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Competitive interactions between endangered kit foxes and nonnative red foxes

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COMPETITIVE INTERACTIONS BETWEEN ENDANGERED KIT FOXES AND NONNATIVE RED FOXES

Howard O. Clark, Jr.^{1,2,3}, Gregory D. Warrick⁴, Brian L. Cypher¹, Patrick A. Kelly¹,
Daniel F. Williams¹, and David E. Grubbs²

ABSTRACT.—We investigated interference and exploitative competition between endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) and nonnative red foxes (*V. vulpes*). Seven kit foxes and 16 red foxes were radio-collared and tracked via radiotelemetry near Lost Hills, California. One kit fox was killed by a red fox. Home ranges of the 2 species did not overlap extensively. Although both species used similar habitats, they used different parcels of land. Kit foxes and red foxes primarily consumed rodents on the study site, and dietary overlap was considerable. Red foxes also may have been using dens formerly used by kit foxes. Thus, red foxes were engaging in both interference and exploitative competition with kit foxes, and red foxes constitute a potentially significant threat to kit foxes. Coyotes (*Canis latrans*) co-occur with kit foxes and may limit red fox abundance and distribution. Therefore, although they occasionally kill kit foxes, the presence of coyotes may benefit kit foxes by excluding red foxes.

Key words: California, competition, endangered species, kit fox, red fox, *Vulpes macrotis mutica*, *Vulpes vulpes*.

The San Joaquin kit fox is a federally endangered and state threatened species occurring in the San Joaquin Valley, California (United States Fish and Wildlife Service 1998). The historic range of the San Joaquin kit fox has been significantly reduced by habitat loss due to agricultural, industrial, and urban development. Remaining kit fox populations are threatened by continuing habitat conversion, as well as rodenticide use and interspecific competition (United States Fish and Wildlife Service 1998). Nonnative red foxes are increasing in abundance in the San Joaquin Valley (Jurek 1992, Lewis et al. 1999) and potentially could compete with kit foxes. Competitive interactions between kit foxes and red foxes have not been investigated.

Red foxes were introduced into the Sacramento Valley of California from the midwestern United States in the 1870s (Grinnell et al. 1937, Lewis et al. 1999) and since have spread as far south as San Luis Obispo, Orange, and Los Angeles Counties, California (Jurek 1992). Red foxes also have appeared throughout the San Joaquin Valley, including habitats occupied by kit foxes. Adverse impacts to kit foxes

from red foxes have been documented. Ralls and White (1995) reported 2 San Joaquin kit fox mortalities due to red foxes. Also, red foxes have been observed using dens previously occupied by kit foxes (B. Cypher personal observation). Other potential impacts include competition for food and disease transmission (Cypher et al. 2001). Red foxes also have been found to adversely affect other fox species such as arctic foxes (*Alopex lagopus*; Frafjord et al. 1989, Hersteinsson and Macdonald 1992) and swift foxes (*V. velox*; A. Moehrensclager personal communication). Thus, it is important to quantify competitive interactions between kit foxes and red foxes to determine whether red foxes are a potential threat to remaining kit fox populations.

We examined competitive interactions between San Joaquin kit foxes and nonnative red foxes near Lost Hills, California, during 1998–1999. Our objectives were (1) to examine sources of mortality and space use patterns of both species to determine whether interference competition was occurring, and (2) to examine habitat use and food habits of both species to determine whether exploitative competition was occurring.

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METHODS

Study Area

We conducted our study along an approximately 32-km segment of the California Aqueduct (aqueduct) near the community of Lost Hills, Kern County, California (Fig. 1). Kit foxes and red foxes co-occur in this area. The study area is predominantly flat with elevations ranging from approximately 80 m in the east to 150 m along the Lost Hills anticline. The Lost Hills, forming the western edge of the study area, are gentle, rolling hills that run in a northwest to southeast direction paralleling the aqueduct.

Climate is characterized by hot, dry summers and wet, cool winters with thick fog (National Climatic Data Center 2000). Weather data recorded 40 km east of Lost Hills in Wasco, California, indicate that average daily maximum temperatures range from 13.4°C in December to 37.5°C in July, and average daily minimums range from 2.1°C in December to 18.7°C in July. Precipitation, which averages 18.6 cm annually, was 41.6 cm in 1998 and 14.7 cm in 1999.

