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SOCIAL MONOGAMY IN KIT FOXES: FORMATION, ASSOCIATION, DURATION, AND DISSOLUTION OF MATED PAIRS

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Social monogamy is characterized by long-term pair-bonds, but there is extensive variation among socially monogamous species in the timing of pair formation, the extent to which pair-mates associate throughout the year, the duration of pair-bonds, and the frequency with which pair-bonds are dissolved while both partners are living. We studied these aspects of social monogamy in kit foxes (*Vulpes macrotis*) at 1 urban and 2 nonurban sites. Behavior was similar across sites despite differences in ecological conditions. Pair formation occurred throughout the year, often within a month after the loss of a mate. Pair-mates associated throughout the year. Some pairs remained associated for more than 1 breeding season. Death of a pair-mate was the most common reason for the dissolution of a pair (14 of 16 cases). Two pairs dissolved while both partners were still living: 1 due to abandonment by a male of his pair-mate and territory and 1 due to displacement of a male by another male. These characteristics of social monogamy in kit foxes may be related to year-round territoriality, and may optimize individual fitness by enhancing survival and ultimately reproductive success.

Key words: kit fox, monogamy, pair-bond, *Vulpes macrotis*

Long-term partnerships, or pair-bonds, characterize social monogamy, a social system that is rare in mammals (Kleiman 1977; Reichard and Boesch 2003), although common in birds (Black 1996). Although polygyny occurs in some socially monogamous species (e.g., Kamler et al. 2004; Zabel and Taggart 1989), it is generally infrequent: for example, birds are considered socially monogamous only if the frequency of polygyny is less than 5% (Black 1996). However, saying that a species is socially monogamous provides little insight into the details of these long-term partnerships, because there is a great deal of behavioral variation among socially monogamous species. Such variation includes the time of year when pair-bonds are formed, the degree to which pair-mates associate throughout the year, whether or not pair-mates remain together for successive breeding seasons, and the probability of pair dissolution and re-pairing while both partners are still alive. Long-term studies of socially monogamous birds have shown that there are species in which the mated male and female

remain together for life, such as barnacle geese (*Branta leucopsis*—Black et al. 1996) and others where they remain together for only a single breeding season, such as house sparrows (*Passer domesticus*—Veiga 1992). Even in the birds exhibiting perennial monogamy, that is, those species in which most partnerships persist from year to year, there is variation in the amount of time pair-mates associate throughout the year, ranging from species in which mates remain together every month of the year to those where mates are together for less than a month each year (Black 1996). The probability of pair dissolution and re-pairing while both partners are still alive ranges from 0% to 50% per year (Black 1996). Although there are fewer good long-term field studies of socially monogamous mammals and such details are often lacking, most of these species are thought to exhibit some form of perennial monogamy (Reichard 2003).

Many canids are socially monogamous, with breeding pairs known to form long-lasting pair-bonds that persist across multiple breeding seasons. Such male–female partnerships exist across a range of group sizes and are known both in species that form large groups, such as wolves (*Canis lupus*), and those in which the mated male and female are often the only adults in their home range, such as many smaller foxes (Geffen et al. 1996; Ikeda 1991; Moehlman 1989). The kit fox

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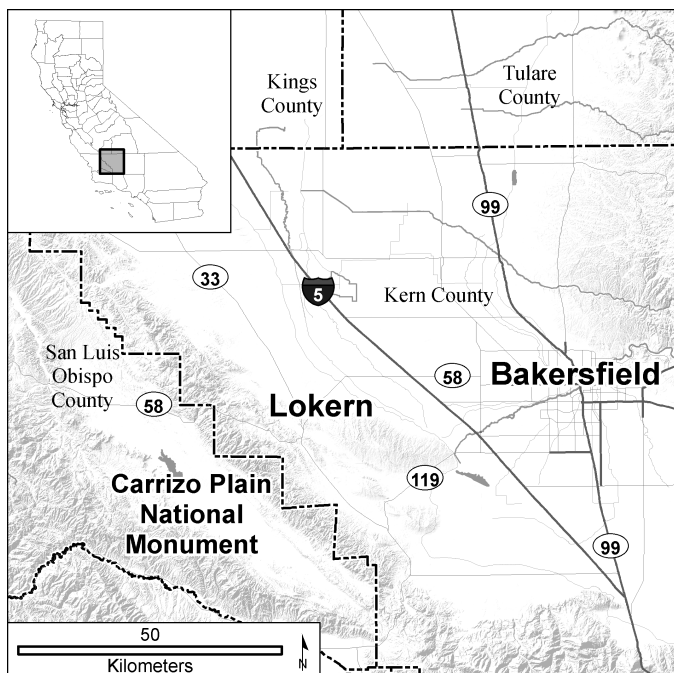


FIG. 1.—General locations of the areas in California where kit foxes have been studied. White and Ralls (1993) worked in the Carrizo Plain, Morrell (1972) and Spiegel (1996) in the Lokern area, and Bjurlin et al. (2005) in the city of Bakersfield. The Lokern area and Bakersfield are in the southern part of the San Joaquin Valley, whereas the Carrizo area is in a much smaller adjacent valley.

(*Vulpes macrotis*) and the closely related swift fox (*V. velox*) are socially monogamous (Moehrenschrager et al. 2004), although social groups occasionally include other adults, which, based on molecular genetic evidence, are usually closely related (offspring or siblings) to at least 1 of the pair-mates (Kitchen et al. 2006; Ralls et al. 2001).

