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Exploitative competition between desert kit foxes and coyotes in the Mojave Desert

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Abstract. Exploitative competition between two sympatric guild members can influence the composition and dynamics of an ecological community. We assessed potential exploitative competition between desert kit foxes (*Vulpes macrotis arsipus*) and coyotes (*Canis latrans*) by comparing food habits of the two species from 2009 to 2014 on a study site in the Mojave Desert in California. Desert kit foxes specialised on heteromyid rodents and invertebrates, while the most frequently occurring items consumed by coyotes were lagomorphs and rodents. Both species consumed a variety of food items throughout the study, but relative use of these items varied with year and season. Also, precipitation affected prey abundance, and this influenced prey consumption by the two species. The diets of desert kit foxes and coyotes overlapped extensively, which indicated possible exploitative competition. Desert kit foxes consistently had lower dietary diversity than coyotes, indicating that desert kit foxes are more specialist consumers while coyotes are more generalists. Dietary specialisation by kit foxes on smaller items may help reduce competition with coyotes and facilitate coexistence. Coyotes consumed anthropogenic material at much higher frequencies than desert kit foxes, and this subsidisation could increase competitive pressures on kit foxes if it results in greater coyote abundance. Desert kit foxes in California are not a protected species although formal protection has been proposed due to increasing human encroachment. Conservation strategies should include measures to maintain an abundance and diversity of natural food items and limit anthropogenic subsidisation of coyotes.

Additional keywords: drought, optimal foraging theory, prey availability, resource partitioning.

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Introduction

Competitive interactions between species influence the composition and dynamics of an ecological community. Competition can be detrimental to one or both of the species involved (Pianka 1978). Exploitative competition, which occurs when two species are using the same resources, is one of the two primary forms of competition that can occur between sympatric species, with the other being interference competition (Pianka 1978; Maurer 1984; White *et al.* 1995).

Coyotes (*Canis latrans*) are the main predator and competitor of the kit fox (*Vulpes macrotis*) and are sympatric throughout the range of the kit fox, including the Mojave Desert in California, USA (Cypher and Spencer 1998; Cypher 2003; Arjo *et al.* 2007). Both canids consume many of the same foods, resulting in the potential for exploitative competition. The competitive exclusion principal emphasises that no two competing species can reside in the same community if they both utilise the same niche (Lotka 1925; Volterra 1926; Gause 1934; Hardin 1960). Therefore, for coyotes and desert kit foxes (*V. m. arsipus*) to occur together there must be sufficient differentiation in their ecological niches to permit coexistence or resources must be sufficiently abundant to not be a limiting factor.

Resource partitioning can reduce the effects of competitive interactions between species (Cypher and Spencer 1998; Nelson *et al.* 2007; Kozlowski *et al.* 2008). Kit foxes may partition food with coyotes by using different items or by using the same items, but in different proportions (White *et al.* 1995; Cypher and Spencer 1998). In a study conducted at the Naval Petroleum Reserves in California, San Joaquin kit foxes (*V. m. mutica*) consumed many of the same prey items as coyotes, but did so in different proportions, reflecting differences in preferred prey (Cypher and Spencer 1998). Conversely, in the Great Basin Desert of western Utah, USA, resource partitioning between desert kit foxes and coyotes was not very pronounced (Kozlowski *et al.* 2008). Competitive pressures on the kit fox population in this area were very high but may have been mitigated somewhat by spatial partitioning (Kozlowski *et al.* 2008).

The intensity of exploitative competition can increase during times of decreased resource availability (White *et al.* 1995; Cypher and Spencer 1998). For example, exploitative competition may be exacerbated during drought years when prey abundances are lower and prey choices are limited (White *et al.* 1995; Cypher and Spencer 1998). Results from a multiyear study of coyotes and San Joaquin kit foxes on the Carrizo Plain

National Monument, California, indicated that dietary overlap increased as prey availability decreased during drought conditions (White *et al.* 1995). Competition between species may also be heightened further by habitat loss and human encroachment as animals are forced into smaller habitat patches.

For the San Joaquin kit fox, a USA federally listed endangered and state-listed threatened subspecies, habitat destruction is a major factor influencing population instability and decline (United States Fish and Wildlife Service 1983, 1998; Cypher *et al.* 2013). While the Mojave Desert kit fox population has not yet been impacted by such widespread land conversion as the San Joaquin kit fox, this may change in the coming decades as habitat is increasingly being lost or fragmented by on-going developments (e.g. urban, recreational, renewable energy facilities). In particular, large expanses of the Mojave Desert are at risk for habitat loss and fragmentation from numerous constructed and proposed utility-scale solar plants (Leitner 2009; Lovich and Ennen 2011). Anthropogenic changes could result in increased stress, disease, and predation risk for kit foxes as competition for food and space increases (Nelson *et al.* 2007; Kozlowski *et al.* 2008; Clifford *et al.* 2013).

Currently, desert kit foxes in California are considered a common subspecies and therefore lack the protections granted to the San Joaquin kit fox (United States Fish and Wildlife Service 1998). The desert kit fox is state-listed as endangered in Colorado, state-listed as threatened in Oregon, and listed as endangered in Mexico, whereas populations in California have no formal protections aside from being a protected furbearer species (United States Fish and Wildlife Service 1998; Moehrenschlager *et al.* 2004). In recent years, however, desert kit foxes in California have been increasingly treated as a Species of Special Concern, and in 2013 a petition was filed by the Center for Biological Diversity to protect the subspecies under the *California Endangered Species Act* (D. Kadaba, I. Anderson, C. Bradley, S. Wolf unpubl. report). The petition was ultimately rejected by the California Department of Fish and Wildlife due to lack of information on desert kit foxes in California (D. Kadaba, pers. comm.).

