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Spatial response of coyotes to removal of water availability at anthropogenic water sites

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Abstract

Features containing year-round availability of free water (hereafter water sites) and areas affiliated with water sites (i.e., riparian zones) occurring within arid landscapes represent a potential limiting resource for some desert dwelling vertebrates. Little is known about the relationship between water sites and mammalian carnivores. An increase of water sites in portions of the Great Basin Desert in Utah reportedly contributed to an increase in coyote (*Canis latrans*) abundance. We examined frequency of visitation and spatial affinity of resident coyotes for water sites at the home range scale extent. Visitation to sites with available water averaged 13.0 visitations/season (SD = 13.5) and ranged from zero to 47. We documented no visits to water sites in 16% (10 of 64) of seasonal home-ranges, <5 visits within 39% (25 of 64) of home ranges, and 25% (28 of 113) of coyote home-ranges did not contain a water site. Water sites associated with riparian vegetation experienced higher visitation than guzzlers (no riparian vegetation present). We found no evidence that removal of water influenced home range size or spatial shifting of home range areas. Water sites, especially guzzlers, do not represent a pivotal resource for the coyote population in our study area.

Keywords: canid, desert, free water, guzzler, home-range

Introduction

Identifying the extent to which organisms utilize certain resources on a given landscape, and the impact of such use, has become a central tenet of animal ecology. Investigations determining the spatial relationships between animals and the resources they utilize can guide conservation and management strategies (Morris, 2003; Onorato et al., 2011; Briggs et al., 2012) and predict the impacts of varying land use (Wilson et al., 2014) and climate change scenarios (Costa et al., 2010). It has been long established that resources available to animals in a given spatial mosaic are often used at variable levels (Manly et al., 2002; Begon et al., 2005). Resources can serve as a requisite component of species habitat (Shroeder et al., 2004; Cain et al., 2012; Edgel et al., 2013), while other resources may be utilized, they are not required. (Manly et al., 2002).

Landscape features with year-round availability of free water (hereafter water sites) and adjacent areas affiliated with water sites (i.e., riparian zones) occurring within arid landscapes represent a potential limiting resource. Many species of terrestrial vertebrates are dependent on water sites (Gill, 2006; Vaughan et al., 2010); regular intervals of free water uptake are needed to maintain metabolic functions necessary for an individual's survival (Silanikove, 1994; Larsen et al., 2012). Other species of vertebrates utilize water sites for drinking as a resource subsidy; they have the ability to persist on preformed or metabolic forms of water alone (Harrington et al., 1999; Cain et al., 2008; Hall et al., 2013). In most cases, investigations focusing on water uptake and wildlife have documented overall use (e.g., visitations to or activity/sign at water sites) at the species or community level (e.g., an index) rather than determining patterns of individual water use (Rosenstock, 2004; Morgart et al., 2005; Jennifer et al., 2010; Whiting et al., 2010). Such individual based investigations are needed to determine water site visitations per individual, the

proportion of a population utilizing water sites, and to determine the relevancy of water sites as a habitat component (Shields et al., 2012). In addition to providing water uptake opportunities, water sites can facilitate establishment of riparian vegetation that provide resources that confer a reproductive, nutritional, safety, or thermoregulatory benefit to a degree greater than areas not affiliated with water sites (Bock and Bock, 1984; Doyle, 1990; Schulz and Leininger, 1991; Shalfroth et al., 2005).

Water sites influence individual space use and species habitat quality for a host of terrestrial vertebrates (Harrington, 1999; Allen, 2012; Cain et al., 2012; Ogutu et al., 2014), or can have little to no impact (Krausman and Etchberger, 1995; Cain et al., 2008). The majority of investigations focused on populations of large herbivores in xeric landscapes, where water sites are more influential than in mesic landscapes (Larsen et al., 2012). Such an emphasis on this group of animals is likely due to a host of factors including, but not limited to, logistical (e.g., VHF or GPS transmitter mass) and political (e.g., the disproportionate amount of research funding allocated toward game versus nongame animals) factors (Simpson et al., 2011).

Infrequent investigations have examined the relationship between water sites, water use, and the influence of such use on mammalian carnivores. Allen (2012) reported that 100% of GPS-collared dingoes (*Canis lupus dingo*) regularly visited water sites, though the frequency of visitations varied by individuals and temporal factors, and suggested the dingo population was dependent on water sites. However, determining patterns of use and the impact of water sites on many desert dwelling carnivores has not been achieved; to date, investigations have only chronicled indexes of visitations to water sites (Rosenstock et al., 2004; Atwood et al., 2011; Hall et al., 2013) or indexed activity for areas distant from and close to water sites (Hall et al., 2013).

Coyotes (*Canis latrans*) occur in a host of wildland, rural, and urban landscapes across a broad spectrum of mesic and arid environments (Bekoff and Gese, 2003), but the degree to which this species utilizes water sites, and the relationship between water sites and space use remains unexplored. Coyote populations are often managed due to issues relating to human-wildlife conflict (Knowlton et al., 1999; Conner et al., 2008; Poessel et al., 2013) or conservation of threatened or imperiled species competing with coyotes (Cypher et al., 2000; Moehrenschrager et al., 2007). It has been posited that the distribution and abundance of coyotes in the Great Basin Desert has increased in part due to the addition of water sites, by way of relaxing the limitation of arid systems to coyotes (Arjo et al., 2007; Kozlowski et al., 2008), thus increasing overall habitat quality for coyotes (Kozlowski et al., 2012). As a result, discerning the relevancy of water sites to coyotes has both management and conservation implications.

