

Variation in the social system of the red fox

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The existing literature on the ranging behaviour, territoriality, sociality and mating system of the red fox (*Vulpes vulpes*) is reviewed. Red fox home ranges are often unstable, varying in size suddenly or seasonally, shifting, and drifting; excursions are common. Floating individuals often occur in populations, but it is unclear whether they do not have an home range or range over stable areas much larger than those of resident foxes. Territoriality seems not very strict. Sociality is limited to co-operation in the raising of cubs. Evidence for both monogamy and polygyny is present. The red fox social structure might have evolved as fairly tolerant assemblages under the pressure of larger predators.

KEY WORDS: red fox, *Vulpes vulpes*, home range, territoriality, sociality, mating system.

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INTRODUCTION

The cosmopolitan red fox (*Vulpes vulpes*) is one of the most studied carnivores in Europe (ZIMEN 1980) and in North America (ABLES 1975). Its reproduction and feeding ecology are relatively well known (CAVALLINI & VOLPI 1995, CAVALLINI & SANTINI 1996, for short reviews). Because of practical difficulties (foxes are notori-

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ously elusive and difficult to catch), questions involving the direct observation of foxes are less clearly understood, despite the number of field studies conducted. Earlier studies depicted the fox as a territorial animal living in families of one male, one female, and their cubs until about 6 months old (SCOTT 1943). Later, evidence grew that additional females may remain inside the range of the family (MACDONALD 1981, VON SCHANTZ 1984a). There is social flexibility, not only geographically (VOIGT & MACDONALD 1984), but temporally also within the same locality (LINDSTRÖM 1989, ZABEL & TAGGART 1989).

The objectives of this paper are to describe the variation in ranging behaviour, territoriality, sociality, and mating system of red foxes, and to propose an argument linking this variation to selection pressure from larger carnivores. Because several issues are not theoretically clear (e.g. What is an home range? What is territoriality?) and have been used with different meanings in earlier literature, the definitions used are explicitly stated and the observations are described within these frameworks.

DO FOXES HAVE FIXED HOME RANGES?

Definition

According to a classical definition, a "home range is the area over which an animal normally travels in pursuit of its routine activities" (JEWELL 1966: 103). The word "normally" is difficult (or impossible) to define rigorously. Some researchers have approached this problem by excluding some of the locations where the foxes were found, whereas others included all the locations. The criteria for excluding locations have been based on: (i) subjective and/or behavioural grounds, excluding "excursions" (e.g. HARRIS 1980, MACDONALD et al. 1980a, WOOLLARD & HARRIS 1990). The concept of "excursion" may be ambiguous, because it is often defined as a movement outside the home range when it is the home range that is to be defined. Even regular movements outside the home range have been called excursions (NIEWOLD 1980, KOLB 1986); (ii) a variety of statistical methods: discarding either some percentage of locations at some distance from a centre, or least used cells in a grid (e.g. CAVALLINI 1992). There is usually no objective method for selecting a particular percentage for exclusion. The discrepancy among techniques makes it impossible to compare different studies accurately.

Prediction

For an animal with a completely fixed range, one would expect a complete overlap between the ranges of the same animal measured at different times. The home range size should therefore stop increasing within the time scale of the study. If, at the other extreme, foxes are nomadic, total home ranges should increase with time without reaching an asymptote. The minimum convex polygon (the most widely used technique) is not an ideal method to test for this, because it is dependent on the number of observations and is particularly sensitive to outliers (FORD & MYERS 1981, BOULANGER & WHITE 1990), thus leading to an underestimate of the number of ranges reaching an asymptote.

Test

Due to differences in methodology, a variable number of the reviewed papers ($n = 37$; Table 1) provided useful information for each variable. One of the papers (DONCASTER & MACDONALD 1991) reported two widely different situations (stable ranges in suburban habitat, drifting ranges in the city), and is hereafter treated as two separated studies. Most of the studies that reported data on ranging behaviour did not provide evidence on range stability (54%); of those that did ($n = 17$), most (69%) reported stability of ranges, but in only four cases was the stability quantitatively demonstrated (Table 2). Five studies from very different areas found a continuous increase in total home range size with time. For instance, only 29.5% of range was retained after 9 months for foxes in Australia (MARLOW 1992). Excursions were explicitly or implicitly reported by most studies. Other changes included: seasonal size variations (8), shifts (8), sudden enlargements (7), drifts (2), and commuting (1). The distinction between shifts (movements of the activity centre), drifts (continuous sliding of the range) and enlargements was not always clear. The reported causes of such changes included food (foxes can make excursions to feed), sex (males travel widely during the breeding season), cover (foxes can make use of resting sites far from their usual range) and social factors (after the death of a neighbour, foxes can move to areas not previously used).

