EFFECTS OF VARYING HABITATS ON COMPETITION BETWEEN

ENDANGERED SAN JOAQUIN KIT FOXES (*VULPES MACROTIS MUTICA*)

AND COYOTES (*CANIS LATRANS*)

by

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ABSTRACT

Coyotes (*Canis latrans*) are the primary predator of endangered San Joaquin kit foxes (*Vulpes macrotis mutica*). Coyotes often associate with cover-rich habitats while kit foxes use grasslands, alkali shrublands, and urban environments. Effects of varying habitats on coyote and kit fox competition are relatively unknown. I assessed exploitation and interference competition between coyotes and kit foxes in grassland and shrubland habitats to determine if kit foxes are niche displaced by coyotes. I evaluated habitat and spatial partitioning, diet, and prey abundance of kit foxes and coyotes, as well as survival and fecal glucocorticoid levels (GC) of kit foxes at the Lokern Natural Area in central California from January 2003 through June 2004. Kit foxes partitioned habitat, space, and diet with coyotes. Coyotes primarily used shrubland habitats while kit foxes selected for burned grasslands that coyotes avoided. Kit foxes and coyotes had high dietary overlap, though coyotes had higher dietary breadth than kit foxes, creating significant differences in their diets. Kit fox scats recovered in grasslands showed preference for the larger kangaroo rat, *Dipodomys heermanni*, which was closely tied to shrub habitats. Predation was the primary source of mortality for kit foxes and was greater in the shrublands than grasslands. As a result of increased predation in shrublands, kit foxes with home ranges containing greater proportions of shrub had lower survival rates than foxes residing in grasslands. Despite increased predation risk in shrublands, I detected no difference in kit fox GC levels in shrubland versus grassland habitats, indicating that use of shrub habitats did not produce a physiological stress response in kit foxes. Results suggest that a heterogeneous landscape may allow for the parsimonious coexistence of San Joaquin kit foxes and coyotes. I also analyzed fecal glucocorticoid levels of kit foxes in rural and urban environments to assess the effect of various environments on kit fox stress responses. I detected no difference in glucocorticoid levels in kit foxes residing in urban compared to rural environments, suggesting that the niche shift from traditional rural habitats to the urban setting does not carry physiological costs due to chronic stress responses.

INTRODUCTION

Stable coexistence of competing species is possible when the species are able to minimize competition through niche segregation (Gause 1934). Niche segregation encompasses many forms of resource division, including partitioning of space, habitat, time, and food (Schoener 1974). Animals compete by two different methods: exploitation competition and interference competition. Exploitation competition occurs when animals share the same resources, while interference competition involves direct interaction, which may include predation or physical impairment.

Gause's (1934) experiments with yeast and bacteria demonstrated that competing species can suppress population densities. He showed that the number of *Paramecium* cells in a pure species culture far exceeded the number of cells in a mixed species culture where competition was present. Since those simple experiments, this model has been verified in countless other taxa. A well known example is the introduced North American grey squirrel (*Sciurus carolinensis*) out-competing the European red squirrel (*Picea abies*) by suppressing red squirrel fecundity (Gurnell et al. 2004).

Both exploitation and interference competition can influence the ecological niches of competing populations. A study on cavity-nesting birds in the northwest showed that exploitation competition had an important role in nest site selection of red-naped sapsuckers (*Sphyrapicus nuchalis*) and Northern flickers

(*Colaptes auratus*) (Dobkin et al. 1995). Interference competition between lions (*Panthera Leo*) and wild dogs (*Lycaon pictus)* caused wild dogs to alter habitat use, switching to habitats with low prey densities in order to decrease encounters with lions (Creel and Creel 2002; Creel and Creel 1996).

Intraguild predation (IGP) occurs when competing species also interact as predator and prey. IGP is a common form of interference competition in carnivores and is thought to play a large role in defining niche separation between competing species (Polis et al. 1989). IGP is highly prevalent in canids. In North America, wolves (*Canis lupus*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*) all engage in direct predation of other canid species, which often influences space and habitat use (Cypher et al. 2001; Cypher and Spencer 1998; Gosselink et al. 2003; Harrison et al. 1989; Kitchen et al. 1999; Mech 1970; White et al. 1994).

In an ecosystem with unstable resources, or in threatened and endangered species, interference competition can potentially drive a species to extinction (Rosenzweig and MacArthur 1963). If a population has spatial refugia, such as dens or tree cover, rare species may still be able to persist at low densities (Gotelli 2001). "Competition refuges" are areas where weaker competitors can avoid superior competitors or predators, and can be as simple as using a different microhabitat. For example, cheetahs (*Acinonyx jubatus*) in the Serengeti used areas of low-density prey in order to avoid lions and hyenas (Durant 1998).

In the absence of refugia, superior competitors could have a substantial negative effect on populations. This theory is described by the Lotka-Volterra model: the presence of competition can lead to exclusion of one species by the other if the effects of the competitive species on each other are not balanced or they do not have competition refuges. Examples include Gause's (1936) lab experiments with bacteria where *Didinium* eliminated *Paramecium* from test tubes through direct predation, and the introduction of brown trout (*Salmo trutta*) in New Zealand that led to local extinction of several native fish species (Townsend 1996).

Competition may also elicit physiological stress responses in animals. Con-specific aggression in animals with dominance hierarchies, as well as lynx (*Lynx canadensis*) predation on snowshoes hares (*Lepus americanus*), resulted in increased physiological stress responses of the researched species (Boonstra et al. 1998; Creel 2001). Circumstances or habitats that increase competition from superior competitors may produce physiological stress responses in inferior competitors. Steroid hormones, called glucocorticoids (GCs), regulate stress responses in animals allowing the animal to mediate social and environmental stressors. Animals that encounter frequent stressors, such as regular contact with predators, can experience impaired regulatory stress responses that can chronically elevate basal GC levels. Prolonged elevated GC levels can have deleterious effects on animals, including reproductive and immune system suppression (Sapolsky 2002; Sapolsky et al. 2000). The effects of environmental

perturbations, such as perceived risk from competition or predation, on threatened or endangered species may be of special concern if stress responses are negatively effecting a population.

This study examined the effects of coyote competition on endangered San Joaquin kit foxes (*Vulpes macrotis mutica*). San Joaquin kit foxes coexist with coyotes throughout San Joaquin kit fox range. The principle of competitive exclusion (Hardin 1960) suggests that when resources are limited, kit foxes will partition resources with coyotes to decrease intraguild competition. I evaluated niche segregation between kit foxes and coyotes and examined effects of coyote predation on kit fox glucocorticoid stress (GC) levels. In the first chapter of this thesis, I address kit fox and coyote habitat use, space use, diet, and survival. I use these data to determine the extent to which interference and exploitation competition from coyotes influence kit fox demography and survival. In the second chapter, I analyze glucocorticoid levels of kit foxes to evaluate if proximity to coyotes has a physiological effect on kit foxes due to stress. Both chapters in this thesis represent individual manuscripts and therefore have some overlap in content but address different aspects of how interspecific competition with coyotes influences San Joaquin kit fox demographics, survival, and physiological stress responses.

SPACE USE, HABITAT USE, DIET, AND DEMOGRAPHY OF SAN JOAQUIN

KIT FOXES AND COYOTES

Introduction

San Joaquin kit foxes are small, endangered foxes endemic to arid portions of central California. In addition to narrow endemism, competition from predators, specifically from coyotes, is one potential threat to the survival of San Joaquin kit fox populations (Cypher and Spencer 1998; Cypher et al. 2000; Ralls and White 1995; U.S. Fish and Wildlife Service 1998). Coyotes exhibit both interference and exploitative competition with kit foxes through direct mortalities and overlapping prey use. However, kit foxes may mitigate competition through dietary partitioning and diurnal den use (Cypher and Spencer 1998; Ralls and White 1995). Competition with coyotes affects kit fox survival though the degree to which coyotes may influence kit fox space use and habitat selection is unknown.

Coyotes are the primary predator of kit foxes, as well as swift foxes (*Vulpes velox*) (Kamler et al. 2003; Kitchen et al. 1999; Olson and Lindzey 2002), red foxes (*Vulpes vulpes*) (Gosselink et al. 2003; Sargent et al. 1987), and grey foxes (*Urocyon cinereoargenteus*) (Wooding 1984). Predators, mostly coyotes, were responsible for 75% - 78% of San Joaquin kit fox mortalities on the Carrizo Plain, Lokern Natural Area, and the Naval Petroleum Reserve (Cypher and Spencer 1998; Disney and Spiegel 1992; Ralls and White 1995). Swift foxes are

phylogenetically and ecologically similar to kit foxes, and in studies of swift foxes throughout the western United States, coyote predation has reportedly ranged from 27% - 89 % of swift fox mortalities (Kamler et al. 2003; Kitchen et al. 2000; Olson and Lindzey 2002; Sovada et al. 1998).

In an attempt to decrease coyote-caused kit fox mortalities, a coyote control program was implemented on the Naval Petroleum Reserve between 1985 and 1988. The control program negatively affected coyote numbers, but kit foxes also declined during this period. Both fox and coyote densities were positively correlated with lagomorph densities, suggesting that kit foxes are affected more by prey abundance than predator abundance (Cypher and Scrivner 1992). White and Garrott (1997) determined that predation on juvenile kit foxes by coyotes is probably density dependent and that interference competition by coyotes may regulate fox populations.

On the other hand, coyote removal proved successful in restoring depressed swift fox populations in northwestern Texas (Kamler et al. 2003). Also, Sargent (1987) reported that red foxes in North Dakota that resided among low densities of coyotes were not regularly harassed. In short, it appears that coyotes can have at least locally strong effects on the demography and dynamics of smaller canids, including kit foxes, but the extent to which coyotes regulate or contribute to the decline of San Joaquin kit foxes is not fully resolved.

Kit foxes have evolved adaptive strategies to co-exist with coyotes (Cypher et al. 2001; Egoscue 1962; White et al. 1994). Two of these strategies

are food partitioning and year round den use (Cypher and Spencer 1998; Cypher et al. 2000). Dens are thought to aid foxes in escaping predators (Egoscue 1962; Kitchen et al. 1999; Morrell 1972; White et al. 1994), which could explain the high spatial overlap between kit foxes and coyotes found in previous studies. By using dens as refuges, foxes can perhaps use areas from which they would otherwise be excluded by interference competition or intraguild predation. White and Ralls (1994) reported that all kit foxes had a greater than 30% home range overlap by coyotes, and as much as 100% overlap, on the Carrizo Plain. Similarly, swift foxes, which also use dens diurnally and year-round, have been found to overlap coyote home ranges by as much as 100% (Kitchen et al. 1999).

Another way inferior competitors may coexist with superior competitors is by colonizing habitats seldom used by the dominant competitor. Habitat partitioning decreases intraguild competition (Tilman 1987) and may be a strategy kit foxes employ to coexist with coyotes. Gosselink et al. (2003) found that rural red foxes avoided the cover-rich habitats that coyotes selected for, and also reported that red foxes selected for the human-disturbed areas that coyotes avoided. Similarly, red foxes appeared to exclude arctic foxes (*Alopex lagopus*) from lower elevation areas during the mating season in Sweden (Tannerfeldt and Angerbjorn 1998). Other species, such as wild dogs in the Selous (Creel and Creel 2002; Creel and Creel 1996) and cheetahs in the Serengeti (Durant 2000) showed use of "competition refuges" (Durant 1998) by utilizing areas where competitor densities were low. For wild dogs, avoidance of competitors

(particularly lions) carried a cost, because wild dogs and their competitors have substantial overlap in prey, and refuge habitats yielded lower rates of encounter with prey. This pattern suggests that habitat partitioning was driven by competition and not by the distribution of food. Jackals (*Canis adustus* and *Canis mesomelas*) in Zimbabwe (Loveridge and Macdonald 2003), red squirrels (*Picea abies*) and grey squirrels (*Sciurus carolinensis*) in Scotland (Bryce et al. 2002), and pumas (*Puma concolor*) and jaguars (*Panthera onca*) in Venezuela (Scognamillo et al. 2003) also exhibited habitat partitioning on fine-scale levels despite apparent overlap between the species.

Coyotes often associate with habitats that provide large amounts of vegetative cover because, unlike kit foxes, they do not commonly use dens for protective cover except when raising pups (Gese et al. 1988a; Gosselink et al. 2003). San Joaquin kit foxes occupy a variety of habitats, including grassland and shrubland habitats, as well as grazed grasslands, oil fields, and urban areas (Morrell 1972; O'Farrell 1980; White et al. 1995). Kit foxes may minimize their use of shrub areas by selecting for habitats less frequented by coyotes. Coyotes may be spatially excluding kit foxes, forcing them into substandard habitat, as in the case of red foxes and coyotes (Gosselink et al. 2003; Harrison et al. 1989). Although some studies have looked at habitat use by kit foxes and coyotes (White et al. 1995), implications for competitive interactions and spatial overlap in these habitats have not been addressed. Further knowledge on the spatial relationship between kit foxes and coyotes in varying landscapes, explicitly

related to the distributions of their primary foods, is necessary to better manage lands for kit fox conservation.

The primary purpose of this study was to explore how to manage lands appropriately to allow for the co-existence of San Joaquin kit foxes and coyotes. This study specifically addressed differences in kit fox and coyote demography in intact habitats versus habitats altered by fire. I hypothesized that kit foxes were displaced from the best foraging habitats by coyotes. Specifically, I predicted that 1) coyotes select for shrubs and unburned habitats, 2) kit foxes select for grasslands and burned habitats where coyotes are less prevalent, 3) kit foxes spatially avoid coyotes, 4) kit foxes and coyotes partition diet, and 5) coyote predation is the primary source of kit fox mortality. I tested these predictions by first determining the habitat selection of both kit foxes and coyotes, then assessing interference and exploitative competition between kit foxes and coyotes in the varying habitats.

<div align="center">Methods</div>

Study Area

I conducted my research on 100 km^2 of the Lokern Natural Area, in western Kern County, approximately 60 km west of Bakersfield, CA. Lokern is part of one of the designated core areas of recovery for San Joaquin kit foxes (U.S. Fish and Wildlife Service 1998). Vegetation at Lokern was classified as Valley Grassland (Heady 1977) and consisted of non-native grasses and forbs

with a community of arid shrublands, primarily desert saltbush (*Atriplex polycarpa*). Other shrubs included spiny saltbush (*A. spinifera*), cheesebush (*Hymenocle salsola*), and bladderpod (*Isomeris aborea*). Annual grasses and forbs were dominated by red brome (*Bromus madritensis rubens*) and red-stemmed filaree (*Erodium cicutarium*) (Cypher et al. 2000). Lokern soils were poorly drained alkali soils (Heady 1977) and were predominantly sandy loams and clay loams (U.S. Department of Agriculture Undated*a;* U.S. Department of Agriculture Undated*b*).

