PREDATION ON SAN JOAQUIN KIT FOXES BY LARGER CANIDS

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A better understanding of the relationships between endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) and sympatric larger canids that prey on them is important for conservation efforts toward kit foxes. We used radiotelemetry to monitor the survival and cause of death of 41 San Joaquin kit foxes and 24 coyotes (*Canis latrans*) on the Carrizo Plain Natural Area, California, during the 1989–1991 drought. The estimated minimum-annual-survival rate for all coyotes was 0.88. Estimated annual-survival rates for juvenile foxes (0.21–0.41) were somewhat less than those for adult foxes (0.58–0.61). Survival rates for foxes were similar across years and sexes. Larger canids accounted for 78% of 23 verified deaths of kit foxes: 15 killed by coyotes; 2 by non-native red foxes (*Vulpes vulpes*); 1 by a domestic dog. High predation by larger canids, coupled with poor reproduction in kit foxes due to reduced prey availability during the drought, contributed to a significant decrease in density of kit foxes (from 0.24 to 0.12 foxes/km^2) during the study. Although coyotes can have a significant impact on populations of kit foxes, larger non-native red foxes may pose a greater threat in some areas.

Key words: *Canis latrans, Vulpes macrotis mutica,* coyote, kit fox, intraguild predation

A better understanding of the relationships between the endangered San Joaquin kit fox (*Vulpes macrotis mutica*; Mercure et al., 1993) and larger canids is important for conservation efforts toward kit foxes, because large canids can depress sympatric populations of smaller canids. For example, coyotes fare poorly when wolves (*Canis lupus*) are numerous (Carbyn, 1987; Dekker, 1989; Schmidt, 1991), and red foxes (*Vulpes vulpes*) fare poorly when coyotes are abundant (Johnson and Sargeant, 1977). Sterile red foxes have been used to eradicate Arctic foxes (*Alopex lagopus*) on islands (Bailey, 1992).

The San Joaquin kit fox is sympatric with the much larger coyote over much of its range, and larger non-native red foxes are invading some areas of its range (R. M. Jurek, in litt.; J. C. Lewis et al., in litt.). Furthermore, development of the habitat of kit foxes is exposing them to domestic dogs. Coyotes (*Canis latrans*) and domestic dogs are known to kill kit foxes (Cypher and Scrivner, 1992; Disney and Spiegel, 1992; O'Neal et al., 1987). There is no documented death of kit fox due to red foxes, although red foxes are known to kill Arctic foxes (Bailey, 1992; Hersteinsson and Macdonald, 1992). The impact of these larger canids on populations of kit foxes is not well understood. Several studies have reported increased densities of various species of foxes after coyote-control programs (Covell, 1992; Henke, 1992; Kilgore, 1969; Linhart and Robinson, 1972; Robinson, 1953, 1961), but capture indices and survival rates of the San Joaquin kit fox did not increase after 4 years of coyote control at the Naval Petroleum Reserves, California (Cypher and Scrivner, 1992).

We studied survival, causes of death, and population densities in sympatric coyotes and San Joaquin kit foxes on the Carrizo Plain Natural Area in California from 1989 to 1991. The Carrizo Plain Natural Area contains ca. 800 km^2 of habitat that is increasingly important for the conservation of the San Joaquin kit fox, as human activities continue to destroy and degrade natural habitats in the San Joaquin Valley (Williams, 1992).

Study Area

The study was conducted in the western portion of the Carrizo Plain Natural Area (39°15'N, 119°W), San Luis Obispo Co., California (White and Ralls, 1993: fig. 1). The 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 in Twisselmann (1956) and White and Ralls (1993). Nocturnal rodents were the principal prey of both coyotes and kit foxes (C. A. Vanderbilt White, pers. comm.); prey species are listed in White and Ralls (1993). Average annual precipitation in the study area was 26 cm, occurring primarily as winter rains. However, the study was conducted during a drought. Annual precipitation was only 11.5 cm in 1989, 5.0 cm in 1990, and 16.5 cm in 1991. The drought reduced populations of small mammals, which led to reduced reproductive success in kit foxes (White and Ralls, 1993).