Competitive interactions between coyotes and kit foxes have been investigated, but not in the vast Mojave Desert in California. Interest in the conservation of the desert kit fox is increasing and additional information on factors affecting this subspecies, including potential exploitative competition with sympatric coyotes, could contribute to future conservation efforts. We assessed food item use by coyotes and desert kit foxes in the Mojave Desert in California. Our objectives were to compare diets between desert kit foxes and coyotes to determine the degree of dietary overlap and to assess prey use relative to prey abundance to determine the effects of food availability on competition intensity between desert kit foxes and coyotes.

Materials and methods

Study area

We collected data in a 1500-km^2 study site located in the Mojave Desert north of Barstow, California, USA (Cypher *et al.* 2018*a*). This area is bounded by the Fort Irwin National Training Center and the China Lake Naval Air Weapons Station to the north and Interstate 15 and State Route 58 to the south (Fig. 1). The study area was characterised as typical Mojave Desert scrub vegetation dominated by creosote bush (*Larrea tridentata*) and a ground cover of subshrubs, forbs, and grasses ranging from 1 to 29% (United States Bureau of Land Management 1980; Turner 1994; Esque *et al.* 2010). Elevation ranged from 500 to 900 m and the terrain consisted of flat, dry lake beds, alluvial fans, sand dunes, steep, rugged hills, and wide expanses of land dotted with natural soil crusts and sparse vegetation cover (United States Bureau of Land Management 1980). Consistent with an arid desert environment, the mean annual precipitation for Barstow is only 13.4 cm (United States Climate Data 2014). Much of the study area comprises public lands managed by the United States Bureau of Land Management with interspersed private property. Human densities and influences were greatest around Barstow (population 23 835) followed by the small towns of Hinkley, CA (population 1915), and Harvard, CA (unincorporated community with population fewer than 100); included in Newberry Springs, CA (unincorporated community with a population of 2895), and declined quickly with distance from these towns (Esque *et al.* 2010).

Study design

From autumn 2009 to summer 2014, we collected coyote and desert kit fox scats as part of an investigation of coyote predation on Agassizi's desert tortoises (*Gopherus agassizii*) (Cypher *et al.* 2018*a*). In arid environments, food availability and abundance are particularly influenced by precipitation (Noy-Meir 1973). In the western Mojave Desert, the wet season occurs from autumn through spring (United States Climate Data 2014). Thus, to better pair canid foraging patterns with annual prey availability, years were defined as October to September. We determined annual precipitation totals using data from United States Climate Data (2014). We defined the seasons as autumn (October–December), winter (January–March), spring (April–June), and summer (July–September). To locate scats, a crew of two people slowly (i.e. <15 km h^{-1}) drove along dirt roads within the research site for three consecutive days during each season. Each scat that we located was individually bagged in a small brown paper bag and labelled with the date and corresponding location (Lat/Long WGS 84). We also opportunistically collected scats during prey transect surveys and camera station surveys (Kelly 2017). Only fresh scats were collected; any scats that were dry and bleached white were not used in our study.

Back in the laboratory, we heated all scats in a drying oven for 24 h at 60°C to destroy any eggs and cysts of the zoonotic parasitic hydatid tapeworm (*Echinococcus multilocularis*) (Spiegel *et al.* 1996; Cypher *et al.* 2018*a*). After drying, we placed each scat inside a nylon pantyhose that was tied with an identification marker. We then put wrapped scats into a mesh laundry bag, washed them in a standard household washing machine, and dried them in a household dryer for 60–120 min. This process removed soluble material, leaving undigested food item remains.

To analyse each scat, we spread the remaining undigested material from each scat on a paper towel and carefully sorted through to find different food items. If there were mammalian teeth in the scat, we identified the prey item down to species using published guides and reference specimens (Glass 1981;

