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Resource partitioning between kit foxes (*Vulpes macrotis*) and coyotes (*Canis latrans*): a comparison of historical and contemporary dietary overlap

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Abstract: Range expansions by generalists can alter communities and introduce competitive pressures on native species. In the Great Basin Desert, USA, coyotes (*Canis latrans* Say, 1823) have colonized and are now sympatric with native kit foxes (*Vulpes macrotis* Merriam, 1888). Since both species have similar diets, dietary partitioning may facilitate coexistence. We analyzed coyote and kit fox diets, then compared our results to an earlier study. Because populations are dynamic, we expected that decreases in prey or increases in predator abundance could alter dietary patterns. We found no significant changes in population-level prey diversity for kit foxes or coyotes, but found high levels of dietary overlap between species. We did detect a significant decrease in the relative importance of leporids (family Leporidae) in the diets of both canids, but they remained important for coyotes. The relative importance of small mammals was greater for kit foxes than coyotes, but their importance had not changed significantly over time. We detected significant declines in prey diversity per sample (scat-level dietary diversity) for both canids, suggesting that during a foraging event, individuals may encounter less diverse prey now than historically. These findings suggested that kit foxes and coyotes were not limited by prey, despite high dietary overlap.

Key words: *Canis latrans*, competition, coyote, diet, intraguild predation, kit fox, *Vulpes macrotis*.

Résumé : L'expansion des aires de répartition de généralistes peut modifier des communautés et introduire des pressions concurrentielles sur les espèces indigènes. Les coyotes (*Canis latrans* Say, 1823) ont colonisé le désert du Grand Bassin (États-Unis) et y vivent maintenant en sympatrie avec les renards nains (*Vulpes macrotis* Merriam, 1888) indigènes. Comme les deux espèces ont des régimes alimentaires semblables, le partage différentiel des ressources alimentaires pourrait faciliter leur coexistence. Nous avons analysé les régimes alimentaires de coyotes et de renards nains, puis comparé les résultats à ceux d'une étude antérieure. Parce que les populations sont dynamiques, nous nous attendions à ce que des baisses de l'abondance de proies ou des augmentations de l'abondance de prédateurs puissent modifier les habitudes alimentaires. Nous n'avons décelé aucun changement significatif de la diversité des proies au niveau de la population pour les renards nains ou les coyotes, mais avons noté des degrés élevés de chevauchement des régimes alimentaires des deux espèces. Nous avons toutefois détecté une baisse significative de l'importance relative des léporides (famille des léporidés) dans l'alimentation des deux canidés, même si ces proies demeureraient importantes pour les coyotes. L'importance relative des petits mammifères était plus grande chez les renards nains que chez les coyotes, mais leur importance n'a pas changé significativement avec le temps. Nous avons décelé des baisses significatives de la diversité des proies par échantillon (diversité des aliments dans les excréments) pour les deux canidés, ce qui indiquerait que, durant les épisodes d'approvisionnement, les individus pourraient trouver une moins grande diversité de proies que par le passé. Ces constatations donnent à penser que les renards nains et les coyotes ne sont pas limités par les proies, malgré l'important chevauchement de leurs régimes alimentaires. [Traduit par la Rédaction]

Mots-clés : *Canis latrans*, concurrence, coyote, régime alimentaire, prédation intraguilde, renard nain, *Vulpes macrotis*.

Introduction

Novel interactions among species are predicted to become increasingly common as species continue to alter their ranges in response to climate change and anthropogenic disturbances (Parmesan 2006; Urban et al. 2012; Engler et al. 2013). Among carnivores, range expansions and colonization of new habitats by dominant generalist species can alter carnivore communities and negatively impact subordinate specialist carnivores through com-

petition (Gompper 2002; Larivière 2004; Arjo et al. 2007; Kamler et al. 2007). The intensity of competition between carnivores increases with increasing dietary overlap and taxonomic relatedness. Additionally, the probability of interspecific competitive killing (an extreme form of interference competition; Lourenço et al. 2014) is highest when the dominant carnivore is sufficiently large relative to the subordinate species that the probability of the aggressor being injured or killed during an interaction is low

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(Donadio and Buskirk 2006). The consequences of an invading generalist carnivore may range from coexistence to extirpation of a native carnivore (Polis et al. 1989). Under conditions leading to coexistence, competition with a dominant species may limit the distribution and density of a subordinate carnivore (Hardin 1960; Schoener 1983; Glen and Dickman 2008; Sidorovich et al. 2010), which can make the population less resilient to changes in habitat or resource availability. Thus, the ability to minimize competition through resource partitioning may be critical for the long-term persistence of specialist carnivore populations facing novel competitive pressures.

Resource partitioning is a multidimensional process involving temporal, spatial, and (or) dietary shifts in a species' resource use, which lessens niche overlap among species (Schoener 1974; Garneau et al. 2007; Kamler et al. 2012) and reduces negative encounters between competitors (Polis et al. 1989; Donadio and Buskirk 2006). For carnivores, temporal partitioning may be restricted by activity patterns and availability of prey resources (Palomares and Caro 1999; Kozłowski et al. 2008). Spatial partitioning requires spatial heterogeneity or structural diversity in habitats, whereas dietary partitioning requires a diverse prey base (Hughes and Grabowski 2006; Arjo et al. 2007; Moehrensclager et al. 2007).

