

Competition Dynamics within Communities of Desert Organisms at Water Sources

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RESEARCH OBJECTIVES

For this dissertation, I will be testing hypotheses related to resource competition among different communities of desert animals in the Great Basin and Mojave Deserts of Utah. Chapter one will evaluate the influence of exotic horses (*Equus caballus*) on patterns of water use by communities of native birds and mammals. Chapter two will discuss the potential dual role of interspecific competition from exotic horses and increased aridity on drinking patterns of pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). Chapter three will determine which best explains activity patterns of subordinate carnivores at water sources: presence of dominant carnivores or habitat preferences. Chapter four will assess the role of interspecific competition and flight maneuverability among desert bats when water is experimentally reduced. Work from this dissertation will culminate in four full-length publications.

CHAPTER 1

Influence of exotic horses on the use of water by communities of native wildlife in a semi-arid environment

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INTRODUCTION

Competition for limiting resources influences the organization and structuring of biotic communities (Schoener 1974, Carothers and Jakšić 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 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.

Communities with species that have co-evolved likely have better developed strategies for coexistence than newly formed communities that have not been subject to evolutionary time. For example, within the community of native herbivores in semi-arid Africa that compete for access to limited water, there is evidence that the large-bodied elephant (*Loxodonta africana*) influences community structure at waterholes (Valeix et al. 2007a). Smaller herbivores that compete with elephants tend to avoid peak times of elephant visitation to waterholes. These smaller herbivores have co-existed with elephants for a long time 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 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, 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). Communities with large-bodied, behaviorally dominant exotic species may be susceptible to disruptions in community structure due to a lack of time for subordinate competitors to evolve adaptations for resource partitioning.

The horse (*Equus caballus*) is a large, exotic 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). Exotic horses (and burros [*E. asinus*]) have also displaced native ungulates from preferred habitats and water sources (Ostermann-Kelm et al. 2008, Attum et al. 2009, Girard et al. 2013). Water can be limiting for species inhabiting arid or semi-arid environments (Rautenstrauch and Krausman 1989, Cain III et al. 2006, Cain III et al. 2012) and there may be implications for species that compete with horses for water. Horses are gregarious, behaviorally dominant, and water-limited (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 other species at water sources. However, little is known concerning the degree

to which horses compete with communities of native species for water in environments where water is scarce.

Our objective is to determine the influence of horses on the use of water by communities of native wildlife in the semi-arid Great Basin Desert. We will monitor water sources where horses have drinking access (horse included; hereafter HI) and water sources where horses are excluded with fencing (hereafter HE) to determine if there are differences in 1) composition of native communities or 2) temporal patterns of visitation by native species. We expect native species to alter either spatial or temporal use of water (indirect evidence of competition) to minimize overlap with horses. If spatial partitioning occurs, we predict that communities of wildlife will be less species-rich and less diverse at HI water sources compared to HE water sources. If temporal partitioning occurs, we predict that native species will alter visitation patterns to reduce potential interactions with horses.

METHODS & MATERIALS

Study area

We conducted this study on 631 km² 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 domestic livestock for more than 60 years allowing us to assess the influence of exotic horses on wildlife communities at water sources without this potential confounding influence.

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). 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 Re却onyx PC900 covert infrared cameras (Re却onyx, 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 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.

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.

CHAPTER 2

Predicting impacts of warming climates and competition from exotic horses on access to water by native ungulates

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INTRODUCTION

Managing the effects of exotic species is an increasing global problem (Sanders et al. 2003, Pimentel et al. 2005, Preston et al. 2012). Exotic species can have dramatic impacts on ecosystems by altering and degrading habitats as well as negatively affecting native species (Bradley 2010, Dorcas 2012, Porter et al. 2014). Attempts to control exotic species are often faced with multiple challenges, but control efforts can be even more difficult with exotic species that have shared close relationships with humans over time (Vanak and Gompper 2010, Graham et al. 2012, Krauze-Gryz et al. 2012). Managing exotic species that are or have been domesticated (e.g., feral cats) can present public and political challenges, because of societal viewpoints, furthering the inability to appropriately manage these species.

The horse (*Equus caballus*) is a domesticated exotic ungulate that was introduced to North America in the 16th century (Mills and McDonnell 2005). Since its introduction, the horse has become widespread in western North America. Populations currently exceed appropriate management levels and are increasing by 15 to 20% per year (Palmer et al. 2013). However, horses are commonly perceived as an iconic species of the American West and public opinion and sentiment often precede conservation priorities for ecosystems (Taggart 2008, Bies et al. 2011). The federal protection of horses makes effective management problematic, costly, and controversial (Linklater et al. 2002, Bies et al. 2011). Despite efforts to manage horses,

current practices and methodologies appear to be inadequate to achieve desired population levels (Palmer et al. 2013).

Increased numbers of horses have been linked to impacts on arid and semi-arid landscapes and some of the species inhabiting these environments (Beever 2003, Beever and Aldridge 2011, Davies et al. 2014). Horses have been implicated in disturbing habitat features such as soil and vegetation via trampling, excessive nutrient deposition, and overgrazing (Loydi and Zalba 2009, Ostermann-Kelm et al. 2009, de Villalobos et al. 2011, Parvage et al. 2011). Horses have also been negatively associated with decreased diversity and abundance of fossorial invertebrates and small vertebrates (Beever and Brussard 2004, Beever and Herrick 2006). Yet, despite horses being a large-bodied, behaviorally dominant species, there has been relatively little work assessing their ability to outcompete their closest native competitors (i.e., ungulates) for limiting resources.

