



Spatial relationships between mesocarnivores and domestic species in an urban environment and implications for endangered San Joaquin kit foxes

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Abstract

In the city of Bakersfield, CA, endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) occur with raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*), all of which share the urban landscape with an abundance of domestic dogs (*Canis familiaris*) and cats (*Felis catus*). Interactions between domestic and wild carnivores range from ambivalent to competitive and coexistence may be facilitated by partitioning space, time, and resources. An understanding of these mechanisms among increasing urbanization is of particular importance for the conservation of San Joaquin kit foxes. We used annual survey data and quantified urban land uses in multi-scaled χ^2 spatial analyses and occupancy modeling to explore how kit foxes and three other mesocarnivores manage cohabitation with dogs and cats. Cat occupancy was driven by a negative association with open spaces, skunk occupancy was driven by a negative association with commercial land uses and a positive association with industrial land uses, and opossum occupancy was driven by a negative association with open spaces as well as a positive association with parks. Kit foxes occurred mostly independently of dogs and cats, though showed some fine-scale spatial avoidance of cats. Opossums exhibited fine-scale spatial avoidance of dogs while raccoons and skunks exhibited fine-scale spatial coexistence with cats. Ultimately, these species select for different urban landscapes and mesocarnivores show varying changes in space use when sharing a landscape immediately with domestic species which may help facilitate coexistence between wild mesocarnivores and domestic species in Bakersfield.

Keywords Adaptation · Mesocarnivore · Domestic species · Endangered species · Trail cameras · Urban wildlife

Introduction

Over half of the world's human population currently resides in urban areas, with this figure projected to increase to nearly 70% by 2050 (United Nations, Department of Economic and Social Affairs, Population Division 2019). With habitat loss the leading cause of extinction in wild animals, species in areas of encroaching urban development must adapt or risk extinction (Gehrt 2010; Primack and Morrison 2013). As compared to natural ecosystems, urban environments have increased ambient temperature, available surface water, light and noise pollution, non-native species, and habitat

heterogeneity and fragmentation (Gehrt 2010). Wildlife in urban areas may benefit from additional available resources including anthropogenic foods and refuge, though may be impeded by unfamiliar dangers such as roads, pollutants, poisons, parasites, and disease (Fuller et al. 2010; Gehrt 2010). Urban wildlife also share the landscape with an abundance of domestic dogs (*Canis familiaris*) and cats (*Felis catus*). Dogs and cats are typically the most abundant and ubiquitous carnivores in urban areas due to their close relationship with humans (Baker et al. 2010). Dogs and cats may serve as competitors, predators, or prey to urban wildlife and can be hosts for contagious pathogens (Beck 1973; Bradley and Altizer 2006; Gehrt 2010). Activity patterns of free-roaming dogs and cats concentrate around available food, water, and shelter that are often provided by human caretakers, as well as the availability of reproductive conspecifics (Baker et al. 2010). Both dogs and cats will avoid areas frequented by larger predators and are commonly observed after dark (Berman and Dunbar 1983; Baker et al. 2010).

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Wild carnivores in urban environments may exhibit changes in home range sizes, primary food sources, litter sizes, and survival rates as compared to conspecifics in natural environments (Iossa et al. 2010). Several mesocarnivores are found in the city of Bakersfield, California, including coyotes (*C. latrans*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), San Joaquin kit foxes (*V. macrotis mutica*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*). Red foxes and opossums are not native to the area and San Joaquin kit foxes (hereafter, kit fox) are listed as federally Endangered and Threatened in California due to habitat loss and degradation (Gardner 1982; Lewis et al. 1993; United States Fish and Wildlife Service 1998). In urban environments these species are generally nocturnal, occur in higher densities with smaller home ranges, den in a variety of landscape features including under or within man-made structures, and will opportunistically consume anthropogenic food sources (Rosatte and Larivière 2003; Cypher 2010; Gehrt and Riley 2010; Hadidian et al. 2010; Rosatte et al. 2010; Soulsbury et al. 2010; Wright et al. 2012; Lombardi et al. 2017). Proclivity for certain landscapes within the urban matrix by carnivores may be a result of microhabitat preferences as well as avoidance of predators or competitors (Crooks et al. 2010). Patterns in past studies on urban carnivores suggest coyotes, red foxes, and gray foxes will select for more natural or undeveloped fragments in the urban landscape (Ansell 2004; Gehrt and Riley 2010; Soulsbury et al. 2010; Kapfer and Kirk 2012). Kit foxes and skunks prefer maintained green spaces with large yards such as schools, golf courses, and churches, and will also select for open space such as water catchment basins and canals (Rosatte et al. 1991, 2010; Frost 2005; Deatherage et al. 2021). Raccoons and opossums prefer areas near water and raccoons further select for tree cover and use residential areas, focusing activity around anthropogenic food sources such as picnic areas and garbage receptacles (Bozek et al. 2007; Hadidian et al. 2010; Fidino et al. 2016).

Interactions among domestic and wild carnivores range from ambivalent to competitive and are dependent on habitat type, species abundances, food habits, resource availability, body size differences, and behavior, and can have dramatic consequences on the structure of carnivore communities (Crooks et al. 2010; Fuller et al. 2010). Larger carnivores will sometimes kill smaller carnivores for food or competitive reasons; coyotes will attack all the smaller species, larger dogs will also attack coyotes and the smaller species, and red foxes will occasionally attack cats, kit foxes, and skunks (Harris 1981; Crooks and Soulé 1999; Kamler et al. 2003; Cypher 2003; Farias et al. 2005; Gosselink et al. 2007; Baker et al. 2010; Hadidian et al. 2010; Shedden et al. 2020). Ecologically similar species can facilitate coexistence with antagonistic competitors by partitioning time, space, and

resources (Schoener 1974). Consequently, cats and opossums have been shown to have consistent negative spatial and temporal relationships with coyotes in San Diego, CA (Crooks and Soulé 1999). Conversely, cats and skunks have been observed denning simultaneously with kit foxes and each other (Cypher 2010).

Changes in frequency and intensity of interspecific interactions are anticipated in urban areas as distributions are limited by impeding development and population densities tend to be elevated (Cypher 2010; Hadidian et al. 2010; Riley et al. 2010). The fragmentation of urban landscapes tends to concentrate some carnivores into remaining natural or green spaces, leading to an increase in interactions (Parsons et al. 2019). Little is known about how species respond to frequent encounters in urban areas, particularly between wild mesocarnivores and novel domestic competitors. While coexistence between domestic and wild carnivores is a necessary adaptation for urban living, risks of high population densities include increased competition, predation, and disease transmission. These risks are of particular concern for endangered species like the kit fox.