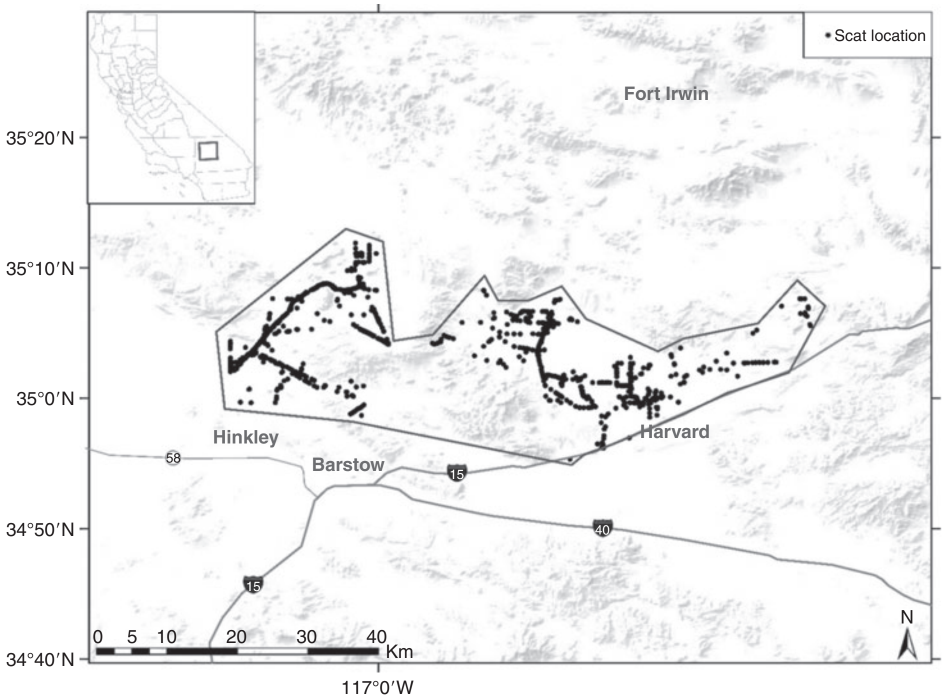

Fig. 1. Study area located in the Mojave Desert in California, United States (inset), which is bound by the Fort Irwin National Training Center to the north and Interstate 15 and State Route 58 to the south. The blue boundary is the specific study area and the black dots denote every location a scat or multiple scats were collected during the five-year project.

Roest 1986). We identified other undigested mammalian remains by examining macroscopic hair characteristics (e.g. length, texture, colour, banding patterns), nail characteristics, and bone fragments, and we compared these items to published guides and reference specimens (Adorjan and Kolenosky 1969; Moore *et al.* 1974; Glass 1981; Roest 1986). For other items, such as a reptile scales and insect exoskeletons, we identified the remains to the lowest taxonomic level possible. We identified fleshy fruits at least to genus based on seed characteristics (Young and Young 1992). We also classified anthropogenic items based on the presence of domestic animal remains or indigestible items (e.g. plastic, paper, foil).

As part of the investigation of predation on Agassizi's desert tortoises, we collected prey availability data (Cypher *et al.* 2018*a*). We used these data to assess the annual abundance of the following prey items: leporids (primarily black-tailed jackrabbits (*Lepus californicus*), and desert cottontails (*Sylvilagus audubonii*)), kangaroo rats (*Dipodomys* spp.), pocket mice (*Perognathus* spp. and *Chaetodipus* spp.), and squirrels (*Xerospermophilus* spp.) and the white-tailed antelope squirrel (*Ammospermophilus leucurus*). To assess prey abundance, we conducted annual surveys along 60 1-km transects on United States Bureau of Land Management and California Department of Fish and Wildlife public lands throughout the study area. The transects began ~25 m from a dirt road and were oriented perpendicular to the road. To increase sampling efficiency, transects were established in pairs with transects oriented parallel to each other and separated by 250 m. Pairs of transects were spaced at least 2 km apart and located in areas with typical habitat conditions for the region. We clearly marked the beginning and end of each transect with a wooden stake and we recorded a global positioning system (GPS) point.

We conducted prey abundance assessments once each spring. We performed the assessments by having two observers slowly walk along each transect. The first observer used a GPS unit to navigate to the end of the transect and also counted all active rodent burrows within 1 m of either side of the transect. We characterised burrows as either large (burrow opening ≥3 cm) or small (burrow opening <3 cm). Large burrows were assumed to be those used by kangaroo rats or ground squirrels while small burrows were assumed to be those used by mice, particularly pocket mice. Inactive burrows, characterised by openings obstructed by vegetation or spider webs, were not counted. The second observer followed behind the first and counted all fresh lagomorph pellets within 1 m of either side of the transect and recorded all data. Fresh pellets were characterised as having a golden to dark brown colour and a smooth surface whereas old pellets were characterised by a grey colour and a rough, weathered appearance.

Analyses

Food items were identified in desert kit fox and coyote scats and the frequency of occurrence (FOO) of each item (number of scats with a particular item divided by the total number of scats) was determined for all years combined (Kelly 2017; Cypher *et al.* 2018*a*). For statistical analyses, we grouped items into the following seven broad categories: lagomorph, rodent, bird, reptile, invertebrate, fruit, and anthropogenic items. We calculated Shannon diversity indices (H') for both desert kit foxes and coyotes for each year, each season by year, and the total project length by using the equation:

$$H' = \left(N \log N - \sum n_i \log n_i\right)/N$$

where N is the total number of occurrences of all items and n_i is the number of occurrences of item i (Brower and Zar 1984). We used a two-sample *t*-test, after determining parametric assumptions were met, to compare both mean annual and seasonal H' between species. We also determined Horn's index of similarity between both species for each year, for each season, and for all years combined by using the equation:

$$R_o = (H_{\max} - H_{\mathrm{obs}})/(H_{\max} - H_{\min})$$

where H is the Shannon diversity measure (Horn 1966). To compare mean Horn's index of similarity values between seasons, we used a one-way analysis of variance (ANOVA) with multiple range tests if a significant difference was found.

We performed Spearman-rank correlation analysis to compare rankings of items between species for each season, year, and all years combined. To examine the effect of annual precipitation, we conducted Spearman-rank correlation analysis on precipitation versus annual Spearman-rank correlation coefficients and precipitation versus annual Horn index of similarity values. We also compared annual Horn indices to annual counts of rabbit pellets, large holes, and small holes using Spearman-rank correlation analyses.