The southern portion of the study site consisted of rolling hills contiguous with the Naval Petroleum Reserve, while the northern portion was generally flat with a gentle downward slope toward the north. A concrete waterway, the California Aqueduct, bordered the eastern edge of the study area while deep drainages were scattered throughout the area. Lokern had a Mediterranean climate with hot, dry summers and cool, wet winters. The annual mean maximum and minimum temperatures in summer were 36° C and 18° C, respectively, while annual mean maximum and minimum temperatures in winter were 16° C and 2° C, respectively (U.S. National Oceanic and Atmospheric Administration 2002). Annual precipitation for the area ranged from 5.0 cm - 15.0 cm, and occurred mostly as rainfall from October through April (U.S. National Oceanic and Atmospheric Administration 1996; U.S. National Oceanic and Atmospheric Administration 2002)

The Lokern study area encompassed land owned by numerous entities with different land management strategies, which created a mosaic of land attributes. Three major 2-lane highways traversed the study area. Since 1997, a cattle-grazing study was conducted on 5 sections of land in the center of the study area, although cattle were not present during this study. Sheep grazed parts of the study site seasonally, usually in the spring. Two hazardous waste clean-up facilities were located at the north and west ends of the study area. In 1998 a major wild fire swept through much of Lokern destroying shrublands. Controlled burns on other sections of the study area followed the wildfires. Both the controlled burns and attempts to stop wildfires by building road breaks created abrupt and distinct boundaries between shrubland and grassland habitats. The local pattern of ecological succession is burn, grassland, shrubland. Grassland habitats in Lokern are the result of repeated burns and the subsequent failure of shrub re-establishment. The only major difference between grasslands and burned areas was the fact that the grasslands had more time to recover from burns, and contained scattered shrubs and thicker herbaceous layers. Shrublands were mostly unburned habitats, although there were small patches of land that were previously burned and began to re-colonize with shrubs (Figure 1). Grasslands and burned habitats were highly correlated, as were shrublands and unburned habitats. For that reason, I analyzed habitat data according to shrubland versus grassland and burned versus unburned, although

the results of burned and grassland, and shrubland and unburned, were often very similar.

Determining Home Ranges and Habitat Use

This study was conducted in parallel with an existing kit fox study that was conducted from August 2001 to June 2004. Therefore, data on kit foxes relating to survival came from 2001-2004, but all the demographic and dietary data relating to kit fox and coyote competition, as well as prey abundances, were collected from January 2003 – June 2004. I trapped, ear-tagged, and radio collared 62 kit foxes from August 2001 – June 2004. I trapped kit foxes using wire mesh box traps covered with a tarp, and baited overnight with meat. I handled all foxes in cloth bags without chemical immobilization.

I captured 10 coyotes via helicopter net gunning in January 2003 (for methods see Gese et al. 1987). The helicopter flew transects over the entire study area and attempted to capture all coyotes. One group at the southwest end of the study area escaped capture; however I captured at least one individual in all other known groups. I radio collared coyotes and kit foxes with Advanced Telemetry Systems transmitters and ear-tagged, sexed, aged (adult or juvenile), weighed, and physically examined all animals. I collected tissue samples from foxes, blood samples from coyotes, and hair and scat samples from both species.

From January 2003 - June 2004, I monitored the movements of 49 kit foxes and 7 coyotes. I tracked animals nocturnally with vehicle mounted null

telemetry systems consisting of dual H-antennas. Telemetry error, determined by reference transmitters, averaged +/-3.0°. Two observers in separate vehicles at known locations took simultaneous bearings to each animal. Locations with inter-bearing angles outside 20º - 160º were discarded. I tracked each animal a minimum of two nights per week, recording only one point per animal per night. Direct observations of animals replaced telemetry locations for those animals for that night.

I produced home ranges using the Home Range Extension (HRE) for ArcView (Rodgers and Carr 2002). I analyzed all data over a one year period (Jun. 16, 2003- Jun. 15, 2004) as well as seasonally. I divided the year into two seasons of equal length, pupping and mating, based on kit fox reproductive behavior. The pupping season (Jan. 16- Jun. 15) included the periods of pregnancy and caring for pups while the mating season (Jun. 16 – Jan. 15) included the periods of dispersal and mating. I used a minimum of 25 locations for kit fox home range analyses based on area observation curves (Odum and Kuenzler 1955) and a minimum of 29 locations for coyote home ranges. I produced fixed kernel ranges using least-squares cross-validation (LSCV) and x-variance smoothing parameters. Hereafter, I call 95% kernels 'home ranges', and 50% kernels (the area of most intense use) 'core areas'.

To test for habitat selection, I employed logistic regression, corrected for over-dispersion, to predict species (fox or coyote) from proportion of habitat in an animal's home range. I used the Wilcoxon Matched Pairs Test to test for

differences in proportion of habitat in core areas versus home ranges for both species. To determine effect of habitat on home range size, I used simple linear regression with home range size regressed on proportion of habitat in an animals' home range. To assess spatial avoidance, I compared the actual overlap of foxes and coyotes to the overlap from 100 simulations of randomly generated home ranges. I created the random home ranges by buffering random points with the average radius of home ranges for foxes and coyotes. I averaged the overlap of the random ranges and compared this to the actual overlap by using a test of proportions. To look at spatial avoidance in specific habitats, I generated random points across the study area (repeated over 100 simulations) to determine the probability of overlap of foxes and coyotes in varying habitats, as if the animals were using the study site at random. I then compared the average of the randomly generated points to the actual overlap of foxes and coyotes in these habitats.

In addition to the night-time fixes described above, I monitored kit foxes diurnally a minimum of once per week by tracking foxes to their dens or day resting locations. I assessed diurnal habitat selection of foxes by using log-odds ratios and χ^2 tests comparing fox dens, weighted by number of times used, to random locations within a fox's home range. To test whether habitat affected natal den placement, I computed differences in natal den distance from shrub habitat versus non-natal dens using analysis of covariance (ANCOVA) with fixed (den type) and random (fox ID) variables.

I also monitored coyote diurnal locations bi-weekly by calculating locations from biangulations or triangulations by a single observer using a 3-element hand-held antenna. Coyote day locations served to verify that day ranges did not differ from nocturnal ranges. The error for hand-held antennas averaged +/- 8.1º. I computed all statistics in STATISTICA, except for χ^2 analyses that were greater than 2 x 2 contingency tables, which I computed by hand in MS Excel, then entered into STATISTICA to obtain p-values. All statistics were considered significant if $P < 0.05$. All data are reported as means ± 1 SE unless otherwise stated.

Measures of Prey Abundance

I conducted surveys for relative abundance of nocturnal rodents and lagomorphs in the varying habitats four times during the study. I trapped nocturnal rodents using Sherman live-traps, baited with seed at sunset. I checked all traps a minimum of two hours after sunset, with the starting transects rotated each night to avoid a time bias. Each trapping session included four transects, consisting of 25 traps each, placed in shrub and grass habitats over four consecutive nights. I analyzed rodent data as number of individuals per 100 trap nights using a three-way analysis of variance (MANOVA) to look at differences in abundance of rodent species, habitat, and season.

I used scent stations to measure lagomorph abundance between shrub and grass habitats. Stations were approximately 1 m^2 in size and placed a minimum distance of 0.5 km apart, based on the approximate home range radius

of black-tailed jackrabbits (*Lepus californicus*) (Dunn et al. 1982; Smith 1990). All scent stations were cleared of vegetation and debris, covered with fine soil, and baited with a carrot oil scented plaster disc and a small handful of alfalfa pellets, based on a pre-study trial of effective scent lures. I tested for differences in lagomorph presence among habitats using χ^2 tests.

Diet Determinations

To determine dietary preferences of and dietary partitioning between kit foxes and coyotes, I analyzed scats for prey contents. Potential prey species for kit foxes and coyotes at the Lokern Natural Area included three species of kangaroo rats (giant kangaroo rats [*Dipodomys ingens*], short-nosed kangaroo rats [*D. nitratoides*], and Heermann's kangaroo rats [*D. heermanni*]), San Joaquin antelope squirrels (*Ammospermophilus nelsoni*), San Joaquin pocket mice (*Perognathus inornatus*), deer mice (*Peromyscus maniculatus*), Southern grasshopper mice (*Onychmys torridus*), desert cottontails (*Sylvilagus audubonii*), black-tailed jackrabbits, Jerusalem crickets (Gryllacridae [*Stenopelmatus cahuilaensis*]), and grasshoppers (Acrididae) (Cypher et al. 2000).

I collected 396 coyote scats and 472 kit fox scats at traps, scent stations, dens, along road transects, and opportunistically. I did not collect scats that were clearly desiccated or bleached to ensure collection of fresh scats. I stored scats in paper bags, then baked them for 24 hours to kill parasites, and finally washed and dried them in nylon stockings in a household washing machine and dryer. I identified prey items to the lowest taxonomic scale possible and recorded

presence or absence of each prey species in all scats. For analysis, I divided

prey into eight categories, namely kangaroo rat, other rodent, rabbit, insect, fruit,

sheep, bird, and other. I measured dietary diversity using the Shannon-Weiner

index (Krebs 1989), dietary overlap of foxes and coyotes using Horn's index

(Horn 1966), and preference for kangaroo rats by foxes using Manly's alpha

(Manly 1974) and probability of capture. I used χ^2 analyses to determine

differences in diet between species, habitat, and season, and computed all

indices in MS Excel.

<u>Survival</u>

I performed necropsies on all animals found dead to determine cause of

death. I used logistic regression to identify factors affecting fox survival and

considered the following *a priori* potential predictors: categorical predictors

included sex, age, year, and season; the continuous predictor was the proportion

of the fox's range that was shrubland (preferred coyote habitat, see results).

Only foxes with night location data were included in the survival analysis, which

limited the survival model to the years 2002-2004. In the model I weighted each

fox seasonally by a function of the number of locations for that animal. This gave

more weight to foxes with a lot of data and less to foxes that died or disappeared

early in the season. I used a traditional hypothesis-testing framework to consider

the effects of each predictor on fox survival, but confirmed the generality of these

results in a model-selection framework using AICc. However, due to data

limitations (i.e. the data set of foxes with proportion shrub in their home ranges

varied by season and year, some combinations of covariates resulted in a

survival of 1, and AICc will not compare more than 2 categorical covariates at

once), I could not run AICc on the full set of predictors. Thus, to check the

results of the all subsets logistic regression in AICc, I used 4 model sets that

included proportion shrub plus 2 covariates that could interact (results in Table

4). Logistic regression produced mean probabilities of survival for foxes from

2002-2004 under the various classes defined by the predictors. To determine if

proportion of shrub habitat in kit fox home ranges posed a predation risk, I used a

χ^2 analysis to compare the amount of shrub habitat in the ranges of foxes that

survived with the amount of shrub habitat in the ranges of foxes killed by

predators.

Results

Home Range and Habitat Use

I obtained 2,231 night locations for kit foxes and 648 night locations for

coyotes between Jan 16, 2003 - June 15, 2004. Kit fox annual home ranges

averaged 5.91 km^2 ± 0.44 (n = 32), while coyote annual home ranges averaged

6.89 km^2 ± 0.49 (n = 6). Coyote annual home range sizes decreased with

increasing shrub habitat within ranges (R^2 = 0.812, $F_{1,4}$ = 17, P = 0.014);

however, their home range sizes did not differ seasonally ($F_{2,14}$ = 2.724, P =

0.100). I did not analyze the effect of sex on coyote range size due to an

insufficient sample size. Annual fox home range sizes did not vary by sex (t =

0.854, df = 30, P = 0.400) or habitat (R^2 = 0.106, $F_{1,30}$ = 3.354, P = 0.070), nor did they vary seasonally by habitat ($F_{2,46}$ = 0.939, P= 0.398).

Coyotes used significantly more shrub habitat than foxes over all seasons in both their core areas (Table 1: Wald stat. = 18.246, df = 1, P <0.001) and home ranges (Table 1: Wald stat. = 16.540, df =1, P < 0.001). This pattern was consistent through time, as the amount of shrub used by each species did not vary by season (Table 1: 95 Kernel: Wald stat. = 0.325, P = 0.908, Core: Wald stat. = 0.661, df =1, P = 0.416). Foxes used significantly more burned habitat (with little cover) than coyotes over all seasons in both their core areas (Table 1: Wald stat. = 12.196, df =1, P < 0.001) and home ranges (Table 1: Wald stat. = 14.495, df =1, P < 0.001). Foxes used significantly less burned habitat in the pupping season than in the mating season, both in their core areas (Table 1: Wald stat. = 5.879, df =1, P =0.015) and home ranges (Table 1: Wald stat. = 6.769, df =1, P = 0.009). This may be the result of increased foraging in the shrub habitat where prey abundances were higher (see results on prey abundances by habitat) during the pup-rearing season.

Table 1. Mean ± SE Proportion of Shrub and Burn Habitat in Home Ranges and Core Areas of Kit Foxes and Coyotes at the Lokern Natural Area in California During 2001-2004.

Season	Home Range Area	Mean Proportion Burned Habitat in Home Range		Mean Proportion Shrub Habitat in Home Range	
		Coyote	Kit Fox	Coyotes	Kit Foxes
Annual	Core Area	0.00 ± 0.000	0.714 ± 0.061	0.716 ± 0.128	0.184 ± 0.057
	Home Range	0.051 ± 0.035	0.676 ± 0.058	0.607 ± 0.104	0.222 ± 0.054
Pupping*	Core Area	0.008 ± 0.008	0.568 ± 0.067	0.710 ± 0.078	0.268 ± 0.059
	Home Range	0.041 ± 0.019	0.540 ± 0.062	0.685 ± 0.072	0.294 ± 0.055
Mating*	Core Area	0.010 ± 0.010	0.810 ± 0.066	0.720 ± 0.134	0.161 ± 0.075
	Home Range	0.054 ± 0.036	0.765 ± 0.060	0.948 ± 0.119	0.194 ± 0.066

* Pupping and mating season ranges are subsets of annual ranges. Pupping season included the periods of pregnancy and caring for pups (Jan. 16 – Jun. 15). Mating season included the periods of dispersal and mating (Jun. 16 – Jan. 15).

