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Urban landscape attributes affect occupancy patterns of the San Joaquin kit fox during an epizootic

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Abstract. The federally endangered and California state threatened San Joaquin kit fox (*Vulpes macrotis mutica*) persists in relatively high density in the urban environment of Bakersfield, California, USA. Coyotes (*Canis latrans*), red foxes (*V. vulpes*), and gray foxes (*Urocyon cinereoargenteus*) are natural competitors of San Joaquin kit foxes, and their presence in Bakersfield potentially impacts kit foxes. We used annual camera survey data in 111 randomly selected 1-km^2 grid cells to investigate the influence of landscape attributes and the presence of canid competitors on San Joaquin kit fox occupancy from 2015 to 2019 in Bakersfield. Of 59 candidate models, our results indicated that occupancy patterns of urban kit foxes were driven primarily by a selection for campuses (e.g. schools, churches, and medical centres), followed by an avoidance of paved roads. Presence of other canids was associated with kit fox presence during surveys but did not have a discernable effect on occupancy, possibly due to a relatively low number of detections. Kit fox occupancy was estimated to have declined by 40% in Bakersfield over the 5-year study, likely due to sarcoptic mange (canis variety skin mite, *Sarcoptes scabiei*) disease as evidenced by a 37–49% extinction probability as a result of mange. Despite mange, the San Joaquin kit fox population in Bakersfield is one of the largest remaining populations. Awareness of the selection for campuses and avoidance of paved roads by San Joaquin kit foxes can help to develop effective land management and mitigation policy for kit foxes affected by urban development.

Keywords: fox, Kern County, multi-season occupancy modelling, paved roads, San Joaquin kit, single-species occupancy modelling, urban development, *Vulpes macrotis mutica*.

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Introduction

The San Joaquin kit fox (*Vulpes macrotis mutica*) is a federally endangered and California state-threatened canid species in the USA, imperiled primarily due to habitat loss as a result of human development (Cypher 2010). The San Joaquin kit fox is a subspecies of kit fox (*V. macrotis*), which ranges throughout flat, semiarid, open desert, shrubland, and grassland habitats in southwestern North America (McGrew 1979). San Joaquin kit foxes (hereafter kit fox) are endemic to the San Joaquin Valley of Central California (Cypher *et al.* 2001). They select for open saltbush (*Atriplex* spp.) scrub and use subterranean dens for shelter from climatic conditions and to escape predators such as coyotes (*Canis latrans*), golden eagles (*Aquila chrysaetos*), and red foxes (*V. vulpes*; Cypher 2003; Cypher *et al.* 2001, 2013). The kit fox population in the city of Bakersfield, California constitutes one of the largest remaining populations of kit foxes, and as such is important to the recovery of this subspecies (Cypher and Van Horn Job 2012). More recently, the Bakersfield population has dramatically declined due to a sarcoptic mange epizootic caused by a highly contagious skin infestation of the *Canis* variety of skin mite, *Sarcoptes scabiei* (Cypher *et al.* 2001; Pence and Ueckermann 2002; Cypher *et al.* 2017). The disease has been studied extensively in red foxes in which mortality can occur 3–4 months following infestation (Stone *et al.* 1972) and due to the similar biology of red foxes and kit foxes it is likely that time-to-mortality is similar for kit foxes, with data indicating the disease is 100% fatal in untreated kit foxes (Cypher 2003; Cypher *et al.* 2017).

Urbanisation as a result of human development creates new environments dominated by infrastructure (e.g. buildings and roads) and characterised by an increase in temperature and noise, year-round water, diverse microhabitats, and non-native wildlife (Grimm *et al.* 2008; Gehrt 2010). Urban landscapes possess hard, linear boundaries, with features such as roads and walls that act as wildlife barriers resulting in fragmentation, isolation, and edge effects on natural habitat (Crooks 2002; Riley *et al.* 2010). Conversely, urban environments can offer increased resource availability for wildlife including pet food or intentional feeding of wildlife, food refuse, planted fruits and vegetables, permanent water sources, and human-built structures that provide shelter (Harrison 1997; Fuller *et al.* 2010). This has led to range expansion into urban areas by opportunistic species that readily adapt to human-modified environments, including kit foxes and other canids (Ditchkoff *et al.* 2006; Cypher 2010; Bateman and Fleming 2012; Lombardi *et al.* 2017).

In Bakersfield, kit foxes are sympatric with three other canids – coyotes, red foxes, and gray foxes (*Urocyon cinereoargenteus*) – with which they share spatial, dietary, and temporal requirements, resulting in the potential for interference competition (Cypher *et al.* 2001; Nelson *et al.* 2007; Cypher 2010; Soulsbury *et al.* 2010). Interference competition can lead to predation, harassment, spatial exclusion, or interspecific killing of smaller, less dominant fox species by larger, more dominant foxes and coyotes, thereby limiting species distributions or encouraging niche differentiation (Case and Gilpin 1974; Kitchen *et al.* 1999; Cypher *et al.* 2001). In some non-urban areas in the San Joaquin Valley, kit foxes make greater use of less optimal habitat with lower food availability due to prominent use of optimal habitat by coyotes, indicating habitat partitioning to reduce competition (Cypher *et al.* 2001; Nelson *et al.* 2007).

Landscape attributes and relative density of urban development may have a stronger effect on carnivore spatial dynamics than temporal activity of competitors or human activity (Bateman and Fleming 2012; Moll *et al.* 2018). Additionally, larger predators are often less tolerated by humans and subjected to higher human-caused mortality than smaller carnivores. This can create areas where larger predators are absent, thereby providing spatial refuge for smaller species and facilitating competitor sympatry within the urban landscape (Lesmeister *et al.* 2015; Moll *et al.* 2018). Past studies indicate that coyotes need larger, connected open space, and are regularly observed in areas within urban environments with more natural habitat (Crooks 2002; Gehrt *et al.* 2009; Gese *et al.* 2012). Red foxes avoid coyotes by being better adapted to intermediate human-modified habitats (i.e. suburbs with house densities of <20 houses/ha; Gosselink *et al.* 2003; Lesmeister *et al.* 2015). Gray foxes tend to select for urban edges or more natural, tree-covered areas (Riley 2006; Mathewson *et al.* 2008; Lesmeister *et al.* 2015). In the Great Basin Desert of western Utah, USA, desert kit foxes (*V. m. arsipus*) in urban areas foraged and denned near highly developed areas that afforded protection from coyotes (Kozlowski *et al.* 2008).