The kit fox is one of the smallest North American canids, inhabiting arid lands west of the Rocky Mountains. Reviews of its general biology are provided by Moehrenschrager et al. (2004) and Cypher (2003). Kit foxes are opportunistic foragers and eat a variety of foods but rodents and leporids usually form a large part of their diet. Annual mortality of adults is often about 50% in nonurban populations and few adults live to be more than 7 years old (Cypher et al. 2000). Predators, primarily coyotes (*Canis latrans*), which caused over 75% of the deaths in several studies, but also domestic dogs (*C. familiaris*) and bobcats (*Lynx rufus*), are a major source of mortality in nonurban populations (Cypher et al. 2000; Ralls and White 1995; Spiegel 1996; Standley et al. 1992). In contrast, annual mortality in urban Bakersfield, California, is lower (about 30%) and motor vehicles are the major cause of death (Bjurlin et al. 2005). No sex or seasonal differences in vulnerability to predation are known.

Kit foxes are monestrous (Asa and Valdespino 2003) and give birth to 1 litter of 1–7 young each year. Mating occurs from mid-December to mid-January and whelping from mid-February to mid-March. Pups are independent at about 5–6 months of age. They typically disperse from their natal home

range before they are 1 year old, although a few, usually females, remain on their natal home range after adulthood. An additional adult fox was associated with 3 of 12 pairs in the Carrizo Plain National Monument (White and Ralls 1993) and 2 of 18 pairs in the Lokern Natural Area (Spiegel 1996) but the proportion of nondispersing pups likely varies with environmental conditions, increasing with population density and food availability. Females can give birth at 1 year of age. Males bring food to lactating females and older pups (Girard 2001).

Unlike many other species of foxes, which use dens only when rearing pups, kit foxes spend the day in an underground burrow or den throughout the year. Dens provide protection from predators and high environmental temperatures during the day. There are multiple dens available to the foxes in most home ranges and these dens are used almost exclusively by members of the social group inhabiting that home range (Cypher et al. 2003; Spiegel 1996; Tannerfeldt et al. 2003). Pair-mates frequently, but not always, share the same den on the same day (Koopman et al. 1998; Ralls and White 2003).

Relatively little is known about the formation and duration of kit fox pairs, the degree of association between pair-mates at different times of year, and the frequency of pair dissolution while both pair-mates are living. The literature is conflicting. Egoscue (1962) and O'Neal et al. (1987), working in Utah and Nevada, respectively, reported that kit foxes formed long-lasting pair-bonds similar to those reported for other canids, although Egoscue did not have radiocollared individuals and O'Neal's study lasted for only 1 year. Morrell (1972), based on a small sample of radiocollared individuals in California, described a different picture, similar to that found in many passerine birds (Black 1996), with an annual cycle in which new pairs are formed each year in late fall and early winter, pair-mates stay together only until their pups are raised, and adult foxes are unpaired and solitary during the summer and early fall, after which they begin to form new pairs in preparation for the next breeding season.

To obtain a better understanding of the formation, association, duration, and dissolution of male–female pairs in kit foxes, we compiled data from 3 multiyear radiotelemetry studies of San Joaquin kit foxes (*V. m. mutica*). We present data on the times of year when new pairs formed, the degree of association between pair-mates over the course of the yearly reproductive cycle, the length of time pair-mates remained together, and the dissolution of pair-bonds.

MATERIALS AND METHODS

Study sites.—We compiled data from radiotelemetry studies of kit foxes at 3 locations in California near the southern end of the San Joaquin Valley (Fig. 1). We studied nonurban foxes in 2 areas, the Carrizo Plain National Monument (Carrizo) and the Lokern Natural Area (Lokern), and an urban population in the city of Bakersfield. The climate of the southern San Joaquin Valley is characterized by hot, dry summers, and cool, wet winters. Average daily temperatures in Bakersfield range from 4°C to 14°C in December to 21°C to 37°C in July. Average annual precipitation is highly variable but ranged from 26 cm

in Carrizo (White and Ralls 1993) to about 14 cm in Lokern (Spiegel 1996) and Bakersfield (National Oceanic and Atmospheric Administration 1996). Detailed descriptions of the study sites are available in previous publications, so we provide only brief accounts here. The Carrizo study was conducted in the western part of the Carrizo Plain National Monument (39°15'N, 119°W), San Luis Obispo County, in a small valley separated from the southern San Joaquin Valley by the Temblor Range to the east (White and Ralls 1993). The principal habitat types within the study area were valley grasslands, alkali sink, and fallow grain fields. The Lokern study was conducted on the eastern side of the Temblor Range near the small town of McKittrick, approximately 40 km west of Bakersfield, in Kern County (Spiegel 1996). Foxes in the Lokern study were monitored on 3 subsites representing undisturbed land (no oil development), an area with a moderate level of development for oil production (105 oil pumps/km²), and an area with an intensive oil production (243 oil pumps/km²). The Bakersfield study was conducted in the southwestern quarter of the Bakersfield Metropolitan Area. As of January 2003, the entire metropolitan area was approximately 580 km² (224 mile²) with some 394,234 residents and the city is growing rapidly (Bakersfield Chamber of Commerce 2006). Kit fox habitat in Bakersfield includes the campus of California State University, Bakersfield, golf courses, vacant lots, and drainage sumps. Coyotes, a major cause of kit fox mortality, were common at the Carrizo (Ralls and White 1995) and Lokern (Spiegel 1996) sites but were rare in urban Bakersfield.

