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Coyotes in the Great Basin desert do not exhibit a spatial response following the removal of anthropogenic water sources

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A R T I C L E I N F O

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A B S T R A C T

Coyote (*Canis latrans*) range expansion into desert ecosystems has highlighted the role of anthropogenic water sources in arid ecosystems. Despite hypotheses that additional water facilitated this expansion, previous studies reported that coyotes did not exhibit a spatial or dietary response to removal of anthropogenic water. We used GPS data to examine if coyotes responded to water removal at a finer spatial scale than previously investigated. Our integrated step selection analysis did not find evidence that coyotes adjusted their distance to water following water removal. Vegetation was an important factor in habitat selection of coyotes, with riparian and agricultural areas being the most selected among vegetation types. Coyotes selected for locations where hunting and trapping was prohibited. Possibly the cause of increased coyote abundance in our study area was not due to the introduction of anthropogenic water sources but rather due to the cessation of regional lethal predator control programs. These two management decisions both occurred in the 1970s, therefore, their influences on the subsequent increase of coyote abundance may have been conflated. Our results, in combination with previous studies, provide evidence that coyotes are desert-adapted carnivores that do not rely on anthropogenic water sources.

1. Introduction

Water is a vital resource for all organisms. However, water can be scarce in certain ecosystems such as deserts. Many organisms have developed adaptations to survive in these reduced water environments (Costa, 2012). Even with these adaptations, water can still be a limiting resource for organisms. Wildlife resource managers have constructed anthropogenic water developments intended to benefit wildlife populations in arid environments; in 1997 as many as 10 western state wildlife agencies had active water development programs, and collectively had constructed at least 5859 water developments (Rosenstock et al., 1999). Despite their long running and widespread use, the utilization and benefits of water developments by wildlife populations is understudied (Simpson et al., 2011). As global temperatures continue to rise and human populations in the arid west increase, drought and water shortages are expected to increase (Fort, 2002). Therefore, the potential mitigation value of water developments may also likely increase (Rich et al., 2019), necessitating a firm understanding of how these anthropogenic water sources impact wildlife populations and communities.

Following the reduction of large carnivores across North America, midsized carnivores such as coyotes (*Canis latrans*) expanded their distribution >40% from their historic range of the 18th and 19th centuries (Laliberte and Ripple, 2004). This range expansion included a push into arid environments; coyotes now occur in most areas having abundant kit fox (*Vulpes macrotis*) populations (Ralls and White, 1995). Kit foxes are listed as vulnerable in the state of Utah (NatureServe, 2022), and intraguild predation (Polis et al., 1989) by coyotes on kit foxes is the leading cause of kit fox mortality (Ralls and White, 1995; Kozlowski et al., 2008; Kluever and Gese, 2017). Researchers have proposed that increasing coyote populations drove a decline of kit fox numbers in the west desert of Utah, mainly via intraguild predation and competition (AGEISS EnvironmentalInc, 2001; Arjo et al., 2007; Kozlowski et al.,

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2008).

One suggested explanation for the increase of coyotes in the west desert was the increased presence of anthropogenic water sources. The "indirect effect of water" hypothesis states that anthropogenic water sources are helping non-desert adapted animals, such as coyotes, gain purchase in environments that were considered unsuitable to their ecological needs, and they are now outcompeting endemic species specifically adapted to this climate, such as kit foxes (Hall et al., 2013). The basis of this hypothesis is the reliance on anthropogenic water by non-desert adapted animals. Addition of water to arid environments has been shown to reduce physiological stress and increase survival of large predators (Brawata and Neeman, 2011). This facilitates the persistence of large predators and increases the potential for conflict with intraguild prey (Atwood et al., 2011). Kit foxes do not require free water and can satisfy their water requirements through consumption of prey items, while it has been hypothesized that coyotes need to consume 3.5 times the amount of prey to meet their water requirements in the absence of available water during the summer (Golightly and Ohmart, 1984). Therefore, a lack of permanent freestanding water is not a deterrent to kit foxes occupying desert environments and may have provided them suitable habitat free from competition with or predation by coyotes.

The Dugway Proving Ground (DPG) is a United States Army installation in Tooele County, Utah, USA, covering ~3000 km^2 of Great Basin desert habitat. The DPG has been the site of ecological research since the 1950s, when Egoscue (1956) performed preliminary studies of kit foxes and found they were the most common carnivore on the DPG. Other records indicated coyotes were rare at the DPG during the mid-20th century (Shippee and Jollie, 1953). In the early 2000s, coyotes were reported as the most abundant carnivore on the DPG, while kit fox populations had declined (AGEISS EnvironmentalInc, 2001). Anthropogenic water sources were introduced to the DPG in the 1970s, and it was believed that these new water sources permitted coyotes to inhabit territories that were previously inaccessible to them due to a lack of sufficient freestanding water (Arjo et al., 2007; Kozlowski et al., 2008). In support of this theory, coyote core home ranges in the DPG all radiated from permanent water sources, and the recommendation was made that removing or excluding coyotes from these water sources could potentially change coyote spatial patterns and reduce coyote presence on the DPG (AGEISS EnvironmentalInc, 2001).

Kluever and Gese (2016) was one of the first studies to move past observational research and implement a before-after-control-impact (BACI) study design aimed at examining the impact of anthropogenic water sources on individual coyote spatial distributions by manipulating water availability on the landscape. Kluever and Gese (2016) found no change or shift in home ranges of coyotes following removal of water sources, which contradicted the postulations of Arjo et al. (2007) and Kozlowski et al. (2008). The coyotes whose only water sources were turned off did not leave the area, nor did they adjust their home ranges to include additional permanent water sources, and survival was not affected (Kluever and Gese, 2016). The only resultant change was a decrease in the frequency of visits to water resource sites that had been turned off. However, there were sample size limitations for both individual coyotes and VHF based location data, resulting in little to no statistical inference.

Hall et al. (2013) also found no evidence to support the indirect effect of water hypothesis for coyotes and kit foxes. Coyote occurrence was associated with factors other than the presence of free water and more research was needed to determine those factors (Hall et al., 2013). In addition, coyotes on the DPG during the Kluever and Gese (2016) study did not compensate for the removal of artificial water sources by altering their diets to larger prey which contain more preformed water (Hodge et al., 2022). Since coyotes on the DPG did not alter their home ranges (Kluever and Gese, 2016) or diet (Hodge et al., 2022) in response to removal of water sources, then possibly they were impacted by the water manipulation at a finer scale of habitat selection, the within home range scale, known as 3rd order habitat selection (Johnson, 1980).

Therefore, the objective of this study was to examine space use of coyotes pre- and post-water manipulation to evaluate if the removal of anthropogenic water sources impacted fine-scale habitat selection and distance to the closest water source. The indirect effect of water hypothesis rests on the assumption that coyotes cannot persist in desert ecosystems without the additional anthropogenic water sources. This study evaluated whether coyotes continued to use the same geographic areas both with access to anthropogenic water and after access to anthropogenic water sources was reduced. If coyotes chose to remain in locations without anthropogenic water, it was likely that water access was not a limiting factor to their fitness.

Our proposed hypothesis was that water manipulation would not impact coyote habitat use patterns. If this hypothesis was supported, we would expect to see a higher relative intensity of use in locations with larger distances to the nearest water source once anthropogenic water was removed. For example, within a certain geographic area if the number of available water sources declines, the average distance to remaining water sources in that geographic area would increase. If anthropogenic water sources do not influence coyote space use patterns, we would expect that once water sources are removed, coyotes appear to use locations that are further from the nearest water source. If, however, coyotes rely on anthropogenic water, we would expect to see coyotes maintain the same intensity of use of locations with shorter distances to nearest water, as coyotes would need to shift their space use patterns to account for the reduction in available water sources.