The physiological demands and behavioral characteristics of coyotes are such that water sites are more likely to be utilized than more desert-adapted carnivore species, like the sympatric kit fox (*Vulpes macrotis*) (Golightly and Omart, 1983), a species of conservation concern in several western states (Dempsey et al., 2014). For example, in the absence of water, coyotes theoretically need to consume 3.5 times the number of prey items than kit foxes to meet energetic requirements (Golightly and Ohmart, 1984). Thus, if prey items are a limiting factor on a landscape the addition of free water sites could serve as a resource subsidy to coyotes. Coyotes in the Great Basin Desert were classified as rare during the 1950s (Shippee and Jollie, 1953) and coyote abundance in this area has increased since the 1970s (Arjo et al., 2007). Further, kit fox density has been found to be negatively correlated with coyote abundance (Arjo et al. 2007), and it has been posited that a marked increase of permanent water sites in the Great Basin Desert since the mid-twentieth century may have indirectly decreased available kit fox

habitat by way of increased interspecific competition and intraguild predation from coyotes, leading to reduced kit fox abundance (Arjo et al., 2007; Kozlowski et al., 2008; Kozlowski et al., 2012).

Clearly, further investigation is needed to determine the extent to which water sites are utilized by coyotes in arid landscapes, and if water sites represent a requisite habitat component for coyotes in arid regions. If water sites represent a limiting factor for a coyote population, it would be expected that coyote home ranges will overlap with water sites and that these water sites would be regularly utilized by coyotes, thus a reduction of available water sites would prompt a spatial response by coyotes. Elucidating the relationship between water sites and coyotes has the potential to influence kit fox conservation strategies and coyote management programs, as well as increase our general understanding of the effects of free water on wildlife in arid environments. The overall objective of our study was to determine the impacts of water sites on coyotes in an arid landscape. Specifically, we aimed to determine: 1) the frequency of water site visitations by individual coyotes, 2) whether removal of water availability at water sites reduces coyote visits to water sites, 3) if the removal of water availability at water sites facilitates a change in coyote home range sizes, and 4) if removal of water availability at water sites facilitates a shift of coyote home range areas.

Methods

Study Area

We conducted our research on 1127 km² of the eastern portion of the U.S Army Dugway Proving Ground (DPG) and the adjoining lands managed by Bureau of Land Management (BLM), located approximately 128 km southwest of Salt Lake City, in Tooele County, Utah, USA (Figure 1). Elevations ranged from 1302 m to 2137 m. The study site was located in Great Basin

Desert, where winters were cold, summers were hot and dry, with the majority of precipitation occurring in the spring. Annual weather consisted of mean air temperatures of 12.7°C (range: -20.0 to 40.6°C) and mean precipitation of 150 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). In the study area, we identified 23 permanent water sites consisting of 10 guzzlers, 4 natural springs, and 9 man-made ponds/catchments. Guzzlers were designed to allow no run-off or access to water by rooted vegetation. Thus, there was no riparian vegetation component associated with guzzlers. In addition, the eastern portion of the study area managed by the BLM contained 3 livestock tanks that were at times operational during winter and spring cattle grazing (November 1 to April 1). 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). Thus, the ratio of anthropogenic to natural water sites within the study area was at least 3:1, with slight seasonal variability occurring due to the turning on/off of livestock tanks. We inspected all permanent water sites (e.g., ponds, springs, guzzlers) and livestock tanks within the study area monthly to confirm water availability. Water sites were considered permanent if they contained water during ≥ 3 of the monthly checks for each 4-month canid biological season and year (e.g., 2011 breeding season; Dempsey et al., 2014). There was no free-flowing water present on the study area. Additional water sites (e.g., hardpans, rainfall, drainages) were ephemeral pools (< 1 week); thus we assumed they were homogenous throughout the study area and did not influence overall space use of coyotes relative to water sites.

The study area consisted of predominately flat playa punctuated with steep mountain ranges. The lowest areas consisted of salt playa flats sparsely vegetated with pickleweed

(*Allenrolfea occidentalis*). Slightly higher elevation areas were less salty and supported a cold desert chenopod shrub community consisting predominately of shadscale (*Atriplex confertifolia*) and gray molly (*Kochia America*). At similar elevations, greasewood (*Sarcobatus vermiculatus*) communities were found with mound saltbrush (*Atriplex gardneri*) and Torrey seepweed (*Suaeda torreyana*). Higher elevations consisted of vegetated sand dunes including fourwing saltbush (*Atriplex canescens*), greasewood, rabbitbrushes (*Chrysothamnus* spp.), shadscale, and horsebrush (*Tetradymia glabrata*). Near the bases of the higher steep mountains were shrub steppe communities of sagebrush (*Artemisia* spp.), rabbitbrush, Nevada ephedra (*Ephedra nevadensis*), greasewood, and shadscale. The highest elevation was a Utah juniper (*Juniperus osteosperma*) community including black sagebrush (*Artemisia nova*) and bluebunch wheatgrass (*Elymus spicatus*). Where wildfires had occurred along the foothills, cheatgrass (*Bromus tectorum*), tall tumble-mustard (*Sisymbrium altissimum*), and Russian thistle (*Salsola kali*) was common within communities of sagebrush, rabbitbrush and juniper (Arjo et al., 2007).

