



Evaluating the influence of water developments on the demography and spatial ecology of a rare, desert-adapted carnivore: the kit fox (*Vulpes macrotis*)

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Constructing water developments to support anthropogenic activities and particular fauna is pervasive across many arid regions of the globe. Despite their prevalence and a predicted increase as a management and conservation tool, water developments may have complex and unanticipated impacts on wildlife. For example, the addition of water developments to the Great Basin Desert in the western United States may have indirectly contributed to a decrease in distribution and abundance of kit foxes (*Vulpes macrotis*). From 2010 to 2013, we examined survival, relative abundance, and habitat characteristics of kit foxes in relation to water developments on the U.S. Army Dugway Proving Ground, Utah, using a before-after control-impact design. We collected 2 years of baseline data prior to reducing availability of water and continued data collection for another 2 years after removal of water on one-half of the study area. We found no evidence that removing water influenced survival or abundance of kit foxes. In addition, we found areas associated with the majority of water developments differed from current kit fox territories in elevation, soil type, and dominant cover type; historical use by kit foxes of areas associated with water developments is largely unknown. One explanation for our inability to find support for a water effect is that observed changes in the kit fox population and canid community in the Great Basin are attributable to changes in coyote management practices that temporally coincided with, but were largely unrelated to increases in water availability.

Key words: home range, indirect effect, intraguild predation, kit fox, relative abundance, survival, water development

Adding anthropogenic water sites (hereafter, water developments) to arid environments occurs across the globe. These water developments can have several goals, including promoting urban development (Kristan and Boarman 2007), improving grazing habitat for livestock (Harrington et al. 1999; Holecheck et al. 2010; Allen 2012; LaBaume 2013; Ndaimani, et al. 2016), and benefiting target wildlife species (Harrington et al. 1999; Larsen et al. 2012; Krausman and Cain 2013; Ndaimani et al. 2016). Programs to construct and maintain water developments to support wildlife have been adopted by land management agencies (Harrington et al. 1999; Simpson et al. 2011; Larsen et al. 2012; Ndaimani et al. 2016), natural resource extraction companies (Haynes and Klopatek 1979), and military training installations (Broyles and Cutler 1999; Hall et al. 2013), and their use is predicted to increase (Larsen et al. 2012). However, a growing body of literature has suggested that the impacts of

water developments on certain species can be adverse (Broyles 1995; Harrington et al. 1999; DeStefano et al. 2000; Arjo et al. 2007) or not in accordance with management objectives (Krausman and Etchberger 1995; Broyles and Cutler 1999; Cain et al. 2008). An overall understanding of the impacts of water developments on wildlife is lacking (Simpson et al. 2011; Larsen et al. 2012; Krausman and Cain 2013).

Impacts of water developments on wildlife can be direct or indirect. Direct effects are those associated with the intake of free water. Indirect effects include changes to competition, vulnerability to predation, wildlife-habitat relationships, and host-parasite and disease interactions caused by increased availability of free water (Larsen et al. 2012). A specific indirect effect of water has been hypothesized for kit foxes (*Vulpes macrotis*) on and near the U.S. Army Dugway Proving Ground (DPG), Utah. Kit foxes were historically reported as the most

abundant and widely distributed carnivore on DPG, but these historical findings are largely premised on anecdotal observations and uncertain study area extents and focal areas (Egoscue 1956; Egoscue 1962). More recently, kit foxes were reported to be less abundant and more limited in distribution than coyotes (*Canis latrans*—Arjo et al. 2007; Kozłowski et al. 2012). It has been argued that water developments constructed during the 1970s–1990s on and near DPG removed the arid-system limitations on coyotes (TRIES 1997; Arjo et al. 2007), which compete with kit foxes for habitat, space, and food (Arjo et al. 2007; Nelson et al. 2007; Kozłowski et al. 2008). In addition, asymmetrical intraguild killing has been observed between these 2 species; coyotes were reported as the leading source of mortality for kit foxes at DPG (Arjo et al. 2007).

The indirect effect of water hypothesis is largely premised on the differential physiological demand for free water by coyotes and kit foxes. Golightly and Ohmart (1984) reported that in the absence of available free water, coyotes must consume over 3× the biomass of wet prey to meet water versus energy requirements compared to when water is available, whereas kit foxes need to increase their consumption of wet prey by less than 2×. Thus, coyotes are hypothesized to have expanded their distribution and abundance at DPG as a consequence of adding water developments, which in turn contributed to a reduction of population size and distribution of kit foxes due to increased competition and intraguild killing (TRIES 1997; AGEISS 2001; Arjo et al. 2007; Kozłowski et al. 2012). In an observational study at DPG, Hall et al. (2013) observed no difference in use of areas in proximity to and away from water sites by either coyotes or kit foxes, but found use of water sites by coyotes exceeded that of kit foxes. Kluever and Gese (2016) found that removal of water availability did not result in territory abandonment, increased mortality, or large shifts in coyote territories, although the number of coyotes included in some analyses was small (e.g., $n = 3$ for shifts in coyote territories after removal of access to water). However, Kluever et al. (2017) found that removal of water resulted in a reduction of coyote use of areas formerly containing water availability. Thus, a key assumption of the indirect effect of water hypothesis, that pervasiveness of coyotes is related to water developments, has received mixed support. The inconclusiveness of combined studies on the indirect effect of water hypothesis, lack of research that explicitly includes data on kit foxes, and the designation of kit foxes as requiring conservation attention in several western states (Dempsey et al. 2014) together suggest the relationship between water developments and kit foxes warrants further investigation.

Here, we describe a 4-year investigation involving an experimental manipulation of water developments and its effects on kit foxes in the Great Basin Desert. If the distribution, abundance, and survival of kit foxes have been negatively affected by the addition of water developments according to the indirect effect of water hypothesis, we predicted that 1) visitation to water developments by kit foxes would be minimal, and 2) removal of water developments would increase survival and relative abundance of kit foxes. Further, we predicted that environmental variables associated with water developments (i.e.,

areas no longer regularly used by kit foxes) would be similar to those in areas currently used by kit foxes if the current limited spatial distribution of kit foxes is primarily driven by indirect effects of water developments (e.g., coyote activity) and not habitat characteristics.

