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# Dietary Shifts Related to Water Availability and the Demographic Response to Changing Prey Abundance of Carnivores in the West Desert, Utah

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# DIETARY SHIFTS RELATED TO WATER AVAILABILITY AND THE DEMOGRAPHIC RESPONSE TO CHANGING PREY ABUNDANCE OF CARNIVORES IN THE WEST DESERT, UTAH

by

Ashley E. Hodge

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTERS OF SCIENCE

in

Wildlife Biology

Approved:

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UTAH STATE UNIVERSITY
Logan, Utah

2021

# ABSTRACT

## Dietary Shifts Related to Water Availability and the Demographic Response to Changing Prey Abundance of Carnivores in the West Desert, Utah

by

Ashley E. Hodge, Master of Science

Utah State University, 2021

Major Professor: Dr. Eric M. Gese
Department: Wildland Resources

Across North America, range contraction of large carnivores has allowed many mesocarnivores to assume the role of the apex predator. This reduction of large carnivores on the landscape has favored some mesocarnivores such as coyotes (*Canis latrans*) who have expanded their distribution. Other small carnivores such as kit foxes (*Vulpes macrotis*) have experienced a range reduction across North America and their population status throughout the United States is a growing concern. Researchers have suggested that artificial water sources installed across the western U.S. may have permitted an influx of coyotes into arid environments like the Great Basin Desert. In the late-1980s, energetic models also suggested that coyotes would have to triple their prey biomass consumption in the absence of water to meet energy requirements. More recent coyote research has found no evidence of a water effect to support these claims. We used data collected between 2010 and 2013 on the U.S. Army Dugway Proving Ground (DPG) in Utah's West Desert, to test the coyotes' dependency on free water and to determine how kit foxes respond to changing prey abundance. We examined for a dietary shift towards large-bodied prey (i.e., leporids) based on the percent occurrence of prey in the coyote diet and proximity to water availability. We found no evidence of a dietary shift towards larger prey to meet energy requirements in the treatment areas where there was no available free water. Our results, in addition to previous DPG research, provide strong evidence that coyotes in the West Desert are desert-adapted carnivores and are not influenced by artificial water sources. The 4-year DPG dataset also allowed us to investigate demographic and functional responses of kit foxes to changing prey abundance. We found no correlation between kit fox litter size and local rodent or leporid abundance. However, we found a 3-fold increase in survival for kit fox pups in 2012 when rodent abundance nearly doubled. Diet analysis of kit fox scats showed four prey categories (rodent, insect, kangaroo rat, leporid) represented 78.5% occurrence of all prey items. We infer a functional response by kit foxes to changing kangaroo rat abundance based on kit fox diet composition and kangaroo rat relative abundance indices. As prey resources have changed over the last 60 years, the DPG kit foxes have demonstrated plasticity in their foraging by shifting away from historical leporid use and now heavily rely on rodents. In addition to more research on kit fox population parameters and responses, we recommend that future studies also focus on their prey populations. The health and productivity of the prey community will play a critical role in the future of the kit fox in the West Desert.

(117 pages)

# PUBLIC ABSTRACT

## Dietary Shifts Related to Water Availability and the Demographic Response to Changing Prey Abundance of Carnivores in the West Desert, Utah

Ashley E. Hodge

The decrease in number and range of North American large carnivores, has often allowed smaller carnivores (<15 kg) to fill the role of the top predator. This has favored some carnivores such as coyotes (*Canis latrans*), who have expanded their distribution. Other small carnivores such as kit foxes (*Vulpes macrotis*) have experienced a range shrinkage and their population status throughout the United States is a concern. Historically, western U.S. natural resource management agencies installed artificial water sources to assist desert wildlife, but some researchers believe the access to water allowed more coyotes to live in Utah's West Desert. In the late-1980s, research proposed that without free drinking water, coyotes would have to triple their food consumption to survive. More recent coyote research has found no evidence to support these claims. We used data collected between 2010 and 2013 on the U.S. Army Dugway Proving Ground (DPG) in Utah's West Desert to examine if the coyotes' changed their diet when drinking water was removed and to determine how kit foxes respond to changing prey abundance. We examined coyote scats to see if they shifted towards eating more large-bodied prey (i.e., leporids such as jackrabbits and cottontails) in the areas void of drinking water. We found no evidence of a dietary shift towards larger prey to meet energy requirements in the areas where there was no available free water. Our results, in addition to previous DPG research, provide strong evidence that coyotes in the West Desert are desert-adapted carnivores and are not influenced by artificial water sources. The 4-year DPG dataset also allowed us to investigate if kit fox litter sizes and pup survival changed when prey abundance changed. We found no connection between kit fox litter size and rodent or leporid abundance. However, we found a 3-fold increase in kit fox pup survival in 2012 when rodent abundance nearly doubled. Diet analysis of kit fox scats showed four prey categories (rodent, insect, kangaroo rat, leporid) represented 78.5% occurrence of all prey items. We found that kit foxes changed their diet when kangaroo rat abundance changed. As prey resources have changed over the last 60 years, the DPG kit foxes have shown to be flexible in their diet by shifting away from their historical leporid use to now heavily relying on rodents. In addition to more research on kit foxes, we recommend that future studies also focus on their prey populations to help ensure the future of the West Desert kit fox.

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# CHAPTER 1

# INTRODUCTION

Apex predators are often key drivers of food webs, trophic dynamics, and play a large role in regulating ecosystem health (Polis and Holt, 1992; Richie and Johnson, 2009). As such, the direct and indirect effects of predators on their prey and sub-dominant competing predators have been investigated for several large, charismatic species, but to a lesser extent for smaller species (Roemer et al., 2009). For example, large carnivore research topics have included the functional response of wolves (*Canis lupus*) to different prey abundance (Dale et al., 1994; Bergerud and Elliott, 1998; Winnie Jr. and Creel, 2017) and lion (*Panthera leo*) densities correlated with prey biomass (Ogutu and Dublin, 2004). However, fewer studies have researched how the top predators impact the smaller mesopredators (Richie and Johnson, 2009) and the ecological role of mesocarnivores (Roemer et al., 2009). Carnivore studies frequently discuss theories such as the intraguild predation theory (Holt and Polis, 1997; Lonsinger et al., 2017) and the competitive exclusion principle (Hardin, 1960; Kelly et al., 2020) in an attempt to explain sympatric carnivores. Other research highlights both the positive and negative exchanges between different-sized carnivores (Prugh and Sivy, 2020). Nonetheless, the range contraction of North America's large carnivores is permitting smaller carnivores to fill the role of apex predator in these communities (Laliberte and Ripple, 2004; Roemer et al., 2009).

Across North America, the reduction in large carnivores has favored coyotes (*Canis latrans*), which have expanded their distribution by an estimated 40% in the last 70 years (Laliberte and Ripple, 2004). Coyotes are highly adaptable and possibly the most studied carnivore (Bekoff, 2001). Similar to larger canids, intraguild predation occurs within mesocarnivores such as coyotes killing red foxes (*Vulpes vulpes*; Gosselink et al., 2007), swift foxes (*V. velox*; Kitchen et al., 1999), and kit foxes (*V. macrotis;* White et al., 1995). White and Garrott (1997) analyzed results from kit fox and swift fox studies and reported prey abundance was the major factor regulating fox densities and coyote-related mortalities were a less predominant factor. However, fox population dynamics and densities may be severely affected by the combination of poor resource conditions coupled with high rates of intraguild predation (White and Garrott, 1997). The status of kit fox populations varies by state as the species is vulnerable in Utah (NatureServe, 2021) and listed as threatened in Oregon (Oregon Department of Fish and Wildlife, 2021). A sub-species, the San Joaquin kit fox (*V. macrostis mutica*), is federally listed as endangered and state listed as threatened in California (California Department of Fish and Wildlife, 2021). The status uncertainty of the western kit fox calls for continued research on their population drivers and the most efficient management actions to ensure the future of this small carnivore.

In the western portion of the U.S.A., between the Rocky and Sierra Mountains lies the semi-arid Great Basin Desert (Pellant et al., 2004). The U.S. Army Dugway Proving Ground (DPG), located in Utah's West Desert, is in the northeastern section of the Great Basin Desert and has been a key wildlife research site since the late 1950s when Egoscue (1956) conducted preliminary studies on kit foxes. Coyotes and kit foxes were the primary mammalian carnivores on DPG, which have been investigated for intraguild predation (Kozlowski et al., 2012), reproductive rates and densities (Arjo et al., 2007; Lonsinger et al., 2018), and prey resources (Arjo et al., 2007; Kluever et al., 2016;

Kluever et al., 2017; Byerly et al., 2018). Historically, the kit fox was reported as the most abundant carnivore in the West Desert (Egoscue, 1956, 1962). In the late 1950s, the kit fox density was estimated at 0.15 foxes/km$^2$ (Egoscue, 1956) but by 2014 the density had decreased to 0.02 foxes/km$^2$ (Lonsinger et al., 2018). Conversely, along the same time-scale, the coyote population went from being described as "rare" (Shippee and Jollie, 1953) to < 0.1 coyotes/km$^2$ in the DPG area (Lonsinger et al., 2018).

Utah's West Desert has experienced major ecological and management alterations over the years including changes in fire regimes favoring non-native cheatgrass (*Bromus tectorum*) invasion, shifts in coyote management strategies (e.g., banning of toxicants in 1972), and an increase in artificial water sources throughout the landscape (Arjo et al. 2007, Kluever et al. 2019). State wildlife programs and Federal land management agencies have installed over 6,000 artificial water sources across Utah, Nevada, Arizona, and California alone (Krausman et al. 2006). Several studies have investigated the influences of artificial water sources on wildlife behavior and populations but differ in the relevancy of their conclusions (Rosenstock et al., 1999; Simpson et al., 2011). Kit foxes have adapted to arid desert conditions by meeting energy requirements through preformed water (i.e., water from ingested prey) but this adaptability and independence of free drinking water have not been reported for the coyote (Golightly and Ohmart, 1984). Coyotes have been hypothesized to require more than triple their wet biomass intake, in the absence of water, to meet their energy requirements (Golightly and Ohmart, 1984).

Considering the intraguild competition and proposed energy requirement differences between coyotes and kit foxes, in theory, one could assist the kit fox population recovery by removing DPG water sources therefore forcing the coyotes out of the area. Kluever and Gese (2016) were the first to manipulate water sources in an arid environment while focusing on the spatial response by resident carnivores using a before-after-control-impact (BACI) design. Kluever and Gese (2016) monitored radio-collared coyotes for four years (2010 to 2013) and halfway through the study removed several major water sources to test for a water effect. Surprisingly, the coyotes showed no change in space use regardless of water proximity, nor was coyote survival influenced. The lack of spatial response (Kluever and Gese, 2016) and the presumed coyote energy requirements (Golightly and Ohmart, 1984) inspired our hypothesis that coyotes in the water removal areas must have shifted their diet to larger prey to compensate for the lack of free water. For chapter 2, we used data collected during Kluever (2015) 4-year study of relationships between wildlife and artificial water sources to assess coyote diet for shifts after the water manipulation. For chapter 3, we also used Kluever (2015) datasets but shifted our focus to demographic and functional responses by kit foxes with changing prey abundance.

In chapter 2, we used coyote scats (*n* = 1,861) for our diet analysis, which were collected as a by-product of seasonal scat deposition surveys. These surveys provided a relative abundance index for coyotes across our study site during the 4-year study. Scat deposition surveys were conducted along 15 5-km road-based transects that were assigned as control (i.e., water available throughout the study) or treatment (i.e., water removed in 2012). The coyote scats were processed following protocols from similar diet studies (Kelly, 1991; Bartel, 2003), and prey items were placed into 11 prey categories to be consistent with a previous DPG occurring study: anthropogenic, fruits and plants, scorpion, insect, reptile, bird, rodent, kangaroo rat, leporid, miscellaneous mammal, and ungulate (Kozlowski et al., 2008). The water sites assigned as treatment were blocked or water was completely removed by May 2012, which represented 33% of the artificial water sources on DPG (Kluever and Gese, 2016). Leporids were the most abundant medium-sized prey (Knowlton and Stoddart, 1992) and a principal prey item in the coyote diet (Kozlowski et al., 2008). Therefore, we predicted that coyotes in the treatment areas (i.e., water removed) would respond by increasing the percent occurrence of leporids in their diet after water removal in 2012 due to energetic requirements. North American deserts may become drier and warmer due to climatic changes (Stahlschmidt et al., 2011), and understanding how predators respond to the lack of free water will become even more relevant for management and conservation strategies.

In chapter 3, we explored demographic and functional responses of kit foxes to changing prey abundance. Considering the status uncertainty of kit fox populations across the western United States, continued research is needed to understand which population parameters are affected by changes in prey. We used data from radio-collared kit foxes and remote cameras placed at kit fox natal dens to determine if kit fox litter sizes or the survival of kit fox pups responded to changes in prey abundance. The prey abundance indices were results from rodent trapping surveys and leporid spotlight surveys conducted during the same study period (Kluever et al., 2016; Kluever et al., 2017). We also used kit fox scats ($n = 611$) for diet analysis that were collected during the scat deposition surveys and processed following the diet studies previously described. The prey abundance surveys with the addition of the kit fox diet analysis allowed us to investigate if a functional response occurred based on changes in diet composition and prey abundance.

The results from these two studies will add to the decades of research at the DPG on coyotes, kit foxes, and several prey species. Previous studies have suggested that artificial water sources were partly responsible for the increase in coyote abundance across Utah's West Desert (Arjo et al., 2007), but more recent studies did not find evidence for this claim (Hall et al., 2013; Kluever and Gese, 2016). Our chapter 2 results will provide evidence for or against the presumed coyote energy requirements in the absence of water (Golightly and Ohmart, 1984) using a BACI design and almost 2,000 coyote scats. Our chapter 3 results will add to kit fox studies and increase our knowledge on the demographic responses by kit foxes to changes in prey (White and Ralls, 1993; White and Garrott, 1997), which could also be translational to other small carnivores. We will also use kit fox diet composition and prey abundance indices for inference of any functional responses by kit foxes to changes in prey abundance. These results will provide a better understanding of the sensitivity kit foxes may or may not have to certain prey fluctuations.

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# CHAPTER 2

# DOES WATER AVAILABILITY SHIFT DIETARY PREFERENCES OF COYOTES IN THE WEST DESERT OF UTAH?[1]

## Abstract

Water is one of the most essential resources on the planet and shapes entire ecosystems. Water is utilized by wildlife in three forms (i.e., metabolic, preformed, and free water) but the proportions in which these forms are used varies among species and behavioral state (e.g., migrating, not migrating). Across the western United States since the 1940s, thousands of artificial water sources were installed to assist wildlife populations in arid environments (e.g., the Great Basin Desert). Previous research reported that kit foxes (*Vulpes macrotis*) can live independently of free drinking water but coyotes (*Canis latrans*) would have to more than triple their intake of prey biomass to meet energy requirements. The kit fox population in the West Desert of Utah has declined considerably since the 1950s while the opposite trend has been recorded for coyotes. Intraguild competition with coyotes is one possible reason for the kit fox decline. To assist the recovery of the kit fox population, previous researchers used a before-after control-impact (BACI) design and removed water sources in 2012 with the prediction that resident coyotes would abandon their territories and leave the study area. Surprisingly, coyotes showed no change in space use within the control or treatment (i.e., water removed) areas, nor was survival rates of coyotes influenced by the removal of water sources. Based on energy requirements, we predicted that coyote diets in the

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[1] Co-authors are Eric M. Gese and Bryan M. Kluever; chapter is formatted for Journal of Arid Environments

treatment areas would show an increase in leporids, as a source of preformed water after the water removal to compensate for the lack of free water. However, we found no evidence of a dietary shift by coyotes towards large-bodied prey (i.e., leporids) after the water removal. Percent occurrence of leporids in the coyote diet decreased after water removal in both the control and treatment areas. The top prey categories were consistent with previous findings with rodents, leporids, kangaroo rats, and insects representing 73.8% of the coyotes' diet. Based on this study and previous research in Utah's West Desert, coyotes in the Great Basin ecosystem were not influenced by artificial water sources in a spatial, demographic, or dietary capacity.

## 1. Introduction

Water is one of the most essential resources on the planet (Robbins, 1983; Wolanski et al., 1999; Ogutu et al., 2008; Stahlschmidt et al., 2011; Geremia et al., 2019; Aikens et al., 2020) Water availability influences habitat suitability for large predators in arid ecosystems (Abade et al., 2014) and shapes patterns of desert life (Ochoa et al., 2021). Water is utilized by wildlife in three forms: metabolic (i.e., a byproduct of cellular processes), preformed (i.e., food), and free water (i.e., drinking water) (Robbins, 1983). Depending on the species' physiological, morphological, and behavioral mechanisms, the proportion in which water is used between these three forms can vary (Cain et al., 2006; Golightly and Ohmart, 1984). Some desert bighorn sheep (*Ovis canadensis nelsoni*) populations have been shown to heavily rely on artificial water sources installed by state wildlife agencies (Longshore et al., 2009). Conversely, using a before-after-control-impact (BACI) study design, Cain et al. (2008) reported female desert bighorn sheep did not shift their diet towards more succulent vegetation, change foraging area selection, or alter home-range size after water removal. O'Brien et al. (2006) recorded a variety of species visiting artificial water sources in Arizona including mule deer (*Odocoileus hemionus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), black-tailed jackrabbit (*Lepus californicus*), and kit fox (*Vulpes macrotis*).

In arid environments starting in the mid-1900s, a belief by wildlife managers that many species depend on these artificial water sources, facilitated the installation of thousands of water developments across the western United States (Larsen et al., 2012). State wildlife programs have installed over 4,590 artificial water sources across Utah, Nevada, Arizona, and California alone (Rosenstock et al., 1999). In addition, military installations located in arid environments also installed water sources in an attempt to bolster wildlife populations on the lands they manage. Several studies have investigated the impacts of artificial water sources on wildlife behavior and populations but differed in their conclusions (Rosenstock et al., 1999; Simpson et al., 2011). Germane to this debate is the premise that use of water by wildlife does not equal evidence of need or confer a notable benefit at the individual or population level (O'Brien et al., 2006). Many mammals have adapted to arid environments where water is extremely limited or absent. For example, kangaroo rats (*Dipodomys* spp.) have physiological adaptations for extracting additional water from their urine when needed and do not require free water (Urity et al., 2012). In addition, black-tailed jackrabbits are not dependent on free water sources in desert systems (Best, 1996; Kluever et al., 2017). The kit fox is a specialized desert carnivore found in remote areas lacking free water and utilizes dens to avoid extreme temperatures (Egoscue, 1962; McGrew, 1979; Arjo et al. 2003). All these species occur in the Great Basin Desert, which is part of North America's largest semidesert system (Miller et al., 1994).

