Ann. Zool. Fennici 33: 267–274 ISSN 0003-455X
Helsinki 21 August 1996

Reproduction of the red fox *Vulpes vulpes* in Central Italy

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Received 18 March 1996, accepted 23 May 1996

The reproductive output (ovulation rate, fertility, barrenness, productivity, pre-natal mortality) of the red fox *Vulpes vulpes* (n = 317) has been studied in a Mediterranean region (Pisa province, Central Italy) in 1992 by post-mortem analysis. On average, female foxes shed 5.03 ± 1.27 ova, had 3.95 ± 1.25 placental scars and 3.88 ± 1.55 live embryos. Twenty percent of foxes were barren, and intra-uterine mortality was common: 47% of females lost at least one ovum before implantation; 43.5% of yearlings (≤ 1 year old) lost at least one foetus, whereas only 16.7% of adults did so. Male yearlings had lower testis mass than adults. The reproductive output was higher for heavier females, but marginally so for those with greater head and body length. Barrenness and intra-uterine mortality were not related to body size. Amount of body fat and age were unrelated to reproductive output, with the exception of post-implantation mortality (higher for yearlings). All these results suggest that the reproduction of the red fox was not limited directly by food availability, but rather by social modulation. The reproductive output in this population was low in comparison with other populations, in spite of faster physical development. A review of the literature suggests compensatory reproduction in the red fox, litter size being larger in areas of higher mortality.

1. Introduction

The reproduction of the red fox *Vulpes vulpes* has been widely studied (Hayssen *et al*. 1993). Most features are highly variable, and reproductive output appears dependent on food availability at high latitudes (Englund 1970), whereas at lower latitudes it seems limited by social constraints (Macdonald 1980, Lindström 1989). No data on the reproduction of the red fox are available for the Mediterranean region. Barren females are present in several populations, and their proportion is variable in time and space (e.g. Englund 1970). Those females may be subordinates that help the dominant female to raise cubs (Macdonald 1979). Clumped or otherwise abundant food resources may allow the presence of subordinates, and therefore the formation of groups (Macdonald 1981, Von Schantz 1984a), and territory inheritance may be one of the reasons for helpers to stay in their natal territory (Von Schantz 1984b). Reproduction may be inhibited through a stress-induced, hormonal mechanism (at least in captive foxes: Hartley *et al*. 1994). It is unclear from the available literature, however, which factors modulate reproductive output among females. We formulate two alternative hypotheses: a) if female reproduction is limited by food, fatter females should produce more offspring than leaner females; only leaner females should not reproduce; b) if female reproduction is limited by social factors, reproductive output should correlate with competitive ability (and therefore with body size). Larger females should therefore produce more offspring.

The aims of this paper are two-fold: a) to report data on the reproductive output of the red fox from the Mediterranean region, and to compare these results with those from other areas; in particular, we aim to evaluate the presence of compensatory reproduction at geographical scale (i. e. an increase of reproductive output related to an increase in mortality); and b) to evaluate the physical factors (body size and condition, age) influencing reproductive output of individual foxes.

2. Study area, materials and methods

The study area (Pisa province: 43°N, 10–11°E, Central Italy; 52 km E-W by 75 km N-S; 2 448 km^2) is mostly flat, with high human population density (> 200 km^{-2}) and intensively cultivated (> 50% of the surface; mainly cereals) in the north, becoming increasingly hilly (up to 800 m a.s.l.), less populated (35 km^{-2}) and more wooded (50% of the surface) towards the south (Cavallini 1994b). 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. Monthly means were below 10°C for 3 months, and above 20°C for 4 months. 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 in rainfall is large. In 1992, the least rainy months (less than 20 mm of rain per month) were January, February, March, August, and May (in an ascending order; Cavallini 1994a).