Comparisons of core areas to broader home ranges can reveal habitat preferences because core areas generally reflect areas where an animal spends more of its time. Foxes had significantly more burned habitat (T_{32} = 46.000, P = 0.005) and significantly less shrub habitat (T_{32} = 55.000, P = 0.004) in their core areas than home ranges (Table 1). Coyotes, on the other hand, had significantly more shrub habitat in their core areas than home ranges (Table 1: T_6 = 0.000, P = 0.006). None of the collared coyotes had any burned habitat in their core areas. Foxes used burned habitats 14 times more, and shrub habitats 3 times less, than coyotes (Figure 1).
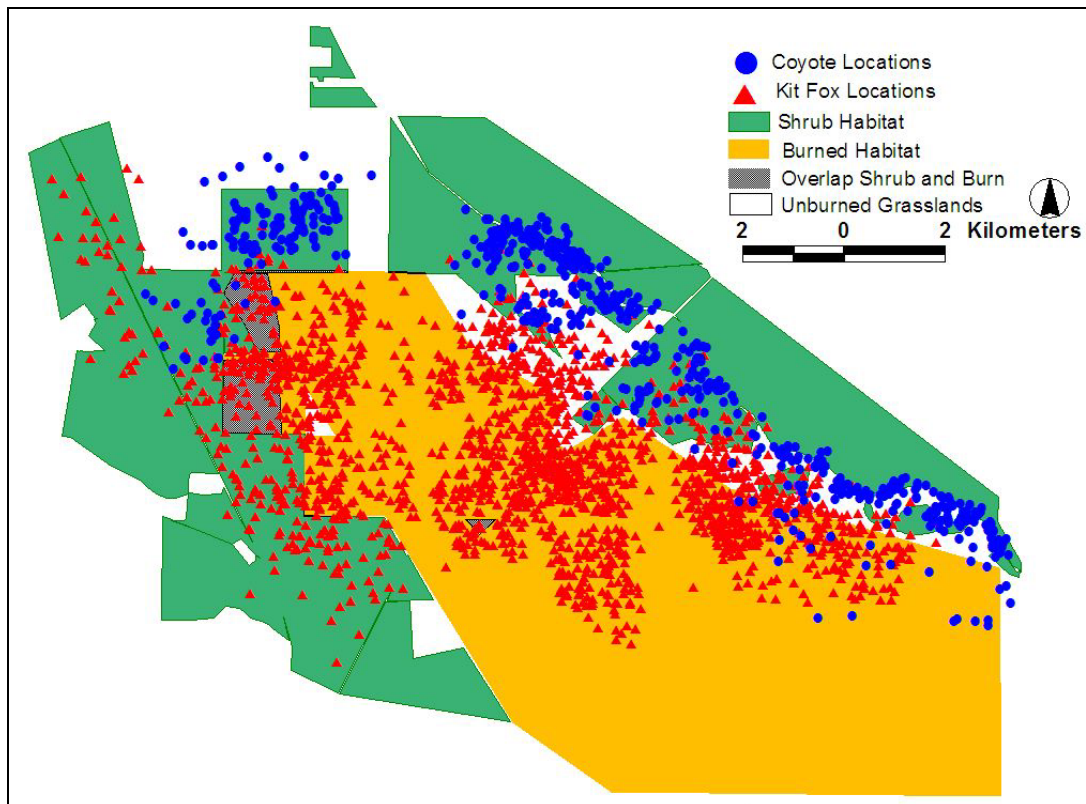
Figure 1. Kit fox (red triangles) and coyote (blue circles) locations, showing spatial partitioning and differences in use of burned habitats (orange) and shrub habitats (green) at the Lokern Natural Area, California, during 2001-2004.

Kit fox and coyote home ranges overlapped significantly less than expected if the two species were using the landscape at random (n = 32, P = 0.031). The probability of kit fox and coyote overlap in the shrublands did not differ from the overlap expected at random. However the probability of kit fox and coyote overlap in the burned areas was 6 times less than expected at random (Figure 2). Annually, 50% (n = 32) of collared kit foxes had home ranges that overlapped with collared coyotes. Those foxes overlapped with coyote home ranges on average by only 20.1% of the foxes' home ranges. Additionally, 34% (n = 32) of foxes had core areas that overlapped with coyotes' home ranges. The average overlap of fox core areas with coyote home ranges was 24.5% of the foxes' core areas. Only 2 foxes had core areas that overlapped with coyote core areas and the overlap was only by 4.0% of those foxes' core areas.

Diurnally, kit foxes used dens in shrub habitats significantly less (χ^2 = 176.70, df = 1, P < 0.001) and dens in burned habitats significantly more (χ^2 = 158.77, df = 1, P < 0.001) than expected over both seasons (Figure 3). There were also significantly fewer dens in shrub habitats (χ^2 = 49.48, df = 1, P < 0.001) and significantly more dens in burned habitats (χ^2 = 65.13, df = 1, P < 0.001) than placement of dens at random. Though not significant, foxes used dens located in their nocturnal core areas more than expected, suggesting a possible preference for dens in core areas. Diurnal ranges of coyotes did not differ from nocturnal ranges. Kit foxes that had pups showed no detectable preference for

or against grassland or shrubland when picking natal dens within their ranges (χ^2 = 1.02, df = 1, P = 0.313). However, foxes did use burned habitats more than expected for natal den sites (χ^2 = 6.45, df = 1, P = 0.011). Fox natal dens generally did not fall within coyote home ranges. Over both years, only one fox natal den fell within one collared coyote home range, and then only by 30 meters. The majority of fox natal dens fell within the core areas of female foxes, however 15.8% (n = 16) of natal dens were located outside female core areas. Coyotes did not tend to use burned habitats and kit fox core areas did not overlap with areas of intensive use by coyotes, so kit fox placement of natal dens allowed them avoid coyotes.
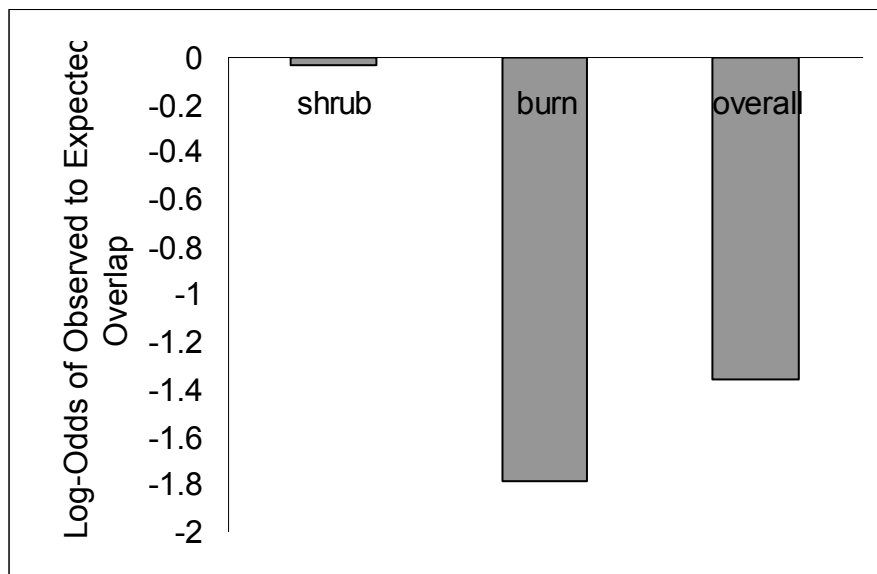
Figure 2. Log-odds ratios (ln) comparing actual kit fox and coyote home range overlap to the overlap expected at random at the Lokern Natural Area in California, from 2001-2004. Log-odds ratios compare observed to expected values. Thus, when the observed value equals the expected value, the log-odds value is 0. A positive value indicates selection for a habitat while a negative value indicates avoidance.
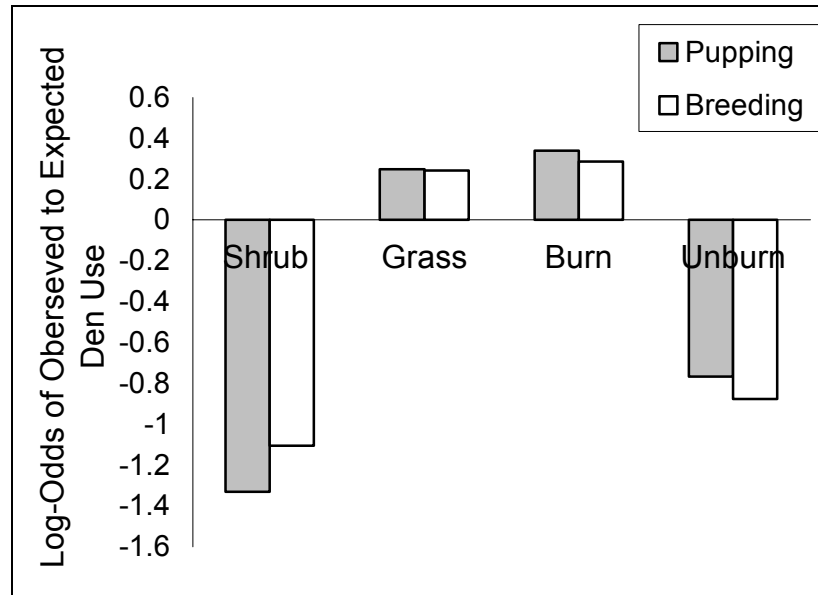
Figure 3. Log-odds ratio comparing kit fox den use by habitat to den use expected at random at the Lokern Natural Area in California during 2001-2004. Log-odds ratios compare observed to expected values. Thus, when the observed value equals the expected value, the log-odds value is 0. A positive value indicates selection for a habitat while a negative value indicates avoidance.

Prey Abundance by Habitat

Some rodent species were more abundant than others both across the entire study site ($F_{5,12}$ = 19.089, P < 0.001) and within habitat types ($F_{5,12}$ = 6.301, P = 0.004). Overall rodent abundance did not vary by season ($F_{1,12}$ = 1.187, P = 0.297). Short-nosed kangaroo rats (DINI) were more abundant in the grass habitats where Heermann's kangaroo rats (DIHE) were rarely trapped, while DIHE were more abundant than DINI in shrub habitats (Figure 4). DIHE were 45% larger (70.6g ± 11.8, n = 223) than DINI (39.2g ± 7.8, n = 728), and thus provided a larger energy package for coyotes and kit foxes. There was an

overall greater abundance of nocturnal rodents in the shrublands and scent

station surveys indicated that leporids were more abundant in the shrublands

(proportion of rabbit presence: 0.552, n = 105) than in the grasslands (proportion

of rabbit presence: 0.394, n = 170) (χ^2 = 6.56, df = 1, P = 0.010). Collectively,

these data indicate that shrublands held a higher biomass of prey than

grassland, for both coyotes and foxes (see below for data on diets).
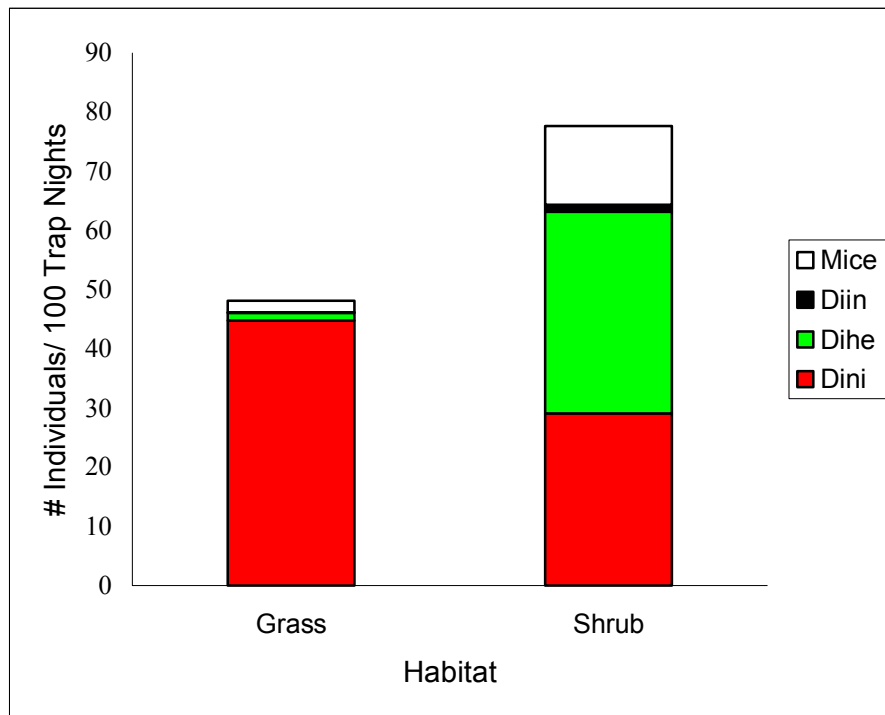
Figure 4. Relative abundance of nocturnal rodents (# individuals/100 trap nights) in grass and shrub habitats at the Lokern Natural Area in California during 2001-2004.

Diet

Coyotes and kit foxes differed significantly in their diets (Figure 5: χ^2 = 513.179, df = 7, P < 0.001). Coyotes had approximately twice the diversity in

their diets than kit foxes (Table 2). Prey items identified in both kit fox and

coyotes scats were DINI, DIHE, giant kangaroo rats, San Joaquin pocket mice,

California pocket mice (*Chaetodipus californicus*), harvest mice

(*Reithrodontomys* spp), grasshopper mice, deer mice, pocket gophers

(*Thomomys bottae*), black rats (*Rattus rattus*), leporids (including both desert

cottontails and black-tailed jack rabbits), insects (primarily Orthoptera, including

grasshoppers and Jerusalem crickets), vegetation (primarily almonds and seeds

from berries), lizards, snakes, birds, fish, domestic sheep (*Ovis aries*), and

garbage.
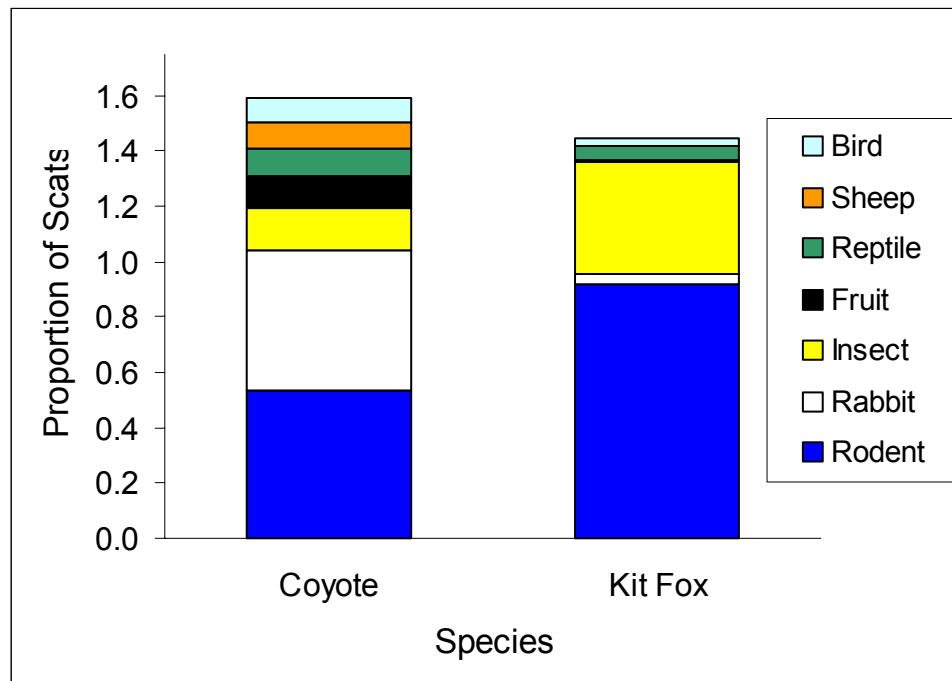
Figure 5. Coyote and kit fox diets, based on proportion of scats containing each prey item, at the Lokern Natural Area in California during 2001-2004.

Table 2. Indices of Diversity (Shannon Weiner) and Overlap (Horn's) in Coyote and Kit Fox Diets at the Lokern Natural Area in California During 2003-2004.