The Great Basin Desert includes Utah's West Desert, which has experienced several major ecological and management alterations, including changes in fire regimes favoring non-native cheatgrass (*Bromus tectorum*) invasion, shifts in coyote management strategies (e.g., banning of toxicants in 1972), and an increase in artificial water sources throughout the landscape (Arjo et al., 2007; Kluever et al., 2019). There are at least 415 artificial water sources in Utah's West Desert alone (L. Hall, pers. comm.) excluding the hundreds of livestock water sources across the area. Historically, the kit fox was reported as the most abundant carnivore in the West Desert (Egoscue, 1956, 1962). Egoscue (1956) estimated kit fox density to be 0.15 foxes/km$^2$, but by 2014 the density had decreased to 0.02 foxes/km$^2$ (Lonsinger et al., 2018). Conversely, the coyote population went from being described as rare in the late 1950s (Shippee and Jollie, 1953) to the most abundant carnivore in the area (Lonsinger et al., 2018). Kit foxes have adapted to arid desert conditions by meeting energy requirements through preformed water and ultimately being independent of free drinking water but the same adaptability has not been reported for the coyote (Golightly and Ohmart, 1984). In the absence of water, coyotes have been hypothesized to require more than triple their wet biomass intake to meet their energy requirements through preformed water (Golightly and Ohmart, 1984). As such, the addition of artificial water sources is a possible cause for increasing coyote abundance in the West Desert of Utah (Arjo et al., 2007).

Factors limiting kit fox populations include habitat changes from native shrubs to invasive herbaceous vegetation resulting in monocultures affecting prey abundance (Arjo et al., 2007; Kluever et al., 2019), high dietary overlap with coyotes (Kozlowski et al., 2008), and intraguild predation (Kozlowski et al., 2012). Based on energy requirements, in theory, one could remove water sources thus forcing coyotes out of an area to release intraguild competition, thereby assisting in kit fox population recovery. Kluever and Gese (2016) were the first to manipulate water sources in an arid environment while focusing on carnivores, using a BACI design, and recording the spatial response of the canid species. Kluever and Gese (2016) monitored radio-collared coyotes and kit foxes for two years, removed several major water sources across the study area, and monitored the two canids for another two years. Surprisingly, the coyotes showed no change in space use within the control or treatment (i.e., water removed) areas, nor were survival rates of coyotes influenced by water removal. The only spatial response was a decrease in coyote visitation to the manipulated water sources after the water was removed.

Our hypothesis that, after water removal, coyotes in the treatment areas would shift their diet towards larger prey was influenced by two primary findings: presumed coyote energy requirements in the absence of water (Golightly and Ohmart, 1984), and the lack of spatial response by coyotes to water removal (Kluever and Gese, 2016). The most abundant medium-sized herbivore throughout Utah’s region of the Great Basin Desert is the black-tailed jackrabbit, which is a principal diet component of the coyote (Knowlton and Stoddart, 1992; Kozlowski et al., 2008; Byerly et al., 2018). Black-tailed jackrabbit was the dominant rabbit species in the area within the family Leporidae, but cottontail species (*Sylvilagus spp.)* do occur, thus the term leporid is more inclusive and used throughout this study. We predicted that the coyotes in the treatment areas (i.e., where water was removed) would have a dietary increase in leporids, whereas coyotes in the control areas (i.e., no water removed) would not show a dietary shift after the water manipulation. An increase in leporid consumption by coyotes in the treatment areas (after water removal), would theoretically increase preformed water uptake and replace water used from artificial water sources. Understanding how predator populations respond to the absence of water may become even more relevant as the climate continues to change. North American deserts are predicted to become drier and warmer within the coming years (Seager et al., 2007; Stahlschmidt et al., 2011), underscoring the need to gain a better understanding of how species and communities may be affected.

## 2. Methods

### *2.1. Study area*

The 879-km$^2$ study area (Figure 2-1) in the Great Basin Desert was 128 km southwest of Salt Lake City, Utah, on the U.S. Army Dugway Proving Ground (DPG) and mainly included the eastern portion of DPG but also the surrounding land managed by the Bureau of Land Management (BLM; Dempsey et al., 2014; Kluever, 2015). Data collection occurred over 4 years (2010 – 2013) when temperatures ranged from -4.7 ºC to 36.7ºC with annual precipitation of 24.5, 26.6, 14.7, and 14.8 cm, respectively (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). The study site was described as a cold desert with predominately flat playa interspersed by steep mountain ranges (Dempsey et al., 2014) and precipitation mainly occurring in the winter and spring. Vegetation included 7 vegetation communities: grassland (including exotic annuals), chenopod, pickleweed, vegetated dune, greasewood, shrubsteppe, and urban (Arjo et al., 2007; Kozlowski et al., 2008, 2012).

### *2.2. Scat Deposition Surveys*

All coyote scats were collected during Kluever's (2015) examination on relationships between water developments and selected mammals on DPG between 2010 and 2013. Scat deposition surveys were conducted to ascertain indices of relative abundance and for dietary data during three biological seasons (i.e., breeding, pup-rearing, dispersal; Gese and Ruff, 1998; Seidler and Gese, 2012). Transects (5-km sections on various roads) were classified as either treatment ($n$ = 5) or control ($n$ = 10) based on the average home range of a DPG coyote and the proximity of the water resources that were drained or altered to be inaccessible by May 01, 2012 (i.e., treatment transects) or remained available throughout the study (i.e., control transects; Figure 2-1). The control transects were "controls" only regarding the water manipulation and no attempt was made to control any other ecological aspects of these transects (e.g., fluctuations in prey abundance).

The elimination of these water sources accounted for 33% (6 of 18) of the study site's anthropogenic water resources (Kluever and Gese, 2016). Predator and prey surveys were conducted two years prior and another two years post water manipulation. Kluever (2015) cleared transects for the scat depositions surveys by using double-observers, walking opposite directions, and collecting scats, then returning 14 days later to again count and collect any coyote deposited scats.  This survey technique provided an index of coyote relative abundance (# of coyote scats/transect/ survey; Kluever, 2015), and the scats collected were used for diet analysis. Scats were identified based on morphology and physical appearance (Murie and Elbroch, 2005). Lonsinger et al. (2015) used molecular species identification on over 800 coyote fecal samples to evaluate field identification methods on the DPG and concluded only 7.1% of coyote scats were misclassified. Prior to water removal, five scat deposition survey sessions were conducted (dispersal 2010, breeding 2011, pup-rearing 2011, dispersal 2011, breeding 2012) and four surveys were conducted post water removal (pup-rearing 2012, dispersal 2012, two surveys within pup-rearing 2013). Species, date, transect name, and UTM coordinates were recorded for each scat collected. Scats were dried under a heat lamp, then frozen until diet analysis.

Lonsinger et al. (2016) tested the persistence of coyote scats on DPG roads and found only 10.6% of coyote scats remained after 42 days over the various road types. Furthermore, an average of 65.6% of scats were removed after 14 days across all roads (i.e., large 90.8%, medium 64.2%, small 41.7%) from vehicle traffic and natural decay. Results from Lonsinger et al. (2016) were particularly applicable because it overlapped with the end of our project (2013 – 2014), was completed in the same general study area, and included our scat deposition transects. Based on Lonsinger et al. (2016) scat persistence research, the coyote scats collected during the initial clearing of the transects added valuable data to our diet analysis. For example, when scats collected during the initial clearing were back-dated two weeks, these samples fell within the same respective survey season (*n* = 8 surveys), and one survey changed to a different season by only a few days.

### *2.3. Diet analysis*

Scat analysis techniques were mechanical in nature and primarily followed Kelly (1991) but also some details from Bartel (2003). The scat sample information on each paper bag was recorded, and the frozen scat was placed in a black nylon bag with a uniquely numbered metal tag, which served as a link to the collection data after the washing process. Samples were thawed in hot soapy water (Kelly, 1991) in 5-gallon buckets for ≥24 hours. After samples were thawed, ≤60 samples at a time (Bartel, 2003) were placed in a standard washing machine on a delicate cycle with a mild detergent to remove fecal material and minimize content loss. Some studies dry the scat samples in a household drier (Cypher et al., 2018; Kelly et al. 2020), but we selected to air dry them outside (weather permitting) for ≥24 hours or inside the building under a laboratory fume hood in an attempt to minimize the content loss that could potentially affect percent volume estimates. Nylon bags were reused, but washed twice on a normal cycle with detergent to minimize the chance of cross-contamination.

Each scat sample was placed in a clear sorting tray, separated, and prey items identified. Prey items (e.g., hair, teeth, and bones) were determined using Utah State University's extensive specimen collection and other existing hair and animal skull identification keys (Moore et al., 1974; Elbroch, 2006). Hair was identified primarily by the characteristics of the hair medulla using a light microscope (Moore et al., 1974). At least one hair slide per sample was created and inspected under a light microscope for unique hair characteristics. Skull fragments and teeth were compared with the specimen collection and identified by features described in Elbroch (2006).

For consistency and comparison, we classified prey/food items into the same 11 categories used by Kozlowski et al. (2008): anthropogenic, fruits and plants, scorpion, insect, reptile, bird, rodent, kangaroo rat, leporid, miscellaneous mammal, and ungulate. Kangaroo rat was singled out of the rodent category due to the species high prevalence in the study area and high use by the resident predators (Kozlowski et al., 2008; Byerly et al., 2018). We identified prey items to a prey category and to species if possible. We defined the percent occurrence of prey categories as the number of occurrences of an item divided by the total number of occurrences of all prey items (Kelly, 1991; Kozlowski et al., 2008; Dowd and Gese, 2012). The percent volume of each prey item within each scat was recorded using a simple grid system under the clear sorting tray to visually estimate to the nearest 10% (Dowd and Gese, 2012; Doherty, 2015; Wysong et al., 2019). As part of Kluever (2015) spatial monitoring of carnivores, coyotes were captured and fitted with radio-collars using helicopter net-gunning and foothold traps around roadkill carcasses (primarily mule deer). Ungulate presence in coyote scats from probable capture carcasses was not included in the diet analysis.

To investigate changes in the coyote diet in response to the water manipulation, we utilized a 4-year BACI study design (Morrison et al., 2001) to examine diet composition before and after the water removal on the control and treatment transects. The percent occurrence of prey within the coyote scats were analyzed by transect type and season to test for changes in prey selection after the water manipulation that might indicate a water effect (i.e., scats collected from treatment transects increased in percent occurrence of leporids after the water was removed). A chi-squared test of independence was performed on the prey occurrence of the top prey categories to examine differences between transect type and before versus after the removal of water (Wright, 2010; Krebs, 2014). We conducted Spearman-rank correlation analysis to assess diet composition between transect types per season.

Because increased biomass of prey consumed would increase defecation rates, we tested that the coyote diet analyses and the coyote relative abundance index were not influenced by higher defecation rates (due to higher prey consumption after water removal on the treatment transects), we examined the rate of prey presence in coyote scats collected during the 14-day scat deposition surveys. The rate of the top three prey categories (i.e., leporid, rodent, kangaroo rat) per transect type was calculated for each survey (i.e., control vs treatment).

### *2.4. Prey Abundance Surveys*

Kluever (2015) conducted leporid and rodent surveys during the same 4-year study as the scat deposition surveys and in association with the same transects. These surveys provided prey indices for comparison to coyote dietary results. Leporid spotlight surveys were conducted at night when they are primarily active (Costa et al., 1976) on the established 15 5-km road transects by slowly driving while two observers scanned with 3 million candlepower spotlights; surveys were run for 3-4 consecutive nights (Kluever et al., 2017). When a leporid was sighted, we recorded species, location, radial distance, and angle to the animal (Kluever et al., 2017). The spotlight surveys provided a relative abundance of leporids (average number of leporids/transect/night/season) across all biological seasons for four years. Despite the seemingly low overall relative abundance, the distance sampling survey method allowed us to calculate absolute annual and seasonal density estimates per transect type (i.e., control, treatment) using the software Distance (Thomas et al., 2010); density estimates per transect were not possible due to low sample size. The half-normal key function with a cosine adjustment best fits our data with a truncation of 70m as leporid sightings beyond this distance contributed little to the shape of the detection function.

Two rodent grids were established for eight different water sources, one proximate (<100 m from the water source) and one distant (>1000 m from the water source) to reduce the chance of overlapping rodent populations, producing 16 trapping grids across the study area (Kluever, 2015). Each 7 x 7 grid contained 49 live traps (Sherman Traps, Inc., Tallahassee, Florida) with 8.3 m spacing and run for 4 consecutive nights during each trapping session (Kluever et al., 2016). Rodents were identified to species, ear-tagged, sexed, reproductive status noted, weighed and foot length recorded before release. Between May 2010 and September 2013, nine trapping sessions across all sixteen grids were completed primarily during the summer months when cold nightly temperatures were not a threat to the captured animals. By the dispersal season of 2010, all surveys had been completed at least once thus for clarity and comparison we used all predator and prey surveys from the 2010 dispersal season to the end of the project in 2013. These surveys provided a rodent relative abundance index based on the number of unique individuals captured per grid/session (Kluever et al., 2016).

### *2.5. Transect-level vegetation*

To possibly elucidate leporid distribution between 2010 and 2013, we used the Rangeland Analysis Platform (RAP; Allred et al., 2020) to investigate potential differences in habitat cover types across the 15 transects surveyed. The RAP categorized four main habitat cover types for our study area: annual forbs and grasses, perennial forbs and grasses, shrubs, and bare ground. Program Distance was not able to estimate leporid density per transect, thus a relative abundance index from the same spotlight data was used for this analysis. To compare leporid relative abundance per transect as a response to the percent cover of each habitat type, we produced five models including a null and four univariate vegetation cover models. Model weights were then compared using the AICctab function (bbmle package) in R (R Core Team, 2020). The leporid abundance data were inspected for constant variance and normality assumptions.

## 3. Results

We completed diet analysis from 1,861 coyote scats collected between January 2010 and August 2013 during seasonal scat deposition surveys (*n* = 9), and when available, collected during radio-collaring capture events. Anthropogenic items found in coyote scats included black rubber, burlap, metal, food and gum wrapper, paper, woven fabric, brown paper bag, clear tape, red string, cigarette, plastic, and a steel ball from a wheel bearing. The fruits and plants category included Utah juniper (*Juniperus osteosperma*), Russian olive (*Elaeagnus angustifolia*), houndstongue (*Cynoglossum officinale*), Indian ricegrass (*Achnatherum hymenoides*), cheatgrass (*Bromus tectorum),* and various other grasses. Scorpions (*Centruroides* spp.) were recorded and insects discovered include various larvae, Mormon cricket (*Anabrus simplex*), Jerusalem cricket (*Stenopenmatus fuscus*), various grasshoppers (*Orthoptera* spp.), and beetles (*Coleoptera* spp.), ladybug (*Coccinellidae* spp.), tick (*Acari* spp.), and various ants (*Formicidae* spp.). Gopher snake (*Pituophis melanoleucus*) and other snake and lizard species (*Squamata* spp.) were documented in the reptile category. Various bird remains included feathers, bones, and eggshell fragments but no efforts were made to identify to species. Rodent was the most diverse category and included desert woodrat (*Neotoma lepida*), bushy-tailed woodrat (*Neotoma cinerea*), western harvest mouse (*Reithrodontomys megalotis*), deer mouse (*Peromyscus maniculatus*), canyon mouse (*Peromyscus crinitus*), montane vole (*Microtus montanus*), meadow vole (*Microtus pennsylvanicus*), Botta's pocket gopher (*Thomomys bottae*), Great Basin pocket mouse (*Perognathus parvus*), little pocket mouse (*Perognathus longimembris*), long-tailed pocket mouse (*Chaetodipus formosus*), Townsend's ground squirrel (*Spermophilus townsendii*), white-tailed antelope squirrel (*Ammospermophilus leucurus*), and least chipmunk (*Tamias minimus*). Ord's kangaroo rat (*Dipodomys ordi*) and chisel-toothed kangaroo rat (*Dipodomys microps*) represented the kangaroo rat species. Leporid included black-tailed jackrabbit and cottontails. Miscellaneous mammals included badger (*Taxidea taxus*), yellow-bellied marmot (*Marmota flaviventris*), porcupine (*Erethizon dorsatum*), long-tailed weasel (*Mustela frenata*), raccoon (*Procyon lotor*), skunk (*Mustelidae* spp.), and one confirmed occurrence of a kit fox. The ungulate category comprised of pronghorn (*Antilocapra americana*), mule deer, cow (*Bos Taurus*), and feral horse (*Equis ferus caballus*).

We found slight seasonal fluctuations in the percent occurrence of prey items, but rodent, leporid, kangaroo rat, and insect were consistently the top prey categories (Table 2-1). The percent occurrence within coyote scats showed 25.4% rodent, 16.5% leporid, 16.3% kangaroo rat, and 15.6% insect being the top prey categories (Table 2-2). The percent volume resulted in the same prey order with 25.5% rodent, 27.2% leporid, 21.6% kangaroo rat, and 9.9% insect leading the prey categories (Table 2-2). The percent occurrence of ungulate, bird, reptile, scorpion, miscellaneous mammal, and anthropogenic were each <10% at 5.8%, 4.3%, 2.8%, 2.3%, 0.5%, and 0.4%, respectively (Table 2-2). Fruits and plants were observed slightly more often at 10.1% and primarily included Russian olive (13.3%) and juniper berries (8.0%). Grass of ≥40% volume was found in 61 scat samples but only 9 were 100% grass by volume. All other plant and fruit occurrences had low (≤30%) percent volume grass and were suspected to be indirect consumption while feeding on other prey items.

Kit fox hair was confirmed in one scat in October 2012 and was presumably from the predation of an uncollared kit fox, as the date did not correspond to a radio-collared kit fox mortality. We found 260 total occurrences of ungulate species for the 4-years of coyote scat data, which included mule deer (38.8%), domestic cattle (13.8%), feral horse (12.3%), and pronghorn (11.5%). There were 67 occurrences of mule deer or pronghorn, but no dorsal hairs were present to identify species. There were six scats with multiple ungulates but all had a combination of horse or cattle and mule deer or pronghorn. Within the kangaroo rat category, Ord's or chisel-toothed kangaroo rat species were confirmed when teeth were available, as hair remains did not differentiate between the two species. Kangaroo rat was present in 723 scats of which prey was identified to species on 182 occurrences with Ord's being the predominant species over chisel-toothed at 84.6% and 17.0%, respectively. This includes three occasions when both species were confirmed in the same scat.

The coyote diet results showed four prey categories were of primary importance (73.8%) and were therefore emphasized in our examination for a water effect. Before and after the water removal, these top prey categories graphically followed the same trends of percent occurrence for both transect types suggesting that no water effect occurred (Figure 2-2A-D). In particular, we found no increase in the higher mass prey category (i.e., leporids) after the water was removed on the treatment transects where no free drinking water was available (Table 2-3, Figure 2-2B). Across both transect types in dispersal season 2012, the percent occurrence of leporids declined as the coyote diet increased in the percent occurrence of rodents and kangaroo rats (Figure 2-2 A-C). Chi-square analysis showed prey occurrence changed similarly in both transect types before and after water removal (Table 2-4). If a water effect occurred in regards to diet of DPG coyotes we would have expected leporid chi-squared results would have been significant on the treatment alone and not on the control transects. However, both transect types were significant indicating leporid use by coyotes changed across the study area and the water removal was irrelevant (Table 2-4). Spearman-rank correlation analysis between transect types across survey seasons, also showed no change in dietary importance of the 11 prey categories by averaging 0.936 (SD = 0.046) with 1.0 being the highest correlation possible (Table 2-5). Shannon diversity index ($H'$) was calculated annually and seasonally with an average of 0.839 ±0.038 (Table 2-1, 2-2).