Field methods.—The same capture and handling methods were used in all 3 studies (Bjurlin et al. 2005; Spiegel 1996; White and Ralls 1993). Thirty-eight foxes were radiotagged in Carrizo from December 1988 to November 1990, 103 in Lokern from August 1989 to September 1993, and 229 in Bakersfield from May 1997 to July 2004. The sex ratio of collared adults was approximately 1:1 at all 3 study sites. We captured foxes with wire-mesh box traps baited with assorted meats. Traps were covered with cloth tarps to protect animals from inclement weather and direct sun. Captured foxes were handled without anesthesia. They were examined for injury and parasites, ear-tagged, age and sex were determined, and they were fitted with a radiocollar (40–55 g; Advanced Telemetry Systems, Isanti, Minnesota) containing a mortality sensor that changed the signal pulse rate if the animal was motionless for 4 h. We released foxes at the site of capture after 0.5–1 h of handling.

The intensity of different types of monitoring varied across studies because of differing study objectives. In Carrizo, we tracked each fox to its den daily throughout the study (Ralls et al. 2001; Ralls and White 2003) and conducted nocturnal radiotracking during specific periods to determine home ranges and fox interaction rates (White and Ralls 1993; White et al. 2000). In Lokern, we monitored foxes for mortality signals 2–5 times per week, tracked foxes to their dens at least 2 times per week, and conducted nocturnal radiotracking during specific periods to determine home ranges (Spiegel 1996). In Bakersfield, we attempted to record at least 1 diurnal resting location and 2 night-activity locations per animal per week (Bjurlin et al. 2005). In all studies, we conducted observations at natal

dens in the spring to determine which male and female adults were associated with each litter.

Capture and handling of foxes were performed in a humane manner following guidelines of the American Society of Mammalogists (Gannon et al. 2007). Each principal investigator (KR, LKS, BC) was authorized to work on San Joaquin kit foxes under a federal Endangered Species Act permit from the United States Fish and Wildlife Service and a Memorandum of Understanding with the California Department of Fish and Game. We followed standard methods, approved by both agencies and specified in detail in our permits, for trapping and handling this species that were designed to minimize chances of stress or injury. Methods used in the Carrizo study were approved by the Institutional Animal Care and Use Committee at the Smithsonian's National Zoological Park.

Data compilation.—An adult male and female were judged to be a pair if they met 2 or more of the following 3 criteria: their home ranges were highly overlapping (e.g., in Carrizo, home ranges of pair-mates overlapped by about 70%, whereas those of foxes in different social groups living on adjacent home ranges overlapped about 14% [White and Ralls 1993]), they were frequently found together in the same den (e.g., Koopman et al. [1998] found pair-mates together on approximately 50% of the days they were located), or they were both seen at the same natal den with a litter of pups. Den sharing between foxes other than pair-mates and their progeny is rare. For example, in Carrizo, den sharing by foxes in the same social group accounted for 97% of 3,797 instances of den sharing (Ralls et al. 2001). Although all pairs met criteria 1 and 2, some pairs did not meet criterion 3, primarily because of poor survival of pups to the age at which they would have appeared aboveground in some years (White and Ralls 1993). When we could score criterion 3, however, results always agreed with those for criteria 1 and 2. When social groups included more than 1 female (Ralls et al. 2001; Spiegel 1996), we used additional information such the relative ages of the 2 females, based on known year of birth or examination of their teeth when year of birth was unknown, or observations of mammae for evidence of suckling by pups to determine which individual was the breeding adult.

If a male and female were both radiocollared and monitored regularly before pair formation, the 1st date they were found together was taken as the date of pair formation. Sometimes a radiocollared fox lost its mate and paired with an uncollared fox. Because none of the studies was specifically designed to obtain information on dates of pair formation, we did not increase the intensity of monitoring after a fox lost its mate. If an uncollared fox was observed, we collared it as soon as possible. However, our permits did not allow us to trap foxes during the reproductive season (15 January–1 May). We then estimated the date of pair formation as the midpoint between the date the old mate died or was found to be missing and the 1st date the fox was found with the new mate. We included only cases in which we could determine the date of pair formation to the nearest month. Rate of observed pair formation was compared among months with a chi-square goodness-of-fit test.

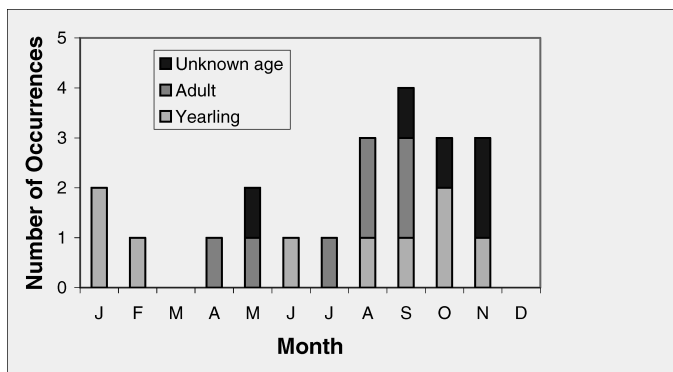


FIG. 2.—Number of pair-formation events occurring each month in kit foxes living in the Carrizo, Lokern, and Bakersfield, California, study areas. Shading indicates age of female involved in the event.