2. Methods

2.1. Study area

We conducted this study in Tooele County, Utah, USA, within the eastern portion of the DPG and adjoining federal lands (Fig. 1). Elevations ranged from 1287 to 3355 m. Annual mean air temperatures were 12.7 °C (range: 20.0 to 40.6 °C) and annual mean precipitation was 21.0 cm (range: 14.7–29.4 cm; U.S. Army Dugway Proving Ground, Meteorological Division). The Palmer Drought Severity Index (PDSI) during our study ranged from −3.0 to 4.3 (mean = −0.3, SD = 2.5) in the summer, and −2.4 to 2.6 (mean = −0.2, SD = 1.4) in the winter. We identified 50 water sources on the landscape, consisting of 15 natural springs, 14 wildlife guzzlers, 16 livestock tanks, and 5 ponds, which represent the vast majority of available water sources in the study area; 11 of the livestock tanks were only active during the grazing season (1 November – 31 March). Guzzlers were primarily placed among or at the base of mountainous areas to benefit populations of chukar partridges (*Alectoris chukar*) and mule deer (*Odocoileus hemionus*), and ponds were primarily located in flat land areas to support urban development (Hall et al., 2013). Guzzlers were designed to allow no run-off or access to water by rooted vegetation. Therefore, guzzlers did not support riparian vegetation while springs and man-made ponds were often associated with riparian communities, primarily comprised of tamarisk (*Tamarix ramosissima*) (Emrick and Hill, 1999). Anthropogenic water sites (i.e., guzzlers, ponds, and livestock tanks) were developed between the 1960s and 1990s (Arjo et al., 2007). 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 and were assumed to be homogenous throughout the study area.

The study area was predominately flat playa punctuated with steep mountain ranges. The lowest areas consisted of salt playa flats sparsely vegetated with iodinebush (*Allenrolfea occidentalis;* Kluever and Gese, 2016). Less salty, slightly higher elevation areas supported a cold desert chenopod shrub community consisting of principally of shadscale (*Atriplex confertifolia*) and greenmolly (*Kochia americana*). At similar elevations, shrub communities dominated by greasewood (*Sarcobatus vermiculatus*) were found. Mid-elevations consisted of vegetated sand dunes. Near the bases of the higher steep mountains were shrub-steppe communities of sagebrush (*Artemisia* sp.). The highest elevations

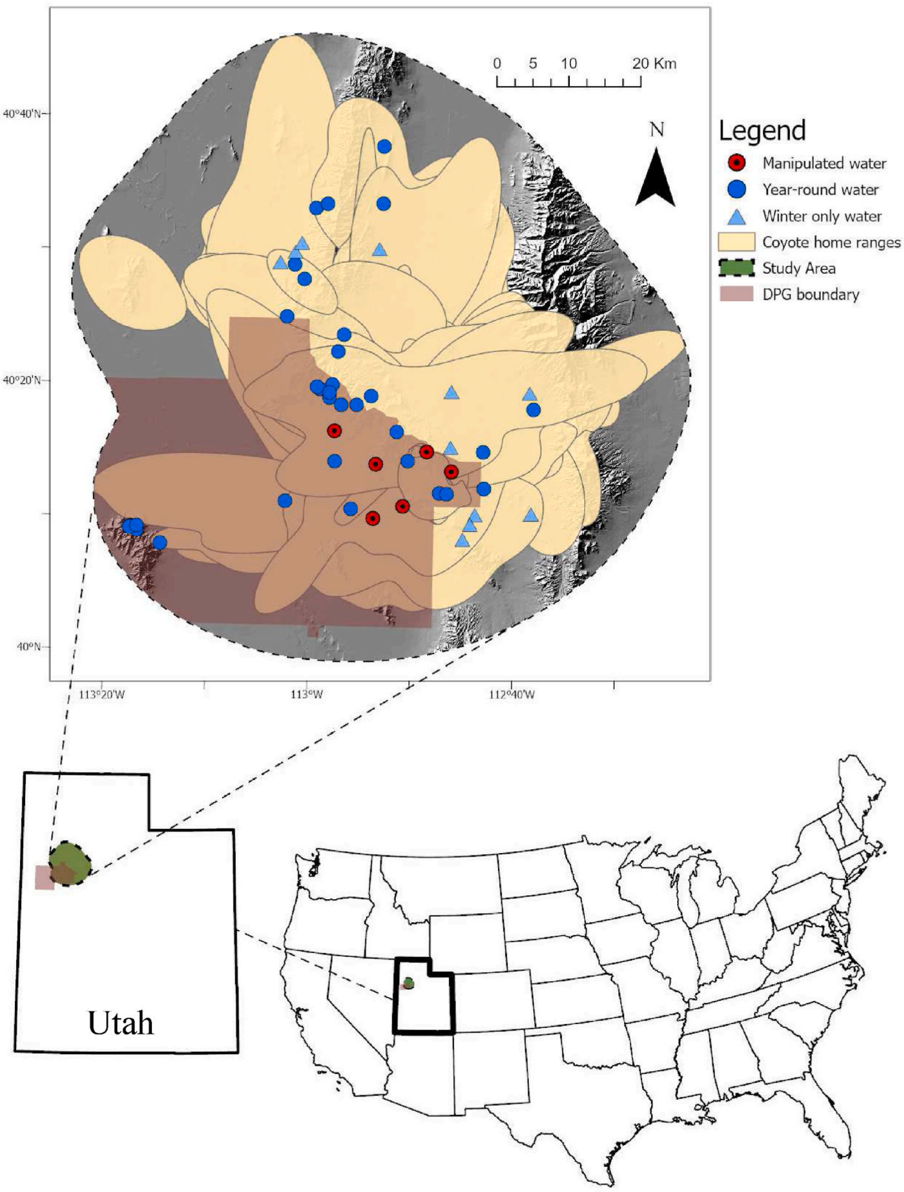

Fig. 1. Free water sites (total n = 50) in study area which were available year-round (n = 39 pre-manipulation, n = 33 post-manipulation) or available only in the winter (n = 11), and those that were manipulated (n = 6). Dugway Proving Ground (DPG) and adjacent public lands, Utah, USA, 2010–2013.

consisted of Utah juniper (*Juniperus osteosperma*) communities including black sagebrush (*Artemisia nova*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). Along the foothills, where wildfires had occurred, cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola kali*), and tall tumble-mustard (*Sisymbrium altissimum*) had invaded communities of sagebrush, juniper, and rabbitbrush (*Chrysothamnus* sp.) (Arjo et al., 2007). We classified the vegetation in our study area into the following categories based on plant physiognomy: barren (22.2%), desert scrub (21.2%), grassland (19.9%), sagebrush (13.8%), forest (12.2%), shrubland (5.8%), developed (1.8%), agriculture (1.1%), riparian (0.1%), and sparsely vegetated (1.9%) (landfire.gov, accessed 2021).

2.2. Animal capture and handling

Methods for coyote capture followed Kluever and Gese (2016). We captured coyotes via helicopter net-gunning (Gese et al., 1987) or foothold traps (#3 Soft Catch, Oneida Victor Inc., Euclid, OH) affixed with a trap tranquilizer device (Sahr and Knowlton, 2000). We staggered captures throughout the study, mainly between January 2010 to December 2012. Processing of coyotes included taking blood samples, affixing ear tags, and recording weight, sex, and morphological measurements. We determined age by tooth wear, tooth eruption and body size (Gier, 1968), and we fitted adults with a 200 g global positioning system (GPS) radio-collar (Model M2220; Advanced Telemetry Systems, Isanti, MN). The GPS collars were store-on-board with a programmed release mechanism that allowed collars to be recovered without recapturing coyotes. We captured coyotes throughout the study area and efforts were made to radio-collar only one individual per social group. We limited capture efforts to October through February of each year so as to not interfere with parturition and pup rearing. 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 coyotes 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).