Water is a communal resource that is limiting in arid and semi-arid landscapes (Valeix et al. 2007b). Water plays an important role for horses and native ungulates such as pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). Water deprivation studies have showed that horses experience significant losses of body mass, extracellular fluid, and plasma volume over a 3 day period (Carlson et al. 1979). Based on calculations of water intake, pronghorn require drinking water in addition to preformed and metabolic sources to survive times of heat stress (Beale and Smith 1970, Fox et al. 2000, Tluczek 2012). Dependence on water by mule deer is largely evident by increased water intake and proximity to water sources during periods of heat stress (Bowyer 1984, Hervert and Krausman 1986, Hazam and Krausman 1988, Rautenstrauch and Krausman 1989, Boroski and Mossman 1996). Water consumption by horses (up to 33 L/day) is significantly greater than that of pronghorn (up to 3 L/day) and mule deer (up to 6 L/day) during biological stress times (Beale and Smith 1970, Groenendyk et al.

1988, Hazam and Krausman 1988, Thluczek 2012). However, during these physiologically demanding times, water is often least available (Valeix et al. 2008). Moreover, projected climate conditions for arid regions are likely to further compound seasonal fluctuations in water availability (Seager et al. 2007, Mamtimin et al. 2011). In the West, temperatures are projected to increase while precipitation decreases (Cook et al. 2004, Seager et al. 2007), with regions projected to experience multi-decadal megadrought conditions over the next 50 years (Ault et al. 2014, Borsa et al. 2014). Further constrained access to an already limited resource will likely lead to intense levels of interspecific competition.

Larger, more competitive species can drive temporal and spatial patterns of water use by smaller species (Valeix et al. 2007a, Valeix et al. 2008, Atwood et al. 2011, Brawata and Neeman 2011). The relatively large body of the horse most likely favors their ability to outcompete smaller, native ungulates for limited water (Miller 1983). Horses may impose direct interference competition on these ungulates at water sources (Miller 1983, Gooch 2014), potentially resulting in injury or disease from direct contact (Atwood et al. 2011). During times of heat stress, horses may also monopolize the already limited amount of available water for native ungulates (i.e., exploitative competition; Miller 1983). However, there is no consensus regarding the ability of horses to drive patterns of water use by native ungulates in arid environments. Previous research has illustrated that horses can exclude native ungulates from water, while other work has demonstrated complete sympatry between horses and native ungulates at water (Meeker 1979, Miller 1983, Ostermann-Kelm et al. 2008). The studies that have attempted to address this issue often lack rigorous temporal and spatial replication in sampling effort, particularly emphasizing interspecific interactions when water is likely most limiting. Overall, we lack an understanding of the competitive role that horses may have on

native ungulates during hot and dry times, which would provide a basis for competitive exclusion.

Our objective was to determine if horses outcompete pronghorn and mule deer for a limiting resource. To achieve this, we compared competition dynamics for horses and native ungulates at water sources along two neighboring mountain ranges in the Great Basin Desert. At the Cedar Mountains, horses and native ungulates are sympatric, but nearly half of the water sources have fencing that exclusively prevent horses from accessing water while allowing native ungulates free access. At the Thomas-Dugway Mountain range, pronghorn and mule deer co-occur in the absence of horses. Our sampling approach will allow us to better determine the influence of horses on temporal and spatial patterns of water use by native ungulates, with particular focus on periods of increased aridity. We predicted that horses will have the greatest impact on native ungulates at the smallest water sources during the times of greatest physiological need for water. We expected pronghorn and mule deer to spatially and/or temporally alter their patterns of drinking to minimize competition with horses.

METHODS & MATERIALS

Study Areas

We conducted this research at two study areas located approximately 40 km apart in the Great Basin Desert of western Utah. The Cedar Mountain study area consisted of 800 km² of land managed by the United States Department of Defense, United States Army Dugway Proving Ground. Elevations across the study area ranged from 1300 to 1800 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). In this study area, we identified 25 permanent water sources (13 fenced sites) consisting of 14 water developments, 9 natural springs, and 2 man-made ponds.

The Thomas-Dugway study area consisted of 700 km² of land managed by United States Department of the Interior, Bureau of Land Management. Elevations in this study area ranged from 1500 to 1900 m. Similar to the Cedar Mountain study area, typical vegetation types also included invasive grasslands mixed with desert shrubs at lower elevations with pinyon-juniper woodlands occurring at higher elevations. Annual weather consisted of mean air temperatures of 14.2° C with mean precipitation of 185 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). At Thomas-Dugway we identified 17 water sources (only 1 fenced site) which included 13 water developments and 4 natural springs.