The proportion of days pair-mates are found in the same den each month can be used as a measure of the degree to which they are associated over the course of the annual breeding cycle (Koopman et al. 1998). We were only able to calculate the proportion of days pair-mates were found in the same den each month for the Carrizo site, because this was the only 1 of the 3 studies in which foxes were tracked to their dens daily (Ralls et al. 2001). Mean proportions were compared between months with a 1-way analysis of variance after arcsine-transforming the proportions (Zar 1984). Mean proportions were similarly compared between the following seasons: breeding (November–January), pup rearing (February–June), and dispersal (July–October). All deaths were confirmed by using the radiosignal to locate the carcass.

RESULTS

Dates of pair formation.—We were able to determine the date in which pair formation occurred to the nearest month in 21 cases (Fig. 2). Although pair formation most commonly occurred from August through November, we also recorded at least 1 pair-formation event in every other month except March

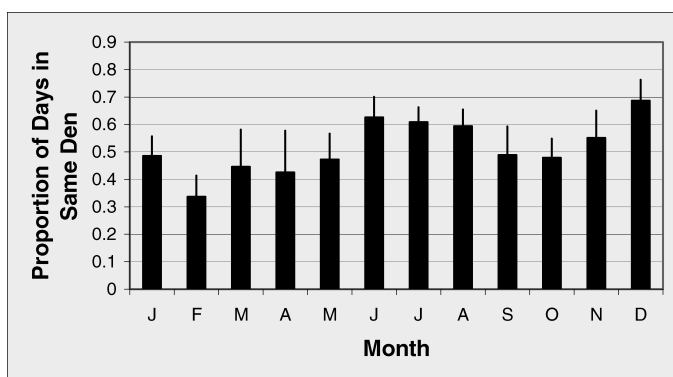


FIG. 3.—Proportion of days each month that kit fox pair-mates in the Carrizo Plain, California, were found sharing the same den. Sample sizes ranged from 6 to 11 pairs per month. Bars indicate standard error of the mean for the number of pairs observed that month.

TABLE 1.—Status of pairs at beginning of monitoring and reasons that monitoring of pairs ended.

Status	Reason for end of monitoring				Total
	Death of 1	Lost signal of 1	End of study	Not found together	
Existing pair	12	7	3	2	24
Newly formed pair	10	6	4	1	21
Total					45

and December. The number of pair-formation occurrences did not differ among months ($\chi^2 = 10.43$, $d.f. = 11$, $P = 0.49$).

Association of pair members over the annual reproductive cycle.—In Carrizo, we radiolocated both members of 6–11 pairs per month at their dens on a daily basis. Pair-mates were found in the same den some of the days each month (Fig. 3). The highest degree of association between pair-mates was in December and the lowest was in February. However, the mean proportion of days that pair-mates shared dens did not differ among months ($F = 1.27$, $d.f. = 11$, 99 , $P = 0.26$). Mean proportion also did not differ between seasons ($F = 1.66$, $d.f. = 11$, 99 , $P = 0.20$).

Duration of pair-bonds.—We monitored 45 pairs: 12 in Carrizo, 16 in Lokern, and 17 in Bakersfield. In 34 of these, the period for which we monitored the pair was an underestimate of the duration of the pair-bond for 1 or more of the following reasons: the pair was in existence when we began monitoring, we lost the signal of 1 pair-mate (likely due to failure of the radiocollar in most cases), or the pair was still in existence when the study ended (Table 1). Nevertheless, we monitored 18 pairs for periods exceeding the length of 1 annual reproductive cycle (range 357–701 days), indicating that pair-mates commonly remain together for multiple breeding seasons.

Pair dissolution and re-pairing.—We observed 16 instances where previously paired foxes formed an association with a new mate. All instances in Carrizo (5) and Lokern (8), where adult foxes were frequently killed by predators (Ralls and White 1995; Spiegel 1996), were preceded by the death of the fox's previous mate. In Lokern, the mean interval between the death of a mate and observation of the unpaired fox with a new mate was 39 days (Spiegel 1996). In Carrizo, we documented 4 foxes with new mates at 7, 73, 114, and 119 days after the death of their previous mate. However, these foxes could have had new mates before we observed them and these data were collected during a serious drought when fox reproduction was very poor (White and Ralls 1993), so potential new mates were likely less numerous than in more normal years. Re-pairing was observed less frequently in urban Bakersfield but we documented 1 case where a fox re-paired after the death of its previous mate and 2 instances, 1 definite and 1 probable, of a fox forming an association with a new mate while its previous mate was still alive. In the definite case, a male, after helping raise a litter of pups, abandoned his mate and territory in the fall and moved to a territory about 5 miles away. On this new territory, he formed a new pair-bond with

a different female with whom he reared pups the following breeding season. The abandoned female stayed on her territory and soon had a new mate with whom she reared pups the following breeding season. In the probable case, 2 unrelated young foxes of opposite sex began denning together and likely would have become a breeding pair. However, an adult male that had recently lost his mate moved into their territory, displaced the young male, and formed a pair-bond with the young female.