Coyote relative abundance across all transects ($n$ = 15) during the 4-year study averaged 5.55 (*SD* = 6.89) scats/transect/survey, ranged from 0 to 46 scats/transect/ survey, and peaked in dispersal season 2012. We found no evidence that the coyote relative abundance was influenced by higher defecation rates due to dietary changes after water removal on the treatment transects. The rate of coyote scats containing leporid showed seasonal fluctuations on the treatment transect, but showed no increase after water removal (Figure 2-3 A). The rate of coyote scats containing rodent or kangaroo rat also displayed seasonal fluctuations and both prey categories increased after water removal in 2012 (Figure 2-3 B-C). However, these increases occurred on both the treatment and control transects indicating that it was not a response to the water removal but probable changes in rodent resources.

Annual rodent relative abundance from trapping surveys between 2010 and 2013 was 13.52, 13.25, 21.72, and 8.50, respectively. The rodent abundance index was nearly double in 2012, which was reflected in the coyote diet across our study site especially during the 2012 dispersal season when the coyote diet shifted away from leporid and towards the two rodent categories (Table 2-1, Figure 2-4). Based on leporid spotlight survey data, estimated annual leporid density was 6.91, 4.30, 9.00, and 6.86 leporids/km$^2$, 2010 to 2013, respectively, and comparable to leporid density estimates in other desert ecosystems (Lightfoot et al., 2010). Leporids appeared to cycle in 2012 reaching the highest recorded densities during the project. Specifically, the treatment transects during pup-rearing 2012 reached our highest density estimate at 26.19 leporids/km$^2$ (Figure 2-5). When separated by transect type, the leporid density estimate on the control transects was 4.92 (*SD* = 2.80) leporids/km$^2$. The treatment transects estimate was higher at 10.45 (*SD* = 7.13) leporids/km$^2$. Despite an increase in leporid density on the treatment transects, the coyote diet did not show a water effect by sustaining a high usage of this prey resource (Figure 2-5).

Leporid relative abundance was not explained by any one RAP transect habitat cover type. All univariate models were ranked by model weight, the null was the top model at 38% followed by bare ground, annual forbs and grasses, shrub, and perennial forbs and grasses at 19%, 16%, 14%, and 13%, respectively (Table 2-6). We also performed the same analysis but focused on 2012 when the leporid population cycled as a response to the 2012 vegetation data. However, we found near-identical model weight results as compared with the original attempt and no evidence that transect-level vegetation explained leporid abundance.

## 4. Discussion

The top prey categories (rodent, leporid, kangaroo rat, insect) in the DPG coyote diet between 2010 and 2013 were consistent with Kozlowski et al. (2012) diet analysis collected 10 years prior to our project. However, the order of these top categories ranked differently showing a shift towards rodents and away from leporids. A decrease in leporid abundance on the DPG has been a growing concern (Arjo et al., 2007) and is exemplified in our percent occurrence of leporid, which dropped to nearly half of Kozlowski et al. (2012) results (Table 2-7). A decrease in percent occurrence of kangaroo rats was also detected but these declines were mainly offset by increased rodent occurrence and slight increases in the fruit and plants, scorpion, insect, reptile, and bird categories.

Byerly et al. (2018) also reported the same top four prey categories in 2013, but defined the percent occurrence differently and eliminated prey categories with <5% occurrence. This resulted in insects (29%) topping the list of most important prey category followed by leporids (26%), kangaroo rats (26%), and rodents (18%). By comparison, we eliminated all prey categories except these top four and recalculated our percent occurrence, which also showed insects (30.5%) were a major prey item for coyotes' in 2013. Our leporid occurrence was slightly lower at 21.9%, and we also found rodents of more importance (29.2%) than kangaroo rats (18.4%). However, data from 2013 are a snapshot in time, and when compared to 4-years of data across all prey categories, the average percent occurrence of insect was 15.6%. Additionally, Byerly et al. (2018) included a larger study area that stretched further across DPG and surrounding BLM land, which may account for some of the variations in the order of prey importance.

Nevertheless, these top prey categories were still the most prevalent in a DPG coyotes' diet but slight annual fluctuations do occur.

Ord's was the predominant kangaroo rat species over the chisel-toothed identified in all coyote scats at 84.6% and 17.0%, respectively, including three occasions when both species were confirmed in the same scat. This species composition was reflected in the rodent surveys with 1,556 unique individual kangaroo rats captured including 1,423 (91.5%) identified as Ord's and 133 (8.5%) identified as chisel-toothed (Kluever et al., 2016). Kangaroo rats represented 72.5% of all individuals captured during rodent surveys. If the categories of rodent and kangaroo rat were combined in the analysis, then kangaroo rats would represent 39.1% of all rodents present in the coyotes' diet. This difference in kangaroo rat abundance, as verified from rodent trapping and the percent occurrence in coyote scats, possibly suggests coyotes were catching a wider variety of rodents than were trapped or disproportionately selecting for certain species. For example, Botta's pocket gophers spend the majority of their lives underground and 90% of their burrowing activity occurs within an area of <50-m$^2$ (Gettinger, 1984). Due to their fossorial behavior, this species was not represented in our rodent trapping surveys. A minimum of 20.8% of all rodent occurrences in the coyote scats included pocket gopher indicating a significant food source. Future studies may want to explore additional rodent surveys appropriate for pocket gophers.

With the exception of three scats, all coyote scats containing domestic cattle were located on the eastern transects closest to the BLM land, which is leased for cattle grazing. The number of scats containing mule deer and pronghorn were minimal with an average number of scats per survey of 6.7 (± 4.3) and 3.3 (± 3.5), respectively. There were increases in the number of scats containing mule deer in the summer of 2012 (*n* = 16) and 2013 (*n* = 11), suggesting coyotes were possibly catching and consuming fawns. Similarly, the number of coyote scats containing pronghorn increased in the summer of 2013 (*n* = 11) but otherwise minimal throughout the study. Presence and percent occurrence data do not translate to the number of animals depredated as one large carcass could be the source of numerous coyote scats collected. However, this data does illustrate trends of available carcasses on the landscape, but whether the ungulates were scavenged or preyed upon is indeterminate. Kit fox deaths attributable to coyotes have been documented on the DPG to be between 48% and 56% (Kozlowski et al., 2008; Kluever and Gese, 2017), which is partially driven by high dietary overlap (Kozlowski et al., 2008) and interspecific competition, but coyotes do not generally feed on the carcass. One coyote scat contained kit fox hair remains with 20% volume and may have been indirectly consumed during a predation event.

The most abundant medium-sized herbivore throughout the Great Basin Desert is the black-tailed jackrabbit, which is a principal diet component of the most abundant predator, the coyote (Knowlton and Stoddart, 1992). For this reason, we hypothesized that if Golightly and Ohmart (1984) water energetic models held true, in the absence of free water coyotes would have to more than triple their prey consumption, then they would most likely increase their consumption of leporids. We found no evidence of a dietary shift in coyotes towards leporids after the water manipulation. Percent occurrence of leporids from both the control and treatment areas synchronously changed across survey seasons (Figure 2-2B). If coyotes' metabolic requirements changed after water removal, we would have expected the percent occurrence of leporids on treatment transects to remain high regardless of leporid availability. According to leporid density estimates, the leporid population cycled during our project in July 2012 and was highest on treatment transects (26.19 leporids/km; Figure 2-5). Following the peak, leporid density declined along with the percent occurrence of leporid in the coyote diet on the treatment transects (Figure 2-5). When processing the coyote scats, it was frequently not possible to quantify how many prey individuals were consumed especially if it was the same species. Depending on the coyotes' total meal size and the size of the rodent, the digestibility of bones and teeth can vary but hair is unaffected (Kelly and Garton, 1997). Hypothetically, if the coyotes intensified their use of rodents after the water removal (instead of leporids) for metabolic reasons, then we should have seen an increase in the percent volume results in the rodent and kangaroo rat categories exclusively on the treatment transects. The percent volume of these prey categories on each transect type per survey season did not illustrate a water effect as seasonal fluctuations in the coyote diet on the treatment transects were also evident on the control transects (Figure 2-6 A-C). Prey percent occurrence and volume analyses measured the proportion of the prey categories within the coyote scats ultimately for dietary inferences. It's perhaps possible that the coyotes in the treatment areas did not change the proportion of prey use, but consumed more prey, and thus defecated more often. Coyote relative abundance surveys showed an increase in abundance in 2012 after water removal, but we found no evidence that this was a result of higher defecation rates. In 2012, the use of rodents in the coyote diet increased as a response to increased rodent abundance across the study area, which possibly benefited coyote demographic parameters (e.g., pup survival) leading to a higher relative abundance of coyotes on the landscape.

There have been reports of leporid population fluctuation cycles every 8 to 10 years on and around the DPG (Eberhardt and Van Voris, 1986; Arjo et al., 2007). Cyclic peaks occurred in 1971 and 1972 then consistently peaked from 1979 to 1982 (Eberhardt and Van Voris, 1986) followed by Arjo et al. (2007) reporting an upward trend in 2000. To directly compare our data with these previous leporid indices, we recalculated our leporid index from average leporid counts per transect per survey to leporids per km (Figure 2-7). The reported leporid peaks occurred in 1971, 1981, 2000, and during our study in 2012 with leporids per km at 4.96, 3.22, 1.03 and 0.73, respectively (Eberhardt and Van Voris, 1986; Arjo et al., 2007). The leporid surveys by Eberhardt and Van Voris (1986) were performed during the day but the studies thereafter were conducted at night when black-tailed jackrabbits are more active (Best, 1996). Despite the differences in survey methods, the leporid numbers illustrate a decline and were possibly underestimated in the earlier studies. Similar cyclic populations have been documented in northern Utah every 10 to 11 years (Bartel et al., 2008). Our overall leporid index across all transects during this peak averaged 0.73 leporids/km, but if separated by transect type, the treatment transect group was the main driver of the increase. During the peak, there were 3-folds more leporids/km observed on the treatment than the control transects at 1.33 and 0.43, respectively. Kluever et al. (2017) found no evidence that water removal influenced leporid abundance, therefore another environmental factor must be driving the higher leporid presence on the treatment transects. Our habitat cover analysis also failed to explain high leporid numbers on the treatment transects. Alternatively, RAP's 30 x 30 m resolution may not be fine-scale enough to detect habitat preferences by leporids within our study site. Kluever et al. (2016) found the increase in rodent abundance in

2012 was possibly a response from the previous year's precipitation, which provided increased plant productivity and thus resources for rodents in 2012. This same mechanism may explain why leporids cycled in 2012, but other research has shown no relationship between leporid densities and precipitation (Cypher et al., 2000).

Several predator and prey species such as the kit fox and kangaroo rat have adapted to water depleted deserts through metabolic (e.g., quickly meeting water requirements through prey consumption) and behavior mechanisms (e.g., using dens during the heat of the day) (Vorhies, 1945; Golightly and Ohmart, 1983). In general, mammals of larger body size have higher water loss rates (Richmond et al., 1962) and "probably influencing the proximity of coyotes to free water" (Golightly, 1981: 134). However, the coyotes on the DPG exhibited no spatial response after the removal of artificial water sources nor was coyote survival influenced (Kluever and Gese, 2016). We followed up on the possibility of a dietary shift towards higher mass prey that would explain how coyotes can persist without free drinking water. No evidence of a dietary shift was detected and based on these two studies, we are proposing that coyotes can be considered a desert-adapted carnivore in the West Desert of Utah even when free water is absent. A coyote (~13 kg body mass) is larger in body size, thus in theory, has greater water and energy requirements than a kit fox (~2 kg) or kangaroo rat (~60 g). Nevertheless, African lions (~200 kg; *Panthera leo*) in the Kalahari Desert "could survive at least eight months with no drinking water" (Owens and Owens, 1984: 242). Similarly, the brown hyena (~40 kg; *Hyaena brunnea*) was also recorded to "go months even years, in times of drought with nothing to drink" (Owens and Owens, 1978; Owens and Owens, 1984: 185). Even the black-backed jackal (~9 kg; *Canis mesomelas*) who is often called the “African coyote” and relatively similar to a coyote in weight, was observed to go without free water for at least three months (Owens and Owens, 1984: 51). Coyotes in the West Desert of Utah have challenged our current knowledge of water conservation mechanisms, and what it truly means for individuals and populations to survive in the absence of free water. It appears the capabilities and adaptability of coyotes to thrive in arid environments such as the Great Basin Desert have been underestimated.

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## Tables and Figures

**Table 2-1:** Percent occurrence of prey categories (top categories in bold) from coyote scats (*n* = 1,861) and the diet diversity index separated by survey between 2010 and 2013 during the respective biological season: D = dispersal, B = breeding, P = pup-rearing season on U.S. Army Dugway Proving Ground, Utah, USA.

| | ***Survey season and year*** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **D_'10** | **B_'11** | **P_'11** | **D_'11** | **B_'12** | **P_'12** | **D_'12** | **P_'13a** | **P_'13b** |
| ***n* scats** | 115 | 355 | 148 | 195 | 166 | 204 | 233 | 227 | 148 |
| ***Prey category*** | | | | | | | | | |
| Anthropogenic | 0.0 | 0.9 | 0.0 | 0.6 | 0.0 | 0.2 | 0.7 | 0.0 | 0.3 |
| Bird | 3.1 | 4.0 | 3.3 | 5.2 | 0.8 | 2.6 | 2.3 | 10.3 | 6.6 |
| Fruit & Plants | 9.7 | 11.2 | 7.9 | 10.3 | 12.7 | 8.5 | 10.8 | 7.1 | 13.7 |
| **Insect** | 18.1 | 6.9 | 4.5 | 23.9 | 10.0 | 19.4 | 17.9 | 15.2 | 29.5 |
| **Kangaroo rat** | 14.6 | 15.8 | 21.8 | 12.3 | 16.8 | 15.9 | 23.2 | 16.2 | 8.4 |
| **Leporid** | 19.4 | 21.6 | 22.1 | 17.1 | 18.4 | 14.5 | 7.1 | 13.9 | 14.0 |
| Misc. mammal | 0.0 | 0.1 | 0.9 | 0.6 | 0.3 | 0.7 | 0.5 | 0.4 | 0.8 |
| Reptile | 2.8 | 1.5 | 1.5 | 2.6 | 0.8 | 4.4 | 3.5 | 3.4 | 5.3 |
| **Rodent** | 21.9 | 26.6 | 28.7 | 22.1 | 31.4 | 24.2 | 30.9 | 23.6 | 14.8 |
| Scorpion | 4.9 | 1.3 | 1.2 | 2.2 | 0.5 | 6.0 | 1.2 | 0.8 | 3.8 |
| Ungulate | 5.6 | 10.2 | 8.2 | 3.2 | 8.1 | 3.7 | 1.8 | 9.1 | 2.8 |
| ***Diversity Index*** | | | | | | | | | |
| Shannon *(H`)* | 0.86 | 0.84 | 0.80 | 0.86 | 0.78 | 0.87 | 0.80 | 0.87 | 0.87 |

**Table 2-2:** Annual and overall percent occurrence (top categories in bold), the diversity index ($H$`), and overall percent volume of the 11 prey categories in coyote scats ($n$ = 1861) collected on U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| | **% Occurrence** | | | | | **% Volume** |
|---|---|---|---|---|---|---|
| ***Prey category*** | **2010** | **2011** | **2012** | **2013** | **Overall** | **Overall** |
| Anthropogenic | 0.0 | 0.6 | 0.3 | 0.2 | 0.4 | 0.1 |
| Bird | 3.0 | 4.2 | 2.1 | 8.4 | 4.3 | 1.9 |
| Fruit & Plants | 10.0 | 10.4 | 10.0 | 9.9 | 10.1 | 5.2 |
| **Insect** | 17.3 | 11.6 | 16.4 | 20.9 | 15.6 | 9.9 |
| **Kangaroo rat** | 15.3 | 15.9 | 18.9 | 12.6 | 16.3 | 21.6 |
| **Leporid** | 19.6 | 20.2 | 12.9 | 15.0 | 16.5 | 27.2 |
| Misc. mammal | 0.0 | 0.4 | 0.6 | 0.5 | 0.5 | 0.5 |
| Reptile | 2.7 | 1.8 | 3.1 | 4.2 | 2.8 | 0.7 |
| **Rodent** | 22.3 | 25.6 | 28.8 | 20.0 | 25.4 | 25.5 |
| Scorpion | 4.7 | 1.5 | 2.8 | 2.1 | 2.3 | 0.4 |
| Ungulate | 5.3 | 7.7 | 3.9 | 6.1 | 5.8 | 7.0 |
| ***Diversity Index*** | | | | | | |
| Shannon ($H'$) | 0.86 | 0.86 | 0.82 | 0.89 | 0.84 | |

**Table 2-3:** Percent occurrence of prey categories (top categories in bold) in coyote scats collected on treatment transects before and after the water removal, and from the control transects (no water removal), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| *Transect Type* | **Treatment** | | **Control** | |
|---|---|---|---|---|
| | **Before** | **After** | **Before** | **After** |
| **water** | **yes** | **no** | **yes** | **yes** |
| *n* coyote scats | 599 | 469 | 435 | 358 |
| ***Prey Category*** | *Percent Occurrence* | | | |
| Anthropogenic | 0.6 | 0.4 | 0.2 | 0.2 |
| Bird | 2.8 | 5.3 | 4.4 | 4.8 |
| Fruit & Plants | 10.5 | 10.8 | 10.4 | 8.2 |
| **Insect** | 13.5 | 19.5 | 10.3 | 20.0 |
| **Kangaroo rat** | 15.1 | 15.6 | 17.6 | 17.7 |
| **Leporid** | 20.7 | 12.4 | 18.4 | 13.1 |
| Misc. mammal | 0.4 | 0.6 | 0.3 | 0.6 |
| Reptile | 1.6 | 3.9 | 2.1 | 4.2 |
| **Rodent** | 24.3 | 23.2 | 29.5 | 25.7 |
| Scorpion | 1.8 | 3.0 | 1.7 | 2.8 |
| Ungulate | 8.8 | 5.3 | 5.0 | 2.7 |

**Table 2-4:** Results from chi-squared analysis comparing occurrence of the top four prey categories in the coyote diet before vs after water removal on the two transect types: control (i.e., water always available) and treatment (i.e., water removed in 2012), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| | *Control transects* | | | *Treatment transects* | | |
|---|---|---|---|---|---|---|
| ***Prey category*** | $\chi^2$ | df | P | $\chi^2$ | df | P |
| Insect | 45.08 | 1 | **<0.001** | 38.08 | 1 | **<0.001** |
| Kangaroo rat | 0.05 | 1 | 0.82 | 2.75 | 1 | 0.098 |
| Leporid | 11.53 | 1 | **<0.001** | 29.67 | 1 | **<0.001** |
| Rodent | 5.30 | 1 | **0.02** | 0.89 | 1 | 0.35 |