Foxes ($n = 317$) were killed by hunters by a variety of methods (shooting, trapping, poisoning) in 1992 from January to May, which is the breeding season (Cavallini & Santini 1995b). The variety of sampling methods may limit the biases in the sample (Lindström 1982). We collected foxes from hunters within 6 h of death and stored them in plastic bags in a refrigerator cell (≤ 48 hours, – 2°C) until dissection. Foxes were weighed (body mass; ± 50 g), placed on a dissection table and measured (± 0.5 cm; head and body length, from the tip of the nose to the first vertebra of the tail; Cavallini 1995).

Female reproductive tracts were removed, from cervix to ovaries included. Ovaries were hand sectioned using a microtome blade and corpora lutea were counted as a measure of fecundity in 1992. Because polyovulation in the fox is rare, and corpora lutea of the previous year have completely regressed by the breeding season (Englund 1970), the number of ovarian bodies (all types pooled: immature follicles, anthral follicles, Graafian follicles, corpora lutea) approximates the number of ova shed in the current year. The uterine horns were opened along their length, and dark and uniformly spaced placental scars were counted (for non-pregnant females only) as a measure of litter size at birth (i.e. fertility; for all counts of placental scars, we followed Lindström 1981). We classified adult females of ≥ 2 years in 1992, and therefore potentially breeding in 1991, without placental scars as barren. Uterine swellings of pregnant females were counted. When embryos were large enough to be measured (> 27 days; Englund 1970), we extracted them and recorded sex, body length and mass. We identified dead and resorbing foetuses by one of three criteria: a) the presence of placental remnants only; b) disintegration of foetus; c) anaemic or flaccid condition, or markedly smaller size (body length ± 1 mm, mass ± 0.1 g) of the foetus compared with others of the same litter. Pre-implantation mortality rate was calculated as the percentage of shed ova that do not give a viable embryo, implanted on the uterine wall. Post-implantation mortality was calculated as the percentage of implanted embryos which died *in utero*. Productivity was calculated as the mean number of placental scars or living foetuses (> 27 days from conception) per female, including barren ones. We removed both testes (including epididymides) from males and weighed them (± 0.1 mg). Average testes mass was taken as an index of males' fertility (Fairley 1970, Lloyd & Englund 1973, Nelson & Chapman 1982). We excluded damaged testes from the sample.

Two indices of body condition were estimated or calculated: a) subcutaneous fat index (on a 1–4 scale); b) logarithm of the mean perirenal fat index (hereafter "lnKFI"; for details on the indices, see Cavallini 1994b). Age was determined from the number of incremental annuli and width of the pulp cavities of canine teeth, and the mass of eye lens (Cavallini & Santini 1995a). Owing to the small number of older foxes, the sample was pooled in two age classes for most analyses: yearlings (1 year old at the time of sampling) and adults (≥ 2 years old).

Results were shown as average ± 1 standard deviation (*S.D.*) unless otherwise specified. We used non-parametric tests for non-normal variables and small sample sizes, and parametric tests in other cases. All tests were two-tailed.

3. Results

3.1. Age distribution

Half of the sampled foxes were yearlings with no

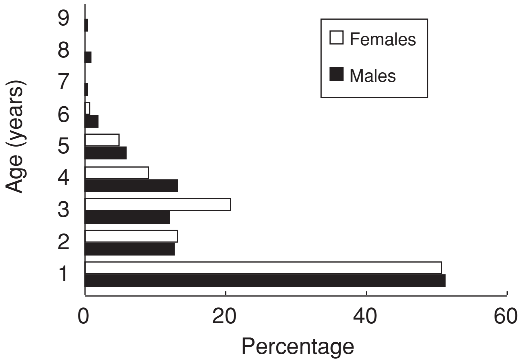

Fig. 1. Age structure of the sampled foxes from Pisa Province, Central Italy, January to May 1992 (*n* = 317).

significant difference in sex ratio (males: 51%; females: 52%; $\chi^2 = 7.65$, $P = 0.18$, *d.f.* = 5, $n = 317$; Fig. 1). There were less 2 years old foxes than expected from a stable age distribution (Fig. 1).