DISCUSSION

We found no evidence for the annual cycle described by Morrell (1972), in which new kit fox pairs are formed each year in late fall and early winter, pair-mates stay together only until their pups are raised, and adult foxes are unpaired and solitary during the summer and early fall. Instead, we found that new pairs formed throughout the year, that pair-mates remained associated throughout the annual reproductive cycle, and that pair-mates who survived to the next breeding season usually remained together, in agreement with the findings of Egoscue (1962) and O'Neal et al. (1987). It is unclear why the findings of Morrell (1972) differ so markedly from those of others who have studied kit foxes because he did not present data to support many of his assertions or explain the criteria he used for determining that 2 foxes were paired. The findings of Morrell (1972) were based on short-term observational data from a small sample of telemetered foxes (14) in a limited area (approximately 520 ha), all of which may have led to inaccurate characterizations of kit fox social ecology.

Intraspecific variation in social behavior due to differences in ecological conditions occurs in many mammalian species (Lott 1984), including canids (Angerbjörn et al. 2004; Kamler et al. 2004; Kitchen et al. 2006; Moehlman 1989; Zabel and Taggart 1989). However, differences in ecological conditions are an unlikely explanation for the unusual results of Morrell (1972), because his study site was near our Lokern study site (Fig. 1). Furthermore, despite differences in ecological conditions between our urban and nonurban sites, the aspects of social monogamy we studied were similar across sites. Urban foxes had access to anthropogenic food resources as well as natural prey, so food was abundant and showed little annual variation in abundance (B. Cypher, in litt.). In contrast, foxes in the 2 nonurban areas experienced dramatic annual variations in prey availability, which were related to annual variation in rainfall (Cypher et al. 2000; Ralls and Eberhardt 1997). Consequently, foxes in nonurban areas had larger home ranges than those in urban areas (B. Cypher, in litt.). Urban and nonurban areas also differed in the intensity of predation by larger predators, which was high in the nonurban areas and low in the urban area, resulting in higher survival rates among urban foxes (B. Cypher, in litt.).

We found that pair formation among kit foxes occurred throughout the year, and not just in the fall immediately before breeding. More occurrences of pair formation did indeed appear to occur in the fall (Fig. 2), which probably reflects pairing by young of the year. However, pair formation also

occurred in other seasons. Kitchen et al. (2005) also found that swift fox pairs formed during all seasons. As kit foxes lose mates due to predation or other factors, they apparently re-pair as soon as they can find another suitable mate. No pair-formation events were recorded in December, when most mating occurs on our study areas (Murdoch 2004), or in March when both parents are caring for their young pups.

Kit fox pair-mates on our study sites continued to associate throughout the year, and not just during breeding and pup rearing. This association was evident from both overlapping space use and den sharing. The high rate of den sharing between pair-mates in December coincided with the peak breeding period (Murdoch 2004). Swift fox pair-mates also associated more closely during the breeding season (Kitchen et al. 2005). The low rate in February coincided with parturition and the presence of very young pups in the dens. Males generally do not den with their mates when very young pups are present, but instead use dens nearby. We failed to document den sharing between the male and female after the whelping period (February–March) for 3 pairs in Bakersfield that were still paired based on their overlapping home ranges and joint rearing of a litter the following year. This was likely because we tracked individuals to their dens relatively infrequently in Bakersfield and pair-mates with older offspring often share a den with some of them rather than each other (Koopman et al. 1998).

Despite underestimation of pair-bond duration, examination of our data indicated that pair-mates commonly remained together for more than a year. Even our longest monitoring period of 701 days was an underestimate of pair duration because the pair was in existence when monitoring started and monitoring of the pair ended only because we lost the signal for the female. However, given the relatively high mortality rates of our foxes, few pairs would be expected to last for more than 3 breeding seasons. For example, assuming an annual adult mortality rate of about 50% (Ralls and White 1995; Spiegel 1996), both pair-mates would be killed in about 25% of pairs each year, 1 in about 50% of pairs, and neither in 25% of pairs. Under these conditions, only 25% of pairs would last for 2 years and about 6% (25% of 25%) for 3 years. Pair-bonds also persist for multiple breeding seasons in other canids. Pair duration in wolves ranged from <1 to >3.5 years in an un hunted population (Meier et al. 1995) and from 1 to 4 years in a heavily hunted one (Jędrzejewski et al. 2005). Pair-bonds among silver-backed jackals (*Canis mesomelas*) can persist for 6–8 years (Moehlman 1989).

Kit foxes in natural habitats generally suffer high mortality rates due to interference competition from coyotes. As a result, death of a pair-mate due to predation was the primary reason for pair dissolution among kit foxes. Similarly, pair dissolution among swift foxes usually resulted from the death of 1 of the pair-mates, typically from predation (Kitchen et al. 2005). Death of a pair-mate also was the major cause of pair dissolution in wolves (Jędrzejewski et al. 2005).

We observed 1 definite occurrence, in Bakersfield, of a pair dissolving while both foxes were still alive. Both foxes re-paired with new mates and produced young with those new

mates during the next breeding season. Kitchen et al. (2006) reported 3 instances of such "mate switching" among swift foxes. In all 3 instances, the males re-paired with younger females. No details were provided on whether the females from the dissolved pairs re-paired.