Season	Shannon Weiner Index of Diversity		Horn's Index of Similarity
	Coyote	Kit Fox	
Pupping[†]	2.242	1.350	0.773
Mating[‡]	2.374	1.386	0.725
Overall	2.374	1.386	0.759
Habitat			
Grass	2.322	1.417	0.813
Shrub	2.384	1.279	0.698

[†] Pupping season included the periods of pregnancy and caring for pups (Jan. 16 – Jun. 15)

[‡] Mating season included the periods of dispersal and mating (Jun. 16 – Jan. 15)

Dietary overlap did not vary by season, though scats from foxes and coyotes recovered in the grass habitats had slightly more dietary overlap than scats found in the shrublands (although short-term movement between habitats weakens this comparison). Coyote diets varied both by habitat (Figure 6: χ^2 = 14.793, df = 7, P = 0.039) and season (Figure 6: χ^2 = 36.605, df = 7, P < 0.001). Coyotes tended to have home ranges dominated by shrub or grass habitats, making it possible to detect differences in diet by habitat. Coyote scats from shrub habitats consisted of more rabbits than scats from grasslands; rodents and sheep were more prevalent in coyote scats during the pupping season, and fruit

was more prevalent during the mating season. Kit fox diets did not differ by habitat (x^2 = 10.674, df = 7, P = 0.153) or season (x^2 = 6.751, df = 7, P = 0.455). However, based on rodent abundances, kit foxes showed strong preference for DIHE, and some avoidance of DINI, in grassland habitats (Table 3). Coyote scats contained significantly more DIHE than kit foxes' scats (x^2 = 30.633, df = 1, P < 0.001).

Table 3. Proportions of Short-nosed Kangaroo Rats (*Dipodomys nitritoides*) and Heermann's Kangaroo Rats (*D. heermanni*) Captured in Grass and Shrub Habitats and Observed in Kit Fox Diets.

	Relative Abundance	Proportion in Diet	Manly's Alpha (1/m = 0.5)[†]
D. nitritoides			
Grass	*0.972*	*0.729*	*0.073*[‡]
Shrub	0.460	0.651	0.687
D. heermanni			
Grass	*0.028*	*0.271*	*0.923*[‡]
Shrub	0.540	0.349	0.313

[†] Manly's alpha values equal 1/m (m is the number of prey species) if there is no preferential selection of prey. In this case values above 0.5 indicate selection for and values below 0.5 indicate selection against a prey species.
[‡] Italicized numbers represent strong preference for or against a prey species.
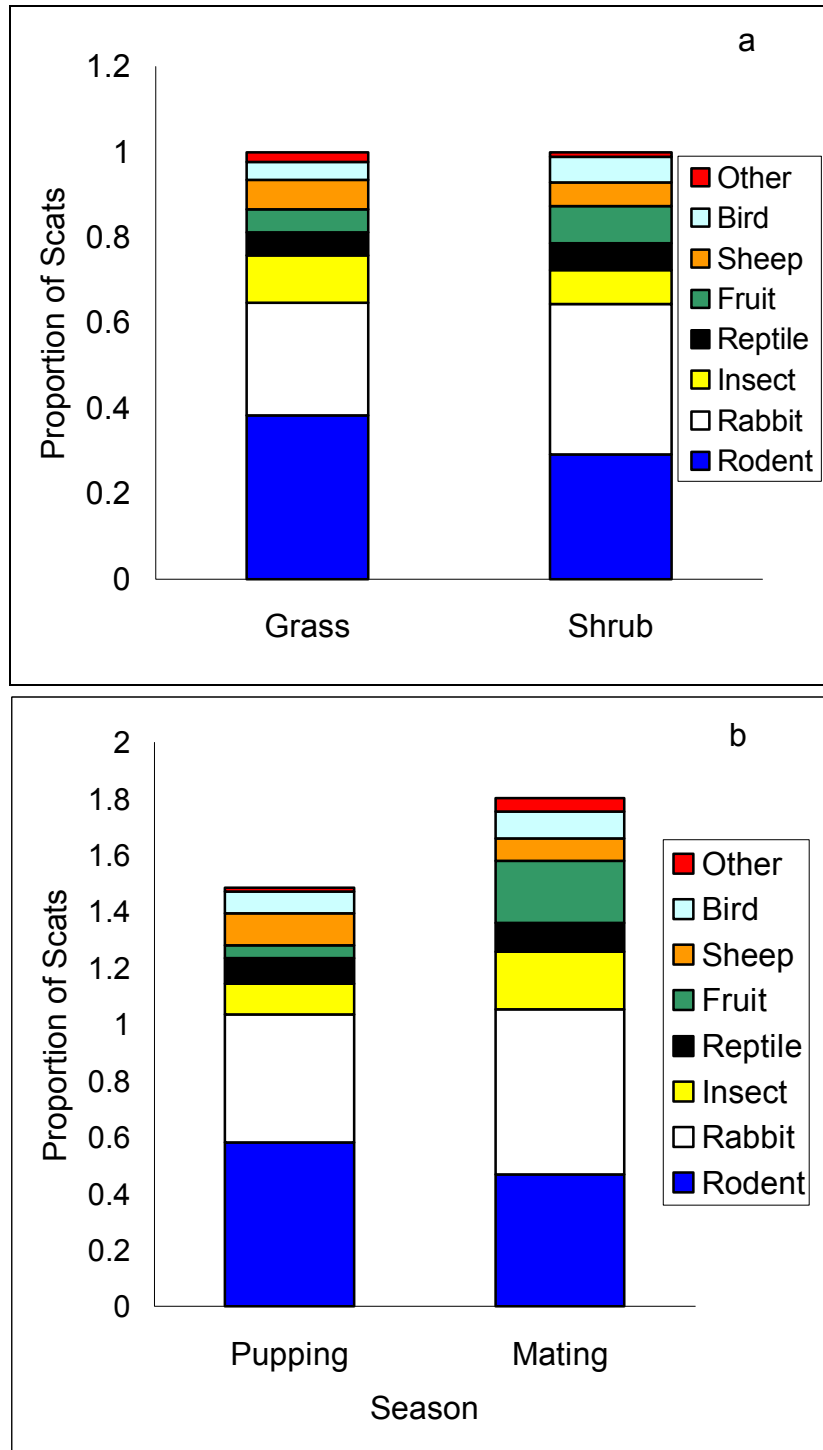
Figure 6. Coyote diets as indicated by proportion of prey items in scats collected in grass and shrub habitats (a) and during pupping and mating seasons (b) at the Lokern Natural Area during 2003-2004.

Survival

From 2001 – 2004 I located 25 freshly dead kit foxes, resulting in an overall survival of 0.40 (n = 25/62). However, this estimate was uninformative as to what drove kit fox survival. Therefore, I modeled kit fox survival using 3 covariates to better understand the factors influencing fox survival (see below). Known predation accounted for 48% (12/25) of total kit fox mortalities, though probable predation and known predation combined constituted 76% (19/25) of total kit fox mortalities. Probable predation included foxes that were found buried, scavenged, or with signs of predation at the carcass, though a cause of death could not be conclusively determined. I was unable to determine any cause of death for 20% (5/25) of kit fox mortalities, and only one fox was killed by a vehicle collision. Only two collared coyotes died during the study: one from a vehicle collision and the other from a gunshot, so no systematic analysis was possible for coyotes.

The final model for kit fox survival included proportion of shrub habitat in a fox's home range, sex, and season as predictors. Given the close association of coyotes with shrub habitats, I was primarily interested in how proportion of shrub habitat in a fox's home range predicted fox survival. However, I also included age, sex, year, and season as covariates in potential models because I thought each may influence fox survival. I allowed all subsets of the full set of predictors to compete, which resulted in proportion shrub and season as the only significant predictors, while sex, age, and year were insignificant predictors. I checked

these results using AICc on four subsets of models (see methods). Proportion

shrub was a top predictor in the best model for all sets of models. Sex and

season were top predictors with proportion shrub for all sets they could be run in,

while year and age were equivocal and not as strong at predicting survival (Table

4). Furthermore, the regression coefficient for proportion shrub (the primary

variable of interest) remained fairly constant regardless of the covariates in the

model, indicating that proportion shrub is a good predictor of fox survival (Figure

7).   Thus I concluded a model including proportion shrub, sex, and season was

the best model for predicting fox survival.
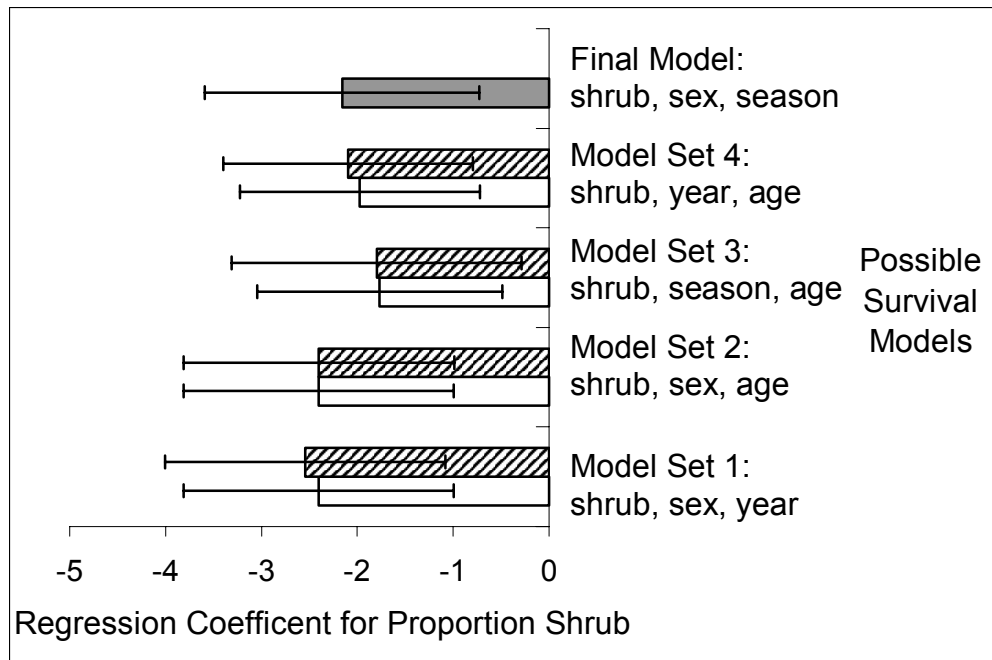
Figure 7. Estimated regression coefficients (with 95% confidence interval whiskers) for regression of survival of proportion shrub habitat in a kit fox's home range using logistic regression models of Table 4 at the Lokern Natural Area in California during 2002-2004. Empty bars represent the best model for each set of predictors according to AIC_c, striped bars represent the second best model for each set of predictors according to AIC_c, and the solid bar is the final model used for kit fox survival estimates.

From 2002-2004, females had higher overall mean survival rates (0.945 ± 0.024) than males (0.780 ± 0.046) (Figure 8 and Table 5: Wald Stat = 12.183, df = 1, P < 0.001) and overall mean survival rates were lower in the mating season (0.809 ± 0.041) than in the pupping season (0.937 ± 0.028) (Figure 9 and Table 5: Wald Stat = 5.322, df = 1, P = 0.021). An increasing proportion of shrub in a fox's home range was associated with poorer survival (Figures 10 and 11 and Table 5: Wald Stat = 8.721, df = 1, P = 0.003).

I found 55% (n = 11/20) of the kit foxes that died from predation or from likely predation torn apart or missing body parts, and 30% (n = 6/20) were buried with coyote sign at the burial site. I also observed coyotes carrying killed prey. Together, these observations make it likely that coyotes sometimes carried fox carcasses to their recovery locations. I did not analyze locations of mortalities (as others have done), because the location of a carcass does not necessarily reveal the location of death. As an alternative method to determine if shrub habitats increased predation risk for kit foxes, I analyzed the amount of shrub habitat in the home ranges of foxes killed by predators and compared this to shrub habitat in surviving foxes' home ranges. Kit foxes that were killed by predators had significantly more shrub habitat in their home ranges than kit foxes that survived (prop. shrub of survivors: 0.210, n = 758; prop. shrub of mortalities: 0.402, n = 338; χ^2 = 44.08, df = 1, P < 0.001).

Table 4. Possible Survival Models: Four Model Sets, as Selected by AIC_c in addition to the Final Survival Model.

Model Set	Predictors in Model Set	AIC_c 1st and 2nd Best Models	ΔAIC	Model Weight[b]
1	proportion shrub, sex, year	1. shrub[a], sex[a]	0	0.736
		2. shrub[a], sex[a], sex*year	2.047	0.264
2	proportion shrub, sex, age	1. shrub[a], sex[a]	0	0.718
		2. shrub[a], sex[a], sex*age	1.871	0.282
3	proportion shrub, age, season	1. shrub[a], season[a]	0	0.689
		2. shrub[a], season, shrub*season	1.589	0.311
4	proportion shrub, age, year	1. shrub[a]	0	0.667
		2. shrub[a], age	1.392	0.333
Final model		proportion shrub[a], sex[a], season[a]		

[a] Significant predictors at $P < 0.05$
[b] Considering only the 1st and second best models in each model set
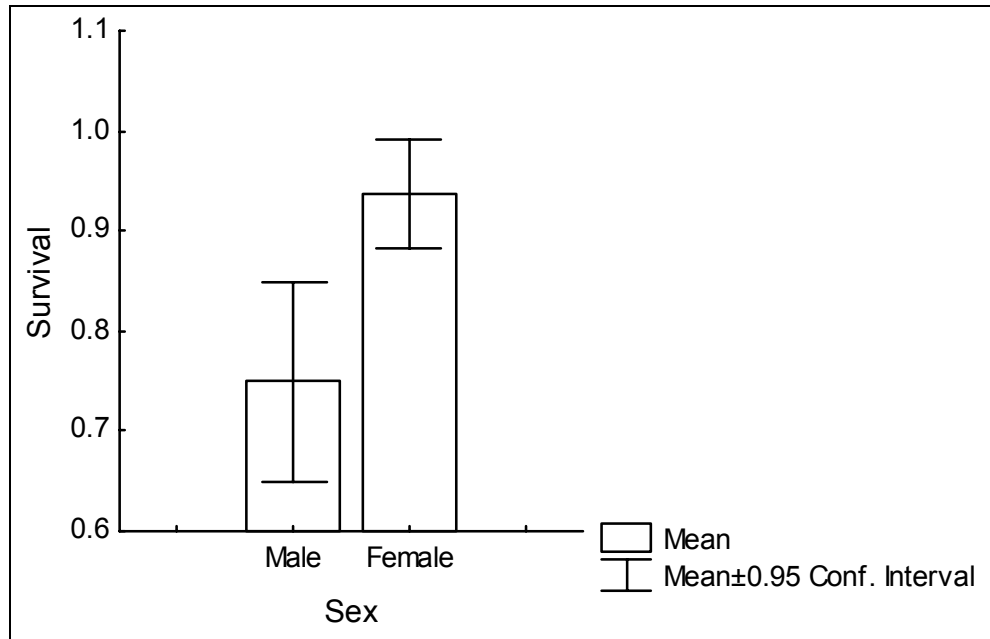
Figure 8. Survival estimates of male and female San Joaquin kit foxes with 95% confidence interval whiskers at the Lokern Natural Areas during 2002-2004.
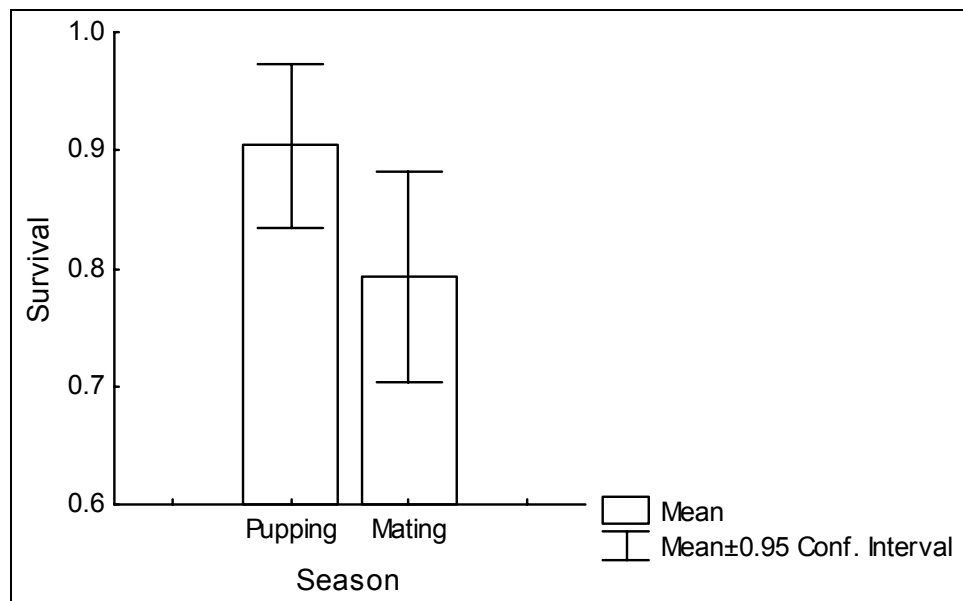
Figure 9. Survival estimates of San Joaquin kit foxes at the Lokern Natural Area, California during the pupping and mating seasons of 2002-2004 with 95% confidence interval whiskers.

