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Competition Dynamics Within Communities of Desert Wildlife at Water Sources

Lucas Keith Hall

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

Competition Dynamics Within Communities of Desert Wildlife at Water Sources

Lucas Keith Hall
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Doctor of Philosophy

Water is a vital resource for species inhabiting arid and semi-arid regions and can shape the biotic communities that we observe. Because water is considered a limiting resource for many species in desert environments, there is the potential for competitive interactions between species to occur at or around water sources. For this dissertation I tested hypotheses related to resource competition among different species of wildlife in the Great Basin and Mojave Deserts of western Utah. Chapter one evaluated the influence of feral horses (*Equus caballus*) on patterns of water use by communities of native birds and mammals. Chapter two determined if feral horses competed with pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) for access to water. In chapters one and two, we found evidence that horses compete with native wildlife for water. In chapter one, horses were associated with decreased richness and diversity of native species at water sources. Native species also had fewer visits and spent less time at water sources frequented by horses. In chapter two, we found that pronghorn and mule deer used water sources less often where horse activity was high. There were also significant differences in temporal activity for pronghorn, but not mule deer, at horse-occupied sites versus sites where horses were absent or uncommon. Our results indicated that horses spatially and temporally displaced other species at water sources providing evidence of a negative influence on how communities of native wildlife access a limited resource in an arid environment. Chapter three assessed whether dominant carnivores (coyote (*Canis latrans*) and bobcat (*Lynx rufus*)) negatively influenced the spatial use of water sources by the subordinate kit fox (*Vulpes macrotis*). Our results did not reveal strong negative associations between kit fox visits to water sources and visits by dominant carnivores; in fact, dominant carnivores contributed very little to the use of water by kit foxes. Instead, kit fox visits were more closely associated with habitat features at water sources. Our findings indicate that dominant carnivores are not the primary driver of use of water sources by subordinate carnivores. Chapter four evaluated whether a simulated loss of water due to climate change/increased human use would differentially affect desert bats based on flight morphology and maneuverability. When we experimentally reduced surface area of water sources, larger, less-maneuverable bats experienced a 69% decrease in drinking success and increased competition with smaller, maneuverable bats. Anticipated reductions in the sizes of water sources due to climate change may lead to species with less maneuverability being unable to access water efficiently and facing increased competition from more agile bats.

Keywords: bats, carnivores, competition, horses, maneuverability, mule deer, kit fox, pronghorn, spatial partitioning, temporal partitioning, ungulates, water development, water source

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CHAPTER 1

INFLUENCE OF FERAL HORSES ON THE USE OF WATER BY COMMUNITIES OF NATIVE WILDLIFE IN A SEMI-ARID ENVIRONMENT

ABSTRACT

Introduced species can impact native communities by altering competition dynamics. Large feral species, such as the horse (*Equus caballus*), may have a competitive advantage over smaller native species and could exclude them from access to limited resources. Our objective was to determine the influence of the feral horse on the use of water by native species in a semi-arid environment where availability of water is limited. From July 2010 to August 2011, we used remote cameras to monitor water sources in the Great Basin Desert where horses had drinking access and where horses were excluded (with fencing) to compare 1) composition of native communities and 2) water usage by native species. We captured 96,601 images representing 40 species of birds (29,396 images) and 13 species of mammals (67,205 images). Of the 67,205 images of mammals, 79% contained horses. Horses were associated with decreased richness and diversity of native species at water sources. Furthermore, native species had fewer visits and spent less time at water sources frequented by horses. Our results indicated that horses displaced other species at water sources providing evidence of a negative influence on how communities of native wildlife access a limited resource in an arid environment.

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INTRODUCTION

Competition for limited resources influences the organization and structuring of biotic communities (Schoener, 1974; Carothers and Jaksić, 1984). Where species co-occur and compete for resources there are often mechanisms that enable coexistence and community stability. Because species differ in their competitive abilities, some species outcompete others for access to resources (Côté, 2005). To ensure coexistence in multi-species environments, subordinate competitors often partition resources with dominant competitors (MacArthur, 1958; Barot and Gignoux, 2004). However, mechanisms that stabilize community structure (e.g., resource partitioning) typically evolve over long periods of time.

Consequently, communities with species that have co-evolved over relatively long periods of time likely have better developed strategies for coexistence than newly formed communities. For example, within the community of native herbivores in semi-arid Africa, there is evidence that the large-bodied elephant (*Loxodonta africana*) influences community structure at waterholes (Valeix et al., 2007). Smaller herbivores that compete with elephants tend to avoid peak times of elephant visitation to waterholes. These smaller herbivores have co-existed with elephants over millions of years and have likely evolved strategies for temporal resource partitioning to minimize competition. In native communities, dominance hierarchies are typically well established, helping to stabilize community organization (Schuette et al., 2013). In communities where relatively new competitors have been introduced (i.e., exotic species), dominance hierarchies and competition dynamics may be altered, negatively influencing resource partitioning and the structure of native communities.

The introduction of exotic species is a global phenomenon that has had far-reaching implications for the stability of native communities (Wolfe and Klironomos, 2005; Lach, 2008;

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Kenis et al., 2009). Many exotic species have a competitive advantage over native species due to a variety of factors related to life history and physiology (e.g., growth rate, reproduction rate, lack of natural predators and/or competitors; Humphrey and Schupp, 2004; Côté, 2005; Preston et al., 2012). In addition, physical attributes such as body size further enable some exotic species to outcompete native species (Gherardi and Cioni, 2004; Reed et al., 2012). Exotic species that are large-bodied and behaviorally dominant can disrupt native communities due to competitive advantages over native species.

The horse (*Equus caballus*) is a large, exotic and feral ungulate that has been introduced around the world since its domestication (Clutton-Brock, 1981; Mills and McDonnell, 2005). Horses have been shown to negatively influence soil, vegetation, small vertebrates and invertebrates in a variety of systems (Beever and Brussard, 2000; Zalba and Cozzani, 2004; Beever and Herrick, 2006; Parvage et al., 2011; Davies et al., 2014). Feral horses (and burros [*E. asinus*]) have also displaced native ungulates from preferred habitats and at water sources (Ostermann-Kelm et al., 2008; Attum et al., 2009; Girard et al., 2013; Gooch, 2014). Species inhabiting arid or semi-arid environments rely on the availability of water (Rautenstrauch and Krausman, 1989; Cain III et al., 2006; Cain III et al., 2012; Bock, 2015) and there may be implications for species that compete with horses for access to water. Horses are gregarious, behaviorally dominant, and water-limited (an individual horse can drink up to 33 L of water/day; Berger, 1985; Groenendyk et al., 1988; Stevens, 1988) and these characteristics may compound competition for native species at water sources. Moreover, horse populations have increased dramatically in arid regions of western North America over the past several decades and are currently exceeding management objectives in many areas (Palmer et al., 2013; Davies et al., 2014). Little is known, however, concerning the degree to which horses compete with

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communities of native species for water in environments where water is scarce or how increased populations of horses may influence native communities.

Our objective was to determine the influence of horses on the use of water by communities of native wildlife in the semi-arid Great Basin Desert. We monitored water sources where horses had drinking access (horse included; hereafter HI) and water sources where horses were excluded with fencing (hereafter HE) to determine if there were differences in 1) composition of native communities or 2) use of water sources by native species. We expected native species to alter use of water (indirect evidence of competition) to minimize overlap with horses. We predicted that communities of wildlife would 1) be less species-rich and less diverse and 2) spend less time at HI water sources compared to HE water sources.

METHODS

Study area

We conducted this study on 631 km^2 of land managed by the United States Department of Defense, United States Army Dugway Proving Ground located in the Great Basin Desert of western Utah, USA. Valley terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats which were dominated by black greasewood (*Sarcobatus vermiculatus*). Along mountain foothills, big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), juniper (*Juniperus osteosperma*), and cheatgrass (*Bromus tectorum*) were common plants. Annual weather consisted of mean air temperatures of 12.3 °C (range: -20.0 to 40.6 °C) and mean precipitation of 146 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). Unlike typical neighboring land managed by the United States Department of the Interior, Bureau of Land Management, this study area had not been grazed by

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domestic livestock for more than 60 years allowing us to assess the influence of feral horses on wildlife communities at water sources without this potential confounding influence. Recent estimates of the horse population in and around our study area suggested herd size was 464 horses (Bureau of Land Management, 2012).

Sampling design & data collection

We monitored 12 HI water sources and 13 HE water sources during June 2010 through August 2011. Water sources included water developments targeted for wildlife (13), overflow ditches and ponds from water treatment facilities (2), and natural springs (10). The majority of water sources were generally small (mean surface area = 2.6 m^2) with the exception of the two overflow water sources (mean surface area = 1620 m^2). To exclude horses at water sources, but not native species, HE water sources were enclosed with a two-tier, barbless cable fence in the late 1990s (AGEISS Environmental, 1998). Different strategies have been used so that perimeter fencing surrounding water sources does not exclude native ungulates such as mule deer (*Odocoileus hemionus*) or pronghorn (*Antilocapra americana*) (Larsen et al., 2011). In our study area, perimeter fencing was ≥ 5 m from the water source, with the top cable 92 cm from the ground, the bottom cable 44 cm from the ground, and a 48 cm space in between both cables, allowing native ungulates ample space to crawl underneath or jump over the fencing and both native ungulates regularly occurred at HE water sources.

To sample species visitation to water sources, we used Reconyx PC900 covert infrared cameras (Reconyx, Inc., Holmen, Wisconsin) at all water sources. We mounted each camera to a metal post and positioned it 40 cm above ground level and approximately 3 m from the water source. Cameras were preset to detect motion and heat and were set to record an image at a

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minimum interval of 30 s. We checked cameras for proper function, battery status, and replaced memory cards every two weeks. We used Exifer v.2.1.5 (www.friedemann-schmidt.com/software/exifer) software to extract metadata (date and time stamps) from each image file. With date and time information for each image, we then sorted photos into species visits. We defined separate "visits" as consecutive images of a species separated by at least 30 minutes (Hall et al., 2013).

Water sources (and fences) were in place prior to our study (AGEISS Environmental, 1998), thus we did not have experimental control over location of water sources. This lack of experimental control created the potential for location and surrounding habitat features to influence species use of water sources and confound our results (Burger and Gochfeld, 1992; Larsen et al., 2007; Larsen et al., 2012). To address this limitation, we collected a suite of habitat variables associated with each water source. We measured vegetation and topographic characteristics up to 100 m around each water source. We estimated cover and density of shrubs with a Random T-Square sampling approach (Krebs, 1999). To measure vegetation height, we used a Robel pole (Robel et al., 1970) and recorded vegetation measurements at 10, 20, 50, 75, and 100 m intervals radiating away from the water source in all four cardinal directions. We also used ocular estimation to classify the area surrounding each water source with the two dominant types of vegetation present at each site. To further describe each water source, we used ArcGIS (ArcMap, version 10.2, Environmental Systems Research Institute, Redlands, California) to calculate slope, aspect, and ruggedness (Sappington et al., 2007) around water sources using a 10 m resolution digital elevation model.

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Data analyses

To address potential differences in wildlife community composition, we compared species richness and Simpson's indices of diversity for birds, mammals, and all species combined among treatments using *t*-tests. We also assessed similarity/dissimilarity of wildlife community composition across treatments (HI or HE) using Non-metric Multi-Dimensional Scaling (NMDS) on a Bray-Curtis similarity matrix (Bray and Curtis, 1957). We used ANOSIM to further support NMDS results and assess variation in community composition between treatment groups (Clarke, 1993). In addition, we used an NMDS analysis to determine if habitat characteristics were different between HE and HI sites. We then compared the number of visits/day (mean visits per site/number of days monitored), duration of visits (min; time from initial photo in a visit subtracted from the time of the last photo), and overall duration/day (min) of wildlife species at HI and HE water sources with *t*-tests. We also compared the amount of time (min/day) spent at all water sources for horses and all native species combined with a Mann-Whitney *U*-test. We performed statistical analyses using Program R and the community analysis package "vegan" (R Development Core Team, 2011; Oksanen et al., 2015). For series of statistical analyses, we used a Holm-Bonferroni correction to avoid type I errors (Holm, 1979; Gaetano, 2013). We set the family-wise alpha level for all significance tests at = 0.05.

RESULTS

We captured 96,601 images representing 53 species of vertebrates including 40 species of birds (29,396 images) and 13 species of mammals (67,205 images). Approximately 0.2% of images ($N = 198$) did not contain sufficient information to confidently identify species. Of the total 67,205 images of mammals, 79% (53,091) contained feral horses. Horses visited all 12

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water sources that did not have exclusionary fencing and were photographed outside fencing at all 13 HE water sources.

Species richness at HE water sources was greater than at HI water sources (Overall: t = 8.20, $P < 0.001$, $N = 25$, Figure 1-1a; birds: $t = 8.98$, $P < 0.001$, Figure 1-1b; mammals: $t = 3.91$, $P < 0.001$, Figure 1-1c). Similarly, species diversity was greater at HE water sources compared to HI water sources (Overall: $t = 3.41$, $P = 0.002$, $N = 25$, Figure 1-2a; birds: $t = 5.89$, $P < 0.001$, Figure 1-2b; mammals: $t = 2.60$, $P = 0.016$, Figure 1-2c). We detected a difference between wildlife community composition between treatment groups (HI and HE) with noticeable between-group compactness (Global $R = 0.77$, $P = 0.001$, Figure 1-3a). We did not, however, detect any differences between habitat characteristics that accounted for the differences we observed in wildlife community composition (Global $R < 0.001$, $P = 0.38$; Figure 1-3b).

Native wildlife visited HE water sources on average over three times more per day than HI water sources (Table 1-1). We did not, however, detect consistent differences in duration of native wildlife visits between HE and HI water sources, with exception of our “other birds” and “small mammals” taxonomic groups (Table 1-1). The overall time/day that native wildlife spent at HE water sources was nearly three times greater than at HI water sources; “raptors” were the only taxonomic group that did not significantly differ in time/day between HE and HI water sources (Table 1-1). On a daily basis, horses were present at water sources almost 10 times longer than all species of wildlife combined ($U = 0.00$, $P < 0.001$, $N = 25$, Figure 1-4).

DISCUSSION

Exotic feral species can disrupt the stability of biotic communities by altering how limited, communal resources are partitioned by multiple species. Our study illustrated that

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horses displaced native species from access to water in a semi-arid environment. Native species tended to avoid times when horses were present at water sources, providing some indirect evidence for interference competition, similar to what has been observed for interactions between bighorns (*Ovis canadensis*) and feral horses (Ostermann-Kelm et al., 2008). We only detected a few instances where native species and horses simultaneously occurring at the same water source. This observation could result from one or several of the following reasons: 1) large body size can confer a competitive advantage (Berger, 1977; Robertson, 1998; Palomares and Caro, 1999), 2) frequent physical intraspecific disputes among horses may deter other species from approaching (Berger, 1977; Stevens, 1988), and 3) the sheer number of horses occupying nearly all of the available space for drinking.

Competition from a large dominant species may drive niche partitioning of other species (Carothers and Jaksić, 1984; Ziv et al., 1993; Schuette et al., 2013). For example, small African herbivores avoided visiting water sources during peak times of visitation by the larger African elephant (Valeix et al., 2007). Likewise in our study, native species avoided water sources occupied by horses. Generally, niche partitioning enables two (or more) competing species to share resources while minimizing potentially costly interspecific interactions (Case and Gilpin, 1974; Schoener, 1974). However, during times of greatest physiological stress (increased temperature, decreased precipitation), horses monopolized access to water sources where they were present up to 73% of the day, leaving limited time for other species. The potential for a feral species, such as the horse, to outcompete native species for a limited communal resource during peak need raises concern for native communities in water-limited environments.

The availability of a limited resource can dictate the competitive environment between species (Dolman, 1995; Hasui et al., 2009). Though elephants have been implicated in altering

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the temporal niche of other herbivores (Valeix et al., 2007), these subordinate herbivores did not avoid waterholes used by elephants (Valeix et al., 2009). The discrepancy between what was observed in Zimbabwe, Africa and what we observed is likely due to at least two factors. First, communities of African wildlife have evolved in the presence of elephants and therefore have likely adapted strategies of minimizing potential conflict. Second, the size (diameter) of water sources in Zimbabwe was on average 14 times larger than the water sources in our study area. Large water sources provide greater availability of shoreline edge where animals can access water, likely minimizing interspecific competition. The relatively small water sources in our study area could accommodate one to a few horses at a time, leaving little to no space for other species to drink. Moreover, the species of wildlife in our study have co-occurred with feral horses for a relatively short time and likely have not completely adapted to the presence of a large, gregarious mammal with high water demand (Groenendyk et al., 1988).

Our results have implications for the conservation of water sources in arid and semi-arid regions. Recent projections of climate change in desert regions, particularly western North America, predict increased temperatures and decreased precipitation (Seager et al., 2007; Mamtimin et al., 2011; Ault et al., 2014; Borsa et al., 2014; Cook et al., 2015). Furthermore, ever increasing anthropogenic use of water and modification of arid landscapes has caused dramatic reductions of water availability which is only predicted to increase in the future (Barnett et al., 2008; Bruins et al., 2012). Increased aridity and reduced availability of water in already water-limited landscapes may magnify the competitive pressures that large feral species have on smaller native species at water sources.

In addition to the effects we observed, horses may also indirectly alter the quality of water and habitat for native species. At unfenced water sources, disturbance to water and

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trampling of the immediate habitat surrounding water sources was prevalent, corroborating other work (Turner, 1987; Stevens, 1988; Davies et al., 2014). Furthermore, some of our photos depicted horses urinating and defecating either in or adjacent to water sources and we commonly found dung piles near water sources. The addition of bodily waste from horses to water sources could also have contributed to the lack of use by wildlife compared to water sources where horses were excluded. There may also be bottom-up effects for aquatic ecosystems due to mechanical (trampling, grazing) and chemical alteration by horses (Levin et al., 2002; Beever and Herrick, 2006; Loydi and Zalba, 2009).

We provide novel information concerning the influence of the feral horse on community use of water by native wildlife in a semi-arid environment. We recognize that our study was observational in nature and that we cannot infer causality. Additional efforts, such as monitoring survival, productivity, and recruitment by native species, are needed to determine if horses exert a biological relevant impact via competition for water. Despite these shortcomings, however, our study is the first to provide a community-level perspective regarding temporal and spatial use of water by native species in the presence of horses. We found strong differences between water use patterns and communities of wildlife at fenced (horses excluded) and unfenced water sources. At water sources where horses had access, wildlife spent less time and communities were less species-rich and less diverse compared to water sources where horses were excluded. Our results indicate that horses displaced other species at water sources providing evidence of a negative influence on how communities of native wildlife access a limiting resource.

