

## Spatiotemporal patterns of San Joaquin kit foxes and an urban canid guild

NICOLE A. DEATHERAGE<sup>1,\*</sup>, BRIAN L. CYPHER<sup>1</sup>, TORY L. WESTALL<sup>1</sup>, AND ERICA C. KELLY<sup>1</sup>

<sup>1</sup>*Endangered Species Recovery Program, California State University, Stanislaus,  
One University Circle, Turlock, CA 95382*

**ABSTRACT.**—The federally endangered and California State–threatened San Joaquin kit fox (*Vulpes macrotis mutica*) forms an ecological guild with coyotes (*Canis latrans*), red foxes (*V. vulpes*), gray foxes (*Urocyon cinereoargenteus*), and domestic dogs (*C. familiaris*) in the city of Bakersfield, California, USA. Where these species are sympatric in natural environments, interference competition occurs, resulting in spatiotemporal avoidance or changes in behavior to avoid conflict. We analyzed camera survey data from 2015 to 2019 from 111 1-km<sup>2</sup> grid cells throughout Bakersfield to investigate spatial associations between San Joaquin kit foxes and canid competitors, as well as differences in temporal activity of kit foxes in the presence of a canid competitor. We found that kit foxes typically did not occur with other canids on a daily, yearly, or 5-year scale. In cells where other canids were immediately present, kit foxes altered their temporal activity to avoid other canids by appearing 3 h later and exhibited less variance in the amount of time spent at a camera trap. Thus, although kit foxes share the urban habitat with multiple larger competitors, they likely use spatial and temporal partitioning to reduce risk and facilitate coexistence.

**RESUMEN.**—El zorro kit de San Joaquín (*Vulpes macrotis mutica*), que se encuentra en la lista federal de especies en peligro de extinción y como especie amenazada en el estado de California, forma un gremio ecológico con los coyotes (*Canis latrans*), los zorros rojos (*V. vulpes*), los zorros grises (*Urocyon cinereoargenteus*) y los perros domésticos (*C. familiaris*) en la ciudad de Bakersfield, California, EE.UU. La competencia por interferencia ocurre entre estas especies, donde son simpátricas en ambientes naturales, lo que resulta en la evasión espacio-temporal o en cambios en el comportamiento para evitar conflictos. Analizamos los datos registrados por una cámara trampa de 2015–2019 de 111 parcelas de muestreo de 1 km<sup>2</sup> en todo Bakersfield, para investigar las asociaciones de espacio entre los zorros kit de San Joaquín y sus competidores cánidos, así como las diferencias en la actividad temporal de los zorros kit en presencia de un competidor cánido. Descubrimos que los zorros kit normalmente no se encontraron con otros cánidos en una escala diaria, anual o de 5 años. En las parcelas de muestreo donde otros cánidos estuvieron presentes, los zorros kit alteraron su actividad temporal para evitarlos, al aparecer 3 horas más tarde y exhibieron menos variación en la cantidad de tiempo que pasaron en una cámara trampa. Por lo tanto, aunque los zorros kit comparten el hábitat urbano con múltiples competidores de mayor tamaño, es probable que utilicen la división espacial y temporal para reducir el riesgo y facilitar la coexistencia.

A competitive ecological guild forms when a group of biologically similar species have overlapping niches, sharing limiting resources (MacKenzie et al. 2006, Freeman 2011). Dominant, typically larger guild members can adversely affect subordinate, typically smaller members through interference competition (Case and Gilpin 1974). Interference competition consists of predation, harassment, or spatial exclusion of subordinate species by dominant species (Case and Gilpin 1974, Cypher et al. 2001). Intraguild predation is an

extreme mechanism of interference competition in which subordinate species are killed or excluded from habitats with abundant resources and must balance risk with access to resources (Polis et al. 1989, Heithaus 2001). Areas with higher risk of predation can lead to increased antipredator behavior in subordinate species, such as vigilance and changes in temporal or spatial foraging (Hall et al. 2013, Wang et al. 2015). Rather than avoiding a site altogether, subordinate species may avoid sites for some period following a visit

\*Corresponding author: ndeatherage@csu.edu

NAD  orcid.org/0000-0002-3485-750X

BLC  orcid.org/0000-0002-7349-545X

TLW  orcid.org/0000-0002-4043-6752

ECK  orcid.org/0000-0002-3033-1607

by a more dominant species, and such temporal partitioning may facilitate coexistence (White et al. 1994, Moll et al. 2018).

San Joaquin kit foxes (*Vulpes macrotis mutica*; hereafter kit fox) are endemic to the San Joaquin Valley of central California and are federally endangered and California State threatened, primarily because of habitat loss and degradation due to human development (Williams et al. 1998, Cypher et al. 2001, Cypher 2003). In natural environments, kit foxes are subject to interference competition from coyotes (*Canis latrans*), red foxes (*V. vulpes*), and gray foxes (*Urocyon cinereoargenteus*) due to overlap in habitat use, activity patterns, and diet (Cypher 2003, Macdonald 2009). Interference competition between canid species is facilitated with the use of scent marking and vocal and visual interspecific communications (Cypher 2003). Coyotes dominate over foxes due to their larger size, and in many locations they are the primary predator of foxes; however, coyotes do not typically consume fox kills, suggesting intraguild competition rather than sustenance as the likely cause of predation (Ralls and White 1995, Kitchen et al. 1999, Cypher et al. 2001, Farias et al. 2005). Because of their smaller stature, kit foxes are also occasionally killed by larger red foxes, which will enter and use kit fox dens (Ralls and White 1995, Williams et al. 1998, Cypher et al. 2001, Clark et al. 2005).

Kit foxes persist in some urban areas in the San Joaquin Valley, including in the city of Bakersfield, California (Williams et al. 1998, Cypher et al. 2013). Kit foxes are uniquely sympatric with coyotes, red foxes, and gray foxes within the city boundary (Cypher 2010), with red foxes being the only nonnative species of the guild in the region (Lewis et al. 1999). Domestic dogs (*C. familiaris*) are an additional canid species occurring in Bakersfield and may also participate in interference competition with wild canids. Free-roaming dogs can include free-ranging pet dogs, as well as semiferal dogs that rely partly on humans for resources (Moodie 1995). Free-roaming dogs tend to congregate where anthropogenic food is abundant (e.g., garbage dumps, accessible trash cans, and dumpsters; Macdonald and Carr 1995, Baker et al. 2010). Coyotes will regularly kill dogs, causing free-roaming dogs to avoid areas where coyotes are present (Quinn 1997, Crooks and Soulé

1999). Likewise, dogs have killed red foxes and kit foxes, and foxes may avoid areas where free-roaming dogs are present (Harris 1981, Cypher 2010).