Table 5. Regression Coefficients of Parameters in the Final Kit Fox Survival Model.

Predictor	Effect	Regression Coefficients	95% Confidence Interval for Coefficient
Proportion Shrub	n/a	-2.158	(-3.591, -0.726)
Sex	Male	-0.988	(-1.542, -0.433)
Season	Pupping	0.626	(0.094, 1.158)
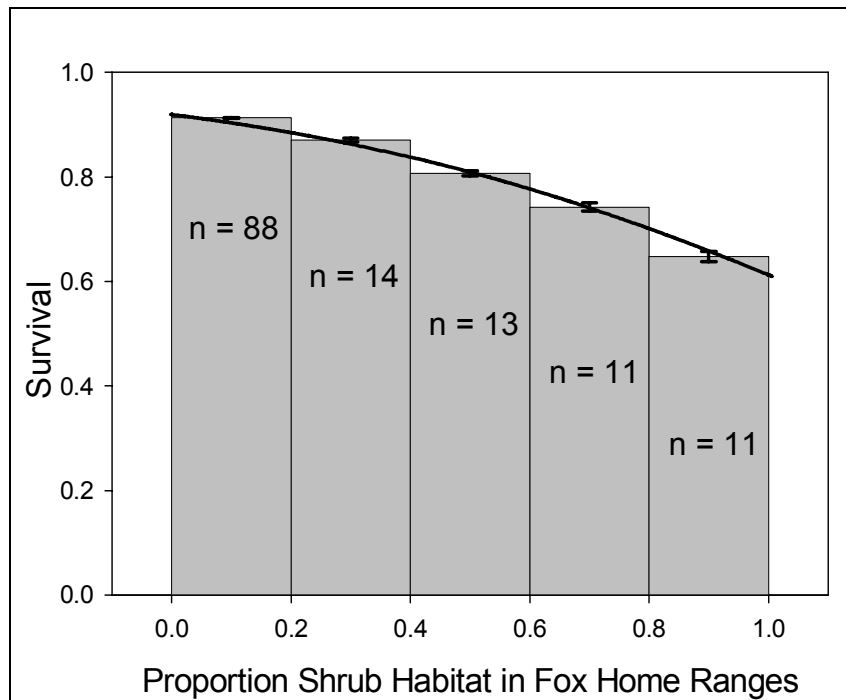
Figure 10. Simple logistic regression of proportion of shrub on probability of fox survival at the Lokern Natural Area in California during 2002-2004. The line represents the simple logistic regression model. Bars show the raw data as mean (± SE bars) for classes of proportion shrub habitat in fox home ranges.
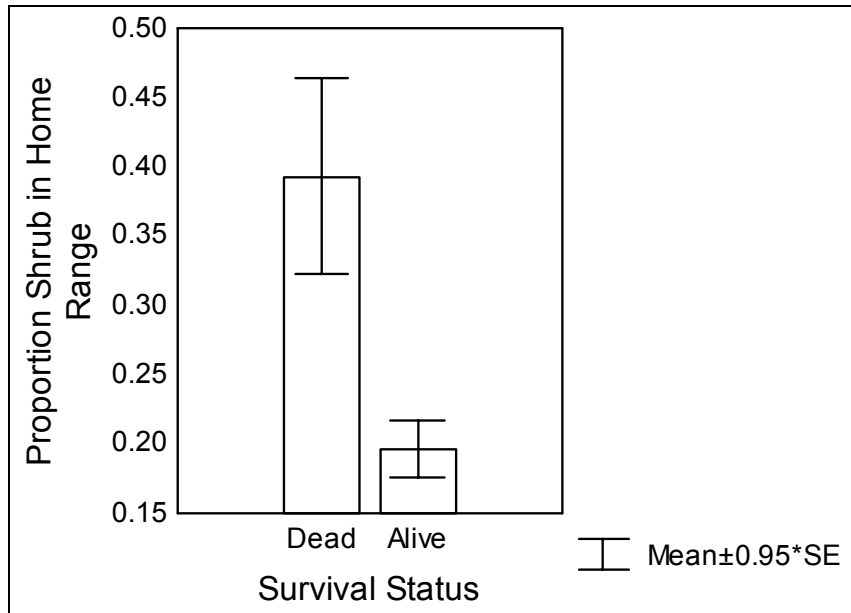
Figure 11. Mean ± SE proportion of shrub habitat in for San Joaquin kit foxes that survived or did not survive the year at the Lokern Natural Area in California during 2002-2004.

Discussion

The results from this study indicate that San Joaquin kit foxes are likely niche displaced by coyotes from shrublands into grassland habitats, affecting kit fox space use and diet. These results are consistent with conventional competition theory, demonstrating that competing species utilize resources differently to minimize conflict (Gause 1934). Kit foxes exhibited habitat and spatial partitioning with coyotes by using burned habitats more intensively and shrub habitats less intensively than coyotes. The details of these patterns suggest that foxes are displaced by coyotes and not vice versa. Though foxes continued to spatially overlap coyotes in some instances, the cost of overlap was an increased probability of death.

The shrub habitats in Lokern had a greater abundance and diversity of prey than the grass habitats. Therefore in the absence of competitors, and assuming habitat does not influence hunting abilities of foxes, foxes should be expected to use shrub habitats more than grass habitats. Contrary to this prediction, kit foxes had less shrub habitat in their core areas than home ranges.

Foxes decreased their chances of encountering coyotes by using burned areas because the probability of kit fox and coyote overlap in burned areas was far less than expected at random. Similar behavior was observed with red foxes that used habitats occupied by predators less than other habitats (Fedriana et al. 1999; Gosselink et al. 2003). Wild dogs also showed preference for habitats with a lower abundance of prey but also lower lion densities (Creel and Creel 2002). Kit foxes capitalized on the safer burned habitats by placing their natal dens within these habitats. This allowed foxes to decrease chances of pup overlap with coyotes. This strategy has also been seen in arctic foxes who placed dens at higher elevations to avoid red foxes (Linnell et al. 1999).

I expected coyote and kit fox use of burned areas to be similar to their use of grassland areas because of the correlation between grasslands and burned habitats (Figure 1). However, coyotes avoided burned habitats more strongly than grassland habitats. This avoidance may be attributed to increased human activity, increased conspicuousness, and lower prey abundances. Their preference for shrub habitats was consistent with other studies that found coyotes prefer cover-rich environments (Gese et al. 1988a; Gosselink et al. 2003;

Quinn 1997). The shrublands contained not only greater abundances of prey,

but also more cover that provided some protection from human hunters.

Many carnivores, including coyotes, decrease their territory size in

response to increasing resource richness (Gese et al. 1988a; Macdonald 1983).

Coyote home range sizes in Lokern increased as the proportion of grasslands

within ranges increased. This was likely due to the lower abundance of prey,

specifically rodents and rabbits, in grass habitats.

Coyote home range sizes in Lokern were small compared to other studies

(Kitchen et al. 1999; White et al. 1994), although Gese (1988a) reported home

ranges as small as 5.5 km^2 in habitats with more vegetative cover. On average,

coyote home range sizes were only 1 km^2 larger than kit foxes' home range

sizes, and ranges of coyote packs were non-contiguous and non-overlapping.

This may explain why I found little overlap between kit foxes and coyotes, while

other studies reported high spatial overlap (White et al. 1994); where coyote

ranges are small with discrete gaps between packs, it may be easier for kit foxes

to avoid them with movements on the scale that foxes typically make. Both

species' core areas only overlapped in a few point locations, further suggesting

spatial avoidance. Other studies that reported as much as 100% spatial overlap

of swift and kit foxes with coyotes also reported that coyote home ranges were

approximately 3 times larger than the coyote ranges in Lokern (Kitchen et al.

1999; White et al. 1994). Where coyotes range widely and occupy the landscape

more fully, fox avoidance of coyotes, in the sense of simple home range overlap,

is more highly constrained. However, such high spatial overlap could also be mediated by temporal avoidance.

Previous studies did not report spatial avoidance between coyotes and kit foxes nor between coyotes and swift foxes (Kitchen et al. 1999; White et al. 1994), though spatial avoidance of coyotes by red foxes has been reported on several occasions (Gosselink et al. 2003; Harrison et al. 1989; Kitchen et al. 1999; Sargent et al. 1987). Previous explanations on how kit foxes and coyotes co-existed have centered on dietary partitioning and den use (Cypher et al. 2001; Egoscue 1962; White et al. 1994). Though both are clearly two methods foxes employ to co-exist with coyotes, Lokern has a heterogeneous landscape that allowed for further resource partitioning in the form of habitat partitioning. Historically most of the central valley was alkali shrub, but habitat degradation has transformed most of the remaining natural lands (Kelly et al. 2005). White et al. (1995) reported that coyotes on the Carrizo Plain tended to prefer shrub areas to grasslands, while kit foxes mostly preferred grasslands. However, coyotes and kit foxes on the Carrizo Plain did not exhibit spatial partitioning to the extent I observed in Lokern. This may be due to the large home ranges of coyote packs observed on the Carrizo Plain, constraining complete spatial avoidance of coyote by foxes.

Complete data on avoidance patterns requires that all individuals of both species be monitored, but not all coyotes in Lokern were captured during this study, and data from some grassland coyotes was likely absent from this

analysis. However, there were clear-cut trends in coyotes' habitat preferences for shrublands and avoidance of burned areas. Coyotes that occupied grass habitats in Lokern did so along the California aqueduct where there was more vegetative structure and higher abundances of prey.

Animals must balance access to resources with exposure to competitors and predators (Stephens and Krebs 1986). Shrublands in Lokern provided cover and high abundances of prey, but also maintained higher densities of coyotes. Continued use of shrub habitats by kit foxes was surprising given the predation risk associated with the shrubs. However, kit foxes showed a preference for the larger kangaroo rat, DIHE, which was closely tied to shrub habitats. Their sustained use of the shrub habitats was likely due to their preference for DIHE over DINI and the energetic benefits of foraging for a larger prey species. If the effort of finding and catching a kangaroo rat does not depend heavily on its size, then the larger DIHE should be an energetically more profitable prey item. Kit fox use of grass habitats, and avoidance of shrub habitats, may carry energetic costs of limited access to their preferred prey, DIHE. In other words, kit foxes occupying grasslands may be at an energetic disadvantage if the primary prey item in grasslands is a smaller energetic package than that which foxes using both grass and shrub habitats prey upon.

Another possible reason that foxes used shrublands despite the increased predation risk of these habitats was that shrub habitats acted as a sink for dispersing foxes from the grasslands. However, there was no age difference in

foxes using shrub habitats versus grass habitats, suggesting that dispersing juveniles foxes were not the only foxes using the shrublands. Furthermore, capture rates of kit foxes did not differ between the habitats. Therefore, optimal foraging seems a more likely explanation and has been seen in countless other species including snowshoe hares (*Lepus americanus*), northern bottlenose whales (*Hyperodon ampullatus*), wild dogs, and white-throated sparrows (*Zonotrichia albicollis*) (Creel and Creel 2002; Morris 2005; Schneider 1984; Wimmer and Whitehead 2004).

The high diversity in coyote diets was consistent with other studies (Andelt et al. 1987; Cypher and Spenser 1994; Kitchen et al. 1999). Coyote diets often reflect variation in prey availability (Andelt et al. 1987; Gese et al. 1988b). Coyote diets varied with habitat and season, eating more rabbits in the shrublands, more fruits and nuts in the fall, and more sheep in the spring. Kit foxes were less opportunistic with fairly narrow diets, consisting almost entirely of rodents and insects. Previous studies reported that leporids were a primary prey item in kit fox diets (Cypher and Spencer 1998; Cypher et al. 2000; White et al. 1995), although I did not find this at Lokern. Kit foxes consumed almost no vegetation, maintaining a mostly carnivorous diet, and did not alter their diet by habitat or season. These results suggest that kit foxes may not be able to adapt to changes in prey communities as well as coyotes. Kit fox populations are closely tied to kangaroo rat abundance (Grinnell et al. 1937; Morrell 1972; White

and Garrott 1999) and in the past kit foxes have shown an inability to switch prey and adapt in years of prey declines (White et al. 1996).

Despite the differences in dietary breadth between kit foxes and coyotes, there was substantial overlap in their diets. High dietary overlap is not uncommon among sympatric canids (Cypher and Spencer 1998; Green and Flinders 1981; Kitchen et al. 2000; Neale and Sacks 2001). Dietary overlap between kit foxes and coyotes was similar to overlap seen on the Carrizo Plain (White et al. 1995) and between swift foxes and coyotes in Colorado (Kitchen et al. 1999). Overlap was higher in the grasslands than the shrublands, presumably because of the decreased diversity of prey in the grasslands.

Kit fox survival at Lokern was much higher than reported in previous studies, though raw survival numbers were comparable. Higher survival may have been due to inclusion of covariates in the survival model, or the result of high prey densities during the years of this study. Other studies reported droughts and declines in prey (Ralls and White 1995), which may have contributed to increased kit fox mortality. Predation was the primary source of kit fox mortality, accounting for 48% - 76% of mortalities. Other studies on San Joaquin kit foxes also reported similar percentages of deaths due to predation (Cypher and Spencer 1998; Disney and Spiegel 1992; White et al. 1994). Fox carcasses were rarely consumed and were often buried, suggesting that interference competition, and not simple predation to obtain food, is the driving force behind fox mortalities. Low densities of foxes could account for the higher

survival I observed in this study, though I was unable to test this hypothesis. White and Garrott (1999) suggested that predation on foxes by coyotes may decrease with lower fox densities as the chances for agonistic encounters would be less likely.