We used presence/absence data to investigate how kit foxes and three other mesocarnivores: raccoons, skunks, and opossums, manage cohabitation with ubiquitous domestic dogs and cats in the urban environment of Bakersfield. We used chi-square analyses to test spatial relationships between domestic species and wild mesocarnivores on two spatial scales. We also used occupancy modeling to investigate urban landscape preferences for the species and further co-occurrence patterns between domestic species and kit foxes. We expected cats and opossums to prefer similar urban landscapes that included easy access to resources such as parks and other maintained green space and expected skunks would select for more undeveloped or open areas. We also expected kit foxes and the other mesocarnivores would occur independently of cats while showing some spatial avoidance of dogs due to the tendency of dogs to kill the smaller species.

Methods

Study area

The city of Bakersfield is located in Kern County, within the southeastern San Joaquin Valley of Central California. The area is generally flat with elevations roughly between 30 and 183 m above sea level (Stachelski and Sanger 2008). Hot, dry summers, and cool, wet winters characterize the desert climate, with average daily maximum temperatures ranging from 14°C in December to 37°C in July and average daily minimum temperatures ranging from 4°C in December to 21°C in July (National

Oceanic and Atmospheric Administration 2020). Annual precipitation averages 16.4 cm but varies greatly between years (National Oceanic and Atmospheric Administration 2020).

Bakersfield is a heavily developed city with a growing population of nearly 380,000 people. Only 25 – 30% of Bakersfield abuts natural environments including arid grasslands, shrublands, and riparian areas, with the remainder bordered by agriculture (Cypher 2010). Bakersfield encompasses a variety of urban land uses including commercial developments, preserved green spaces, agriculture, campuses, residential, recreational, and industrial areas. The Kern River runs through the city though typically only portions of the corridor contain water year-round due to diversion for agriculture. Vegetation in the city consists primarily of a mix of planted native and non-native ornamental trees, shrubs, and flowering plants. A multitude of free-roaming dogs and cats inhabit the area, with approximately 6,600 dogs and 5,500 cats reported as stray intakes at Kern

County Animal Services in 2019 (Kern County Animal Services 2019).

Study design

We conducted annual camera surveys throughout Bakersfield from 2015 to 2021 using camera station methodology developed specifically to survey for kit foxes and other sympatric mesocarnivores (Westall and Cypher 2017). We established a sampling grid of up to 111 1-km² cells to be surveyed each year, randomly selected from a total of 358 cells that contained $\geq 50\%$ urban development, thus sampling approximately 31% of the city (Fig. 1). Each cell was roughly representative of the average kit fox home range of 0.78 km² in urban areas (Cypher et al. 2023). Studies have shown the other species to also have home ranges smaller than or close to 1 km² in urban areas (Rosatte et al. 1991; Gehrt 2004; Baker et al. 2010; Wright et al. 2012). We placed one motion-triggered trail camera (Black Flash

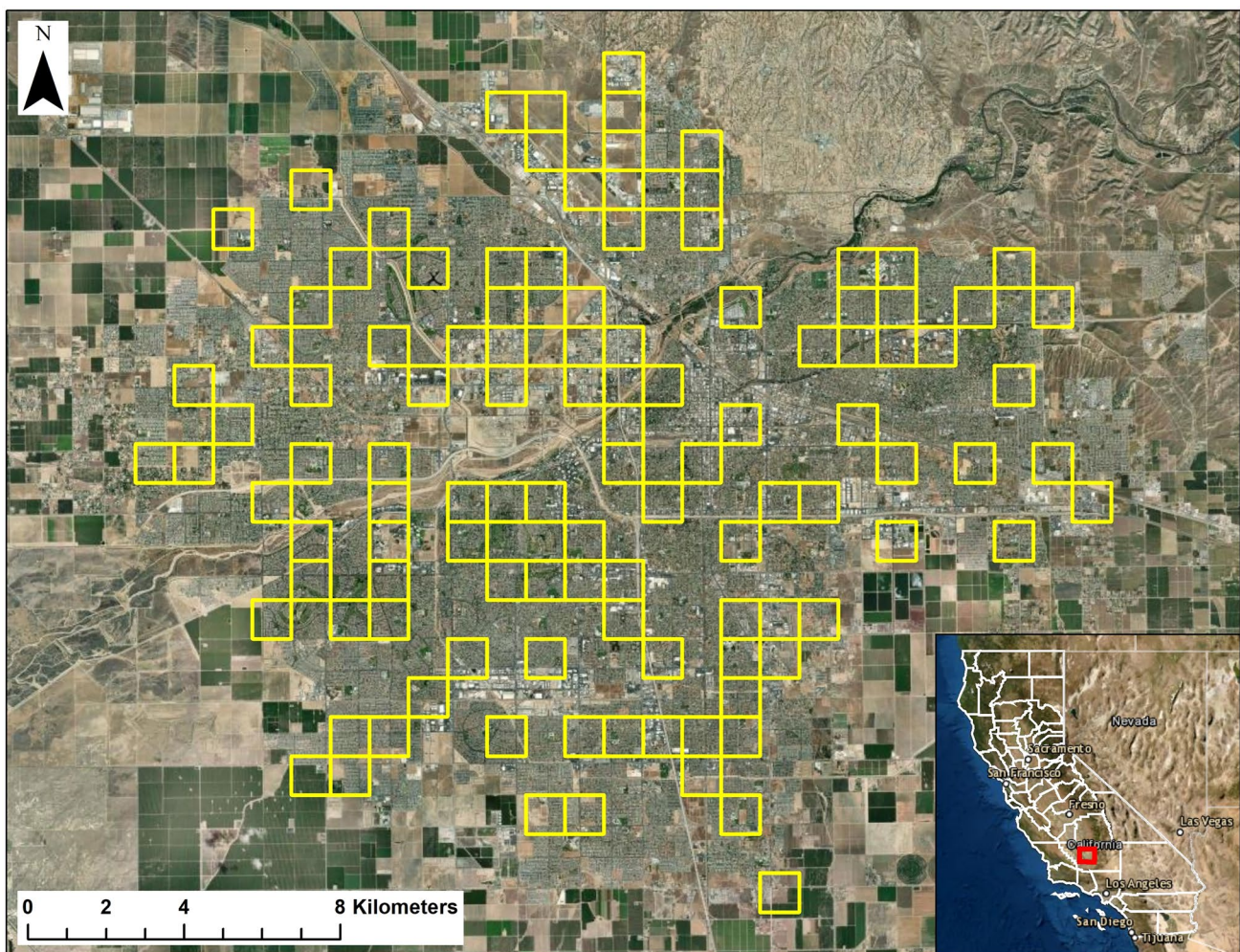


Fig. 1 112 1-km² grid cells throughout Bakersfield, CA surveyed annually from 2015 to 2021 for urban mesocarnivores