Urban areas can provide animals with shelter in human-built structures, permanent water sources, and abundant anthropogenic food sources including refuse, food intentionally left out for animals, and planted fruits and vegetables (Harrison 1997, Fuller et al. 2010). Since opportunistic species such as coyotes and foxes appear in greater abundance within heavily human-populated areas, rapid ecological and behavioral adaptations are observed (Ditchkoff et al. 2006, Fuller et al. 2010, Moll et al. 2018). For instance, coyotes, red foxes, and gray foxes found in or near urban areas have shifted from cathemeral activity patterns observed in natural areas to largely nocturnal activities in response to increased human activity during the day, which may lead to increased temporal overlap and conflict between competitors (Harrison 1997, McClennen et al. 2001, Moll et al. 2018).

Recently, some urban populations of kit foxes have been negatively affected by sarcoptic mange, a highly contagious skin infestation caused by the *canis* variety of skin mite, *Sarcoptes scabiei* (Pence and Ueckermann 2002, Cypher et al. 2017); however, the kit fox population in the city of Bakersfield has constituted one of the largest populations and, as such, has been a central focus of kit fox research over the past 20 years (Cypher and Van Horn Job 2012). Previous studies on urban competition have focused on competitors from different taxonomic families or on intraguild groups consisting of a few species. The purpose of our study was to determine whether kit foxes utilize spatiotemporal partitioning with multiple larger competitors as a mechanism of coexistence within the urban environment. Using 5 years of remote camera data from an annual week-long, city-wide survey from 2015 to 2019, we investigated associations and differences in spatiotemporal activity of kit foxes in relation to other canids within 1-km<sup>2</sup> grid cells on daily, annual, and 5-year scales. Due to the territorial tendencies of larger canids to kill smaller species, we first predicted that kit foxes and other canids would rarely co-occur at camera traps within the same day or year. If kit foxes did occur with other canids within

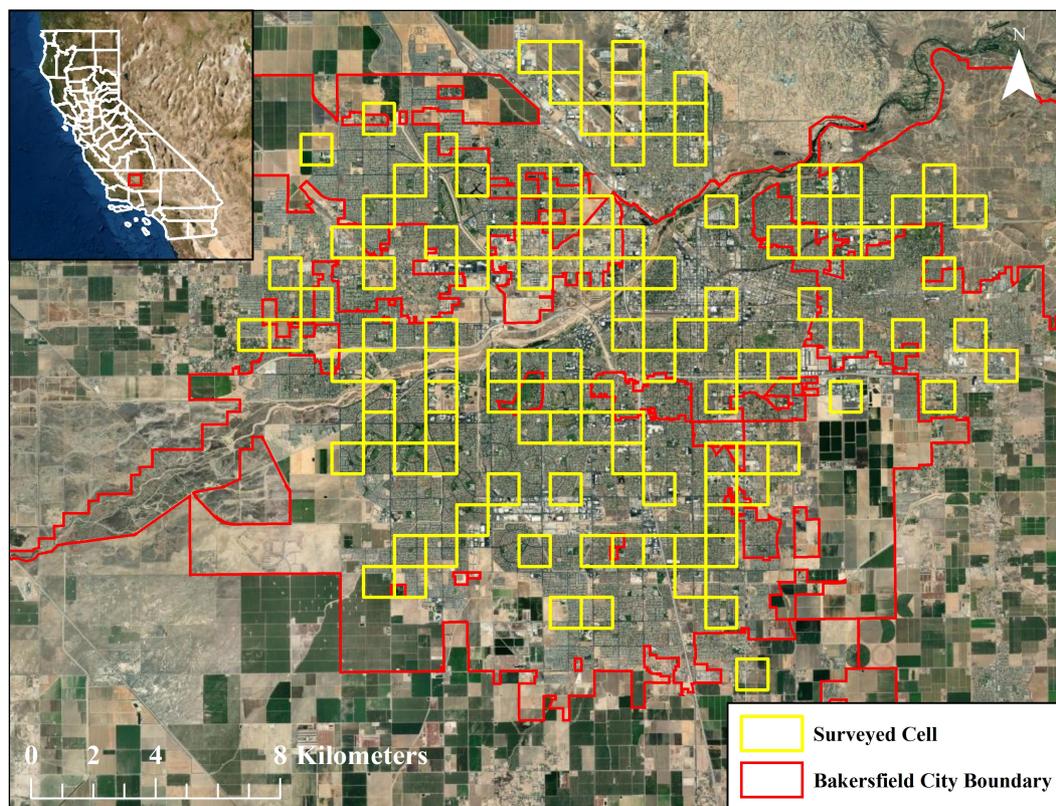


Fig. 1. Distribution of 111 1-km<sup>2</sup> grid cells used to monitor San Joaquin kit foxes (*Vulpes macrotis mutica*) in Bakersfield, California, from 2015 to 2019.

the same day, we further predicted that kit foxes would avoid other canids by delaying visitation to a camera trap when another canid was present and spend less time at the camera.

## METHODS

### Study Area

Bakersfield is located in western Kern County and is characterized by heavy urbanization with natural vegetation on 25%–30% of its boundary, including saltbush (*Atriplex* spp.) scrub, grassland, and riparian areas (Cypher 2010). The city encompasses a variety of urban land uses, including residential and commercial developments, recreational areas, preserved green spaces, industrial centers, agriculture, and campuses. The Kern River runs through the middle of the city and is accessible to the public. Due to water being diverted for agricultural purposes, only portions of the river contain water year-round within the city

(Shigley 2010). Vegetation within Bakersfield consists primarily of a mix of planted native and nonnative ornamental trees, shrubs, and flowering plants. A number of free-roaming dogs inhabit the city, with approximately 6700 dogs reported as stray intakes in Kern County in 2019 (Kern County Animal Services 2019).