Animal Capture & Handling

Beginning in December 2009, we captured 41 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). Captures were staggered and took place from December 2009 through November 2012. Processing of coyotes included taking blood samples, affixing ear tags and recording weight, sex and morphological measurements. We aged individuals as pups (< 9 mo old), yearlings (9–21 mo) or adults based on tooth wear, tooth eruption and body size (Gese et al., 1987). We fitted adult animals with a 200 g very high frequency (VHF) radio-collar (Model M2220; Advanced Telemetry Systems, Isanti, MN). Coyotes were captured throughout the study area and efforts were made to 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.

Radio-telemetry and home range determination

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 $>20^\circ$ but $<160^\circ$ apart, for each animal within 20 minutes (Arjo et al., 2007; Kozłowski et al., 2008). We then calculated coyote locations using program Locate III (Pacer Computing, Tatamagouche, Nova Scotia). For each week, we temporally distributed telemetry sampling by collecting two nocturnal locations and one diurnal location. To reduce auto-correlation and retain temporal independence between locations, we separated each weekly nocturnal and diurnal sample by >12 hours and a difference of >2 hours in the time of day of each location (Swihart and Slade, 1985; Gese et al., 1990). All home ranges were computed using only locations with an error polygon $<0.10 \text{ km}^2$ (Seidler and Gese 2012). We attempted to locate each coyote >3 times weekly in order to obtain 30 locations for each coyote for each biological season as the minimum number of locations needed to adequately describe the home range of a coyote (Gese et al., 1990).

We created seasonal home ranges for all coyotes with >30 locations (Gese et al., 1990; Aebischer et al., 1993) with defined biological seasons based on the behavior and energetic needs of canids for our study area: breeding 15 December – 14 April, pup-rearing 15 April – 14 August and dispersal 15 August – 14 December (Dempsey et al., 2014). We created 95% fixed kernel density estimates (KDE) 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) platform and loaded these polygons into ArcGIS 10.2. (Environmental Systems Research Institute Inc., Redlands, CA). We quantified home range areas using the field calculator tool and determined the number of water sites contained within each home range using theme-intersection routines.

Water site visitations

We examined the relationship between coyotes and seasonal visitations to water sites within each home range by establishing data loggers (model R4500S and model R2100/D5401, ATS, Isanti, MN), following recommendations of Breck et al. (2006). Data loggers cycled through VHF signals associated with radio-collared coyotes and recorded the presence of coyotes at water sites. Data loggers were established at 10 wildlife water developments (hereafter guzzlers) and 3 ponds (hereafter non-guzzlers). These 13 water sites represented 54% (13 of 24) of the potential water sites within the study area and 68% (13 of 19) of anthropogenic water sites. We defined a visit as all data logger recordings of an individual animal occurring within 30 min at a particular water site (Atwood et al., 2011). For each home range we determined both the total number of intersecting water sites and the number of intersecting sites equipped with data loggers. For coyote home ranges containing water sites with data loggers, we summarized the number of visitations, which provided a visitation frequency (# of visitations to water sites/seasonal home range) for further investigation. Because we suspected non-guzzler sites might experience higher visitations than guzzler sites, we also tracked the number of visitations within each home range that occurred at guzzlers versus non-guzzlers. We did not attempt to describe visitations when home ranges contained water sites without data loggers because we had no way of determining individual coyote use of water sites without data loggers, or if visits to sources with

data loggers constituted a small or large portion of overall water use within a coyote's home range.

Water manipulation

At the conclusion of the 2012 breeding season, we drained 5 guzzlers using a generator and submersible pump, and covered drinking portals with plywood (Figure 2). 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. This manipulation effort eliminated water availability at 33% (6 of 18) of 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., 2001) where we assessed home range and visitations before and after eliminating water availability at water sites. Specifically, we assigned home ranges and visitations for the temporal spans prior to and after the water manipulation into two separate periods (pre-period and post-period) and two separate classes (reference or impact). The reference class referred to all home range areas and respective visitations containing water sites not spatially associated with the manipulation. The impact class referred to all home range areas and respective visitations containing water sites slated for manipulation at the onset of the post-period. For example, a home range area and visitation frequency assigned to the pre-period and impact class would be associated with the time period before water manipulation and spatially associated with the water sites to be manipulated (i.e., the home range contained a water site or sites that were to be manipulated at the conclusion of the pre-period). BACI designs are considered superior to observational studies as they better account for variability of response and exploratory variables attributed to temporal (e.g., annual precipitation) and spatial factors (e.g., vegetation heterogeneity across study area)

that cannot always be controlled and/or accounted for under natural environmental conditions (Underwood, 1994; Morrison et al., 2001).

Spatial Separation of Home Ranges

We estimated the impact of water manipulation on spatial separation of coyote home ranges by measuring spatial overlap of 95% fixed kernel home ranges (Atwood and Gese, 2010). We used the *adehabitat* package in R (R Core Team, 2014) to quantify overlap by computing the proportion of a home range for each coyote that was impacted by the water manipulation (i.e., impact class) during the season just prior to the post-period (i.e., breeding 2012) covered by the home-range of the same animal for the first three seasons of the post-period (i.e., pup 2012, dispersal 2012, breeding 2013). This provided us with three home-range overlap values for each individual coyote that had been assigned to the impact class. We compared these overlap values with an equal number of coyotes of the same sex ratio (2 males, 2 females) affiliated with the reference class.