FIGURES

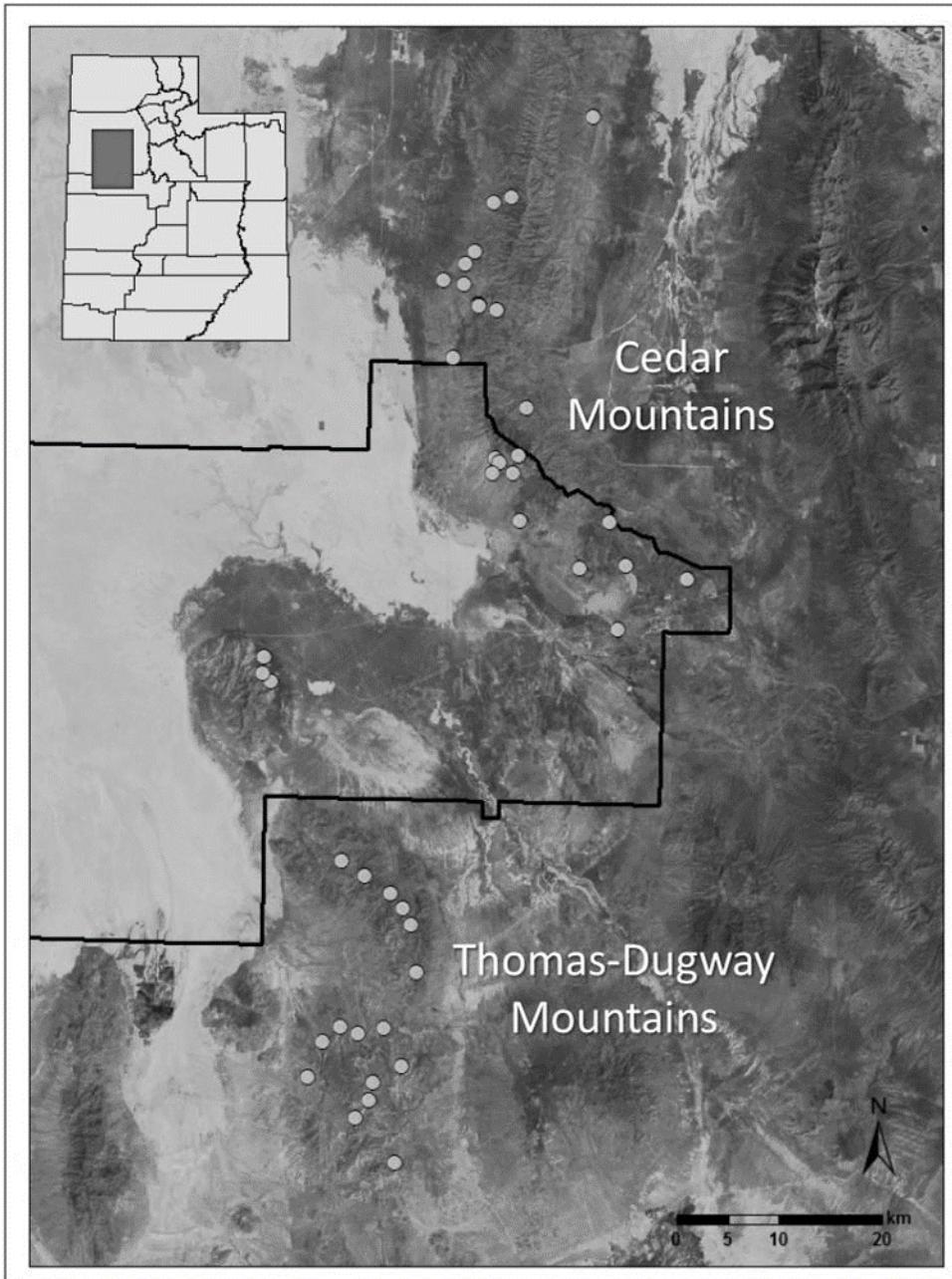


Figure 1. Location of mountain ranges where ungulate data was collected. Black line represents the US Army Dugway boundary. Gray circles represent water sources where camera sampling will occur.

Data Collection

We used infrared-triggered cameras at all known water sources in both study areas to photograph ungulates. By using cameras we avoided the potential effects of direct observation by humans on the behavior of animals (Bridges and Noss 2011). We secured cameras to metal posts and place them approximately 3 m from the edge of water where animals can drink. 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 can drink. We considered proximity to trails and recent sign to determine the location of cameras at ponds and large springs (Atwood et al. 2011). Approximately every two weeks we checked and performed any necessary maintenance to the cameras. We monitored water sources from May to October 2010 to 2014. This seasonal window likely captured the “wet and cool” periods of early and late summer associated with minimal use by ungulates as well as the “hot and dry” periods during mid-summer where visitation rates are greater (Shields et al. 2012).

To determine relative patterns of visitation by ungulates, we first extracted the time and date metadata associated with each camera image. With time and date information, we then categorized images into species visits. We defined a species visit as any sequence of images separated by at least 30 min. Thus, photo sequences occurring more than 30 min apart were considered independent events (Michalski and Peres 2007).

To account for the influence of site characteristics on the use of water by wildlife (Larsen et al. 2007, Larsen et al. 2011, Larsen et al. 2012), we measured sizes of water sources (surface area and shoreline edge), topographical and vegetative characteristics associated with a 30 m area around each water source. We assessed cover and density of vegetation using a Random T-Square sampling design (Krebs 1999). To measure vegetation height (and visibility), 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. Using ArcGIS (ArcMap, version 10.2, Environmental Systems Research Institute, Redlands, California), we calculated topographical obscurity (view-shed) around water sources at 25 m intervals (up to 100 m) using a 10 m resolution digital elevation model.

Statistical Analyses

We used generalized linear mixed models to determine if horses negatively influence spatial patterns of water use by native ungulates. With mixed effects models we were able to treat individual water sources as fixed effects, while including the variability in ungulate visitation and weather as random effects. Our response variables were the number of visits by pronghorn and mule deer per day. In addition, we included model covariates such as water size, habitat characteristics, and weather variables such as temperature ($^{\circ}\text{C}$), number of days since last precipitation event, and relative humidity. We conducted analyses with model covariates to identify the occurrence of autocorrelation, in which case, variables with an r value greater than 0.7 were removed from model analyses (Carpenter et al. 2010).

