

Polygynandry in a red fox population: implications for the evolution of group living in canids?

Philip J. Baker,^a Stephan M. Funk,^{a,b} Michael W. Bruford,^{b,c} and Stephen Harris^a

^aSchool of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK,

^bInstitute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK, and

^cSchool of Biosciences, Cardiff University, PO Box 915, Cathays Park, Cardiff CF10 3TL, UK

Canid social groups are typically thought to consist of extended families, that is, a dominant breeding pair and related nonbreeding subordinates, that principally obtain indirect fitness benefits from helping to raise the offspring of the dominant pair. Consequently, the monogamous pair has been viewed as the basic fundamental unit of canid social organization. However, there have been few genetic studies that have tested this assumption. We analyzed the parentage of red foxes (*Vulpes vulpes*) in a high-density (19.6–27.7 adult foxes/km²) population in Bristol, UK, to determine (1) whether groups typically produced a single litter of cubs annually and (2) whether male and female foxes exhibited monogamous mating strategies. Social monogamy (the production of one litter in a social group) was observed or assumed in 54% of breeding attempts ($N = 13$ group-years). However, polyandrous and polygynous patterns of mating were common. Multiple paternity was confirmed in 38% of litters ($N = 16$) containing offspring with resolved maternity and paternity ($N = 30$ cubs); when including cubs with unresolved paternity ($N = 20$), multiple-paternity may have occurred in 69% of litters. Litters were sired by an average of 1.6 identified males (range = 1–4); when including cubs with unresolved paternity, litters may have been sired by up to seven males. Only 20% (6/30) of cubs with resolved maternity and paternity were sired by males within the social group. Within groups, dominant females did not breed with subordinate males; dominant males did breed with subordinate females. Dominant and subordinate females both produced cubs with dominant and subordinate males from other social groups. Mean adult relatedness in groups typically ranged from 0.15–0.35, indicative of second-order rather than first-order relatives. *Key words:* dominant males/females, maternity, paternity, red foxes, subordinate males/females. [*Behav Ecol* 15:766–778 (2004)]

Most mammalian carnivores are solitary and exhibit a social system of intrasexual territoriality, with larger male ranges encompassing those of several females (Sandell, 1989). By contrast, most canid species exhibit a system of group territoriality comprising a breeding pair and several subordinates (Geffen et al., 1996; Macdonald and Moehlman, 1983; Moehlman, 1989). Some species (grey wolf, *Canis lupus*; African wild dog, *Lycaon pictus*) exhibit complex forms of cooperative behavior (Creel and Creel, 1995; Fanshawe and Fitzgibbon, 1993), whereas others (red fox, *Vulpes vulpes*) form groups numbering up to 10 adults under some circumstances (Baker et al., 2000; Cavallini, 1996) but are predominantly solitary. The social system of the red fox has, therefore, been viewed as one potential step in the evolutionary pathway to more complex societies (Baker and Harris, 2004).

In assessing why red foxes form social groups in the absence of cooperative benefits, particular attention has focussed on the role of resource availability (Bacon et al., 1991a,b; Carr and Macdonald, 1986; Johnson et al., 2002; Macdonald, 1981, 1983; von Schantz, 1984). For example, the resource dispersion hypothesis (RDH) proposes that groups may arise in the absence of any a priori need for interindividual cooperation simply as a consequence of the rules by which the dominant breeding pair configure their territories in order to obtain sufficient resources throughout a period of limited resource availability. As the territory is delimited according to the period of worst resource availability, average resource avail-

ability may be greater than that required solely by the breeding male and female such that subordinate animals may be able to coexist on a territory at little or no cost to the dominant pair. Therefore, within these species, group living may be an epiphenomenon of resource dispersion (Kruuk and Macdonald, 1985).

However, resource availability alone cannot explain this system of organization. To determine the conditions under which subordinates will remain on a territory, it is necessary to consider the relative costs and benefits of dispersing versus those of remaining (Emlen, 1982a,b; Macdonald and Carr, 1989; Vehrencamp, 1983). Generally, fox groups are thought to be extended families, with subordinates being the philopatric offspring of one or both of the dominant breeding pair (Baker et al., 1998; Macdonald, 1979; von Schantz, 1984; but see Zabel, 1986). Because it is widely believed that subordinate reproduction is typically suppressed (Creel and Macdonald, 1995; Moehlman and Hofer, 1997), the major fitness benefits that subordinates may attain are indirect by helping to raise the young of the dominant pair (Macdonald, 1979), and/or direct either by inheriting the territory upon the death of the same-sex parent (Lindström, 1986) or with a limited chance of direct breeding when resource availability permits (Zabel and Taggart, 1989). Therefore, the evolutionary stability of this system relies on a high degree of relatedness between dominants and subordinates. Observations of mate-guarding behavior, interference with copulations, and postcopulatory locks have led researchers to believe that canids are monogamous (Kleiman, 1977), leading to the inference that nonbreeders must be close relatives of the dominant pair (Lehman et al., 1992). During the breeding season, male foxes may closely follow sexually receptive females for several days,

Address correspondence to P. J. Baker. E-mail: p.j.baker@bristol.ac.uk.

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although this is not always the case. Similarly, mating may or may not result in a postcopulatory lock.

Yet there is evidence to suggest that mating may not be exclusively monogamous (Harrington et al., 1982; Sillero-Zubiri et al., 1996). For example, male foxes are known to undergo extraterritorial movements during the breeding season (White et al., 1996; Zimen, 1984), and this appears to be a major source of mortality (Harris and Smith, 1987). In addition, paternal care may be important for cub survival (*sensu* Kleiman and Eisenberg, 1973). Consequently, to offset the mortality risk associated with searching for extraterritorial mates and the potential reduction in survival of an individual's cubs on its home territory should the adult male be killed during an extraterritorial movement, it would be predicted that such movements lead to an increased reproductive output.

The role of alloparental care and territory inheritance are also unclear. For example, von Schantz (1984) rarely recorded alloparental provisioning. In the population studied by Baker et al. (1998), alloparental care was widespread among both male and female subordinates but did not appear to increase cub survival. Although Zabel and Taggart (1989) showed that alloparental care did increase cub survival, this was for an island population where it limited infanticide rather than increased provisioning rates: it is unclear whether intergroup infanticide is common in nonisland populations. The RDH assumes that dominant animals have preferential access to resource supplies (see Macdonald, 1981) such that subordinate mortality rates would be expected to be higher than those of dominant animals; in Bristol, the age at death of dominant animals was much higher than that of subordinates, although it was not clear whether this was due to access to resources (Baker et al., 1998). Under these conditions, most subordinates would not live to inherit a territory. In the absence of these benefits, there would be a strong selective pressure for subordinates to attempt to breed directly. As a consequence, it may be predicted that foxes exhibit a nonmonogamous system of mating, that there are direct fitness benefits from natal philopatry, and that social groups show lower levels of relatedness than hitherto believed.

Since 1990, we have studied a number of fox groups in northwest Bristol, UK. Between 1990–1994, before an outbreak of mange, population density increased from 7.8–37.0 adults/km² as a result of the increased availability of food (Baker et al., 2000, 2001a). From an analysis of the costs and benefits associated with remaining in a social group versus those of dispersing, we concluded that in this population the principal fitness benefit for subordinates was probably the chance to reproduce directly (Baker et al., 1998). However, the true level of breeding by subordinates can only be measured by genetic analysis. In this article, we test the hypothesis that monogamy in this population was rare by parentage testing using microsatellite markers amplified from DNA samples of cubs collected during the period of high fox density. We consider monogamy in two contexts: (1) group reproductive output (hereafter termed social monogamy) and (2) underlying mating strategies (hereafter termed genetic monogamy). However, different investigators have used the term “monogamy” to describe both concepts, whereas in reality they are not synonymous: social monogamy can occur with monogamous, polygynous, and polyandrous mating strategies.

METHODS

Study site and study animals

The study site occupied an area of approximately 1.5 km² in northwest Bristol, UK. Six social groups were studied initially, but two further groups were formed during the study from the

division of two territories. Foxes were captured by using cage-traps set in private residential gardens (Baker et al., 2001b). During the course of the study, one litter of eight cubs was born to a female during trapping and these cubs perished (see Results); no other animals were injured or died as a result of the protocols implemented.