A fraction of the population (called transient, nomadic or floating) roamed widely, crossing the home ranges of other foxes (NIEWOLD 1980, MACDONALD 1981, VON SCHANTZ 1984a, ZIMEN 1984, HARRIS & SMITH 1987, ZABEL & TAGGART 1989, LOVARI et al. 1994). Few authors (ZIMEN 1984, ZABEL & TAGGART 1989, LOVARI et al. 1994) reported information about these animals. The actual frequency of transients was probably underestimated because they are difficult to follow and many researchers excluded them (consciously or not) from analyses (Table 2).

All age and sex classes of individuals, especially yearling males, moved more widely in late summer through spring (from August-September till November-March in the Northern hemisphere), generally until the end of the breeding season (JENSEN 1968, MARCSTROM 1968, PHILLIPS et al. 1972, STORM et al. 1976, ENGLUND 1980, PAGE 1981, VON SCHANTZ 1981, KOLB 1984, MULDER 1985, HARRIS & TREWHELLA 1988, TREWHELLA & HARRIS 1988, TREWHELLA et al. 1988, COMAN et al. 1991, ALLEN & SARGEANT 1993). Resident males increased their range, whereas a nomadic male restricted it during the same period (CAVALLINI 1996). Long-range movements of adult males have also been recorded in summer (July; KOLB 1984). Adult, resident, and possibly breeding males also moved widely in autumn and winter. When animals did not return to their previous range, these movements have been called dispersal. Because recovery distances increased with age class (ALLEN & SARGEANT 1993), dispersal may not be a single event, but rather foxes can move progressively from year to year.

Conclusions

From available data, foxes often seem attached to particular areas, some after a period of dispersal, but the sizes of the areas and their locations varied with time, probably for sexual (MACDONALD 1981), population dynamic (DONCASTER & MACDONALD 1991) and trophic (CAVALLINI & LOVARI 1991) reasons. An unmeasured fraction of the population was either not attached to particular sites, or it ranged over much larger areas, as hypothesized for birds (ZACK & STUTCHBURY 1992: 212). The

Table 1.
Summary of published data on home range size in the red fox.

Reference	Location	Duration of radio-tracking per fox (months)	n/sex	Average HR size (ha)	Method	Habitat	Season
ABLES 1969	Wisconsin, U.S.A.	0.3-5	3 M, 5 F	237	2	marsh, forest, prairie, shrub, farmland	Sp, Su, W
ARTOIS et al. 1990	N France	6	5 M, 6 F	358	2	forest, pastures, farmland	Y
BOITANI et al. 1984	N Italy	6	3 M, 2 F	195	—	alpine pastures	Y
CAVALLINI 1992	S Japan	4	3 M, 3 F	357-631	2	forest, farmland	Sp, Su
CAVALLINI 1996	Central Italy	5	3 M, 1 F	350	2	woodland, farmland	W, Sp
CAVALLINI & Lovari 1994	Central Italy	8	3 M, 2 F	282	2	shrub	Y
COMAN et al. 1991	Victoria, Australia	≤ 1	2 M, 1 F	600	2	pastures, woodland	Sp
COMAN et al. 1991	Victoria, Australia	≤ 1	2 M, 1 F	90	2	suburban	A
DONCASTER & MACDONALD 1991 ^a	England	2-25	17 (F, M)	93.4	4e	urban	Y
DONCASTER & MACDONALD 1991 ^b	England	3-15	29 (F, M)	54.3	4e	suburban	Y
GOSZCZYNSKI 1989 ^b	Poland	—	≥ 4 M, 4 F	412	6e	forest, farmland	W
HARRIS 1980	England	4	7 F	45	1	urban	Y
HARRISON et al. 1989	Maine, U.S.A.	—	3 M, 3 F	1470	2	forest	Y
JONES & THEBERGE 1982	British Columbia, Canada	1.5-3.2	4 M, 3 F	1611	2	alpine shrub	Su
KEENAN 1981	Ontario, Canada	12	1 M, 2 F	674	4e	forest, farmland	Y
KOLB 1984	Scotland	5	15 M	42-460	2	urban	Y
KOLB 1986	Scotland	1-2	9 F	100	1	urban	Y
LLOYD 1980	Wales	—	44 M, 40 F	70-400	1	farmland	Y
LOVARI et al. 1994	Central Italy	7	3 M, 1 F	330	2	woodland	Y
MACDONALD 1981 ^b	England	—	16 (M, F)	71	2, 5	suburban	Y
MARLOW 1992	NSW, Australia	—	2 M, 7 F	513	3	semi-arid	Y
MAUREL 1980	N France	—	3 M	517	4	forest	Sp
MULDER 1985	The Netherlands	—	56 (M, F)	105-200	1	dunes, woodland	Y
NIEWOLD 1980	The Netherlands	—	10 M, 18 F	263	1	dunes, woodland	Y
PHILLIPS & CATLING 1991	NSW, Australia	4	2 M, 1 F	130-528	2	heath, forest	W, Sp
PILS & MARTIN 1978	Wisconsin, U.S.A.	3	3 F	558	2	farmland	W, Sp
POULLE et al. 1994	N France	16	3 M, 3 F	200 ca.	2	farmland	Y

