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Temporal variation in foraging patterns of Desert Kit Foxes (*Vulpes macrotis arsipus*) in the Mojave Desert, California, USA

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ABSTRACT

Ecological studies on the Desert Kit Fox (*Vulpes macrotis arsipus*) in California, USA are severely lacking. Although the Desert Kit Fox does not have any formal protections in California, conservation concern for this subspecies is increasing markedly. We conducted a five-year multi-season dietary study in the Mojave Desert near the city of Barstow, California, USA, in which we collected and analyzed over 1,200 Desert Kit Fox scats. Desert Kit Foxes specialized on heteromyid rodents, even when this preferred prey declined during a drought. Invertebrates were also regularly consumed and use of this prey type increased when rodents decreased. Opportunistic items such as birds, reptiles, and Pistachio (*Pistacia vera*) nuts supplemented the Desert Kit Fox diet. We conclude that Desert Kit Foxes in California are rodent and invertebrate specialists, but they have sufficient ecological plasticity to expand their diet in response to environmental changes, similar to other canids. Management strategies should thus include steps to maintain healthy prey populations as well as a variety of available food options in the event of declines in primary foods. Ecological plasticity may allow Desert Kit Foxes to adapt and persist despite anthropogenic landscape modifications and potential climate change.

1. Introduction

Critical to understanding the biology of a species is determining the foods that optimize its fitness in a given environment. Such investigations provide valuable insight into the life history of a species as well as contribute to management and conservation strategies (Korschgen, 1980). Based on optimal foraging theory, not all prey species available to a predator will be consumed in the same proportions, and some prey items may even be preferred over others (Perry and Pianka, 1997; Pyke et al., 1977; Schoener, 1971). In general, optimal foraging theory predicts that an animal will forage in a way that maximizes energy gain while minimizing the time and energy required to obtain nourishment (Perry and Pianka, 1997; Pyke et al., 1977; Schoener, 1971). Foraging patterns are further mediated by factors that affect food item availability such as habitat quality, temporal variation (e.g., annual and seasonal variation), and competition (Cypher et al., 2018; Fisher, 1981; Spiegel et al., 1996).

Kit Foxes (*Vulpes macrotis*) are opportunistic foragers that rely heavily on rodents and insects for sustenance (Clark et al., 2005; McGrew, 1979; Sheldon, 1992). Kangaroo rats (*Dipodomys* spp.), pocket mice (*Perognathus* and *Chaetodipus* spp.), and ground squirrels (*Xerospermophilus* spp. and *Ammospermophilus* spp.), are common rodent prey items, and Coleopterans and Orthopterans are regularly consumed insects (Cypher et al., 2000; Spiegel et al., 1996). Kit Foxes are also known to consume Leporids (*Lepus californicus* and *Sylvilagus* spp.), birds, reptiles, and a variety of non-insect invertebrates (Fisher, 1981; Spiegel et al., 1996; White et al., 1995).

Although dietary studies have been conducted on the Kit Fox elsewhere (Egoscue, 1956; Kozlowski et al., 2008; Nelson et al., 2007; Spiegel et al., 1996), no investigations have been conducted on the Desert Kit Fox (*V. m. arsipus*) populations in California, USA. In general, little information is available on the life history of this animal. Although the Desert Kit Fox in California is not formally listed as a threatened or endangered species, conservation concern for this subspecies is increasing (D. Kadaba, pers. comm.; McGrew, 1979). Although Kit Foxes in the Mojave Desert in California have been less impacted than the San Joaquin Kit Fox (*V. m. mutica*), which is formally protected under federal and state law, continuing rapid urban sprawl, renewable energy development, and other landscape modifications may jeopardize them in the near future (Leitner, 2009; McGrew, 1979; O'Farrell and Gilbertson, 1986).

To help address current information gaps on Desert Kit Foxes in California, we conducted a multi-year dietary analysis from fall 2009 to summer 2014 to investigate temporal patterns of food item use. We also