2.3. Water manipulation

Halfway through the study period, in March 2012, we drained 5 guzzlers using a generator and submersible pump, then covered the drinking portals with plywood. Drained guzzlers were selected randomly. Guzzler water levels were checked monthly and were re-drained if they reached >2/3 capacity. In addition, one pond was excluded by affixing a 1.2 m chain-link apron to an existing surrounding chain link fence. The pond was not randomly selected for exclusion because it was the only pond on DPG where exclusion was possible with available resources. All manipulated water sources were previously available year-round (Fig. 1). At the time of manipulation, these sites were thought to account for 33% (6 of 18) of the available perennial anthropogenic water sites within the study area. The manipulation allowed us to incorporate a multiple-treatment site, multiple-control site BACI design (Morrison et al., 2008) where we assessed distance to water before and after eliminating water availability at water sites. This allowed us to compare the temporal spans prior to (pre-) and after (post-) the water manipulation.

2.4. Home range determination

Locational data were recorded by GPS-collars every 4 h and used to calculate home ranges of individual coyotes. We evaluated seasonal home ranges using an autocorrelated kernel density estimate (aKDE) that accounts for the inherent spatial-temporal autocorrelation present in GPS data taken at frequent time fixes and reduces home range bias (Fleming et al., 2015). Each annual seasonal home range was based on >30 GPS points analyzed using the **amt** package in R (Signer et al., 2019; R Version 4.0.2, www.r-project.org, accessed Aug 22, 2020). We determined seasons by average snowfall as wet/winter (1 November – 31 March) and dry/summer (1 June – 30 September) to account for the presence of free water across the landscape in the form of snow. We did not include data from April, May, or October as those were transitional months. This allowed us to have a clear delineation between wet and dry seasons.

2.5. Integrated step selection analysis

We investigated the effect of water manipulation on coyotes' relationship with water, as well as general coyote resource selection using a type of step selection function (SSF; Thurfjell et al., 2014) known as an integrated step selection analysis (iSSA; Signer et al., 2019; Avgar et al., 2016). An SSF evaluates which habitat and environmental covariates serve as predictors of wildlife space use and operates at the spatio-temporal scale of each location (Thurfjell et al., 2014) permitting the inclusion of time-varying covariates such as the Palmer Drought Severity Index (PDSI) and other environmental covariates of interest (Table 1). An SSF considers a 'step' to be the straight-line distance between two consecutive GPS points and uses conditional logistic regression to examine how animals move through the landscape (Thurfjell et al., 2014). We used the **amt** package in R to run the iSSA; for each observed step, we generated 10 available steps from the same starting location, with the step length drawn from a gamma distribution and the turn angle drawn from a von Mises distribution (Signer et al., 2019). The randomly generated step locations represented habitat that was available for coyotes to select. The response variable in our models was whether a step was used (confirmed through GPS data) or available (randomly generated). It is important to note that available locations may have been used by coyotes between data collection points.

We split the data into treatment and control groups based on whether coyotes were impacted by the water removal or not. Treatment coyotes were individuals that contained one or more manipulated water source (s) within their seasonal home ranges. Control coyotes had either 1) GPS location data only from the pre-manipulation period, when all free water sites were available, or 2) had GPS location data both pre- and post-manipulation and did not contain a manipulated water source in any of their pre-manipulation seasonal home ranges. Therefore, control individuals were sampled throughout both the pre- and post-manipulation periods and did not experience the water removal treatment, whereas the treatment individuals were sampled throughout the pre- and post-manipulation periods and were exposed to the water removal. This represents a BACI study design where both control and treatment groups are monitored both before and after a treatment.

Table 1
Environmental and demographic covariates used to model coyote (*Canis latrans*) habitat selection on the Dugway Proving Ground, Utah, 2010–2013.

Covariate	Description	Type of Measure	Source
Elevation	Elevation centered and scaled to a standard deviation of 1	Continuous	30 m digital elevation model (DEM; usgs.gov, 2021)
Vegetation	Vegetation type (n = 10) of each 30 m^2 pixel, classified using plant physiognomy	Categorical	LANDFIRE 2012 (LF_130) Existing Vegetation Type (landfire.gov, accessed 2021)
Distance to road	Log transformed Euclidean distance to the closest road	Continuous	Kluever and Gese (2016)
Distance to active water source	Log transformed Euclidean distance to the closest active water source	Continuous	Kluever and Gese (2016)
Distance to inactive water source	Log transformed Euclidean distance to the closest inactive water source	Continuous	Kluever and Gese (2016)
Within/out boundary of DPG	Whether or not the location is inside the boundaries of the DPG	Categorical	Kluever and Gese (2016)
Palmer Drought Severity Index (PDSI)	Measure of drought that incorporates temperature and precipitation data	Continuous	GRIDMET/DROUGHT (Abatzoglou, 2012)
Season	Wet: (1 November – 31 March) Dry: (1 June – 30 September)	Categorical	
Pre/Post	Whether the observed GPS data were collected from before or after the March 2012 water manipulation	Categorical	

We separated our data into treatment and control groups and modeled them separately due to sample size constraints with multiple interactions. For each treatment and control group we used an a-priori modeling approach (Burnham and Anderson, 2002) and evaluated four models: a full model with all covariates (n = 9), a water-only model that focused on distance to active and inactive water sources, a model that excluded all water-related variables, and a model that excluded vegetation (Table 2). We chose these models to evaluate if habitat selection was a mixture of multiple factors (full), if it was driven solely by water (water-only), if water was extraneous (water exclusion), and if vegetation was extraneous (vegetation exclusion). We examined several environmental and demographic covariates (Table 1) for each model (Table 2).

We included three interactions for distance to water. The interaction between distance to water and the water manipulation (pre/post) is a test of the water removal treatment (i.e., we estimate whether there is a difference in the effect of water in the pre-vs post-manipulation periods). In the control group analysis, the estimate from this interaction reflects 'natural' change in the distance to water effect from the pre-to post-manipulation period. We consider this 'natural' change in the distance to water effect because the control group did not experience any water

Table 2
Candidate models of coyote (*Canis latrans*) habitat selection ranked by Akaike's Information Criterion for small sample sizes (AICc) scores. PDSI: Palmer Drought Severity Index. Each model includes the following movement covariates: step length (sl), log-step length (log_sl), and the cosine of the turn angle (cos_ta). Dugway Proving Ground, Utah, 2010–2013.

Model		Treatment		Control	
	df	ΔAIC_c	Weight	ΔAIC_c	Weight
Full Model: Elevation + Vegetation + Road + Water + Inactive + Dugway + (Water: Pre/Post) + (Water * Season) + (Water * PDSI) + sl + log_sl + cos_ta	20	0	1.00	0	1.00
No Water Model: Elevation + Vegetation + Road + Dugway + sl + log_sl + cos_ta + (log_sl * Dugway)	15	145	0	825	0
No Vegetation Model: Elevation + Road + Water + Inactive + Dugway + (Water: Pre/Post) + (Water * Season) + (Water * PDSI) + sl + log_sl + cos_ta	11	380	0	637	0
Water Only Model: Water + Inactive + (Water: Pre/ Post) + (Water * Season) + (Water * PDSI) + sl + log_sl + cos_ta	8	546	0	1229	0

removal manipulation. The same interaction in the treatment group represents the combined 'natural' change expected between the pre- and post-manipulation periods plus the effect of the water removal treatment. Further, we hypothesized that regardless of whether individuals were in the treatment or control group, the effect of distance to water on habitat selection may differ during the season (wet/dry), and based on drought severity (PDSI), as individuals may experience different water limitations during these seasons and drought conditions (Table 2).

