THE SOUTHWESTERN NATURALIST 48(3):432–436 SEPTEMBER 2003

DIURNAL SPACING PATTERNS IN KIT FOXES, A MONOGAMOUS CANID

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ABSTRACT—Kit foxes (*Vulpes macrotis*) are socially monogamous and live in male-female pairs or small family groups. These small desert foxes are nocturnal and spend the day in an underground den. Mated pairs often shared the same den on the same day. However, on days when they did not share the same den, mated pairs did not occupy dens that were closer together (or farther apart) than expected by chance. Closely related foxes on adjacent home ranges also occasionally shared dens. However, foxes living on adjacent home ranges, even when closely related, also did not occupy dens that were closer together or farther apart than expected by chance.

RESUMEN—Las zorritas del desierto (*Vulpes macrotis*) son socialmente monógamas y viven en parejas de macho-hembra o en pequeños grupos familiares. Estas pequeñas zorritas del desierto son nocturnas y pasan el día bajo suelo dentro de sus madrigueras. Parejas apareadas compartieron con frecuencia la misma madriguera durante el mismo día. Sin embargo, en los días cuando no compartieron la misma madriguera, las parejas apareadas se distribuyeron en forma aleatoria, es decir sus madrigueras no estuvieron ni más cercanas ni más lejanas de lo que se esperaba al azar. Las zorritas que están cercanamente emparentadas y que viven en rangos de hogar adyacentes ocasionalmente también compartieron la misma madriguera. Sin embargo, estas zorritas que viven en rangos de hogar adyacentes, aun cuando están cercanamente emparentadas, tampoco ocuparon madrigueras más cercanas ni más lejanas de lo que se esperaba al azar.

Kit foxes (*Vulpes macrotis*) are monogamous, living in male-female pairs or small family groups. These foxes are nocturnal and spend the day in underground dens, thus avoiding the high temperatures of their desert environment and escaping from predators, such as coyotes (*Canis latrans*) (Seton, 1925; Golightly and Ohmart, 1984; Ralls and White, 1995). Kit fox social groups maintain numerous dens in relatively exclusive denning ranges that overlap only slightly, if at all, with the denning ranges of adjacent groups (Spiegel, 1996; Koopman et al., 1998; Ralls and White, unpubl. data). A kit fox typically remains in the same den all day, emerges at night to hunt, and returns to the same den or a different den the next morning.

In some monogamous mammals, such as klipspringers (*Oreotragus oreotragus*) (Dunbar and Dunbar, 1980) and dik-diks (*Madoqua kirki*) (Kranz, 1991), the behavior of pair members tends to be synchronized, and mated males spend much of their time in close proximity to their female partner during both active and resting periods. This male behavior led to the hypothesis that monogamy in dik-diks evolved as a result of males guarding their mates (Brotherton and Manser, 1997).

Unlike the males of small, monogamous antelope species, male kit foxes are constrained by the need to forage independently for small prey, such as kangaroo rats (*Dipodomys*), and thus cannot remain in close proximity to their mate during nocturnal activity periods. Nevertheless, distances between mated foxes are consistently smaller than expected by chance during the night, whereas distances between neighboring foxes (fox dyads living on adjacent or partially overlapping home ranges) are not consistently closer together or farther apart than expected by chance (White et al., 2000). Spacing patterns between kit foxes during their diurnal resting period are not well-known, although the male and female of a mated pair use the same den on about 45% of the days that the dens of both individuals are found (Koopman et al., 1998).

We reasoned that, as in the better-studied monogamous antelopes, spacing patterns of kit

foxes during the day would resemble those during the night. Therefore, we predicted that: 1) the male and female of a mated pair would tend to choose dens that were closer together than expected by chance and 2) neighboring foxes would den randomly with respect to each other, using dens that were neither closer together nor farther apart than expected by chance.

We also speculated that an exception to this random denning pattern between neighbors might occur when neighboring foxes were closely related. Related kit foxes living on adjacent home ranges occasionally share a den (Ralls et al., 2001). These shared dens tend to be near the edge of the home range of one of the adjacent social groups (Ralls et al., 2001), so we predicted that: 3) related foxes on adjacent home ranges would use dens that were closer together than expected by chance.

We tested these 3 hypotheses by radiotracking individual kit foxes to their dens each day and estimating relatedness between individuals based on microsatellites (Ralls et al., 2001).

METHODS—*Study Area*—The study was conducted in the western portion of the Carrizo Plain National Monument (39°15′N, 119°W), San Luis Obispo County, California (see Fig. 1 in White and Ralls, 1993). The study area ranged in size from 85 km^2 in 1989 to 140 km^2 in 1991. The principal habitat types within the study area included valley grassland, alkali sink, and fallow grain fields. Detailed descriptions of the vegetation types, climate, and fauna are provided by Twisselmann (1956) and White and Ralls (1993). Nocturnal rodents were the principal prey of the foxes (White et al., 1996). Average annual precipitation in the study area was 26 cm, occurring primarily as winter rains. Larger canids, particularly coyotes, often killed kit foxes on the study area (Ralls and White, 1995), which resulted in frequent changes in the composition of fox social groups.

