

Ranging behaviour of red foxes during the mating and breeding seasons

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Received 16 May 1995, accepted 10 November 1995

Ranging behaviour (home range size, core area size, activity levels) of four red foxes (*Vulpes vulpes*; three males and one female) was studied by radio-tracking in a rural area of Central Italy during the mating and breeding seasons (January to May). Home range size was equal or smaller than in other areas, ranging from 47 to 320 ha (kernel analysis) or from 57 to 394 ha (minimum convex polygon), with the exception of a yearling male, who ranged over a very large area (2307 ha). Core areas ranged from 11 to 29 ha. Foxes were most active between 19:00 and 00:00 hr, then activity decreased slowly until sunrise. Foxes used about 25% of their range each night, with individually different strategies: the two resident males greatly increased their range in the second half of female fertile period, whereas the nomadic male restricted his large range during the peak of matings. Barking bouts (indices of agonistic and contact behaviour) were most common after median ovulation date. The female decreased her range at the time of births. The range expansion by males during the mating season, also reported by previous studies, was limited to the second half of the females' fertile period. Males could therefore maximise individual reproductive success by roaming only after the oestrus of their mate. Because of the small number of foxes followed, these results should be verified in other studies.

KEY WORDS: red fox, *Vulpes vulpes*, ranging behaviour, mating system, mating season, vocalisation.

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INTRODUCTION

The ranging behaviour of the red fox (*Vulpes vulpes*) has been widely studied in North America, continental Europe, the Mediterranean region, British Isles, Australia, and Japan (e.g. TREWHELLA et al. 1988). Home range size is extremely variable, from 30 ha in urban environments (SAUNDERS et al. 1993) to 1600 ha in the tundra (JONES & THEBERGE 1982). Several authors reported a high frequency of "excursions" (movements outside the usual home range) for males during the mating season (NIEWOLD 1980, VOIGT & MACDONALD 1984, ZIMEN 1984, MULDER 1985, SAUNDERS et al. 1993), whereas others found a yearly stability of ranges (ABLES 1969b, SARGEANT et al. 1987, PHILLIPS & CATLING 1991). Red foxes are sometimes considered monogamous (e.g. SARGEANT 1972, NIEWOLD 1980, SARGEANT et al. 1987), sometimes polygynous (e.g. MACDONALD 1980, VON SCHANTZ 1984, ZABEL & TAGGART 1989). There may be social variation, both between and within populations (MOEHLMAN 1989). In the case of monogamy, male excursions during the mating season would not be expected. Unfortunately, no studies report on the fine-scale temporal variation for males in relation to the breeding season, partly because of the difficulty in determining the ovulation dates accurately. Ovulation dates are determined most reliably by post-mortem analyses (examination of reproductive tracts of females and males; e.g. LLOYD & ENGLUND 1973).

The aims of this paper are: (1) to describe the pattern of ranging behaviour (home range size, core area size, activity levels) for a sample of red foxes from Central Italy, comparing different methods of home range estimation; (2) to quantify the influence of reproductive activities (mating and births) on the use of home range.

STUDY AREA, MATERIALS AND METHODS

The study was carried out in the hilly (< 250 m a.s.l.) central section of the province of Pisa (43°30'N, 10°30'E). Climate was Mediterranean, with mild winters and dry, hot summers. Average monthly temperatures ranged from 6 (January and February) to 25 °C (August). Most of the area (50%) was covered by cultivated fields (mainly cereals). Woodland covered 31% of the area, cultivated poplar trees 10%, and pastures 6%. Human population density was 47/km². In the area, fox mating started at the beginning of February, and stopped at the end of March; half of the matings occurred between 22 February and 3 March; the median date was 25 February (CAVALLINI & SANTINI 1995b).

The examination of a sample of foxes killed in the province of Pisa during predator control operations (n = 330; CAVALLINI & SANTINI 1995b) set the background for this study. Foxes were neck-snared in January and February 1993. Captured foxes were weighed (\pm 10 g), measured (head and body length, from the tip of the nose to the first vertebra of the tail; tail length, from the first vertebra to the tip of the tail; chest girth, immediately behind the fore legs; all linear measurements \pm 1 cm) and equipped with a radio-collar (Telonics Inc., U.S.A.). Physical condition was evaluated by the residuals of the regression of body mass on head and body length of individual mass (calculated separately by sex); values lower than - 0.3 indicate very lean foxes, values over + 0.3 very fat, stocky foxes (CAVALLINI 1994).