In the Great Basin Desert, kit foxes (*Vulpes macrotis* Merriam, 1888) and coyotes (*Canis latrans* Say, 1823) have changed in distributional overlap since the mid-20th century (Arjo et al. 2007). Kit foxes are desert specialists native to North America. They are highly tolerant of arid conditions and can persist in the absence of free-standing water (Golightly and Ohmart 1984). These adaptations have historically enabled kit foxes to spatially partition themselves from potential competitors by occupying desert habitats less suitable for other predators (Egoscue 1962; Kozłowski et al. 2008). Native to the Great Plains of central North America, coyotes are larger bodied generalists that have significantly expanded their range over the last two centuries (Gompper 2002). As recently as the 1950s and 1960s, kit foxes were the most abundant carnivore in the Great Basin and were increasing in abundance (Egoscue 1956; Dempsey et al. 2015), whereas coyotes were rare (Egoscue 1962; Arjo et al. 2007). Since then, coyotes have increased dramatically in abundance (Arjo et al. 2007) to a density 3–4 times greater than that of kit foxes (Lonsinger et al. 2018) and are widespread (Lonsinger et al. 2017). Coyotes require substantially more water than kit foxes and are less efficient in their water usage (Golightly and Ohmart 1984). Consequently, it has been suggested that the increases in coyote abundance in the region may have been, at least in part, related to increased water availability through the development of artificial water sources (Arjo et al. 2007).

Coyote presence has been hypothesized to regulate kit fox populations across their range and increased coyote abundance has been linked to declining kit fox populations in some areas (Cypher and Scrivner 1992; White and Garrott 1997; White et al. 2000; Arjo et al. 2007; Kozłowski et al. 2008). In the Great Basin Desert, kit fox declines have been attributed to the combined influences of increased coyote abundance and the conversion of desert vegetation to exotic grasses (Arjo et al. 2007). At the time of our study, kit fox populations in the region were found to be at their lowest reported density (Lonsinger et al. 2018). As generalists, coyotes can reach greater densities than specialist carnivores such as kit foxes and may limit access to resources through exploitation competition (Gompper 2002). Coyotes may also limit smaller carnivores through interference competition (Crooks and Soulé 1999; Gompper 2002) and interspecific competitive killing of kit foxes by coyotes is believed to be the primary cause of kit fox mortality in some regions (Cypher and Spencer 1998; Kozłowski et al. 2012). Previous research on sympatric kit foxes and coyotes has reported a high degree of dietary overlap (Cypher and Spencer 1998; Kozłowski et al. 2008), which can strongly influence the

potential for competition and negative encounters between sympatric competitors (Neale and Sacks 2001; Donadio and Buskirk 2006).

We analyzed the diets of sympatric kit foxes and coyotes in the Great Basin Desert of Utah, USA, and compared our results to a study conducted in the same region from 1999 to 2001 (~12 years earlier; Kozłowski et al. 2008). Although the high levels of dietary overlap between kit foxes and coyotes previously reported suggested prey may not have been a limiting resource (Kozłowski et al. 2008), systems are dynamic and continued increases in coyote abundance or decreases in prey availability could increase competitive pressures and cause patterns of dietary partitioning to emerge.

To ensure valid comparisons, dietary composition and overlap were evaluated following the procedures of Kozłowski et al. (2008). When dietary overlap was last investigated in this system, coyote abundance and leporid (species of the family Leporidae) density were believed to be on increasing and decreasing long-term trajectories, respectively (Arjo et al. 2007). Consequently, we hypothesized that we would see an overall decrease in dietary overlap between the two species, reflecting increased competition for prey and, accordingly, an increased degree of dietary resource partitioning. It has been hypothesized that water is a limiting factor in this region (Arjo et al. 2007) and that kit foxes and coyotes select for prey that will maximize water intake (Golightly and Ohmart 1984; Kozłowski et al. 2012). We predicted that coyotes would limit kit fox access to higher quality dietary prey, such as leporids, which contain higher water content per capture than smaller mammals, such as kangaroo rats (species of genus *Dipodomys* Gray, 1841) and other rodents (species of the order Rodentia), and nonmammalian prey (e.g., insects, reptiles, birds; Pond 1978). We predicted that kit foxes would respond by increasing their use of small mammals and nonmammalian prey.