Field Methods—From December 1988 through November 1990, we captured San Joaquin kit foxes (*V. m. mutica*) in Tomahawk wire box traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin) baited with sardines. Each captured fox was examined for sex, weighed, and fitted with a radiocollar weighing ca. 45 g. A small sample of blood was drawn from the femoral vein or carotid artery of each fox and immediately placed in a 1-cc ethylenediaminetetraacetic acid disodium salt (EDTA) tube. Samples were refrigerated as soon as possible and mailed overnight in a styrofoam container to the Molecular Genetics Laboratory at the National Zoological Park. When catching and handling foxes, we followed a United States Fish and Wildlife animal-welfare protocol (permit RALLK-4) for the endangered San Joaquin kit fox. We routinely recaptured foxes and replaced their collars.

We monitored radiocollared individuals closely to identify mated pairs and foxes that lived on adjacent home ranges. We tracked each fox to its den daily using a hand-held antenna. We also located foxes at night to determine home ranges. Details regarding radiotelemetry techniques, methods of estimating home ranges, and maps of convex polygon and harmonic mean home ranges within the study area are given in White and Ralls (1993) and White et al. (1994).

Estimation of Relatedness—We estimated kinship between dyads by calculating Grafen's coefficient of relatedness based on 11 microsatellites (highly variable nuclear markers). Details of this procedure are given in Ralls et al. (2001). Grafen's coefficient of relatedness (r) ranges from -1 to $+1$. A positive r-value suggests that 2 individuals are more related than expected by chance, whereas a negative r-value suggests that 2 individuals are less related than expected by chance. First-degree relatives, such as parents and offspring, should have an r of 0.5. Foxes were considered to be closely related if r was 0.5 or higher.

Statistical Analyses—We used the Spatial Ecology Analysis System (J. Cary, University of Wisconsin, Madison) to determine if male-female pairs or 2 foxes with adjacent home ranges simultaneously occupied dens that were closer or farther apart than expected by chance. First, we obtained a distribution of daily inter-den distances for the members of each dyad by calculating the distance between the dens used by each member on each day. We compared this distribution to an expected distribution of inter-den distances, consisting of the distances between 1,000 pairs of randomly selected dens, 1 from the dens used by 1 fox and 1 from the dens used by the other fox, with replacement. We used t-tests to determine if the observed mean distance between the dens simultaneously occupied by the 2 foxes was smaller or larger than expected by chance. A positive t-value suggested that 2 foxes might be using dens that were close together, and a negative t-value suggested that 2 foxes might be using dens that were far apart.

RESULTS—*Social Groups*—We collared 38 foxes during the study. Social units consisted of solitary (unpaired) foxes, male-female pairs (with or without pups), and trios consisting of a male-female pair and an additional adult. We monitored 3 unpaired foxes and 5 groups in

1989, 3 unpaired foxes and 8 groups in 1990, and 5 unpaired foxes and 5 groups in 1991.

Distance Between Simultaneously Occupied Dens- We calculated the distribution of distances between pairs of dens simultaneously occupied by 11 mated male-female pairs based on 2,525 locations. When we compared the mean distance between the dens occupied by pair members to the mean distance between 1,000 pairs of randomly chosen dens (1 from the dens occupied by 1 member of the pair and 1 from the dens used by the other member), all 11 *t*-values were positive and all 11 tests were significant, suggesting that the pair members were denning significantly closer ($P = 0.001$) to each other than expected by chance. However, pair members shared the same den 51% of the time (1,293 of the 2,525 simultaneous locations). When we excluded the 1,293 cases where the pair members were in the same den, the sign of the *t*-statistic was no longer consistent and only 1 of the 11 *t*-tests was still significant, indicating that pair members did not den closer together (or farther apart) than expected by chance on days when they did not share the same den.

We also calculated the distribution of the distances between the dens simultaneously occupied by 27 fox dyads belonging to adjacent social groups (13 male-female dyads, 9 male-male dyads and 5 female-female dyads) based on 5,196 locations of dyads. When we compared the mean distance between the dens occupied by these dyad members with the mean distance between randomly chosen dens, the direction of the *t*-statistic was not consistent, and only 4 of the 27 *t*-tests were significant at the 0.05 level (Table 1). There was no relationship between the relatedness of dyad members and the direction or significance of these *t*-tests (Table 1). Thus, foxes living on adjacent home ranges did not den closer together or farther apart than expected by chance, even if they were closely related.

TABLE 1—Results of *t*-tests for differences between mean distances between dens simultaneously occupied by fox dyads belonging to adjacent social groups and mean distances between pairs of randomly chosen dens from their home ranges. r = coefficient of relatedness between dyad members. * = significant at $P \leq 0.05$.

