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Timing of reproduction in the Red fox, *Vulpes vulpes*

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Abstract

Ovulation date was estimated for 93 female red foxes (*Vulpes vulpes*) collected in central Italy. Three methods were used: ageing embryos, examination of ovarian bodies, and of placental scars. Most females ovulated around 26 February (SD ± 9.5 days). Estimates from different methods gave consistent results. Ovulation date was independent of physical condition and size, but was 5 days earlier in the north of the study area than in the south. The testes of 154 males were also weighed. Male testicular mass decreased after the end of February. Results from this and other studies are consistent with the hypothesis that timing of reproduction in the red fox is constrained by a winter trophic bottleneck in the north, but can be more variable in the south. Small-scale variation in our study area was probably unrelated to food availability.

Introduction

The red fox (*Vulpes vulpes*) is a seasonal breeder. Its reproduction has been studied both in the wild (in North America and in northern Europe) and in fur farms (see Hayssen et al. 1993 for a review). In central and northern Europe, oestrus is later with increasing latitude (i. e. late January to late March at 51°N to 63°N); with 52–53 days of gestation, whelping occurs from mid-March to mid-May (Lloyd and Englund 1973). From the study of Lloyd and Englund (1973), however, no data for northern American red foxes were available. In Scotland, the onset of breeding shows local variation, presumably depending on local food availability (Kolb and Hewson 1980). No interannual variation was recorded (Fairley 1970). Spermatogenesis in males ceases after the female oestrus (e. g. Fairley 1970).

We hypothesised that the onset of breeding in the red fox may be regulated by two different phenomena: (a) in the northern part of its range, where foxes are under nutritional stress during winter (e. g. Lindström 1982), females must postpone the birth season until the increase in environmental productivity. At the same time, a delay of reproduction causes cubs to enter the winter at a younger age. The equilibrium point between the two opposing selective pressures will be positively related to the beginning of productivity pulse (i. e. spring; Geist 1987), which in turn is positively related to latitude; (b) more to the south, where winters are shorter and less rigorous, limiting factors (e. g. food availability and quality in spring or in summer: Cavallini and Lovari 1991; social structure: Lindström 1989) are presumably more variable among areas. Here we can therefore expect a lack of relationship between latitude and onset of breeding at lower latitudes. Data from the southern part of the fox range are therefore important to test these concepts. Unfortunately, no studies have been carried out in Mediterranean environments (except for a recent preliminary report from Spain; Martorell and Gortazar 1993).

Objectives of this study were to: (a) evaluate the seasonality of reproduction in wild red foxes from a Mediterranean region (central Italy), from an area where no data are yet available, (b) compare these results with published results from other areas, and (c) test the above hypothesis on the relation between the timing of ovulation and latitude.

Material and methods

From January to May 1992, during the main fox hunting season, we obtained 330 red foxes (205 M, 125 F) from hunters in the Pisa Province (ca. 43°N, 10–11°E), central Italy. Due to physical damage, sample size was reduced. The area (52 km E–W by 75 km N–S; 2 448 km^2) is mostly flat and intensively cultivated (mainly cereals) in the north, becoming increasingly hilly (up to 800 m a. s. l.) and wooded towards the south. Climate is Mediterranean, with mild winters and dry, hot summers. Foxes were usually collected within 6 hours of death and kept in plastic bags in a refrigerator (≤ 48 hours, –2 °C) until dissection. Before dissection, foxes were weighed (± 0.05 kg) and measured (head and body length; ± 0.5 cm). Complete female reproductive tracts (from cervix to ovaries included) were also removed, and the ovulation date estimated by 3 methods:

(1) ageing embryos by mass and crown-rump method (Layne and McKeon 1956; Englund 1970). Length was measured ± 0.05 mm, mass ± 0.01 g. Dead embryos diagnosed by (a) the presence of placental remnants only; (b) disintegration of the embryo; (c) anaemic and flaccid condition of the embryo compared with others of the same litter (Englund 1970) were excluded. This method is applicable only to embryos ≥ 28 days from the date of conception. For younger embryos, age was estimated (although less accurately) by measuring the major diameter of the corresponding uterine swelling (Englund 1970). To reduce within-litter variability, we used the average for the entire litter both for younger and older embryos.

