Urban Landscape Attributes and Intraguild Competition Affect San Joaquin Kit Fox Occupancy and Spatiotemporal Activity

Nicole Anne Deatherage

Department of Biology, California State University, Bakersfield

ABSTRACT

Human population growth and rapid urbanization have created new, attractive environments for opportunistic animals including some species of wild canids. San Joaquin kit foxes (*Vulpes macrotis mutica*) are a federally listed endangered and California listed threatened canid that persists in the city of Bakersfield, California, where they form a unique ecological guild with three other canid competitors: coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*). These four canids typically exhibit avoidance and/or resource partitioning due to overlapping niches, with smaller fox species avoiding attacks from more dominant foxes and coyotes by selecting alternative resources, finding refuge, occupying different habitat types, or adjusting behavior. Recent carnivore sympatry in urban areas may be due to behavioral adjustments and adaptations to complex urban environments, including heterogeneous landscape matrices and new, abundant resources.

I investigated carnivore sympatry in urban environments using 5 y of remote camera survey data collected throughout the city of Bakersfield to first determine how landscape attributes within heterogeneous urban landscapes influence San Joaquin kit fox occupancy patterns, and if canid competitors (i.e., coyotes, red foxes, and gray foxes) affect San Joaquin kit fox distributions with the use of occupancy modeling. Second, I investigated how the presence

of canid competitors or domestic dogs (*Canis familiaris*) in the same 1-km^2 area affects San Joaquin kit fox spatiotemporal activity with the use of Two-way Contingency Tables, One-way Analysis of Variance, and Kruskal-Wallis tests. I found the most supported occupancy model for San Joaquin kit foxes to be an additive effect of two urban landscape attributes, percentages of paved roads and campuses (e.g., schools, churches, and medical centers) in cells. The percentage of paved roads was a negative predictor of San Joaquin kit fox occupancy while the percentage of campuses was a positive predictor. The percentage of paved roads was ultimately the most supported covariate for predicting San Joaquin kit fox occupancy (or lack thereof) in my study system. Roads are the main source of mortality for urban San Joaquin kit foxes and have greater noise pollution, development, disturbance, and human activity, which may discourage San Joaquin kit foxes from incorporating roads into their urban home ranges. Conversely, campuses have landscaping, sports yards, quadrangles, and walkways that offer open space, which San Joaquin kit foxes select for in natural habitats. These sites also afford security from excess human disturbance and larger predators due to fences and other security measures employed by campuses, as well as anthropogenic food sources from cafeterias and people directly feeding San Joaquin kit foxes. I concluded that San Joaquin kit foxes were avoiding paved roads while selecting for campuses in the urban environment. The presence of coyotes, red foxes, and gray foxes was not a contributing factor of urban San Joaquin kit fox occupancy patterns, though this may have been a result of low sample sizes of other canids compared to San Joaquin kit foxes.

Apart from one association between the number of days in which San Joaquin kit foxes occurred alone and the number of days in which they occur with other canids in 2018, I found no other associations between San Joaquin kit fox and other canid occurrences in cells or on given days. I also found differences between the number of days San Joaquin kit foxes occurred alone and the number of days they occurred with another canid for all years collectively and each year individually. I concluded that urban San Joaquin kit foxes rarely occur with coyotes, red foxes, gray foxes, and domestic dogs in the same 1-km^2 area within the same day, same year, or 5-y span, suggesting spatiotemporal avoidance of canid competitors. In instances when San Joaquin kit foxes and other canids did occur on the same camera on the same survey night, I found San Joaquin kit foxes delay their time to appearance following sunset by about 3 h at camera stations where another canid species appeared. Furthermore, variances in mean consecutive min that San Joaquin kit foxes spent at stations showed that they had the least predictability in the potential window of time spent at the station if another canid visited the camera station on the same night but did not appear first. San Joaquin kit foxes had the most predictability in the potential window of time spent at the station if another canid appeared first. These results indicate that San Joaquin kit foxes may require a more immediate predator presence cue than scent to perceive imminent risk from nearby competitors. Finally, my results show that if multiple canid species did occur there were never more than three, though primarily only two canids occurred in any given cell or on any given day, with a majority of co-occurrences between kit foxes and domestic dogs. Because domestic dogs are abundant in urban areas, they may not be novel or threatening to kit foxes, allowing domestic dogs and kit foxes to co-occur at higher frequencies than kit foxes and other wild canids. Additionally, where coexistence does occur, canids may only be willing to exist with one other canid species at any given time.

In both analyses, I confirm that San Joaquin kit foxes occur in higher abundances than any other wild canid species in Bakersfield. San Joaquin kit foxes may be more receptive and adaptive to highly developed urban areas than other canids and are frequently observed denning in inner city landscapes; whereas past studies show that coyotes require larger, connected ranges and natural habitat, that red foxes avoid coyotes in intermediate human-modified habitats (i.e., suburbs with house densities of < 20 houses/ha), and that gray foxes select for urban edges or more natural, tree covered areas. My results also demonstrated a sizeable decrease in kit fox abundance over the years, with a 69% decrease in San Joaquin kit fox abundance at camera stations and a 40% decrease in probability of San Joaquin kit fox occupancy from 2015 to 2019. This is explained by the recent outbreak of sarcoptic mange (*Sarcoptes scabiei*) skin disease in San Joaquin kit foxes in Bakersfield, which is highly infectious and 100% fatal in untreated kit foxes.

Overall, I conclude that while San Joaquin kit foxes rarely occur with other canid species within a 1-km^2 urban area, they may require immediate predator presence cues to perceive risk from competition, while avoidance of paved roads and selection for campuses as urban landscape characteristics may be of greater importance in explaining occupancy dynamics in urban San Joaquin kit foxes. Understanding how top predators adapt to developing landscapes provides insight towards species conservation and management in urban areas, which is particularly important for the San Joaquin kit fox. Conserving the unique urban population in Bakersfield may be significant for the overall health, survival, and recovery of this species as human development is projected to continue, and upcoming conservation efforts may be particularly critical considering the current mange epidemic within this population.

URBAN LANDSCAPE ATTRIBUTES AND INTRAGUILD COMPETITION AFFECT SAN JOAQUIN KIT FOX OCCUPANCY AND SPATIOTEMPORAL ACTIVITY

By

Nicole Anne Deatherage, B.S.

A Thesis Submitted to the Department of Biology
California State University, Bakersfield
In Partial Fulfillment for the Degree of Masters of Science

Spring 2020

Urban Landscape Attributes and Intraguild Competition Affect San Joaquin Kit Fox

Occupancy and Spatiotemporal Activity

By Nicole Anne Deatherage

This thesis has been accepted on behalf of the Department of Biology by their supervisory committee:

Dr. David J. Germano
Committee Chair

Dr. Brian L. Cypher

Dr. Carl T. Kloock

ACKNOWLEDGEMENTS

My thesis expands on previous work completed by Dr. Brian L. Cypher with the Endangered Species Recovery Program (ESRP) of California State University, Stanislaus. As such, much of the background, research direction, and methods have referenced his and his colleague's published work. My thesis committee chair, Dr. David J. Germano, and committee member, Dr. Carl T. Kloock, of California State University, Bakersfield (CSUB) have assisted with data analysis and writing through guidance and review. In addition, Dr. James Murdoch of University of Vermont provided direction on statistical analysis and occupancy modeling of my data. Funding and materials have been generously provided by the Endangered Species Recovery Program, The San Joaquin Valley Chapter of The Wildlife Society, The Western Section of The Wildlife Society, as well as the Graduate Equity Fellowship and Fairie Decker Memorial Endowment Fund of CSUB.

Preliminary camera data for my analyses were collected and reviewed by ESRP personnel, including Tory Westall, Erica Kelly, Larry Saslaw, and Christine Van Horn Job. Tory and Erica in particular have familiarized me with protocols, helped to develop my datasets, and having both completed a M.S. in Biology at CSUB, have provided invaluable support towards the development and completion of my thesis.

In addition, I thank Angela Madsen of CSUB for her confidence and editing of drafts of my thesis, and Olga Rodriguez of U.S. Geological Survey for aiding with GIS mapping. I thank my parents, Nancy Armendaris and Michael Deatherage, and friends, Jordyn Carkhuff and April Purdy, for providing unconditional encouragement, support, humor, and hard truths. I thank "Aunt Wonderful" for all her support in showing me the natural world and inspiring my love for wildlife. Finally, I thank Philip Schoepfle for his patience, support, and tranquility during my thesis work.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 2

CHAPTER 3

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

Chapter 1

Introduction

Urbanization began during the Industrial Revolution (1760 to 1870) and is defined by an increase in human residents, industry, employment, living conditions, and social public services (Chen et al. 2014). The number of people living in urban areas rose globally from 39% in 1980 to 52% in 2011, and rose to approximately 80% in North America by 2011 with rising trends likely to continue (Chen et al. 2014; Fig. 1). Urbanization is considered the current leading cause of alterations to Earth's ecosystems, and modest increases in development can result in significant changes in biodiversity (Hansen et al. 2005, Grimm et al. 2008).

Urban areas constitute new habitat with an increase in temperature and noise, non-native animals, roads, buildings, and infrastructure (Gehrt 2010). Urbanization creates a habitat gradient in which city centers are densely populated outward to low-density human activity, resulting in different light, noise, microclimate, and microhabitat conditions along the gradient (Šálek et al. 2015). Due to rapid expansion of human development in a historically short period of time, animals must possess ecological plasticity and make immediate behavior adjustments or undergo rapid evolutionary response to persist in urban areas (Ditchkoff et al. 2006). Wild animals may experience changes in fitness, vigilance, or habitat selection as a result of disturbance or perceived risk from human activity (Frid and Dill 2002). Urban habitats can provide animals with access to abundant anthropogenic food sources including refuse, food intentionally left out for animals, planted fruits and vegetables, and permanent water sources, as well as human-built structures that provide shelter (Harrison 1997, Fuller et al. 2010). These

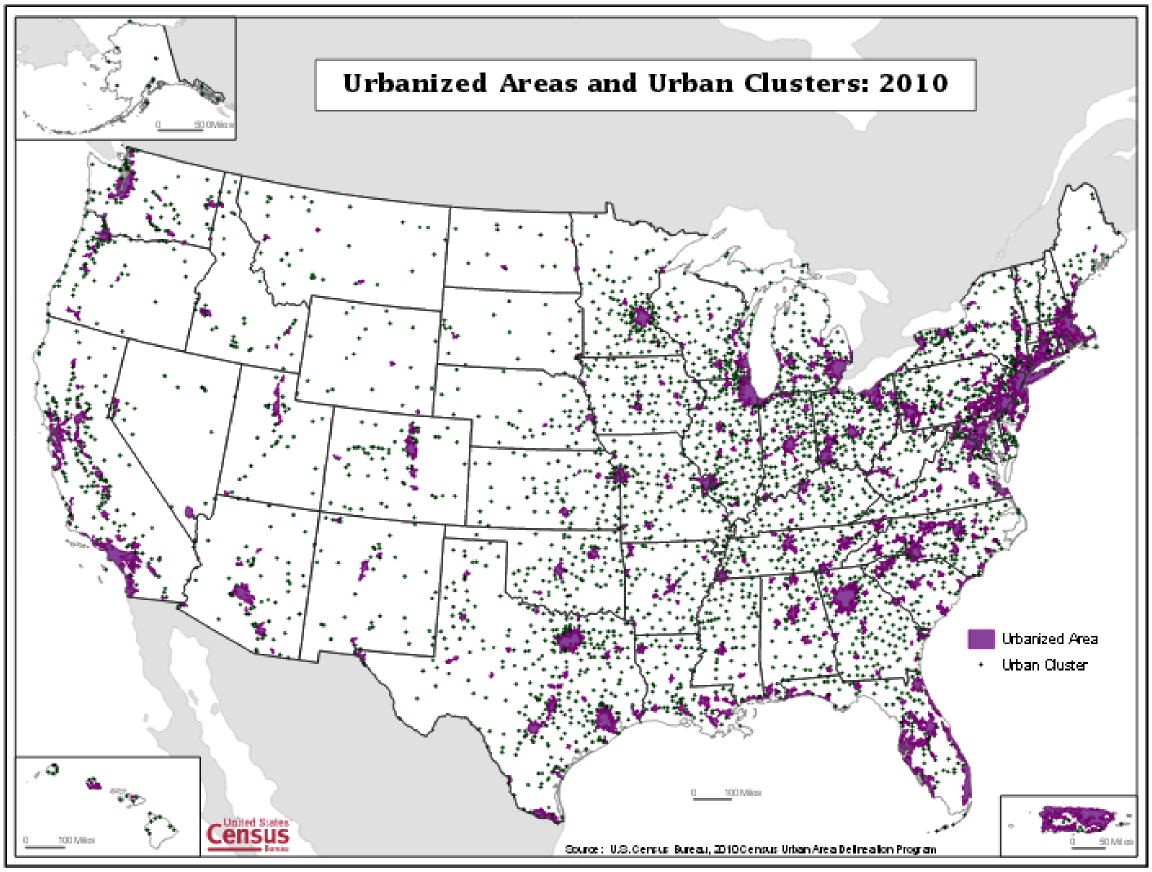


Figure 1. Urban areas (≥ 50,000 people) and urban clusters (≥ 2,500 people) of the United States in 2010. (Map by the United States Census Bureau).

resources can attract high densities of development-tolerant animals, as is the case for many canid species (Gehrt and Riley 2010).

San Joaquin kit foxes (*Vulpes macrotis mutica*) are a development-tolerant canid that is frequently observed in urban areas (Cypher 2010). San Joaquin kit foxes are the smallest wild canid species in North America, weighing 2.1–2.3 kg with a body-plus-tail length of 105.3–110 cm on average and, unlike many other canid species, are known to use multiple daily dens throughout the year (Williams et al. 1998, Cypher 2003). The San Joaquin kit fox is a federally listed endangered and California listed threatened subspecies of the kit fox (*Vulpes macrotis*) and is endemic to the San Joaquin Valley of central California, but was historically also found in the Salinas and Cuyama valleys of California (Williams et al. 1998, Cypher et al. 2001). Kit foxes are adapted to desert environments and are found in flat semi-arid open-desert, shrubland, or grassland habitats throughout Southwestern North America (McGrew 1979, Warrick and Cypher 1998, Cypher 2003). The protected status of the San Joaquin kit fox (hereafter kit fox) is primarily due to habitat loss and degradation from agricultural, industrial, and urban development, although predation by larger carnivores remains the main cause of mortality in natural habitats (Williams et al. 1998, Cypher et al. 2001). Since 2013, kit foxes in urban areas have additionally been negatively affected by sarcoptic mange, a highly contagious skin infection caused by *Sarcoptes scabiei* mites, with varieties that infest many wild and domestic species as well as humans (Pence and Ueckermann 2002, Cypher et al. 2017).

Kit foxes have overlapping niches with three other canids also observed in urban areas throughout the United States: coyotes (*Canis latrans*), red foxes (Vulpes vulpes), and gray foxes (*Urocyon cinereoargenteus*); forming an intraguild assemblage where these species co-occur (Cypher et al. 2001, Cypher 2003, 2010, Lesmeister et al. 2015; Fig. 2). Coyotes and foxes are opportunistic canids of the order Carnivora and inhabit a variety of habitat types, are active at similar times of day (crepuscular or nocturnal), and have meso-carnivore diets including fruits, invertebrates, small mammals, and birds (Voigt and Berg 1987, Cypher 2003, Macdonald 2009, Soulsbury et al. 2010). Their home ranges are fluid and determined by many factors including sex, season, food abundance, habitat quality, and presence of physical barriers (e.g., rivers and lakes), as well as intra- and interspecific competition (Cypher 2003). In North America, coyotes, red foxes, and gray foxes are widely distributed with the coyote as the top predator throughout

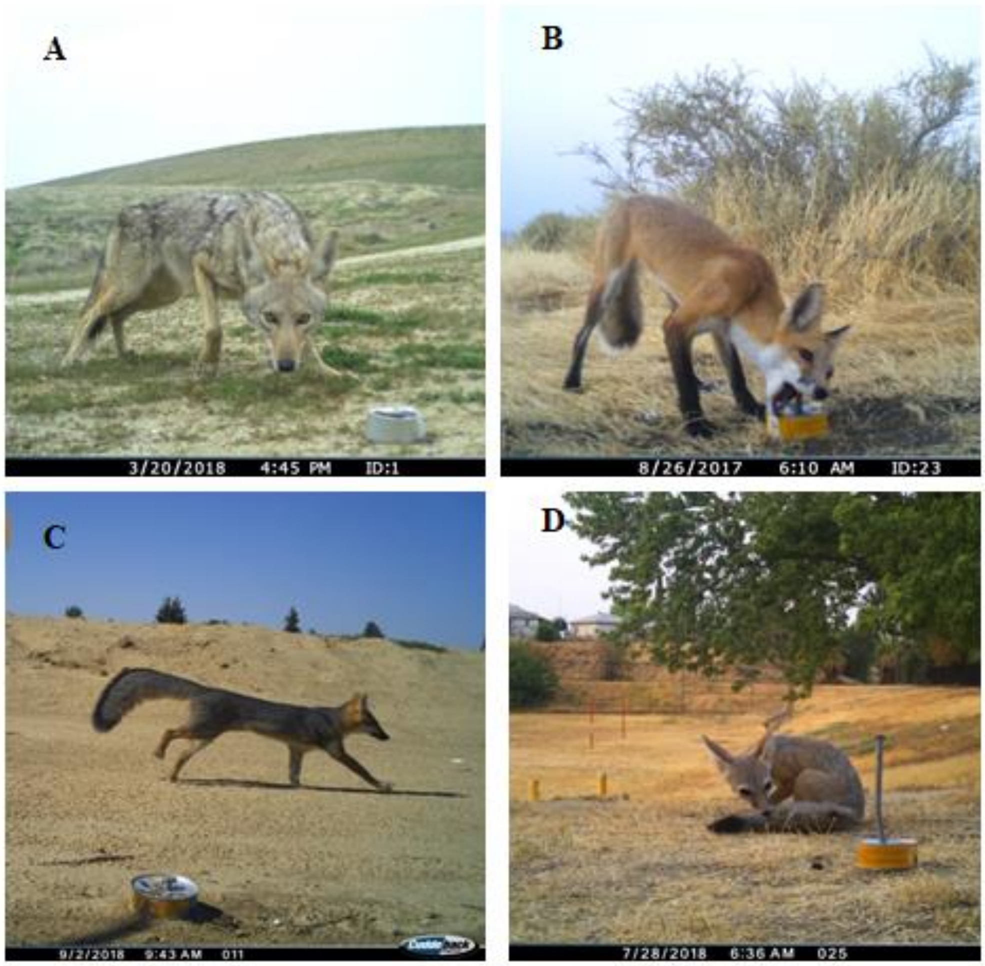


Figure 2. A (A) coyote, (B) red fox, (C) gray fox, and (D) San Joaquin kit fox pictured visiting baited camera stations in or around Bakersfield, California in 2017 and 2018. (Photographs by the Endangered Species Recovery Program, California State University, Stanislaus).

much of its range (Voigt and Berg 1987, Cypher 2003, Gehrt and Riley 2010, Soulsbury et al. 2010).