Coyotes appeared to be the major potential canid predator for kit foxes on the study area. Prior to the establishment of the Carrizo Plain Natural Area in 1988, much of the area was used for sheep and cattle grazing. Private ranchers routinely trapped and shot coyotes, and federal trappers conducted coyote-control programs on several ranches (D. Capelli, pers. comm.). Coyote control was discontinued when the Carrizo Plain Natural Area was established in 1988, and diurnal sightings of coyotes gradually became more frequent, suggesting that the coyote population increased (J. Cochran, pers. comm.). Although non-native red foxes, which are extending their range over large parts of California (R. M. Jurek, in litt.; J. C. Lewis et al., in litt.), have reached the Carrizo Plain Natural Area, they appear to be uncommon there. We observed two natal dens of red foxes just outside the natural area, but none within it. Relatively few humans live in the natural area, and there are few domestic dogs.

Materials and Methods

From December 1988 through November 1990, we captured kit foxes with Tomahawk box traps (Tomahawk Live Trap Company, Tomahawk, WI) and coyotes with padded, Victor 3N longspring traps (Woodstream Corporation, Lititz, PA), modified so that they would not be tripped by an animal the size of a kit fox. Each captured animal was examined for sex, weighed, and fitted with a radiocollar weighing ca. 45 g and containing a mortality sensor (Advanced Telemetry Systems, Inc., Isanti, MN). We followed a United States Fish and Wildlife animal-welfare protocol when catching and handling kit foxes. We routinely recaptured kit foxes and replaced their collars; however, we rarely recaptured coyotes and many of their radiocollars expired during the study.

We calculated daily survival rates and expanded them to annual survival rates, under the assumption of a constant survival rate over the annual cycle (Heisey and Fuller, 1985). To use this method, it is necessary to assume the status of each individual (dead or alive) is known for each day. This assumption generally was true, because we obtained one diurnal radiolocation per day for each collared animal. However, it was violated when animals became missing and we were unable to determine their fate. Only one coyote became missing; to estimate the lowest possible survival rate for coyotes, we assumed that it died. There were four missing foxes, so we bracketed a best estimate of survival by first assuming missing individuals lived and then assuming that they died.

Confidence limits were obtained by bootstrapping (Efron, 1982; Efron and Gong, 1983). The observed set of n survival records was sampled at random, with replacement. Each bootstrap sample included n records, which were used to calculate a survival rate. We repeated this process 2,000 times to produce a frequency distribution of estimated survival rates. We used the percentile method to calculate 95% confidence limits that excluded 2.5% of the observations in each tail of the frequency distribution.

We estimated a single annual-survival rate for all age-sex classes of coyotes due to small samples. We calculated survival rates for juvenile and adult foxes. On the Carrizo Plain Natural Area, kit foxes are born in February and can reproduce at 1 year of age (O'Farrell, 1987); our permit prohibited us from trapping during the reproductive season (defined as 15 January–1 May). We considered young foxes to be juveniles from the date they were first trapped until 1 March of the following year. To compare differences in mortality rates among years and between sexes, we tabulated the number of fox-days on which individuals did or did not die and performed a chi-square test on the resulting contingency table.

We attempted to determine causes of death for collared animals that died during the study, using criteria similar to those used by Disney and Spiegel (1992). We examined each kit-fox carcass for puncture wounds and searched the vicinity for tracks and signs of predators. The diameter of individual puncture wounds and the distance between pairs of puncture wounds were compared with measurements taken from museum specimens, collected in central California, of possible mammalian predators (red foxes; bobcats, *Lynx rufus*; and coyotes) on the study area. We concluded that a kit fox had been killed by a particular predator if puncture wounds on the carcass matched the diameter and spacing of canine teeth on museum specimens and appropriate tracks and signs were found in the vicinity of the carcass. Carcasses of kit foxes were necropsied by veterinarians from the California Department of Fish and Game, who confirmed field assessments of the cause of death. We assumed that kit foxes that died of unknown causes were not killed by other canids. We calculated the yearly probability of a kit fox being killed by a wild canid (coyote or red fox) based on daily survival rates (Heisey and Fuller, 1985).