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Table 1-1. Mean temporal metrics (±SE) of all species of native wildlife (separated into taxonomic groups) at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

	Visits/day			Minutes/visit			Minutes/day		
Group	HE	HI	*p*	HE	HI	*p*	HE	HI	*p*
All wildlife	7.29 ±0.27	2.67 ±0.12	< 0.001*	1.94 ±0.09	1.67 ±0.06	0.175	14.30 ±1.09	4.45 ±0.27	< 0.001*
Birds	4.92 ±0.24	1.68 ±0.07	< 0.001*	1.75 ±0.12	1.31 ±0.15	0.175	8.77 ±0.81	2.23 ±0.28	< 0.001*
Passerines	2.69 ±0.23	1.31 ±0.04	< 0.001*	1.28 ±0.12	0.90 ±0.12	0.180	3.61 ±0.61	1.17 ±0.15	0.001*
Raptors	0.11 ±0.02	0.03 ±0.02	0.028*	2.17 ±0.33	1.47 ±0.24	0.224	0.27 ±0.07	0.09 ±0.06	0.064
Other birds[a]	2.05 ±0.13	0.34 ±0.02	< 0.001*	1.95 ±0.18	1.07 ±0.18	0.016*	4.23 ±0.59	0.37 ±0.06	< 0.001*
Mammals	2.37 ±0.17	0.99 ±0.09	< 0.001*	2.50 ±0.12	2.11 ±0.13	0.180	6.08 ±0.65	2.15 ±0.26	< 0.001*
Ungulates	1.76 ±0.17	0.87 ±0.08	< 0.001*	3.02 ±0.17	2.86 ±0.19	0.551	5.34 ±0.62	2.57 ±0.36	0.004*
Carnivores	0.47 ±0.07	0.08 ±0.01	< 0.001*	1.20 ±0.09	0.63 ±0.05	< 0.001*	0.58 ±0.11	0.05 ±0.01	< 0.001*
Sm. Mammals	0.14 ±0.03	0.04 ±0.01	0.002*	1.24 ±0.25	0.66 ±0.06	0.118	0.22 ±0.08	0.03 ±0.01	0.031*

*Denotes significance at $p < 0.05$.

[a] Other birds included mourning dove (*Zenaida macroura*), chukar (*Alectoris chukar*), northern flicker (*Colaptes auratus*), common poorwill (*Phalaenoptilus nuttallii*), American coot (*Fulica americana*), killdeer (*Charadrius vociferus*), spotted sandpiper (*Actitis macularius*), and white-faced ibis (*Plegadis chihi*).

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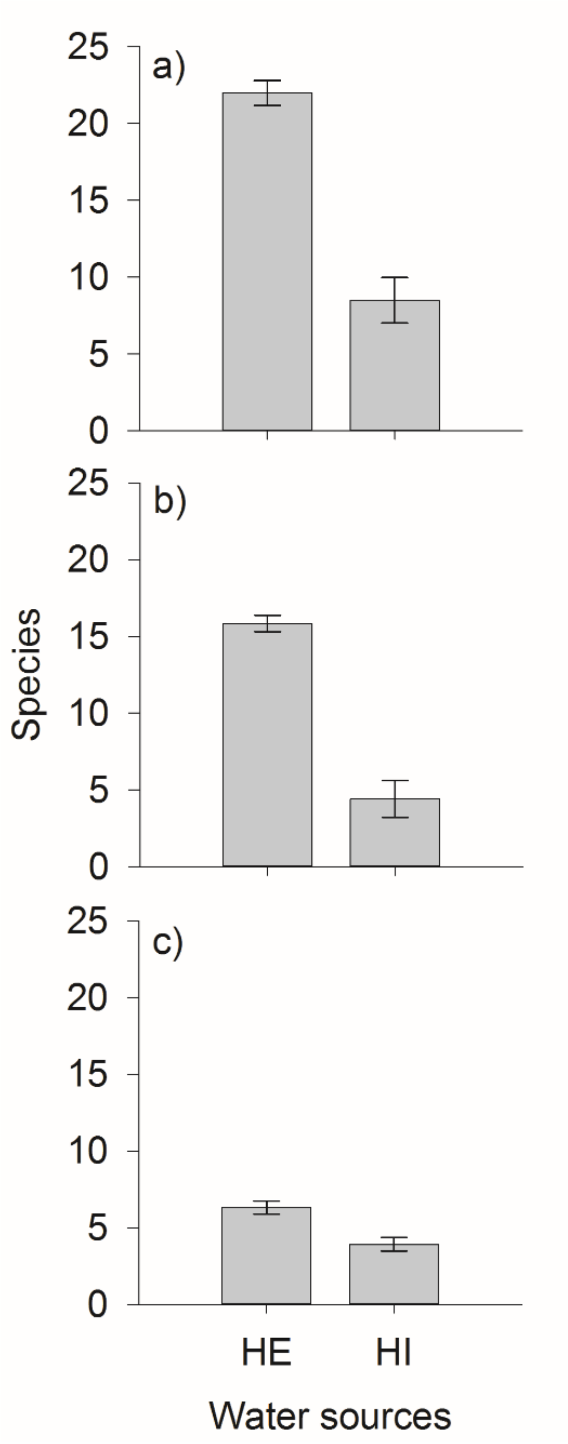

Figure 1-1. Mean (±SE) species richness of a) all species, b) birds, and c) mammals that appeared in images captured by remote cameras at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

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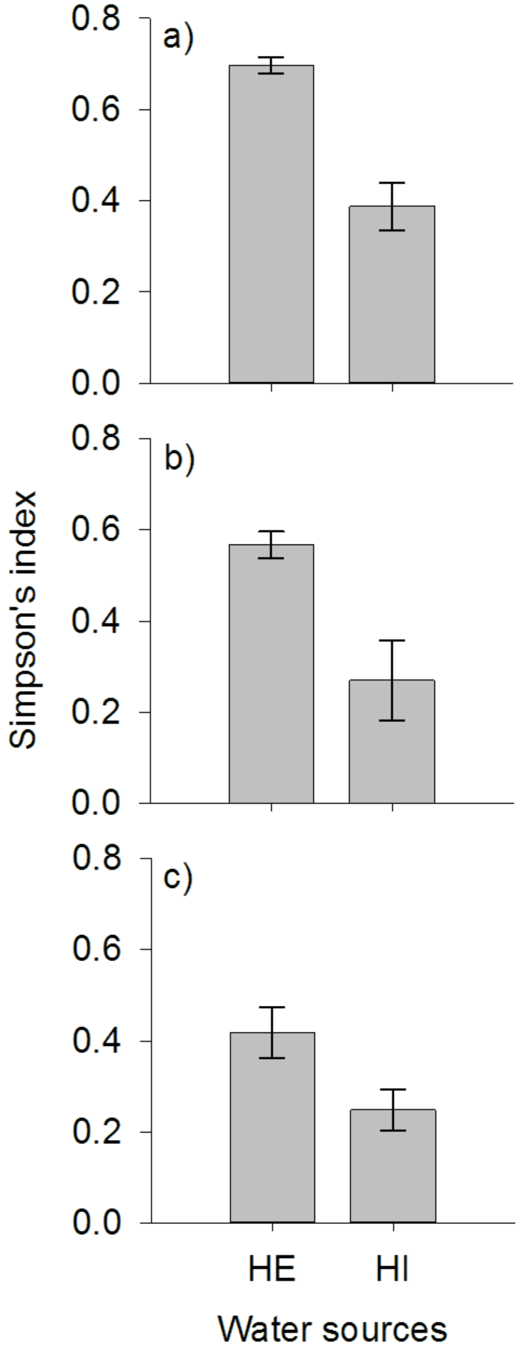

Figure 1-2. Mean (±SE) Simpson's diversity of a) all species, b) birds, and c) mammals that appeared in images captured by remote cameras at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

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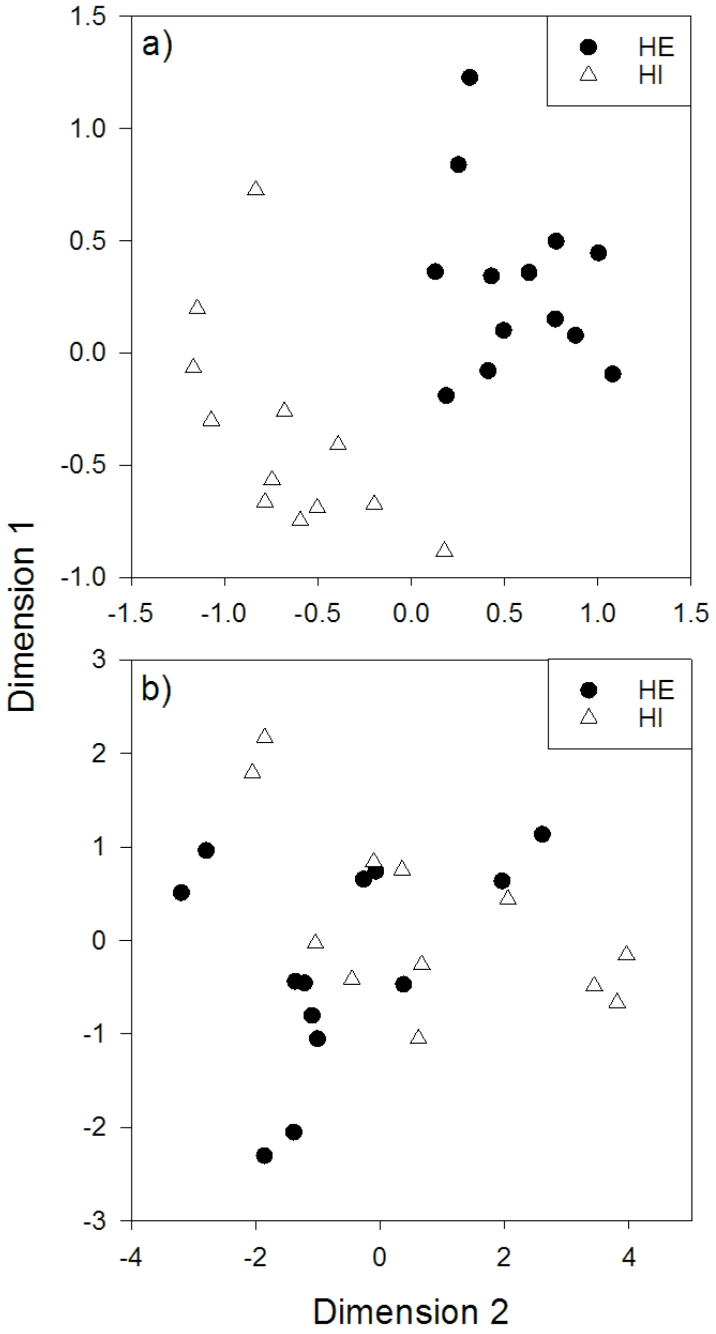

Figure 1-3. Non-metric Multi-Dimensional Scaling (NMDS) ordination map of similarity/dissimilarity for species composition of wildlife communities (panel a) and habitat characteristics (panel b) at water sources in the Great Basin Desert, Utah (USA) where horses (*Equus caballus*) were excluded (HE) and where horses accessed water (HI).

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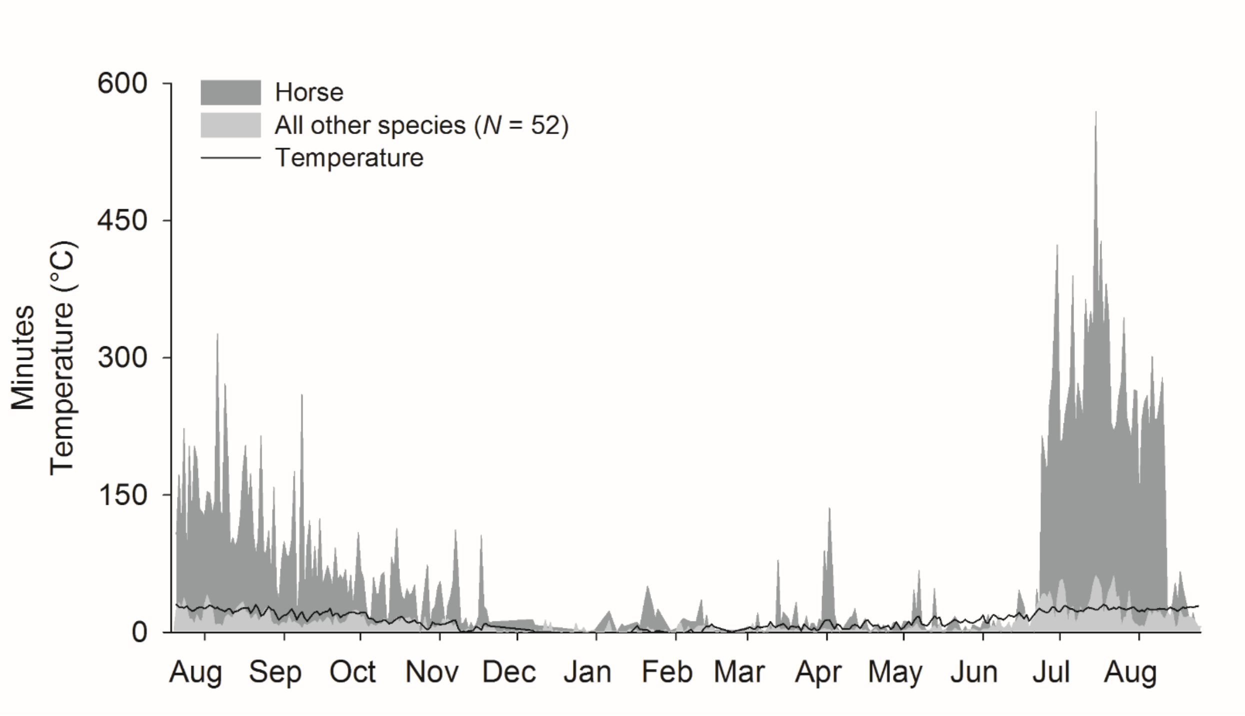

Figure 1-4. Mean duration of time (min/day) spent at water sources by all species of native wildlife compared to that of horses (*Equus caballus*) in the Great Basin Desert, Utah (USA). Diel activity at water sources is presented in relation to mean air temperature and month.

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CHAPTER 2

DO FERAL HORSES COMPETE WITH NATIVE UNGULATES FOR ACCESS TO WATER IN A SEMI-ARID ENVIRONMENT?

ABSTRACT

The horse (*Equus caballus*) is a feral ungulate that currently exceeds target population sizes in many areas of western North America. Anecdotal and unpublished observations suggest that horses are behaviorally dominant over native ungulates and may outcompete the latter for access to water sources. However, we lack empirical data substantiating this claim. Our objective was to determine if horses competed with pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) for access to water sources in a semi-arid environment. If competition was occurring, we expected pronghorn to visit water sources less-frequented by horses or visit when horses were less active. Because mule deer are primarily crepuscular and nocturnal whereas horses are diurnal, we did not expect a difference in visitation patterns by mule deer in response to horse activity. From 2010-2014, we used remote cameras to monitor ungulates at 32 water sources in the Great Basin Desert. We evaluated spatial and temporal partitioning of water sources using generalized linear models and Mann-Whitney *U*-tests. We found that both native ungulates used water sources less often where horse activity was high (β estimate associated with numbers of horse visits in pronghorn models = -1.41, 95% CI = -2.49 to -0.32; β estimate associated with number of horse visits in mule deer models = -1.06, 95% CI = -1.97 to -0.23), indicating that spatial partitioning occurred. Further, we observed significant differences in peak arrival time for pronghorn (p = 0.04), but not mule deer (p = 0.95) at horse-occupied sites versus sites where horses were absent or uncommon indicating that temporal partitioning may be more important for pronghorn than mule deer. Our study provides evidence that horses competed with

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native ungulates as they spatially displaced both pronghorn and mule deer and temporally displaced pronghorn from water sources.

INTRODUCTION

Exotic species can influence ecosystems in a variety of ways. In some cases, exotic species can alter and degrade habitats as well as compete with or even displace native species (Bradley 2010, Dorcas 2012, Porter et al. 2014). In these situations, managers often attempt to minimize impacts of exotic species. However, attempts to control exotic species or offset their effects are often confronted with economical and biological challenges (Pimentel et al. 2005, Preston et al. 2012). Control efforts for exotic species that have been domesticated (and later become feral through intentional and/or unintentional release) may involve an additional societal challenge due to the emotional ties that humans have with these species. Consequently, managing domesticated feral species can be met with public debate and criticism (Symanski 1996, Linklater et al. 2002). Because public opinion and sentiment can take priority over conservation needs for ecosystems, the ability to mitigate the potential negative effects of exotic feral species can be compromised (Linklater et al. 2002, Bies et al. 2011).

The horse (*Equus caballus*) is a domesticated feral ungulate that was introduced to North America during the 16th century (Mills and McDonnell 2005). Since its introduction, the horse has become widespread in western North America. Numbers of horses currently exceed recommended management levels in most herd units and can increase by 15 to 20% per year (Palmer et al. 2013). However, because horses are federally protected and are commonly perceived as an iconic species of the American West, management options are limited, costly, and controversial (Linklater et al. 2002, Taggart 2008, Bies et al. 2011, Garrott and Oli 2013).

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Despite efforts to manage populations of horses, current practices and methodologies appear inadequate to achieve target population sizes in much of western North America (Palmer et al. 2013).

Increased numbers of horses are associated with impacts to arid and semi-arid landscapes and some of the species inhabiting these environments (Beever 2003, Beever and Aldridge 2011, Davies et al. 2014, Hall et al. 2016). Horses can modify habitat features such as soil and vegetation via trampling, excessive nutrient deposition, and overgrazing (Loydi and Zalba 2009, de Villalobos et al. 2011, Parvage et al. 2011). Horse-related shifts in soil and vegetation are linked to altered community composition of fossorial invertebrates and small vertebrates (Beever and Brussard 2004, Beever and Herrick 2006). Increased grazing by horses can result in higher rates of predation for these species by removing vegetative cover used for concealment (Levin et al. 2002, Zalba and Cozzani 2004). While evidence suggests that horses can influence habitat components and relatively small animals, there is little information on how or if larger species (e.g., native ungulates) respond to the presence of horses. Because desert environments are generally resource-low areas, increased numbers of horses may influence resource acquisition by native ungulates (Ostermann-Kelm et al. 2008).

Water is a limiting resource for horses and native ungulates such as pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). Horses have a relatively high water demand (up to 33 L/day; Groenendyk et al. 1988). During periods of water stress, horses increase visitation rates and duration of visits, and can spend the majority (73%) of the day at water sources (Miller 1983, Stevens 1988, Hall et al. 2016). Pronghorn and mule deer drink less water, less frequently than horses (pronghorn up to 3.4 L/day, mule deer up to 6 L/day; Hazam and Krausman 1988, Fox et al. 2000), but still depend on water in periods of water stress,

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particularly during lactation in the summer months (Bowyer 1984, Clemente et al. 1995, Boroski and Mossman 1996, Fox et al. 2000, McKee et al. 2015). However, water is often least available in deserts during these physiologically demanding times. Reduced availability of an already limited resource could heighten competitive interactions between horses and these native ungulates.

Our objective was to determine if horses compete with pronghorn and mule deer for water in the semi-arid Great Basin. Previous work suggests that horses are dominant over native ungulates (Berger 1985, Ostermann-Kelm et al. 2008), however whether they can outcompete pronghorn and mule deer for water is only supported by anecdotal observations and unpublished findings (Miller 1983, Gooch 2014). Observing direct competitive interactions between species can be challenging and time consuming due to rarity of occurrence; therefore we relied on indirect evidence of competition (spatial and temporal partitioning) to determine if competition between these species occurred. If horses are dominant and compete with pronghorn, we would predict pronghorn to avoid water sources frequented by horses (spatial partitioning; Ostermann-Kelm et al. 2008) or alter arrival times to water sources to minimize competition with horses (temporal partitioning; Valeix et al. 2007). Because mule deer are primarily crepuscular and nocturnal whereas horses are diurnal, we did not predict a difference in visitation to water by mule deer in response to horse presence.