Both food abundance and intensity of predation are known to affect the degree of polygyny in some populations of foxes (Kamler et al. 2004; Zabel and Taggart 1989) and could also cause variation (which might be detectable with larger sample sizes) in some of the behaviors we studied. Higher mortality rates could result in a greater frequency of pair formation at times other than late fall, when young of the year are seeking pair-mates, and could shorten the average duration of pairs. Higher mortality rates also might reduce the likelihood of observing the dissolution of pairs due to causes other than death so it might not have been a coincidence that we only observed this in the urban population where foxes had higher survival rates.

Increased fecundity due to more abundant food supplies could decrease the percentage of time pair-mates denned together at some times of year because pair-mates with older pups often den with all or some of their pups rather than each other (Koopman et al. 1998). Regardless of the percentage of time they share the same den, however, pair-mates remain associated over the course of the annual reproductive cycle, as evidenced by exclusive use of the same set of dens and highly overlapping nocturnal home ranges.

The characteristics of social monogamy we observed in kit foxes resemble those in several other socially monogamous mammals, including the swift fox (Kitchen et al. 2005, 2006), the fat-tailed dwarf lemur (*Cheirogaleus medius*—Fietz 2003), the fork-marked lemur (*Phaner furcifer*—Schülke and Kappeler 2003), the Malagasy giant jumping rat (*Hypogeomys antimena*—Sommer 2003), and the rock-haunting possum (*Petropseudes dahli*—Runcie 2000), all of which live in perennial, continuous partnerships.

Theoretical discussions regarding the evolution of monogamy (Brotherton and Komers 2003; Reichard 2003; Wolff and Macdonald 2004) have not addressed the question of why mammals should exhibit perennial, continuous partnerships rather than some other form of social monogamy. In birds, this type of social monogamy has been linked to year-round territoriality (Ens et al. 1996), which also is characteristic of most socially monogamous mammals. In these birds, the possession of a breeding territory is vital for the reproductive success of both sexes, and selection seems to favor both partners remaining on the same territory for more than 1 breeding season. Long-lasting pair-bonds and continuous association of partners throughout the year are thought to be linked to the scarcity of breeding territories and the importance to both sexes of maintaining possession of a territory once acquired (Marzluff et al. 1996; Russell and Rowley 1996; Williams and McKinney 1996).

A similar argument may apply to kit foxes and other socially monogamous mammals that are nonmigratory and remain on the same territory year-round. A kit fox needs both a territory, which provides dens and food resources, and a pair-mate

(because both parents care for the young) for successful reproduction. Once a fox acquires these 2 essentials, it is easy to think of potential costs (and difficult to think of potential benefits) it would incur by abandoning either 1 for part of the annual reproductive cycle as envisioned by Morrell (1972). Remaining on a well-known territory with familiar den locations decreases predation risk (Cypher and Spencer 1998; McGee et al. 2006). When foxes travel into unfamiliar areas they are more vulnerable to predation and many dispersing juveniles die while traveling outside their natal territory (Koopman et al. 2000).

Also, kit foxes may increase fitness by remaining with a compatible, successful mate. Annually searching for a new mate would not only increase predation risk due to travel through unfamiliar territory, but might impose an energetic cost along with the risk of mate incompatibility, and even injury from intraspecific competition for a new mate. Also, delaying pair-bonding until just before the breeding season might add additional risk. Red foxes that do not successfully pair-bond in a timely manner may not reproduce that year (Lloyd 1980).

In summary, kit foxes exhibit a perennially monogamous social system characterized by nonseasonal pair formation, year-round association of pair-mates, and multiyear and generally life-long pair-bonds. This social system likely increases fitness by enhancing survival and ultimately reproductive success.

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LITERATURE CITED

- ANGERBJÖRN, A., P. HERSTEINSSON, AND M. TANNERFELDT. 2004. Arctic foxes: consequences of resource predictability in the arctic fox—two life-history strategies. Pp. 163–172 in *Biology and conservation of wild canids* (D. W. Macdonald and C. Sillero-Zubiri, eds.). Oxford University Press, Oxford, United Kingdom.
- ASA, C. S., AND C. VALDESPINO. 2003. A review of small canid reproduction. Pp. 117–124 in *Ecology and conservation of kit foxes in a changing world* (M. Sovada and L. Carbyn, eds.). Canadian Plains Research Center, University of Regina, Regina, Saskatchewan, Canada.
- BAKERSFIELD CHAMBER OF COMMERCE. 2006. Bakersfield community profile. <http://www.bakersfieldchamber.org/pdf/community-profile.pdf>. Accessed 9 October 2007.
- BJURLIN, C. D., B. L. CYPHER, C. M. WINGERT, AND C. L. VAN HORN JOB. 2005. Urban roads and the endangered San Joaquin kit fox. Endangered Species Recovery Program, Fresno, California.