Kit foxes in Bakersfield are commonly observed using dens in undeveloped lots, storm water catchment basins and canal banks, industrial areas, commercial areas, landscaping features, and powerline and railroad corridors (Cypher and Van Horn Job 2012). These dens are often earthen but may also be constructed in culverts, pipes, rubble piles, or under infrastructure (Frost 2005; Cypher 2010). Radio collared kit foxes have been found to utilise undeveloped lands and water catchment basins disproportionately more than residential areas (Frost 2005); however, it is largely unknown how heterogeneous urban landscape features (e.g. water availability, vegetation cover, land use, and building and infrastructure density) and the presence of competitors drives kit fox occupancy patterns in the city.

We investigated whether specific urban landscape attributes, including the presence of a competitor canid species, affect kit fox occupancy patterns in Bakersfield. We used 5 years of camera trap data from an annual city-wide survey conducted from 2015 to 2019 combined with a suite of urban landscape attributes in occupancy modelling. Although assuming kit fox occupancy would decrease over time due to mange, we predicted kit foxes would continuously select for open spaces within the urban environment while avoiding the outer edges of the city where more natural habitat and dominant canid species may occur. Understanding kit fox associations with specific landscape features in the urban environment will help in developing effective management, mitigation, conservation, and recovery strategies for kit foxes in urban areas.

Materials and methods

Study area

The city of Bakersfield is located in Kern County, in the southwestern portion of the San Joaquin Valley (35.37329°N, –119.01871°W). 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 characterise 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). Land use is comprised of oil and gas production, grazing, agriculture, natural, conserved, and urban lands (Cypher *et al.* 2000).

Bakersfield is a heavily urbanised city with a growing population of 380 000 people (United States Census Bureau 2019). The city is surrounded by natural habitat, including saltbush scrub, grassland, and riparian areas on 25–30% of its boundary with agriculture on the remainder (Cypher 2010). Bakersfield encompasses a variety of urban land uses including residential areas (e.g. single family homes, apartment buildings, townhouses, and nursing homes), commercial developments, recreational areas, preserved green spaces, industrial centres, agriculture, and campuses (e.g. schools, churches, and medical centres). The Kern River runs through the middle of the city though only portions of the river corridor contain water year-round due to water diversion for agricultural purposes (Shigley 2010). Vegetation in the city consists primarily of a mix of planted native and non-native ornamental trees, shrubs, and flowering plants.

Study design

We conducted annual surveys from 2015 to 2019 using camera traps to monitor sarcoptic mange in the Bakersfield kit fox population, and used these data to investigate kit fox occupancy patterns. We set camera traps in 111 randomly selected 1-km^2 grid cells located throughout the 368-km^2 city, thus covering approximately 30% of the city. We selected cell size such that each kit fox mean home range of 1.72 km^2 (Frost 2005) potentially included two cells to maximise our ability to detect kit foxes, as they could likely readily access any feature, including camera locations, within cells (Westall and Cypher 2017). We selected camera locations within cells based on amount of human activity, accessibility by personnel, and accessibility for kit foxes. We secured Cuddeback Black Flash E3 or C3 digital trail cameras (Cuddeback, Green Bay, WI, USA) to t-posts, fences, or vegetation at a height or angle appropriate for capturing images of kit foxes and other canid species via motion sensors. We baited camera traps with a punctured can of commercial cat food secured approximately 1.5 m in front of the camera and added several drops of Carman's Canine Call carnivore lure (Minnesota Trapline Products Inc., Pennock, MN, USA) that can be detected up to 1.6 km away by canid species (Westall and Cypher 2017). 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 stations within 6 nights (Westall and Cypher 2017), we ran cameras annually for 1 week in mid-summer, outside of the kit fox breeding and whelping season that might affect activity. We reviewed images captured by the cameras each year and recorded the number of species detections and if kit foxes appeared to be infested with mange. To test for an association between kit fox and other canid presence, we completed a two-way contingency table and Chi-square test for the total cells and total survey days in which the species occurred across the 5-year sampling period.

We used satellite imagery maps to quantify a suite of urban landscape attributes in all cells to use as covariates in occupancy models. We overlaid cells with a 10 × 10 m point grid in Google Earth Pro, resulting in a total of 100 points/cell. We used imagery dated 26 April 2018 at an eye altitude of 300-m above ground level to characterise grid points and camera locations scaled to 1.0. We characterised each point by the landscape that best described the location of the point (i.e. the land use type on which the majority of the point was located), and recorded if any portion of the point fell on a mature tree or paved road. If a point appeared to fall equally on two different landscape types, we split the proportion of the point between the attributes (0.5:0.5). If a point fell on a water body we characterised it as the closest terrestrial landscape and made note of the water source and additionally noted the presence of other stable water sources within cells. Counts approximated percentages of 13 landscape attributes and whether water was present within each cell. Landscape attributes consisted of paved roads, mature trees, high-density residential areas, low to medium density residential areas, commercial areas, industrial areas, campuses, undeveloped lots, agriculture, parks and green spaces, median or side of roadways, other open spaces, and the Kern River corridor. We tested pairwise correlations between landscape attributes using Spearman's Rank tests and adjusted the resulting P-values using the method proposed by Legendre and Legendre (1998) to account for the inflated risk of a type I statistical error when running multiple tests. Two-way contingency tables, Chi-squares, and correlation tests were completed in Minitab 19 statistical software and analysed at $\alpha = 0.05$ for statistical significance.