To adjust for an increased probability of a Type I error when conducting multiple tests on the same data, we used Hochberg's variation on Holm's method to correct for *P*-values when necessary (Legendre and Legendre 1998). Also, for all statistical analyses, we considered *P*-values to be significant at $\alpha = 0.1$. We chose a more relaxed α value to reduce the risk of committing a Type II error, which is considered more detrimental than a Type I error when making natural resource management and conservation decisions (Taylor and Gerrodette 1993; Di Stefano 2003; Scherer and Tracey 2011). By relaxing the α value, we aimed to reveal potential ecological relationships that can be more fully explored through further investigation. We used Minitab statistical software (Minitab 18 statistical software, Minitab Inc., State College, Pennsylvania) to perform all necessary statistical tests.

Results

During the five-year study, we collected and analysed 1230 desert kit fox scats (range = 76–410 per year and 187–636 per season). Also, 3246 coyote scats (range = 474–801 per year and 738–845 per season) were collected concurrently and analysed (Cypher *et al.* 2018*a*). Overall, we identified 45 different items in the desert kit fox scats and 50 distinct items were identified in the coyote scats (Kelly 2017; Cypher *et al.* 2018*a*). We found many of the same items in the scats of both species, although the proportions differed (Fig. 2).

Desert kit foxes and coyotes both regularly ate rodents. The three kangaroo rat species that potentially occurred in the study area included desert kangaroo rats (*Dipodomys deserti*), Merriam's kangaroo rats (*Dipodomys merriami*), and chisel-toothed kangaroo rats (*Dipodomys microps*). Potential pocket mice species included desert pocket mice (*Chaetodipus penicillatus*), long-tailed pocket mice (*Chaetodipus formosus*), and little pocket mice (*Perognathus longimembris*). Desert kit foxes and coyotes both consumed lagomorphs as well, of which two species occurred in the Mojave Desert: black-tailed jackrabbit and desert cottontail. We found squirrel remains in scats, which we could not identify to species. Species that were potentially prey included round-tailed ground squirrel (*Xerospermophilus tereticaudus*), Mohave ground squirrel (*Xerospermophilus mohavensis*), and white-tailed antelope squirrel.

Invertebrate prey mostly consisted of Orthopteran and Coleopteran species, solpugids, scorpions, larvae, and sand treader crickets (Family Stenopelmatidae). In general, bird, lizard, and snake remains within the scats were not identifiable to species. Anthropogenic items consumed included nuts of pistachios (*Pistacia vera*) and other agricultural crops, man-made materials (e.g. cloth, plastic, food wrappers), domestic pets (i.e. cats and dogs), and livestock and their waste. We suspect that several items that we found within the scats were ingested incidentally, including twigs, pieces of grass, small amounts of plant material, and dirt. These items were most likely ingested while a kit fox or coyote was capturing or consuming an intended food item.

Rankings of food categories in desert kit fox and coyote diets were not correlated in any year, season, or the total diet (Table 1). This indicated that items were consumed in different proportions by the two species in all years, all seasons, and for all years combined (Tables 2 and 3). For desert kit foxes, rodents were the most frequently occurring items in Years 1–3, while invertebrates were the most frequently occurring items in Years 4 and 5 (Table 2). For coyotes, rodents were the most frequently occurring item for Years 1 and 2. In all other years, lagomorphs occurred most frequently. Invertebrates were a primary food item for coyotes as well (FOO >10%), but FOO never exceeded 26% while FOO of this same item category in desert kit foxes never fell below 46%. When all years were combined, rodents and invertebrates had the highest FOO in desert kit fox diets while rodents and lagomorphs had the highest FOO in coyote diets. Also, desert kit foxes only consumed fruits in Year 4 while coyotes consumed fruits every year. Overall, coyotes ate more anthropogenic material than desert kit foxes; frequently they had a FOO of anthropogenic material that was two times higher than that of desert kit foxes. Interestingly, both species exhibited the highest FOO of anthropogenic material in Year 5.

In desert kit fox diets, the occurrence of birds increased yearly while the FOO of birds in coyote diets fluctuated among years, with Year 2 having the lowest FOO and Year 5 having the highest. The FOO of reptiles in desert kit fox scats was lowest in Years 2 and 3 and highest in Year 5. The occurrence of reptiles in coyote scats did not follow an apparent pattern, but coyotes consumed the least number of reptiles in Year 4 and had the highest consumption in Year 2.

Seasonal FOO of grouped food items for desert kit foxes and coyotes also exhibited similarities and differences (Table 3). For both desert kit foxes and coyotes, rodents were the most frequently occurring of all the items consumed in autumn. In the remaining seasons, invertebrates had the highest FOO in desert kit fox scats while lagomorphs were the most frequently occurring item in coyote scats. In desert kit fox scats, the FOO of

