

OVERLAP IN HABITAT AND FOOD USE BETWEEN COYOTES AND SAN JOAQUIN KIT FOXES

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Although coyotes (*Canis latrans*) and endangered San Joaquin kit foxes (*Vulpes macrotis mutica*; Mercure et al., 1993) use a variety of resources, many foods and habitats are apparently utilized by both species. For example, leporids were the primary prey of both coyotes and kit foxes at the Naval Petroleum Reserves in California, and kangaroo rats constituted an important secondary item for both species (Cypher et al., 1994). High overlap in resource utilization could increase the potential for resource competition between these species and, theoretically, result in decreased fox abundance (Case and Gilpin, 1974; Polis et al., 1989). Therefore, a better understanding of the extent of resource overlap between these species could contribute to kit fox

conservation efforts. During 1989–1991, we compared dietary diversity, dietary overlap, and habitat selection between coyotes and San Joaquin kit foxes on the Carrizo Plain Natural Area, California (CPNA).

The CPNA (T31S and T32S, R19E and R20E, San Luis Obispo County) lies adjacent to the southwestern edge of the San Joaquin Valley and is one of the largest continuous habitats (>750 km²) for San Joaquin kit foxes. Our 210 km² study area was located in the western portion of the CPNA and included valley sink scrub, valley saltbush scrub, upper Sonoran subshrub scrub, cismontane juniper woodland and scrub, Interior Coast Range saltbush scrub, non-native annual grassland, and grain field community types (Hol-

land, in litt.). Most of the dry-farmed grain fields had been fallow for one to five years at the onset of the study. One grain field was tilled each autumn, but its vegetative cover was quite similar to that of fallow fields for most of the year. Elevations range from 580 to 850 m and the topography varies from flat plains and rolling hills in the lowlands, to steep draws and dry washes in the Caliente Mountains. The area also includes a 12 km², dry-alkali, evaporative basin (Soda Lake). The climate is semiarid with hot, dry summers and cool, wet winters. Approximate summer high and winter low temperatures are 40°C and -10°C, respectively. Annual precipitation on the CPNA averages about 26 cm and occurs primarily as rain falling between November and April. However, drought conditions existed during the study and annual precipitation was only 11.5 cm in 1989, 5.0 cm in 1990, and 16.5 cm in 1991. This low rainfall resulted in poor plant production and counts of nocturnal rodents were two to five times lower during 1990-1991 than during 1989 (White and Ralls, 1993). Likewise, counts of lagomorphs were two to three times lower during 1990-1991 than during the previous two decades (J. Lidberg, pers. comm.).

We determined habitat use by monitoring 24 radiocollared coyotes and 38 radiocollared kit foxes from January 1989 through November 1991 as described by White et al. (in press). Briefly, we attempted to obtain one diurnal location per day for each collared coyote and fox. Coyotes were located by triangulation using vehicle-mounted, four-element Yagi antennas. Foxes were tracked to their diurnal resting sites using a hand-held H-antenna. Nocturnal locations of both species were obtained using the vehicle-mounted tracking system. One to six locations were obtained per animal per night, and each animal was located at ≥ 1 -h intervals. Nocturnal sampling periods for a given group of animals were generally separated by ≥ 1 week. Each location was plotted to the nearest 100 m using the Locate II plotting program (Pacer, Truro, Nova Scotia, Canada). To reduce error, locations ≥ 3 km from reference points were eliminated from analyses. Telemetry error was determined by reference transmitters to be 165 ± 13 m.

We determined habitat availability by digitizing (PC ARC/INFO 3.4D, ESRI, Redlands, California) community type boundaries that had been delineated on U. S. Geological Survey 7.5-minute topographic maps and orthophotoquads