We log transformed covariates that were 'distance to' features, and elevation was centered and scaled with a standard deviation of 1. Vegetation was a categorical covariate derived from the LANDFIRE 2012 dataset (landfire.gov, accessed 2021) with the following categories classified by plant physiognomy: agriculture, barren, desert scrub, developed, forest, grassland, sparsely vegetated, riparian, sagebrush, and shrubland. We included movement covariates of step length, log step length, and cosine of the turning angle in every model. We checked for correlations between all covariates and any with a correlation higher than 0.7 were excluded from the models to avoid issues of collinearity (Dormann et al., 2013). We used Akaike's Information Criterion with a correction for small sample sizes (AIC_c; Burnham and Anderson, 2002) to determine the best supported model.

We evaluated model fit using used-habitat calibration (UHC) plots (Fieberg et al., 2018). Traditional methods of evaluating resource selection functions, which have also been applied to SSF, quantify the model's ability to classify locations as used or unused (Johnson et al., 2006). These traditional methods are not appropriate to use for a SSF because they cannot account for the inherent stratified nature of the temporally variant data (Fieberg et al., 2018). The UHC plots validate models based on how well they predict the habitat characteristics associated with used locations, which allows them to validate SSFs accounting for stratified data (Fieberg et al., 2018).

As we were working with used-available data (as opposed to used-unused data), we cannot estimate the probability of use of a resource unit since available locations may have been used between data points (Manly et al., 2002), and alternatively estimated the relative selection strength for categorical variables (RSS; Avgar et al., 2017). The RSS compares the probability of selection at one or more location(s) to that of a single reference location and allows for easier interpretation of iSSA results.

3. Results

We radio-collared 31 coyotes (13 females, 18 males) between January 2010–December 2012 and monitored them until December 2013. We established 102 seasonal aKDE home ranges based on a mean of 475 GPS points each (range = 32–878, SD = 240). Individual coyotes had a mean of 2.46 seasonal home ranges (SD = 1.48, range = 1–5) before the 2012 water manipulation, and a mean of 2.75 (SD = 0.92, range = 1–4) after the manipulation. We recorded 16 mortalities of radio-collared coyotes during the study period, 12 (75%) were due to hunting/trapping, 2 (12.5%) were due to predation, and 1 (6.3%) each were due to sepsis and vehicle collision. Of the 31 radio-collared coyotes, 30 (12 females, 18 males) were considered for further analysis (~65,000 GPS locations). The one coyote removed from analysis had data collected every 7 h, and therefore could not be analyzed with the remainder which all had 4 h between locations.

The treatment group consisted of 9 coyotes (1 female, 8 males) which contained at least one manipulated water source(s) in their seasonal home ranges and reported data from 1) both pre- and post-water manipulation (6 males), or 2) only from post-manipulation (1 female, 2 males). The remaining 21 coyotes (11 females, 10 males) were assigned to the control group and had either 1) data only from pre-manipulation (9 females, 9 males), or 2) had data both pre- and post-manipulation and did not contain a manipulated water source in any of their pre-manipulation seasonal home ranges (2 females, 1 male). Due to mortality of study animals during the study only 9 coyotes total provided data both pre- and post-manipulation. We chose to keep additional animals in the analysis to decrease the impact of individual variation on the results.

Based on AIC_c values, the full model, which included all covariates, was the best or both control and treatment groups, with a ΔAIC_c of 637 and 145 to each secondary model, respectively, (Table 2) and carried 100% of model weight. The UHC plots showed that models passed validation checks (Fig. 2).

The BACI design where we monitored both control and treatment groups over time enables us both to estimate 'natural' changes (i.e., not related to treatment effects) in individuals' relationship with distance to water (through the interaction between distance to water and pre/post for the control group), and to account for any initial group differences in the relationship to distance to water before the experimental water removal manipulation. We can use the beta coefficients from the model (Table 3, Supplemental Table 1) to calculate the expected β for treatment individuals post-manipulation if they were not exposed to a treatment (hereafter referred to as 'post no treatment'; Stewart-Oaten and Bence, 2001). This is shown in Equation (1), where PNT is post no treatment, PR is treatment group pre-manipulation, and NC is natural change.

$$\begin{aligned} PNT &= PR + NC \\ PNT &= -0.13 + (-1.16) \\ PNT &= -1.29 \end{aligned} \tag{1}$$

This allowed us to directly compare treatment individuals that received the treatment ($\beta_{Post\ treatment} = -0.49$, Supplemental Table 1) with the theoretical no treatment individuals ($\beta_{Post\ no\ treatment} = -1.29$, Equation (1)). After accounting for the natural variation within the BACI study design, we found that treatment coyotes had a higher intensity of use of locations further from the nearest water source (i.e., a less negative relationship with distance to water; $\beta_{treatment} = -0.49$; $\beta_{no\_treatment} = -1.29$; Supplemental Table 1, Equation (1), Fig. 3).

There was a negative relationship between selection and the log-transformed distance to water sources ($\beta_{control} = -0.56$; $\beta_{treat} = -0.13$), and coyotes selected for lower elevations ($\beta_{control} = -0.75$; $\beta_{treat} = -0.61$; Table 3). Coyotes were ~1.5–2 times more likely to choose a step ending inside DPG boundaries than outside, all other variables