Statistical Analyses

Prior to analyses, we examined all data for normality and homogeneity of variances and used transformations to better meet parametric assumptions, or non-parametric tests when assumptions could not be met (Zar, 1999). We report means, medians, standard deviations and standard errors in the original scale of measurement. We employed generalized linear mixed models (GLMMs) to test the categorical main effects of period (before and after) and class (reference and impact) on the continuous response variables of coyote visitations (visitations/individual/season) and seasonal coyote home-range size (km²). The GLMM approach enables the fitting of random terms and therefore accounts for repeated sampling across error terms. Seasonal home ranges and visitations were derived repeatedly from the same

individuals in different seasons and years, thus we included individual as a random effect in all models (Stoup, 2012). Specifically, we tested for an effect of water site manipulation by including a period by class 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 impact and reference sampling units following some type of manipulation (Underwood, 1992). Inspection of visitation data revealed non-normality that was not remedied by data transformations. As a result we fitted the following model families: lognormal, Poisson, quasi-Poisson, and negative binomial. Models that did not converge were eliminated and we assessed remaining models based on the generalized chi-square fit statistic (Stroup, 2012). For the visitations and home range area data, the final model family used was negative binomial and lognormal, respectively. We separately tested for differences in visitations by water site type (i.e., guzzlers versus non-guzzlers) using a Wilcoxon signed-rank test (Zar, 1999). For this test, we only included visitation data from home ranges that contained both guzzler and non-guzzlers that were monitored by data loggers. For all statistical tests we interpret p-values in terms of relative evidence of differences (Ramsey and Schafer, 2002). All statistical analyses were conducted using R (R Development Program Team, 2014).

Results

We developed 149 seasonal home ranges from 41 coyotes spanning from the 2010 pup rearing season to the 2013 dispersal season. We excluded 23% (35 of 149) of home ranges and respective visitations from further description because they partially occurred outside of our study area. Prior to the water manipulation (i.e., the pre-period), 88% (61 out of 69) of home ranges contained at least one water site. On average, 2 water sites (min = 1, max = 9) were contained within each home range prior to removal of water sites. Following reduction of water

availability, 56% (25 of 45) of home ranges contained at least one water site. Of these, 83% (19 of 23) contained only water sites monitored by data loggers that remained following water availability removal. On average, one (min = 1, max = 4) water site was contained within each seasonal home following removal of water availability.

We excluded 31% (35 of 114) of remaining home ranges and associated visitations from additional description and analyses due to home ranges either containing water sites within our study area that were not monitored by data loggers or containing zero water sites; except for home ranges and respective visitations associated with post-period and impact class (see methods for full description). We also censored remaining home ranges derived from transient coyotes ($n = 6$) because they were only associated with the reference class of home ranges, and could have introduced bias into further analyses (Kamler and Gipson, 2000). This left 72 home ranges from 21 individual coyotes for further description and analysis.

Coyote seasonal visitations to water sites averaged 13.0 visitations/season ($SD = 13.5$) and ranged from zero to 47 visits. We found evidence that elimination of water availability reduced coyote visits to former water sites (period x class interaction: $t = 2.06$, $P = 0.05$, $df = 1$, 49; Figure 2). Frequency of visitation to water sites that were manipulated decreased from 8.46 visits/season during the before period ($SE = 2.52$) to 4.22 visits/season ($SE = 1.69$) following removal of water. Conversely, visitations to water sites that were not removed increased from 12.17 visits/season ($SE = 1.90$) during the pre-period to 19.79 visits/season ($SE = 1.62$) during the post-period. We found no evidence that period alone influenced coyote visitations ($t = -2.47$, $P = 0.35$, $df = 1$, 49). There was evidence that visitations were higher at water sites associated with the reference class ($t = 2.58$, $P = 0.03$, $df = 1$, 49). Average visitation within home ranges associated with the reference and impact classes were 15.58 ($SE = 0.81$) and 7.10 ($SE = 1.78$)

visitations/season, respectively. We found evidence that visitations were higher at non-guzzlers (Wilcoxon rank sum test, $Z = -3.58$, $P = < 0.01$, $n = 19$). For example, median seasonal visitations by coyotes whose home ranges contained at least one guzzler and non-guzzler were 0 and 7 visits, respectively (Figure 3). We found no evidence that removal of water influenced home range size (period x class interaction: $t = -0.96$ $P = 0.34$, $df = 1, 49$; Figure 4). Similarly, there was no evidence to suggest that period ($t = -0.95$ $P = 0.33$, $df = 1, 49$), or class ($t = -1.37$ $P = 0.17$, $df = 1, 49$) had an influence on home range size (Figure 4). We compared seasonal home range overlap for 2 males and 2 female coyotes from each home range class (i.e., impact or reference). Percent seasonal overlap of fixed kernel home ranges for coyotes assigned to the reference and impact classes were 78% (SE = 11.5) and 85% (SE = 9.2), respectively.

Discussion

Our study was the first to quantify individual based visitations to water sties for coyotes and the first to incorporate a resource manipulation design to evaluate the effects of water sites on space use of a canid species in an arid environment. Overall, we found a portion of coyotes did not utilize water sites, coyote visitations to water sites were reduced following removal of water availability, reducing water availability did not influence coyote home range size, and reducing water availability did not influence spatial shifts of home ranges.