Materials and methods

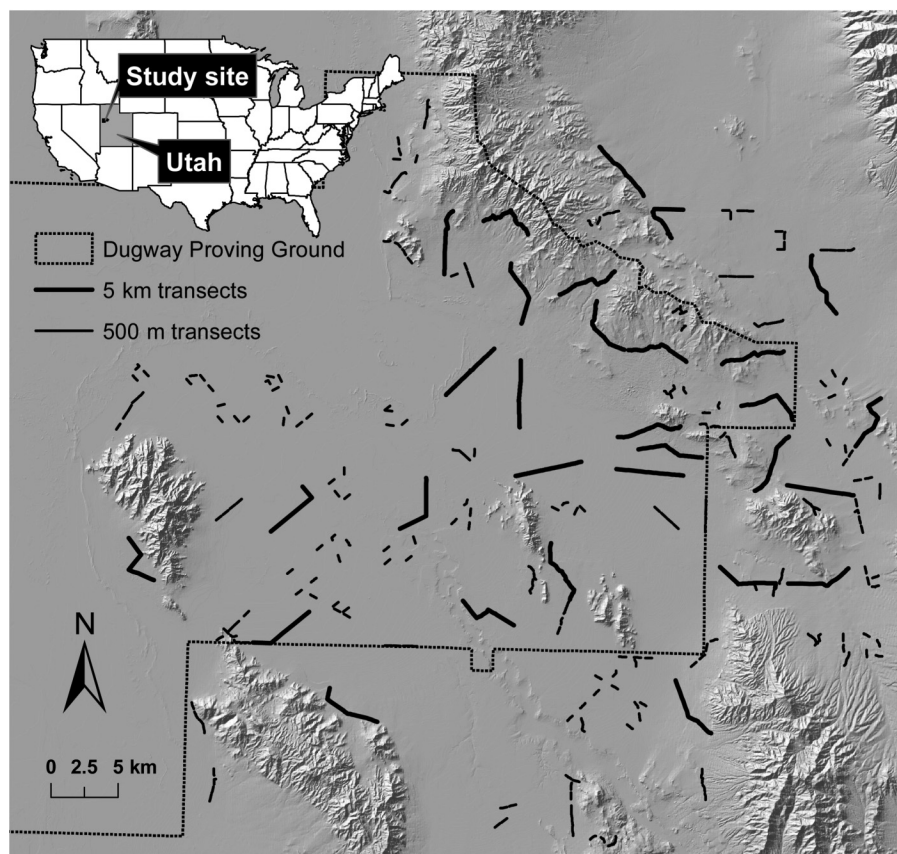
Study area

This study was conducted in the Great Basin Desert of western Utah, USA. Sampling occurred on the U.S. Army's Dugway Proving Ground and surrounding federal lands managed by the U.S. Bureau of Land Management (collectively hereafter Dugway; Fig. 1). Dugway is characterized by flat lowlands separated by abrupt, steep mountains (Kozłowski et al. 2008). The region tends towards cold winters and moderate summers; January is the coldest month (mean high = 3.3 °C; mean low = 8.8 °C) and July is the warmest month (mean high = 34.7 °C; mean low = 16.3 °C) (Lonsinger et al. 2015a). Dugway receives ~20 cm of precipitation annually and evaporation exceeds precipitation, limiting the availability of naturally occurring free-standing water (Arjo et al. 2007; Kozłowski et al. 2012). Habitat types within the region include arid shrub-steppe, greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) shrubland, cold desert chenopod shrubland, cold desert playa, native and exotic grasslands, vegetated and unvegetated dunes, open juniper (species of the genus *Juniperus* L.) woodland complexes, and isolated human developments (Kozłowski et al. 2012; Lonsinger et al. 2017). Our contemporary study complemented a study investigating canid abundance (Lonsinger et al. 2018) and occupancy patterns (Lonsinger et al. 2017), for which the extent was ~3015 km² (Fig. 1). Our study extent encompassed the spatial extent of the historical study implemented by Kozłowski et al. (2008), as well as sites used to study kit fox ecology from 1951 to 1958 (Egoscue 1956; Egoscue 1962; Arjo et al. 2007).

Sample collection and processing

Kit fox and coyote fecal samples were collected along 270 km of transects. Surveys were conducted during winter (January–March) and summer (July–August) of 2013. During these two seasons, 30 transects (5 km each) were surveyed 3 (summer) to 4 (winter) times

Fig. 1. Location of 5 km and 500 m transects surveyed within and around the U.S. Army's Dugway Proving Ground in western Utah, USA, for coyote (*Canis latrans*) and kit fox (*Vulpes macrotis*) scats in the winter and summer of 2013.



(Fig. 1), with consecutive surveys separated by ~14 days. Additionally, 240 shorter transects (500 m each; Fig. 1) were each surveyed once in each season. Researchers were trained to identify scats with samples of known origin. During surveys, scats were identified to species based on morphology, overall size, shape, color, and odor, as well as associated sign (e.g., tracks; Kozłowski et al. 2012), and species identification was later confirmed using mitochondrial DNA (mtDNA) fragment analysis (De Barba et al. 2014). Fecal DNA sample collection and mtDNA species identification followed procedures detailed in Lonsinger et al. (2017). At the time of collection, samples were placed in paper bags and frozen. Samples were subsequently thawed, individually packaged in nylon material, soaked in warm water for approximately 2 h, and washed with detergent in a standard washing machine for 2–3 cycles to remove fecal material. Samples were then dried at 70 °C in drying ovens for 24 h. The remaining indigestible remnants (e.g., hair, teeth, bones, feathers, and scales) were analyzed using site-specific voucher specimens and dichotomous keys (for full list see Gosselin et al. 2017).

Data analysis

Dietary items were separated into 1 of 11 classes following Kozłowski et al. (2008). Dietary classes included leporids, rodents, kangaroo rats (separated from other rodents because of their high frequency and historical importance in the diets of both canids), insects, birds, fruits and plants, reptiles, anthropogenic materials, ungulates, and miscellaneous mammals. The presence or absence of each dietary class was recorded for each scat. Proportions of dietary classes were calculated by percent occurrence (PO), which we defined as the number of occurrences of a dietary class/total number of scat samples, and relative percent occurrence (RPO), which we defined as the number of occurrences of a dietary class/

total number of occurrences of all dietary classes (Loveridge and Macdonald 2003). PO estimates the frequency a prey item is used by the species, whereas RPO estimates the frequency of a prey item compared with other prey items, providing an estimate of a prey item's relative importance in the diet (Loveridge and Macdonald 2003; van der Merwe et al. 2009). To facilitate data analysis and minimize bias, dietary items with a PO < 5% in both species were considered trace and excluded from subsequent PO and RPO analyses (Kamler et al. 2007). We also estimated PO and RPO by season. For both species, population-level PO decreased across primary dietary classes between historical and contemporary sampling periods (see Results). We suspected these results could reflect decreases in dietary diversity on a per-scat basis. Differences in mean number of classes per scat for both kit foxes and coyotes between sampling periods were tested for significance using Welch's *t* test (Welch 1947).

