Spatial Patterns and Population Performance of Mule Deer: Responses to Water Provisioning in Mojave National Preserve, California

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources and Environmental Science

by

Cody J. McKee

Dr. Kelley M. Stewart/Thesis Advisor

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We recommend that the thesis
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CODY J. MCKEE

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MASTER OF SCIENCE

Kelley M. Stewart, Ph. D., Advisor

James S. Sedinger, Ph. D., Committee Member

Vernon C. Bleich, Ph. D., Committee Member

Thomas P. Albright, Ph. D., Graduate School Representative

Marsha H. Read, Ph. D., Dean, Graduate School

May, 2012
THESIS ABSTRACT

There are four habitat components essential for vertebrate species: food, cover, space, and water (Mackie 1981). In areas where water is limited, but those other 3 components are readily available, the provisioning of water is expected to benefit populations of wildlife. Development of water sources in arid regions of the western United States has been a common practice used by wildlife and range managers in both state and federal agencies since the early 20th century (Broyles 1995, Rosenstock et al. 2001, Krausman et al. 2006). As evidence of the considerable popularity of this practice, water development programs were present in 10 of 11 state wildlife agencies in 1997, accounting for over 6000 developed water sources (Rosenstock et al. 1999).

Despite widespread use of water developments in wildlife and range management, few empirical studies have adequately evaluated the effects of those water sources on wildlife ecology (Broyles 1995, Krausman et al. 2006, Cain et al. 2008). Broyles (1995) questioned the utility of water developments, and further suggested the necessity, benefits, and harmful side effects had not yet been evaluated. Conversely, others contend that water developments provide intrinsic benefits to wildlife populations (Rosenstock et al. 1999, Bleich 2005, Krausman et al. 2006). Although the provision of water for wildlife has developed into a controversial topic, investigators agree that there is a need for more experimental research evaluating the influence of water developments on species ecology (Broyles 1995, Broyles and Cutler 1999, Rosenstock et al. 1999, Krausman et al. 2006, Simpson et al. 2011).
Over the last 2 decades, research evaluating the effects of water developments on wildlife has increased (Krausman and Etchberger 1995, Broyles and Cutler 1999, Dolan 2006, Marshal et al. 2006a, Cain et al. 2008). None of those studies, however, have conclusively determined the ecological benefits of anthropogenic water developments on wildlife. In a study of desert sheep (*Ovis canadensis nelsoni*) in Arizona, USA, Broyles and Cutler (1999) argued that desert sheep obtained adequate water to meet metabolic demands from available forage and, thus, were not reliant on available free-water. Nonetheless, Rosenstock et al. (2001) identified several flaws in their experimental design and interpretation of data, and ultimately determined the conclusions of Broyles and Cutler (1999) to be “useless.” Cain et al. (2008b) evaluated the response of desert sheep to the removal of water developments and found little change in spatial patterns or population performance. The results of that research were, however, confounded by cool temperatures and above-average precipitation during the treatment (water-removal) phase of their experiment (Cain et al. 2008). Other published literature has been mostly subjective and the conclusions anecdotal (Dolan 2006).

Based on the lack of definitive results, a long-term, experimental study was needed to account for factors such as environmental stochasticity encountered in Cain et al.’s (2008b) research or the design flaws inherent in previous research (Broyles and Cutler 1999, Rosenstock et al. 2001). The goal of my research was to identify the effects of water developments on mule deer (*Odocoileus hemionus*) inhabiting a Mojave Desert ecosystem. I focused my research efforts on those ungulates because many water development projects are implemented to induce changes in their spatial patterns and population performance (Broyles 1995, Krausman and Etchberger 1995, Dolan 2006,
The results of my research could have profound implications for wildlife management in desert ecosystems, as well as for water management in the west.

Mule deer are widely distributed throughout western North America and occupy a variety of habitat types, including the Canadian boreal forest, the Great Basin Desert, the Colorado Plateau, and the Mojave Desert (Wallmo 1981). The ability to adapt to extreme temperatures and precipitation gradients distinguishes mule deer from many other species of ungulate (Wallmo 1981). In areas of low habitat productivity, such as desert ecosystems, mule deer require large areas to maintain viability of populations (Marshal et al. 2006b). Nutritional quality and availability of forage (Rautenstrauch and Krausman 1989, Marshal et al. 2005), cover (Ordway and Krausman 1986), natal sites (Fox and Krausman 1994), and availability of free-standing water (Marshal et al. 2006a) are all used to assess suitability of those large areas for long-term persistence of mule deer. During times of water scarcity, mule deer are particularly reliant on the availability of free-standing water (Rautenstrauch and Krausman 1989, Rosenstock et al. 1999). In arid regions and particularly during the hot-dry season, the availability of permanent sources of water may be the most important component of habitat for mule deer.

Spatial distributions of mule deer are intimately linked to availability of resources on the landscape. Seasonal changes in space use due to changes in resource availability have been documented in a variety of ungulate species including desert sheep (Cain et al. 2008) and desert mule deer (O. h. crooki; Relyea et al. 2000). During times of water scarcity, typically the hot-dry season, water content of forage is also limited. Mule deer have been reported to change distribution and home range to incorporate permanent sources of water during the hot-dry season (Rautenstrauch and Krausman 1989).
Conversely, when permanent water sources are unavailable, mule deer have been shown to increase daily movements and home range size to locate sources of water (Hervert and Krausman 1986), which is likely an expensive energetic allocation. Mule deer inhabiting resource-limited environments exhibit larger home ranges and increased movements to meet their energetic demands and, alternatively, they exhibit smaller home ranges and decreased movements in environments with abundant resources (Ordway and Krausman 1986, Relyea et al. 2000, Marshal et al. 2006a, Bender et al. 2007). If water is a limiting resource in desert landscapes inhabited by mule deer, then patterns of space use would be influenced by changes in the availability of that resource.

Changes in density and distribution of ungulate populations are often linked to changes to changes in body condition, productivity, and survival (McCullough 1979, Eberhardt 2002, Cook et al. 2007, Bishop et al. 2009). Moreover, populations constrained by density-dependent processes exhibit poor body condition, low productivity, and low survival when at or near ecological carrying capacity (McCullough 1979, Kie et al. 1980, Stewart et al. 2005). The underlying mechanisms of population dynamics dictating density dependence are driven primarily by the availability and quality of resources on the landscape (Kie and White 1985, Stewart et al. 2002, Bender et al. 2007, Bishop et al. 2009, Parker et al. 2009). Mule deer inhabiting desert ecosystems occur at low densities with large ranges (Marshal et al. 2006b) presumably due to limited availability of resources on the landscape (Marshal et al. 2005, Bender et al. 2007, Bleich et al. 2010). If availability of permanent sources of water is limiting in desert environments, then mule deer should reduce their effort spent acquiring free-water when
sources of permanent water are provided. Mule deer could then reallocate those efforts to foraging, which could, ultimately, improve body condition, productivity, and survival.

In chapter 1, I evaluated movements, distribution, and resource selection (i.e., patterns of space use) of mule deer in response to provisioning of water developments in Mojave National Preserve, California, USA from 2008-2011. I hypothesized that deer would alter movements and distribution to improve access to permanent water, particularly during times of water scarcity. I also hypothesized that proximity to permanent water would be a significant component of resource selection by mule deer, and that mule deer would exhibit selection for sites near those sources. I used general linear models with random effects for individual mule deer to evaluate the influence of water availability and season on daily movements and area of mule deer distributions. I used nonlinear mixed-effects models to evaluate the importance of water in models of resource selection by mule deer and to determine the magnitude of that water effect.

In chapter 2, I evaluated responses in body condition and traits of demography of mule deer to provisioning of water developments. I hypothesized that mule deer with improved access to permanent sources of water would exhibit greater body fat, greater fetal rates, and higher survival than those in areas where water was limited. I used general linear models to evaluate the influence of water availability and climatic conditions on body condition. I then modeled the effects of water availability, body condition, and climatic conditions on fetal rates using logistic regression. Finally, I used the known fates package in Program MARK to evaluate the effects of water provisioning, climatic conditions, and individual characteristics on survival patterns of mule deer and to estimate monthly and annual probabilities of survival.
LITERATURE CITED


DEDICATION

I dedicate this thesis to all who have a passion for wildlife and to those who treasure the intrinsic beauty of the desert.
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First and foremost, I thank my parents for introducing me to the outdoors and teaching me the value of hard work and perseverance. I also thank my family and friends for their unconditional love and support. I gratefully acknowledge financial and technical support from the National Park Service, California Department of Fish and Game, Nevada Department of Wildlife, University of Nevada in Reno, Safari Club International, the California Deer Association, and the Boone and Crockett Club. I thank my thesis advisory committee K. Stewart, V. Bleich, J. Sedinger, and T. Albright for guidance and many helpful comments of this manuscript. I thank N. Darby and D. Hughson of the National Park Service, as well as B. Pierce, K. Monteith, T. Stephenson, and B. Gonzalez of California Department of Fish and Game for field and methodological assistance. I also thank technicians N. Simpson, C. Morris, D. Gonzalez, T. Brown, J. Zweifel, I. Knight, J. Saenz, and numerous volunteers who helped collect data used in this thesis. All capture and handing of mule deer were compliant with procedures outlined by the California Department of Fish and Game, were approved by the University of Nevada Reno’s Institutional Animal Care and Use Committee (IACUC: 00058), and were consistent with the guidelines established by the American Society of Mammalogists for care and use of wild mammals in research (Gannon et al. 2007).
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SPACE USE PATTERNS OF MULE DEER IN RESPONSE TO EXPERIMENTAL WATER PROVISIONING IN A BURNED MOJAVE DESERT LANDSCAPE

Cody J. McKee¹*, Kelley M. Stewart¹, James S. Sedinger¹, Vernon C. Bleich¹, and Neal W. Darby²

¹Department of Natural Resources and Environmental Science, University of Nevada-Reno, 1664 N. Virginia Street, Reno, Nevada 89557, USA
²National Park Service, 2701 Barstow Road, Barstow, California 92311, USA

*Correspondence author. E-mail: cmckee@cabnr.unr.edu
Providing permanent water to habitats that are water-limited has been assumed to provide both practical and intrinsic benefits to wildlife populations in arid regions of the western United States. Recent studies attempting to delineate costs and benefits of providing permanent water to wildlife have been inconclusive due to a variety of confounding factors. We investigated the effects of water provisioning and natural wildfire on patterns of space use by mule deer (*Odocoileus hemionus*) in 3 study areas (i.e., control area, water-provided area, and water-limited area) of Mojave National Preserve, California, 2008-2011. We used general linear models to evaluate differences in daily movements and area of 95% and 50% utilization distributions (UDs) of 39 mule deer in response to water provisioning. We also used nonlinear mixed-effects models to evaluate the importance of permanent water in selection of resources of 40 mule deer. We detected differences among study areas in daily movements, area of the 95% UD, and area of the 50% UD. Pairwise comparisons indicated daily movements were similar in the water-provided area and water-treatment area but significantly less than the control area. Area of the 95% and 50% UD were significantly smaller in the water-provided area than both the water-limited area and control area. We found use of water to be important in models of resource selection among the 3 study areas but the use of that resource in the water-provided area was influenced by wildfire disturbance. Our results suggest wildfire has confounded our ability to detect an effect of water-provisioning and may also explain, in part, the differences observed in UDs of mule deer among the 3 study areas. Wildfire

1 The plural pronoun “We” will be used instead of “I” for the remainder of this thesis to indicate other authors in the two manuscripts submitted for publication.
often promotes the regeneration of high-quality forage to mule deer, which likely contains higher content of preformed water. Mule deer in the water-provided area may be able to meet both their nutritional and hydration needs while foraging in areas disturbed by wildfire, reducing the overall importance of access to sources of permanent water. We urge future investigators to consider multiple landscape-level effects when evaluating spatial patterns of species in arid environments.

Key Words: California, daily movement, Mojave Desert, *Odocoileus hemionus*, resource selection, utilization distribution, wildfire, water developments

INTRODUCTION

Development of water sources in arid regions of western North America has been a widely implemented management tool by state and federal wildlife agencies since the 1940s (Broyles 1995, Rosenstock et al. 2001, Krausman et al. 2006). Over the last 2 decades, a fervent dispute regarding the realized benefits of these developments on ecology of desert wildlife has become firmly rooted in the field of wildlife management (Broyles 1995, Broyles and Cutler 1999, Rosenstock et al. 1999, Krausman et al. 2006). Studies evaluating the influence of water developments on wildlife have been inconclusive and confounded by issues with experimental design (Broyles and Cutler 1999; see Rosenstock et al. 2001), were based on subjective information (Dolan 2006), postulated a lag effect in response to water provisioning (Marshal et al. 2006a), and experienced cool and wet years after removal of water sources (Cain et al. 2008b). Each
of these authors suggested further research is needed to adequately evaluate the influence of water source developments on ecology of desert wildlife.

The goal of development of water sources for wildlife is to provide a resource in landscapes perceived to be water-limited. Use of such developments by targeted wildlife has been the most common measure of success utilized by practitioners (Simpson et al. 2011). Several studies have documented use by wildlife at these water sources yet were unable to determine the effects of these resources on movements, distribution, or population performance (Krausman and Etchberger 1995, Marshal et al. 2006a, Cain et al. 2008b). Nonetheless, claims of poor quality of water, entrapment, increased predation, and competition (Broyles 1995, Rosenstock et al. 1999, Krausman et al. 2006) have been largely unsubstantiated (Andrew et al. 2001, Bleich et al. 2006, Simpson et al. 2011). Although the negative effects of water developments have been largely dismissed, positive influences of water developments on population performance of wildlife have not been identified, aside from increased abundance and distribution of various ungulate and upland game bird species (Rosenstock et al. 1999). Addressing the anticipated benefits of water developments on distribution and range, resource preferences, and population performance would provide a better understanding of the overall utility of water developments for wildlife (Simpson et al. 2011).