To assess the influence of horses on temporal patterns of drinking by native ungulates, we identified periods of proportional peak activity for each species (Adams and Thibault 2006). We determined peak activity by calculating the proportion of visits that occur each hour of the day. We then generated temporal use curves using proportional activity for horses, pronghorn, and mule deer. With G -tests, we statistically compared temporal use curves between study areas and horse-excluded and horse-included water sources to determine if horses are associated with altered temporal patterns of native ungulates in early (May to mid-June), mid (mid-June through August), and late summer (September through October). We performed all analyses using

Program R (R Development Core Team 2011). We will set the level of significance for all statistical tests at $\alpha = 0.05$.

CHAPTER 3

Do subordinate carnivores alter temporal and spatial activity to reduce competitive interactions
with dominant carnivores at water sources?

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INTRODUCTION

Where communal resources are limiting, the likelihood of interspecific competition increases (Ronconi and Burger 2011, Robles et al. 2012). In resource-limited scenarios, partitioning can play a significant role in mediating competitive interactions between species, thus minimizing interspecific competition and promoting coexistence (Albrecht and Gotelli 2001, Amarasekare 2003, Cristescu et al. 2013). While there can be multiple factors influencing how resources are partitioned, body size is an important attribute conferring strong competitive advantages to large species (Bloch et al. 2011, Nascimento et al. 2011, Reed et al. 2012). For example, within carnivore communities, larger species not only tend to outcompete smaller species for resources, but examples of interspecific killings are common (Palomares and Caro 1999, Fedriani et al. 2000, Moehrenschlager et al. 2007, Cupples et al. 2011). Intense resource competition coupled with the likelihood of mortality, results in well-defined dominance hierarchies between species of carnivores (Berger and Conner 2008, Levi and Wilmers 2012, Cristescu et al. 2013). Where asymmetric competitive interactions occur between dominant and subordinate species, there is a greater risk for the subordinate species to directly interact or compete with the dominant species. Thus, it has been proposed that subordinate species will modify or adjust their behavior and activity to avoid or minimize potential competitive interactions with dominant species (Switalski 2003, Scheinin et al. 2006, Nakayama and Fuiman 2010).

Evidence of partitioning of food and habitat resources is relatively common within carnivore communities in a variety of systems (Fedriani et al. 1999, Thornton et al. 2004, Borchert et al. 2008, Schuette et al. 2013). However, subordinate carnivores generally face a more difficult trade-off between resource acquisition and mortality compared to dominant carnivores. Subsequently, subordinate carnivores are likely to be relegated to “fringe” or marginal habitat to minimize the risk of mortality as a result of intense competition by dominant carnivores (Durant 1998, Fedriani et al. 1999). For example, kit foxes (*Vulpes macrotis*) primarily used disturbed habitats with low prey availability and avoided more productive habitats where coyotes (*Canis latrans*) were present (Warrick and Cypher 1998, Nelson et al. 2007, Kozlowski et al. 2008, Kozlowski et al. 2012). Examples of larger, dominant carnivores driving behavior and activity patterns of smaller, subordinate carnivores are evident (Jones 1998, Atwood and Gese 2008, Mukherjee et al. 2009). However, there is little information regarding the impact that dominant carnivores may have on subordinate carnivores for access to drinking water in arid and semi-arid systems.

Water is a spatially and temporally constraining resource in arid landscapes (Thrash et al. 1995, Valeix et al. 2008, Valeix 2011). The increased physiological demand of water during periods of increased aridity may lead to heightened competitive interactions between competing species (Miller 1983, Valeix et al. 2007a). Previous work has indicated that larger carnivores may be exerting competitive pressures on smaller carnivores at water sources (Atwood et al. 2011, Brawata and Neeman 2011). Gray foxes (*Urocyon cinereoargenteus*) were observed occupying rugged, seemingly low-value habitat and conforming patterns of temporal activity towards nocturnal hours (Atwood et al. 2011). However, there may be other reasons (aside from the presence of larger competitors) that are accounting for patterns of habitat use and temporal activity of smaller carnivores.

Our objective was to test the hypothesis that dominant carnivores drive temporal and spatial activity of subordinate carnivores at water sources. We monitored water sources in two North American deserts where dominant carnivores, such as the coyote and bobcat (*Lynx rufus*), are present and determine their relative impacts on the spatial and temporal activity of the American badger (*Taxidea taxus*), gray fox, and kit fox. If larger carnivores negatively influence the activity of smaller carnivores, then we expected that subordinate species will reduce spatial and temporal overlap with dominant carnivores to minimize the likelihood of competitive interactions.

METHODS

Study Areas

This study was conducted at sites in both the Great Basin and Mojave Deserts. The Great Basin Desert study area consisted of 915 km² of land managed by the United States Department of Defense, United States Army Dugway Proving Ground in west-central Utah. The terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats that were dominated by black greasewood (*Sarcobatus vermiculatus*). Where wildfires had occurred along the foothills, cheatgrass (*Bromus tectorum*) was common within communities of big sagebrush (*Artemisia* spp.), rabbitbrush (*Chrysothamnus* spp.), and juniper (*Juniperus osteosperma*) (Arjo et al. 2007). Elevations across the study area ranged from approximately 1300 to 1800 m. Annual weather consisted of mean air temperatures of 12.69° C (range: -20.02 to 40.58° C) and mean precipitation of 150 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). In this study area, we identified 22 permanent water sources consisting of 11 water developments for wildlife, 6 natural springs, and 5 man-made ponds.