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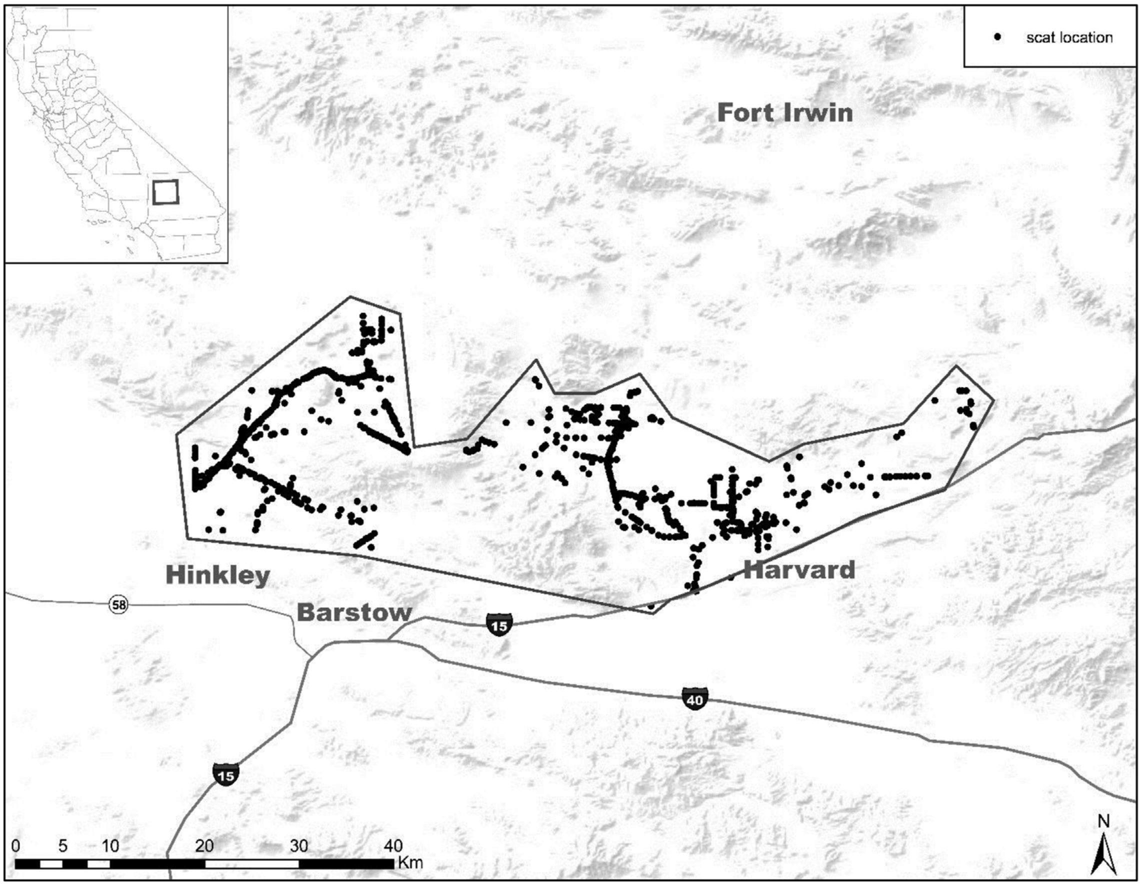

Fig. 1. Study area located in the Mojave Desert in California, USA (inset), which is bound by the Fort Irwin National Training Center to the north and Interstate 15 and State Route 58 to the south. The gray boundary is the specific study area and the black dots denote every location a scat or multiple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

incorporated annual prey abundance data collected concurrently to assess the effects of relative item availability on Kit Fox diet. Our objectives were to quantify annual and seasonal use of food items by Desert Kit Foxes and to determine the relationship between annual item use and relative prey abundance. This information will help to define ecological relationships, identify resources important for Desert Kit Foxes, and contribute to the development of effective conservation strategies.

2. Methods

2.1. Study area

We collected our data from a 1500-km^2 study site located in the Mojave Desert north of Barstow, California, USA (Cypher et al., 2018; Fig. 1). The study area, as described in Cypher et al. (2018), represents typical Mojave Desert scrub habitat (Turner, 1994) and, consistent with an arid desert environment, the mean annual precipitation for this location is only 13.4 cm (U.S. Climate Data 2014). The majority of the study area is comprised of public lands managed by the USA Bureau of Land Management (BLM) with interspersed private inholdings (BLM 1980; Cypher et al., 2018). Human densities and impacts to our study site were greatest in and around the relatively small towns of Barstow, Hinkley, and Harvard, California.

2.2. Study design

From fall 2009 to summer 2014, the Endangered Species Recovery Program (ESRP) of California State University, Stanislaus, USA conducted a food habits study on Coyotes (*Canis latrans*) at this study site as part of an investigation of predation on Mohave Desert Tortoises (*Gopherus agassizii*; Cypher et al., 2018). During that study, we opportunistically collected Desert Kit Fox scats for future dietary analysis by following the study design described in Cypher et al. (2018). Scat collections were conducted each season, which were defined as fall (October–December), winter (January–March), spring (April–June), and summer (July–September).