MATERIALS AND METHODS

Study area.—We conducted our research in the Great Basin Desert on the eastern portion of DPG and adjoining federal lands, Tooele County, Utah, United States. Elevations ranged from 1,302 to 2,137 m. Average annual long-term (1953–2009) and study-duration (2010–2013) temperatures derived from monthly mean maxima were 17°C (range: 11–21) and 17°C (range: 15–19), respectively. Long-term and study-duration annual precipitation averaged 24.5 cm (range: 7.9–42.3) and 18.1 cm (range: 8.0–26.6; National Oceanic and Atmospheric Administration, National Centers for Environmental Information; <https://www.ncdc.noaa.gov/data-access>, accessed October 2014). In the study area, we identified 19 permanent free-water sites consisting of 15 water developments (10 wild-life waterers, 5 ponds or catchments) and 4 natural springs. Four additional ponds were run-off based and ephemeral. In addition, the eastern portion of the study area, managed by the Bureau of Land Management (BLM), contained 3 livestock tanks that were at times operational during winter and spring cattle grazing (1 November to 1 April). Water developments were constructed between the 1960s and 1990s (Arjo et al. 2007). The ratio of water developments to natural water sites within the study area was at least 4:1, with slight seasonal variability due to the turning on or off of livestock tanks and ephemeral catchment ponds. There was no free-flowing water present on the study area. Additional water sites (e.g., hardpans, rainfall, drainages) were ephemeral pools lasting < 1 week; we assumed they were homogenous throughout the study area.

The terrain consisted of isolated small mountains, a portion of the Cedar Mountains, sand dunes, and alkaline flats that were dominated by black greasewood (*Sarcobatus vermiculatus*), big sagebrush (*Artemisia tridentata*), and juniper (*Juniperus osteosperma*—Dempsey et al. 2014). Where wildfires had occurred, 40% of historical juniper woodland and shrub communities had been replaced by exotic herbaceous vegetation (Emrick and Hill 1999). Rodents, especially Ord's kangaroo rats (*Dipodomys ordii*), were the primary prey of kit foxes (Kozłowski et al. 2008; P. Byerly, University of Louisiana, pers. comm.). Coyotes occurred throughout DPG, but distribution of kit foxes was limited (Kozłowski et al. 2012; Dempsey et al. 2015); habitat use by kit foxes at DPG represented spatial and behavioral strategies designed to minimize spatial overlap with coyotes while maximizing access to resources (Kozłowski et al. 2012).

Study design.—From January 2010 to March 2012, we captured, radiocollared, and radiotracked kit foxes for 2 years as the “baseline” monitoring period. At the conclusion of the 2012 breeding season (April), we initiated the “manipulation” period, when we drained 5 water developments using a

generator and submersible pump and excluded 1 pond by affixing a 1.2-m chain-link apron to an existing surrounding chain-link fence. This manipulation eliminated water availability at 31% (6 of 19) of the permanent water developments within the study area. An investigation of space use and abundance of kit foxes by [Dempsey et al. \(2014\)](#) revealed that, despite intensive trapping and survey efforts, kit foxes were not detected in the northern and northeastern areas of DPG where the majority of water sources were located; kit foxes were only captured and found to utilize the western and southern portions of DPG. Therefore, we chose to eliminate water availability at a subset of water sources that experienced a high frequency of visits by coyotes, were logistically feasible to manipulate, and appeared to be located on the periphery of areas used by kit foxes as determined by [Dempsey et al. \(2014\)](#). This design allowed us to test whether our overall water manipulation influenced survival of kit foxes at the study-site level using a before-after design. In addition, we tested whether individually manipulated water sources influenced kit foxes using a before-after control-impact (BACI) design by monitoring areas associated with and unassociated with manipulated water developments prior to and following the water manipulation. BACI designs are considered superior to observational studies because they better account for variability of responses and explanatory variables attributed to temporal (e.g., annual precipitation) and spatial (e.g., vegetation heterogeneity across study area) factors that cannot always be controlled or accounted for under natural environmental conditions ([Morrison et al. 2001](#)).

Capture and radiotracking of kit foxes.—Between January 2010 and November 2013, we captured 84 kit foxes via road-based transect trapping ([Schauster et al. 2002](#); [Dempsey et al. 2014](#)) and at known den sites ([Kluever et al. 2013](#); [Dempsey et al. 2014](#)) using box traps (25 × 25 × 80 cm; Model 107; Tomahawk Live Trap LLC, Hazelhurst, Wisconsin) baited with hot dogs. Of these, we classified 43 as adults and 41 as juveniles (< 1 year old) at time of capture. Trapping transects were distributed to provide maximum coverage of the area and allow for increased likelihood of capturing most of the kit foxes occupying the study area ([Dempsey et al. 2014](#)). We deployed traps in the evening and checked them early morning each day. We conducted road-based trapping each year on each transect for at least 8 nights during the breeding (15 December–14 April) and dispersal seasons (15 August–14 December). Due to concerns of overheating and the demands of natal care on female foxes, we did not conduct road-based trapping during the pup-rearing season (15 April–14 August—[Dempsey et al. 2013](#)) but did trap and capture juvenile kit foxes at natal dens between 15 July and 14 August each year. Capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees (IACUC) at the United States Department of Agriculture's National Wildlife Research Center (QA-1734) and Utah State University (#1438). Permits to capture and handle kit foxes were obtained from the Utah Division of Wildlife Resources (COR #4COLL8322). All capture and handling procedures were in accordance with guidelines endorsed by the American Society of Mammalogists ([Sikes et al. 2016](#)).