The Mojave Desert study area consisted of 1,064 km² of public land managed by the United States Department of the Interior, Bureau of Land Management. The Mojave study area was located in extreme southwestern Utah, northwestern Arizona, and southeastern Nevada and was approximately 360 km south of our Great Basin study area. The Mojave study area was characterized by an alternating landscape of rolling hills/ridges and dry desert washes radiating from the Beaver Dam Mountains and emptying into the Beaver Dam Wash to the southwest near the intersection of the Utah-Nevada-Arizona state borders (Hall et al. 2013). In burned areas, exotic grasses (e.g., *B. rubens*) were prevalent and interspersed among surviving communities of native vegetation. Along the foothills, the vegetation primarily consisted of sagebrush and juniper, transitioning to pinyon pine (*Pinus edulis*) at higher elevations. Elevations across the Mojave 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). We identified 66 permanent water sources in this study area consisting of 35 water developments for wildlife, 18 water troughs/tanks for livestock, 11 natural springs, and 2 man-made ponds.

FIGURES

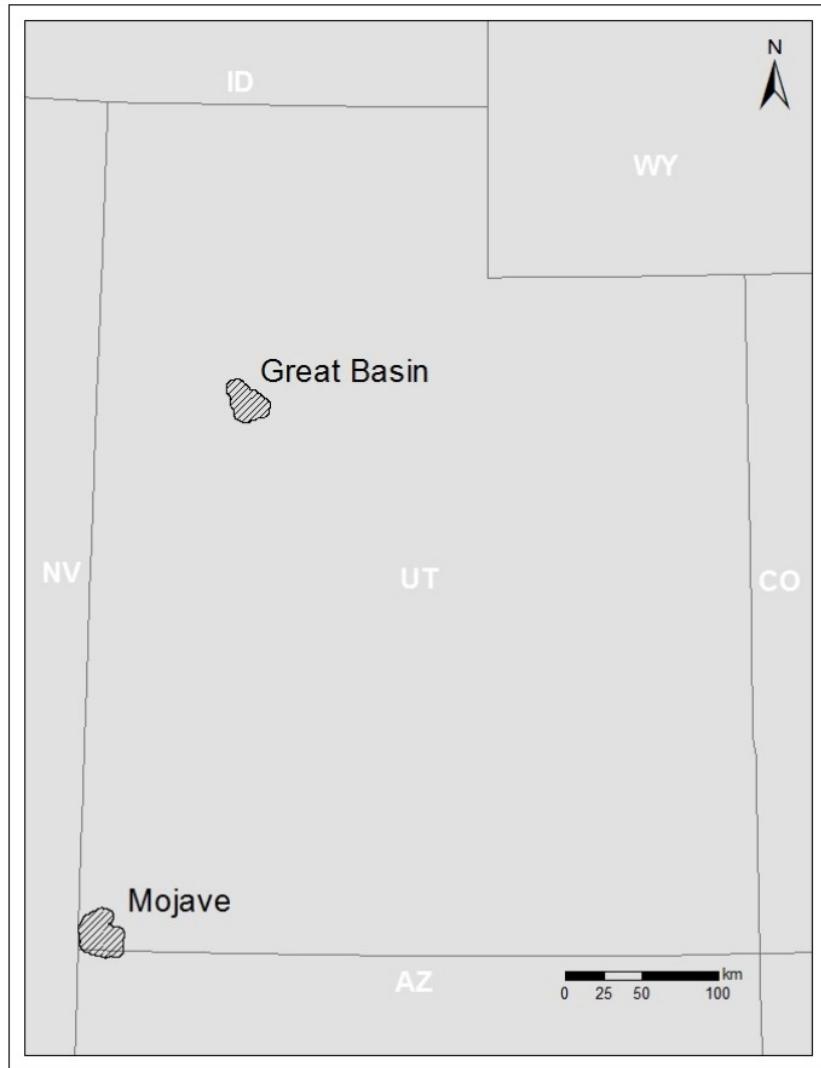


Figure 1. Location of study areas where carnivore data was collected.

Data Collection

To evaluate relative rates of visitation to water sources by canids, we monitored all known water sources at the Great Basin and Mojave study areas. From May to October, 2010 to 2012, we used infrared-triggered cameras to detect canids at water sources. We randomly sampled water sources with cameras at both study areas for approximately two-week periods. To determine which water sources to sample for a given period, we generated random points within each study area using ArcGIS (ArcMap, version 10, Environmental Systems Research Institute, Redlands, California). We then identified the nearest water source to a random point and camera-sampled as many water sources as possible (up to 15 sites). We attached cameras to metal posts and placed them approximately three meters from water sources. At large water sources with multiple locations of drinking access, we positioned cameras at a minimum of two locations where animals can drink. We considered proximity to trails and recent sign as determinants for the location of cameras at large water sources (Atwood et al. 2011). Our estimates of visitation by canids at large water sources are likely be conservative due to the inability to monitor all potential locations where canids can access water. We assumed however, that any potential bias is similar at large water sources from both study areas.

We used date and time stamps associated with photos from the cameras to generate visits of carnivores at water sources. We then calculated indices of relative activity for each species of carnivore at each water source by dividing the number of visits by the number of days that cameras were operable. We considered a visit as all photo occurrences of a single species within 30 min and treat these as independent events (Michalski and Peres, 2007).

Since habitat can be an influential determinant of space use by carnivores (Anderson 1990, Horne et al. 2009, Graham et al. 2012), we measured vegetation characteristics and conducted geospatial analyses up to 100 m around each water source. We estimated cover and

density of vegetation with a Random T-Square sampling approach (Krebs 1999). To measure visibility (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. Using ArcGIS (ArcMap, version 10, Environmental Systems Research Institute, Redlands, California), we calculated topographical obscurity (view-shed) and ruggedness around water sources at 25 m intervals (up to 100 m) using a 10 m resolution digital elevation model. Some water sources had structural roof cover that could influence carnivore behavior (Hall et al. 2013) and captured this variation by categorizing each water source as covered or uncovered.