3.2. Ovulation rates

Mean ovulation rate (= number of ovarian bodies) for 1992 was 5.03 ± 1.27 (range: 3–8; $n = 66$; Fig. 2a). For 34 yearling females it was 4.94 ± 1.25, whereas for 30 adult vixens it was 5.23 ± 1.25, a non-significant difference (Mann-Whitney $U = 432.5$, $P = 0.281$, $n = 64$). Females that ovulated more ova than average (> 5) were heavier (5.15 ± 0.77 kg) than females that ovulated less ova than average (< 5; 4.69 ± 0.66 kg) ($U = 154.5$, $P = 0.029$, $n = 45$), but not detectably longer ($U = 145.5$, $P = 0.168$, $n = 43$) nor fatter (lnKFI: $U = 154.5$, $P = 0.59$, $n = 38$). Subcutaneous fat was not related to ovulation rate (Kruskal-Wallis ANOVA, $H = 0.769$, $P = 0.86$, $n = 50$).

3.3. Female fertility

On average, foxes that conceived had 3.95 ± 1.25 placental scars (range: 1–7; $n = 37$; Fig. 2b), with no difference between adults (4.00 ± 1.08) and yearlings (3.83 ± 1.59) (Mann-Whitney $U = 139.5$, $P = 0.72$, $n = 37$). Females with more scars than average (> 4) were heavier (5.21 ± 0.46 kg) than females that had fewer scars (< 4; 4.82 ± 0.33 kg) ($U = 38$, $P = 0.01$, $n = 27$), but not detectably longer ($U = 57$, $P = 0.106$, $n = 27$) nor fatter (lnKFI: $U = 72$, $P = 0.52$, $n = 26$). Subcutaneous fat was not related to number of scars (Kruskal-Wallis ANOVA, $H = 2.233$, $P = 0.52$, $n = 34$).

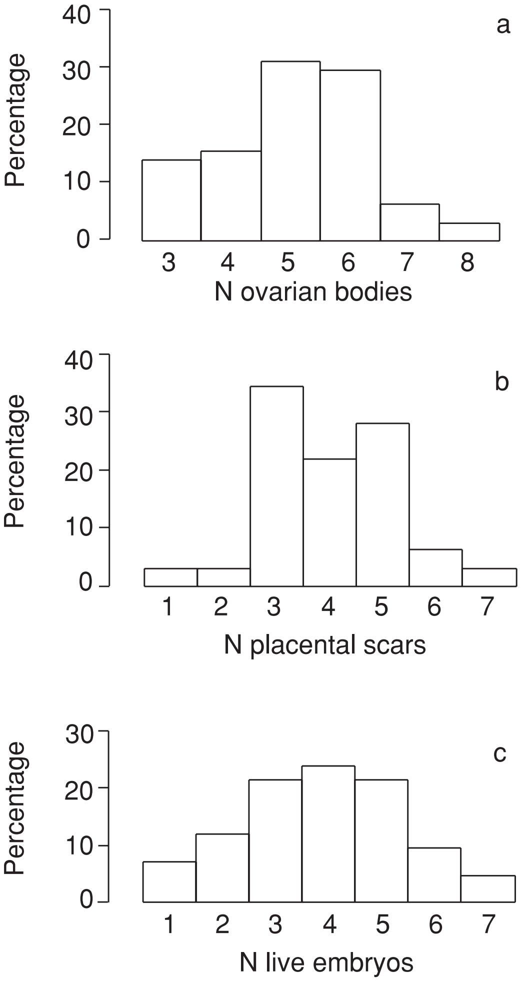

Fig. 2a–c. Frequency distribution of: — a: ovarian bodies in red fox female (*n* = 66); — b: placental scars in red fox females (*n* = 37; excluding those who did not conceive); — c: live embryos in red fox females (*n* = 42) from Pisa Province, Central Italy, January to May 1992.