(continued)

Table 1 (continued)

Reference	Location	Duration of radio-tracking per fox (months)	n/sex	Average HR size (ha)	Method	Habitat	Season
SARGEANT 1972	N Dakota, U.S.A.	—	32	700 ca.	—	woodland, farmland, marshes	Y
SARGEANT et al. 1987	N Dakota, U.S.A.	1-5	8 M, 11 F	1190	2	pastures	Su
SAUNDERS et al. 1993	England	14	3 M, 3 F	30	2	urban	Y
SCOTT 1943	Iowa, U.S.A.	—	≥ 3F, 3M	400	6	farmland	W
STORM et al. 1976	Midwestern U.S.A.	2	2 M, 2 F	1000 ca.	—	farmland	Au
TAKEUCHI & KOGANEZAWA 1992	Central Japan	1-8	2 M, 1 F	650	2	pairie, woodland	W, Sp, Su
VOIGT & MACDONALD 1984	Ontario, Canada	—	34 (M, F)	900	1	farmland	Y
VOIGT & MACDONALD 1984 ^a	England	—	11 (M, F)	86	1	urban	Y
VOIGT & MACDONALD 1984 ^b	England	—	7 (M, F)	45	1	suburban	Y
VOIGT & MACDONALD 1984	England	—	3 (M, F)	234	1	farmland	Y
VON SCHANTZ 1981 ^c	S Sweden	8-12	3 M, 6 F	—	—	pastures, wood, marsh	Y
VON SCHANTZ 1984 ^a	S Sweden	—	5 M, 8 F	—	—	pasture, wood, marsh	Y
WOOLLARD & HARRIS 1990	England	3.8	9 M	52	2	urban	W
ZABEL & TAGGART 1989	Bering Sea	4	ca. 30 (M, F)	27-30	5	arctic island	Su
ZIMEN 1984	Germany	—	58 (M, F)	473	—	farmland, forest	Y
ZIMEN 1984	Germany	—	—	133	—	forest, urban	Y

HR = home range. Season: Sp = spring, Su = summer, A = autumn, W = winter, Y = year-round. Methods are: 1 = subjective polygon; 2 = minimum convex polygon; 3 = Fourier transform (ANDERSON 1982); 4 = grid (4e = excluding excursions); 5 = direct observations; 6 = snow tracking (6e = excluding excursions). When not mentioned, dispersing animals have been excluded. Studies marked with ^a, ^b, ^c were probably based on some of the same foxes.

Table 2.
Summary of published data on home range stability and territoriality in the red fox.