METHODS

Study area

We conducted this study in the Great Basin Desert of western Utah, USA (Figure 2-1). Our study area consisted of 1,200 km^2 of land managed by the U.S. Department of Defense, U.S.

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Army Dugway Proving Ground and the U.S. Department of the Interior, Bureau of Land Management. Elevations across the study area ranged from 1300 to 1850 m. The terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats that were dominated by black greasewood (*Sarcobatus vermiculatus*). Along the foothills, invasive annual grasslands (*Bromus tectorum*) were commonly mixed with desert shrubs (*Chrysothamnus* spp.), big sagebrush (*Artemisia* spp.), and juniper (*Juniperus osteosperma*), transitioning to pinyon (*Pinus edulis*)-juniper woodlands at higher elevations. Annual weather consisted of mean air temperatures of 13.6° C and mean precipitation of 160 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center).

Data collection

We used infrared-triggered cameras (Reconyx PC900 Hyperfire, Holmen, WI) to monitor ungulate activity at 32 water sources in our study area (Figure 2-1). These water sources consisted of 9 water developments for wildlife (i.e., guzzlers), 8 livestock troughs, 11 natural springs/seeps, and 4 ponds. We secured cameras to metal posts and placed them approximately 3 m from the edge of water where animals accessed water for drinking. At water sources with multiple locations of drinking access (e.g., paired tanks of water, ponds), we placed cameras at a minimum of two locations where animals could drink. We considered proximity to trails and recent sign to determine the location of cameras at larger ponds or springs. We checked the battery status, changed memory cards, and performed any necessary maintenance to cameras approximately every two weeks. Cameras were set to trigger on both motion and heat following which they recorded an image every 30 seconds. We monitored 16 water sources from June to October 2010 to 2014 and monitored an additional 16 water sources (for a total of 32 water

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sources) from June to October 2013 to 2014. This seasonal window captured periods of increased temperatures and decreased precipitation where visitation rates to water by ungulates were greatest (Shields et al. 2012).

To determine relative patterns of visitation by ungulates, we first summarized the images of ungulate species captured by remote cameras. We extracted the time and date associated with each camera image. With date and time information, we then sorted camera images into species visits. Due to the difficulty of identifying individuals (particularly females and juveniles), we followed the methodology of previous research using remote cameras to monitor wildlife and defined independent visits as consecutive images of a species separated by at least 30 minutes (Michalski and Peres 2007, Day et al. 2016, Hall et al. 2016).

To account for the potential influence of site characteristics on the use of water by wildlife (Larsen et al. 2012, Hall et al. 2013), we measured vegetative and topographical characteristics within a 1,785 m radius around each water source (Larsen et al. 2011). We selected a 1,785 m radius based on summer home range sizes and daily distances travelled for pronghorn and mule deer (Gregg 1955, Kitchen 1974, Yoakum 1978, Hoskinson and Tester 1980, Garrott et al. 1987, Hayes and Krausman 1993, O'Gara and Yoakum 2004). We used tree cover and topographical ruggedness (terrain roughness) as our primary habitat variables to follow what has been done with pronghorn and mule deer at water sources in the Great Basin Desert (Larsen et al. 2011). We derived tree cover using vegetative cover types available in LANDFIRE (2013). We defined tree cover as the proportion of pixels within a 1,785 m radius around water sources containing vegetation dominated by trees (Larsen et al. 2011). Using ArcGIS (ArcMap, version 10.3, Environmental Systems Research Institute, Redlands, CA), we calculated ruggedness within the 1,785 m radius buffer around water sources using a 30 m

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resolution digital elevation model. We set the ruggedness neighborhood to a 3 x 3 cell size to follow the methods of Sappington et al. (2007).

Statistical analyses

We employed a two-stage modelling approach to determine if spatial partitioning occurred between horses and native ungulates. In the first stage, we identified the most appropriate statistical distribution (Gaussian, Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial) for visitation rates (counts) of mule deer and pronghorn (Larsen et al. 2011). Count data for wildlife at water sources can often result in atypical distributions that do not meet the assumptions of normality for standard linear models. These data are not easily normalized via transformations sometimes due to the presence of large numbers of zero counts (where no target species were detected). Within the last two decades, however, statistical distributions designed to handle non-normal data with large numbers of zeros have been developed and used in ecological modelling. To determine the best distribution for ungulate data we used model selection and AIC scores to evaluate the relative performance of a simple model (ungulate visits as a function of elapsed sampling time (number of camera days)) with each of the distributions.

In the second stage, we created two sets of models to measure any influence that horses may have on water source use by native ungulates (Larsen et al. 2011). One model of each set contained an environmental covariate such as mean daily temperature (°C), mean precipitation (cm), tree cover, or ruggedness. The other model of each set was identical to the first but differed in that we included horse activity (number of pictures of horses at a water source) as an additional parameter. We included the elapsed sampling time in each model to account for

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differences in sampling time across water sources. We limited our models to no more than three variables considering our overall sample size of water sources was rather modest (n = 32) and the general rules of thumb regarding model selection and linear models (Burnham and Anderson 2002). Prior to model selection, we conducted correlation analyses with all variables. In the case where variables were highly correlated ($|r|$ value greater than 0.6), we retained the variable that had a lesser AIC_c score and provided more model support. Using AIC_c values and model weights (w_i), we ranked competing models (Burnham and Anderson 2002). We considered models to be competing if they were within 2 ΔAIC_c of each other (Burnham and Anderson 2002). We then evaluated both the log likelihood and AIC_c values associated with top models to identify any models with uninformative parameters. We judged parameters as uninformative when competing models differed from the top model by a single parameter and little to no improvement in log likelihood was evident (Burnham and Anderson 2002, Anderson 2008, Arnold 2010). This model comparison coupled with the β estimates allowed us to evaluate the relative influence of horses on the visitation of ungulates after accounting for environmental influences.

The second component of our objective was to determine if native ungulates experienced temporal shifts or altered time usage (Valeix et al. 2007) at water sources due to high activity of horses. To achieve this objective, we identified hour of peak arrival for pronghorn and mule deer at each water source. We then compared hour of peak arrival for native ungulates at water sources where horses were common and absent or rare using Mann-Whitney U-tests. We considered water sources as “horse common” if horses visited more than once per day. This categorization occurred at a natural break in horse activity and resulted in 17 water sources that were “horse common” and 15 that were “horse absent or rare”. On average, activity of horses

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was 16.5 times greater at “horse common” water sources compared to “horse absent or rare” water sources. We performed all analyses using Program R (R Development Core Team 2014). We set the level of significance for all statistical tests at $\alpha = 0.05$.

RESULTS

From 2010 to 2014 we accrued a total of 69,271 pictures of pronghorn and mule deer in 27,700 camera days. Of these pictures, there were 7,465 visits of pronghorn and 7,363 visits of mule deer. Horses accounted for an additional 780,452 pictures resulting in 92% of all ungulate pictures at water sources. All three ungulates occurred at the majority of water sources that we sampled. Pronghorn visited 26 of the 32 water sources (81%), mule deer visited 29 water sources (91%), and horses visited 23 water sources (72%).

From stage one of our modelling, we determined that a zero-inflated negative binomial distribution best fit the pronghorn data. This distribution had a better AIC score (381) than negative binomial (386), Gaussian (462), zero-inflated Poisson (8355), and Poisson (11423). A negative binomial distribution best fit the mule deer data. The AIC score of the negative binomial distribution (393) was lower than zero-inflated negative binomial (396), Gaussian (472), zero-inflated Poisson (11648), and Poisson (13076) distributions.

In stage two we found that in nearly all analyses, the model that contained horse activity was best supported by the data. In fact, models with the horse activity covariate comprised 92% of model weight for pronghorn and 76% of model weight for mule deer. The top model for pronghorn showed that tree cover and horse activity were the most influential covariates. This top model for pronghorn improved the AIC_c score by 3.38 (Table 2-1). The model with ruggedness and horse activity was the best model explaining variation in visitation to water for

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mule deer. The top model for mule deer outcompeted the next best model by 3.24 ΔAIC_c points (Table 2-2). Based on results from the top models, horse activity was negatively correlated with visitation to water by both pronghorn (β = -1.41, 95% CI = -2.49 to -0.32; Table 2-3) and mule deer (β = -1.06, 95% CI = -1.97 to -0.23; Table 2-4).

Native ungulates exhibited relatively distinct patterns of temporal activity at water sources whereas horses were active throughout day, but most active during diurnal hours (Figure 2-2). Horse activity did not appear to influence arrival times to water by pronghorn and mule deer in the same fashion. At water sources where horses were common, pronghorn exhibited differences in arrival times compared to water sources where horses were absent or rare (U = 81.00, p = 0.04; Figure 2-3). There was also a greater amount of variation in arrival times for pronghorn where horses were common (Figure 2-3). Alternatively, there were no differences in arrival time to water for mule deer regardless of horse activity (U = 159.00, p = 0.95; Figure 2-4).

DISCUSSION

Our study demonstrated that feral horses competed with native ungulates for a limited resource. As such, these data provide robust support of previous suggestions (Miller 1983, Ostermann-Kelm et al. 2008, Gooch 2014). We observed resource partitioning (indirect evidence of competition) between horses and native ungulates. Specifically, we found evidence for spatial partitioning as pronghorn and mule deer avoided water sources more heavily used by horses. We also observed temporal shifts in water use by pronghorn in response to increased activity of horses. However, we did not detect temporal shifts for mule deer in response to horse activity, likely due to horses being primarily diurnal, suggesting horses may impact pronghorn more than mule deer.

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Large competitive herbivores can drive patterns of water use by smaller, less competitive species (Valeix et al. 2007, Valeix et al. 2008, Hall et al. 2016). For example, relatively small African herbivores generally avoided times of peak visitation to waterholes by elephants (Valeix et al. 2007). Desert bighorn sheep (*Ovis canadensis*) exhibited a similar pattern using alternative water sources when a horse was a present at a regularly used water source (Ostermann-Kelm et al. 2008). Similarly, Nubian ibex (*Capra nubiana*) avoided water sources that had been recently used by feral donkeys (*E. africanus asinus*) in northern Africa (Attum et al. 2009). In each of these examples larger, dominant herbivores competed with smaller herbivores for water over space and time. Moreover, the latter two studies highlight how a feral equid can influence patterns of resource acquisition by smaller native species (Ostermann-Kelm et al. 2008, Attum et al. 2009).

Competing for limiting resources can result in trade-offs for the species involved. In arid and semi-arid regions, many species face a trade-off associated with accessing limited water resources and minimizing conflict with more competitive species (Atwood et al. 2011, Edwards et al. 2015). In our study system, there may be fitness costs associated with the trade-off of directly competing with horses versus using different water sources or allocating use at different times, when horses are absent. Prior work conducted in the Great Basin Desert on use of water by horses and pronghorn found the latter devoted more time to vigilance behavior and foraged and drank less in the presence of horses (Gooch 2014). While the long-term implications of this behavioral modification are largely unknown and may be negligible, our work supports previous research indicating that horses can alter drinking patterns of pronghorn (Gooch 2014).

Given the influence of climatic variables on use of water by mule deer and pronghorn, our study raises conservation concerns. With models of global climate change predicting

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increased desertification in many arid and semi-arid regions, water will likely become less available for species (including humans) inhabiting these areas (Ault et al. 2014, Cook et al. 2014, Wanders et al. 2015). While reduction in water availability is not a novel concept for desert species, the rapid loss of water in these systems (due to contemporary climate change) will likely pose new challenges for desert biota. Water already serves as a major selective force in warm and dry environments (Noy-Meir 1973). Further loss of water from the environment combined with competition with increasing populations of feral species will likely create additional conservation and management issues for native species.

Our study provides a multi-year perspective on how a behaviorally dominant, feral species such as the horse can compete with native species for a limited resource. While we did not experimentally manipulate the density of horses to identify a causal relationship for the patterns that we observed, we did take advantage of differences in horse activity across water sources. We also camera-sampled multiple water sources over multiple years providing both spatial and temporal context to our findings. We provide evidence that horses competed with native ungulates and spatially displaced both pronghorn and mule deer. Our study suggested that horses also temporally displaced pronghorn, but not mule deer from water sources. Our findings indicated that feral horses further constrained access to an already limited resource for native species in a semi-arid environment.

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Table 2-1. Model selection results for visits to water sources of pronghorn (*Antilocapra americana*) using a zero-inflated negative binomial distribution. Data were collected in the Great Basin Desert of western Utah, USA from June to October 2010 to 2014.

Model[a]	K[b]	AIC$_c$[c]	ΔAIC$_c$[d]	w_i[e]	LL[f]
EST + Trees + Horse	8	438.72	0.00	0.75	-207.20
EST + Rugged + Horse	8	442.09	3.38	0.14	-208.90
EST + Trees	7	443.81	5.09	0.06	-212.60
EST + Horse	7	445.18	6.47	0.03	-213.30
EST + Rugged	7	447.63	8.91	0.01	-214.50
EST	5	448.95	10.23	0.00	-219.80
EST + Temp	7	449.29	10.58	0.00	-215.30
EST + Precip + Horse	8	450.41	11.70	0.00	-213.10
EST + Temp + Horse	8	450.47	11.75	0.00	-213.10
EST + Precip	7	451.17	12.45	0.00	-216.30

[a] EST, elapsed sampling time; Trees, proportion of pixels identified as trees within 1,785 m of each water source (representing home range tree cover); Horse, activity (# of pictures) of horses; Rugged, ruggedness metric calculated within 1,785 m of each water source using a 30 m resolution digital elevation model; Temp, mean daily temperature over sample period; Precip, mean precipitation over sample period.
[b] Number of parameters.
[c] Akaike's Information Criterion corrected for small samples.
[d] Change in AIC$_c$ value compared to top model.
[e] AIC$_c$ weight.
[f] Model log-likelihood.

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Table 2-2. Model selection results for visits to water sources by mule deer (*Odocoileus hemionus*) using a negative binomial distribution. Data were collected in the Great Basin Desert in western Utah, USA from June to October 2010 to 2014.

Model[a]	K[b]	AIC$_c$[c]	ΔAIC$_c$[d]	w_i[e]	LL[f]
EST + Rugged + Horse	4	374.92	0.00	0.61	-181.72
EST + Rugged	3	378.16	3.24	0.12	-184.65
EST + Trees + Horse	4	378.64	3.72	0.09	-183.68
EST + Trees	3	378.82	3.90	0.09	-184.98
EST + Horse	3	380.85	5.93	0.03	-186.00
EST	2	381.69	6.77	0.02	-187.64
EST + Precip + Horse	4	382.25	7.33	0.02	-185.39
EST + Temp + Horse	4	383.47	8.55	0.01	-185.99
EST + Temp	3	383.72	8.80	0.01	-187.43
EST + Precip	3	383.92	9.00	0.01	-187.53

[a] EST, elapsed sampling time; Trees, proportion of pixels identified as trees within 1,785 m of each water source (representing home range tree cover); Horse, activity (# of pictures) of horses; Rugged, ruggedness metric calculated within 1,785 m of each water source using a 30 m resolution digital elevation model; Temp, mean daily temperature over sample period; Precip, mean precipitation over sample period.

[b] Numbers of parameters.

[c] Akaike's Information Criterion corrected for small samples.

[d] Change in AIC$_c$ value compared to top model.

[e] AICc$_c$ weight.

[f] Model log-likelihood.

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Table 2-3. Coefficients, associated p-values, and 95% confidence intervals from the top (zero-inflated negative binomial) model for pronghorn (*Antilocapra americana*) visits to water sources. Data were collected in the Great Basin Desert in western Utah, USA from June to October 2010 to 2014.

Coefficient	Estimate	SE	*z*	*p*	Lower 95%	Upper 95%
Count						
Intercept	6.56	0.62	10.61	<0.01	5.35	7.77
EST[a]	0.002	0.0007	3.10	0.002	0.0008	0.003
Trees[b]	4.02	3.38	1.19	0.23	-2.61	10.65
Horse[c]	-1.41	0.55	-2.55	0.01	-2.49	-0.32
Log(theta)	-0.27	0.28	-0.96	0.34	-	-
Zero-inflation						
Intercept	-2.47	1.76	-1.40	0.16	-5.92	0.99
EST	0.002	0.002	0.72	0.47	-0.003	0.006
Trees	14.53	7.27	2.00	0.05	0.29	28.77
Horse	-2.74	1.92	-1.43	0.15	-6.50	1.02

[a] Elapsed sampling time.

[b] Home range tree cover, defined as the proportion of pixels within a 1,785 m radius around water sources containing vegetation dominated by trees

[c] Activity (# of pictures) of horses.

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Table 2-4. Coefficients, associated p-values, and 95% confidence intervals from the top (negative binomial) model for mule deer (*Odocoileus hemionus*) visitation to water sources. Data were collected in the Great Basin Desert of western Utah, USA from June to October 2010 to 2014.

Coefficient	Estimate		*z*	*p*	Lower 95%	Upper 95%
Intercept	3.26	0.50	6.51	<0.01	2.15	4.41
EST[a]	0.003	0.0005	5.58	<0.01	0.002	0.004
Rugged[b]	166.79	54.03	3.09	0.002	59.98	283.64
Horse[c]	-1.06	0.43	-2.47	0.01	-1.97	-0.23

[a] Elapsed sampling time.

[b] Home range tree cover, defined as the proportion of pixels within a 1,785 m radius around water sources containing vegetation dominated by trees.

[c] Activity (# of pictures) of horses.