Interspecific interactions are complex mechanisms that can regulate populations and community structure. When a group of species have overlapping niches due to selection for the same limiting resources (e.g., habitat or food) they experience interspecific competition (Cypher et al. 2001, Mackenzie et al. 2006). Interference competition occurs when one species kills, harasses, or spatially excludes another, resulting in decreased use of an area by the less dominant species (Case and Gilpin 1974, Cypher et al. 2001). Intraguild predation is an extreme mechanism of interference competition in which predators compete for shared resources with larger, dominant species killing smaller, subordinate species and selecting for resource rich habitats, while subordinate species must balance risk with access to resources (Polis et al. 1989, Heithaus 2001). Intraguild competition can lead to exclusion or alternative stable states among guilds (Polis et al. 1989). In these situations, natural selection favors adaptive behaviors of individuals to avoid confrontation and death, leading to niche differentiation and ultimately, coexistence (Holt and Polis 1997, Freeman 2011). When coexistence occurs, avoidance of competitors may reduce interference competition, but can limit the distribution of the subordinate competitor (Kitchen et al. 1999, Freeman 2011). Under the intraguild predation model, coexistence is possible if predation by the top predator on the lesser predator is infrequent enough for the lesser predator to persist, and if the lesser predator is capable of exploiting alternative resources not used by the top predator (Holt and Polis 1997).

Intraguild species may be capable of specialization and/or resource partitioning over time and space to avoid conflict (Lesmeister et al. 2015). In many places where coyotes and foxes are sympatric, coyotes are the number one predator of foxes and more successful in attacks when foxes are further from protective den or day use sites; however, coyotes often do not consume these kills suggesting competition rather than sustenance as the likely cause of predation (Ralls and White 1995, Kitchen et al. 1999, Cypher et al. 2001, Moehrenschlager et al. 2001, Farias et al. 2005, Nelson et al. 2007; Fig. 3). While coyotes select habitat with natural cover and high prey abundance, foxes may select habitats with less prey but more escape cover to avoid

Figure 3. A coyote (right) chases a San Joaquin kit fox (left) into a den at Carrizo Plain National Monument, California. The kit fox enters the den at 0244 on 5 May 2018, followed by the coyote at 0245 on the same date. (Photographs by the Endangered Species Recovery Program, California State University, Stanislaus).

interference competition with coyotes (Theberge and Wedeles 1989, Gosselink et al. 2003, Kozlowski et al. 2008, Lesmeister et al. 2015, Lonsinger et al. 2017).

Coyotes occur in a variety of habitat types from open country to alpine zones, and their dominance over foxes has been credited to their larger size, weighing 9–16 kg with a body-plus-tail length of 160–180 cm on average (Voigt and Berg 1987, Fedriani et al. 2000, Macdonald 2009). Red foxes are the largest North American fox, weighing 3.5–7.0 kg with a body-plus-tail length of 100–110 cm on average (Voigt 1987). They are the most widely distributed canid worldwide due to their highly variable ecology and behavior, though generally they prefer more open, mesic habitats (Storm et al. 1976, Macdonald 1980, Cypher 2003). Although somewhat smaller than red foxes, there is evidence for gray foxes (weighing 3–7 kg with a body-plus-tail length of 107.5–156.0 cm on average) being dominant over red foxes (Hall 1981, Tullar and Berchielli 1982). Gray foxes are primarily found in densely vegetated or woodland habitat and, unlike other canid species, are known for their arboreal abilities (Fritzell 1987, Lesmeister et al. 2015). Human related issues, including hunting and automobile collisions, are the number one cause of mortality for coyotes, red foxes, and gray foxes (Fritzell 1987, Voigt 1987, Voigt and Berg 1987).

Past studies have shown kit foxes, red foxes, and gray foxes avoid coyotes both temporally and spatially in non-urban environments (Warrick and Cypher 1998, Crooks and Soulé 1999, Fedriani et al. 2000, Cypher et al. 2001, Cypher 2003, Nelson et al. 2007, Lesmeister et al. 2015, Moll et al. 2018). In central California, kit foxes were observed using a greater variety of habitat types than coyotes, primarily selecting habitats with lower prey availability perhaps to avoid coyotes (Nelson et al. 2007). Kit fox abundance has been observed to decrease coinciding with an increase in coyote abundance, and similarly, gray fox and red fox abundance has increased following the removal of coyotes at treatment sites in western Texas and Wyoming, respectively, suggesting spatial avoidance of coyotes by foxes (Linhart and Robinson 1972, Henke and Bryant 1999, White et al. 2000).

An increase in coyote and fox densities when coupled with high levels of human activity in urban environments is likely to cause ecological and behavioral changes in intraguild dynamics (Fuller et al. 2010, Moll et al. 2018). Notable ecological changes exhibited by coyotes and foxes in urbanized areas as compared to natural areas include a decrease in home range or territory size, utilization of man-made structures, and the consumption of anthropogenic food sources. Kit foxes utilize manmade structures for denning and home range size decreases from an estimated mean of 4.61 km^2 in non-urban areas to 1.72 km^2 in urban areas (Knapp 1978, White and Ralls 1993, Koopman 1995, Zoellick et al. 2002, Frost 2005, Cypher 2010). Urban kit foxes consume mostly small mammals, insects, and anthropogenic food (White and Ralls 1993, Newsome et al. 2010). Coyotes maintain variable home range sizes, although a decrease in mean home range size from 17.0 km^2 in non-urban areas to 13.4 km^2 in urban areas has been observed (Gehrt and Riley 2010). Coyote activity is negatively correlated with human development and activity and urban coyotes consume mostly small mammals (Ng et al. 2004, Gehrt and Riley 2010, Moll et al. 2018). Red foxes hold territory sizes on the smaller end of their wide range of values, may climb or dig under buildings for refuge, and consume mostly anthropogenic food in urban areas (Cavallini 1996, Goszczyński 2002, Soulsbury et al. 2010). Space partitioning has been observed between coyotes and red foxes within an urban environment in Madison, Wisconsin, but to a lesser extent than is observed in natural lands (Mueller et al. 2018). Gray foxes exhibit greater home range complexity, utilize old agricultural fields and human-facilitated areas, and consume mostly small mammals and ornamental fruits in urban areas (Fuller 1978, Harrison 1997).

Kit foxes, coyotes, red foxes, and gray foxes are sympatric in the city of Bakersfield, California, located on the southern end of the San Joaquin Valley (Fig. 4). While kit foxes, coyotes, and gray foxes are native to the valley, red foxes were introduced from the mid-western United States in the 1870s for hunting and fur, with abundant anthropogenic water sources the likely reason for their successful colonization of the valley (Lewis et al. 1999, Cypher et al. 2001). The kit fox population in Bakersfield is of particular importance as, prior to the recent mange outbreak, it has been a stable population with a majority of individuals residing exclusively within an urbanized area (Cypher 2010). Considerable interest lies in this

Figure 4. A coyote (left) and San Joaquin kit fox (right) in urban areas of Bakersfield, California in 2014 and 2015. (Photographs by the Endangered Species Recovery Program, California State University, Stanislaus).

population's ecology and how it may inform recovery and conservation efforts (Cypher 2010). Previous studies in the San Joaquin Valley show coyotes continue to be a significant cause of fox mortality, and red foxes will on occasion kill smaller kit foxes and gray foxes and may enter or make use of kit fox dens (Cypher and Spencer 1998, Cypher et al. 2001, Clark et al. 2005, Farias et al. 2005). Domestic dogs (*Canis familiaris*) are an additional canid species in valley and interference competition may also occur between dogs and wild canids (Vanak and Thaker 2009).

Three possible mechanisms facilitating the coexistence of sympatric canids in Bakersfield are (1) diverse urban landscapes create more environmental complexity and niche availability; (2) larger predators are limited in urban areas resulting in competitive release for smaller species; and (3) resources are abundant in urban areas, thereby significantly reducing competition (B. L. Cypher, unpublished data). While radio collared kit foxes in Bakersfield have been observed utilizing undeveloped lands and water catchment basins disproportionately more than residential areas (Frost 2005), how kit fox occupancy and activity patterns are affected by heterogeneous urban landscapes and competitive interactions with four other canids in an urban environment is largely unknown (Cypher et al. 2001). I investigated mechanisms facilitating sympatry of five canids in Bakersfield by first determining which landscape features within the urban environment have the greatest influence on kit fox occupancy patterns, and whether coyotes, red foxes, and gray foxes affect kit fox distribution. Second, I investigated spatiotemporal avoidance of more dominant canid competitors, including domestic dogs, by kit foxes in the urban environment. My research provides insight into the complex ecology of a unique canid guild comprised of native, non-native, domestic, and endangered predators in an urban environment. With an increasing number of carnivores in urban areas, an understanding of their adaptations in response to urbanization becomes imperative for appropriate management and conservation practices, in particular for the imperiled kit fox.

My research is presented in the following two chapters, each of which has been formatted as manuscripts to be submitted to peer-reviewed journals. Chapter Two, "Urban landscape attributes affect San Joaquin kit fox occupancy patterns", presents my results on how landscape features and the presence of coyotes, red foxes, and gray foxes affect kit fox occupancy patterns within the urban environment. Chapter Two is formatted for Pacific Conservation Biology journal. Chapter Three, "Spatiotemporal patterns of San Joaquin kit foxes and an urban canid guild", presents my results on spatiotemporal activity patterns of urban kit foxes in the presence of coyotes, red foxes, gray foxes, and domestic dogs. Chapter Three is formatted for Western North American Naturalist journal. Finally, Chapter Four provides a summary of my research presented in Chapters Two and Three, and highlights implications for future research, conservation, and management of kit foxes in the urban environment.

LITERATURE CITED

Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences of the United States of America 71: 3073-3077.

Cavallini, P. 1996. Variation in the social system of the red fox. Ethology Ecology & Evolution 8: 323-342.

Chen, M., H. Zhang, L. Weidong, and W. Zhang. 2014. The global pattern of urbanization and economic growth: evidence from the last three decades. PLoS ONE 9(8): e103799. doi:10.1371/journal.pone.0103799.

Clark, H. O. Jr., G. D. Warrick, B. L. Cypher, P. A. Kelly, D. F. Williams, and D. E. Grubbs. 2005. Competitive interactions between endangered kit foxes and nonnative red foxes. Western North American Naturalist 65: 153-163.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400: 563-566.

Cypher, B. L. 2003. Foxes. Pages 511-546 *in*: Wild Mammals of North America: Biology, Management, and Conservation. 2nd Ed. Feldhamer, G. A., B. C. Thompson, and J. A. Chapman, editors. John Hopkins University Press, Baltimore, MD.

Cypher, B. L. 2010. Kit foxes (*Vulpes macrotis*). Pages 49-57 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. The Johns Hopkins University Press, Baltimore, MD.

Cypher, B. L., C. O. J. Howard, P. A. Kelly, C. Van Horn Job, G. D. Warrick, and D. F. Williams. 2001. lnterspecific interactions among wild canids: implications for the conservation of endangered San Joaquin kit foxes. Endangered Species Update 18: 171-174.

Cypher, B. L., J. L. Rudd, T. L. Westall, L. W. Woods, N. Stephenson, J. E. Foley, D. Richardson, and D. L. Clifford. 2017. Sarcoptic mange in endangered kit foxes (*vulpes macrotis mutica*): case histories, diagnoses, and implications for conservation. Journal of Wildlife Diseases 53: 46-53.

Cypher, B. L., and K. A. Spencer. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79: 204-214.

Ditchkoff, S. S., S. T. Saalfeld, and C. J. Gibson. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecosystems 9: 5-12.

Farias, V., T. K. Fuller, R. K. Wayne, and R. M. Sauvajot. 2005. Survival and cause-specific mortality of grey foxes (*Urocyon cinereoargenteus*) in southern California. The Zoological Society of London 266: 249-254.

Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125: 258-270.

Frost, N. 2005. San Joaquin kit fox home range, habitat use, and movements in urban Bakersfield. Master's thesis. Humboldt State University, Arcata, CA.

Freeman, S. 2011. An introduction to ecology. Pages 993-1127 *in*: Biological Science. 4th Ed. Wilbur, B., B. Ruden, S. DiVittorio, A. Fugate, M. Lerner-Nelson, W. O'Neal, S. Teahan, K. Murphy, B. Golden, and L. Allen, editors. Pearson Education, Inc., San Francisco, CA.

Frid, A. and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6: 11.

Fritzell, E. K. Gray fox and island grey fox. 1987. Pages 410-420 *in*: Wild Furbearer Management and Conservation in North America. Novak, M., J. A. Baker, M. E. Obbard, and B. Malloch, editors. The Ontario Trappers Association, Ontario, Canada.

Fuller, T. K. 1978. Variable home range sizes of female gray foxes. Journal of Mammalogy 59: 446-449.

Fuller, T. K., S. Destefano, and P. S. Warren. 2010. Carnivore behavior and ecology, and relationship to urbanization. Pages 18-19 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. Johns Hopkins University Press, Baltimore, MD.

Gehrt, S. D. 2010. The urban ecosystem. Pages 6-9 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. Johns Hopkins University Press, Baltimore, MD.

Gehrt, S. D., and S. P. D. Riley. 2010. Coyotes (*Canis latrans*). Pages 85-89 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. Johns Hopkins University Press, Baltimore, MD.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and M. G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. The Journal of Wildlife Management 67: 90-103.

Goszczyński, J. 2002. Home ranges in red fox: territoriality diminishes with increasing area. Acta Theriologica 47, Supplement 1: 103-114.

Grimm, N. B., D. Foster, P. Groffman, J. M. Grove, C. S. Hopkinson, K. J. Nadelhoffer, D. E. Pataki, and D. P. C. Peters. 2008. The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. The Ecological Society of America: Frontiers in Ecology and the Environment 6: 264-272.

Hall, E. R. 1981. The mammals of North America. Volume 2. John Wiley & Sons, New York, NY.

Hansen, A. J., R. L. Knight, J. M. Marzluff, S. Powell, K. Brown, P. H. Gude, and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15: 1893-1905.

Harrison, R. L. 1997. A comparison of grey fox ecology between residential and undeveloped rural landscapes. The Journal of Wildlife Management 61: 112-122.

Heithaus, M. R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild. Oikos 92: 542-554.

Henke, S. E., and F. C. Bryant. 1999. Effects of coyote removal on the faunal community in western Texas. The Journal of Wildlife Management 63: 1066-1081.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. The American Naturalist 149: 745-746.

Kitchen, A. M., E. M. Gese, and E. R. Schauster. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77: 1645-1656.

Knapp, D. K. 1978. Effects of agricultural development in Kern County, California, on the San Joaquin kit fox in 1977. California Department of Fish and Game, None-game Wildlife Investigations Final Report, Project E-1-1, Job V-1.21, Fresno, CA.

Koopman, M. E. 1995. Food habits, space use, and movements of the San Joaquin kit fox on the Elk Hills Naval Petroleum Reserves in California. Master's thesis. University of California, Berkeley, Arcata, CA.

Kozlowski, A. J., E. M. Gese, and W. M. Arjo. 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. The American Midland Naturalist 160: 191-208.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. Wildlife Monographs 191: 1-61.

Lewis, J. C., K. L. Sallee, and R. T. Jr. Golightly. 1999. Introduction and range expansion of nonnative red foxes (*Vulpes vulpes*) in California. American Midland Naturalist 142: 372-381.

Linhart, S. B., and W. B. Robinson. 1972. Some relative carnivore densities in areas under sustained coyote control. Journal of Mammalogy 53: 880-884.

Lonsinger, R. C., E. M. Gese, L. L. Bailey, and L. P. Waits. 2017. The roles of habitat and intraguild predation by coyotes on the spatial dynamics of kit foxes. Ecosphere 8 3: e01749.10.1002/ecs2.1749.

Macdonald, D. W. 1980. Habitat requirements of the red fox. Pages 7-25 *in*: The Red Fox. Volume 18. Zimen, E., editor. Biogeographica, The Hague, The Netherlands.

Macdonald, D. W., editor. 2009. Carnivores. Pages 598-611 *in*: The Princeton Encyclopedia of Mammals. Princeton University Press, Princeton, NJ.

MacKenzie, D. I., J. A. Royle, J. D. Nichols, J. E. Hines, K. H. Pollock, and L. Bailey. 2006. Occupancy Estimation and Modeling, Inferring Patterns and Dynamics of Species Occurrence. Academic Press, Burlington, MA.

McGrew, J. C. 1979. *Vulpes macrotis.* Mammalian Species 123: 1-6.

Moehrenschlager, A., R. List, and D. W. Macdonald. 2001. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. Jourmal of Mammalogy 88: 1029-1039.

Moll, R. J., J. D. Cepek, P. D. Lorch, P. M. Dennis, T. Robison, J. J. Millspaugh, and R. A. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21: 765-778

Mueller, M. A., D. Drake, M. L. Allen. 2018. Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. PLoS ONE 13(1): e0190971. https://doi.org/10.1371/journal.pone.0190971.

Nelson, J. L., B. L. Cypher, C. D. Bjurlin, and S. Creel. 2007. Effects of habitat on competition between kit foxes and coyotes. The Journal of Wildlife Management 71: 1467-1475.

Newsome, S. D., K. Ralls, C. Van Horn Job, M. L. Fogel, and B. L. Cypher. 2010. Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). Journal of Mammalogy 91: 1313-1321.

Ng, S. J., J. W. Dole, R. M. Sauvajot, S. P. D. Riley, and T. J. Valone. 2004. Use of highway undercrossings by wildlife in southern California. Biological Conservation 115: 499-507.

Pence, D. B., and E. Ueckermann. 2002. Sarcoptic mange in wildlife. Scientific and Technical Review of the Office International des Epizooties 21: 385-398.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20: 297-330.

Ralls, K., and P. J. White. 1995. Predation on San Joaquin kit foxes by larger canids. Journal of Mammalogy 76: 723-729.

Šálek, M., L. Drahníková, and E. Tkadlec. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Review 45: 1-14.

Soulsbury, C. D., P. J. Baker, G. Iossa, and S. Harris. 2010. Red foxes (*Vulpes vulpes*). Pages 63-75 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. Johns Hopkins University Press, Baltimore, MD.

Storm, G. L., R. D. Andrews, R. L. Philips, R. A. Bishop, D. B. Siniff, and J. R. Tester. 1976. Morphology, reproduction, dispersal and mortality of midwestern red fox populations. Wildlife Monographs 49: 3-82.

Theberge, J. B., and C. H. R. Wedeles. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67: 1285-1290.

Tullar, B. F. Jr., and L. T. Jr. Berchielli. 1982. Comparison of red foxes and gray foxes in central New York with respect to certain features of behavior, movement and mortality. New York Fish and Game Journal 29: 127-133.

Vanak, A. T., and M. Thaker. 2009. Experimental examination of behavioural interactions between free-ranging wild and domestic canids. Behavioral Ecology and Sociobiology 64: 279-287.

Voigt, D. R. 1987. Red fox. Pages 380-392 *in*: Wild Furbearer Management and Conservation in North America. Novak, M., J. A. Baker, M. E. Obbard, and B. Malloch, editors. The Ontario Trappers Association, Ontario, Canada.

Voigt, D. R., and W. Berg. 1987. Coyote. Pages 345-356 *in*: Wild Furbearer Management and Conservation in North America. Novak, M., J. A. Baker, M. E. Obbard, and B. Malloch, editors. The Ontario Trappers Association, Ontario, Canada.

Warrick, G. D., and B. L. Cypher. 1998. Factors affecting the spatial distribution of a kit fox population. The Journal of Wildlife Management 62: 707-717.

White, P. J., W. H. Berry, J. J. Eliason, and M. T. Hanson. 2000. Catastrophic decrease in an isolated population of kit foxes. The Southwestern Naturalist 45: 204-211.

White, P. J., and K. Ralls. 1993. Reproduction and spacing patterns of kit foxes relative to changing prey availability. The Journal of Wildlife Management 57: 861-867.