The mean number of live foetuses was 3.88 ± 1.55 per pregnant female (range: 1–7; $n = 42$; Fig. 2c). Sex ratio of embryos was 23 M:22 F, not different from 1:1 ($\chi^2 = 0.01$, $P = 0.9$, *d.f.* = 1). Young females had 3.62 ± 1.75 foetuses, whereas adults had 4.26 ± 1.28; the difference was not significant (Mann-Whitney $U = 156$, $P = 0.230$, $n = 40$). Including all age classes, females with more foetuses than average (> 4) were heavier (5.49 ± 0.68 kg) than females with fewer foetuses (< 4; 4.88 ± 0.68 kg) ($U = 170.5$, $P = 0.046$, $n = 27$); they were longer (63.8 ± 2.8 cm vs. 60.9 ± 3.5 cm; $U = 162.5$, $P = 0.029$, $n = 30$) but not significantly leaner (lnKFI: 0.436 ± 0.120 vs. 0.529 ±

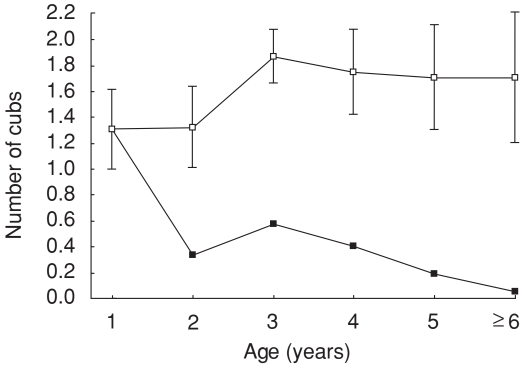

Fig. 3. Female reproductive output as a function of female age in Pisa Province, Central Italy, January to May 1992. Open squares = age-specific number of female offspring per female (bx = mean number of female offspring to a x-aged vixen, with standard errors); black squares = age-specific total reproductive output (the proportion surviving at the start of each age interval, lx, multiplied by bx; Krebs 1978). Ages ≥ 6 years were pooled because of small sample sizes.

0.139; $U = 51.5$, $P = 0.094$, $n = 26$). Subcutaneous fat was not related to number of foetuses (Kruskal-Wallis ANOVA, $H = 2.855$, $P = 0.415$, $n = 40$).

Estimates of litter size based on placental scars and on the number of live foetuses did not differ (Mann-Whitney $U = 761.5$, $P = 0.88$, $n = 79$; it was not possible to count placental scars and foetuses in the same fox). We therefore pooled both estimates in a new variable (hereafter "litter size") to obtain larger samples. There was no difference in the litter size of yearling and adult females ($U = 727.5$, $P = 0.330$, $n = 72$). Females with litters larger than average (> 4) were heavier (5.38 ± 0.61 kg) than females with fewer foetuses (< 4, excluding females that did not reproduce; 4.86 ± 0.55 kg) ($U = 202.5$, $P = 0.003$, $n = 55$), longer (63.9 ± 4.4 cm vs. 61.0 ± 3.0 cm; $U = 209.5$, $P = 0.009$, $n = 54$) but not leaner (lnKFI: $U = 343$, $P = 0.378$, $n = 49$). Subcutaneous fat was not related to litter size (Kruskal-Wallis ANOVA, $H = 1.162$, $P = 0.762$, $n = 67$). There was no difference in litter size between the North and the South of the study area ($U = 761.5$, $P = 0.171$, $n = 72$).

3.4. Barren vixens and productivity

Of 35 females ≥ 1 year old in 1991, 7 (20%) were barren. Barren females were either 1 year old (2 of the 8 yearling females sampled), 2 (4 of 14), or 3 years old (1 of 8). Barren females were therefore mostly young, but their age distribution was not different from that of fertile females. However, statistical testing is suspect because of small sample size. Percentage of barren females was not calculated for 1992, because the high incidence of hunting at reproductive dens would have biased the results. These foxes were not included in further calculations of productivity. Barren females were shorter (60.9 ± 3.7 vs. 62.4 ± 4.2 cm), lighter (4.59 ± 0.80 vs. 5.07 ± 0.46 kg), and fatter (lnKFI: 0.491 ± 0.131 vs. 0.464 ± 0.162) than females that conceived, but differences were very small and not significant ($U < 133.5$, $P > 0.097$, $n = 34$). Including barren females, total population productivity was therefore 3.16 ± 2.0 cubs per female. Although individual yearling females produced slightly fewer cubs on average, the yearlings produced more cubs in total, owing to their larger proportion in the population (Fig. 3).