Red foxes are mainly nocturnal (e.g. EGUCHI & NAKAZONO 1980, WEBER et al. 1994). Therefore radio-tracking sessions lasted from sunset (17:00-19:00 hr) to sunrise (06:30-07:00 hr), for a total of 12-14 hr per night. To avoid the influence of capture stress, foxes were not tracked in the first week after the capture. A hand-held, three-element Yagi antenna and a portable receiver were used. From sightings of collared animals while radio tracking, error radii were < 50 m in most conditions. For each fix, activity (based on signal amplitude fluctu-

ations, GARSHELIS & PELTON 1980) was recorded. In the first eight tracking nights, fox locations were recorded every 15 min. The autocorrelation between consecutive locations was computed (SWIHART & SLADE 1985). The time-to-independence, as calculated by Schoener's index, may be over-estimated for highly mobile species (ANDERSEN & RONGSTAD 1989), and only high autocorrelation influences home range estimation (CRESSWELL & SMITH 1992). The use of very long intervals sacrifices biologically significant information, and autocorrelated data may provide a better estimate of true home-range sizes (REYNOLDS & LAUNDRÉ 1990). I therefore chose a time-to-independence just sufficient to avoid serious autocorrelation (Schoener's index > 1 instead of 2 as in SWIHART & SLADE 1985; see also McNAY et al. 1994). Every available method for the evaluation of the size of the home range has its flaws, and direct comparisons of sizes estimated by different methods is impossible (e.g. KENWARD 1987, WHITE & GARROTT 1990). I therefore computed home range size of the sample animals using four methods: (1) minimum convex polygon (MCP) including all locations recorded for each animal (HAYNE 1949); (2) MCP excluding the 5% of locations furthest from the harmonic centre (MCP 95); (3) kernel analysis including 95% of locations (KE 95; WORTON 1989); (4) harmonic mean including 95% of locations (HM 95, DIXON & CHAPMAN 1980, with SPENCER & BARRETT 1984 modification); this estimator was computed in spite of its mathematical inappropriateness (WORTON 1987) to allow comparison with previous studies. The core area was estimated by the kernel analysis and the harmonic mean, both including 50% of locations (KE 50 and HM 50 respectively). All occurrences of barking bouts (calls suited to agonistic and contact functions: NEWTON-FISHER et al. 1993) during tracking sessions were recorded, and their localisation estimated by acoustical triangulation (using the same system as for the radio signals). Because of difficulties in distinguishing different types of barks, all types were pooled: yell, normal, staccato and wow-wow barks (NEWTON-FISHER et al. 1993).

RESULTS

Four adult foxes (three males and one female) were captured between 15 January and 6 February 1993; the female (3F) was in very good physical condition, whereas males were either in average condition (2M), lean (1M) or very lean (4M; Table 1). The male 4M was shot after the end of the study. From the count of the incremental annuli of the teeth (JENSEN & NIELSEN 1968, CAVALLINI & SANTINI 1995a), he was born in the spring 1992 (1 year before this study).

From 137 to 265 locations were recorded for each fox (total = 828). No location was missing (i.e. when searched for the animal was always found). Sampling effort seemed sufficient to evaluate home range size: the ranges of two foxes (2M

Table 1.

Characteristics of foxes radio-tracked in the province of Pisa, Central Italy, from January to June 1993. Physical condition was evaluated by the residuals for the regression of body mass on head and body length of individual mass (calculated separately by sex; see text).

	Fox number and sex			
	1M	2M	3F	4M
Capture date	19 Jan 93	6 Feb 93	15 Jan 93	15 Jan 93
Body mass (kg)	5.93	6.2	5.33	5.25
Head and body length (cm)	68	69	63	68
Tail length (cm)	37	40	37	38
Chest girth (cm)	38	39	36	37
Physical condition	-0.17	-0.04	0.35	-0.85

and 4M) did not increase after 110 locations (98-100% of total MCP range), whereas most of the MCP ranges of other foxes (1M: 83% and 3F: 86% of total range) were described after 190 and 140 locations, respectively. Autocorrelation (Schoener's index) between successive locations was ≥ 1 at 60 min for all foxes (1M = 1.2; 2M = 1.7; 3F = 1.6; 4M = 1.0); only locations separated by at least 1 hr were therefore used for home range estimation.