Reference	Degree of HR overlap	Stability of HR n =	Nature of changes in HR size	Known causes	Transients n =
ABLES 1969	large	6 asymptotes	no change	—	0
ARTOIS et al. 1990	small	linear increase	drift, 1 M + 1 F increased	1 social	0
BOITANI et al. 1984	large (M), small (F)	—	—	—	—
CAVALLINI 1992	large (1 F, 2 M)	—	1 M shifted, excursions enlargements, 1 M shift	—	0
CAVALLINI 1996	—	2, quantitative	1 M shifted, excursions	—	1
CAVALLINI & LOVARI 1994	—	4, qualitative	no change	—	0
COMAN et al. 1991	small	—	no change	—	0
COMAN et al. 1991	small	—	no change	—	0
DONCASTER & MACDONALD 1991 ^a	large (non simultaneous)	0	drift (faster in winter), excursions	mortality	excluded
DONCASTER & MACDONALD 1991 ^b	small	asymptotes	excursions	—	excluded
GOSZCZYNSKI 1989 ^b	small	—	excursions	—	excluded
HARRIS 1980	large	—	no change	—	excluded or 0
HARRISON et al. 1989	large (3 M, 1 F)	—	no change	—	0
JONES & THEBERGE 1982	large	—	smaller in spring, larger in summer; excursions smaller in Jan-Feb, larger in Apr-Jun),	—	0
KEENAN 1981	large	no asymptotes	wandering, excursions, shifts	—	0
KOLB 1984	—	≥ 1, qualitative	2 excursions, expansion, 1 shift	—	0
KOLB 1986	large	most foxes (qualitative)	1 commuting	food, cover	1 juv (excluded)
LLOYD 1980	large	—	excursions	—	—
LOVARI et al. 1994	large	1, qualitative	expansions, contractions	—	0
MACDONALD 1981 ^b	large	—	excursions, males travel widely in Jan-Feb	sex	excluded
MAULOW 1992	4-75%	0	shifts (average 6 km) throughout the year	—	0
MAUREL 1980	none	—	no change	—	0
MULDER 1985	small	qualitative	excursions, males travel widely in Jan	—	0 (only dispersal)
NI EWOLD 1980	small	qualitative	excursions, shifts (common Jun-Dec), males travel widely during mating	resting sites	≥ 1 (excluded)
PHILLIPS & CATLING 1991	small	—	no change	—	0
PILS & MARTIN 1978	—	—	1 F shift	—	0

(continued)

Table 2 (continued)

Reference	Degree of HR overlap	Stability of HR n =	Nature of changes in HR size	Known causes	Transients n =
POULLE et al. 1994	large	—	high seasonal variability	—	0
SARGEANT 1972	small	—	1 expansion	social	0
SARGEANT et al. 1987	large (1 M, 3 F)	—	no change	—	0
SAUNDERS et al. 1993	—	qualitative	male excursions in winter	—	0
SCOTT 1943	—	—	smaller when close to the breeding period	—	excluded
STORM et al. 1976	small	—	no change	—	0
TAKEUCHI & KOGANEZAWA 1992	large	0	expansions, contractions, excursions	mortality, reproduction	0
VOIGT & MACDONALD 1984	small	qualitative	males travelling during the mating season, dispersal, female visiting parents, excursions	—	—
VOIGT & MACDONALD 1984 ^a	small	qualitative	males travelling during the mating season, dispersal, excursions	—	—
VOIGT & MACDONALD 1984 ^b	small	qualitative	idem	—	—
VOIGT & MACDONALD 1984	small	qualitative	idem	—	—
VON SCHANTZ 1981 ^c	large	—	no change	—	excluded
VON SCHANTZ 1984 ^a	large	—	—	—	1
WOOLLARD & HARRIS 1990	—	all, quantitative	no change in the residents	—	12 dispersers
ZABEL & TAGGART 1989	large	—	shift of the den	—	43-63%
ZIMEN 1984	—	—	excursions, enlargements, shift	food, sex (males), dispersal, rabies	few

HR = home range. Large home range overlap is $\geq 20\%$. When not mentioned, dispersing animals have been excluded. Studies marked with ^a, ^b, ^c were probably based on some of the same foxes.

latter possibility has usually been dismissed (except for LOVARI *et al.* 1994) without supporting data. Also, the dichotomy between the ranging patterns of resident and transient foxes may not be absolute. A fox can acquire a major proportion of its daily food requirements in a short time from a concentrated, easily acquired food source (CAVALLINI & LOVARI 1991). The energetic importance of excursions may have been underestimated, and the importance of the restricted home range for feeding may have been overestimated.

ARE FOXES TERRITORIAL?

Definitions

The evidence for territoriality has usually relied on the occupation of (i) a defended area (NOBLE 1939), or (ii) an exclusive area (SCHOENER 1968), or both (with a large variability across studies: MAHER & LOTT 1995). To test for this requires data usually not available for a nocturnal, secretive species like the red fox. A less restricted, and more statistically testable definition is: (iii) animals are territorial when they are spaced further apart than would be expected from a random occupation of suitable habitats (KREBS 1978). Other definitions, like that of WILSON (1975), which includes spatio-temporal (or "floating") range defence in the concept of territory, are probably too vague and impossible to distinguish from simple intolerance. Territories have been classified variously: all-purpose (feeding, mating, and breeding), feeding, mating (the food may be collected outside it), and reproductive territories (a small area close to the nest or den; e.g. WILSON 1975).