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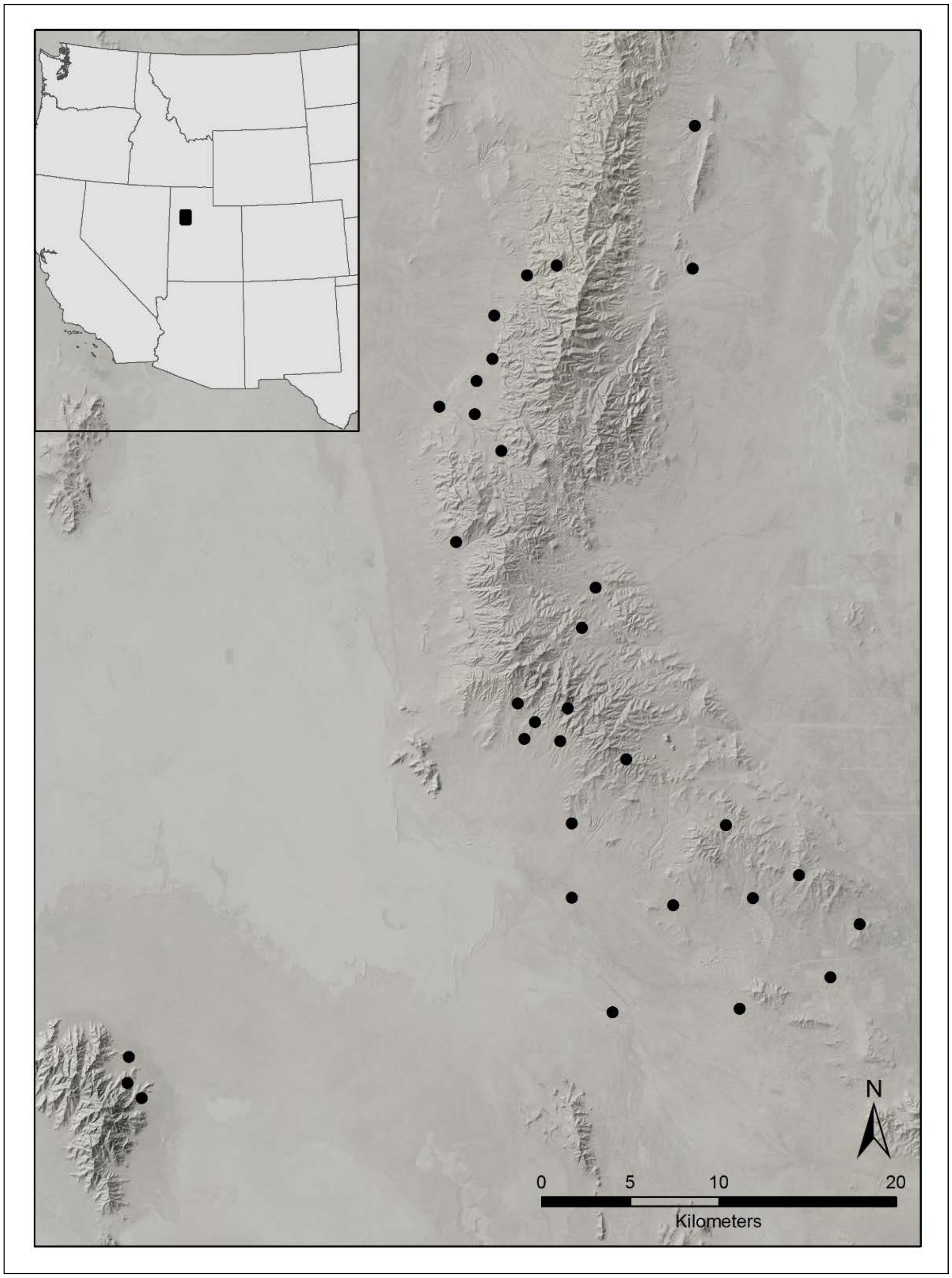

Figure 2-1. Distribution of water sources that were monitored with remote cameras for pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and horses (*Equus caballus*) in the Great Basin Desert of western Utah, USA from June to October 2010 to 2014.

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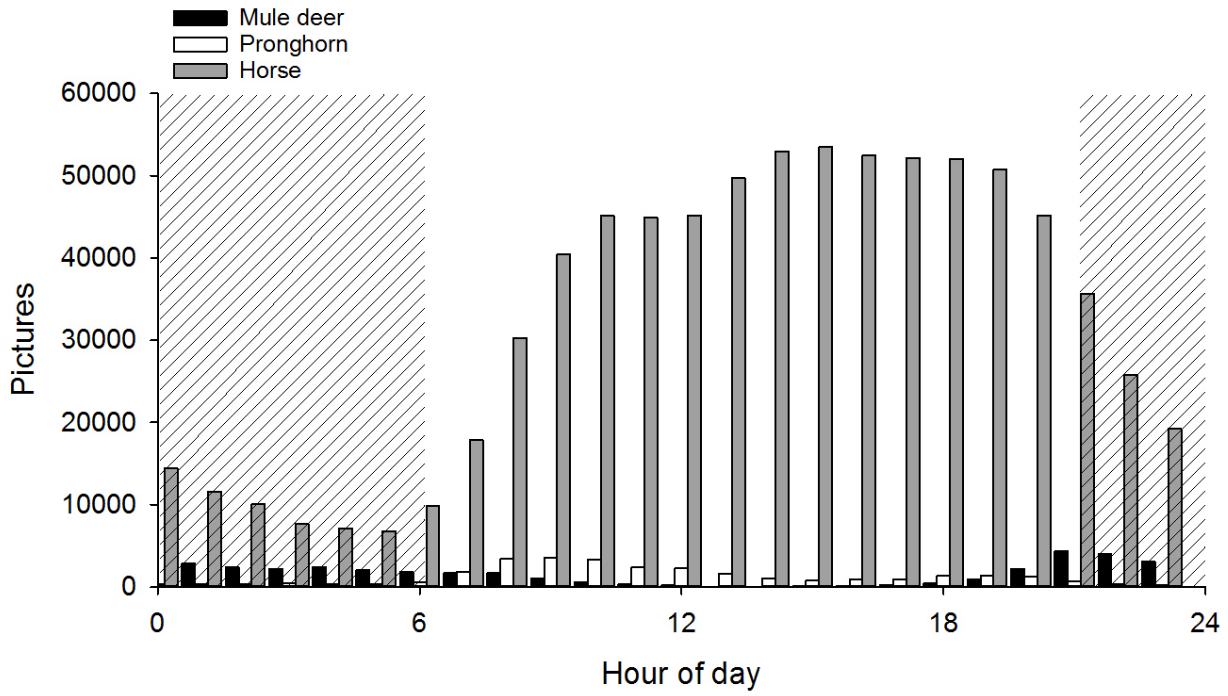

Figure 2-2. Temporal activity (number of pictures from remote cameras by hour of day) of pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and horses (*Equus caballus*) at water sources in the Great Basin Desert of western Utah, USA from June to October 2010 to 2014. Hatched (shaded) regions depict nocturnal hours.

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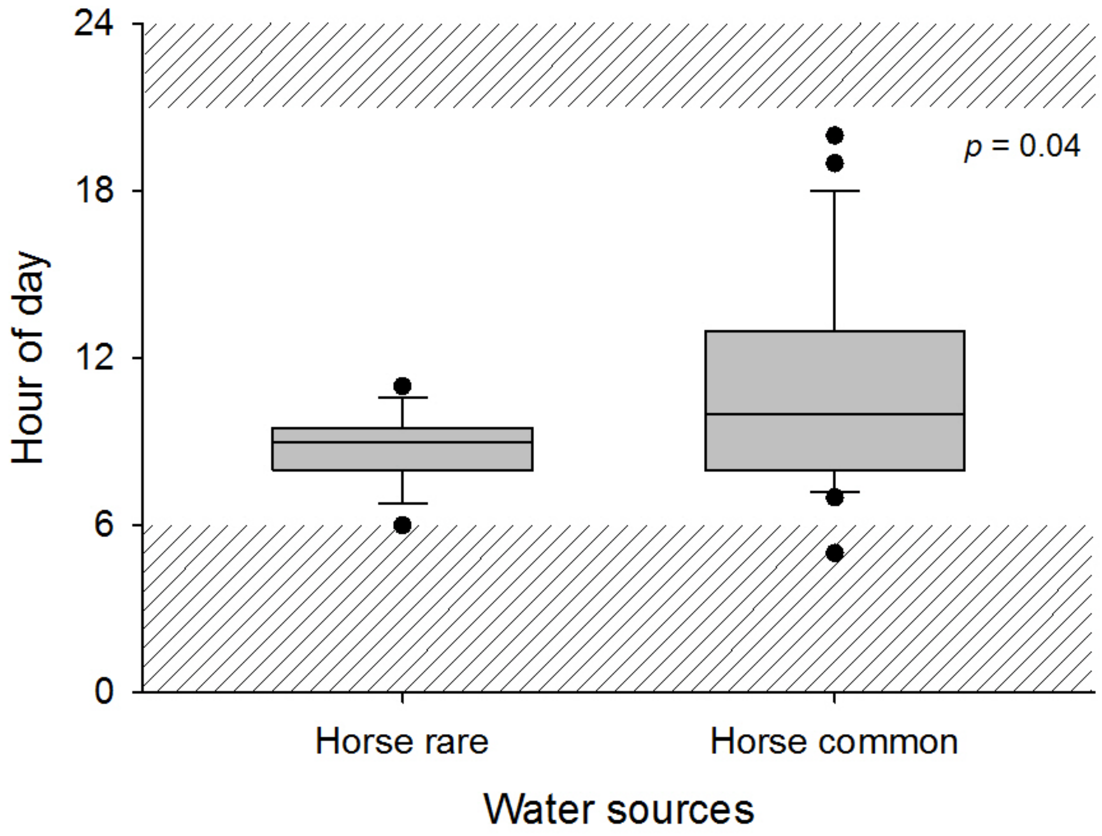

Figure 2-3. Peak arrival hour for pronghorn (*Antilocapra americana*) at water sources where horses (*Equus caballus*) were rare (or absent) and where horses were common. Hatched (shaded) regions depict nocturnal hours. Data were collected in the Great Basin Desert of western Utah, USA from June to October 2010 to 2014.

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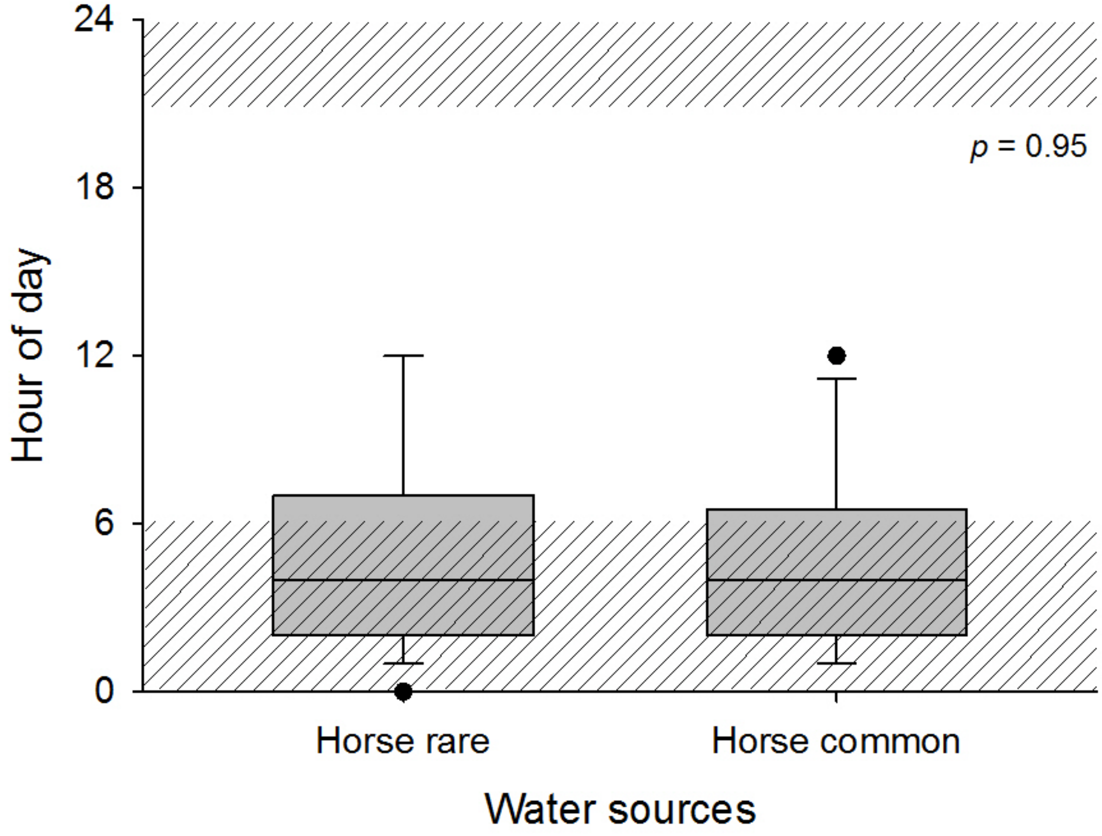

Figure 2-4. Peak arrival hour for mule deer (*Odocoileus hemionus*) at water sources where horses (*Equus caballus*) were rare (or absent) and where horses were common. Hatched (shaded) regions depict nocturnal hours. Data were collected in the Great Basin Desert of western Utah, USA from June to October 2010 to 2014.

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CHAPTER 3

DO DOMINANT CARNIVORES DRIVE THE USE OF A LIMITING RESOURCE BY A SUBORDINATE CARNIVORE?

ABSTRACT

Determining how species interactions impact community structure across landscapes has been a long-standing goal in ecology. In carnivore communities, larger dominant species can intensely compete with and often kill smaller subordinate species. To minimize competition and the risk of fatal interactions, subordinate carnivores often avoid dominant carnivores. While this avoidance behavior by subordinate carnivores has been observed in several studies, only a few of these studies have focused on how dominant carnivores influence the use of water by subordinate carnivores in deserts. Our objective was to test this hypothesis with three years of camera-trapping data from 66 water sources in the Mojave Desert where coyotes (*Canis latrans*) and bobcats (*Lynx rufus*)--known predators and competitors of kit foxes--are sympatric with the smaller kit fox (*Vulpes macrotis*). Based on this hypothesis, we predicted that there would be strong negative associations between visits to water by kit foxes and dominant carnivores. We used generalized linear mixed effects models to evaluate the influence of coyotes and bobcats on the use of water by kit foxes after accounting for habitat characteristics that could influence kit fox occurrence. Our modelling efforts did not reveal strong negative associations between kit fox visits to water sources and visits by dominant carnivores. In fact, according to our models, dominant carnivores contributed very little to the use of water by kit foxes. Instead, kit fox visits were more closely associated with habitat features at water sources. The results of our study contrast with much of what has been observed among desert carnivores at water sources. Our

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findings indicate that dominant carnivores are not the primary driver of use of water sources by subordinate carnivores.

INTRODUCTION

Determining how species interactions impact community structure across landscapes has been a long-standing goal in ecology. In some communities, strong interspecific interactions can govern how communities are spatially organized. For example, within carnivore communities, larger species have been observed to influence the spatial dynamics of smaller species (Vanak and Gompper 2010, Harihar et al. 2011, Levi and Wilmers 2012, Forsyth et al. 2014). The ability of large carnivores to drive the spatial dynamics of small carnivores is primarily due to differences in body size which confer direct competitive advantages to the larger species (Bloch et al. 2011, Nascimento et al. 2011, Reed et al. 2012). However, larger species of carnivores not only outcompete smaller species for resources, they also pose a direct risk of mortality as they will often kill subordinate species competing for the same resources (Palomares and Caro 1999, Fedriani et al. 2000, Donadio and Buskirk 2006, Moehrenschlager et al. 2007, Cupples et al. 2011). As a result, there is a greater risk for small subordinate carnivores to directly interact or compete with dominant carnivores.

To minimize competition and the risk of fatal interactions, subordinate carnivores often avoid dominant carnivores. Subordinate carnivores achieve this by modifying behavior, activity, or use of habitat to avoid larger carnivores (Fedriani et al. 1999, Switalski 2003, Scheinin et al. 2006, Leo et al. 2015). Cheetahs (*Acinonyx jubatus*), for example, avoid nocturnal hours and areas of high prey density to minimize conflict with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) which are competitors and predators of cheetahs (Durant 1998,

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Cristescu et al. 2013). If we consider mesocarnivores, we find many examples of larger species negatively influencing the occurrence of smaller species (Major and Sherburne 1987, Warrick and Cypher 1998, Fedriani et al. 1999, Fedriani et al. 2000, Kozlowski et al. 2008, Vanak and Gompper 2010, Kozlowski et al. 2012, Gehrt et al. 2013, Vanak et al. 2014). Intensive effort has been invested in understanding how subordinate carnivores minimize the effects of competition with dominant carnivores for habitat and food resources (Jones 1998, Atwood and Gese 2008, Mukherjee et al. 2009, Cupples et al. 2011). However, we are still acquiring information regarding the impacts that dominant carnivores may have on the use of water by subordinate carnivores in arid and semi-arid regions.

Water is a spatially and temporally constraining resource in arid and semi-arid landscapes (Thrash et al. 1995, Valeix et al. 2008, Valeix 2011). Water is considered a limiting resource for a variety of desert organisms and shapes biotic communities (Noy-Meir 1973). Often, water is in greatest demand by desert species when it is least available during the hottest and driest times of the year (Hall et al. 2016). Consequently, water sources serve as ideal locations to survey the occurrence of desert species, particularly for carnivores (Edwards et al. 2016). However, the increased demand of water by multiple species during periods of high temperature and aridity can lead to heightened competitive interactions between species at water sources (Valeix et al. 2007, Atwood et al. 2011).

The few studies conducted on the use of water by sympatric carnivores in deserts have indicated that dominant carnivores can negatively influence the occurrence of smaller carnivores (Atwood et al. 2011, Brawata and Neeman 2011, Edwards et al. 2015). Gray foxes (*Urocyon cinereoargenteus*) in the Chihuahuan Desert, for example, generally avoided water sources that were frequented by coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Atwood et al. 2011).

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Similarly, foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) in Australia were less likely to occur at water sources where dingoes (*C. lupus dingo*) were present (Brawata and Neeman 2011). However, the hypothesis positing that dominant carnivores drive the spatial use of water by subordinate carnivores has only been evaluated within a few desert landscapes and subordinate species over a sub-sample of the available water sources. To determine if this hypothesis is more widely applicable, additional sampling across deserts, species, and water sources is warranted.

Our objective was to test this hypothesis with three years of camera-trapping data from 66 water sources in the Mojave Desert where coyotes and bobcats (known competitors and predators of kit foxes; Cypher et al. 2000) are sympatric with the smaller kit fox (*V. macrotis*). Only until recently, drinking behaviors of kit foxes were seldom observed and it was presumed that this species rarely drank water (O'Farrell 1999, O'Brien et al. 2006). However, recent work has illustrated that kit foxes frequent water sources in the Mojave Desert (Hall et al. 2013a, Hall et al. 2013b) and larger carnivores may influence their spatial patterns of water use. If coyotes and bobcats affect visitation patterns to water by kit foxes, we predicted that with our multi-year dataset we would observe strong negative associations between visits of carnivores at water sources; similar to what has been found in other studies (Atwood et al. 2011, Brawata and Neeman 2011).

METHODS

Study area

The Mojave Desert study area consisted of 400 km^2 of public land managed by the Bureau of Land Management located in extreme southwestern Utah (Figure 3-1). Common vegetation at lower elevations included creosote (*Larrea tridentata*), Joshua-tree

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(*Yucca brevifolia*), black-brush (*Coleogyne ramosissima*), and red brome (*Bromus rubens*). Along the foothills, vegetation consisted of sagebrush (*Artemisia* spp.) and juniper (*Juniperus osteosperma*), transitioning to pinyon pine (*Pinus edulis*) at higher elevations. Elevations across the study area ranged from approximately 800 to 2000 m. Annual weather consisted of mean air temperatures of 19.18° C (range: -10.04 to 41.70° C) and mean precipitation of 113 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center).