To process and analyze the Desert Kit Fox scats, we followed the techniques outlined by Cypher et al. (2018). We dried scats in a drying oven at 60 C for at least 24 h to destroy any eggs and cysts of zoonotic parasites. We then placed each scat inside an individually marked nylon pantyhose and washed and dried the scats to remove any soluble material. To analyze each scat, we spread the undigested material on a paper towel and carefully sorted through to find identifiable food items. We identified mammalian teeth down to species and identified other undigested mammalian remains to the lowest taxonomic level possible by examining macroscopic (e.g., length, texture, color, banding patterns) hair characteristics, nail characteristics, and bone fragments. For other items, such as a reptile scales and insect exoskeletons, we also identified the remains to the lowest taxonomic level possible. We were able to identify fleshy fruits to genus and we classified anthropogenic items based on the presence of domestic animal remains or indigestible items (e.g., plastic, rope, foil).

Prey availability data were collected during the Coyote study (Cypher et al., 2018) and these data also were used in this project. To assess annual abundance of prey, 60 1-km transects were established on BLM and California Department of Fish and Wildlife lands throughout the study area and surveys were conducted each spring. Fresh leporid

Table 1
Frequency of occurrence of food items found in Desert Kit Fox (*Vulpes macrotis arsipus)* scats collected in the Mojave Desert, California, USA, for all years combined (October 2009 to September 2014). Primary food items (> 10% frequency of occurrence) are in bold.

Frequency of occurrence (%)	
Food item	All Years (n = 1230)
Kangaroo rats (*Dipodomys* spp.)	**30.16**
Pocket mice (*Perognathus* spp. and *Chaetodipus* spp.)	**20.65**
Deer Mouse (*Peromyscus maniculatus*)	0.57
House Mouse (*Mus musculus*)	0.24
Western Harvest Mouse (*Reithrodontomys megalotis*)	0.08
Squirrels (*Xerospermophilus* spp. and *Ammospermophilus* spp.)	3.25
Desert Woodrat (*Neotoma lepida*)	0.49
Valley Pocket Gopher (*Thomomys bottae*)	0.08
Unknown rodent	**22.36**
Lagomorphs (*Lepus californicus* and *Sylvilagus audubonii*)	9.02
Unknown small mammal	2.52
Unknown mammal	2.52
Birds (Class Aves)	**14.47**
Snakes (Order Squamata)	8.86
Common Chukwalla (*Sauromalus ater*)	0.08
Desert Iguana (*Dipsosaurus dorsalis)*	0.08
Desert Horned Lizard (*Phrynosoma platyrhinos*)	0.41
Other lizards (Order Squamata)	**10.65**
Mohave Desert Tortoise (*Gopherus agassizii*)	0.57
Unknown reptile	1.46
Eggshells	0.41
Unknown vertebrate	1.95
Field crickets (Family Gryllidae)	0.16
Jerusalem crickets (Family Stenopelmatidae)	6.34
Sand treader crickets (Family Stenopelmatidae)	**10.24**
Grasshoppers (Order Orthoptera)	**11.63**
Unknown Orthopterans	**12.36**
Scarab beetles (Family Scarabaeoidea)	9.35
Tenebrionid beetles (Family Tenebrionidae)	3.74
Weevils (Family Curculionidae)	0.08
Other beetles (Order Coleoptera)	**27.56**
Earwigs (*Forficula auricularia*)	0.41
True bugs (Order Hemiptera)	0.16
Unknown insect	**26.91**
Bot fly larvae (Family Oestridae)	0.08
Larvae	**12.85**
Solpugids (Order Solifugae)	**20.08**
Scorpions (Order Scorpiones)	**11.38**
Invertebrate	0.24
Boxthorn (plant) (*Lycium* spp.)	0.08
Plant material	0.65
Pistachio nuts (plant) (*Pistacia vera*)	6.10
Domestic animal (pets, farm animals)	0.16
Domestic animal gut contents/feces	0.41
Man-made material (cloth, paper)	2.11

pellets, large (≥ 3 cm diameter) rodent burrows, and small (< 3 cm diameter) rodent burrows were counted in a 2-m wide belt along each transect. These data were used to derive an annual index of abundance for leporids (primarily Black-tailed Jackrabbits and Desert Cottontails [*S. audubonii*]), larger rodents (e.g., kangaroo rats and squirrels), and small rodents (e.g., pocket mice).