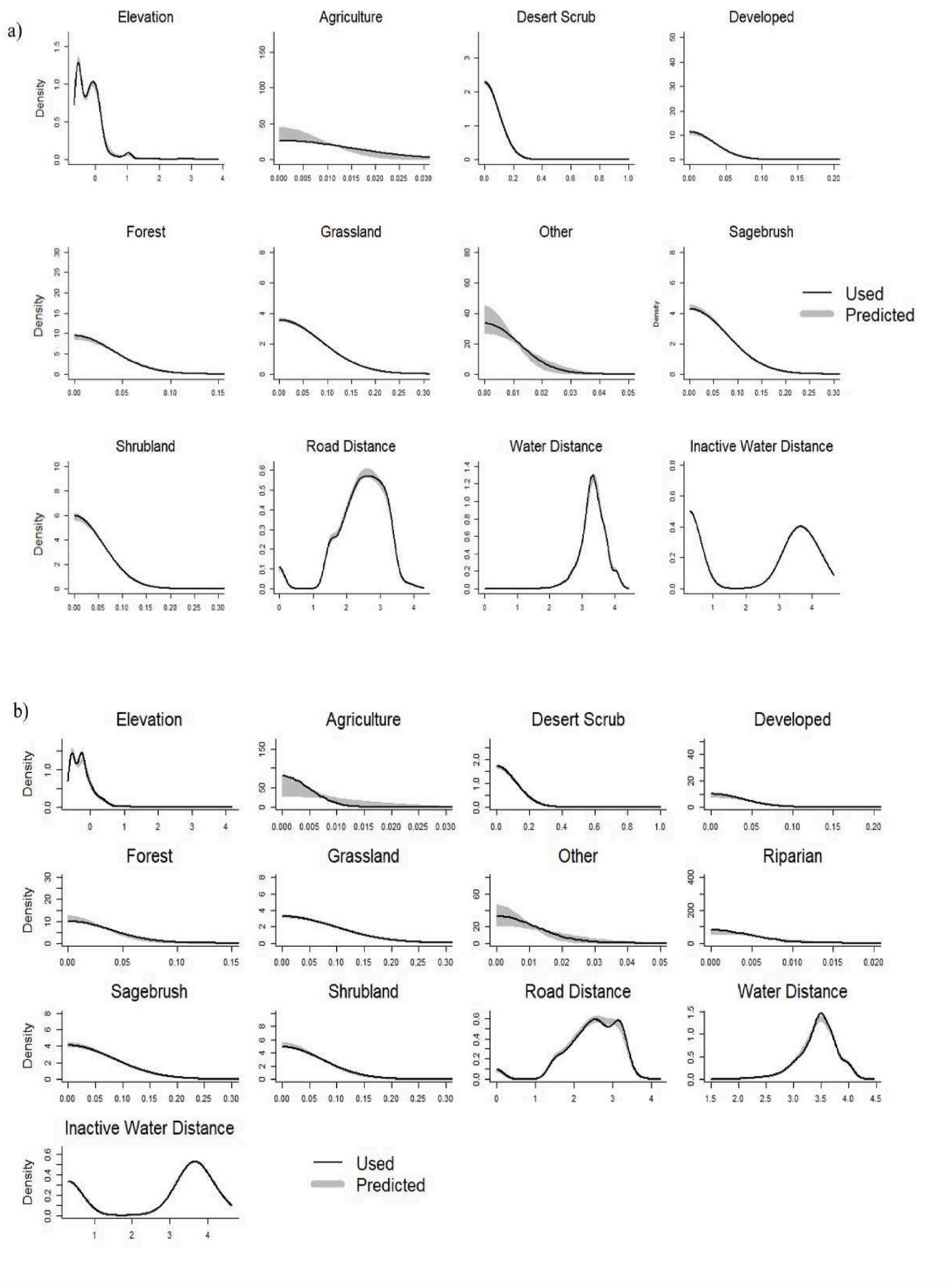

Fig. 2. Used-Habitat Calibration (UHC) plots for control (a) and treatment (b) iSSA models. Control does not include riparian because it was insignificant in the model. The observed distribution of each environmental covariate is the test data set and is represented by the solid black lines, with a 95% simulation envelope for the distribution being represented by the gray bands. Predictive distributions were formed using a model fit to training data. The model is well calibrated if the observed distributions (solid black lines) fall within the simulation envelopes. Dugway Proving Ground (DPG) and adjacent public lands, Utah, USA, 2010–2013.

being constant ($\beta_{control} = 0.60$, $logRSS_{control} = 1.82$; $\beta_{treatment} = 0.37$, $logRSS_{treatment} = 1.44$; Table 3). Distance to roads had a small positive influence on control coyotes ($\beta_{control} = 0.074$) but was insignificant in the treatment model ($\beta_{treatment} = 0.012$, $p = 0.44$; Table 3). The interaction between distance to water and season had opposite effects on control and treatment coyotes but was insignificant for control; control coyotes used areas farther from water during the wet season ($\beta_{control} = 0.10$, $p = 0.11$) while treatment coyotes used areas closer to water during the wet season ($\beta_{treatment} = -0.29$; Table 3). The interaction between distance to water and PDSI was not significant for either model

Table 3
Variables from the top integrated step selection analysis (iSSA) for control and treatment coyotes (*Canis latrans*), Dugway Proving Ground, Utah, 2010–2013.

	Control			Treatment		
Covariate	β Estimate	Std. Error	p value	β Estimate	Std. Error	p value
Dugway (Inside)	0.60	0.041	<0.0001	0.37	0.056	<0.0001
Elevation	−0.75	0.040	<0.0001	−0.61	0.058	<0.0001
Vegetation: Agriculture	1.45	0.14	<0.0001	1.62	0.30	<0.0001
Vegetation: Desert Scrub	0.87	0.048	<0.0001	1.07	0.079	<0.0001
Vegetation: Developed	1.20	0.067	<0.0001	1.41	0.099	<0.0001
Vegetation: Forest	0.89	0.066	<0.0001	1.16	0.11	<0.0001
Vegetation: Grassland	0.73	0.050	<0.0001	0.82	0.081	<0.0001
Vegetation: Sparsely Vegetated	1.12	0.13	<0.0001	0.72	0.18	0.001
Vegetation: Riparian	0.48	0.43	0.27	1.99	0.60	0.003
Vegetation: Sagebrush	0.99	0.052	<0.0001	1.12	0.083	<0.0001
Vegetation: Shrubland	1.10	0.052	<0.0001	1.21	0.084	<0.0001
Distance to Road	0.074	0.013	<0.0001	0.012	0.16	0.44
Distance to Water	−0.56	0.055	<0.0001	−0.13	0.098	<0.0001
Distance to Inactive Water	0.029	0.064	0.65	0.31	0.073	<0.0001
Dist. Water * Post-Manipulation	−1.16	0.088	<0.0001	−0.36	0.13	0.003
Dist. Water * PDSI	−0.0026	0.018	0.88	0.0067	0.032	0.83
Dist. Water * Wet Season	0.10	0.065	0.11	−0.29	0.090	<0.0001

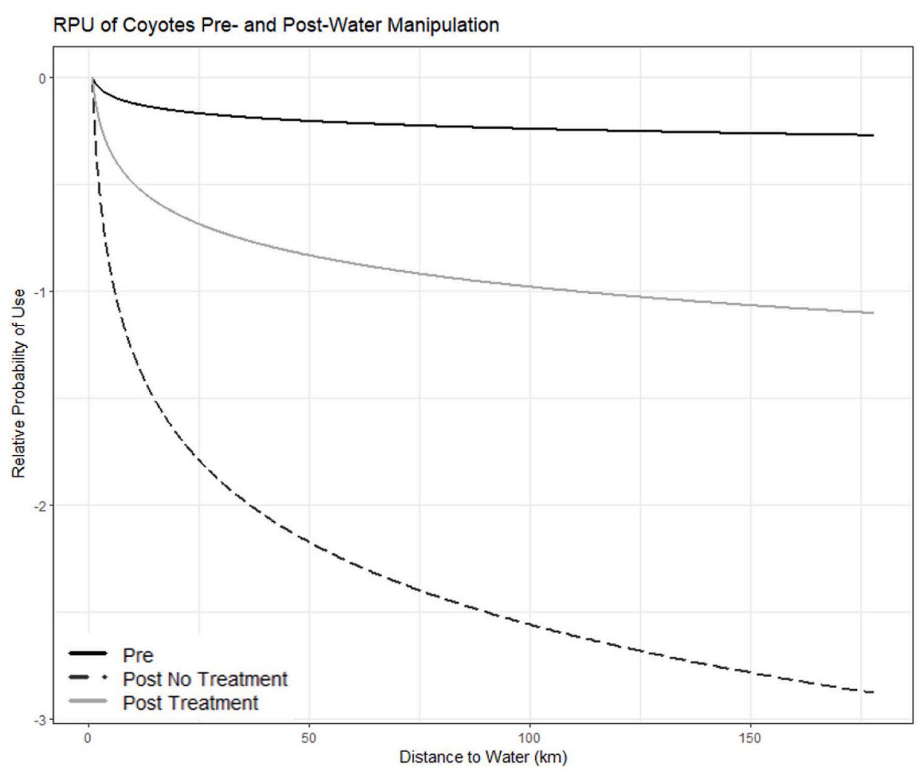

Fig. 3. Relative probability of use (RPU) with changing distance to water for treatment coyotes (*Canis latrans*) pre-manipulation (pre, solid black), post-manipulation (post treatment, solid light gray), and if no treatment had been applied (post no treatment, dashed dark gray). Dugway Proving Ground (DPG) and adjacent public lands, Utah, USA, 2010–2013.

($\beta_{control} = -0.003$, $p_{control} = 0.88$; $\beta_{treatment} = 0.007$, $p_{treatment} = 0.83$; Table 3).

Using log relative selection strength (logRSS) to compare the likelihood of selecting a location in differing vegetation types over barren showed riparian, agriculture, and developed as the most selected for. Riparian vegetation was the most selected for vegetation for treatment coyotes ($\beta_{treatment} = 1.99$, $logRSS_{treatment} = 7.3$), but was insignificant for control coyotes ($\beta_{control} = 0.48$, $p = 0.27$; Table 3). Agriculture had the second highest selection for treatment and the highest for control ($\beta_{control} = 1.45$, $logRSS_{control} = 4.3$; $\beta_{treatment} = 1.62$ $logRSS_{treatment} = 5.0$), followed by developed for control ($\beta_{control} = 1.20$, $logRSS_{control} = 3.3$; Table 3, Fig. 4).