### Field Methods

We conducted annual surveys from 2015 to 2019 to monitor the urban kit fox population in Bakersfield and used these data to investigate kit fox spatiotemporal activity in relation to canid competitors. We set one camera in each of 111 randomly selected 1-km<sup>2</sup> grid cells located throughout the 368-km<sup>2</sup> city, thus covering approximately 30% of the city (Fig. 1). We selected the cell size such that the average kit fox home range of 1.72 km<sup>2</sup> (Frost 2005) potentially included 2 cells, thus optimizing detection of kit foxes. Within cells, we selected camera locations that were accessible and

minimized potential theft. With a few exceptions due to human disturbance, camera locations remained consistent over the 5-year sampling period. Because 97.1% of kit foxes are typically detected at camera traps within 6 nights (Westall and Cypher 2017), we ran cameras for one week in midsummer outside of canid breeding and whelping season which might affect activity (Macdonald 2009). We programmed Cuddeback Black Flash E3 or C3 digital trail cameras (Cuddeback, Green Bay, Wisconsin, USA) to the highest sensitivity. We programmed the cameras to capture one image during the daylight hours after a 15-s delay and 2 images at night as fast as possible, triggered by motion sensors. We secured the cameras to t-posts, fences, or vegetation using zip ties at a height and angle appropriate for capturing images of kit foxes and other canid species. Excessive vegetation was removed within 2 m of camera setup to minimize unnecessary triggers and provide a clear view of the target. We baited camera traps with a punctured 5.5-oz can of wet cat food staked approximately 2 m in front of the camera with 30-cm nails. We added several drops of Carman's Canine Call carnivore scent lure to the can and surrounding vegetation (Minnesota Trapline Products, Inc., Pennock, Minnesota, USA). Canids can detect this scent lure from up to 1.6 km away (Westall and Cypher 2017).

We reviewed images captured by the cameras each year and recorded species and minimum number of individuals. Unless animals could be distinguished as different individuals (by size, sex, markings, or tags affixed to individuals during other projects), we counted multiple appearances of a species on a camera during a given session as the same individual because of the territoriality tendencies of canids. We reviewed photographs from camera traps where kit foxes, coyotes, red foxes, gray foxes, or dogs occurred, and recorded the number of cells and days these species visited. For each survey night on cameras where our target species occurred, we used the image date and time stamps to calculate the minutes elapsed between sunset and first appearances by the canid and also the consecutive minutes that kit foxes spent at a camera trap. If a kit fox was not detected for more than 10 min, time calculation ceased with the last kit fox image, which marked the

cutoff for a new encounter. We used sunset (United States Naval Observatory 2019) as our reference time due to the nocturnal nature of our target species.

#### Spatial Analyses

To determine whether there were associations among the occurrences of kit foxes and other canid species, we used two-way contingency tables to compare the number of days with and without visits by kit foxes to the number of days with and without visits by both kit foxes and at least one other canid within each survey year and across all survey years combined (Gotelli and Ellison 2013). Data were heteroscedastic in an *F* test for equal variances (all *P* values < 0.001; Gotelli and Ellison 2013); thus, we used Kruskal–Wallis tests to determine whether there was a difference between the median number of days that each camera trap was visited by only kit foxes and the median number of days a camera trap was visited by kit foxes and at least one other canid for each survey year and across all survey years combined.

#### Temporal Analyses

In instances where both kit foxes and other canids occurred, we tested for differences in the timing of visits by kit foxes in relation to other canids for all survey nights collectively using one-way analysis of variance and Tukey's honestly significant difference tests to compare the mean time to appearance (minutes from sunset to first kit fox appearances) on nights when (1) only kit foxes visited, (2) both kit foxes and other canids visited but kit fox appeared first, and (3) both kit foxes and other canids visited but other canids appeared first (Gotelli and Ellison 2013). We then compared the median time (number of consecutive minutes) that kit foxes spent at camera traps in each of the 3 scenarios using a Kruskal–Wallis test, as these data were heteroscedastic in a Bartlett's test for equal variances (Gotelli and Ellison 2013). To reduce bias from the strong influence humans have on the activity of pet dogs, we excluded dogs that appeared to be restricted-ranging pets—based on their visiting camera traps during daylight or having a collar or leash—from the finer-scaled temporal analysis (Moodie 1995). All statistical tests were run in Minitab 19 statistical software and significance was determined by an  $\alpha$  value of 0.05.

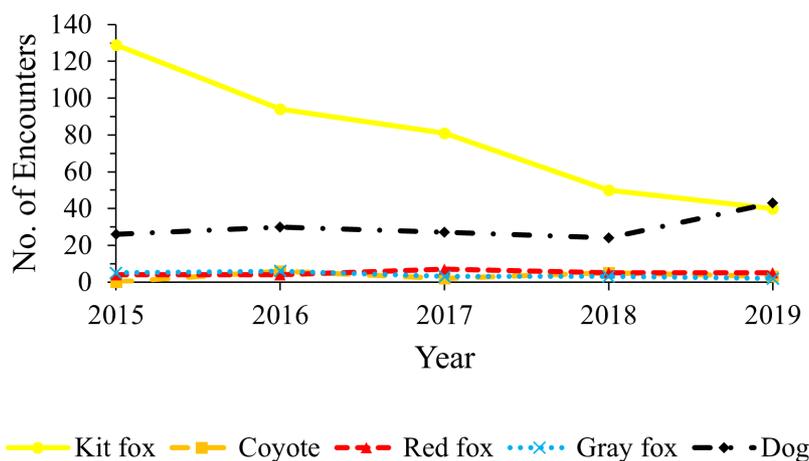


Fig. 2. Total number of encounters for San Joaquin kit fox (*Vulpes macrotis mutica*), domestic dog (*Canis familiaris*), red fox (*V. vulpes*), gray fox (*Urocyon cinereoargenteus*), and coyote (*C. latrans*) each year during a week-long, city-wide camera survey with  $n = 604$  target species encounters in Bakersfield, California, from 2015 to 2019.

TABLE 1. Total number of encounters (Enc.) as well as the number of grid cells in which, and survey days on which, each canid species occurred during an annual week-long, city-wide camera survey in Bakersfield, California, from 2015 to 2019. SJKF = San Joaquin kit fox (*Vulpes macrotis mutica*), dog = domestic dog (*Canis familiaris*), RF = red fox (*V. vulpes*), GF = gray fox (*Urocyon cinereoargenteus*), Coy = coyote (*C. latrans*). Sample size ( $n$ ) is given in the last line of the table.