Dietary overlap was calculated using the Morisita–Horn similarity index (hereafter M–H index; Horn 1966), in which overlap was based on the proportion of prey classes in the diet, and was measured on a scale of 0 (no dietary overlap) to 1 (complete dietary overlap). All 11 dietary classes were included in measurements of overlap and diversity. Seasonal and annual dietary overlap was assessed within each canid species between contemporary and historical periods. Dietary overlap was also assessed between kit foxes and coyotes for the contemporary sampling period. Breadth of dietary diversity for contemporary samples was calculated using the Shannon–Weiner diversity index (hereafter *H'*; Shannon 1948). Dietary diversity was measured both annually and for winter and summer sampling periods and differences in diversity were tested for significance using Hutcheson's *t* test (Hutcheson 1970). Differences in RPO between species and between historical

and contemporary studies were tested for significance using Pearson's χ^2 test (Zar 1996). Contribution to diet was calculated for each primary dietary class individually with a single-sample proportions test with continuity correction. All analyses were completed with the R statistical programming language (R Core Team 2014).

Sensitivity to misidentification

Carnivore scats collected from 1999 to 2001 were identified to species based on scat morphology, including color, odor, overall size, and physical appearance (Kozłowski et al. 2008, 2012); misidentification of scats associated with this approach may bias inferences (Lonsinger et al. 2015b). We assumed that field-based scat misclassification levels during the 2013 sampling adequately represented misidentification levels during the historical time period and we used 2013 samples to evaluate the sensitivity of our statistical approaches to misidentification. Using the field identification of scats, we randomly selected n samples from each species without replacement, evaluating sample sizes (n) of 50 to 250 (by 50). For each n , we repeated this procedure 1000 times, each time evaluating the dietary overlap between species, testing for significant differences in H' with Hutcheson's t test, and comparing RPO between species with Pearson's χ^2 tests as described above. Across the 1000 replicate subsamples for each n , we then calculated the mean difference between the M–H index derived from the full data set and based on mtDNA species identification and the M–H index derived from each replicate subsample. Similarly, we compared the statistical results of the Hutchinson's t test and Pearson's χ^2 tests across replicates for each n to that from the full data set identified with mtDNA and calculated the proportion that were in agreement.

Habitat proportions

Variation in prey availability and abundance may be associated with variation in habitat types (Arjo et al. 2007; Kozłowski et al. 2012); consequently, observed differences in dietary composition between historical and contemporary sampling periods may be an artifact of differences in the habitat proportions sampled within each spatial extent. Temporally relevant vegetation type layers were acquired from the LANDFIRE database (<http://www.landfire.gov/>) for each sampling period, with vegetation layers from 2001 and 2012 being used to characterize habitat proportions from historical and contemporary sampling periods, respectively. We used ArcGIS version 10.0 (ESRI 2010) to reclassify habitat types as woodland, shrubland, subshrubs, grassland, sparsely vegetated, or developed. For each sampling period, we calculated the proportion of each habitat type within a linear polygon 5 km on each side of scat deposition transects. Changes in habitat proportions within a single spatial extent can provide additional information on habitat patterns observed. For the contemporary spatial extent, we also calculated the proportion of each habitat type based on 2001 vegetation data and compared this to the patterns observed with 2012 vegetation data.

Results

Sample collection and processing

We analyzed 776 coyote and 266 kit fox scats obtained during the winter and summer sampling periods. Only four dietary classes — leporids, rodents, kangaroo rats, and insects — had >5% PO in the diets of both species. Some representative species identified in the main dietary classes included black-tailed jack-rabbit (*Lepus californicus* Gray, 1837), Ord's kangaroo rat (*Dipodomys ordii* Woodhouse, 1853), deer mouse (*Peromyscus maniculatus* (Wagner, 1845)), grasshopper mouse (species of the genus *Onychomys* Baird, 1857), white-tailed antelope squirrel (*Ammospermophilus leucurus* (Merriam, 1889)), vole (species of the genus *Microtus* Schrank, 1798), Mormon cricket (*Anabrus simplex* Haldeman, 1852), and various beetles (order Coleoptera). Additional classes included varied

Table 1. Morisita–Horn similarity index (M–H index) of dietary overlap over time between historical samples collected by Kozłowski et al. (2008) and contemporary samples collected in 2013 for coyotes (*Canis latrans*) (historical: $n = 1131$; contemporary: $n = 776$) and kit foxes (*Vulpes macrotis*) (historical: $n = 294$; contemporary: $n = 266$) and estimates of dietary diversity (Shannon–Weiner diversity index (H')).

Species	Season	M–H index	H'	
			Historical	Contemporary
Coyote	Annual	0.97	0.80	0.87
	Winter	0.97	0.77	0.74
	Summer	0.94	0.81	0.85
Kit fox	Annual	0.97	0.75	0.78
	Winter	0.87	0.69	0.61
	Summer	0.96	0.76	0.76

Note: M–H index indicates overlap within each sampling season (winter and summer) and annually (winter and summer combined).

items such as mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), domestic cattle (*Bos taurus* Linnaeus, 1758; likely scavenged), juniper cones, Horned Larks (*Eremophila alpestris* (Linnaeus, 1758)), Gopher Snakes (*Pituophis catenifer* (Blainville, 1835)), and scorpions (various species). No kit fox remains were detected in coyote scats.