A strip of habitat approximately 60 m wide occurs along both sides of the aqueduct. This habitat is typical of Valley Grassland vegetation (Heady 1977), with red brome (*Bromus madritensis*) and filaree (*Erodium* spp.) dominating the herbaceous vegetation. Common shrubs include desert saltbush (*Atriplex polycarpa*) and spiny saltbush (*A. spinifera*). Honey mesquite (*Prosopis glandulosa*) occurs within the southern portion of the study area, and a few feral almond and pistachio trees are found in areas where the aqueduct borders orchards. Farmland covers most of the study area outside the aqueduct corridor. Major crops include cotton, barley, almonds, and pistachios. Less abundant crops are alfalfa, onions, lettuce, watermelon, olives, tomatoes, and vineyards. Annual crops are typically planted in late winter and harvested in the fall. After crops are harvested, the ground is disked and left bare until the following spring. Pistachio and almond groves are drip-irrigated and harvested in October of each year.

The west side of the study area is bounded by the Lost Hills oil field (approximately 1.5 km west of the aqueduct), which is primarily owned and operated by private oil companies. Although some portions of the oil field are heavily de-

veloped, significant expanses of natural vegetation typical of the Valley Grassland are present.

Field Methods

Kit foxes were captured during the non-breeding season (April–September) using Tomahawk™ wire-mesh traps (38 × 38 × 107 cm; Tomahawk, MI) baited with canned mackerel, wieners, bacon, or chicken. We captured red foxes during the dispersal season by plunging them from drainage culverts into handling bags. The plunger consisted of lengths of plastic pipe attached together with a foam ball taped to an end (O'Farrell 1987). Foxes were ear-tagged, measured, weighed, and fitted with radio-collars (Advanced Telemetry Systems, Isanti, MN). Collars contained mortality sensors that activated after 8 hours of nonmovement. Each radio-collar weighed approximately 50 g, or <3% of the animal body mass (Cypher 1997). We released the foxes at their individual capture sites and then radio-tracked them from January 1998 to December 1999 (Clark 2001).

Radio-collared foxes found dead were necropsied to determine cause of death. If the fox had contusions caused by tooth punctures, we considered predators the cause of death (Roy and Dorrance 1976). When possible, we measured distances between canine puncture wounds to determine which species caused the death (Disney and Spiegel 1992). If the cause of death could not be determined because the carcass was badly decomposed or scavenged, it was classified as unknown.

To determine space use patterns, foxes were radio-tracked weekly using 2 truck-mounted null tracking systems with paired 2-element antennae (White 1985). Stations were located along access roads of the aqueduct and separated by approximately 800 m. Researchers at 2 adjacent stations simultaneously took bearings on foxes. Four azimuths (referencing true north) were obtained: the azimuth to the fox from the south antenna, the azimuth to the fox from the north antenna, the azimuth from the south antenna to the north antenna, and vice versa. Survey grade GPS units (Pathfinder Pro XR/XRS, Trimble Navigation Limited, Sunnyvale, CA) were used to determine the locations of the antenna stations. We initiated telemetry sessions approximately 1 hour before sunset and continued for approximately 4.5 hours. The first 3–5 hours after sunset is typically

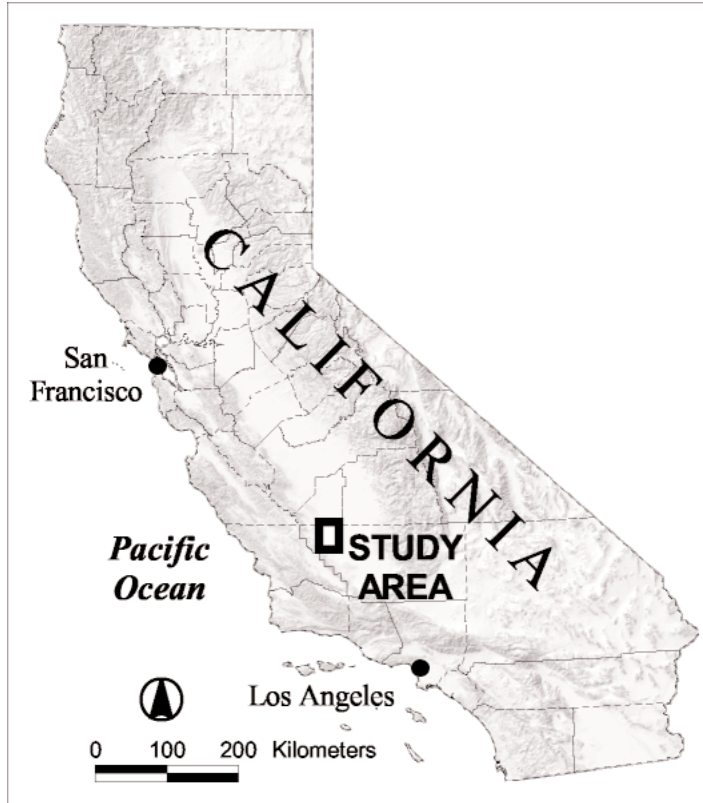


Fig. 1. Location of study site near Lost Hills, California.