Our visitation results provided support that the availability of perennial free water does not appear to be a requisite resource component for coyotes in our study area. We observed zero visits during 16% (10 of 64) of seasonal observations, and <5 visits during 39% (25 of 64) of observations; these null to low frequency of visitation were observed across all three season types and years of the study. Allen (2012) found that all radio-collared dingoes in the Strzelecki Desert visited water sites every season, and dingoes rarely went >5 days without visiting a water

site. Clearly, more investigations are needed to determine frequency of water site visitations for canids at the individual level, especially for species and populations deemed to benefit from the presence of such sites.

Our manipulation revealed that visitations to water sites decreased once water was no longer available, but visitations to these sites did not altogether cease (Figure 2). Coyotes may have returned to impacted water sites following the manipulation in order to re-investigate the availability of water, to engage in scent-marking (Gese and Ruff 1997), to forage at waters' edge, or a combination thereof. We observed that coyote visitations within home ranges containing water sites unassociated with the water manipulation (i.e., the reference class) experienced higher visitations (Figure 2). We speculate that this finding was at least partially attributed to a disparity of water site types among design classes. Manipulated water sites consisted of only one non-guzzler, while water sites affiliated to the reference class contained two non-guzzlers that were associated with riparian vegetation, which was rare on our study site (Emrick and Hill 1999). Such riparian vegetation may have provided coyotes with foraging and/or bedding opportunities at the waters' edge that were not available at guzzlers, which ostensibly resulted in non-guzzlers providing additional resources when compared to guzzlers. De Boer et al. (2010) observed that lion (*Panthera leo*) prey availability was higher at ponds and rivers when compared to random locations, but investigations that test whether water sites with riparian vegetation provide additional resources for coyotes or other desert canids are lacking. We did not visually monitor coyote behavior at water sites during this study, nor did we assess coyote prey availability at water sites or non-water sites. Thus, we cannot make any firm conclusions regarding the mechanisms driving this finding.

Our assessment of home ranges in relation to water sites provided additional support that access to water sites was not an obligatory resource component for coyotes. For example, 25% of home ranges occurring exclusively within our study area did not contain a single water site. Further, 33% (36 of 108) of the home ranges we investigated either did not contain a water site or contained a water site that was not visited for an entire season (e.g., approx. 120 day period). In addition, our water site manipulation did not appear to influence home range sizes (Figure 4) or the overlap of home ranges.

We were only able to track seasonal overlapping of home ranges for three coyotes that belonged to the impact class for the three consecutive seasons following the manipulation. Such a small sample size and resulting lack of statistical inference warrants caution. However, all three of these animals maintained a spatial affinity to their home ranges' following the manipulation (i.e., they did not die, disperse or abandon their home ranges after water was no longer available), and none of the animals adjusted their movements in a manner where post-manipulation home ranges included a water site. Anthropogenic modifications to landscapes can influence coyote home range selection, which is considered a second-order selection process (Johnson, 1980). Boisjoly et al. (2010) determined that clear-cutting activities in boreal forests increased coyote habitat quality by increasing food accessibility, and posited that such anthropogenic activity may have allowed coyotes to establish home ranges. Hidalgo-Mihart et al. (2004) found coyotes utilizing landfills had home ranges less than half the size of coyotes that occurred in vegetation zones predominantly unaltered by anthropogenic modification. Conversely, Atwood et al. (2004) found coyote home range sizes were largest in areas with the highest levels of anthropogenic modification to the landscape. Clearly, the influence of

anthropogenic factors on coyote selection processes is highly variable and contingent upon myriad factors that can differ across time and space.

It has been revealed or postulated that anthropogenic water sites can directly alter the distributions and densities of ungulates, birds, and mammalian carnivores (de Leeuw et al., 2001; Kristian and Boarman, 2003; Cain et al., 2012; Allen et al. 2012), but empirical evidence of water sites engendering indirect effects are sparse. Harrington et al. (1999) documented a population crash of roan antelope (*Hippotragus equinus*) following an increase of water developments in the northern portion of Kruger National Park. They speculated that these water sites served as a subsidized resource facilitating a population increase of more water dependent species [i.e., zebra (*Equus quagga*) and wildebeest (*Connochetes taurinus*)], which engendered increased lion numbers and lion predation on roan antelope. These claims were substantiated when the removal of water developments coincided with a roan antelope population recovery (Harrington et al., 1999). An indirect effect of increased water sites has been proposed as a factor contributing to reduced kit fox abundance and distribution in the Great Basin Desert; additions of water sites in the mid to late twentieth century coincided with increased abundance of coyotes (Arjo et al., 2007; Kozlowski et al., 2008). Depressing coyote populations has been shown to positively alter the abundance of gray foxes (*Urocyon cinereoargenteus*) (Henke and Bryant 1999) and swift foxes (Kamler et al., 2003). Similarly, Kamler et al. (2013) found that areas void of black-backed jackals (*Canis mesomelas*) experienced higher densities of Cape foxes (*Vulpes chama*) when compared to areas occupied by jackals. Thus, the proposition that water sites have impacted the carnivore community in our study area is rational.