model C3 or E3, Cuddeback, Green Bay, WI, USA) in each cell, secured within protective cases (CuddeSafe E Model 3327, Cuddeback, Green Bay, WI, USA) to t-posts, fences, or vegetation with zip-ties and cable locks. We selected camera locations based on permission to survey properties, accessibility for mesocarnivores, and minimal risk of human disturbance. We attempted to find locations toward the center of cells to place cameras such that stations in adjacent cells would be separated by approximately 1 km, though cameras were not placed in locations without a means of entry by our target species (e.g., areas completely enclosed within tall, solid walls) and were hidden out of view (e.g., within vegetation or behind structures) in areas with consistent high human activity. With a few exceptions due to human disturbance, cells surveyed and camera locations remained consistent each year. In locations where cameras were tampered with or stolen, efforts were made to place cameras in different locations within the same cell; however, if this was not possible another cell was used as a replacement or the cell was omitted in any given year. This resulted in 112 different cells being surveyed over the seven-year sampling period.

We used 30-cm nails to secure a perforated 163-ml can of cat food approximately 2 m in front of each camera, added several drops of a carnivore scent lure (Carman's Canine Call, Minnesota Trapline Products Inc., Pennock, MN, USA) as bait, and clipped back excess vegetation from the camera's field of view. We programmed cameras to wide view and the highest resolution (20 MP) to collect one image following a 15-s delay during daylight (to reduce images of vegetation and human activity) and three images as fast as possible after dark. We deployed cameras in up to 15 cells at a time between June and September each year. Cameras were deployed for seven nights and then images were reviewed for the number of species detections each night, defined as 1200 through 1159 the following day. Images went through two rounds of review, first by two to three researchers concurrently to confirm species presence and a second time by a single researcher to record the specific number of individuals and number of nights they were detected in each cell. Individual animals were distinguished from others of the same species based on size, sex, fur patterns, or markings. If no distinguishing characteristics were discernable, we counted multiple appearances of a species on camera during the 7-n session as the same individual.

Landscape attributes

We used satellite imagery maps to quantify urban landscape attributes in surveyed cells to use in analyses. We superimposed cells with a 10×10 m point grid (100 points/cell) in Google Earth Pro and used 2018 imagery at an eye altitude

of 300-m above-ground-level to characterize points and camera locations scaled to 1.0. We characterized each point by the landscape that best described that location (i.e., the terrestrial land use on which the point was located or nearest to), recorded if the point fell on a mature tree, and noted the presence of stable water sources within cells (e.g., water catchment basins, recreational ponds and lakes, agricultural water supply, the Kern River, and other large bodies of water). Point counts approximated percentages of 12 landscape attributes in cells (Table 1).

Course-scale spatial analyses

To assess spatial relationships between domestic species and mesocarnivores within urban landscapes, we compared the total number of detections in landscape attributes specifically describing camera locations for each pairwise relationship between dogs or cats and kit foxes as well as other smaller mesocarnivores (raccoons, skunks, and opossums combined into one account of "smaller mesocarnivores" due to low detections) using a χ^2 contingency table test for association and Yate's corrected χ^2 goodness of fit tests (Gotelli and Ellison 2013).

Fine-scale spatial analysis

To assess spatial relationships between domestic species and mesocarnivores on a more refined scale, we tested for associations among species presence on nights when they occurred for each pairwise relationship between dogs or cats and kit foxes, raccoons, skunks, or opossums using χ^2 two-way contingency tables (Gotelli and Ellison 2013). We tested these relationships across all cells from all years collectively, as well as each year individually for associations with cats. All tests were analyzed at an α -level of 0.05 for significance.

Occupancy modeling

We used occupancy modeling to investigate associations between urban land uses and species occupancy in surveyed cells, as well as interaction patterns between domestic species and kit foxes within the urban landscape (MacKenzie et al. 2018). We used detection histories to estimate single-species occupancy probabilities (ψ) for cats, opossums, and skunks in relation to landscape attributes in a single-season framework (MacKenzie et al. 2018). Dogs and raccoons performed poorly in single-species occupancy modeling so were excluded from this analysis. Campuses with large maintained green yards (e.g., schools and churches) and paved roads, particularly highways, have been previously described as likely positive and negative, respectively, influential landscape attributes for urban kit fox occupancy (Deatherage

Table 1 Descriptions of 12 landscape attributes quantified for 112 1-km² grid cells, surveyed annually from 2015 to 2021 for urban mesocarnivores in Bakersfield, CA. Included are the percentage of grid cells (Cells) that had a stable water source, $\geq 20\%$ mature tree cover, or that were predominantly characterized by each given attrib-

ute, as well as the percentage of cameras that were located in each attribute (Cams, $n=119$), whether the attribute was supported as a covariate in occupancy modeling, and the degree(s) of urban development that each attribute was categorized as a priori for occupancy modeling

Attribute	Description	Cells	Cams	Covariate	Urban development
water	Stable water source present (yes/no)	63%	n/a	No	Green
tree	Mature tree cover ($\geq 20\%$ tree cover summarized)	28%	n/a	Yes	High, green
road	Percentage of paved roads (vehicular rights-of-way, parking lots, medians, or side of the roadway)	8%	3%	No	High
rail	Percentage of railroad tracks	0%	0%	No	Low
res	Percentage of residential areas (high-density (HDR): single-family homes, or low-to-medium density (LMDR): apartments, nursing homes))	65%	1%	Yes	High, intermediate
OOS	Percentage of other open space (undeveloped lots, airport runways, canals, water catchment basins, power lines, dirt roads, or farms)	18%	48%	Yes	Intermediate, low
com	Percentage of commercial development (shopping and service areas or businesses)	2%	8%	Yes	High, intermediate
ind	Percentage of industrial development (pipe yards, oil fields, factories, junk yards, solar panel lots, or large storage lots)	5%	3%	Yes	High, intermediate
camp	Percentage of campuses (schools, churches, or medical centers)	0%	34%	Yes	High, intermediate, low, green
KR	Percentage of the Kern River corridor	0%	0%	No	Green
ag	Percentage of crop agriculture (row crops or orchards)	2%	0%	No	Green
park	Percentage of parks or other green space (golf courses, cemeteries, or large lawns)	1%	3%	Yes	Intermediate, low, green

et al. 2021; Cypher et al. 2023). These attributes were used in co-occurrence modeling for kit foxes. Important attributes identified for cats from single-species modeling were also included in co-occurrence modeling for cats and kit foxes. We calculated species co-occurrence (ϕ) and co-detection (δ) factors in a two-species, single-season framework for dogs or cats and kit foxes (MacKenzie et al. 2018).