when kit fox activity is highest (Zoellick 1990). We collected locations on all collared foxes in the vicinity, and successive locations on individual foxes were separated by ≥ 10 min. When bearings intersected < 20 degrees, we discarded locations. Locations of foxes were calculated using methodology described in White and Garrott (1990), and we entered these locations into a GIS layer for analyses using ARC/INFO (Environmental Systems Research Institute, Redlands, CA).

Accuracy of the telemetry system was determined by having 2 observers gather bearings on radio-collars ($n = 30$) placed at locations known only by a 3rd person. Locations derived from telemetry were then compared to the actual locations of the radio-collars (recorded using a survey grade GPS unit) to determine the average telemetric error (Springer 1979), which was 38 ± 7 m (range = 4–186 m). Eighty percent of triangulated locations had an error of < 45 m. Tracking vehicles averaged 552 ± 35

m (range = 74–1318 m) from the reference transmitters.

To evaluate spatial overlap of foxes, we used the points collected throughout the year to delineate home ranges and core areas for each fox, but only for those with > 30 locations (Chamberlain and Leopold 2000). Home ranges were delineated using the minimum convex polygon (MCP) method, which provides a conservative estimate of space use. Core areas were delineated using the adaptive kernel method (Worton 1989). Areas within the home range that fell within the 25% probability contour were considered core areas, defined as the portion of an animal's home range that exceeded an equal-use pattern (Samuel et al. 1985). Core areas can be used to denote central areas of consistent or intense use (Kaufmann 1962). An ArcView program extension was used to delineate home ranges and core areas (Hooge and Eichenlaub 1997). Spatial overlap between kit foxes and red foxes was calculated for each

animal by determining the percentage of each range that was overlapped by an individual of the other species.

To determine habitat use by the 2 fox species, we entered into an ARC/INFO layer the habitat information gathered using GPS units, United States Geological Survey maps, and ground mapping. Fox locations were plotted in ArcView, and each location was assigned a habitat type. Only those kit foxes and red foxes with overlapping home ranges were included in the habitat selection analysis. In 1998 home range overlap between species occurred only in the southern portion of the study area, and in 1999 only in the northern portion of the study area. One adult male kit fox in 1998 with an analyzed overlapping home range with a red fox had an analyzed overlapping home range in 1999; all other foxes were different individuals. To ensure data independence, we selected a single random location per fox per telemetry session (Swihart and Slade 1985). Available habitat was defined as being within 1.6 km of the aqueduct and 1.6 km from the most southerly and most northerly fox locations. Utilization-availability analysis was conducted using the method described in Neu et al. (1974) and Byers et al. (1984). To test whether foxes used each habitat category in proportion to its occurrence within the available area, we used the chi-square method described in Neu et al. (1974).

Habitat types included orchard, row crops, aqueduct right-of-way (ROW), vineyard, grassland, residential, and other. Orchards included almonds, olives, and pistachios. Annual row crops included cotton, barley, and tomatoes. Residential referred to any farmhouse, equipment staging area, or farm equipment storage yard. The category "other" included small parcels of tilled and miscellaneous land. Habitat types differed between 1998 and 1999 due to fox home range overlap occurring in different portions of the study area.

To assess overlap in food use, we analyzed scats collected from trapped foxes and known fox dens. A *scat* is defined as all fecal material deposited in 1 event. Scats were oven-dried for 24 hours at 60°C to facilitate handling and to destroy cysts of zoonotic parasites. Prey remains were identified using hairs (Mayer 1952, Stains 1958) and by comparing teeth, bones, scales, skin, exoskeletons, and seeds with reference specimens (Roest 1991). Food items

were grouped to simplify analyses. Horn's index (Horn 1966), R_0 , was calculated to determine the amount of overlap between diets. A Shannon index of dietary diversity, H' , was calculated for each species. A 2×10 contingency table chi-square test was conducted on the dietary data, and a 2×2 contingency table chi-square test was conducted on each item to determine if proportional use by the 2 fox species was similar (Zar 1999).