Prior studies on swift foxes analyzed the distance between swift fox carcasses and den locations to determine the importance of dens in predator avoidance (Kitchen et al. 1999). However, because coyotes often carry prey items the size of kit foxes for substantial distances, I did not assume the location of their carcass was the mortality location. On one occasion I witnessed a coyote pick up and carry a dead kit fox that had been in a prior location for at least 8 hours. For this reason I am hesitant to conclude that foxes were more susceptible to predation when far from familiar dens.

Foxes killed by predators had significantly more shrub habitat in their home ranges than surviving foxes, and kit fox survival decreased as the proportion of shrub habitat in a fox's home range increased. These results highlight the predation risk for kit foxes in shrub habitats (habitats which would otherwise provide good access to preferred prey).

Survival rates of female kit foxes were greater than male foxes, and survival was higher in the pupping season than the mating season. These results were likely due to male biased dispersal of kit foxes. Male foxes are often exploring potential mates in neighboring territories during the mating season, and might be more susceptible to predation. Age was not a predictor of fox survival

in the model. Although juvenile foxes had slightly lower survival than adults, the sample size of juvenile foxes may have been too low to detect any true differences. If juvenile survival is density dependent, then juvenile survival may also have been higher during this study than other studies due to lower fox densities. This might explain the lack of association between age and survival, as seen in other studies.

This study confirms other studies that identify coyotes as the primary predator of foxes. I also observed dietary overlap and dietary preferences of foxes and coyotes similar to other studies. However, I found more spatial partitioning between the two species than previous studies reported. The results of this study are also consistent with competition theory demonstrating that inferior competitors coexist with superior competitors by expanding their niche breadth, primarily using poorer quality habitats and partitioning limited resources. In this case, kit foxes use a greater variety of habitats than coyotes (shrub, grass, and burned), kit foxes primarily used grass habitats with lower abundances of prey, and kit foxes partitioned both habitat and prey possibly to ameliorate competition with coyotes. All of these results suggest that kit fox use of grasslands is likely the result of habitat displacement by coyotes.

Despite the fact that coyotes continue to be the primary predator of kit foxes, the two species appear to partition resources adequately to allow for co-existence. Although coyote control programs have been effective in some locations with swift foxes, the control programs were unsuccessful with kit foxes.

Coyotes are a perseverant species that will thrive in almost any environment and are expanding their range across North America. Habitat degradation within the central valley of California has made co-existence between coyotes and kit foxes difficult due to decreased habitat availability.

Managing for a heterogeneous landscape may provide predator refuges for San Joaquin kit foxes, and thus may be an effective management strategy. If given a homogenous landscape, coyotes will establish themselves anywhere. However, in a mosaic of habitat types, coyotes can occupy the cover-rich (and prey-rich) habitats, leaving the more open grasslands for use by San Joaquin kit foxes. Land managers should consider a maintaining a heterogeneous landscape to allow for the co-existence of both species.

RESPONSES OF ENDANGERED SAN JOAQUIN KIT FOXES TO HIGH

PREDATION RISK AND URBAN HABITATS AS INDICATED BY FECAL

GLUCOCORTICOID LEVELS

Introduction

Animals have evolved physiological stress responses to deal with social and environmental perturbations such as predation, con-specific agonistic interactions, environmental catastrophes, and food shortages (Wingfield et al. 1998). When an animal perceives a stressor, the hypothalamus signals the anterior pituitary to release andrenocorticotropic hormone (ACTH), which in turn signals the adrenal cortex to release steroid hormones, including glucocorticoids (GCs), to help the animal mediate the stressor (Sapolsky 2002; Wingfield and Sapolsky 2003). The release of GCs elicits a series of short-term physiological responses including immune and reproductive system suppression, increased blood glucose, and redirection of energy in order to facilitate behavioral responses such as the "fight-or-flight" response (Romero 2004; Sapolsky et al. 2000; Wingfield et al. 1998). If the stressor is resolved, GC levels quickly return to a base level through a negative feedback loop, directly controlled by the elevated GC levels themselves, and the GC-controlled mediating responses of the animal return to their previous state (Sapolsky et al. 2000; Wingfield et al. 1998). However, if animals have chronically elevated GC levels, resulting from prolonged exposure to stressors, this negative feedback loop may become

impaired (Sapolsky et al. 2000). The basal GC levels in animals experiencing chronic stress responses remain high and prevent animals from mounting acute stress responses (Romero 2004). Chronically elevated levels of GCs can have deleterious effects including reproductive and immune system suppression, ulcers, and impaired growth from muscular atrophy (Sapolsky 2002; Sapolsky et al. 2000). In some cases, the effects of chronically elevated GC levels could be fatal (Wingfield 2005; Wingfield et al. 1998) and thus, are of special concern in threatened or endangered species.

Chronically elevated GC levels can occur both at the individual level and at the population level. Individual dominant animals in cooperatively breeding species often have higher basal GC levels than subordinate animals, suggesting that dominance in individuals carries a physiological cost (Creel 2001; Creel 2005). Few studies reported cases of elevated levels of GCs in populations. Two examples of such cases include populations of elk (*Cervus elaphus*) and wolves (*Canis lupus*) that showed elevated GC levels in response to snowmobiles in Yellowstone National Park (Creel et al. 2002), and a population of snowshoe hares that showed elevated GC levels in response to predation by lynx in the Yukon, Canada (Boonstra et al. 1998).

McEwen and Wingfield (2003) defined chronically elevated GC levels as allostatic overload type 2. Allostasis refers to the physiological ability of animals to maintain stable physiological systems necessary for survival when confronted with both predictable and unpredictable perturbations. Though animals

experiencing chronically elevated GC levels (allostatic overload type 2) may suffer deleterious effects, animals can also sustain elevated GC levels if stored energy or increased food intake can maintain homeostasis of the animals' physiological systems (McEwen and Wingfield 2003).

When considering stress responses of animals, biologists must consider the predictability and perception of stressors to the population of interest (Levine 2000; Romero 2004). If a potential threat is controllable or predictable, it may not be perceived as a stressor and a stress response will not be mounted (Levine 2000). For example, Weiss (1968) demonstrated that the degree of control (control is predictable) rats possessed over a stressor determined the hormonal response of the rat. Other experiments with rats showed that an increase or decrease in GC levels depended on the perception of animals to their present condition compared to their previous condition (Levine and Coover 1976).

San Joaquin Kit Foxes

San Joaquin kit foxes (*Vulpes macrotis mutica*) are an endangered species inhabiting areas in the San Joaquin Valley in central California. Remaining San Joaquin kit foxes exist in subpopulations that are often isolated and variable in size (U.S. Fish and Wildlife Service 1998), though generally small. Kit foxes inhabit both rural and urban environments (U.S. Fish and Wildlife Service 1998). The largest populations of San Joaquin kit foxes are located within western Kern County, including the Lokern Natural Area and the city of Bakersfield (U.S. Fish and Wildlife Service 1998). Kit foxes inhabit both rural

and urban environments (U.S. Fish and Wildlife Service 1998). Primary sources of mortality for urban foxes and rural foxes are vehicle collisions and predation (mostly by coyotes), respectively (Bjurlin et al. 2005; Cypher and Spencer 1998; Disney and Spiegel 1992; Ralls and White 1995).

The movement of foxes into urban environments has lead to differences in sources of mortality, diet, mass, and habitat use of the animals. Urban kit foxes are larger than rural foxes (Cypher and Frost 1999; Cypher et al. 2000) and feed on a variety of food items from natural prey to human refuse (Cypher and Warrick 1993). Rural foxes, on the other hand, prey mostly upon rodents and insects (Cypher et al. 2000, Nelson 2005, Chapter 2). Urban foxes inhabit a variety of human altered environments including residential neighborhoods, parking lots, schools, and parks (Bjurlin et al. 2005).

Rural kit foxes reside in grassland or shrubland habitats. Coyotes, the primary predator of kit foxes, are closely associated with shrub habitats and as a result, predation of foxes is greater in the shrublands than the grasslands (Nelson 2005, Chapter 2). As a result of increased predation in shrublands, kit foxes with home ranges containing greater proportions of shrub have lower survival rates than foxes residing in grasslands (Nelson 2005, Chapter 2). Kit foxes also spatially avoid coyotes, suggesting they perceive the predation risk associated with coyotes. However, despite the increased predation risk associated with shrublands, kit foxes continue to enter these habitats, presumably to forage for their preferred prey species, Heermann's kangaroo rats

(*Dipodomys heermanni*), which are closely associated with shrub habitats. (Nelson 2005, Chapter 2).

Constant stressors, such as frequent encounters with predators and humans or constant human disturbances, may lead to "permanent perturbations" (see Wingfield et al. 1998) that could result in chronic stress responses in kit foxes. Chronic stress responses can have deleterious effects on survival and reproduction (Sapolsky et al. 2000; Wingfield et al. 1998). Both urban and rural kit foxes may be susceptible to chronic stress responses. Urban foxes may perceive continual stressors from constant human disturbance leading to chronic stress responses that could elevate GC levels in this population. Rural foxes may perceive constant stressors from food shortages or the increased presence of predators causing them to experience chronic stress responses in certain areas where food is limited and/or predators are abundant.

Rural kit foxes that enter shrublands may experience increased GC levels due to the perceived increased predation risk associated with the shrublands. However, the stress response elicited by entering shrub habitats would likely be an acute stress response that would subside once the animal leaves the situation (returns to the grasslands). Thus, this is a different potential stress response from urban foxes whose basal GC levels may be chronically elevated from perceived constant stressors (humans) in their environment. Unlike rural foxes, urban foxes can not leave the urban habitat and escape the stressors.

I examined levels of GCs in San Joaquin kit foxes to assess the potential threat posed to the species from differing stressors in rural and urban environments.   I specifically determined 1) if the niche shift to an urban environment resulted in chronically elevated levels of GCs in San Joaquin kit foxes and 2) within the rural environment, whether using shrub habitats produced an acute stress response in rural foxes. I hypothesized that foxes in urban environments would have higher basal GC levels than rural foxes, based on increased human disturbance, and that rural foxes in shrub habitats would have higher GC levels than foxes in the grass habitats due to increased predation risk in the shrublands.

Drawing Inferences About Populations from GC Results

Drawing reliable conclusions about the impact of stressors on population parameters using GCs as a measure of stress response can be difficult. External stressors can affect animals directly or indirectly. Direct effects may include predation or decreased mating and fecundity, whereas indirect effects can result from elevated GC levels that may have deleterious effects on animals, such as immune system suppression, which could lead to decreased survival (Figure 12).

A failure to elicit a GC response can occur for several reasons: the animals do not perceive the perturbation as a stressor in the narrow sense of triggering a hypothalamic-pituitary response, the animals have habituated to regular perturbations and no longer perceive the perturbations as stressors (Romero 2004; von der Ohe and Ser);heen 2002), or the animals still perceive

the stressor but are unable to mount stress responses . In these situations the physiological costs of elevated GCs are avoided through habituation (the stressor is no longer perceived as a stressor) or non-response (the stressor is still perceived as a stressor but the animal fails to elicit a GC response), though the inferences drawn about the effects of stressors on the populations of interest may be incorrect. For example, humans suffering from posttraumatic stress disorder (PTSD) have lower basal cortisol levels than humans without PTSD (Yehuda et al. 2000; Yehuda et al. 1996). Therefore it is possible that animals exposed to chronic stressors experience an impairment of the negative feedback loop that actually hinders the release of GCs in general. In this situation a biologist may conclude that the population with the higher GC levels is experiencing a chronic stress response, when in reality, the population with the lower GC levels perceives or perceived chronic stressors and can no longer mount an appropriate hormonal stress response, but still may incur the direct costs of the stressor.

Despite the difficulties associated with interpreting GC results, evaluation of GC levels in San Joaquin kit foxes can still be informative as to whether urban environments have resulted in higher basal GC levels of foxes over rural environments from which they evolved in. Interpretation of these results will depend on whether or not foxes can mount acute stress responses, demonstrating that their stress response system is not impaired. Within rural environments, analysis of fox GC levels can be informative as to whether or not

high predation risk habitats produce acute stress responses in kit foxes, which

could pose physiological threats if these responses occurred regularly.
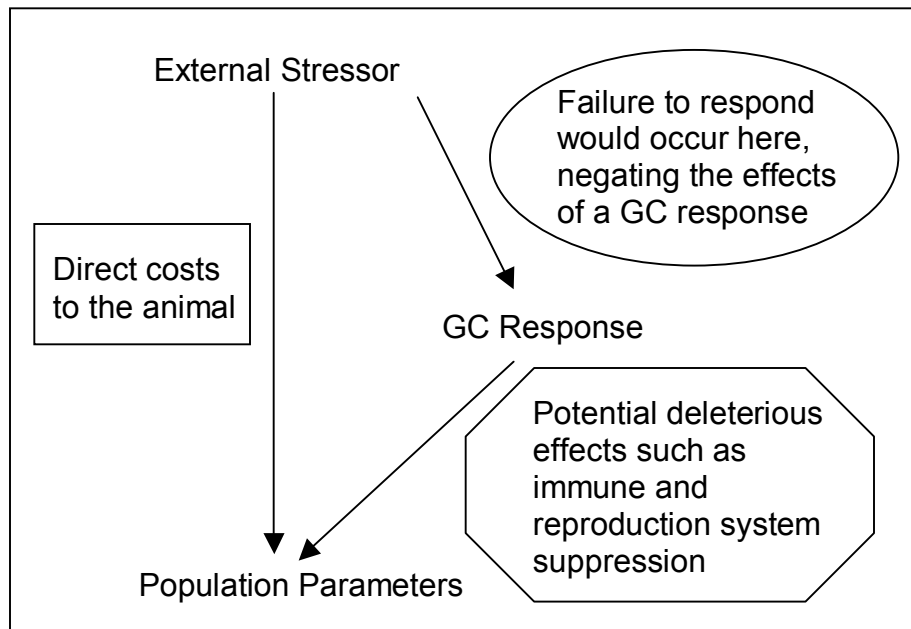
Figure 12. Diagram of the stress response process showing when direct and indirect effects of external stressors influence population parameters.

Methods

Study Sites

The study area comprised two study sites, rural and urban, in

southwestern Kern County in central California. Site 1 (rural) was located at the

Lokern Natural Area on approximately 100 km^2 of land approximately 60 km west

of Bakersfield, CA. Major land features consisted of undeveloped habitats of

distinct grassland (non-native grasses and forbs) and shrubland (primarily desert

Saltbrush [*Atriplex polycarpa*]), created from road breaks built to control wildfires. Other land features in the area included the California aqueduct, three 2-lane highways, and two hazardous waste clean-up facilities. Despite its proximity to highways and human facilities, Lokern remained fairly undisturbed with few people using the land.

Site 2 (urban) encompassed approximately 100 km^2 in the southwest portion of the city of Bakersfield, CA. In stark contrast to Lokern, Bakersfield was a developed urban environment with very few unaltered areas. Bakersfield had a population of around 280,000 people during this study and was one of the fastest growing cites in the United States. Land uses in the study area included residential neighborhoods, golf courses, California State University—Bakersfield campus, strip malls, and construction sites.