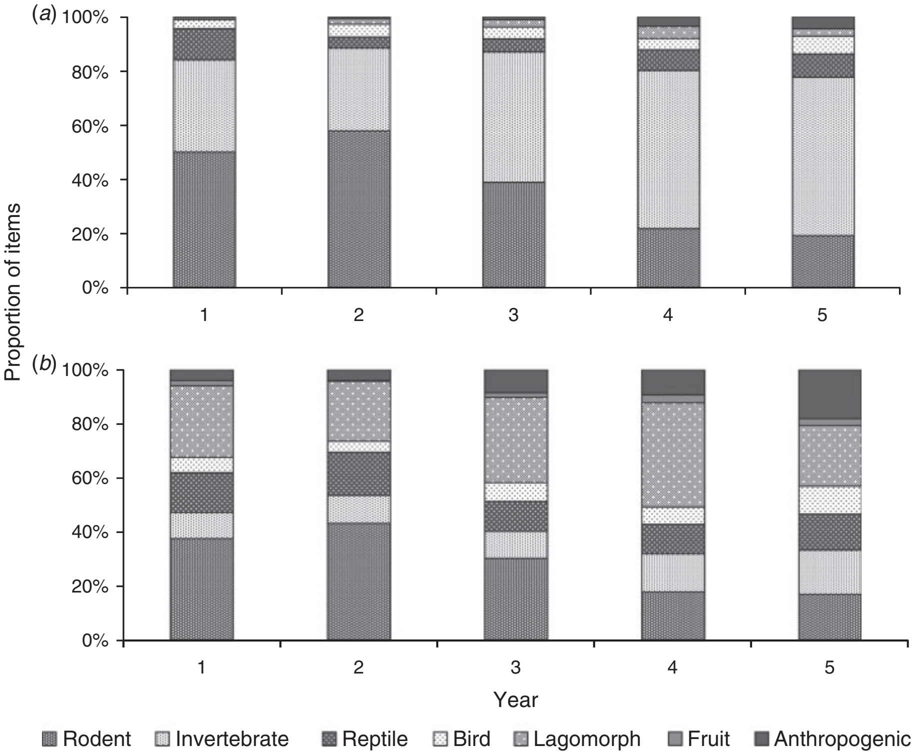

Fig. 2. Yearly proportions of grouped items for both (*a*) desert kit foxes (*Vulpes macrotis arsipus*) and (*b*) coyotes (*Canis latrans*) from the Mojave Desert, California, USA, during October 2009 to September 2014.

Table 1. Spearman rank correlations analysis to compare rankings of items between coyotes (*Canis latrans*) and desert kit foxes (*Vulpes macrotis arsipus*) for each year, season, and total

Scats from both species were collected from the Mojave Desert, California, USA, from October 2009 to September 2014. Years span October–September and seasons were defined as: Autumn, October–December; Winter, January–March; Spring, April–June; Summer, July–September

Period	r_s	t	P
Year 1	0.75	2.54	0.261
Year 2	0.68	2.07	0.281
Year 3	0.54	1.43	0.430
Year 4	0.71	2.25	0.281
Year 5	0.07	0.16	0.879
Autumn	0.68	2.07	0.375
Winter	0.21	0.48	0.645
Spring	0.54	1.43	0.588
Summer	0.46	1.16	0.588
All years/seasons	0.46	1.16	0.294

anthropogenic items, fruit, and lagomorphs was highest in winter, FOO of birds was highest in spring, and FOO of reptiles was highest in summer. The FOO of anthropogenic items in coyote scats was also the highest in winter, but the FOO of birds was highest in spring, and the FOO of fruits, invertebrates, and reptiles was highest in summer. In desert kit fox scats, the FOO of birds and invertebrates were lowest in autumn, the FOO of reptiles was lowest in winter, the FOO of lagomorphs was lowest in spring, and the FOO of rodents and anthropogenic material were lowest in summer. For coyotes, the FOO of lagomorphs and anthropogenic items in their scats were lowest in autumn while the FOO of all other grouped items were lowest in winter.

The annual H' of both species varied slightly between years (Table 4). The H' for both desert kit foxes and coyotes was lowest in Year 2 ($H' = 0.48$ and 0.65, respectively) and highest in Year 5 ($H' = 0.66$ and 0.80, respectively). Overall, coyotes exhibited a higher H' than desert kit foxes ($H' = 0.75$ and 0.62, respectively). The mean annual H' for desert kit foxes was significantly lower than that for coyotes ($t_8 = -3.50$, $P = 0.008$).

Mean H' for desert kit foxes was highest in spring and lowest in autumn (Table 5). Mean H' for coyotes was highest in summer and lowest in winter. Mean H' for desert kit foxes was significantly lower than that for coyotes in autumn, spring and summer, but similar between species in winter (Table 5).

Horn's similarity indices were high in all years and seasons (Tables 4 and 5), indicating high overlap between desert kit fox and coyote diets. The diets were most similar in Years 2 and 5 (Table 4). Seasonally, mean Horn's similarity indices were not significantly different ($F_{3,16} = 0.32$, $P = 0.808$) (Table 5).

Annual precipitation was relatively high during the first two years of the study and markedly lower afterward (Table 4) such that precipitation in the last three years constituted drought conditions. Consequently, the mean number of large rodent burrows, small rodent burrows, and lagomorph pellets declined markedly during the study (Table 4). The overall trend across

Table 2. Annual frequency of occurrence (FOO) for item categories in desert kit fox (*Vulpes macrotis arsipus*) (Kelly 2017) and coyote (*Canis latrans*) (Cypher *et al.* 2018*a*) scats collected in the Mojave Desert, California, USA, from October 2009 to September 2014

Years span October–September

Item category	Desert kit fox FOO (%)						Coyote FOO (%)					
	Year 1	Year 2	Year 3	Year 4	Year 5	Total	Year 1	Year 2	Year 3	Year 4	Year 5	Total
Scat total (*n*)	127	76	229	388	410	1230	625	474	631	801	715	3246
Lagomorph	1.6	4.0	7.0	13.4	9.3	9.0	48.3	42.0	58.2	67.5	41.4	52.5
Rodent	92.9	96.1	90.0	62.4	59.3	71.7	53.1	65.4	46.3	24.3	26.4	40.6
Bird	7.1	9.2	10.9	12.1	22.0	14.5	10.4	6.5	12.8	10.9	19.0	12.3
Reptile	23.6	7.9	12.2	20.6	25.9	20.3	20.3	26.2	19.3	17.9	21.8	20.7
Invertebrate	53.5	46.1	69.0	77.6	83.7	73.6	14.4	15.6	16.6	20.4	25.7	19.0
Fruit	0.0	0.0	0.0	0.3	0.0	0.1	3.5	0.4	2.9	4.5	4.5	3.4
Anthropogenic	0.8	1.3	2.2	9.8	12.9	8.0	7.2	4.9	14.9	14.7	28.7	14.9