**Table 2-5:** Spearman-rank correlation results using percent occurrence of the 11 prey categories from coyote scat analysis for each transect type (i.e., control and treatment) during scat deposition surveys ($n$ = 9) collected during the respective biological season, U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| ***Survey Season*** | | $r_s$ | $t$ | $P$ |
|---|---|---|---|---|
| **Dispersal** | **2010** | 0.968 | 11.553 | < 0.001 |
| **Breeding** | **2011** | 0.936 | 8.002 | < 0.001 |
| **Pup-rearing** | **2011** | 0.959 | 10.114 | < 0.001 |
| **Dispersal** | **2011** | 0.871 | 5.319 | < 0.001 |
| **Breeding** | **2012** | 0.852 | 4.887 | 0.001 |
| ***water removal*** | | | | |
| **Pup-rearing** | **2012** | 0.959 | 10.140 | < 0.001 |
| **Dispersal** | **2012** | 0.995 | 31.321 | < 0.001 |
| **Pup-rearing** | **2013** | 0.954 | 9.573 | < 0.001 |
| **Pup-rearing** | **2013** | 0.927 | 7.430 | < 0.001 |

**Table 2-6:** Model results of leporid abundance per transect as a response to four habitat cover types and the null model on U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| Model | ΔAICc | df | *w* |
|---|---|---|---|
| Null | 0.0 | 2 | 0.38 |
| Bare ground | 1.4 | 3 | 0.19 |
| Annual forbs & grasses | 1.7 | 3 | 0.16 |
| Shrub | 2.0 | 3 | 0.14 |
| Perennial forbs & grasses | 2.1 | 3 | 0.13 |

**Table 2-7:** Percent occurrence of 11 prey categories (top categories in bold) in coyote scats during two studies on U.S. Army Dugway Proving Ground, Utah, USA; 1999 to 2001 by Kozlowski et al. (2012), 2010 to 2013 by this study, and the overall dietary diversity index for both studies.

| ***Prey category*** | ***1999-2001*** | ***2010-2013*** |
|---|---|---|
| Anthropogenic | 0.3 | 0.4 |
| Bird | 2.7 | 4.3 |
| Fruit & Plants | 2.2 | 10.1 |
| **Insect** | 13.0 | 15.6 |
| **Kangaroo rat** | 25.6 | 16.3 |
| **Leporid** | 31.9 | 16.5 |
| Misc. mammal | 0.6 | 0.5 |
| Reptile | 2.1 | 2.8 |
| **Rodent** | 14.8 | 25.4 |
| Scorpion | 1.1 | 2.3 |
| Ungulate | 5.8 | 5.8 |
| ***Diversity Index*** | | |
| Shannon (*H`*) | 0.78 | 0.84 |

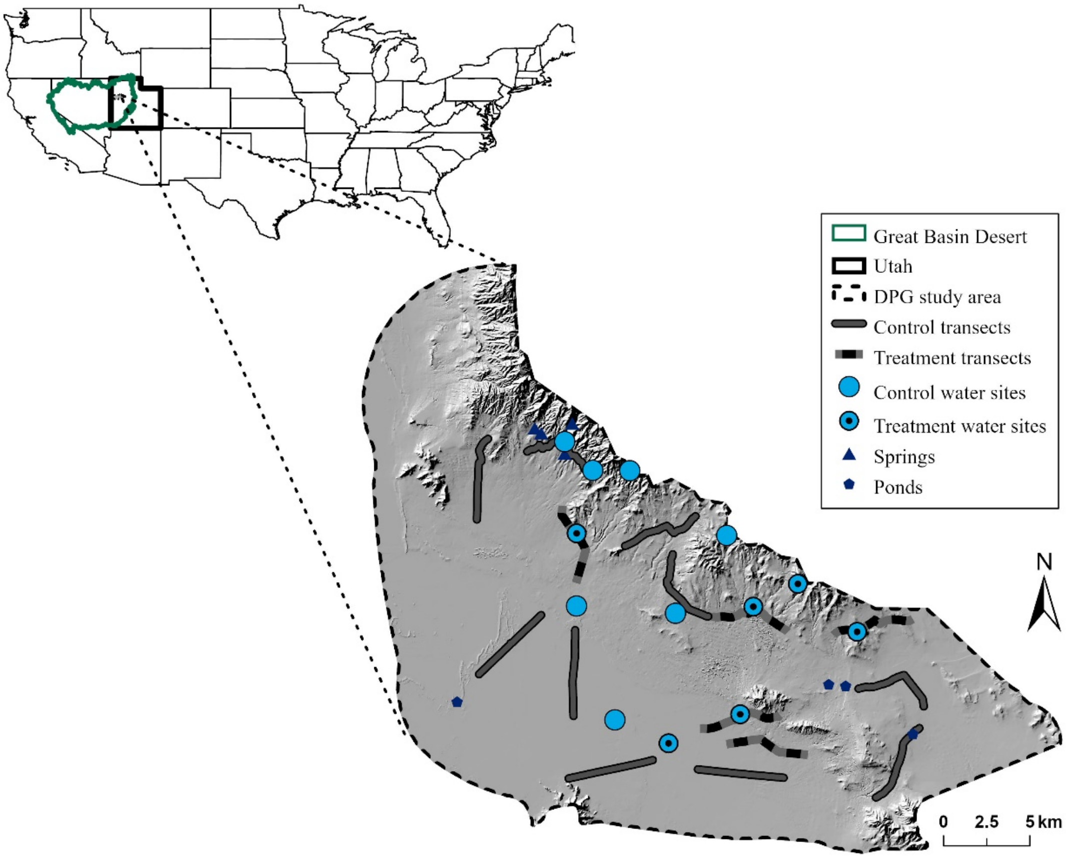
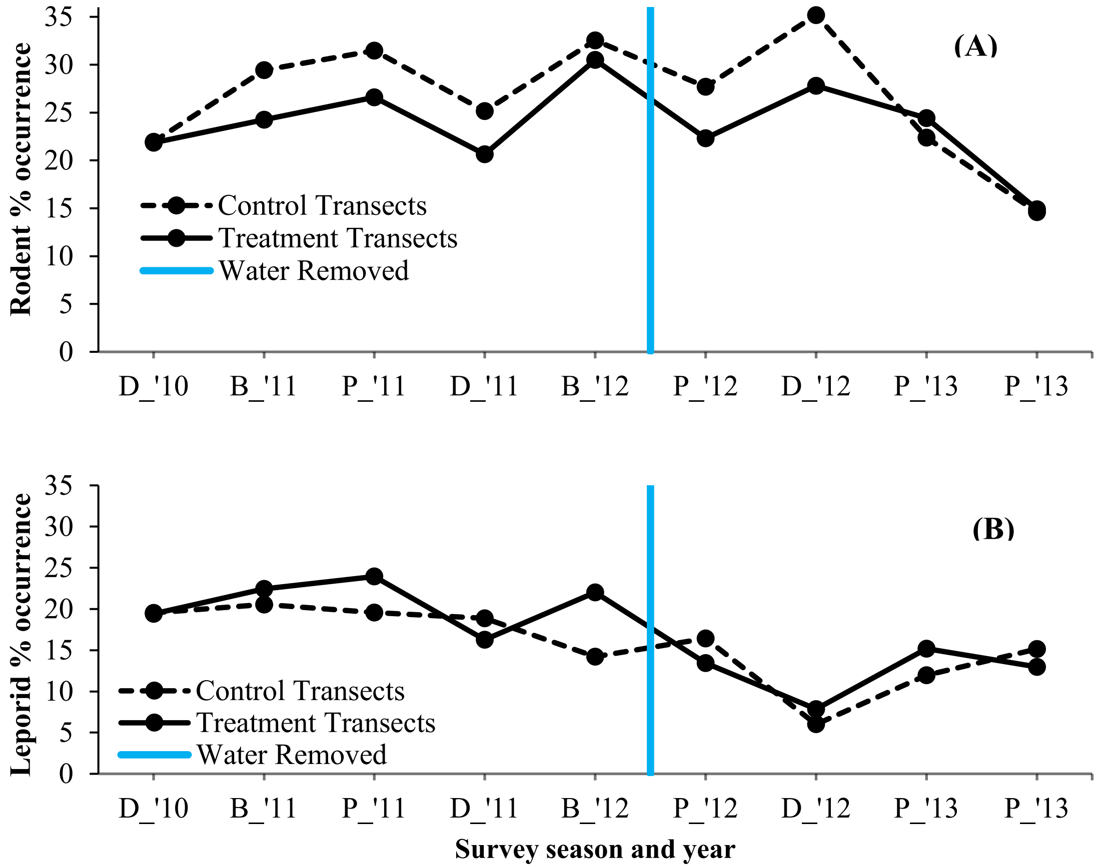


**Figure 2-1:** The 879 km$^2$ study area within the Great Basin Desert encompassing our control transects (*n* = 10), treatment transects (*n* = 5), control water sites (i.e., water always available), treatment water sites (i.e., water removed in 2012), and ephemeral water sites (i.e., springs and ponds) within and adjacent to the U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.


(A)
Rodent % occurrence
35
30
25
20
15
10
5
0
Control Transects
Treatment Transects
Water Removed
D_'10
B_'11
P_'11
D_'11
B_'12
P_'12
D_'12
P_'13
P_'13
(B)
Leporid % occurrence
35
30
25
20
15
10
5
0
Control Transects
Treatment Transects
Water Removed
D_'10
B_'11
P_'11
D_'11
B_'12
P_'12
D_'12
P_'13
P_'13
Survey season and year

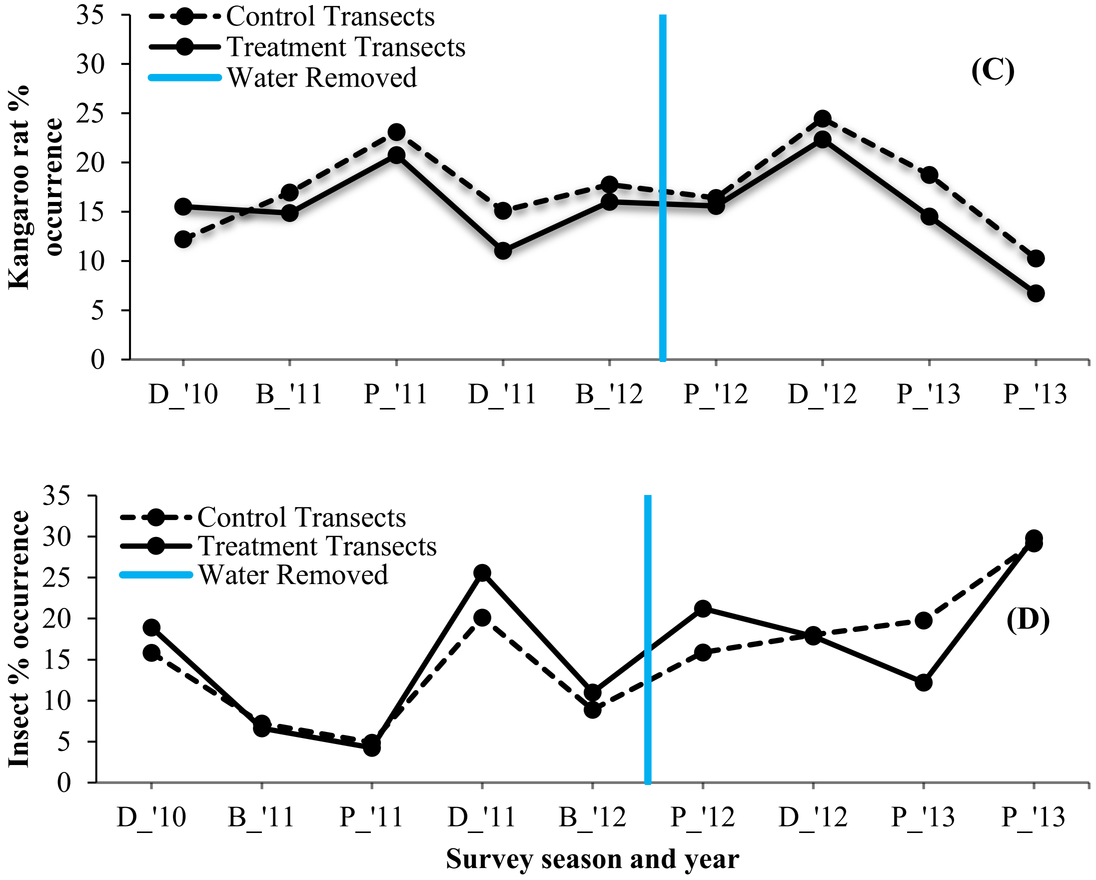


**Figure 2-2 A-D:** Percent occurrence of prey categories (**A**) rodent, (**B**) leporid, (**C**) kangaroo rat, and (**D**) insect, in coyote scats on control (dashed line) and treatment (solid line) transects across the nine surveys and the corresponding biological season: D = dispersal, B = breeding, P = pup-rearing on U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

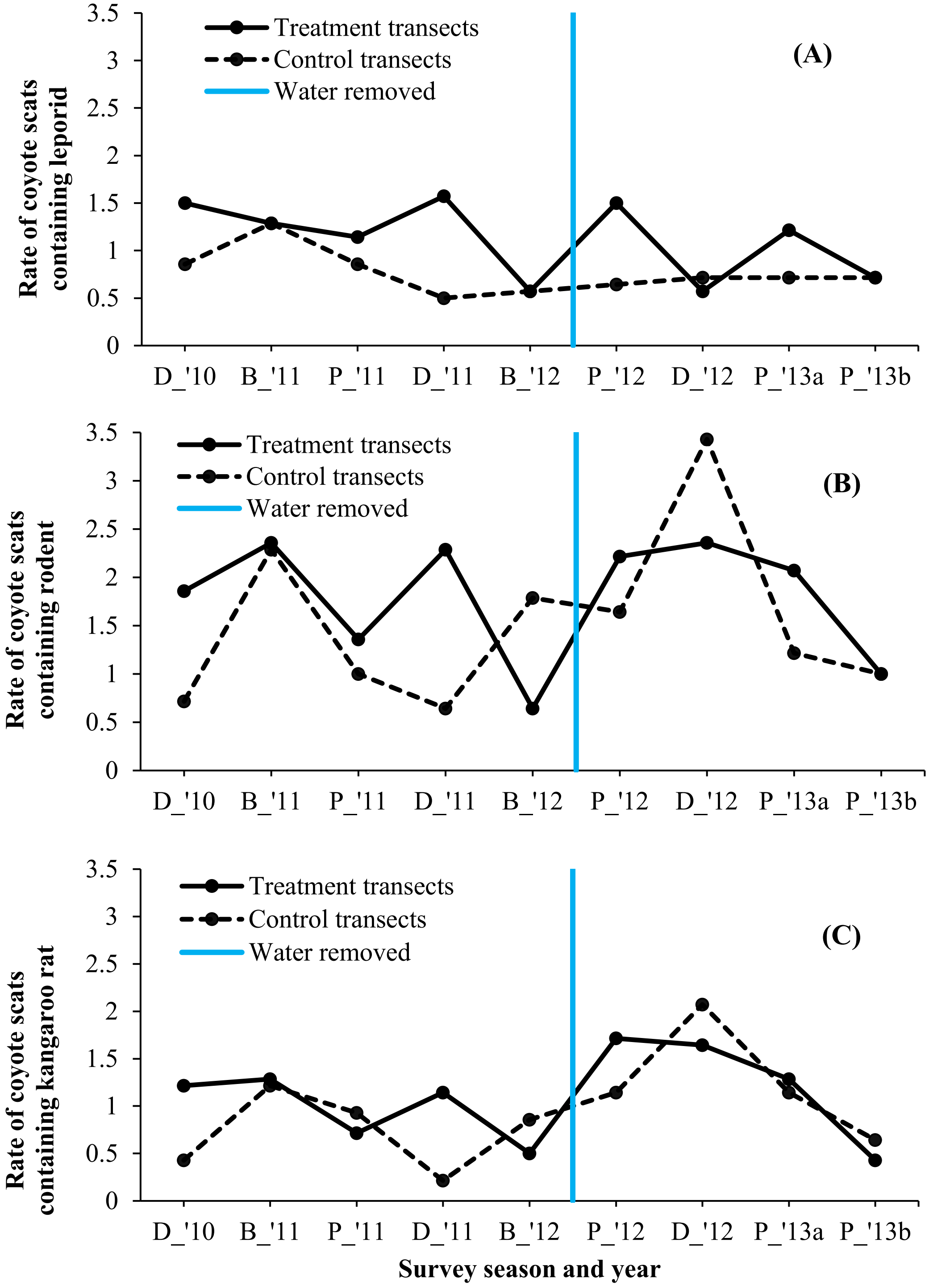


**Figure 2-3 A-C:** The rate of top prey categories **(A)** leporid, **(B)** rodent, and **(C)** kangaroo rat present in coyote scats collected during nine scat deposition surveys and the corresponding biological season: D = dispersal, B = breeding, P = pup-rearing on U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

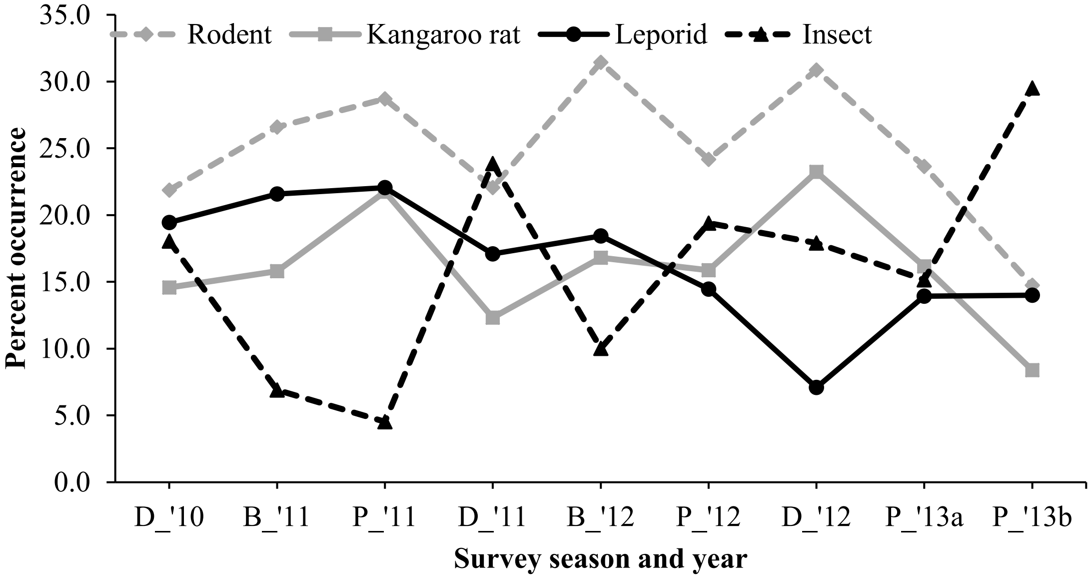


**Figure 2-4:** Percent occurrence of the top four prey categories (rodent, leporid, kangaroo rat, insect) in the coyote diet across the nine scat deposition surveys and the corresponding biological season: D = dispersal, B = breeding, P = pup-rearing on U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