2.3. Analytical methods

We determined the frequency of occurrence of each food item (number of scats with a particular item divided by the total number of scats) found in Desert Kit Fox scats for each season and year, and for all years combined. Kit foxes commonly masticated items, particularly smaller ones, to the point of not being able to count individuals. Also, our objective was to assess the relative frequency of item use versus calculating caloric intake. Therefore, we used frequency of occurrence to quantify food item use (Corbett, 1989). For statistical analyses, we grouped items into seven broad categories per Cypher et al. (2018): lagomorph, rodent, bird, reptile, invertebrate, fruit, and anthropogenic. We used Kendall's coefficient of concordance (W) to compare rankings of items among seasons and among years. We compared the use of each food category among seasons and among years by performing contingency table analyses employing a chi-square test for heterogeneity using the item counts (Cypher et al., 2018; Zar, 1984). If the relative frequencies of scats with an item varied among seasons or years, we repeated the chi-square test for each pair of seasons or years. For these 2 × 2 contingency tables, we applied Yates' correction for continuity and, to adjust for an increased probability of a Type I error, we used Hochberg's variation on Holm's method to correct for P-values (Legendre and Legendre, 1998). We also calculated Shannon diversity indices (H') for seasonal and annual diets by using the equation:

$$H' = (N \log N - \Sigma n_i \log n_i)/N$$

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). H′ range from 0 to 1, with 0 being no dietary richness or evenness within a season or year. Also, the higher the H′, relative to each other, the more diverse the diet.

We conducted Spearman-rank correlation analysis to assess annual item use relative to the annual availability of that item and also relative to annual precipitation. We examined the relationship between: frequency of occurrence of kangaroo rats relative to average large burrow counts, frequency of occurrence of pocket mice relative to average small burrow counts, and the frequency of occurrence of lagomorphs relative to average pellet counts. To understand how precipitation affected food habits, we examined the relationship between annual precipitation and the broader food categories. Lastly, we examined the relationship between annual precipitation and Shannon diversity indices.

We used Minitab statistical software to perform all statistical tests. As in Cypher et al. (2018), we considered P-values to be significant at $\alpha \le 0.1$ for all statistical analyses. We chose a more relaxed alpha value to reduce the risk of committing a Type II error, which is considered more detrimental than a Type I error when making wildlife management decisions and within the field of conservation biology (Di Stefano, 2003; Taylor and Gerrodette, 1993). By relaxing the alpha value we hoped to identify any potential differences and relationships as these could be important for the management and conservation of Desert Kit Foxes. Significant differences and relationships were explored further in our study and also form the basis of topics warranting further investigation in future studies on Desert Kit Foxes.

3. Results

During the five-year study, we collected and analyzed 1,230 Desert Kit Fox scats (range 76–410 per year and 187–636 per season). Overall, we identified 45 different items in the scats, including various rodents, birds, reptiles, and invertebrates, and a few anthropogenic items (Table 1). Invertebrates, rodents, reptiles, and birds appeared to be primary food items for Desert Kit Foxes (categories with frequency of occurrence for all years combined > 10%). Primary invertebrate prey were Orthopteran and Coleopteran species, solpugids, scorpions, larvae, grasshoppers, and sand treader crickets (Family Stenopelmatidae). Kangaroo rats and pocket mice had the highest frequency of occurrence among rodents. The three kangaroo rat species that potentially occurred in the study area included Desert Kangaroo Rat (*D. deserti*), Merriam's Kangaroo Rat (*D. merriami*), and Chisel-toothed Kangaroo Rat (*D. microps*). Potential pocket mice species included Desert Pocket Mouse (*C. penicillatus*), Long-tailed Pocket Mouse (*C. formosus*), and Little Pocket Mouse (*P. longimembris*). In general, birds, lizards, snakes, and invertebrate remains were not identifiable to species. Anthropogenic items, including nuts of Pistachios (*Pistacia vera*) and man-made materials, had a total frequency of occurrence of 7.97%. A

Table 2
Annual frequency of occurrence for item categories in Desert Kit Fox (*Vulpes macrotis arsipus*) scats collected in the Mojave Desert, California, USA, during October 2009 to September 2014. Years span October–September. *P*-values in bold are significant.

Item category	Frequency of occurrence (%)					X^2_6 [a]	*P*
	Year 1 (*n* = 127)	Year 2 (*n* = 76)	Year 3 (*n* = 229)	Year 4 (*n* = 388)	Year 5 (*n* = 410)		
Lagomorph	1.57B [b]	3.95 AB	6.99 AB	13.40 A	9.27 A	21.22	< **0.001**
Rodent	92.91 A	96.05 A	89.96 A	62.37 B	59.27 B	135.88	< **0.001**
Bird	7.09 B	9.21 B	10.92 B	12.11 B	21.95 A	29.91	< **0.001**
Reptile	23.62 A	7.89 B	12.23 B	20.62 A	25.85 A	25.14	< **0.001**
Invertebrate	53.54 D	46.05 D	69.00 C	77.58 B	83.66 A	82.93	< **0.001**
Fruit	0.00	0.00	0.00	0.26	0.00	n/a	n/a
Anthropogenic	0.79 B	1.32 B	2.18 B	9.79 A	12.93 A	39.48	< **0.001**
Diversity[c]	0.50	0.48	0.54	0.64	0.66		