Species	Enc.	Cells	Days
SJKF	394	205	690
Dog	150	80	170
RF	25	15	38
GF	19	18	31
Coy	16	10	19
Sample size ( $n$ )	604	545	3806

## RESULTS

Over the 5-year sampling period, we completed 545 week-long camera surveys for a total of 3806 survey days, completing 735 to 775 survey days within each year. The number of encounters, cells, and days in which focal species were detected in images was highest for kit foxes, followed by dogs, red foxes, gray foxes, and then coyotes (Table 1, Figs. 2, 3, 4). Although 2015 had the lowest number of survey days, this year had the highest number of kit fox encounters (33% of the total kit fox encounters) and the highest number of cells (25% of the total cells) and days (33% of the total days) in which kit foxes occurred across all survey years (Table 2). Kit fox encounters

declined annually through 2019, which had 763 survey days and 10% of the total number of kit fox encounters, as well as 7% of the total cells and 9% of the total days in which kit foxes occurred across all survey years (Table 2, Figs. 2, 3, 4). Overall, there was a 69% decrease in kit fox encounters over the 5-year sampling period (Table 2).

For any given cell or day each year, kit foxes occurred alone more frequently than they did with any other canid, occurring alone in 30% of the total cells and 17% of the total days across all years (Table 3). Less frequently, kit foxes occurred with dogs in 5% of cells and <1% of days across all years, then with coyotes and gray foxes in 1% of cells and <1% of days across all years, followed by red foxes in <1% of cells and days across all years (Table 3). Kit foxes occurred with 2 other canid species, gray fox and dog, at one camera trap in 2016, but they did not occur on the same day (Table 3). Due to low occurrences of other canids compared to kit foxes, we grouped coyote, red fox, gray fox, and dogs into a combined category for subsequent analysis.

## Spatial Analyses

We found one association between the number of days kit foxes occurred alone and the number of days kit foxes occurred with other canids in 2018 ( $\chi^2 = 4.922$ ,  $df = 1$ ,  $P = 0.027$ ), with no associations in the remaining

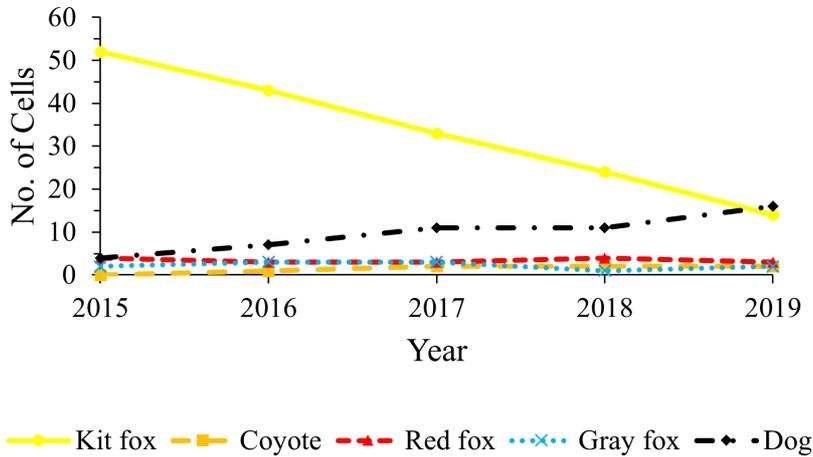


Fig. 3. Total number of grid cells in which San Joaquin kit fox (*Vulpes macrotis mutica*), domestic dog (*Canis familiaris*), red fox (*V. vulpes*), gray fox (*Urocyon cinereoargenteus*), and coyote (*C. latrans*) occurred each year during a week-long, city-wide camera survey of  $n = 105$  to 111 cells, depending on the year, in Bakersfield, California, from 2015 to 2019.

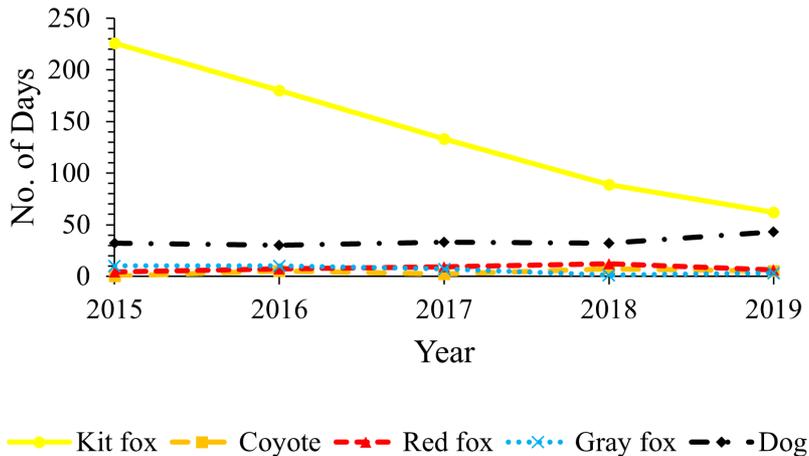


Fig. 4. Total number of days in which San Joaquin kit fox (*Vulpes macrotis mutica*), domestic dog (*Canis familiaris*), red fox (*V. vulpes*), gray fox (*Urocyon cinereoargenteus*), and coyote (*C. latrans*) occurred each year during a week-long, city-wide camera survey of  $n = 735$  to 775 survey days, depending on the year, in Bakersfield, California, from 2015 to 2019.

tests ( $\chi^2$  values range from 0.002 to 3.058, all  $df = 1$ , all  $P$  values  $> 0.05$ ). The number of days that camera traps were visited by only kit foxes was higher than the number of days that camera traps were visited by both kit foxes and other canids in all tests ( $H$  values range from 11.6 to 99.22, all  $df = 1$ , all  $P$  values  $< 0.001$ ). We observed a similar trend in mean days visited by kit foxes relative to that of other canids, with a decrease in days visited by kit foxes over the 5-year sampling period (Fig. 5).

#### Temporal Analyses

We found that kit foxes delayed visiting camera traps on nights when other canids appeared first but not on nights when only kit foxes occurred or nights when both kit foxes and other canids occurred but the kit fox appeared first ( $F_{2,556} = 4.82$ ,  $P = 0.008$ ; Tukey HSD:  $P \leq 0.05$ ; Fig. 6). Mean time to appearance for kit foxes was 3 h (492 min) later on nights when other canids appeared first and 2 h (178 min) earlier on nights when other canids occurred but did not appear first

TABLE 2. Total number of encounters (Enc.) as well as grid cells and days that each canid species occurred each year during a city-wide camera survey in Bakersfield, California, from 2015 to 2019. SJKF = San Joaquin kit fox (*Vulpes macrotis nuttica*), dog = domestic dog (*Canis familiaris*), RF = red fox (*V. vulpes*), GF = gray fox (*Urocyon cinereoargenteus*), Coy = coyote (*C. latrans*). Sample size ( $n$ ) is given in the last line of the table.