Statistical Analyses

We evaluated support for spatial partitioning among carnivores using generalized linear mixed effects models and AIC model selection (Burnham and Anderson 2002). We employed a two-stage approach for AIC model selection (Carpenter et al. 2010). First, we used stepwise regression to identify candidate models using habitat variables that best explain variation in our response variables (relative activity of subordinate carnivores). We considered candidate models to be competing if ΔAICc (adjusted for small sample sizes) scores were within two AICc points of the lowest AICc value (Burnham and Anderson 2002).

Second, with our top competing candidate models, we then constructed additional models by solely adding the relative activity of dominant carnivores as a model covariate. Again, we evaluated top models by assessing ΔAICc scores. We then evaluated both the log likelihood and AICc values associated with top models to identify any models with uninformative parameters. We judged model parameters as uninformative if 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 approach permitted us to determine the relative importance of dominant carnivores on the activity of subordinate species with habitat as a potential alternative explanation.

To determine if dominant carnivores drive temporal patterns of activity by subordinate species, we first generated measures of proportional activity for each species. We identified peak activity for each occurring species by calculating the proportion of visits that occur during each hour of the day (Razgour et al. 2011). We then created temporal use curves using proportional activity for carnivore species. Using *G*-tests, we statistically compared patterns of temporal activity, focusing specifically on periods of peak activity, between dominant and subordinate carnivores. We also compared temporal activity for each subordinate species between sites where dominant carnivores are common and where they are rare or absent. We performed all analyses using JMP Pro 11 (SAS, Cary, North Carolina, USA). We set the level of significance for all statistical tests at $\alpha = 0.05$.

CHAPTER 3

Importance of competition and flight maneuverability for desert bats in a changing climate
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INTRODUCTION

Global climate change will lead to decreases in availability and size of water sources in arid environments (MacDonald 2010, Woodhouse et al. 2010, Dai 2011, Seager et al. 2013, Wada et al. 2013, Ault et al. 2014, Borsa et al. 2014, Cook et al. 2014, Cook et al. 2015). Increased anthropogenic use of natural sources of water will only exacerbate these decreases (Taylor et al. 2013, Wada 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). Prolonged drought in the Colorado River Basin of western North America and decreased availability of surface water has increased human reliance on, and unsustainable use of, groundwater reserves (Castle et al. 2014). Future availability of water is a defining crisis for western North America as mega-droughts are projected to occur over the next several decades (Seager et al. 2007, Ault et al. 2014, Cook et al. 2015, Wanders et al. 2015).

The consequences of climate change and continued water loss will likely impact resource availability and the stability of biotic communities (Williams and Jackson 2007, Lecomte et al. 2009, Williams et al. 2012, Peterman and Semlitsch 2014). Water is a communal resource that is temporally and spatially limiting in arid systems, making it a major and driving influence in arid environments (Hillel and Tadmor 1962, Noy-Meir 1973, Hawkins et al. 2003). The ability to access and compete for limited water will become increasingly important among species of desert communities as water becomes scarce. However, while climate change and water loss are predicted to alter community dynamics and composition (Walther et al. 2002, McCain 2007,

Sinervo et al. 2010, Dawson et al. 2011, Razgour et al. 2013), mechanisms underlying the differential responses of desert species to accelerated rates of warming and unprecedeted loss of water are largely unknown (Loarie et al. 2009, Sherwin et al. 2013).

Bats are a species-rich taxa common to arid environments, despite physiological predispositions to water loss (e.g., high surface area to volume ratios, large membranous wings, etc; Hattingh 1972, Webb et al. 1995). The sensitivity of bats to rising temperatures and concomitant loss of water makes them important indicators of climate change (Jones et al. 2009, Newson et al. 2009, Adams 2010, Razgour et al. 2013). Bats rely on open access to free (drinking) water, especially for reproduction (Kurta et al. 1989, Adams and Hayes 2008). Consequently, desert water sources are focal points for multiple species of bats (Arlettaz 1999, Korine and Pinshow 2004, Williams and Dickman 2004, Rebelo and Brito 2007). However, while desert bats have evolved differing morphologies/flight characteristics to minimize competition for insect prey, loss of water will make it increasingly necessary for bats to compete for access to declining water sources (Adams and Thibault 2006, Razgour et al. 2011, Adams et al. 2012).

Because bats drink in flight their ability to compete for and access water is dependent on their maneuverability. Larger, 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, Franci 2008, Razgour et al. 2010). Fewer available water sources with smaller dimensions may disadvantage larger, less maneuverable species, leading to a compositional shift in the structure of bat communities towards more maneuverable species that can better access smaller bodies of water. The potential for morphological differences between ecologically-similar species to drive responses to contemporary climate change has received very little attention. Understanding how bat communities respond to reduced water sources is integral for

the conservation of bat communities, particularly as water becomes increasingly scarce in arid and semi-arid regions (McCain 2007, Adams and Hayes 2008, Adams 2010, Jones and Rebelo 2013, Sherwin et al. 2013).

Our objective was to determine if less maneuverable bats were more affected than more maneuverable bats in accessing and competing for water when water was reduced under a simulated climate change scenario. We first used an observational approach and acoustically sampled water sources in two deserts of western North America to determine the influence of surface area (hereafter SA) on presence and activity of low and high maneuverability bats (hereafter LM and HM, respectively). We then experimentally reduced the SA of water sources to assess changes in drinking behavior and interspecific competition between bat species. We predicted that LM bats would 1) frequent and drink less at small water sources (observational and experimental), and 2) experience increased interspecific competition (e.g., temporal partitioning) with HM bats when SA was reduced.