[a] Chi-square analyses conducted on item counts.
[b] Means with similar letters were not significantly different.
[c] Shannon diversity index.

number of items that we found within the scats appeared to be consumed incidentally and included twigs, grass, small amounts of plant material, and dirt. These items were most likely consumed while the Kit Fox was capturing or consuming a food item.

When we grouped items into broader food categories, 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). The occurrence of birds increased yearly while the frequency of occurrence for reptiles decreased from Years 1–2 and then increased in Years 3–5.

We found that fruits were only consumed in Year 4. The occurrence of anthropogenic items increased yearly and by Year 5 we found these items in > 10% of scats. When we grouped scats by season, rodents were the most frequently occurring item in the fall while invertebrates had the highest frequency of occurrence in all other seasons (Table 3). The frequency of occurrence of anthropogenic items, fruit, and lagomorphs were highest in winter, bird was highest in spring, and reptile was highest in summer.

Precipitation may have had an effect on prey abundance (Fig. 2). Annual precipitation fluctuated throughout the study with drought conditions during the last three years of the study. For Years 1–5, annual precipitation was 16.9 cm, 28.2 cm, 7.3 cm, 7.5 cm, and 8.0 cm, respectively. Annual precipitation for this location averages 13.2 cm. As annual precipitation changed, so did dietary patterns of the Desert Kit Foxes. As precipitation decreased in the last three years of the study, the occurrence of rodents decreased while the occurrence of invertebrates increased. Also, when precipitation was low, Desert Kit Foxes consumed a greater variety of items. As precipitation decreased, the consumption of anthropogenic items and birds increased. When precipitation was at its peak, so was the occurrence of rodents while the occurrence of reptiles was at its lowest. As rainfall declined from Years 2–5, we found that the percentage of invertebrates consumed showed an inverse relationship by steadily increasing through these same years. In all years, regardless of precipitation, rodents and invertebrates comprised over 70% of the items consumed.

Based on the Shannon diversity indices, Desert Kit Fox diets were less diverse in the first two years of the study and more diverse in the latter two years (Table 2). Seasonally, Shannon diversity indices fluctuated slightly with fall being less diverse and winter more diverse than the other seasons (Table 3). In all, Desert Kit Fox diets were the most diverse in Year 5 as well as during the winter season.

Among years, the ranks of item categories exhibited significant concordance ($W_6 = 0.943$, $X^2 = 28.29$, $P < 0.001$) indicating that the relative use of items was similar across years. However, the relative frequency of each of the item categories varied among years (Table 2). We did not include the fruit category in the chi-square analyses because Desert Kit Foxes did not eat fruit for most of the years and seasons. Rodent use by Desert Kit Foxes fluctuated substantially, from a low frequency of occurrence of 59% to a high of 96%. The relative frequency of invertebrates varied significantly between all years except between Years 1 and 2 (Table 2).

Among seasons, the ranks of item categories also exhibited significant concordance ($W_6 = 0.920$, $X^2 = 22.07$, $P = 0.001$) indicating that the relative use of items was similar across seasons. The relative frequency of lagomorph and rodent categories lacked significant variation among seasons (Table 3) whereas the relative frequency of reptiles was significantly different for all seasons except between spring and summer ($X^2 = 1.60$, $df = 1$, $P = 0.206$). The relative frequency of

Table 3
Seasonal frequency of occurrence for item categories in Desert Kit Fox (*Vulpes macrotis arsipus*) scats collected in the Mojave Desert, California, USA, during October 2009 to September 2014. Seasons were defined as Fall = October–December; Winter = January–March; Spring = April–June; Summer = July–September. *P*-values in bold are significant.