We weighed, determined sex of, ear tagged, and fitted each kit fox with a 30- to 50-g radiocollar (Model M1930; Advanced Telemetry Systems, Isanti, Minnesota) weighing < 5% of body mass. Collars included a mortality sensor that activated after 4 h. Upon detecting a mortality signal, we immediately recovered the transmitter and remains of the kit fox. We determined the cause of mortality by examining the carcass for external and internal injuries, puncture wounds, and hemorrhaging. If we did not observe any gross trauma, we sent animals to the Utah State University (Logan, Utah) or Wyoming State University (Laramie, Wyoming) Veterinary Diagnostic Laboratory for necropsy and diagnosis.

We located animals > 3 times per week using a portable receiver (Model R1000; Communications Specialists, Inc., Orange, California) and a handheld 3-element Yagi antenna. We triangulated an animal's location using ≥ 3 compass bearings, each > 20° but < 160° apart, recorded within 20 min ([Arjo et al. 2007](#); [Kozłowski et al. 2008](#)). We then calculated locations using program Locate III (Pacer Computing, Tatamagouche, Nova Scotia, Canada). We temporally distributed telemetry sampling by collecting 2 nocturnal locations and 1 den (resting) location each week. We reduced autocorrelation using methods described by [Gese et al. \(1990\)](#). We computed home ranges using only locations with an error polygon < 0.10 km² ([Seidler and Gese 2012](#)). We attempted to locate each kit fox > 3 times per week in order to obtain 30 locations for each kit fox for each biological season as the minimum number of locations needed to adequately describe the home range ([Gese et al. 1990](#)). We then developed seasonal home ranges for all kit foxes with > 30 locations within the 3 biological seasons ([Dempsey et al. 2013](#)). We created 95% fixed kernel density estimates (KDEs) following recommendations of [Walter et al. \(2011\)](#) by calculating Gaussian kernels with a plug-in bandwidth estimator (cell size = 30) using the Geospatial Modeling Environment (GME) platform ([Beyer 2012](#)). We then created home range polygons using GME and loaded these polygons into ArcGIS 10.2 (Environmental Systems Research Institute Inc., Redlands, California).

Visitation rates to water developments by kit foxes.—We examined the frequency of seasonal visits to water developments by kit foxes by establishing data loggers (model R4500S and model R2100/D5401; ATS, Isanti, Minnesota) at 13 water developments, following recommendations of [Breck et al. \(2006\)](#). These 13 sites ([Fig. 1](#)) represented 68% (13 of 19) of the permanent water developments within the study area. When we initiated the study, we had assumed kit foxes had access to all the water sources, but subsequent determination of home ranges showed many water sources outside these home ranges ([Fig. 1](#)). Therefore, when the water manipulation phase began, we were limited to shutting off water at only a few of the water developments contained in these home ranges. We defined a visit as all data-logger recordings of an individual animal occurring within 30 min at a particular water development (i.e., multiple recordings of the same individual within 30 min were counted as a single visit—[Atwood et al. 2011](#)). For kit foxes with home ranges that contained water developments with data

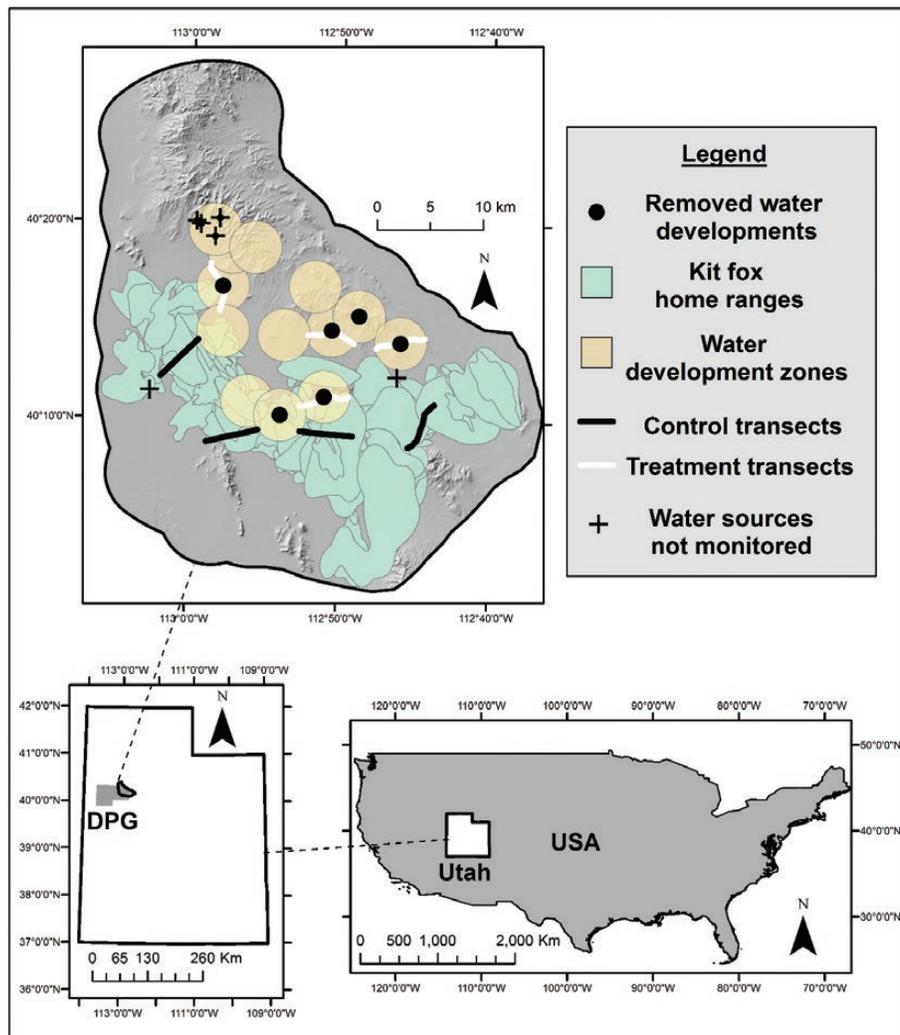


Fig. 1.—Map of 95% fixed kernel seasonal home ranges for kit foxes (*Vulpes macrotis*), water development zones (an area equal to the average home range size of a kit fox, centered around a water source), and survey transects on and around the U.S. Army Dugway Proving Ground (DPG), Utah, United States, 2010–2013.

loggers, we summarized the number of visits to water developments per seasonal home range. We did not attempt to describe visitations when home ranges contained water developments without data loggers because we could not determine if visits to the water sources with data loggers constituted a small or large portion of overall water use by the kit fox occupying that home range.