Table 3. Seasonal frequency of occurrence (FOO) for item categories in desert kit fox (*Vulpes macrotis arsipus*) (Kelly 2017) and coyote (*Canis latrans*) (Cypher *et al.* 2018*a*) scats collected in the Mojave Desert, California, USA, from October 2009 to September 2014

Seasons were defined as: Autumn, October–December; Winter, January–March; Spring, April–June; Summer, July–September

	Desert kit fox FOO (%)				Coyote FOO (%)			
Item category	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Scat total (*n*)	209	636	198	187	845	834	738	829
Lagomorph	7.2	10.7	5.6	9.1	46.8	54.2	52.2	57.1
Rodent	74.6	71.4	71.7	69.5	51.1	34.4	38.8	37.8
Bird	9.6	14.5	19.2	15.0	11.7	10.1	14.5	13.3
Reptile	18.2	12.6	31.3	37.4	19.5	15.0	24.1	24.6
Invertebrate	65.6	72.2	76.3	84.5	16.6	15.6	20.3	23.6
Fruit	0.0	0.2	0.0	0.0	3.8	2.8	3.4	3.6
Anthropogenic	3.8	13.4	1.5	1.1	12.2	17.0	14.2	16.3

Table 4. Annual Shannon diversity indices for coyotes (*Canis latrans*) and desert kit foxes (*Vulpes macrotis arsipus*) and Horn's index of similarity along with prey availability indices and annual precipitation in the Mojave Desert, California, USA, from October 2009 to September 2014

Years span October–September

	Year 1	Year 2	Year 3	Year 4	Year 5	Total
Diversity						
Kit foxes	0.50	0.48	0.54	0.64	0.66	0.62
Coyotes	0.70	0.65	0.72	0.72	0.80	0.75
Similarity	0.83	0.88	0.80	0.82	0.86	0.85
Annual Precipitation (cm)	16.9	28.2	7.3	7.5	8.0	
Average large burrows	50	42	36	7	9	
Average small burrows	24	19	20	15	15	
Average lagomorph pellets	77	130	1227	343	31	

years was that annual H' for both species increased as precipitation decreased (Fig. 3). Precipitation was not related to either annual Horn's similarity indices ($r = 0.90$, $t_3 = 3.58$, $P = 0.187$) or annual correlation coefficients between desert kit fox and coyote diets ($r = 0.30$, $t_3 = 0.54$, $P = 0.873$). Furthermore, annual Horn's similarity indices were not correlated with annual abundance of rabbit pellets ($r = -0.70$, $t_3 = -1.70$, $P = 0.752$), large rodent burrows ($r = 0.30$, $t_3 = 0.54$, $P = 0.873$), or small rodent burrows ($r = -0.10$, $t_3 = -0.17$, $P = 0.873$).

Discussion

Desert kit foxes and coyotes in the Mojave Desert in California consumed many of the same food items, but generally in different proportions, with both species exhibiting preferences (Fig. 2). Kit foxes primarily consumed rodents and invertebrates while coyotes primarily consumed lagomorphs and rodents. These results are similar to those from previous studies on kit foxes and coyotes in California (Ferrel *et al.* 1953; White *et al.*

Table 5. Shannon diversity indices for coyotes (*Canis latrans*) and desert kit foxes (*Vulpes macrotis arsipus*) and Horn's index of similarity calculated for each season across all years in the Mojave Desert, California, USA, from October 2009 to September 2014

Seasons were defined as: Autumn, October–December; Winter, January–March; Spring, April–June; Summer, July–September. Means with similar letters were not significantly different

	Autumn	Winter	Spring	Summer
Diversity				
Kit fox	0.49 ± 0.07	0.56 ± 0.04	0.57 ± 0.02	0.53 ± 0.03
Coyote	0.70 ± 0.02	0.65 ± 0.04	0.72 ± 0.03	0.73 ± 0.02
t	−2.58	−1.77	−3.50	−4.92
P	−0.033	0.115	0.008	0.001
Similarity	0.81 ± 0.02A	0.80 ± 0.03A	0.82 ± 0.02A	0.83 ± 0.02A

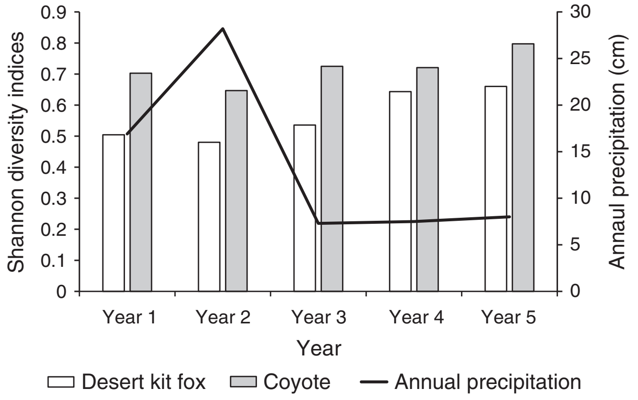

Fig. 3. Annual Shannon diversity indices for both desert kit foxes (*Vulpes macrotis arsipus*) and coyotes (*Canis latrans*) with annual precipitation totals from the Mojave Desert, California, USA, during October 2009 to September 2014.

