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Abstract—San Joaquin kit foxes (*Vulpes macrotis mutica*) are typically socially monogamous. During the 2012 breeding season in Bakersfield, California, where food is abundant, population density is high, and dispersal potential is low, we documented two cases of social polygyny. Both groups had two litters; we documented allonursing in one group. In both groups the two mothers were not closely related and the "helper" was not closely related to the other adults. All four reproducing females had at least one pup sired by an extragroup male. One female had three inbred pups that resulted from matings with first-degree relatives. The unique conditions associated with the urban environment may alter kit fox social ecology.

Resumen—El comportamiento social de los zorros de San Joaquín (*Vulpes macrotis mutica*) es típicamente monógamo. Durante la temporada de reproducción de 2012 en Bakersfield, California, donde la comida es abundante, la densidad poblacional es alta y el potencial de dispersión bajo, documentamos dos casos de poliginia social. Ambos grupos tuvieron dos camadas; documentamos crianza cooperativa en un grupo. En ambos grupos, las dos madres no estuvieron estrechamente relacionadas entre sí y la "cooperante" no estuvo estrechamente relacionada con los demás adultos. Las cuatro hembras reproductoras tuvieron al menos un cachorro engendrado por un macho externo al grupo. Una hembra tuvo tres crías consanguíneas provenientes de apareamientos con parientes de primer grado. Las particulares condiciones asociadas al entorno urbano pueden alterar la ecología social de los zorros de San Joaquín.

Monogamous mating systems are rare in mammals as a whole but relatively common in some groups, such as primates and canids (Kleiman, 1977). When advances in molecular genetics enabled wide-spread paternity testing, monogamy was further classified as social monogamy (breeding adults live together in pairs) or genetic monogamy (paired adults breed exclusively with each other; Gowaty, 1996). It is thought that social monogamy evolved, in most cases, from an ancestral condition in which females were solitary and widely spaced due to scarce resources (Lukas and Clutton-Brock, 2013), although there are exceptions (Kappeler, 2014). Males help with care of the offspring in some socially monogamous species but not in others, and phylogenetic reconstructions suggest that monogamy evolved more often in the absence than the presence of paternal care, indicating that paternal care is usually a consequence rather than a cause of social monogamy (Lukas and Clutton-Brock, 2013). However, paternal care has been proposed as a driving force in the evolution of monogamy in red foxes (*Vulpes vulpes*; Baker and Harris, 2004).

Canids are unusual among mammals because most species are monogamous and paternal care is also common (Kleiman, 1977; Malcolm, 1985; Asa and Valdespino, 1998). Although small foxes are typically socially monogamous, they can form polygynous trios or more complex social groups when resources are abundant (Zabel and Taggart, 1989; Lemons et al., 2003; Kamler et al., 2004). Genetic testing has revealed that extrapair copulations are common in some species of foxes (Baker et al., 2004; Kitchen et al., 2006; Cameron et al., 2011). Extrapair copulations may occur more frequently when resources are more abundant and population densities are high (Cameron et al., 2011).

The San Joaquin kit fox (*Vulpes macrotis mutica*) is a small desert-adapted canid endemic to the San Joaquin Desert in California (Morrell, 1972; Germano et al., 2011). These foxes have one litter per year in the early spring. They are typically socially monogamous and a social group usually consists of a breeding pair and their current offspring, although occasionally one or more pups will delay dispersal and remain in the natal home range during the next breeding season (Ralls et al., 2001,

2007). As a result of habitat loss, the San Joaquin kit fox has been federally listed as endangered and listed by California as threatened (United States Fish and Wildlife Service, 1998). As a result of agricultural, industrial, and urban development, the San Joaquin kit fox exists in a meta-population consisting of several small satellite populations and three core areas (Cypher et al., 2013). In addition, a fourth substantial population has adapted to living in the urban environment in Bakersfield, California (Cypher and Frost, 1999; Cypher, 2010).