Dietary overlap and diversity

A comparison of diet by species and season using the M–H index revealed high levels of dietary overlap between historical and contemporary periods for both kit foxes (M–H index = 0.97) and coyotes (M–H index = 0.97; Table 1). Within the contemporary period, dietary overlap between kit foxes and coyotes was found to be high in both winter (M–H index = 0.93) and summer (M–H index = 0.91) and was comparable to dietary overlap in the historical period (winter: M–H index = 0.87; summer: M–H index = 0.90). Population-wide dietary diversity of both species was also similar between historical and contemporary periods, as seen in the comparison of H' (Table 1), and significant differences in dietary diversity between historical and contemporary periods were detected only when diversity declined for kit foxes in winter ($t_{[256]} = 2.15$, $P < 0.05$). Overall dietary diversity of the contemporary samples was higher in summer than in winter for both species, and annual H' was significantly higher for coyotes than kit foxes ($t_{[492]} = -3.77$, $P < 0.05$).

Kit fox diet analysis

Kangaroo rats had the greatest RPO (41%) in annual kit fox diets during the historical period, followed by rodents (25%), insects (21%), and leporids (13%) (Table 2). Similarly, for annual kit fox diets during the contemporary period, kangaroo rats had the greatest RPO (36%), followed by rodents (35%), insects (22%), and leporids (7%) (Table 2). A significant increase in annual RPO was observed between historical and contemporary periods for the rodent ($\chi^2_{[1]} = 7.80$, $P = 0.01$) class and a significant decrease for the leporid ($\chi^2_{[1]} = 5.1$, $P = 0.02$) class (Table 2). In winter kit fox scats, we observed a significant decrease in the RPO of insects ($\chi^2_{[1]} = 12.47$, $P < 0.01$) and a significant increase in the RPO of rodents ($\chi^2_{[1]} = 9.44$, $P < 0.01$) relative to the historical period (Table 2). Leporid RPO decreased significantly in summer kit fox scats ($\chi^2_{[1]} = 12.20$, $P < 0.01$) when compared with the historical period. No other significant seasonal differences were observed between contemporary and historical periods. Significant decreases in annual dietary PO were observed across all analyzed classes (Fig. 2). We found a significant decrease in the per-sample dietary diversity between historical and contemporary periods for both summer ($t_{[245.5]} = -9.0$, $P < 0.01$) and winter ($t_{[207.5]} = -9.0$, $P < 0.01$).

Coyote diet analysis

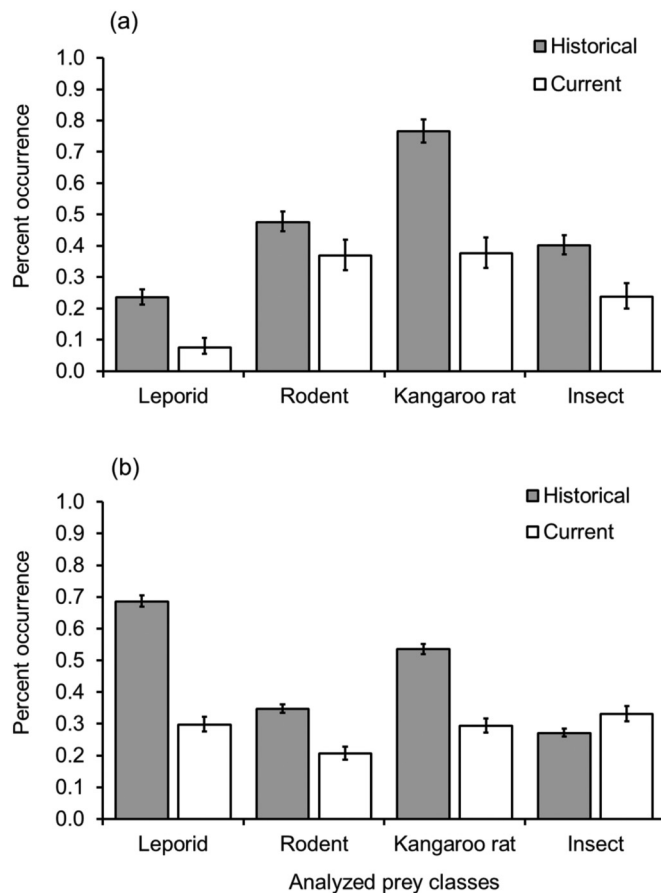
For coyote annual diets, leporids had the highest RPO in the historical period (37%), followed by kangaroo rats (29%), rodents

Table 2. Relative percent occurrence (RPO) of dietary classes representing >5% occurrence for kit fox (*Vulpes macrotis*) populations based on historical (HS; 1999–2001) and contemporary (CS; 2013) scat samples collected in western Utah, USA.

Dietary class	Annual		Winter		Summer	
	HS	CS	HS	CS	HS	CS
Leporid	0.13	0.07*	0.13	0.15	0.12	0.02*
Rodent	0.25	0.35*	0.31	0.49*	0.26	0.20
Kangaroo rat (species of genus <i>Dipodomys</i>)	0.41	0.36	0.44	0.36	0.38	0.35
Insect	0.21	0.22	0.12	0.00*	0.37	0.29
Sample size	294	266	146	113	148	153

Note: Asterisk indicates significant difference ($P < 0.05$) between historical and contemporary RPO.