Predictions

If foxes are territorial, home ranges should not overlap (definitions i and ii), or overlap less than expected by chance (definition iii). Experimental removal should lead to an enlargement of neighbours' ranges. A resident territorial animal should be dominant over an intruder always, whereas non-territorial animals should rank according to fighting ability. Territoriality should also lead to more frequent and intense aggression against transients, and therefore to greater transient mortality caused by intraspecific fighting. The frequency of activity radii should show a platikurtic (truncated) distribution if boundaries occurred (ABLES 1969). Fighting, patrolling and marking at range boundaries should also be expected. If fox territories are all-purpose, marked seasonal variation in the extent of territorial behaviour of the two sexes is not expected. In the instance of mating or reproductive territories, maximum territoriality should be shown in the respective seasons, whereas ranges used as feeding territories should become more exclusive during periods of food shortage.

Test

Because of the variety of methods used for the home range estimation, the results of different studies cannot be compared reliably. The concept of territoriality has been misused in earlier studies, in which it is equated to site attachment

(e.g. SCOTT 1943). In many studies (38%, of those that reported data $n = 29$) only a slight overlap between breeding animals of the same sex was reported (Table 2). In Wisconsin, only 3 of 8 foxes (all females) showed a platykurtic distribution of activity radii (ABLES 1969). However, sample sizes are usually small, and there is the possibility that some unmarked animal had overlapping ranges. The majority of studies (62%, $n = 29$) reported at least one instance of large home range overlap or (in one instance in an unusual environment) a complete lack of territorial behaviour (ZABEL & TAGGART 1989) among breeding animals. Very high density, limited emigration opportunities and possibly high inbreeding might be factors explaining the occurrence of a complete lack of territoriality (ZABEL & TAGGART 1989). A "group" of at least three females and one male showed large but variable overlap during a 20-month period; the same animals (and also a male from an adjacent range) frequently associated during daytime rest (POULLE et al. 1994). By contrast, in a high density urban area incursions in adjacent territories were rare (except in winter), encounters between foxes belonging to different groups were avoided (and were almost always aggressive), and intra-group encounters were uniformly common and non-aggressive throughout the year (WHITE & HARRIS 1994).

A rigorous test of prediction (iii) was attempted only by HEWSON (1986) and, with a smaller sample size, VON SCHANTZ (1984b), who showed a significantly uniform distribution of breeding dens. This strongly suggests intraspecific avoidance, at least during breeding. In Switzerland, however, both breeding and non-breeding dens were randomly spaced (MEIA & WEBER 1992), possibly because of a shortage of den sites (HEWSON 1994). Borders between non-related foxes were rigid and non-overlapping near the den, but more flexible at other points, both in a large enclosure (PRESTON 1975) and in the wild (KEENAN 1981). There was some evidence of smaller female ranges (and therefore less overlap) during breeding (SCOTT 1943, KEENAN 1981, POULLE et al. 1994). However, infrequent but widespread communal denning has been reported (SHELDON 1950, STORM et al. 1976, TULLAR et al. 1976, PILS & MARTIN 1978, TULLAR & BERCHIELLI 1980).

The period of more intense territoriality differs among studies: borders seemed less rigid during autumn and winter (dispersal and mating times; NIEWOLD 1980), late summer and autumn (dispersal time; MULDER 1985) or spring and summer (breeding season; PILS & MARTIN 1978). Increased male movements during the mating season (January to March in the Northern hemisphere) imply that the range overlap was at a maximum (thus, territoriality was at a minimum) in this period (Table 2). Aggressive vocalisations (NEWTON-FISHER et al. 1993) and physical injuries (WHITE & HARRIS 1994, DUFF & HUNT 1995) peaked during the same period. However, the home ranges of males in Edinburgh were smaller in January-February, and larger in April-June (KOLB 1984). Many studies reported no seasonal change in home range size (Table 2). Sudden home range shifts were common in June-December (NIEWOLD 1980), and drift was faster in the winter (DONCASTER & MACDONALD 1991). The ranges of two or more males can overlap widely (MURIE 1961, NIEWOLD 1980, HARRIS & SMITH 1987, CAVALLINI 1992). The overlapping males may have been related (MURIE 1961, NIEWOLD 1980). The home range of a breeding female can overlap that of non-breeding (MACDONALD 1981, VON SCHANTZ 1981) or breeding females (HARRIS 1980, KOLB 1986). Younger vixens had restricted movements within the range of older ones (HARRIS 1980, VON SCHANTZ 1981, KOLB 1986). Although no removal experiment was attempted, range expansions have been related to the disappearance of neighbouring foxes (SARGEANT 1972, NIEWOLD 1980, ARTOIS et al. 1990).

