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Article

# Influence of free water availability on a desert carnivore and herbivore

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## Abstract

Anthropogenic manipulation of finite resources on the landscape to benefit individual species or communities is commonly employed by conservation and management agencies. One such action in arid regions is the construction and maintenance of water developments (i.e., wildlife guzzlers) adding free water on the landscape to buttress local populations, influence animal movements, or affect distributions of certain species of interest. Despite their prevalence, the utility of wildlife guzzlers remains largely untested. We employed a before–after control-impact (BACI) design over a 4-year period on the US Army Dugway Proving Ground, Utah, USA, to determine whether water availability at wildlife guzzlers influenced relative abundance of black-tailed jackrabbits *Lepus californicus* and relative use of areas near that resource by coyotes *Canis latrans*, and whether coyote visitations to guzzlers would decrease following elimination of water. Eliminating water availability at guzzlers did not influence jackrabbit relative abundance. Coyote relative use was impacted by water availability, with elimination of water reducing use in areas associated with our treatment, but not with areas associated with our control. Visitations of radio-collared coyotes to guzzlers declined nearly 3-fold following elimination of water. Our study provides the first evidence of a potential direct effect of water sources on a mammalian carnivore in an arid environment, but the ecological relevance of our finding is debatable. Future investigations aimed at determining water effects on terrestrial mammals could expand on our findings by incorporating manipulations of water availability, obtaining absolute estimates of population parameters and vital rates and incorporating fine-scale spatiotemporal data.

**Key words:** arid, black-tailed jackrabbit, *Canis latrans*, coyote, *Lepus californicus*.

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The manipulation of limited resources on the landscape in an attempt to benefit individual species and communities is a practice commonly employed by wildlife management agencies, sportsmen groups, and conservation organizations. One such action in arid regions is the construction and maintenance of wildlife water developments (i.e., wildlife guzzlers), which adds availability of free water on a landscape in order to buttress populations, influence animal movements, or affect the distributions of species of interest, particularly certain game species or endangered species (Simpson et al. 2011; Larsen et al. 2012). For example, at the end of the last century, 10 of 11 state wildlife

management agencies in the western United States reported ongoing water development programs with combined annual expenditures >US\$1,000,000 (Rosenstock et al. 1999), and as of 2013, nearly 7,000 water developments had been constructed (Simpson et al. 2011). Furthermore, water developments are being utilized as a mitigation technique to offset military activities (Broyles 1995) and are forecasted to increase as a wildlife conservation and management tool in the western United States (Simpson et al. 2011). In addition, water developments are commonly used by ranchers in arid regions to improve habitat for livestock (Holecheck et al. 2010).

Despite their prevalence, little is known in regards to the influence of water developments on wildlife. First, the utility of artificial water developments has been questioned. Researchers speculate whether increased availability of free water benefits or harms species that are adapted to desert or arid conditions (Burkett and Thompson 1994; Cain et al. 2008). Essentially, the general notion that the direct uptake of free water by wildlife translates to a biological benefit (Leopold 1933) or that water use always equates to water need, has been challenged under certain conditions (Cain et al. 2008; Simpson et al. 2011). Second, researchers have posited that water developments may be deleterious, either by spreading disease, encouraging exotic species, hindering wilderness values, or negatively influencing populations of non-water dependent wildlife by increasing predation, predation risk, or competition (Broyles 1995; DeStefano et al. 2000; Bleich 2005; Larsen et al. 2012; Hall et al. 2013). Currently, the numbers of published works that merely discuss or debate water developments appear to outnumber data-driven field investigations.

Despite their prevalence, the utility of artificial water developments has been questioned. Researchers speculate whether increased availability of free water benefits or harms species that are adapted to desert or arid conditions (Burkett and Thompson 1994; Cain et al. 2008). Essentially, the general notion that the direct uptake of free water by wildlife translates to a biological benefit (Leopold 1933) or that water use always equates to water need has been challenged under certain conditions. Furthermore, others have posited that water developments may be deleterious, either by spreading disease, encouraging exotic species, hindering wilderness values, or negatively influencing populations of non-water dependent wildlife by increasing predation, predation risk, or competition (Broyles 1995; DeStefano et al. 2000; Bleich 2005; Larsen et al. 2012; Hall et al. 2013).

Investigations lending empirical insight to the impacts of water developments on wildlife are rare, because the majority of studies have only chronicled the uptake of free water at said developments (Cambell and Remington 1979; Rosenstock et al. 2004; Morgart et al. 2005; Lynn et al. 2006). Though such studies have merit, they are unable to determine whether use of free water translates to a biological or ecological effect. Adding further complexity is the notion that effects of water developments on wildlife can be either direct or indirect. Larsen et al. (2012) defined the direct effects of water as those associated with the intake of free water (e.g., increased chukar *Alectoris chukar* survival due to chukar water intake [Larsen et al. 2010]). In contrast, indirect effects may include, but were not limited to, exploitative or interference competition with other species or conspecifics, or altered vulnerability to predation (e.g., a decrease in black-tailed jackrabbit *Lepus californicus* survival may hypothetically be due to an increase in coyote [*Canis latrans*] survival or activity near water points engendered by coyote water intake at water developments [DeStefano et al. 2000]).

Investigations on direct effects of water developments on wildlife are sparse. Larsen et al. (2010) found chukars were influenced by water sources only in certain mountain ranges. In a study including a before–after control-impact (BACI) design, Cain et al. (2008) found bighorn sheep *Ovis Canadensis* were not impacted by reduction of water sources. Hall et al. (2013) observed similar coyote activity in areas with and without water developments and springs despite regular coyote use at water sites, suggesting no direct effect of water consumption for this species. Investigations into the potential indirect effects of water developments on wildlife are also lacking. Cutler and Morrison (1998) found measures of species richness