Our results suggest that under the environmental conditions present during our study, water sites did not appear to constitute a requisite resource for adult resident coyotes, or a

resource that influenced home-range size. We found no spatial shifts in home ranges, no increase in home range size, as well as no abandonment of their home range or reduced survival (i.e., no coyotes died) following the cessation of water availability in their home range. We speculate that the observed increase of coyotes (Arjo et al. 2007) may be more attributable to changes in coyote management practices, or habitat change (i.e., invasion of cheatgrass). Within a study area that encompassed our own, Egoscue (1956) argued that coyote abundance was suppressed by way of intensive coyote control efforts, including regular usage of baited toxicants spaced at intervals aimed to maximize lethality to coyotes rather than carnivores with smaller home ranges (i.e., kit foxes). The use of baited toxicants was a common predator control tactic in Utah, including DPG, during the mid-twentieth century (Shippee and Jollie, 1953). In 1972, the enacting of Executive Order 11643 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 that relied heavily on toxicants were more effective at suppressing coyote populations than contemporary methods. Therefore, the observed increase of coyote numbers observed by Arjo et al. (2007) over the latter half of the twentieth century may be in part tied to changes in coyote management practices that temporally coincided, but were largely unrelated, to the additions of anthropogenic water sites.

Our study was the first to incorporate a manipulation design to test the effects of water sites on canids. Our findings provide evidence that water sites, especially guzzlers, do not represent a pivotal resource for coyotes in our study area, during the temporal span the investigation was conducted. That being said, we recommend some caution be exercised in relation to our findings. Our investigation focused on one study area, spanned only a 4 year

period, and focused primarily on second and fourth-order selection processes (Johnson, 1980).

We recommend future investigations on the impact of free water on coyotes, and other species of interest, should consider designs with replication at the study site level (Cain et al., 2008), a longer temporal span (i.e., several generation times of the species of interest), an examination/comparison of population state variables and/or vital rates, and selection processes at other orders (i.e., first and third-order).

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References

- Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data *Ecology* 74, 1313-1325.
- Allen, B.L., 2012. Do desert dingoes drink daily? Visitation rates at remote waterpoints in the Strzelecki Desert. *Aust. Mammal.* 34, 251-256.
- 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. *West. North Am. Naturalist* 67, 389-401.
- Atwood, T.C., Fry, T.L., Leland, B.R., 2011. Partitioning of Anthropogenic Watering Sites by Desert Carnivores. *J. Wildl. Manage.* 75, 1609-1615.
- Atwood, T.C., Gese, E.M., 2010. Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids. *J. Mammal.* 91, 490-499.
- Atwood, T.C., Weeks, H.P., Gehring, T.M., 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. *J. Wildl. Manage.* 68, 1000-1009.
- Begon, M., Townsend, C.R., Harper, J.L., 2005. *Ecology: from individuals to ecosystems*, 4th ed. Wiley Blackwell, West Sussex, England.
- Bekoff, M.a.E.M.G., 2002. Coyote, in: Feldhamer, G.A., Thompson, B.C., and J.A. Chapman (Ed.), *Wild mammals of North America: biology, management, and conservation*. Johns Hopkins University Press, Baltimore, Maryland, USA, pp. 467-481.
- Beyer, H., 2012. *Geospatial Modeling Environment (Version 0.6.0.0)*.
- Bock, C.E., Bock, J.H., 1984. Importance of sycamores to riparian birds in southeastern Arizona. *J. Field Ornithol.* 55, 97-103.
- Boisjoly, D., Ouellet, J.P., Courtois, R., 2010. Coyote Habitat Selection and Management Implications for the Gaspesie Caribou. *J. Wildl. Manage.* 74, 3-11.
- Breck, S.W., Lance, N., Bourassa, J., 2006. Limitations of Receiver/Data Loggers for Monitoring Radiocollared Animals. *Wildl. Soc. Bull.* 34, 111-115.
- Briggs, B.D.J., Hill, D.A., Gosler, A.G., 2012. Habitat selection and waterbody-complex use by wintering Gadwall and Shoveler in South West London: Implications for the designation and management of multi-site protected areas. *J. Nat. Conserv.* 20, 200-210.
- 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.* 1-32.
- Cain, J.W., Owen-Smith, N., Macandza, V.A., 2012. The costs of drinking: comparative water dependency of sable antelope and zebra. *J. Zool.* 286, 58-67.
- Conner, M.M., Ebinger, M.R., Knowlton, F.F., 2008. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. *Ecol. Model.* 219, 234-247.
- Costa, D.P., Crocker, D.E., Goebel, M.E., Fedak, M.A., McDonald, B.I., Huckstadt, L.A., 2010. Climate Change and Habitat Selection of Seals in the Western Antarctic Peninsula. *Integr. Comp. Biol.* 50, E34-E34.
- Cypher, B.L., Warrick, G.D., Otten, M.R.M., O'Farrell, T.P., Berry, W.H., Harris, C.E., Kato, T.T., McCue, P.M., Scrivner, J.H., Zoellick, B.W., 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. *Wildl. Monogr.* 1-43.
- de Boer, W.F., Vis, M.J.P., de Knegt, H.J., Rowles, C., Kohi, E.M., van Langevelde, F., Peel, M., Pretorius, Y., Skidmore, A.K., Slotow, R., van Wieren, S.E., Prins, H.H.T., 2010. Spatial distribution of lion kills determined by the water dependency of prey species. *J. Mammal.* 91, 1280-1286.
- de Leeuw, J., Waweru, M.N., Okello, O.O., Maloba, M., Nguru, P., Said, M.Y., Aligula, H.M., Heitkonig, I.M.A., Reid, R.S., 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biol. Conserv.* 100, 297-306.
- Dempsey, S.J., Gese, E.M., Kluever, B.M., 2014. Finding a Fox: An Evaluation of Survey Methods to Estimate Abundance of a Small Desert Carnivore. *Plos One* 9, 8.
- Dorrance, M.J., Roy, L.D., 1976. Predation losses of domestic sheep in Alberta. *J. Range Manage.* 29, 457-460.