Once captured, animals were sexed, weighed, aged by incisor wear (Harris, 1978), and marked with plastic ear tags (Rototags, Dalton Supplies Ltd). Full-grown animals were fitted with radio-collars manufactured at the University of Bristol, which were covered in colored electrical insulating tape to aid individual identification in the field. Collar units weighed 200–250g. The mean (\pm SD) weight of resident and nonresident foxes collared was 6.0 ± 0.8 kg (range = 4.3–8.5 kg; $N=91$); at fitting, collars were selected such that they never exceeded 5% of the animal's mass. All animals were assumed to have been born on 1 April (Harris and Trehwella, 1988): each fox-year corresponds to the period 1 April–31 March. The term “cub” denotes animals less than 6 months old; “subadult,” animals 6–12 months old; and “adult,” any animal more than 12 months old.

Genetic samples were collected from January 1992–June 1994 inclusive. In this article, we consider the maternity and paternity relationships only of those animals born in 1992 and 1993: animals born in 1994 have been excluded as this coincided with an outbreak of sarcoptic mange and was associated with large population perturbations (Baker et al., 2001a). Adult animals were assigned to social groups on the basis of information derived from trapping, nocturnal radio tracking, diurnal rest sites, observations at feeding sites, and the recovery of dead individuals (Baker et al., 1998, 2000, 2001b). During 1990–1994, animals were trapped on 458 occasions, and 28 sightings recorded by members of the general public, more than 1000 sightings made during 360 nights of radio tracking, and more than 3500 daytime rest sites were recorded (Baker et al., 2001b). Any individual found on the same territory for two successive records was assumed to have been resident on that territory for the intervening period. Territory configurations were determined by radio tracking and expressed as minimum convex polygons (see Saunders et al., 1993). Adult social status was assessed from observations at feeding sites and during radio tracking sessions. Dominant animals were individuals that elicited submissive behavior from all other animals in the same social group. All other adults were classed as subordinate. Each group was composed of a dominant male and female and a variable number of subordinate adults.

Animals captured or recovered dead as cubs were assigned to the group in whose territory they were caught or found and considered resident from 1 April. Animals captured as subadults and adults and subsequently confirmed as resident on a territory were considered resident from 1 April of the corresponding fox-year; any animal disappearing within a period of 1 week after its release was considered to be a nonresident individual. Untagged animals recovered dead as subadults were not considered resident because most dispersal occurs in this age class and it is a period of high mortality (Harris and Trehwella, 1988).

Genetic analyses

Genetic analysis was conducted on tissue taken during ear tagging or from spleens taken from dead individuals. Samples were stored in 25% w/v dimethylsulphoxide in 6 M NaCl (ear tissue) or frozen (-80°C , spleen) before analysis. DNA was extracted by using standard phenol/chloroform extraction procedures (Bruford et al., 1998). Parentage analysis was carried out by using 10 canine microsatellite markers: c2001, c2006, c2010, c2017, c2054, c2075, c2088 (all tetranucleotide

repeat microsatellites; Francisco et al., 1996), aht130 (dinucleotide repeat; Holmes et al., 1994), ucb466, and ucb642 (dinucleotide repeats; Ostrander et al., 1995; GenBank accession numbers for u642 are L29310 and L29318) (Table 1). All forward primers were fluorescently labeled with one of three dyes (FAM, HEX, or TET) suitable for semiautomated genotyping. PCR was carried out in a 10 µl volume containing 50 ng DNA, 2 nmol of each dNTP, either 5 pmol (dinucleotides) or 1 pmol of each primer (tetranucleotides), 0.25 U of *Taq* polymerase, and 10% 10× KCl *Taq* buffer (IGI). Two triplex amplification systems were designed for the tetranucleotides. PCR was carried out in a 15 µl volume containing 50 ng DNA, 4 nmol of each dNTP, 0.5 U of *Taq* polymerase, and 10% (v/v) 10× KCl *Taq* buffer. One system contained 1 pmol of each primer of the markers 2006, 2054, and 2088, and the second contained 1 pmol of each primer of the marker 2001 and 1.8 pmol of each primer of the markers 2010 and 2017, respectively.

Amplifications were carried out by using a Perkin Elmer Cetus 9600 thermal cycler using the following parameters: one 5-min denaturation at 94°C, followed by 32 cycles of 15 s at 94°C, 30 s at annealing temperature, and 1 min at 72°C, followed by a final extension step at 72°C for 30 min. PCR products, including TAMRA 350 size standard (Applied Biosystems), were electrophoresed by using an Applied Biosystems 377 DNA sequencer with Genescan Analysis software for Macintosh following the manufacturer's instructions. Multiplex systems were designed for genotyping of foxes on the basis of primers annealing at 58°C and compatibility of primers (using the AssemblyLign software for Macintosh; International Biotechnologies, Inc.). Genotype confirmation and analysis was carried out by using GeneScan Analysis 2.0 and Genotyper 1.1 software.

Parentage was analyzed both by exclusion and inclusion. For the exclusion analysis, adults that were present in the study area during the period of conception and for whom a genetic sample was obtained (i.e., potential parents) were excluded if they did not possess an allele in the offspring, either singly or in combination with the other putative parent. Analyses were carried out by using POPASSIGN 4.0 (Goossens et al., 2002) to calculate the number of loci for which there was an allelic exclusion for all potential mothers and fathers, and for combinations of males and females, resulting in an exclusion probability for each parent-offspring combination (after the method of Chakraborty et al., 1988).

For inclusion analyses, we used likelihood analysis in the program CERVUS 1.0 (Marshall et al., 1998) to identify the most likely parent from a number of potential parents by correlating the genotypes of the adult sample to the most likely genotype of the parent (Coltman et al., 1998; Constable et al., 2001). With this approach, a potential parent can be implicated if the number of loci is not sufficient to exclude all other males and if not all potential fathers have been included in the tests. This program was also used to assess the possible occurrence of null (nonamplifying) alleles.

The number of individuals that were candidates for maternity or paternity for each offspring was estimated from field observations based upon sightings of known females and males present at the time of conception of each offspring. The proportion of candidate females and males sampled was 0.76 ($N = 16/21$) and 0.87 ($N = 20/23$), respectively (two animals of unknown sex excluded). The proportions of loci typed (0.95) and the loci mistyped (0.05) are average values for both sexes across the 10 loci typed. We estimated the rate of typing error from the frequency of single allele mother and father-offspring mismatches (see criteria below). Parentages were analyzed at 80% and 95% levels of confidence, and 10,000 simulations were generated.

Table 1

Genetic diversity of markers used in this study

Microsatellite	Annealing temperature	Size range	Alleles (N)	Polymorphic information content
2001	58	127–151	6	0.59
2006	58	193–297	6	0.55
2010	58	220–240	5	0.16
2017	58	266–298	10	0.67
2054	58	144–200	10	0.76
2075	58	149–206	7	0.44
2088	58	127–159	6	0.51
Ucb466	59	139–153	7	0.53
Ucb642	58	146–182	13	0.80
AHT-130	55	111–123	7	0.77

Parentages were considered assigned using the decision matrix in Figure 1. In general, individual adults with a single allelic exclusion with the offspring, or male-female pairs with a single combined allelic exclusion with the offspring, were considered as potential parents to allow for mistyping or the extremely unlikely event of a mutation. Females were assigned to cubs unequivocally if she was the only female who had zero allelic exclusions with the cub *and* the female was observed performing maternal behavior with that cub or if the female was known to be a member of the group into which the cub was born at the time of conception. If more than one female presented zero or one exclusions, then inclusion analysis using CERVUS was performed: females were accepted as parents only if a single mother was identified at 80% or 95% confidence. In all other cases, maternity was not assigned.