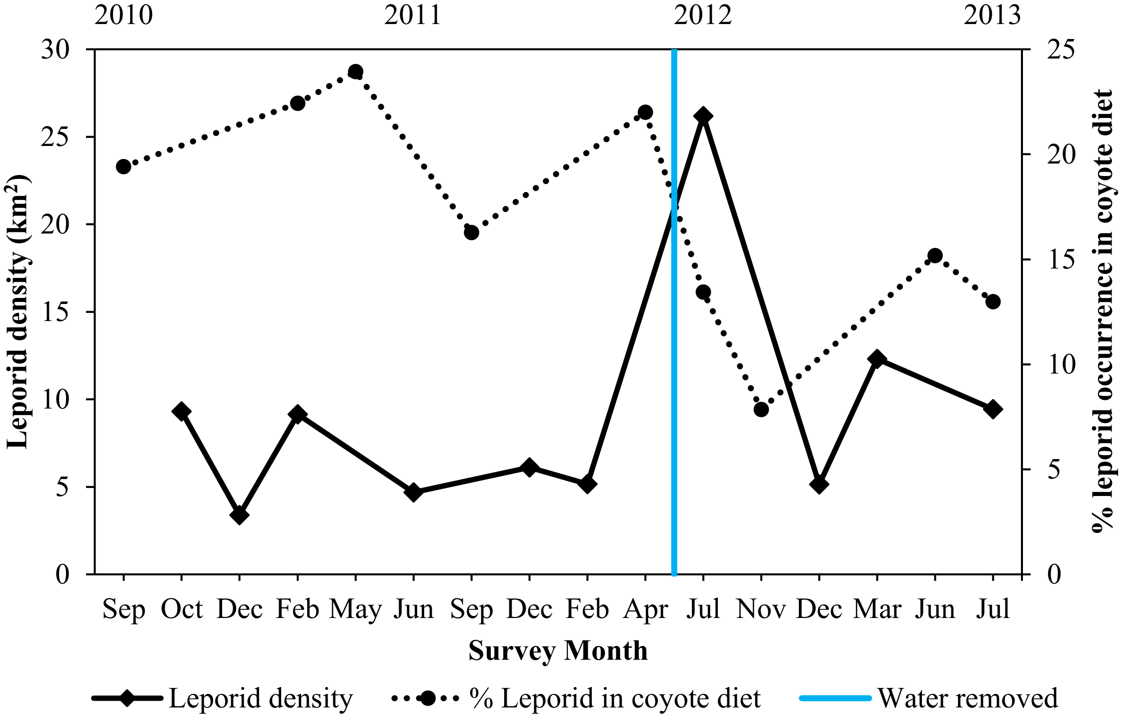


**Figure 2-5:** Leporid density (leporids/km$^2$) estimates using program Distance compared with percent occurrence of leporid in coyote scats from scat deposition surveys by month specifically on the treatment transects, U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

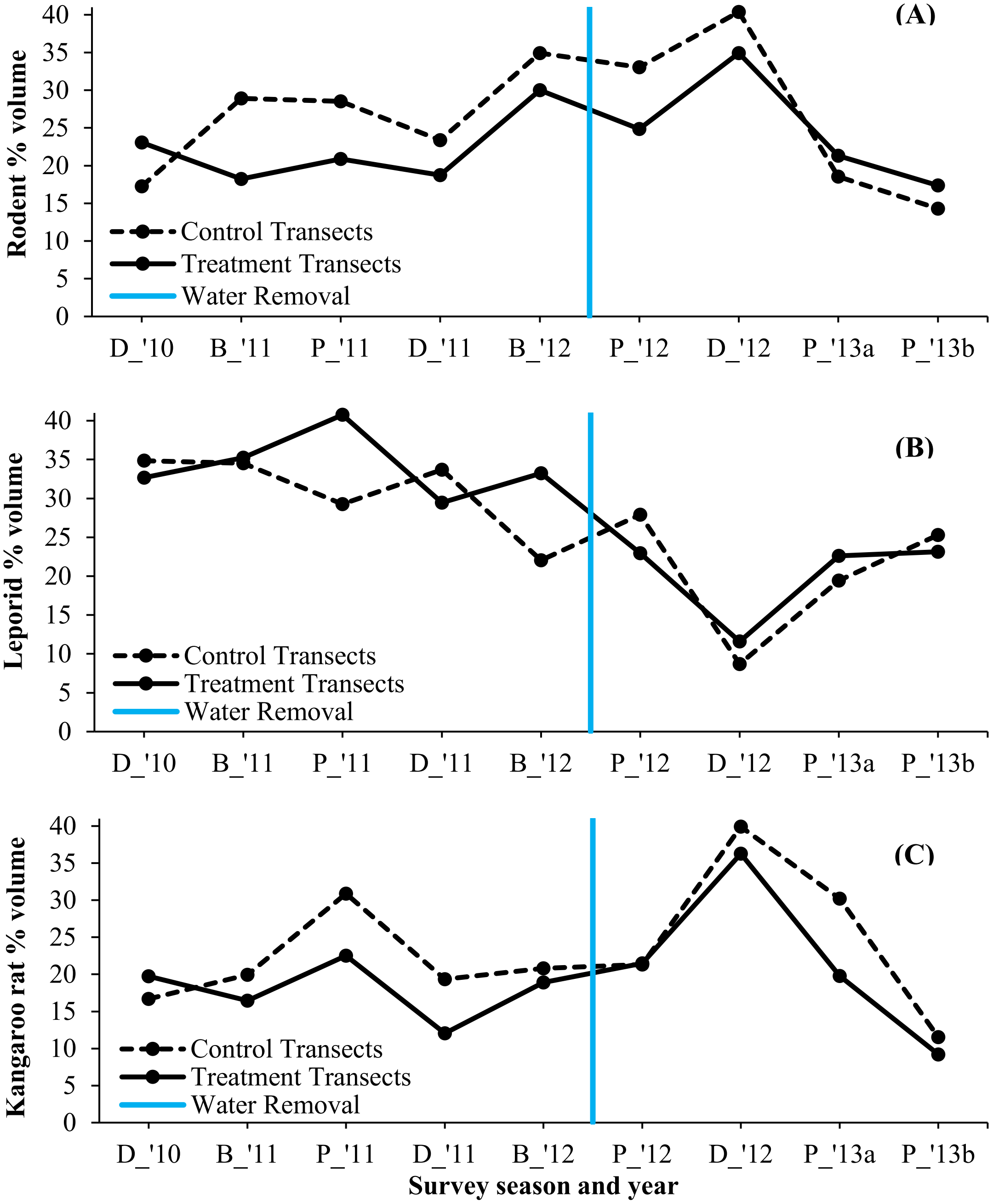


**Figure 2-6 A-C:** Percent volume of prey categories (**A**) rodent, (**B**) leporid, and (**C**) kangaroo rat, in coyote scats on control (dashed line) and treatment (solid line) transects across the nine surveys and the corresponding biological season: D = dispersal, B = breeding, P = pup-rearing on U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

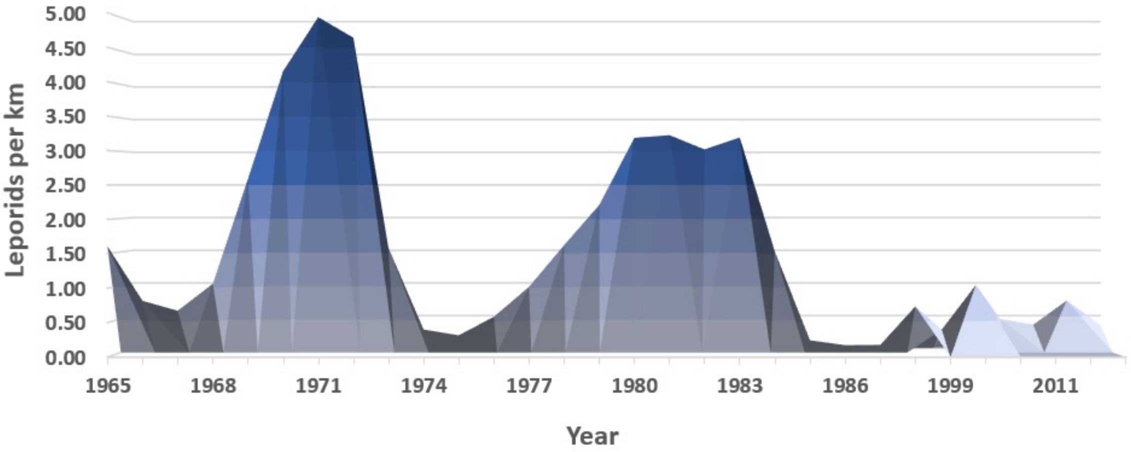


**Figure 2-7:** Historical leporid abundance compared to more current data on and near U.S. Army Dugway Proving Ground, Utah, USA, showing a decreasing trend of leporids but cycles still occurring. Data from Eberhardt and VanVoris 1965-1986, TRIES 1996-1997, Arjo 1999-2000, Kluever 2010-2013.

# CHAPTER 3

# DEMOGRAPHIC AND FUNCTIONAL RESPONSES OF KIT FOXES TO CHANGING PREY ABUNDANCE[2]

## Abstract

Large carnivores are often the focus of research and management, but range contraction of large carnivores across North America can permit smaller carnivores to fill the role of apex predator in these communities. These smaller carnivores (<15 kg), also termed mesocarnivores, can function as important ecosystem drivers and are more diverse in their behavior, ecology, and have higher species richness than their larger carnivore counterparts. The kit fox (*Vulpes macrotis*) is one of the smallest foxes in North America (~2 kg) and is considered a vulnerable species in Utah and the Intermountain West. We investigated demographic and functional responses of kit foxes to prey abundance using a 4-year (2010-2013) predator and prey data set collected on the U.S. Army Dugway Proving Ground in Utah's West Desert. Our objectives were to determine: 1) if kit fox litter size corresponded with changing prey abundance, 2) if kit fox pup survival responded to changes in prey abundance, and 3) if a functional response occurred between diet composition of kit foxes and changes in prey abundance. Rodent abundance and leporid density peaked in 2012 with both prey categories nearly doubling when compared to the previous year. Kit fox litter size and pup survival data from remote den cameras and radio-collared pups resulted in 26 potential natal dens with 14 litters having a total of 41 pups of known fate. During the 4-years, mean litter size was 3.9 (±

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[2] Co-authors are Eric M. Gese and Bryan M. Kluever; chapter is formatted for Journal of Arid Environments

1.4) pups/litter and we found no correlation between kit fox litter size and local rodent or leporid abundance. Survival rates for pups was 0.07, 0.01, 0.46, and 0.16, for 2010 to 2013, respectively, and we found a correlation between pup survival rates and local rodent abundance; leporid abundance appeared to not influence pup survival. Diet analysis showed the top four prey categories were rodent, insect, kangaroo rat, and leporid with overall percent occurrences of 31%, 22%, 18%, and 7%, respectively. Based on diet composition, we can infer that kit foxes demonstrated a functional response to changes in kangaroo rat availability as percent occurrence of kangaroo rat in the kit fox diet closely followed changes in kangaroo rat abundance. The occurrence of rodents in the kit fox diet followed declines in rodent abundance (excluding *Dipodomys* spp.). Seasonal leporid use by kit foxes was not correlated to leporid density. Kit fox demographics were dependent on rodent abundance and more specifically kangaroo rat availability. Historically, leporids reportedly filled this dietary role, but with the continuous decline of leporids since the 1950s, the kit fox appears to have switched to rodents as their primary prey. Understanding which population parameters of kit foxes are influenced by different prey species is critical information for the management and conservation of this vulnerable mesocarnivore.

## 1. Introduction

Food availability is required for the survival and growth of animal populations. Populations of specialist carnivores such as the common weasel, *Mustela nivalis*, and Canadian lynx, *Lynx canadensis*, have been found to cycle with their main prey (Stenseth et al., 1997; Mougeot et al., 2019). Other carnivore species have also been reported to track prey densities, including coyotes (*Canis latrans;* O'Donoghue et al., 1997), red foxes (*Vulpes vulpes*; Lindström, 1989), bobcats (*Felis rufus*; Knick, 1990), wolves (*Canis lupus*; Messier, 1994), and spotted hyenas (*Crocuta crocuta*; Hofer and East, 1995). Range contraction of large carnivores across North America is permitting the smaller carnivores to fill the role of apex predator in these communities (Laliberte and Ripple, 2004; Roemer et al., 2009). These smaller carnivores (<15kg), termed mesocarnivores, can function as important ecosystem drivers and are more diverse in their behavior, ecology, and their communities exhibit higher species richness than their larger carnivore counterparts (Roemer et al., 2009). There is some terminology debate whether these carnivores should be subdivided into mesocarnivores, as the mid-sized carnivores (e.g., coyotes, lynx, bobcats), and smaller carnivores (e.g., foxes, small wild cats) considered as small carnivores (Prugh and Sivy, 2020).

The kit fox (*Vulpes macrotis*) is one of the smallest foxes in the world, and is known for its fossorial behavior (Arjo et al., 2003) and occurrence in harsh arid ecosystems (Golightly and Ohmart, 1983). This mesocarnivore ranges from the southern borders of Oregon and Idaho to central Mexico (McGrew, 1979; Cypher and List, 2014). The kit fox is highly adapted to desert environments and is independent of free drinking water by utilizing preformed water from ingested prey (Golightly and Ohmart, 1984). Kit foxes use dens to rear their young, escape extreme temperatures, and for protection from predators (Arjo et al., 2003). The slim but quick and cryptic colored carnivore (McGrew, 1979) has a mass equal to one of its common prey items, the black-tailed jackrabbit (~2kg; *Lepus californicus*). The majority of their diet is comprised of rodents, leporids, and insects (Kozlowski et al., 2008; Byerly et al., 2018; Kelly et al., 2019). Kit fox populations have shown numerical responses to leporid abundance (Egoscue, 1975;

White and Garrott, 1997, 1999), but more recent research has shown rodents to be of greater dietary importance than leporids (Kozlowski et al., 2008; Kelly et al., 2019). This dietary change aligns with the reported decline of leporids across the Great Basin Desert (Arjo et al., 2007).

Cypher et al. (2000) found precipitation-mediated prey abundance was the key driver of a kit fox population in southern California. Other recognized kit fox population regulating factors include habitat loss (Cypher and List, 2014), and interspecific competition with other predators (White and Garrott, 1997; Clark et al., 2005). In California, kit fox populations were limited by high habitat fragmentation, and Cypher et al. (2013) urged future conservation efforts to focus on providing habitat connectivity and protection of high suitability habitat zones. Habitat conversion from native shrubs to invasive herbaceous vegetation and affecting prey abundance is another habitat related concern (Arjo et al., 2007; Kluever et al., 2019). Sources of kit fox mortalities differ between populations, but a principal source is typically coyote predation (White et al., 1995; Moehrenschlager et al., 2007; Kluever and Gese, 2017). Other predators have been documented to kill kit foxes such as golden eagles (*Aquila chrysaetos;* Kluever and Gese, 2017), red foxes (Clark et al., 2005; Ralls and White, 1995), and domestic dogs (*Canis lupus familiaris;* Ralls and White, 1995). In Mexico, a higher kit fox survival rate may have been due to smaller home ranges (decreased encounter rate with coyotes), and refuge holes in prairie dog towns (Moehrenschlager et al., 2007).

Kit foxes were once the most abundant carnivore in the West Desert of Utah at 0.15/km$^2$ (Egoscue, 1956, 1962). However, by 2014 the density had declined to 0.02/km$^2$ (Lonsinger et al., 2018), and is considered a vulnerable species in Utah (NatureServe, 2021). A sub-species, the San Joaquin kit fox (*V. macrotis mutica*), is federally listed as endangered and state listed as threatened in California (California Department of Fish and Wildlife, 2021). The uncertainty of the population status of the kit fox calls for additional research on the potential drivers of their population numbers and demographics. Kluever (2015) studied the relationships between wildlife and artificial water sources in Utah's West Desert, and as a result created robust carnivore and prey data sets that allowed for additional research examinations. Our study also overlapped with an evaluation of survey methods for detecting and estimating kit fox abundance (Dempsey et al., 2014). We investigated the demographic and functional responses of kit foxes to changing prey abundance using data collected during Kluever's (2015) 4-year study. Specifically, our objectives were to determine if: 1) litter size of kit foxes responded to changes in prey abundance, 2) the survival of kit fox pups responded to changes in prey abundance, and 3) a functional response occurred based on changes in diet composition and prey abundance.

## 2. Methods

### *2.1. Study area*

We collected data in the Great Basin Desert on the eastern portion of the U.S. Army Dugway Proving Ground (DPG) and surrounding land managed by the Bureau of Land Management (BLM) (Figure 3-1; Dempsey et al., 2014; Kluever and Gese, 2017). All surveys were conducted between 2010 and 2013 when mean daily temperatures ranged from -4.7 ºC to 36.7ºC with annual precipitation of 24.5, 26.6, 14.7, and 14.8 cm, respectively (MesoWest, Bureau of Land Management & Boise Interagency Fire Center).

The study area was categorized as a cold desert, and elevations ranged from 1302 to 2137m (Kluever et al., 2017). This area was home to a variety of mammals including kit foxes, coyotes, mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and feral horses (*Equis ferus caballus)*. The DPG has not been subjected to livestock grazing in over 60 years (Kluever, 2015), but domestic cattle (*Bos taurus*) were present on adjacent BLM land during this study. Primary vegetation communities included grassland (including exotic annuals), chenopod, pickleweed, vegetated dune, greasewood, shrubsteppe, and urban (Arjo et al., 2007; Kozlowski et al., 2008). These vegetation types support rodent species from the Heteromyidae and Cricetidae families, and leporid species including black-tailed jackrabbit and cottontails (*Sylvilagus spp.*).

### *2.2. Prey and predator abundance surveys*

All carnivore and prey abundance surveys were conducted on or in relation to 15 5-km road transects established across the study area (Figure 3-1; Dempsey et al., 2015). Road transects provided a framework for established survey methods such as scat deposition and spotlight surveys (Barnes and Tapper, 1985; Ralls and Eberhardt, 1997; Warrick and Harris, 2001). The dispersal season of 2010 marked the first time period when all carnivore and prey abundance surveys were completed. For clarity and analysis, we used surveys from this season onward. Survey results and analysis were organized into the three biological seasons for kit foxes: breeding (15 December—14 April), pup-rearing (15 April—14 August), and dispersal (15 August—14 December; Dempsey et al., 2014; Kluever and Gese, 2017).

Rodent abundance surveys were repeated across 16 sites with 49 live traps (Sherman Traps, Inc., Tallahassee, Florida) in a 7 x 7 grid pattern (for more study design details see Kluever et al., 2016). These surveys were restricted by temperature to warmer months (i.e., May to early October) due to weather concerns and the overnight safety of the live-trapped animals. Seven trapping sessions were completed between dispersal season 2010 and pup-rearing season 2013, which provided a rodent relative abundance index based on the number of unique individuals captured per grid/session (Kluever et al., 2016). Kangaroo rats (*Dipodomys spp)* were such a large portion of all prey that we analyzed them as a separate category from all other rodents.