To determine if densities of coyotes and kit foxes changed during the study, we estimated the number of adult coyotes and kit foxes on the study area each month as described by Andelt (1985). We calculated the proportion of the locations of each individual that were within the study area and summed over individuals to obtain an estimate of collared-animal use. As all of the kit foxes were resident within the study area (White et al., in press), these proportions were all equal to one and the estimate of collared-animal use was equal to the number of collared foxes each month. However, several of the collared coyotes traveled outside the study area, so estimates of collared-animal use were less than the number of collared coyotes. The estimate of collared-animal use then was combined with an estimate of the number of uncollared animals using the study area based on opportunistic sightings of the species. These sightings were recorded as we drove throughout the study area for reasons other than locating collared animals; sightings were not recorded during radiotracking sessions. The estimate of the number of uncollared animals (uncollared-animal use) was obtained by multiplying the proportion of opportunistic sightings that were uncollared animals by the collared-animal use. Finally, the total estimated number of animals of each species (collared-animal use + uncollared-animal use) was divided by the size of the study area to obtain a density estimate. We calculated densities of kit foxes each month during the study and averaged these monthly estimates to obtain yearly estimates for 1989, 1990, and 1991. Densities of coyotes were estimated each month from May 1990 to May 1991, the period when we had the largest number of collared coyotes. We used a one-sample runs test for randomness (Daniel, 1990:63) and analysis of variance to determine whether the pattern of monthly densities varied within and among years, respectively. We used a one-tailed sign test to determine whether monthly densities of kit foxes declined after June 1990.

RESULTS

We radiocollared 41 kit foxes (9 adult females, 15 adult males, 9 juvenile females, and 8 juvenile males). Because animals were captured throughout the study and some juveniles survived to adulthood, the number of collared individuals in the various age-sex classes monitored per month differed from these totals. The numbers of radiocollared foxes monitored per month were 3–10 adult females, 3–10 adult males, 0–6 juvenile females, and 0–5 juvenile males. We radiocollared 24 coyotes (nine adult males, eight adult females, three juvenile females, and four juvenile males).

TABLE 1.—*Estimated annual survival rates (Heisey and Fuller, 1985) and 95% confidence limits (in parentheses) for kit foxes and coyotes radiocollared on the Carrizo Plain Natural Area, California, 1989–1991. Confidence limits are asymmetrical because they were calculated by the percentile method.*

		Survival rates		*n*	
Species	Age	Assuming missing animals lived	Assuming missing animals died	Radiodays	Individuals
Kit fox	Adult	0.61 (0.50–0.74)	0.58 (0.47–0.70)	13,339	33
	Juvenile	0.41 (0.18–0.83)	0.21 (0.06–0.56)	1,641	17
Coyote	All		0.88 (0.74–0.98)	11,376	24

The estimated minimum annual-survival rate for coyotes was 0.88, considerably higher than those for kit foxes (Table 1). Estimates for kit foxes radiocollared as juveniles were lower than those for adults (Table 1). Survival rates for kit foxes did not vary among years or between sexes ($P > 0.05$).

Three radiocollared coyotes died during the study: one shot; two of unknown causes. Twenty-two radiocollared kit foxes died during the study: 17 killed by larger canids; 1 by a vehicle; 1 when its den caved in during a flash flood; 3 of unknown causes. Based on the size of puncture wounds on the carcasses and nearby tracks and signs, 14 kit foxes were killed by coyotes, 2 by red foxes, and 1 by a domestic dog. One uncollared young kit fox also was killed by a coyote. Thus, larger canids accounted for 78% (18/23) of verified deaths of kit foxes. The estimated annual probability of an adult kit fox being killed by a wild canid (coyote or red fox) was 0.48 in 1989, 0.13 in 1990, and 0.21 in 1991. Nine of the 15 kit foxes killed by coyotes were partially eaten. Both of the kit foxes killed by red foxes were partially eaten and completely buried; red foxes typically cache food in this way (Henry, 1986). Several carcasses of kit foxes had a broken rear leg, and many had freshly broken canine teeth and claws. Tracks often indicated that there had been a short pursuit, with the larger canid chasing the kit fox as it tried to escape.

There were 10–17 radiocollared coyotes using portions of the study area during May 1990 to May 1991. However, uncollared coyotes accounted for 69% of our 109 opportunistic sightings of coyotes, and we estimated that 20–22 coyotes were using portions of the study area. The mean monthly density of adult coyotes was $0.14/km^2$ ($SE = 0.01$) during this period, and the pattern of monthly density estimates was random ($P > 0.05$).

Uncollared kit foxes accounted for only 5.8% of 87 opportunistic sightings of kit foxes. Therefore, we estimated that 22–27 kit foxes were using some portion of the study area during 1989–1991. The standard error of the monthly mean density estimates was 0.01 for all 3 years. Minimum densities of adult kit foxes were $0.24/km^2$ in 1989, $0.23/km^2$ in 1990, and $0.15/km^2$ in 1991. The density of adult kit foxes was significantly lower during 1991 than in 1989 and 1990 (White and Ralls, 1993). Densities of kit foxes declined each month from June 1990 through November 1991 ($P < 0.01$).