Fathers were assigned conditionally with respect to the mother's genotype if a mother had been assigned (see above); if no mother had been identified, males were assigned unconditionally. Paternity was assigned unequivocally if the individual was the sole adult male with zero to one pair-offspring allelic exclusions or zero to one father-offspring allelic exclusions *and* had 80% or higher inclusion likelihood using CERVUS. CERVUS paternity inclusion analysis was always carried out unconditionally on the maternal genotype. If several potential fathers satisfied the above criteria, paternity was assigned only if there was clear behavioral or demographic evidence that would exclude all except one competing male. In the case of several nonexcluded and ecologically plausible males being implicated, sole paternity was ascribed if only one of these males had a 95% or greater likelihood inclusion confidence estimate.

Group reproductive output

For all groups we determined the frequency of singular and plural breeding. Singular breeding is defined as those instances in which all offspring whose maternity was confirmed originated from a single female. Plural breeding is defined as those instances in which offspring whose maternity was confirmed originated from more than one female. Litter size was determined retrospectively based on genetic analyses, as litters of females in the same social group were typically pooled and reared communally such that it was not possible to assign cubs to individual females on the basis of behavioral observations. Overall, the present study encompassed 13 group-years.

Sex-specific reproductive output

Male and female reproductive output was calculated for all resident adult foxes that had been sampled in the study

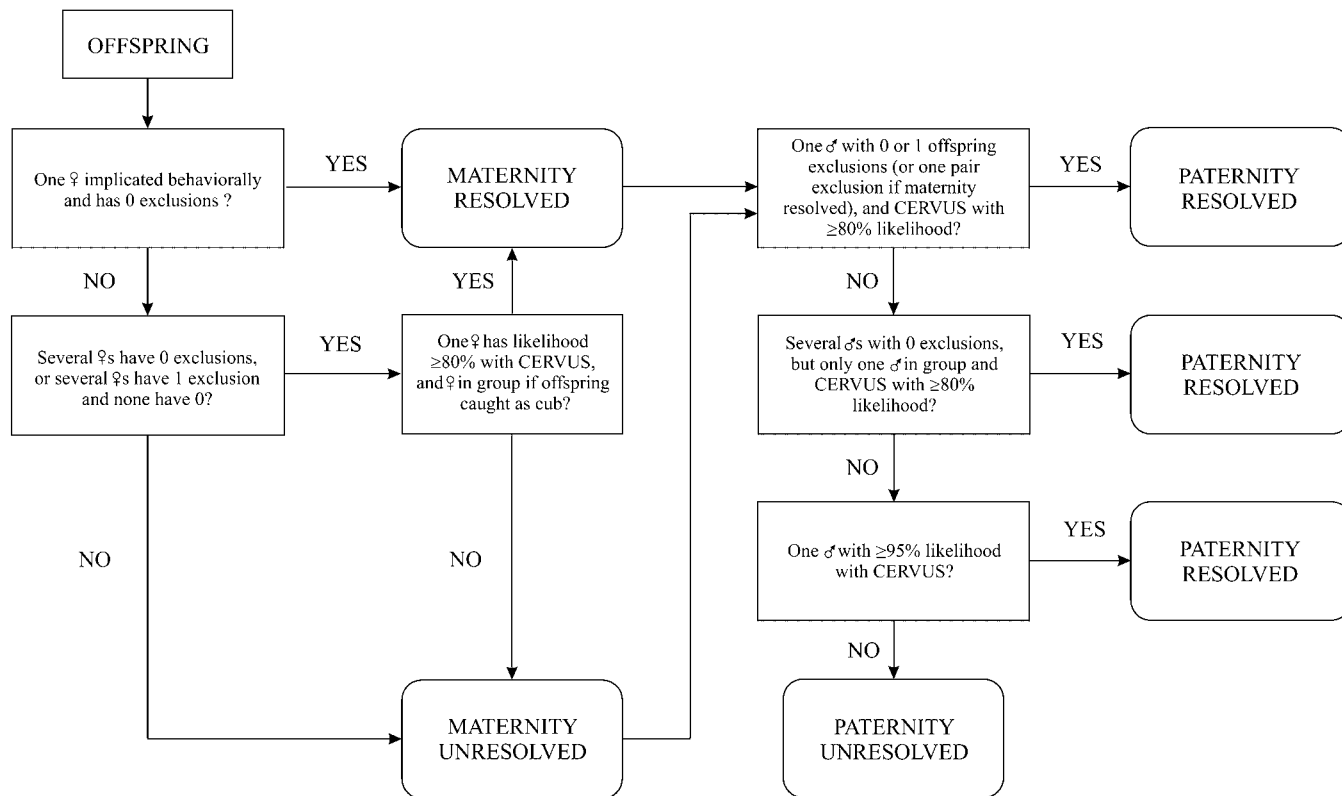


Figure 1
Hierarchical decision matrix for assigning maternity and paternity.

groups, including those instances in which no cubs had been captured on a territory in a given year, as cubs from these ranges could have been captured as subadults making extraterritorial movements onto neighboring ranges. Mating patterns were derived from the number of animals of the opposite sex within and outside the focal individual's social group with which that individual produced cubs. For each individual, we calculated the minimum and maximum number of partners with which that individual produced cubs. For females, the minimum number of males breeding with the focal individual was calculated assuming all cubs in the litter with unconfirmed paternity were also sired by males that were identified; the maximum number of males was calculated assuming each unidentified cub in the litter with unconfirmed paternity was sired by a separate male. Reproductive output and mating patterns were calculated separately for dominant and subordinate animals. Figures are presented (1) for all subordinate animals and (2) only for those subordinate individuals that were confirmed as having reproduced. In all cases, figures are minimum values for postemergent young, as some offspring may have been missed during the trapping and sampling program.

In order for reproduction as a subordinate to increase individual fitness, those cubs produced by subordinate individuals must survive. As it is believed that dominant animals may kill the cubs of subordinate animals, we compared the survival rate for those cubs with resolved maternity. Each cub's age was taken as the last month (April of year of birth = 0) for which we had information for that cub. The fate of each cub was classified as died or lost: lost animals were those individuals for which we had no definitive date of death and relate to the animal's last date of capture or observation. Statistical analyses were conducted using SPSS (Kinnear and Gray, 2000).

Relatedness within and between groups

Pairwise and mean group or cohort relatedness values were calculated according to the method of Queller and Goodnight (1989) using POPASSIGN 4.0. Standard deviations for group relatedness values were produced by jackknifing across loci and individuals. Rarefaction analysis (Altmann et al., 1996) was first carried out, which confirmed that the 10 markers used were adequate to summarize relatedness values accurately within and among groups. Pairwise relatedness values were estimated for all possible parent-cub and presumed sib comparisons (including between adults within social groups). Group and cohort values were also estimated for each year (mean among adults, mean among cubs with maternity resolved, and mean among all cubs and between all adults and all cubs).

RESULTS

Study site and study animals

A minimum of 46 adult foxes were resident in the study groups (Table 2), comprising 36 tagged (16♂, 20♀) and 10 untagged (5♂, 3♀, 2 unknown sex) animals; these data include two females whose cubs were frequently trapped on a territory but which had not been confirmed as resident in that group on the basis of behavioral observations. Tagged adults were assigned to groups by using the following criteria: 31 were radio-collared (70% of all identified adults), four (9%) were recovered dead as adults on their natal group, and one (2%) was confirmed as resident by a member of the general public. Fifteen individuals (7♂, 8♀) were present in both years, seven (4♂, 1♀, 2 unknown sex) were present in 1992 only, and 24 (10♂, 14♀) in 1993 only. Minimum (\pm SD) group size in 1992 and 1993 was 4.4 ± 2.2 ($N = 5$) and 4.9 ± 2.2 ($N = 8$),

Table 2

The number of adult foxes resident in the study groups and the number of putative offspring from the 1992 and 1993 cohorts trapped and sampled during the study