In Bakersfield, it is more common for kit fox social groups to have an extra adult, likely because of the abundance of anthropogenic food (Cypher and Frost, 1999; Newsome et al., 2010). These are thought to be mainly pups from the previous year and are termed "helpers" (Macdonald, 1979; Ralls et al., 2001). Field observations have been conducted on the Bakersfield kit foxes since 1997. In 2012, while conducting a larger study on parental care (Westall, 2015), we observed two social groups that each had one male, two adult females, a helper, and two litters. We documented the behavior of these groups through direct observations and determined the genetic relationships among individuals using 11 microsatellite markers.

We trapped foxes in early January 2012 to gather relevant biological information and samples. We captured foxes with wire-mesh box traps ($38 \times 38 \times 107$ cm) that were baited with cat food, hot dogs, and sardines. For the animals' protection, we placed traps in secure locations away from well-trafficked areas and covered the traps with oiled cloth tarps to guard against the elements. We examined each fox to determine age, sex, and reproductive condition and applied a uniquely numbered ear-tag to every individual. Females were ear-tagged on the right and males were ear-tagged on the left to help visually distinguish sex of individuals. Each ear-tag had a four-digit number, which we use only when mentioning male foxes identified as the fathers of pups that resulted from extrapair copulations. We collected hair and tissue samples from all foxes for genetic analysis. We collected tissue samples from the ear using a 2-mm biopsy punch (Inegra® Miltex®, Model 33-31, York, Pennsylvania) and stored samples in 95% ethanol. We marked each fox with a unique pattern using a permanent nontoxic dye (Nyanzol-D; Albinal Dyestuff, Inc., Jersey City, New Jersey) to allow for the identification of individuals over the course of the project. We monitored the two social groups during the 2012 breeding season. We performed direct observations at each den for a session of 2 h one to two times per week, between January and May. We categorized foxes into three roles—group male, mother, or helper (Macdonald, 1979)—based on direct observations and genetic analysis.

We genotyped individuals using the molecular methods described in Wilbert et al. (2015). Briefly, we extracted DNA using DNeasy blood and tissue kits (QIAGEN®, Hilden, Germany). We genotyped each sample at 11 tetranucleotide microsatellite loci (*FH2137, FH2140, FH2226, FH2535, FH2561, Pez19, AHTh171, FH2054, FH2328, FH2848,* and *Ren162*) that had previously been proven to be reliable for kit fox (Smith et al., 2006). For each DNA extract, we performed two to three polymerase chain reaction replicates of each microsatellite to ensure reproducible genotypes, with two replicates for heterozygous loci and three replicates for homozygous loci. We used fluorescently labeled forward primers (TET, HEX, or FAM) to visualize the products on an ABI PRISM 3130 Genetic Analyzer (Applied Biosystems, Foster City, California). We scored the size of each fragment using Genemapper® (Thermo Fisher Scientific, Waltham, Massachusetts) software. Every microsatellite was genotyped with a positive and negative control to eliminate any contamination and to standardize allele sizes across all data.

We compared the genotypes of individuals in our two groups with 342 individuals captured in Bakersfield from 2000 to 2011 that had already been genotyped at the same loci (unpubl. data). The larger data set did have Hardy-Weinberg disequilibrium and linkage disequilibrium, but this is expected given that the samples include family groups. In addition, the individuals are only sampled from certain areas of Bakersfield and not the entire population of kit foxes, which is likely to produce Hardy-Weinberg disequilibrium and linkage disequilibrium. However, we do not believe these issues are large enough to affect parentage of assignment.

We estimated the coefficient of relationship (r) between individuals within each social group using the Queller-Goodnight estimator (Queller and Goodnight, 1989) as implemented by the program GenAlEx 6 (Peakall and Smouse, 2006, 2012). This measure of relatedness ranges from -1 to $+1$. Pairs of individuals with positive r values are more closely related than average and those with negative r values are less closely related than average. First-degree relatives such as parents or offspring have an expected $r = 0.5$, first cousins an $r = 0.125$, and pairs of randomly chosen individuals an $r = 0$. The accuracy and precision of these estimates increases with the number of markers used. We had only 11 markers, so our calculations provide only general estimates of the degree to which two individuals are related.