Occupancy modelling

We first estimated raw kit fox occupancy as,

$$\hat{\psi} = \frac{\hat{x}}{s},$$

where $\hat{\psi}$ is the estimated probability of kit fox occupancy, $\hat{x}$ is the estimated number of sites occupied by kit foxes, and s is the number of sites surveyed, i.e. grid cells (MacKenzie *et al.* 2018). To account for detection uncertainty, we used single-species dynamic occupancy modelling to produce probability estimates of kit fox occupancy, defined by the equation,

$$\hat{\psi}_{MLE} = \frac{s_D}{(s\hat{p}^*_{MLE})},$$

where $\hat{\psi}_{MLE}$ is the maximum-likelihood estimate for the probability of occupancy of a kit fox, i.e. the value for kit fox occupancy that maximises the likelihood function given the observed data; s_D is the number of cells at which a kit fox was detected using survey detection histories (h); and $s\hat{p}^*_{MLE}$ is the maximum-likelihood estimate for the probability of detecting a kit fox at least once during a survey (k), given kit foxes were present (MacKenzie *et al.* 2018). We estimated relationships between kit fox occupancy and landscape attributes, the presence of a stable water source, and the total number of canid competitors detected in cells as covariates, defined by the linear regression equation in the logit function,

$$\hat{\psi}_i = \frac{\exp(\hat{\beta}_0 + \hat{\beta}_1 x_{i1})}{1 + \exp(\hat{\beta}_0 + \hat{\beta}_1 x_{i1})},$$

where $\hat{\psi}_i$ is the estimated probability of kit fox occupancy at cell i; $\hat{\beta}_0$ is the estimated intercept term; $\hat{\beta}_1$ is the estimated slope of the effect of covariate 1; and x_{i1} is the value of the continuous predictor variable, i.e. the value of covariate 1 at cell i (MacKenzie *et al.* 2018). We determined estimated probability of kit fox occupancy in subsequent seasons following season 1 in multi-season modelling, defined by the equation,

$$\psi_{t+1} = \psi_t(1 - \epsilon_t) + (1 - \psi_t)\gamma_t,$$

where ψ_{t+1} is the probability of kit fox occupancy in the season following season t; ϵ_t is the extinction probability, i.e. the probability an occupied cell in season t is unoccupied by kit foxes in season $t + 1$; γ_t and is the colonisation probability, i.e. the probability that a cell unoccupied in season t is occupied by kit foxes in season $t + 1$ (MacKenzie *et al.* 2018). Cells occupied by kit foxes the following season, $t + 1$, are a combination of cells occupied in the given season, t, where kit foxes did not go locally extinct, $\psi_t(1 - \epsilon_t)$, and cells that are currently unoccupied by kit foxes that are colonised before next season, $(1 - \psi_t)\gamma_t$ (MacKenzie *et al.* 2018). We assumed no unmodelled heterogeneity in our data, that occupancy state at each site did not change over surveys within a sampling season, and that target species were never falsely detected (MacKenzie *et al.* 2018). We treated each year of the study as individual seasons ($T = 5$) and each day camera stations were run in cells within seasons as individual surveys ($K = 7$).

We developed a set of 59 candidate models that included combinations of covariates in cells (Table 1 and see Supplementary Material 1; MacKenzie *et al.* 2018). Covariates that

Table 1. Covariates used in candidate occupancy models for San Joaquin kit foxes (*Vulpes macrotis mutica*) from 2015 to 2019 in Bakersfield, California, USA

Covariate	Description
OC	Total number of other individual canids (coyote, red fox, gray fox) recorded in cell
water	Presence of a stable water source in cell
tree	Percentage of mature tree cover in cell
road	Percentage of paved roads in cell
HDR	Percentage of cell characterised by high-density residential land use (single family homes)
LMDR	Percentage of cell characterised by low to medium density residential land use (apartment buildings, nursing homes)
com	Percentage of cell characterised by commercial land use (shopping and service areas, businesses)
ind	Percentage of cell characterised by industrial land use (pipe yards, oil fields, factories, junk yards, lots under construction, solar panel lots, large storage lots)
camp	Percentage of cell characterised by campus land use (schools, churches, medical centers, and large corporations)
UL	Percentage of cell characterised by undeveloped lots
KRC	Percentage of cell characterised by the Kern River corridor
ag	Percentage of cell characterised by agriculture land use (row crops and orchards)
PGS	Percentage of cell characterised by parks and green space land use (golf courses, parks, cemeteries, large lawns)
MSR	Percentage of cell characterised by roadway median or side of roadway land use
OOS	Percentage of cell characterised by other open space land use (natural areas, airport runways, canals, water catchment basins, powerlines, dirt roads)

Table 2. Total number of grid cells (no. of cells), survey days (no. of surveys), and cells and surveys with San Joaquin kit foxes (*Vulpes macrotis mutica*, kit fox) or other canids (includes coyotes, *Canis latrans*; red foxes, *V. vulpes*; and gray foxes, *Urocyon cinereoargenteus*), as well as the number of cells in which San Joaquin kit foxes possessed sarcoptic mange disease (canis variety skin mite, *Sarcoptes scabiei*) each season (year) from 2015 to 2019 in Bakersfield, California, USA