With the exception of 4M, home range size varied from 47 to 320 ha (KE 95) and from 57 to 394 ha (MCP); the female had the smallest range (Table 2). The yearling, very lean male (M4) ranged at first (until 24 January) over a very large area (4Ma: MCP = 2307 ha; KE 95 = 1929 ha); it then (25 January-9 March, i.e. during the mating season: CAVALLINI & SANTINI 1995b) occupied a much smaller range (4Mb: MCP = 183 ha; KE 95 = 137 ha) completely overlapping that of 3F. A male was shot around 20 January by local game wardens in the same area. Finally, 4M moved 5 km south, where it remained until the end of the study (13 May 1993). In this area it was followed for 2 nights only; its last range was therefore incompletely described (4Mc: MCP = 34 ha; KE 95 = 31 ha). Excluding the 5% of locations furthest from the harmonic centre (MCP 95) the ranges were all substantially smaller ($68.3\% \pm 10.9$ SD of MCP). Differences between KE 95 and HM 95 were large and unpredictable (HM was from 15 to 220% of KE; average = $112\% \pm 66$ SD). Core areas ranged from 11 to 29 ha (KE 50; excluding 4a and 4c; Table 2), i.e. $18.6\% \pm 9.8$ SD of total ranges (KE 95). Again, HM estimates were largely different from KE estimates, and generally equal or smaller (8 to 111% of KE; average = $80\% \pm 38$ SD). Foxes started their activity after 18:00 hr and were almost always active at 19:00 hr. The activity level remained high until 00:00 hr, then decreased slowly, and dropped below 50% after 06:00 hr (Fig. 1). After sunrise movements were very limited. Sporadic fixes during the day ($n = 15$) never revealed activity.

Radioed foxes used about 25% of their total range (MCP) each night, without significant individual differences (Kruskal-Wallis ANOVA = 2.06, $P = 0.56$, $df = 3$, $n = 37$; Table 3). The two resident males (1M and 2M) greatly increased their range

Table 2.
Home range size (hectars) of the radioed foxes.

Fox number and sex	No. locations	No. tracking nights	MCP	MCP 95	KE 95	HM 95	KE 50	HM 50
1M	238	9	120.9	64.4	98.3	215.7	14.5	16.1
2M	137	9	394.3	290.7	319.9	289.4	28.9	27.8
3F	188	10	57.0	33.8	46.8	57.7	10.7	8.7
4M	a	2	2307.0	1645.0	1929.3	284.7	699.4	53.5
	b	5	183.3	153.8	137.1	172.2	22.3	23.5
	c	2	33.6	22.9	30.6	30.6	3.8	3.0
Average			188.9	135.7	150.5	183.8	19.1	19.0

MCP = minimum convex polygon; MCP 95 = minimum convex polygon excluding 5% of locations furthest from the harmonic centre; KE 95 and 50 = kernel analysis including 95% and 50% of locations, respectively; HM 95 and 50 = harmonic mean analysis including 95% and 50% of locations, respectively. KE 50 and HM 50 are indices of the core area. The average is computed excluding the a and c ranges of fox 4M (see text).

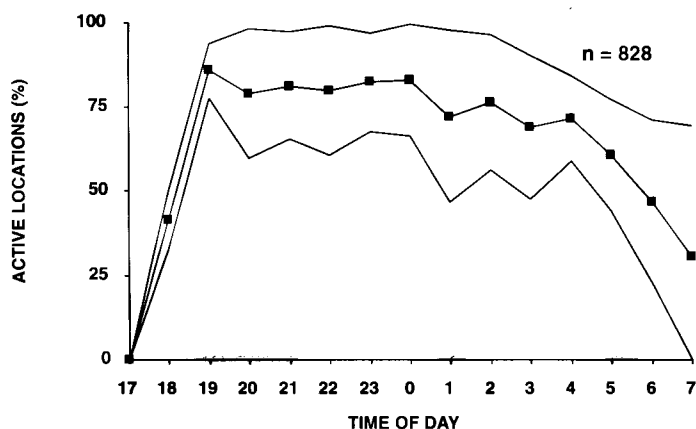


Fig. 1. — Activity patterns of four red foxes in Central Italy (January–May 1993) (with standard deviation among individual foxes). The sample size is the total number of locations.