Species	2015			2016			2017			2018			2019		
	Enc.	Cells	Days												
SJKF	129	52	226	94	43	180	81	33	133	50	24	89	40	14	62
Dog	26	4	32	30	7	30	27	11	33	24	11	32	43	16	43
RF	4	4	4	4	3	7	7	3	9	5	4	12	5	3	6
GF	5	2	10	6	3	10	3	3	7	3	1	1	2	2	3
Coy	0	0	0	6	1	5	2	2	2	5	2	7	3	2	5
Sample size ( $n$ )	164	105	735	140	111	775	120	109	763	87	110	770	93	110	763

TABLE 3. Number of grid cells and days that San Joaquin kit foxes occurred alone or with another canid species each year and across all years during a city-wide camera survey in Bakersfield, California, from 2015 to 2019. SJKF = San Joaquin kit fox (*Vulpes macrotis nuttica*), dog = domestic dog (*Canis familiaris*), RF = red fox (*V. vulpes*), GF = gray fox (*Urocyon cinereoargenteus*), Coy = coyote (*C. latrans*). Sample size ( $n$ ) is given in the last line of the table.

Species	2015			2016			2017			2018			2019			2015–2019		
	Cells	Days	Days	Cells	Days	Days												
SJKF only	52	212	172	43	172	127	33	127	24	88	14	55	166	654				
SJKF, Dog	12	13	5	5	6	6	6	6	3	1	1	4	27	29				
SJKF, RF	2	0	0	0	0	0	0	0	0	0	0	0	2	0				
SJKF, GF	2	1	1	1	1	0	0	0	0	0	1	0	4	2				
SJKF, GF, Dog	0	0	0	1	0	0	0	0	0	0	0	0	1	0				
SJKF, Coy	0	0	2	2	0	0	1	0	1	0	2	3	5	5				
Sample size ( $n$ )	105	735	775	111	775	763	110	770	110	770	110	763	545	3806				

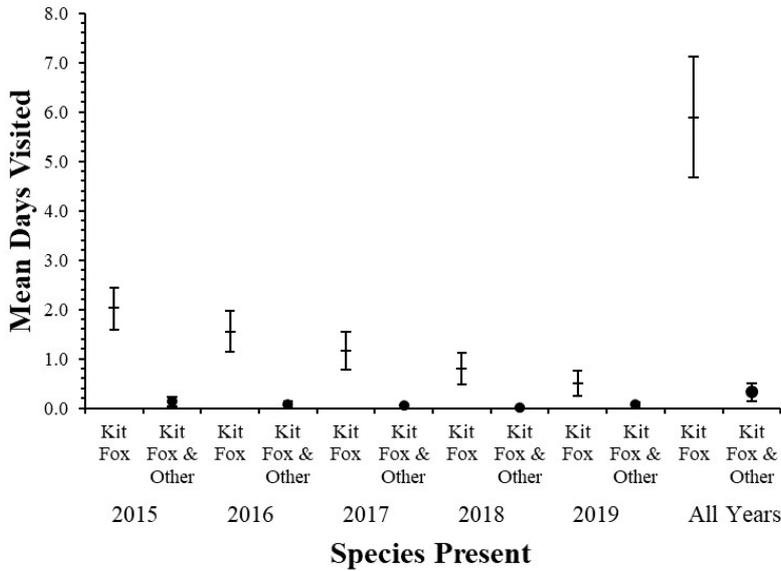


Fig. 5. Mean number of days (with 95% confidence interval bars) that camera traps were visited by only San Joaquin kit foxes (*Vulpes macrotis mutica*) (lines) or by kit foxes and coyotes (*Canis latrans*), red foxes (*V. vulpes*), gray foxes (*Urocyon cinereoargenteus*), or domestic dogs (*C. familiaris*) (circles) each year from 2015 to 2019, as well as for all years combined, during an annual survey consisting of  $n = 735$  to 775 days, depending on the year, in Bakersfield, California.

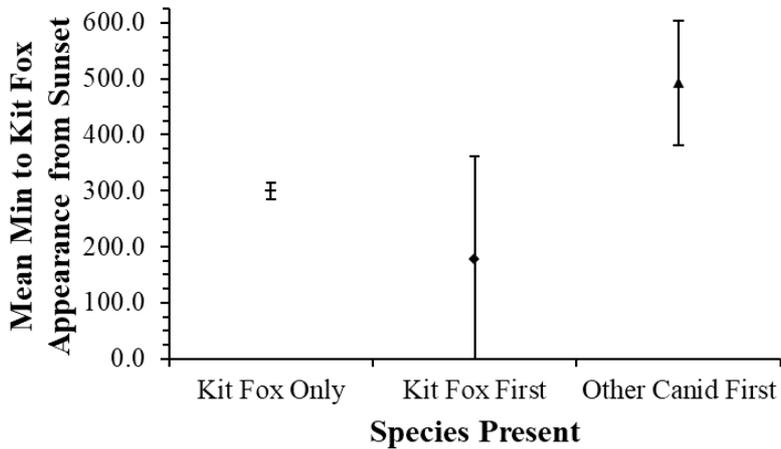


Fig. 6. Mean number of minutes (with 95% confidence interval bars) to first San Joaquin kit fox (*Vulpes macrotis mutica*) appearances at camera traps following sunset during an annual camera survey in Bakersfield, California, from 2015 to 2019. The dash represents nights when only kit foxes occurred ( $n = 549$ ); the diamond represents nights when both kit foxes and other canids (coyotes [*Canis latrans*], red foxes [*V. vulpes*], gray foxes [*Urocyon cinereoargenteus*], or domestic dogs [*C. familiaris*]) occurred, but the kit fox appeared on camera first ( $n = 4$ ); and the triangle represents nights when both kit foxes and other canids occurred, but the other canid appeared on camera first ( $n = 6$ ).

when compared to appearances on nights when only kit foxes visited, which occurred 5 h (300 min) after sunset (Fig. 6). We did not find differences between the median time that kit foxes spent at cameras traps in any of the