- BLACK, J. M. 1996. Introduction: pair bonds and partnerships. Pp. 3–20 in *Partnerships in birds: the study of monogamy* (J. M. Black, ed.). Oxford University Press, Oxford, United Kingdom.
- BLACK, J. M., S. CHOUDHURY, AND M. OWEN. 1996. Do barnacle geese benefit from lifelong monogamy? Pp. 91–117 in *Partnerships in birds: the study of monogamy* (J. M. Black, ed.). Oxford University Press, Oxford, United Kingdom.
- BROTHERTON, P. N. M., AND P. E. KOMERS. 2003. Mate guarding and the evolution of social monogamy in mammals. Pp. 42–58 in *Monogamy: mating strategies and partnerships in birds, humans and other mammals* (U. H. Reichard and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom.
- CYPHER, B. L. 2003. Foxes. Pp. 511–546 in *Wild mammals of North America: biology, management, and conservation* (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.
- CYPHER, B. L., P. A. KELLY, AND D. F. WILLIAMS. 2003. Factors influencing populations of endangered San Joaquin kit foxes. Pp. 125–137 in *Ecology and conservation of kit foxes in a changing world* (M. Sovada and L. Carbyn, eds.). Canadian Plains Research Center, University of Regina, Regina, Saskatchewan, Canada.
- CYPHER, B. L., AND K. A. SPENCER. 1998. Competitive interactions between San Joaquin kit foxes and coyotes. *Journal of Mammalogy* 79:204–214.
- CYPHER, B. L., ET AL. 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. *Wildlife Monographs* 145:1–43.
- EGOSCUE, H. J. 1962. Ecology and life history of the kit fox in Toole County, Utah. *Ecology* 43:481–497.
- ENS, B. J., S. CHOUDHURY, AND J. M. BLACK. 1996. Mate fidelity and divorce in monogamous birds. Pp. 344–401 in *Partnerships in birds: the study of monogamy* (J. M. Black, ed.). Oxford University Press, Oxford, United Kingdom.
- FIETZ, J. 2003. Pair living and mating strategies in the fat-tailed dwarf lemur (*Cheirogaleus medius*). Pp. 214–231 in *Monogamy: mating strategies and partnerships in birds, humans and other mammals* (U. H. Reichard and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom.
- GANNON, W. L., AND R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild animals in research. *Journal of Mammalogy* 88:809–823.
- GEFFEN, E., M. E. GOMPPER, J. L. GITTLEMAN, H. LUH, D. W. MACDONALD, AND R. WAYNE. 1996. Size, life-history traits, and social organization in the Canidae: a reevaluation. *American Naturalist* 147:140–160.
- GIRARD, I. 2001. Foxes make good fathers: high paternal investment in the kit fox, *Vulpes macrotis*. Abstract, Ecological Society of America 86th Annual Meeting, Madison, Wisconsin.
- IKEDA, H. 1991. Comparative socioecology of canids. *Japanese Journal of Ecology* 41:263–277.
- JĘDRZEJEWSKI, W., ET AL. 2005. Genetic diversity and relatedness within packs in an intensely hunted population of wolves *Canis lupus*. *Acta Theriologica* 50:3–22.
- KAMLER, J. F., W. B. BALLARD, P. R. LEMONS, AND K. MOTE. 2004. Variation in mating system and group structure in two populations of swift foxes, *Vulpes velox*. *Animal Behaviour* 68:83–88.
- KITCHEN, A. M., E. M. GESE, S. M. KARKI, AND E. R. SCHAUSTER. 2005. Spatial ecology of swift fox social groups: from group formation to mate loss. *Journal of Mammalogy* 86:547–554.
- KITCHEN, A. M., E. M. GESE, L. P. WAITES, S. M. KAARKI, AND E. R. SCHAUSTER. 2006. Multiple breeding strategies in the swift fox, *Vulpes velox*. *Animal Behaviour* 71:1029–1038.
- KLEIMAN, D. G. 1977. Monogamy in mammals. *Quarterly Review of Biology* 52:39–69.
- KOOPMAN, M. E., B. L. CYPHER, AND J. H. SCRIVNER. 2000. Dispersal patterns of San Joaquin kit foxes (*Vulpes macrotis mutica*). *Journal of Mammalogy* 81:213–222.
- KOOPMAN, M. E., J. H. SCRIVNER, AND T. T. KATO. 1998. Patterns of den use by San Joaquin kit foxes. *Journal of Wildlife Management* 62:373–379.
- LLOYD, H. G. 1980. The red fox. B. T. Batsford Ltd., London, United Kingdom.
- LOTT, D. F. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266–325.
- MARZLUFF, J. M., G. E. WOOLFENDEN, J. W. FITZPATRICK, AND R. P. BALDA. 1996. Breeding partnerships of two New World jays. Pp. 138–161 in *Partnerships in birds: the study of monogamy* (J. M. Black, ed.). Oxford University Press, Oxford, United Kingdom.
- MCGEE, B. K., W. B. BALLARD, K. L. NICHOLSON, B. L. CYPHER, P. R. LEMONS II, AND J. F. KAMLER. 2006. Effects of artificial escape dens on swift fox populations in northwest Texas. *Wildlife Society Bulletin* 34:821–827.
- MEIER, T. J., J. W. BURCH, L. D. MECH, AND L. G. ADAMS. 1995. Pack structure and genetic relatedness among wolf packs in a naturally-regulated population. Pp. 293–302 in *Ecology and conservation of wolves in a changing world: proceedings of the second North American symposium on wolves* (L. N. Carbyn, S. H. Fritts, and D. R. Seip, eds.). Canadian Circumpolar Institute, Occasional Publication 35:1–642.
- MOEHLMAN, P. D. 1989. Intraspecific variation in canid social systems. Pp. 143–163 in *Carnivore behavior, ecology, and evolution* (John L. Gittleman, ed.). Cornell University Press, Ithaca, New York.
- MOEHRENSCHLAGER, A., B. CYPHER, K. RALLS, R. LIST, AND M. SOVADA. 2004. Comparative ecology and conservation priorities of swift and kit foxes. Pp. 185–198 in *Biology and conservation of wild canids* (D. W. Macdonald and C. Sillero-Zubiri, eds.). Oxford University Press, Oxford, United Kingdom.
- MORRELL, S. 1972. Life history of the San Joaquin kit fox. *California Fish and Game* 58:162–174.
- MURDOCH, J. 2004. Scent-marking behavior of San Joaquin kit fox. M.S. thesis, University of Denver, Denver, Colorado.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1996. Local climatological data, Bakersfield, California. National Climatological Data Center, Asheville, North Carolina.
- O'NEAL, G. T., J. T. FLINDERS, AND W. P. CLARY. 1987. Behavioral ecology of the Nevada kit fox (*Vulpes macrotis nevadensis*) on a managed desert rangeland. Pp. 443–481 in *Current mammalogy* (H. H. Genoways, ed.). Plenum Press, New York.
- RALLS, K., AND L. L. EBERHARDT. 1997. Assessment of abundance of San Joaquin kit fox by spotlight surveys. *Journal of Mammalogy* 78:65–73.
- RALLS, K., K. L. PILGRIM, P. J. WHITE, E. E. PAXINOS, M. K. SCHWARTZ, AND R. C. FLEISCHER. 2001. Kinship, social relationships, and den-sharing in kit foxes. *Journal of Mammalogy* 82:858–866.
- RALLS, K., AND P. J. WHITE. 1995. Predation on San Joaquin kit foxes by larger canids. *Journal of Mammalogy* 76:723–729.
- RALLS, K., AND P. J. WHITE. 2003. Diurnal spacing patterns in kit foxes, a monogamous canid. *Southwestern Naturalist* 48:432–436.