3.5. Intra-uterine mortality

Minimum pre-implantation mortality was 11.7 ± 20.0% of ova shed per female, and it was independent of age class (Mann-Whitney $U = 165$, $P = 0.87$, $n = 36$). About a half of females (47%) lost at least one ovum before implantation. Those females were neither lighter ($U = 159$, $P = 0.74$, $n = 37$) nor shorter ($U = 166.5$, $P = 0.63$, $n = 35$) then females without pre-implantation mortality. They were marginally fatter according to the kidney fat index (lnKFI = 0.558 ± 0.164 vs. 0.447 ± 0.152; $U = 59$, $P = 0.073$, $n = 28$), but not according to the subcutaneous fat ($U = 137$, $P = 0.378$, $n = 36$).

Minimum post-implantion mortality was 12.3 ± 21.8% (range: 0–75%; $n = 41$). It was higher in young vixens (19.5 ± 26.6% of foetuses, range: 0–75%), than in old ones (3.3 ± 10.3%, range: 0–40%; Mann-Whitney $U = 253$, $P = 0.023$, $n = 39$). A total of 43.5% of yearling females lost from 1 to 3 foetuses, whereas only 16.7% of adult females lost 1 or 2 foetuses. Females that lost foetuses were neither lighter ($U = 139$, $P = 0.53$, $n = 38$) nor shorter ($U = 143$, $P = 0.68$, $n = 38$), and they were marginally fatter (lnKFI = 0.586 ± 0.111 vs. 0.481 ± 0.170; $U = 51.5$, $P = 0.067$, $n = 31$; subcutaneous fat: 3.0 ± 0.6 vs. 2.5 ± 0.6; $U = 99$, $P = 0.055$, $n = 39$). In two uteri the number of embryos was larger than the number of corpora lutea, probably due to polyembryony.

3.6. Male fertility

During the period of sample collection, testes mass was constant for one month and a half, then it decreased (Cavallini & Santini 1995b). When considering the date of sampling, average testes mass was higher in adult dog foxes than in yearlings (adjusted least squares mean was 5.77 ± 0.171 g (*S.E.*) for yearlings, and 6.67 ± 0.166 g (*S.E.*) for adults; ANCOVA with date of sampling as covariate, F (age class) = 14.44, $P = 0.0002$, F(date) = 162.8, $P < 0.0001$, $n = 140$; Fig. 4).

4. Discussion

In our study area, the reproductive effort (ovulation rate and litter size) was higher for heavier female red foxes than for lighter ones, whereas body length was less related to reproduction. Foetuses and placentae could have increased body mass of pregnant females, but greater body mass was also related to higher fecundity when this was measured by counting placental scars (non-pregnant vixens) or ovarian bodies (vixens in the early stages of gestation). The proportion of barren females was 20% of all females. Barren females were not significantly smaller or lighter than fertile ones. Intra-uterine mortality was not related to physical dimensions. Body fat was not related to reproductive effort. Barren females were insignificantly fatter than fertile females, and intra-uterine mortality was positively related to fat level. In synthesis, reproductive output correlates with body mass (and probably competitive ability) rather than with fat reserves (and probably food availability). Our results from a Mediterranean environment are therefore consistent with the hypothesis of a social modulation of reproduction, but not with a direct limitation by food availability. This follows the hypothesis formulated by Lindström (1989) according to which foxes at high latitudes are directly food-limited (e.g. northern Sweden; Englund 1970), whereas more to the south the populations are socially regulated (e.g. British cities; Macdonald 1981). Factors determining reproductive suppression are less clear (possibly also because of small sample size), but seem more related to body size than to fat reserves.