Fig. 2. Percent occurrence of primary dietary classes for (a) kit fox (*Vulpes macrotis*) and (b) coyote (*Canis latrans*) populations as determined through analysis of scat samples collected in western Utah, USA, during historical (1999–2001) and contemporary (2013) sampling periods. Error bars represent Wilson's 95% confidence intervals.



(19%), and insects (15%), respectively (Table 3). For the contemporary period, insects had the highest RPO (29%), followed by leporids (26%), kangaroo rats (26%), and rodents (18%) (Table 3). A significant increase was observed in annual insect RPO between historical and contemporary periods ($\chi^2_{[1]} = 84.4$, $P < 0.01$), whereas annual leporid content decreased ($\chi^2_{[1]} = 32.15$, $P < 0.01$; Table 3). The contemporary RPO of rodents in winter coyote diets increased significantly since the historical period ($\chi^2_{[1]} = 8.13$, $P < 0.01$), whereas kangaroo rat RPO ($\chi^2_{[1]} = 8.87$, $P < 0.01$) and insect RPO ($\chi^2_{[1]} = 9.5$, $P < 0.01$) decreased (Table 3). In summer coyote diets, the

contemporary RPO of insects increased significantly ($\chi^2_{[1]} = 53.66$, $P < 0.01$), whereas leporid RPO decreased ($\chi^2_{[1]} = 41.58$, $P < 0.01$) since the historical period (Table 3). No other significant seasonal differences in RPO were seen between contemporary and historical periods. Similar to patterns observed in kit foxes, significant decreases in dietary PO were seen for all analyzed dietary classes since the historical period, with the exception of the insect class, which increased between historical and contemporary periods ($\chi^2_{[1]} = 84.14$, $P < 0.01$; Fig. 2). A significant decrease in per-sample dietary diversity was observed between historical and contemporary periods for both summer ($t_{[888.162]} = 10.239$, $P < 0.01$) and winter ($t_{[896.753]} = 18.764$, $P < 0.01$) periods.

Sensitivity to misidentification

When scat misidentification was present, the mean change in the estimated M–H index was negligible across sample sizes considered. At small sample sizes, results of the Hutcheson's t tests from replicated subsamples including field-based misidentification were in low to moderate agreement with the full data set based on mtDNA. At the lowest sample size, 73% of the data sets produced results that were not in agreement with the full data set (Supplementary Table S1).¹ As sample size increased, however, the influence of misidentification decreased; at the largest sample size evaluated, 85% of replicates were in agreement with the full data set without misidentification (Supplementary Table S1).¹ Results of the Pearson's χ^2 tests from replicate subsamples including field-based misidentification were in high agreement with the full data set based on mtDNA, even with small sample sizes; when replicate sample sizes were ≥ 100 scats per species, $\geq 99\%$ of replicates were in agreement (Supplementary Table S1).¹

Habitat proportions

The proportions of habitat types were similar between historical and contemporary sampling periods when using temporally aligned vegetation data. Subshrub habitats (historical = 49.9%; contemporary = 41.5%) constituted the most widely distributed habitat type within each sampling period and spatial extent, followed by shrubland (historical = 21.8%; contemporary = 19.4%) and grassland (historical = 20.5%; contemporary = 23.5%) habitats. Sparsely vegetated (historical = 5.5%; contemporary = 9.4%) and woodland (historical = 1.2%; contemporary = 5.8%) habitats were less common. Developed areas comprised only 1.2% and 0.4% of the historical and contemporary spatial extents, respectively. When considering changes in habitat proportions within the contemporary spatial extent, grassland (2001 = 16.9%; 2012 = 23.5%), subshrub (2001 = 45.3%; 2012 = 41.5%), and shrubland (2001 = 22.2%; 2012 = 19.4%) habitats experienced the greatest change. Little or no change was observed for sparsely vegetated (2001 = 9.2%; 2012 = 9.4%), developed (2001 = 0.5%; 2012 = 0.4%), and woodland (2001 = 5.8%; 2012 = 5.8%) habitats.

¹Supplementary Table S1 is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0246>.

Table 3. Relative percent occurrence (RPO) of dietary classes representing >5% occurrence for coyote (*Canis latrans*) populations based on historical (HS; 1999–2001) and contemporary (CS; 2013) scat samples collected in western Utah, USA.

Dietary class	Annual		Winter		Summer	
	HS	CS	HS	CS	HS	CS
Leporid	0.37	0.26*	0.39	0.45	0.35	0.18*
Rodent	0.19	0.18	0.21	0.29*	0.169	0.13
Kangaroo rat (species of genus <i>Dipodomys</i>)	0.29	0.26	0.34	0.24*	0.23	0.27
Insect	0.15	0.29*	0.06	0.01*	0.26	0.42*
Sample size	1131	776	671	276	460	500

Note: Asterisk indicates significant difference ($P < 0.05$) between historical and contemporary RPO.

Discussion

Our primary objectives were to evaluate dietary diversity and overlap between kit foxes and coyotes and to determine if the diets of these species have diverged since an earlier study conducted at the same study site that found high levels of dietary similarity (Kozłowski et al. 2008). We expected that increased exploitative competition between native kit foxes and nonnative coyotes could be driven by continued increases in coyote abundance, decreases in prey availability, or both. We predicted that increased competitive pressure would be indicated by a decrease in dietary overlap between kit foxes and coyotes, with coyotes concentrating on larger bodied shared prey (i.e., leporids) and limiting their availability to subordinate kit foxes. Instead, we observed little change, with the diets of both species having high overlap (97%) between historical and contemporary periods. Dietary overlap between the two species also remained high (91% annually). Interestingly, our results suggested that the frequency at which a prey class was used (as characterized by PO) decreased across prey classes for both species (with the exception of insect use by coyotes), and we have related this pattern to significant declines in the number of dietary classes per scat for both species.