Year	Social group ^a	Minimum group size and composition ^b	Range size (ha) ^c	Putative offspring captured (N) ^d	Putative offspring sampled (N) ^d	Maternity only resolved ^d	Paternity only resolved ^d	Maternity and paternity resolved ^d	Maternity and paternity not resolved ^d
1992	AR	2 [1,1]	28.3	3 (0 + 3)	3 (0 + 3)	0 (—)	0 (—)	0 (—)	3 (0 + 3)
	BC	6 [4,2]	23.6	9 (8 + 1)	8 (7 + 1)	1 (1 + 0)	0 (—)	4 (4 + 0)	3 (2 + 1)
	LAR	6 [4,2]	20.2	7 (2 + 5)	7 (2 + 5)	1 (0 + 1)	2 (1+1)	2 (0 + 2)	2 (1 + 1)
	S	6 [1,3,2?]	18.1	14 (12 + 2)	13 (12 + 1)	3 (3 + 0)	5 (5+0)	2 (2 + 0)	3 (2 + 1)
	WD	2 [1,1]	21.8	5 (0 + 5)	4 (0 + 4)	2 (0 + 2)	0 (—)	0 (—)	2 (0 + 2)
	Subtotal	22 [11,9,2?]		38 (22 + 16)	35 (21 + 14)	7 (4 + 3)	7 (6 + 1)	8 (6 + 2)	13 (5 + 8)
1993	AR	2 [1,1]	28.3	3 (2 + 1)	3 (2 + 1)	1 (1 + 0)	0 (—)	1 (0 + 1)	1 (1 + 0)
	BC	5 [1,4]	14.3	13 (12 + 1)	11 (11 + 0)	3 (3 + 0)	0 (—)	7 (7 + 0)	1 (1 + 0)
	BR	3 [2,1]	9.4	5 (4 + 1)	5 (4 + 1)	1 (1 + 0)	1 (1 + 0)	2 (2 + 0)	1 (0 + 1)
	CR	3 [2,1]	14.0 ^e	0 (—)	0 (0 + 0)	0 (—)	0 (—)	0 (—)	0 (—)
	DCD	4 [1,3]	15.6 ^e	16 (10 + 6)	15 (9 + 6)	7 (5 + 2)	2 (1 + 1)	1 (1 + 0)	5 (2 + 3)
	LAR	7 [3,4]	20.2	12 (6 + 6)	12 (6 + 6)	0 (—)	0 (—)	6 (6 + 0)	6 (0 + 6)
	S	8 [4,4]	18.1	11 ^f (9 + 2)	2 (1 + 1)	0 (—)	0 (—)	0 (—)	2 (1 + 1)
	WD	7 [3,4]	21.8	19 (12 + 7)	18 (11 + 7)	2 (2 + 0)	0 (—)	7 (5 + 2)	9 (4 + 5)
	Subtotal	39 [17,22]		79 (55 + 24)	66 (44 + 22)	14 (12 + 2)	3 (2 + 1)	24 (21 + 3)	25 (9 + 16)
	Total	46 [21,23,2?]		117 (77 + 40)	101 (65 + 36)	21 (16 + 5)	10 (8 + 2)	32 (27 + 5)	38 (14 + 24)

Putative offspring are reported on the basis of the location where they were captured.

^a For comparative purposes, groups are labeled in accordance with the method of Baker et al. (2000).

^b Figures in brackets denote the number of males and number of females. In the case of group S in 1992, two additional untagged animals of unknown sex were also present.

^c Range size was determined by nocturnal radio tracking unless otherwise stated. Where a group was not radio tracked in a given year, those data from the previous or following years have been used.

^d Figures in parentheses indicate the number of animals captured as cubs and as subadults/adults, respectively.

^e Range size estimated from position of diurnal refuges.

^f Includes a litter of eight cubs born during trapping that have been excluded from all subsequent analyses.

respectively; corresponding range size was 22.4 ± 3.9 and 17.7 ± 5.8 ha. These figures indicate approximate prebreeding densities of 19.6 and 27.6 adult foxes/km², respectively.

One hundred seventeen putative offspring were captured (Table 2): 109 were sampled. Excluding the litter of cubs that died during trapping, estimates of reproductive output and patterns of mating are based upon a sample of 101 animals. Maternity only, paternity only, both maternity and paternity, and neither maternity nor paternity were resolved for 21%, 10%, 32%, and 38% of individuals sampled, respectively.

Group reproductive output

A minimum of 22 litters was identified (Table 3). In five instances, groups contained only a single female. For one group, monogamy was confirmed by genetic analyses. In the remaining four groups, cubs were observed in the respective territories, but only one cub was caught and its maternity was not resolved. These groups have been assumed to represent instances of monogamy.

Eight groups contained more than one female. In five groups all females were sampled; in three groups all but one female was sampled. Polygyny and monogamy was confirmed by genetic analyses in five groups and one group, respectively. In one group (S-1992), polygyny was assumed as the maternity of only five of 12 cubs was resolved, and it is unlikely that a single female would produce 12 emergent cubs: maximum pre-emergent litter size of 399 breeding females examined post mortem from Bristol between 1977–1990 was nine cubs (0.3% of females examined; Harris S, unpublished data). In one group (S-1993), a single female gave birth during capture, and the cubs perished. A single cub was also recovered dead in this

territory, but this was believed to have represented a case of intergroup infanticide: the cub was found in good condition, showed clear evidence of having been killed by an animal (intercanine distance was consistent with that of a fox), and had been observed being tossed about by an adult fox, and despite intensive field searches, no other cubs were located on that territory in that year. Consequently, this group was classified as having one litter in that year. In summary, singular breeding was confirmed or assumed in seven groups (54%) and plural breeding in six groups (46%).

Female reproductive output and mating patterns

The mothers of 53 individuals (43 cubs, 10 subadults/adults) were identified. Fifty offspring were born to females on the study groups (Table 3), including one cub and three subadults captured off their natal range. Three animals were assigned to females in neighboring groups. In addition, the known mother of the eight cubs that perished during trapping was identified as the parent of those cubs.

Nineteen individuals representing 23 potential breeding opportunities from nine social groups were used for estimates of female reproductive output and patterns of mating (Table 4). Three females were present as both a dominant and subordinate animal, four only as a dominant, and 12 only as a subordinate, including one female that was present in both years. Multifemale groups comprised a larger proportion of the subsample (89%) than in the study as a whole (62%): the possible effects of this selection on the likelihood of breeding, litter size and patterns of mating by dominant females are discussed. Parameter values for subordinate females are unaffected as single-female groups did not contain subordinate individuals.

Table 3
The outcome of maternity relationships established

Year	Social group	Minimum adult females (N [N sampled]) ^a	Minimum litters identified (N)	Young with resolved maternity (N) ^b	Cubs with unresolved maternity (N)	Included in analyses of female mating patterns? ^c
1992	AR	1 [1,0]	1 ^d	0 (—)	0	
	BC	2 [1,1]	2	5 (3,2)	2	yes [1,1]
	LAR	2 [1,1]	1	4 (4)	2	yes [1,1]
	S	3 [1,1]	2	5 (5,?) ^e	7	yes [1,1]
	WD	1 [0,0]	1 ^d	0 (—)	0	
1993	AR	1 [1,0]	1 ^d	0 (—)	1	
	BC	4 [1,3]	3	10 (1,1,8)	1	yes [1,3]
	BR	1 [1,0]	1	3 (3)	1	yes [1,0]
	CR	1 [0,0]	1 ^d	0 (—)	0	
	DCD	3 [1,2]	3	9 (3,1,5)	3	yes [1,2]
	LAR	4 [1,3]	3	8 (2,1,5)	0	yes [1,3]
	S	4 [1,2]	1 ^f	0 (—)	1 ^g	yes [0,2]
	WD	4 [0,3]	2	6 (3,3)	4	yes [0,3]
Total	31 [10,16]	22	50 (21,29)	22	9 [7,16]	

The number of young with resolved maternity includes animals captured on other territories but assigned to the group indicated; therefore, figures for each group do not necessarily correspond with those listed in Table 1.

^a Figures in brackets indicate the number of dominant and subordinate females sampled respectively.

^b Figures in parentheses indicate minimum litter size for individual females. Litter size of dominant female given first.

^c Figures in brackets indicate the number of dominant and subordinate females used to derive figures presented in Table 4.

^d Cubs were observed on territory, but not sampled; we assumed only a single litter was produced.

^e Subordinate female assumed to have bred based on large number of cubs captured ($N = 12$), but could not determine litter size because this female was not sampled.

^f Cubs of dominant female died during trapping; we assumed that female would have bred in that year.

^g Single cub sampled was assumed to represent case of intergroup infanticide.