Yearling females had a higher post-implantation mortality, but in all other respects they were indistinguishable from older ones, and their contribution to population reproductive output is the highest of all age classes (Fig. 3). Also in North America, total litter losses are very frequent in yearlings (28.3%) and partial litter losses occur with a higher incidence than in adult vixens (Allen 1984). Our results contrast with other studies from northern Europe and the British Isles (Englund 1970, Harris 1979) where yearling females produced significantly fewer cubs than adults. In North America, the reproductive performance increases as a function of female age (Allen 1984). Our results are in accordance with studies from other areas (northern France: Artois *et al.* 1982; northeastern Spain: Martorell & Gortazar 1993; southern Germany: Vos 1994). In a food-rich environment, yearling females may develop faster (Cavallini & Santini 1995a), possibly because of milder winters and lack of a definite winter bottleneck in food availability (Cavallini & Volpi 1996). They can therefore compete successfully with older females, thus having a high reproductive output since their first reproductive season.

Spermatogenetic activity appears lower in males at their first reproductive season, at least judging from testis mass (Fig. 4). This would not necessarily lead to a lower reproductive success of yearling males, but rather to a possible disadvantage in case of sperm

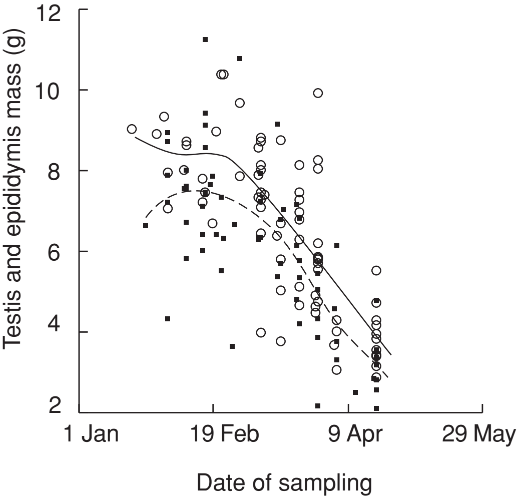

Fig. 4. Testes mass of male red foxes (yearlings = open circles and dashed line; $n = 68$; adults = black squares and upper line; $n = 72$) from Pisa Province, Central Italy, January to May 1992. The smoothing lines are locally weighted regressions (LOWESS; smoothing factor (F) = 0.5; Cleveland 1981).

competition (red foxes may have multiple mating; Ables 1975, Niewold 1980, Lloyd & Hewson 1986; see Cavallini 1996, for a review).

The number of 2-years-old foxes was lower than expected for a stable population. This may be due to a *Sarcoptes scabiei* epizootic noticed in 1990 (Prof. A. Poli, pers. comm.), which may have lowered recruitment in that year. In 1990, in fact, the number of foxes shot was lower (about 500) than in previous years (1983–1989: 800–1 250 foxes shot; Cavallini 1994b).

In spite of their fast physical maturation (Cavallini & Santini 1995a) and good average body condition (Cavallini 1994b), the reproductive output of foxes in our study area was low in comparison with other populations (Table 1): a) Italian foxes had fewer corpora lutea, embryos and placental scars than foxes in most areas except Australia and Spain; captive foxes had higher ovulation rate, but lower litter size (Jalkanen 1992); b) the percentage of barren vixens was relatively high in our study area; c) pre-implantation mortality (12% in this study) was similar to other studies (Allen 1984: 7–21% of ova shed, Englund 1970: 9%, Layne & McKeon 1956: 14%) but lower than in Australia (McIntosh 1963: 22%, Ryan 1976: > 30%); d) post-implantation mortality was more variable (Allen 1984: 0–22% of embryos implanted, Englund 1970: 14%, Fairley 1970: 8%, Layne & McKeon 1956: 5%, McIntosh 1963: 0%); e) total intra-uterine mortality was similar across field studies (from 20 to 24%; Layne & McKeon 1956, McIntosh 1963, Englund 1970, Lindström 1982, Allen 1984) and slightly higher in captivity (27%; Jalkanen 1992). However, some of these differences might be due to differences in methods used.