during ground surveys in 1989 (E. Hubert and K. Kakiba-Russell, pers. comm.). Habitat use was then determined by overlaying coyote and fox location points with the digital community type polygons. To improve our ability to detect differences in habitat preference during selection analyses (White and Garrott, 1986), we generalized similar community types into four habitat categories: saltbush (valley saltbush scrub and valley sink scrub; 30.3% of study area), grassland (non-native annual grassland; 29.6%), fallow fields (fallow and tilled grain fields; 34.5%), and mountain scrub (cismontane juniper woodland and scrub, Interior Coast Range saltbush scrub, and upper Sonoran subshrub scrub; 5.6%). The area encompassed by Soda Lake was deleted from selection analyses since $< 0.1\%$ of the estimated canid locations occurred in this area. We evaluated if coyotes and kit foxes consistently used some habitats more (or less) than the availability of those habitats using Friedman's method, as described by Alldredge and Ratti (1986), and compositional analysis (Aebischer et al., 1993). Use-availability data were analyzed at two levels of selection: comparing proportional habitat use within minimum convex polygon home ranges with proportions of total available habitat types, and comparing the proportions of radio locations for each animal in each habitat type with the proportion of each habitat type within the social group's home range (Johnson, 1980; Thomas and Taylor, 1990; Aebischer et al., 1993). Home range locations and configurations were estimated using the minimum convex polygon method (Mohr, 1947). Since the activities of members of a coyote or fox social group may be correlated (Doncaster, 1990), we combined locations from each member of a group to calculate the group's home range. Coyotes were considered to belong to a specific social group if they lived in the same area during the same year (Sargeant, 1972). Foxes were considered to belong to a specific social group if they frequently and concurrently shared the same dens (White and Ralls, 1993). Diurnal and nocturnal habitat selection were analyzed separately. Only groups with ≥ 60 diurnal locations and ≥ 60 nocturnal locations were used in the analyses to minimize the likelihood of Type II errors (Alldredge and Ratti, 1986).

Dietary diversity and overlap between coyotes and kit foxes were estimated using scat analysis. From January 1989 to October 1991, we opportunistically collected coyote and kit fox scats from

den sites and along roads. Each scat was handled and processed as described by Vanderbilt White (1994). Skeletal and hair reference collections and hair keys (Moore et al., 1974) were used to identify food items. Food items were categorized as birds, feral pigs, insects, juniper berries, leporids, livestock, reptiles, rodents, and other mammals, and identified to species where possible. Indigestible plant fragments were found in most scats, but were not included as a food category since their ingestion was likely incidental. Percentages of occurrence of items in scats (number of occurrences of a food item divided by the total number of occurrences of all food items; Kelly, 1991) were determined by year and season (wet season, 1 November to 30 April; dry season, 1 May to 31 October). We used loglinear models (Everitt, 1977) to identify covariates that explained substantial variability in coyote and kit fox diets. Covariates considered included year, season, and food item. The occurrence of items in coyote and kit fox scats were compared using contingency table analysis (Everitt, 1977). We calculated a Shannon diversity index (Krebs, 1989) for each species, and used a *t*-test to determine whether dietary diversity differed significantly between species (Hutcheson, 1970). Horn's similarity index (Horn, 1966) was used to estimate dietary overlap between species.

We obtained 4,865 diurnal locations of coyotes and 10,069 diurnal locations of kit foxes. We also obtained 1,255 nocturnal locations of coyotes and 3,106 nocturnal locations of foxes. Habitats were ranked similarly from 'least' to 'most preferred' by Friedman's method (Alldredge and Ratti, 1986) and compositional analysis (Aebischer et al., 1993). Both species generally rested during the day, but were active at night. Kit fox social groups ($n = 12$) consistently ($P < 0.001$) used fallow fields and grasslands within the study area and, also, within their home ranges more than expected by availability. Foxes in six social groups preferentially used fallow fields for their diurnal resting sites, whereas six social groups used grasslands (Table 1). Similarly, kit foxes in five social groups preferentially used fallow fields for their nocturnal activities, whereas six social groups used grasslands and one group used saltbush (Table 1). Coyote social groups ($n = 8$) avoided ($P = 0.01$) fallow fields during diurnal hours, probably since fallow fields provided less cover than other habitat types and were generally located closer to human activities. Coyotes in five social groups

preferentially used saltbush or mountain scrub for their diurnal resting sites, whereas three social groups used grasslands (Table 1). At night, coyote social groups used all habitats as expected by their availability ($P = 0.72$). Coyotes in two social groups preferentially used fallow fields, whereas five social groups used saltbush or mountain scrub and one group used grasslands (Table 1). Thus, some coyotes often foraged in habitats also favored by foraging kit foxes.