METHODS

Study Areas

We conducted this study at water sources in the Mojave and Great Basin Deserts. The Mojave Desert study area consisted of 635 km² of public land in extreme southwestern Utah managed by the US Department of the Interior, Bureau of Land Management. The Mojave study area was characterized by an alternating landscape of rolling hills/ridges and dry desert washes radiating from the Beaver Dam Mountains and emptying into the Beaver Dam Wash to the southwest near the intersection of the Utah-Nevada-Arizona state borders. Invasive annual grasses such as red brome (*Bromus rubens*) were well established among creosote (*Larrea*

tridentata), Joshua-tree (*Yucca brevifolia*), and blackbrush (*Coleogyne ramosissima*) communities. Along the foothills, the vegetation primarily consisted of big sagebrush (*Artemesia tridentata*) and juniper (*Juniperus osteosperma*), transitioning to pinyon pine (*Pinus edulis*) at higher elevations. Elevations across the Mojave study area ranged from approximately 800 to 2000 m. Annual weather consisted of mean air temperatures of 19.91° C (range: -10.20 to 40.10° C) and mean precipitation of 126 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). We identified 66 permanent water sources in this study area consisting of 34 water developments for wildlife, 18 water troughs/tanks for livestock, 11 natural springs, and 3 man-made ponds.

The Great Basin Desert study area consisted of 675 km² of land managed by the US Department of Defense, US Army Dugway Proving Ground and the US Department of the Interior, Bureau of Land Management. The Great Basin study area was located in west-central Utah, approximately 360 km north of Mojave. The terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats that were dominated by black greasewood (*Sarcobatus vermiculatus*). Cheatgrass (*B. tectorum*) was common within communities of big sagebrush, rabbitbrush (*Chrysothamnus* spp.), and juniper. Elevations across the study area ranged from approximately 1300 to 1800 m. Annual weather consisted of mean air temperatures of 13.27° C (range: -20.00 to 40.60° C) and mean precipitation of 156 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). In this study area, we identified 25 permanent water sources consisting of 10 water developments for wildlife, 1 water tank for livestock, 8 natural springs, and 6 man-made ponds.