Season (year)	No. of cells	No. of surveys	No. of cells with kit fox	No. of surveys with kit fox	No. cells with other canids	No. surveys with other canids	No. cells with kit fox + other canids	No. of surveys with kit fox + other canids	No. cells with kit fox mange
1 (2015)	105	735	68	226	8	14	4	1	9
2 (2016)	111	775	52	180	11	22	4	3	7
3 (2017)	109	763	39	133	8	18	0	0	6
4 (2018)	110	770	28	89	9	20	1	0	5
5 (2019)	110	763	18	62	7	14	3	3	2
1–5 (2015–2019)	545	3806	205	690	43	88	12	7	29

were correlated based on significant *P*-values were never included in the same multi-covariate model (Burnham and Anderson 2002; Lesmeister *et al.* 2015; Lombardi *et al.* 2017). We fit models first with no occupancy covariates (null model), followed by each covariate individually, as well as with combinations of covariates following four a priori modelling categories representing various degrees of urban development and prominent city characteristics: (1) less development and/or the presence of other canids, (2) heavy development, (3) high density of paved roads, and (4) high density of vegetation and/or the presence of other canids (see Supplementary Material 1). We included other canids in the first and fourth categories as they are more likely to be occurring in less developed or highly vegetated areas within the urban environment. While we were primarily interested in estimating occupancy probability, the inclusion of mange presence in cells as an extinction covariate allowed us to partly control for the population wide effects of mange across the 5 years of the study (MacKenzie *et al.* 2018). We held extinction, colonisation, and detection parameters constant across seasons and survey occasions.

We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c, number of cells surveyed/maximum number of model parameters <40; Burnham and Anderson 2002) and β values to rank each model in the set (MacKenzie *et al.* 2018). The lower the AIC_c value and the larger the AIC_c weight (w, the measure of support for the given model being the best model of the data), the better the model explained the data (MacKenzie *et al.* 2018). We considered models strong descriptors of the data when the ΔAIC_c value between the best fit model and the given model was <2.00, and moderate descriptors of the data when $2.00 \leq \Delta AIC_c < 4.00$ (Burnham and Anderson 2002). All models were run in PRESENCE 2.12.34 (Hines 2006).

Results

We detected kit foxes at 38% of the total cells and during 18% of the total surveys over the 5-year sampling period (Table 2). The number of kit fox detections was highest in season 1 (2015) and consistently declined through season 5 (2019), resulting in a 74% decrease in the number of cells and 73% decrease in number of surveys in which kit foxes were detected (Table 2).

Table 3. Number of grid cells characterised by a majority percentage of urban landscape attributes, as well as with > 20% paved roads or mature trees and the presence of a stable water source out of 111 cells from 2015 to 2019 in Bakersfield, California, USA

Landscape characterisation	Number of cells
% High-density residential	73.5
% Undeveloped lot	18.5
% Commercial	8.0
% Industrial	5.0
% Agricultural	2.0
% Campus	1.5
% Parks and green space	1.0
% Other open space	1.0
% Kern River corridor	0.5
% Low to medium density residential	0.0
% Median or side of roadway	0.0
>20% mature trees	28.0
>20% paved roads	33.0
Stable water source present	70.0

Table 4. Correlated pairwise habitat attributes including Spearman correlation test statistic (*t*) and Spearman correlation coefficient (r_s) values for a total of 111 survey grid cells from 2015 to 2019 in Bakersfield, California, USA

Degrees of freedom = 109 and *P*(adjusted) <0.001 for each correlation

Habitat attribute correlation	*t*	r_s
Tree × HDR	10.064	0.694
Road × MSR	5.806	0.486
UL × OOS	5.469	0.464
Road × HDR	5.173	0.444
Ind × OOS	4.382	0.387
Tree × PGS	3.965	0.355
LMDR × camp	3.863	0.347
Tree × road	3.838	0.345
Tree × UL	–9.604	–0.677
HDR × UL	–7.224	–0.569
HDR × OOS	–5.775	–0.484
Tree × ind	–5.394	–0.459
HDR × ind	–4.818	–0.419
Road × UL	–4.748	–0.414
LMDR × UL	–4.625	–0.405
Tree × OOS	–4.516	–0.397
HDR × com	–4.449	–0.392
UL × PGS	–4.289	–0.380
Road × OOS	–4.029	–0.360
LMDR × OOS	–3.600	–0.326

Similarly, we observed kit foxes with mange in 14% of the total cells in which kit foxes were detected over the 5-year sampling period with the number of cells with mange highest in season 1 and slightly declining through season 5, resulting in a 2% decrease in the number of cells with kit foxes possessing mange (Table 2). Our cameras detected kit foxes in 4.7 times as many cells and 7.8 times as many surveys as other canids combined, with kit foxes occurring with another canid in 6% of total cells and 1% of total surveys in which kit foxes were detected (Table 2). Kit fox presence was not associated with other canid presence in cells ($X^2 = 2.182$, d.f. = 1, $P = 0.140$) but was associated with other canid presence on survey days across the 5-year sampling period ($X^2 = 6.283$, d.f. = 1, $P = 0.012$).

Occupancy modelling

The dominant landscape attribute in most cells was high-density residential (66% of cells; Table 3). Campuses, parks and green spaces, other open spaces, and the Kern River corridor were dominant in ≤1% of cells and low to medium density residential and median or side of the roadway attributes were not dominant in any of the cells (Table 3). Fewer than half of the cells had > 20% paved roads or mature tree cover (30 and 25% of cells, respectively), and more than half had a stable water source (63% of cells; Table 3). We found eight positive correlations and 12 negative correlations between landscape attributes (Table 4).

Apart from the best ranking model, six models had strong empirical support with ΔAIC_c <2.00, including the null model (Table 5). Roads, campuses, low to medium density residential areas, the presence of water, and parks and green spaces were the covariates represented respectively in the six models (Table 5). Of the six models, two were additive models, one including both roads and low to medium density residential covariates and one including both water and campuses as covariates, respectively (Table 5). Roads and campuses were the only two covariates to appear in two of the six models (Table 5) with roads the only negative predictor of kit fox occupancy (Table 6). Two additional models were supported with ΔAIC_c < 2.00 (see Supplementary Material 1) although they were excluded from our analysis as all had covariate beta 95% confidence intervals that encompassed 0 for one or more occupancy parameters, providing insufficient evidence to conclude an effect on kit fox occupancy (β range = 0.02 to 0.17, 95% CI range = –0.35 to 0.48).