Feeding aggregations have been reported (HARRIS 1980, JONES & THEBERGE 1982, KOLB 1986). No boundary patrolling (SARGEANT 1972, SERVÍN *et al.* 1991) or scent marking at range borders (GOSZCZYNSKI 1990) have been reported, but in two instances, indirect evidence for boundary defence was noted (NIEWOLD 1980). Resident males were dominant over introduced males in only a minority of encounters in a large enclosure (PRESTON 1975), and complex male hierarchies can be established (VINCENT 1958, PRESTON 1975). However, continual harassment by the resident male finally resulted in the exclusion of the introduced one (PRESTON 1975). Foxes trapped close to one another often showed dominance-subordination relationships (BARASH 1974). The vocal repertoire is large and complex, which suggests some social tolerance (NEWTON-FISHER *et al.* 1993). Frequencies of inter- and intra-group aggressive encounters were broadly similar in an urban environment (WHITE & HARRIS 1994). Intraspecific fights were a rare source of mortality in an urban habitat (< 4%), and their importance was greater at very high density (7%; HARRIS & SMITH 1987). No data are available on the differential mortality of transients.

Conclusions

The question of fox territoriality is of particular importance, because territoriality is at the basis of most hypotheses on the social behaviour of foxes (e.g. LINDSTRÖM 1986). The Resource Dispersion Hypothesis (MACDONALD 1981, 1983), which recently received much attention, both theoretical (e.g. CARR & MACDONALD 1986) and empirical (e.g. GEFFEN *et al.* 1992), implies exclusive "territories containing sufficient resources to meet or exceed their [the animal's] requirements for a critical proportion of feeding periods" (CARR & MACDONALD 1986).

In early studies the existence of territorial behaviour in the red fox was not conclusively demonstrated (ABLES 1975). Various lines of evidence suggest occasional and not very strict exclusivity of ranges: (i) the high mobility of ranges; (ii) the inconsistency between the results of different studies in different areas; (iii) the generalised (but not yet quantified) presence of wide-ranging movements; and (iv) the existence of a proportion of foxes without a fixed home range that traverse the ranges of other foxes. A few authors describe the social system of the red fox as "widespread intraspecific tolerance" (PHILLIPS 1971, TULLAR & BERCHIELLI 1980). The common evidence of "excursions" directed to exploit feeding and mating opportunities diminish the likelihood of the presence of feeding or mating territories. Furthermore, defending resources year-round implies generalised food limitation, for which there is no hard evidence, except in northern areas (LINDSTRÖM 1989). Catholic feeding habits (e.g. DONCASTER *et al.* 1990, CAVALLINI & LOVARI 1991, JEDRZEJEWSKI & JEDRZEJEWSKA 1992) make food limitation unlikely in most habitats, at least outside reproduction. Defence of females implies female territoriality and restricted movements in the mating season (DAVIES 1991). The protection of females from harassment and the prevention of intraspecific predation (infanticide; ZABEL & TAGGART 1989) may be a function of intraspecific intolerance near the den. The advantage of an intimate knowledge of an area, which may enhance feeding efficiency (CAVALLINI & LOVARI 1991) or reduce susceptibility to capture (LAUNDRE & KELLER 1983, TRAVAINI *et al.* 1993) may explain the general residential tendency of foxes.

ARE FOXES SOLITARY?

Definition

An animal is solitary when it never co-operates with conspecifics, except for mating (SANDELL 1989). For a carnivore, co-operation is most likely to arise in hunting (e.g. PACKER & RUTTAN 1988), in the rearing of young (e.g. MACDONALD & MOEHLMAN 1982), in defence of a territory (e.g. KRUUK & MACDONALD 1985) or from predators (e.g. RASA 1986). A different definition is: "solitary species are those whose members are usually found alone" (WASER & JONES 1983).

Prediction

If solitary, no co-operation should be shown, and individuals should be seen alone.

Test

Foxes are usually found alone (BURROWS 1968, ABLES 1975, KEENAN 1981, LLOYD & HEWSON 1986). No co-operation in defence of a territory or from predators has been observed in the red fox. Communal defence, however, may have been overlooked because of practical difficulties in observing foxes. Co-operation in hunting is not expected, because of the average small size of fox prey (e.g. ABLES 1975, LLOYD & HEWSON 1986, CATLING 1988), but has been observed for foxes hunting roe deer in deep snow (LINDSTRÖM 1982). Communal denning gives foxes the opportunity of co-operation in reproduction. Some barren or lactating vixens fed the cubs of dominant females, both in the wild and in captivity, and non-breeding females may adopt the cubs on the death of the mother (MACDONALD 1980, VON SCHANTZ 1981).