Both study sites have Mediterranean climates with hot, dry summers and cool, wet winters. Annual mean minimum and maximum temperatures were 2°C and 36°C, respectively. Annual precipitation ranged from 5.0 - 15.0 cm and mostly fell from October through April (U.S. National Oceanic and Atmospheric Administration 1996; U.S. National Oceanic and Atmospheric Administration 2002).

Fecal Collection and Hormone Extraction

From January 2003–June 2004, I collected 284 San Joaquin kit fox scats from small mammal traps, open fox traps, scent stations, and fox dens for measurement of glucocorticoid hormones by enzyme-linked immunosorbent

assays (ELISA). To ensure fecal collection and extraction within 24 hours of fox defecation, I only collected scats from sites I visited and cleared the previous day. I also collected fecal samples from trapped foxes in both Lokern and Bakersfield. The samples from trapped foxes served to verify that the procedure detected acute stress responses in San Joaquin kit foxes. I stored fecal samples in 5 ml screw cap tubes marked with date, time of collection, time of defecation (if known), and location (determined by GPS location). I placed samples in a cooler in the field during hot months, immediately stored them in a –20°F freezer upon returning from the field, and logged the time of freezing to record lag time between collection and freezing.

I extracted steroid hormones using published methods (Creel et al. 2002). I homogenized samples manually using metal spatulas, and then dried fecal samples in a rotary evaporator without heat, weighing all samples before and after drying to determine water content of the feces. I weighed approximately 0.180-0.220 g of dried feces (to 0.01 g), using an analytic balance (Mettler Toledo AB204), and boiled this known mass of feces in 10 ml of 95% ethanol for 20 minutes. After boiling I centrifuged the mixture, decanted off the supernatant with the extracted hormone, and recorded the mass of the saturated pellet after decanting (again using an analytic balance). I evaporated the ethanol and reconstituted the hormone in 5ml of ethanol by vortexing for 15 seconds and placing the sample in an ultrasonic glass cleaner for 15 seconds. I repeated the evaporation process and finally reconstituted the hormone in 1 ml of 100%

methanol, vortexed it for 1 minute, and placed it in an ultrasonic glass cleaner for 30 seconds. I then transferred each extract into 1ml cryovials and froze them at –20° F until analysis.

I measured cortisol concentrations by ELISA using cortisol kits from R and D Systems that I validated for San Joaquin kit fox fecal extract using standard tests for accuracy, specificity, and precision. I prepared all reagents and hormones according to the R and D instruction manual. Prior to immunoassay, I determined the dilution by plotting a series of 2-fold dilutions, ranging from undiluted extract to a 2048-fold dilution, on the curve produced by the standard cortisol concentrations (range 0 – 10 ng cortisol). I used the dilution that fell in the steepest part of the curve, producing the most accurate results. I diluted samples to a 9:1 ratio of assay buffer to cortisol for all assays. To determine the interassay coefficient of variation (CV) and as a quality control, I created a control sample consisting of equal amounts of 10 random samples. This control was included in all assays. Mean (± SE) recovery of cortisol added to the pooled control sample (range 0.312-5 ng), and averaged over two assays, was 90.75% ± 7.28 (ng measured = 0.85x ng cort. added – 0.117, R^2 = 0.994, P < 0.001). I excluded nine samples with CV values over 50% from analyses and quality control tests. The intra- and interassay CVs were 6.7% and was 13.4%, respectively. The slopes of the lines from the standard curve and the dilution series did not differ (Figure 13: $F_{1,13}$ = 1.423, P = 0.254), indicating that this assay was suitable for use with San Joaquin kit foxes.

I used analysis of variance (ANOVA) to test differences in GC concentrations due to habitat and season of rural foxes, and t-tests to assess GC differences between trapped versus non-trapped, and urban versus rural foxes. Excepting the trapped versus non-trapped tests, all tests included only non-trapped foxes. Kit fox seasons were based on kit fox reproductive behavior, and consisted of two periods of equal length: pupping and mating. The pupping season (Jan. 16- Jun. 15) included the periods of pregnancy and caring for pups while the mating season (Jun. 16 – Jan. 15) included the periods of dispersal and mating. All statistical tests were conducted with STATISTICA and all results are expressed as means ± 1 SE of ng cortisol/ g dry feces.
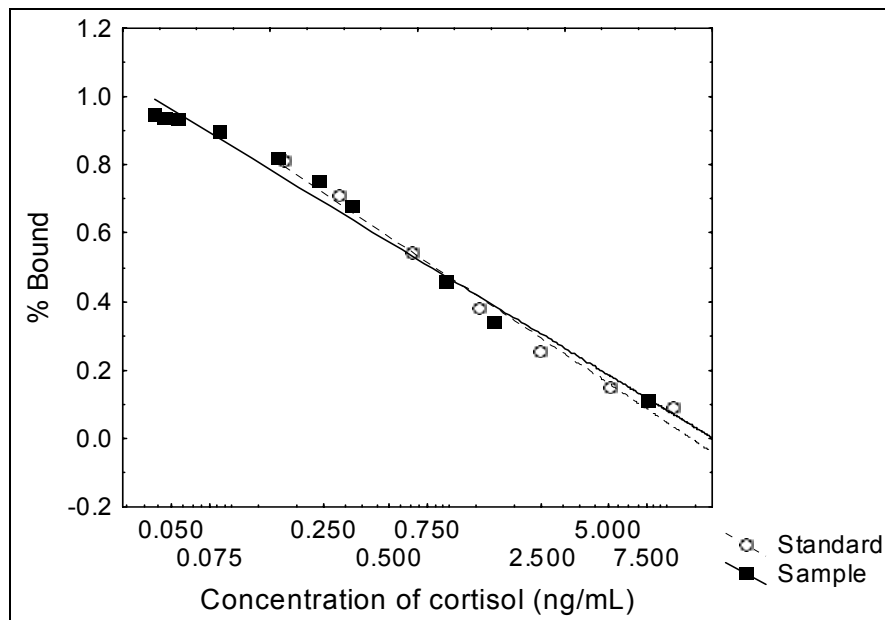

Figure 13. Parallelism between increasing concentrations of a pooled sample of extracted cortisol from San Joaquin kit foxes and standard cortisol concentrations. The regressions lines for standard cortisol and sample cortisol are %Bound$_{standard}$ = -0.43*log10(standard concentration) + 0.46 and %Bound$_{sample}$ = -0.39*log10(sample concentration) + 0.46, respectively.

Results

Trapped foxes had significantly higher mean GC levels than non-trapped foxes (Figure 14: t_{269} = -1.972, df = 268, P = 0.0496) at both the urban and rural sites. The mean GC levels of trapped foxes versus non-trapped foxes were 34.498 ± 26.897 and 4.780 ± 0.560, respectively. I detected no differences between trapped urban (6.043 ± 3.273) versus trapped rural (9.465 ± 1.802) foxes (Figure 15: t = -0.889, df = 57, P = 0.377), although mean GC levels of trapped rural foxes were higher. The difference in GC levels between trapped and non-trapped foxes shows the methods can detect acute, short-term stress responses in kit foxes.
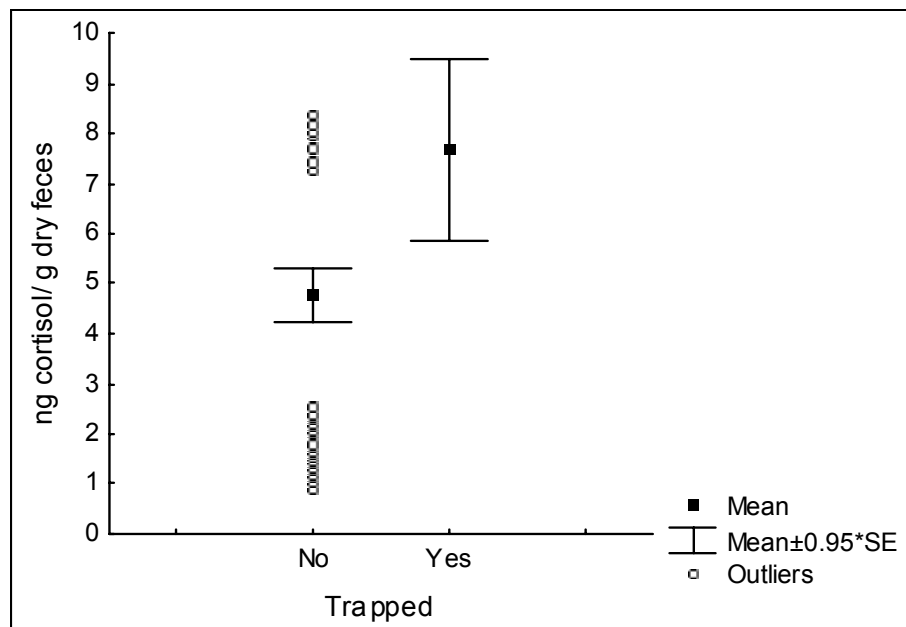
Figure 14. Mean ± SE of cortisol concentrations (ng cortisol / g dry feces) in non-trapped (a) and trapped (b) kit foxes at the Lokern Natural Area and Bakersfield, California during 2003-2004.

I detected no differences in GC levels between urban (5.291 ± 2.153) and rural (4.688 ± 0.540) foxes (Figure 15: t_{209} = -0.385, P = 0.701), or in GC levels of rural kit foxes occupying grassland (4.291 ± 0.754) versus shrubland (4.504 ± 1.641) habitats (Figure 17: $F_{1,175}$ = 0.014, P = 0.906). Furthermore, I detected no differences in seasonal fox GC levels (pupping: 3.756 ± 1.630, mating: 5.039 ± 0.776; $F_{1,175}$ = 0.504, P = 0.479).

Figure 15. Distribution of cortisol concentrations in trapped rural and urban kit foxes at the Lokern Natural Area and Bakersfield, California during 2003-2004. Bins contain 1ng and range from 0-50 with the last bin containing cortisol levels above 50 ng. Only one value from rural and urban locations each fell in the 50+ bin.

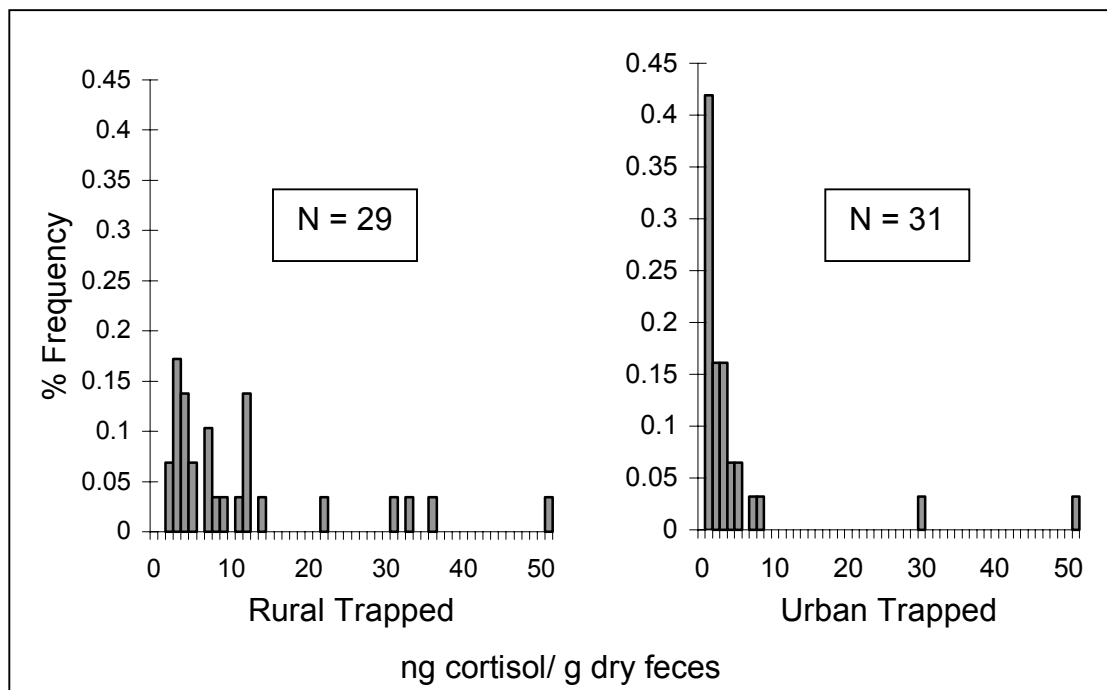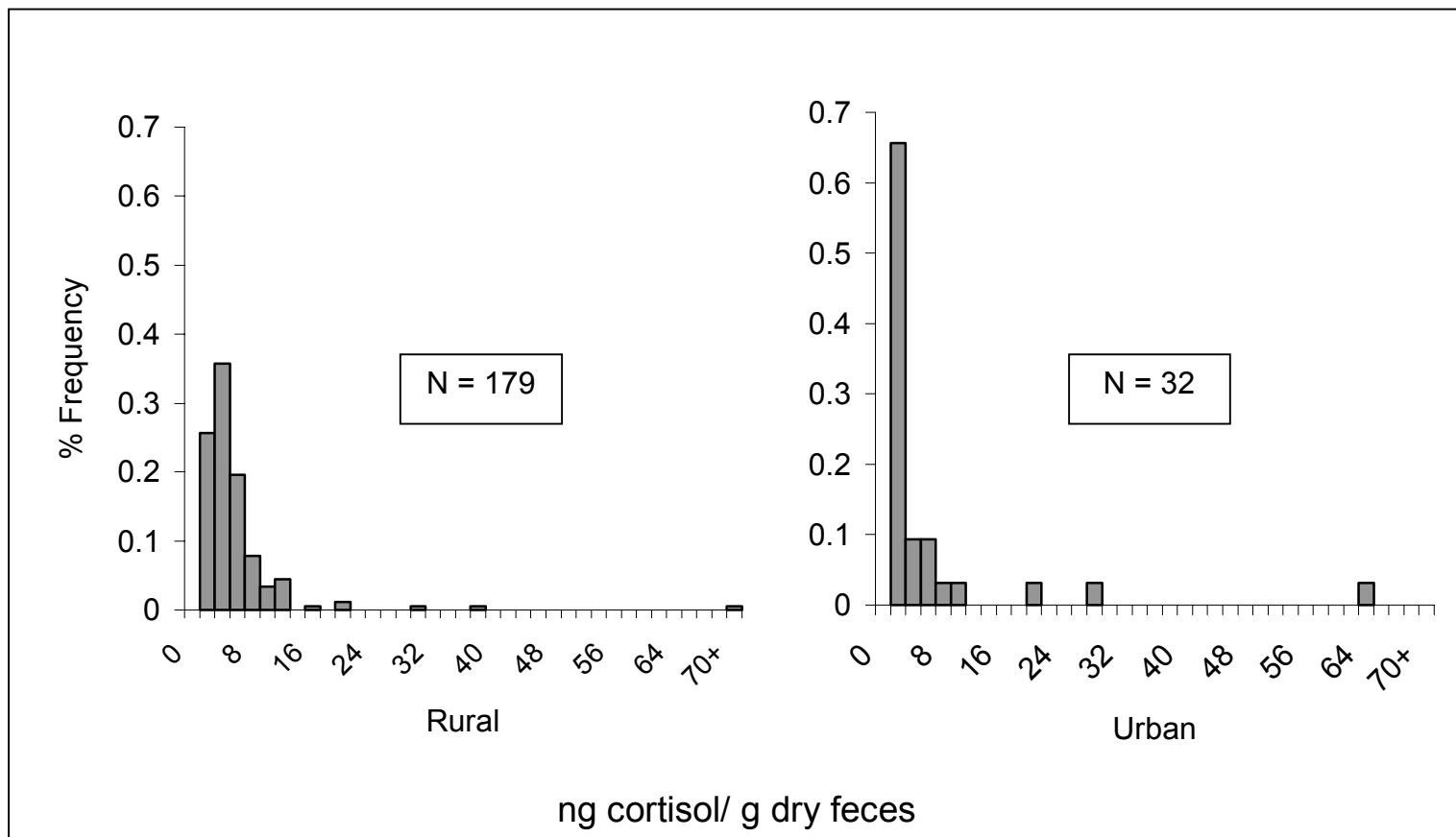Figure 16. Distribution of cortisol concentrations in rural and urban kit foxes at the Lokern Natural Area and Bakersfield, California during 2003-2004. Bins contain 2 ng and range from 0-70 with the last bin containing cortisol levels above 70 ng. Only one value from rural locations fell in the 70+ bin.
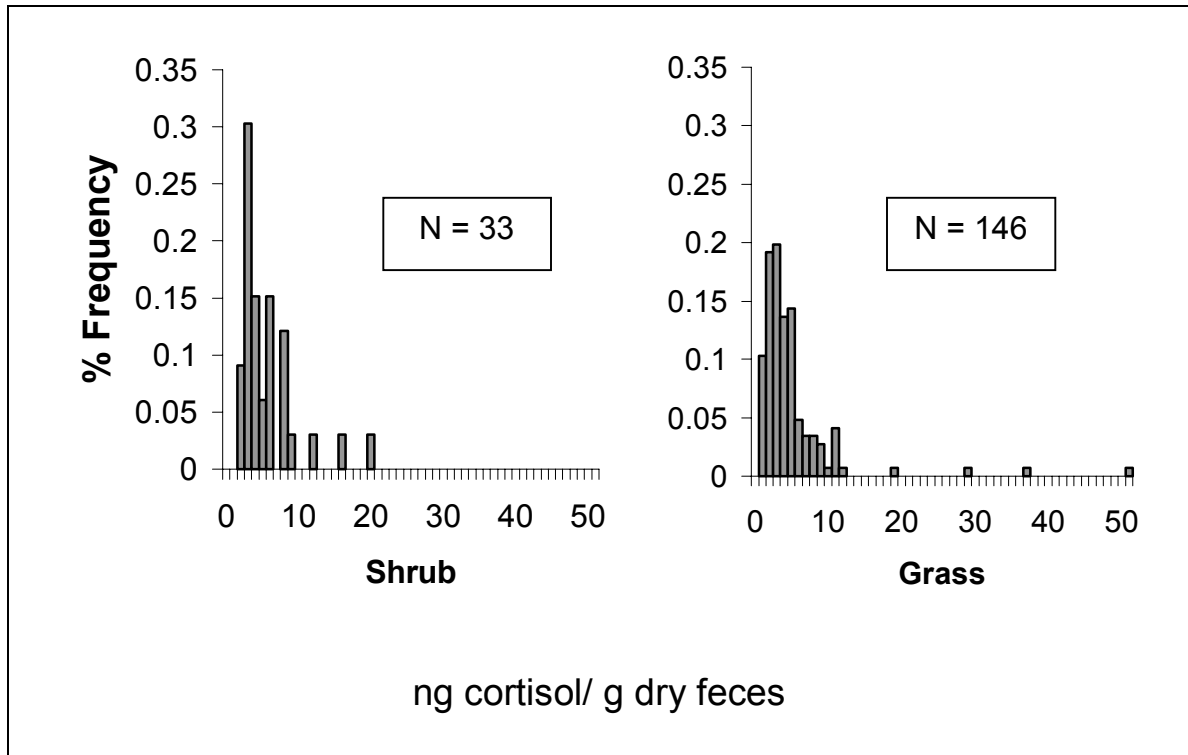
Figure 17. Distribution of cortisol concentrations in kit foxes using shrub habitats and grass habitats at the Lokern Natural Area in California during 2003-2004. Bins contain 1 ng and range from 0-50 with the last bin containing cortisol levels above 50 ng. Only one value from grass locations fell in the 50+ bin.