Despite recognition of the various issues confounding the investigation of water developments on wildlife, even the most robust experimental designs have not been resilient to stochastic events that are frequently encountered in large-scale ecological studies (Douglas and Leslie 1986, Oehler et al. 2003, Cain et al. 2008b). Unfortunately, the potential impacts of ecological conditions on results are often considered post hoc.
The capability to identify these phenomena \textit{a priori} would provide a more robust
approach to addressing issues surrounding complex ecological relationships, such as the
role of water developments in the ecology of desert wildlife.

In addition to increasing availability of permanent water in arid environments,
several authors suggest fire could improve habitat of ungulate populations across western
North America (Wallmo et al. 1981, Rogers et al. 2004), particularly in fire-adapted
experimental studies investigating the influence of fire on ungulate populations involve a
mosaic of burned and unburned habitats created by small prescribed fires, with the goal
of stimulating growth of high-quality herbaceous forage (Ruthven et al. 2000, Long et al.
2008, Meek et al. 2008). Nevertheless, the influence of large wildfires on ungulate
populations is under-represented in the current body of literature (Holl et al. 2004, Bleich
et al. 2008, Biggs et al. 2010), especially in desert ecosystems. The response of ungulates
to wildfire in a water-limited ecosystem is speculative and, in regions that have
experienced both wildfire activity and development of water sources, individuals may
select for areas that maximize allocation of water and forage of high productivity.
Alternatively, ungulates in these conditions may exhibit a preference for areas with
access to high quality forage or a preference for areas with access to permanent water.
Certainly, trade-offs associated with selection of resources have been documented in
desert ungulates, such as the Sonoran pronghorn (\textit{Antilocapra americana sonoriensis}),
which have been reported to select forage with high preformed water content but of low
nutritional quality (Fox et al. 2000). Variation in selection of resources by ungulates to
maximize nutrient intake in a burned landscape could confound experimental results and
lead to difficulties in interpretation of the responses of those animals to the development of permanent sources of water.

Mule deer (*Odocoileus hemionus*) are widely distributed throughout western North America and occupy a variety of habitat types, including the Canadian boreal forest, the Great Basin Desert, the Colorado Plateau, the Mojave Desert, and the Sonoran Desert (Wallmo et al. 1981). Indeed, the ability to adapt to extreme temperatures and precipitation gradients distinguishes mule deer from other ungulates (Wallmo et al. 1981). In areas of low productivity, such as desert ecosystems, mule deer require large areas to maintain viable populations (Bleich 2005, Marshal et al. 2006c). Characteristics commonly used to assess suitability of habitat for mule deer are nutritional quality and availability of forage (Rautenstrauch and Krausman 1989, Marshal et al. 2005a), cover (Ordway and Krausman 1986), natal sites (Fox and Krausman 1994), and availability of free-standing water (Marshal et al. 2006a). During times of water scarcity, mule deer are especially reliant on permanent sources of water (Rautenstrauch and Krausman 1989, Rosenstock et al. 1999). In arid regions, particularly during the hot-dry season, water may be the most important component of habitat for mule deer.

We evaluated movement patterns and resource selection of mule deer in response to provisioning of permanent sources of water in a Mojave Desert ecosystem. We were also interested in the influence of a large-scale wildfire on those responses. Our goal was to determine the relative importance of permanent water on spatial patterns of mule deer inhabiting a burned ecosystem. We hypothesized that deer will alter movements to improve access to permanent water, particularly during times of water scarcity such as the summer season. Thus, we predicted that individuals will exhibit restricted
movements and smaller utilization distributions (UD) where access to water is highest and that those metrics would vary by season. Additionally, we hypothesized that proximity to permanent water will be a significant component of resource selection by mule deer, and that they will exhibit selection for sites near those sources. We suspected, however, that use of permanent water may be confounded by severity of wildfire. We also predicted that access to water and wildfire severity, where applicable, would be significant parameters in competitive models of resource selection by mule deer.

**STUDY AREA**

We studied a population of mule deer in Mojave National Preserve (hereafter Mojave) in San Bernardino County, California, USA (35°00´N, 115°28´W) from January 2008 until March 2011. The general boundaries of Mojave are delineated on the north by Interstate Highway 15, on the south by Interstate Highway 40, and on the east by the California-Nevada state border (Fig 1). Mojave encompass nearly 650,000 ha and includes components of 3 of the 4 major desert ecosystems of North America: the Mojave, the Sonoran, and the Great Basin (National Park Service 2011). The overlap of these desert ecosystems has created a heterogeneous landscape characterized by distinct, rugged, mountain ranges composed of granite, basalt, and igneous rock separated by bajadas, playas, and dunes with elevations ranging from 270 m to 2400 m (Thorne et al. 1981). We concentrated our research efforts in the Cima Dome, Mid Hills, and New York Mountain regions of eastern Mojave (Fig. 1)
The climate of Mojave is representative of the arid southwestern USA. However, wide temperature and precipitation gradients occur between low and mid- to upper-elevations. Maximum temperatures at low elevations average 40.5°C in summer and 19°C in winter (Desert Studies Center 2011). Temperatures at mid- to upper-elevations are more moderate in the summer with mean maximum temperatures of 33°C and mean maximum temperatures of 13°C in the winter (United States Geological Survey 2010). Precipitation patterns are distinctly bi-modal with a cool season peak occurring during winter and a warm season peak occurring during the summer (Fig. 2). Mean annual precipitation at low elevation sites is 8.5 cm (1980-2005, Soda Springs, northern Mojave), while mean annual precipitation at mid- to upper-elevation sites is 27 cm (1958-1996, Mitchell Caverns Natural Preserve, southern Mojave).

We delineated seasons with a climograph (Stewart et al. 2002) developed from historical temperature and precipitation patterns collected at Mitchell Caverns Natural Preserve in southern Mojave from 1958-1996. The Mitchell Caverns weather station was ideal for our research objectives because it provided a long-term dataset of climatic conditions at a similar elevation to our study sites (1,300 m) and experienced similar weather phenomena. We identified four seasons as follows: winter (cool, wet) began approximately 1 December and lasted until 31 March, spring (warm, dry) began 1 April to 31 May, summer (warm, wet) began around 1 June and lasted until 31 September, and autumn (cool, dry) began 1 October to 30 November (Fig. 2).

Vegetation communities vary by elevation and precipitation gradient in Mojave. Creosote bush (*Larrea tridentate*) was abundant in low elevation bajadas and valleys. Mid-elevations <1,600 m with shallow, rocky, soils were characterized by cholla cactus
(Opuntia spp.), barrel cactus (Ferocactus spp.), blackbush (Coleogyne ramosissima), Spanish bayonet (Yucca spp.) and Joshua tree woodlands (Yucca brevifolia; Thorne et al. 1981). Mid-elevations >1,600 m contained Great Basin sagebrush (Artemesia tridentata), Utah juniper (Juniperus osteosperma), and pinyon pine (Pinus spp.; Thorne et al. 1981). White fir (Abies concolor) communities were present in the upper elevations (>1,800 m) of 2 mountain ranges (Clark Mountain and New York Mountains).

Various natural and developed sources of permanent water were present and available to mule deer before initiation of our research activities (Fig. 1). Natural and developed springs were predominately found in the New York Mountains and the Mid Hills, while water availability on Cima Dome was limited primarily to ground-water wells with above-ground catchments. Depending on climatic conditions, ephemeral springs, seeps, and tenajas can provide additional sources of water during winter, spring, and early summer. Wildlife documented to use permanent sources of water in Mojave include mule deer, desert tortoise (Gopherus agassizii), spotted skunk (Spilogale gracilis), mountain lion (Puma concolor), and Gambel’s Quail (Callipepla gambelii; N. Darby, unpublished data).

On 22 June 2005, a series of lightning strikes sparked several wildfires, occurring primarily in the Mid Hills area of Mojave. By 23 June 2005, these wildfires merged to form the Hackberry Complex Fire, which burned 28,700 ha (Fig. 1). The Hackberry Complex Fire created large expanses of sparsely vegetated desert habitat with few unburned remnant patches (Fig. 3). Many of the dominant species of vegetation in the pre-burned landscape (e.g. Utah juniper, Great Basin sagebrush, and barrel cactus) will take many decades to reestablish. Nevertheless, other native species including annual
and perennial herbaceous vegetation such as globemallow (*Sphaeralcea* spp.) and four o’clock (*Mirabilis* spp.), as well as some perennial shrubs, including bitterbrush (*Purshia tridentata* var. *glandulosa*) and desert almond (*Prunus fasciculata*), now dominate the post-fire landscape.

**METHODS**

**Experimental Design**

Mojave was primarily administered as livestock rangeland before designation as a unit of the National Park Service. During early settlement, numerous ground-water wells with above-ground catchments were developed to provide water for domestic livestock and homesteads. Most of these wells were instituted in the early 20th century. Not only did those developments provide a reliable source of water for livestock, they were also used by wildlife. After establishment of Mojave National Preserve (United States Congress 1994), many livestock wells were allowed to become inactive, effectively removing a permanent source of water for many species of wildlife.

We divided the central region of Mojave, where the overlap of mule deer and presence of wells (both active and inactive) was highest, into 3 study areas. Study area 1, Cima Dome, did not experience well deactivation. Those sources of permanent water have been available to mule deer since before the establishment of Mojave (hereafter control area). In study area 2, Mid Hills, deactivated livestock wells were reactivated in the fall of 2008 (hereafter water-provided treatment). In study area 3, New York Mountains, livestock wells were not reactivated (hereafter water-limited treatment).
Additionally, we added exclusionary fencing around the majority of permanent springs in the water-limited area to prevent access by mule deer but allowed for access by other wildlife. We investigated the response in movements and habitat selection patterns of mule deer in the three areas by comparing results among study areas, seasons, activity period (i.e., crepuscular hours and resting hours), and wildfire disturbance.

**Animal Capture and Handling Procedures**

We captured adult female mule deer during the winter or spring of each year of our study. Each individual was caught with a net-gun fired from a helicopter (Krausman et al. 1985a). We selected only one adult female per social group when conditions permitted. We transported captured individuals to a central processing location where they were fitted with Global Positioning System (GPS) radiocollars (Wildlife GPS Datalogger, Sirtrack, Havelock North, New Zealand) and were marked uniquely with ear-tags. We programmed each GPS collar to obtain one location every 1.5 hours (up to 16 locations per day) using GPS satellites and to remotely release from the deer approximately 1 year after deployment. A Very High Frequency (VHF) radio signal was incorporated into the design of each collar to allow for the immediate collection of dropped GPS radiocollars by ground crews. When the capture location was less than 1 km from the processing location, we released individuals from the central processing site. We transported individuals back to the capture location via vehicle or helicopter when it was greater than 1 km from the central processing site.
**Individual Heterogeneity**

We derived multiple data points related to patterns of movements, distribution, and selection of resources for each individual mule deer in Mojave. We anticipated that those data would vary among individuals and that multiple data points from the same individual would be correlated (Gillies et al. 2006, Duchesne et al. 2010). We therefore incorporated a random effect for telemetered mule deer into all models of spatial patterns and resource selection, which accounted for variation in the magnitude of response of individuals in those models and, ultimately, designated the individual as the sample unit (Gillies et al. 2006). Although we were interested in population-level responses to our water-provisioning experiment, incorporating a random effect for individual mule deer effectively controlled for pseudoreplication and incorporated the overall contribution of variation by individual level differences in our analyses.

**Patterns of Movement**

We imported locations from GPS radiocollars into a GIS (ArcGIS 9.3, Environmental Systems Research Institute [ESRI], Redlands, California, USA) for calculation of movement parameters. We used the Hawth’s Analysis Tools extension (Beyer 2004) to connect consecutive GPS locations with a straight-line and calculate distance moved between locations. We then summed straight-line segments to obtain distance traveled per day (km) for each animal. We also used the Hawth’s Analysis Tools extension (Beyer 2004) to calculate the 95% and 50% fixed kernel density (kde) estimates as a metric for estimation of area of an individual’s utilization distribution among seasons (UD; Worton 1989, Seaman and Powell 1996). We used the area (ha) of
the 95% kde to represent an individual’s entire UD and area of the 50% kde to represent an individual’s core area of use. We implemented least-squares cross-validation to estimate the smoothing parameter ($h$) of our kernel density estimates (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999).

We assessed distributions of movement data for normality (SAS Institute 9.2, Cary, NC) and performed a natural log transformation on both UD and daily movements. We used a mixed-effects analysis of variance (hereafter ANOVA) to evaluate differences in movement patterns of mule deer among study areas and seasons, in addition to an interaction between both of those main effects (PROC MIXED; SAS 9.2, Cary, NC). We evaluated homoscedasticity of errors of independent variables and distribution of model residuals for level 1 (random) and level 2 (main) effects using the SAS 9.2 macro MIXED_DX (Bell et al. 2010). We did not include a year effect in our ANOVA because logistical constraints resulting from a total helicopter crash during 2010 prevented collection of representative samples of individuals from each study area, and limited our power to detect differences among years (control area: 2 individuals, water-provided treatment area: 11 individuals, water-limited area: 2 individuals). As a result, only one year (2009) contained representative samples of individual mule deer from each study area. We employed the least-squared means procedure to evaluate pairwise differences in movement patterns. For this analysis, variation among study areas were interpreted as variation among treatment applications.
**Resource Selection**

We were first interested in identifying patterns of high and low activity that may be influencing resource selection by mule deer. We expected seasonal climatic conditions and photoperiod to influence these activity patterns and ultimately the selection of resources. Mule deer are most active during crepuscular hours when availability of resources is assumed to be a strong predictor of habitat selection (Johnson et al. 2000). During periods of low activity, mule deer may use landscape features unrelated to foraging or free-water acquisition such as accessing thermal refugia (Cain et al. 2006, Cain et al. 2008a) or predator avoidance (Geist 1998). Consequently, access to permanent sources of water may be more important during periods of high activity than during periods of low activity. Although errors in GPS locations were small (i.e. missed GPS fixes), we divided distances moved between consecutive locations by the number of hours elapsed between the two locations to obtain a movement rate (m/h; Cain et al. 2008b). We then calculated the mean of movement rates ($\bar{x} \pm SE$) by hour during the 24 hour cycle to identify periods of high activity (hereafter active) and periods of low activity (hereafter resting). Lastly, we assigned activity period (i.e., active or resting) to each location by visually identifying the times of day, by season, when animals are most active and least active.