Survival of kit foxes in relation to water developments.—We estimated survival probability using the known fate model in the RMark package in R (R Development Core Team 2014). We developed encounter histories at the season temporal scale and used the Delta method to approximate variances of annual survival probability (Powell 2007). The model was age-structured, allowing juveniles to graduate into the adult cohort after surviving through April of the year following their birth (Gese and Thompson 2014). We tested for an effect of our water manipulation by incorporating a bivariate temporal variable (i.e., before and after water manipulation). We included additional individual-based (i.e., age, sex) and time-varying (i.e., season, year, rodent prey base) covariates that we felt had the

potential to influence survival of kit foxes based on previous investigations of kit foxes (White and Garrott 1997; Arjo et al. 2007). For the prey base covariate, we utilized annual estimates of rodent abundance from Kluever et al. (2016) that exhibited a nonlinear trend, with consistent abundance over the first 2 years of the study, an increase the following year, and a decrease during the final years (i.e., prey base covariate = years 1 and 2: moderate, year 3: high, year 4: low). We developed a candidate set of 15 a priori models containing univariate, 2-way additive, and 2-way interactive combinations based on our primary research question and previous investigations of kit fox ecology (Burnham and Anderson 2002). We examined the evidence in support of candidate models by examining the combination of evidence ratios and 95% CI overlap of real (i.e., survival) and beta estimates (Anderson 2008).

Abundance of kit foxes in relation to water developments.—We established four 5-km road-based survey transects whose midpoints were adjacent to water developments (model Dual Big Game; Boss Tanks, Elko, Nevada). We considered these treatment transects because they were associated with a water

development. The average distance from treatment transects to the next nearest perennial water source (i.e., pond, water development, sewage lagoon) was 4.10 km ($SD = 0.54$). We used ArcGIS (version 9.3; Environmental Systems Research Institute Inc., Redlands, California) to create 4 additional 5-km control transects distributed randomly along available non-paved roads with the constraints of occurring on lengths of road with no angles $> 60^\circ$, a minimum distance of 2.6 km from treatment transects, and a minimum distance of 2.6 km from a perennial water source. We did not establish survey transects associated with 2 manipulated water sources (i.e., 1 wildlife waterer and 1 pond) due to lack of road coverage. Surveys taking place on transects prior to the water manipulation period were considered the “baseline period,” while surveys following the water manipulation were considered the “manipulation period.”

For survey transects, we employed a multiple-treatment site, multiple-control site BACI design where we monitored all transects prior to and after eliminating water availability at water developments. We conducted scat deposition surveys (Knowlton 1984; Schauster et al. 2002) along the eight 5-km transects to estimate the relative abundance of kit foxes (see Dempsey et al. 2014 for full description). Scat deposition counts provided an index of kit fox abundance: the number of kit fox scats per transect per survey. Scat surveys have been reported as an effective index for tracking kit fox abundance over time and space (Dempsey et al. 2014) and have outperformed other non-invasive surveys for mammalian carnivores (Knowlton 1984; Harrison et al. 2002; Long et al. 2007; Dempsey et al. 2014). We also conducted scent station surveys as a second estimate of relative abundance of kit foxes (see Dempsey et al. 2014 for full description). These surveys provided a count of scent station visits (i.e., total number of visits, with a maximum possible number of visits of 44) as a measure of relative abundance. We elected not to convert count data to proportions due to excessive zeros (Zar 2010). Scent station surveys have also been described as an effective means to assess trends in carnivore populations (Roughton and Sweeny 1982; Thacker et al. 1995).

We employed generalized linear mixed models (GLMMs—Stroup 2012) to test the categorical main effects of period (baseline and manipulation) and transect type (control and treatment) on the continuous response variables of relative abundance of kit foxes: scats/transect/survey and scent station visits/transect/survey. Specifically, we tested the impact of water development manipulation by including a period-by-transect type interaction in our model (Underwood 1992). Within the framework of a BACI design, such an interaction tests for a differential change (i.e., non-parallelism) between treatment and control sampling units following manipulation (Underwood 1992). Inspection of the raw data revealed non-normality and a high frequency of zeros. Therefore, we fit the following model families: lognormal, Poisson, quasi-Poisson, and negative binomial. Models not converging were eliminated, and we assessed remaining models based on the generalized chi-square fit statistic (Stroup 2012). We compared the remaining model families with zero-inflated models of the same model family using a Vuong test; zero-inflated regression models outperform traditional models of the same family when excess zeros are generated by a

separate process from the count values (Everitt and Hothorn 2009). For the scat and scent station data, we selected the Poisson model family for our final models. For both measures of relative abundance, we conducted multiple surveys on each transect for both periods. To reduce model complexity and better account for residual variance, we collapsed our original data sets across surveys. By doing so, data were analyzed within a balanced split plot in a time-model framework (Aho 2014). To account for variability among survey transects, and variability among survey transects within treatments, we included a survey transect (i.e., treatment or control) by period (baseline and manipulation) random effect (Demidenko 2013). All statistical analyses for relative abundance were performed using the glmm and pscl packages in R.