4. Discussion

Our results support our hypothesis that coyotes do not necessarily rely on anthropogenic water sources to determine their step selection patterns. As predicted, after anthropogenic water sources were removed from the landscape, treatment coyotes had higher intensity of use in locations with greater distances to water compared with control individuals, indicating that treatment coyotes did not need to shift their space use patterns to remain within a constant, shorter distance to water following the removal of anthropogenic water. Rather, after accounting for the natural change in habitat selection that occurred over time in the control group (i.e., part of the BACI design), we found a positive treatment effect, with treatment coyotes being more tolerant of increased

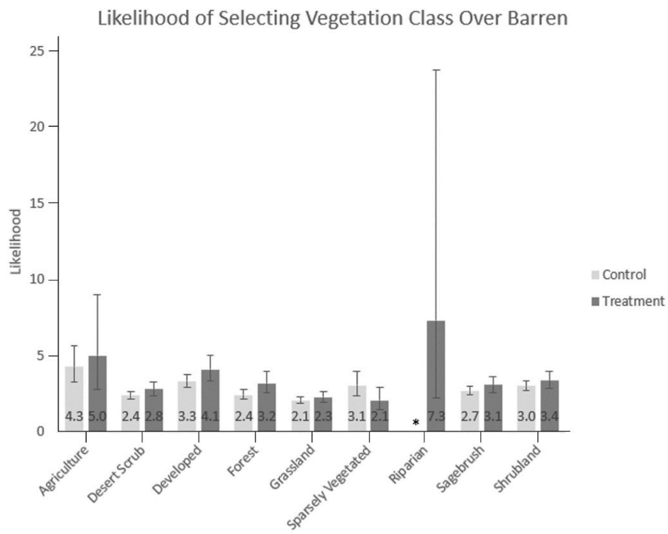

Fig. 4. Likelihood of control (light gray) and treatment (dark gray) coyotes (*Canis latrans*) selecting for a vegetation class if all other variables are constant, as compared to barren, with 95% confidence intervals represented by error bars. For example, a coyote would be ~2 times as likely to select for grassland than for barren. *Riparian vegetation was insignificant for control, so it has been excluded. Dugway Proving Ground (DPG) and adjacent public lands, Utah, USA, 2010–2013.

distance to water.

If water was a limiting resource on the landscape for coyotes, we would have expected them to adjust their space use following water removal to maintain a certain constant distance to water to be able to meet their water needs. The desert bighorn sheep (*Ovis canadensis mexicana*), a desert adapted ungulate, also did not adjust their distance to water following the removal of artificial water sources (Cain et al., 2008). This further contributes to evidence that coyotes are a desert adapted species. Our work builds on studies in the DPG which established that after the removal of anthropogenic water sources, coyotes did not alter their home range boundaries to include additional water sources (Kluever and Gese, 2016), nor did they adjust their diet to increase intake of larger prey containing more preformed water (Hodge et al., 2022).

Vegetation type also played an important role in coyote habitat selection. We found treatment coyotes selected highly for riparian vegetation, which has also been found by multiple other studies (Morin, 2015; Gifford et al., 2017). Conversely, some studies found coyotes avoided riparian vegetation (Hinton et al., 2015), although this may have been due to human activity in those areas (Mastro et al., 2019). Selection for riparian vegetation may be due to several causes. Gifford et al. (2017) posited it was part of a risk-avoidance behavior to prevent predation by cougars (*Puma concolor*), though only one of our tagged coyotes was killed by a cougar during our study. Morin (2015) also suggested that these areas provided refuge for coyotes, by way of avoiding human development. Possibly the coyotes we investigated selected riparian vegetation for its protective cover and the thermoregulation benefits of shade provided by the dense vegetation found there.

Other benefits of riparian vegetation could be foraging and/or bedding opportunities, supported by the fact that McAdoo et al. (2006) found that rodent numbers were highest in riparian aspen woodland compared to other vegetation types in the Great Basin desert. We did not assess small mammal abundance in riparian zones in our study area, but this could be an aspect of future studies. Riparian vegetation was rare within our study area (0.1%; Emrick and Hill, 1999), so its relative rareness could inflate the observed selection with only a few used locations in this vegetation type (Mysterud and Ims, 1998). This uncertainty can be seen in the large 95% confidence intervals for riparian selection in our treatment model, and the fact that it was insignificant in our control model (Fig. 4).

Agriculture was another vegetation type strongly selected for by coyotes, which has been found in other studies (Hinton et al., 2015), possibly due to increased prey availability (Byrne et al., 2014). Coyotes also selected for areas of lower elevation, a selection preference that has been seen in wolves (*Canis lupus*) relative to prey availability and ease of movement (Uboni et al., 2015). Coyotes in high elevation environments have been known to utilize snowmobile trails to facilitate movement (Gese et al., 2013). Coyotes selected for steps ending within DPG boundaries, which was expected as those areas were protected from hunting and trapping, which was the leading cause of coyote mortality in this study. This shows that when coyotes were near the border of the DPG, they preferred to be inside rather than outside. Mammalian carnivores often select for areas of refugia, especially from human impacts (Duarte et al., 2022).

We did not find a significant relationship between drought severity and the distance to artificial water sources. This was surprising, as we anticipated that distance to water would be shorter when drought severity values indicated drier conditions. We did not see support for our hypothesis that the distance to a water source would be greater in the wet season as ephemeral pools, snow, and other temporary water sources were more available across the landscape reducing the need to travel to a permanent water source. The treatment model showed coyotes closer to water in the wet season, while the control model was insignificant. Our water only model was the least supported model according to AICc, indicating that while water was an important component of habitat selection by desert coyotes, it was not the sole factor.

This study was part of one of the first ever to use a BACI design aimed at testing the spatial response of coyotes to removal of artificial water sources on the landscape. Our results, when considered in combination with the results of several other studies on coyotes in the DPG, suggest that the indirect effect of water hypothesis is unsubstantiated for coyotes in the desert system we investigated (Hall et al., 2013; Kluever and Gese, 2016; Hodge et al., 2022). Coyote reliance on anthropogenic water sources is the basis of the indirect effect of water hypothesis, and without evidence of that reliance the rest of the hypothesis is not supported. Postulations regarding the metabolic water requirements of coyotes may have overestimated the amount of water coyotes require to survive in desert ecosystems (Golightly and Ohmart, 1984). Future research of interest given our findings could be to investigate the metabolic requirements of coyotes in a captive research facility where water and food intake can be regulated.

Our research contributes to elucidating how access to water influences coyote space use and behavior in desert habitats. Based on our findings, the observed increase in coyotes in and around the DPG was not solely the result of increased anthropogenic water sources on the landscape, as previously posited (Arjo et al., 2007; Kozlowski et al., 2008). Rather, it may be that the effects of changes in predator management have been conflated with the introduction of anthropogenic water sources. During the mid-20th century, when coyotes were rare on the DPG, baited toxicants were commonly used as a form of predator control (Shippee and Jollie, 1953). The use of baited toxicants on federal lands was banned in 1972 then highly limited for use only by federal agencies in 1976 (restricted use under the Environmental Protection Agency), which coincided with the introduction of anthropogenic water sources to the DPG in the 1970s (Executive Order No. 11917, 1976; Arjo et al., 2007; Kozlowski et al., 2008). Having found no evidence to suggest that the additional water sources contributed to the coyote population increase, it may be that the reduction in predator control was the cause of the observed increase. Further studies into the impacts of reduced predator control may be necessary to confirm this hypothesis.