RESULTS

Causes of Mortality

During 1998–1999 we captured and radio-collared 4 adult (2 female, 2 male) and 3 juvenile male kit foxes, and 16 red fox juveniles (10 females, 6 males). It is likely that representatives from all kit fox and red fox family units were radio-collared during this 2-year period. Four radio-collared kit foxes (2 adults, 2 juveniles) were killed, 3 (1 adult, 2 juveniles) by coyotes and 1 adult by a red fox. Eleven radio-collared red foxes were found dead, 9 killed by coyotes. Cause of death could not be determined conclusively for 1 red fox (although probably a predator kill). The signal from the collar of another was emanating from the aqueduct and this fox was presumed to be dead.

Spatial Overlap

In 1998 we delineated space use for 4 kit foxes and 4 red foxes. The home ranges of 3 kit foxes were not overlapped by any radio-collared red foxes. The home range of the remaining kit fox was overlapped by 4 juvenile red foxes. Average home range overlap was 31% (range 14%–48%) for the kit fox and 55% (range 40%–81%) for the red foxes. The core area for this kit fox was partially overlapped by the home range of 1 red fox, but core areas of the 2 species did not overlap. The adult male kit fox with a home range overlapped by 4 juvenile red foxes moved 10 km north in December 1998 to pair bond with an adult female kit fox (see Clark 2003). He remained in the area throughout 1999.

In 1999 space use was delineated for 10 red foxes and 4 kit foxes (2 adults and 2 juveniles). The kit foxes were members of the same family group. Home ranges of 9 of the red foxes did not overlap home ranges of any radio-collared kit foxes. The home range of the remaining red fox overlapped home ranges of the 4 kit

foxes. Average overlap was 24% (range 14%–36%) for the kit foxes and 11% (range 5%–14%) for the red fox. Core areas for all 4 kit foxes were overlapped by the home range of the red fox, but the core area of the red fox was overlapped by the home range of only 1 kit fox. Core areas of the 2 species did not overlap.

On 3 occasions kit foxes and red foxes were located in the same general vicinity, providing an opportunity to observe interactions. It is unknown whether foxes not radio-collared or other animals in the area (e.g., coyotes) influenced these movements. On 26 August 1998, an adult kit fox and 4 juvenile red foxes were located within 0.5 km of each other. During a 1-hour period the kit fox maneuvered south through the 4 red foxes and continued south away from them. One red fox also moved south, but for a shorter distance than that traveled by the kit fox.

On 18 November 1998 we recorded an encounter between 2 kit foxes and 1 red fox. An adult male and an adult female kit fox were located within 250 m of a juvenile red fox during a 20-minute period. The female kit fox moved toward the initial location of the red fox, while the red fox and the male kit fox moved away from each other.

On 30 September 1999 we observed a juvenile red fox as it moved in a direction away from an approaching adult kit fox. It then moved back toward the kit fox and finally away again. The shortest distance between the 2 foxes was approximately 300 m within a 1-minute window. On 22 November 1999 these 2 foxes again were located in close proximity, and both foxes moved away from each other. The shortest distance between the 2 foxes was approximately 100 m.

Habitat Use

Habitat use by kit foxes was disproportionate to availability in both 1998 ($\chi^2 = 20.0$, $df = 3$, $P < 0.01$) and 1999 ($\chi^2 = 86.4$, $df = 5$, $P < 0.01$). Likewise, habitat use by red foxes was disproportionate to availability in both 1998 ($\chi^2 = 240.6$, $df = 3$, $P < 0.01$) and 1999 ($\chi^2 = 88.4$, $df = 4$, $P < 0.01$). In 1998 use of orchards by kit foxes was higher than expected while use of row crops and other habitats was lower than expected (Fig. 2). For red foxes in 1998, use of the aqueduct ROW and orchards was higher than expected while use of row crops was lower than expected (Fig. 2). In

1999 use of the aqueduct ROW and orchards by kit foxes was higher than expected while use of row crops and other habitats was lower than expected (Fig. 3). For red foxes in 1999, use of the aqueduct ROW was higher than expected while use of row crops was lower than expected (Fig. 3). During the study red foxes sometimes used residential areas, grasslands, and vineyards, whereas kit foxes never were located in these habitats.