We used PRESENCE 2.13.10 (Hines 2006) to fit occupancy models using all surveyed cells ($s=112$). We set each year to represent a survey ($K=7$) and set detection (p or r) parameters to remain constant over surveys (MacKenzie et al. 2018). We felt this model design was appropriate for our data because changes in habitat composition in the urban environment are minimal once developed and the specific year a cell was surveyed would therefore have minimal effect on occupancy. Further, covariates affecting detection probabilities were not measured in this study as we were primarily concerned with occupancy probabilities and felt detection variation was limited year-to-year due to consistencies in cells surveyed each year, time of year cells were surveyed, use of bait and lure, and a relatively short survey period. We used alternate parameterization in PRESENCE and set landscape attribute covariates to vary between the two species for co-occurrence models (Hines 2006; MacKenzie et al. 2018). Single-species candidate models included a null model (no covariates), a global model (including all covariates considered most likely to influence occupancy for a given species), univariate

models, and additive pairwise combinations of covariates following four a priori categories representing varying degrees of urban development: high, intermediate, low, and green space (Table 1). We tested pairwise correlations between covariates using Spearman's Rank tests and corrected the resulting P -values (Legendre and Legendre 1998). We considered an r_s value $> \pm 0.50$ as moderately correlated and such covariates were not included in the same model (Burnham and Anderson 2002).

We calculated Pearson's χ^2 goodness-of-fit statistic and an overdispersion factor (\hat{c}) using 1,000 bootstraps for global models at an α -level of 0.05 (Burnham and Anderson 2002). We used Akaike's Information Criterion adjusted for overdispersion (QAIC, $\chi^2 P$ -value < 0.05 and $\hat{c} \gtrsim 1.00$) and small sample sizes (AIC_c , sample size/maximum number of model parameters < 40) where appropriate (Burnham and Anderson 2002). We examined discontinuity in ΔAIC values (the difference between the AIC of the top model in the set and the AIC of the given model) to rate model adequacy and then examined the direction and relative magnitude of covariate coefficient estimates (β) to evaluate covariate effects for a given species (Burnham and Anderson 2002). For co-occurrence models, we considered ϕ or δ values < 1.00 to signify a negative association between species (i.e., avoidance or exclusion), ϕ or δ values > 1.00 to signify a positive association, and ϕ or δ values ≈ 1.0 to signify independence (MacKenzie et al. 2018).

Results

Camera results are summarized over all surveyed cells from all seven years in Table 2. Detections were highest for cats (58% of detections), followed by kit foxes (17%), dogs (8%), skunks and opossums (both 5%), and finally raccoons (4%). Cats occurred in more cells and on more nights than any other species each year (80% of surveyed cells and 43% of surveyed nights) followed by kit foxes (35% of surveyed cells and 16% of surveyed nights). Dogs occurred in frequencies similar to raccoons, skunks, and opossums, with dogs occurring in the most cells (17%) and opossums occurring on the most nights (6%).

Landscape attributes

Of the 112 cells, most were dominant in residential land use, followed by other open space, paved road, industrial, commercial and agriculture, and finally park land uses (Table 1). Over half the cells had a stable water source available and nearly one third had $\geq 20\%$ mature tree cover. Camera stations were located in one of eight different landscape

characterizations (Table 1). There were 119 camera locations due to seven cameras being moved to different locations within the cell throughout the study. The average distance between camera locations was 1.06 km (± 0.10 km), with a minimum distance of 0.41 km. Cameras that were classified in the roadway attribute were always located on the side of the road and cameras that were classified in the other open space attribute were specified as either undeveloped lot (13 cameras) or other open space (primarily water catchment basins, 44 cameras). Most cameras were located in other open space (37% of cameras) and campuses (34%), followed by undeveloped lots (11%), commercial areas (8%), and industrial areas, side of the roadway, and parks (all 3%), with the least number of cameras located in residential areas ($< 1\%$).

Course-scale spatial analyses

We found associations between species occurrences and land use at camera locations ($\chi^2 = 358.15$, $df = 21$, $P < 0.001$). Dogs occurred more frequently than kit foxes along roadways than would be expected if they occurred equally in the attribute (i.e., 50:50 frequencies; $\chi^2 = 24.45$, $df = 1$,

Table 2 Number of individuals detected for six urban carnivores, and number of grid cells and nights in which they occurred on trail cameras during an annual survey from 2015 to 2021 in Bakersfield, CA

Species	2015 Individuals Cells (<i>n</i> = 105)	2016 Individuals Cells (<i>n</i> = 111)	2017 Individuals Cells (<i>n</i> = 109)	2018 Individuals Cells (<i>n</i> = 111)	2019 Individuals Cells (<i>n</i> = 110)	2020 Individuals Cells (<i>n</i> = 108)	2021 Individuals Cells (<i>n</i> = 108)	All years Individuals Cells (<i>n</i> = 762)
	Nights (<i>n</i> = 735)	Nights (<i>n</i> = 775)	Nights (<i>n</i> = 751)	Nights (<i>n</i> = 778)	Nights (<i>n</i> = 770)	Nights (<i>n</i> = 753)	Nights (<i>n</i> = 756)	Nights (<i>n</i> = 5311)
Dog	26	30	27	24	43	35	42	227
	16	14	17	15	22	20	25	129
	32	31	46	33	43	41	60	286
Cat	252	260	246	252	228	202	193	1633
	84	91	90	93	87	82	82	609
	318	354	353	377	347	302	253	2303
Kit fox	129	94	81	52	43	41	43	483
	68	52	39	29	23	28	24	263
	226	180	133	95	67	78	66	845
Raccoon	14	11	13	20	13	27	19	117
	8	3	8	8	6	18	14	65
	12	11	10	17	11	19	19	99
Skunk	21	24	26	21	17	20	16	145
	19	20	23	16	15	19	12	124
	27	40	57	41	31	36	28	260
Opossum	21	19	24	19	14	22	24	143
	16	13	19	13	12	21	19	113
	54	47	70	49	27	37	35	319

$P < 0.001$). Dogs also occurred more frequently than other smaller mesocarnivores along roadways as well as in parks (χ^2 range = 5.33 – 19.45, all $df = 1$, P range = < 0.001 – 0.02). Dogs occurred less frequently than kit foxes in all other land uses apart from park and industrial (χ^2 range = 4.98 – 49.77, all $df = 1$, P range = < 0.001 – 0.03) and less frequently than other smaller mesocarnivores in all other land uses apart from residential areas or undeveloped lots (χ^2 range = 4.98 – 99.05, all $df = 1$, P range = < 0.001 – 0.03). Dogs did not have an association with kit foxes in parks or industrial areas (χ^2 range = < 0.01 – 0.05, all $df = 1$, P range = 0.83 – 1.00), nor with other smaller mesocarnivores in residential areas or undeveloped lots (χ^2 range = < 0.01 – 0.05, all $df = 1$, P range = 0.48 – 1.00). Cats occurred more frequently than kit foxes in most land uses (χ^2 range = 9.80 – 381.03, all $df = 1$, all $P < 0.001$) and more frequently than other smaller mesocarnivores in all land uses than would be expected if the species occurred equally (χ^2 range = 9.60 – 283.45, all $df = 1$, P range = < 0.001 – 0.02). Cats did not have an association with kit foxes in residential areas or undeveloped lots (χ^2 range = 0.01 – 0.70, all $df = 1$, P range = 0.40 – 0.94).