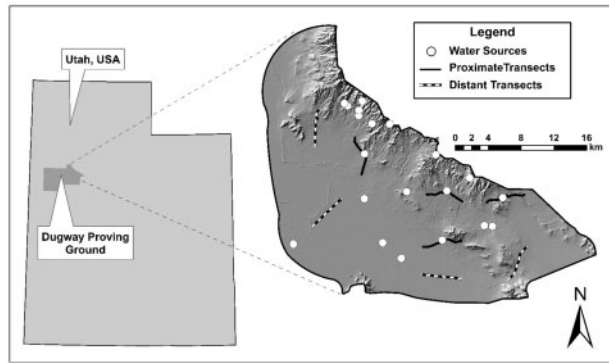
and relative abundance for desert-adapted reptiles, and rodents did not differ in relation to areas adjacent to dry or wet water developments, suggesting that predation rates at sites did not differ or that increased predation was compensatory. Hall et al. (2015) found that native species had fewer visits and spent less time at water sources frequented by exotic horses. DeStefano et al. (2000) observed a negative relationship between leporid (black-tailed jackrabbit and desert cottontail *Sylvilagus audubonii*) and coyote relative use in relation to proximity to water developments in the Sonoran Desert. Conversely, Hayden (1966) observed that black-tailed jackrabbit relative abundance was higher near water sources in the Mojave Desert, and believed this finding was attributed to leaky or overflowing water tanks supporting patches of vegetation with high levels of preformed water, which was preferred forage for jackrabbits.

The limited, dissimilar, and predominantly observational findings speaking to direct and indirect impacts of water developments on wildlife species revealed the need for additional investigations, especially studies with an experimental component (DeStefano et al. 2000; Simpson et al. 2011; Larsen et al. 2012). Two appropriate candidate species for such a study are the coyote and the black-tailed jackrabbit. Coyotes have been shown to regularly utilize water developments (Rosenstock et al. 2004; Hall et al. 2013), and it has been proposed that physiological constraints and behavioral tendencies make them more likely to utilize and be dependent on free water than other desert-dwelling carnivores (Golightly and Ohmart 1983; Golightly and Ohmart 1984). Specifically, it has been posited that increases in anthropogenic water sources may be responsible for increases in coyote populations in arid regions of the Great Basin (Arjo et al. 2007; Kozłowski et al. 2008). Black-tailed jackrabbits, on the other hand, appear to persist by utilizing preformed water alone (Johnson and Anderson 1984; Woffinden and Murphy 1989; Rosenstock et al. 2004). Populations of these 2 species have been considered ecologically linked; jackrabbits often comprise the majority of coyote diet throughout areas of the western United States (Johnson and Hansen 1979; Kitchen et al. 1999; Kozłowski et al. 2008; Hernández et al. 2011). Coyote populations have also been shown to exhibit functional and numerical responses to changing jackrabbit numbers in certain areas (Clark 1972; Johnson and Hansen 1979; Stoddart et al. 2001; Hernández et al. 2011), whereas other works support the idea that coyotes can limit jackrabbit populations (Wagner and Stoddart 1972; Henke 1995). The overall objective of our study was to elucidate the effects of water developments on 2 desert-dwelling mammals, coyotes and black-tailed jackrabbits. Specifically, we used a BACI design to determine: (1) whether water developments influence black-tailed jackrabbit abundance (e.g., an indirect effect), (2) whether water developments influence coyote activity (e.g., a direct effect), and (3) whether coyote visitations to water developments are reduced following elimination of water availability.

## Materials and Methods

### Study area

We conducted our research on 879 km<sup>2</sup> of the eastern portion of the US Army Dugway Proving Ground (DPG) located approximately 128 km southwest of Salt Lake City, in Tooele County, UT, USA (Figure 1). Elevations ranged from 1,302 m to 2,137 m. The study site was in the Great Basin and was characterized as a cold desert. Winters were cold; summers were hot and dry, with the majority of precipitation occurring in the spring. Annual weather, derived from daily averages, consisted of mean air temperatures of 12.69 °C



**Figure 1.** Study area (1,127 km<sup>2</sup>), permanent water sites, and survey transects at the US Army DPG, USA, 2010–2013.

(range: –20.02 to 40.58 °C) and mean precipitation of 20.99 cm (range 14.71–29.38; US Army DPG, Meteorological Division). 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 (Cluever et al. 2016). The dominant vegetation types comprising the study area were shrubland (62%), exotic herbaceous grassland (16%), barren (13%), and pinon juniper woodland (5%; LANDFIRE 2012).

Besides several species from the families Heteromyidae and Cricetidae, the black-tailed jackrabbit was considered the most common mammalian species on DPG and surrounding areas (Eberhardt and Van Voris 1986). Mountain cottontails *S. nuttalli*, pronghorn *Antilocapra americana*, mule deer *Odocoileus hemionus*, and feral horses *Equus ferus* were also present. Grazing of livestock had not taken place on DPG for over 60 years. Coyotes were considered the most abundant mammalian carnivore on DPG (Kozlowski et al. 2008). Other resident carnivores included cougars *Puma concolor*, bobcats *Lynx rufus*, kit foxes *Vulpes macrotis*, and badgers *Taxidea taxus* (Hall et al. 2014). No predator control program had occurred on DPG since the 1980s.

**Experimental design and sampling**

We established four 5-km road-based survey transects on which midpoints were adjacent to wildlife water development sites (hereafter wildlife guzzlers [model Dual Big Game, Boss Tanks, Elko,

NV, USA]). Guzzlers were installed during 1970–1990. These transects (hereafter proximate transects) served as our treatment transects because they were associated with a water development. The average perpendicular distance of guzzlers from proximate transects was 11.5 m (standard deviation [SD]=5.6). Average distance between nearest neighbor proximate transects was 4.9 km (SD = 2.5). The average distance from proximate transects to the next nearest perennial water source (i.e., pond, water development, sewage lagoon) was 3.45 km (SD = 0.97, range 2.9–4.9). We used ArcGIS (version 9.3, Environmental Systems Research Institute, Redlands, CA) to create 4 additional 5-km transects (hereafter distant transects), which were distributed randomly along available non-paved roads with the constraints of occurring on lengths of road with no angles >60°, a minimum spacing distance of 2.6 km from proximate transects, and a minimum spacing of 2.6 km from the nearest perennial water source. This minimum distance was derived from the square root of home ranges for coyotes inhabiting a semi-arid environment similar to our study area (Nelson et al. 2007; Hall et al. 2013). The square root of the home range is a linear measure used to approximate average daily movements of mammals (Bowman et al. 2002) and has been encouraged and incorporated into the spatial design of water development investigations in general and within our study area (Simpson et al. 2011; Hall et al. 2013). Black-tailed jackrabbit home ranges have consistently been reported as being smaller than coyotes (Feldhamer et al. 2007), so we were confident that 2.6 km was a distance greater than average daily movements for black-tailed jackrabbits and coyotes. Proximate transects had the same spacing and orientation requirements as distant transects except for being centrally associated with a guzzler.