Diet

In 1999 we collected 207 kit fox scats, with most (204) being found at known dens during April (32.4%), June (64.3%), and July (1.9%). Rodents were the most frequently occurring item in kit fox scats (88.4%), followed by insects (18.4%), other arthropods (11.6%), leporids (8.7%), human-derived items (6.3%), and birds (1.9%). Species of rodents occurring in kit fox scats include house mice (*Mus musculus*, 34.3%), deer mice (*Peromyscus maniculatus*, 17.9%), pocket gophers (*Thomomys bottae*, 9.7%), California voles (*Microtus californicus*, 3.9%), harvest mice (*Reithrodontomys megalotis*, 3.4%), and San Joaquin pocket mice (*Perognathus inornatus*, 1.5%). In addition, 27.0% of the scats contained murid rodents that could not be identified to species, and 4.8% of the scats contained rodents that could not be identified to species. Insect species include field crickets (family Gryllidae, 9.7%), grasshoppers (family Acrididae, 4.4%), ants (family Formicidae, 4.4%), and beetles (order Coleoptera, 2.9%). Other arthropod remains were not identifiable. Bird remains in scats typically consisted of a few feathers and were not identified to species. Human-derived items included plastic (1.9%), string (1.9%), paper (1.5%), and rubber (1.0%).

In 1999 we gathered 140 scats from known red fox dens in February (10%), June (67%), and September (23%). Murids were the most frequently occurring item in red fox scats (91.4%), followed by insects (16.4%), leporids (11.4%), birds (7.1%), and human-derived items (4.9%). Species of rodents that occurred in red fox scats include California voles (31.4%), house mice (28.6%), deer mice (4.3%), pocket gophers (2.9%), and harvest mice (0.7%). In addition, 27.1% of the scats contained murid rodents that could not be identified to species, and 6.4% of the scats contained rodents that could not be identified to species. Insect species included ants (7.9%), field crickets (7.1%), and beetles

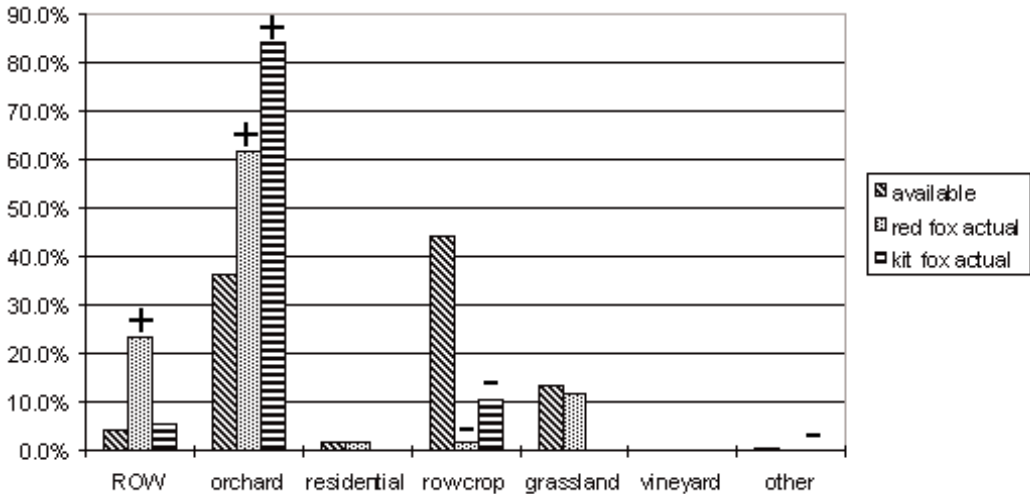


Fig. 2. Proportional availability and use of habitat types by kit foxes and red foxes at Lost Hills, California, in 1998. A plus (+) indicates habitats for which use was greater than expected, and a minus (-) indicates habitats for which use was less than expected.

(1.4%). Bird remains in scats typically consisted of a few feathers and were not identified to species. Human-derived items included paper (2.8%), plastic (0.7%), string (0.7%), and rubber (0.7%). Most of the scats contained some vegetation, such as grass and seeds of brome. Four scats (2.8%) contained almonds, and 1 scat contained a barley seed head.