Fine-scale spatial analysis

Opossum nightly presence was lower when dogs were also present across all years combined ($\chi^2 = 7.91$, $df = 1$, $P = 0.005$); kit fox nightly presence was lower when cats were also present in 2016, 2020, and across all years (χ^2 range = 6.68 – 23.86, all $df = 1$, P range = < 0.001 – 0.004); raccoon nightly presence was higher when cats were also present in 2020 and across all years (χ^2 range = 4.32 – 14.28, all $df = 1$, P range = < 0.001 – 0.04); skunk nightly presence was higher when cats were also present in 2016, 2018, and across all years (χ^2 range = 5.62 – 36.60, all $df = 1$, P range = < 0.001 – 0.02) though was lower when cats were present in 2015 ($\chi^2 = 28.88$, $df = 1$, $P = < 0.001$); and opossum nightly presence was higher when cats were also present in 2016 ($\chi^2 = 13.01$, $df = 1$, $P = < 0.001$) though the opposite was found in 2021 ($\chi^2 = 6.21$, $df = 1$, $P = 0.01$). The remaining 24 pairwise relationships between nightly presence were independent (χ^2 range = < 0.01 – 3.29, all $df = 1$, P range = 0.07 – 0.96).

Occupancy modeling

Five of the 12 landscape attributes: water, road, rail, KR, and ag, were excluded from single-species occupancy analyses due to overall poor performance in models (i.e., did not converge or produced large standard errors for β values across the species). Of the viable covariates, five of the pairwise combinations were moderately correlated: tree + OOS ($r_s = -0.57$), res + ind ($r_s = -0.56$), res + OOS ($r_s = -0.55$), tree + ind ($r_s = -0.52$), and tree + res ($r_s = 0.75$; all $df = 356$,

all P (corrected) < 0.001). The other 23 combinations were less than moderately correlated (r_s range = -0.39 – 0.37 , all $df = 356$, P (corrected) range = < 0.001 – 1.736).

Single-species

Including the global and null models, we developed 29 candidate models for cats and 25 candidate models for skunk and opossum single-species modeling (Online Resource 1). The res covariate was differentiated into low-to-medium density residential and high-density residential attributes to test for more fine-scale effects of residential land use on cats (Table 1). The cat global model included HDR, LMDR, com, camp, and park covariates and resulted in the use of QAIC for cats ($K = 8$, $\chi^2 = 800.03$, $P = 0.03$, $\hat{c} = 2.31$). The skunk global model included OOS, tree, camp, and park covariates ($K = 6$, $\chi^2 = 395.80$, $P = 0.36$, $\hat{c} = 1.07$), and the opossum global model included res, com, camp, and park covariates ($K = 6$, $\chi^2 = 400.34$, $P = 0.31$, $\hat{c} = 1.10$). The number of sites divided by the highest number of parameters led to the use of AIC_c for all single-species models ($112/8 = 14$; Table 3). The dog global model did not converge and resulted in very poor fit ($K = 7$, $\chi^2 = 10456.71$, $P < 0.001$, $\hat{c} = 35.44$) and raccoon modeling resulted in no candidate model outperforming the null and large standard errors, so these two species were excluded from our single-species occupancy analysis.

We considered models with $\Delta\text{AIC}_c < 4.00$ for cat single-species occupancy which resulted in nine models with a cumulative w of 95% (Table 3). These models included OOS and tree univariate models followed by the additive model tree + camp, four additive models including OOS and one other covariate, and finally two additive models including tree and one other covariate (Table 3). However, all covariates apart from OOS had β confidence intervals that crossed 0 so were not considered reliable covariates for cats (Table 4). In the top model, OOS had a relatively weak negative effect on cat occupancy (Table 4). We considered other open space to be the most important land use for cat occupancy in our analysis. Considering the OOS univariate model, the lowest occupancy probability for cats (0.08) occurred in the cell with the most open space (82% OOS) and the highest occupancy probability (1.00) occurred in cells where there was no open space (Table 5). The lowest occupancy probability for cats was still higher than the other modeled species and cats also had a higher detection probability than the other modeled species (Table 5).

We considered models with $\Delta\text{AIC}_c < 3.00$ for skunk single-species occupancy which resulted in three models with a cumulative w of 72% (Table 3). The three top models included the additive models com + ind followed by res + com and OOS + ind. Across the top models, com and res had a weak negative effect on skunk occupancy and ind and OOS had a weak positive effect (Table 6). We

Table 3 Akaike Information Criterion (AIC) values, including model weight (w , the probability of the given model being the best approximating model among those evaluated), number of parameters estimated in the model (No. parms), and model deviance (-2LogLike) from top-ranking single-species, single-season occupancy models for domestic cats, striped skunks, and Virginia opossums. AIC was adjusted for overdispersion for cats (QAIC) and was adjusted for small sample sizes for all species (AIC_c). Modeling was completed using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Model	AIC	Δ AIC	w	No. parms	-2logLike
Cat	QAIC _c	Δ QAIC _c	QAIC _c w		
psi(OOS),p(.)	273.00	0.00	0.227	4	619.49
psi(tree),p(.)	273.91	0.91	0.144	4	621.63
psi(tree + com),p(.)	274.19	1.18	0.126	5	617.13
psi(OOS + camp),p(.)	274.41	1.40	0.113	5	617.65
psi(OOS + com),p(.)	275.08	2.07	0.081	5	619.22
psi(OOS + ind),p(.)	275.17	2.16	0.077	5	619.44
psi(OOS + park),p(.)	275.19	2.18	0.076	5	619.48
psi(tree + camp),p(.)	275.66	2.65	0.060	5	620.58
psi(tree + park),p(.)	276.08	3.07	0.049	5	621.56
Skunk	AIC _c	Δ AIC _c	AIC _c w		
psi(com + ind),p(.)	558.66	0.00	0.3164	4	550.29
psi(res + com),p(.)	558.73	0.07	0.3055	4	550.36
psi(OOS + ind),p(.)	561.02	2.36	0.0972	4	552.65
Opossum	AIC _c	Δ AIC _c	AIC _c w		
psi(OOS + park),p(.)	541.70	0.00	0.4887	4	533.33
psi(park),p(.)	544.79	3.09	0.1043	3	538.57
psi(res + park),p(.)	545.12	3.42	0.0884	4	536.75
psi(tree + park),p(.)	545.60	3.90	0.0695	4	537.23