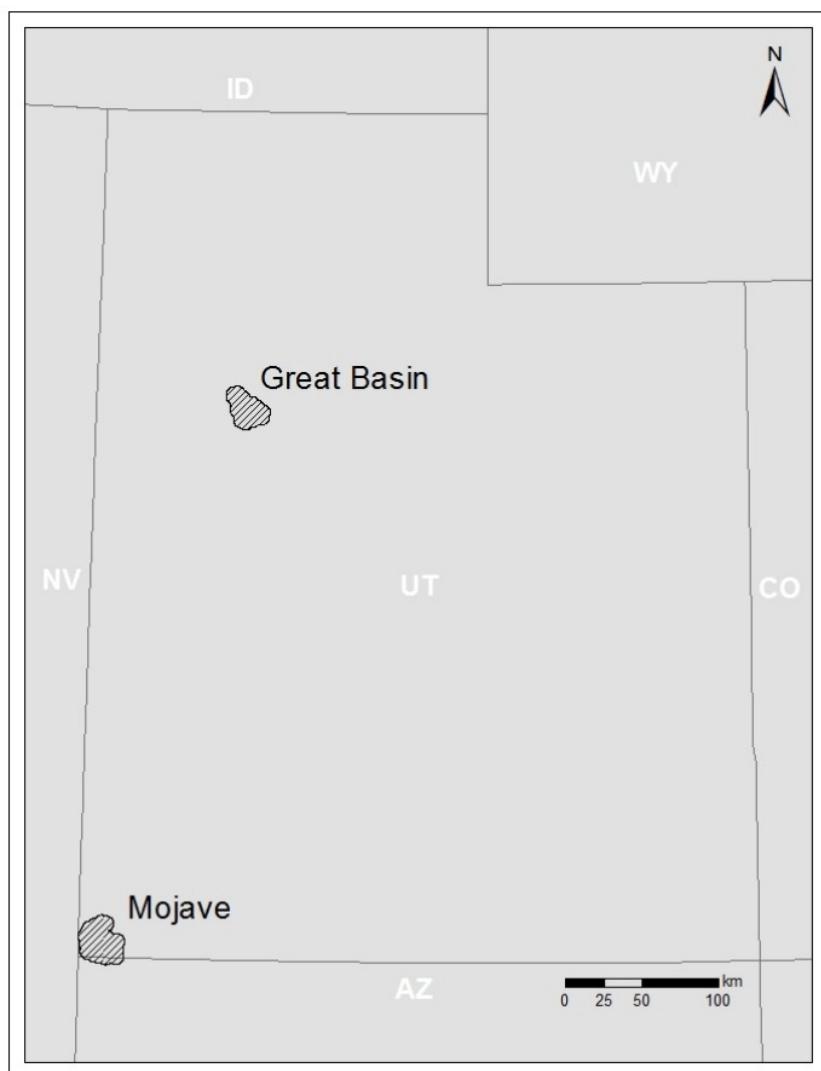


Figure 1. *Location of study areas where bat data were collected.*

Observational Data Collection

From May to August of 2010 and 2011 we used AR125 bat detectors and FR125-III data recorders (Binary Acoustic Technology, Tucson, Arizona, USA) at both study areas. We selected water sources using a clustered sampling scheme by randomly selecting a point in space within a geographic information system (GIS) and then locating the nearest known water source. From that water source we then located the next two nearest water sources for sampling and deploy bat detectors at our three selected water sources for one night. We sampled with replacement so each water source was eligible for re-sampling. During equipment setup, we positioned microphones on tripods approximately 3 m away from water sources. Acoustic recording began at 2100 hr (approximately at sunset) and ended at 0100 (total of 4 hr), which time period corresponded to nearly all bat activity for the species in this region (Jones 1965, O'Farrell et al. 1967, Ruffner et al. 1979). On windy nights (wind speed surpassing 15 km/hr), we avoided acoustic sampling (O'Farrell et al. 1967, O'Farrell and Bradley 1970). Following acoustic sampling, we used Sonobat software version 3 (Sonobat, Arcata, California, USA) to identify bat calls to species. We set our acceptance classification criteria for bat calls at 90% (i.e., 90% of each recorded call will have to match a known reference of a bat call).

We categorized each water source into one of three sizes (large ≥ 5 m, medium < 5 m and ≥ 2 m, or small < 2 m) of surface water length. To account for the influence of obstructions on accessibility of water by bats, we assessed characteristics of the surrounding habitat (Jackrel and Matlack 2010). We considered water sources as being obstructed based on low levels of water and the presence of potential obstacles (e.g., vegetation, rocks, catchment canopies, fences) adjacent to water sources.

Experimental Data Collection

We conducted our SA experiment at Mojave because of high diversity and activity of bats in this area. In late July through August of 2011, we monitored two water tanks for livestock frequented by bats. We ensured that both tanks had consistent levels of water during our study period. The tanks were 3.5 km apart and located in similar habitat (i.e., creosote flats with Joshua trees). Both tanks were void of any obstructions in the immediate vicinity that could negatively influence flight maneuverability of bats. Each tank was 0.6 m tall and circular in design, measuring 6.25 m in diameter and providing 30.66 m² of SA. 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 at each tank. We initiated video and audio recording at 2100 h and concluded at 0100 h. We analyzed video recordings to differentiate between drinking and nondrinking passes using The Observer XT10 behavioral analysis software (Noldus, Leesburg, Virginia, USA) (Adams & Simmons 2002). We then matched timestamps between the audio and video files to determine drinking behavior of identified species (Razgour et al. 2010).



Figure 2. *Water storage tank that was used for surface area manipulation experiment in the Mojave Desert.*

We imposed SA restrictions on each of the two water tanks. After monitoring two control nights on each tank, we restricted the SA dimensions on one tank to 2.25 m^2 (average SA for small water sources from both study areas) for five subsequent nights. During this time, we continued monitoring the other water tank unmodified. Following the five night manipulation period, we removed SA restrictions from the first water tank. One night later, we repeated the process for the second water tank while monitoring the first tank unmodified. We used the unmodified periods before and after manipulation as control nights. In total, we accumulated 7 control and 5 treatment nights for each tank.

Statistical Analyses

To analyze use of water sources by bats based on maneuverability, we first classified all species into LM and HM groups based on aspect ratios, wing-load ratios, and average mass of species (Norberg and Rayner 1987, Brigham 1988, Holloway and Barclay 2001). Low maneuverability bats will include *Eptesicus fuscus*, *Euderma maculatum*, *Tadarida brasiliensis*, *Lasiurus cinereus*, *Lasionycteris noctivagans*, and *L. blossevillii*, which are relatively heavier bats with faster, less maneuverable flight. High maneuverability species consisted of all occurring Myotis species (*M. californicus*, *M. ciliolabrum*, *M. lucifugus*, *M. evotis*, *M. thysanodes*, *M. yumanensis*, and *M. volans*), *Parastrellus hesperus*, *Antrozous pallidus*, and *Corynorhinus townsendii*, all of which have lower wing-load ratios and higher aspect ratios with slower, more maneuverable flight.

For our observational data, we used generalized linear regression and model selection to determine the influence of water size on maneuverability groups of bats (Burnham and Anderson 2002). We first established base models which included temperature (a known predictor of bat activity (Korine and Pinshow 2004)), presence of obstructions near water (Jackrel and Matlack 2010), nearest neighbor distances (average distance of the 3 nearest water sources (Ruffner et al. 1979, Razgour et al. 2011)), and study area (Great Basin or Mojave). We then added a water size variable to each of these models to determine the relative influence of the size of water sources on the activity and occurrence of the different maneuverability groups. We used Akaike's Information Criterion adjusted for small sample size (AICc) to compare base models to water models (Akaike 1974). We considered models to be competing if they were within two ΔAICc values of the model with the lowest AICc value (Burnham and Anderson 2002).

For our experimental data, we compared drinking behaviors and activity patterns of bats between control and treatment nights. First, we compared the number of non-drinking and

drinking passes between LM and HM groups using one-tailed *t*-tests. Second, we sorted activity times into 30 minute intervals for LM and HM groups. To determine if our SA experiment induced changes in temporal partitioning, we compared peak arrival times and proportional activity within both groups (Adams and Thibault 2006, Razgour et al. 2011). We used *G*-tests of independence (Sokal and Rohlf 1981) to determine if proportional activity differed between control and treatment nights for LM and HM groups. We also compared the proportional activity within these groups using *G*-tests. We used JMP Pro 11 (SAS, Cary, North Carolina, USA) for all statistical analyses. We set the level of significance at $\alpha = 0.05$ and use Bonferroni adjusted α -levels for series of statistical analyses (*t*-test $\alpha = 0.125$; *G*-test $\alpha = 0.006$).

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