Leporid spotlight surveys were conducted at night from vehicles along the same 15 5-km road transects previously described (Barnes and Tapper, 1985). Surveys were initiated an hour after dusk for three consecutive nights during clear and calm weather conditions using two 3 million candlepower spotlights (Kluever et al., 2017). At every leporid sighting we recorded location of vehicle, radial distance to the animal, angle to the animal, and species. Leporid spotlight surveys were conducted across all biological seasons and provided a relative abundance index (average number of leporids/transect/night/season). Leporid counts were insufficient for program Distance (Thomas et al., 2002) to calculate transect-level density estimates, but absolute annual and seasonal leporid density estimates were possible. Within the Distance software, we used the half-normal key function with a cosine adjustment to best fit our data and truncation of 70-m for leporid sightings for optimal detection function shape. We used leporid density estimates for annual and seasonal analysis, but when we required more spatially specific leporid numbers, we used relative abundance from the raw count data.

For estimating the relative abundance of resident predators, scat deposition surveys were performed along the established 15 5-km transects starting dispersal season

2010 for a total of nine surveys until the study concluded in late 2013. Scats collected during these surveys were used for our kit fox diet analysis. Transects were cleared by collecting scats using double-observers and walking opposite directions, and then returning 14 days later for the survey to again count and collect any deposited scats for abundance estimates (Gese, 2001; Schauster et al., 2002; Kluever, 2015). Relative abundance indices for the primary carnivores in our study area (i.e., kit fox and coyote) were calculated as the number of scats collected per transect per 14-day period (Davison, 1980; Kluever, 2015). Species, date, transect name, and UTM coordinates were recorded for each scat collected. Scats were dried under a heat lamp, then frozen until diet analysis.

### *2.3. Litter size and prey availability*

Remote infrared motion-triggered cameras (model NF4300; Cuddeback Digital, De Pere, WI) were placed at potential natal kit fox dens (i.e., a pair of kit foxes were displaying pup-rearing behaviors) to assess the reproductive success and litter sizes. A successfully reproductive female was defined by pups observed or captured at the den site (Cypher et al., 2000). Kluever et al. (2013) concluded that remote cameras at kit fox den sites produced more reliable counts than human observers. The highest number of pups recorded by the den cameras was consistent with the highest number of juveniles trapped and radio-collared at each den. On one occasion 3 pups were recorded on camera and 4 juveniles were later captured at that natal den.

Kit fox litter sizes were compared with prey abundance data to examine a demographic response. We used the average annual rodent and leporid abundance as litter size is probably determined by the females' condition prior to pupping (February/March; McGrew, 1979; Bronson, 1989), and our overall annual prey survey efforts may have detected artifact prey population fluctuations. For correlation analysis, we compared each litter size with the local prey levels from the closest rodent and leporid abundance surveys.

### *2.4. Pup survival and prey availability*

Pup survival analysis was based on remote camera data from each den site paired with telemetry data. The pups were radio-collared as they transitioned to juveniles and prior to potential dispersal. Dempsey et al. (2014) conducted trapping efforts across the study area but was primarily successful in the central and southern section of DPG. Radio-collared adult kit foxes from trapping efforts were then located at den sites and provided opportunistic capture of the entire or most of the fox family (Dempsey et al., 2014). For pup survival, we included pups of known fate to the end of the year determined by remote cameras and radio-collars. In 2011, we had two situations where the attending mother died early in the pup-rearing season and den cameras revealed a rapid decrease in pups present at the den; we assumed the death of these pups ($n = 7$) given their young age (≤ 3 months). We excluded any dispersals or resident juveniles with unknown time and cause of death (e.g., only the radio-collar was located), which reduced the 14 litters to 12 litters for analysis. Program MICROMORT (Heisey and Fuller, 1985) was used to calculate pup survival rates based on the interval of time each pup survived to the end of the year then we averaged pup survival across litters. Unfortunately, sample sizes were limited, and more robust pup survival analysis was not possible. Pup survival rates were compared to local prey abundance data using Pearson's correlation coefficient and linear regressions in R to test the relationship between pup survival and prey indices (i.e., rodent and leporid) (R Core Team 2020).

### 2.5. *Diet*

Lonsinger et al. (2016) studied the persistence of scats across the same study area roadways and concluded that minimal scats remained after 42 days. Furthermore, vehicle traffic and natural decay over 14 days resulted in an average of 65.6% scat removed. Thus, Lonsinger et al. (2016) research supplied a justification for including the scats during the clear portion of the scat deposition survey resulting in us including all kit fox scats collected during both the clear and the survey for each scat deposition session to add to our diet analysis.

Each frozen scat was placed in a black nylon bag with a uniquely numbered metal tag. Samples were thawed in hot soapy water (Kelly, 1991) in 5-gallon buckets for ≥24 hours. No more than 60 samples at a time (Bartel, 2003) were then placed in a standard washing machine on a delicate cycle with a mild detergent to remove fecal matrix material. In an attempt to minimize content loss, scats were air-dried outside (weather permitting) for ≥24 hours or inside the building under a laboratory fume hood. Each scat sample was separated in a clear sorting tray and prey items were identified. Prey items (e.g., hair, teeth, and bones) were determined using Utah State University's extensive specimen collection, a dorsal guard hair guide (Moore et al., 1974), and an animal skull identification key (Elbroch, 2006).

Following Kozlowski et al. (2008), we classified prey/food items into the same 11 categories: anthropogenic, fruits and plants, scorpion, insect, reptile, bird, rodent, kangaroo rat, leporid, miscellaneous mammal, and ungulate. We defined percent occurrence of prey categories as the number of occurrences of an item divided by the total number of occurrences of all prey items (Kelly, 1991; Kozlowski et al., 2008; Dowd and Gese, 2012). The percent volume of each prey item within each scat was estimated to the nearest 10% using a simple grid system (Dowd and Gese, 2012; Wysong et al., 2019). Concurrent projects required the trapping and radio-collaring of kit foxes (Dempsey et al., 2014; Kluever and Gese, 2017), which provided additional scat samples that were frequently available and collected during capture efforts. The Shannon diversity index with base 10 log (Shannon and Weaver, 1964) was calculated per year to compare between years, and to a previous kit fox diet study occurring within the same spatial extent as ours (Kozlowski et al., 2008).

### 2.6. *Functional response based on diet composition*

We plotted the relative rodent abundance and leporid density against their associated percent occurrence in the kit fox diet across each biological season during the 4-year study. Rodent trapping was restricted to the warmer months and only overlapped with scat deposition surveys five times. Therefore, we were unable to statistically compare the two data sets, but there were notable trends between certain prey use and availability. We deemed the kangaroo rat genus such an important item in the kit fox diet that we divided the rodents into two categories: kangaroo rat and non-kangaroo rat. For qualitative analysis, we separately compared the percent occurrence of two rodent categories with abundance estimates from trapping surveys. The non-invasive leporid spotlight surveys were conducted during all weather conditions and resulted in eight surveys that overlapped with scat deposition surveys. We compared the percent occurrence of leporid in the kit fox diet with leporid densities both qualitatively and quantitatively. Regression analysis were performed in R to test the relationship between leporid occurrence in the kit fox diet and leporid density (R Core Team 2020). We made no attempt to quantify the actual number of prey consumed, but other studies have used diet composition and prey abundance to infer a functional response (Forsyth et al., 2018).

## 3. Results

The percent of potential natal dens that successfully reared pups was 67% for 2012, and 50% for the other three years of the study (Table 3-1). The number of potential natal dens with pairs exhibiting pup-rearing behavior was 6 for the first three years and 8 dens during the last year of the study for a total of 26 dens (Table 3-1). We had 14 litters with a total of 41 pups with known fate over the 4-year study. Between 2010 and 2013, we documented 33 radio-collared females with a confirmed home range during pup-rearing season. There was only one juvenile female (1-year-old) and she did not reproduce in 2010. All other reproductive females (successful or not) were adults. During 2010 to 2013, the number of successfully reproductive females was 3, 3, 4, and 4, respectively. The number of unsuccessfully reproductive females was 6, 4, 4, and 5, from 2010 to 2013, respectively.

The annual rodent abundance index was similar in 2010 and 2011, but then nearly doubled in 2012 before dropping to the lowest recorded abundance during the study in 2013 (Table 3-1). Indices of kangaroo rat accounted for 77% (*SD* = 4.6%) of the rodent abundance every season (Figure 3-2A) when compared to all other rodents (Figure 3-2B). However, both prey categories experienced similar fluctuations across survey seasons (r = 0.71; Figure 3-2A, B). Kluever et al. (2016) found the increase in 2012 rodent abundance was likely a result of the previous year's precipitation, which lead to higher plant productivity and increased rodent vital rates. Program Distance annual leporid density estimates averaged 6.77 (*SD* = 1.92) leporids/km$^2$, over the 4-years with a peak in

2012 (Table 3-1). The highest leporid density recorded was during pup-rearing 2012 (14.4 leporids/km$^2$) when the population appeared to cycle (Figure 3-2C). Our estimated leporid densities were comparable to Lightfoot et al. (2010) in the Chihuahuan Desert.

Kit fox and coyote relative abundance indices, based on nine scat deposition surveys, showed both canids followed similar seasonal fluctuations (Figure 3-3). In dispersal season 2012, coyote relative abundance was 2-fold greater than previous dispersal seasons, and kit fox relative abundance also at its highest. Considering the surges in rodent abundance and leporid density in 2012, it would appear the increase in prey resources favored both predators.

Mean litter size varied annually (Table 3-1) and we found no correlation between kit fox litter size and local rodent abundance (r = -0.06, F = 0.05, P = 0.83) or leporid abundance (r = -0.29, F = 1.09, P = 0.32). In 2012, litter sizes did not increase despite overall rodent abundance and leporid density nearly doubling across the study area nor was there an increase in litter sizes the following year after increased prey resources (Table 3-1, Figure 3-4). Annual survival rates for kit fox pups was 0.07, 0.01, 0.46, and 0.16, 2010 to 2013, respectively (Table 3-1, Figure 3-5). We found some evidence for a correlation between pup survival rates and local rodent abundance (r = 0.48, F = 3.05, P = 0.11; Figure 3-6A). We found no correlation between pup survival rates and local leporid abundance (r = 0.06, F = 0.34, P = 0.86; Figure 3-6B).

We completed diet analysis of 611 kit fox scats. No anthropogenic items were found in any kit fox scats. The fruits and plants category contained Russian olive (*Elaeagnus angustifolia*), Indian ricegrass (*Achnatherum hymenoides*), cheatgrass (*Bromus tectorum),* and various other grasses. Scorpions (*Centruroides* spp.) were recorded, and insects found included Mormon cricket (*Anabrus simplex*), Jerusalem cricket (*Stenopenmatus fuscus*), ladybug (*Coccinellidae* spp.), various grasshoppers (*Orthoptera* spp.), and beetles (*Coleoptera* spp.). The reptile category included one gopher snake (*Pituophis melanoleucus*) and several lizard species (*Squamata* spp.). Various bird remains were documented but were not identified to species. Rodents were the most diverse category and included desert woodrat (*Neotoma lepida*), western harvest mouse (*Reithrodontomys megalotis*), deer mouse (*Peromyscus maniculatus*), montane vole (*Microtus montanus*), Botta's pocket gopher (*Thomomys bottae*), Great Basin pocket mouse (*Perognathus parvus*), long-tailed pocket mouse (*Chaetodipus formosus*), Townsend's ground squirrel (*Spermophilus townsendii*), and white-tailed antelope squirrel (*Ammospermophilus leucurus*). Ord's kangaroo rat (*Dipodomys ordi*) and chisel-toothed kangaroo rat (*Dipodomys microps*) represented the kangaroo rat category. Predominantly black-tailed jackrabbit (*Lepus californicus*), but also cottontails (*Sylvilagus* spp.), were documented in the leporid category. The miscellaneous mammals included a single occurrence of porcupine (*Erethizon dorsatum*). The ungulate category comprised of mule deer, cow, and feral horse.

The top four prey categories over the 4-years of data were rodent, insect, kangaroo rat, and leporid with overall percent occurrences of 31.4, 22.3, 18.2, and 6.6%, respectively (Table 3-2). These prey categories encompassed 78.5% of all prey occurrences within the kit fox diet while the other 7 categories were each <10% (Table 3-2). All of the top prey categories seasonally fluctuated to some degree, but it was the insect category that illustrated the most extreme seasonal fluctuations (Figure 3-7). Percent volume indicated the same importance of the top four prey categories within the kit fox food habits but slightly changed in the ranking. Kangaroo rats provided more prey by volume than the insect category (Table 3-2). Out of the 53 scats with fruit or plant present, only 12 scats contained >50% grass by volume. The single occurrence of a porcupine was recorded as <10% by volume. The Shannon diversity indices (*H'*) per year averaged 0.77 (range: 0.71 to 0.82) during our 4-year study (Table 3-2).

Based on changes in diet composition, we infer that kit foxes demonstrated a functional response to changes in kangaroo rat availability as percent occurrence of kangaroo rat in the kit fox diet closely followed kangaroo rat abundance (Figure 3-2A). Percent occurrence of other rodents (excluding the kangaroo rat genus) corresponded to declines in rodent abundance, but rodent use did not follow changes in availability every season (Figure 3-2B). Percent occurrence of leporid in the kit fox diet did not closely follow leporid availability (Figure 3-2C). Seasonal leporid use by kit foxes was not correlated to leporid density (r = 0.06, F = 0.03, P = 0.88).

## 4. Discussion

We found kit fox litter sizes averaged 3.9 pups/litter, which was consistent with other kit fox studies that typically average around 4 pups/litter (Moehrenschlager et al., 2004). Cypher et al. (2000) had a mean litter size of 3.8 in a 16-year dataset on San Joaquin kit foxes. However, a lower mean litter size was reported in a different area of California, at 2.7 pups/litter in a 2-year study (Randel, 2016). In 2010, we had one litter of 7 pups, but this was likely the result of cooperative parenting and polygyny, as two lactating adult females were captured with the pups. This phenomenon has been previously observed in kit foxes and genetically determined in swift foxes, *Vulpes velox* (Kitchen et al., 2006; Kluever et al., 2013). The ecological significance and drivers of litter size have been long-term questions in ecology and life history theory (Lack, 1948). Biologists have reported several important mechanisms affecting litter size, and one common deduction is maternal condition driven by food supply (Bronson, 1989; Lack, 1948; Stearns, 1992). Demographic parameters such as litter size contribute to an overall numerical response of a population (Holling, 1959; Krebs, 2001). In arctic foxes, *Alopex lagopus,* litter and population sizes were determined by food availability (Tannerfeldt and Angerbjorn, 1998). Numerical responses by kit foxes have been reported when prey is scarce (Egoscue, 1975; White and Ralls, 1993). Therefore, we predicted kit fox litter sizes would respond accordingly to any changes in prey abundance. In 2012, both rodent and leporid levels nearly doubled, but litter sizes remained between 2 and 5 pups/litter in both 2012 and 2013. In 2013, rodent abundance was the lowest of the 4-years, and yet litter size remained unaffected. Our study had 3 to 4 successfully reproductive females every year despite changing prey levels. Using the most spatially relevant rodent and leporid abundance data for each den area, we found no correlation between kit fox litter size and local prey abundance.

In contrast to litter size, survival rates of pups were correlated with rodent abundance, with both peaking in 2012. Interval survival rates for pups was 0.07, 0.01, 0.46, and 0.16, 2010 to 2013, respectively, suggesting a demographic response by kit foxes in 2012 to the increase in rodent abundance. Leporid abundance appeared to not influence pup survival rates. A low sample size of pups per year resulted in wide confidence intervals, which is a recurring problem among investigations on mammalian carnivores. But a small sample size should not discredit the importance of the research question (Bissonette, 1999). These results were consistent with survival models conducted on the same kit fox population showing survival was mainly influenced by age and rodent prey base (Kluever and Gese, 2017). Furthermore, Arjo et al. (2007) concluded in the early 2000s that the DPG kit fox population depended on the survival of its juveniles, which is dependent on prey populations. Low prey abundance probably leads to lower hunting efficiency (Erlandsson et al., 2017), and possibly reduces the frequency of food provided to the pups (McGrew, 1979). Lower hunting efficiency may expose the parental foxes to higher predation risk, leaving the den undefended longer, and possibly increasing juvenile predation and starvation risks (Erlandsson et al., 2017). The high prey base we documented in 2012 was the highest during our study, but not high enough to create a response in kit fox litter size. However, it did increase pup survival, but we do not know the exact mechanism (i.e., hunting efficiency, parental care, predation risk, increased philopatry). In arctic foxes, litter size and juvenile survival followed rodent population cycles, thereby affecting the population structure of arctic foxes (Elmhagen et al., 2000; Meijer et al., 2013). Variations in vole abundance can alter red fox diet, growth, ovulation rate, and mean litter size (Lindström, 1982, 1983, 1989). It is also possible that female kit foxes in general may be physiologically unable to produce larger litter sizes (e.g., > 7 pups; O'Neal et al., 1987; Cypher et al., 2000).

Pup survival from this study and the overall effects of rodent abundance on juvenile survival (Kluever and Gese, 2017) were consistent with our diet analysis ranking rodents as the most important food category. Diet analysis showed the top four prey categories were rodents, insects, kangaroo rats, and leporids with overall percent occurrences of 31.4, 22.3, 18.2, and 6.6%, respectively. In 2012, rodent and kangaroo rat categories were 52.8% occurrence of all prey items in the kit fox diet, which was the highest out of the 4-year study and consistent with the increase in the rodent abundance index for that year. Based on diet composition, we infer that kit foxes demonstrated a functional response to changes in kangaroo rat availability as percent occurrence of kangaroo rat in the kit fox diet closely followed kangaroo rat abundance. Percent occurrence of other rodents did not closely follow rodent availability at every time step, but the kit fox diet did correspond to the decline in rodent abundance. Kelly et al. (2019) reported a dietary response by kit foxes to increased anthropogenic food items when primary native prey had declined.

Seasonal dietary use of leporids by kit foxes was not correlated to leporid density. Our results suggest that kit fox demographics were highly dependent on rodent abundance and more specifically, the abundance of kangaroo rats. Historically, leporids reportedly filled this dietary role, but with the continuous decline of leporids since the 1950s, the kit fox appears to have switched to rodents as their primary prey. Egoscue (1962) reported jackrabbits accounted for 94% of prey items by weight within 64 days based on prey remains around den sites. Despite our different approaches for examining prey use than Egoscue (1962), we feel our results suggest a substantial decrease in leporid use as our overall percent volume of leporids was <10% of kit fox scats. Similarly, the seasonal percent occurrence of leporids illustrated constant use as a prey item, which never exceeded 11.1% (Figure 3-7). More contemporary studies on DPG than the works of Egoscue have also confirmed a decrease in leporid use by kit foxes, and an increase in the dietary importance of the rodent categories. Kozlowski et al. (2012) reported on the percent occurrence data from kit fox scats collected between 1999 and 2001, and showed kangaroo rats to be the most important prey item, but our data suggest the kit fox diet has become slightly more generalized towards all rodents (Figure 3-8). The percent occurrence of leporids has declined between the two studies from 11.1% to 6.6%, respectively. The Shannon diversity index indicated that the kit fox diet has slightly increased over the 10 years from 0.73 to 0.77 between studies. Kozlowski et al. (2008) had a low presence of anthropogenic items, but we did not observe any such items during this study. The work of Byerly et al. (2018) overlapped in temporally with ours in 2013, but calculated percent occurrence differently using only the top four prey categories in addition to surveying an overall larger area. However, all three DPG kit fox diet studies since 1999 have indicated all rodents and insects were of higher dietary importance than leporids. Percent occurrence can over-represent a physically small prey category (e.g., insects) as all prey occurrence categories must equal 100% (Ciucci et al., 1996), but the percent volume of insects indicated it was still in the top four prey categories (Table 3-2).