Fox numbers	r	t	df
Male–male dyads			
104–108	0.5	−0.39	1189
104–134	0.5	−0.63	1250
112–124	0.1	−0.08	1099
103–104	0.0	−0.69	1129
110–133	0.0	0.09	1291
110–134	0.0	−0.12	1260
110–124	−0.2	−0.20	1367
104–131	no data	−1.11	1093
128–130	no data	−1.55	1021
Female–female dyads			
125–126	0.6	−0.84	1219
105–109	0.6	−0.63	1244
101–114	0.5	−2.15*	1224
111–120	0.2	0.52	1329
111–121	0.0	0.61	1314
Male–female dyads			
103–105	0.3	−0.11	1125
110–102	0.3	0.84	1435
134–111	0.2	−0.68	1175
108–105	0.1	−1.23	1201
110–121	0.1	−3.21*	1335
104–101	0.0	−0.01	1092
124–114	−0.3	0.89	1246
132–109	−0.4	−0.57	1078
128–126	−0.5	−1.28	1127
131–109	no data	−0.27	1092
110–127	no data	1.90*	1111
112–127	no data	−3.71*	1076
130–125	no data	−1.42	1020

DISCUSSION—The males of small socially monogamous antelopes spend much of their time in close proximity to their mate regardless of whether they are resting or active (Dunbar and Dunbar, 1980; Kranz, 1991). Because males, in general, follow the female, this behavior has been interpreted as a form of mate guarding that reduces the risk of extra-pair fertilizations and has led to the hypothesis that monogamy in dik-diks evolved because of the need for males to guard mates (Brotherton and Manser, 1997).

Kit foxes also are socially monogamous, but they differ from monogamous antelopes in many respects. Among the most important are the need for mated males and females to forage independently for small prey during nocturnal activity periods and the much greater role of male kit foxes in rearing young. The inability of a lone female to rear young successfully is thought to be largely responsible

for the evolution of monogamy in canids (Kleiman, 1977). It is not known whether or not kit foxes engage in extra-pair copulations, although in the socially monogamous island fox (*Urocyon littoralis*) 4 of 16 pups resulted from extra-pair fertilizations (Roemer et al., 2001).

Mated male and female kit foxes did not use dens that were closer together than expected by chance on days when they did not share the same den. This suggests that males do not guard their mates by using nearby dens and that mate-guarding is not an important function of den-sharing by mated pairs. The risk that a mated female alone in a den will encounter a neighboring male is likely low, because kit fox social groups have nearly exclusive denning ranges and foxes rarely move between dens during the day. Perhaps each member of the mated pair simply chooses a nearby den when they find themselves in different parts of their denning range at the end of their nocturnal activity. On the other hand, aerial radiotelemetry and observations showed that mated pairs of wild wolves (*Canis lupus*) sleep closer together during the mating season than afterwards (Mech and Knick, 1978). However, wolves live in packs, so the risk of extra-pair fertilizations during the day might be greater for wolves than for kit foxes. If male kit foxes do guard their mates during the day, they should choose dens closer to the den used by their mate and share dens with her more often during the mating season. Because male kit foxes play a major role in rearing pups, mated pairs also might use dens that were closer together than expected by chance when they have pups.

As predicted, neighboring foxes used dens that were neither closer together nor farther apart than expected by chance. Contrary to predictions, this was true even for closely related foxes living on adjacent home ranges. If kit foxes do engage in extra-pair copulations, it is possible that males and females on adjacent ranges might den closer together than expected by chance during the mating season. It seems likely, however, that the risk of extra-pair fertilizations is greater during the nocturnal activity period than during the day, so that males might exhibit more mate guarding primarily at night. Mates are closer together than expected by chance during the night (White et al., 2000), but they might stay closer together during the mating season than at other times a year.

Thus, a more detailed analysis of the diurnal and nocturnal spacing patterns between mated and neighboring kit foxes during the mating and pup-rearing seasons could add further insights into kit fox behavioral ecology.

We thank J. M. Hurl and our other field assistants for data collection and offer special to thanks to D. B. Siniff and J. R. Cary for their contributions to the study. We thank K. Pilgrim and M. Schwartz for analyzing the microsatellites and R. C. Fleischer for kinship calculations, J. Maldonado for the Spanish abstract, the Bureau of Land Management and The Nature Conservancy for logistical support, and the United States Fish and Wildlife Service and the California Department of Fish and Game for the necessary permits and memoranda of understanding. The Nature Conservancy; The Friends of the National Zoo; the Abbott, Baird, Nelson, and Witherspoon Funds of the Smithsonian Institution; and California Department of Water Resources supported our work.

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Submitted 28 October 2001. Accepted 23 August 2002. Associate Editor was Cheri A. Jones.