Williams, D. F., E. A. Cypher, P. A. Kelly, K. J. Miller, N. Norvell, S. E. Phillips, C. D. Johnson, and G. W. Colliver. 1998. San Joaquin kit fox (*Vulpes macrotis mutica*). Pages 122-136 *in*: Recovery Plan for Upland Species of the San Joaquin Valley, California. U.S. Fish and Wildlife Service, Region 1, Portland, OR.

Zoellick, B. W., C. E. Harris, B. T. Kelly, T. P. O’Farrell, and T. T. Kato. 1987. Reproduction of the San Joaquin kit fox on Naval Petroleum Reserve No. 1, Elk Hills, California, 1980-1985. U.S. Department of Energy Topical Report No. EGG 10282-2144.

CHAPTER 2

Urban landscape attributes affect San Joaquin kit fox occupancy patterns

Nicole A. Deatherage[A, B, C], *Brian L. Cypher*[B], *James Murdoch*[D], *Tory L. Westall*[B], *Erica C. Kelly*[B], *and David J. Germano*[A]

[A]Department of Biology, California State University – Bakersfield, 9001 Stockdale Highway, Bakersfield, CA 93311, USA

[B]Endangered Species Recovery Program, California State University – Stanislaus, One University Circle, Turlock, CA 95382, USA

[C]Corresponding author. Email: ndeatherage@csub.edu

[D]Wildlife and Fisheries Biology Program, University of Vermont, Burlington, VT 05405, USA

Conflicts of Interest

The authors declare no conflicts of interest.

Acknowledgements

The Endangered Species Recovery Program (ESRP) of California State University, Stanislaus, provided preliminary data as well as equipment and funding to complete camera surveys for our analysis. ESRP personnel Larry Saslaw and Christine Van Horn Job assisted in data collection and analysis. Dr. Carl T. Kloock of California State University, Bakersfield assisted with data analysis and edited drafts of this manuscript, and Olga Rodriguez with U.S. Geological Survey assisted with GIS mapping. Funding for this study was generously provided by ESRP, the San Joaquin Valley Chapter of The Wildlife Society, and the Western Section of The Wildlife Society.

Abstract. The federally listed endangered and California state-listed threatened San Joaquin kit fox (*Vulpes macrotis mutica*) persists in the urban environment of Bakersfield, California. Urbanization can create complex habitats and provide abundant, diverse resources for animals capable of habituation to altered environments and human activity. Coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*) are natural competitors of San Joaquin kit foxes, and their presence in Bakersfield potentially impacts kit foxes. We investigated landscape attributes and the presence of canid competitors in association with San Joaquin kit fox occupancy. We used 5 y of annual camera survey data gathered on 1-km^2 grid cells distributed throughout the city of Bakersfield in occupancy modeling to determine important landscape features for San Joaquin kit foxes. Urban San Joaquin kit fox occupancy patterns were driven primarily by avoidance of paved roads and selection for campuses (e.g., schools, churches, and medical centers); however, we found no association between the presence of other canids and occupancy of an area by San Joaquin kit foxes. Understanding San Joaquin kit fox usage of urban landscapes can help to develop effective land management and mitigation policy for San Joaquin kit foxes affected by urban development.

Additional keywords: campus, canid, competition, habitat, road

Online table of contents summary: The imperiled San Joaquin kit fox (*Vulpes macrotis mutica*) persists in the urban environment of Bakersfield, California. In this study, we found kit fox occupancy patterns were affected by a negative association with paved roads and a positive association with campuses in the urban landscape.

Running head: San Joaquin kit fox urban habitat attributes

Introduction

The San Joaquin kit fox (*Vulpes macrotis mutica*) is federally listed as endangered and California state-listed as threatened in the United States, primarily due to habitat loss as a result of human development. The San Joaquin kit fox is a subspecies of the kit fox (*Vulpes macrotis*), which ranges throughout flat semi-arid open desert, shrubland, and grassland habitats in Southwestern North America (McGrew 1979). Endemic to the San Joaquin Valley of central California (Cypher *et al.* 2001), the San Joaquin kit fox (hereafter kit fox) selects for open saltbush (*Atriplex* spp.) scrub and grassland habitats, and uses numerous dens daily to escape predators such as coyotes (*Canis latrans*), golden eagles (*Aquila chrysaetos*), and red foxes (*Vulpes vulpes*; Ralls and White 1995, Cypher *et al.* 2001, 2013, Cypher 2003). The kit fox population in the city of Bakersfield, California has constituted one of the largest subpopulations of kit foxes in the valley, and as such, has been a prime focus of kit fox research over the past 20 y (Cypher and Van Horn Job 2012). More recently, the Bakersfield population has dramatically declined due to an outbreak of sarcoptic mange, a highly contagious skin infection caused by the canis variety of the skin mite *Sarcoptes scabiei* (Cypher *et al.* 2001, Pence and Ueckermann 2002, Cypher *et al.* 2017).

Urbanization results in new environments dominated by infrastructure (e.g., buildings and roads) that are characterized by an increase in temperature and noise, year-round water, diverse vegetation, and non-native wildlife (Grimm *et al.* 2008, Gehrt 2010). Urban landscapes possess hard, linear boundaries and features such as roads and walls that may act as wildlife barriers which can result in fragmentation, isolation, and edge effects on natural habitat (Crooks 2002, Riley *et al.* 2010). Conversely, urban environments can offer increased resource availability such as refuse, food intentionally left out for animals, 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 canid species (Prange and Gehrt 2004, Ditchkoff *et al.* 2006, McKinney 2006, Cypher 2010, Bateman and Fleming 2012, Haverland and Veech 2017, Lombardi *et al.* 2017).

In Bakersfield, kit foxes are sympatric with three other canids, coyotes, red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*) in Bakersfield and share habitat, activity, and diet preferences with these species, resulting in interference competition (Voigt and Berg 1987, Cypher *et al.* 2001, Cypher 2003, MacKenzie *et al.* 2006, Nelson *et al.* 2007, Macdonald 2009, Soulsbury *et al.* 2010, Freeman 2011). Interference competition can lead to predation, harassment, or spatial exclusion of smaller, less dominant fox species by larger, more dominant foxes and coyotes, limiting species distributions or encouraging niche differentiation (Case and Gilpin 1974, Kitchen *et al.* 1999, Cypher *et al.* 2001, Freeman 2011). In some non-urban areas in the valley, kit foxes exhibit 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).

Relative density of urban development has the strongest effect on carnivore spatial dynamics when compared to 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 are subjected to higher human-caused mortality than smaller carnivores (Lesmeister *et al.* 2015). This can create areas within urban environments where larger predators are absent, thereby creating spatial refuge for smaller species and facilitating competitor sympatry (Lesmeister *et al.* 2015, Moll *et al.* 2018). Past studies indicate that coyotes need larger, connected open space and are more often observed in areas within urban environments with more natural habitat present (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 (*Vulpes macrotis arsipus*) in urban areas foraged and denned near highly developed areas that afforded protection from coyotes (Kozlowski *et al.* 2008). In Bakersfield, kit foxes are commonly observed using dens constructed in undeveloped lots, storm water catchment basins, industrial areas, commercial areas, landscaping features, and powerline and railroad corridors (Cypher and Van Horn Job 2012). Radio-collared kit foxes utilize undeveloped lands and water catchment basins disproportionately more than residential areas; however, it is largely unknown how heterogeneous urban landscape features (e.g., water availability, vegetation cover, land use, and building and infrastructure cover) and the presence of competitors drives kit fox occupancy patterns in the city (Frost 2005).

We investigated if heterogeneous urban landscape attributes, including the presence of a competitor species, affect kit fox occupancy patterns in Bakersfield. We used occupancy modeling to analyze 5 y of remote camera data from an annual city-wide survey from 2015 to 2019 combined with a suite of quantified urban landscape attributes (MacKenzie *et al.* 2006). Occupancy modeling uses species presence/absence data to estimate the probability of occupancy of a species while accounting for imperfect survey detections (Donovan and Hines 2007). Occupancy modeling can test for effects of environmental covariates (e.g., habitat characteristics at a site) on occupancy and detection probabilities of a species (MacKenzie *et al.* 2006, Donovan and Hines 2007, Wiens *et al.* 2015). Multi-season occupancy models may explain changes in occupancy and detection dynamics over time by assessing colonization and extinction probabilities at sites (MacKenzie *et al.* 2006, Donovan and Hines 2007). While 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 species associations with specific landscape features in the urban environment will help to develop effective future management, conservation, and recovery strategies for kit foxes in urban areas.

Materials and methods

Study area

Bakersfield, California is a large city with a growing population of 380,000 people (U.S. Census Bureau 2018). It is located in the San Joaquin Desert of Kern County, an area comprised of oil and gas production, grazing, agriculture, natural, conserved, and urban lands (Cypher *et al*. 2000; Fig. 1). Bakersfield is characterized by heavy urbanization interlaced with natural habitat including saltbush (*Atriplex* spp.) scrub, grassland, and riparian areas on 25 to 30% of its boundary (Cypher 2010). The city encompasses a variety of urban land use including residential areas (e.g., single-family homes, apartment buildings, townhouses, and nursing homes), commercial developments, recreational areas, preserved green spaces, industrial centers, agriculture, and campuses (e.g., schools, churches, medical centers, and large corporations with landscaped grounds). The Kern River runs north-east to south-west through the middle of the city and is accessible by the public. Due to water being diverted for agricultural purposes, only portions of the river contain water year-round within the city (Shigley 2010). Vegetation in Bakersfield consists primarily of a mix of planted native and non-native ornamental trees, shrubs, and flowering plants.

Study design

We conducted annual surveys using camera stations from 2015 to 2019 to monitor sarcoptic mange in the Bakersfield kit fox population and used these data to investigate kit fox occupancy patterns. We set camera stations in 111 randomly selected 1-km^2 grid cells located throughout the 368-km^2 city, thus covering approximately 30% of the city (Fig. 2). We selected cell size such that each kit fox home range (mean of 1.72 km^2; Frost 2005) potentially could include two cells, thus optimizing detection of foxes. We selected camera locations within cells based on amount of human activity, access by personnel, and accessibility for kit foxes. We secured Cuddeback Black Flash E3 or C3 trail cameras that were digital and motion triggered (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. We baited camera stations 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. With a few exceptions due to human disturbance, camera locations remained consistent over the 5-y sampling period. We ran stations annually for one 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 species and number of individuals. Unless animals could be distinguished as different individuals (by size, sex, markings, and/or tagging), we counted each species of canid that appeared on one camera during a given session as the same individual.

We used satellite imagery maps to quantify a suite of urban landscape attributes in all camera station cells to use as covariates in occupancy models. We overlaid cells with a 10 × 10 m dot grid in Google Earth Pro, resulting in a total of 100 dots/grid. We used Google Earth Pro imagery dated 26 April 2018 at an eye altitude of 300-m Above Ground Level to characterize grid dots and camera locations scaled to 1.0. We characterized each dot by the landscape that best described the location of the dot (i.e., the land use type on which the majority of the dot was located), and recorded if any portion of the dot fell on a mature tree or paved road. If a dot appeared to fall equally on two different landscape types, we split the proportion of the dot equally between the attributes (0.5:0.5). Because kit foxes are terrestrial animals, if a dot fell on a water body we characterized 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 and side of roadways, other open spaces, and the Kern River corridor (Table 1).

Occupancy analysis

We used multi-season occupancy modeling and assumed no un-modeled 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.* 2006). We first tested for pair-wise correlations between all landscape attributes covariates using Spearman's Rank tests in Minitab 19 statistical software (Mackridge and Rowe 2018). We did not include the total number of other canids in the correlation tests as we were interested in explicitly testing the effects of other canids on kit fox occupancy. We 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 on data (12 tests on each covariate). Correlated covariates were never included in the same multi-covariate model to minimize model overfitting and excessive model testing (Burnham and Anderson 2002).

We used single-species occupancy modeling 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 given species, i.e., the value for kit fox occupancy that maximizes the likelihood function given the observed data; S is the number of sites, i.e., grid cells; S_D is the number of cells at which a kit fox was detected using survey detection histories (h); and $\hat{P}^*_{MLE}$ 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,

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

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_i is the value of the continuous predictor variable, i.e., the covariate value at cell *i* (MacKenzie *et al.* 2018). We determined the estimated probability of kit fox occupancy in subsequent seasons following season 1 in multi-season modeling, 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 probability an occupied cell in season *t* is unoccupied by kit foxes in season *t* + 1; and γ_t is the probability that a cell unoccupied in season t is occupied by kit foxes in season *t* + 1 (MacKenzie *et al.* 2006). In other words, cells occupied by kit foxes next season, *t* + 1, are a combination of cells occupied this 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 colonized before next season, $(1 - \psi_t)\gamma_t$ (MacKenzie *et al.* 2018). We modeled our 5 y of annual data as individual seasons (*T* = 5) and each day camera stations were run in each cell as individual surveys (*K* = 7) in the occupancy modeling program PRESENCE 2.12.34 (Hines 2006). We explored covariate effects on kit fox occupancy by fitting models first with no covariate (null model) followed by each covariate individually, as well as combinations of covariates to test the following four a priori hypotheses: (1) if two open space specific covariates, the percentages of undeveloped lot and other open space (e.g., natural areas, canals, water catchment basins, dirt roads, etc.), had an additive effect when paired, and/or when combined with the presence of other canids, (2) if four human development specific covariates, the percentages of high-density residential, low to medium density residential, commercial, and industrial areas, had an additive effect when paired, (3) if six road specific covariates, the percentages of low to medium density residential, commercial, campus, high-density residential, median and side of roadway areas, and paved roads had an additive effect when paired, and (4) if six vegetative specific covariates, the percentages of mature trees, campus, Kern River corridor, parks and green space, agriculture, and the presence of a stable water source had an additive effect when paired, and/or when combined with the presence of other canids. As we were primarily interested in modeling kit fox occupancy, we held colonization, extinction, and detection parameters constant across sites and survey occasions.

We used β values (logit parameter probability estimates from observed data in a maximum-likelihood function), real parameter probability estimates (logit estimations for each site, i.e., grid cell, from β and covariate values in a linear regression function), and Akaike Information Criterion (AIC) output by PRESENCE to determine which models best fit the data (MacKenzie *et al.* 2006). The lower the AIC value and the higher the AIC 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.* 2006). Using parsimonious model selection, we considered models in our analysis when the ΔAIC value between the best fit model and the given model was < 2.00 (Burnham and Anderson 2002).

Results

Our cameras captured the highest number of kit foxes in season 1 (year 2015), followed by a decline in the number of kit foxes through season 5 (year 2019), resulting in a 69% decrease in kit fox abundance over the 5-y sampling period (Table 2). Our cameras captured approximately 6.6 times as many kit foxes as other canids combined, with approximately 5.6 times as many total camera survey days with kit foxes as with other canids (Table 2). We found that kit foxes occurred with another canid during approximately 4% of the total surveys in which kit foxes were detected, and other canids occurred with kit foxes during approximately 20% of the total surveys in which other canids were detected (Table 2).

Occupancy analysis

The dominant landscape attribute in a majority of the cells was high-density residential (approximately 66% of cells) followed by undeveloped lot (approximately 16% of cells), commercial (approximately 7% of cells), industrial (approximately 6% of cells), and agricultural (approximately 2% of cells; Table 3). Campuses, parks and green space, other open space, and the Kern River corridor were dominant in ≤ approximately 1% of cells (Table 3). Low to medium density residential and median and side of the roadway attributes were not dominant in any of the cells (Table 3). Fewer than half the cells had > 20% paved roads or mature tree cover (approximately 30% and 25% of cells, respectively), and more than half had a stable water source (approximately 63% of cells; Table 3).

We found eight positively correlated landscape attributes which were, in order from strongest pair-wise correlation to weakest, mature trees and high-density residential, paved roads and median and side of the roadway, undeveloped lot and other open space, paved roads and high-density residential, industrial and other open space, mature trees and parks and green space, low to medium density residential and campus, and finally, mature trees and paved roads (Table 4). We found 12 negatively correlated landscape attributes which were, in order from weakest negative pair-wise correlation to strongest, low to medium density residential and other open space, paved roads and other open space, undeveloped lot and parks and green space, high-density residential and commercial, mature trees and other open space, low to medium density residential and undeveloped lot, paved roads and undeveloped lot, high-density residential and industrial, mature trees and industrial, high-density residential and other open space, high density residential and undeveloped lot, and finally, mature trees and undeveloped lot (Table 4).

We fit 59 kit fox occupancy models and found our third *a priori* hypothesis, that two road specific covariates would have an additive effect on kit fox occupancy, to be the only supported hypothesis. Our top ranking model included paved roads and campuses as covariates, with percentage of paved roads a weak negative predictor of kit fox occupancy and percentage of campuses a weak positive predictor (Tables 5 and 6; Figs. 3 and 4). According to our top model, the mean probability of kit fox occupancy was 66% in 2015 (ψ $\beta = 0.66$, 95% CI = 0.58-0.73), 41% in 2016 (ψ $\beta = 0.41$, 95% CI = 0.37-0.45), 31% in 2017 (ψ $\beta = 0.31$, 95% CI = 0.28-0.35), 28% in 2018 (ψ $\beta = 0.28$, 95% CI = 0.24-0.31), and 26% in 2019 (ψ $\beta = 0.26$, 95% CI = 0.23-0.29), thus representing a 40% decrease in mean occupancy probability over time (Fig. 5). The other models with $\Delta AIC < 2.00$, from second highest ranking to lowest, included percentages of paved roads and campuses as individual covariates, a model including both roads and low to medium density residential as covariates, and the null model (Table 5). For the single covariate models, the percentage of paved roads remained a negative predictor of kit fox occupancy, while percentage of campuses and the null model were positive predictors of occupancy (Table 6). In the additive model that included paved roads and low to medium density residential areas, percentage of paved roads was again a negative predictor of kit fox occupancy while percentage of low to medium density residential areas was a positive predictor (Table 6). The percentage of paved roads covariate occurred in three of the five ranking models, which had a cumulative AIC weight of 0.1668 (approximately 17%), while percentage of campuses occurred in two of the top ranking models with a cumulative AIC weight of 0.1213 (approximately 12%; Table 5). Two additive models that included percentages of Kern River corridor and campuses (ψ(KRC) β = 0.17, 95% CI = -0.03 to 0.37) as well as percentages of campuses and the presence of a stable water source (ψ β = 0.06, 95% CI = -0.29 to 0.43) as covariates also had ΔAIC values < 2.00; however, they had β 95% confidence intervals that included zero making them poor models for predicting kit fox occupancy. The number of other canids in grids was a moderate negative predictor of kit fox occupancy in all models fit with other canids as a covariate (18 models; AIC = 2636.26-2640.96, ΔAIC = 2.65-7.35, w = 0.0191-0.0018), though all models had at least one parameter with a β 95% confidence interval that included zero making the presence of canids a poor predictor of kit fox occupancy in our modeling.

Discussion

While the most supported kit fox occupancy model in our system was an additive effect of percentages of paved roads and campuses in cells, paved roads was ultimately the most important factor for determining whether a cell was occupied by kit foxes in our study. We found a 4% higher cumulative weight from all ranking models containing percentage of paved roads as a covariate compared to the cumulative weight for percentage of campuses in all ranking models. Roads are inhospitable to kit foxes and are the main source of mortality in urban areas (Bjurlin *et al.* 2005). Additionally, roads are characterized by increased noise pollution, development, disturbance, and human activity, which likely discourages urban kit foxes from utilizing paved roads in their home ranges (Bjurlin *et al.* 2005). In San Diego, California, gray foxes were similarly found to be negatively associated with the presence of roads (Markovchick-Nicholls *et al.* 2008). Conversely, 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). These open spaces also support populations of potential prey for kit foxes including California ground squirrels (*Otospermophilus beecheyi*), Valley pocket gophers (*Thomomys bottae*), birds, and insects. Further, campuses often have food courts, cafeterias, or picnic tables where patrons drop food or even feed animals directly (Cypher 2010). Additionally, campuses commonly have security measures or fencing, which may limit human activity overnight when kit foxes are most active, and help to exclude larger predators such as coyotes. Percentage of low to medium density residential areas in grids was also a considerable positive predictor of kit fox occupancy. We considered low to medium density residential areas to include apartment buildings, townhouses, and nursing home living situations. Similar to campuses, this type of infrastructure provides landscaped yards, recreation areas, and walkways as open space for kit foxes. These results support our third *a priori* hypothesis, that kit fox occupancy would be affected by a combination of two road specific covariates and were consistent with our prediction that kit foxes would select for open space areas within the urban environment.