Dominant and subordinate females reproduced in 100% and 56% of breeding opportunities, respectively. Therefore, the likelihood of breeding by dominant females was not affected by the presence of subordinate females. The confirmed reproductive output of dominant females was greater than for subordinate females, but this difference was not significant (Mann Whitney U test: $U = 30.0$, $N_1 = 7$, $N_2 = 16$, $p > .05$). Average reproductive output across all breeding opportunities was 2.2 cubs per female per annum (i.e., 50/23: range = 0–8). The minimum litter size resolved for dominant females in groups with one litter was greater (mean = 3.5, range = 3–4: $N = 2$) than in groups with more than one litter (mean = 2.8, range = 1–5: $N = 5$), although sample sizes were small and the observed range in the latter was large. Furthermore, 22 cubs captured on these territories had unresolved maternities (Table 3). Consequently, it is unclear whether dominant females suffered a reduced reproductive output in the presence of subordinate litters.

There was no significant difference between dominant and subordinate females in the number of cubs subsequently recovered dead ($N = 37$) and those with no definitive fate ($N = 13$) (chi-squared test: $\chi^2_1 = 2.75$, $p > .05$). The pattern of last information for these cubs is illustrated in Figure 2. There was no significant difference with respect to female status in either the age at death of offspring (Mann Whitney U test: $U = 15.5$, $N_1 = 5$ dominant females and 13 cubs recovered dead, $N_2 = 8$ subordinate females and 24 cubs recovered dead, $p > .05$; age at death averaged for all cubs assigned to an individual female) or age at which cubs were lost (Mann Whitney U test: $U = 9.0$, $N_1 = 5$ dominant females and 8 cubs, $N_2 = 5$ subordinate females and 5 cubs, $p > .05$; age at last

information averaged for all cubs assigned to an individual female). Consequently, the survivorship of cubs did not appear to be affected by their mother's social status.

Paternity was determined for 30 offspring (60%) born to resident females: 12 of 21 (57%) cubs assigned to dominant females and 18 of 29 (62%) to subordinate females (Table 4). Overall, the 30 offspring were sired by 13 individual males (Figure 3). Two males were identified as a father in 1992 only ($N = 2$ cubs), eight were identified as fathers in 1993 only ($N = 17$ cubs), and three males sired cubs in both years ($N = 11$ cubs). The average number of paternities resolved for cubs of dominant (mean = 1.7, range = 0–3) versus breeding subordinate females (mean = 2.0, range = 0–5) was not significantly different ($U = 30.0$, $N_1 = 7$, $N_2 = 9$, $p > .05$). Multiple fathers were identified in six litters (38%), four litters were composed of only a single cub (25%), one litter (6%) containing more than one cub had just one father, and in five litters (31%) only a single male was confirmed by genetic analyses but additional cubs with unresolved paternity were also present; in the latter, multiple paternity could not be excluded. Therefore, these data indicate a mixed-paternity rate within litters of 38–69%. A minimum of two fathers were also identified for the litter of eight cubs that perished during trapping.

Overall, breeding females sired cubs with one to seven males (Table 4). There was no significant difference in the minimum number of males siring cubs with dominant (mean = 1.4, range = 1–3) and subordinate females (mean = 1.8, range = 1–4; $U = 26.0$, $N_1 = 7$, $N_2 = 9$, $p > .05$), that is, assuming all cubs with unresolved paternity were sired by males already identified for that litter. This was also the case for the maximum number of males siring cubs with dominant (mean = 2.6, range = 1–4)

Table 4
Pattern of paternity for those offspring born to females in the study groups

Social Group	Female	Minimum litter size	Male within group		Male outside group		Male of unknown status	Paternity unresolved	Observed sires (n)	Maximum sires (n)
			Dominant	Subordinate	Dominant	Subordinate				
BC-1992	F2	3	1 (M2)			1 (m13)	1 (A)	0	3	3
LAR-1992	F4	4	2 (M6)					2	1	3
S-1992	F6	5				2 (m9)		3	1	4
BC-1993	F3	1				1 (m18)		0	1	1
BR-1993	F12	3			1 (M9)		1 (G)	1	2	3
DCD-1993	F14	3						3	1	3
LAR-1993	F17	2				2 (m21)		0	1	1
Subtotal	N = 7	21	3	0	1	6	2	9	mean = 1.4	mean = 2.6
BC-1992	f3	2				1 (m9)		1	1	2
LAR-1992	f5	0						—	—	—
S-1992	f7	0						—	—	—
BC-1993	f2	0						—	—	—
	f10	1				1 (m21)		0	1	1
	f11	8			2 (M14)		3 (E,F,G)	3	4	7
DCD-1993	f15	1						1	1	1
	f16	5					1 (H)	4	1	5
LAR-1993	f4	1				1 (m18)		0	1	1
	f5	0						—	—	—
	f18	5	1 (M6)		2 (M9)			2	2	4
S-1993	f19	0						—	—	—
	f20	0						—	—	—
WD-1993	f21	0						—	—	—
	f22	3		2 (m21)			1 (H)	0	2	2
	f23	3					3 (A,E,J)	0	3	3
Subtotal	N = 16	29	1	2	4	3	8	11	mean = 1.8	mean = 2.9
N = 9 groups	N = 23	50	4	2	5	9	10	20	mean = 1.6	mean = 2.9

Individual identification codes for males and females correspond to those illustrated in Figure 3.

and subordinate females (mean = 2.9, range = 1–7; $U = 31.5$, $N_1 = 7$, $N_2 = 9$, $p > .05$), that is, assuming all cubs with unresolved paternity were each sired by a male not already identified for that litter.

Overall, 20% (six of 30) of offspring of females with resolved paternity were sired by males within the female’s social group, 80% (24/30) by males from other groups (Table 4). Dominant females produced more cubs with males from their own social group (25%, 3/12) than did subordinate females (17%, three of 18). However, for two groups, not all resident males had been sampled, and this would potentially reduce estimates of

within-group paternity. Dominant and subordinate females both produced cubs with dominant and subordinate males from other social groups. Dominant females did not produce cubs with subordinate males from their own group (Table 4); that is, dominant females in single- and multifemale groups both mated only with the dominant male from their own group or with males from another group. Therefore, it is unlikely that the exclusion of the four monogamous groups from the analysis biased the observed pattern of mating by dominant females. In contrast, subordinate females did produce cubs with subordinate males from their own group.

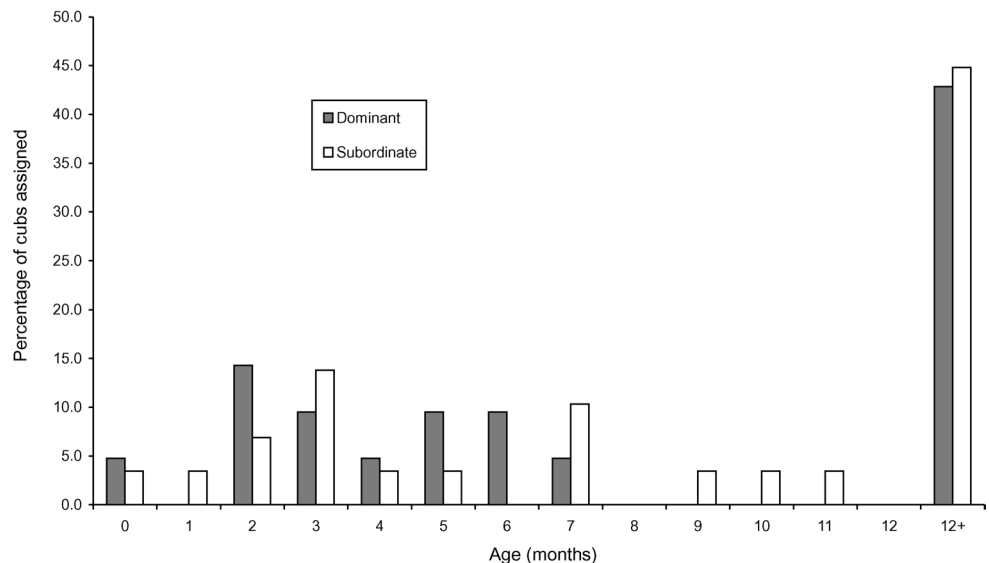


Figure 2
 The pattern of recovery of those cubs assigned to dominant ($N = 21$) and subordinate ($N = 29$) females. Age is indicated in months, with April of the year of birth taken as month zero.