Four models had moderate empirical support with 2.00 ≤ ΔAIC_c < 4.00, which included the presence of water, mature trees, and commercial areas as individual covariates and an additive model including low to medium density residential and commercial areas (Table 5). Of the four models, commercial areas were the only negative predictor of kit fox occupancy (Table 6). Twenty-five other models were supported with 2.00 ≤ ΔAIC_c < 4.00 (see Supplementary Material 1) although they were excluded from our analysis as all had covariate beta 95% confidence intervals that encompassed 0 for one or more occupancy parameters (β range = <–0.01 to 0.32, 95% CI range = –0.52 to 0.89).

The best ranking model in our set included an additive combination of paved roads and campuses in cells (Table 5). Paved roads had a negative effect on kit fox occupancy and campuses had a positive effect, with campuses having a slighter larger effect on occupancy than paved roads (Table 6). Occupancy probability increased from 0.73 with 0% campus to 0.94 with 100% campus while holding roads at 0% (Fig. 1). Occupancy probability decreased from 0.73 with 0% roads to 0.30 with 100% roads while holding campus at 0% (Fig. 1). Across the study area, probability of occupancy was highest near campuses and lowest near large roads when considering the effect of both parameters across the 5-year sampling period (Fig. 2). Mean occupancy probability across cells declined 40% over time from 0.66 in 2015 to 0.26 in 2019 with raw occupancy estimates following a similar pattern and declining by 49% over time from 0.65 in 2015 to 0.16 in 2019 (Fig. 3). The best model

Table 5. Model selection results for occupancy modelling of San Joaquin kit foxes (*Vulpes macrotis mutica*) from 2015 to 2019 in Bakersfield, California, USA

The candidate model set includes 59 models and those with strong to moderate empirical support ($\Delta \text{AIC}_c < 4.00$) are shown

Model ranking	Model name	*K*	AIC$_c$	ΔAIC$_c$	*w*	–2LogL
1	$\psi(\text{road} + \text{camp}),\gamma(),\varepsilon(\text{mange}),p()$	7	2634.38	0.00	0.0698	2619.29
2	$\psi(\text{road}),\gamma(),\varepsilon(\text{mange}),p()$	6	2634.68	0.30	0.0601	2621.87
3	$\psi(\text{camp}),\gamma(),\varepsilon(\text{mange}),p()$	6	2634.88	0.50	0.0543	2622.07
4	$\psi(\text{road} + \text{LMDR}),\gamma(),\varepsilon(\text{mange}),p()$	7	2635.44	1.06	0.0411	2620.35
5	$\psi(\text{water} + \text{camp}),\gamma(),\varepsilon(\text{mange}),\text{p}()$	7	2635.76	1.38	0.0350	2620.67
6	$\psi(),\gamma(),\varepsilon(),p()$	4	2635.85	1.47	0.0335	2627.47
7	$\psi(\text{PGS}),\gamma(),\varepsilon(\text{mange}),p()$	6	2636.19	1.81	0.0282	2623.38
8	$\psi(\text{water}),\gamma(),\varepsilon(\text{mange}),p()$	6	2636.41	2.03	0.0253	2623.60
9	$\Psi(\text{tree}),\gamma(),\varepsilon(\text{mange}),p()$	6	2636.57	2.19	0.0233	2623.76
10	$\psi(\text{com}),\gamma(),\varepsilon(\text{mange}),p()$	6	2636.86	2.48	0.0202	2624.05
11	$\psi(\text{LMDR} + \text{com}),\gamma(),\varepsilon(\text{mange}),p()$	7	2637.84	3.46	0.0214	2622.75

predicted a 0.15 colonisation probability (95% CI = 0.11 to 0.20) and a 0.46 detection probability (95% CI = 0.43 to 0.48), meaning over the course of the seven surveys within a season we had a 98.7% chance of detecting a kit fox.

Mange presence in kit foxes was a negative predictor of extinction in the 11 supportive models (Table 6). The best model predicted a 0.49 extinction probability (95% CI = 0.40 to 0.57) in sites where mange was not present in kit foxes over the 5-year sampling period and an 0.37 extinction probability (95% CI = 0.24 to 0.50) in sites where mange was present, meaning there was a 12% greater chance of kit fox extinction at sites that did not already have mange present. The number of other canids was a negative predictor of occupancy in all 18 models fit with other canids as a covariate, although these were excluded from our analysis as all had covariate beta 95% confidence intervals that encompassed 0 (β range = –0.04 to –0.01, 95% CI range = –0.11 to 0.07).

Discussion

The high number of kit fox detections relative to those for coyotes, red foxes, and gray foxes demonstrated that kit foxes may be better adapted to highly developed urban environments. Although they may exhibit preferences, kit foxes are frequently observed using many urban landscape types unlike coyotes, red foxes, and gray foxes. In general, mammals with smaller body sizes are more likely to fare better in urban environments (Crooks 2002) because larger canids may have more limited utilisation of these areas due to greater open space requirements, lower human tolerance, and other factors (Gehrt and Riley 2010; Riley and White 2010; Soulsbury *et al.* 2010).

With campuses and paved roads the two most important landscape attributes in our modelling, our results most closely align with our third *a priori* modelling category, that kit fox occupancy would be affected by urban areas with high densities of paved roads. Campuses may be the most important single landscape attribute for kit fox occupancy. Campuses were a positive predictor of kit fox occupancy which was consistent with our prediction that kit foxes would select for open space areas within the urban environment. Campuses have large landscaped grounds (e.g. sports fields, courtyards, quadrangles, lawns, and walkways) that offer open space for kit foxes (Cypher and Van Horn Job 2012). Campuses also offer abundant and inviting denning opportunities for kit foxes underneath large storage containers, modular buildings, sheds, garbage dumpsters, and other man-made structures or debris (Frost 2005). Additionally, campuses often have food courts, cafeterias, or picnic tables where patrons drop food or feed kit foxes and other animals directly (Cypher 2010), and these spaces support populations of kit fox prey including California ground squirrels (*Otospermophilus beecheyi*), valley pocket gophers (*Thomomys bottae*), birds, and insects (Cypher 2010). Further, campuses commonly have security measures or fencing which may limit human activity overnight when kit foxes are most active and help to exclude larger terrestrial predators such as coyotes.