The colonization of nonnative species can alter carnivore communities and drive resource partitioning. For example, European mink (*Mustela lutreola* (Linnaeus, 1761)) shifted their diet in response to invading American mink (*Neovison vison* (Schreber, 1777)), and patterns of dietary partitioning varied with changes in time since invasion and fluctuations in prey populations (Sidorovich et al. 2010). Coyotes likely colonized the Great Basin by the early 1900s and coyote control programs had been implemented by the 1950s (Egoscue 1956). Still, coyotes were believed to be rare until the mid-20th century, after which coyote relative abundance increased steadily (Arjo et al. 2007). The earliest studies of kit fox diets at Dugway reported that foxes used a diverse prey base, but that leporids made up a significant portion of their diet (up to 90%; Egoscue 1962; Arjo et al. 2007). Subsequent analyses of canid diets at Dugway from 1999 to 2001 suggested that kit foxes had shifted their diet in response to increasing coyote abundance, with leporids representing the smallest proportion of kit fox diets and the greatest proportion of coyote diets, relative to other prey class (Kozłowski et al. 2008).

Leporid populations are believed to be declining at Dugway, with the population experiencing reduced amplitude in ~10 year population cycles (Arjo et al. 2007). Considering the relative importance that leporids have had in canid diets at Dugway, we expected that continued increases in coyote abundance and (or) decreases in leporid abundance could lead to increased dietary competition between kit foxes and coyotes. Our population-level results suggested that the annual RPO of leporids continued to decrease significantly in kit fox diets. In contrast to our predictions, population-level annual RPO of leporids also decreased significantly for coyotes. Although we did not estimate leporid densities, a concurrent study suggested that leporid relative abundance was lower during our study than during the historical period (Arjo et al. 2007; Kluever et al. 2017). Declines in RPO of

leporids in both populations was likely related to overall population declines in leporid abundance and therefore availability.

Cypher and Spencer (1998) found sympatric coyotes and San Joaquin kit foxes (*Vulpes macrotis mutica* Merriam, 1902) relied more heavily on leporids and small mammals, respectively, and that this allocation of prey resources aligned with predictions that species may partition resources based on their body size. Although we observed high levels of dietary overlap between kit foxes and coyotes, the relative importance of prey classes (as characterized by RPO) suggested similar patterns. Even with declines in the RPO of leporids since the historical period, leporids were still more important for coyotes than kit foxes. Both species used kangaroo rats and other rodents, but these classes combined to a relative importance of 71% in kit fox diets compared with 44% in coyote diets. When compared with historical estimates, these values represent only a nominal increase in RPO of kit fox diets and decrease in RPO of coyote diets, suggesting that partitioning of prey based on size likely occurred prior to the historical study. Insects constituted a relatively important prey class for both canids, but it was the prey class with the highest annual RPO for coyotes. Cypher and Spencer (1998) suggested that coyotes may not be able to efficiently exploit some small mammals and they may therefore rely more on insects when leporid availability is low. Neither kit foxes nor coyotes used other nonmammalian dietary classes (e.g., reptiles, birds) at significantly higher levels, but instead relied upon the same primary dietary classes — rodents, kangaroo rats, rabbits, and insects — as during the historical period.

Despite some changes in the RPO of prey classes, dietary overlap remained high between kit foxes and coyotes (and between historical and contemporary periods for each canid), suggesting that the prey resources were likely not a limiting factor in this ecosystem and that partitioning of dietary resources was not necessary for kit fox and coyote coexistence. It has been suggested that kit foxes and coyotes may coexist at Dugway through spatial partitioning (Kozłowski et al. 2012), but other studies have failed to detect these patterns (Hall et al. 2013). Lonsinger et al. (2017) found patterns that reconciled these seemingly disparate results: kit foxes and coyotes employed broad-scale habitat partitioning, but where they co-occurred, kit fox space use was higher in areas with greater coyote activity. These patterns could result from either (i) kit foxes and coyotes aggregating in areas with more abundant prey resources or (ii) coyotes actively hunting kit foxes. Although Lonsinger et al. (2017) could not directly test these two hypotheses, our data supports the former. We observed high levels of dietary overlap, which highlights that both species targeted similar prey, and supports the conclusions of Kozłowski et al. (2012) that, despite apparent broad-scale spatial partitioning, kit foxes still used prey classes in proportions similar to those of coyotes. Furthermore, neither Kozłowski et al. (2008) nor our study, through the collective analysis of >1900 coyote scats, found evidence of kit fox remains in coyote diets, suggesting that coyotes were likely not actively hunting kit foxes for food.

It is not uncommon for mammalian intraguild predators to kill and not consume a subordinate intraguild competitor when prey resources are not limited (Palomares and Caro 1999). For example, consumption of kit foxes or swift foxes (*Vulpes velox* (Say, 1823)) was rare when resources were abundant (Cypher and Spencer 1998; Kitchen et al. 1999), but common when prey resources were limited (Ralls and White 1995). At Dugway, interspecific killing by coyotes has been identified as a primary cause of kit fox mortality (41%–67% of mortalities; White and Garrott 1997; Kozłowski et al. 2008; Kluever and Gese 2017), despite a lack of evidence that kit foxes were consumed. This suggests that prey resources were not limiting. Competitive pressure of coyotes on kit foxes was likely restricted to interference competition. Interference competition may restrict kit fox space use. For example, broad-scale kit fox local extinction at Dugway was higher in areas with greater coyote activity (Lonsinger et al. 2017). Thus, high levels of dietary overlap as demonstrated in this study may lead to heightened risk of kit foxes encountering coyotes while foraging, increasing the potential for interspecific competitive killing. If key prey classes for coyotes such as leporids continue to decline at Dugway, then this dynamic relationship could change and exploitative competition could further limit kit foxes.