Because the number of campuses is expected to increase as human population continues to grow (Chen *et al.* 2014), there is potential for urban kit fox populations to persist. Common concerns regarding kit foxes on campuses include kit foxes attacking patrons, leaving fecal matter, spreading disease or parasites, damaging property, or having implications for property owners when a protected species resides on their property (Cypher and Van Horn Job 2012). Property owners may be more tolerant of foxes residing on campuses given education and outreach efforts to assure minimal risk of kit fox-human conflict, informing of established protocols to aid landowners with handling fox nuisance issues (Cypher 2010, Cypher and Van Horn Job 2012), and appropriate response actions during a kit fox encounter. 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) and to date, with 57 reported occurrences and 22 kit fox fatalities to date in Bakersfield due to stress, exhaustion, or suffocation when trapped in a net for an extended period of time (Cypher and Van Horn Job 2012; unpublished data). This presents an additional conflict that could be addressed through education and outreach by informing schools of the dangers of leaving sports nets out overnight or posting signage reminding personnel to tie nets off the ground when not in use.

Nonetheless, as urbanization increases, the abundance of paved roads will also increase (Bjurlin *et al.* 2005). An increase in paved roads not only presents risk to kit fox survival, but also reduces the amount of suitable kit fox habitat within the urban environment.

Percentage of paved roads was the strongest predictor of kit fox occupancy in our system, therefore, a high proportion of paved roads in urban areas that also support campuses may benefit from informative 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 road crossing structures considering the use of open landscaping, fencing to keep larger predators out, and/or denning structures would likely be inviting for kit foxes (Bjurlin et al. 2005, Frost *et al.* 2005, Cypher 2010, Bateman and Fleming 2012, Cypher and Van Horn Job 2012).

The high number of kit fox detections and estimated individuals relative to those for coyotes, red foxes, and gray foxes demonstrate that kit foxes may be more adaptable to urban environments than other wild canids. Although they exhibit preferences for campuses, kit foxes are frequently observed using many urban landscape types unlike coyotes, red foxes, and gray foxes (Frost 2005, Cypher 2010, Cypher and Van Horn Job 2012). Additionally, mammals with smaller body sizes are more likely to fare better in urban environments in general (Crooks 2002).

Current occupancy modeling 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). Further, effects of species interactions may not be accurately assessed if detection rates of species are highly disproportionate (MacKenzie *et al.* 2018), as was the case with our sample sizes for kit foxes (n = 395) and other canid species ($n \leq 25$). To better assess the effects of other canid presence on occupancy patterns of kit foxes further research may require a study designed to capture a more equivalent number of kit foxes to other canids, such as increased cell sizes that assess occupancy on a different scale.

Our top-ranking kit fox occupancy models had AIC weights between 2 and 7%, meaning the weight of evidence for any of our models being acceptable representations of kit fox occupancy was relatively low (Burnham and Anderson 2002). Further, our remaining three *a priori* hypotheses, how open space, human development, or vegetative specific covariates would affect kit fox occupancy, were not supported by any models. Therefore, additional research may require a more refined set of covariate models or the use of a different type of analysis such as logistic regression to further assess the effects of habitat covariates on kit fox occupancy patterns (MacKenzie *et al.* 2018). Specifically, additional research regarding roads may approach with a finer scaled assessment of road type (e.g., local, collector, arterial, or highway) to reveal more detailed kit fox occupancy patterns in relation to roads.

Lastly, the 69% decline in kit fox detections over the 5-y study span highlights the significant negative effects of sarcoptic mange on the urban kit fox population currently in Bakersfield. The disease has been studied extensively in red foxes in which mortality can occur 3–4 mo following infection (Stone *et al.* 1972). Due to the similar biology of red foxes and kit foxes, it is likely that time-to-mortality for kit foxes is similar, and the disease is 100% fatal in untreated kit foxes (Cypher 2003, 2017). The mange epidemic was further reflected in our kit fox occupancy modeling with the probability of occupancy decreasing by 40% over the 5-y sampling span.

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.

An understanding of local kit fox occupancy dynamics and how they are affected by changes in habitat can lead to effective conservation or management when planning urban development or identifying suitable areas for kit foxes within cities (MacKenzie *et al.* 2006). Informed decisions and planning can facilitate the long-term sustainability of kit fox populations in urban environments.

References

Bateman, P. W., and Fleming, P. A. (2012). Big city life: carnivores in urban environments. *Journal of Zoology* **287**, 1–23.

Bjurlin, C. D., Cypher, B. L., Wingert, C. M., and Van Horn Job, C. L. (2005). Urban roads and the endangered San Joaquin kit fox. California Department of Transportation, Endangered Species Recovery Program Final Report Contract No. 65A0136, Fresno, CA.

Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodal Inference: a Practical Information Theoretic.' 2nd Edn. (Springer–Verlag New York, Inc.: New York, NY.)

Case, T. J., and Gilpin, M. E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America* **71**, 3073–3077.

Chen, M., Zhang, H., Weidong, L., and Zhang, W. (2014). The global pattern of urbanization and economic growth: evidence from the last three decades. *PLoS ONE* **9**(8), e103799. doi:10.1371/journal.pone.0103799

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* **16**, 488–502.

Cypher, B. L. (2003). Foxes. In ‘Wild Mammals of North America: Biology, Management, and Conservation’. 2nd Edn. (Eds G. A. Feldhamer, B. C. Thompson, and J. A. Chapman.) Chapter 24, pp. 511–546. (John Hopkins University Press: Baltimore, MD.)

Cypher, B. L. (2010). Kit foxes (*Vulpes macrotis*). In ‘Urban Carnivores, Ecology, Conflict, and Conservation’. (Eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher.) Chapter 5, pp. 49–57. (The Johns Hopkins University Press: Baltimore, MD.)

Cypher, B. L., Howard, C. O. J., Kelly, P. A., Van Horn Job, C., Warrick, G. D., and Williams, D. F. (2001). Interspecific interactions among wild canids: implications for the conservation of endangered San Joaquin kit foxes. *Endangered Species Update* **18**, 171–174.

Cypher, B. L., Philips, S. E., and Kelly, P. A. (2013). Quantity and distribution of suitable habitat for endangered San Joaquin kit foxes: conservation implications. *Canid Biology & Conservation* **16**, 25-31.

Cypher, B. L., Rudd, J. L., Westall, T. L., Woods, L. W., Stephenson, N., Foley, J. E., Richardson, D., and Clifford, D. L. (2017). Sarcoptic mange in endangered kit foxes (*Vulpes macrotis mutica*): case histories, diagnoses, and implications for conservation. *Journal of Wildlife Diseases* **53**, 46–53.

Cypher, B. L., and Van Horn Job, C. L. (2012). Management and conservation of San Joaquin kit foxes in urban environments. In ‘Proceedings of the Vertebrate Pest Conference’. p. 347–352. (University of California: Davis, CA.)

Cypher, B. L., Warrick, G. D., Otten, M. R. M., O’Farrell, T. P., Berry, W. H., Harris, C. E. H., Kato, T. T., McCue, P. M., Scrivner, J. H., and Zoellick, B. W. (2000). Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. *Wildlife Monographs* **145**, 1–43.

Ditchkoff, S. S., Saalfeld, S. T., and Gibson, C. J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems* **9**, 5–12.

Donovan, T. M., and Hines, J. (2007). 'Exercises in Occupancy Modeling and Estimation.' Available at http://www.uvm.edu/envnr/vtcfwru/spreadsheets/occupancy.htm [accessed 27 January 2020].

Freeman, S. (2011). An introduction to ecology. In 'Biological Science'. 4th Edn. (Eds B. Wilbur, B. Ruden, S. DiVittorio, A. Fugate, M. Lerner-Nelson, W. O'Neal, S. Teahan, K. Murphy, B. Golden, and L. Allen.) Chapter 50, pp. 993–1127. (Pearson Education, Inc.: San Francisco, CA.)

Frost, N. (2005). San Joaquin kit fox home range, habitat use, and movements in urban Bakersfield. M.Sc. Thesis, Humboldt State University, Arcata.

Fuller, T. K., Destefano, S., and Warren, P.S. (2010). Carnivore behavior and ecology, and relationship to urbanization. In 'Urban Carnivores, Ecology, Conflict, and Conservation'. (Eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher.) Chapter 2, pp. 18–19. (The Johns Hopkins University Press: Baltimore, MD.)

Gehrt, S. D. (2010). The urban ecosystem. In 'Urban Carnivores, Ecology, Conflict, and Conservation'. (Eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher.) Chapter 1, pp. 6–9. (The Johns Hopkins University Press: Baltimore, MD.)

Gehrt, S. D., Anchor, C., and White, L. A. (2009). Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *Journal of Mammalogy* **90**, 1045–1057.

Gese, E. M., Morey, P. S., and Gehrt, S. D. (2012). Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. *Japan Ethological Society and Springer* **30**, 413–425.

Gosselink, T. E., Van Deelen, T. R., Warner, R. E., and Joselyn, M. G. (2003). Temporal habitat partitioning and spatial use of coyotes and red foxes in east–central Illinois. *The Journal of Wildlife Management* **67**, 90–103.

Grimm, N. B., Foster, D., Groffman, P., Grove, J. M., Hopkinson, C. S., Nadelhoffer, K. J., Pataki, D. E., and Peters, D. P. C. (2008). The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *The Ecological Society of America: Frontiers in Ecology and the Environment* **6**, 264–272.

Harrison, R. L. (1997). A comparison of grey fox ecology between residential and undeveloped rural landscapes. *The Journal of Wildlife Management* **61**, 112–122.

Haverland, M.B., and Veech., J. A. (2017). Examining the occurrence of mammal species in natural areas within a rapidly urbanizing region of Texas, USA. *Landscape and Urban Planning* **157**, 221–230.

Hines, J. E. (2006). 'PRESENCE– Software to estimate patch occupancy and related parameters.' (USGS–PWRC).

Kitchen, A. M., Gese, E. M., and Schauster, E. R. (1999). Resource partitioning between coyotes and swift foxes: space, time, and diet. *Canadian Journal of Zoology* **77**, 1645–1656.

Kozlowski, A. J., Gese, E. M., and Arjo, W. M. (2008). Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. *The American Midland Naturalist* **160**, 191–208.

Legendre, P., and Legendre, L. (1998). ‘Numerical Ecology.’ 2nd Edn. (Elsevier Science B.V.: Amsterdam, The Netherlands.)

Lesmeister, D. B., Nielsen, C. K, Schauber, E. M., and Hellgren, E. C. (2015). Spatial and temporal structure of a mesocarnivore guild in midwestern North America. *Wildlife Monographs* **191**, 1–61.

Lombardi, J. V., Comer, C. E., Scognamillo, D. G., and Conway, W. C. (2017). Coyote, fox, and bobcat response to anthropogenic and natural landscape features in a small urban area. *Urban Ecosystems* **20**, 1239–1248.

Macdonald, D. W. (2009). Carnivores. In ‘The Princeton Encyclopedia of Mammals’. pp. 598–611 (Princeton University Press: Princeton, NJ.)

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., and Hines, J. E. (2018). ‘Occupancy Estimation and Modeling, Inferring Patterns and Dynamics of Species Occurrence.’ 2nd Edn. (Academic Press: San Diego, CA.)

MacKenzie, D. I., Royle, J. A., Nichols, J. D., Hines, J. E., Pollock, K. H., and Bailey, L. L. (2006). ‘Occupancy Estimation and Modeling, Inferring Patterns and Dynamics of Species Occurrence.’ (Academic Press: Burlington, MA.)

Mackridge, A., and Rowe, P. (2018). Choosing a statistical test. In ‘A Practical Approach to Using Statistics in Health Research, From Planning to Reporting’. pp. 27–38. (John Wiley & Sons, Inc.: Hoboken, NJ.)

Markovchick–Nicholls, L., Regan, H. M., Deutschman, D. H., Widyanata, A., Martin, B., Noreke, L., and Hunt, T. A. (2008). Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conservation Biology* **22**, 99–109.

Mathewson, P. D., Spehar, S. N., and Cooper, D. S. (2008). An initial carnivore survey of Griffith Park, Los Angeles, California. *Bulletin of the Southern California Academy of Sciences* **107**, 57–67.

McGrew, J. C. (1979). *Vulpes macrotis. Mammalian Species* **123**, 1–6.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127**, 247–260.

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Robison, T., Millspaugh, J. J., and Montgomery, R. A. (2018). Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems* **21**, 765–778.

Nelson, J. L., Cypher, B. L., Bjurlin, C. D., and Creel, S. (2007). Effects of habitat on competition between kit foxes and coyotes. *Journal of Wildlife Management* **71**, 1467–1475.

Nicholson, J. M., and Van Manen, F. T. (2009). Using occupancy models to determine mammalian responses to landscape changes. *Integrative Zoology* **4**, 232–239.

Pence, D. B., and Ueckermann, E. (2002). Sarcoptic mange in wildlife. *Scientific and Technical Review of the Office International des Epizooties* **21**, 385–398.

Prange, S. and Gehrt, S. D. (2004). Changes in mesopredator–community structure in response to urbanization. *Canadian Journal of Zoology* **82**, 1804–1817.

Ralls, K., and White, P. J. (1995). Predation on San Joaquin kit foxes by larger canids. *Journal of Mammalogy* **76**, 723–729.

Riley, S. P. D. (2006). Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. *The Journal of Wildlife Management* **70**, 1425–1435.

Riley, S. P. D., Gehrt, S. D., and Cypher, B. L. (2010). Urban carnivores, final perspectives and future directions. In ‘Urban Carnivores, Ecology, Conflict, Conservation’. (Eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher.) Chapter 17, pp. 223–232. (The Johns Hopkins University Press: Baltimore, MD.)

Shigley, P. 2010. Bakersfield hopes to restore water to Kern River. *Planning; Chicago* **76**, 8.

Soulsbury, C. D., Baker, P. J., Iossa, G., and Harris, S. (2010). Red foxes (*Vulpes vulpes*). In ‘Urban Carnivores, Ecology, Conflict, and Conservation’. (Eds S. D. Gehrt, S. P. D. Riley, and B. L. Cypher.) Chapter 6, pp. 63–75. (The Johns Hopkins University Press: Baltimore, MD.)

Stone, W. B., Parks, E., Weber, B. L., and Parks, F. J. (1972). Experimental transfer of Sarcoptic mange from red foxes and wild canids to captive wildlife and domestic animals. *New York Fish and Game Journal* **19**, 1–11.

Voigt, D. R., and Berg, W. (1987). Coyote. In ‘Wild Furbearer Management and Conservation in North America’. (Eds M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch.) pp. 345–356. (The Ontario Trappers Association: Ontario, Canada.)

Wiens, J. D., Kolar, P. S., Fuller, M. R., Hunt, W. G., and Hunt, T. (2015). Estimation of occupancy, breeding success, and predicted abundance of golden eagles (*Aquila chrysaetos*) in the Diablo Range, California, 2014. U. S. Geological Survey Open-File Report 2015–1039. doi.org/10.3133/ofr20151039

Figure captions

Fig. 1. Land use and cover of the San Joaquin Valley of central California in 2004. The city of Bakersfield is located in the southeast part of the valley.

Fig. 2. Distribution of 120 1-km^2 grid cells used to monitor sarcoptic mange disease in San Joaquin kit foxes in Bakersfield, California in 2015. Of these, 105 to 111 cells were surveyed annually (depending on the year) through 2019 using remote camera stations.

Fig. 3. Occupancy probability estimates (ψ) for San Joaquin kit foxes as a function of percentages of paved roads and campuses (covariates) in 111 grid cells in Bakersfield, California from 2015 to 2019. As percentage of paved roads decreases and percentage of campuses increases, probability of kit fox occupancy increases. Kit fox detection histories and covariate values used in models were from 7-d annual surveys.

Fig. 4. Mean estimated probability of occupancy (ψ) for San Joaquin kit foxes in the city of Bakersfield, California from 2015 to 2019. In the top model the percentages of paved roads and campuses in 111 grid cells throughout the city had an additive effect on kit fox occupancy, with paved roads a negative predictor and campuses a positive predictor of kit fox occupancy. Kit fox detection histories and covariate values used in models were from 7-d annual surveys.

Fig. 5. Mean estimated probability of occupancy (ψ), with 95% confidence interval bars, for San Joaquin kit foxes in Bakersfield, California from 2015 to 2019 from the top ranking occupancy model, an additive effect of percentages of paved roads and campuses as covariates in 111 grid cells. Kit fox detection histories and covariate values used in models were from 7-d annual surveys.

Fig. 1.

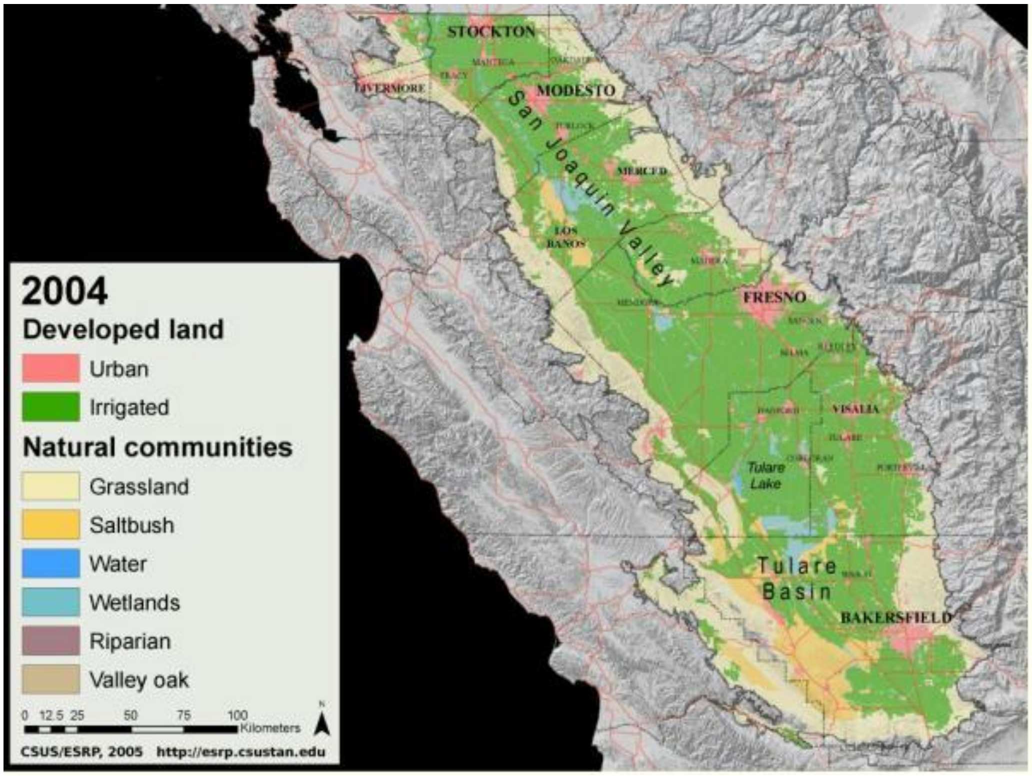

STOCKTON
LIVERMORE
MODESTO
San Joaquin Valley
MERCED
LOS BANOS
FRESNO
VISALIA
Tulare Lake
Tulare Basin
BAKERSFIELD
2004
Developed land
Urban
Irrigated
Natural communities
Grassland
Saltbush
Water
Wetlands
Riparian
Valley oak
0 12.5 25 50 75 100
Kilometers
CSUS/ESRP, 2005 http://esrp.csustan.edu

Fig. 2.