One way to measure the ability of molecular marker data to assign paternity is to calculate the probability of identity (P_{id}) and probability of sibship (P_{sib}). P_{id} is the probability that two individuals in a population will have the same genotypes at all loci due to chance (Nei and Feldman, 1972), while P_{sib} is the probability that two siblings will have the same genotype due to chance (Evett and Weir, 1998). We estimated these values with the program GenAlEx 6 (Peakall and Smouse, 2006, 2012).

Parentage was determined by a likelihood-based

TABLE 1—Relatedness (*r*) and parentage (indicated by *) in San Joaquin kit foxes (*Vulpes macrotis mutica*) in the CSUB-S group at California State University, Bakersfield, and the BC-2012 group at Bakersfield College during the 2012 breeding season.

CSUB-S	Group male	Mother A	Mother B	Helper female
Group male	X			
Mother A	−0.050	X		
Mother B	0.170	0.290	X	
Helper female	0.203	−0.094	−0.068	X
Pup 1	0.445*	0.405*	0.299	0.128
Pup 2	0.395	0.277	0.516*	0.199
Pup 3	0.060	0.564*	0.063	0.112
Pup 4	0.354*	0.526*	0.360	0.450

BC-2012	Group male	Mother C	Mother D	Helper male
Group male	X			
Mother C	−0.246	X		
Mother D	0.515	−0.311	X	
Helper male	−0.509	−0.421	−0.941	X
Pup 5	0.213	0.588*	0.059	−0.743
Pup 6	0.480*	0.591*	0.166	−0.523
Pup 7	0.446*	0.420	0.433*	−0.803
Pup 8	0.219	0.049	0.336*	−0.369
Pup 9	0.507	0.611*	0.343	−0.273
Pup 10	0.256	0.739*	0.149	−0.422

method using the program CERVUS (Kalinowski et al., 2007), which uses the allelic frequencies from all individuals to calculate the likelihood of parentage for each individual. We used the genotypes from all 342 individuals to calculate allele frequencies and perform simulations in CERVUS. CERVUS can tolerate moderate deviations from Hardy-Weinberg equilibrium and weak associations between loci. We simulated maternity, paternity, and parental pair data using the following parameters: 10,000 offspring; 8 candidate mothers, fathers, and pairs; 85% mothers, fathers, and pairs sampled; 90% loci typed; 1% missing data; and a minimum of six loci genotyped. We then calculated the likelihood that the adults in each social group were the parents of the pups sampled from that group. All parents assigned by CERVUS could not be excluded based on direct comparisons of gentoypes.

We used a two-step procedure to assign parentage with CERVUS following Dugdale et al. (2007). If CERVUS identified a male–female pair as the parents of a pup with a likelihood of >80%, we considered that both parents had been identified. If CERVUS did not assign a pair with this level of probability, we examined the likelihood that individual foxes were parents and accepted a female as the mother if her likelihood of maternity was >95% and a male as the father if his likelihood of paternity was >95%. A relaxed likelihood of 80% is acceptable for defining pairs

(Dugdale et al., 2007), but the online manual for CERVUS recommends a minimum likelihood of 95% when defining individual parents (http://www.fieldgenetics.com/pages/aboutCervus_Method.jsp). Additional parentage analysis with the program COLONY (Jones and Wang, 2010) also assigned 12 of the 14 assigned parents by CERVUS and included the other two assignments as potential parents.