We collected and analyzed 337 coyote scats and 774 kit fox scats (Table 2). Neither coyote nor kit fox diets were dominated by a single food item. Rodent remains were the most frequently occurring items in coyote scats (30.4% of occurrences), followed by insects (27.9%), leporids (12.9%), feral pigs (10.7%), and juniper berries (10.7%). Rodent remains also were the most frequently occurring items in kit fox scats (48.2% of occurrences), followed by insects (35.2%), birds (8.6%), leporids (4.3%), and reptiles (1.5%). The most common rodent remains in coyote scats were California ground squirrels (*Spermophilus beecheyi*; 8.8% of occurrences), pocket mice (*Chaetodipus californicus*, *Perognathus inornatus*; 8.8%), and kangaroo rats (*Dipodomys heermanni*, *D. ingens*; 8.7%). The most common rodent remains in kit fox scats were pocket mice (19.4% of occurrences), deer mice (*Peromyscus maniculatus*; 9.8%), and kangaroo rats (7.9%). Other rodent remains in coyote or kit fox scats included San Joaquin kangaroo rats (*D. nitratoides*), San Joaquin antelope ground squirrels (*Ammospermophilus nelsoni*), pocket gophers (*Thomomys bottae*), wood rats (*Neotoma lepida*), and grasshopper mice (*Onychomys torridus*). Identifiable insect remains in coyote and kit fox scats consisted primarily of beetles (mostly *Eleodes* spp.; 57% of insect occurrences), Jerusalem crickets (Gryllacrididae; 25%), and grasshoppers (Acrididae; 16%). The overall contribution of insects to coyote and kit fox diets was likely overestimated since insect remains accounted for <20% of the total scat volume in half of the scats containing insects. Desert cottontails (*Sylvilagus audubonii*) comprised 65 and 77% of the identifiable leporid remains in coyote and kit fox scats, respectively, with black-tailed jack rabbits (*Lepus californicus*) comprising the remainder. Livestock remains included cattle and sheep. Other mammalian remains in coyote or kit fox scats included elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and skunk

TABLE 1—Diurnal and nocturnal habitat selection by social groups of coyotes and San Joaquin kit foxes, Carrizo Plain Natural Area, California, 1989–1991. The differences between use and availability of four habitat types within each social group's home range are provided and ranked from the highest (4) to lowest (1) value.

Pair no.	Diurnal habitat selection				Nocturnal habitat selection				
	Saltbush	Mountain scrub	Grassland	Fallow field	Saltbush	Mountain scrub	Grassland	Fallow field	
Fox	1	0.01 (3)	-0.08 (2)	0.19 (4)	-0.12 (1)	0.32 (4)	-0.07 (2)	-0.05 (3)	-0.20 (1)
	2	-0.20 (2)	N ^a	0.02 (3)	0.18 (4)	-0.16 (2)	N	0.01 (3)	0.15 (4)
	3	-0.22 (2)	N	-0.03 (3)	0.25 (4)	-0.07 (3)	N	-0.03 (2)	0.10 (4)
	4	N	N	0.40 (4)	-0.40 (3)	N	N	-0.19 (3)	0.19 (4)
	5	-0.07 (2)	-0.16 (1)	-0.03 (3)	0.26 (4)	-0.06 (2)	-0.12 (1)	-0.02 (3)	0.20 (4)
	6	-0.21 (2)	N	-0.15 (3)	0.36 (4)	-0.12 (2)	N	0.22 (4)	-0.10 (3)
	7	N	N	0.12 (4)	-0.12 (3)	N	N	0.34 (4)	-0.34 (3)
	8	-0.06 (2.5)	-0.06 (2.5)	0.35 (4)	-0.23 (1)	-0.04 (3)	-0.05 (2)	0.23 (4)	-0.14 (1)
	9	N	N	-0.10 (3)	0.10 (4)	N	N	-0.04 (3)	0.04 (4)
	10	N	-0.16 (3)	0.35 (4)	-0.19 (2)	N	-0.14 (2)	0.15 (4)	-0.01 (3)
	11	N	-0.12 (3)	-0.43 (2)	0.55 (4)	N	-0.09 (2)	0.06 (4)	0.03 (3)
	12	-0.28 (2)	N	0.49 (4)	-0.21 (3)	-0.14 (2)	N	0.11 (4)	0.03 (3)
Coyote	1	-0.07 (2)	0.13 (3)	0.18 (4)	-0.24 (1)	-0.10 (2)	-0.01 (3)	-0.13 (1)	0.24 (4)
	2	-0.03 (3)	N	0.16 (4)	-0.13 (2)	-0.59 (2)	N	-0.06 (3)	0.65 (4)
	3	-0.02 (2)	0.14 (4)	-0.01 (3)	-0.11 (1)	-0.01 (2)	0.06 (4)	0.04 (3)	-0.09 (1)
	4	N	0.53 (4)	-0.09 (3)	-0.44 (2)	N	0.21 (4)	-0.06 (3)	-0.15 (2)
	5	-0.02 (2)	0.05 (3)	0.07 (4)	-0.10 (1)	0.00 (2)	0.02 (3)	0.25 (4)	-0.27 (1)
	6	0.12 (4)	0.11 (3)	-0.01 (2)	-0.22 (1)	0.14 (4)	-0.04 (3)	-0.05 (1.5)	-0.05 (1.5)
	7	N	0.37 (4)	-0.08 (3)	-0.29 (2)	N	0.02 (4)	-0.01 (2.5)	-0.01 (2.5)
	8	0.11 (4)	0.05 (3)	0.03 (2)	-0.19 (1)	0.06 (4)	-0.02 (2)	0.04 (3)	-0.08 (1)

^a None of this habitat type occurred within the social group's home range.