We employed a multiple-treatment site, multiple-control site BACI design (Morrison et al. 2001) where we monitored all transects prior to and after eliminating water availability at water developments. BACI designs are considered superior to observational studies because 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 (Morrison et al. 2001). Following recommendations of Morrison et al. (2001) and Smith (2002), we only included variables explicitly associated with our BACI design (e.g., period and transect type) in our analyses. In April 2012, we drained the 4 wildlife guzzlers associated with proximate transects using a generator (model 4000-Watt, Champion Power Equipment, Santa Fe Springs, CA, USA) and submersible pump (model 1/2 HP, Wayne Pumps, Harrison, OH, USA), and drinking portals were covered with plywood. Water levels were checked monthly and we drained them if they reached >2/3 capacity. Surveys taking place on proximate and distant transects prior to the water manipulation period were considered the pre-period (September 2010–April 2012), whereas surveys following the water manipulation were considered the post-period (May 2012–August 2013).

We used nocturnal vehicle-based spotlight surveys (Barnes and Tapper 1985) to estimate relative abundance of jackrabbits along the eight 5-km transects. While driving a vehicle along transect at approximately 10–15 km/h, 2 observers scanned their respective side of the road and the road itself with a 3 million candlepower spotlight (Ralls and Eberhardt 1997). Surveys were conducted under clear and calm conditions between 1 h after dusk and 1 h before sunrise for 3 consecutive nights, resulting in a total of 24 separate spotlight counts per survey (i.e., 3 counts for each transect). Spotlight counts associated with each transect were then pooled across the 3

survey days. The order of transects surveyed in a given night was randomized. Once an animal was sighted the driver stopped the vehicle and the species of leporid was identified. Species, location, distance, and bearing to the animal were recorded for each sighting. Surveys were conducted along the eight 5-km transects previously described. Surveys were temporally spaced so that we conducted 1 survey within each 4-month season based on energetic needs of coyotes: breeding 15 December–14 April, pup-rearing 15 April–14 August, and dispersal 15 August–14 December (Gese and Ruff 1998; Siedler and Gese 2012). Seasonal surveys were randomly selected across the 4-month period. When possible, we performed additional intra-season surveys, with  $\geq 2$ -month spacing between surveys, during the pre- (2 extra surveys) and post-period (1 extra survey). Spotlight surveys took place between September 2010 and August 2013. Spotlight counts provided an index of relative abundance; the number of jackrabbits observed per transect per night. Investigations utilizing spotlight counts similar or lower survey effort to our own have been shown to.

A combination of our survey effort/design and a seemingly low jackrabbit density during our study (Egosuce 1975; Eberhardt and Van Voris 1986; Arjo et al. 2007) did not allow for the minimum number of observations needed to robustly estimate absolute abundance using distance sampling (Buckland et al. 2001) or N-mixture models (Joseph et al. 2009). We felt justified in utilizing spotlight counts as an index of relative abundance; they have been utilized to quantify hare and jackrabbit relative abundance across time and space (Moreno et al. 2007; Hernández et al. 2011), and have been shown to be highly correlated with absolute abundance estimates that account for detection probabilities, when data sets are robust enough for such comparisons (Reid and Montgomery 2007; Barrio et al. 2010). We felt that our sampling design, which called for sampling the same transects over time, further justified the use of total counts as a surrogate of abundance, as detectability/sightability issues were likely less influential than if survey transects were spatially unique during each survey season.

We conducted scat deposition surveys along roads of proximate and distant transects (Knowlton 1984; Schauster et al. 2002; Dempsey et al. 2014) to estimate the relative use of coyotes. As a passive technique, scat deposition surveys do not require the target species to investigate an attractant or lure. This may be beneficial, especially with species such as coyotes which can be wary of novel cues and exhibit high levels of behavioral plasticity (Sequin et al. 2003). Surveys were conducted by initially walking the transect to clear any scat from the road surface, then returning 14 days later to walk and count the number of scats (Schauster et al. 2002). Following recommendations from Knowlton (1984), each transect was walked in both directions to reduce missed detections of scats. Surveys were conducted along the same eight 5-km transects as the jackrabbit surveys. Scat surveys were temporally spaced in the same manner as jackrabbit surveys. Hence, each survey consisted of 8 scat deposition counts (i.e., 1 scat deposition count per transect). Scat deposition surveys took place between September 2010 and August 2013. We identified coyote scats based on guidelines described in Murie and Elbroch (2005). Scat deposition counts provided an index of use; the number of coyote scats per transect per survey. Scat surveys have been reported as an effective index for tracking coyote use and abundance over time and space (Knowlton 1984; Stoddart et al. 2001), have low mis-identification rates (Lonsinger et al. 2015) and have outperformed other non-invasive surveys for mammalian carnivores (Schauster et al. 2002; Dempsey et al. 2014).

During the pre- and post-periods we monitored coyote monthly visitation rates to the water developments using a sample of adult radio-collared coyotes inhabiting DPG. We monitored visitation of radio-collared coyotes to the water development sites with data loggers (model R4500S and model R2100/D5401, ATS, Isanti, MN, USA) and an omnidirectional antenna following recommendations of Breck et al. (2006). We defined a visit as all data logger recordings of an individual animal occurring within 30 min at a particular water source (Atwood et al. 2011; Hall et al. 2013). For example, an animal visiting a water source and then visiting the same water source greater than 30 min later was classified as 2 separate visits. Data loggers were calibrated to detect a signal at an average distance of 10 m from the antennae, which were placed 8 m from guzzler drinking portals. The area of signal detection uncertainty (Breck et al. 2006) was  $< 3$  m at all data logger sites. We considered all data logger detections as visits to guzzlers.