3 scenarios ( $H = 1.12$ ,  $df = 2$ ,  $P = 0.571$ ); however, variances in consecutive minutes that a kit fox spent at a camera trap between the 3 scenarios were heteroscedastic ( $B = 27.02$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 7). Kit foxes

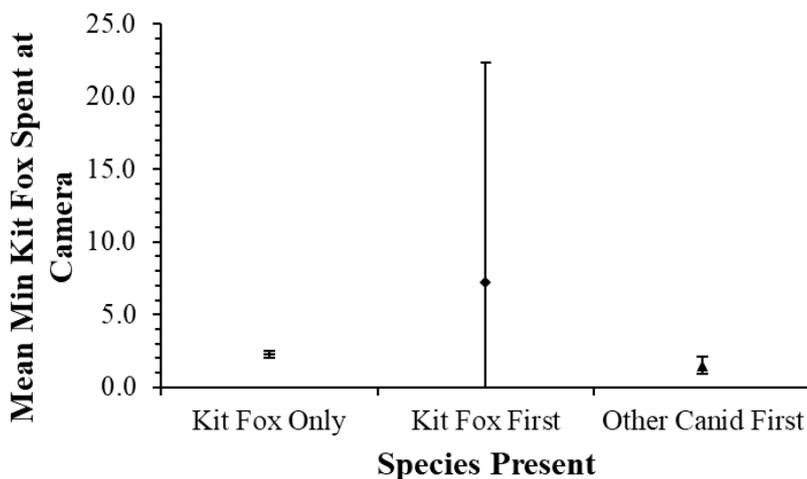


Fig. 7. Mean consecutive minutes (with 95% confidence interval bars) in which a San Joaquin kit fox (*Vulpes macrotis mutica*) appeared on camera traps during an annual camera survey in Bakersfield, California, from 2015 to 2019. The dash represents nights when only kit foxes occurred ( $n = 549$ ); the diamond represents nights when both kit foxes and other canids (coyotes [*Canis latrans*], red foxes [*V. vulpes*], gray foxes [*Urocyon cinereoargenteus*], or domestic dogs [*C. familiaris*]) occurred, but the kit fox appeared on camera first ( $n = 4$ ); and the triangle represents nights when both kit foxes and other canids occurred, but the other canid appeared on camera first.

exhibited greater variation in the amount of time spent at a camera trap on nights when both kit foxes and other canids occurred but the kit fox appeared first ( $s^2 = 89.58$ ), followed by nights when kit foxes were the only canid visitor ( $s^2 = 10.13$ ). Kit foxes exhibited the lowest variation in time spent at a camera trap on nights when both kit foxes and other canids occurred, but the other canid appeared first, with kit foxes spending up to 2 min at a camera trap ( $s^2 = 0.30$ ).

#### DISCUSSION

Kit foxes primarily did not occur or were not associated with other canids on days across all years collectively and within most years, suggesting spatial partitioning among kit foxes and other canids in Bakersfield. Our results are consistent with our prediction that kit foxes would rarely occur with other canids at the same camera trap within the same day and year, and they further show that kit foxes rarely occur with other canids within a 5-year span. Past studies in urban areas have found that red foxes prefer suburbs (<20 houses/ha), gray foxes prefer urban edges or heavily vegetated areas, and coyotes prefer suburbs or more natural habitat within cities (Gosselink et al. 2003, Gehrt et al.

2009, Lesmeister et al. 2015). Kit foxes are commonly observed denning in man-made structures throughout Bakersfield (Cypher and Van Horn Job 2012), and kit fox occupancy in the city may be driven by a selection for campus-type land use, such as manicured school and church grounds, as urban habitat (Deatherage et al. 2021). Campuses may provide kit foxes with protection from larger predators like coyotes with the use of security fencing (Deatherage et al. 2021). In the Great Basin Desert of western Utah, USA, desert kit foxes (*V. m. arsipus*) in urban areas also foraged and denned near highly developed areas that afforded protection from coyotes (Kozlowski et al. 2008).

On a finer spatial scale, in instances where kit foxes and other canids did co-occur, the presence of another canid did not discourage the use of that area by kit foxes on the same night unless the other canid arrived first, in which case kit foxes appeared later and showed reduced variance in the time spent in the area. These results also align with our prediction that other canids would discourage a kit fox from approaching bait. Studies involving other canid guilds have demonstrated similar patterns of temporal avoidance as a means of minimizing competition. In northeastern Argentina, pampas foxes (*Lycalopex gymnocercus*) reduced

their activity at times when a more dominant competitor, the crab-eating fox (*Cerdocyon thous*), was highly active (Di Bitetti et al. 2009). In central India, Indian foxes (*V. bengalensis*) reduced their visitation rates to food stations, spent less time at the food, and increased their vigilant behavior when a dog was visible; however, the presence of dog odors had little effect on fox activity (Vanak et al. 2009). Similarly, in Israel, the presence of jackals (*Canis aureus*) prevented red foxes from visiting food stations, yet jackal odors had little effect on behavior (Scheinin et al. 2006). Because there is a trade-off between predator avoidance, foraging efficiency, and overall fitness, a more immediate predator presence may be required to produce a discernable effect on perceived risk to the subordinate species (Haswell et al. 2018). This was observable in our results, as kit foxes only altered activity in response to another canid having already arrived at the camera station.

Our camera surveys detected mostly kit foxes, followed by dogs. Kit foxes apparently occur in higher abundances in urban areas than in nonurban habitats (B.L. Cypher unpublished data) due to their generalist foraging and habitat requirements, ability to utilize anthropogenic structures, modest space requirements, small size, and minimal conflict with humans (Cypher 2010). Dogs also persist in close proximity to human development due to their dependence on anthropogenic food sources (Vanak and Gompper 2009) and are abundant in urban areas. Therefore, sign of dog presence such as odor may not be novel or threatening to kit foxes (Vanak et al. 2009), allowing kit foxes and dogs to be detected in higher numbers in our study. Additionally, canids may only be capable of coexistence with one other canid species at any given time (Lesmeister et al. 2015), which is consistent with our study in which kit foxes occurred alone more frequently than with another canid, followed by occurrences only with dogs.