Covariate definitions: OOS – other open space (undeveloped lots, canals, etc.), tree – mature tree cover, com – commercial properties (shopping, service areas, businesses), camp – campuses (schools, churches, medical centers), ind – industrial areas (pipe yards, oil fields, factories, large storage lots, etc.), park – parks and other maintained green spaces, res – residential areas (single family homes, apartment buildings)

considered the additive effect of commercial and industrial to be the most important land uses for skunk occupancy in our analysis. Considering the com + ind additive model, the lowest occupancy probability (0.02) occurred in a cell with no industrial land use and 41% commercial land use, while the highest occupancy probability (0.96) occurred in a cell with 66% industrial land use and 8% commercial land use (Table 5; Fig. 2).

We considered models with Δ AIC_c < 4.00 for opossum single-species occupancy which resulted in four models with a cumulative w of 75% (Table 3). These models included the additive model OOS + park followed by the park univariate model, and two other additive models, res + park and tree + park. However, tree had a β confidence interval that crossed 0 by 0.02 so was not considered a reliable covariate for opossums (Table 7). Across the considered models, OOS had a weak negative effect on opossum occupancy while res had a weak positive effect and park had a moderate positive effect (Table 7). We considered the additive effect of other open space and parks to be the most important land use for opossum occupancy in our analysis. From this model, the lowest occupancy probability (0.06) occurred in a cell with 74% open space and no parks, while the highest occupancy probability (0.98) occurred in a cell with 31% open space and 32% parks (Table 5; Fig. 3).

Co-occurrence

We developed three co-occurrence models for dogs and kit foxes and four for cats and kit foxes (Online Resource 2). We designated the domestic species as the dominant species (Species A) in both model sets. The number of sites divided by the highest number of parameters also led to the use of AIC_c for co-occurrence modeling ($112/10 = 11.20$). Both co-occurrence model sets resulted in the null model as the single top model holding 71% of the model weight for dogs and kit foxes and 100% for cats and kit foxes (Table 8). Considering the null models, kit foxes had a positive occupancy probability given dog or cat presence (Table 9). Cats being present and detected had a slight negative effect on kit fox detection, though the same effect was not observed with dogs (Table 9). Ultimately, kit foxes occurred independently of dogs and cats (Table 10).

Discussion

Overall, kit foxes appear to occur independently of dogs and cats though there is some evidence of fine-scale spatial avoidance of cats by kit foxes. Cats are generally two or three times heavier than kit foxes and in Bakersfield, kit foxes have been observed deferring to cats at feeding

Table 4 Parameter estimates (β) for occupancy probability (ψ) and detection probability (p), with 95% confidence intervals, from single-species, single-season occupancy modeling for domestic cats using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Cat models	β	LCI	UCI
psi(OOS),p(.)			
ψ	6.55	1.95	11.15
$\psi(\text{OOS})$	-0.11	-0.20	-0.02
p	1.77	1.45	2.09
psi(tree),p(.)			
ψ	-0.03	-1.89	1.84
$\psi(\text{tree})$	0.40	-0.03	0.83
p	1.77	1.45	2.09
psi(tree + com),p(.)			
ψ	-0.89	-3.26	1.48
$\psi(\text{tree})$	0.39	-0.02	0.80
$\psi(\text{com})$	0.29	-0.27	0.84
p	1.77	1.45	2.09
psi(OOS + camp),p(.)			
ψ	5.92	1.10	10.74
$\psi(\text{OOS})$	-0.10	-0.20	-0.01
$\psi(\text{camp})$	0.23	-0.58	1.03
p	1.77	1.45	2.09
psi(OOS + com),p(.)			
ψ	6.14	1.19	11.10
$\psi(\text{OOS})$	-0.10	-0.20	-0.01
$\psi(\text{com})$	0.09	-0.49	0.66
p	1.77	1.45	2.09
psi(OOS + ind),p(.)			
ψ	6.65	1.80	11.49
$\psi(\text{OOS})$	-0.11	-0.20	-0.02
$\psi(\text{ind})$	-0.01	-0.14	0.12
p	1.77	1.45	2.09
psi(OOS + park),p(.)			
ψ	6.58	1.59	11.56
$\psi(\text{OOS})$	-0.11	-0.21	-0.01
$\psi(\text{park})$	-0.01	-0.65	0.63
p	1.77	1.45	2.09
psi(tree + camp),p(.)			
ψ	-0.14	-2.05	1.78
$\psi(\text{tree})$	0.37	-0.06	0.79
$\psi(\text{camp})$	0.17	-0.51	0.86
p	1.77	1.45	2.09
psi(tree + park),p(.)			
ψ	-0.05	-1.93	1.84
$\psi(\text{tree})$	0.41	-0.05	0.88
$\psi(\text{park})$	-0.05	-0.50	0.40
p	1.77	1.45	2.09

Covariate definitions: OOS – other open space (undeveloped lots, canals, etc.), tree – mature tree cover, com – commercial properties (shopping, service areas, businesses), camp – campuses (schools, churches, medical centers), ind – industrial areas (pipe yards, oil fields, factories, large storage lots, etc.), park – parks and other maintained green spaces, res – residential areas (single family homes, apartment buildings)

Table 5 Occupancy probability (ψ) and detection probability (p) estimates for domestic cats, striped skunks, and Virginia opossums from the most supported single-species occupancy model for each using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Species	Covariate (effect)	ψ range	p (\pm CI)
Cat	Other open space (-)	0.08 – 1.00	0.85 (\pm 0.04)
Skunk	Commercial (-), industrial (+)	0.02 – 0.96	0.39 (\pm 0.06)
Opossum	Other open space (-), park (+)	0.06 – 0.98	0.34 (\pm 0.06)

stations established for feral cats (Cypher 2010). These results somewhat contradict our prediction that kit foxes would occur independently of cats but might avoid dogs. However, while there may be some avoidance of cats by kit foxes where possible, both are highly ubiquitous and probably mostly ignore each other (Cypher 2010). Despite the risk of predation by dogs, kit foxes may occur independently of dogs due to the influence humans have over dog location and activity. Because many people own pet dogs, they occur ubiquitously throughout the city and are often confined on leashes or within fences. Therefore, dogs may not be as threatening to kit foxes as other predators.