Habitat differences between home ranges of kit foxes and water developments.—We delineated circular buffers equal in area to the average home range of kit foxes at DPG around each data logger monitoring a water development (Fig. 1). This allowed us to compare environmental characteristics of kit fox home ranges with areas associated with water developments at a spatial extent germane to our focal species (Larsen et al. 2012). We only assessed environmental characteristics of water developments monitored with data loggers. At each site, we quantified 3 environmental variables previously reported as important habitat components for kit foxes: elevation (McGrew 1976; Fitzgerald 1996), dominant vegetation type (Kozlowski et al. 2008), and soil type (Egoscue 1962; Fitzgerald 1996; Robinson et al. 2014). Elevation and soil type data were obtained from GIS databases (Utah Automated Geographic Reference Center; <http://gis.utah.gov>, accessed October 2014). Soils were classified into 4 major classes: silt, fine sand, blocky loam, and gravel (Dempsey et al. 2015). We eliminated the gravel soil type from analyses because it constituted $< 5\%$ of the area associated with home ranges of kit foxes and water development areas. Data on dominant vegetation cover were obtained from the Landfire database (<http://landfire.cr.usgs.gov/>), accessed October 2014) and were classified into 3 major types: herbaceous, shrub, or barren. These 3 classes comprised 94% of the total area encompassed within home ranges of kit foxes and water development areas. We used the GME platform (Beyer 2012) to obtain mean elevation for each home range and water development area, and the proportion of each home range and water development area comprised of each soil type and vegetation class.

We employed 2-tailed permutation tests with 20,000 resamples (Manly 2006) to test for differences between home ranges and water development areas in our 3 environmental variables. To better meet the assumption of independence of observations, we collapsed summary data of environmental characteristics across the home ranges of individual foxes. We selected this test because inspection of data on environmental variables revealed skewness and unequal variances that could not be remedied with data transformations. Permutation tests are distribution-free in the sense that probabilities of obtaining extreme test statistic values given the truth of the null hypothesis (type I errors) are based on permutations of the data from randomization theory and are not based on an assumed

population distribution (Manly 2006). Permutation tests were performed using the blossom package in R. For all statistical tests we interpreted *P*-values in terms of relative evidence of differences (Ramsey and Schafer 2002).

RESULTS

During the study, 7,256 locations were recorded on the 84 collared foxes, allowing for the calculation of 114 seasonal home ranges (37 in breeding, 30 in dispersal, 47 in pup-rearing) from the 2010 pup-rearing season through the 2013 dispersal season. The mean number of days a fox was monitored from radiocollaring to either death, loss of signal, or conclusion of the study was 246 days ($SD = 292.71$). We found seasonal 95% KDE home-range sizes for kit foxes averaged 19.45 km² ($n = 114$, $SD = 15.1$). For all years combined, average home-range size of kit foxes was largest during the breeding season ($\bar{x} = 24.25$ km², $n = 37$, $SD = 20.91$), followed by the dispersal season ($\bar{x} = 19.56$ km², $n = 30$, $SD = 10.34$) and pup-rearing season ($\bar{x} = 15.93$ km², $n = 47$, $SD = 11.32$).

A total of 50 kit foxes died during the study (25 adults, 25 juveniles). Of these deaths, 24 (48%) were confirmed coyote predation, 7 (14%) were eagle predation, 6 (12%) were suspected predation, 5 (10%) were unknown cause, 4 (8%) were vehicle collision, 1 (2%) was bobcat predation, 1 (2%) was esophageal feed impaction, 1 (2%) was suspected rattlesnake bite, and 1 (2%) was study influenced. The study-influenced death was censored in survival analyses. Many of the suspected predation events involved recovery of a torn, bloody, or buried radiocollar and only remnants of a carcass. We were unable to conduct a necropsy on these individuals. Thus, suspected and confirmed predation accounted for 76% of the kit fox deaths with coyote predation being the leading cause of death.

Visitation rates to water developments by kit foxes.—We determined 72 seasonal home ranges of our radiocollared kit foxes for the period prior to the water manipulation (i.e., baseline monitoring period). Of these, only 12 of 72 (17%) seasonal home ranges contained a water development. These 12 home ranges overlapped with 5 water developments we monitored with data loggers and zero that were not monitored (Fig. 1); 3 of these 5 water developments then received our manipulation of removing accessibility to water. Following reduction of water availability (i.e., manipulation period), we determined 42 seasonal home ranges of the radiocollared kit foxes. However, only 2 of these 42 (2%) seasonal home ranges of the surviving radiocollared kit foxes contained a water development. One home range included 1 water development we monitored with data loggers and the other home range contained a water development that was not monitored. Overall, kit foxes with water developments within their home ranges averaged 2.8 ($SD = 3.1$) seasonal visitations to those water developments, but only 4 monitored water developments were visited by kit foxes during the entire study. We recorded only 2 seasonal water development visitations by 1 individual kit fox during the manipulation period; both of these visits occurred at 1 of the manipulated water sources the season following the manipulation.

Kluever and Gese (2016) used the same methods and reported that coyotes averaged 13.0 ($SD = 13.5$) seasonal visitations to water developments during this same time period.

Survival of kit foxes in relation to water developments.—The percentage of kit fox mortalities caused by coyotes prior to and following our water manipulation was 44% (12 of 27) and 48% (12 of 23), respectively. The water manipulation did not appear to influence survival of kit foxes; the model containing only the water manipulation variable did not outperform the null model (Table 1). Age appeared to have the strongest influence on survival probabilities of kit foxes as this parameter was included in the 9 highest-ranked models and was included in 82% (9 of 11) of candidate models outperforming the null model (Table 1). The prey base parameter was associated with the 2 top-ranked models (Fig. 2), but the 95% survival probabilities associated with prey base years, and all other time-varying parameters, highly overlapped for both adults and juveniles. Annual survival probabilities for adults and juveniles averaged across all years were 55.50% ($SD = 2.73$) and 27.93%

Table 1.—Results from age-structure known fate survival models for radiocollared kit foxes (*Vulpes macrotis*) on and adjacent to the U.S. Army Dugway Proving Ground, Utah, 2010–2013. *K* refers to the number of parameters (including intercept), W_i the model weight, and ER the evidence ratio. Models shown are those that outperformed the null (age-structured) model.