Table 1. Comparison of reproductive parameters of the red fox in the world. Average is given for each variable. When several years or localities were studied, the range of variation of individual averages is reported. Standard deviation of the mean is seldom available in original papers, and is therefore not included here.

Area	*N* corpora lutea	*N* embryos	*N* placental scars	% barren	Reference
N Dakota, USA	5.0–6.3	2.8–5.0	–	–	Allen 1984
France	–	4.6	4.3	3.8	Artois *et al.* 1982
Sweden	5.0–7.0	3.6–6.0	3.7–6.9	11–79	Englund 1970
Ireland	6.0	5.4	5.4	9.8	Fairley 1970
Bristol & London	–	–	4.7	15.4–20.3	Harris & Smith 1987
London	–	–	4.6	24	Harris 1979
Indiana, USA	–	6.8	–	–	Hoffman & Kirkpatrick 1954
Captivity	5.9	2.6–3.0#	–	–	Jalkanen 1992
Scotland	5.6–7.8	–	4.6–7.3	–	Kolb & Hewson 1980
New York, USA	5.9	–	5.4	2.1–16.6	Layne & McKeon 1956
Sweden	–	4.1§	–	40	Lindström 1982
England & Wales	5.1–6.8	4.2–5.4	–	8.6–25.0	Lloyd 1980
NSW, Australia	–	–	2.9	–	Marlow 1992
NE Spain	–	–	3.2	18.4	Martorell & Gortazar 1993
ACT, Australia	5.0	3.8	4.3	2.6	McIntosh 1963
Maryland, USA	6.0	–	5.0	–	Nelson & Chapman 1982
Wisconsin, USA	–	6.4	5.5	–	Pils & Martin 1978
Wisconsin, USA	–	6.9	5.5	–	Pils *et al.* 1981
NSW, Australia	4.5	4.0	–	–	Ryan 1976
New York, USA	–	–	5.4	4.7	Sheldon 1949
Illinois & Iowa, USA	–	6.8	–	5	Storm *et al.* 1976
Germany	–	–	4.8	15.3	Vos 1995
Pisa	5.03	3.88	3.95	20.0	This study

n of cubs at birth

§ placental scars and embryos >27 days old pooled

There was an indication of compensatory reproduction: the percentage of yearlings in the sample (an index of mortality; Lloyd 1980) was positively correlated with ovulation rate, number of placental scars, and of embryos ($r_s = 0.480–0.657$) across studies. Compensatory reproduction, and the wide range of physiologically possible litter sizes (from 2.8 to 7.3; Table 1) may explain the exceptional resistence of the red fox to eradication attempts (e.g. Stubbe 1980). For this analysis, averages for each study involving several years or localities were used. However, the percentage of yearlings in the sample may be influenced also by other factors (e.g. timing of major hunting period: Pils *et al.* 1981, capture method: Lindström 1982). Because of this, and due to small sample size (*n* of studies with available data ranges from 5 to 10) we did not attempt statistical testing. Data available in the literature are too sparse also to test the relative importance of various factors likely to influence reproduction (e.g. population density, food availability and distribution). Further studies in different environments are therefore needed to collect baseline data.

Acknowledgements. Funding for this study has been provided by the Amministrazione Provinciale di Pisa (M. Franceschini). Hunters and game wardens collaborated for sample collection. T. Volpi greatly helped during collection and laboratory analyses. Prof. A. Poli and his staff assisted with dissection and laboratory facilities. The guidance and support of late Prof. R. Nobili, Prof. F. Dessì-Fulgheri, Prof. S. Lovari and Prof. R. Dallai made this study possible. The Museum of Natural History of the University of Pisa and the Museum of Natural History of Livorno also provided logistic support. Prof. S. Creel kindly revised the manuscript, making useful comments on it. All these individuals and institutions are gratefully acknowledged.

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