We then developed a resource selection probability function (hereafter RSPF) to determine if resources were being used disproportionally to availability (Manly et al. 2002). We were not interested in building a predictive map from the resulting RSPF, but we were interested in understanding the relative effects of resources on likelihood of mule deer use. We evaluated resource selection by mule deer among the 3 study areas.
(hereafter global dataset) and explicitly within the water-provided treatment area
(hereafter watered dataset). This approach allowed us to investigate general patterns of
resource selection across the entire Mojave region, as well as conditions that were
specific to the water-provided study area (i.e. presence of springs, catchments, and
wildfire). We subsampled GPS location data from individual mule deer by randomly
selecting a single GPS location per day by assigned activity period to minimize spatial
 autocorrelation (Stewart et al. 2002). We limited our dataset to used locations occurring
between 1 October 2008, coinciding with the activation of water-developments, and 31
March 2011, the most recent date that deployed collars released from animals. We
subsequently evaluated selection of resources from 21,487 used locations collected from
40 individuals in the global dataset and 9,803 used locations from 20 individuals in the
watered dataset.

We evaluated resource selection within an individual’s UD (3rd order selection;
Johnson 1980) because mule deer in Mojave were constrained to habitable mountain
ranges that are separated by low elevation bajadas, playas, and sand dunes (i.e. 1st and 2nd
selection decisions would be based on availability of suitable mountain ranges; Johnson
1980). Furthermore, evaluation of UDs prior to analyses indicated that landscape
placement was strongly associated to those mountain ranges, as well as sources of
permanent water. We were explicitly interested in how individual mule deer used those
water sources within their UD rather than the general placement of their UD. We
therefore expected 3rd order selection patterns by mule deer to be the most impacted by
the supplementation of water sources. To quantify available resources within an
individual mule deer’s UD, we buffered used locations by the mean distance traveled per
day for each study area and season. This procedure bounds the distribution of available resources at a used location by the distance an individual may travel in a given day (Boyce et al. 2003, Johnson et al. 2006). We then matched used locations with two random locations from the bounded distribution of available resources to represent resource availability in our models of selection (Boyce et al. 2003, Johnson et al. 2006). We estimated the spatial error of locations by placing GPS collars in a known location for approximately 7 days, which was approximately 15 m. We subsequently buffered used and available locations by 15 m to reduce the effects of spatial error in our analysis of resource selection (Rettie and McLoughlin 1999).

We used a GIS to calculate landscape metrics expected to influence selection of resources at a 10 m x 10 m pixel resolution (Table 1). In accordance with our hypotheses, we included predictive covariates relating distance of used and available locations to nearest source of permanent water, as well as distance to water catchments and distance to springs. We delineated between types of water source because the water-provided area contained multiple springs before and during our research activities in Mojave. We suspected that the importance of springs in the area would provide insight into the overall importance of free water to mule deer if there was a lag effect by mule deer in response to activation of water catchments, documented by Marshal et al. (2006b). To quantify the effect of anthropogenic activity, we calculated the distance from used and available locations to maintained roads (i.e., high volume of traffic) and unmaintained roads (i.e., low volume of traffic). We evaluated the importance of the abiotic predictors, elevation, slope, ruggedness (Sappington et al. 2007), east-west aspect (aspect transformed by sine function), and north-south aspect (aspect transformed by
cosine function) calculated from a Digital Elevation Model (DEM; United States Geological Survey 2011) at used and available locations. We determined a coarse habitat type from land cover data obtained from the United States Geological Survey (USGS; Thomas et al. 2002). To better understand the influence of the Hackberry Complex wildfire on resource selection in the water-provided treatment area, we included 4 categorical variables related to wildfire severity, i.e. unburned, low severity, moderate severity, and high severity, which were based on changes in biomass, soil exposure, and byproducts of fire (Monitoring Trends in Burn Severity 2010). Finally, we included 4 categorical variables representing winter, spring, summer, and autumn season to evaluate seasonal differences in selection of resources.

We assessed explanatory variables for normality and implemented natural logarithmic and arcsine square root data transformations when appropriate (Zar 2010). We also evaluated correlations between variables (PROC CORR; SAS Institute, Cary, NC) and when 2 variables were correlated we removed one of highly correlated variables ($r \geq 0.60$; Long et al. 2008) from our models of resource selection. Distance of locations to water catchments and distance of locations to springs were strongly and positively correlated in the control area and strongly and negatively correlated in the water-limited treatment area. As a result, we modeled only the proximity of mule deer locations to nearest source of permanent water when evaluating our global dataset. We investigated the importance of springs and catchments, in addition to wildfire severity, in the water-provided treatment area only. Finally, we standardized covariates prior to model evaluation (Zar 2010).
We developed a candidate set of *a priori* models of resource selection (22 models in each dataset) and implemented mixed-effects logistic regression (Boyce et al. 2003, Fortin et al. 2009, Duchesne et al. 2010) to analyze the validity of the hypothesized relationships among model parameters and the probability of use. We included only parameter’s known to be meaningful from previous research or from our observations in the field as additive effects, fixed effects, and interactions (Boyce et al. 2003). We used non-linear mixed models (PROC NLMIXED; SAS Institute, Cary, NC), which implements adaptive Gaussian quadrature to maximize the true likelihood of model parameters (Pinheiro and Bates 1996, Duchesne et al. 2010). The implementation of mixed-effects models also allowed us to control for heterogeneity in resource availability among individuals (Gillies et al. 2006, Duchesne et al. 2010). Akaike’s Information Criterion (AIC; Akaike 1973, Anderson et al. 2000) was used to evaluate model support. Models with the lowest AIC score were designated as the most parsimonious. We evaluated AIC weights ($w_i$) and parameter estimates ($\beta_i$) of any model within 2 AIC units of the most parsimonious model to determine the best supported model because Akaike’s underlying formula incorporates a 2-unit penalty for each model parameter (Akaike 1973). The estimates of $\beta_i$ from the top-ranked models of resource selection were used to determine the direction and magnitude of influence (+/-) of model parameters. We determined significance of those estimates by evaluating 95% confidence intervals. Confidence intervals of $\beta_i$ that did not over-lap zero were determined to be a significant component of resource selection by mule deer.
RESULTS

Patterns of Movement

We evaluated patterns in daily movement and UD of 39 mule deer consisting of 11 individuals from the control area, 20 individuals from the water-provided treatment area, and 8 individuals from the water-limited treatment area. We detected differences among treatment areas (\(F_{2,36} = 6.87, P < 0.003\)), season (\(F_{3,84} = 11.26, P < 0.001\)), and treatment \(\times\) season (\(F_{6,84} = 24.87, P < 0.001\)) for daily distance traveled by mule deer in Mojave. In general, mule deer in the control area moved longer distances than mule deer in both treatment areas, while daily movements of mule deer in the water-provided area and water-limited areas were similar (Fig. 4). For area of the 95% UD, we identified differences among treatment areas (\(F_{2,36} = 17.15, P < 0.001\)) and seasons (\(F_{3,83} = 9.03, P < 0.001\)) but not treatment \(\times\) season (\(F_{6,83} = 1.25, P = 0.290;\) Table 2). Mule deer in the control area had the largest 95% UD among all seasons, followed by mule deer in the water-limited area, while mule deer in the water-provided area exhibited the most restricted 95% UD among seasons (Fig. 5a). We detected differences in area of the 50% core UD among treatment areas (\(F_{2,36} = 13.71, P < 0.001\)) and among seasons (\(F_{3,83} = 10.97, P < 0.001\)) but not treatment \(\times\) season (\(F_{6,83} = 1.43, P = 0.213;\) Table 2). Area of the 50% core UD was smallest in the water-provided area, during all seasons, while areas of the 50% core UD in the control area and water-limited area were similar among each area and season, but consistently larger than the 50% core UD of the water-provided area (Fig. 5b).
Patterns of activity by hour indicated distinct segregation of periods of active and resting behavior during each season. Peak activity occurred during the early morning and late evening hours. Mule deer generally exhibited moderate levels of activity throughout the night and the most restricted levels of activity during the middle of the day (Fig. 6). Movements were similar at mid-day and at mid-night during winter only (Fig. 6d). Length of photoperiod influenced the duration of crepuscular behavior. During the spring and summer, when length of photoperiod was maximum, we identified active behavior as movements occurring 06:00-09:00 and 20:00-23:00 PDT and resting behavior as those movements occurring 11:00-19:00 PDT (Fig. 6a and c). During autumn and winter, when duration of photoperiod was minimized, we identified active behavior as movements occurring 07:00-10:00 and 18:00-21:00 PST and resting behavior as movements occurring 11:00-17:00 PST (Fig. 6b and d). We incorporated those periods of resting and active behavior into subsequent models of resource selection by mule deer in Mojave.

**Resource Selection**

Our top-ranked model of resource selection for adult female mule deer identified from the global dataset (control: \( n = 12 \), water-provided: \( n = 20 \), water-limited: \( n = 8 \)) contained effects of water, roads, ruggedness, elevation, slope, and included fixed effects of treatment area, habitat type, and season, as well as a two-way interaction between each covariate and treatment area (\( w_i = 0.60 \); Table 3). Additionally, all supported models contained a random effect of individual mule deer in our analysis (Table 3). The second ranked model (\( w_i = 0.33 \)) from the global dataset contained an additional fixed effect of
activity period but evaluation of the parameter estimate for this effect indicated activity
did not substantially influence selection of resources ($\beta_i = 0.015$, $95\% \text{ CI} = -0.020–0.050$; Table 3). The final model of resource selection containing support from the global
dataset included all parameters from the top model, as well as additional interactions
among east-west aspects and treatment area and among north-south aspects and treatment
area ($w_i = 0.07$; Table 3). Further evaluation of parameter estimates indicated that neither
the additive effects of the northness of aspect ($\beta = -0.022$, $95\% \text{ CI} = -0.053–0.008$) or
westness of aspect ($\beta_i = -0.017$, $95\% \text{ CI} = -0.047–0.014$) nor an aspect×area interaction
(northness×water-provided: $\beta_i = 0.036$, $95\% \text{ CI} = -0.004–0.077$; northness×water-limited:
$\beta_i = -0.002$, $95\% \text{ CI} = -0.049–0.077$; westness×water-provided: $\beta_i = 0.003$, $95\% \text{ CI} = -0.038–0.043$; westness×water-limited: $\beta_i = 0.018$, $95\% \text{ CI} = -0.028–0.066$) were
significant determinants of resource selection. Models investigating an influence of
season on selection of covariates in the global dataset were not supported ($\Delta AIC =
2109.22$; Table 3). We were unable to detect a significant influence of a two-way
interaction of activity period and selection of resources ($\Delta AIC = 2283.20$; Table 3).

The top ranked model of resource selection for mule deer in the watered dataset
included a two-way interaction among wildfire severity and all landscape covariates
identified as significant predictors of resource selection in the global dataset (i.e. roads,
elevation, ruggedness, and slope), as well as proximity to water by type of water source
($w_i = 0.64$; Table 4). The top model also included fixed effects of season and habitat
type, in addition to a random effect of individual mule deer (Table 4). The second-
ranked model contained all parameters from the top model plus a fixed effect of activity
period and was the only other model to receive support ($w_i = 0.36$; Table 4). Models of
selection containing the interactions between covariates and season (ΔAIC = 440.82) or covariates and activity period were not supported (ΔAIC = 485.94; Table 4). The best-competing model containing only proximity to nearest water source, not water source by type, was also not competitive (ΔAIC = 35.82; Table 4), which supported our delineation of type of water source in models of selection in the watered dataset.

Parameter estimates from the top model in the global dataset indicated mule deer selected sites closer to sources of permanent water than at random in all 3 study areas of Mojave (Table 5). Mule deer in the water-limited treatment area and individuals in the control area displayed a higher probability of selecting for sites near sources of permanent water, while individuals in the water-provided area displayed weaker selection for these sites (Fig. 7a). Probability of use by mule deer increased as distance to maintained roads increased, while the negative effect of main roads was the strongest on individuals in the control area and weakest on individuals in the water-provided area (Fig. 7b). Mule deer in the control area and water-limited area avoided unmaintained roads, while individuals in the water-provided area displayed neither selection nor avoidance of roads of this classification (Fig. 7c). We detected a significant, positive relationship between probability of use and landscape ruggedness in Mojave, although the magnitude of effect was strongest in the control and water-limited area and weakest in the water-provided area (Fig. 7d). Mule deer selected lower elevations and steeper slopes in the control area and water-limited area but selected higher elevations and no selection of slope in the water-provided area (Fig. 7e and f). We detected an overall negative effect of the summer season on resource selection but only when compared to the winter ($\beta = -0.066$, 95% CI = -0.113 to -0.014). Overall, mule deer in Mojave exhibited selection for
desert washes, Joshua tree woodlands, and pinyon woodlands and avoidance of black brush and Great Basin sagebrush communities (Table 5).

Wildfire severity exhibited a strong influence on resource selection in the watered dataset, particularly on selection of water sources (Table 6). The slope of the response by mule deer to the presence of springs \( \beta_i = -0.368, 95\% \text{ CI} = -0.446– -0.289 \) was steeper than the slope of the response to catchments \( \beta_i = -0.228, 95\% \text{ CI} = -0.302– -0.153 \) but only in undisturbed sites (Fig. 8a). In low severity wildfire areas and in moderate severity wildfire areas, mule deer exhibited little preference for either springs or catchments (Figs. 8b and c), although the parameter estimate for catchment×moderate wildfire interaction overlapped zero \( \beta_i = 0.087, 95\% \text{ CI} = -0.010–0.184 \). The influence of high severity wildfire on selection of catchments \( \beta_i = -0.258, 95\% \text{ CI} = -0.871–0.356 \) or selection of springs \( \beta_i = -0.413, 95\% \text{ CI} = -0.911–0.086 \) was not different than selection for these sources of water in unburned areas.