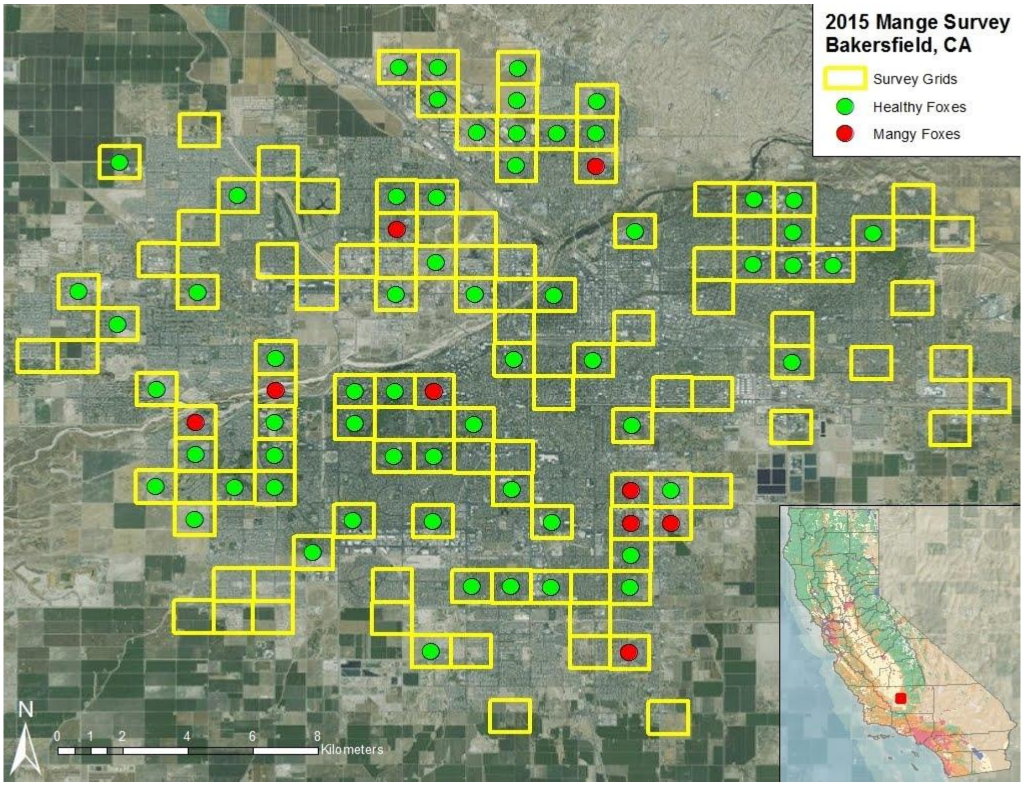

2015 Mange Survey
Bakersfield, CA
Survey Grids
Healthy Foxes
Mangy Foxes
N
0 1 2 4 6 8
Kilometers

Fig. 3.

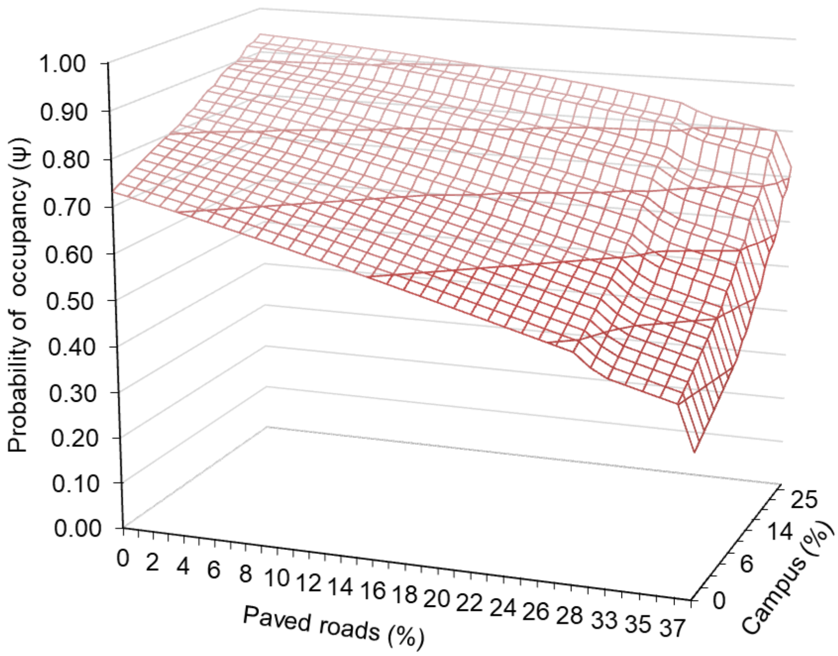

Probability of occupancy (ψ)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 33 35 37
Paved roads (%)
0 6 14 25
Campus (%)

Fig. 4.

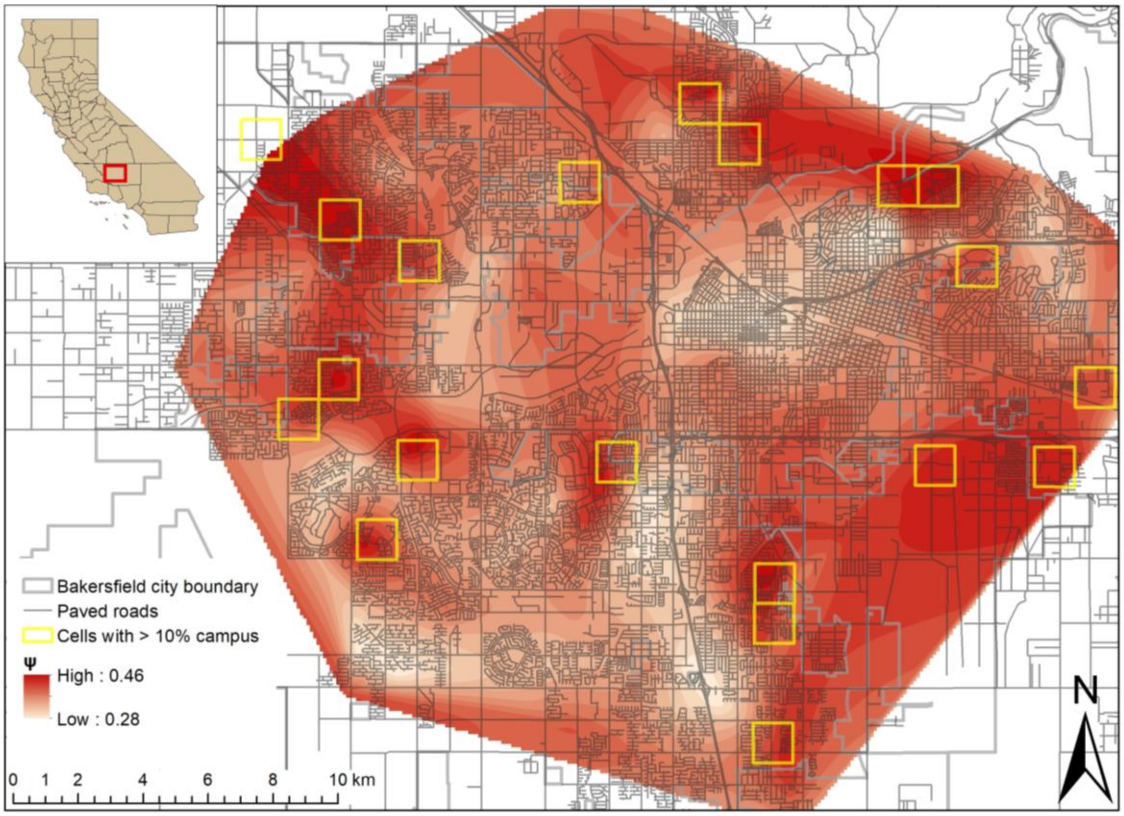
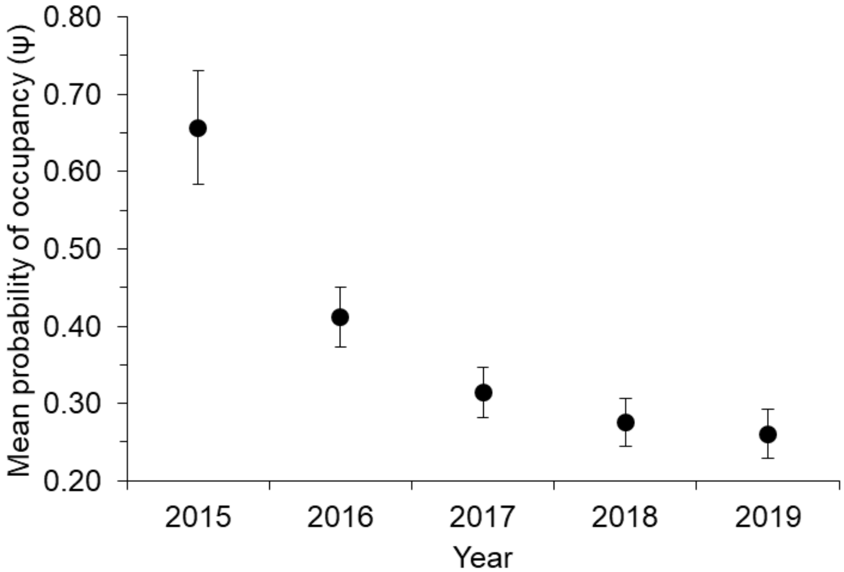

Bakersfield city boundary
Paved roads
Cells with > 10% campus
ψ
High : 0.46
Low : 0.28
0 1 2 4 6 8 10 km
N

Fig. 5.


Mean probability of occupancy (ψ)
0.80
0.70
0.60
0.50
0.40
0.30
0.20
2015
2016
2017
2018
2019
Year

Tables

Table 1. Covariate abbreviations and descriptions used in San Joaquin kit fox occupancy modeling of grid cells surveyed annually from 2015 to 2019 in Bakersfield, California

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

Table 2. The total number of surveys, species counts, and surveys with kit foxes and/or other canids (coyotes, red foxes, and gray foxes) from an annual remote camera survey of grid cells in Bakersfield, California from 2015 to 2019

Season (year)	Surveys (*n*)	Kit foxes	Coyotes	Red foxes	Gray foxes	Surveys with kit foxes	Surveys with other canids	Surveys with kit foxes and another canid
1 (2015)	735	129	0	4	5	232	37	19
2 (2016)	775	94	6	4	6	180	27	3
3 (2017)	763	81	2	7	3	133	24	0
4 (2018)	770	50	5	5	3	89	21	0
5 (2019)	763	40	3	5	2	62	15	3
Totals	3806	394	16	25	19	696	124	25

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

Landscape characterization	Number of cells
% High-density residential	73.5
% Undeveloped lot	18.5
% Commercial	8
% Industrial	5
% Agricultural	2
% Campus	1.5
% Parks and green space	1
% Other open space	1
% Kern River corridor	0.5
% Low to medium density residential	0
% Median and side of roadway	0
> 20% mature trees	28
> 20% paved roads	33
Stable water source present	70

Table 4. Correlated pair-wise habitat attributes and Spearman correlation test statistic (*t*), adjusted *P* value (*P*), and Spearman correlation coefficient values (r_s) for a total of *n* = 111 survey grid cells from 2015 to 2019 in Bakersfield, California

trees = percentage of mature trees in cells, HDR = percentage of high-density residential areas in cells, roads = percentage of paved roads in cells, MSR = percentage of median and side of roadway areas in cells, UL = percentage of undeveloped lot in cells, OOS = percentage of other open space in cells, ind = percentage of industrial areas in cells, PGS = percentage of parks and green spaces in cells, LMDR = percentage of low to medium density residential areas in cells, camp = percentage of campuses in cells, and com = percentage of commercial area in cells. *P* values were adjusted to account for the inflated risk of a type I statistical error when running multiple tests on data (Legendre and Legendre 1998). df (degrees of freedom) = 109 for each correlation

Habitat attribute correlation	*t*	*P(adjusted)*	r_s
trees x HDR	10.064	< 0.001	0.694
roads x MSR	5.806	< 0.001	0.486
UL x OOS	5.469	< 0.001	0.464
roads x HDR	5.173	< 0.001	0.444
ind x OOS	4.382	< 0.001	0.387
trees x PGS	3.965	< 0.001	0.355
LMDR x camp	3.863	< 0.001	0.347
trees x roads	3.838	< 0.001	0.345
LMDR x OOS	-3.600	< 0.001	-0.326
roads x OOS	-4.029	< 0.001	-0.360
UL x PGS	-4.289	< 0.001	-0.380
HDR x com	-4.449	< 0.001	-0.392
trees x OOS	-4.516	< 0.001	-0.397
LMDR x UL	-4.625	< 0.001	-0.405
roads x UL	-4.748	< 0.001	-0.414
HDR x ind	-4.818	< 0.001	-0.419

Habitat attribute correlation	*t*	*P(adjusted)*	r_s
trees x ind	-5.394	< 0.001	-0.459
HDR x OOS	-5.775	< 0.001	-0.484
HDR x UL	-7.224	< 0.001	-0.569
trees x UL	-9.604	< 0.001	-0.677

Table 5. Model ranking, name, number of parameters (no. par), Akaike Information Criterion value (AIC), the difference in AIC values between the given model and the top ranking model (ΔAIC), and the AIC weight (*w*) from San Joaquin kit fox occupancy modeling in Bakersfield, California from 2015 to 2019

roads+camp = percentages of paved roads and campuses in grid cells in an additive covariate model as well as single covariates, roads+LMDR = percentages of paved roads and low to medium density residential areas in cells, and no covariate listed = null model. Kit fox detection histories and covariate values used in models were compiled from 105 to 111 cells (depending on the year) surveyed annually for 7 d

Model ranking	Model	no.par	AIC	ΔAIC	*w*
1	ψ(roads+camp),γ(),ε(),p()	6	2633.61	0.00	0.0717
2	ψ(roads),γ(),ε(),p()	5	2634.21	0.60	0.0531
3	ψ(camp),γ(),ε(),p()	5	2634.35	0.74	0.0496
4	ψ(roads+LMDR),γ(),ε(),p()	6	2634.68	1.07	0.042
5	ψ(),γ(),ε(),p()	4	2635.47	1.86	0.0283

Table 6. Model ranking, name, and maximum-likelihood estimate for the given parameters of the model (β) with 95% confidence intervals (CI) from San Joaquin kit fox occupancy modeling in Bakersfield, California from 2015 to 2019

Covariates are listed in parentheses following the parameter of interest (ψ, or species occupancy): roads+camp = percentages of paved roads and campuses in grid cells in an additive covariate model as well as single covariates, roads+LMDR = percentages of paved roads and low to medium density residential areas in cells, and no covariate listed = null model. Kit fox detection histories and covariate values used in models were compiled from 105 to 111 cells (depending on the year) surveyed annually for 7 d

Model ranking	Model	Parameter	β	Lower CI	Upper CI
1	ψ(roads+camp),γ(),ε(),p()	ψ	1.00	0.53	1.48
		ψ(roads)	-0.04	-0.06	-0.02
		ψ(camp)	0.05	0.02	0.08
2	ψ(roads),γ(),ε(),p()	ψ	1.33	0.89	1.77
		ψ(roads)	-0.04	-0.06	-0.02
3	ψ(camp),γ(),ε(),p()	ψ	0.37	0.11	0.63
		ψ(camp)	0.05	0.02	0.09
4	ψ(roads+LMDR),γ(),ε(),p()	ψ	1.22	0.77	1.66
		ψ(roads)	-0.04	-0.07	-0.02
		ψ(LMDR)	0.05	0.01	0.09
5	ψ(),γ(),ε(),p()	ψ	0.65	0.44	0.86

CHAPTER 3

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

NICOLE A. DEATHERAGE[1,2,*], BRIAN L. CYPHER[2,4], TORY L. WESTALL[2,5], ERICA C. KELLY[2,6], AND CARL T. KLOOCK[1,7]

[1]*Department of Biology, California State University, Bakersfield, 9001 Stockdale Highway, Bakersfield, CA 93311*

[2]*Endangered Species Recovery Program, California State University, Stanislaus, One University Circle, Turlock, CA 95382*

[*]Corresponding author: ndeatherage@csub.edu

[4]Author: bcypher@esrp.org

[5]Author: twestall@esrp.org

[6]Author: ekelly@esrp.org

[7]Author: ckloock@csub.edu

Running head: COMPETITION IN URBAN CANIDS

ABSTRACT.—The federally listed endangered and California state-listed threatened San Joaquin kit fox (*Vulpes macrotis mutica*) forms an ecological guild with coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*) in the city of Bakersfield, California. Interference competition occurs between these species where they are sympatric, resulting in spatiotemporal avoidance or changes in behavior to avoid harassment or death in natural environments. To investigate the effects of canid competitors and semi-feral domestic dogs (*Canis familiaris*) on San Joaquin kit fox spatiotemporal activity, we used 5 y of annual camera survey data from 1-km^2 grid cells gathered throughout Bakersfield in Two-way Contingency Table, One-way Analysis of Variance, and Kruskal-Wallis tests. We found that San Joaquin kit foxes typically did not occur with other canids within cells on a daily, yearly, or 5-y scale, and when other canids were immediately present, San Joaquin kit foxes altered temporal activity in avoidance by appearing later on cameras and possessing less variance in the amount of time spent at a camera (i.e., a smaller window of potential consecutive min spent at a camera). Our analysis provides a more comprehensive understanding of interactions between San Joaquin kit foxes and their competitors within the urban environment, providing implications for conservation efforts regarding this species.

A competitive ecological guild forms when a group of biologically similar species have overlapping niches and share limiting resources (Mackenzie et al. 2006, Freeman 2011). Interference competition consists of predation, harassment, or spatial exclusion and occurs when the presence of one species in an area results in the decreased use of that area by a less dominant species (Case and Gilpin 1974, Cypher et al. 2001). Intraguild predation is an extreme mechanism of interference competition in which larger, dominant species kill or exclude subordinate species from habitats with abundant resources, and subordinate species must balance risk with access to resources (Polis et al. 1989, Heithaus 2001). Areas with higher risk of predation can lead to increased antipredator behavior by subordinate species such as vigilance and changes in temporal or spatial foraging (Hall et al. 2013, Wang et al. 2015). Rather than avoiding a site altogether subordinate species may avoid sites for some period of time following a visit by a more dominant species, and such temporal partitioning may facilitate coexistence (White et al. 1994, Moll et al. 2018).