(2) Ovarian bodies were examined both macro- and microscopically, and were classified in: (a) primary follicles (characterised by several layers of cells surrounding the ovum); we estimated that these bodies were present about 8 days before ovulation; (b) mature follicles, where the cells surrounding the ovum secrete an oestrogen-rich fluid that fills the cavity (antrum) and surrounds the egg; they develop after the primary follicles, but before ovulation. We therefore estimated that they occur approximately 5 days before ovulation; (c) de Graafian follicles, protruding above the surface of the ovary with the liquor folliculi under pressure; they are present before ovulation (approximately 2 days); (d) after release of the ovum, the follicular cavity fills with blood and lymph, which is gradually replaced by granulosa cells to form the corpus luteum; we called these bodies transition structures, and estimated their occurrence as about 14 days after ovulation (Valtonen 1992; Valtonen and Jalkanen 1993; L. Jalkanen, pers. comm.). When one of the ovaries was damaged, the sample was excluded.

(3) After parturition, placental scars are swollen (Kirkpatrick 1980). We estimated that about 4 days intervened between parturition and sampling (56 days from conception) when traces of blood were still visible in the swollen area. We assumed that 2 days intervened between ovulation and conception, and 52 days between conception and parturition (Hayssen et al. 1993). No adequate reference figures on the macroscopic development of the ovary during ovulation and conception are available in the literature. All our estimates are therefore approximations only.

Mass of testes is higher (about 8 g) during the spermatogenetic period, and vital spermatozoa are found only during the 2 or 3 months of peak testicular mass. When testicular mass decreases, no vital spermatozoa are present in male reproductive tracts (Fairley 1970; Lloyd and Englund 1973; Nelson and Chapman 1982). Both testes (including epididymes) were therefore removed from males and weighed (± 0.1 mg). Damaged testes were excluded from the sample. Age was determined by measuring eye lens mass and canine teeth pulpar width, and by counting the incremental annuli in the cementum of canine teeth (Jensen and Nielsen 1968; Cavallini and Santini 1995). The logarithm of the kidney fat index was used to evaluate nutritional status (e. g. LaJeunesse and Peterson 1993; Cavallini 1994).

We used parametric statistical tests (regression analysis) for normally distributed variables (as determined by Lilliefors test, a modified version of the Kolmogorov-Smirnov test; Lilliefors 1967), nonparametric tests (Kruskal-Wallis ANOVA, Mann-Whitney's two-sample test) for the remaining variables.

Results and discussion

Date of ovulation was determined for 93 females. Estimates for different methods ranged from day 54 (swollen placental scars, N = 8) to day 60 (mature follicles, N = 8) from the beginning of the year. Most ovulation dates were determined by embryo ageing (mean date = 54.8 days ±9.6 SD, N = 30) and by immature follicles (57.9 days ± 9.6 SD, N = 24). Difference among methods was not significant (Kruskal-Wallis Test, H = 5.72, p = 0.33, 5 d.f., N = 93). Births were highly synchronised: half of the females ovulated between 22 February and 3 March (median: 25 February; average: 57th day from the beginning of the year ±9.5 SD; range: 2 February–21 March); therefore most births took place around the end of April.

Ovulation date was independent from the age class of the female (Mann-Whitney Test, U = 1 177, p = 0.18, N = 90), from nutritional status (logarithm of the kidney fat index: regression analysis, $r^2 = 0.02$, p = 0.20, N = 80) and from physical dimensions (head and body length: regression analysis, $r^2 = 0.002$, p = 0.69, N = 86). Females from the north of the study area ovulated on average 5 days earlier than those in the south (north: 54.8 days ± 9.5 SD, N = 59; south: 60.2 days ± 8.6 SD, N = 34; Mann-Whitney Test, U = 717.5, p = 0.022).