in the second half of the female fertile period. The third male (4M) showed the opposite pattern, restricting its range exactly during the peak of matings (when he frequented the range of 3F; see above) and increasing it immediately afterwards. The female used a smaller proportion of total area, particularly before the peak of matings; her range decreased markedly after 18 April (peak of births; Fig. 2). Barks were not recorded until the beginning of matings (2 February). The only exception was a barking bout recorded at the first appearance of 4M inside the home range of 3F (25 January), which could be related to the contact function of this call (NEWTON-FISHER *et al.* 1993). The two radioed foxes were very close to each other (≤ 50 m) at the time of barking and for 1 hr afterwards. No barks were recorded during the following 7 nights of tracking until the median ovulation date (25 February). After that date, barking bouts were heard each night (26 February–6 March; 4 tracking nights). From 8 March until the end of this study, no barks were recorded.

Table 3.

Percentage of total range (minimum convex polygon) covered each night by each study fox. The first, nomadic period of 4M was excluded from the analysis (see text).

	Fox number and sex				General average
	1M	2M	3F	4M	
Average	23.9	19.8	16.9	30.7	23.4
SD	21.2	23.1	9.3	28.5	21.0
Min	3.4	2.7	4.0	3.7	2.7
Max	67.9	75.6	30.4	73.1	75.6

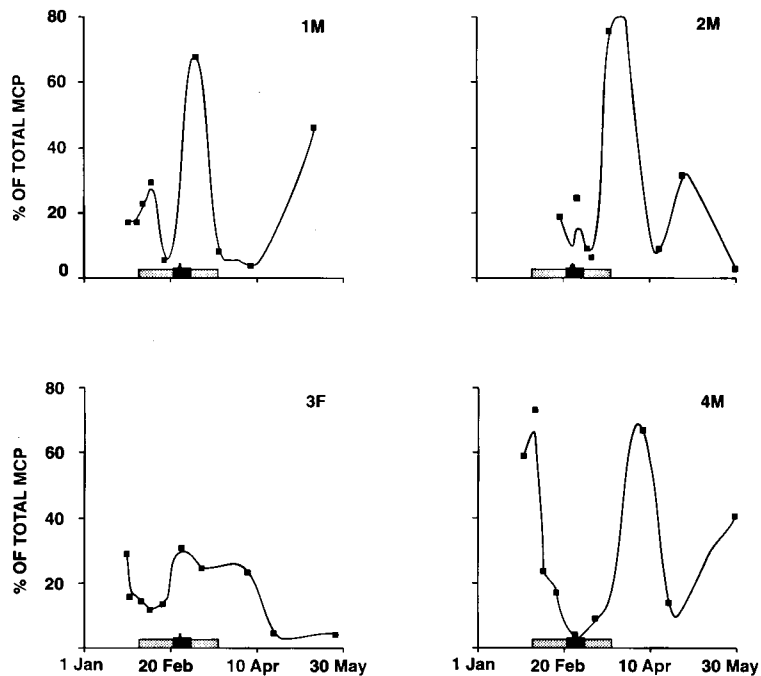


Fig. 2. — Range use (percentage of total minimum convex polygon covered each night) of four red foxes in Central Italy during the mating and breeding season (January-May 1993). The smoothing curve is distance weighed least squares (tension = 0.001; McLAIN 1974). The mating period is indicated by the bar on the abscissa axis: stippled area = range; black area = inter-quartile range (peak of matings); vertical bar = median.