Fieldwork was approved and sanctioned by the US Department of Agriculture's National Wildlife Research Center and the US Army's DPG. Permission to access land on the DPG was obtained from the US Army. Capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees (IACUC) at the US Department of Agriculture's National Wildlife Research Center (QA-1734) and Utah State University (#1438). The Utah State University and National Wildlife Research Center IACUC committees specifically approved this study. Permits to capture, handle, and radio-collar coyotes were obtained from the Utah Division of Wildlife Resources (COR#4COLL8322). All applicable institutional and/or national guidelines for the care and use of animals were followed.

## Data analysis

We employed generalized linear mixed models (GLMMs; Stroup 2012) to test the categorical main effects of period (pre- and post-manipulation) and transect type (proximate and distant) on the continuous response variables of jackrabbit relative abundance and coyote relative use. Specifically, we tested the impact of water development manipulation by including a period by transect type interaction in our model (Underwood 1992). Within the framework of a BACI design, such an interaction tests for a differential change (i.e., non-parallelism) between impact and control sampling units following some type of manipulation (Underwood 1992). Inspection of raw data revealed non-normality for both data sets. As a result, we fit 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 jackrabbit and coyote data, the final model family used was quasi-Poisson and lognormal, respectively. Though we conducted multiple surveys on each transect for the pre- and post-periods, we collapsed our survey data across surveys to reduce model complexity and better account for residual variance. By doing so, data were analyzed within a balanced split plot in a time model framework (Aho 2014). In order to account for variability among survey transects, and variability among survey transects within treatments, we included a survey transect (i.e., proximate or distant) by period (pre- and post-manipulation) random effect (Demidenko 2013). GLMM analyses were performed using the GLIMMIX procedure in SAS (version 9.4, Cary, NC, USA). Following recommendations of Morrison et al. (2001) and Smith (2002), we only included variables explicitly associated with our BACI design (e.g., period and transect type) in our analyses

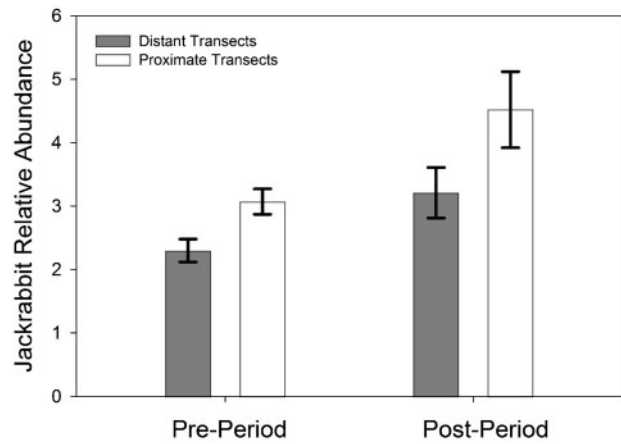
We determined if the number of radio-collared coyote visits to water developments decreased by comparing the number of monthly data logger visitations prior to and following our manipulation. To ensure the visitation data were not biased by sample size, we compared the number of radioed coyotes available for data logger recording each month for both periods. We used a 1-way analysis of variance (ANOVA) in SAS for these comparisons. For all statistical tests we interpreted *P* values in terms of relative evidence of difference (Ramsey and Schafer 2002). Reported means, standard deviations, standard errors, and 95% CIs were derived from the raw data, rather than model driven estimates.

**Results**

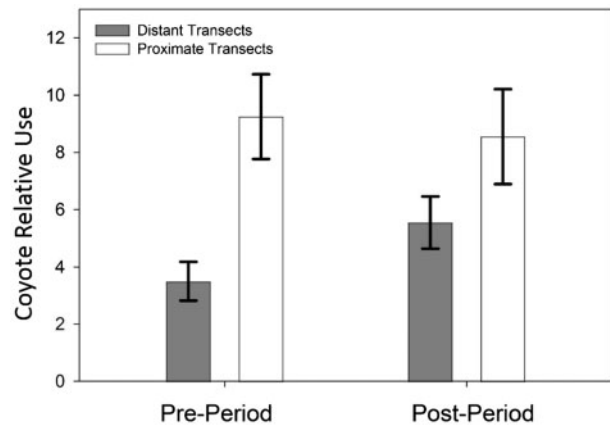
Between September 2010 and August 2013, we conducted 7 jackrabbit surveys prior to and 5 surveys following our manipulation. Jackrabbit relative abundance across all surveys averaged 3.07 rabbits/transect/night (SD = 2.60) and ranged from 0 to 19 rabbits/transect/night. We found no evidence that elimination of water at guzzlers impacted jackrabbit relative abundance (period x transect type interaction:  $F = 0.41, P = 0.54, df = 1, 6$ ; Figure 2). There was evidence that period influenced jackrabbit relative abundance ( $F = 5.76, P = 0.05, df = 1, 6$ ; Figure 2). There was no evidence that transect type influenced jackrabbit relative abundance ( $F = 1.40, P = 0.28, df = 1, 6$ ). Average jackrabbit relative abundance before and after manipulation for all transects was 2.68 (standard error [SE] = 0.13) and 3.87 (SE = 0.35) rabbits/transect/night, respectively.

Between September 2010 and August 2013, we conducted 4 seasonal coyote scat deposition surveys prior to and following our manipulation. Overall, coyote relative use averaged 6.01 scats/transect/survey (SD = 5.91) and ranged from 0 to 27 scats/transect/survey. We found evidence that elimination of water at guzzlers influenced coyote relative use (period x transect type interaction:  $F = 10.61, P = 0.02, df = 1, 6$ ; Figure 3). The number of coyote scats observed on distant transects increased from 3.50 scats/transect during the pre-period (SE = 1.06) to 5.50 scats/transect (SE = 1.62) during the post-period. Conversely, the number of coyote scats observed on proximate transects decreased slightly from 9.25 scats/transect (SE = 2.79) during the pre-period to 8.50 scats/transect (SE = 1.62) during the post-period. We found some evidence that period influenced coyote relative use ( $F = 4.22, P = 0.09, df = 1, 6$ ). There was no evidence that transect type influenced coyote relative use on its own ( $F = 2.58, P = 0.15, df = 1, 6$ ). Average relative use during the pre- and post-manipulation periods for all transects was 6.35 (SE = 0.81) and 7.10 (SE = 0.86) cats/transect/survey, respectively.