Proportional item use by kit foxes differed significantly from that of red foxes ($\chi^2 = 78.0$, $df = 9$, $P < 0.01$; Fig. 4). Proportional use of voles ($\chi^2 = 47.7$, $df = 1$, $P < 0.01$) and birds ($\chi^2 = 4.6$, $df = 1$, $P = 0.03$) was greater among red foxes than kit foxes. Conversely, proportional use of deer mice ($\chi^2 = 12.9$, $df = 1$, $P < 0.01$), gophers ($\chi^2 = 5.0$, $df = 1$, $P = 0.03$), and other items ($\chi^2 = 3.9$, $df = 1$, $P = 0.05$) was greater among kit foxes than red foxes, and use of orthopterans ($\chi^2 = 3.3$, $df = 1$, $P = 0.07$) and arthropods ($\chi^2 = 2.9$, $df = 1$, $P = 0.09$) was marginally greater. Proportional use of house mice ($\chi^2 = 1.0$, $df = 1$, $P = 0.31$), unknown murids ($\chi^2 = 2.0$, $df = 1$, $P = 0.92$), and leporids ($\chi^2 = 0.4$, $df = 1$, $P = 0.51$) did not differ significantly between kit foxes and red foxes. Diets are identical if their R_0 value = 1.0; a value of zero means the diets have no dietary items in common. The calculated R_0 value between kit fox and red fox diets was 0.87, indicating the diet overlap between the

fox species was high. The Shannon diversity indices for kit fox and red fox diets were 0.91 and 0.90, respectively.

DISCUSSION

Interference Competition

Interference competition can consist of direct mortality, spatial exclusion, or avoidance behavior. During this investigation, 1 kit fox was killed by a red fox, as has been observed elsewhere (Ralls and White 1995). Red foxes are larger than kit foxes (3–7 kg vs. 2–3 kg), and therefore kit foxes are at greater risk of injury or death in agonistic interactions. Red foxes also have been reported to kill other fox species such as arctic foxes (Frafjord et al. 1989, Bailey 1992) and swift foxes (A. Moehrenschrager personal communication).

Space use patterns of kit foxes and red foxes on the study site provided some evidence of spatial partitioning. Kit fox and red fox family groups occupied separate areas, although some interspecific home range overlap was observed. Core areas were only rarely overlapped. We could not determine whether the observed partitioning was a result of antagonism or exploitative competition.

Movement patterns of kit foxes and red foxes monitored simultaneously suggested possible avoidance behavior, although there was no way

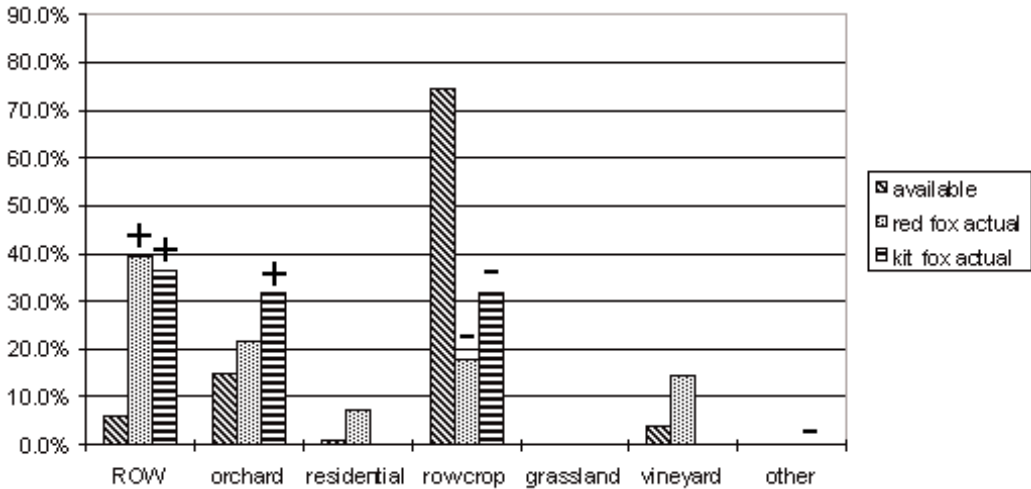


Fig. 3. Proportional availability and use of habitat types by kit foxes and red foxes at Lost Hills, California, in 1999. A plus (+) indicates habitats for which use was greater than expected, and a minus (-) indicates habitats for which use was less than expected.

to verify causation. Kit foxes were observed to move away from red foxes on 2 occasions. Both instances involved adult kit foxes avoiding red foxes. Red foxes also were observed to move away from kit foxes on 2 occasions. However, both instances involved juvenile red foxes. Although larger than adult kit foxes, juvenile red foxes may be more cautious than adult red foxes in interspecific encounters.