For the remaining parameters of models of resource selection in the watered dataset, mule deer avoided maintained and unmaintained roads in areas disturbed by wildfire (Table 6). Wildfire severity did not change the response of mule deer to elevation. Animals preferred higher elevations regardless of wildfire severity \( \beta_i = 0.541, 95\% \text{ CI} = 0.469–0.613 \); Table 6). Mule deer preferred less rugged terrain in unburned areas, but exhibited no preference for landscape ruggedness in sites burned at moderate to low severity (Table 6). Individuals preferred gentle slopes in unburned areas but exhibited negligible preference for slopes in areas burned at low or moderate severity (Table 6). Summer imposed an overall negative effect on likelihood of selection but only in relation to winter \( \beta_i = -0.150, 95\% \text{ CI} = -0.227– -0.073 \). We detected an overall
preference by mule deer in the water-provided area for Joshua tree and pinyon woodlands, avoidance of black brush and Great Basin sagebrush communities, and no preference for desert wash systems or Mojave yucca vegetation communities (Table 6).

DISCUSSION

Mule deer in the water-provided treatment area exhibited the most restricted daily movements and had smaller total and core UD's than individuals in the control area or water-limited area, which lends support to our original predictions of restricted movements and distribution where sources of water were enhanced. We expected individuals in the control area to express that same pattern in movements and UD’s as the water-provided area because they have had long-term access to sources of permanent water. Surprisingly, mule deer in the control area of Mojave moved longer distances each day and utilized larger areas than individuals from both the water-provided and water-limited treatment areas across all seasons. We did detect support for a seasonal shift in distances traveled each day, but the influence of season varied by area.

Consistent with our original hypothesis and predictions, however, was a seasonal shift in both the 95% UD and the 50% core UD. In general, the UD's of mule deer among the 3 study areas were the largest during the cool, wet winter months and the most restricted during the warm summer months (Fig. 5).

Observed movement and UD patterns of mule deer in the control area of Mojave could be a result of instinctive knowledge of the long-term presence of reliable sources of water in the area. Under this hypothesis, movements of individuals may not be
constrained by the uncertainty of 1) exploration for new sources of free-standing water and 2) evaporation of known sources of water. Nonetheless, a more likely explanation for the observed differences in movement parameters is related to habitat productivity. Several authors have documented the importance of forage quality to free-ranging ungulates (Relyea et al. 2000, Stewart et al. 2000, Marshal et al. 2006a, Stewart et al. 2006). As a result, movements and distribution of free-ranging ungulates is closely tied to distribution and quality of forage (Marshal et al. 2006a). Ungulates inhabiting habitats of low productivity exhibit larger home ranges and increased movements to meet their energetic demands and, alternatively, they exhibit smaller home ranges and decreased movements in habitats of high productivity. The control area of Mojave is comprised of dense concentrations of Joshua trees. Although there is little information available about habitat productivity in Mojave Desert ecosystems to ungulates (Bleich et al. 1997), areas comprised of Joshua tree communities may be of low productivity, resulting in the movement and UD patterns exhibited by mule deer in the control area. Additional research quantifying the quality of vegetation communities to mule deer in Mojave would likely provide a better understanding of the proposed relationship between habitat productivity and the observed patterns of movement.

The results of our selection analysis (i.e., global dataset) largely corroborated selection patterns exhibited by mule deer across their geographic range. Marshal et al. (2006a) determined mule deer in the Sonoran Desert preferred higher elevations in summer and autumn but lower elevations in winter and spring, selected for steeper slopes in 3 out of 4 seasons, and a weak avoidance of roads in summer and autumn. Although Marshal et al. (2006a) postulated that varying selection for elevation by season may be an
anti-predator strategy during the fawning period; we did not detect this relationship. In Mojave, mule deer preferred lower elevations in the control area and water-limited area but higher elevations in the water-provided area. Selection preferences for elevation by mule deer in control and water-limited area may be explained, in-part, by the distribution of permanent water sites, which occurred at lower elevations on the landscape. Water sites within these 2 areas are either naturally occurring springs (water-limited area) or gravity filled water catchments (control area) and, given the underlying hydrology of these systems, free-water from watershed recharge or aquifers would travel vertically through sub-surface flow paths from accumulation at higher elevations to discharge at springs or catchments at lower elevations (Patten et al. 2008). Free-water available at catchments in the water-provided area were not constrained by this hydrological process because they are filled by a series of underground wells where free-water is pumped to the surface by windmills.

Ordway and Krausman (1986) also identified selection by female mule deer for moderate to steep slopes (11-75%) but avoidance of gentle slopes (0-10%). Few recent studies evaluating selection patterns of mule deer have investigated the effect of landscape ruggedness on likelihood of use. Those studies that incorporated some component of terrain heterogeneity, however, identified a strong and positive effect of this landscape metric on probability of selection, which corroborates our findings of preferences by mule deer for steeper slopes and rugged terrain in Mojave (Fox and Krausman 1994, Sanchez-Rojas and Gallina 2000). Preference for slopes and ruggedness likely represents a predator avoidance strategy, which allows for 1) long distance detection of risk and 2) rapid escape (Geist 1998). These relationships are especially
important during the fawning period (Fox and Krausman 1994), although we did not detect differences in preferences for slopes or ruggedness among seasons.

Consistent with other work assessing resource preferences of ungulates in desert ecosystems (Blong 1993, Krausman et al. 1985b) our results detected a general preference for desert wash systems. Forage availability and quality have been identified by multiple investigators as important components of ungulate habitat (Relyea et al. 2000, Stewart et al. 2000, Marshal et al. 2006a, Stewart et al. 2006), and vegetation communities found along wash systems often provide primary sources of forage and cover to ungulates in desert systems (Andrew et al. 2001, Krausman et al. 1998, Marshal et al. 2005b, Marshal et al. 2006a). Although vegetation communities in Mojave are likely more diverse than other water-limited systems due to the overlap of 3 of the 4 major desert ecosystems, our detection of desert washes as a significant component of resource selection by mule deer in Mojave highlights the overall importance of this habitat component to desert-dwelling herbivores.

We incorporated an interaction term in our candidate models for selection by season, in which we allowed the response in selection of model parameters to vary by season. Other investigations have reported seasonal differences in use of landscape features such as elevation, slope, roads, and water (Ordway and Krausman 1986, Nicholson et al. 1997, Sanchez-Rojas and Gallina 2000, Marshal et al. 2006a). We employed this approach to detect differences in in the magnitude of response in resource selection among seasons. Nonetheless, our best model of resource selection incorporating the season interaction term was not supported in the model selection process ($\Delta AIC = 2109.22$; Anderson et al. 2000). Our top-ranked model of selection in
the 3 study areas indicated that the effect of an interaction with treatment area on selection of landscape features was stronger than an interaction with season (Table 3). We expected that variation in phenology of forage and temperature gradients resulting from changes in climatic conditions throughout the year would influence selection of resources by mule deer at varying magnitudes (Marshal et al. 2005a, b). Nonetheless, that expectation was not supported in our analysis. We detected an overall negative influence of summer on the probability of resource use but only when compared with winter. This finding indicates that mule deer in Mojave exhibit a restriction in selection patterns in response to climatic variation but the response to individual components of the landscape to seasonal variation does not fluctuate.

We observed a strong response by mule deer to the presence of sources of permanent water in patterns of resource selection, particularly in the control and water-limited areas. Across all 3 study areas, individuals exhibited a higher probability of use near a water site than further away. The importance of water in patterns of resource selection by desert ungulates is often postulated (Rosenstock et al. 1999, Bleich 2005, Krausman et al. 2006, Simpson et al. 2011) but preference is rarely detected (Krausman and Etchberger 1995, Bleich et al. 1997, Marshal et al. 2006a, Cain et al. 2008b). We identified a strong response by mule deer to presence of sources of permanent water in both the control area and the water-limited area but a weak response in the water-provided area. In landscapes where availability of a critical resource, such as water, is limited in both availability and distribution, species inhabiting those systems may exhibit a strong preference for that resource. Conversely, in areas where a critical resource is abundant, species inhabiting those areas may exhibit weak selection or no response for
that resource (Mysterud and Ims 1998). Those variations likely represent a dynamic shift in preferences by species to fluctuations in availability of a resource on the landscape (Mysterud and Ims 1998, Beyer et al. 2010). The distribution and density of permanent sources of water are much more restricted in the control area (total sites: 8) and in the water-limited area (total sites: 3) than in the water-provided area (total sites: 23). Our findings of preferences of varying magnitudes for permanent water among the 3 study areas likely suggest a dynamic shift in patterns of use by mule deer where water is limited (high preference) to areas where water is abundant (low preference), as described by Mysterud and Ims (1998).

The spatial scale (3rd order selection) of our analysis may also explain the variation in preference for sites in proximity to sources of permanent water among the 3 areas. Several authors suggest evaluation of resource selection at multiple spatial scales to assess resource preferences of free-ranging ungulates (Kie et al. 2002, Boyce et al. 2003). We may not be able to detect a strong preference for sites close to sources of permanent water by mule deer in the water-provided area because their movement patterns and distribution were already constricted to areas close to those sources. Thus, evaluation of factors influencing placement of the home range on the landscape (2nd order selection; Johnson 1980) may have been more appropriate (Kie et al. 2002). Evaluation of UDs prior to analyses, however, indicated that landscape placement of UDs were strongly associated with known sources of permanent water. We were explicitly interested in how individuals used those sources within their UD rather than the general placement of their UD, warranting the 3rd order spatial scale implemented in our analysis of resource selection. Moreover, we identified strong selection for proximity to
permanent water in both the control area and the water-limited area using this approach, which provides further support of our methodology.

The influence of Hackberry Complex Fire may explain, in-part, the weak selection of water by mule deer in the water-provided treatment area. Selection for water sites by mule deer in unburned regions of the water-provided area (Fig. 8a) was similar in the magnitude of preference for water sites in the control area and the water-limited area of Mojave (Fig. 7a). In areas disturbed by low severity wildfire, mule deer exhibited no selection for springs and catchments, whereas in areas disturbed by moderate severity wildfire, individuals displayed no preference for springs and a weak selection for catchments. We were unable to identify an influence of high-severity wildfire on probability of use of springs or catchments, likely due to few areas disturbed by this classification of wildfire.

Disturbance to the Mojave landscape due to the Hackberry Complex Fire has likely created a diminishing impact of the overall importance of sources of permanent water to mule deer in the water-provided area. In fire-adapted ecosystems, disturbance from fire often promotes the regeneration of forage of high nutritional quality to ungulates (Ruthven et al. 2000, Holl et al. 2004, Bleich et al. 2008, Long et al. 2008, Meek et al. 2008). Prior to the Hackberry Complex Fire, the water-provided area was comprised of dense Utah juniper stands, and late seral Great Basin big sagebrush and bitterbrush communities, in addition to various Mojave Desert cacti spp. (Thorne et al. 1981). Previous work has shown that although dense vegetation communities, such as those existing before the Hackberry Complex Fire, can provide important security cover, they are of low nutritional quality to ungulates (Van Dyke and Darragh 2006, Bender et
al. 2007, Bishop et al. 2009, Halbritter and Bender 2011). The effective removal of these late seral habitats via wildfire has resulted in an increase in vegetation of high nutritional value (e.g. annual forbs, globemallow, bitterbrush; Wallmo and Regelin 1981, Krausman et al. 1997, Bishop et al. 2001). Moreover, early seral vegetation is often more digestible (Marshal et al. 2005b) and may have greater content of preformed water than mature vegetation communities. The removal of those juniper communities, due to the Hackberry Complex Fire, has also resulted in an increase in availability of free-water (N. Darby, unpublished data) likely due to a reduction in plant uptake. Thus, mule deer in the water-provided area of Mojave may be able to meet both their nutritional and hydration needs while foraging in areas disturbed by the Hackberry Complex Fire, reducing the overall importance of access to sources of permanent water. Improved access to habitats of high productivity may also explain the patterns of restricted movements and distribution exhibited by mule deer in the water-provided area. Additional research characterizing the quality of vegetation communities following the Hackberry Complex Fire would provide additional insight into the relationship between wildfire disturbance and use of permanent water in the water-provided area.

Although our analysis supported the delineation between proximity of mule deer locations to springs and proximity to catchments in the water-provided area rather than solely modeling the proximity to any source of permanent water (ΔAIC = 35.82), the magnitude of difference in selection for springs and catchments was equivocal. Nevertheless, mule deer were more likely to be closer to springs than further away, while a similar response to catchments was not as evident, although overlap in the parameter estimates of these two types of water sources indicated no statistical difference (Table 6).
We detected marginal responses by mule deer to either springs or catchments in burned areas, which was likely a result of the location of those sources within the burned area. We found the result of similar use of springs and catchments to be surprising because the vegetation structure at springs and at catchments is fundamentally different. Springs in Mojave contain a vertical vegetation component immediately surrounding the source, which may provide important thermal refugia for mule deer during the hottest times of the year (Cain et al. 2006, Cain et al. 2008a). Also, forage is more concentrated and, likely, of higher quality at spring sites than other areas of the landscape in Mojave, which may provide an additional nutritional component to the diet of mule deer that use those sources. Continued evaluation of patterns of resource selection for water sources will help to determine if there is a difference in use of springs and water catchments by mule deer in Mojave.

CONCLUSIONS

Our results supported our original predictions of constricted distributions and the overall importance of free-water in patterns of resource selection demonstrated by mule deer in response to the provision of water catchments in Mojave. Those results have undoubtedly been confounded, however, from landscape disturbance caused by the Hackberry Complex Fire. Indeed, we encountered many of the same issues as our predecessors investigating the utility of water provisioning for desert ungulates (Broyles and Cutler 1999, Marshal et al. 2006a, Cain et al. 2008b). Attributing our findings in movement and selection exclusively to improved density and distribution of permanent
sources of water would be a misleading interpretation of the results from our research. Further evaluation of habitat structure and nutritional quality of forage in Mojave, particularly in the water-provided area, would address the hypothesis of variable habitat conditions between the 3 treatment areas. Additionally, assessment of parameters related to population performance, such as survival, body condition, productivity, as well as juvenile survival and recruitment could disentangle the influence of those habitat conditions from improved access to sources of permanent water.

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Table 1. Descriptions of parameters and abbreviations used in models of resource selection by mule deer in Mojave National Preserve, California, USA, 2008-2011.