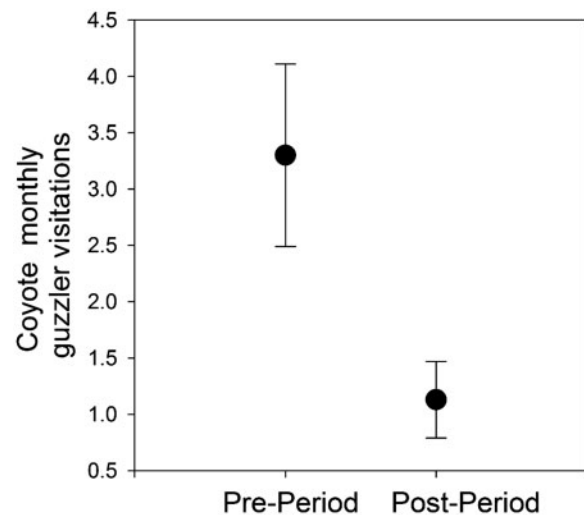
For the pre-period and post-period, we monitored visitations of radio-collared coyotes at wildlife guzzlers from May 2010 to April 2012 and May 2012 to August 2013, respectively. There was no evidence that the number of radio-collared coyotes (i.e., number available for monthly data logger recording) differed prior to and following water removal ( $F = 1.05, P = 0.31, df = 1, 37$ ). The monthly sample size of marked coyotes during pre-period and post-period averaged 18.74 (SE = 0.94) and 20.25 (SE = 1.13), respectively. There was evidence that monthly visitations by radio-collared coyotes to wildlife guzzlers was influenced by the elimination of water ( $F = 6.19, P = 0.02, df = 1, 37$ ) with the elimination of water reducing visitation by coyotes (Figure 4).



**Figure 2.** Black-tailed jackrabbit relative abundance ( $\pm$  SE) observed on 5-km proximate and distant to guzzler transects prior to (pre-period) and following (post-period) removal of water availability at guzzlers on the US Army DPG, Utah, USA, 2010–2013.



**Figure 3.** Coyote relative use ( $\pm$  SE) observed on 5-km proximate and distant to guzzler transects prior to (pre-period) and following (post-period) removal of water availability at guzzlers on the US Army DPG, Utah, USA, 2010–2013.



**Figure 4.** Average monthly visitations ( $\pm$  SE) of a marked coyote population prior to (pre-period) and following (post-period) removal of water availability at guzzlers on the US Army DPG, Utah, USA, 2010–2013.

## Discussion

Our study was the first to incorporate a resource manipulation design to evaluate the potential effects of water developments on canids and leporids in an arid environment. Overall, we found evidence that abundance of jackrabbits was not indirectly impacted by manipulation of water developments, but found support that our manipulation influenced relative use of coyotes, and that coyote visitations to water developments declined following removal of water availability.

A potential indirect effect of water developments is suppressed populations of prey species of water dependent carnivores (Rosenstock et al. 1999; DeStefano et al. 2000; Simpson et al. 2011). Our findings differ from those of DeStefano et al. (2000) in that we found no evidence of an indirect impact of water developments on black-tailed jackrabbits. This disparity may be attributed to several factors. First, our experimental design may have allowed us to account for sources of bias that can go undetected with purely observational studies (Underwood 1992). For example, if jackrabbit abundance had been greater near proximate rather than distant transects, our BACI design would have allowed us to determine whether any such disparity was attributed to water developments, and not some other factor(s). Second, our sampling design (5-km transects) may have better captured changes in the trend of the jackrabbit population across a larger landscape. Alternatively, the spatial scale of our transects may have been too large to detect differences in jackrabbit abundance occurring at close proximity (e.g., >1 km) to guzzlers.

We found no evidence suggesting treatment type influenced the relative abundance of jackrabbits. This seems contradictory based on visual inspection of the data (Figure 2). This can be explained by the majority of the variation among treatments occurring due to variation at the survey transect level, rather than the transect type level. This likely occurred because proximate and distant transects were not established across uniform vegetation classes. That is, we did not stratify across vegetation classes, or other spatial factors that may have influenced jackrabbit relative abundance. The reason for this was 2-fold. First, DPG contains high levels of vegetation heterogeneity (see methods for full description). As a result, we felt the establishment of transects partitioned by vegetation classes would not have provided sample sizes needed to adequately address our central research questions. Second, efforts aimed at discerning the role of vegetation on populations of black-tailed jackrabbits, and closely related species, have already been undertaken (Anderson and Shumar 1986; Portales et al. 2004; Hernández et al. 2011). Heterogeneity of vegetation within and across transects likely influenced detection of jackrabbits. However, because we sampled the same transects over time and vegetation communities near transects did not change over the course of our study (i.e., no major disturbance events), we feel our inability to account for detection did not inhibit our ability to detect a water effect.

Jackrabbit relative abundance appeared to be partially driven by temporal factors, as we observed higher relative abundance during the post-manipulation period of the study (Figure 2). It was not our objective in this study to identify the suite of factors influencing the jackrabbit population at DPG, but we speculate that this temporal trend was at least partially a result of a time lag effect between precipitation and jackrabbit abundance. Hernández et al. (2011) reported a positive relationship between the previous 12 months of precipitation and both primary productivity and jackrabbit abundance. Similarly, Ernest et al. (2000) reported rodent abundance

was positively correlated to precipitation occurring during the previous season or seasons. Monthly precipitation rates at DPG during 2009 (i.e., a span potentially influencing pre-period jackrabbit relative abundance) and 2011 (i.e., a span potentially influencing post-period jackrabbit relative abundance) averaged 1.14 (SE = 0.25) and 1.96 cm (SE = 0.66), and a precipitation spike of 10.06 cm occurred in May of 2011, 11 months prior to our manipulation (US Army DPG, West Desert Test Center Meteorological Division). Thus, a general trend of increased primary productivity leading up to the post-manipulation period may have resulted in increased jackrabbit reproductive output, facilitating an increase in overall jackrabbit abundance. Further analyses are needed to establish the drivers of jackrabbit abundance at DPG and the Great Basin Desert.