Table 6 Parameter estimates (β) for occupancy probability (ψ) and detection probability (p), with 95% confidence intervals, from top ranking single-species, single-season occupancy models for striped skunks using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Skunk models	β	LCI	UCI
psi(com + ind),p(.)			
ψ	-0.35	-0.86	0.15
$\psi(\text{com})$	-0.09	-0.17	0.00
$\psi(\text{ind})$	0.06	0.02	0.11
p	-0.45	-0.70	-0.21
psi(res + com),p(.)			
ψ	1.22	0.25	2.19
$\psi(\text{res})$	-0.03	-0.05	-0.01
$\psi(\text{com})$	-0.08	-0.14	-0.01
p	-0.46	-0.70	-0.21
psi(OOS + ind),p(.)			
ψ	-0.96	-1.55	-0.37
$\psi(\text{OOS})$	0.02	0.00	0.04
$\psi(\text{ind})$	0.04	0.00	0.08
p	-0.45	-0.70	-0.21

Covariate definitions: OOS – other open space (undeveloped lots, canals, etc.), tree – mature tree cover, com – commercial properties (shopping, service areas, businesses), camp – campuses (schools, churches, medical centers), ind – industrial areas (pipe yards, oil fields, factories, large storage lots, etc.), park – parks and other maintained green spaces, res – residential areas (single family homes, apartment buildings)

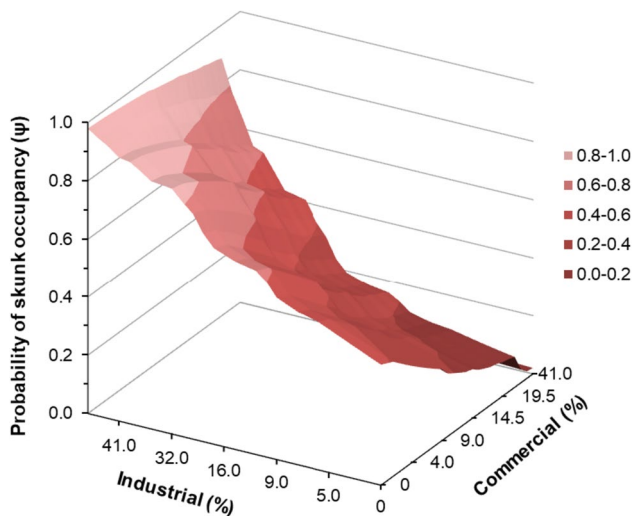


Fig. 2 Occupancy probability (ψ) for striped skunks in relation to percentage of industrial and commercial land uses in 112 1-km² grid cells, using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Among the other smaller mesocarnivores, there was some evidence of fine-scale spatial avoidance of dogs by opossums. Interactions between dogs and opossums are not well

Table 7 Parameter estimates (β) for occupancy probability (ψ) and detection probability (p), with 95% confidence intervals, from single-species, single-season occupancy modeling for Virginia opossums using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Opossum models	β	LCI	UCI
psi(OOS + park),p(.)			
ψ	-0.17	-0.87	0.53
$\psi(\text{OOS})$	-0.03	-0.06	0.00
$\psi(\text{park})$	0.14	0.01	0.27
p	-0.64	-0.90	-0.39
psi(park),p(.)			
ψ	-0.75	-1.25	-0.25
$\psi(\text{park})$	0.18	0.04	0.32
p	-0.64	-0.90	-0.38
psi(res + park),p(.)			
ψ	-1.22	-2.04	-0.41
$\psi(\text{res})$	0.01	0.00	0.03
$\psi(\text{park})$	0.16	0.03	0.30
p	-0.64	-0.90	-0.39
psi(tree + park),p(.)			
ψ	-1.18	-2.09	-0.28
$\psi(\text{tree})$	0.03	-0.02	0.09
$\psi(\text{park})$	0.16	0.02	0.30
p	-0.65	-0.90	-0.39

Covariate definitions: OOS – other open space (undeveloped lots, canals, etc.), park – parks and other maintained green spaces, res – residential areas (single family homes, apartment buildings), tree – mature tree cover

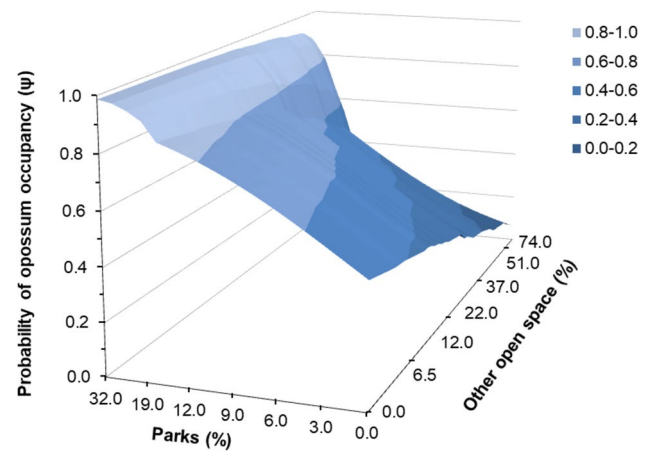


Fig. 3 Occupancy probability (ψ) for Virginia opossums in relation to percentage of other open space and parks land uses in 112 1-km² grid cells, using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

documented, though opossums may avoid dogs to some extent due to risk of predation. Opossums have also shown negative associations with dog presence in San Francisco Bay Area, CA (Reilly et al. 2016). Raccoons and skunks exhibited fine-scale spatial coexistence with cats. Positive associations between cats and smaller mesocarnivores may be explained by low competitive pressure due to none of the species being overtly territorial and all having opportunistic feeding patterns (Hopkins and Forbes 1980; Gardner 1982; Leyhausen 1979; Pearre and Maass 1998; Hadidian et al. 2010; Rosatte et al. 2010).

Cats are the most frequently detected urban carnivore in Bakersfield, followed by kit foxes and then dogs. The pervasive distributions of urban mesocarnivores, immense heterogeneity of the urban environment, and human influence over animal activity, particularly for domestic species, makes it difficult to discern clear occupancy patterns for the species in our study; however, we found open space to be an important negative predictor of cat and opossum occupancy. Cats and opossums are likely avoiding open spaces due to a lack of cover and increased risk of predation by coyotes or red foxes. Less human presence in open spaces also makes it less likely that cats and opossums will find accessible meals from people leaving out pet food. Cats and opossums may find refuge from predators in isolated fragments of more natural environments (e.g., parks and green space) surrounded by development in part due to mesopredator release, in which smaller carnivores are freed from larger, competitive predators that are unfit to inhabit small and isolated fragments (Crooks and Soulé 1999; Crooks 2002). It is unsurprising that dogs occurred more frequently along roadways than other species as pet dogs are routinely guided along sidewalks adjacent to roads while on walks with their owners.