Item category	Frequency of occurrence (%)				X^2_6 [a]	*P*
	Fall (*n* = 209)	Winter (*n* = 636)	Spring (*n* = 198)	Summer (*n* = 187)		
Lagomorph	7.18 A[b]	10.69 A	5.56 A	9.09 A	5.93	0.115
Rodent	74.64 A	71.38 A	71.72 A	69.52 A	1.36	0.715
Bird	9.57 B	14.47 AB	19.19 A	14.97 AB	7.66	**0.054**
Reptile	18.18 B	12.58 C	31.31 A	37.43 A	72.72	< **0.001**
Invertebrate	65.55 C	72.17 BC	76.26 AB	84.49 A	19.77	< **0.001**
Fruit	0.00	0.16	0.00	0.00	n/a	n/a
Anthropogenic	3.83 B	13.36 A	1.52 B	1.07 B	53.53	< **0.001**
Diversity[c]	0.58	0.63	0.60	0.60		

[a] Chi-square analyses conducted on item counts.
[b] Means with similar letters were not significantly different.
[c] Shannon diversity index

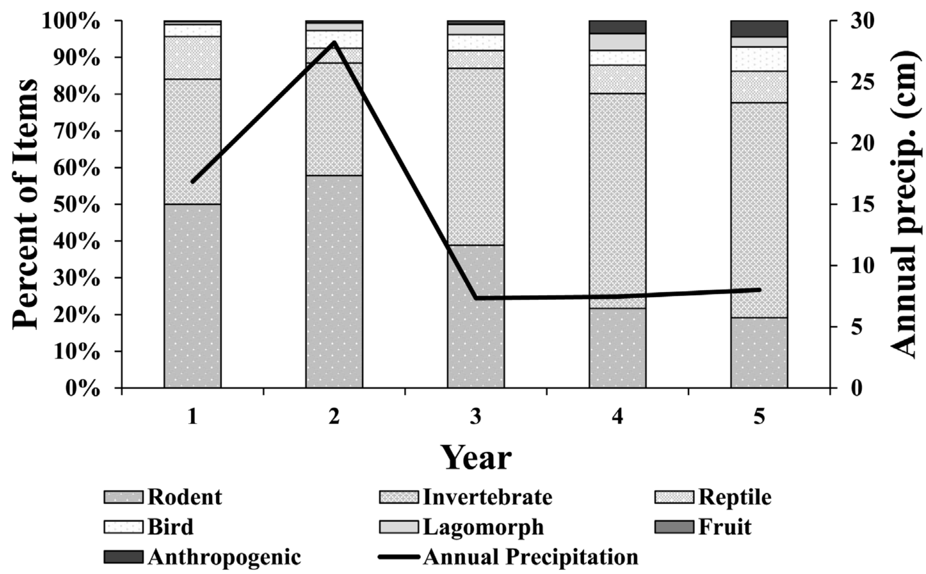

Fig. 2. Yearly percent of grouped items with the annual precipitation trend from the Mojave Desert, California, USA, during October 2009 to September 2014.

anthropogenic items was significantly different between winter and all other seasons (X^2 = 14.61–23.11, *df* = 1, *P* = < 0.001).

We conducted 12 combinations of Spearman-rank correlation analyses between food category use, prey indices, and precipitation (Table 4). From the prey transect data we collected annually, the average number of large burrows was 50, 42, 36, 7, and 9; the average number of small burrows was 24, 19, 20, 15, 15; and the average number of lagomorph pellets was 77, 130, 1227, 343, and 31, for the five years respectively (Cypher et al., 2018). There was a strong, positive significant correlation between annual precipitation and frequency of occurrence of pocket mice ($r = 1.00$, $t_3 > 38.70$, $P = < 0.001$). All remaining Spearman-rank correlations resulted in varying degrees of correlation, but none were significant (all *P*-values > 0.100).

4. Discussion

Our results suggest that Desert Kit Foxes in the Mojave Desert in California rely heavily on rodents and invertebrates for food, but will consume a variety of other items especially when the number of preferred prey is low. The primary use of rodents, specifically kangaroo rats and pocket mice, and invertebrates by this Desert Kit Fox population is similar to Desert Kit Foxes in Utah (Kozlowski et al., 2008) and San Joaquin Kit Foxes in California (Clark et al., 2005; White et al., 1995). Contrary to some studies that have found lagomorphs prevalent in the diet of foxes (Cypher and Spencer, 1998; White and Garrott, 1997), lagomorphs were not a major food item for this kit fox population. This may be due to multiple factors, including a possible low density of lagomorphs, a high number of rodents and invertebrates, or prey avoidance to potentially decrease competition with Coyotes that are also present in the area (Cypher et al., 2018; Kelly, 2017; White et al., 1995). Vanak and Gompper (2009) found that Indian Foxes (*V. bengalensis*) in Central India consume a lower proportion of anthropogenic food items than they predicted, particularly agricultural crops, and attributed it to potential competition from the larger free-ranging domestic dogs that were present in their study area.