It can be assumed that the number of campuses will increase as the human population continues to grow (Chen *et al.* 2014), which may continue to support urban kit fox populations. Human–kit fox conflict on campuses include concerns that kit foxes may attack people, leave abundant faecal matter, spread disease or parasites, damage property by digging dens, or have implications for property owners when a protected species resides on their property (Cypher and Van Horn Job 2012); however, actual incidents are rare. Property owners may be more tolerant of foxes residing on campuses given education and outreach efforts that provide information on minimal risks, established protocols to aid landowners with handling fox nuisance issues, and appropriate response actions during a kit fox encounter (Cypher 2010; Cypher and Van Horn Job 2012). One significant risk to kit foxes associated with school campuses is that they may tangle themselves in sports nets (e.g. soccer nets, batting cage nets, and tennis nets), leading to stress, exhaustion, or suffocation when trapped in a net for an extended period of time (Cypher and Van Horn Job 2012). To-date, there have been 57 reported occurrences and 22 kit fox fatalities in Bakersfield due to sport net entanglement (B. L. Cypher, unpubl. data). This issue could also be addressed through education and outreach by informing schools of the consequences of leaving sports nets out overnight or posting signage reminding personnel to tie nets off the ground when not in use.

Nonetheless, paved roads were also an important negative predictor of kit fox occupancy and as urbanisation increases, the abundance of paved roads will also increase (Bjurlin *et al.* 2005). An increase in paved roads not only presents risk to kit

Table 6. Parameter estimates with 95% confidence intervals for best ranking occupancy models of San Joaquin kit foxes (*Vulpes macrotis mutica*) from 2015 to 2019 in Bakersfield, California, USA

The candidate model set includes 59 models and those with strong to moderate empirical support ($\Delta AIC_c < 4.00$) are shown

Model ranking	Model and parameters	β	Lower CI	Upper CI
1	ψ(road + camp),γ(),ε(mange),*p*()			
	ψ	1.01	0.54	1.49
	ψ(road)	–0.04	–0.06	–0.02
	ψ(camp)	0.05	0.02	0.08
	γ	–1.72	–1.90	–1.54
	ε	–0.05	–0.22	0.13
	ε(mange)	–0.51	–0.84	–0.17
	p()	–0.18	–0.23	–0.12
2	ψ(road),γ(),ε(mange),*p*()			
	ψ	1.34	0.89	1.78
	ψ(road)	–0.04	–0.06	–0.02
	γ	–1.72	–1.90	–1.54
	ε	–0.04	–0.22	0.13
	ε(mange)	–0.51	–0.84	–0.17
	p()	–0.18	–0.23	–0.12
3	ψ(camp),γ(),ε(mange),*p*()			
	ψ	0.37	0.11	0.63
	ψ(camp)	0.05	0.02	0.09
	γ	–1.72	–1.90	–1.54
	ε	–0.05	–0.23	0.12
	ε(mange)	–0.50	–0.83	–0.17
	p()	–0.18	–0.23	–0.12
4	ψ(road + LMDR),γ(),ε(mange),*p*()			
	ψ	1.23	0.78	1.67
	ψ(road)	–0.04	–0.07	–0.02
	ψ(LMDR)	0.05	0.01	0.09
	γ	–1.72	–1.90	–1.54
	ε	–0.05	–0.22	0.13
	ε(mange)	–0.51	–0.84	–0.17
	p()	–0.18	–0.23	–0.12
5	ψ(water + camp),γ(),ε(mange),*p*()			
	ψ	0.07	–0.30	0.43
	ψ(water)	0.51	0.08	0.95
	ψ(camp)	0.05	0.02	0.09
	γ	–1.72	–1.91	–1.54
	ε	–0.05	–0.23	0.12
	ε(mange)	–0.50	–0.83	–0.17
	p()	–0.18	–0.23	–0.12
6	ψ(),γ(),ε(),*p*()			
	ψ	0.65	0.44	0.86
	γ	–1.73	–1.91	–1.54
	ε	–0.19	–0.34	–0.04
	p()	–0.18	–0.24	–0.13
7	ψ(PGS),γ(),ε(mange),*p*()			
	ψ	0.49	0.25	0.73
	ψ(PGS)	0.06	0.01	0.10
	γ	–1.72	–1.9	–1.54
	ε	–0.05	–0.23	0.13
	ε(mange)	–0.50	–0.83	–0.17
	p()	–0.18	–0.23	–0.12
8	ψ(water),γ(),ε(mange),*p*()			
	ψ	0.32	0.00	0.65
	ψ(water)	0.54	0.11	0.97
	γ	–1.72	–1.91	–1.54
	ε	–0.05	–0.22	0.13
	ε(mange)	–0.50	–0.84	–0.17
	p()	–0.18	–0.23	–0.12
9	ψ(tree),γ(),ε(mange),*p*()			
	ψ	0.23	–0.18	0.63
	ψ(tree)	0.03	<0.01	0.05
	γ	–1.72	–1.90	–1.54
	ε	–0.05	–0.22	0.13
	ε(mange)	–0.50	–0.84	–0.17
	p()	–0.18	–0.23	–0.12
10	ψ(com),γ(),ε(mange),*p*()			
	ψ	0.82	0.55	1.09
	ψ(road)	–0.02	–0.03	<–0.01
	γ	–1.72	–1.90	–1.54
	ε	–0.05	–0.22	0.13
	ε(mange)	–0.51	–0.84	–0.17
	p()	–0.18	–0.23	–0.12
11	ψ(LMDR + com),γ(),ε(mange),*p*()			
	ψ	0.70	0.41	0.98
	ψ(LMDR)	0.04	<0.01	0.09
	ψ(com)	–0.02	–0.03	<–0.01
	γ	–1.72	–1.90	–1.54
	ε	–0.05	–0.22	0.13
	ε(mange)	–0.50	–0.84	–0.17
	p()	–0.18	–0.23	–0.12