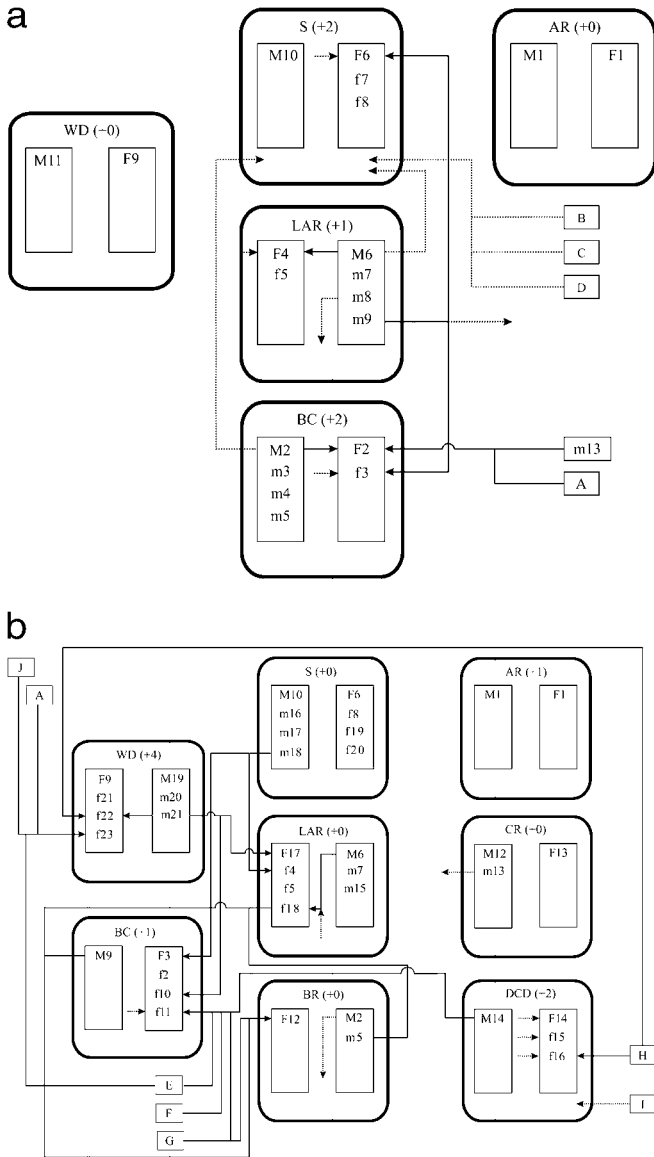


Figure 3
 The spatial and temporal pattern of matings identified. Groups are indicated in bold: group codes are indicated at the top of each symbol; figures in parentheses indicate the number of additional putative offspring captured as cubs but for which neither maternity nor paternity was resolved. Groups are arranged in an approximation of their true spatial distribution. Solid arrows indicate instances in which a male was identified as the father of the female indicated: for clarity, the number of cubs sired by that male with that female is not indicated. A dotted arrow pointing to a female indicates one or more offspring born to that female but with unresolved paternity. A dotted arrow from a male to a group but not a specified female indicates that the male sired a cub captured on that territory but for which maternity was not resolved. F indicates dominant female; f, subordinate female; M, dominant male, and m, subordinate male. Letters A through J denote nonresident males of unknown status.

Male reproductive output and mating patterns

Estimates of male reproductive output were derived from a subsample of 11 individuals for which we had estimates of both within-group and between-group mating (Table 5). Overall, the data set encompassed six dominant and 10 subordinate breeding opportunities: two males were present as dominant animals in both 1992 and 1993, one was present as

both a dominant and a subordinate, and two were present as a subordinate in both 1992 and 1993. The remainder were present only as a dominant ($N = 1$) or subordinate ($N = 5$) in 1 year.

Dominant males reproduced every year, whereas subordinate males only reproduced in 40% of breeding opportunities (Table 5). In four of six breeding opportunities (67%), dominant males sired cubs in their own group, compared with two of 10 (20%) for subordinate males: comparable figures for outside the individual's social group were four of six (67%) and three of 10 (30%), respectively. The confirmed reproductive output of dominant males was greater than for subordinate males, but not significantly ($U = 14.0$, $N_1 = 6$, $N_2 = 10$, $p < .05$). Average reproductive output across all breeding opportunities was 1.4 cubs per male per annum (22/16).

Forty-five percent of offspring of dominant males were produced within the individual's social group, compared with 27% for subordinate males (Table 5). Subordinate males were never recorded to have produced cubs with the dominant female from their own group, although in one group the mother of a single cub sired by a subordinate male was not identified. Both dominant and subordinate males sired cubs with dominant and subordinate females on other groups. On average, dominant and subordinate males produced young with 1.2 (range = 1–2; $N = 6$) and 1.8 (range = 1–3; $N = 4$) females, respectively: these are minimum estimates, as males may have sired cubs with females in groups neighboring the study site.

In addition to the 22 offspring sired by the focal males, a further 20 cubs had resolved paternity: 13 were born to known females in the main study groups and two were born to known females in neighboring groups, and for five cubs, we were not able to resolve maternity. These were sired by 14 individual males, comprising six adults ($N = 7$ cubs), seven subadults ($N = 11$ cubs), and one individual who sired cubs both as a subadult and an adult ($N = 2$ cubs). Nine males were of unknown origin and probably represented adult animals making extraterritorial movements in search of estrus females ($N = 5$ males, 6 cubs) and dispersing juveniles ($N = 4$ males, 5 cubs). Five individuals were of known origin: two males ($N = 4$ cubs) were resident in the main groups but were excluded from the analyses of mating patterns as we did not have data on the cubs within their groups, one male ($N = 1$ cub) was known to be resident in a neighboring group, and two were juveniles ($N = 4$ cubs) that dispersed from the main study groups. The maximum distance a male was known to have traveled to sire cubs (point of capture to point of subsequent observation) was 1.5 km. This was equivalent to a straight-line movement of 2.7 territories (average territory size = 0.25 km^2 , average territory diameter = 0.56 km). Two of the adult males were recovered dead shortly after the mating season.

Patterns of relatedness

Pairwise relatedness estimates for confirmed parent-offspring pairs were close to the expected value of 0.5 (Figure 4). The relatedness values for maternal and paternal sib pairs were higher than, but in the range of, those expected for half siblings ($r = .25$) (Figure 4). Consequently, these reflect a mixture of predominantly half sibs in the litters, in accordance with the parentage data.

Mean adult relatedness in groups with 10 or more pairwise comparisons ranged from unrelated ($r = .054$) to second-order relatives ($r = .271$), with the majority of values ranging from 0.15–0.35 (Appendix). This confirms the presence of close relatives in seven out of nine groups of adults present in 1992 and 1993. Relatedness between cubs from the same social group varied between 0.099 ± 0.023 where unrelated cubs

Table 5
The pattern of mating by males in the study groups

Social group	Male	Minimum cubs sired	Female within group			Female outside group			Observed mates (N)	Maximum mates (N)
			Dominant	Subordinate	Maternity unresolved	Dominant	Subordinate	Maternity unresolved		
BC-1992	M2	2	1 (F2)		0			1	1	2
LAR-1992	M6	3	2 (F4)		0			1	1	2
BC-1993	M9	2			0	1 (F12)	1 (f18)	0	2	2
BR-1993	M2	1			1			0	1	1
DCD-1993	M14	2			0		2 (f10)	0	1	1
LAR-1993	M6	1		1 (f18)	0			0	1	1
Subtotal	N = 6	11	3	1	1	1	3	2	mean = 1.2	mean = 1.5
BC-1992	m3	0			—			—	—	—
	m4	0			—			—	—	—
	m5	0			—			—	—	—
LAR-1992	m7	0			—			—	—	—
	m8	1			1			0	1	1
	m9	4			0	2 (F6)	1 (f3)	1	2	3
BR-1993	m5	1			0		1 (f18)	0	1	1
LAR-1993	m7	0			—			—	—	—
WD-1993	m20	0			—			—	—	—
	m21	5		2 (f22)	0	2 (F17)	1 (f10)	0	3	3
Subtotal	N = 10	11	0	2	1	4	3	1	mean = 1.8	mean = 2.0
N = 6 groups	N = 16	22	3	3	2	5	6	3	mean = 1.4	mean = 1.7

Individual identification codes for males and females correspond to those illustrated in Figure 3.

predominated the cohort, and 0.491 ± 0.057 where nearly all cubs were likely to be full sibs. As with the adults, most cohort relatedness values varied between 0.15 and 0.35.