Changes in diets of species may be subtle and the scale of inference may limit our understanding of dynamic processes. We found no significant changes in population-level diets over time for either species through dietary overlap analysis. However, our analyses found significant decreases in overall PO (i.e., frequency of use) for the primary dietary classes for both kit foxes and coyotes between the historical and contemporary periods (apart from an increase in insect PO for coyotes). These results indicated that although kit foxes and coyotes used the same primary prey classes at the population level and over longer periods (i.e., seasonally or annually), prey classes were used less frequently. We attributed these results to a significant decrease in number of prey classes per sample (i.e., a decrease in scat-level diversity) for both species since the historical period. It is possible that this reduction of scat-level dietary diversity was the result of spatial or temporal variation in the availability of the primary prey classes in our study region. The land cover in the Great Basin Desert has been altered considerably over the last half of the 20th century, with over 50% of the natural shrub–steppe vegetation having been replaced by monoculture grasslands dominated by invasive species such as cheatgrass (*Bromus tectorum* L.) (Arjo et al. 2003; Bartel et al. 2008; Ostojka and Schupp 2009). Homogenous habitats dominated by nonnative plants can lead to decreased diversity of small mammals (Bartel et al. 2008; Litt and Steidl 2011). Arjo et al. (2007) and Kozłowski et al. (2012) found increased rodent abundances at Dugway, but they noted that overall species diversity was low and that the increase in abundance was likely due to an influx of habitat generalists. Proportions of habitat types between historical and contemporary spatial extents and periods were similar, but we did observe a decrease in shrub and subshrub cover and an increase in grassland and sparsely vegetated cover since the historical sampling period, indicating a continuation of the trend towards landscape homogeneity. Decreased scat-level diversity for both kit foxes and coyotes may therefore be reflective of a less diverse prey base within the cover types present in each individual canid's home range. These results highlight the importance of considering the sensitivity of the analysis in evaluating change over time in natural systems, as subtle or finer scale changes may not be detectable through broad-scale analyses such as dietary overlap.

Our main goal was to evaluate changes in dietary partitioning over time for two sympatric canids, and we therefore elected to use the same dietary analysis methods as previously employed (Kozłowski et al. 2008) to facilitate a comparison of trends. Our research suggested that population-level dietary resource partitioning between kit foxes and coyotes had not changed significantly over ~12 years in our study region. These findings

suggested that prey resources were sufficiently high to support coexistence of native kit foxes and nonnative coyotes. Our results also highlight the subtleties of assessing changes in diet over time. Although population-level analyses suggested little change in dietary overlap, we found evidence that diets may have changed at the foraging level. Although this pattern may have been related to homogenization of habitats within individual canid home ranges, additional research is needed to further explore this relationship. It is important to note that our findings may have been influenced by our shorter sampling period, which could influence our results through natural fluctuations in the prey base. However, we believe that our results are reflective of what we would expect as average conditions. The only major change that we saw was in the decrease of leporid occurrence in the data, which is consistent with the predicted and observed long-term declines of jackrabbits in this region (Arjo et al. 2007; Kluever et al. 2017). As leporid populations are believed to be on a 10 year cycle in this region (Arjo et al. 2007), it is unlikely that adding another sampling year would have altered these results.

Kit fox populations are believed to be declining across their range and have been shown to be declining at Dugway (Lonsinger et al. 2018). These declines have been commonly attributed to broad-scale habitat conversion, decreased prey abundances, and competition with coyotes (White and Garrott 1997; White et al. 2000; Arjo et al. 2007; Moehrensclager et al. 2007; Kozłowski et al. 2012). Although exploitative competition did not appear to be limiting the kit fox population, prey diversity and abundance were predicted to decrease in our study region due to the effects of climate change and habitat conversion (Arjo et al. 2007; Bartel et al. 2008; Ostojka and Schupp 2009). Decreases in resource availability may alter competitive dynamics between kit foxes and coyotes, with possible negative consequences for future kit fox persistence in the region.

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Supplementary material

Table S1. Results of a sensitivity analysis evaluating the influence of scat misidentification between coyote (*Canis latrans*) and kit fox (*Vulpes macrotis*) scats collected in western Utah, USA, in 2013, with percent misclassified (%MC) indicating the mean misclassification rate among 1000 replicate subsamples for each samples size, and mean change and standard deviation (SD) indicating the difference between the Morisita–Horn similarity index (M–H index) of dietary overlap for the full data set (including all samples with species identification based on unambiguous genetic analyses) and replicate subsamples based on field identification (including misidentification).

Sample size	%MC	M–H index		Proportion in agreement	
		Mean change	SD	Hutchinson's <i>t</i> test	Pearson's χ^2
50	8.59	0.022	0.018	0.27	0.84
100	8.73	0.015	0.012	0.39	0.99
150	8.58	0.011	0.008	0.52	1.00
200	8.61	0.009	0.007	0.69	1.00
250	8.62	0.008	0.005	0.85	1.00