San Joaquin kit foxes (*Vulpes macrotis mutica*) engage in interference competition with coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*) where these species are sympatric due to overlapping habitat use, activity patterns, and diets (Voigt and Berg 1987, Cypher 2003, Macdonald 2009, Soulsbury et al. 2010). These canids display scent marking as well as vocal and visual communications (Cypher 2003). Coyotes dominate over foxes due to their larger size and are the primary predator of foxes in many locations; however, coyotes do not typically consume fox kills, suggesting competition rather than sustenance as the likely cause of intraguild predation (Voigt and Berg 1987, Ralls and White 1995, Kitchen et al. 1999, Fedriani et al. 2000, Cypher et al. 2001, Moehrenschlager et al. 2001, Farias et al. 2005, Nelson et al. 2007). Of the four species, San Joaquin kit foxes are the smallest and consequently are also killed by larger red foxes, which will occasionally enter and make use of kit fox dens (Ralls and White 1995, Voigt 1987, Williams et al. 1998, Cypher et al. 2001, Clark et al. 2005). In New Mexico, desert kit foxes (*Vulpes macrotis arsipus*) were described as superior exploitative competitors capable of occupying prey-poor habitat that coyotes could not exploit, because the large body size of coyotes requires higher metabolic needs than that of desert kit foxes (Robinson et al. 2014). Desert kit foxes also had a higher probability of visiting camera stations that coyotes had not previously visited (Robinson et al. 2014). Gray foxes are only slightly smaller than red foxes and their interactions with other canids are not well known (Hall 1981).

While coyotes, red foxes, and gray foxes are widespread throughout North America, San Joaquin kit foxes are a subspecies of the kit fox (*Vulpes macrotis*) endemic to the San Joaquin Valley of central California, and are federally listed endangered and California state-listed threatened in the United States (Voigt and Berg 1987, Cypher et al. 2001, Cypher 2003, Gehrt and Riley 2010, Soulsbury et al. 2010). The endangerment of the San Joaquin kit fox (hereafter kit fox) is primarily due to habitat loss and degradation from human development; however, kit foxes persist in some urban areas in the Valley (Williams et al. 1998, Cypher et al. 2013). In recent years, some urban subpopulations have been affected by sarcoptic mange, a highly contagious skin infection caused by the canis variety of the skin mite *Sarcoptes scabiei* (Pence and Ueckermann 2002, Cypher et al. 2017).

Urbanization continues to be the leading cause of alterations to Earth's ecosystems as human population continues to increase (Grimm et al. 2008). Urban areas create new environments characterized by an increase in temperature and noise, year-round water, green and diverse vegetation, non-native wildlife, roads, buildings, and infrastructure (Gehrt 2010). Urban areas can provide animals with abundant anthropogenic food sources including refuse, food intentionally left out for wildlife or pets, planted fruits and vegetables, permanent water sources, as well as human-built structures that can provide shelter (Harrison 1997, Fuller et al. 2010). As opportunistic species such as coyotes and foxes appear in greater abundance within heavily human-populated areas, immediate ecological and behavioral changes in intraguild dynamics is expected in order for species to persist (Ditchkoff et al. 2006, Fuller et al. 2010, Moll et al.

2018). For instance, coyotes, red foxes, and gray foxes found in or near urban areas have shifted from both diurnal and nocturnal activity patterns observed in natural areas to largely nocturnal in response to increased human activity during the day, which may lead to more temporal overlap and conflict between competitors (Harrison 1997, McClennen et al. 2001, Moll et al. 2018).

Kit foxes are sympatric with coyotes, red foxes, and gray foxes in the urban environment of Bakersfield, California, located on the southern end of the San Joaquin Valley. While coyotes, gray foxes, and kit foxes are native to the valley, red foxes are introduced (Lewis et al. 1999). Domestic dogs (*Canis familiaris*) are an additional canid species occurring in Bakersfield, and semi-feral dogs in urban areas tend to congregate where anthropogenic food is abundant such as garbage dumps (Macdonald and Carr 1995, Baker et al. 2010). Coyotes will regularly kill dogs, causing free-roaming dogs to avoid areas where coyotes are present (Quinn 1997, Crooks and Soulé 1999); however, dogs have killed red foxes and kit foxes and consequently foxes may avoid areas where free-roaming dogs are present (Harris 1981, Cypher 2010).

The kit fox population in the city of Bakersfield has constituted one of the largest subpopulations and as such has been a central focus of kit fox research over the past 20 y (Cypher and Van Horn Job 2012). The canid guild in Bakersfield is unique as it involves five species comprised of native, non-native, domestic, and endangered canid species. Previous studies on urban competition have focused on competitors from different taxonomic families or on intraguild groups consisting of two to three species. Using 5 y of remote camera data from an annual city-wide survey from 2015 to 2019, we investigated spatiotemporal activity of kit foxes in relation to other canids within 1-km^2 grid cells on a daily, annual, and 5-y basis. Due to the territorial tendencies of larger canids to kill smaller species, we first predicted that kit foxes and other canids would rarely co-occur in the same 1-km^2 area within the same day or year. If kit foxes did occur with other canids within the same night, we further predicted that kit foxes would practice caution by delaying visitation to a camera station when another canid was present and spend less time at the camera station. Our study aims to provide a more comprehensive understanding of interactions between an imperiled species of kit fox and canid competitors in the urban environment.

METHODS

Study Area

Bakersfield, California is located in the San Joaquin Desert of Kern County, California, and is characterized by heavy urbanization with natural habitat including saltbush (*Atriplex* spp.) scrub, grassland, and riparian areas on 25 to 30% of its boundary (Cypher 2010). The city encompasses a variety of urban land use including residential and commercial developments, recreational areas, preserved green spaces, industrial centers, agriculture, and campuses. The Kern River runs north-east to south-west through the middle of the city and is accessible by the public. Due to water being diverted for agricultural purposes, only portions of the river contain water year-round within the city (Shigley 2010). Vegetation within Bakersfield consists primarily of a mix of planted native and non-native ornamental trees, shrubs, and flowering plants. A number of semi-feral and free-roaming domestic dogs inhabit the city, with approximately 6,700 dogs reported as stray intakes in Kern County in 2019 (Kern County Animal Services Directors Monthly Report December 2019).

Field Methods

We conducted annual surveys using camera stations from 2015 to 2019 to monitor sarcoptic mange in the Bakersfield kit fox population and used these data to investigate kit fox spatiotemporal activity in relation to canid competitors. We set camera stations in 111 randomly selected 1-km^2 grid cells located throughout the 368-km^2 city, thus covering approximately 30% of the city (Fig. 2). We selected cell size such that each kit fox home range (mean of 1.72 km^2; Frost 2005) potentially could include two cells, thus optimizing detection of foxes. We selected camera locations within cells based on amount of human activity, access by personnel, and accessibility for kit foxes. We secured Cuddeback Black Flash E3 or C3 trail cameras that were digital and motion triggered (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. We baited camera stations 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. With a few exceptions due to human disturbance, camera locations remained consistent over the 5-y sampling period. We ran stations annually for one 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 species and number of individuals. Unless animals could be distinguished as different individuals (by size, sex, markings, and/or tagging), we counted each species of canid that appeared on one camera during a given session as the same individual.

We reviewed photographs from camera stations where kit foxes, coyotes, red foxes, gray foxes, and/or domestic dogs occurred, and recorded the number of cells and days these species visited. For each survey night on cameras where our target species occurred, we used the image date and time stamps to calculate the min elapsed between sunset and first appearance by kit foxes, and the consecutive min that kit foxes spent at a camera station. If a kit fox was not detected for more than 10 min, time calculation ceased with the last kit fox image. We used sunset as our reference time due to the nocturnal nature of our target species. We collected sunset times from the United States Naval Observatory Astronomical Applications Department Data website (https://aa.usno.navy.mil/data/docs/RS_OneYear.php).

Spatial Analyses

To determine if there were associations among the occurrences of kit foxes and other canid species, we used Two-way Contingency Tables to compare the number days with and without visits by kit foxes to the number of days with and without visits by both kit foxes and at least one other canid within each survey year and across all survey years combined (Gotelli and Ellison 2013). We then used Kruskal-Wallis tests to compare the median number of days that each camera station was visited only by kit foxes to the median number of days a station was visited by kit foxes and at least one other canid for each survey year and across all survey years combined as these data were not homoscedastic in a Bartlett's test for equal variances (Gotelli and Ellison 2013).

Temporal Analyses

To test for differences in the timing of visits by kit foxes in relation to other canids for all survey nights collectively, we used One-way Analysis of Variance and Tukey Honestly Significant Difference tests to compare the mean number of min from sunset to first kit fox appearances on nights when (1) only kit foxes visited, (2) both kit foxes and other canids visited, but the kit fox appears first, and (3) both kit foxes and other canids visited, but the other canid appears first (Gotelli and Ellison 2013). We then compared the median number of consecutive min that kit foxes spent at camera stations in each of the three scenarios using a Kruskal-Wallis test as these data were not homoscedastic in Bartlett's test for equal variances (Gotelli and Ellison 2013). We included domestic dogs in our temporal analysis only if they appeared to be semi-feral based on visiting camera stations after sunset, not having a collar, and not being on a leash. All statistical tests were run in Minitab 19 statistical software and analyzed at $\alpha = 0.05$.

RESULTS

Over the 5-y sampling period, we completed 545 camera surveys for a total of 3,806 survey nights. The number of individuals, survey cells in which they were detected, and survey nights in which they were detected was highest for kit foxes followed by domestic dogs, red foxes, gray foxes, and coyotes (Table 1). In a given survey cell or on a given survey day, we found that kit foxes occurred alone more frequently than with other canids (approximately 31% of survey cells and 17% of survey days). Less frequently, kit foxes occurred with domestic dogs (approximately 5% of survey cells, less than 1% of survey days), then coyotes, gray foxes, or red foxes (< 1% of survey cells and days with coyotes or gray foxes; < 1% of survey cells and no days with red foxes; Table 1). Domestic dogs occurred with either red foxes or gray foxes in < 1% of the survey cells and survey days and did not occur with coyotes on any occasion (Table 1). Due to highly inequivalent numbers of kit foxes visits to visits by other canids, we grouped coyote, red fox, gray fox, and domestic dog occurrences into a combined Other Canids category for subsequent analyses.

We completed 735 to 775 survey days in each of the 5 y of our study. Although 2015 had the lowest number of survey days (735), this year had the highest number of kit fox individuals (approximately 33% of the total number of kit foxes across all years), number of survey cells in which they occurred (approximately 31% of the total survey cells across all years), and number of survey days in which they occurred (approximately 32% of the total survey days across all years; Tables 1 and 2). Our 2015 survey year also had the highest number of survey cells in which kit foxes occurred with one other canid species (approximately 3% of total survey cells across all years; Tables 1 and 2). No coyotes were detected on our cameras in 2015 (Table 2). Kit fox numbers declined annually through 2019, which had 763 survey days and approximately 10% of the total number of kit foxes and approximately 8% of the total survey cells and total survey days in which they occurred across all years (Tables 1 and 3). Overall, there was a 69% decrease in kit fox abundance over the 5 y sampling period (Tables 2 and 3). Kit foxes occurred with two other canid species, gray fox and dog, at one camera station in 2016, but they did not occur on the same day (Table 3). Additionally, in each individual survey year there were few occurrences of kit foxes and other canids detected in the same cell or on the same day (Tables 2 and 3).

Spatial Analyses

We found one association between the number of days kit foxes occurred alone and the number of days kit foxes occurred with Other Canids in 2018 ($X^2 = 4.922$, df = 1, $P = 0.027$), with no associations in the remaining tests ($X^2 = 0.002$-3.058, all dfs = 1, all P-values > 0.05). The number of days that cameras were visited by only kit foxes was higher than the number of days that cameras were visited by both kit foxes and Other Canids in all tests ($H = 11.6$-99.22, all dfs = 1, all P-values < 0.001). We observed a similar trend in mean days visited by kit foxes relative to that of Other Canids, with a decrease in the mean days visited by kit foxes over the 5-y sampling period (Fig. 2).

Temporal Analyses

We found kit foxes only delayed their min to appearance from sunset at camera stations on nights when Other Canids appeared first when compared to nights when only kit foxes occurred and nights when both kit foxes and Other Canids occurred but the other canid did not appear first ($F_{2,556} = 4.82$, $P = 0.008$; Tukey HSD, $P \leq 0.05$; Fig. 3). Trends in mean min to appearances from sunset show kit foxes appear about 2-h earlier on nights when Other Canids occurred but did not appear first, and about 3-h later on nights when Other Canids appeared first when compared to kit fox appearances on nights when only kit foxes visited, which occurred about 5 h following sunset (Fig. 3). We did not find differences between the median consecutive min kit foxes spent at stations on nights when only kit foxes occurred, nights when both kit foxes and Other Canids occurred but the other canid did not appear first, and nights when both kit foxes and Other Canids occurred but the other canid appeared first ($H = 1.12$, df = 2, $P = 0.571$). Trends in mean consecutive min that a kit fox spent at a station showed that kit foxes spent about 5 more minutes at stations when another canid visited on the same night but did not appear first, and spent about 2 min at a station when kit foxes were the only visitor or another canid had already appeared on camera (Fig. 4). Additionally, variances in mean consecutive min that a kit fox spent at a station between the three groups were heteroscedastic ($B = 27.02$, df = 2, $P < 0.001$; Fig. 4). Kit foxes exhibited greater unpredictability in the amount of time spent at a station on nights when both kit foxes and Other Canids occurred but the other canid did not appear first ($s^2 = 89.58$), followed by nights when kit foxes were the only canid visitor ($s^2 = 10.13$), and finally, kit foxes exhibited the most predictability in the amount of time spent at a station on nights when both kit foxes and Other Canids occurred but Other Canids appeared first ($s^2 = 0.30$). Kit foxes spent between 1 and 21 min at a station on nights when Other Canids occurred but did not appear first, between 1 and 35 min at a station on nights when kit foxes were the only visitor, and up to 2 min at a station on nights when another canid appeared first on camera. Because there were at least 543 more observations for kit foxes as the only visitor, kit foxes had the largest variance in the potential time window spent at a station on nights when another canid also visited but kit foxes appeared first, followed by a smaller variance in the potential time window when kit foxes were the only visitor, and the smallest variance in the potential time window when another canid had already visited the station.

DISCUSSION

Kit foxes primarily did not occur or were not associated with other canids on days across all years collectively or within most years suggesting spatial partitioning among kit foxes and other canids in Bakersfield. The 2018 survey was the only year that kit foxes did not occur with other canids on any given day when ignoring domestic dogs, with only one day of overlap between kit foxes and domestic dogs, which may explain why 2018 had the only association between the number of days kit foxes occurred alone and with another canid within years. These results are consistent with our prediction that kit foxes would rarely occur with other canids in the same 1-km^2 area within the same day and year, but further show kit foxes rarely occur with other canids within a 5-y span.

On a finer spatial scale, in instances where kit foxes and other canids did co-occur the presence of another canid did not discourage the use of that area by kit foxes on the same night unless the other canid arrived first. Kit foxes were the least predictable in the amount of time spent at stations if another canid was in the area on the same night but did not appear at a station first, in which case kit foxes appeared later and were the most predictable in the amount of time spent at a station. Studies involving other canid guilds have demonstrated similar patterns of temporal avoidance as a means of minimizing competition. In northeastern Argentina, pampas foxes (*Lycalopex gymnocercus*) reduced their activity at times when a more dominant competitor, the crab-eating fox (*Cerdocyon thous*), was highly active (Di Bitetti et al. 2009). In central India, Indian foxes (*Vulpes bengalensis*) reduced their visitation rates to food stations, spent less time at the food, and increased vigilant behavior when a domestic dog (*Canis familiaris*) was visible; however, the presence of dog odors had little effect on fox activity (Vanak and Thaker 2009). Similarly, in Israel, the presence of jackals (*Canis aureus*) prevented red foxes from visiting food stations, yet jackal odors had little effect on behavior (Scheinin et al. 2006). Because an increase in vigilance can affect time allocation for foraging, apprehension, and other behaviors, a more immediate predator presence cue than scent, such as a visual of the competitor, may be required to produce an effect in perceived risk to subordinate competitors (Haswell et al. 2018), which is consistent with our results regarding San Joaquin kit foxes. These results were partially consistent with our prediction that other canids in the area would discourage a kit fox from approaching bait.

Our camera surveys detected mostly kit foxes followed by domestic dogs. Past studies in urban areas have found that red foxes prefer suburb areas (< 20 houses/ha) and gray foxes prefer urban edges or heavily vegetated areas, while coyotes prefer suburbs or more natural habitat within cities (Gosselink et al. 2003, Riley 2006, Mathewson et al. 2008, Gehrt et al. 2009, Gese et al. 2012, Lesmeister et al. 2015). San Joaquin kit foxes apparently occur in higher abundances in urban areas than in non-urban habitats, and domestic dogs persist in close proximity to human development due to dependence on anthropogenic food sources (Vanak and Gompper 2009, unpublished data), which may explain why these two species were detected in higher numbers. Additionally, domestic dog odors are abundant in urban areas, meaning that the presence of domestic dog odors may not be novel and therefore are not threatening to kit foxes (Vanak and Thaker 2009). Because we found all canids occurred alone more frequently than with another canid, followed by occurrences with just one other canid, which primarily occurred between kit foxes and domestic dogs, our camera results are consistent with other findings that canid species may only be capable of coexistence with one other canid at any given time (Lesmeister et al. 2015).

By 2019 kit fox numbers had decreased in our camera surveys by approximately 69% from 2015 highlighting the severe negative impact of sarcoptic mange in Bakersfield which was first noted in urban kit foxes in 2013 and is 100% fatal in untreated kit foxes (Cypher et al. 2017). The disease has been studied extensively in red foxes in which mortality can occur 3–4 mo following infection (Stone et al. 1972). Due to the similar biology of red foxes and kit foxes, it is likely that time-to-mortality for kit foxes is similar (Cypher 2003). Interestingly, our cameras did not capture any coyotes in 2015, when kit fox abundance was highest. Urban coyotes are also susceptible to sarcoptic mange, and it was first noted in coyotes in the San Joaquin Valley in 2007 (Cypher et al. 2017). While sarcoptic mange is not 100% fatal for coyotes, the infection results in higher mortality, particularly for fragmented populations, which is often the case for animals living in patchy habitat in urban landscapes (Pence et al. 1983, Pence and Ueckermann 2002, Gehrt 2010). It is possible that mange reduced coyote abundance in the Bakersfield population by 2015.

Overall, our study shows that kit foxes rarely occur with other canids in the urban environment. Understanding how species respond to development will allow for more effective species management or conservation plans. Conserving the kit fox population in Bakersfield is important for the conservation of this species as a whole. Future conservation strategy as it pertains to urban areas where this imperiled fox persists, such as selection of habitat mitigation lands, habitat restoration, or relocation of kit foxes should take into consideration the presence of other canid species and their activity patterns.

ACKNOWLEDGMENTS

The Endangered Species Recovery Program (ESRP) of California State University, Stanislaus provided preliminary data as well as equipment and funding to complete camera surveys for our analysis. ESRP personnel Larry Saslaw and Christine Van Horn Job assisted in data collection and analysis. Dr. David J. Germano of California State University, Bakersfield assisted with data analysis and edited drafts of this manuscript. Funding for this study was generously provided by ESRP, the San Joaquin Valley Chapter of The Wildlife Society, and the Western Section of The Wildlife Society.

LITERATURE CITED

Baker, P.J., C.D. Soulsbury, G. Iossa, and S. Harris. 2010. Domestic cat (*Felis catus*) and domestic dog (*Canis familiaris*). Pages 157–171 in S.D Gehrt, S.P.D. Riley, and B.L. Cypher, editors, Urban carnivores, ecology, conflict, and conservation. The Johns Hopkins University Press, Baltimore, MD.

Case, T.J., and M.E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences of the United States of America 71:3073–3077.

Clark, H.O.Jr., G.D. Warrick, B.L. Cypher, P.A. Kelly, D.F. Williams, and D.E. Grubbs. 2005. Competitive interactions between endangered kit foxes and nonnative red foxes. Western North American Naturalist 65:153–163.

Crooks, K.R., and M.E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Cypher, B.L. 2003. Foxes. Pages 511–546 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors, Wild mammals of North America: biology, management, and conservation. 2nd edition. The John Hopkins University Press, Baltimore, MD.