Model	ΔAIC_c	W_i	<i>K</i>	ER
Age * prey base	0.00	0.35	6	1.00
Age + prey base	1.04	0.21	5	1.68
Age	2.02	0.11	2	2.74
Age * water manipulation	2.40	0.10	5	3.32
Age + water manipulation	2.98	0.08	4	4.43
Age * year	3.72	0.05	7	6.42
Age + year	4.17	0.04	6	8.04
Age + sex	5.77	0.02	3	17.90
Season + age	6.95	0.01	5	32.30
Prey base	9.81	> 0.01	4	134.96
Season + prey base	10.57	> 0.01	7	197.35

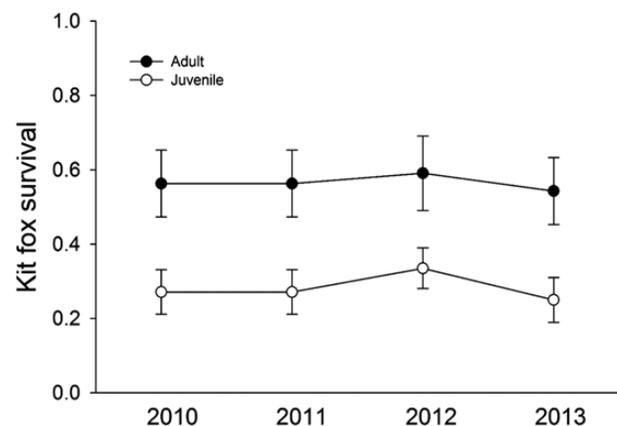


Fig. 2.—Kit fox (*Vulpes macrotis*) annual survival probabilities ($\pm SE$) derived from models age*prey base, age + prey base, and age, on and around the U.S. Army Dugway Proving Ground, Utah, United States, 2010–2013. Water availability was experimentally manipulated in 2012.

($SD = 3.99$), respectively (Fig. 2). The top-ranked model (age * prey base) had 3.3 times more support than the highest-ranked model containing the water manipulation parameter (age * water).

Abundance of kit foxes in relation to water developments.—Between September 2010 and August 2013, we conducted 5 seasonal scat deposition surveys prior to and following our water manipulation. On average, we observed 3.26 scats/transect/survey ($SD = 5.99$), with a range of 0–29 scats/transect/survey. We found no evidence that elimination of water at developments influenced relative abundance of kit foxes (period × transect type interaction: $t_6 = 0.42$, $P = 0.44$). We found convincing evidence that relative abundance of kit foxes differed by transect type ($t_6 = -2.42$, $P < 0.01$; Fig. 3A), but found no evidence that relative abundance differed by period ($t_6 = -0.82$, $P = 0.41$). The numbers of kit fox scats observed on control transects were 5.50 ($SE = 1.77$) scats/transect during the baseline period and 6.35 ($SE = 1.66$) scats/transect during the manipulation period (Fig. 3A). The numbers of kit fox scats observed on treatment transects during the baseline period and manipulation period were 0.55 ($SE = 0.17$) and 0.65 ($SE = 0.22$) scats/transect, respectively (Fig. 3A).

Between September 2010 and August 2013, we conducted 5 seasonal scent station surveys prior to and following our water manipulation. On average, 2.27 visits/transect/survey ($SD = 3.15$) were observed and counts ranged from 0 to 15

visits/transect/survey. We found no evidence that elimination of water at developments influenced relative abundance of kit foxes (period × transect type interaction: $t_6 = 1.12$, $P = 0.26$). We found convincing evidence that relative abundance of kit foxes differed by transect type ($t_6 = -1.85$, $P < 0.01$; Fig. 3B), but found no evidence that relative abundance differed by period ($t_6 = -0.11$, $P = 0.48$). The numbers of scent station visits by kit foxes observed at control transects during the baseline period and manipulation period were 3.54 ($SE = 0.77$) and 4.05 ($SE = 0.88$) visits/transect, respectively (Fig. 3B). The numbers of scent station visits observed on treatment transects during the baseline period and manipulation period were 0.60 ($SE = 0.19$) and 0.79 ($SE = 0.22$), respectively (Fig. 3B).

Habitat differences between home ranges of kit foxes and water developments.—We found convincing evidence that elevation of kit fox home ranges differed from that of water development areas ($n = 51$, $P < 0.001$). Average elevation within kit fox home ranges and water development areas averaged 1,387 m ($SE = 18.62$) and 1,491 m ($SE = 35.84$), respectively. We found suggestive evidence that kit fox home ranges and water development areas contained different proportions of cover by barren land ($n = 51$, $P < 0.08$), and convincing evidence of differences in proportions of cover by shrubland ($n = 51$, $P < 0.001$) and herbaceous ($n = 51$, $P < 0.001$) dominant cover types (Fig. 4A). We also found convincing evidence that home ranges and water development areas were characterized by

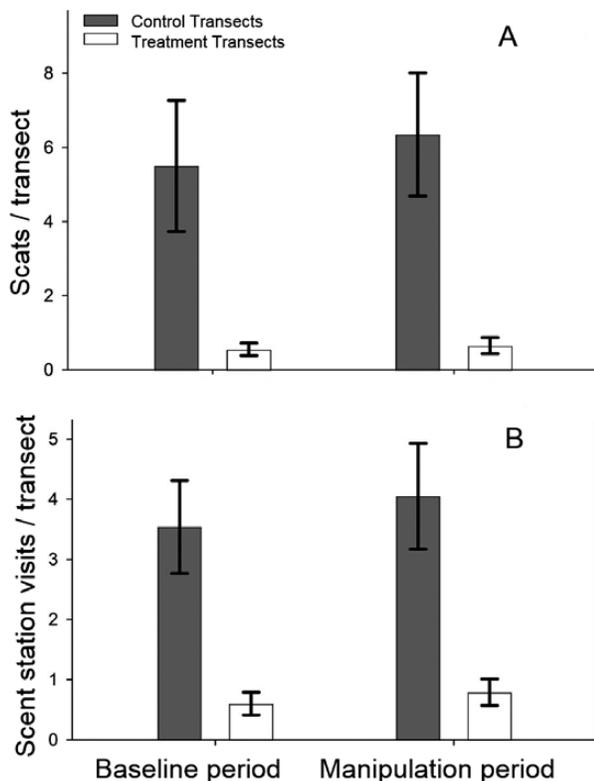


Fig. 3.—Kit fox (*Vulpes macrotis*) scats (A) and scent station visits (B) observed on 5-km treatment and control transects prior to (baseline period) and following (manipulation) removal of water availability at water developments on the U.S. Army Dugway Proving Ground, Utah, United States, 2010–2013.