Data collection

We monitored all known water sources in our study area (Figure 3-1) with infrared-triggered cameras to evaluate use of water sources by kit foxes and other carnivores. We identified 66 permanent water sources consisting of 35 water developments for wildlife, 18 water troughs/tanks for livestock, 11 natural springs, and 2 man-made ponds. From June 2010 to Oct 2012, we selected water sources using a clustered sampling scheme by randomly selecting a point in space within a geographic information system using ArcGIS (ArcMap, version 10, Environmental Systems Research Institute, Redlands, California) and then locating the nearest known water source. From that water source we located the nearest water sources and camera-sampled as many as possible (up to 15 sites) with Reconyx (PC900 Hyperfire model, Holmen, WI, USA) and Cuddeback (Attack IR model, De Pere, WI, USA) cameras. We camera-monitored water sources for two-week periods over three seasons: summer (1 Jun - 30 Sep), fall-winter (1 Oct - 31 Jan), and spring (1 Feb - 31 May) to follow what has been done previously for desert carnivores (Atwood et al. 2011). We attached cameras to metal posts and placed them approximately two meters from water sources. Cameras were programmed to trigger upon both motion and heat and take one photo every 30 seconds. We used date and time stamps associated

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with photos from the cameras to generate visits of carnivores at water sources. We defined two separate visits as two consecutive images of a single species separated by at least 30 min and we treated visits as independent events (Michalski and Peres 2007, Atwood et al. 2011, Hall et al. 2013b).

To determine if larger carnivores influenced the occurrence of the smaller kit fox at water sources, we first accounted for habitat characteristics that could underlie the spatial distribution of kit foxes. Previous work indicates that kit foxes selected certain vegetative and topographical characteristics in desert landscapes. Generally, kit foxes have been associated with lowland valleys and desert steppe characterized by sparse vegetation and relatively little topographical relief (Egoscue 1956;1962, McGrew 1979, Warrick and Cypher 1998, List and Cypher 2004). Kit foxes are thought to occupy these relatively flat, open areas to maximize visibility of approaching predators (Egoscue 1956). Therefore, we measured several vegetative, visibility, and topographical variables around each water source.

We included four vegetation measurements in our vegetative category. We classified the primary vegetation type for each water source using the Dominant Vegetation layer from the Utah Division of Wildlife Resources (http://gis.utah.gov/data). Since a substantial portion of our study area has been affected by wildfires over the last decade, we also categorized water sources as “burned” if they occurred within a burned area. We estimated cover and height of vegetation at water sources using the Random T-Square sampling approach along 30 m transects in all cardinal directions (Krebs 1999).

Our visibility category was represented by eight variables at water sources. We used a Robel pole (Robel et al. 1970) to measure visual obscurity along transects at 5, 10, 15, 20, 50, 75, and 100 m intervals radiating away from the water source in all cardinal directions (Hall et

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al. 2013a). At nearly a third of the water sources that we sampled, there was structural roof cover over the water to serve as a rain catchment and also to minimize evaporative water loss. Due to the low-profile nature of catchment canopies, these structures often served as obstructions to visibility for species using these water sources (Hall et al. 2013a). Thus, we accounted for this variation by considering water sources as either covered or uncovered.

We also measured four topographical characteristics at water sources. We used ArcGIS to calculate terrain ruggedness around water sources up to 90 m using a 30 m resolution digital elevation model (Sappington et al. 2007, Atwood et al. 2011). We included a surrogate metric of terrain ruggedness by measuring the distance from a water source to the nearest rocky outcrop or cliff. We also recorded the elevation (m) of each water source, since kit foxes typically have occurred at lower elevations (List and Cypher 2004). Lastly, since kit foxes rely on the year-round use of dens/burrows (White et al. 1995, Moehrenschlager et al. 2007) they usually have occurred in areas with loose textured soils (List and Cypher 2004). Therefore, we included soil type at each water source and considered sandy and loamy soils to be suitable for burrowing (Soil layer from the U.S. Department of Agriculture, Natural Resources Conservation Service; http://gis.utah.gov/data).

Statistical analyses

Photo-count data from remote cameras can result in some sites not detecting the focal species, producing sites with zero counts. The inability to detect species at all sites is particularly true for desert carnivores that already occur at relatively low densities. To effectively deal with the issues that arise from excess zeroes in photo-count data, we used generalized linear mixed effects models with a zero-inflated negative binomial distribution.

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Zero-inflated models allowed us to simultaneously assess the influence of explanatory variables on photo-counts and the probability of a zero count (Larsen et al. 2011).

We used a two-stage modelling approach (Carpenter et al. 2010, Hall et al. 2013a) to determine if larger carnivores drive the spatial patterns of water use by kit foxes. In the first stage, we created simple habitat models and allowed them to compete among other models within their respective habitat category (i.e., vegetation, visibility, topography). These models included a single habitat variable while controlling for temperature (°C) and days since rainfall. To account for the variation between seasons, years, cluster samples, and water sources, we included these variables as random effects in our models. Because we sampled with replacement, water sources were camera-sampled more than once and by including "water source" as a random effect we accounted for the potential dependency between samples. The "cluster sample" and "water source" variables helped account for any lack of independence between neighboring samples due to individual carnivores potentially visiting more than one water source in a single two-week sample. We evaluated top models within habitat categories by assessing ΔAIC*c* scores (Burnham and Anderson 2002). We considered models to be competing if they were within 2 ΔAIC*c* points of each other. Top models were identified as having the lowest ΔAIC*c* score(s) and comprising the majority of model weight (w_i). Stage one of our modelling allowed us to identify the most influential vegetative, visibility, and topographical variables that we measured and we could then advance these variables to the second stage of model analysis.

In the second stage, we first conducted analyses to detect multicollinearity between variables. When explanatory variables were highly correlated ($|r| > 0.6$), we retained the variable that had the lowest AIC*c* score from stage one of model comparison. We then used the

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remaining top variables from each habitat category to construct a baseline habitat model accounting for variation in temperature, days since rainfall (precipitation), vegetation, visibility (visual obscurity), and topography. Once we created our baseline habitat model, we then individually added the number of visits from coyotes and bobcats to the habitat model. Using AIC*c* scores and model weights, we ranked these models in order of model support (Burnham and Anderson 2002). We then evaluated both the log likelihood and AIC*c* values associated with these models to identify if carnivore variables enhanced model fit or were uninformative parameters. We considered parameters to be uninformative when little to no improvement in log likelihood and AIC*c* values was evident (Burnham and Anderson 2002, Anderson 2008, Arnold 2010). We also evaluated β-estimates from these models to assess whether the activity of dominant carnivores was negatively associated with that of kit foxes. This two-stage process allowed us to determine whether dominant carnivores influenced the use of water by smaller kit foxes after accounting for habitat characteristics in a single statistical framework. We performed all analyses using Program R (R Development Core Team 2014). We used the glmmADMB package (http://glmmadmb.r-forge.r-project.org/) to run generalized linear mixed models in Program R.

RESULTS

In a total of 6,522 camera days from 2010-2012, we recorded 1,582 independent visits of kit foxes. We also observed 350 visits of coyotes and 172 visits of bobcats. During our 3-year study we detected kit foxes at 28 out of a possible 66 sites (42%), which resulted in many of our sites (and re-sampled sites) with zero visits (Figure 3-2). Of the 28 sites where we recorded visits of kit foxes, dominant carnivores were present at 26 of those sites. Dominant carnivores

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were more common across our study area with coyotes and bobcats being present at 65% and 59% of the sites that we sampled, respectively. In addition to our focal species, we also captured pictures of other mesocarnivores such as the American badger (*Taxidea taxus*), gray fox, northern raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and western spotted skunk (*Spilogale gracilis*). However, visitations from these other carnivores were rare and insufficient for data analysis.

In stage one of our model selection process we identified top variables in each of our habitat categories. Type of dominant vegetation had the lowest AIC*c* value in our vegetative category (Table 3-1). Visual obscurity measured with the Robel pole at 20 m from the water source was the best variable in the visibility category, closely outcompeting the next best variable at 2.40 ΔAIC*c* points (Table 3-1). Upon initial inspection of the model comparison in the topography category, there did not appear to be a clear top variable as distance to outcrop, elevation, and soil were all within 2 ΔAIC*c* points (Table 3-1). However, we excluded the elevation and soil variables due to multicollinearity (with vegetation type) and slightly poorer performance in comparison to distance to outcrop (Table 3-1).

From the results of stage one, we created a baseline habitat model with vegetation type, visual obscurity at 20 m, and distance to outcrops (Table 3-2). Each of these variables had strong correlations with visits to water by kit foxes (Table 3-3). For vegetation type, kit fox visits were positively correlated with the presence of creosote (β = 2.24, 95% CI = 0.85 – 3.64; Table 3-3) which occurred at higher elevations along the foothills. Visual obscurity at 20 m was also negatively correlated with visitation to water by kit foxes (i.e., as obscurity decreased, visits of kit foxes increased; β = -0.03, 95% CI = -0.06 – -0.01; Table 3-3). Distance to outcrops, however, was positively associated with kit fox use of water (β = 0.001, 95% CI =

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0.0001 – -0.001; Table 3-3) indicating that kit fox visits increased as water sources were increasingly farther from rugged terrain.

After we individually included the visits of coyotes and bobcats to the baseline habitat model, we did not observe model improvement (Table 3-2). In fact, the habitat model without dominant carnivores ranked as the top model outcompeting the next best model (habitat + bobcat) at 2.10 ΔAIC*c* points (Table 3-2). Coyotes had a negative association with use of water by kit foxes (β = -0.03, 95% CI = -0.12 – 0.06; Table 3-3). However, this association was not strong and meaningful as the confidence intervals of the estimate overlapped zero (Table 3-3). Bobcats had a slight positive association with use of water by kit foxes, but this also was not a meaningful result as confidence intervals overlapped zero (β = 0.14, 95% CI = -0.03 – 0.30; Table 3-3).

DISCUSSION

We found no evidence that dominant carnivores negatively influenced the spatial use of water by subordinate kit foxes. Our repeated sampling of 66 water sources over three years did not provide support that kit foxes avoided the use of water sources frequented by coyotes and bobcats. Our findings contrast with what has been observed in other studies at water sources from other deserts with different subordinate species (Atwood et al. 2011, Brawata and Neeman 2011). Our results indicate that visitation patterns of kit foxes were primarily based on habitat characteristics surrounding water sources and not the relative occurrence of dominant carnivores. These findings reveal an additional perspective on the interspecific relationships between desert carnivores at water sources in an arid environment.

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One possible explanation for the lack of model support for dominant carnivores may relate to the variety of tactics that subordinate species use to coexist with larger competitors and predators. For example, gray foxes used hardwood stands and rugged escape terrain as refuges to escape potential predation by coyotes and bobcats (Atwood et al. 2011, Lesmeister et al. 2015). Although our models with dominant carnivores received less support than our baseline habitat model, it was interesting to note a consistency between kit foxes and gray foxes. Vegetation type (a surrogate for sandy and loamy soil suitable for burrowing) was associated with kit fox visits, similar to hardwood stands and rugged terrain with gray foxes (Atwood et al. 2011, Lesmeister et al. 2015). In other studies, kit foxes have mitigated interspecific conflict with larger carnivores by using refuges, such as burrows (Egoscue 1962, Moehrenschlager et al. 2007). Our findings our at least consistent with the idea that kit foxes may be using burrows to coexist with larger carnivores since the latter were present at all but two water sources used by kit foxes.

The interaction between spatial scale and resource abundance is an important factor that can govern relationships between competing species. We found that the interspecific relationships documented in the Chihuahuan Desert between coyotes, bobcats, and gray foxes (Atwood et al. 2011) were not observed in our study. In the Chihuahuan Desert, there were fewer water sources concentrated in an area approximately half the size of our study area. In our study area, however, there were nearly twice as many water sources available than in the Chihuahuan Desert study area. While the relative densities of water sources were approximately equal between both deserts, there was more space available in our study area. Increased availability of space likely reduced the possibility of interspecific interaction between carnivores in the Mojave Desert. In fact, this finding was substantiated in that we did not detect a single

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direct encounter between our focal carnivores, whereas researchers in the Chihuahuan Desert observed 23 encounters between carnivores (Atwood et al. 2011). The behavioral adaptations of subordinate carnivores critical for mediating the effects of interspecific competition (e.g., spatial avoidance) may not be as important where resources are relatively abundant over large spatial scales.

Negative interspecific interactions between competing carnivores has been shown to be an important factor structuring carnivore communities (Vanak and Gompper 2010, Harihar et al. 2011, Levi and Wilmers 2012, Forsyth et al. 2014). However, we did not detect strong inverse correlations between dominant carnivores and kit foxes at water sources. Corroborating studies have shown that dominant and subordinate carnivores can coexist and overlap in space use (Mattisson et al. 2011, Schuette et al. 2013, Lesmeister et al. 2015, Gompper et al. 2016). Specifically, in our case where coyotes are widely understood to be predators and competitors of kit foxes, coyotes do not necessarily exclude kit foxes from access to resources (White et al. 1994, White et al. 1995, Robinson et al. 2014). The degree to which subordinate carnivores partition space with dominant carnivores is likely dependent upon several interacting factors (e.g., density of dominant species, availability of prey, etc.), evidenced by the mixed results across deserts, spatial scales, and species that have been observed in this and other studies.

Previous work has shown how important habitat features are for the occurrence of kit foxes. Similar to what others have found kit foxes selected areas of relative low elevation with little topographical relief (McGrew 1979, Daneke et al. 1984, Warrick and Cypher 1998). In addition, kit foxes visited sites more frequently that had relatively sparse vegetation (Egoscue 1956, McGrew 1979), primarily consisting of creosote and Joshua trees (Zoellick et al. 1989). While competitors and predators have been observed to influence the spatial dynamics of kit

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foxes (Warrick and Cypher 1998, Fedriani et al. 2000, Nelson et al. 2007), our study indicates that habitat was a major driver of selection of water sources by kit foxes. Habitat characteristics play an important role in the spatial ecology of kit foxes and other small carnivores (Gompper et al. 2016) which is likely related to the habitats occupied by their small mammal prey (White et al. 1996, Dennis and Otten 2000).

Our study did not support previous research indicating that dominant carnivores influenced the spatial use of resources by a smaller subordinate species. But, it is difficult to exclude the possibility that dominant carnivores played a larger role in water use by kit foxes. Within the context of our study, we did not experimentally manipulate the presence and abundance of coyotes and bobcats which would have provided additional inference and ability to draw stronger conclusions. In light of this deficiency, other observational studies have detected an effect of dominant carnivores on subordinate carnivores with substantially less sampling effort (Atwood et al. 2011, Edwards et al. 2015). Given our rather extensive sampling effort, we would have expected to find similar evidence of an effect of dominant carnivores, if it existed in our study area. Instead, we found that kit fox visits were more closely associated with habitat features at water sources. Our findings indicate that dominant carnivores are not the primary driver of the spatial use of water sources by subordinate carnivores.

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Table 3-1. Model selection results for zero-inflated negative binomial models of kit fox (*Vulpes macrotis*) visits as a function of vegetative, topographical, and visibility explanatory variables. We advanced competing models (within two AIC*c* values of the top model) to stage two of analysis. Data were collected in the Mojave Desert in southwestern Utah, USA from 2010 to 2012.

Model[a]	K[b]	AIC$_c$[c]	ΔAIC$_c$[d]	w_i[e]	LL[f]
Vegetation					
Temp + RainDays + VegType	9	1692.81	0.00	1.00	-833.79
Temp + RainDays + Burned	9	1716.51	23.70	0.00	-845.67
Temp + RainDays + ShrbCover	9	1717.71	24.90	0.00	-846.24
Temp + RainDays (null)	8	1722.23	29.41	0.00	-849.85
Temp + RainDays + ShrbHeight	9	1722.61	29.80	0.00	-848.68
Topography					
Temp + RainDays + DistOutcrop	9	1701.61	0.00	0.51	-838.21
Temp + RainDays + Elevation*	9	1703.01	1.40	0.25	-838.90
Temp + RainDays + Soil*	9	1703.11	1.50	0.24	-838.96
Temp + RainDays + Rugged	9	1716.11	14.50	0.00	-845.47
Temp + RainDays (null)	8	1722.23	20.61	0.00	-849.85
Visibility					
Temp + RainDays + Robel20	9	1700.11	0.00	0.70	-837.47
Temp + RainDays + Robel15*	9	1702.51	2.40	0.21	-838.63
Temp + RainDays + Robel10*	9	1705.41	5.30	0.05	-840.11
Temp + RainDays + Robel50	9	1705.91	5.80	0.04	-840.33
Temp + RainDays + Robel5*	9	1711.11	11.00	0.00	-842.96
Temp + RainDays + Canopy	9	1719.71	19.60	0.00	-847.24
Temp + RainDays + Robel75	9	1721.81	21.70	0.00	-848.32
Temp + RainDays (null)	8	1722.23	22.11	0.00	-849.85
Temp + RainDays + Robel100*	9	1722.71	22.60	0.00	-848.73

[a] Temp, mean daily temperature over sample period; RainDays, number of days since last rainfall; VegType, type of dominant vegetation present; Burned, whether the area immediately surrounding the water source had been recently burned (within last decade); ShrbCover, shrub cover within 30 m; ShrbHeight, mean shrub height within 30 m; DistOutcrop, distance to nearest rocky outcrop or cliff; Soil, presence of sandy or loamy soil; Rugged, ruggedness metric calculated within a 100 m radius using a 10 m resolution digital elevation model; Robel, visibility measurements (height of obstructions, e.g., vegetation, rocks, etc.) taken at 5, 10, 15, 20, 50, 75, and 100 m intervals; Canopy, presence of structural roof cover over water sources.

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[b] Number of parameters.
[c] Akaike's Information Criterion corrected for small samples.
[d] Change in AIC$_c$ value compared to top model.
[e] AIC$_c$ weight.
[f] Model log-likelihood.
* Variable removed due to multicollinearity with other variable(s).

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Table 3-2. Model selection results for zero-inflated negative binomial models of kit fox (*Vulpes macrotis*) visits to water sources as a function of top habitat (from stage 1 of model selection) and predator/competitor explanatory variables. Data were collected in the Mojave Desert in southwestern Utah, USA from 2010 to 2012.

Model[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	LL[f]
Temp + RainDays + VegType + DistOutcrop + Robel20	11	1679.29	0.00	0.60	-823.20
Temp + RainDays + VegType + DistOutcrop + Robel20 + Bobcat	12	1681.39	2.10	0.21	-824.77
Temp + RainDays + VegType + DistOutcrop + Robel20 + Coyote	12	1682.89	3.60	0.10	-824.50
Temp + RainDays (null)	8	1722.23	42.94	0.00	-849.85

[a] Temp, mean daily temperature over sample period; RainDays, number of days since last rainfall; VegType, type of dominant vegetation present; DistOutcrop, distance to nearest rocky outcrop or cliff; Robel20, visibility measurements (height of obstructions, e.g., vegetation, rocks, etc.) taken at 20 m using a Robel pole; Bobcat, number of bobcat (*Lynx rufus*) visits; Coyote, number of coyote (*Canis latrans*) visits.
[b] Number of parameters.
[c] Akaike's Information Criterion corrected for small samples.
[d] Change in AIC_c value compared to top model.
[e] AIC_c weight.
[f] Model log-likelihood.

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Table 3-3. Coefficients, associated p-values, and 95% confidence intervals from the top (zero-inflated negative binomial) model for kit fox (*Vulpes macrotis*) visits to water sources. Data were collected in the Mojave Desert in southwestern Utah, USA from 2010 to 2012.