One of the groups we studied was at California State University, Bakersfield (CSUB-S; N35.348096 W-119.103716) and the other at Bakersfield College (BC-2012; N35.407837 W-118.971824). Each group consisted of two mothers, one father, one helper, and pups. We investigated the relatedness of 8 of the 10 individuals associated with the CSUB-S social group (Table 1) and the relatedness of 10 of the 14 individuals associated with the BC-2012 social group (Table 1). We were unable to capture the other individuals, all of which were pups. With the exception of one individual from BC-2012, we were able to genotype at least 8 of 11 microsatellite loci for the sampled individuals, and most of them were genotyped at all 11 loci. Overall, we had a low level of dropout (estimated null allele frequencies ranged from 0.00 to 0.06) and sufficient data for identification of parentage ($P_{id} = 1.44 \times 10^{-9}$; $P_{sib} = 2.47 \times 10^{-4}$; calculated in GenAlEx).

The CSUB-S group had two litters with three pups in each litter. The second litter emerged 3 weeks after the first, and the size and developmental differences between them were obvious. We documented allonursing in this group because we observed both mothers nursing pups from both litters. The BC-2012 group had two litters that totaled 10 pups, but the number of pups in each litter was unknown because all pups emerged simultaneously and appeared to be the same age developmentally. Both mothers showed signs of actively nursing pups, such as enlarged nipples and rufus belly fur, but we could not determine if allonursing occurred because we could not visually distinguish pups from each litter.

The adults in the CSUB-S group were not closely related (Table 1). The closest relationship was between the two mothers, but the *r* value for this pair was only 0.290, roughly the same as half sibs, so they might have been litter-mates with different fathers. The female helper was not closely related to either of the mothers but had an *r* of 0.203 with the group male. The group male sired two of the four pups (pup 1 and pup 4) that we were able to sample, and mother A was the mother of both the pups that he sired (Table 1). We only genetically sampled one pup born to mother B and it was the result of an extrapair copulation; therefore, we could not determine whether he also mated with this female. Both mothers had at least one pup that was the result of an extrapair copulation but CERVUS did not assign a father to either of them. The helper was not the mother of any pups (Table 1).

The two mothers in the BC-2012 group were unrelated and the male helper was not related to any of the group members (Table 1). Both the group male and mother D

were captured as pups of the same litter in 2011. The group male had an $r = 0.515$ with mother D, confirming that he was her brother. The group male sired at least one pup with each of the mothers and both mothers also had pups resulting from extrapair copulations (Table 1). CERVUS assigned fathers to two pups (8 and 9) that were the result of extrapair copulations. Male #6547 was assigned as the father of pup 8. He was the group male in the BC group in 2011, but died in November 2011 before the main mating season in December. However, the pups in the BC-2012 group were born a month earlier than the majority of the 2012 litters and he must have mated with mother D before he died. Male #6547 was thought to be the father of mother D because he was the male in the BC social group when she was born in 2011 and this was supported by high r value (0.515) between them, which suggested that they were first-degree relatives (Table 1). The father of pup 9 is uncertain. CERVUS assigned male #6523 as its most likely father. Male #6523 was born in the BC social group in 2011 when #6547 was still the group male. He was thought to be the brother of mother D based on field observations and this was supported by the high r value between them (0.501). Male #6523 had disappeared by 2012. Pup 9 was also closely related to the group male with an $r = 0.507$, so he could also have been its father (Table 1). The group male and male #6523 were closely related ($r = 0.670$). Field data indicated that #6523, which was born in 2010, was probably an older sibling of the group male and this was supported by the high r value between them. Regardless of which male sired pup 9, it was inbred because it was the result of a brother–sister mating.

Our results are the first documentation of social and genetic polygyny in San Joaquin kit foxes, although social polygyny has been observed in desert kit foxes (*Vulpes macrotis arsipus*; Egoscue, 1962). The primary cause of this shift from social monogamy to social polygyny in some fox groups is probably the abundant food available in the urban environment, in accordance with the predictions of the Resource Dispersion Hypothesis (Macdonald, 1983), which posits that a pair of carnivores can tolerate additional group members when resources are abundant as long as the breeding pair has sufficient resources throughout periods of limited food availability. Shifts from monogamy to polygyny when food is plentiful have been observed in bat-eared foxes (*Otocyon megalotis*; Pauw, 2000), arctic foxes (*V. lagopus*; Strand et al., 2000), swift foxes (*V. velox*; Kamler et al., 2002; Kitchen et al., 2006) and red foxes (Macdonald, 1983; von Schantz, 1984; Baker, et al. 2004). Urban environments tend to have more consistent and abundant food and more cover for small canids than do natural lands (Cypher and Frost, 1999; Gosselink et al., 2010). As a result, dominant females may be more tolerant of conspecifics and allow other females to reproduce within their home range, assuming there is no detriment to their reproductive