- Doyle, A.T., 1990. Use of riparian and upland habitats by small mammals J. Mammal. 71, 14-23.
- Edgel, R.J., Pierce, J.L., Larsen, R.T., 2014. Pygmy rabbit (*Brachylagus idahoensis*) habitat selection: does sagebrush (*Artemisia* spp.) age influence selection? West. North Am. Naturalist 74, 145-154.
- Egosuce, H.J., 1956. Preliminary studies of the kit fox. J. Mammal. 37, 351-357.
- Emrick, V., Hill, A., 1999. Classification of Great Basin plant communities occurring on Dugway Proving Ground, Utah. Construction Engineering Research Laboratories, Champaign, IL, USA, 47 pp.
- Gese, E.M., Andersen, D.E., Rongstad, O.J., 1990. Determining home-range size of resident coyotes from point and sequential locations. J. Wildl. Manage. 54, 501-506.
- Gese, E.M., 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., Ruff, R.L., 1997. Scent-marking by coyotes, *Canis latrans*: The influence of social and ecological factors. Anim. Behav. 54, 1155-1166.
- Gill, F.B., 2006. Ornithology, Third ed. W. H. Freeman and Company, New York, New York, USA.
- Golightly, R.T., Ohmart, R.D., 1983. Metabolism and body temperature of two desert canids - coyotes and kit foxes J. Mammal. 64, 624-635.
- Golightly, R.T., Ohmart, R.D., 1984. Water economy of two desert canids - coyote and kit fox J. Mammal. 65, 51-58.
- Hall, L.H., Larsen, R.T., Knight, R.N., Bunnell, K.D., McMillian, B.R., 2013. Water developments and canids in two North American deserts: A test of the indirect effect of water hypothesis. Plos One 8, 8 pp.

- Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R., Funston, P., 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biol. Conserv.* 90, 69-78.
- Henke, S.E., Bryant, F.C., 1999. Effects of coyote removal on the faunal community in western Texas. *J. Wildl. Manage.* 63, 1066-1081.
- Hidalgo-Mihart, M.G., Cantu-Salazar, L., Lopez-Gonzalez, C.A., Fernandez, E.C., Gonzalez-Romero, A., 2004. Effect of a landfill on the home range and group size of coyotes (*Canis latrans*) in a tropical deciduous forest. *J. Zool.* 263, 55-63.
- Jennifer, P., Nishantha, H.G., Janaka, H.K., Isler, K., Fernando, P., 2010. Water-body use by Asian elephants in Southern Sri Lanka. *Trop. Conserv. Sci.* 3, 412-422.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65-71.
- Kamler, J.F., Gipson, P.S., 2000. Space and habitat use by resident and transient coyotes. *Can. J. Zool.* 78, 2106-2111.
- Kamler, J.F., Stenkewitz, U., Macdonald, D.W., 2013. Lethal and sublethal effects of black-backed jackals on cape foxes and bat-eared foxes. *J. Mammal.* 94, 295-306.
- Kozlowski, A.J., Gese, E.M., and W.M. Arjo, 2012. Effects of Intraguild Predation: Evaluating Resource Competition between Two Canid Species with Apparent Niche Separation. *Inter. J. Ecology* 2012, 12.
- 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, 191-208.
- Krausman, P.R., Etchberger, R.C., 1995. Response of desert ungulates to a water project in

- Arizona J. Wildl. Manage. 59, 292-300.
- Kristan, W.B., Boarman, W.I., 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology 84, 2432-2443.
- Larsen, R.T., J.A. Bissonette, J.T. Flinders, and J.C. Whiting, 2012. Framework for understanding the influences of wildlife water developments in the western United States. California Fish and Game 98, 148-163.
- Mitchell, B.R., Jaeger, M.M., Barrett, R.H., 2004. Coyote depredation management: current methods and research needs. Wildl. Soc. Bull. 32, 1209-1218.
- Moehrensclager, A., List, R., Macdonald, D.W., 2007. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. J. Mammal. 88, 1029-1039.
- Morgart, J.R., Hervert, J.J., Krausman, P.R., Bright, J.L., Henry, R.S., 2005. Sonoran pronghorn use of anthropogenic and natural water sources. Wildl. Soc. Bull. 33, 51-60.
- Morris, D.W., 2003. How can we apply theories of habitat selection to wildlife conservation and management? Wildl. Res. 30, 303-319.
- Morrison, M.L., W.M. Block, M.D. Strickland, and W.L. Kendall, 2001. Wildlife Study Design. Springer New York, USA.
- Nunley, G., 1986. The extirpation and reestablishment of coyotes in Edwards Plateau of Texas., Texas Proceedings of Great Plains Wildlife Damage Control, Lubbock, Texas, USA., pp. 9-27.
- Ogutu, J.O., Reid, R.S., Piepho, H.P., Hobbs, N.T., Rainy, M.E., Kruska, R.L., Worden, J.S., Nyabenge, M., 2014. Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human-wildlife conflicts. Biodivers.