Coefficient					Lower 95%	Upper 95%
Habitat						
Intercept	-1.140	0.649	-1.760	0.079	-2.411	0.131
Temp[a]	0.079	0.014	5.600	0.000	0.051	0.106
RainDays[b]	0.005	0.009	0.540	0.591	-0.013	0.024
VegType[c]	2.243	0.712	3.150	0.002	0.848	3.638
DistOutcrop[d]	0.001	0.000	2.380	0.017	0.000	0.001
Robel20[e]	-0.034	0.011	-3.080	0.002	-0.055	-0.012
Habitat + coyote						
Intercept	-1.134	0.643	-1.760	0.078	-2.393	0.126
Temp	0.079	0.014	5.660	0.000	0.052	0.107
RainDays	0.005	0.009	0.550	0.580	-0.013	0.024
VegType	2.227	0.706	3.160	0.002	0.844	3.611
DistOutcrop	0.001	0.000	2.390	0.017	0.000	0.001
Robel20	-0.033	0.011	-3.050	0.002	-0.054	-0.012
Coyote[f]	-0.034	0.046	-0.730	0.463	-0.124	0.057
Habitat + bobcat						
Intercept	-1.162	0.652	-1.780	0.075	-2.439	0.115
Temp	0.075	0.014	5.300	0.000	0.047	0.103
RainDays	0.006	0.010	0.670	0.500	-0.012	0.025
VegType	2.246	0.716	3.130	0.002	0.842	3.650
DistOutcrop	0.001	0.000	2.470	0.014	0.000	0.001
Robel20	-0.034	0.011	-3.120	0.002	-0.056	-0.013
Bobcat[g]	0.139	0.084	1.660	0.096	-0.025	0.303

[a] Mean daily temperature over sample period.
[b] Number of days since last rainfall.
[c] Type of dominant vegetation present.
[d] Distance to nearest rocky outcrop or cliff.
[e] Visibility measurements (height of obstructions, e.g., vegetation, rocks, etc.) taken at 20 m using a Robel pole.
[f] Number of coyote (*Canis latrans*) visits.
[g] Number of bobcat (*Lynx rufus*) visits.

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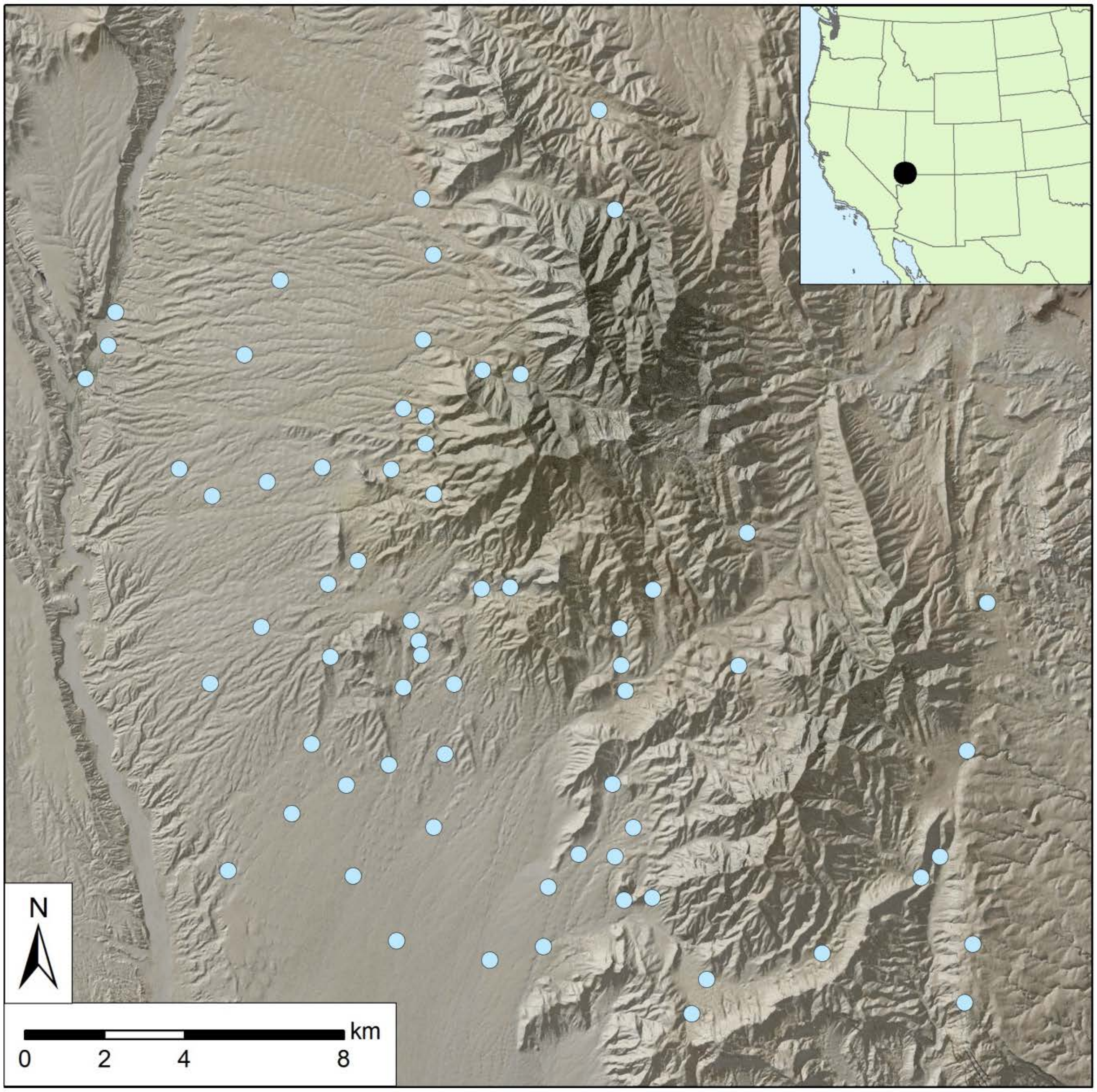

Figure 3-1. Distribution of water sources (blue circles) that were monitored with infrared-triggered cameras for carnivores in the Mojave Desert in southwestern Utah, USA from 2010 to 2012.

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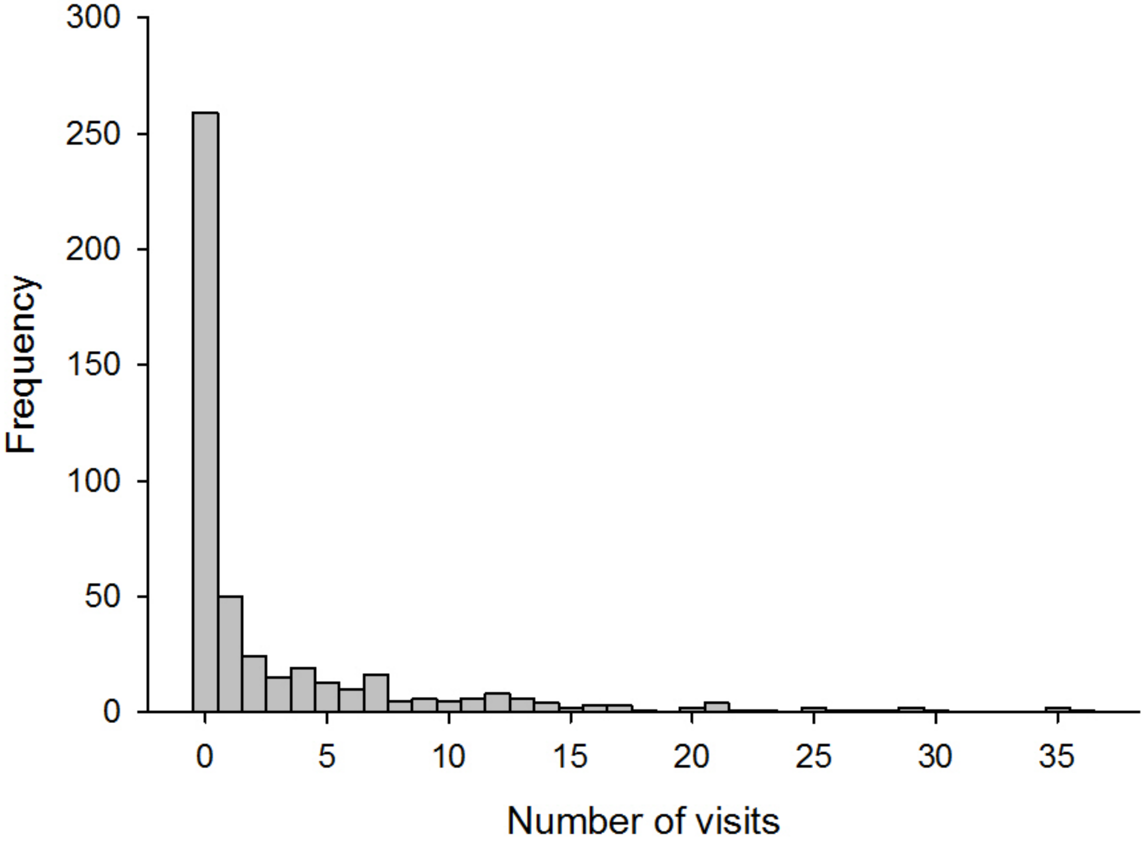

Figure 3-2. Frequency of kit fox (*Vulpes macrotis*) visits at water sources in the Mojave Desert in southwestern Utah, USA. Data were collected from 2010 to 2012.

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CHAPTER 4

WILL CLIMATE CHANGE LEAVE SOME DESERT BAT SPECIES THIRSTIER THAN OTHERS?

ABSTRACT

The combined effects of global climate change and increased anthropogenic use of free water are likely to cause decreases in availability and surface area of water in arid environments. Climate change and water loss are predicted to alter community dynamics, but identifying mechanisms underlying differential responses of species remains a critical conservation challenge. Bats drink in flight and rely on accessible water sources, yet the ability to access water is a function of flight maneuverability. By reducing the size of water sources (to simulate predicted water loss due to climate change/increased human use), we demonstrated species-specific responses by desert bats based on differences in morphology and flight maneuverability. Under natural conditions, less-maneuverable bats selected larger water sources while maneuverable bats exhibited no preference. When we experimentally reduced surface area, larger, less-maneuverable bats experienced a 69% decrease in proportion of drinking passes ($p < 0.05$) and increased competition with smaller, maneuverable bats. Our study illustrates how morphology can mediate access to a resource and highlights conservation implications as water becomes more limited in arid environments. Selection for differences in wing morphology and flight ability in insectivorous bats has allowed for coexistence and high species richness at a local scale. However, anticipated reductions in the sizes of water sources due to climate disruption may lead to species with less maneuverability being unable to access water efficiently and facing increased competition from more agile bats.

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INTRODUCTION

Models of global climate change predict decreasing availability of free water in arid environments due to increased aridity and frequency of drought (Ault et al. 2014; Cook et al. 2015; Dai 2011; Seager et al. 2013). Western North America, for example, recently lost 63 trillion gallons of surface water due to long-term drought (Borsa et al. 2014). Decrease of water coupled with increasing human demand is expected to further reduce water availability in arid regions (MacDonald 2010; Taylor et al. 2013; Wada et al. 2013). The combined effects of climate change and loss of water will likely have profound impacts on biotic communities (Brusca et al. 2013; Lecomte et al. 2009; Maestre et al. 2015; Ogston et al. 2016; Parmesan and Yohe 2003; Walther et al. 2002; Westphal et al. 2016), but there is little information regarding mechanisms that predict how species will respond to these changes. Understanding how variability among species can lead to differential responses to a rapidly changing climate will increase our ability to forecast shifts in biotic communities (Chen et al. 2011; Jump and Peñuelas 2005; Sherwin et al. 2013; van Gils et al. 2016).

The sensitivity of bats to rising temperatures and concomitant loss of water makes them important indicators of climate change (Adams 2010; Jones et al. 2009; Razgour et al. 2013). Although many species of bats have adaptations that help them locate water sources (Greif and Siemers 2010) and limit evaporative water loss (Bell et al. 1986; Geluso 1978; Muñoz-Garcia et al. 2016), most species face challenges associated with water retention (Carpenter 1969; Hattingh 1972; Studier 1970; Webb et al. 1995). Consequently, bats rely on access to free water for thermoregulation in addition to foraging and reproduction (Adams and Hayes 2008; Carpenter 1969; Hagen and Sabo 2012; Kurta et al. 1989; Kurta et al. 1990). Significant decreases in surface area of water sources in a water-limited environment may increase inter- and

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intraspecific competition among bats attempting to drink and result in reductions in local and regional species richness and/or reductions in reproductive yields for some species (Adams 2010; McCain 2007; Razgour et al. 2011).

Because bats drink in flight, their ability to access water is dependent on their maneuverability. Larger, less-maneuverable bats forage high off the ground or in open areas where obstacles are few and speed is favored over maneuverability, while smaller maneuverable bats forage near the ground or on and around vegetation where avoiding obstacles and collisions is critical (Norberg and Rayner 1987). Thus, less-maneuverable bats are more likely affected by reduced surface area of water sources than smaller, more maneuverable species (Cross 1986; Rabe and Rosenstock 2005; Razgour et al. 2010). The potential for morphological differences between ecologically-similar species to drive responses to contemporary climate change has received little attention. Understanding how biotic communities respond to increasingly limited water is integral for their conservation, particularly as free water becomes less available in arid and semi-arid regions (Adams 2010; Jones and Rebelo 2013; Maestre et al. 2015; Ogston et al. 2016).

We studied bat communities to determine if reduced water availability (an expected outcome of climate change) leads to species-specific responses based on morphological traits. Bats provide a model system because they have evolved differing morphologies for flight maneuverability to partition foraging niches, but are still reliant upon and compete for access to water sources (Adams and Hayes 2008; Findley and Wilson 1982). We used corroborating lines of evidence by first employing an observational approach to acoustically sample 60 water sources across two North American deserts to determine if surface area of water sources predicted the presence of bats based on morphology. Second, we experimentally reduced the

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surface area of water sources to assess changes in drinking behavior and competition between maneuverable and less-maneuverable bats. Since competition can be difficult to observe directly, we relied on indirect evidence for the occurrence of competition (e.g., temporal shifts in resource use to minimize direct competitive interactions). We hypothesized that less-maneuverable species of bats would occur less frequently at smaller water sources and respond more strongly to reductions in surface area of water sources than more maneuverable species. Specifically, we predicted that 1) surface area would positively correlate with the presence of less-maneuverable bats under natural conditions, 2) the ratio of drinking passes to non-drinking passes would decrease for less-maneuverable bats when water sources were experimentally reduced, and 3) less-maneuverable bats would experience altered temporal partitioning with maneuverable bats when surface area of water was reduced.

METHODS

Study areas

We conducted this study at water sources in the Mojave and Great Basin Deserts. The Mojave Desert study area was located in extreme southwestern Utah (Figure 4-1) and was characterized by alternating rolling ridges and dry washes. Common vegetation included red brome (*Bromus rubens*), creosote (*Larrea tridentata*), Joshua tree (*Yucca brevifolia*), and blackbrush (*Coleogyne ramosissima*). The Great Basin Desert study area was located in west-central Utah, approximately 360 km north of Mojave (Figure 4-1), and was characterized by dune systems and alkaline flats. Vegetation characteristic of this area included greasewood (*Sarcobatus vermiculatus*), cheatgrass (*B. tectorum*), big sagebrush (*Artemisia tridentata*), and juniper (*Juniperus osteosperma*).

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Observational data collection

From May to August of 2010 and May to July 2011 we sampled 35 water sources at Mojave and 25 water sources at Great Basin with AR125 full-spectrum, time-expansion bat detectors and FR125-III data recorders (Binary Acoustic Technology, Tucson, AZ, USA). Water sources consisted of natural springs and ponds (16), water tanks for livestock (13), water developments for wildlife (27), and water treatment ponds and ditches (4). Only two of the water sources that we sampled were routinely filled with water; the other water sources were considered self-maintaining and contained water throughout the duration of our study. Surface area of water sources ranged from 0.25 to 10,000 m^2 (mean: 186.60 m^2, SE: 99.10 m^2). We categorized water sources into three size groups based on surface length: small (surface length < 2 m), medium (surface length between 2 and 5 m), and large (surface length > 5 m). We considered all known perennial (or near perennial) water sources within our study areas for acoustic sampling, but not all were sampled. We selected water sources using a clustered sampling scheme by randomly selecting a point in space within a geographic information system and then locating the nearest known water source. From that water source we located the two nearest water sources and deployed bat detectors at all three sites for one night (due to equipment limitations, we could only sample three locations each night). On average, water sources selected for sampling were 2.35 km apart (range: 0.60 to 6.20 km). The following evening, a new random point was chosen and three new water sources were selected for sampling. We sampled with replacement so each water source was eligible for re-sampling. We positioned microphones at 45° angles on tri-pods (1 m in height) approximately 3 m from the edge of the water (Adams and Simmons 2002; Jackrel and Matlack 2010; Razgour et al. 2010). We oriented microphones over the center of the water source and placed them at the longest edge to capture

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the majority of airspace above water (Razgour et al. 2011). We recorded bat activity from 2100 hr (approximately sunset) to 0100 hr (4 hrs total; this time period encompassed nearly all bat activity for species in this region (Cockrum and Cross 1964; O'Farrell et al. 1967; Ruffner et al. 1979)).

Experimental design

Our surface area experiment occurred in August of 2011 at two livestock water tanks located 3.51 km apart in Mojave. These tanks were selected because they were the largest water sources available in our study area, identical in design, void of flight obstructions, had been filled with water during the summers of 2010 and 2011, and were still close enough to be found within the same habitat (i.e., creosote flats with Joshua trees). Each tank was 0.60 m tall and circular in design, measuring 6.25 m in diameter and provided 30.66 m^2 of surface area. At each tank, we used an infrared video camera (Sony Handycam DCR-DVD610) and a supplemental infrared lamp along with an AR125 bat detector and FR125-III recorder for species identification. We initiated video and audio recording at 2100 and concluded at 0100. We used The Observer XT10 behavioral analysis software (Noldus, Leesburg, VA, USA) to view video recordings and record observations related to drinking and non-drinking passes. We considered a drinking pass when a bat made contact with the surface of the water (Adams and Simmons 2002). We then matched timestamps between audio and video files to determine drinking behavior of identified species (Razgour et al. 2010).

We conducted our surface area experiment using a “crossover” design (Jackrel and Matlack 2010; Tuttle et al. 2006). At Tank A, we restricted the surface area to 2.25 m^2 (average surface area of small water sources from both study areas) using a plywood cover while Tank B

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was unmodified. After one night (to allow bats to adjust to the experimental modification (Jackrel and Matlack 2010)), we recorded bat activity and behavior for five subsequent nights. Following the five night manipulation period, we switched the surface area restrictions from Tank A onto Tank B. One night later, we recorded for another five nights with Tank B as our treatment and Tank A as our control. This "crossover" design allowed each tank to serve as the control and the experimental unit (Tuttle et al. 2006).