Prey availability can influence kit fox recruitment rates, but high prey abundance does not guarantee an increase in kit fox population size (Warrick et al., 1999). Coyotes can be a source of exploitative and interference competition for kit foxes (Cypher and Spencer, 1998; Lonsinger et al., 2017), which kit foxes attempt to alleviate by spatially minimizing their overlap with coyotes (Kozlowski et al., 2012). White and Garrott (1997) examined kit fox and swift fox studies and concluded fox populations may be regulated by both prey abundance and competition by coyotes. However, coyote control operations aiming to relieve this competition, and improve kit fox populations have been unsuccessful. Cypher and Scrivner (1992) found no increase in kit fox numbers or survival rates after almost 600 coyote removals, and there was no reduction in predator-caused fox mortalities. The increase in kit fox pup survival rates and overall survival (Kluever and Gese, 2017) in 2012, provided the potential for kit fox numbers to improve the following year (2013) due to recruitment. However, kit fox relative abundance estimates from seasonal scat deposition surveys in 2013 were consistent with previous seasons (Figure 3-3). Dempsey et al. (2014) concluded that scat depositions surveys had the highest detection probability and correlation to kit fox abundance when conducted in the breeding season. Unfortunately, the two scat deposition surveys conducted in 2013 were in the pup-rearing season, and we do not have abundance estimates for the breeding season. However, the scat deposition survey during the dispersal season 2012 exhibited the highest recorded kit fox abundance index during the study, which is consistent with our increased pup survival for that year resulting in more juveniles on the landscape. Higher relative abundance during dispersal seasons are expected as juveniles are highly mobile and dispersing from natal areas (Schauster et al., 2002).

Kluever and Gese (2017) reported 48% of kit fox mortalities were due to coyote predation. We analyzed these same mortalities annually to determine if high prey abundance possibly lead to lower encounter rates with coyotes, thus a lower percentage of kit foxes killed by coyotes. In 2012, we observed the highest prey abundance, and yet percent mortalities attributable to coyotes was also at an annual high (Table 3-3). During 2010 to 2013, coyote predation accounted for 43.8, 30.0, 66.7, and 53.3% of all radio-collared kit fox mortalities, respectively. Therefore, an increase in prey populations did not appear to decrease interference competition between kit foxes and coyotes. However, our total number of kit fox mortalities was lowest in 2012, and mortalities caused by other sources were lower. Eagle predation was the cause of 7 kit fox mortalities during this study, but none of these mortalities occurred in 2012 when prey abundance was high. The status of the local eagle populations was not monitored, and any conclusions beyond this observation would be speculative. However, golden eagles (*Aquila chrysaetos*) have been reported as the second highest cause of mortalities of swift foxes in Canada (Moehrenschlager et al., 2007). A synchronous numerical increase in the coyote population could explain the higher proportion of kit foxes killed by coyotes in 2012 despite higher prey availability. Coyote litter size has been shown to be more variable than kit foxes (Gese 2005), which could have led to the species benefiting more than kit foxes from increased prey availability. The relative abundance of coyotes based on the scat deposition surveys indicated an increase in coyotes on the landscape particularly during dispersal 2012 (Figure 3-3). The percent of kit foxes killed by coyotes out of all radio-collared kit foxes monitored each year was relatively constant (18.8 ± 3.1%) within our population (Table 3-3). During this study, 1,861 coyote scats were also processed for percent occurrence into the same 11 prey categories and according to Horn's similarity index, there was high dietary overlap with kit foxes (Horn, 1966). The dietary overlap between coyote and kit fox was similar to previous research (0.885; Kozlowski et al. 2008), and overlap was high throughout our study at 0.894 ± 0.037 with a value of 1.0 indicating complete dietary overlap (Table 3-3). The high dietary overlap between the two carnivores, and the constant predation of kit foxes by coyotes, were consistent with Lonsinger et al. (2017) findings that kit fox detection and probability of local extinction were both positively related to coyote activity.

Another possible explanation for the lack of a numerical response by the kit fox population in our specific study area could be compensatory dispersal and a saturated carrying capacity. Karki et al. (2007) found swift fox juveniles had higher survival, but dispersed sooner in coyote removal areas, thereby not changing the population density because all suitable habitat was occupied. Karki et al. (2007) reported a swift fox density of 0.26 foxes/km$^2$ while Lonsinger et al. (2018) found the kit fox population in our study area to be 0.02 foxes/km$^2$ in 2013 and 2014. While these study sites differ in fox densities, habitat, and prey base, the same population pressures of resource dependent saturation could still apply to the DPG kit foxes. Unfortunately, we did not have enough dispersal data to test the timing of our juvenile dispersals. In 2015 and 2016, scent stations were used to examine kit fox detectability and occupancy across Utah including the DPG (Richards, 2017). Out of the 5 sites sampled in the Great Basin Desert, DPG had the lowest rate of occupancy despite having the highest relative probability of use as determined by kit fox habitat models (Richards, 2017). Based on Richards (2017) findings, it would appear the general DPG kit fox population status has not improved since our data was collected two years prior. Alternatively, low sample size could also explain the lack of observed numerical response.

Based on our results, kit fox litter size did not respond to changing prey abundance, but a demographic response was observed in kit fox pup survival the year which exhibited higher prey abundance. Our inference of a functional response by kit foxes to kangaroo rats was based on kit fox diet composition and kangaroo rat abundance. Future kit fox diet studies should strive for temporally larger datasets for a more statistically robust functional response analysis. Understanding which kit fox population parameters are influenced by prey abundance, and if they’re more sensitive to changes in certain prey species, is critical information for the management and conservation of this vulnerable mesocarnivore.

Lonsinger et al. (2020) provided a thorough review and recommendations on kit foxes in the Great Basin Desert, and advocates for more studies on kit fox metapopulation dynamics. These knowledge gaps should be addressed, but habitat conversion is of greater concern and likely one of the main long-term threats to kit fox persistence (Cypher and List, 2014). The DPG kit fox population is safe from agricultural habitat conversion, but invasive cheatgrass, *Bromus tectorum,* has changed the grasslands across the Great Basin Desert (Chambers et al., 2007). We suggest that future research efforts also focus on prey populations and habitat health. Rodent-cheatgrass studies have shown a negative correlation with cheatgrass cover (Hall, 2012; Bachen et al., 2018). Some rodent species can tolerate or even benefit from the invasive annual grass to a certain degree, but eventually exhibit a negative response as cheatgrass becomes more pervasive (Smith et al., 2017; Kluever et al., 2019). The kit foxes in the West Desert of Utah have shown foraging plasticity by shifting their diet towards rodents with the decline in leporid availability over the last 60 years. Prey abundance has a direct positive influence on kit fox density and reproductive rates (White and Garrott, 1999; Cypher et al., 2000). To promote positive kit fox population responses (i.e., functional and demographic) to changing prey, future kit fox conservation strategies must also focus on improving prey and habitat conditions, especially in harsh arid environments.

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## Tables and Figures

**Table 3-1:** Annual number of potential natal dens (i.e., kit fox pairs showing pup-rearing behavior), natal dens with confirmed pups (via observations and remote cameras), litter sizes, radio-collared pups with known fate, pup survival rates, and measures of prey abundance, U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| **Year** | **# potential natal dens (# natal dens with pups)** | **Mean litter size (±SD)** | **# pups of known fate** | **Pup survival rate** | **Rodent abundance index** | **Leporid density (#/ km$^2$)** |
|---|---|---|---|---|---|---|
| **2010** | 6 (3) | 4.7 ± 2.1 | 12 | 0.07 | 13.52 | 6.91 |
| **2011** | 6 (3) | 4.0 ± 2.0 | 10 | 0.01 | 13.28 | 4.30 |
| **2012** | 6 (4) | 3.5 ± 0.6 | 12 | 0.46 | 21.72 | 9.00 |
| **2013** | 8 (4) | 3.3 ± 1.3 | 7 | 0.16 | 8.50 | 6.86 |

**Table 3-2:** Annual percent occurrence, overall percent occurrence, and overall percent volume of 11 prey categories (top categories are in bold) in kit fox scats ($n = 611$), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| | **% Occurrence** | | | | | **% Volume** |
|---|---|---|---|---|---|---|
| ***Prey category*** | **2010** | **2011** | **2012** | **2013** | **Overall** | **Overall** |
| Anthropogenic | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Bird | 0.0 | 6.2 | 3.2 | 6.2 | 4.8 | 1.7 |
| Fruit & plants | 6.0 | 4.1 | 3.8 | 3.8 | 4.1 | 3.0 |
| **Insect** | 25.0 | 21.1 | 23.3 | 21.8 | 22.3 | 16.2 |
| **Kangaroo rat** | 15.5 | 16.0 | 19.6 | 20.6 | 18.2 | 27.0 |
| **Leporid** | 2.6 | 7.5 | 4.6 | 9.1 | 6.6 | 7.9 |
| Misc. mammal | 0.0 | 0.0 | 0.3 | 0.0 | 0.1 | 0.0 |
| Reptile | 2.6 | 1.7 | 2.4 | 2.4 | 2.2 | 0.7 |
| **Rodent** | 33.6 | 32.8 | 33.2 | 26.5 | 31.4 | 37.0 |
| Scorpion | 14.7 | 9.8 | 8.0 | 8.2 | 9.3 | 5.4 |
| Ungulate | 0.0 | 0.9 | 1.6 | 1.5 | 1.2 | 1.2 |
| ***Diversity Index*** | | | | | | |
| Shannon *H’* | 0.71 | 0.79 | 0.77 | 0.82 | 0.77 | |

**Table 3-3:** Annual kit fox mortalities based on radio-collared individuals, and Horn's similarity index between kit fox and coyote scats, U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

| **Year** | **Total # kit fox mortalities** | **# killed by coyote** | **% killed by coyote** | **# kit fox monitored that year** | **% all monitored kit foxes killed by coyote** | **Horn's index** |
|---|---|---|---|---|---|---|
| 2010 | 16 | 7 | 43.8% | 31 | 22.6% | 0.842 |
| 2011 | 10 | 3 | 30.0% | 20 | 15.0% | 0.895 |
| 2012 | 9 | 6 | 66.7% | 33 | 18.2% | 0.918 |
| 2013 | 15 | 8 | 53.3% | 41 | 19.5% | 0.922 |
| ***total*** | ***50*** | ***24*** | | | | |

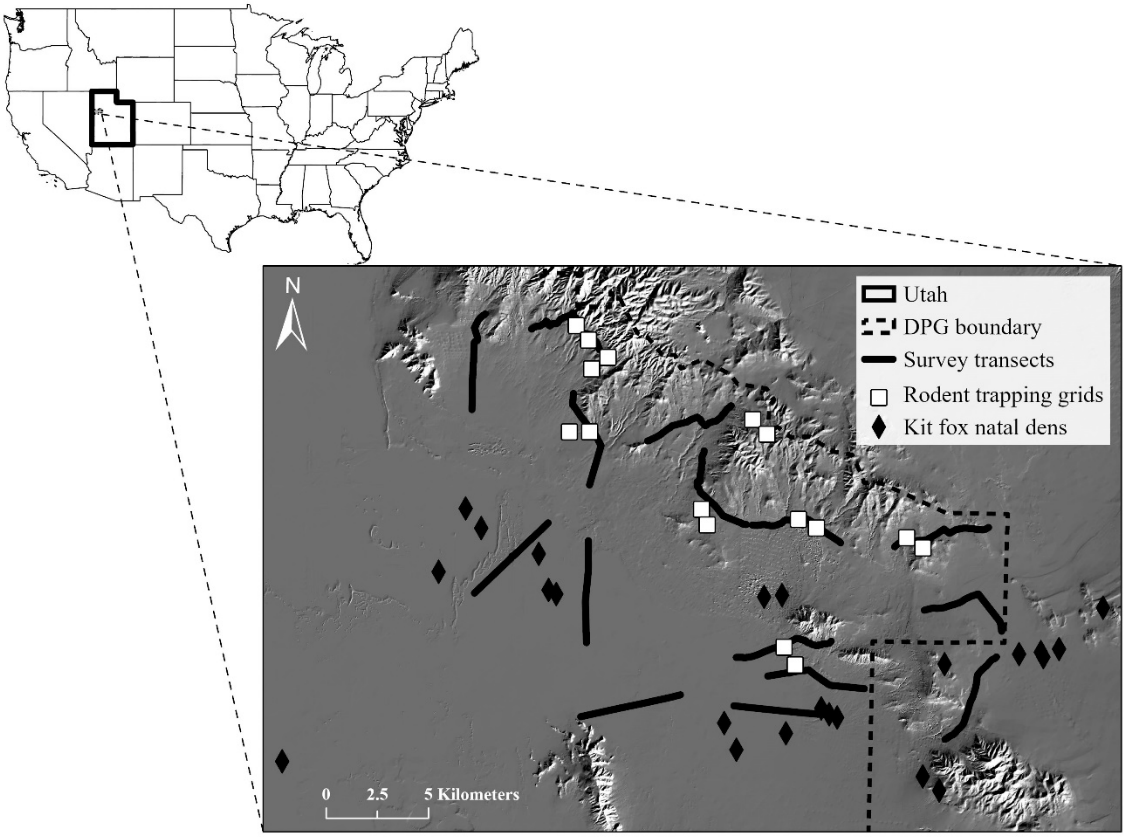

**Figure 3-1:** Locations of scat deposition and leporid spotlight survey transects, rodent trapping grids, and kit fox natal dens, U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

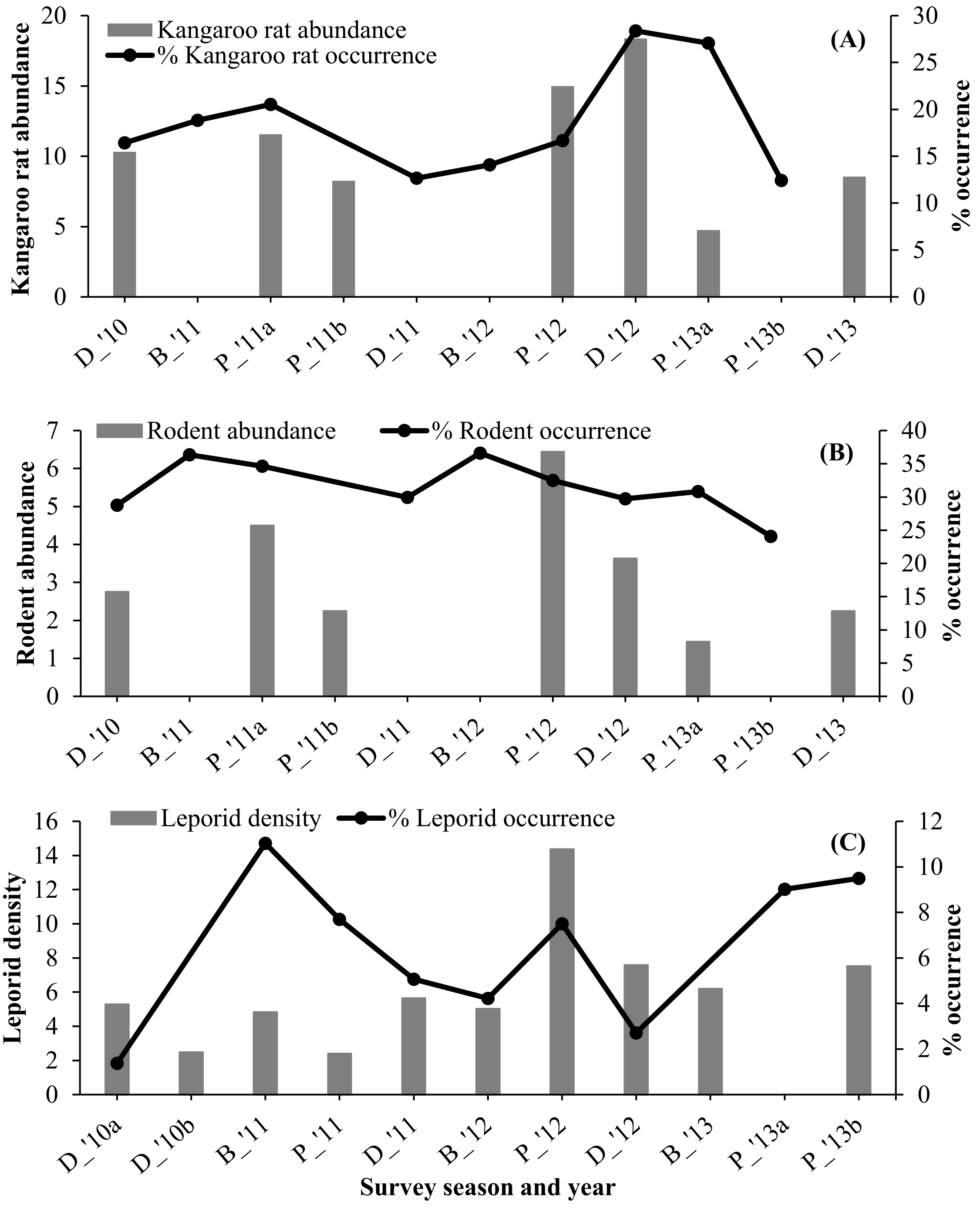

**Figure 3-2:** Seasonal relationship between (**A**) kangaroo rat abundance, (**B**) other rodent abundance (excluding kangaroo rats), and (**C**) leporid density (leporids/km$^2$), and the associated prey percent occurrence in the kit fox diet within each biological season: D = dispersal, B = breeding, P = pup-rearing, U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

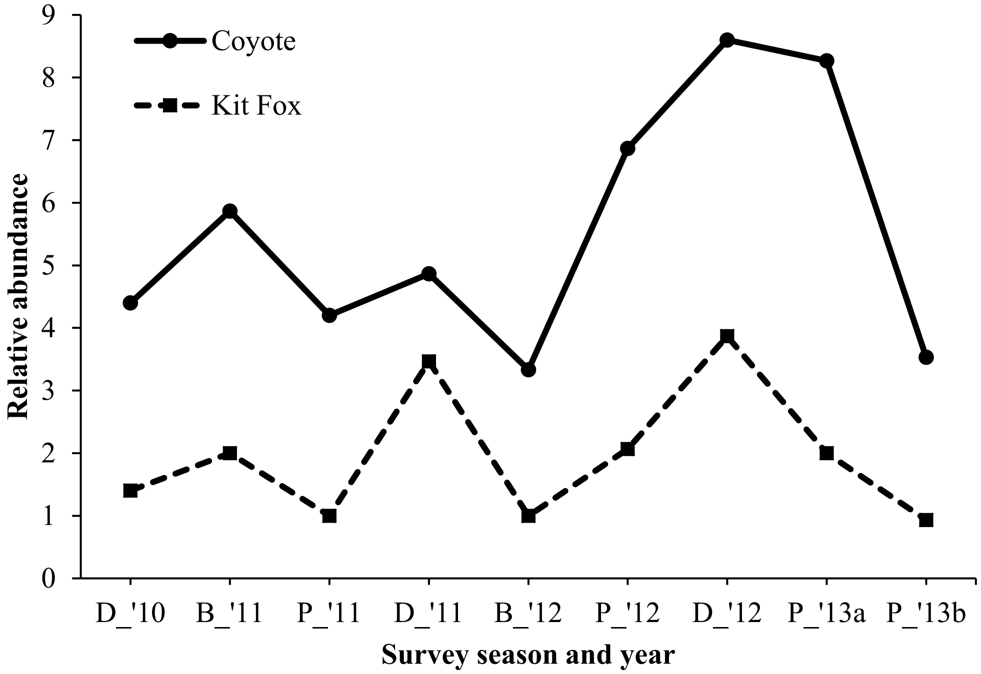

**Figure 3-3:** Estimates of coyote and kit fox relative abundance across seasons based on nine scat deposition surveys (# scats/transect/survey), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