Mass of testes from 145 foxes was constant from January until the end of February. After mid-March it decreased rather abruptly (Fig. 1).

The different methods used to estimate ovulation date gave consistent results, and therefore can be compared, and each can be used in future studies. Female red foxes in central Italy ovulated around the end of February, and the fertile period for males presumably ended after mid-March. This was substantially later than determined in all other studies conducted at low latitudes, and close to values for northern Sweden (Tab. 1). The relationship between latitude and ovulation date is approximately linear, positive and very strong at northern latitudes (>55°N; $r^2 = 0.900$, p = 0.004, N = 6), as shown in an earlier study (Lloyd and Englund 1973). Below 55°N, this relationship disappears ($r^2 = 0.020$, p = 0.68, N = 11), and the scatter among studies is very large (Fig. 2; about

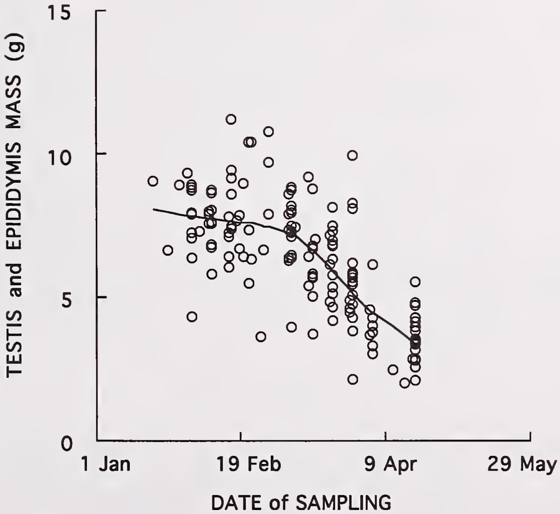

Fig. 1. Decrease of mean testis and epididymis mass with date of death for 145 male red foxes collected between January and May 1992 in the Province of Pisa, central Italy. The curve indicates LOWESS smoothing (Cleveland 1981).

40 days among the fox populations living between 41.5°N and 43.5°N). Within the Mediterranean area, Spanish foxes ovulate about 20 days earlier than Italian foxes (Tab. 1). These results are in accordance with our hypothesis: timing of reproduction of foxes ap-

Table 1. Ovulation date of the red fox (*Vulpes vulpes*) in various areas (in N–S order) compared to the present study

Reference	Area	Ovulation date
LLOYD and ENGLUND (1973)	Jarmtland, Sweden	22 March [a]
LLOYD and ENGLUND (1973)	Varmland, Sweden	5 March [a]
LLOYD and ENGLUND (1973)	Uppland, Sweden	20 February [a]
KOLB and HEWSON (1980)	NE Scotland, U. K.	26 January [b]
KOLB and HEWSON (1980)	W Scotland, U. K.	5 February [b]
LLOYD and ENGLUND (1973)	Skane, Sweden	30 January [a]
LLOYD and ENGLUND (1973)	Wales, U. K.	28 January [a]
LLOYD and ENGLUND (1973)	England, U. K.	22 January [a]
FAIRLEY (1970, 1971)	NE Ireland, U. K.	20 January [b]
ARTOIS et al. (1982)	N France	24 January [b]
ALLEN (1984)	N Dakota, U. S. A.	6 February [b]
SHELDON (1949)	New York, U. S. A.	18 January [b]
STORM et al. 1976	Iowa and Illinois, U. S. A.	2 February [b]
PILS and MARTIN (1978)	Wisconsin, U. S. A.	12 February [b]
MARTORELL and GORTAZAR (1993)	NE Spain	5 February [b]
MCINTOSH (1963)	ACT, Australia	15 July [b]
This study	Pisa, central Italy	26 February [c]