Including the origins of adults known to be resident in the study groups before 1992, four incestuous pairings were recorded ($N = 6$ cubs): mother and son ($N = 1$ pair, $N = 2$ cubs in two different years), father and daughter ($N = 2$ pairs, $N = 3$ cubs), and half-brother and half-sister ($N = 1$ pair, $N = 1$ cub). For three pairings, mating occurred while the animals were still in the same social group; for one pairing, one individual had left the natal group. In addition, there were three further cases in which animals mated with more distantly related animals (e.g., half-nephew) with which they may not have had an experiential history.

DISCUSSION

Canids have been classified as behaviorally monogamous (Kleiman, 1977), with groups comprising a dominant mated pair and one or more related but reproductively suppressed subordinates. Evidence for the assumption of social monogamy includes extensive overlap of home ranges of paired males and females (Geffen and Macdonald, 1992), cooperation in the care of the young (Pauw, 2000; Vergara, 2000), and the presence of paternity assurance mechanisms, such as mate-guarding and a postcopulatory lock (Asa and Valdespino, 1998). However, in the present study, social monogamy was recorded in only 54% of group-years. Furthermore, this represents the maximum rate of social monogamy in this population, as maternity was not resolved for 22 out of 65 animals (34%) captured as cubs.

In our population, genetic monogamy appeared extremely rare, with both males and females frequently reproducing with more than one partner. Levels of mixed paternity (38–69% of 16 litters) were substantially higher than were levels recorded in other canids (11% of nine litters in African wild dogs: Girman et al. 1997; 25% of 16 cubs in Island foxes, *Urocyon littoralis*: Roemer et al. 2001) and carnivores (19% of 21 litters in dwarf mongooses, *Helogale parvula*: Keane et al. 1994). For

males, the number of successful partners identified is likely to be a minimum, as the frequency of mating in neighboring groups off the study site was probably underestimated. The maximum straight-line distance recorded for a male on an assumed extraterritorial mating foray was equivalent to the diameter of 2.7 territories, that is, approximately two territories from the center of the animal's own range; assuming a hexagonal arrangement of territories, this would imply that each male could potentially sire cubs in 18 neighboring groups. The 11 males used to determine male reproductive output originated from five contiguous social groups, and these may have sired cubs in a maximum of 32 neighboring groups. Given that cubs from only eight groups were sampled during the study, we may have underestimated intergroup mating success by up to a factor of four. However, it is plausible that extraterritorial movements may be much more restricted (Baker P, Harris S, unpublished data), such that a maximum output of twice the recorded intergroup mating success is perhaps more realistic.

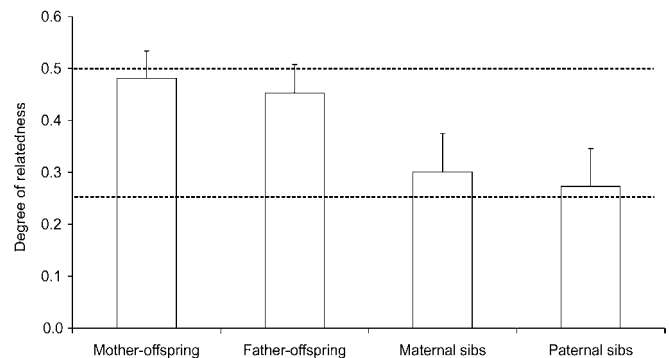


Figure 4

Average pair-wise relatedness values for mother-offspring ($N = 69$), father-offspring ($N = 53$), maternal sibs ($N = 166$), and paternal sibs ($N = 74$). Dashed lines indicate relatedness values of 0.5 and 0.25.

In the 1992 and 1993 cohorts, dominant individuals did not produce cubs with subordinate individuals within the same social group, whereas subordinate individuals did produce cubs with each other. Therefore, there is evidence for selective mate choice within groups, whereas outside the social group, dominant and subordinate individuals successfully mated with animals of either rank. This pattern is very similar to that observed in Ethiopian wolves, *Canis simensis*, in which dominant females frequently mated outside the social group (with alpha, beta, and lower category males), whereas all matings within the group were confined to the dominant male (Sillero-Zubiri et al., 1996). By contrast, within dwarf mongoose packs, matings between dominant and subordinate animals were common, with 24% of the young produced by the pack sired by subordinate males, and 15% of young born to subordinate females (Keane et al., 1994). Similarly, in the white-nosed coati, *Nasua narica*, band offspring are sired by several males (Gompper et al., 1997).

However, evidence of incestuous matings between resident adults (based on adult lineages) suggests that successful intragroup dominant-subordinate matings may occur in red foxes, but presumably at a low rate. This is in contrast to studies of gray wolves (Smith et al., 1997) and African wild dogs (McNutt, 1996), in which there was little evidence of any mating between close relatives. Incest occurred both between animals with and without an experiential history of one another, implying that either (1) foxes do not actively avoid mating with close relatives, although the low levels of successful mating between dominants and subordinates appears to contradict this (assuming that this is indicative of mating *per se*), or (2) a close association over a long period of time (parent and philopatric offspring) is not an infallible incest avoidance mechanism in this species. The extraterritorial movements of female Ethiopian wolves has been viewed as one means to avoid inbreeding (Sillero-Zubiri et al., 1996), and Gompper et al. (1998) observed male coatis making temporary long-distance movements away from their normal home range, which generally overlaps the range of a band of related females, presumably to avoid inbreeding. We were not able to quantify any potential costs to inbreeding because of small sample sizes.

Dominant males and females reproduced at every breeding opportunity, whereas subordinate males and females reproduced on 40% and 56% of breeding opportunities, respectively. Consequently, the annual reproductive output of dominant individuals was higher, but not significantly greater, than that of subordinates. The annual reproductive output of dominant females was 1.7 times that of subordinate females; the corresponding figure for males was 1.6. In this population, the mean age at death for dominant foxes was 4.5 years and 2.1 years for subordinates (Baker et al., 1998); that is, on average, dominant animals may reproduce up to four times in their life, whereas subordinates breed only twice. Therefore, the lifetime reproductive output for dominant males and females was as much as 3.2 and 3.4 times greater than that for subordinate males and females, respectively.

The frequency of breeding by subordinate females observed in the present study is substantially higher than that recorded for other canids in other habitats. For example, Geffen and Macdonald (1992) observed no evidence of plural breeding in groups of Blanford's foxes (*Vulpes cana*); Tannerfeldt and Angerbjörn (1996) document only one possible instance of multiple breeding in arctic fox *Alopex lagopus* groups; and in two populations of African wild dogs, only 6–17% of subordinate females reproduced annually (Creel et al., 1997). Social monogamy has also been routinely observed in captive red fox (Macdonald, 1979) and arctic fox (Kullberg and Angerbjörn, 1992) studies. However, in a review of wolf studies,

Harrington et al. (1982) indicated plural breeding rates of 22–41% and 39% in wild and captive packs, respectively.

The high level of polygyny detected in Bristol may have arisen from two interrelated factors: female dependence on male care and population density. Small (less than 6.0 kg) canids may have a tendency to produce smaller litters of more precocial young that require reduced male investment, such that females are less reliant on male care to produce young successfully (Moehlman, 1989). As a result, these species may have an inherent tendency to higher levels of polygyny than do larger canid species (but see Geffen et al., 1996). However, at the present time, there is a paucity of genetic studies on patterns of mating within canids of different size.