Acoustic analysis

We used SonoBat version 3 (SonoBat, Arcata, CA, USA) to identify call sequences to species. SonoBat uses a decision-based engine to quantitatively analyze recorded call sequences from the field against known recordings from species and has an identification accuracy rate of 98% (J. Szewszak, Humboldt State University, unpubl. data). Prior to analysis of call sequences, we removed any noise or low-quality call sequences. SonoBat then classified call sequences based on several parameter values (e.g., maximum and minimum frequency, duration of call, frequency of the knee, steepness of the slope, etc.) and estimated probabilities for identified call sequences using a discriminate function model trained on calls from a reference library from the western U.S. (J. Szewszak, Humboldt State University, unpubl. data; Clement et al. 2014; Slough et al. 2014). We used call sequences for species identification with an estimated probability of correct identification ≥ 95% (Barnhart and Gillam 2014; Clement et al. 2014). Despite a high accuracy rate, SonoBat can have difficulty distinguishing fragmented calls between pairs of certain species, such as *Tadarida brasiliensis/Lasiurus cinereus*, *Myotis lucifugus/M. volans*, *M. thysanodes/Corynorhinus townsendii*, and *Eptesicus fuscus/Lasionycteris noctivagans* (J. Szewszak, Humboldt State University, unpubl. data). However, none of these pairings included

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species with differing maneuverability and any misclassification between these species was unlikely to influence our results.

Data analysis

We used a non-metric multidimensional scaling (NMDS) analysis to assign bats into less-maneuverable or maneuverable groups based on aspect and wing-loading ratios (Brigham 1988; Holloway and Barclay 2001; Norberg and Rayner 1987). Species of bats that are more morphologically similar with regards to characters conducive to different types of flight will tend to "cluster" in ordinal space, whereas species that are more morphologically distinct will be farther apart. We plotted each species in ordinal space and then looked for a natural break to assign individuals into a group.

With our observational data we used mixed-effects logistic models and model selection to determine if the size of water sources influenced the presence of maneuverable and less-maneuverable bats (Burnham and Anderson 2002). We established base models for both groups of bats that included temperature (°C; Korine and Pinshow 2004), mean wind speed (m/sec) over the 4-hr sample period (O'Farrell et al. 1967), nearest neighbor distances (average distance of the 3 nearest water sources to the sampled water source (Razgour et al. 2010; Ruffner et al. 1979)), and flight obstructions (e.g., vegetation, rocks, catchment canopies, fences) adjacent to the water and taller than 0.5 m (Jackrel and Matlack 2010). Since our microphones were set 3 m away from water sources, potential obstructions adjacent to water sources did not influence our general set up procedure for bat detectors. To account for the variation between study areas (Great Basin and Mojave), cluster samples, and water sources, we included these variables as random effects in our models. Because we sampled with replacement some water sources were re-sampled

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more than once on different nights and by including “water source” as a random effect we accounted for the potential dependency between samples. The “cluster sample”, “water source”, and “nearest neighbor” variables helped account for any potential lack of independence between neighboring samples due to individual bats potentially visiting > 1 water source in a single night. In addition, we conducted Mantel tests with Monte-Carlo permutations for each study area to identify if spatial patterns of bat activity occurred (Besag and Diggle 1977; Mantel 1967). This way, we ensured that the proximity of water sources (regardless of their size and associated habitat features) was not a driving influence on our analysis.

After creating base models incorporating temperature, wind, nearest neighbor distance, obstructions, study area, cluster sample, and water source variables, we then included a “water size” variable to each of the base models to determine the relative influence of the size of water sources on the presence of different maneuverability groups. We used Akaike’s Information Criterion adjusted for small sample size (AIC_c) to compare base models to water models (Akaike 1974). We considered models to be competing if they were within two ΔAIC_c values of the model with the lowest AIC_c value and accounted for the majority of model weight (w_i) (Burnham and Anderson 2002). We also included both marginal (variance explained by fixed effects) and conditional (variance explained by fixed and random effects) R^2 values to provide a measure of model strength (Nakagawa and Schielzeth 2013).

For our experimental data we first compared drinking behaviors of maneuverability groups between control and treatment nights. Since our crossover design resulted in a treatment and control measure for each night, we did not incorporate temperature or wind into this analysis since the same climatic patterns occurred at both tanks each night (an assumption based on the relative proximity of the two tanks). We also excluded the nearest neighbor distance covariate

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(used in the logistic regression) because it was an unlikely contributor to drinking ratios (drinking passes/total passes). We compared measures of drinking ratios for each group between treatment and control nights using a mixed-effects ANOVA. In this model, we included “group” (maneuverability group), “treatment”, and a “group x treatment” interaction as fixed effects. The group x treatment interaction allowed us to simultaneously test for relative differences in drinking ability between both groups of bats and between control and treatment nights. To account for variation associated with differences between sample nights and experimental tanks, we included “night” and “tank” as random effects in our model. We then calculated least-squares means for each treatment and group combination.

Second, we compared two measures of bat activity for both maneuverability groups between control and treatment nights: peak arrival times (time when the majority of bat activity occurred at the water source) and proportional activity (number of calls during each 30-min interval/total number of calls for that group in a night) (Adams and Thibault 2006; Razgour et al. 2011). We used 30-min intervals to make our results comparable with previous studies conducted in the American Southwest (Cockrum and Cross 1964; Kuenzi and Morrison 2003; O'Farrell and Bradley 1970; O'Farrell et al. 1967). We used *G*-tests of independence (Sokal and Rohlf 1981) to determine if the proportion of activity differed between 30-min intervals on control and treatment nights at each tank. This analysis allowed us to evaluate shifts in temporal partitioning (indirect evidence of competition) at each tank when water was significantly reduced. If competition occurred, we would expect the less competitive species to exhibit shifts (differences) in proportional activity when the resource was reduced to minimize competition with the more competitive species. Since activity measures used for comparison occurred across multiple nights at a single tank, there existed the possibility of climatic variability to influence

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our comparisons. However, there were no differences in mean temperature ($t = 0.11$, $df = 4$, $p = 0.92$) or wind speed ($t = 0.31$, $df = 4$, $p = 0.77$) between the first five and latter five nights based on two-sample *t*-tests. Furthermore, precipitation was not a factor as it did not rain during the experiment. Therefore, we did not include these climatic variables in the analyses for our experiment. We used Program R for all statistical analyses (R Development Core Team 2014). We set the level of significance for all statistical tests at $\alpha = 0.05$ and used Bonferroni adjusted α-levels of $\alpha = 0.025$ for Mantel tests and $\alpha = 0.013$ for *G*-tests.

RESULTS

The groups of bats that we studied exhibited relatively distinct aspect and wing-loading ratios based on the clustering apparent in the NMDS analysis (Global $R = 0.98$, $p < 0.01$; Figure 4-2). Species of less-maneuverable bats included *E. fuscus*, *Euderma maculatum*, *L. noctivagans, L. blossevillii*, *L. cinereus*, and *T. brasiliensis*, which have greater aspect and wing-loading ratios and are relatively larger bats with faster, less maneuverable flight. Maneuverable species consisted of *Antrozous pallidus*, *C. townsendii*, *M. californicus*, *M. ciliolabrum*, *M. evotis*, *M. lucifugus*, *M. thysanodes*, *M. volans*, *M. yumanensis*, and *Parastrellus hesperus*, all of which have lower aspect and wing-loading ratios and slower, more maneuverable flight.

During our observational data collection from May to August of 2010 and May to July 2011, we sampled 60 water sources from Mojave and Great Basin Deserts (Figure 4-1). We were able to re-sample 23 of these water sources on > 1 night resulting in 92 total nights of sampling. We detected 16 species at Mojave and 13 species at Great Basin (Table 4-1). During our surface area experiment at Mojave in August of 2011, we detected 15 species over the 10 night period (Table 4-1). Mantel tests did not reveal spatial aggregations of bat activity at

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Mojave ($p = 0.46$) or Great Basin ($p = 0.35$). Our modelling efforts demonstrated that the size of water sources was significantly correlated with the presence of less-maneuverable, but not maneuverable bats (Table 4-2, Figure 4-3). Including “water size” as a variable better explained variation in species presence for less-maneuverable bats, but not maneuverable bats (Tables 4-2, 4-3).

Data from our experiment indicated that maneuverability groups responded differently to restricted surface areas in terms of drinking. The “group x treatment” interaction for drinking ratios was significant ($p < 0.01$) in the mixed-effects ANOVA model (Table 4-4). After inspecting the least-squares means for this model, we found that less-maneuverable bats exhibited a 69% decrease ($p < 0.05$) in drinking ratios during treatment nights relative to control nights (Figure 4-4). Conversely, maneuverable bats only experienced a 13% decrease in drinking ratios which was not different ($p > 0.05$) between control and treatment nights (Figure 4-4).

We also detected differences in peak arrival times and proportional activity for less-maneuverable bats during our experiment. During control nights, peak arrival times for both groups overlapped; however, during treatment nights, peak arrival time for less-maneuverable bats was delayed 30 min (Figure 4-5). Maneuverable bats did not appear to alter peak arrival time at either tank, which occurred 1 hour after sunset on control and treatment nights. The proportional activity of less-maneuverable bats during treatment nights differed significantly compared to control nights ($G = 20.08$, $df = 7$, $p < 0.01$; Figure 4-5). However, the proportional activity of maneuverable bats did not differ between control and treatment nights ($G = 1.59$, $df = 7$, $p = 0.98$; Figure 4-5).

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DISCUSSION

Using observational and experimental approaches, we demonstrated that less-maneuverable species of bats occurred less frequently at smaller water sources and responded more strongly to reductions in surface area than maneuverable species. During our observational surveys, we detected less-maneuverable bats at larger water sources more often than at smaller water sources, corroborating previous work (Rabe and Rosenstock 2005; Razgour et al. 2010). Logistic models showed that the presence of less-maneuverable bats was positively correlated with surface area, which supported our first prediction. However, this correlation was not apparent for maneuverable bats. In fact, there was no difference in the presence of maneuverable bats at water sources of different sizes. Experimentally manipulating the size of water sources allowed us to examine the mechanisms likely underlying the differential visitation to small water sources by bats and test our other two predictions.

Our experimental findings revealed that reduced surface area of water affected drinking success and timing of use by less-maneuverable bats. Our prediction that less-maneuverable bats would experience lower drinking ratios upon reduction of water sources was supported. Maneuverable bats, on the other hand, did not exhibit significantly reduced drinking ratios when surface areas were restricted. Data also supported our prediction that less-maneuverable bats would experience altered temporal partitioning (i.e., competition) with maneuverable bats. We detected shifts in peak arrival times and proportional activity by less-maneuverable, but not maneuverable bats when water size was reduced. On nights when the surface area of the water source was not restricted, the peak arrival of both groups of bats occurred at the same time, suggesting a lack of competition. However, during nights when surface area of water was restricted, less-maneuverable bats arrived at water sources 30 min later than on control nights.

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This temporal shift in activity is likely a response to restricted surface area of water and the resulting increase in competition with maneuverable bats. A half-hour delay in drinking may be of no fitness consequence to bats. However, since bats have high metabolic rates (Voigt et al. 2010) and can lose significant amounts of water while roosting (Webb et al. 1995), visiting water sources shortly after sunset is likely necessary to recover water lost during roosting (Adams and Hayes 2008). Therefore, a delay or increased difficulty in drinking during hot and dry conditions may have physiological consequences for bats, especially for lactating females that have an increased demand for water (Adams 2010; Adams and Hayes 2008).

The competitive advantage of maneuverable bats in accessing experimentally-restricted water likely contributed to the decrease in drinking ratios by less-maneuverable bats. There is a high risk of collisions during flight around small water sources, thus, bats coordinate their drinking passes using a "runway" system where one bat drinks at a time (an observation we confirmed in our videos) (Adams and Simmons 2002). The difficulty of accessing small water sources coupled with competition from maneuverable bats will likely create additional challenges for less-maneuverable bats as water becomes increasingly limited. Decreases in surface area of water sources across arid landscapes will likely lead to heightened competition for this increasingly limited resource as species concentrate on fewer, smaller bodies of water. Our study provides additional evidence that climate change may alter competition dynamics within biotic communities.

We recognize the limitations inherent in sampling only two water sources for an experiment. To minimize the limitations, we implemented a crossover design using each water tank as both treatment and control over multiple nights of sampling. While sample size may limit the inference of our experiment, the experimental design and significant results allowed us

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to identify potential mechanisms leading to the differential ability of some bats to better access water than others. Despite reducing the surface area on only two experimental tanks, we were able to detect differences in drinking success and peak arrival time for less-maneuverable bats, both of which supported our predictions and helped explain large-scale patterns of water source use observed across our study areas. The logistically and cost-intensive nature of video-monitoring over multiple nights naturally limits sample sizes and our approach was consistent with previous studies that have investigated drinking patterns of bats (Adams and Thibault 2006; Jackrel and Matlack 2010; Razgour et al. 2010; Tuttle et al. 2006).

Bats are considered bioindicators of climate change due to their sensitivity to environmental conditions (Jones and Rebelo 2013; Sherwin et al. 2013). Due to the high demand of water by lactating females, loss of water due to climate change will likely impact reproduction (Jones and Rebelo 2013). Bats have experienced decreased reproduction and undersized young during times of prolonged drought (Tuttle 1976). Decreased reproduction is likely unsustainable for *k*-selected species, which lends credence to the predicted distributional shifts of some bat species as climates continue to warm (Jones and Rebelo 2013; McCain 2007; Razgour et al. 2013; Sherwin et al. 2013). Our study further supports the forecasted impacts of climate change on bat communities and proposes a morphological mechanism which may lead to community divergence as water loss continues in arid environments.

While our results propose that less-maneuverable bats will encounter added difficulty in accessing and competing for water when it is reduced, we recognize that these species are still well adapted to the challenges of inhabiting arid environments. Less-maneuverable bats are typically large in body size, which likely allows them to maintain better water balance than smaller species (Carpenter 1969). Larger bats with fast flight can also more efficiently cover

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longer distances to locate suitable water sources while expending less energy than smaller bats (Chambers et al. 2011; Robinson and Stebbings 1997). Also, some larger bats can consume larger prey items that provide greater water content than can smaller-bodied, more agile species (Barclay and Brigham 1991). Less-maneuverable bats may be able to persist in a rapidly changing climate with limited water availability as long as they can commute to large water sources (with minimal energy loss) to meet basic water demands. However, if trends of water loss continue as projected it may become energetically unfeasible for large, less-maneuverable bats to inhabit areas of increasingly limited water availability.

It is presumed that water sources introduced by humans can help stabilize the unpredictable nature of water availability in desert landscapes (Longshore et al. 2009). Nonetheless, it is unknown whether anthropogenic water sources can completely mitigate the predicted effects of climate change. The majority of water sources that we sampled during our study were anthropogenic, however all but two were self-maintaining and relied on natural occurring precipitation (i.e., rain, snow, and springs). Therefore, it could be expected that even these anthropogenic water sources would be subjected to the effects of future drying projected over the course of this century (Ault et al. 2014; Cook et al. 2015; Seager et al. 2013; Wada et al. 2013). If water availability significantly decreases, it is likely that efforts would be made to maintain these water sources via supplementation. But these efforts would be costly, time-intensive, and likely short-lived due to the difficulty of maintaining water availability in so many water sources across such a large area.

Our study provides evidence that the reduction of water can differentially impact competing species of bats based on their morphologies. In addition, these findings illustrate how ecomorphology mediates access to a resource and highlights conservation implications as water

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becomes more limited in arid environments. Based on our findings, less-maneuverable species of bats will likely experience difficulty or delayed access from increasingly smaller bodies of water as water loss continues throughout desert regions. Selection for differences in wing morphology and flight ability in insectivorous bats has allowed for coexistence and high species richness at a local scale. However, anticipated reductions in the sizes of water sources due to climate disruption may lead to less-maneuverable species being unable to access water efficiently or being outcompeted by more agile fliers.

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Table 4-1. Distribution of bat calls across species at Mojave and Great Basin Deserts during our observational and experimental sampling from May to August 2010-11. Observational sampling occurred at 60 water sources of different sizes over a total of 92 nights. Experimental sampling occurred at two large water tanks (30.66 m2) over a total of 10 nights.

	Number of calls		
Species	Mojave^{obs}	Mojave^{exp}	Great Basin^{obs}
Less-maneuverable			
Eptesicus fuscus	182	129	11
Euderma maculatum	74	*	6
Lasionycteris noctivagans	10	3	7
Lasiurus blossevillii	3	7	*
Lasiurus cinereus	58	3	8
Tadarida brasiliensis	82	20	7
Maneuverable			
Antrozous pallidus	46	74	3
Corynorhinus townsendii	65	30	1
Myotis californicus	1563	2095	9
Myotis ciliolabrum	127	238	1163
Myotis evotis	6	5	*
Myotis lucifugus	3	23	39
Myotis thysanodes	31	6	8
Myotis volans	4	20	6
Myotis yumanensis	100	77	*
Parastrellus hesperus	3923	9404	68

^{obs} Observational sampling (surveys).
^{exp} Surface area experiment.
* denotes lack of detection of species.

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Table 4-2. Coefficients from mixed-effects logistic models for the presence of less-maneuverable and maneuverable bats. Data were collected at 60 water sources in the Mojave and Great Basin Deserts from May to August 2010 and May to July 2011.

Model	Coefficient	Estimate	SE	*p*
Less-maneuverable base[a]	Intercept	-2.72	1.52	0.07
	NearNeighbor[c]	0.00	0.00	0.15
	Obstructed[d]	0.00	0.00	0.82
	AvgTemp	0.11	0.05	0.04
	AvgWind	0.16	0.10	0.13
Less-maneuverable water[b]	Intercept	-6.30	3.40	0.06
	WaterSize	2.61	1.17	0.03
	NearNeighbor[c]	0.00	0.00	0.24
	Obstructed[d]	0.00	0.00	0.79
	AvgTemp	0.18	0.11	0.09
	AvgWind	0.15	0.16	0.36
Maneuverable base[a]	Intercept	-6.29	17.36	0.44
	NearNeighbor[c]	0.01	0.03	0.66
	Obstructed[d]	0.04	0.53	0.95
	AvgTemp	5.66	6.50	0.38
	AvgWind	-1.46	12.56	0.91
Maneuverable water[b]	Intercept	-4.80	12.09	0.06
	WaterSize	-3.78	4.85	0.16
	NearNeighbor[c]	0.02	0.01	0.07
	Obstructed[d]	0.05	0.08	0.51
	AvgTemp	7.18	2.91	0.01
	AvgWind	-5.44	2.39	0.02

[a] Base models accounted for variation in site (random effect), cluster sample (random effect), water source (random effect), temperature (°C), average wind speed (m/sec), presence of flight obstructions, and nearest neighbor distances (m) for water sources.
[b] Water models were identical to base models with the exception of the "WaterSize" variable.
[c] Mean distance (m) from the three nearest water sources to water source sampled.
[d] Obstruction of ≥ 0.5 m in height adjacent to the water source.

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Table 4-3. Mixed effects logistic models for the presence of less-maneuverable and maneuverable bats. Data were collected from May to August 2010 and May to July 2011 at 60 water sources in the Mojave and Great Basin Deserts.