<table>
<thead>
<tr>
<th>Model Parameter</th>
<th>Abbr</th>
<th>Description</th>
<th>Parameter Category</th>
<th>Effect Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Activity</td>
<td>ACT</td>
<td>Level of activity (active vs. resting)</td>
<td>Behavior</td>
<td>Fixed</td>
</tr>
<tr>
<td>Area</td>
<td>AREA</td>
<td>Treatment Type</td>
<td>Influence of treatment</td>
<td>Fixed</td>
</tr>
<tr>
<td>Catchment</td>
<td>CTH</td>
<td>Distance to nearest water catchment (m)</td>
<td>Proximity to water‡</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Mule Deer</td>
<td>DEER</td>
<td>Individual mule deer</td>
<td>Individual heterogeneity</td>
<td>Random</td>
</tr>
<tr>
<td>Elevation</td>
<td>ELEV</td>
<td>Elevation (m)</td>
<td>Topographic</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Fire</td>
<td>FIRE</td>
<td>Fire severity</td>
<td>Influence of fire‡</td>
<td>Fixed</td>
</tr>
<tr>
<td>Water</td>
<td>H2O</td>
<td>Distance to nearest source of water (m)</td>
<td>Proximity to water</td>
<td>Fixed</td>
</tr>
<tr>
<td>Landcover</td>
<td>LCOV</td>
<td>Landcover type</td>
<td>Influence of habitat</td>
<td>Fixed</td>
</tr>
<tr>
<td>Maintained Roads</td>
<td>MR</td>
<td>Distance to nearest maintained road (m)</td>
<td>Proximity to roads</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Northness</td>
<td>NRT</td>
<td>Cosine of aspect (-1 to 1)</td>
<td>Topographic</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Season</td>
<td>SEAS</td>
<td>Season</td>
<td>Influence of season</td>
<td>Fixed</td>
</tr>
<tr>
<td>Slope</td>
<td>SLOPE</td>
<td>Degree of slope</td>
<td>Topographic</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Spring</td>
<td>SPR</td>
<td>Distance to nearest spring (m)</td>
<td>Proximity to water‡</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>VRM</td>
<td>Vector ruggedness metric (0 to 1)</td>
<td>Topographic</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Westness</td>
<td>WST</td>
<td>Sine of aspect (-1 to 1)</td>
<td>Topographic</td>
<td>Covariate‡</td>
</tr>
<tr>
<td>Unmaintained Roads</td>
<td>4X4</td>
<td>Distance to nearest unmaintained road (m)</td>
<td>Proximity to roads</td>
<td>Covariate‡</td>
</tr>
</tbody>
</table>

†Parameter z-standardized prior to model analysis.
‡Effect investigated in water-provided treatment area only.
Table 2. Estimates (ha) and standard errors (SE) of the 95% and the 50% utilization distributions (UD) of mule deer by study area in Mojave National Preserve, California, USA, autumn 2008 through winter 2011. For the 95% UD, differences were detected between treatment areas ($F_{2,11} = 46.66, P < 0.001$) and between seasons ($F_{3,11} = 4.29, P = 0.006$) but not treatment × season ($F_{6,11} = 0.51, P = 0.797$). For the 50% UD, differences between treatment areas ($F_{2,11} = 34.34, P < 0.001$) and between seasons ($F_{3,11} = 5.96, P < 0.001$) were also detected but not treatment × season ($F_{6,11} = 0.72, P = 0.634$). Sample sizes indicated in table (n).

<table>
<thead>
<tr>
<th>Study Area</th>
<th>n</th>
<th>95% UD ha</th>
<th>SE</th>
<th>50% UD ha</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Control Area</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>11</td>
<td>2359</td>
<td>237</td>
<td>429</td>
<td>46</td>
</tr>
<tr>
<td>Summer</td>
<td>10</td>
<td>1995</td>
<td>310</td>
<td>366</td>
<td>53</td>
</tr>
<tr>
<td>Autumn</td>
<td>10</td>
<td>1830</td>
<td>281</td>
<td>420</td>
<td>51</td>
</tr>
<tr>
<td>Winter</td>
<td>14</td>
<td>2654</td>
<td>307</td>
<td>576</td>
<td>62</td>
</tr>
<tr>
<td><strong>Water-Limited Area</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>20</td>
<td>1035</td>
<td>81</td>
<td>249</td>
<td>20</td>
</tr>
<tr>
<td>Summer</td>
<td>18</td>
<td>836</td>
<td>103</td>
<td>186</td>
<td>17</td>
</tr>
<tr>
<td>Autumn</td>
<td>15</td>
<td>1010</td>
<td>191</td>
<td>238</td>
<td>37</td>
</tr>
<tr>
<td>Winter</td>
<td>14</td>
<td>1285</td>
<td>164</td>
<td>328</td>
<td>55</td>
</tr>
<tr>
<td><strong>Water-Provided Area</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>9</td>
<td>2060</td>
<td>158</td>
<td>523</td>
<td>53</td>
</tr>
<tr>
<td>Summer</td>
<td>9</td>
<td>1751</td>
<td>198</td>
<td>394</td>
<td>53</td>
</tr>
<tr>
<td>Autumn</td>
<td>8</td>
<td>1581</td>
<td>314</td>
<td>347</td>
<td>57</td>
</tr>
<tr>
<td>Winter</td>
<td>9</td>
<td>1840</td>
<td>185</td>
<td>458</td>
<td>50</td>
</tr>
</tbody>
</table>
Table 3. Candidate models of resource selection, which evaluated preferences of mule deer in 3 study areas (control: $n = 12$, water-provided: $n = 20$, water-limited: $n = 8$) of Mojave National Preserve, California, USA, 2008-2011. Models were analyzed using mixed effects logistic regression and evaluated for competitiveness using differences in Akaike’s Information Criterion values ($\Delta$AIC) and model support (AIC wt). Also included is number of model parameters ($k$) and an estimate of the negative log-likelihood ($\text{-LogL}$). See Table 1 for parameter descriptions.

<table>
<thead>
<tr>
<th>Model†</th>
<th>$k$</th>
<th>$\text{-LogL}$</th>
<th>$\Delta$AIC</th>
<th>AIC wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>H2O×AREA ELEV×AREA VRM×AREA MR×AREA 4X4×AREA SLOPE×AREA LCOV SEAS DEER</td>
<td>33</td>
<td>38851.85</td>
<td>0.00</td>
<td>0.60</td>
</tr>
<tr>
<td>H2O×AREA ELEV×AREA VRM×AREA MR×AREA 4X4×AREA SLOPE×AREA LCOV ACT SEAS DEER</td>
<td>34</td>
<td>38851.46</td>
<td>1.22</td>
<td>0.33</td>
</tr>
<tr>
<td>H2O×AREA ELEV×AREA VRM×AREA MR×AREA 4X4×AREA SLOPE×AREA NRT×AREA WST×AREA SEAS LCOV DEER</td>
<td>39</td>
<td>38848.03</td>
<td>4.36</td>
<td>0.07</td>
</tr>
<tr>
<td>H2O×SEAS ELEV×SEAS VRM×SEAS MR×SEAS 4X4×SEAS SLOPE×SEAS LCOV DEER</td>
<td>37</td>
<td>39902.46</td>
<td>2109.22</td>
<td>0.00</td>
</tr>
<tr>
<td>H2O×ACT ELEV×ACT VRM×ACT MR×ACT 4X4×ACT SLOPE×ACT DEER</td>
<td>26</td>
<td>40000.45</td>
<td>2283.20</td>
<td>0.00</td>
</tr>
<tr>
<td>H2O ELEV VRM MR 4X4 SLOPE AREA LCOV SEAS DEER</td>
<td>21</td>
<td>40025.54</td>
<td>2323.38</td>
<td>0.00</td>
</tr>
<tr>
<td>INTERCEPT</td>
<td>1</td>
<td>41030.34</td>
<td>4292.98</td>
<td>0.00</td>
</tr>
</tbody>
</table>

†If interaction term (×) is present in model then linear term is included by default. See Table 1 for parameter descriptions.
Table 4. Candidate models of resource selection, which evaluated fine-scale preferences of $n = 20$ mule deer in the water-provided treatment area of Mojave National Preserve, California, 2008-2011. Models were analyzed using mixed effects logistic regression and evaluated for competitiveness using differences in Akaike’s Information Criterion values ($\Delta$AIC) and model support (AIC wt). Also included is number of model parameters ($k$) and an estimate of the negative log-likelihood (-LogL). See Table 1 for parameter descriptions.

<table>
<thead>
<tr>
<th>Model†</th>
<th>$k$</th>
<th>-LogL</th>
<th>$\Delta$AIC</th>
<th>AIC wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>CTH×FIRE SPR×FIRE ELEV×FIRE VRM×FIRE SLOPE×FIRE MR×FIRE 4X4×FIRE LCOV SEAS DEER</td>
<td>42</td>
<td>16908.85</td>
<td>0.00</td>
<td>0.64</td>
</tr>
<tr>
<td>CTH×FIRE SPR×FIRE ELEV×FIRE VRM×FIRE SLOPE×FIRE MR×FIRE 4X4×FIRE LCOV ACT SEAS DEER</td>
<td>43</td>
<td>16908.42</td>
<td>1.14</td>
<td>0.36</td>
</tr>
<tr>
<td>H2O×FIRE ELEV×FIRE VRM×FIRE SLOPE×FIRE MR×FIRE 4X4×FIRE LCOV SEAS DEER</td>
<td>38</td>
<td>16930.76</td>
<td>35.82</td>
<td>0.00</td>
</tr>
<tr>
<td>CTH×SEAS SPR×SEAS ELEV×SEAS VRM×SEAS MR×SEAS 4X4×SEAS LCOV FIRE DEER</td>
<td>38</td>
<td>17133.26</td>
<td>440.82</td>
<td>0.00</td>
</tr>
<tr>
<td>CTH×ACT SPR×ACT ELEV×ACT VRM×ACT MR×ACT 4X4×ACT LCOV FIRE SEAS DEER</td>
<td>27</td>
<td>17166.82</td>
<td>485.94</td>
<td>0.00</td>
</tr>
<tr>
<td>CTH SPR ELEV VRM MR 4X4 LCOV FIRE SEAS DEER</td>
<td>20</td>
<td>17182.29</td>
<td>502.88</td>
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</tr>
<tr>
<td>INTERCEPT</td>
<td>1</td>
<td>18719.25</td>
<td>3538.80</td>
<td>0.00</td>
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</tbody>
</table>

†If interaction term (×) is present in model then linear term is included by default.
Table 5. Parameter estimates ($\beta$), standard errors (SE), and 95% confidence intervals from best competing model of resource selection by mule deer from 3 study areas of Mojave National Preserve, California, USA. The top model included interactions between study area and the effects of proximity to water, elevation, ruggedness, proximity to maintained and unmaintained roads, and slope. The top model also included fixed effects of season and landcover type, and supported the inclusion of a random effect for individual deer. See Table 1 for parameter descriptions.

<table>
<thead>
<tr>
<th>Model Parameter</th>
<th>$\beta$</th>
<th>SE</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Individual Heterogeneity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEER</td>
<td>0.136</td>
<td>0.032</td>
<td>0.071</td>
<td>0.199</td>
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<tr>
<td><strong>Study Area (Control as reference)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water-provided</td>
<td>-0.159</td>
<td>0.147</td>
<td>-0.456</td>
<td>0.138</td>
</tr>
<tr>
<td>Water-limited</td>
<td>-0.079</td>
<td>0.179</td>
<td>-0.441</td>
<td>0.282</td>
</tr>
<tr>
<td><strong>Proximity to Water†</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H2O</td>
<td>-0.453</td>
<td>0.024</td>
<td>-0.503</td>
<td>-0.404</td>
</tr>
<tr>
<td>H2O×Water-provided</td>
<td>0.433</td>
<td>0.030</td>
<td>0.371</td>
<td>0.494</td>
</tr>
<tr>
<td>H2O×Water-limited</td>
<td>0.331</td>
<td>0.034</td>
<td>0.261</td>
<td>0.401</td>
</tr>
<tr>
<td><strong>Proximity to Roads†</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MNRDS</td>
<td>0.607</td>
<td>0.051</td>
<td>0.503</td>
<td>0.710</td>
</tr>
<tr>
<td>MNRDS×Water-provided</td>
<td>-0.506</td>
<td>0.055</td>
<td>-0.618</td>
<td>-0.395</td>
</tr>
<tr>
<td>MNRDS×Water-limited</td>
<td>-0.621</td>
<td>0.057</td>
<td>-0.736</td>
<td>-0.506</td>
</tr>
<tr>
<td>4X4RDS</td>
<td>0.425</td>
<td>0.023</td>
<td>0.378</td>
<td>0.471</td>
</tr>
<tr>
<td>4X4RDS×Water-provided</td>
<td>-0.622</td>
<td>0.028</td>
<td>-0.678</td>
<td>-0.565</td>
</tr>
<tr>
<td>4X4RDS×Water-limited</td>
<td>-0.356</td>
<td>0.031</td>
<td>-0.418</td>
<td>-0.294</td>
</tr>
<tr>
<td><strong>Topographic†</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ELEV</td>
<td>-0.091</td>
<td>0.031</td>
<td>-0.154</td>
<td>-0.028</td>
</tr>
<tr>
<td>ELEV×Water-provided</td>
<td>0.979</td>
<td>0.043</td>
<td>0.893</td>
<td>1.066</td>
</tr>
<tr>
<td>ELEV×Water-limited</td>
<td>-0.136</td>
<td>0.044</td>
<td>-0.226</td>
<td>-0.046</td>
</tr>
<tr>
<td>VRM</td>
<td>0.579</td>
<td>0.042</td>
<td>0.494</td>
<td>0.665</td>
</tr>
<tr>
<td>VRM×Water-provided</td>
<td>-0.568</td>
<td>0.047</td>
<td>-0.661</td>
<td>-0.475</td>
</tr>
<tr>
<td>Factor</td>
<td>Coefficient</td>
<td>Standard Error</td>
<td>t-value</td>
<td>p-value</td>
</tr>
<tr>
<td>------------------------------</td>
<td>-------------</td>
<td>----------------</td>
<td>---------</td>
<td>---------</td>
</tr>
<tr>
<td>VRM×Water-limited</td>
<td>-0.406</td>
<td>0.048</td>
<td>-0.503</td>
<td>-0.308</td>
</tr>
<tr>
<td>SLOPE</td>
<td>0.253</td>
<td>0.043</td>
<td>0.166</td>
<td>0.339</td>
</tr>
<tr>
<td>SLOPE×Water-provided</td>
<td>-0.273</td>
<td>0.046</td>
<td>-0.367</td>
<td>-0.179</td>
</tr>
<tr>
<td>SLOPE×Water-provided</td>
<td>-0.014</td>
<td>0.051</td>
<td>-0.116</td>
<td>-0.089</td>
</tr>
</tbody>
</table>