1995; Cypher and Spencer 1998). The rodents consumed by kit foxes were primarily heteromyids (e.g. kangaroo rats, pocket mice: Kelly *et al.* 2019), as has been found in other locations (Morrell 1972; Fisher 1981; White *et al.* 1995; Koopman *et al.* 2001). Kit foxes are considered specialists on this group of rodents (Grinnell *et al.* 1937; Laughrin 1970) and kit fox populations in California typically are most dense and demographically robust where these rodents are abundant (Cypher *et al.* 2013).

The FOO of lagomorphs in coyote scats was, on average, more than five times higher than that in desert kit fox scats. Even when our prey transect surveys indicated that lagomorph numbers were low, the FOO of lagomorphs in coyote scats was always >40%. This implies that even when lagomorph densities declined, coyotes still preferentially consumed this prey type (Cypher *et al.* 2018*a*). A marked preference for lagomorphs by coyotes is similar to results from other coyote dietary studies performed in Utah (Kozlowski *et al.* 2008), south-eastern Idaho (MacCracken and Hansen 1987), southern Illinois (Cypher 1993), north-eastern North Carolina (McVey *et al.* 2013), and other locales in California (Ferrel *et al.* 1953; Cypher *et al.* 1994; Cypher and Spencer 1998). In some previous studies, lagomorphs were prevalent in the diet of kit foxes (Egoscue 1962; Morrell 1972; Cypher *et al.* 2000), but that was not the case in our study where the annual FOO of lagomorphs in kit fox scats usually was <10%. The consumption of invertebrates as a primary food source by kit foxes also has been well documented for San Joaquin kit foxes (Spiegel *et al.* 1996; Cypher *et al.* 2014), desert kit foxes in Utah (Arjo *et al.* 2007; Kozlowski *et al.* 2008), and many other arid-land fox species (Sheldon 1992).

Lagomorphs, birds, reptiles, and fruits appeared to be consumed more opportunistically by kit foxes, while birds, reptiles, invertebrates, and fruits appeared to be consumed more opportunistically by coyotes. Both species consumed some anthropogenic items, with use by coyotes being greater than that of kit foxes. However, use generally was low and the FOO of anthropogenic items in scats did not suggest that either species was dependent upon these resources. Some seasonal variation was evident in use of items by the two species, but this variation was not extensive. Of primary note, the use of reptiles and invertebrates was higher in spring and summer when these items are more active due to warmer temperatures, and use of anthropogenic foods was higher in winter when natural prey are less active.

Dietary diversity was markedly higher for coyotes in all years and seasons. Coyotes are larger and able to more effectively exploit larger prey such as jackrabbits, larger snakes, and desert tortoises (Cypher *et al.* 2018*a*). The coyote is also more of an opportunistic foraging generalist (Bekoff and Gese 2003) while the kit fox exhibits facultative specialisation on heteromyid rodents. Dietary diversity for both species increased in the latter years of the study due to drought-induced declines in lagomorphs and rodents, the primary prey for coyotes and kit foxes, respectively. As the availability of these items decreased, concomitant increases were observed in the proportions of birds, reptiles, and invertebrates in kit fox diets, and the proportions of birds and invertebrates in coyote diets. Use of anthropogenic foods by both species also increased markedly as natural foods became less available.

Our findings were consistent with optimal foraging theory predictions (Pyke *et al.* 1977; Pianka 1978; Stephens and Krebs 1986). Both coyotes and kit foxes appeared to optimise energy acquisition through their selection of food items and foraging strategies. Coyotes selected larger items, particularly lagomorphs, while kit foxes selected smaller items, particularly rodents and invertebrates. Similar prey selection patterns have been observed among sympatric coyotes and kit foxes in other studies (White *et al.* 1995). In our study, coyotes and kit foxes both exhibited greater dietary specialisation when these resources were abundant, and then expanded dietary breadth when these resources became less abundant. Similar shifts in dietary patterns in response to declining resource abundance have been documented among other canids, including coyotes elsewhere (MacCracken and Hansen 1987; Cypher *et al.* 1994), dingoes (*Canis lupus dingo*) (Corbett 1995; Paltridge 2002), and red foxes (*Vulpes vulpes*) (Errington 1937; Spencer *et al.* 2017).

Based on our results, the potential for exploitative competition between coyotes and kit foxes on our study site was substantial. Dietary overlap between the two species was extensive. Most of the food items identified during the study were found in the scats of both species. Also, dietary similarity indices were relatively high (≥0.8) in all years and seasons;

however, competition can only be inferred from the above because we did not manipulate food abundance or populations of the study species (Schoener 1974).

The competitive exclusion principal predicts that two species cannot coexist sympatrically if they occupy the same niche (Lotka 1925; Volterra 1926; Gause 1934; Hardin 1960). For such coexistence to occur, competition must be ameliorated in some manner. Coyotes and kit foxes were not spatially partitioning the study site, as has been found in some other locations (Zoellick *et al.* 1989; Nelson *et al.* 2007; Kozlowski *et al.* 2008). Based on camera station data from the last three years of the study, both species were detected at 60% of the stations and just 10% of the stations detected only coyotes (Kelly 2017). Thus, kit foxes did not appear to be avoiding areas used by coyotes on our study site. Clearly, other mechanisms were facilitating sympatric coexistence of these two species. One such mechanism is year-round den use by kit foxes and the occurrence of multiple dens (providing escape cover) throughout the home range of each fox (White *et al.* 1994; Cypher and Spencer 1998; Koopman *et al.* 1998).