Our data suggested that relative use of coyotes was impacted by water availability with the elimination of water availability at water developments facilitating a reduction of coyote use in areas associated with our treatment (Figure 3). This reduction coincided with an increase in coyote use in areas not associated with our manipulation (i.e., distant transects). This finding partially substantiates the hypothesis that additional free water on desert landscapes may have prompted coyote population increases in the Great Basin Desert (Arjo et al. 2007; Kozłowski et al. 2008) and similar increases for other carnivores in other arid ecosystems (Brawata and Neeman 2011). However, because we measured relative use, and not demography of coyotes, further investigations are required to substantiate this theory. Kluever and Gese (2016) found that resident adult coyotes did not shift or abandon home ranges following the elimination of available free water sources within home ranges. These findings, coupled with our investigation, support the idea that water developments can influence fine scale movements within coyote territories, but are not needed for coyotes to establish or maintain territories. In other words, “coyote use” of free water does not appear to translate to “coyote need” for free water in our study system. It is possible that free water sources are more important to transient and juvenile coyotes, but our study was not explicitly designed to test this possibility.

Our findings differ from those of Hall et al. (2013), despite both investigations encompassing similar spatiotemporal boundaries and utilizing indices of coyote activity. Several mechanisms may be responsible for this discrepancy. First, the behavioral ecology of coyotes may be a driving factor. The sampling technique we employed (scat deposition survey) requires an animal only engage in evacuation behavior in order to be detected/counted. Other sampling techniques, such as scent-station surveys (Hernández et al. 2011; Hall et al. 2013) require that an animal behaviorally react to a novel olfactory cue. Coyotes have been shown to be wary of novel cues (Sequin et al. 2003). As a result, the use of novel cues as part of a sampling technique may introduce sources of bias, especially in a species like the coyote, where variability across the bold/shy continuum occurs (Darrow and Shivik 2009). In addition, human exploitation is often a predominant source of coyote mortality (Bekoff and Gese 2002) with the use of olfactory lures at traps a commonly utilized exploitation method (Bullard et al. 1983) and such efforts are not always successful (i.e., some animals encounter but escape/elude traps; [Skinner and Todd 1990; Linhart and Dasch 1992]). As a result, olfactory cues intended to serve as an attractant may actually deter a portion of coyotes in a given area due to behavioral tendencies engendered by innate and/or learned mechanisms. Hence, the use of more passive, less behavioral dependent sampling techniques (i.e., scat surveys) may reduce sampling bias. Second, the larger size of our sampling units (5-km transects vs. 3-m plots) may

be more appropriate for capturing activity changes/trends of coyotes. Finally, our manipulation of water developments may have captured an effect that would often go undetected with purely observational studies. Our investigation was not designed to determine the ultimate causes responsible for the reduced relative use that we observed, but rather to test whether water sources are an influential factor. For example, our manipulation may have facilitated abandonment by some resident coyotes, shifts of home range boundaries and space use, increased dispersal rates of juveniles (i.e., a reduction of philopatry tolerance among packs or breeding pairs), reduced fecundity, or a combination thereof.

We observed over a 3-fold reduction in use of monitored water developments by coyotes following elimination of water (Figure 4). Our data on visitations were for marked individuals only, and alone cannot fully explain our relative abundance findings, as visitations were relatively low. Our visitation results would have been buttressed if we could report the same relationship for all DPG coyotes that visited treatment water developments, rather than a radio-collared sample. In addition, determining whether coyote visitations increased at other water sources within the study area following our manipulation would have helped elucidate the importance of free water to coyote populations. Marked coyotes were captured throughout the study area using several techniques (e.g., helicopter net gunning, leg-hold trapping) and efforts were made to mark only 1 individual per social group. In addition, from 2011 to 2012, Hall et al. (2013) recorded 869 coyote visitations (i.e., drinking events) at water developments within a study area that encompassed DPG. This investigation, however, concluded near the onset of our manipulation. Given the aforementioned, we feel that our coyote visitation findings are germane with respect to our other study findings, and provide at least partial evidence that overall coyote visitations to water developments were reduced following our manipulation.

Our study was one of the first to utilize a study design with a resource manipulation component in order to determine the effect of water developments on wildlife (Cain et al. 2008). Though we did not determine an indirect effect of water developments on black-tailed jackrabbits, our findings revealed a differential change in coyote activity in relation to elimination of water. In addition, we observed that visitations of coyotes at water sources were reduced following our water manipulation. At first glance, our findings suggest that coyote populations may be affected by water developments, but caution is warranted. First, falsely equating statistical significance to biological relevance is a real and seemingly often ignored risk in ecological investigations (Martinez-Abraín 2008). Second, Cluever and Gese (2016) provided evidence that free water availability is not a requisite habitat component for resident coyotes, but were unable to determine the influence of water developments on coyote space use within territories. Lastly, despite their common validation (Hopkins and Kennedy 2004; Kays et al. 2008; Barrio et al. 2010) indices of abundance and use can be problematic (White 2005; Edwards et al. 2014). As such, we recommend future investigations on the effects of water developments on individual species and ecological interactions incorporate absolute estimates of abundance, rather than indices, into their study design. When possible, such studies should also incorporate fine scale spatiotemporal data and population vital rates.

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### References

Aho KA, 2014. *Foundational and Applied Statistics for Biologists Using R*. Boca Raton: CRC Press.

Anderson JE, Shumar ML, 1986. Impacts of black-tailed jackrabbits at peak population densities on sagebrush-steppe vegetation. *J Ran Man* 39:152-156.

Arjo WM, Gese EM, Bennett TJ, Kozłowski AJ, 2007. Changes in kit fox - coyote - prey relationships in the Great Basin Desert, Utah. *West North Am Natur* 67:389-401.

Atwood TC, Fry TL, Leland BR, 2011. Partitioning of anthropogenic watering sites by desert carnivores. *J Wildl Manag* 75:1609-1615.

Barnes RFW, Tapper SC, 1985. A method for counting hares by spotlight. *J Zool* 206:273-276.

Barrio IC, Acevedo P, Tortosa FS, 2010. Assessment of methods for estimating wild rabbit population abundance in agricultural landscapes. *Eur J Wildl Res* 56:335-340.

Bekoff M, Gese EM, 2002. Coyote. In: Feldhamer GA, Thompson BC, Chapman JA, editors. *Wild Mammals of North America: Biology, Management, and Conservation*. Baltimore: Johns Hopkins University Press, 467-481.