TABLE 2.—Seasonal percentage of occurrence of food items in coyote and San Joaquin kit fox scats, Carrizo Plain Natural Area, California, 1989–1991. Dietary data for kit foxes were derived from Vanderbilt White et al. (in litt.), and are presented here for comparative purposes.

Item	Percentage of occurrence (%)											
	Coyotes						Kit foxes					
	1989		1990		1991		1989		1990		1991	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Rodents	37.3	39.3	29.7	14.7	24.9	36.6	44.8	49.0	44.2	47.3	55.0	48.6
Kangaroo Rats	11.8	6.1	7.9	4.9	8.3	13.2	6.6	5.3	7.2	2.5	8.6	17.4
Deer Mice	0.0	1.2	3.9	0.0	0.0	2.9	5.9	9.0	14.9	8.6	14.0	6.1
Pocket Mice	7.8	7.4	6.7	4.9	8.3	17.6	14.5	22.1	10.8	25.8	22.6	20.6
Ground Squirrels	11.8	20.8	5.6	3.3	8.3	2.9	10.5	6.5	9.1	7.3	7.6	1.0
Wood Rats	2.0	0.0	0.0	0.0	0.0	0.0	0.7	0.8	0.2	0.0	1.1	1.6
Pocket Gophers	3.9	4.3	5.6	1.6	0.0	0.0	6.6	5.3	2.0	3.1	1.1	1.9
Leporids	13.7	14.2	13.5	3.2	20.8	11.7	4.0	6.8	7.2	0.6	3.7	3.6
Desert Cottontails	5.9	9.2	7.3	1.6	0.0	2.9	3.3	2.8	4.7	0.0	1.6	1.3
Black-tailed Jack Rabbits	7.8	2.5	3.4	0.0	8.3	4.4	0.7	1.2	1.4	0.6	0.5	0.0
Unidentified	0.0	2.5	2.8	1.6	12.5	4.4	0.0	2.8	1.1	0.0	1.6	2.3
Livestock (cattle, sheep)	0.0	3.7	6.2	0.0	4.2	0.0	4.6	0.0	1.1	0.0	0.0	0.0
Other mammals (elk, deer, antelope, skunks)	0.0	1.8	1.7	1.6	0.0	2.9	0.0	1.2	0.2	0.0	0.0	0.0
Feral Pigs	5.9	4.9	20.8	8.2	16.7	7.4	0.0	0.0	2.3	1.2	0.5	0.3
Birds	2.0	1.2	3.9	0.0	4.2	4.4	5.9	6.1	13.3	3.1	16.1	6.8
Insects	33.3	34.4	24.1	27.9	16.7	30.8	38.8	36.0	30.5	43.6	23.7	38.4
Beetles	9.8	3.1	6.7	8.2	4.2	10.3	14.5	17.6	16.5	22.1	15.1	18.4
Grasshoppers	2.0	14.7	2.8	3.3	0.0	4.4	3.3	4.9	1.4	4.3	0.5	3.2
Crickets	7.8	8.0	7.9	9.8	12.5	13.2	5.9	6.1	2.9	3.7	2.2	6.8
Unidentified	13.7	8.6	6.7	6.6	0.0	2.9	15.1	7.4	9.7	13.5	5.9	10.0
Juniper Berries	2.0	0.0	0.6	45.9	12.5	2.9	0.7	0.4	0.7	1.2	0.5	0.0
Reptiles	5.9	1.8	1.1	0.0	0.0	5.9	1.3	2.0	0.7	3.1	0.5	2.3
Number of scats	24	91	118	45	14	45	73	111	234	83	105	168

(*Mephitis mephitis*). Identifiable bird remains were primarily those of ground-dwelling species such as Horned Larks (*Eremophila alpestris*) and Western Meadowlarks (*Sturnella neglecta*). Birds comprised <3% of coyote diets, but accounted for 10% of kit fox diets during the drought (1990–1991). Reptiles included unidentifiable snakes and lizards. Juniper berries comprised <1% of kit fox diets, but accounted for 46% of coyote diets during the dry season of 1990 when the drought was at its peak and mammalian prey was scarce.