The sizable decrease in kit fox encounters over the course of our study presumably demonstrates the negative impact of sarcoptic mange in the Bakersfield population, which was first noted in 2013 and is 100% fatal in untreated kit foxes (Cypher et al. 2017). Sarcoptic mange affects over 100 mammalian species, including humans (Pence and Ueckermann 2002), although the mite is highly variable and often host restricted (Rasero et

al. 2010, Rudd et al. 2020). Mite varieties that affect kit foxes may also affect other canids, although kit foxes in Bakersfield may be more at risk due to the high densities at which they occur within the city (Rudd et al. 2020). Sarcoptic mange could further impact intraguild dynamics that depend on species densities (Case and Gilpin 1974). At lower kit fox densities due to mange, spatiotemporal overlap with other canids may be reduced, and kit foxes may not need to rely as heavily on partitioning space and time with larger competitors. Conversely, at higher kit fox densities, in areas or time periods where mange is not prevalent, kit foxes might overlap more with other canids and may need to rely more on such partitioning for coexistence.

Our study demonstrated that kit foxes in an urban environment reduce risk from sympatric, larger intraguild competitors through spatial and temporal partitioning. Understanding behavioral dynamics within canid guilds in urban areas can aid conservation strategies for kit fox areas affected by urbanization. Conservation efforts such as discouraging kit foxes from urban construction projects and locating and managing mitigation or refuge lands should consider the presence and abundance of larger competitors. Conserving the kit fox population in Bakersfield would help to encourage and maintain the number of remaining populations and individuals of this endangered species (Cypher 2010).

#### ACKNOWLEDGMENTS

The Endangered Species Recovery Program (ESRP) personnel Larry Saslaw and Christine Van Horn Job assisted in data collection and analysis. Dr. David J. Germano and Dr. Carl T. Kloock of California State University, Bakersfield, assisted with data analysis and edited drafts of this manuscript. Funding for this study was generously provided by ESRP, the San Joaquin Valley Chapter of The Wildlife Society, and the Western Section of The Wildlife Society.

#### LITERATURE CITED

- BAKER, P.J., C.D. SOULSBURY, G. IOSSA, AND S. HARRIS. 2010. Domestic cat (*Felis catus*) and domestic dog (*Canis familiaris*). Pages 157–171 in S.D. Gehrt, S.P.D. Riley, and B.L. Cypher, editors, Urban carnivores: ecology, conflict, and conservation. Johns Hopkins University Press, Baltimore, MD.

- CASE, T.J., AND M.E. GILPIN. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences of the United States of America 71:3073–3077.
- CLARK, H.O., JR., G.D. WARRICK, B.L. CYPHER, P.A. KELLY, D.F. WILLIAMS, AND D.E. GRUBBS. 2005. Competitive interactions between endangered kit foxes and non-native red foxes. *Western North American Naturalist* 65:153–163.
- CROOKS, K.R., AND M.E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- CYPHER, B.L. 2003. Foxes. Pages 511–546 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors, *Wild mammals of North America: biology, management, and conservation*. 2nd edition. Johns Hopkins University Press, Baltimore, MD.
- CYPHER, B.L. 2010. Kit foxes (*Vulpes macrotis*). Pages 49–57 in S.D. Gehrt, S.P.D. Riley, and B.L. Cypher, editors, *Urban carnivores: ecology, conflict, and conservation*. Johns Hopkins University Press, Baltimore, MD.
- CYPHER, B.L., H.O. CLARK JR., P.A. KELLY, C. VAN HORN JOB, G.D. WARRICK, AND D.F. WILLIAMS. 2001. Interspecific interactions among wild canids: implications for the conservation of endangered San Joaquin kit foxes. *Endangered Species Update* 18:171–174.
- CYPHER, B.L., S.E. PHILIPS, AND P.A. KELLY. 2013. Quantity and distribution of suitable habitat for endangered San Joaquin kit foxes: conservation implications. *Canid Biology and Conservation* 16:25–31.
- CYPHER, B.L., J.L. RUDD, T.L. WESTALL, L.W. WOODS, N. STEPHENSON, J.E. FOLEY, D. RICHARDSON, AND D.L. CLIFFORD. 2017. Sarcoptic mange in endangered kit foxes (*Vulpes macrotis mutica*): case histories, diagnoses, and implications for conservation. *Journal of Wildlife Diseases* 53:46–53.
- CYPHER, B.L., AND C.L. VAN HORN JOB. 2012. Management and conservation of San Joaquin kit foxes in urban environments. Pages 347–352 in Proceedings of the Vertebrate Pest Conference, 1 January 2012. University of California, Davis, CA.
- DEATHERAGE, N.A., B.L. CYPHER, J. MURDOCH, T.L. WESTALL, E.C. KELLY, AND D.J. GERMANO. 2021. Urban landscape attributes affect occupancy patterns of the San Joaquin kit fox during an epizootic. *Pacific Conservation Biology*. <https://doi.org/10.1071/PC20059>
- DI BITETTI, M.S., Y.E. DI BLANCO, J.A. PEREIRA, A. PAVIOLO, AND I.J. PÍREZ. 2009. Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cerdocyon thous*) and pampas foxes (*Lycalopex gymnocercus*). *Journal of Mammalogy* 90:479–490.
- DITCHKOFF, S.S., S.T. SAALFELD, AND C.J. GIBSON. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems* 9:5–12.
- FARIAS, V., T.K. FULLER, R.K. WAYNE, AND R.M. SAUVAJOT. 2005. Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in southern California. *Journal of Zoology* 266:249–254.
- FREEMAN, S. 2011. An introduction to ecology. Pages 993–1127 in B. Wilbur, B. Ruden, S. DiVittorio, A. Fugate, M. Lerner-Nelson, W. O’Neal, S. Teahan, K. Murphy, B. Golden, and L. Allen, editors, *Biological science*. 4th edition. Pearson Education, Inc., San Francisco.
- FROST, N. 2005. San Joaquin kit fox home range, habitat use, and movements in urban Bakersfield. Master’s thesis, Humboldt State University, Arcata, CA.
- FULLER, T.K., S. DESTEFANO, AND P.S. WARREN. 2010. Carnivore behavior and ecology, and relationship to urbanization. Pages 18–19 in S.D. Gehrt, S.P.D. Riley, and B.L. Cypher, editors, *Urban carnivores, ecology, conflict, and conservation*. Johns Hopkins University Press, Baltimore, MD.
- GEHRT, S.D., C. ANCHOR, AND L.A. WHITE. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *Journal of Mammalogy* 90:1045–1057.
- GOSSELINK, T.E., T.R. VAN DEELEN, R.E. WARNER, AND M.G. JOSELYN. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. *Journal of Wildlife Management* 67:90–103.
- GOTELLI, N.J., AND A.M. ELLISON. 2013. *A primer of ecological statistics*. Sinauer Associates, Inc., Sunderland, MA.
- HALL, L.K., C.C. DAY, M.D. WESTOVER, R.J. EDGEL, R.T. LARSEN, R.N. KNIGHT, AND B.R. MCMILLAN. 2013. Vigilance of kit foxes at water sources: a test of competing hypotheses for a solitary carnivore subject to predation. *Behavioural Processes* 94:76–82.
- HARRIS, S. 1981. An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. *Journal of Applied Ecology* 18:455–465.
- HARRISON, R.L. 1997. A comparison of grey fox ecology between residential and undeveloped rural landscapes. *Journal of Wildlife Management* 61:112–122.
- HASWELL, P.M., K.A. JONES, J. KUSAK, AND M.W. HAYWARD. 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia* 187:573–583.
- HEITHAUS, M.R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos* 92:542–554.
- KERN COUNTY ANIMAL SERVICES. 2019. Director’s yearly report. PDF document; [accessed January 2021]. <https://www.kerncountyanimalservices.org/media/1795/monthlyreport201912.pdf>
- KITCHEN, A.M., E.M. GESE, AND E.R. SCHAUSTER. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *Canadian Journal of Zoology* 77:1645–1656.
- KOZŁOWSKI, A.J., E.M. GESE, AND W.M. ARJO. 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. *American Midland Naturalist* 160:191–208.
- LESMEISTER, D.B., C.K. NIELSEN, E.M. SCHAUBER, AND E.C. HELLGREN. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. *Wildlife Monographs* 191:1–61.
- LEWIS, J.C., K.L. SALLEE, AND R.T. GOLIGHTLY. 1999. Introduction and range expansion of nonnative red foxes (*Vulpes vulpes*) in California. *American Midland Naturalist* 142:372–381.
- MACDONALD, D.W., EDITOR. 2009. Carnivores. Pages 598–611 in *The Princeton encyclopedia of mammals*. Princeton University Press, Princeton, NJ.
- MACDONALD, D.W., AND G.M. CARR. 1995. Variation in dog society: between resource dispersion and social flux. Pages 199–216 in J. Serpell, editor, *The domestic dog: its evolution, behaviour and interactions with people*. Cambridge University Press, Cambridge, U.K.
- MACKENZIE, D.I., J.A. ROYLE, J.D. NICHOLS, J.E. HINES, K.H. POLLOCK, AND L. BAILEY. 2006. Occupancy

- estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Burlington, MA.
- MCCLENNEN, N., R.R. WIGGLESWORTH, AND S.H. ANDERSON. 2001. The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). *American Midland Naturalist* 146: 27–36.
- MOLL, R.J., J.D. CEPEK, P.D. LORCH, P.M. DENNIS, T. ROBISON, J.J. MILLSPAUGH, AND R.A. MONTGOMERY. 2018. Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems* 21:765–778.
- MOODIE, E. 1995. The potential for biological control of feral cats in Australia. Report. Australian Nature Conservancy Agency, Canberra, Australia.
- PENCE, D.B., AND E. UECKERMANN. 2002. Sarcoptic mange in wildlife. *Scientific and Technical Review of the Office International des Epizooties* 21:385–398.
- POLIS, G.A., C.A. MYERS, AND R.D. HOLT. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- QUINN, T. 1997. Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. *Northwest Science* 71:1–5.
- RALLS, K., AND P.J. WHITE. 1995. Predation on San Joaquin kit foxes by larger canids. *Journal of Mammalogy* 76:723–729.
- RASERO, R., L. ROSSI, D. SOGLIA, S. MAIONE, P. SACCHI, L. RAMBOZZI, S. SARTORE, R.C. SORIGUER, V. SPALENZA, AND S. ALASAAD. 2010. Host taxon-derived *Sarcoptes* mite in European wild animals revealed by microsatellite markers. *Biological Conservation* 143: 1269–1277.
- RUDD, J.L., D.L. CLIFFORD, B.L. CYPHER, J.M. HULL, A.J. RINER, AND J.E. FOLEY. 2020. Molecular epidemiology of a fatal sarcoptic mange epidemic in endangered San Joaquin kit foxes (*Vulpes macrotis mutica*). *Parasites and Vectors* 13:456.
- SCHEININ, S., Y. YOM-TOV, U. MOTRO, AND E. GEFFEN. 2006. Behavioral responses of red foxes to an increase in the presence of golden jackals: a field experiment. *Animal Behavior* 71:577–584.
- SHIGLEY, P. 2010. Bakersfield hopes to restore water to Kern River. *Planning* (Chicago, Ill.: 1969) 76:8.
- UNITED STATES NAVAL OBSERVATORY. 2019. Astronomical Applications Department Data. [Accessed September 2019]. <https://www.usno.navy.mil/USNO/astromical-applications/data-services>
- VANAK, A.T., AND M.E. GOMPPER. 2009. Dogs *Canis familiaris* as carnivores: their role and function in intra-guild competition. *Mammal Review* 39:265–283.
- VANAK, A.T., M. THAKER, AND M.E. GOMPPER. 2009. Experimental examination of behavioural interactions between free-ranging wild and domestic canids. *Behavioral Ecology and Sociobiology* 64:279–287.
- WANG, Y., M.L. ALLEN, AND C.C. WILMERS. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation* 190:23–33.
- WESTALL, T.L., AND B.L. CYPHER. 2017. Latency to first detection of kit foxes (*Vulpes macrotis*) during camera surveys. *Canid Biology and Conservation* 20:32–37.
- WHITE, P.J., K. RALLS, AND R.A. GARROTT. 1994. Coyote–kit fox interactions as revealed by telemetry. *Canadian Journal of Zoology* 72:1831–1836.
- WILLIAMS, D.F., E.A. CYPHER, P.A. KELLY, K.J. MILLER, N. NORVELL, S.E. PHILLIPS, C.D. JOHNSON, AND G.W. COLLIVER. 1998. San Joaquin kit fox (*Vulpes macrotis mutica*). Pages 122–136 in *Recovery plan for upland species of the San Joaquin Valley, California. Region 1*, U.S. Fish and Wildlife Service, Portland, OR.

Received 18 January 2021

Revised 11 June 2021

Accepted 9 July 2021

Published online 15 March 2022