Relative abundance of kangaroo rats and pocket mice, as indicated by our annual prey transect data, decreased from Year 1–5. Rodents remained a primary food item for all years and seasons, despite the apparent decline in this specific prey, suggesting that rodents are a preferred food item for Desert Kit Foxes. Kit foxes are considered specialists on heteromyid rodents (Cypher et al., 2000; Fisher, 1981; Laughrin, 1970), and our study supports this observation. However, as the availability of this primary food item declined at our site, kit foxes increased their consumption of other food items, which is an expected response based on optimal foraging theory (Pyke et al., 1977). As the availability of rodents declined from years 3–5, there was a substantial increase in the consumption of invertebrates. An increase in invertebrate predation during drought conditions has been noted in other kit fox dietary studies (Cypher et al. unpubl. results; Spiegel et al., 1996), further indicating that this type of food provides an important supplement when rodent prey is less available.

Even prior to drought conditions, use of invertebrates by Desert Kit Foxes was on the order of that of a primary food item. The use of invertebrates as a primary food source also has been documented in San Joaquin Kit Foxes (Cypher et al. unpubl. results) and Desert Kit Foxes in Utah (Arjo et al., 2007; Kozlowski et al., 2008). Other arid-land fox species also regularly consume invertebrates (Sheldon, 1992). For example, Burruss et al. (2017) found that Pale Foxes (*V. pallida*) in Niger, Africa primarily prey upon invertebrates and only occasionally consume rodents. Paltridge (2002) also found that invertebrates, particularly Coleopterans, were an important prey item for Red Foxes (*V. vulpes*) in the Tanami Desert of Australia. In our study, invertebrates were a significant component in the Desert Kit Fox diet regardless of climatic conditions, and reliance on this food item may increase during periods of lower rodent abundance.

The frequency of occurrence of birds, reptiles, and anthropogenic

Table 4
Spearman-rank correlations analysis on various annual values collected from the Mojave Desert, California, USA from October 2009 to September 2014. Annual frequency of occurrence of prey items, annual precipitation in cm, average annual large and small burrows, and average annual pellet counts were used for the various analysis combinations. *P*-values in bold are significant.

Annual values tested	r_s	t	P
Kangaroo rat vs. large burrows	0.60	1.30	0.285
Pocket mice vs. small burrows	0.20	0.35	0.747
Lagomorphs vs. pellets	0.20	0.35	0.747
Precipitation vs. kangaroo rat	−0.20	−0.35	0.873
Precipitation vs. pocket mice	1.00	> 38.70	< **0.001**
Precipitation vs. lagomorphs	−0.60	−1.30	0.873
Precipitation vs. bird	−0.50	−1.00	0.873
Precipitation vs. reptile	−0.10	−0.17	0.873
Precipitation vs. invertebrate	−0.60	−1.30	0.873
Precipitation vs. fruit	−0.35	−0.65	0.873
Precipitation vs.anthropogenic	−0.50	−1.00	0.873
Precipitation vs. H′	−0.60	−1.30	0.873

material also increased at our site when rodent numbers declined. Based on optimal foraging theory, as the preferred food type decreased (i.e., rodents), it would be expected that Desert Kit Foxes would increase their consumption of less preferred food items (Perry and Pianka, 1997; Pyke et al., 1977). By the final year of our study, the Mojave Desert was in the third year of below-average rainfall. It was during this year that the frequency of occurrence of rodents was at its lowest and the frequency of occurrence of these other items were at their highest. Also, based on the Shannon diversity indices, the diet in Year 5 was more diverse than any other year. This likely reflected a broadening of the diet as natural food items became less abundant.

We also found a significant correlation between annual precipitation and frequency of occurrence of pocket mice. As annual precipitation decreased, so did the consumption of pocket mice. We did not find similar correlations between precipitation and other items, but this may have been because the effects of rainfall are not necessarily immediate. There can be a lag between the amount of annual precipitation and the response by prey populations (Brown and Harney, 1993; Cypher et al., 2000; Otten and Holmstead, 1996). However, pocket mice may exhibit a more immediate response to changes in annual rainfall patterns than other species (Cypher et al., 2000; Otten and Holmstead, 1996).