It is important to consider that our findings and suggestions are based on a small sample size, with only 4 of 30 coyotes providing data pre- and post-manipulation for both seasons, and an additional 5 coyotes that had pre-manipulation data only for the wet season, and post-manipulation data for both seasons. Additionally, we did not account for differences between sexes, and our treatment group only contained one female. Furthermore, during study design the belief was that the coyotes would remain closer to the boundaries of the DPG, and therefore the manipulated water sources were thought to account for 1/3 of all accessible water sources. However, the coyotes covered a much larger range than initially anticipated, which included additional water sources not originally accounted for in the 2012 water manipulation, but which we took into consideration during this analysis. Perhaps if a higher proportion of water sources had been manipulated, we could have seen more of an effect on coyote habitat selection.

Artificial water developments are present extensively across the globe for both human and wildlife use. Understanding the intended and unintended impacts they may have on both target and nontarget species could inform wildlife management and conservation. Anthropogenic water sources provide additional water sources for ungulates during dry seasons that can impact migration as well as home ranges (Bennitt et al., 2022), and can serve as feeding locations for bats (Lisón and Calvo, 2011). However, artificial water sources do not always benefit wildlife species. Lisón and Calvo, 2011 found that bat activity at canals increased for common bat species but not for species of conservation concern. A study in Australia found that dusky hopping-mice (*Notomys fuscus*) were most strongly influenced by environmental effects of resource availability and rainfall as opposed to human effects such as artificial water availability (Allen et al., 2018). Additionally, anthropogenic water sources can have indirect negative impacts such as extreme degradation of the area surrounding the water source up to 0.5 km away, an increase in unpalatable perennial shrubs, and a decrease in the abundance of palatable native perennial grasses (James et al., 1999). Whenever the possibility of artificial water developments arises, no matter the purpose, it is imperative to consider what consequences it may have on the surrounding wildlife and landscape.

Several studies have created resource selection functions (RSFs) for coyotes, however, none have focused on desert coyotes or water dependency (Hinton et al., 2015). Only two previous studies implemented an SSF for coyotes and they occurred in boreal and deciduous forest habitats (Ellington et al., 2020), or urban environments containing deciduous and mixed-woods stands (Thompson et al., 2021). This was the first study to utilize an SSF to investigate desert coyotes, especially related to selection for permanent water sites, and how water influences coyote movement on the landscape. Thompson et al. (2021) found that urban coyotes select for natural cover compared to developed habitat types, showing a similar selection for refugia that we found in regard to the DPG.

Our results suggest that coyote presence in the west desert is not reliant on artificial water sources. They appear to be a desert adapted carnivore with an increasing population abundance in the Great Basin desert. Kit fox populations appear to be declining due to the increased coyote abundance. Coyotes are the leading cause of kit fox mortality, far above any other causes (Ralls and White, 1995; Arjo et al., 2007; Kozlowski et al., 2008; Kluever and Gese, 2017). In our study system a conversion from native vegetation to homogenous stands of cheatgrass reduced the prey base shared by kit foxes and coyotes, though intermediate levels of cheat grass can be beneficial to rodents (Smith et al., 2018). Removing a small proportion of anthropogenic water sources has not been shown to be a viable solution to decrease coyote presence or abundance. Given the abundant use of artificial water sources for cattle in the surrounding areas, it may be difficult to turn off enough water sources to see an effect on coyote space use. Wildlife managers concerned about declining and sensitive kit fox populations may consider what other strategies might either feasibly allow for the coexistence of these two species or find ways to reduce coyote abundance (NatureServe, 2022).

CRediT authorship contribution statement

Nadine A. Pershyn: Methodology, Validation, Formal analysis, Writing – original draft, Visualization. **Eric M. Gese:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **Erica F. Stuber:** Methodology, Validation, Formal analysis, Writing – review & editing, Supervision. **Bryan M. Kluever:** Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2023.105097.

References

Abatzoglou, J.T., 2012. Development of gridded surface meteorological data for ecological applications and modeling. Int. J. Climatol. 33 (1), 121–131. https://doi.org/10.1002/joc.3413.

AGEISS Environmental, Inc, 2001. Final Report for the Carnivore Ecology Study at Dugway Proving Ground. Final Report to the Directorate of Environmental Programs. U.S. Army Dugway Proving Ground, Dugway, Utah.

Allen, B.L., Fawcett, A., Anker, A., Engeman, R.M., Lisle, A., Leung, L.K.-P., 2018. Environmental effects are stronger than human effects on mammalian predator-prey relationships in arid Australian ecosystems. Sci. Total Environ. 610, 451–461. https://doi.org/10.1016/j.scitotenv.2017.08.051. *–611*.

Arjo, W.M., Gese, E.M., Bennett, T.J., Kozlowski, A.J., 2007. Changes in Kit Fox-Coyote-Prey Relationships in the Great Basin Desert, Utah, vol. 67. Western North American Naturalist, pp. 389–401. https://doi.org/10.3398/1527-0904(2007)67[389:CIKFRI]2.0.CO;2.

Atwood, T.C., Fry, T.L., Leland, B.R., 2011. Partitioning of anthropogenic watering sites by desert carnivores. J. Wildl. Manag. 75 (7), 1609–1615. https://doi.org/10.1002/jwmg.225.

Avgar, T., Lele, S.R., Keim, J.L., Boyce, M.S., 2017. Relative selection strength: quantifying effect size in habitat- and step-selection inference. Ecol. Evol. 7 (14), 5322–5330. https://doi.org/10.1002/ece3.3122.

Avgar, T., Potts, J.R., Lewis, M.A., Boyce, M.S., 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods Ecol. Evol. 7 (5), 619–630. https://doi.org/10.1111/2041-210X.12528.

Bennitt, E., Bradley, J., Bartlam-Brooks, H.L.A., Hubel, T.Y., Wilson, A.M., 2022. Effects of artificial water provision on migratory blue wildebeest and zebra in the Makgadikgadi Pans ecosystem, Botswana. Biol. Conserv. 268, 109502 https://doi.org/10.1016/j.biocon.2022.109502.