fox survival, but also reduces the amount of suitable kit fox habitat within the urban environment. Roads are inhospitable to kit foxes and are the main source of mortality in urban areas (Bjurlin *et al.* 2005). Additionally, roads are characterised by increased noise pollution, development, disturbance, and human activity which likely discourages kit foxes from utilising areas near paved roads (Bjurlin *et al.* 2005). In San Diego, California, USA, gray foxes were similarly found to be negatively associated with the presence of roads (Markovchick-Nicholls *et al.* 2008). A high proportion of paved roads in urban areas that also support campuses may benefit from cautionary signage, reduced speed limits after sunset, or road crossing structures or corridors that support kit fox movements between open space habitat patches. Kit foxes have been observed using culverts and bridges to move under roads, and kit fox specific crossing structures (incorporating open landscaping, fencing to keep larger predators out, and denning structures) may benefit kit foxes (Frost 2005; Cypher 2010).

Low to medium density residential areas, a continuous water source, and parks and green spaces were also considerable positive predictors of kit fox occupancy. We considered low to medium density residential areas to include apartment building or nursing home style living situations and parks and green space to include golf courses, cemeteries, large lawns, and other parks. These areas keep open, landscaped spaces in the form of yards, recreation areas, and walkways which also provide open space for kit foxes similar to campuses. Kit foxes are adapted to meet their metabolic water needs through their prey and therefore do not need to consume water, although they may drink water if it is readily available (Morrell 1972; O'Brien *et al.* 2010; Hall *et al.* 2013*a*).

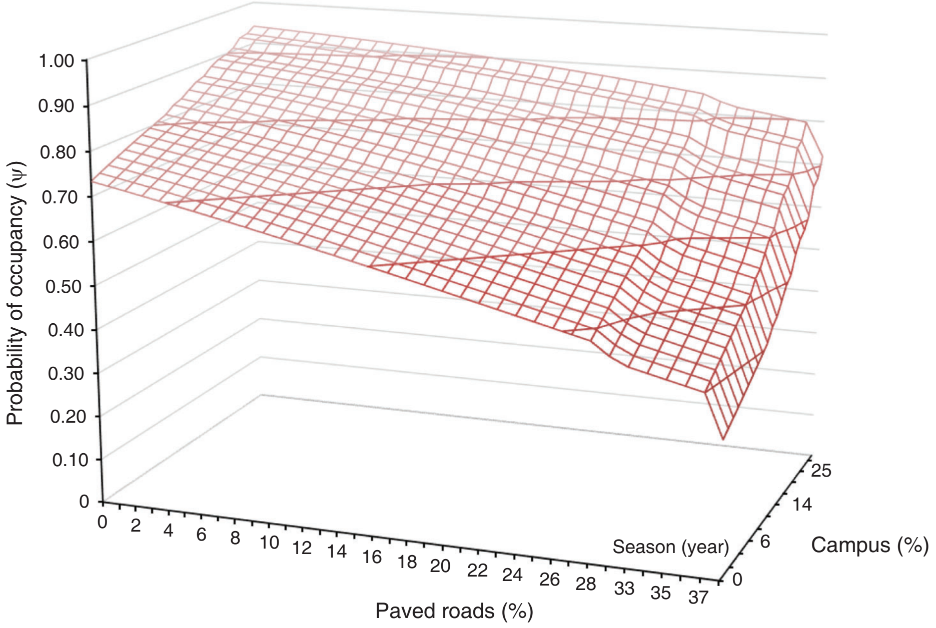

Fig. 1. San Joaquin kit fox (*Vulpes macrotis mutica*) occupancy probability estimates (ψ) as a function of percentages of paved roads and campuses in Bakersfield, California, USA, from 2015 to 2019.

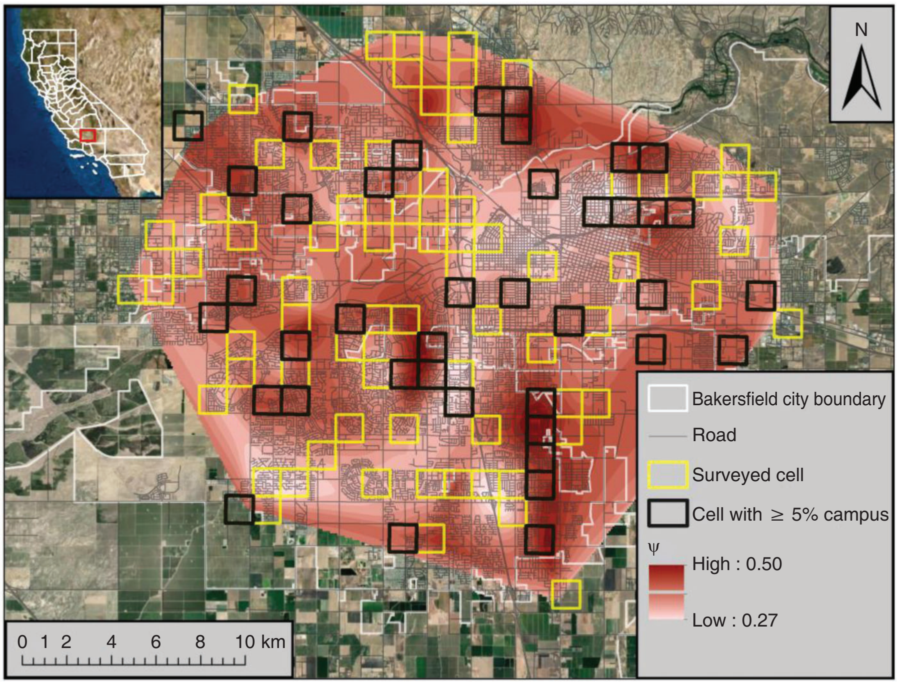

Fig. 2. Mean San Joaquin kit fox (*Vulpes macrotis mutica*) occupancy probability (ψ) in Bakersfield, California, USA across years from 2015 to 2019. City-wide occupancy probabilities were calculated and interpolated from San Joaquin kit fox detection/non-detection data as a function of landscape attribute data in 111 randomly selected 1-km^2 grid cells located throughout the city.