Model	K[a]	AIC_c[b]	$\Delta\mathrm{AIC}_c$[c]	LL[d]	w_i[e]	R^2_{marg}[f]	R^2_{cond}[g]
Less-maneuverable bats							
Base[h] + Water size	8	104.50	0.00	-43.20	1.00	0.49	0.81
Base[h]	7	122.40	18.25	-53.20	0.00	0.25	0.53
Maneuverable bats							
Base[h]	7	72.20	0.00	-36.20	0.70	0.05	0.71
Base[h] + Water size	8	73.50	1.71	-36.30	0.30	0.02	0.57

[a] Numbers of parameters.
[b] Akaike's Information Criterion corrected for small samples.
[c] Change in AIC_c value compared to top model.
[d] Model log-likelihood.
[e] AIC_c weight.
[f] Marginal R-squared values (variance explained by fixed effects).
[g] Conditional R-squared values (variance explained by fixed and random effects).
[h] Base models accounted for variation in site (random effect), cluster sample (random effect), water source (random effect), temperature (°C), average wind speed (m/sec), presence of flight obstructions, and nearest neighbor distances (m) for water sources.

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Table 4-4. Coefficients from a mixed effects ANOVA model comparing drinking ratios (number of drinking passes/total passes) between control and treatment nights for less-maneuverable and maneuverable bats. Data were collected at two livestock water tanks in the Mojave Desert that were experimentally manipulated in a crossover fashion over 10 nights in August of 2011.

Coefficient			*df*	*t*	*p*
Intercept	0.70	0.05	12.68	14.82	< 0.01
Group[a]	0.11	0.07	35	1.65	0.11
Treatment[b]	-0.13	0.07	35	-1.91	0.06
Group[a] x Treatment[b]	-0.56	0.09	35	-5.93	< 0.01

[a] Maneuverability group (i.e., maneuverable and less-maneuverable).
[b] Experimental reduction of surface area.

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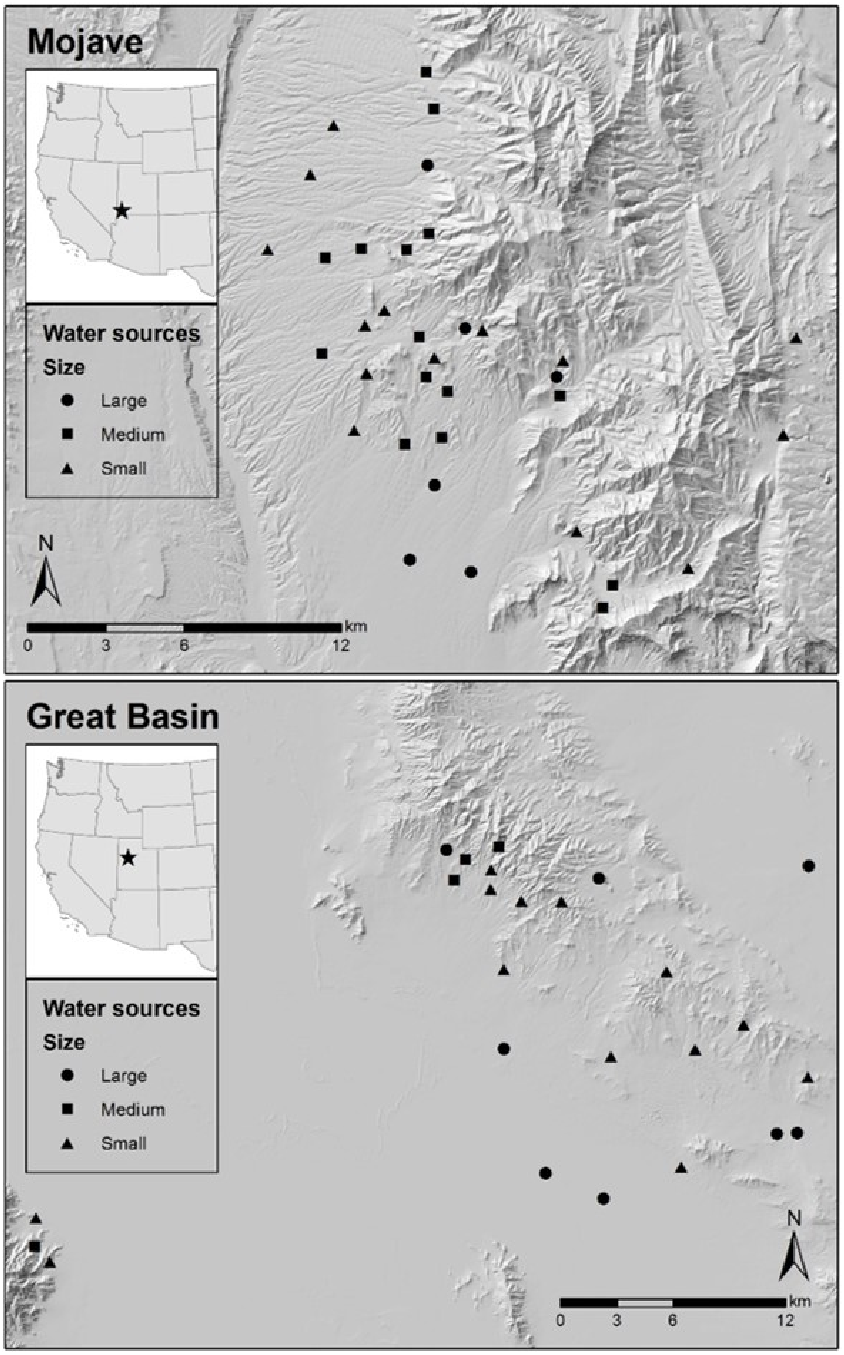

Figure 4-1. Distribution of water sources acoustically sampled from May to August 2010 and May to July 2011 in the Mojave (top panel) and Great Basin (bottom panel) Deserts. Small water sources had a surface length < 2 m, medium water sources had a surface length between 2 and 5 m, and large water sources had a surface length > 5 m.

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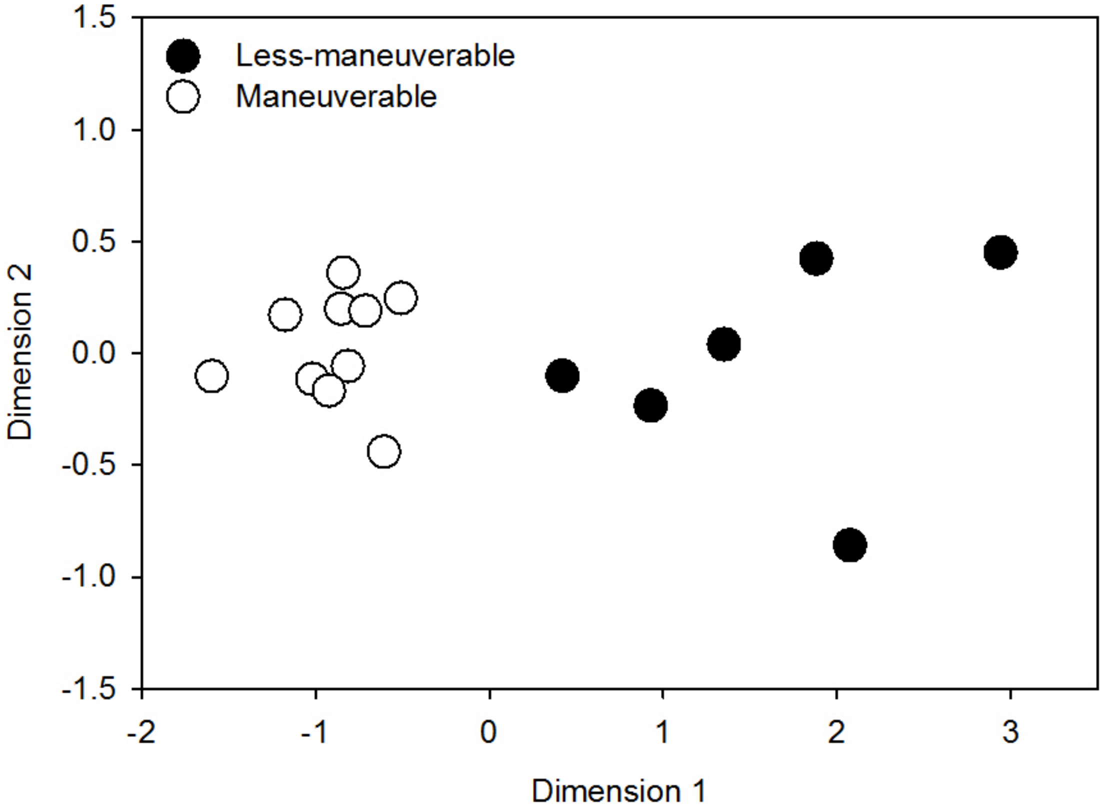

Figure 4-2. Non-metric multidimensional scaling (NMDS) plot illustrating differences between less-maneuverable and maneuverable species of bats based on aspect and wing-loading characteristics that influence flight maneuverability ($p < 0.01$).

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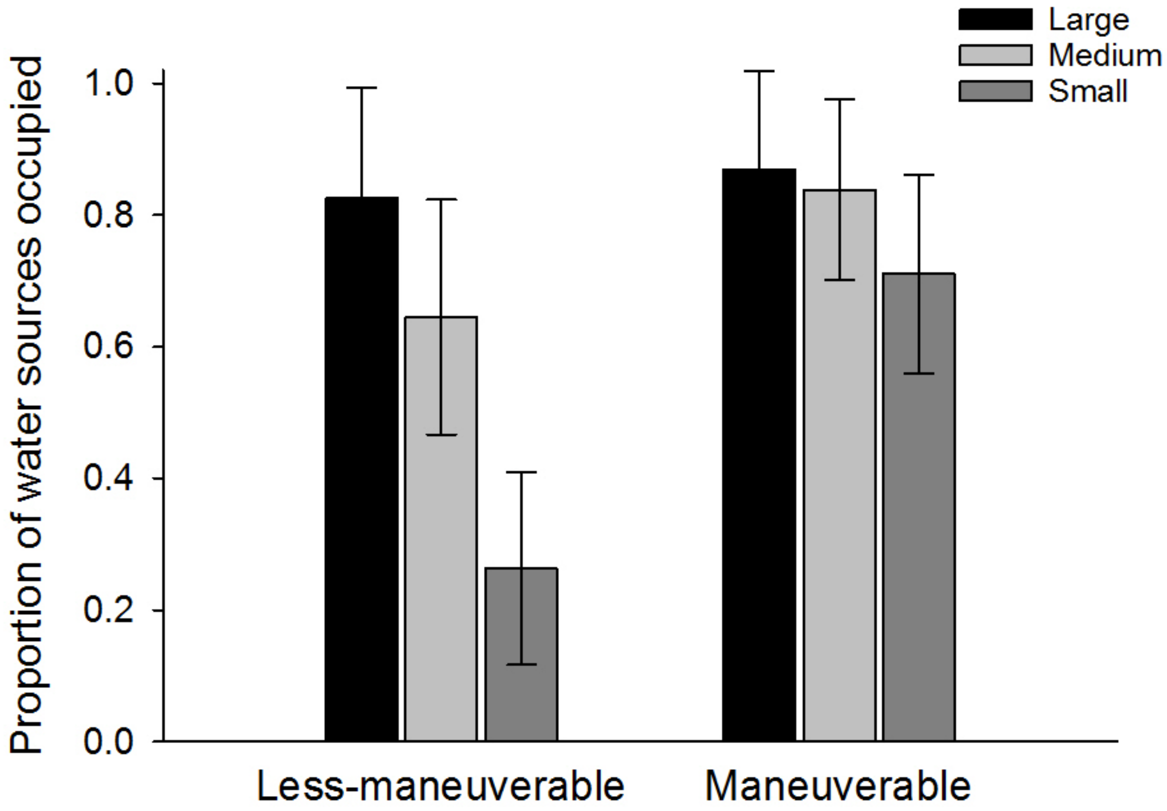

Figure 4-3. Proportion of water sources (±95% CI) where less-maneuverable and maneuverable bats were present. Data were collected across 60 water sources of different sizes in Mojave and Great Basin Deserts from May to August 2010 and May to July 2011. Small water sources had a surface length < 2 m, medium water sources had a surface length between 2 and 5 m, and large water sources had a surface length > 5 m.

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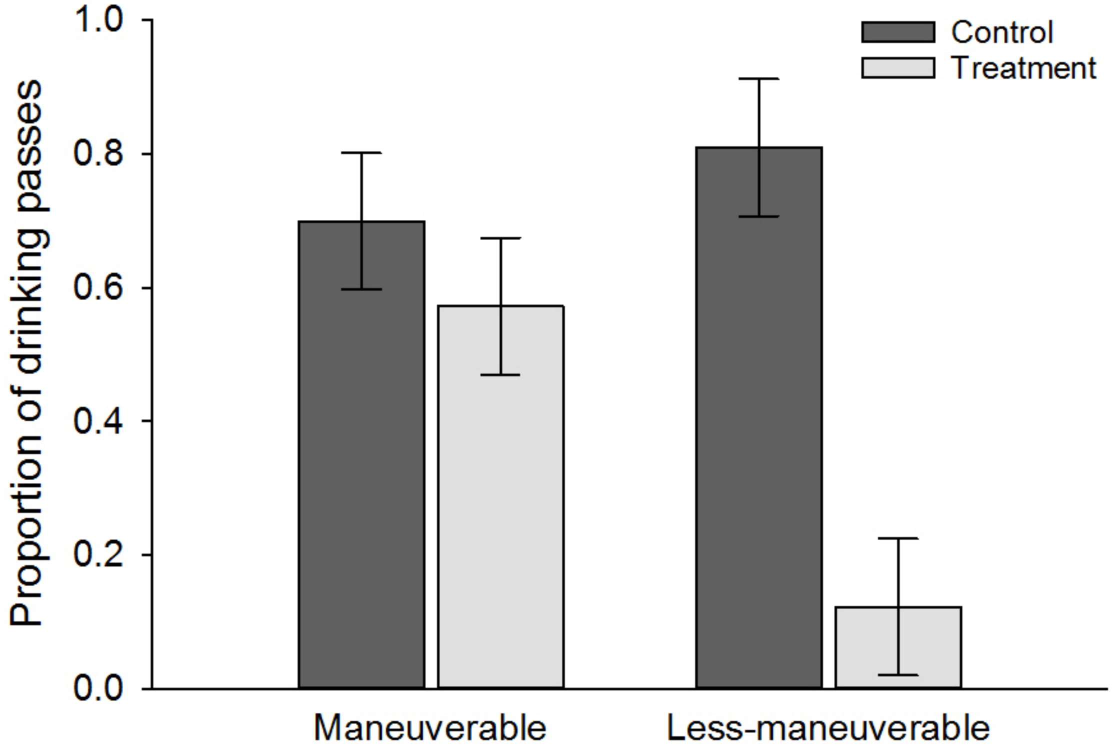

Figure 4-4. Mean drinking ratios (i.e., number of drinking passes/total number of passes; ±95% CI) for less-maneuverable and maneuverable bats at two water tanks on control and treatment nights when we experimentally reduced surface area in a crossover design. On treatment nights, less-maneuverable bats experienced a reduction of drinking ratios, whereas maneuverable bats did not. Data were collected in August 2011 in the Mojave Desert.

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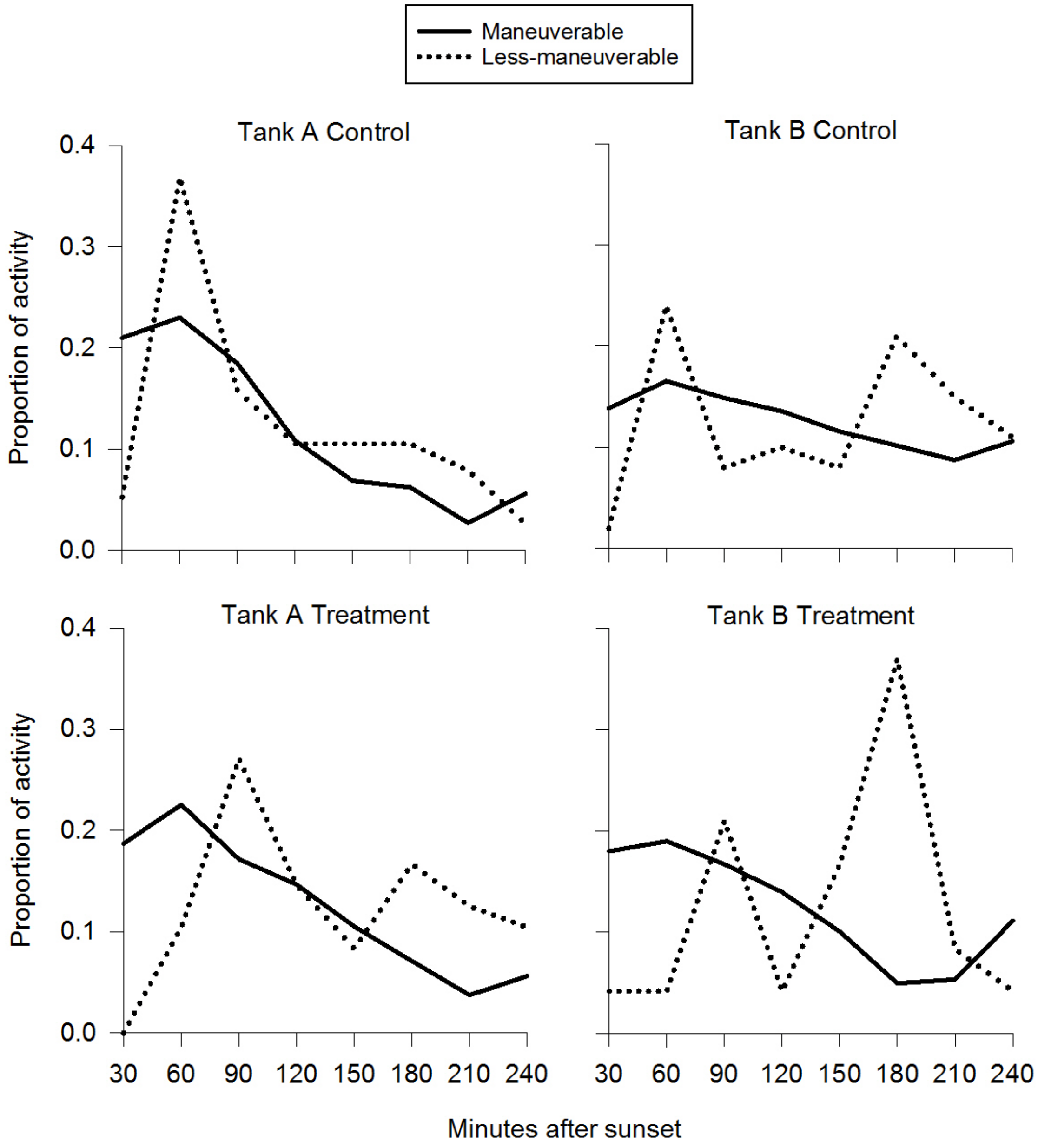

Figure 4-5. Proportion of activity (number of calls during each 30-min interval/total number of calls for that group in a night) of less-maneuverable and maneuverable bats at each experimental water tank on control and treatment nights where surface area was experimentally reduced. There was a difference in proportional activity (plotted lines) between control and treatment nights for less-maneuverable bats ($p < 0.01$), but not maneuverable bats ($p = 0.98$). Data were collected in August 2011 in the Mojave Desert.

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