Conclusions

Red foxes can occasionally co-operate in raising young, and this behaviour may drive the evolution of grouping (e.g. MACDONALD & MOEHLMAN 1982). Foxes have a relatively high cost of reproduction which, within Carnivora, is associated with helping (CREEL & CREEL 1991). It is unclear whether co-operation in reproduction is an adaptive trait *per se* or it is a by-product of ranging behaviour imposed by the patchy distribution of food sources (MACDONALD 1981). However, the propensity of foxes to adopt even unrelated pups may question the adaptive value of this behaviour, especially where contagious diseases are widespread (TULLAR et al. 1976).

ARE FOXES MONOGAMOUS?

Definitions

Monogamy is when one male and one female form a pair bond. Genetic monogamy implies that all the offspring of one male are the offspring of one female

only, and vice versa. The monogamy may be limited to one breeding season, or it may extend through the lifetime. It can be distinguished from promiscuity, in which there is no pair bond, and each individual can mate with several others. Polygyny (simultaneous or sequential) consists of a male mating with several females (DAVIES 1991).

Predictions

The most conclusive evidence is provided by genetic paternity. If monogamous, a male fox should stay with a female at least during the mating season. Weaker correlates of monogamy are sexual monomorphism and similar home range size between sexes. The sex ratio among breeding adults provides a simple (although not accurate) measure of the potential for polygyny (COCKBURN 1988).

Test

Unfortunately, no genetic data are available on parentage in the fox. I have therefore to rely on observational data. Some authors have referred to the basic social structure of the fox as a "family", suggesting monogamy (SARGEANT 1972, SARGEANT et al. 1987). Male and female have been radio-tracked travelling together from December till June (NIEWOLD 1980). In other studies, males expanded their range during the mating season (Table 2), thus suggesting the opportunity for scramble competition. Males have been observed to compete directly for a female during the mating season (ABLES 1975, NIEWOLD 1980, LLOYD & HEWSON 1986). Communal denning may have resulted from the same male mating with more than one female (MACDONALD 1980). In years of high food abundance, probably more than one female mated with the same male (MACDONALD 1980, VON SCHANTZ 1984a, ZABEL & TAGGART 1989). A male range overlapped those of two females whose activity was concentrated close to two separate dens (KEENAN 1981, POULLE et al. 1994), suggesting the occurrence of polygyny. Male co-operation in whelping has been reported (SARGEANT & EBERHARDT 1975, MACDONALD 1980, ZABEL & TAGGART 1989). A lone female was unable to raise its pups because of interference from males and insufficient feeding (ZABEL & TAGGART 1989). Sexual dimorphism is comparatively slight, males averaging 1.1-1.2 times heavier than females (e.g. LLOYD 1980). Home range size may be similar between sexes (ARTOIS 1985, CAVALLINI 1992), or larger for males (KEENAN 1981, SAUNDERS et al. 1993). The pair bond, when present, did not seem to last more than one year (NIEWOLD 1980, MARLOW 1992).

Parental investment and sexual selection theory predicts that when males contribute less to reproduction (as is likely when food is more abundant, and litter size is reduced), there will be a tendency toward polygyny, the adult sex ratio will skew toward females, and males will disperse (TRIVERS 1972, MOEHLMAN 1989). Foxes show a tendency toward polygyny, and more subadult males than subadult females disperse; the sex ratio among breeding adults was not known. In some samples females were under-represented, but this was thought to reflect greater vulnerability of males to shooting and trapping (e.g. YONEDA & MAEKAWA 1982).