Habitat use by kit foxes and red foxes generally was similar. Both species selectively used some habitats (e.g., aqueduct ROW, orchards) and avoided others (e.g., annual row crops). These similar habitat use patterns likely increase the potential for interspecific encounters.

Exploitative Competition

Exploitative competition occurs between 2 sympatric species when both use the same resources. Such overlapping use patterns can result in resource availability being limited for 1 or both species. For kit foxes and red foxes, food and dens could be limiting factors. Overlapping habitat use patterns observed on our study site increased the potential for exploitative competition. However, competitive pressure probably was reduced because the 2 species frequently used different parcels of land. Red foxes also used some habitats that kit foxes did not use, which also may have reduced competition.

The aqueduct ROW may have been selectively used by both fox species due to a relatively high abundance of food. Small mammal diversity and abundance were higher along the aqueduct ROW relative to row crops and orchards (Clark 2001). Also, jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) were observed more frequently in the aqueduct ROW compared with other habitats (H. Clark personal observation). Conversely, food items did not appear to be abundant in orchards (Clark 2001). Thus, the reason for the disproportionately high use of orchards by both fox species is unclear.

Both fox species may have avoided row crops due to relatively low food availability and frequent disturbance. Abundance of small mammals and other foods (e.g., leporids) was relatively low in row crops (Clark 2001). Also, row crops were subjected to weekly inundation during irrigation. This impedes foraging and precludes the establishment of earthen dens. Other frequent disturbances in row crops included cultivation, fertilization, and pesticide application.

Both fox species consumed a diversity of food items. During prey surveys conducted in 1998 and 1999, murid rodents were the most frequently captured small mammals on the study site (Clark 2001), and these rodents were important food items in the diets of both

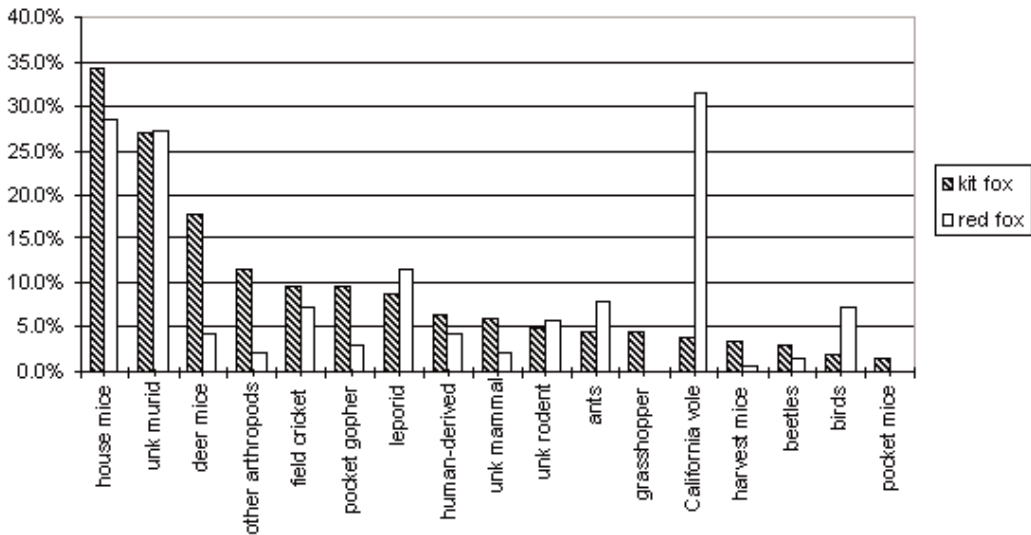


Fig. 4. Food item use by kit foxes and red foxes at Lost Hills, California, 1999. Bars are the proportion of scats with each food item.

fox species. Kit foxes also commonly consumed other rodents including deer mice and gophers. Both fox species commonly consumed invertebrates, although use by kit foxes generally was higher than that of red foxes. This may be an artifact of gathering scat samples at pupping dens, where most of the scats probably were from pups. Pups are not very experienced at capturing prey and consume a high proportion of invertebrates, which are more easily captured than vertebrate prey (Cutter 1958). Red foxes exhibited high use of California voles, which are a commonly used food item in many other parts of their range (Samuel and Nelson 1982). Voles were not captured during small mammal surveys (Clark 2001), and the habitat(s) in which red foxes were finding voles is not known.