Brawata, R., Neeman, T., 2011. Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. Wildl. Res. 38, 426–436. https://doi.org/10.1071/WR10169.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. Springer Science & Business Media, New York, NY.
Byrne, M.E., Clint McCoy, J., Hinton, J.W., Chamberlain, M.J., Collier, B.A., 2014. Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. J. Anim. Ecol. 83 (5), 1234–1243. https://doi.org/10.1111/1365-2656.12205.
Cain, J.W., Krausman, P.R., Morgart, J.R., Jansen, B.D., Pepper, M.P., 2008. Responses of desert bighorn sheep to removal of water sources. Wildl. Monogr. 171, 1–32.
Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.
Duarte, H.O.B., Boron, V., Carvalho, W.D., de Toledo, J.J., 2022. Amazon islands as predator refugia: jaguar density and temporal activity in Maracá-Jipioca. J. Mammal. 103 (2), 440–446. https://doi.org/10.1093/jmammal/gyab142.
Egoscue, H.J., 1956. Preliminary studies of the kit fox in Utah. J. Mammal. 37 (3), 351–357. https://doi.org/10.2307/1376734.
Emrick, V., Hill, A., 1999. Classification of Great Basin Plant Communities Occurring on Dugway Proving Ground. U.S. Army Corp of Engineers Research Laboratories, Utah. Report 57.
Executive Order No. 11917, 3 C.F.R, 1976. Amending Executive Order No. 11643 of February 8, 1972, Relating to Environmental Safeguards on Activities for Animal Damage Control on Federal Lands.
Fieberg, J.R., Forester, J.D., Street, G.M., Johnson, D.H., ArchMiller, A.A., Matthiopoulos, J., 2018. Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. Ecography 41 (5), 737–752. https://doi.org/10.1111/ecog.03123.
Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., Calabrese, J.M., 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96 (5), 1182–1188. https://doi.org/10.1890/14-2010.1.
Fort, D., 2002. Water and population in the American west. Human Population and Freshwater Resources: U.S. Cases and International Perspectives 107, 17–23.
Gese, E., Rongstad, O.J., Mytton, W.R., 1987. Manual and net-gun capture of coyotes from helicopters. Wildl. Soc. Bull. 15, 444–445.
Gese, E.M., Dowd, J.L.B., Aubry, L.M., 2013. The influence of snowmobile trails on coyote movements during winter in high-elevation landscapes. PLoS One 8 (12), e82862. https://doi.org/10.1371/journal.pone.0082862.
Gier, H.T., 1968. *Coyotes In Kansas (Revised)*. Kansas State College Agricultural Experiment Station Bulletin, vol. 393. https://www.ksre.k-state.edu/historicpublications/pubs/SB393.pdf.
Gifford, S.J., Gese, E.M., Parmenter, R.R., 2017. Space use and social ecology of coyotes (*Canis latrans*) in a high-elevation ecosystem: relative stability in a changing environment. J. Ethol. 35 (1), 37–49. https://doi.org/10.1007/s10164-016-0488-2.
Golightly Jr., R.T., Ohmart, R.D., 1984. Water economy of two desert canids: coyote and kit fox. J. Mammal. 65 (1), 51–58. https://doi.org/10.2307/1381199.
Hall, L.K., Larsen, R.T., Knight, R.N., Bunnell, K.D., McMillan, B.R., 2013. Water developments and canids in two North American deserts: a test of the indirect effect of water hypothesis. PLoS One 8 (7). https://doi.org/10.1371/journal.pone.0067800.
Hinton, J.W., Manen, F. T. van, Chamberlain, M.J., 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS One 10 (7), e0132203. https://doi.org/10.1371/journal.pone.0132203.
Hodge, A.E., Gese, E.M., Kluever, B.M., 2022. Does water availability shift dietary preferences of coyotes in the west desert of Utah? J. Arid Environ. 206, 104833 https://doi.org/10.1016/j.jaridenv.2022.104833.
James, C.D., Landsberg, J., Morton, S.R., 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. J. Arid Environ. 41 (1), 87–121. https://doi.org/10.1006/jare.1998.0467.
Johnson, C.J., Nielsen, S.E., Merrill, E.H., Mcdonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. J. Wildl. Manag. 70 (2), 347–357. https://doi.org/10.2193/0022-541X(2006)70[347:RSFBOU]2.0.CO;2.
Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61 (1), 65–71.
Kluever, B.M., Gese, E.M., 2016. Spatial response of coyotes to removal of water availability at anthropogenic water sites. J. Arid Environ. 130, 68–75. https://doi.org/10.1016/j.jaridenv.2016.03.009.
Kluever, B.M., Gese, E.M., 2017. Evaluating the influence of water developments on the demography and spatial ecology of a rare, desert-adapted carnivore: the kit fox (Vulpes macrotis). J. Mammal. 98 (3), 815–826. https://doi.org/10.1093/jmammal/gyx038.
Kozlowski, A.J., Gese, E.M., Arjo, W.M., 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin desert of Western Utah. Am. Midl. Nat. 160 (1), 191–208.
Laliberte, A.S., Ripple, W.J., 2004. Range contractions of North American carnivores and ungulates. Bioscience 54 (2), 123. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2.
Lisón, F., Calvo, J.F., 2011. The significance of water infrastructures for the conservation of bats in a semiarid Mediterranean landscape. Anim. Conserv. 14 (5), 533–541. https://doi.org/10.1111/j.1469-1795.2011.00460.x.
Manly, B.F.J., McDonald, L.L., Thomas, D.L., 2002. Resource Selection by Animals, second ed. Kluwer Academic Publishers, New York, NY http://link.springer.com/book/10.1007/978-94-011-1558-2.
Mastro, L.L., Morin, D.J., Gese, E.M., 2019. Home range and habitat use of West Virginia *Canis latrans* (Coyote). Northeast. Nat. 26 (3), 616–628. https://doi.org/10.1656/045.026.0318.
McAdoo, J.K., Barrington, M.R., Ports, M.A., 2006. Habitat affinities of rodents in Northeastern Nevada rangeland communities. Western North American Naturalist 66 (3), 321–331. https://doi.org/10.3398/1527-0904(2006)66[321:HAORIN]2.0.CO;2.
Morin, D.J., 2015. Spatial Ecology and Demography of Eastern Coyotes (Canis latrans) in Western Virginia. Virginia Polytechnic Institute and State University, Blacksburg, VA. https://vtechworks.lib.vt.edu/bitstream/handle/10919/54942/Morin_DJ_D_2015.pdf?sequence=1&isAllowed=y.
Morrison, M.L., Block, W.M., Strickland, M.D., Collier, B.A., Peterson, M.J., 2008. Wildlife Study Design. Springer Science & Business Media.
Mysterud, A., Ims, R.A., 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79 (4), 1435–1441. https://doi.org/10.2307/176754.
NatureServe, 2022. *Vulpes macrotis.* NatureServe Explorer [web Application]. NatureServe, Arlington, Virginia. (Accessed: March 24, 2022).
Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu. Rev. Ecol. Systemat. 20, 297–330.
Ralls, K., White, P.J., 1995. Predation on San Joaquin kit foxes by larger canids. J. Mammal. 76 (3), 723–729. https://doi.org/10.2307/1382743.
Rich, L., Beissinger, S., Brashares, J., Furnas, B., 2019. Artificial water catchments influence wildlife distribution in the Mojave Desert. J. Wildl. Manag. 83, 855–865. https://doi.org/10.1002/jwmg.21654.
Rosenstock, S.S., Ballard, W.B., Devos, J.C., 1999. Viewpoint: benefits and impacts of wildlife water developments. J. Range Manag. 52 (4), 302. https://doi.org/10.2307/4003538.
Sahr, D.P., Knowlton, F.F., 2000. Evaluation of tranquilizer trap devices (TTDs) for foothold traps used to capture gray wolves. Wildl. Soc. Bull. 28 (3), 597–605.
Shippee, E.A., Jollie, W.P., 1953. Report of Predator Control Operations. Ecology of the Great Salt Lake Desert, Semi-annual Report. University of Utah, Salt Lake City, Utah.
Signer, J., Fieberg, J., Avgar, T., 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol. Evol. 9 (2), 880–890. https://doi.org/10.1002/ece3.4823.
Simpson, N., Stewart, K., Bleich, V., 2011. What have we learned about water developments for wildlife? Not enough. Calif. Fish Game 97, 190–209.
Stewart-Oaten, A., Bence, J.R., 2001. Temporal and spatial variation in environmental impact assessment. Ecol. Monogr. 71 (2), 305–339. https://doi.org/10.1890/0012-9615(2001)071[0305:TASVIE]2.0.CO;2.
Smith, T.N., Gese, E.M., Kluever, B.M., 2018. Evaluating the impact of an exotic plant invasion on rodent community richness and abundance. Western North American Naturalist 77 (4), 515–525. https://doi.org/10.3398/064.077.0411.
Thompson, C., Malcolm, J., Patterson, B., 2021. Individual and temporal variation in use of residential areas by urban coyotes. Frontiers in Ecology and Evolution 9. https://doi.org/10.3389/fevo.2021.687504.
Thurfjell, H., Ciuti, S., Boyce, M.S., 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2 (1), 4. https://doi.org/10.1186/2051-3933-2-4.
Uboni, A., Smith, D.W., Mao, J.S., Stahler, D.R., Vucetich, J.A., 2015. Long- and short-term temporal variability in habitat selection of a top predator. Ecosphere 6 (4). https://doi.org/10.1890/ES14-00419.1 art51.