DISCUSSION

Our estimated survival rates for adult kit foxes (0.58–0.61) are moderately high compared with other reported estimates. The average estimates for the Naval Petroleum Reserves were 0.47 from 1980–1984 and 0.32 from 1985–1990 (Cypher and Scrivner, 1992). Disney and Spiegel (1992) obtained estimates of 0.40 and 0.68 for 1990 and 1991, respectively, when they combined data on kit foxes in undeveloped land and oil fields. Our lower survival rates for juveniles are consistent with other studies

(Cypher and Scrivner, 1992; Disney and Spiegel, 1992), although exact estimates for juveniles are not comparable across studies due to differences in the dates juveniles were trapped and the way juveniles were defined.

Predation appears to be the main cause of mortality of kit foxes throughout San Luis Obispo and Kern counties, California, although the principal predators vary from site to site. Coyotes were the main predators on our study area and the Naval Petroleum Reserves (Cypher and Scrivner, 1992). Coyotes, domestic dogs, and bobcats were the main predators at the Lokern Natural Area and oil fields other than Naval Petroleum Reserves (Disney and Spiegel, 1992). Coyotes on the Carrizo Plain Natural Area fed on more than one-half the kit foxes they killed, although Disney and Spiegel (1992) reported that coyotes rarely ate carcasses of kit foxes.

High predation by larger canids, combined with poor reproduction in kit foxes due to reduced prey availability during the drought (White and Ralls, 1993), contributed to a decrease in density of kit foxes on the study area during 1989–1991. Similar circumstances may have contributed to the decline of a population of kit foxes on the Naval Petroleum Reserves (Cypher and Scrivner, 1992). During 1984–1987, lagomorphs, the primary prey of kit foxes there, declined from ca. 175 to 50 individuals/km^2. Population levels of kit foxes were related to density of lagomorphs and also declined over this period. As in the Carrizo Plain Natural Area, predation by coyotes was the main cause of mortality for kit foxes. Thus, coyotes can have a significant adverse impact on populations of kit foxes, at least during periods of low reproduction in kit foxes.

If low recruitment and high predation persisted for many years, coyotes could conceivably eliminate kit foxes from some areas, but this seems unlikely. It may be that when conditions are poor for kit foxes, they also are poor for coyotes. Although survival of coyotes was high on our study area throughout the drought, reproduction in coyotes may have been depressed, and Cypher and Scrivner (1992) documented declining abundance of coyotes along with declining abundance of lagomorphs during the drought. Furthermore, droughts and corresponding declines in the availability of prey in habitat of the San Joaquin kit fox are episodic and temporary. As rainfall and prey abundance increase, kit foxes have the capacity to recover rapidly from their losses, because females can produce three to five offspring per year (O'Farrell, 1987). Quarterly spotlight surveys for kit foxes in the Carrizo Plain area, conducted by the California Department of Fish and Game, indicate fluctuations but no overall decrease in the population over the past 24 years (J. Lidberg, pers. comm.). With the increased rainfall since 1991, populations of kit foxes on the Carrizo Plain Natural Area (J. Lidberg, pers. comm.) and the Naval Petroleum Reserves appear to be increasing (B. Cypher, pers. comm.).

The two kit foxes killed by red foxes on our study area are the first documented cases of mortality of kit foxes due to red foxes. The rapidly expanding population of non-native red foxes in California (R. M. Jurek, in litt.; J. C. Lewis et al., in litt.) complicates the relationship between coyotes and kit foxes and the overall impact of coyotes on populations of the San Joaquin kit fox. Red foxes are invading habitat of kit foxes and appear to be largely replacing kit foxes in some areas. For example, recent surveys in the northern part of the range of kit foxes (Alameda County) found no kit fox but large numbers of red foxes (H. Bell et al., in litt.). Furthermore, sightings of red foxes are becoming more common in the southwestern San Joaquin Valley (B. Cypher, pers. comm.). Thus, red foxes may be a greater threat to kit foxes than are coyotes in some areas. Coyotes exclude red foxes (Harrison et al., 1989; Sargeant et al., 1987; Voigt and Earle, 1983) but not kit foxes (White et al., 1994) from their home ranges.

Unfortunately, the details of red fox-kit fox interactions and the extent to which healthy populations of coyotes might slow or prevent the invasion of red foxes into habitat of kit foxes are unknown.

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