Bleich VC, 2005. In my opinion: politics, promises, and illogical legislation confound wildlife conservation. *Wildl Soc Bull* 33:66-73.

Bowman J, Jaeger JAG, Fahrig L, 2002. Dispersal distance of mammals is proportional to home range size. *Ecology* 83:2049-2055.

Brawata RL, Neeman T, 2011. Is water the key? Dingo management, intra-guild interactions and predator distribution around water points in arid Australia. *Wildl Res* 38:426-436.

Breck SW, Lance N, Bourassa J, 2006. Limitations of receiver/data loggers for monitoring radiocollared animals. *Wildl Soc Bull* 34:111-115.

Broyles B, 1995. Desert wildlife water developments: questioning use in the Southwest. *Wildl Soc Bull* 23:663-675.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL et al., 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. New York: Oxford University Press.

Bullard RW, Turkowski FJ, Kilburn SR, 1983. Responses of free ranging coyotes to lures and their modifications. *J Chem Ecol* 9:877-888.

Burkett DW, Thompson BC, 1994. Wildlife association with human-altered water sources in semiarid vegetation communities. *Conserv Biol* 8:682-690.

Cain JW, Krausman PR, Morgart JR, Jansen BD, Pepper MP, 2008. Responses of desert bighorn sheep to removal of water sources. *Wildl Monogr* 1-32.

Cambell BH, Remington R, 1979. Bighorn use of artificial water sources in the Buckskin Mountains, Arizona. *Des Bigho Coun Trans* 23:50-56.

Clark FW, 1972. Influence of jackrabbit density on coyote population change. *J Wildl Manag* 36:343-356.

Cutler TL, Morrison ML, 1998. Habitat use by small vertebrates at two water developments in southwestern Arizona. *Southw Nat* 43:155-162.

Darrow PA, Shivik JA, 2009. Bold, shy, and persistent: variable coyote response to light and sound stimuli. *Appl Anim Behav Sci* 116:82-87.

Demidenko E, 2013. *Mixed Models: Theory and Applications with R*, 2nd edn. Hoboken: John Wiley & Sons.