- Conserv. 23, 573-596.
- Onorato, D.P., Crifffield, M., Lotz, M., Cunningham, M., McBride, R., Leone, E.H., Bass, O.L., Hellgren, E.C., 2011. Habitat selection by critically endangered Florida panthers across the diel period: implications for land management and conservation. *Anim. Conserv.* 14, 196-205.
- Poessel, S.A., Breck, S.W., Teel, T.L., Shwiff, S., Crooks, K.R., Angeloni, L., 2013. Patterns of human-coyote conflicts in the Denver Metropolitan Area. *J. Wildl. Manage.* 77, 297-305.
- Rosenstock, S.S., M.J. Rabe, C.S. O'Brien and R.B. Waddell, 2004. Studies of wildlife water developments in Southwestern Arizona: wildlife use, water quality, wildlife diseases, wildlife mortalities, and influences of native pollinators. Arizona Game and Fish Department, Research Branch Technical Guidance Bulletin, Phoenix, AZ, p. 15.
- Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Deibert, P.A., Gardner, S.C., Hilliard, M.A., Kobriger, G.D., McAdam, S.M., McCarthy, C.W., McCarthy, J.J., Mitchell, D.L., Rickerson, E.V., Stiver, S.J., 2004. Distribution of Sage-Grouse in North America. *Condor* 106, 363-376.
- Schulz, T.T., Leininger, W.C., 1991. Nongame wildlife communities in grazed and ungrazed riparian sites *Gt. Basin Nat.* 51, 286-292.
- Seidler, R.G., Gese, E.M., 2012. Territory fidelity, space use, and survival rates of wild coyotes following surgical sterilization. *J. Ethol.* 30, 345-354.
- Shafroth, P.B., Cleverly, J.R., Dudley, T.L., Taylor, J.P., Van Riper, C., Weeks, E.P., Stuart, J.N., 2005. Control of Tamarix in the Western United States: Implications for water salvage, wildlife use, and riparian restoration. *Environ. Manage.* 35, 231-246.
- Shields, A.V., Larsen, R.T., Whiting, J.C., 2012. Summer Watering Patterns of Mule Deer in the

- Great Basin Desert, USA: Implications of Differential Use by Individuals and the Sexes for Management of Water Resources. *Sci. World J.*, 9.
- 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., Ecology of the Great Salt Lake Desert, semi-annual report. University of Utah, Salt Lake City.
- Silanikove, N., 1994. The struggle to maintain hydration and osmoregulation in animals experiencing severe dehydration: the story of ruminants. *Exp. Physiol.* 79, 281-300.
- Simpson, N.O., K.M. Stewart, and V.C. Bleich, 2011. What have we learned about water developments for wildlife? Not enough! *California Fish and Game* 97, 190-209.
- Stroup, W.W., 2012. Generalized linear mixed models: modern concepts, methods and applications. CRC Press, Boca Raton, Florida, USA.
- Swihart, R.K., Slade, N.A., 1985. Influence of sampling interval on estimates of home-range size *J. Wildl. Manage.* 49, 1019-1025.
- Underwood, A.J., 1992. Beyond BACI: The detection of environmental impacts on populations in the real, but variable world. *J. Exp. Mar. Biol. Ecol.* 161, 145-178.
- Underwood, A.J., 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecol. Appl.* 4, 3-15.
- Walter, W.D., Fischer, J.W., Baruch-Mordo, S., VerCauteren, K.C., 2011. What is the proper method to delineate home range of an animal using today's advanced GPS telemetry systems: the initial step, in: Krejcar, O. (Ed.), *Modern Telemetry*. InTech Publication, p. 470.
- Whiting, J.C., Bowyer, R.T., Flinders, J.T., Bleich, V.C., Kie, J.G., 2010. Sexual segregation and use of water by bighorn sheep: implications for conservation. *Anim. Conserv.* 13, 541-

548.

- Wilson, R.R., Horne, J.S., Rode, K.D., Regehr, E.V., Durner, G.M., 2014. Identifying polar bear resource selection patterns to inform offshore development in a dynamic and changing Arctic. *Ecosphere* 5, 24.
- Zar, J.H., 2010. *Biostatistical Analyses*, Fifth ed. Pearson Prentice Hall, Upper Saddle River, New Jersey, USA.

Figure 1. Study area (1127 km²) and permanent/ephemeral free water sites (n = 26) within and adjacent to the U.S. Army Dugway Proving Ground, USA, 2010–2013.

Figure 2. Mean coyote seasonal water site visitations ($\pm$ SE) observed within seasonal home ranges prior to (Pre-Period) and following (Post-Period) removal of water availability at a subset of water sites on the U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013 (n = 69).

Figure 3. Box plot of coyote seasonal water site visitations observed within home ranges that contained guzzler and non-guzzler water sites with water availability and monitored by data loggers (n = 21) on the U.S. Army Dugway Proving Ground, Utah, USA, 2010-2013.

Figure 4. Mean coyote seasonal home range area (km²) ($\pm$ SE) observed prior to (Pre-Period) and following (Post-Period) removal of water availability at a subset of water sites on a study area encompassing U.S. Army Dugway Proving Ground and adjacent BLM land, Utah, USA, 2010-2013 (n = 69). Reference home ranges refers to coyote home ranges that contained water sites with water availability during both periods. Impact home ranges refers to coyote home ranges that contained water sites until water availability was removed at the onset of the Post-Period.

Figure 1

Figure 2

Figure 3

Figure 4