The percentage of occurrence of food items in both coyote and kit fox scats varied significantly between seasons (coyotes: $\chi^2 = 240.2$, $d.f. = 50$, $P < 0.001$; kit foxes: $\chi^2 = 76.9$, $d.f. = 53$, $P = 0.02$) and years (coyotes: $\chi^2 = 157.6$, $d.f. = 32$, $P < 0.001$; kit foxes: $\chi^2 = 64.3$, $d.f. = 38$, $P < 0.005$). Coyote scats contained more feral pig and leporid remains during the wet season than the dry season. Kit fox scats contained fewer insect remains, but more bird and ground squirrel remains, during the wet season than the dry season. Coyote scats contained fewer insect and ground squirrel remains, but more feral pig and juniper berry remains, during the drought (1990–1991) than during 1989. Kit fox scats contained fewer ground squirrel and pocket gopher remains, but more bird remains, during the drought. Interactions between food item and season were independent of those between food item and year for coyotes ($\chi^2 = 1.13$, $d.f. = 2$, $P = 0.53$) and kit foxes ($\chi^2 = 0.03$, $d.f. = 2$, $P = 0.98$), suggesting that the relative compositions of seasonal diets were similar among years. Therefore, we combined data among years to compare seasonal dietary overlap and diversity between species. Horn's similarity index indicated that dietary overlap between coyotes and foxes was high (0.85) during both wet and dry seasons. However, coyotes had more diverse diets than kit foxes (wet season: $t = -2.24$, $P < 0.02$; dry season: $t = -4.10$, $P < 0.001$), and the percentage of occurrence of food items in coyote and kit fox scats was significantly different ($\chi^2 > 427.0$, $d.f. = 13$, $P < 0.001$) during both seasons. Coyotes consumed more larger-sized prey such as leporids and feral pigs, whereas kit foxes consumed more smaller-sized prey such as nocturnal rodents and birds. Thus, although coyote and kit fox diets overlapped extensively, both species exhibited specializations for food items that reflected their respective body sizes and energetic requirements.

The substantial overlap in diet and nocturnal

habitat selection between coyotes and San Joaquin kit foxes indicates a high potential for resource competition. Such competition may be amplified by low mammalian prey availability during droughts, which are quite common in this region. However, coyotes may attempt to lessen resource competition with the smaller kit foxes by killing them. Sixty-five percent (15 of 23) of the fox mortalities during our study were attributable to coyotes (Ralls and White, in press). Coyotes also commonly kill kit foxes in other areas of California (Orloff et al., 1986; Disney and Spiegel, 1992) and Utah (O'Neal et al., 1987). These killings constitute interference competition, but their effects on kit fox population dynamics are uncertain. Interference competition, coupled with poor kit fox reproduction due to reduced prey availability during the drought (1990–1991), contributed to a significant decrease in kit fox density during our study. However, kit fox numbers increased during 1992 and 1993 after rainfall and prey abundance had also increased (Ralls and White, in press). Kit fox capture indices and survival rates did not increase after four years of extensive coyote control at the Naval Petroleum Reserves, California (Cypher and Scrivner, 1992), suggesting that coyote-induced mortality may be partially compensatory or that coyote densities were not reduced sufficiently to observe an effect. In contrast, several studies of closely-related swift foxes (*Vulpes velox*) have reported increased fox densities after the implementation of coyote control programs (Robinson, 1961; Kilgore, 1969; Linhart and Robinson, 1972; Covell, 1992; Henke, 1992). Coyote predation also hindered the reintroduction of swift foxes in southern Alberta, Canada (Scott-Brown et al., in litt.). These results suggest that coyotes could have a significant adverse impact on remnant or reintroduced kit fox populations, at least during periods of high resource competition and low fox reproduction. However, it is unlikely that the long-term impacts of coyote-induced mortalities would be severe for most kit fox populations. Kit foxes have the capacity to rapidly replace these losses because females can produce three to five pups per year. Furthermore, kit foxes have likely coevolved with coyotes and can apparently avoid competitive exclusion, perhaps through slight differences in resource selection and year-round use of dens to avoid agonistic encounters. Kit foxes on the CPNA ate more smaller prey species than coyotes, and were more

selective in their habitat use, thereby partitioning the available resources to some extent. Kit foxes also maintain numerous (>20) dens within their home ranges, which apparently facilitate escape from predators such as coyotes in addition to serving as daytime refuges (Morrell, 1972; White et al., in press).

In summary, high resource overlap between coyotes and San Joaquin kit foxes likely contributes to competition for resources. Coyotes may reduce this competition by killing the smaller foxes (interference competition). However, kit foxes are able to coexist with coyotes, probably due to resource partitioning, the year-round use of dens to avoid agonistic encounters, and their high reproductive potential. Thus, most kit fox populations should be able to endure periods of intense resource competition and high coyote-induced mortality without the need for human intervention (coyote removal).

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