The use of anthropogenic items was the highest in Year 5 and during winter. The most common anthropogenic item consumed was Pistachio nuts, which had a frequency of occurrence > 10% during both time periods. Other fox species, including Red Foxes (Contesse et al., 2004), Swift Foxes (*V. velox*; Kamler et al., 2007), and Indian Foxes (Vanak and Gompper, 2009), commonly include available agricultural crops in their diets. Small Pistachio orchards were present within portions of our study area. Interestingly, Desert Kit Foxes rarely ate native fruits found within our study site, although these were readily consumed by sympatric Coyotes (Cypher et al., 2018). In California, Pistachio nuts tend to be harvested from late August to early September, but this is not when they were most consumed by Desert Kit Foxes (Perry and Sibbett, 1998). Instead, the foxes ate the nuts that remained after harvesting during winter, when preferred prey were less abundant. During winter, reptiles and many invertebrates are underground in a dormant state, overall prey densities are lower, and preferred prey is harder to obtain. This may cause Kit Foxes to forage more for anthropogenic items. The increased frequency of Pistachio nuts in Year 5 also may be a result of continued drought conditions in the Mojave Desert. Similar to use of anthropogenic items during winter, Kit Foxes may have foraged more for nuts due to a decrease in available natural prey. This is analogous to San Joaquin Kit Fox diets during a study in western Kern County, California, USA where the use of human-derived foods decreased as rainfall increased (Spiegel et al., 1996).

Desert Kit Foxes consumed agricultural and other anthropogenic items at a higher rate when natural prey abundance declined. Therefore, the kit fox population may be receiving some amount of anthropogenic subsidization during years with decreased prey availability. This potentially can cause unnaturally higher predation pressure on secondary food items (Cypher et al., 2018; Newsome and van Eeden, 2017; Rodewald et al., 2011), as has been demonstrated between Common Ravens (*Corvus corax*) and Mohave Desert Tortoises in the Mojave Desert (Boarman, 1992), Western Gulls (*Larus occidentalis*) and Steelhead (*Oncorhynchus mykiss*) near Monterey Bay, California (Osterback et al., 2015), and Coyotes and Desert Kit Foxes in the Great Basin Desert, Utah, USA (Arjo et al., 2007).

There was significant agreement in the yearly ranks of item categories used by foxes, although the relative frequency of items varied among years. This result was somewhat unexpected given the marked fluctuations in precipitation and item availability. However, rainfall affects the abundance of all food categories except for anthropogenic items. Thus, the fluctuations in precipitation and item availability may have been sufficient to alter the relative frequency of items between years, but they may not have been sufficient to significantly alter the rankings of items. Even as the percentage of items varied among years, Desert Kit Foxes still primarily consumed rodents and insects.

Desert Kit Foxes did not exhibit a strong functional response to varying item availability, as evidenced by the dietary similarity among years and seasons. However, they could have experienced a numerical response, although we did not assess population trends. Many studies have documented a positive correlation between primary prey densities and relative canid abundance (Egoscue, 1975; White and Ralls, 1993; Spiegel et al., 1996). For example, the population of San Joaquin Kit Foxes residing within the Carrizo Plain Natural Area of central California had decreased reproductive success and thus lower Kit Fox densities during a time of decreased primary prey availability (Ralls and White, 1995; White et al., 1996; White and Ralls, 1993). Also, during a time of low primary prey availability for a population of Desert Kit Foxes in Utah, many of the individuals failed to reproduce (Egoscue, 1975). In our study, the consumption of invertebrates increased in the dry years when vertebrates presumably were less abundant. Although invertebrates can adequately sustain adult foxes (Cypher et al. unpubl. results; Poessel and Gese, 2013), these items may not be deliverable to weaning offspring in a den and might therefore result in poor reproductive success (Geffen and Macdonald, 1992; Poessel and Gese, 2013; White and Ralls, 1993).

The consumption of some secondary food items exhibited notable seasonal variation. Use of reptiles, primarily snakes and lizards, was highest in spring and summer when these species are active due to warmer temperatures. Birds were consumed most frequently in spring when adults are tending to nests and young birds are vulnerable, flightless, and easier targets for Desert Kit Foxes. A number of bird species in the Mojave Desert are ground nesting, making them more vulnerable to predation by mammals, such as kit foxes (Degregorio et al., 2016).

A better understanding of Desert Kit Fox foraging dynamics and the factors affecting these dynamics provides information useful for developing effective management and conservation strategies for this subspecies. As human impacts, particularly development, increase in the Mojave Desert and more Desert Kit Fox habitat is converted and fragmented, such management and conservation strategies may be necessary to maintain viable populations of these animals and prevent them from becoming imperiled. Conservation strategies should include steps to maintain healthy prey populations and a variety of available food options in the event of declines in primary food items. This may best be achieved by conserving large tracts of intact, high-quality habitat when possible. In areas where this is not feasible due to habitat development, it would be beneficial to provide corridors between smaller tracts of remaining habitat. Due to their foraging plasticity, Desert Kit Foxes exhibited a marked increase in consumption of anthropogenic food resources when primary prey items declined. The population and ecological effects of this subsidization are unknown and warrant further investigation, particularly given the ongoing increase in human presence in the Mojave Desert.

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