- Dempsey SJ, Gese EM, Kluever BM, 2014. Finding a Fox: an evaluation of survey methods to estimate abundance of a small desert carnivore. *PLoS ONE* 9:8.
- DeStefano S, Schmidt SL, deVos JC, 2000. Observations of predator activity at wildlife water developments in southern Arizona. *J Ran Man* 53: 255–258.
- Eberhardt LE, Van Voris P, 1986. Historical wildlife dynamics on Dugway proving ground: population and disease trend in jack rabbits over two decades. Richland, Washington, USA: Pacific Northwest Laboratory, 300.
- Edwards CTT, Bunnefeld N, Balme GA, Milner-Gulland EJ, 2014. Data-poor management of African lion hunting using a relative index of abundance. *Proc Natl Acad Sci USA* 111:539–543.
- Egosome HJ, 1975. Population dynamics of the kit fox in western Utah. *Ecology* 43:481–497.
- Ernest SKM, Brown JH, Parmenter RR, 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88:470–482.
- Feldhamer GA, Drickamer LC, Vessey SH, Merritt JF, Krajewski C, 2007. *Mammalogy: Adaptation, Diversity, Ecology*. Baltimore: John Hopkins University Press.
- Gese EM, Ruff RL, 1998. Howling by coyotes *Canis latrans*: variation among social classes, seasons, and pack sizes. *Can J Zool* 76:1037–1043.
- Golightly RT, Ohmart RD, 1983. Metabolism and body temperature of two desert canids: coyotes and kit foxes. *J Mammal* 64:624–635.
- Golightly RT, Ohmart RD, 1984. Water economy of two desert canids: coyote and kit fox. *J Mammal* 65:51–58.
- Hall LH, Larsen RT, Knight RN, Bunnell KD, McMillan BR, 2013. Water developments and canids in two North American deserts: a test of the indirect effect of water hypothesis. *PLoS ONE* 8:8.
- Hall JT, Hall LK, Larsen RT, Knight RN, McMillan BR, 2014. *Do Subordinate Carnivores Alter Temporal and Spatial Activity to Reduce Competition with Dominate Carnivores at Water Sources?* Utah Chapter of the Wildlife Society, Annual Meeting, St. George, Utah.
- Hall LH, Larsen RT, Westover MD, Day CC, Knight RN et al., 2015. Influence of exotic horses on the use of water by communities of native wildlife in a semi-arid environment. *J Arid Env* 127:100–105.
- Hayden P, 1966. Seasonal occurrence of jackrabbits on jackass flat, Nevada. *J Wildl Manag* 30:835–838.
- Henke SP, 1995. Effects of coyote control on their prey: a review. Coyotes in the Southwest: a Compendium of Knowledge; 1995 Dec 13–14; San Angelo, Texas, USA.
- Hernández L, Laundre JW, Grajales KM, Portales GL, Lopez-Portillo J et al., 2011. Plant productivity, predation, and the abundance of black-tailed jackrabbits in the Chihuahuan Desert of Mexico. *J Arid Environ* 75:1043–1049.
- Holecheck JL, Pieper RD, Herel CH, 2010. *Range Management: Principles and Practices*. 6th edn. Upper Saddle River: Prentice Hall.
- Hopkins HL, Kennedy LL, 2004. An assessment of indices of relative and absolute abundance for monitoring populations of small mammals. *Wildl Soc Bull* 32:1289–1296.
- Johnson MK, Hansen RM, 1979. Coyote food habits on the Idaho National Engineering Laboratory. *J Wildl Manag* 43:951–956.
- Johnson RD, Anderson JE, 1984. Diets of black-tailed jack rabbits in relation to population density and Vegetation. *J Ran Man* 37:79–83.
- Joseph LN, Elkin C, Martin TG, Possingham HP, 2009. Modeling abundance using N-mixture models: the importance of considering ecological mechanisms. *Ecol Appl* 19:631–642.
- Kays RW, Gompper ME, Ray JC, 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. *Ecol Appl* 18:1014–1027.
- Kitchen AM, Gese EM, Schauster ER, 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *Can J Zool* 77:1645–1656.
- Kluever BM, Gese EM, 2016. Spatial response of coyotes to removal of water availability at anthropogenic water sites. *J Arid Env* 130:68–75.
- Kluever BM, Gese EM, Dempsey SJ, 2016. The impact of wildlife water developments on a rodent community in the Great Basin Desert. *J Mammal*. doi: 10.1093/jmammal/gyw077.
- Knowlton FF, 1984. *Feasibility of Assessing Coyote Abundance on Small Areas: Final Report*. Denver: Denver Wildlife Research Center.
- Kozłowski AJ, Gese EM, Arjo WM, 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.
- LANDFIRE, 2012. Existing vegetation type layer. LANDFIRE 1.1.0 USA Department of the Interior, Geological Survey [cited 2014 September 15]. Available from: <http://landfire.cr.usgs.gov/viewer/>.
- Larsen RT, Bissonette JA, Flinders JT, Whiting JC, 2012. Framework for understanding the influences of wildlife water developments in the western United States. *Calif Fis Gam* 98:148–163.
- Larsen RT, Bissonette JA, Flinders JT, Hooten MB, Wilson TL, 2010. Summer spatial patterning of chukars in relation to free water in western Utah. *Landsc Ecol* 25:135–145.
- Leopold A, 1933. *Game Management*. New York: Charles Scribner's Sons.
- Linhart SB, Dasch GJ, 1992. Improved performance of padded jaw traps for capturing coyotes. *Wildl Soc Bull* 20:63–66.
- Lonsinger RC, Gese EM, Dempsey SJ, Kluever BK, Johnson TR et al., 2015. Balancing sample accumulation and DNA degradation rates to optimize noninvasive genetic sampling of sympatric carnivores. *Mol Ecol Res* 15:831–842.
- Lynn JC, Chambers CL, Rosenstock SS, 2006. Use of wildlife water developments by birds in southwest Arizona during migration. *Wildl Soc Bull* 34:592–601.
- Martinez-Abraín A, 2008. Statistical significance and biological relevance: a call for a more cautious interpretation of results in ecology. *Acta Oecol* 34:9–11.
- Moreno S, Beltran JF, Cotilla I, Kuffner B, Laffite R et al., 2007. Long-term decline of the European wild rabbit, *Oryctolagus cuniculus*, in south-western Spain. *Wildl Res* 34:652–658.
- Morgart JR, Hervert JJ, Krausman PR, Bright JL, Henry RS, 2005. Sonoran pronghorn use of anthropogenic and natural water sources. *Wildl Soc Bull* 33:51–60.
- Morrison ML, Block WM, Strickland MD, Kendall WL, 2001. *Wildlife Study Design*. New York: Springer.
- Murie OJ, Elbroch M, 2005. *Peterson Field Guides: Animal Tracks*. Boston: Houghton Mifflin Company.
- Nelson JL, Cypher BL, Bjurlin CD, Creel S, 2007. Effects of habitat on competition between kit foxes and coyotes. *J Wildl Manag* 71:1467–1475.
- Portales GL, Hernández L, Cervantes FA, Jw L, 2004. Reproduction of black-tailed jackrabbits (Lagomorpha: *Lepus californicus*) in relation to environmental factors in the Chihuahuan Desert, Mexico. *Southw Nat* 49: 356–366.
- Ralls K, Eberhardt LL, 1997. Assessment of abundance of San Joaquin kit foxes by spotlight surveys. *J Mammal* 78:65–73.
- Ramsey FR, Schafer DW, 2002. *The Statistical Sleuth: a Course in Methods of Data Analysis*. Pacific Grove: Duxbury.
- Reid N, Montgomery WI, 2007. Is naturalisation of the brown hare in Ireland a threat to the endemic Irish hare? *Biol Environ Proc R Irish Acad* 107B: 129–138.
- Rosenstock SS, Rabe MJ, O'Brien CS, Waddell RB, 2004. *Studies of Wildlife Water Developments in Southwestern Arizona: Wildlife Use, Water Quality, Wildlife Diseases, Wildlife Mortalities, and Influences of Native Pollinators*. Vol. 8. Phoenix: Arizona Game and Fish Department, Research Branch Technical Guidance Bulletin.
- Rosenstock SS, Ballard WB, Devos JC, 1999. Viewpoint: Benefits and impacts of wildlife water developments. *J Ran Man* 52:302–311.
- Schauster ER, Gese EM, Kitchen AM, 2002. An evaluation of survey methods for monitoring swift fox abundance. *Wildl Soc Bull* 30:464–477.
- Seidler RG, Gese EM, 2012. Territory fidelity, space use, and survival rates of wild coyotes following surgical sterilization. *J Ethol* 30:345–354.
- Sequin ES, Jaeger MM, Brussard PF, Barrett RH, 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. *Can J Zool* 81:2015–2025.
- Simpson NO, Stewart KM, Bleich VC, 2011. What have we learned about water developments for wildlife? Not enough! *Calif Fis Gam* 97:190–209.
- Skinner DL, Todd AW, 1990. Evaluating the efficiency of footholding devices for coyote capture. *Wildl Soc Bull* 18:166–175.

- Smith EP, 2002. BACI design. In: El-Shaarawi AH, Piegorisch WW, editors. *Encyclopedia of Environmetrics*. Chichester: John Wiley & Sons Ltd.
- Stoddart LC, Griffiths RE, Knowlton FF, 2001. Coyote responses to changing jackrabbit abundance affect sheep predation. *J Ran Man* 54:15–20.
- Stroup WW, 2012. *Generalized Linear Mixed Models: Modern Concepts, Methods and Applications*. Boca Raton: CRC Press.
- Underwood AJ, 1992. Beyond BACI: The detection of environmental impacts on populations in the real, but variable world. *J Exp Mar Biol Ecol* 161:145–178.
- Wagner FH, Stoddart LC, 1972. Influence of coyote predation on black-tailed jackrabbit populations in Utah. *J Wildl Manag* 36:329–342.
- White GC, 2005. Correcting wildlife counts using detection probabilities. *Wildl Res* 32:211–216.
- Woffinden ND, Murphy JR, 1989. Decline of a ferruginous hawk population: a 20 year summary. *J Wildl Manag* 53:1127–1132.