Consuming free water may reduce time and energy kit foxes spend searching for prey, also reducing the likelihood of encounters with competitors or predators, and may compensate for extra water loss by females during lactation due to milk production (Hall *et al.* 2013*b*), thereby benefiting kit foxes residing near free water in urban areas.

The least important, albeit still considerable, landscape attributes for kit fox occupancy in our study were mature trees,

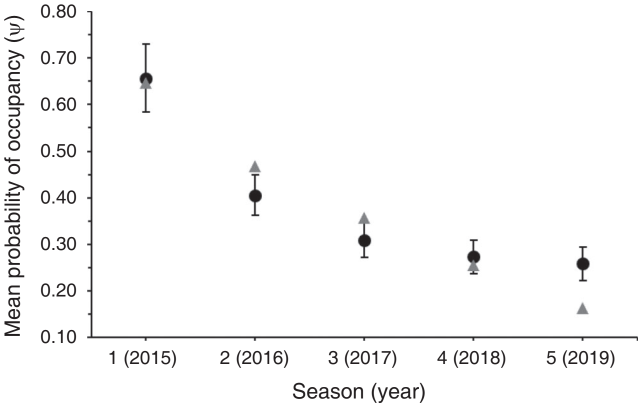

Fig. 3. Mean San Joaquin kit fox (*Vulpes macrotis mutica*) occupancy probability (ψ) across survey sites by season (years 2015 to 2019) in Bakersfield, California, USA. Probability estimates from a model of occupancy as a function of percentages of paved roads and campuses in cells (i.e. adjusted for detection probability, squares with 95% confidence intervals) and raw occupancy calculations (triangles) are included.

which were a positive association for kit foxes, and commercial areas, which were a negative association for kit foxes. While mature trees are not a typical landscape feature in natural kit fox habitat, kit foxes are opportunistic foragers and have been observed climbing trees on rare occasions, perhaps to forage for insects (Murdoch *et al.* 2009). Scattered trees may assist with thermoregulation by shading areas in the summer and insulating areas in the winter or provide concealing protection from predators (Hall *et al.* 2013*b*). Conversely, commercial areas such as shopping areas, service centres, and businesses are dense with paved roads, vehicular traffic, and human activity that often extends past nightfall when kit foxes are most active which may discourage kit foxes from commercial areas.

Because mange prevalence in kit foxes remained mostly consistent over the 5-year study, the drastic decline in kit fox abundance likely reflects the strong negative effect of sarcoptic mange on the urban kit fox population. Mange resulted in high kit fox extinction probabilities at sites, which was at least 22% higher than the kit fox colonisation probability at sites. This confirms that sites are becoming unoccupied by kit foxes at a faster rate than they are becoming occupied. Because mange transmission between foxes may be frequency-dependent as opposed to density-dependent (Devenish-Nelson *et al.* 2014; Carricondo-Sanchez *et al.* 2017; Scott *et al.* 2020), the higher probability of extinction at sites not displaying mange compared with sites confirmed to have mange over the 5-year study may be due to healthy foxes spending more time foraging, interacting with other individuals, or dispersing due to better body conditions (Newman *et al.* 2002; Carricondo-Sanchez *et al.* 2017). Increased activity of healthy individuals compared with already sick individuals may increase the likelihood of infection and therefore extinction at a previously healthy site (Devenish-Nelson *et al.* 2014; Carricondo-Sanchez *et al.* 2017; Scott *et al.* 2020). While multi-state occupancy modelling may have been an alternative method to assess the effects of mange on kit fox occupancy, we used a less robust multi-season analysis due to relatively low sample size and mange occurrence compared with the relatively high number of parameters used in multi-state modelling (MacKenzie *et al.* 2018).

Current occupancy modelling techniques are not sensitive enough to accurately estimate occupancy probability for extremely small detection rates, as we observed for coyotes, red foxes, and gray foxes (MacKenzie *et al.* 2018). Additionally, effects of species interactions in multi-species modelling cannot be accurately assessed if detection rates differ substantially (MacKenzie *et al.* 2018) as they did in our study. Although our modelling results suggest that other canid effects on kit fox occupancy were negligible, there was an association between the presence of kit foxes and other canids during surveys. Issues of sample size and other factors that can affect competition not measured in this study (e.g. prey abundance) create uncertainty about the extent of co-occurrence and impacts on distributions.

In summary, kit foxes are highly urban-compatible species with the ability to use small, moderately developed habitat patches such as campuses while avoiding paved roads. Although kit foxes show preferences for or against certain urban landscape characteristics, none of the covariates used in our analysis produced overwhelming evidence towards kit fox occupancy. The generalist tendencies of kit foxes may make it difficult to find a covariate or model with great support for kit fox occupancy. Nonetheless, an understanding of local kit fox occupancy dynamics and how they are affected by changes in habitat can lead to effective conservation or management policy when planning urban development mitigation and identifying suitable areas for kit foxes within cities. Informed decisions and planning can facilitate the long-term sustainability of kit fox populations in urban environments and contribute to the recovery of this endangered species.

Conflicts of interest

The authors declare no conflicts of interest.

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