success (Zabel and Taggart, 1989). In urban red foxes, dominant females and subordinate females reproduced in 100 and 56% of breeding opportunities, respectively, indicating no effect on dominant female reproduction (Baker et al., 2004). In swift fox populations, all groups in a low-density population were made up of monogamous pairs, while 30% of groups in a high-density population were polygynous trios (Kamler et al., 2002).

The high cost of dispersal in high-density urban populations may also promote the formation of groups with more than one breeding female. There are fewer dispersal opportunities in urban environments because there is less habitat available, it is highly fragmented (increasing the distance that dispersers must travel and thus the risk of dispersal), and usually it is already occupied (Gosselink et al., 2010). The lack of good dispersal opportunities in urban environments is thought to promote the formation of larger social groups because offspring tend to remain longer in their natal home ranges. In one of our groups, the group male appeared to be the brother of one of the two mothers. However, the two mothers were not first-degree relatives in either group, so one mother could not have been an offspring of the other. Similarly, the helper was not an offspring of any of the breeding adults in either of our groups. Thus, it seems that neither of these large groups resulted primarily from philopatric offspring remaining in their parents' home range.

A polygynous breeding system provides the opportunity for communal litters and alloparental care. The Polygyny Threshold Model predicts that the polygyny threshold is reached when the cost of sharing a male with another female is exceeded by the benefit of raising offspring cooperatively (Zabel and Taggart, 1989). In swift foxes, more adult group members resulted in an increase in the amount of time at least one adult was present at the den (Elmhagen et al., 2014), providing more constant defense of the den, as well as reducing the amount of time each mother had to remain away from the den where she was more exposed to danger.

We documented one case of allonursing. Potential benefits of allonursing include reduced peak energetic costs to both mothers when the two litters are of different ages, and indirect benefits of assisting relatives. Offspring may benefit from a reduced a risk of starvation and immunological advantages of receiving milk from more than one mother (Clutton-Brock, 2016). Allonursing has been reported in other canids, including red, arctic, bat-eared, and Bengal foxes (*V. bengalensis*), as well as gray (*Canis lupus*) and Ethiopian (*C. simensis*) wolves, chillas (*Lycalopex griseus*), and African wild dogs (*Lycaon pictus*; Macdonald et al., 2004), but the bat-eared fox is the only species in which this seems to be common (Maas and Macdonald, 2004). This is the first study to document allonursing in kit foxes.

Our finding of extrapair matings by all four mothers

was not unexpected because high levels of extrapair paternity have been reported in several fox species (e.g., red foxes [Baker et al., 2004], swift foxes [Kitchen et al., 2006], arctic foxes [Cameron et al., 2011]) and has been interpreted as a safeguard against inbreeding (Baker et al., 2004; Cameron et al., 2011). However, two of the six pups resulting from extrapair copulations in our study resulted from matings between one female and at least two different first-degree relatives, suggesting that either most of the potential mates available to that female were close relatives or that avoidance of inbreeding may not be the primary or only benefit of extrapair copulations in kit foxes. Other possible benefits to females that mate with multiple males include reduced risk of infertility or total breeding failure, opportunities to engage in cryptic mate choice by biasing paternity after copulation, and increased genetic diversity in litters. There are also potential costs such as the energetic costs associated with multiple mating, increased risk of acquiring disease, and punishment, harassment, or reduced parental investment by the group male (Clutton-Brock, 2016). Kitchen et al. (2006) suggested that male swift foxes may be unable to detect unrelated pups and the same may be true of kit foxes.

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