Our data indicated that another likely mechanism was resource partitioning in regards to diet. Specifically, we documented disproportionate use of food items by the two species and facultative dietary specialisation when resources were abundant. This outcome is predicted by intraguild competition theory (Holt and Polis 1997; Donadio and Buskirk 2006) and has been reported previously between sympatric canids such as coyotes and kit foxes (White *et al.* 1995; Cypher and Spencer 1998), coyotes and grey foxes (Smith and Danner 1990; Neale and Sacks 2001), coyotes and red foxes (Major and Sherburne 1987; Theberge and Wedeles 1989), dingoes and red foxes (Paltridge 2002; Cupples *et al.* 2011), and grey foxes and red foxes (Hockman and Chapman 1983).

We also found that competitive interactions between coyotes and kit foxes may be temporally dynamic. Regardless of degree of overlap in resource use, competition occurs only when the availability of one or more important resources becomes limiting (Lotka 1925; Volterra 1926; Gause 1934). The abundance of primary food items declined in the latter three years of the study in response to drought conditions, and the reduced availability of these items may have become a limiting factor based on observed changes in food item use by both coyotes and kit foxes. In addition to a broadening of dietary breadth by both species, use of anthropogenic foods by both species increased, as did use of lagomorphs by kit foxes. Thus, exploitative competition may have intensified. Also, increased use of the same food items by coyotes and kit foxes potentially could have enhanced interference competition. Encounters may become more frequent as dietary overlap increases between two species and they forage for similar food items (Donadio and Buskirk 2006). This would be detrimental to kit foxes as coyotes are larger and are the primary cause of kit fox mortality in most locations (Cypher 2003; Moehrenschlager *et al.* 2004). In a recent study conducted on two adjacent study areas in California, kit fox survival was lower in the area where dietary overlap with coyotes was higher (Cypher *et al.* 2018*b*).

The presence of anthropogenic foods on the study site potentially could alter competitive interactions between coyotes and kit foxes. Human habitations, the sources of anthropogenic foods, were infrequent and widely dispersed. Thus, there were limited locations where such foods were available thereby increasing the potential for encounters between coyotes and kit foxes. Also, although use of anthropogenic foods did not appear to be extensive in most years, such foods were present in almost 30% of coyote scats in the last year of the study. Such a high FOO could indicate that coyotes were being subsidised to some degree. Subsidisation potentially could maintain or increase coyote abundance, and this could enhance predation pressure on co-occurring species (Esque *et al.* 2010; Cypher *et al.* 2018*a*), including kit foxes. Sustained coyote abundance during periods of low abundance of natural foods also could enhance the depletion of remaining food supplies (Rodewald *et al.* 2011; Newsome and van Eeden 2017). Thus, subsidisation could increase both interference and exploitative competition between coyotes and kit foxes, likely to the detriment of foxes.

Consistent with findings from other locations, competitive interactions likely occur between coyotes and kit foxes in the Mojave Desert; however, these interactions currently do not appear to be limiting kit foxes, at least on our study site. In camera station surveys conducted during the last three years of our study (Kelly 2017), kit foxes were detected at 78 of 87 (90%) stations (coyotes were detected at 70% of the stations). Kit foxes appear to be mitigating exploitative competitive pressure from coyotes through facultative specialisation on smaller items (e.g. rodents, invertebrates) on which foraging efficiency of coyotes may be lower. Dietary overlap, potentially along with competition intensity, increases when rodent abundance is low, such as during droughts. Understanding these ecological relationships will facilitate the development of management and conservation strategies as change affects this ecosystem.

Two factors that could alter future competitive interactions between coyotes and kit foxes are climate change and the increasing human presence in the Mojave Desert. Projected increased variation in precipitation (Bachelet *et al.* 2016) in the Mojave Desert may result in more frequent and extended droughts, thereby forcing kit foxes and coyotes to compete for more limited resources. Increasing availability of anthropogenic foods (Esque *et al.* 2010) could provide a competitive advantage to coyotes as they seem to more effectively exploit these foods compared with kit foxes. The maintenance of large tracts of intact, high-quality habitat with a diversity of natural foods and restricted human presence may help reduce the probability that kit foxes will decline to the point of requiring protective measures.

On the basis of the results of our study, we conclude that (1) desert kit foxes and coyotes on our study site consumed many of the same food items, but in varying proportions; (2) desert kit foxes specialised on heteromyid rodents and invertebrates while coyotes preferentially consumed rodents and lagomorphs, similar to results elsewhere; (3) the potential for exploitative competition between the two species does exist, but it may be mitigated to some extent by a disproportionate use of prey items; (4) dietary diversity was always substantially higher for coyotes than for desert kit foxes and dietary diversity for both species increased during drought conditions; (5) the frequency of occurrence of anthropogenic items was always more than two times higher for coyotes than for desert kit foxes, which poses potential negative consequences for desert kit foxes; and (6) coyotes and desert kit foxes were not spatially partitioning the study site, unlike in other studies, indicating that alternative mechanisms must be facilitating sympatric coexistence of the two species.

Conflicts of interest

The authors declare no conflict of interest.

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