Conclusions

The red fox is not completely monogamous. Polygyny is reached through different strategies: males roaming in search of receptive females, males mating with more than one female in the same range, and males monopolising the ranges of two vixens. Theoretically it is expected that different strategies should be related to social variables such as density and population dynamics. However, the data available do not show any consistent trend. For instance, male excursions during mating were common both in Oxford, U.K. (high density, low mortality) and in Ontario, Canada (low density, high mortality; VOIGT & MACDONALD 1984). With a variable litter size (the average litter size ranges from < 3 to > 7 ; CAVALLINI & SANTINI 1996), female parental investment (and therefore the need for male assistance) also varies. The role of transient males in breeding is unclear. It has been demonstrated that female brown hyenas (*Hyaena brunnea*), aardwolf (*Proteles cristatus*), Abyssinian wolves (*Canis simiensis*) and Eurasian badgers (*Meles meles*) may copulate with immigrant males rather than with those they usually associate with within the clan (EVANS et al. 1989, MILLS 1989, KOEHLER & RICHARDSON 1990, SILLERO-ZUBIRI & GOTTELLI 1994). The simultaneous occurrence of different mating systems is possible, as demonstrated for the dunnock *Prunella modularis* (DAVIES 1985) and suggested for the Egyptian mongoose *Herpestes ichneumon* (PALOMARES 1993). If male investment in parental care occurs, it may be a protection against infanticide, as in primates (SCHAIK & DUNBAR 1990) and voles (COCKBURN 1988); if so, a male is expected to remain with the female he has impregnated. Many questions remain open: are there mating preferences? (e.g. with dominant males or females or with previous partners); is there multiple paternity? Is there sperm competition? What is the function (if any) of the postcopulatory lock?

GENERAL CONCLUSIONS

Variability in ranging behaviour, territoriality, sociality, and mating system of the red fox is large, both within and between populations. Most studies are based on small samples ($n < 10$ individuals), and their more or less anecdotal nature does not allow the causes of such variation to be clarified, or uncover systematic associations between ecological and sociological variables to be uncovered. The available data are only partly consistent either with the vision of the fox as monogamous, living in family territories or with the "helpers" model (MACDONALD 1981). A fair degree of intraspecific tolerance is apparent (PHILLIPS 1971, TULLAR & BERCIELLI 1980).

The red fox has evolved in environments with larger canids (wolves, *Canis lupus*, jackals, *C. aureus*, and coyotes, *C. latrans*) and other large predators, which are important sources of mortality for foxes (MECH 1966, SARGEANT & ALLEN 1989, STEPHENSON et al. 1991, RALLS & WHITE 1995). Examples are: (i) the lynx *Felis lynx* may be a cause of a decline of red fox populations in Alaska (STEPHENSON et al. 1991); (ii) coyotes are the main cause of mortality for the kit fox, *Vulpes velox* (WHITE & RALLS 1993); (iii) after the extinction of the wolf in North-Eastern Spain, fox populations increased (RUIZ-OLMO et al. 1990). Furthermore, wolves can eat red foxes (MERIGGI et al. 1991). One or two species of larger canids are common (or they were in the recent past) throughout the geographical range of the red fox (Fox

1975). The smaller canids tend to occupy "buffer zones" between the home ranges of larger ones (MACDONALD et al. 1980b, VOIGT & EARLE 1983, SARGEANT et al. 1987, HARRISON et al. 1989, SARGEANT & ALLEN 1989, THEBERGE & WEDELES 1989, PACQUET 1991). In this context, a rigid social and spatial structure would have been maladaptive, forcing some of the foxes to live within the home range of larger predator. The ability to shift, drift, enlarge, shrink and overlap their home ranges (together with the catholic diet) may have evolved as an adaptation to the spatial constraints imposed by the ranging behaviour of larger predators (unpredictable from a fox's point of view). If so, the main limiting factor in the evolutionary history of foxes might have been the availability of areas free from larger carnivores. The same argument used to explain the acceptance of conspecifics within a territory (low cost of keeping subordinates; CARR & MACDONALD 1986, MACDONALD & CARR 1989) may also explain a more generalised tolerance (e.g. WASER 1988).

This hypothesis is not easily testable, because it involves long-term adaptations characterized by phylogenetic inertia: tolerance may be a phylogenetically determined character (BALHARRY 1993) difficult to acquire (TAYLOR et al. 1990). However, I predict that the reintroduction of a larger canid would profoundly affect the ranging behaviour, territoriality, sociality, and mating system of the red fox. Within the limitations imposed by larger canid distribution, or in their absence, food distribution would determine the fine-scale use of habitat by foxes. Indeed, resource-based models have best been tested in areas free from larger predators (e.g. MACDONALD 1981, ZABEL & TAGGART 1989). The red fox usually selects the areas of greatest environmental diversity (CAVALLINI & LOVARI 1994). The selection of more uniform areas in the presence of the coyote (THEBERGE & WEDELES 1989) could therefore lend partial support to my prediction. The reintroduction of a larger canid (wolf, coyote) could provide a more thorough test of this hypothesis. Monitoring of red fox populations before, during, and after such an event would therefore be worthwhile. Also a comparison of fox societies living under different kinds of predation pressure could help to test the hypothesis.

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