Cypher, B.L. 2010. Kit foxes (*Vulpes macrotis*). Pages 49–57 in S.D Gehrt, S.P.D. Riley, and B.L. Cypher, editors, Urban carnivores, ecology, conflict, and conservation. The Johns Hopkins University Press, Baltimore, MD.

Cypher, B.L., C.O.J. Howard, P.A. Kelly, C. Van Horn Job, G.D. Warrick, and D.F. Williams. 2001. lnterspecific interactions among wild canids: implications for the conservation of endangered San Joaquin kit foxes. Endangered Species Update 18:171–174.

Cypher, B.L., S.E. Philips, and P.A. Kelly. 2013. Quantity and distribution of suitable habitat for endangered San Joaquin kit foxes: conservation implications. Canid Biology & Conservation 16:25–31.

Cypher, B.L., J.L. Rudd, T.L. Westall, L.W. Woods, N. Stephenson, J.E. Foley, D.Richardson, and D.L. Clifford. 2017. Sarcoptic mange in endangered kit foxes (*Vulpes macrotis mutica*): case histories, diagnoses, and implications for conservation. Journal of Wildlife Diseases 53:46–53.

Cypher, B.L., and C.L. Van Horn Job. 2012. Management and conservation of San Joaquin kit foxes in urban environments. Pages 347–352 in Proceedings of the Vertebrate Pest Conference. University of California, Davis, CA.

Cypher, B.L., G.D. Warrick, M.R.M. Otten, T.P. O'Farrell, W.H. Berry, C.E.H. Harris, T.T. Kato, P.M. McCue, J.H. Scrivner, and B.W. Zoellick. 2000. Population dynamics of San

Joaquin kit foxes at the Naval Petroleum Reserves in California. Wildlife Monographs 145:1–43.

Di Bitetti, M.S., Y.E. Di Blanco, J.A. Pereira, and A. Paviolo. 2009. Time partitioning favors the coexistence of sympatric crab-eating foxes (*cerdocyon thous*) and pampas foxes (*lycalopex gymnocercus*). Journal of Mammalogy 90:479–490.

Ditchkoff, S.S., S.T. Saalfeld, and C.J. Gibson. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecosystems 9:5–12.

Farias, V., T.K. Fuller, R.K. Wayne, and R.M. Sauvajot. 2005. Survival and cause-specific mortality of grey foxes (*Urocyon cinereoargenteus*) in southern California. The Zoological Society of London 266:249–254.

Fedriani, J.M., T.K. Fuller, R.M. Sauvajot, and E.C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Freeman, S. 2011. An introduction to ecology. Pages 993–1127 in B. Wilbur, B. Ruden, S. DiVittorio, A. Fugate, M. Lerner-Nelson, W. O'Neal, S. Teahan, K. Murphy, B. Golden, and L. Allen, editors, Biological science. 4th edition. Pearson Education, Inc., San Francisco, CA.

Fuller, T.K., S. Destefano, and P.S. Warren. 2010. Carnivore behavior and ecology, and relationship to urbanization. Pages 18–19 in S.D Gehrt, S.P.D. Riley, and B.L. Cypher, editors, Urban carnivores, ecology, conflict, and conservation. The Johns Hopkins University Press, Baltimore, MD.

Gehrt, S.D. 2010. The urban ecosystem. Pages 6–9 in S.D Gehrt, S.P.D. Riley, and B.L. Cypher, editors, Urban carnivores, ecology, conflict, and conservation. The Johns Hopkins University Press, Baltimore, MD.

Gehrt S.D., C. Anchor, and L.A. White. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045–1057.

Gese, E.M., P.S. Morey, and S.D. Gehrt. 2012. Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. Japan Ethological Society and Springer 30:413–425.

Gehrt, S.D., and S.P.D. Riley. 2010. Coyotes (*Canis latrans*). Pages 85–89 in S.D Gehrt, S.P.D. Riley, and B.L. Cypher, editors, Urban carnivores, ecology, conflict, and conservation. The Johns Hopkins University Press, Baltimore, MD.

Gosselink, T.E., T.R. Van Deelen, R.E. Warner, and M.G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. The Journal of Wildlife Management 67:90–103.

Gotelli, N.J., and A.M. Ellison. 2013. A primer of ecological statistics. Sinauer Associates, Inc. Sunderland, MA.

Grimm, N.B., D. Foster, P. Groffman, J.M. Grove, C.S. Hopkinson, K.J. Nadelhoffer, D.E. Pataki, and D.P.C. Peters. 2008. The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. The Ecological Society of America: Frontiers in Ecology and the Environment 6:264–272.

Hall, E.R. 1981. The mammals of North America. Volume 2. John Wiley & Sons, New York, NY.

Hall, L.K., C.C. Day, M.D. Westover, R.J. Edgel, R.T. Larsen, R.N. Knight, and B.R. Mcmillan. 2013. Vigilance of kit foxes at water sources: a test of competing hypotheses for a solitary carnivore subject to predation. Behavioural Processes 94:76–82.

Harris, S. 1981. An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. Journal of Applied Ecology 18:455–465.

Harrison, R.L. 1997. A comparison of grey fox ecology between residential and undeveloped rural landscapes. The Journal of Wildlife Management 61:112–122.

Haswell, P.M., K.A. Jones, J. Kusak, and M.W. Hayward. 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. Oecologia 187:573–583.

Heithaus, M.R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild. Oikos 92:542–554.

Kitchen, A.M., E.M. Gese, and E.R. Schauster. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77:1645–1656.

Lesmeister, D.B., C.K. Nielsen, E.M. Schauber, and E.C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. Wildlife Monographs 191:1–61.

Lewis, J.C., K.L. Sallee, and R.T.Jr. Golightly. 1999. Introduction and range expansion of nonnative red foxes (*Vulpes vulpes*) in California. American Midland Naturalist 142:372–381.

Macdonald, D.W., editor. 2009. Carnivores. Pages 598–611 in The Princeton encyclopedia of mammals. Princeton University Press, Princeton, NJ.

Macdonald, D.W., and G.M. Carr. 1995. Variation in dog society: between resource dispersion and social flux. Pages 199–216 in J. Serpell, editor, The domestic dog: its evolution, behaviour and interactions with people. Cambridge University Press, Cambridge, England.

MacKenzie, D.I., J.A. Royle, J.D. Nichols, J.E. Hines, K.H. Pollock, and L. Bailey. 2006. Occupancy estimation and modeling, inferring patterns and dynamics of species occurrence. Academic Press, Burlington, MA.

Mathewson, P.D., S.N. Spehar, and D.S. Cooper. 2008. An initial carnivore survey of Griffith Park, Los Angeles, California. Bulletin of the Southern California Academy of Sciences 107:57–67.

Mcclennen, N., R.R. Wigglesworth, and S.H. Anderson. 2001. The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). The American Midland Naturalist 146:37–36.

Moll, R.J., J.D. Cepek, P.D. Lorch, P.M. Dennis, T. Robison, J.J. Millspaugh, and R.A. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21:765–778

Moehrenschlager, A., R. List, and D.W. Macdonald. 2001. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. Jourmal of Mammalogy 88:1029–1039.

Nelson, J.L., B.L. Cypher, C.D. Bjurlin, and S. Creel. 2007. Effects of habitat on competition between kit foxes and coyotes. Journal of Wildlife Management 71:1467–1475.

Pence, D.B, L.A. Windberg, B.C. Pence, and R. Sprowls. 1983. The epizootiology and pathology of sarcoptic mange in coyotes, *Canis latrans*, from South Texas. The Journal of Parasitology 69:1100–1115.

Pence, D.B., and E. Ueckermann. 2002. Sarcoptic mange in wildlife. Scientific and Technical Review of the Office International des Epizooties 21:385–398.

Polis, G.A., C.A. Myers, and R.D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297–330.

Quinn, T. 1997. Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. Northwest Science 71:1–5.

Ralls, K., and P.J. White. 1995. Predation on San Joaquin kit foxes by larger canids. Journal of Mammalogy 76:723–729.

Riley, S.P.D. 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. The Journal of Wildlife Management 70:1425–1435.

Robinson, Q.H., D. Bustos, and G.W. Roemer. 2014. The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. Ecology 95:3112–3123.

Scheinin, S., Y. Yom-Tov, U. Motro, and E. Geffen. 2006. Behavioral responses of red foxes to an increase in the presence of golden jackals: a field experiment. Animal Behavior 71:577–584.

Shigley, P. 2010. Bakersfield hopes to restore water to Kern River. Planning; Chicago 76:8.

Soulsbury, C.D., P.J. Baker, G. Iossa, and S. Harris. 2010. Red foxes (*Vulpes vulpes*). Pages 63–75 in S.D Gehrt, S.P.D. Riley, and B.L. Cypher, editors, Urban carnivores, ecology, conflict, and conservation. The Johns Hopkins University Press, Baltimore, MD.

Stone, W.B., E. Parks, B.L. Weber and F.J. Parks. 1972. Experimental transfer of Sarcoptic mange from red foxes and wild canids to captive wildlife and domestic animals. New York Fish and Game Journal 19:1–11.

Vanak, A.T., and M.E. Gompper. 2009. Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. Mammal Review 39:265–283.

Vanak, A.T., and M. Thaker. 2009. Experimental examination of behavioural interactions between free-ranging wild and domestic canids. Behavioral Ecology and Sociobiology 64:279–287.

Voigt, D.R. 1987. Red fox. Pages 380–392 in M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors, Wild furbearer management and conservation in North America. The Ontario Trappers Association, Ontario, Canada.

Voigt, D.R., and W. Berg. 1987. Coyote. Pages 345–356 in M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors, Wild furbearer management and conservation in North America. The Ontario Trappers Association, Ontario, Canada.

Wang, Y., M.L. Allen, and C.C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

White, P.J., K. Ralls, and R.A. Garrott. 1994. Coyote-kit fox interactions as revealed by telemetry. Canadian Journal of Zoology 72:1831–1836.

Williams, D.F., E.A. Cypher, P.A. Kelly, K.J. Miller, N. Norvell, S.E. Phillips, C.D. Johnson, and G.W. Colliver. 1998. San Joaquin kit fox (*Vulpes macrotis mutica*). Pages 122–136 in Recovery plan for upland species of the San Joaquin Valley, California. U. S Fish and Wildlife Service. Region 1, Portland, OR.

TABLES

TABLE 1. The total number of individuals (*n* = 604 for individual species, *n* = 2,693 for species combinations), surveyed grid cells (*n* = 545), and surveyed days (*n* = 3,806) that each canid species (SJKF = San Joaquin kit fox, Coy = coyote, RF = red fox, GF = gray fox, Dog = domestic dog), or species combination, occurred during an annual camera survey of 105 to 111 cells (depending on the year) in Bakersfield, California from 2015 to 2019.

Species	Total no. of individuals	Total no. of survey cells	Total no. of survey days
SJKF	394	166	654
Dog	150	49	139
RF	25	15	37
GF	19	9	28
Coy	16	5	14
SJKF, Dog	544	27	29
SJKF, Coy	410	5	5
SJKF, GF	413	4	2
SJKF, RF	419	2	0
SJKF, GF, Dog	563	1	0
GF, Dog	169	2	1
RF, Dog	175	1	1

TABLE 2. The number of individuals (n = 164 for total individual species, n = 772 for total species combinations), surveyed grid cells (n = 105), and surveyed days (n = 735) that each canid species (SJKF = San Joaquin kit fox, Coy = coyote, RF = red fox, GF = gray fox, Dog = domestic dog), or species combination, occurred during a camera survey of 105 cells in Bakersfield, California in 2015.

Species	No. of individuals	No. of survey cells	No. of survey days
SJKF	129	52	212
Dog	26	4	19
GF	5	2	9
RF	4	2	4
Coy	0	0	0
SJKF, Dog	155	12	13
SJKF, GF	134	2	1
SJKF, RF	133	2	0
SJKF, Coy	129	0	0
SJKF, GF, Dog	160	0	0
RF, Dog	30	0	0
GF, Dog	31	0	0

TABLE 3. The number (No.) of individuals, surveyed grid cells, and surveyed days that each canid species (SJKF = San Joaquin kit fox, Coy = coyote, RF = red fox, GF = gray fox, Dog = domestic dog), or species combination, occurred during an annual camera survey in Bakersfield, California from 2016 to 2019. The number of observations (*n*) is included for each year below each heading; for number of individuals, the total number of observations for single species (Sgl) and total number of observations for species in combinations (Com) are included.

Year	2016			2017			2018			2019		
	No. of individuals	No. of cells	No. of days	No. of individuals	No. of cells	No. of days	No. of individuals	No. of cells	No. of days	No. of individuals	No. of cells	No. of days
n	Sgl = 140 Com = 622	111	775	Sgl = 120 Com = 538	109	763	Sgl = 87 Com = 370	110	770	Sgl = 93 Com = 391	110	763
Species												
SJKF	94	43	172	81	33	127	50	24	88	40	14	55
Dog	30	7	24	27	11	27	24	11	30	43	16	39
Coy	6	1	3	2	2	2	5	2	7	3	0	2
GF	6	3	8	3	3	7	3	1	1	2	0	3
RF	4	3	7	7	3	9	5	4	11	5	3	6
SJKF, Dog	124	5	5	108	6	6	74	3	1	83	1	4
SJKF, Coy	100	2	2	83	0	0	55	1	0	43	2	3
SJKF, GF	100	1	1	84	0	0	53	0	0	42	1	0
SJKF, RF	98	0	0	88	0	0	55	0	0	45	0	0
SJKF, GF, Dog	130	1	0	111	0	0	77	0	0	85	0	0
RF, Dog	34	0	0	34	0	0	29	1	1	48	0	0
GF, Dog	36	1	1	30	0	0	27	0	0	45	1	0

FIGURES

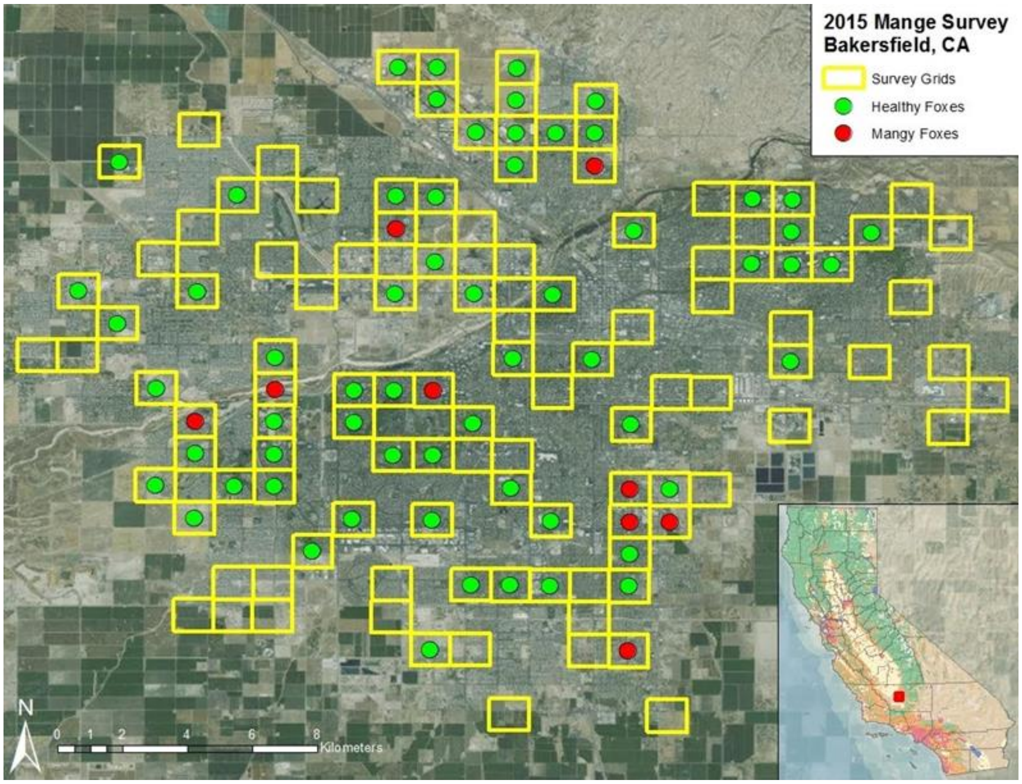


Fig. 1. Distribution of 120 1-km^2 grid cells used to monitor sarcoptic mange disease in San Joaquin kit foxes in Bakersfield, California in 2015. Of these, 105 to 111 cells were surveyed annually (depending on the year) through 2019 using remote camera stations.

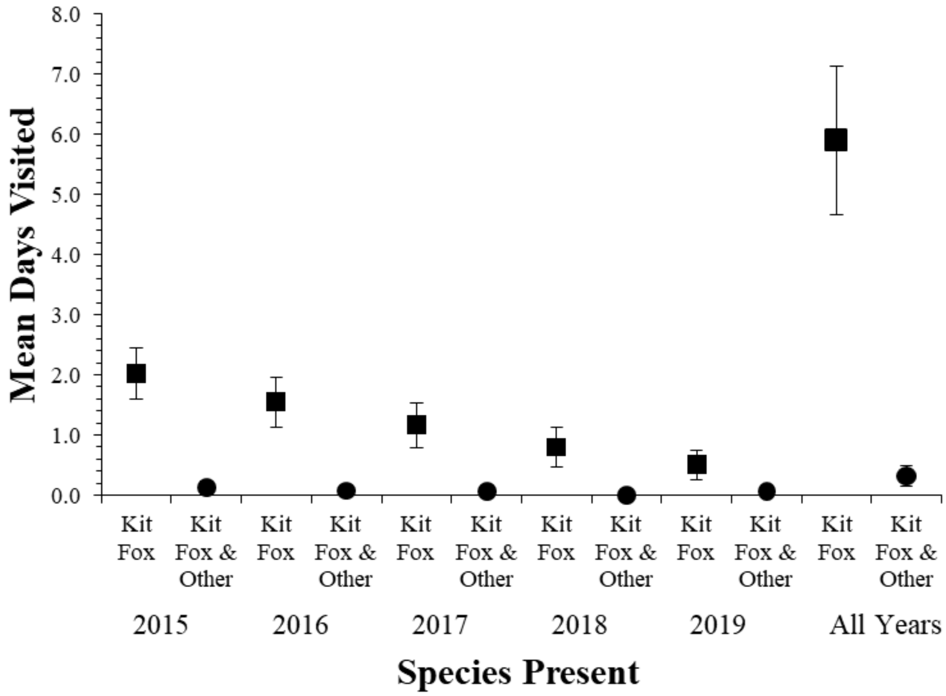


Fig. 2. Mean number of days, with 95% confidence interval bars, camera stations were visited by only San Joaquin kit foxes (squares) or by kit foxes and coyotes, red foxes, gray foxes, or domestic dogs (Kit Fox & Other, circles) each year from 2015 to 2019, as well as for all years combined during a 7-d annual camera survey of n = 105 to 111 grid cells (depending on the year) in Bakersfield, California.