[a] median
[b] recalculated average (approximate)
[c] average

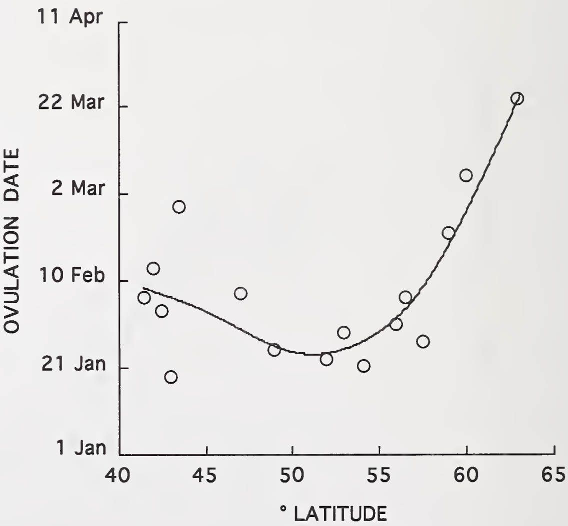

Fig. 2. Relationship between mean (or median, when the mean is unavailable) ovulation date in female red foxes and degrees of latitude North across different studies. The curve indicates distance weighted least squares smoothing (MCLAIN 1974). For references to individual studies, see table 1.

pears strongly constrained by the winter trophic bottleneck in the north (Lindström 1982), but is more variable among localities in the south. The few studies from the southern hemisphere (Australia; 35°30′ S; McIntosh 1963; Ryan 1976) indicate that most oestruses here occurred in mid-July, corresponding to mid-January in the northern hemisphere.

Within our study area, variations in the date of ovulation cannot be attributed to age or physical conditions. In contrast, local variation in timing is small but significant even at such a small scale (<70 km). This result, although surprising, is consistent with the findings of a study in Scotland: cubs in the west were born on average 10 days later than in the northeast (separated by approximately 150 km), probably because the peak in food availability is different in the two areas (Kolb and Hewson 1980). In the Province of Pisa, north-south differences in food consumption are limited to a few secondary food items (Cavallini 1994), so that this is not a likely candidate to explain the difference in ovulation dates within such a small area. Habitat, hunting pressure, external morphology, and female fat levels are different between the north and the south of our study area (Cavallini 1994; Cavallini in Press). The relative influence of these factors on the small-scale timing of reproduction, however, is unclear.

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Zusammenfassung

Zeitliche Abstimmung der Fortpflanzung beim Rotfuchs, Vulpes vulpes.

Das Eisprungdatum wurde für 93 Rotfuchsfähen, die in Zentralitalien gesammelt wurden, geschätzt. Es wurden drei unterschiedliche Methoden eingesetzt, und zwar: Altersbestimmung des Embryos, Untersuchung der Eierstöcke und der Gebärmutternarben. Bei den meisten Weibchen setzte der Eisprung um den 26. Februar ein (SD ± 9.5 Tage). Schätzungen durch die verschiedenen Methoden ergaben konsistente Ergebnisse. Der Eisprung war unabhängig vom Körperzustand und der Körpergröße, setzte aber im Norden des Studiengebietes 5 Tage früher ein als im Süden. Auch die Hoden von 154 Rüden wurden gewogen, und es wurde festgestellt, daß deren Masse nach Ende Februar abnahm. Die Ergebnisse dieser und anderer Studien unterstützen die Annahme, daß die zeitliche Abstimmung der Fortpflanzung beim Rotfuchs durch winterlichen Futtermangel im Norden eingeschränkt wird, im Süden jedoch variabler ist. Unterschiede kleineren Maßstabes in unserem Studiengebiet waren wahrscheinlich mit Futteranwesenheit nicht korreliert.

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