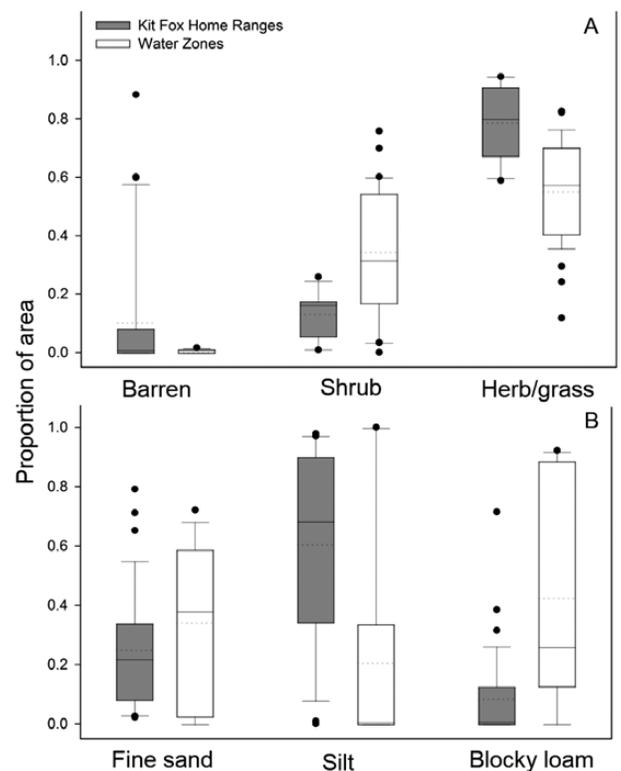


Fig. 4.—Box plots of (A) proportions of soil types and (B) dominant vegetation observed within seasonal kit fox (*Vulpes macrotis*) home ranges pooled by individual foxes ($n = 38$) and areas associated with water developments ($n = 13$) on and near the U.S. Army Dugway Proving Ground, Utah, United States, 2010–2013.

different proportions of silt ($n = 51$, $P < 0.001$) and blocky loam ($n = 51$, $P < 0.001$), where home ranges contained a greater proportion of silt and water development areas contained a greater proportion of blocky loam (Fig. 4B). We found no evidence of a difference for fine sand ($n = 51$, $P = 0.19$; Fig. 4B).

DISCUSSION

Our study did not support the indirect effect of water hypothesis for the decline of the kit fox population at DPG. We confirmed our prediction that use of water developments by kit foxes was rare, and that kit foxes visited water developments much less often than coyotes (Kluever and Gese 2016). Although this comparison supports an important assumption of the hypothesis, we did not find an increase in survivorship or abundance of kit foxes after our manipulation to decrease availability of water at DPG. Furthermore, we found differences in elevation, cover type, and soil type between water developments and current home ranges of kit foxes that suggest habitat selection, either directly by kit foxes or indirectly through habitat use by coyotes, could play a role in determining the current distribution of kit foxes at DPG.

The low visitation rate of kit foxes to water developments in our study provided additional support that kit foxes at DPG are an arid-adapted species that rarely needs to utilize free water (Hall et al. 2013). However, Hall et al. (2013) observed regular visits to water sites by kit foxes in the Mojave Desert, where water sites were more uniformly distributed throughout the landscape. Rosenstock et al. (2004) recorded 76 drinking events by kit foxes at water developments in Arizona, suggesting kit foxes will utilize free water when available in the Sonoran Desert. Given these disparate findings, and the limited number of investigations regarding kit foxes and free water, we caution against range-wide generalizations regarding use of free water by kit foxes.

Our prediction that removal of water availability would influence survival of kit foxes was not confirmed. Similarly, Cain et al. (2008) observed that removal of water availability did not influence survival of desert bighorn sheep (*Ovis Canadensis nelsoni*) in the Sonoran Desert, but Harrington et al. (1999) suggested that survival of roan antelope (*Hippotragus equinus*) increased following a reduction of water developments in the Kalahari Desert. Our findings, in concert with those of Kluever and Gese (2016) for coyotes in our study area, suggest that the influence of water developments on canids in our study system may be overemphasized. Unfortunately, estimation of annual survival per se was not possible in the kit fox investigations that occurred prior to the marked increase of free water at DPG (Egoscue 1956, 1962). Our finding that age class had a large influence on survival was similar to results from other investigations on swift foxes (*Vulpes velox*), a congener of kit foxes (Rongstad et al. 1989; Karki et al. 2007; Gese and Thompson 2014). Our overall estimate of annual adult survival fell within the range previously reported at DPG and in other portions of the species' range (White and Garrott 1997; Arjo et al. 2007). The percentage of kit foxes killed by coyotes was not reduced

following the reduction of water availability, was similar to that observed at DPG by Arjo et al. (2007), and fell within the lower range of coyote-caused death rates observed for kit foxes across their range (White and Garrott 1997). If increased intraguild predation by way of increased availability of free water on DPG was primarily responsible for reductions in population size and distribution of kit foxes, we expected our reduction of water availability to influence coyote predation on kit foxes.

Our prediction that abundance of kit foxes would increase due to removal of water availability was not supported, even though the BACI design associated with this component of our study has repeatedly been reported as superior to purely observational studies (Underwood 1992; Morrison et al. 2001). Our findings resemble that of an investigation at DPG by Hall et al. (2013), where an observational, non-road based scent station survey design was utilized and found that relative abundance of kit foxes and coyotes did not differ between wet and dry areas. Kluever et al. (2016) found that removal of water availability reduced relative abundance of coyotes near manipulated areas, but speculated this statistically significant finding may not have equated to an ecologically relevant impact on the canid community at DPG.