Table 8 Akaike Information Criterion values from single-season, co-occurrence occupancy modeling for domestic dogs and domestic cats with San Joaquin kit foxes using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Model	AIC _C	ΔAIC _C	w	No. parms	-2logLike
Dog + kit fox psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa	1591.66	0.00	0.71	8	1574.26
Cat + kit fox psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa	1575.77	0.00	1.00	8	1558.37

Raccoons, skunks, and opossums have been known to avoid smaller roadways while cats and kit foxes primarily display avoidance of major roadways; however, these avoidances are likely a result of the inhospitality and risk of mortality at roads and not a result of frequent dog occurrences (Barratt 1997; Prange et al. 2003; Bjurlin et al. 2005; Greenspan et al. 2018; Cypher et al. 2023).

We also found commercial and industrial areas to be important negative and positive predictors, respectively, of skunk occupancy. In Toronto, Ontario, both industrial and commercial areas have supported skunk densities as high as 36 individuals/km², though it was presumed that close proximity to empty fields is what attracted skunks to those areas (Rosatte et al. 1991). In Bakersfield, industrial areas

tend to abut open spaces or even encompass such land uses (e.g., large dirt roads or power line lots), and open space was also a positive predictor for skunks in our study. Skunks may refine their selection for industrial areas as refuge from neighboring heavily populated and developed commercial areas in Bakersfield, which might not have been possible for skunks at densities as high as 36 individuals/km² in Toronto. These results, as well as our prediction that cats and opossums would share landscape preferences, are consistent with our predictions on urban land use selection by these species.

Overall positive or indifferent associations between domestic species and kit foxes or other smaller mesocarnivores could enhance the risk of disease transmission. Feeding stations for feral cats throughout Bakersfield are known to attract foxes, raccoons, skunks, and opossums (Cypher 2010). Primary transmittable diseases between the species include rabies, distemper, parvovirus, leptospirosis, and a variety of endo and ectoparasites (Baker et al. 2010). Disease may spread through the environment, direct contact, waste material, or arthropod vectors (Baker et al. 2010). An aggressive skin disease called sarcoptic mange, caused by an infectious mite (*Sarcoptes scabiei*), has been detected in urban kit foxes in Bakersfield since 2013 and is fatal for kit foxes without intervention (Rudd et al. 2020).

Table 9 Parameter estimates with 95% confidence intervals from single-season, co-occurrence occupancy modeling for domestic dogs and domestic cats with San Joaquin kit foxes using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA

Model	β	LCI	UCI
Dog + kit fox			
psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa			
ψ ^A	0.60	0.06	1.15
ψ ^{BA}	1.55	0.88	2.23
ψ ^{Ba}	1.43	0.24	2.62
p ^A	-0.47	-0.98	0.04
p ^B	-0.97	-1.67	-0.26
r ^A	-1.16	-1.48	-0.85
r ^{BA}	-0.19	-0.59	0.21
r ^{Ba}	0.04	-0.22	0.30
Cat + kit fox			
psiA,psiBA,psiBa,pA,pB,rA,rBA,rBa			
ψ ^A	2.71	1.94	3.47
ψ ^{BA}	1.33	0.82	1.85
ψ ^{Ba}	24.3	-138648.57	138697.12
p ^A	1.86	1.34	2.38
p ^B	0.82	0.21	1.43
r ^A	1.74	1.51	1.98
r ^{BA}	-0.44	-0.64	-0.25
r ^{Ba}	-0.10	-0.55	0.34

Table 10 Probability estimates from single-season, co-occurrence occupancy modeling for domestic dogs and domestic cats with San Joaquin kit foxes using detection histories from annual surveys from 2015 to 2021 in Bakersfield, CA. 95% confidence intervals are included in parentheses

Parameter	Dog + kit fox	Cat + kit fox
φ	1.01 (0.92 – 1.10)	0.98 (0.79 – 1.17)
δ	0.91 (0.73 – 1.09)	0.97 (0.62 – 1.32)
ψ ^A	0.65 (0.51 – 0.76)	0.94 (0.87 – 0.97)
ψ ^B	0.82 (-0.14 – 1.78)	0.80 (0.34 – 1.27)
ψ ^{BA}	0.83 (0.71 – 0.90)	0.79 (0.69 – 0.86)
ψ ^{Ba}	0.81 (0.56 – 0.93)	1.00 (0.00 – 1.00)
p ^A	0.38 (0.27 – 0.51)	0.87 (0.79 – 0.92)
r ^A	0.24 (0.19 – 0.30)	0.85 (0.82 – 0.88)
p ^B	0.28 (0.16 – 0.43)	0.69 (0.55 – 0.81)
r ^{BA}	0.45 (0.36 – 0.55)	0.39 (0.35 – 0.44)
r ^{Ba}	0.51 (0.44 – 0.57)	0.47 (0.37 – 0.58)

Our camera surveys have documented a decline in the once robust Bakersfield kit fox population by nearly 70% since 2015 (Kelly et al. 2022). The outbreak in kit foxes has been attributed to a potential spillover event from dogs or coyotes (Rudd et al. 2020). Efforts are underway to monitor, capture, and treat kit foxes with sarcoptic mange, though response can be costly and time consuming as advanced cases require keeping individuals in captivity for at least one month of intensive treatment (Cypher et al. 2017). Vaccinations have proven to be an effective management technique against the spread of other diseases, particularly rabies, among these species, though large-scale vaccinations and treatment of wild carnivores in urban areas is novel and challenging due to the fragmented landscapes and risks to humans, pets, and other wildlife (Baker et al. 2010; Hadidian et al. 2010; Soulsbury et al. 2010).

Wild mesocarnivores living in Bakersfield exhibited varying degrees of spatial partitioning with domestic dogs and cats. The apparent indifference of kit foxes towards domestic species may help kit foxes persist more widely and in higher densities in the urban environment than other urban mesocarnivores. The conservation of urban populations of kit foxes can be beneficial for the long-term persistence of this species as their natural habitat continues to be developed. Conservation initiatives should explore disease prevention in detail, particularly at cat feeding stations or other urban sites where the species may congregate. Because both wild and domestic carnivores commonly co-occur within urban environments, understanding their adaptations to urbanization and novel sympatry allows for management strategies that facilitate coexistence and promote conservation of the wild species, particularly San Joaquin kit foxes.

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Author contributions Nicole A. Deatherage and Brian L. Cypher contributed to the study conception and design and performed data analysis. Material preparation and data collection were performed by all authors. The first draft of the manuscript was written by Nicole A. Deatherage and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and material Data for this manuscript are provided in supplementary information and can be available upon request.

Declarations

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study because all data was collected non-invasively via remote cameras and did not require direct interaction with the species.

Competing interests The authors declare no competing interests.

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