DISCUSSION

The average home range size of foxes found in this study (MCP, 190 ha) was smaller than in many other areas (France: 360 ha, ARTOIS *et al.* 1990; Japan: 500 ha, CAVALLINI 1992; Australia: 600 ha, COMAN *et al.* 1991; U.S.A.: 1470 ha, HARRISON *et al.* 1989; Canada: 1600 ha, JONES & THEBERGE 1982; Central Italy: 330 ha, LOVARI *et al.* 1994; Australia: 330 ha, PHILLIPS & CATLING 1991; U.S.A.: 560 ha, PILS & MARTIN 1978; U.S.A.: 1200 ha, SARGEANT *et al.* 1987; Germany: 470 ha, ZIMEN 1984), but similar to that reported for other areas (North America: 240 ha, ABLES 1969b; Central Italy: 240 ha, CAVALLINI & LOVARI 1994; rural England: 230 ha, VOIGT & MACDONALD 1984, including only studies that reported the MCP values). Foxes in urban and suburban environments have smaller ranges (e.g. DONCASTER & MACDONALD 1991). The difference between harmonic mean and kernel analyses is large when compared to another study (where HM 95 was $100.7\% \pm 25.7$ SD of KE 95, CAVALLINI & LOVARI 1994). Average core area size (50% harmonic mean: 19 ha) was intermediate

between the large areas of rural Japanese foxes (39.5 ha; CAVALLINI 1992) and the small ones in a Mediterranean coastal ecotone (9 ha; CAVALLINI & LOVARI 1994). Excursions had an influence on total range size comparable to that found in the coastal ecotone (MCP 95 was $68.3\% \pm 10.9$ SD of MCP in this study vs $54.7\% \pm 20.0$ SD in Maremma; Mann-Whitney $U = 28$, $P = 0.109$, $n = 12$; CAVALLINI & LOVARI 1994). Both environmental productivity (JONES & THEBERGE 1982), distribution of food (MACDONALD 1981) and presence of larger competitors (e.g. coyote, *Canis latrans* and wolf, *Canis lupus*; HARRISON et al. 1989) may explain this variability. The high level of nocturnal activity (especially in the first half of the night) is coherent with the findings from previous studies (e.g. ABLES 1969a, EGUCHI & NAKAZONO 1980, WEBER et al. 1994).

The tendency towards wider movements by males during the breeding season (NIEWOLD 1980, VOIGT & MACDONALD 1984, ZIMEN 1984, MULDER 1985, SAUNDERS et al. 1993) is confirmed for this population. The fine temporal scale of the analysis showed that resident males moved over larger areas in the period immediately following the oestrus of most females. The nomadic, lean male showed the opposite trend, restricting its movements during the mating period. Barks (more frequent in winter and spring than in the rest of the year; NEWTON-FISHER et al. 1993), followed the same fine-scale trend, being common only after the peak of matings. The female did not show any range increase during the same period. This behaviour of males has never been reported for foxes, and may be interpreted as an attempt by resident males to maximise their reproductive success by "staying home" until the oestrus of the resident female(s), then roaming in search of additional matings. Females may counteract this strategy by attempting to synchronise their oestruses, thereby devaluating the male excursions. As can be expected, oestruses are synchronised among red foxes within each population, whereas they are widely different in distant areas (LLOYD & ENGLUND 1973, CAVALLINI & SANTINI 1995b). The male behaviour appears to be flexible, and dependent on physical condition and social status. A strong range reduction by lactating females (as found in this study) has been measured in other populations (PHILLIPS & CATLING 1991, TRAVAINI et al. 1993).

Alternative hypotheses are possible (e.g. the small, nomadic male could have restricted his range because of the vacancy left by the male that was killed), and the small sample size does not allow the generalisation of my results. Because of the difficulty in catching foxes, such small samples are typical of many studies: the median sample size for 28 home range studies of red foxes was 7, and in 21% of the studies the sample was equal to or smaller than the present one (CAVALLINI 1994). It is therefore necessary to test these ideas on other populations, evaluating both ranging behaviour and reproductive timing.

ACKNOWLEDGEMENTS

Funding for this study was provided by the Amministrazione Provinciale di Pisa (M. Franceschini). Foxes were captured by the game wardens of the Amministrazione Provinciale di Pisa (P. Cerelli and M. Vierucci). S. Santini and T. Volpi helped during field work and laboratory analyses. The guidance and support of late Prof. R. Nobili, Prof. S. Lovari and Prof. R. Dallai made this study possible. The Museo di Storia Naturale e del Territorio dell'Università di Pisa and the Museo di Storia Naturale di Livorno also provided logistic support. All these individuals and institutions are gratefully acknowledged.

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