- REICHARD, U. H. 2003. Monogamy: past and present. Pp. 3–25 in *Monogamy: mating strategies and partnerships in birds, humans and other mammals* (U. H. Reichard and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom.
- REICHARD, U. H., AND C. BOESCH (EDS.). 2003. *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, Cambridge, United Kingdom.
- RUNCIE, M. J. 2000. Biparental care and obligate monogamy in the rock-haunting possum, *Petropseudes dahlia*, from tropical Australia. *Animal Behaviour* 59:1001–1008.
- RUSSELL, E., AND I. ROWLEY. 1996. Partnerships in promiscuous splendid fairy-wrens. Pp. 162–176 in *Partnerships in birds: the study of monogamy* (J. M. Black, ed.). Oxford University Press, Oxford, United Kingdom.
- SCHÜLKE, O., AND P. M. KAPPELER. 2003. So near and yet so far: territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. *Animal Behaviour* 65:331–343.
- SOMMER, S. 2003. Social and reproductive monogamy in rodents: the case of the Malagasy giant jumping rat (*Hypogeomys antimena*). Pp. 109–124 in *Monogamy: mating strategies and partnerships in birds, humans and other mammals* (U. H. Reichard and C. Boesch, eds.). Cambridge University Press, Cambridge, United Kingdom.
- SPIEGEL, L. K. 1996. Studies of the San Joaquin kit foxes in undeveloped and oil-developed areas. California Energy Commission, Sacramento.
- STANDLEY, W. C., W. H. BERRY, T. P. O'FARRELL, AND T. T. KATO. 1992. Mortality of the San Joaquin kit fox (*Vulpes velox macrotis*) at Camp Roberts Army National Guard Training Site, California. National Technical Information Service, Springfield, Virginia, United States Department of Energy Topical Report EGG 10617-2157:1–12.
- TANNERFELDT, M., A. MOEHRENSCHLAGER, AND A. ANGERBJÖRN. 2003. The den ecology of swift, kit and arctic foxes: a review. Pp. 167–181 in *Ecology and conservation of kit foxes in a changing world* (M. Sovada and L. Carbyn, eds.). Canadian Plains Research Center, University of Regina, Regina, Saskatchewan, Canada.
- VEIGA, J. P. 1992. Why are house sparrows predominately monogamous? A test of hypotheses. *Animal Behaviour* 43:361–370.
- WHITE, P. J., AND K. RALLS. 1993. Reproduction and spacing patterns of kit foxes relative to changing prey availability. *Journal of Wildlife Management* 57:861–867.
- WHITE, P. J., K. RALLS, AND D. B. SINIFF. 2000. Nocturnal encounters between kit foxes. *Journal of Mammalogy* 81:456–461.
- WILLIAMS, M., AND F. MCKINNEY. 1996. Long-term monogamy in a river specialist—the blue duck. Pp. 73–90 in *Partnerships in birds: the study of monogamy* (J. M. Black, ed.). Oxford University Press, Oxford, United Kingdom.
- WOLFF, J. O., AND D. W. MACDONALD. 2004. Promiscuous females protect their offspring. *Trends in Ecology and Evolution* 19:127–134.
- ZABEL, C. J., AND S. J. TAGGART. 1989. Shift in red fox, *Vulpes vulpes*, mating system associated with El Niño in the Bering Sea. *Animal Behaviour* 38:830–838.
- ZAR, J. H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

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