**Season (Winter as reference)**

<table>
<thead>
<tr>
<th>Season</th>
<th>Coefficient</th>
<th>Standard Error</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn</td>
<td>0.003</td>
<td>0.029</td>
<td>-0.056</td>
<td>0.062</td>
</tr>
<tr>
<td>Spring</td>
<td>0.018</td>
<td>0.026</td>
<td>-0.036</td>
<td>0.073</td>
</tr>
<tr>
<td>Summer</td>
<td>-0.066</td>
<td>0.023</td>
<td>-0.113</td>
<td>-0.019</td>
</tr>
</tbody>
</table>

**Landcover Type (Juniper as reference)**

<table>
<thead>
<tr>
<th>Landcover Type</th>
<th>Coefficient</th>
<th>Standard Error</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Desert wash system</td>
<td>0.426</td>
<td>0.079</td>
<td>0.266</td>
<td>0.586</td>
</tr>
<tr>
<td>Black brush shrubland</td>
<td>-0.358</td>
<td>0.103</td>
<td>-0.565</td>
<td>-0.151</td>
</tr>
<tr>
<td>Lava bed and cinder cone</td>
<td>-0.728</td>
<td>0.142</td>
<td>-1.014</td>
<td>-0.441</td>
</tr>
<tr>
<td>Creosote bush shrubland</td>
<td>0.170</td>
<td>0.208</td>
<td>-0.250</td>
<td>0.590</td>
</tr>
<tr>
<td>Joshua tree woodland</td>
<td>0.505</td>
<td>0.039</td>
<td>0.427</td>
<td>0.583</td>
</tr>
<tr>
<td>Pinyon woodland</td>
<td>0.424</td>
<td>0.035</td>
<td>0.354</td>
<td>0.494</td>
</tr>
<tr>
<td>Big sagebrush shrubland</td>
<td>-1.177</td>
<td>0.076</td>
<td>-1.330</td>
<td>-1.024</td>
</tr>
<tr>
<td>Mojave yucca scrub</td>
<td>0.133</td>
<td>0.032</td>
<td>0.014</td>
<td>0.252</td>
</tr>
</tbody>
</table>

†Indicates standardized beta coefficient
Table 6. Parameter estimates ($\beta$), standard errors (SE), and 95% confidence intervals from best competing model of resource selection of mule deer in the water-provided treatment area of Mojave National Preserve, California, USA, 2008-2011. The best model included interactions between wildfire severity and the effects of proximity to water catchments and springs, elevation, ruggedness, proximity to maintained and unmaintained roads, and slope. The top model also included fixed effects of season and landcover type, and supported the inclusion of a random effect for individual deer. See Table 1 for parameter descriptions.

<table>
<thead>
<tr>
<th>Model Parameter</th>
<th>$\beta$</th>
<th>SE</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual Heterogeneity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEER</td>
<td>0.210</td>
<td>0.070</td>
<td>0.063</td>
<td>0.356</td>
</tr>
<tr>
<td>Fire Severity (Unburned as reference)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>-0.454</td>
<td>0.049</td>
<td>-0.557</td>
<td>-0.350</td>
</tr>
<tr>
<td>Moderate</td>
<td>-0.103</td>
<td>0.050</td>
<td>-0.207</td>
<td>0.001</td>
</tr>
<tr>
<td>High</td>
<td>0.331</td>
<td>0.256</td>
<td>-0.163</td>
<td>0.825</td>
</tr>
<tr>
<td>Proximity to Water†</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CTH</td>
<td>-0.228</td>
<td>0.036</td>
<td>-0.302</td>
<td>-0.153</td>
</tr>
<tr>
<td>CTH×Low</td>
<td>0.254</td>
<td>0.046</td>
<td>0.157</td>
<td>0.351</td>
</tr>
<tr>
<td>CTH×Moderate</td>
<td>0.087</td>
<td>0.046</td>
<td>-0.010</td>
<td>0.184</td>
</tr>
<tr>
<td>CTH×High</td>
<td>-0.258</td>
<td>0.293</td>
<td>-0.871</td>
<td>0.356</td>
</tr>
<tr>
<td>SPR</td>
<td>-0.368</td>
<td>0.037</td>
<td>-0.446</td>
<td>-0.289</td>
</tr>
<tr>
<td>SPR×Low</td>
<td>0.271</td>
<td>0.047</td>
<td>0.173</td>
<td>0.369</td>
</tr>
<tr>
<td>SPR×Moderate</td>
<td>0.404</td>
<td>0.045</td>
<td>0.311</td>
<td>0.498</td>
</tr>
<tr>
<td>SPR×High</td>
<td>-0.413</td>
<td>0.238</td>
<td>-0.911</td>
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</tr>
<tr>
<td>Proximity to Roads†</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MNRDS</td>
<td>-0.201</td>
<td>0.042</td>
<td>-0.290</td>
<td>-0.112</td>
</tr>
<tr>
<td>MNRDS×Low</td>
<td>0.195</td>
<td>0.049</td>
<td>0.092</td>
<td>0.298</td>
</tr>
<tr>
<td>MNRDS×Moderate</td>
<td>0.360</td>
<td>0.049</td>
<td>0.258</td>
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<tr>
<td>MNRDS×High</td>
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<td>0.255</td>
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<tr>
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<td>0.029</td>
<td>-0.091</td>
<td>0.030</td>
</tr>
<tr>
<td>Landcover Type (Juniper as reference)</td>
<td>β</td>
<td>SE</td>
<td>t</td>
<td>p</td>
</tr>
<tr>
<td>-------------------------------------------------------------</td>
<td>------</td>
<td>-----</td>
<td>-------</td>
<td>------</td>
</tr>
<tr>
<td>Desert wash system</td>
<td>0.073</td>
<td>0.144</td>
<td>-0.228</td>
<td>0.374</td>
</tr>
<tr>
<td>Black brush shrubland</td>
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<tr>
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<tr>
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<td>-2.239</td>
<td>-1.730</td>
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<tr>
<td>Mojave yucca scrub</td>
<td>0.045</td>
<td>0.116</td>
<td>-0.198</td>
<td>0.288</td>
</tr>
<tr>
<td>Season (Winter as reference)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Autumn</td>
<td>-0.063</td>
<td>0.045</td>
<td>-0.157</td>
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<tr>
<td>Spring</td>
<td>-0.022</td>
<td>0.042</td>
<td>-0.110</td>
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</tr>
<tr>
<td>Summer</td>
<td>-0.150</td>
<td>0.037</td>
<td>-0.227</td>
<td>-0.073</td>
</tr>
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</table>

†Indicates standardized beta coefficient
FIGURE LEGENDS

Figure 1. Location of control and treatment areas in Mojave National Preserve, southwestern California, USA, where the effects of permanent water provisioning on mule deer were investigated, 2008-2011. Also identified is the disturbance boundary of the Hackberry Complex wildfire, which occurred predominately in the Mid Hills and the Hackberry Mountains region of Mojave National Preserve, California, USA. The Hackberry Complex wildfire was ignited by a series of lightning strikes in June 2006 and burned over 28,000 ha.

Figure 2. Annual temperature and precipitation pattern used to delineate seasons in Mojave National Preserve (hereafter Mojave), California, USA. Solid lines indicate grouped (by month) seasons. Winter was identified as December-March, spring as April-May, summer as June-September, and autumn as October-November. Gradient-filled circles identify mid-winter (February) and mid-summer (August) precipitation peaks, exhibiting a distinct bi-modal pattern of annual precipitation. Climatological data were collected at Mitchell Caverns in central Mojave from 1958-1996.

Figure 3. (top) The Mid Hills range in Mojave National Preserve, California, USA. The Hackberry Complex wildfire created large expanses of sparsely vegetated desert habitat with relatively few unburned remnant habitat patches. (bottom) The post-wildfire landscape is now dominated by annual and perennial herbaceous vegetation, e.g. globemallow (*Spaerelcea* spp.) and four o’clock (*Mirabilis* spp.), as well as some
perennial shrubs, e.g. bitterbrush (*Purshia tridentata* var. *tridentata*) and desert almond (*Prunus fasciculata*).

**Figure 4.** Mean daily distance traveled (km ± SE) by mule deer for 3 study areas in Mojave National Preserve, California, USA, autumn 2008 through winter 2011. We evaluated distance traveled for *n* = 11 in the control area, *n* = 20 in the water-provided area, and *n* = 8 in the water-limited area using mixed-effects analysis of variance. Pairwise comparisons from a least-square means procedure indicated differences in daily distance traveled between the control and water-limited area (*P* = 0.025) and the control and water-provided area (*P* < 0.001) but no difference between the water-limited and water-provided area (*P* = 0.482). On average (± SE), mule deer moved 3.47 ± 0.11 km/day in the control area, 2.86 ± 0.11 km/day in the water-limited treatment area, and 2.55 ± 0.07 km/day in the water-provided treatment area.

**Figure 5.** Estimates of utilization distribution (ha ± SE) for a) 95% total area and b) 50% core area used by mule deer for treatment area and season in Mojave National Preserve, California, USA, autumn 2008 through winter 2011. We evaluated utilization distribution of mule deer for *n* = 11 in the control area, *n* = 20 in the water-provided area, and *n* = 8 in the water-limited area using mixed-effects analysis of variance. For the 95% utilization distribution, differences were detected among treatment areas (*F*₂,₃₆ = 17.15, *P* < 0.001) and among seasons (*F*₃,₈₃ = 9.03, *P* < 0.001), but not the treatment × season interaction (*F*₆,₈₃ = 1.25, *P* = 0.290). For the 50% utilization distribution, differences among treatment areas (*F*₂,₃₆ = 13.71, *P* < 0.001) and among seasons (*F*₃,₈₃ = 10.97, *P* <
were also detected, but not the treatment × season interaction ($F_{6,83} = 1.43$, $P = 0.211$).

**Figure 6.** Hourly movement rates (m/h) of $n = 40$ mule deer for each season in Mojave National Preserve, California, USA, 2008-2011. Values on the x-axis have been converted from UTC to PDT for a) spring and b) summer and from UTC to PST for c) autumn and d) winter. Error bars represent standard error of movement rates.

**Figure 7.** Relative probability of selection of $n = 40$ mule deer, while holding other model parameters constant (see Table 5), for a) proximity to water, b) proximity to maintained road, c) proximity to unmaintained roads, d) terrain ruggedness, e) elevation, and f) slope in Mojave National Preserve, California, USA, 2008-2011. Results are presented as response of mule deer to parameter by study area where dotted curve represents study control area, solid curve represents water-provided treatment area, and dashed curve represents water-limited treatment area.

**Figure 8.** Relative probability of selection of $n = 20$ mule deer, while holding other model parameters constant (see Table 5), for a) proximity to water in an unburned landscape ($\beta_{\text{catchment}} = -0.228$, 95% CI = -0.302--0.153; $\beta_{\text{spring}} = -0.368$, 95% CI = -0.446--0.289), b) proximity to water in a low burned landscape ($\beta_{\text{catchment}} = 0.254$, 95% CI = 0.157--0.351; $\beta_{\text{spring}} = 0.271$, 95% CI = 0.173--0.369), and c) proximity to water in a moderately burned landscape ($\beta_{\text{catchment}} = 0.087$, 95% CI = -0.010--0.184; $\beta_{\text{spring}} = 0.404$, 95% CI = 0.311--0.498) of a water-provided treatment area of Mojave National Preserve,
California, USA, 2008-2011. Results are presented as response of mule deer to proximity to nearest source of permanent water by source type where dashed curve represents water catchments and solid curve represents springs.
Mojave National Preserve, 1958-1996

Figure 2
Figure 4
Figure 5

a) 95% Utilization Distribution

- Control
- Water-Limited
- Water-Provided

Kernel Density (ha)

Season
- Spring
- Summer
- Autumn
- Winter

b) 50% Core Utilization Distribution

Kernel Density (ha)

Season
- Spring
- Summer
- Autumn
- Winter
Figure 6
Selection Probability

Proximity to Water (m)

- **a) Permanent Water**
  - Control
  - Water-Provided
  - Water-Limited

Proximity to Maintained Roads (m)

- **b) Maintained Roads**
  - Control
  - Water-Limited
  - Water-Provided

Proximity to Unmaintained Roads (m)

- **c) Unmaintained Roads**
  - Control
  - Water-Provided
  - Water-Limited

Ruggedness

- **d) Ruggedness**
  - Control
  - Water-Provided
  - Water-Limited
Figure 7
a) Unburned Landscape

Selection Probability

Proximity to Water (m)

b) Low Severity Wildfire

Selection Probability

Proximity to Water (m)
c) Moderate Severity Wildfire

Selection Probability vs. Proximity to Water (m)

- Catchment
- Spring

Figure 8
POPULATION PERFORMANCE OF MULE DEER: RESPONSES IN DEMOGRAPHY TO EXPERIMENTAL WATER PROVISIONING IN A MOJAVE DESERT ECOSYSTEM

Cody J. McKee, Kelley M. Stewart, James S. Sedinger, Vernon C. Bleich, and Neal W. Darby

1Department of Natural Resources and Environmental Science, University of Nevada-Reno, 1664 N. Virginia Street, Reno, Nevada 89557, USA

2National Park Service, 2701 Barstow Road, Barstow, California 92311, USA

*Correspondence author. E-mail: cmckee@cabnr.unr.edu
ABSTRACT

Providing permanent water to habitats that are water-limited has been assumed to provide both practical and intrinsic benefits to wildlife populations in arid regions of the western United States. Recent studies attempting to delineate costs and benefits of providing permanent water to wildlife have been inconclusive due to a variety of confounding factors. We investigated the effects of water provisioning on body condition and traits of demography of adult female mule deer (*Odocoileus hemionus*) in 3 study areas (i.e., control area, water-provided area, and water-limited area) of Mojave National Preserve, California, 2008-2011. We used general linear models to evaluate the influence of water availability and climatic conditions on body condition, and logistic regression to model the effects of water availability, body condition, and climatic conditions on probability of producing twins. We used Program MARK to evaluate the effects of water-provisioning, climatic conditions, and individual characteristics on survival patterns of mule deer and to estimate monthly and annual probabilities of survival. We did not detect an effect of water-provisioning on body condition but did identify a significant, positive, effect of total accumulation of precipitation from the previous year. Our top model of probability of producing twins did not contain an effect of study area but did suggest a positive influence of body condition. We were unable to identify an effect of water-provisioning in patterns of survival but detected higher annual survival in the control area in comparison with the water-provided area and the water-limited area. Our results highlight the importance of precipitation on body condition and, in turn, body condition on twinning probability. We were, however, unable to infer twinning rates to survival
and subsequent recruitment of those young into the breeding population. Moreover, survival of adult female mule deer is generally resilient to variations in resource availability on the landscape, which was a relationship identified in our experiment. The description of baseline information related to body condition and demography, nonetheless, provide an understanding of the general dynamics of a formerly unstudied population of desert-dwelling herbivores. An appropriate next step in evaluating the overall influence of water-provisioning on population dynamics of mule deer would be to investigate variation in birth rates, survival, and recruitment of juveniles.