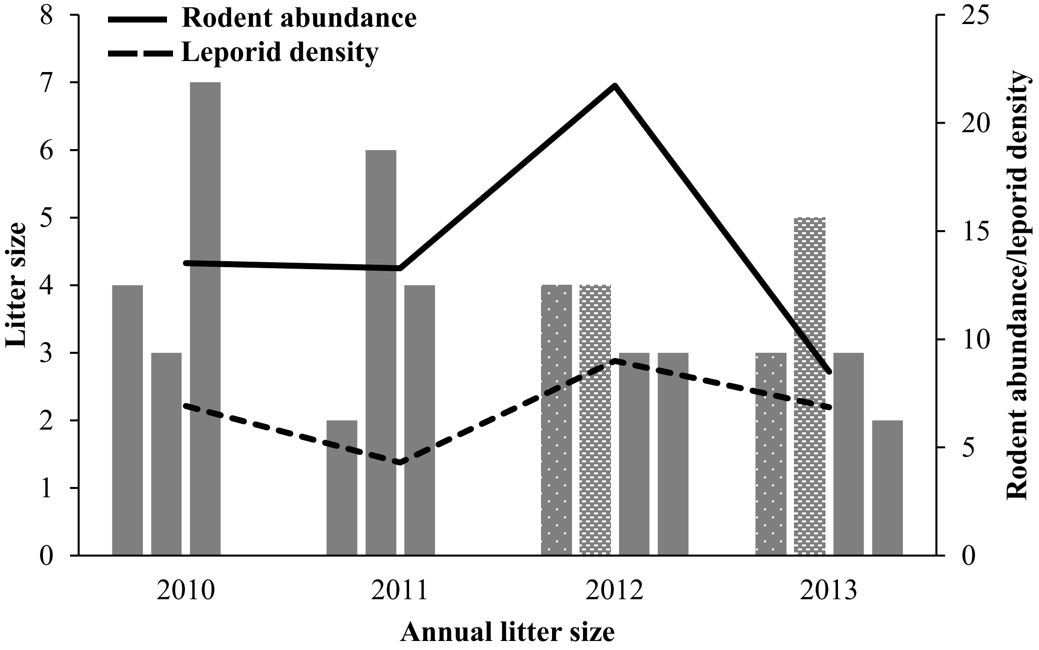

**Figure 3-4:** Annual kit fox litter sizes compared to changes in overall rodent abundance and leporid density (leporid/km$^2$), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013. Only two radio-collared females survived and successfully produced two annual litters: F44 (dots) and F31 (stripes).

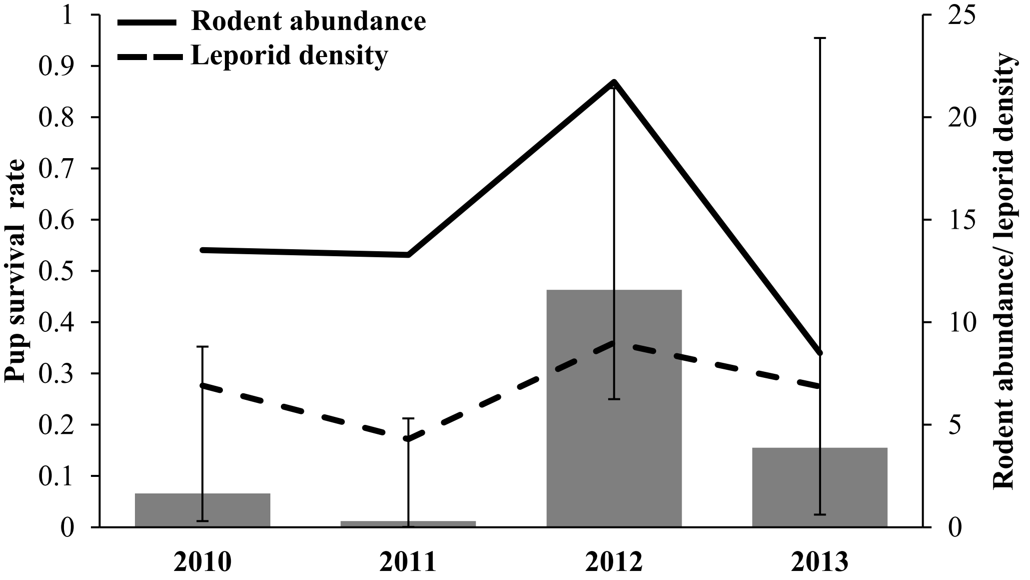

**Figure 3-5:** Annual kit fox litter survival rates and 95% confidence intervals and overall rodent abundance and leporid density (leporids/km$^2$), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

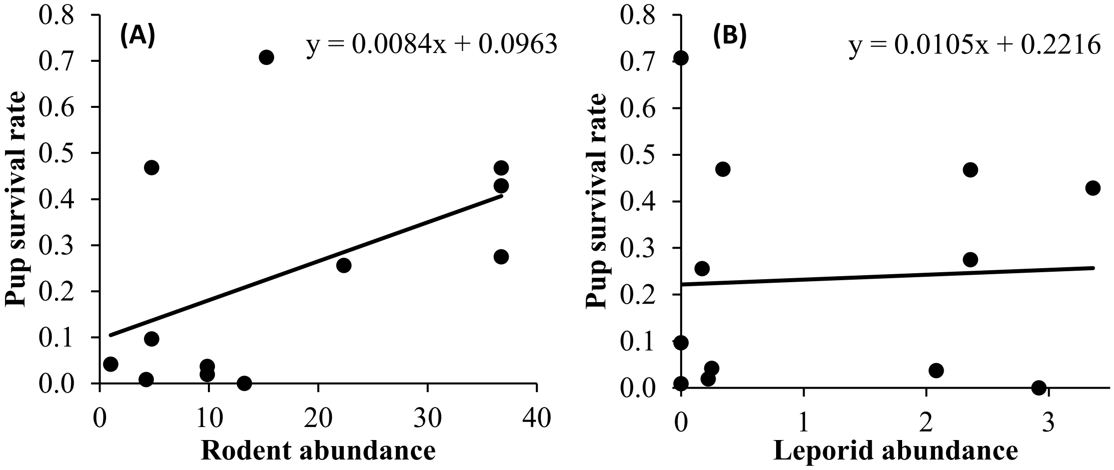

**Figure 3-6:** Relationship between survival rates of kit fox pups and (**A**) small mammal abundance, and (**B**) leporid abundance, U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

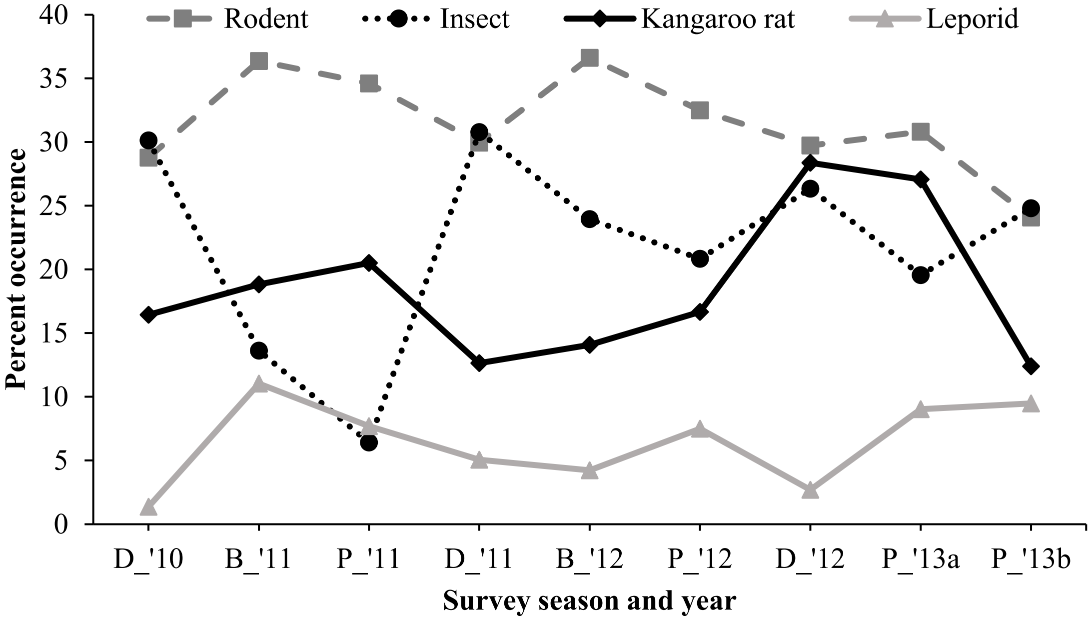

**Figure 3-7:** Seasonal fluctuations of percent occurrence in the top four prey categories in kit fox scats (*n* = 611), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

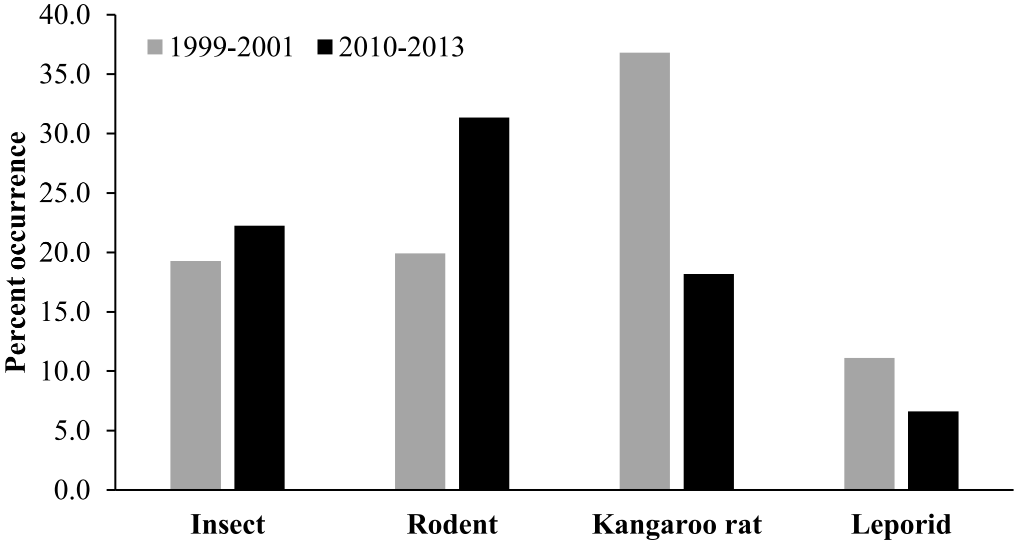

**Figure 3-8:** Annual percent occurrence of the top four prey categories in kit fox scats from Kozlowski et al. (2012) collected between 1999 and 2001 (*n* = 294), and this study (*n* = 611), U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

# CHAPTER 4

# CONCLUSIONS

We investigated dietary shifts related to water availability and the demographic response to changing prey abundance of carnivores in the West Desert, Utah, using 4-years (2010 to 2013) of data collected during Kluever's (2015) study. Estimates of prey abundance were available from rodent trapping results (Kluever et al., 2016) and leporid spotlight surveys (Kluever et al., 2017). Scat deposition road-based surveys (Kluever, 2015) provided relative abundance indices for carnivores. However, we processed and analyzed the collected carnivore scats (*n* = 1,861 coyote; *n* = 611 kit fox) for diet analyses by following protocols from other diet studies (Kelly, 1991; Bartel, 2003). Scat prey items were separated into 11 categories to be consistent with previous on-site studies (Kozlowski et al., 2008; Byerly et al., 2018). We used the original leporid counts from Kluever (2015) spotlight surveys for annual and seasonal absolute density estimates using program Distance software (Thomas et al., 2010). Data from remote cameras placed at natal kit fox dens (Kluever et al., 2013) and radio-collared kit foxes (Kluever and Gese, 2017), provided information for our kit fox litter size and pup survival analyses. The variety of predator and prey data sets collected between 2010 and 2013 on DPG allowed us to: 1) determine if coyotes responded to a water manipulation by shifting their diet towards larger prey to meet energy requirements (chapter 2) and 2) to study any demographic or functional responses by kit foxes to changing prey abundance (chapter 3).

In chapter 2, we compared our coyote diet results with previous on-site studies by comparing the percent occurrence of prey categories and dietary diversity. We found

DPG coyote diet was consistent with previous studies and heavily relied on four prey categories (rodent, leporid, kangaroo rat, insect), which represented 73.8% of all percent occurrence of prey. However, the percent occurrence of leporid has dropped to nearly half of Kozlowski et al. (2008) results, which were collected on-site 10 years before our study. This decline in leporid use was consistent with a decline in leporid numbers since the 1960s. To compare our leporid data with historical trends, we transformed our count data into leporids per km, which showed a steady decline even during their ± 10-year cycles: 5 (1971), 3 (1981), and <1 leporids/km (2000s). The Shannon dietary diversity index (*H'*) of DPG coyotes increased slightly between Kozlowski et al. (2008) study in 1999 to 2001 and our study conducted in 2010 to 2013, from 0.78 to 0.84, respectively. Kit fox hair was identified in one coyote scat and most likely from the predation of an uncollared kit fox. Summer increases in the number of coyote scats containing mule deer were observed in 2012 and 2013 suggesting coyotes were possibly catching and consuming fawns. Similarly, an increase in the number of coyote scats containing pronghorn was observed in the summer of 2013. However, the presence of any ungulate in the coyote diet was minimum throughout the study with the percent occurrence of ungulates averaging at 5.8%.

In 2012, water was removed from the treatment areas (i.e., water sources blocked or drained) while water remained available for wildlife use in the control areas (Kluever and Gese, 2016). To address any shifts in the coyote diet after water removal, we analyzed prey items in coyote scats collected from both the treatment (*n* scats = 1,068) and control (*n* scats = 793) areas. Coyote diet analysis of the top four prey categories on both transect types graphically followed the same trends throughout the 4-year study, which provided no evidence for a water effect. After the water removal in the treatment areas, we expected coyotes to shift their diet towards larger mass prey (i.e., leporids) and continue high use to meet energy requirements; however, this did not occur. Synchronous changes in the percent occurrence of leporids were illustrated on both transect types after water removal. The presence of leporid in the coyote diet indicated that changes occurred before and after the water removal regardless of water proximity suggesting prey resources changed but the water removal was irrelevant.

Total meal size and the size of the prey can alter the digestibility of bones and teeth but hair is unaffected by the coyotes' digestive system (Kelly and Garton, 1997). Hypothetically, after water removal, the coyotes in the treatment areas could have intensified their use of rodents (instead of leporids). If this situation occurred then the percent volume results in the rodent and kangaroo rat categories would have exclusively increased on the treatment transects. We found no evidence of a water effect under these conditions as the percent volume of the rodent and kangaroo rat categories graphically followed the same fluctuations regardless of transect type. Furthermore, no changes in the dietary importance of the 11 prey categories were found when comparing the coyote diet per season based on water proximity and availability using Spearman-rank correlation analysis.

In chapter 3, we found that 67% of natal kit fox dens reared pups in 2012 and 50% for the other three years of the study. Our 4-year analyses included 3 to 4 successfully reproductive females per year resulting in 41 pups from 14 litters. The mean litter size for this study was 3.9 pups/litter, which is consistent with previous kit fox studies (Cypher et al., 2000). We found pup survival to be 0.07, 0.01, 0.46, and 0.16, 2010 to 2013, respectively, based on the 41 pups of known fate to the end of the year determined by remote cameras and radio-collars. In the diet analysis of 611 kit fox scats, we emphasized the top four prey categories, which represented 78.5% of all prey occurrences (31.4% rodent, 22.3% insect, 18.2% kangaroo rat, 6.6% leporid). The percent volume of the same prey categories showed similar prey importance as the percent occurrence data, but kangaroo rat provided more by volume than insects (37.0% rodent, 27.0% kangaroo rat, 16.2% insect, 7.9% leporid). DPG kit fox diet analysis from 1999 to 2001 (Kozlowski et al., 2008) found kangaroo rat to be the highest occurring prey item but our study, 10-years later, suggests kit foxes have become more generalized towards all rodents. Also, leporid use by kit foxes has decreased as the percent occurrence of leporids has dropped from 11.1% to 6.6%. Between the two studies, the percent occurrence of insects were similar at 19.3% and 22.3% as well as Shannon diversity index at 0.73 and 0.77.

We found no evidence of a demographic response of kit fox litter sizes to changing prey abundance. In 2012, rodent indices nearly doubled and leporid densities were also elevated, and yet kit fox litter sizes remained close (3 to 4 pups/litter) to the 4-year study average of 3.9 pups/litter. Similarly, no lag effect was seen in kit fox litter sizes the following year as the four natal dens with confirmed pups ranged from 2 to 5 pups/litter. Despite no response by kit fox litter sizes, we found evidence that pup survival responded to changing prey abundance. In 2012, when prey resources were at our 4-year study high, pup survival increased 3-fold compared to the other three years. A correlation was found between pup survival and rodent abundance index but not leporid densities. For our last objective, we found qualitative evidence to infer a functional response by kit fox to kangaroo rat abundance based on kit fox diet composition and kangaroo rat abundance. Percent occurrence of kangaroo rat in the kit fox diet closely followed kangaroo rat abundance estimates.

Our chapter 2 results support other coyote research in the Great Basin Desert who found no support for the indirect water hypothesis (Hall et al., 2013) and no influence on coyote home ranges or survival after water removal (Kluever and Gese, 2016). Our results do not support Golightly and Ohmart (1984) water economy models that coyotes would have to triple wet prey biomass in the absence of water to meet energy requirements. Coyotes in the West Desert, Utah have challenged our understanding of their physiology and capabilities of adapting to arid environments absent of free water. Our chapter 3 results showed evidence of foraging plasticity by DPG kit foxes as they have shifted their diet away from leporids and towards rodents. This diet adaptation was consistent with changes in the DPG prey resources over the last 60 years. Our kit fox litter size and pup survival analyses showed that demographic responses can occur in one demographic parameter and not in another. For the management and conservation of vulnerable mesocarnivores such as kit foxes, it is critical that we understand which population parameters are influenced by changing prey resources and if they are more sensitive to certain prey species (e.g., kangaroo rat).

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