An alternative explanation for our study not supporting the indirect effect water hypothesis is that 2 years may not have been a long enough time for coyotes to decrease in abundance in response to our water manipulation, as modifications to resources on the landscape may require more time to affect the distribution and abundance of coyotes. As such, we recommend that future investigations including a manipulation of water availability include temporal durations more germane to the population dynamics of the focal species (Larsen et al. 2012). For example, durations based on generation time (Stearns 1992) may be more appropriate.

We were unable to derive actual estimates of kit fox abundance using our survey transect design because the low capture rates (< 1 fox captured/100 trap nights) did not allow for robust use of capture-mark-recapture methods. We recommend future studies allow for actual estimates of abundance (e.g., via genetic analysis). It is important to note that the water developments we manipulated were located on the periphery of the current distribution of kit foxes at DPG. Future investigations on the impacts of free water on kit foxes, and wildlife in general, should consider manipulating (i.e., reducing or adding) free water in areas that fall within the species' current distribution. Nonetheless, if water developments were influencing the distribution of kit foxes in our study area, we expected increased relative abundance on treatment transects following our manipulation, if these areas then represented suitable habitat for kit foxes.

Our prediction that areas associated with water developments would be similar to areas associated with the current distribution of kit foxes for key habitat characteristics was not met. We feel this finding may lend support to the notion that the majority of water developments, at DPG, specifically those constructed along the Cedar Mountains, are located in areas outside of the historical distribution of kit foxes. Elevation has been reported as an important habitat component for kit foxes through its

indirect influence on vegetation assemblages (McGrew 1976; Fitzgerald 1996), and we found home ranges of kit foxes were consistently associated with areas of lower elevation when compared to water development areas. Kit foxes have traditionally been described as a species that primarily utilizes lowland flat areas (Egoscue 1975; Zoellick and Smith 1992), which also seems to be the case for the kit fox population at DPG.

We found home ranges of kit foxes and areas around water developments varied by proportions of blocky loam soil and silt. Using a resource selection function, Dempsey et al. (2015) found that the distribution of kit foxes at DPG was influenced by soil type, where kit foxes rarely occurred in areas with large blocky soils, which would be difficult for den excavation. Den sites are considered to be important to kit foxes as they provide shelter from temperature extremes, a moist microclimate, a place to rear young (Arjo et al. 2003), and are a critical part of the survival strategy of kit foxes (Gerrard et al. 2001). Proper denning conditions (i.e., soil type) may therefore be required to support kit foxes at DPG. We speculate that because the majority of soil in areas associated with water developments do not appear to represent suitable denning substrate, it is possible that these areas were not historically utilized on a regular basis by kit foxes at levels previously posited; it is unlikely that the distribution of various soil types at DPG has markedly changed over the past century. However, Egoscue (1962) observed that kit foxes denned in close proximity to areas that currently contain 2 water developments.

Our findings about differences in dominant vegetation type are more difficult to interpret, as portions of DPG and surrounding areas have undergone encroachment by exotic herbaceous vegetation (e.g., cheat grass, *Bromus tectorum*) in recent decades (Emrick and Hill 1999; Arjo et al. 2007). The impact of this landscape-level change on canid distribution and population sizes at DPG and other portions of the Great Basin Desert remain unclear. The extent to which the distribution of shrublands and barren cover types has changed since the construction of water developments also is unknown. Because the historical reports of wide distribution and high abundance of kit foxes at DPG were based primarily on information considered largely anecdotal by today's scientific standards (Egoscue 1956, 1962), a rigorous determination of the spatial and demographic properties of the historical kit fox population at DPG is not possible.

Support for the indirect effect of water hypothesis for the canid community at DPG is predicated on observed and hypothesized changes in coyote and kit fox populations and canid-habitat relationships following a period of marked increases in water developments (Arjo et al. 2007; Kozłowski et al. 2008, 2012). We posit that other factors may have contributed to such changes. Within a study area that encompassed our own, Egoscue (1956) argued that abundance of coyotes was suppressed by intensive coyote control efforts, including regular use of baited toxicants spaced at intervals aimed to maximize lethality to coyotes rather than carnivores with smaller home ranges (i.e., kit foxes). In addition, Shippee and Jollie (1953) reported coyotes were historically controlled on and near DPG using a host of methods including spring den hunting, shooting, trap sets, poison pellets, cyanide guns, and poisoned sheep

carcasses; > 80 coyotes were harvested in 1951–1952 alone. It seems intuitive that this suite of control factors may have been a driving force behind the seemingly low coyote numbers reported at DPG in 1953 (Shippee and Jollie 1953). In 1972, Executive Order 11,643 banned the use of baited toxicants, and additional restrictions have been placed on the use of toxicants for predator control by the Environmental Protection Agency (Mitchell et al. 2004). Dorrance and Roy (1976) and Nunley (1986) suggested that coyote control programs relying heavily on toxicants were more effective at suppressing coyote populations than contemporary methods. Thus, the implementation of less intense and lethal coyote management practices that temporally coincided with the marked increase of water developments on and around DPG may have bolstered coyote populations, which in turn reduced the abundance and distribution of kit foxes. However, the impact of coyote population control on populations of kit foxes has not been directly investigated. Kamler et al. (2003) observed coyote removal increased survival, density, and recruitment of swift foxes, and Karki et al. (2007) observed an increase in juvenile survival. Similarly, Henke and Bryant (1999) found that relative abundance of mesocarnivores increased following intense coyote control.

In closing, the observed commonness of kit foxes (Egoscue 1956, 1962) and rarity of coyotes (Shippee and Jollie 1953; Egoscue 1956; Arjo et al. 2007) during the mid-20th century may be at least in part tied to changes in coyote control management practices that temporally coincided, but were largely unrelated to, the additions of water developments. However, habitat invasion by cheat grass cannot be ruled out as having influenced the distribution and abundance of kit foxes over the last 50 years. The combination of these changes may in fact have contributed to a synergy that caused a decline in kit fox habitat and population size in the Great Basin. We caution against general inferences regarding the role of water developments on individual species and communities in arid environments. Specific investigations, preferably those that include experimental manipulation and more substantive temporal spans than we undertook, are needed when addressing this complex topic.

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