**Key Words:** Body condition, California, ingesta-free body fat, Mojave Desert, *Odocoileus hemionus*, precipitation, population performance, productivity, Program MARK, survival, twinning rates, water developments

**INTRODUCTION**

Development of water sources and its effect on wildlife inhabiting arid ecosystems has received considerable attention since Broyles (1995) questioned the use of this popular practice in wildlife management (Krausman et al. 2006; Rosenstock et al. 1999; Simpson et al. 2011). Many of the hypothesized negative side-effects of water developments, such as poor quality of water, habitat degradation, increased predation, and entrapment are now known to be relatively unimportant (Andrew et al. 2001; Bleich et al. 2006; Marshal et al. 2006b; Rosenstock et al. 2001; Simpson et al. 2011). Provisioning of water in an otherwise water-limited ecosystem has been hypothesized to
increase the distribution and abundance of species and to improve population performance (Dolan 2006; Rautenstrauch and Krausman 1989; Rosenstock et al. 1999; Simpson et al. 2011). Nonetheless, efforts to identify the benefits of water developments on population performance have been unsuccessful and subject to a variety of confounding factors (Broyles and Cutler 1999; Cain et al. 2008; Krausman and Etchberger 1995; Marshal et al. 2006c). As the availability of natural sources of perennial water diminish, likely resulting from predicted changes to global climate and human development (Longshore et al. 2009), understanding the influence of water developments on species inhabiting arid ecosystems will become ever more important.

Changes in density and distribution of ungulate populations are often linked to changes in body condition, productivity, and survival (Bishop et al. 2009; Cook et al. 2007; Eberhardt 2002; McCullough 1979). Moreover, populations constrained by density-dependent processes exhibit low survival, poor body condition, and low productivity when at or near ecological carrying capacity (Kie et al. 1980; McCullough 1979; Stewart et al. 2005). The underlying mechanisms of population dynamics dictating density dependence are driven primarily by the availability and quality of resources on the landscape (Bender et al. 2007; Bishop et al. 2009; Kie and White 1985; Parker et al. 2009; Stewart et al. 2002). Mammalian herbivores inhabiting desert ecosystems occur at low densities with large ranges (Marshal et al. 2006c) presumably due to limited availability of resources on the landscape (Bender et al. 2007; Bleich et al. 2010; Marshal et al. 2005b). If availability of permanent sources of water in arid environments is limiting to desert ungulates, we would expect those species to reduce their effort spent acquiring free-water when sources of permanent water are provided. Species could then
reallocate those efforts to foraging, which could, ultimately, improve body condition, productivity, and survival.

A strong causal relationship between climatic conditions, especially rainfall, and habitat productivity has been identified for a variety of desert ecosystems (Marshal et al. 2005a, 2005b; Oehler et al. 2003; Rautenstrauch and Krausman 1989). Furthermore, rainfall accumulations, functioning through changes in plant phenology, have been directly related to body condition of desert dwelling ungulates (Marshal et al. 2008). During times of decreased precipitation, ungulates exhibited poor body condition (Fox et al. 2000; Marshal et al. 2008), while a positive relationship between increased precipitation and body condition and survival has been detected (Cain et al. 2008; Marshal et al. 2008). Certainly, variation in environmental conditions can exhibit a critical influence on components of ungulate demography (Gaillard et al. 2000). As rainfall patterns become more unpredictable and drought conditions persist, the ability to enhance availability of a critical resource, such as sources of permanent water, may become increasingly important to ensure the persistence of populations of large herbivores.

Several studies have identified the importance of water (Morgart et al. 2005; Rautenstrauch and Krausman 1989; Whiting et al. 2010) and ruggedness (Bleich et al. 1997; Fox and Krausman 1994; Sanchez-Rojas and Gallina 2000) in patterns of resource selection by ungulates inhabiting a desert ecosystem. Furthermore, a negative relationship between anthropogenic activity and resource use has also been identified (Marshal et al. 2006a). Although a link between resource use and fitness of ungulates have been hypothesized (Boccadori et al. 2008), to our knowledge, there have been few
attempts to understand the effects of decisions about resource use on demography (Dussault et al. 2005; Mahoney and Virgl 2003). Understanding how the use of water sources, ruggedness, and avoidance of roads by desert ungulates and the consequences of those patterns of use on population performance would provide valuable insight into general ecology of the species, as well as a better understanding of the overall importance of a potentially limiting resource, such as water.

Our objectives were to evaluate body condition and demographic responses (i.e., survival, productivity) of mule deer (*Odocoileus hemionus*) inhabiting a desert ecosystem to provisioning of permanent sources of water, as well as environmental conditions. Moreover, decisions in selection of resources by mule deer are not made haphazardly and specific resources are likely used or avoided to increase overall fitness. Thus, we considered the relationship between resource use and the effect of those decisions on demography. We predicted that mule deer with improved access to permanent sources of water would exhibit higher survival, greater body fat, and greater fetal rates than mule deer in areas where water was limited. We expected that stochastic variation in climatic conditions among seasons and years would influence those demographic traits. Finally, we predicted that deer closer to sources of permanent water, in more rugged terrain, and further from roads would exhibit higher survival than deer further from water, in less rugged terrain, and closer to roads. Detection of such enhancements to population performance would lend support to the use of water as a management tool for ungulates.
STUDY AREA

We studied mule deer in Mojave National Preserve (hereafter Mojave), located in San Bernardino County, California, USA (35°00´N, 115°28´W) from January 2008 through December 2011. The general boundaries of Mojave are delineated to the north by Interstate Freeway 15, to the south by Interstate Freeway 40, and to the east by the California-Nevada state border (Fig. 1). The borders of Mojave encompass nearly 650,000 ha and include components of 3 of the 4 major deserts of North America: the Mojave, the Sonoran, and the Great Basin (National Park Service 2011). The overlap of these desert ecosystems has created a heterogeneous landscape characterized by distinct, rugged, mountain ranges composed of granite, basalt, and igneous rock separated by bajadas, playas, and dunes (Thorne et al. 1981). Elevations ranged from 270 m to 2400 m. Our research efforts were concentrated in the Cima Dome, Mid Hills, and New York Mountain regions of Mojave (Fig. 1).

The climate of Mojave is representative of the arid southwestern USA, although wide temperature and precipitation gradients are distinguishable between low and mid- to upper- elevations. Maximum temperatures at low elevations average 40.5°C in summer and 19°C in the winter (Desert Studies Center 2010). Temperatures at mid- to upper- elevations are more moderate in the summer with mean maximum temperatures of 33°C and mean maximum temperatures of 13°C in the winter (United States Geological Survey 2010). Precipitation patterns are distinctly bi-modal with a cool season peak occurring during winter and a warm season peak occurring during the summer. Mean annual precipitation at low elevation sites is 8.5 cm (1980-2005, Soda Springs, northern
Mojave), while mean annual precipitation at mid- to upper-elevation sites is 27 cm (1958-1996, Mitchell Caverns Natural Preserve, southern Mojave).

We delineated seasons with a climograph (Stewart et al. 2002) developed from historical temperature and precipitation patterns collected at Mitchell Caverns Natural Preserve in southern Mojave from 1958-1996. The Mitchell Caverns weather station was ideal for our research objectives because it provided a long-term dataset of climatic conditions at a similar elevation to our study sites (1,300 m). Winter (cool, wet) began approximately 1 December and lasted to 31 March, spring (warm, dry) began 1 April to 31 May, summer (warm, wet) began around 1 June and lasted until 31 September, and autumn (cool, dry) began 1 October to 30 November (Fig. 2).

Vegetation communities vary by elevation and precipitation gradient in Mojave (Thorne et al. 1981). Creosote bush (Larrea tridentata) was abundant in low elevation bajadas and valleys (Thorne et al. 1981). Mid-elevations <1,600 m with shallow, rocky, soils were characterized by cholla cactus (Opuntia spp.), barrel cactus (Ferocactus spp.), blackbush (Coleogyne ramosissima), Spanish bayonet (Yucca spp.) and Joshua tree woodlands (Yucca brevifolia; Thorne et al. 1981). Mid-elevations >1,600 m contained Great Basin sagebrush (Artemesia tridentata), Utah juniper (Juniperus osteosperma), and pinyon pine (Pinus spp.; Thorne et al. 1981). White fir (Abies concolor) communities were present in the upper elevations (>1,800 m) of 2 mountain ranges (Clark Mountain and New York Mountains; Thorne et al. 1981).

Various natural and developed sources of permanent water were present and available to mule deer before initiation of our study (Fig. 1). Natural and developed springs were predominately found in the New York Mountains and the Mid Hills, while
water availability in Cima Dome was primarily limited to ground-water wells with above-ground catchments. Depending on climatic conditions, ephemeral springs, seeps, and tenajas can provide additional sources of water during the winter spring, and early summer months. Species of wildlife that have been documented using those permanent sources of water in Mojave includes mule deer, desert tortoise (*Gopherus agassizii*), spotted skunk (*Spilogale gracilis*), mountain lion (*Puma concolor*), and Gambel’s Quail (*Callipepla gambelii*; N. Darby, unpublished data).

**METHODS**

**Study Design**

We evaluated the response in body condition, productivity, and survival of adult female mule deer to the reactivation of livestock wells in Mojave. We divided the central region of Mojave, where the overlap of mule deer and presence of wells (both active and inactive) was highest, into 3 study areas (Fig. 1). Study area 1, Cima Dome, did not experience well deactivation before our study. Permanent sources of water have been available to mule deer since before the establishment of Mojave. We did not manipulate water developments in Cima Dome (hereafter control area). In study area 2, Mid Hills, livestock wells deactivated in 1994 were reinstituted in the fall of 2008 (hereafter water-provided treatment). In study area 3, New York Mountains, livestock wells were not reactivated (hereafter water-limited treatment). Additionally, we added exclusionary fencing around 2 permanent springs in the water-limited area to prevent access by mule deer but allow for access by other species of wildlife.
Animal Capture and Monitoring Procedures

We captured adult female mule deer during the winter or spring of each year from 2008-2011. We targeted 1 adult female per social group using a net-gun fired from a helicopter (Krausman et al. 1985). We hobbled and blind-folded each animal and transported captured individuals via helicopter to a central processing location. We fitted each individual with either a Global Positioning System radiocollar (GPS; Sirtrack, Havelock North, New Zealand) or a standard Very High Frequency radiocollar (VHF; Advanced Telemetry Systems, Isanti, Minnesota, USA). Each GPS radiocollar was programmed to remotely release approximately 1 year after deployment, while VHF radiocollars remained on the female until the animal died. We employed ultrasonography to measure deposition of subcutaneous fat at its thickest point immediately cranial to the cranial process of the tuber ischium (hereafter MAXFAT; Stephenson et al. 2002) and to determine pregnancy status and fetal rates (Stephenson et al. 1995). MAXFAT measurements were supplemented by palpations of the sacral ridge and the sacro-sciatic ligament to determine a body condition index (hereafter rBCS; Cook et al. 2007). An rBCS of 1 indicated the condition of the individual was generally poor, while incremental increases to 6 of the rBCS indicated an improvement in overall body condition (Cook et al. 2007). We also obtained body mass measured to the nearest 1 kg using a 100 kg hanging scale (Pesola Scales, Baar, Switzerland). When the capture location was less than 1 km from the processing location, we released the individual from the central processing site. We returned the animal to the capture location via helicopter or vehicle when it was greater than 1 km from processing location.
We monitored radiocollar status at the first of each month by fixed wing aircraft, as well as opportunistically by ground crews in Mojave. We recorded signal status as live, mortality, or no signal detected. If a mortality signal was detected a ground crew investigated the signal and performed a field necropsy, if possible (Wade and Browns 1985). We classified cause of mortality as predation (e.g., mountain lion predation), unknown predation, or unknown mortality. We censored all mortalities occurring <2 weeks after capture from our survival analysis.

**Local Weather Patterns**

We obtained annual and seasonal temperature and precipitation data from a MesoWest weather station (University of Utah, Salt Lake City, Utah, USA) located in the MidHills range of Mojave. We calculated mean daily temperature (°C), collected over the 24 hour daily cycle, and total accumulation of precipitation (cm) for both year and season by year. We used the Palmer Drought Severity Index (PDSI; Palmer 1965), which uses rainfall and temperature data to assess dryness, to determine annual and season by year drought conditions (National Climate Data Center 2012). We then related these environmental variables to body condition, productivity, and survival of mule deer.