The high overlap in kit fox and red fox diets indicates potential competition for food resources. However, frequencies of occurrence of food items differed between species, indicating that both species used similar items but did not consume them in the same proportions. These differences in diet would contribute to resource partitioning, which would help ameliorate competition.

Competition for dens was difficult to assess. Kit foxes are obligatory den users and are found in a den almost every day (Grinnell et al. 1937, Morrell 1972). Dens are used for bear-

ing and rearing young, diurnal resting cover, escaping predators, and avoiding temperature extremes. Thus, dens are a critical aspect of kit fox ecology. Conversely, red foxes primarily use dens just during pup rearing. White et al. (2000) reported that red foxes usurped several dens that were used by kit foxes during previous years at a study site. Red foxes have been observed using kit fox dens in the city of Bakersfield (B. Cypher unpublished data). Dens being used by red foxes are unavailable to kit foxes. Similarly, red foxes are expanding into arctic fox range in Norway and usurping arctic fox dens (Frafjord 2003).

Role of Coyotes in Kit Fox–Red Fox Interactions

Coyotes engage in both interference and exploitative competition with kit foxes. In many locations coyotes are the primary cause of kit fox mortality (Ralls and White 1995, Spiegel 1996, Cypher et al. 2000), as was the case on our study site. Coyotes also use some of the same foods as kit foxes (Cypher and Spencer 1998). However, kit foxes have coevolved with coyotes and have adaptive strategies for coexisting with coyotes including year-round den use, efficient exploitation of certain food resources not extensively used by coyotes (e.g., heteromyid rodents; White et al. 1995, Cypher and Spencer 1998), and possibly some level of

habitat partitioning (White et al. 1995, Warrick and Cypher 1998). In general, coyotes do not competitively exclude kit foxes, and both species co-occur in most areas.

Coyotes also engage in both interference and exploitative competition with red foxes. Coyotes are a significant source of mortality for red foxes (Sargeant and Allen 1989). On our study site coyotes were the predominant cause of mortality for red foxes, killing over half the red foxes we monitored. The historic ranges of red foxes and coyotes may have been relatively disjunct (Kamler and Ballard 2002), and therefore red foxes may not have evolved strategies for coexisting with coyotes. Thus, coyotes may significantly influence red fox abundance and distribution (Dekker 1983, Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987).

Because of the negative effects of coyote-fox interactions to red foxes, kit foxes actually might benefit from the presence of coyotes (Cypher et al. 2001). Coyotes may limit red fox abundance and even prevent them from colonizing certain areas within the kit fox range. Red foxes are rarely observed in areas where coyotes are abundant (Ralls and White 1995, Spiegel 1996, Cypher et al. 2000). White et al. (2000) cautioned against the removal of coyotes in kit fox habitat where red foxes also are present. In essence, coyotes may constitute a biological control strategy for red foxes. Indeed, coyotes have been proposed as a control agent for red foxes in coastal areas of California where foxes are preying on endangered California Least Terns (*Sterna antillarum browni*) and California Light-footed Clapper Rails (*Rallus longirostris levipes*; Jurek 1992). Coyotes also have been recommended for controlling red foxes in the Prairie Pothole Region of North America to reduce red fox predation on duck nests (Sargeant and Arnold 1984).

CONCLUSIONS

Red foxes engage in interference competition with kit foxes through direct mortality and possibly through spatial exclusion. Predator escape mechanisms of kit foxes, such as den use, may not be as effective against red foxes, as the relatively similar size of the 2 species permits red foxes to enter kit fox dens. Kit fox mortality attributable to red foxes may be additive, as the presence of red foxes does

not reduce the abundance of coyotes, which are the primary source of kit fox mortality. Red foxes also may engage in exploitative competition with kit foxes through use of kit fox dens and overlapping habitat use and food habit patterns. Furthermore, the 2 species are congeneric, increasing the potential for disease transmission. Thus, nonnative red foxes in the San Joaquin Valley constitute a potentially significant threat to kit foxes (Cypher et al. 2001).

The threat of red foxes to kit foxes may be somewhat ameliorated by several factors. Red foxes are less adapted to arid lands than kit foxes and may have limited ability to colonize kit fox habitat in which free water is scarce or not present. Also, the presence of coyotes may limit red fox abundance in optimal kit fox habitat. Conservation of large blocks of quality arid habitat with healthy coyote populations, as called for in recovery strategies for San Joaquin kit foxes (U.S. Fish and Wildlife Service 1998), should help limit impacts of red foxes on kit foxes.

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