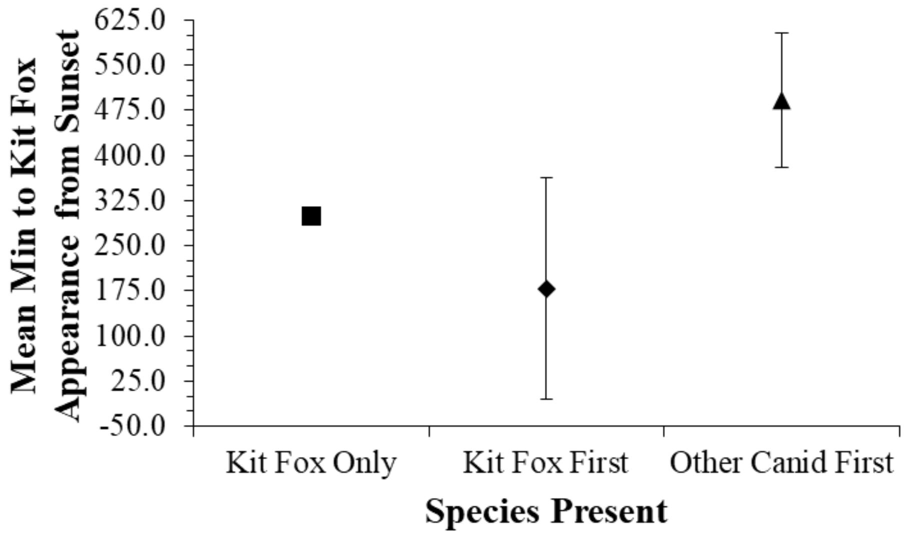


Fig. 3. Mean number of min, with 95% confidence interval bars, to first San Joaquin kit fox appearances at camera stations following sunset during an annual camera survey of 105 to 111 grid cells (depending on the year) in Bakersfield, California from 2015 to 2019. The square represents nights when only kit foxes occurred (*n* = 549), the diamond represents nights when both kit foxes and other canids (coyotes, red foxes, gray foxes, or domestic dogs) occurred but kit foxes appeared on camera first (*n* = 4), and the triangle represents nights when both kit foxes and other canids occurred but the other canid appeared on camera first (*n* = 6).

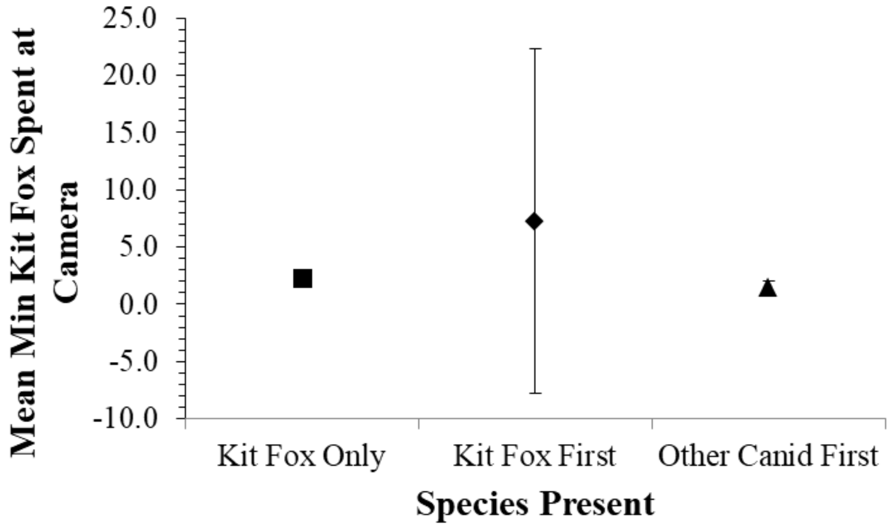


Fig. 4. Mean consecutive min, with 95% confidence interval bars, a San Joaquin kit fox appeared on camera stations on nights during an annual camera survey of 105 to 111 grid cells (depending on the year) in Bakersfield, California from 2015 to 2019. The square represents nights when only kit foxes occurred (*n* = 549), the diamond represents nights when both kit foxes and other canids (coyotes, red foxes, gray foxes, or domestic dogs) occurred but kit foxes appeared on camera first (*n* = 4), and the triangle represents nights when both kit foxes and other canids occurred but the other canid appeared on camera first (*n* = 6).

CHAPTER 4

SUMMARY OF RESEARCH AND IMPLICATIONS

Spatial heterogeneity of landscapes and space use by wildlife are influenced by anthropogenic, natural, physical, and biotic processes (Constible et al. 2006). Interspecific competition is one such process that has been studied extensively in a variety of field and laboratory settings, yet an understanding of how humans and urban development interfere with such processes is a topic that warrants continued investigation as species are increasingly subjected to encroaching human development. Conservation and management policy is often focused on managing landscape change through restoration, mitigation, and protection (Wiens et al. 2015). Understanding how landscape changes affect intra- and interspecific processes is therefore critical in the development of effective policy in the face of rapid landscape change (Wiens et al. 2015). In this study, I first investigated San Joaquin kit fox (*Vulpes macrotis mutica*; hereafter kit fox) urban habitat preferences and how these might relate to the presence of three other canid competitors residing in the city of Bakersfield, California: coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*). Second, I investigated spatiotemporal partitioning among kit foxes, coyotes, red foxes, gray foxes, as well as domestic dogs (*Canis familiaris*) in Bakersfield. From these two analyses I collectively conclude that kit foxes rarely occur with other canids in Bakersfield, though selection for or against certain urban landscape characteristics may be the primary determinate of kit fox occupancy patterns.

Urban landscape attributes affect San Joaquin kit fox occupancy patterns

Results from my first analysis suggest that kit foxes are selecting for campuses (e.g., schools, churches, medical centers, and large corporations) in the urban landscape while avoiding paved roads, as the most supported kit fox occupancy model included the percentages of paved roads and campuses as covariates within1-km^2 grid cells. Percentage of paved roads was a negative predictor of kit fox occupancy and percentage of campuses was a positive predictor. Across all ranking models, percentage of paved roads was ultimately the most supported covariate for predicting kit fox occupancy. Roads are the main source of mortality for urban kit foxes and are characterized by human-caused noise pollution, development, disturbance, and activity which may discourage urban kit foxes from utilizing roads (Bjurlin et al. 2005). Conversely, campuses offer open space with landscaping, sports yards, quadrangles, and walkways, as well as security from excess human disturbance and larger predators with fences and other security measures employed by campuses. Campuses also support rodent, insect, and bird prey for kit foxes and offer anthropogenic food sources from cafeterias and people directly feeding kit foxes (Cypher 2010).

Results from my first analysis confirm that kit foxes occur in higher abundances than any other wild canid species in Bakersfield (B. L. Cypher, unpublished data). Kit foxes may be better able to adapt to highly developed urban areas than other canids. This is consistent with previous studies on urban habitat selection that show that coyotes need larger, connected ranges and are more often observed in urban areas with more natural habitat (Crooks 2002, Gehrt et al. 2009, Gese et al. 2012), that red foxes avoid coyotes by being better adapted to intermediate human modified habitats (e.g., suburbs with house densities of < 20 houses/ha; Gosselink et al. 2003, Lesmeister et al. 2015), and that gray foxes tend to select for urban edges or more natural, tree covered areas (Riley 2006, Mathewson et al. 2008, Lesmeister et al. 2015); however, kit foxes are frequently observed denning in inner city landscapes (Cypher and Van Horn Job 2012). My results also show a significant decrease in kit fox abundances in recent years with a 69% decrease in kit fox numbers at camera stations and a 40% decrease in probability of kit fox occupancy over the past 5 y as a result of sarcoptic mange (*Sarcoptes scabiei*; Cypher et al. 2017).

While the presence of other canids was not a supported model for urban kit fox occupancy, this does not necessarily imply that other canids have no effect on kit fox occupancy patterns. Small sample sizes of other canid detections relative to that of kit foxes may have been inadequate for my modeling to fully assess the effect of competitor presence on kit fox occupancy patterns (MacKenzie et al. 2018). Also, the scale of my sampling design (1-km^2 cells) may not have been optimal for assessing occupancy by the larger canids. The results from my second analysis allowed me to infer more definite kit fox spatiotemporal patterns in relation to the presence of other canids.

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

Apart from one association in the number of days that kit foxes occurred alone and the number of days kit foxes occurred with another canid in 2018, I found no other associations between kit fox and other canid occurrences on days on a yearly scale and across all five survey years collectively. I also found differences between the median numbers of days that kit foxes occurred alone or with another canid on a yearly scale and across all 5 y. My results suggest that kit foxes rarely occur with other canids in a 1-km^2 area within the same day, year, or 5-y span. This is consistent with a study in southern Illinois that found that higher coyote activity on remote cameras resulted in a decreased number of gray foxes overall, as well as during time periods with more coyote detections (Lesmeister et al. 2015).

I found that kit foxes delay their time to appearance at camera stations where another canid species came by first on the same night by about 3 h. Additionally, kit foxes were least predictable, or possessed more variance, in the window of time spent at the station if another canid visited the station but did not appear first, spending between 1 and 21 min at a station. San Joaquin kit foxes had the most predictability in the potential window of time spent at the station if another canid appeared first, spending up to 2 min at a station. Thus, kit foxes may require a more immediate predator presence cue to perceive imminent risk from nearby competitors, as is consistent with a number of other studies on temporal avoidance of larger predators by fox species as a means of minimizing competition (Scheinin et al. 2006, Vanak and Thaker 2009, Haswell et al. 2018).

I found that single canid species were detected more frequently than multiple species in particular cells and on specific days. If more than one canid did occur there were never more than three, though primarily only two species co-occurred, with a majority of co-occurrences between kit foxes and domestic dogs. Because domestic dogs are abundant in urban areas, they may not be novel or threatening to kit foxes, allowing domestic dogs and kit foxes to co-occur at higher frequencies than kit foxes and other wild canids (Vanak and Thaker 2009). Based on these results, canids may only coexist with one other canid species at any given time and location. Thus, some degree of spatial partitioning may occur within the urban environment between kit foxes, coyotes, red foxes, gray foxes, and domestic dogs (Gosselink et al. 2003, Riley 2006, Mathewson et al. 2008, Gehrt et al. 2009, Gese et al. 2012, Lesmeister et al. 2015).

Urban carnivore conflicts and concerns

Effective conservation and management of urban carnivores will address human needs while conserving species diversity and ecosystem interconnectedness. Urban carnivores may generate human-carnivore conflict by damaging property, taking livestock and pets, attacking humans, and exposing humans and domestic animals to disease and parasites (Hudenko et al. 2010). Urban carnivores can create social controversy as both charismatic symbols of the wild and potential nuisances (Hudenko et al. 2010). Because wild canids are often top predators and keystone species in ecosystems, studying their ecology is imperative for understanding how management and conservation practices might also affect lower trophic levels or interspecific interactions (Letnic et al. 2009).

Carnivores are at a relatively high risk for extinction due to low population densities and intrinsic growth rates, dependency on other species for food, and high subjection to persecution by humans (Macdonald 2009). Overall, human development results in significant reductions in species abundances as a result of natural habitat loss, degradation, and fragmentation (Cypher et al. 2010). Urban carnivores are further subjected to urban diseases, pollution, and particularly, road casualties (Gehrt 2010). As human population and urbanization continue to increase, roads will also grow wider, carry more traffic, and become more inhospitable to wildlife (Bjurlin et al. 2005). As roads expand, the risk of vehicle-caused mortality increases while the amount of suitable habitat decreases for many urban carnivores (Bjurlin et al. 2005). Measures to reduce vehicle collisions with wildlife will not only benefit animals but may also reduce unsafe driving conditions for people (Bjurlin et al. 2005).

Urban San Joaquin kit fox conservation and management

In the San Joaquin Valley, which encompasses the city of Bakersfield, native wildlife habitat was reduced to approximately 4% of its historical range by 1979 due to urbanization, agriculture, and industrial development (Olson and Magney 1992). As loss of natural habitat continues, urban carnivore populations may become more important for species persistence (Bjurlin et al. 2005). Conserving populations of kit foxes persisting in urban areas can contribute to the overall health, survival, and recovery of this federally listed endangered and California listed threated species. The Bakersfield population contributes to range-wide abundance and genetic diversity, as well as positive educational outreach in the city (Cypher 2010). Outreach is arguably the most important component of conservation in cities (Cypher et al. 2010). Informing the public of the relatively minimal risks associated with urban kit foxes and the appropriate responses in encounters will facilitate public acceptance and support for urban kit foxes.

My results suggest mitigation lands, habitat restoration, or potential relocation efforts should take into consideration the presence and densities of paved roads and other canid species that deter kit foxes and campus-like habitat characteristics such as open space that may be inviting for kit foxes. Because roads are an important source of kit fox mortality, understanding kit fox occupancy patterns in urban areas aids in the development of effective kit fox exclosures or wildlife crossings (Fritzell 1987, Voigt 1987, Voigt and Berg 1987, Egoscue 1962). As kit foxes repeatedly use the same locations and intersections to navigate roadways and are most frequently killed at road intersections, these locations would be ideal candidates for conservation measures (Bjurlin et al. 2005). Kit foxes have been observed using culverts and bridges to cross under roads, therefore road intersections nearby campuses where probability of kit fox occupancy is highest would likely be efficient locations for kit fox-specific road crossings that employ open landscaping, fencing to keep larger predators out, and/or denning structures

(Bjurlin et al. 2005, Frost 2005, Cypher 2010, Bateman and Fleming 2012, Cypher and Van Horn Job 2012).

Disease is an additional and significant source of kit fox mortality. Due to similarities in biology, all canids addressed in my research have the potential to spread disease to one another (Cypher et al. 2017). In studying how these species interact with one another, conservation and management practices may be better able to control the spread of disease, including sarcoptic mange which is of current concern for the kit fox in urban areas (Cypher et al. 2017). My study suggests that urban kit foxes rarely occur with other canids and are selecting campuses as habitat, which may help future mange studies pinpoint the origin of mange in kit foxes.

Conservation plans would benefit from continued study of kit foxes, and future studies might wish to address competitive interactions on a finer scale by assessing competitive behaviors of canids at urban edges, a comprehensive food habits assessment of these four species in urban areas, or a more detailed study of kit fox home ranges as it relates to campuses or roads within the urban areas. Additional areas of study should focus on connectivity and dispersal between city subpopulations within the meta-population of kit foxes in the San Joaquin Valley. Apart from Bakersfield, the cities of Taft, Maricopa, and Coalinga host urban kit fox populations and connectivity between these cities would be ideal (Bjurlin et al. 2005, Cypher 2010). Movements between populations may prevent local extinctions or allow species to recolonize lands where they were previously extirpated, and wildlife corridors will allow for more natural social ecology, space use, and genetic exchange (Bjurlin et al. 2005).

LITERATURE CITED

Bateman, P. W., and P. A. Fleming. 2012. Big city life: carnivores in urban environments. Journal of Zoology 287: 1-23.

Bjurlin, C. D., B. L. Cypher, C. M. Wingert, and C. L. Van Horn Job. 2005. Urban roads and the endangered San Joaquin kit fox. California Department of Transportation, Endangered Species Recovery Program Final Report, Contract Number 65A0136, Fresno, CA.

Constible, J. M., M. J. Chamberlain, and B. D. Leopold. 2006. Relationships between landscape pattern and space use of three mammalian carnivores in central Mississippi. The American Midland Naturalist 155: 352-362.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16: 488-502.

Cypher, B. L. 2010. Kit foxes (*Vulpes macrotis*). Pages 49-57 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. The Johns Hopkins University Press, Baltimore, MD.

Cypher, B. L., S. P. D. Riley, and R. M. Sauvajot. 2010. Conservation of urban carnivores. Pages 213-220 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. The Johns Hopkins University Press, Baltimore, MD.

Cypher, B. L., J. L. Rudd, T. L. Westall, L. W. Woods, N. Stephenson, J. E. Foley, D. Richardson, and D. L. Clifford. 2017. Sarcoptic mange in endangered kit foxes (*vulpes macrotis mutica*): case histories, diagnoses, and implications for conservation. Journal of Wildlife Diseases 53: 46-53.

Cypher, B. L., and C. L. Van Horn Job. 2012. Management and conservation of San Joaquin kit foxes in urban environments. Pages 347-352 *in*: Proceedings of the Vertebrate Pest Conference. University of California, Davis, CA.

Egoscue, H. J. 1962. Ecology and life history of the kit fox in Tooele County, Utah. Ecology 43: 481-497.

Frost, N. 2005. San Joaquin kit fox home range, habitat use, and movements in urban Bakersfield. Master's thesis. Humboldt State University, Arcata, CA.

Fritzell, E. K. Gray fox and island grey fox. 1987. Pages 410-420 *in*: Wild Furbearer Management and Conservation in North America. Novak, M., J. A. Baker, M. E. Obbard, and B. Malloch, editors. The Ontario Trappers Association, Ontario, Canada.

Gehrt, S. D. 2010. The urban ecosystem. Pages 6-9 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. The Johns Hopkins University Press, Baltimore, MD.

Gehrt S. D., C. Anchor, and L. A. White. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90: 1045-1057.

Gese, E. M., P. S. Morey, and S. D. Gehrt. 2012. Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. Japan Ethological Society and Springer 30: 413-425.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and M. G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. The Journal of Wildlife Management 67: 90-103.

Haswell, P. M., K. A. Jones, J. Kusak, and M. W. Hayward. 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. Oecologia 187: 573-583.

Hudenko, H. W., W. F. Siemer, and D. J. Decker. 2010. Urban carnivore conservation and management, the human dimension. Page 24 *in*: Urban Carnivores, Ecology, Conflict, and Conservation. Gehrt, S. D., S. P. D. Riley, and B. L. Cypher, editors. The Johns Hopkins University Press, Baltimore, MD.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. Wildlife Monographs 191: 1-61.

Letnic, M., F. Koch, C. Gordon, M. S. Crowther, and C. R. Dickman. 2009. Keystone effects of an alien top-predator stem extinctions of native mammals. Proceedings: Biological Sciences 276: 3249-3256.

Macdonald, D. W., editor. 2009. Carnivores. Pages 598-611 *in*: The Princeton Encyclopedia of Mammals. Princeton University Press, Princeton, NJ.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2018. Occupancy Estimation and Modeling, Inferring Patterns and Dynamics of Species Occurrence. 2nd Ed. Academic Press, San Diego, CA.

Mathewson, P. D., S. N. Spehar, and D. S. Cooper. 2008. An initial carnivore survey of Griffith Park, Los Angeles, California. Bulletin of the Southern California Academy of Sciences 107: 57-67.

Olson, T. E., and D. L. Magney. 1992. Distribution of sensitive plant and wildlife species along transmission line corridors in southwestern San Joaquin Valley, California. Page 169 *in*: Endangered and Sensitive Species of the San Joaquin Valley. Williams, D. F., S. Byrne, and T. A. Rado, editors. The California Energy Commission, Sacramento, California.

Riley, S. P. D. 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. The Journal of Wildlife Management 70: 1425-1435.

Scheinin, S., Y. Yom-Tov, U. Motro, and E. Geffen. 2006. Behavioral responses of red foxes to an increase in the presence of golden jackals: a field experiment. Animal Behavior 71: 577-584.

Vanak, A. T., and M. Thaker. 2009. Experimental examination of behavioural interactions between free-ranging wild and domestic canids. Behavioral Ecology and Sociobiology 64: 279-287.

Voigt, D. R. 1987. Red fox. Pages 380-392 *in*: Wild Furbearer Management and Conservation in North America. Novak, M., J. A. Baker, M. E. Obbard, and B. Malloch, editors. The Ontario Trappers Association, Ontario, Canada.

Voigt, D. R., and W. Berg. 1987. Coyote. Pages 345-356 *in*: Wild Furbearer Management and Conservation in North America. Novak, M., J. A. Baker, M. E. Obbard, and B. Malloch, editors. The Ontario Trappers Association, Ontario, Canada.

Wiens, J. D., P. S. Kolar, M. R. Fuller, W. G. Hunt, and T. Hunt. 2015. Estimation of occupancy, breeding success, and predicted abundance of golden eagles (*Aquila chrysaetos*) in the Diablo Range, California, 2014. U. S. Geological Survey Open-File Report 2015-1039. doi.org/10.3133/ofr20151039.