The high density observed in the study population is likely to have affected a number of aspects of the animal's behavior. In this population, the mortality rate of dominant individuals was much lower than that of subordinate animals (Baker et al., 1998). Therefore, juveniles and subordinate adults were probably constrained in their ability to disperse successfully; this may have favored the formation of large social groups (*sensu* Emlen 1982a,b). In turn, in large groups dominant males may be less able to monopolize access to all females by, for example, mate guarding; at high densities males may also be more likely to find sexually receptive females during extraterritorial movements. However, the patterns of mating behavior described in the present study have been recorded (or can be inferred) in fox populations at lower densities and in other canids: extraterritorial forays during the mating season (Niewold, 1980; Voigt and Macdonald, 1984; Zimen, 1984), multiple males in the presence of estrus females (Lloyd, 1980; Niewold, 1980), and plural breeding in groups (Macdonald, 1980; Pils and Martin, 1974; Storm et al., 1976; Zabel and Taggart, 1989). Therefore, the levels of polygyny observed for urban fox populations may represent the maximum along a continuum of fox densities, but they are not likely to be an atypical result associated with a particular type of habitat. Consequently, there is the need to consider the effect of population density on the frequency of these mating patterns.

The presence of extrapair mating strategies will also affect the fitness benefits associated with paternal and alloparental care. Both processes would generally be favored where there was a high degree of relatedness between the dominant male and the cubs, and between subordinate helpers and cubs. Typically, individuals within groups are thought to be first-order relatives such as parents and offspring and/or full sibs. However, the high levels of polygyny and polyandry observed in the present study resulted in levels of relatedness between adult group members, between cubs, and between adults and cubs indicative of second-order relatives. Furthermore, dominant males were only identified as the father of offspring in their own social group in 67% of breeding opportunities, and for only a fraction of the total number of cubs present, for subordinate males this figure was 20%.

Despite this low level of within-group paternity, the majority of dominant and subordinate males did help to rear cubs (Baker et al., 2000), implying that individuals frequently helped to raise offspring to which they were (at best) only distantly related, particularly where litters were pooled and reared communally. Such behavior may arise because males are not able to discriminate between cubs they have sired and those they have not. Also, male foxes are not able to enhance their fitness in other ways during the period of cub rearing: boreal canids are annually monestrous (Asa and Valdespino, 1998), and in the red fox, the period of sexual receptivity is only a few days (Tembrock, 1957). As females are not in estrus during the period of cub rearing, males do not encounter a trade-off between helping to rear young versus abandoning the female and attempting to find additional mating opportunities.

Under such conditions, paternal care may evolve in which this increases cub survival and/or imposes few costs on the male, even if the male does not sire most of the cubs in the litter. However, this does assume that (1) males do mate with females that they subsequently help and (2) males sire at least some of the offspring; it is unclear whether these two provisions are met for subordinate males mating with dominant females. Paternal care may be expected to evolve particularly where it is indivisible between cubs, such as vigilance against predators or conspecifics (Zabel, 1986). This may have been the case in the evolutionary history of the red fox, as cubs are known to be vulnerable to a range of other predators that are now absent from much of its geographical range. However, males also frequently provision young, and such activity could result in significant foraging costs (*sensu* Lindström, 1994; Lovari and Parigi, 1995; but see Baker et al., 1998, 2000) and the feeding of unrelated rather than related young; it is unclear whether selective provisioning of young occurs in canids. Under these foraging constraints and with high levels of polygynandry, high levels of investment by males may not be evolutionarily stable. Alternatively, helping to rear offspring may simply represent a form of "rent" for remaining on a territory in order to reap future benefits such as the inheritance of the territory or dominant status.

From the perspective of females, polyandry may represent selection for an increased likelihood of conceiving, selective mate choice, a means of soliciting subsequent male care, and/or as a means of promoting outbreeding within the group (Hoogland, 1998; Hunter et al., 1993; Reynolds, 1996; Tregenza and Wedell, 2002). Promoting outbreeding may be particularly important where territories are inherited by successive generations, as was observed in this population (Baker et al., 1998). Extrapair mating and patterns of mate choice have been widely investigated in socially monogamous birds (Birkhead and Møller, 1992; Ligon 1999), with females generally selecting partners of "superior quality." In the 1992 and 1993 cohorts, dominant individuals did appear to avoid breeding with subordinate animals within their own group (Tables 3 and 4), although some of those instances of incest recorded involved matings between dominant and subordinate animals within the same group. Consequently, there is evidence for selective mate choice by dominant females. However, dominant females frequently mated with both dominant and subordinate males from neighboring groups, implying that females are not able to easily assess male quality; mate quality is not as important as, for example, the need to obtain sperm for successful breeding; or our assessments of social status were incorrect or different to the factor(s) used by females to assess male quality. There is, therefore, the need for further investigation into these aspects of female mating strategies.

In summary, hypotheses for the evolution of group living in canids have extensively focussed on the impact of the spatial and temporal availability of resources in allowing subordinate animals to remain within the territory of dominant individuals. However, simultaneous consideration must also be given to the cost-benefit trade-off between, for example, the strategies of remaining on the natal group as a subordinate and dispersing and attempting to become the dominant animal in a nonnatal group. Key components of individual fitness within canid groups include the likelihood of breeding directly and indirect fitness benefits from alloparental care: these are related to patterns of mating and intragroup relatedness. In this population of red foxes, social monogamy occurred in a maximum of 54% of group-years. Genetic monogamy was extremely rare, resulting in low levels of relatedness between adult group members and cubs. High population density (more than 19 adults/km²) may have contributed to the very high frequency of polygyny and polyandry observed. However,

similar mating strategies have been observed in other red fox populations at lower densities and in other canid species. We suggest therefore that, rather than being indicative of genetic monogamy, the presence of paternity-assurance mechanisms such as a postcopulatory lock and mate-guarding appear to be indicative of an evolutionary history of extrapair copulations, and extrapair mating may be widespread in canid species. Consequently, this may reduce the direct and indirect benefits associated with paternal and alloparental care, and the direct reproductive output of subordinate individuals may be greater than previously assumed. These factors need to be investigated in other canid species, and in populations across a range of densities.

APPENDIX

Relatedness within social groups: (a) between adults; (b) between those cubs for which maternity had been resolved; (c) between all cubs; (d) between adults and cubs, including only those cubs for which maternity had been resolved; and (e) between adults and all cubs

Comparison	Social group	Year	Pairwise comparisons (n)	Mean relatedness (r)	Jackknived (loci) SD
(a)	BC	1992	15	0.271	0.041
	LAR	1992	15	0.054	0.038
	S	1992	1	0.558	0.041
	BC	1993	10	0.173	0.048
	BW	1993	3	0.352	0.067
	DCD	1993	6	0.297	0.043
	LAR	1993	15	0.230	0.043
	S	1993	15	0.203	0.059
	WD	1993	6	0.008	0.023
	(b)	BC	1992	10	0.220
LAR		1992	6	0.276	0.073
S		1992	6	0.337	0.081
BC		1993	45	0.241	0.037
BW		1993	3	0.365	0.077
DCD		1993	36	0.181	0.032
LAR		1993	21	0.261	0.017
S		1993	28	0.491	0.057
WD		1993	15	0.163	0.111
(c)		BC	1992	21	0.279
	LAR	1992	15	0.286	0.035
	S	1992	45	0.167	0.055
	BC	1993	55	0.248	0.034
	BW	1993	6	0.321	0.053
	DCD	1993	66	0.099	0.023
	LAR	1993	21	0.261	0.017
	S	1993	28	0.491	0.057
	WD	1993	36	0.182	0.047
	(d)	BC	1992	30	0.300
LAR		1992	24	0.204	0.034
S		1992	8	0.289	0.040
BC		1993	50	0.240	0.036
BW		1993	9	0.376	0.035
DCD		1993	36	0.278	0.022
LAR		1993	42	0.291	0.015
S		1993	48	0.260	0.031
WD		1993	24	0.120	0.034
(e)		BC	1992	42	0.301
	LAR	1992	36	0.174	0.039
	S	1992	20	0.193	0.039
	BC	1993	55	0.245	0.033
	BW	1993	12	0.375	0.034
	DCD	1993	48	0.212	0.022
	LAR	1993	42	0.291	0.015
	S	1993	48	0.260	0.031
	WD	1993	36	0.115	0.026

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