Discussion

The failure to detect differences in GC levels between urban and rural San Joaquin kit fox populations indicates that the urban population likely does not have higher basal GC levels than the rural population. This result does not imply that both populations are not experiencing chronic stress responses due to different chronic perturbation factors. However, the lack of difference in basal GC levels suggests that the urban environment does not carry additional physiological costs over the rural environment due to environmental stressors.

Furthermore, the results from trapped versus non-trapped foxes show that these populations of kit foxes are able to mount acute stress responses, indicating that their stress response system is not impaired due to chronically elevated GC levels.

Though I was unable to detect a difference, trapped rural foxes demonstrated higher mean GC levels than trapped urban foxes (Figure 14). This failure to detect a difference may have been due to lack of power in the test from smaller sample sizes of trapped foxes. The distribution of trapped fox GC levels hints that rural foxes may have greater stress responses to capture than urban foxes. Two possibilities for the greater stress response by rural foxes are that urban foxes do not perceive humans as stressors (possibly due to habituation from birth) or the inability of urban foxes to mount acute stress responses due to chronically elevated GC levels. If the latter is true, then urban foxes may, in fact, be experiencing chronic stress responses that could lead to physiological impairments. However, both rural and urban populations had similar basal GC levels, and rural foxes could still clearly mount a stress response, suggesting that the former is a more likely possibility. Urban foxes are also larger than rural foxes (Cypher and Frost 1999), indicating that muscular atrophy, a possible effect of chronic stress responses (Sapolsky 2002), is not prevalent in the urban population. Furthermore, litter sizes are comparable between urban and rural populations (Cypher unpublished data), indicating that reproductive physiology is

not impaired in the urban population (another possible effect of chronic stress responses).

Wingfield (1998) suggested that human disturbances could generate "permanent perturbations", leading to chronic stress responses in animals. Urban San Joaquin kit foxes do not appear to be experiencing such chronic stress responses. The failure of urban foxes to elicit a GC response may be attributed to one of three causes 1) urban foxes do not perceive humans as a stressor and therefore do not exhibit a stress response, 2) foxes have habituated from birth to the presence of humans in their environment and therefore do not elicit a stress response, or 3) foxes are unable to mount stress responses due to impairment of their GC response system from prolonged exposure to chronic stressors. Under the third condition I would expect urban foxes to have lower basal GC levels that rural foxes, based on the cortisol levels in patients with PTSD (Yehuda et al. 1996). Given the lack of difference in the basal GC levels of the two populations, the third explanation is unlikely.

Urban foxes encounter humans, or human activity (i.e. vehicles, buildings, etc.) daily and so mounting an acute stress response to human activity may be maladaptive. Furthermore, kit foxes are curious animals and have quickly habituated to humans observing them in urban studies (Murdoch 2004), suggesting that perhaps the lack of GC response is due to habituation from birth. Under this hypothesis, rural foxes that are un-habituated to humans should perceive humans as a stressor. However, rural foxes often approached our field

vehicles and equipment suggesting that kit foxes may not perceive humans as a stressor and therefore would not elicit a stress response from humans unless directly pursued in a harmful manner. These hypotheses could be better explored by longitudinally monitoring the GC levels of immigrants to the urban population.

I detected no difference in rural foxes using shrub versus grass habitats, suggesting that the mere existence (i.e. scent, scat, tracks) of coyotes in the shrublands is not enough to produce a stress response from kit foxes. As in the case of the urban foxes, there are three possibilities for the lack of GC response in rural foxes: 1) foxes do not perceive the high predation risk habitats as a stressor, 2) foxes have habituated to coyotes and their preferred habitats from birth, or 3) foxes are unable to mount stress responses due to prolonged exposure to chronic stressors. Given the similarity between urban and rural fox basal GC levels, the third explanation remains unlikely. Thus, the first two explanations are more probable.

Kit foxes and coyotes have evolved and co-existed throughout San Joaquin kit fox range. Coyote presence may simply be a part of everyday life for rural foxes, and therefore foxes do not perceive the presence of coyotes as a stressor. Foxes may also have habituated to coyotes from birth, though this seems a less plausible explanation given that encounters between foxes and coyotes would likely be agonistic and may result in the death of kit foxes.

Stress responses in an animal may be related to the predictability of stressors in their environment (Wingfield 2005). For example, seasons change yearly and therefore do not produce acute stress responses from animals. However, extreme weather conditions and predation can be unpredictable events that would likely mount a stress response. Humans are fairly predictable in that after 10pm human activity in urban environments generally subsides. Foxes are nocturnal animals and urban foxes may be able to behaviorally control their physiological stress responses by increasing their activity peaks when humans minimize their activity (habituation). Kit foxes in Bakersfield wait longer after sunset to leave their diurnal den locations in winter, when the sun sets earlier, than in summer, when the sun sets later (Cypher unpublished data), while kit foxes in the rural environments leave their dens at sunset (Cypher unpublished data).

Rural foxes may perceive coyotes as either predictable or unpredictable. If kit foxes perceive coyotes as unpredictable, they still may not elicit a stress response because coyotes are a part of every day life for kit foxes. In other words, mounting a stress response every time a fox senses a coyote would be maladaptive. By inhibiting stress responses from the presence of predators in their environment, kit foxes can continue their daily activities and maintain reproductive and immune system function, without diverting energy resources elsewhere.

Kit foxes could also perceive coyotes as predictable. Coyotes have defined territories that kit foxes actively avoid (Nelson 2005, Chapter 2). Kit fox spatial avoidance of coyotes may result in their perception of coyotes as predictable. Kit foxes may rely on their senses to behaviorally mediate their physiological stress responses by avoiding encounters with coyotes. A direct encounter with a coyote, in the form of a chase or attack, would likely elicit an acute stress response from rural foxes. The non-elevated levels of GCs in San Joaquin kit foxes in this study indicate that high-risk and unnatural habitats do not carry additional hidden costs for this species due to physiological stress responses.

SUMMARY

San Joaquin kit foxes and coyotes at the Lokern Natural Area interacted by both exploitation and interference competition. Coyotes engaged in intraguild predation on San Joaquin kit foxes, which likely resulted in habitat displacement of kit foxes from the shrublands. Competition appeared to result in niche separation in the form of habitat, spatial, and dietary partitioning. Although other studies have not reported spatial avoidance of coyotes by kit foxes (Cypher and Spencer 1998; White et al. 1994), this result was not unexpected based on other canids' behaviors. Wild dogs (Creel and Creel 1996), red foxes (Gosselink et al. 2003), artic foxes (Tannerfeldt et al. 2002), crab-eating foxes (*Dusicyon thous*) (Jacomo et al. 2004), and culpeo foxes (*Dusicyon culpaeus*) (Johnson and Franklin 1994) all spatially avoid larger competitors through habitat segregation.

A surprising result of this study was coyotes' avoidance of burned habitats. Foxes capitalized on coyotes' avoidance of burned habitats by using them more than expected, especially for natal dens. Use of the burned and grassland areas provided kit foxes with a refuge from coyotes, but at the cost of a less diverse prey base (specifically, rodent species) including their preferred prey item, Heerman's kangaroo rats. The grasslands had an abundance of short-nosed kangaroo rats, but almost no Heerman's kangaroo rats, which are the larger of the two species. Heerman's kangaroo rats are more abundant in shrub habitats than grass habitats. Kit foxes in the grasslands showed strong

preference for the less abundant Heerman's kangaroo rats, suggesting that foxes in the grasslands either selectively hunted Heerman's kangaroo rats or entered the shrub habitats to hunt. Assuming Heerman's kangaroo rats are not easier to hunt than short-nosed kangaroo rats, the conclusion from either of the aforementioned actions is the same: coyotes displaced kit foxes from the best quality foraging habitat, the shrublands.

Kit foxes had a narrower dietary breadth than coyotes, relying mostly upon rodents and insects. Kit fox dietary requirements appeared to be more rigid than coyote requirements, suggesting that kit foxes may be less opportunistic in their feeding. As a result, coyotes likely have an advantage over kit foxes in years of prey declines because coyotes can switch food sources more readily. Kit foxes need access to specific habitats that provide adequate amounts of the proper prey base. Although coyotes displaced foxes from the food-rich shrublands, there is no evidence to suggest that the grasslands do not provide an adequate prey base for foxes. Short-nosed kangaroo rats and certain mice species were abundant in the grasslands.

Kit fox habitat segregation with coyotes may also increase fox survival. Kit fox survival in shrub habitats was lower than grass habitats and predation in shrub habitats was higher than grass habitats. Although predation was the primary source of mortality for kit foxes, high predation rates did not seriously impair kit fox survival, as survival rates of kit foxes were higher in this study than previous studies. I can not conclusively relate higher survival rates of foxes to

habitat segregation with coyotes. However, habitat partitioning was beneficial to kit foxes in grasslands as it provided a refuge for foxes that increased their chances for survival by decreasing predation.

The presence of coyotes in close proximity to foxes could have also physiologically impaired foxes by causing an increase in fox glucocorticoid. However, foxes in the coyote-dense shrub habitats did not have significantly higher GC levels than foxes in grasslands. Thus, coyotes did not carry additional physiological costs for foxes due to increased stress levels in foxes using shrub habitats.

In summary, competition between San Joaquin kit foxes and coyotes at the Lokern Natural Area was prevalent. Coyotes 1) out-competed kit foxes for prime foraging habitat, 2) competed for similar prey species (though foxes and coyotes consumed prey in different proportions), and 3) regularly killed kit foxes in interference competition. Nonetheless, coyotes did not appear to have a negative affect on kit fox survival. I conclude that habitat partitioning substantially contributed to the stable coexistence between San Joaquin kit foxes and coyotes at the Lokern Natural Area.

Management Implications for San Joaquin Kit Foxes and Coyotes

San Joaquin kit foxes are an umbrella species for many threatened and endangered plant and animal species in the San Joaquin Valley. Protection and conservation of San Joaquin kit foxes is vital in conserving necessary land for the

survival of threatened and endangered species. Coyotes will continue to occupy remaining natural habitats within the central valley of California. Therefore land managers should consider managing lands with diverse habitats to allow for the coexistence of San Joaquin kit foxes and coyotes.

Partitioning of habitat, space, and diet in a heterogeneous landscape appeared to allow for stable coexistence of kit foxes and coyotes in Lokern. I stress the importance of maintaining a heterogeneous landscape when managing lands for San Joaquin kit foxes. The existence of habitats less frequented by coyotes affords kit foxes some refuge from coyotes. Though many land managers may first opt for coyote control programs, coyote control proved ineffective in boosting San Joaquin kit fox populations in the past. Coyote control programs with swift foxes were successful in some locations; however, coyote control is a short-term solution to help depressed fox populations, not a long-term solution to fox survival. Through maintaining a heterogeneous landscape, land managers may allow for the long-term co-existence of San Joaquin kit foxes and coyotes in California

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