**Landscape Covariates**

Previous work evaluating patterns of resource selection by mule deer in Mojave has identified preferences by individuals for permanent sources of water, terrain heterogeneity, and an avoidance of well-used roads (McKee 2012). We used ArcGIS 10.0 (Environmental Systems Research Institute [ESRI], Redlands, California, USA) to
derive landscape metrics known to influence selection of resources by mule deer and related them to patterns of survival. We first estimated the spatial error of locations by placing GPS collars in a known location for 7 days. Evaluation of those GPS collars indicated locations occurred within 15 m of the true location. We subsequently buffered locations obtained from deployed GPS radiocollars by 15 m to reduce the effects of spatial error in our evaluation of resource use, which created a polygon 30 m in diameter representing each GPS location. We used a Digital Elevation Model (DEM; United States Geological Survey 2011) to derive a metric of terrain ruggedness (Sappington et al. 2007). We then used the Geospatial Modeling Environment (version 0.5.3, Beyer 2011) to determine straight-line distance of buffered locations of each animal to nearest source of permanent water, nearest maintained road, and landscape ruggedness. We calculated an annual and seasonal mean of landscape metrics for each individual. We evaluated annual and seasonal use of landscape covariates on survival patterns because body condition and productivity at capture were likely influenced by habitat use the previous year but for which we did not have data.

**Statistical Analysis**

A strong relationship between MAXFAT measurements and total body composition of ingesta-free body fat (hereafter body fat) in mule deer has been identified but only when there are measurable deposits of subcutaneous fat (Stephenson et al. 2002). Thus, we derived body fat (%) from MAXFAT measurements and the integration of rBCS scaled for body mass using protocol developed and validated by Cook et al. (2010). We investigated differences in body fat among treatment area, body mass,
pregnancy and twinning status, and precipitation from previous year. We evaluated the distributions of independent variables and implemented a cubic transformation on the negatively skewed variable of body mass prior to statistical analysis (Zar 2010). We used factorial analysis of covariance (ANCOVA) to evaluate relationships of body fat and independent variables (PROC GLM; SAS Institute 9.2, Cary, NC). We incorporated study area and twinning status as main effects in the ANCOVA, while precipitation and body mass were included as covariates. We tested homoscedasticity of errors of independent variables using the homogeneity of variance test (HOVTEST) and evaluated distribution of ANCOVA residuals (PROC UNIVARIATE; SAS 9.2). We employed the least-squared means procedure to evaluate pairwise differences in body fat among main effects and a post hoc regression analysis to evaluate the relationship between body fat and rainfall (PROC REG; SAS 9.2).

Mule deer with low body fat reserves have a high probability of becoming pregnant (Tollefson et al. 2010), although the ability of a female to produce twins maximizes her reproductive success (Johnstone-Yellin et al. 2009) and may be more closely associated with body condition (Johnstone-Yellin et al. 2009; Tollefson et al. 2010). Twinning status of females in Mojave was more variable than pregnancy status and likely provided a better indicator of the efficacy of our treatments. We evaluated the influence of study area, body fat, body mass, and precipitation from previous year on likelihood of a female to produce twins. We modeled the relationship using stepwise logistic regression (PROC LOGISTIC; SAS 9.2) with a relaxed stepwise sequence (α to enter and stay = 0.157; Steyerberg et al. 2001). We assigned an individual carrying twins at capture a ‘1’ and females carrying a single fetus or were not pregnant received a ‘0’.
We evaluated correlations among explanatory variables (PROC CORR; SAS 9.2) and standardized the covariates of body fat, body mass, and precipitation prior to analysis (Zar 2010). We used a chi-squared ($x^2$) goodness-of-fit test to determine model fit (Hosmer and Lemeshow 1978) and a Likelihood-Ratio test ($LR x^2$) to determine significance of the resulting model from a null model of twinning probability. Parameter estimates ($\beta_i$) from the model were used to determine the direction and magnitude of influence (+/-) of model parameters on probability of twinning. We determined significance of $\beta_i$ by evaluating 95% confidence intervals. Estimates with 95% confidence intervals that did not over-lap 0 were determined to be significant components of twinning probability for mule deer in Mojave.

We used the known-fates package in Program MARK (version 6.1, Cooch and White 2009) to analyze monthly patterns of survival of mule deer, which corresponded to our monthly efforts of monitoring status of radiocollars. The known-fates package uses a binomial model to estimate probabilities of survival in a capture-mark-recapture framework where capture occasions for individuals are recorded as 1) signal was heard and animal was alive, 2) signal was heard and a mortality signal was detected, or 3) animal was not heard and was censored from the capture occasion (Cooch and White 2009). To address our hypothesis that mule deer would have higher survival in the water-provided area of Mojave, we first investigated the fixed effects of the 3 study areas on overall probability of survival. We then evaluated models of general variation in survival among months, seasons, and years. Next, we modeled climatic conditions as time-varying group covariates to identify influence of annual and seasonal variation in temperature, precipitation, and drought conditions on female survival. Finally, we
assessed the influence of individual-level conditions on patterns of survival (Table 1). We included body fat and fetal rates as individual covariates, and the landscape metrics of proximity to permanent sources of water, proximity to well-used roads, and ruggedness as time-varying individual covariates. We did not have data related to body condition and landscape metrics for individuals during all seasons and years, so we standardized all individual and group covariates prior to model evaluation (Zar 2010). This approach allowed the distribution of data to be centered on $x$ where all individual covariates missing those data could be assigned a ‘0’ and subsequently evaluated in models of survival in Mojave.

We used Akaike’s Information Criterion adjusted for small sample sizes (AIC$_c$; Akaike 1973) to evaluate candidate models of survival of mule deer in Mojave (Anderson et al. 2000; Burnham and Anderson 2001). Models with the lowest AIC$_c$ were determined to be the most parsimonious (Burnham and Anderson 2002). We evaluated AIC$_c$ weights ($w_i$) of all models within 2 AIC$_c$ of the most parsimonious model to determine the best supported model because the underlying formula incorporates a 2-unit penalty for each model parameter to reduce over-fitting of data (Akaike 1973). We derived model-averaged estimates of monthly survival of all models occurring within 2 AIC$_c$ units of the top model by using weighted averages of survival probabilities (Burnham and Anderson 2002). We calculated monthly and annual survival rates and bootstrapped standard errors for the 3 study areas. We used estimates of $\beta_i$ from the top-ranked model(s) of survival probability to determine the direction and magnitude of influence (+/-) of treatments, weather patterns, body condition, productivity, and landscape metrics. We determined significance of estimates by evaluating 95%
confidence intervals; those that did not over-lap 0 were determined to be significant components of patterns of survival exhibited by mule deer in Mojave.

RESULTS

We captured and monitored 81 unique female mule deer in Mojave between 2008 and 2011. Most individuals were monitored for 10-12 months corresponding to the length of GPS radiocollar deployment. Of the 81 animals, we investigated 17 confirmed mortalities during the course of our study. Three of those mortalities occurred ≤ 2 weeks post-capture and were censored before our analysis of survival. We confirmed the cause of death in 6 of 14 mortalities; mountain lion (*Puma concolor*) predation was the primary cause of death (5 of 6 events). We were unable to determine cause of death for most mortalities (8 of 14 events).

Logistical constraints during mule deer capture activities in 2010 prevented the collection of MAXFAT and productivity measurements during that year. Thus, we only evaluated differences in composition of body fat and productivity of mule deer in Mojave from 2008, 2009, and 2011. We estimated composition of body fat for 76 adult females consisting of 25 animals in the control area, 34 animals in the water-provided area, and 17 animals in the water-limited area. Depositions of body fat of mule deer in Mojave ranged from a minimum of 1.05% and a maximum of 8.83%. We did not detect a difference in composition of body fat among treatment area (*F*<sub>2,66</sub> = 0.59, *P* = 0.555), body mass (*F*<sub>1,66</sub> = 0.40, *P* = 0.529), or a two-way interaction of treatment area by precipitation (*F*<sub>2,66</sub> = 0.45, *P* = 0.643). We detected a relationship between body fat and
total precipitation from previous year \((F_{1,66} = 27.31, P < 0.001; \text{Fig. } 3)\). Our post hoc regression analysis indicated that total precipitation from previous year explained substantial variation in annual deposition of body fat \((r^2 = 0.70)\).

We evaluated twinning rates from a total of 74 adult females in the control \((n = 23)\), water-provided \((n = 34)\), and water limited \((n = 17)\) areas. We determined that 69 of 74 females were pregnant at capture, while 44 of 74 females were carrying twins. The logistic procedure produced a significant model \((LR x^2 = 6.17, P = 0.046)\) that distinguished females carrying twins at capture from those without twins. Parameter estimates from the final model all overlapped 0 but only marginally. The resulting model included an intercept term \((\beta_i = 0.381, 95\% \text{ CI}= -0.104–0.865)\) and additive effects of both body fat \((\beta_i = 0.443, 95\% \text{ CI}= -0.047–0.933)\) and mass \((\beta_i = 0.453, 95\% \text{ CI}= -0.079–0.985)\). We were unable to identify effects of treatment area, precipitation, or two-way interactions of body fat by body mass, body fat by precipitation, or treatment area by body fat. The goodness-of-fit test indicated the resulting model was consistent with a logistic fit \((x^2 = 11.04, P = 0.199)\).

Our best model of monthly survival for 78 mule deer contained a fixed effect of the control area and additive effects of fetal rate, ruggedness, proximity to permanent sources of water, and proximity to maintained roads \((AIC_c = 146.39, w_i = 0.07; \text{Table } 2)\). The highest ranked model differentiating probabilities of survival between the water-provided treatment area and the water-limited area was not supported \((\Delta AIC_c = 3.20, w_i = 0.014; \text{Table } 2)\). We detected marginal support for models containing an effect of total accumulation of precipitation during the preceding summer \((\Delta AIC_c = 1.10, w_i = 0.04; \text{Table } 2)\) but confidence intervals for the parameter representing this effect overlapped 0.
(β_i = 0.567, 95% CI= -0.583–1.717). Models of survival containing effects of
temperature and drought conditions were less supported than the null model (ΔAICc =
5.47, w_c = 0.005; Table 2) and were not considered informative.

Estimates of parameters from our top-ranked model of monthly survival
suggested the control area produced a positive effect on probability of survival for
animals inhabiting that area but the 95% confidence intervals overlapped 0 (Table 3). A
positive, but marginally supported, effect of fetal rate on probability of survival was
detected in the spring, summer, and autumn months following capture (Table 3). We
identified a negative effect of terrain ruggedness on probability of monthly survival
during the autumn, winter, and spring months but did not detect that relationship during
the summer months (Fig. 4; Table 3). We also detected a negative, but marginally
supported, effect of proximity to nearest source of water in the spring and a positive
effect of proximity to maintained roads during autumn (Table 3).

We derived model-averaged probabilities of survival from all models ≤ 2 AICc
units of the top ranked model, which comprised 60% of the cumulative model weights.
Estimates of monthly survival (S ± SE) in the control area were constant during the
biological year (June through May) at 0.997 ± 0.001 (Fig. 5), which resulted in an annual
survival rate of 0.97 ± 0.004 (Fig. 6). Estimates of monthly survival in the treatment
areas were more variable where they fluctuated from 0.987 ± 0.002 during the summer
months to 0.984 ± 0.004 during the autumn and early winter months (Fig. 5). Variation
in monthly survival for the 2 treatment areas resulted in an annual estimate of survival of
0.852 ± 0.009 for both areas (Fig. 6).
DISCUSSION

We were unable to detect differences in body condition, productivity, or survival where availability of water was improved compared to areas where access to water was limited. Marshal et al. (2006a) postulated that adult mule deer with established home ranges in a Sonoran Desert ecosystem were less likely to utilize recently developed sources of water than younger animals without established home ranges, ultimately suggesting a population level lag-effect in response to the presence of water developments. Two of capture occasions where we collected data related to body condition and productivity occurred before (2008) or immediately after (2009) livestock catchments in the water-provided treatment area were reinstated in the autumn of 2008. During only one capture occasion (2011), were those data collected >1 year after the establishment of new sources of water. Lack of differentiation in body condition of mule deer among the 3 study areas could have resulted from a lag in response to the augmentation of water sources.

Our findings highlight the importance of rainfall on body condition and subsequent productivity of mule deer inhabiting a desert ecosystem, consistent with other work investigating the influence of climatic conditions on demography of desert ungulates (Cain et al. 2008; Fox et al. 2000; Marshal et al. 2008). The effects of increased precipitation on mule deer is likely manifested through an increase in forage availability and quality (Esparza-Carlos et al. 2011; Marshal et al. 2005a, 2005b), in addition to increasing the availability of ephemeral sources of water. Following years of high accumulations of rainfall, mule deer in Mojave exhibited a higher percentage of
body fat than following years of low rainfall. Interestingly, following the year of highest rainfall (19.38 cm, 2010), mule deer did not have the highest percentage of body fat. Nearly 15 cm of rainfall occurred during the winter months of 2010, while the subsequent summer received substantially less (0.51 cm). In contrast, nearly 11 cm of rainfall occurred during the summer of 2007, comprising 60% of the total rainfall from that year. Mule deer captured during the subsequent winter exhibited the highest levels of body fat during our study. Those results not only highlight the importance of total precipitation but also indicate the importance of the timing of precipitation on body condition of an ungulate inhabiting an arid environment.

Although composition of body fat and body mass contained marginal support in our analysis of twinning rates of mule deer, our results suggest a positive effect of body condition on likelihood of twinning. Furthermore, annual pregnancy rates of mule deer in Mojave were generally high indicating nutritional condition of females was adequate to support ovulation (Cook et al. 2004; Tollefson et al. 2010). Larger females, and those with higher levels of body fat, were more likely to be carrying twins at capture than smaller females and those with low levels of body fat. Our results corroborate the findings of Tollefson et al. (2010) who observed that similar measures of body condition were good predictors of twinning rates in captive mule deer. We were, however, unable to identify an effect of water availability on productivity of females among our 3 study areas. Bishop et al. (2009) also were unable to detect increases in fecundity of a mule deer population in response to enhanced nutritional conditions in southern Colorado, USA. Those authors, however, observed a significant effect of their treatment on survival of juveniles. Females carrying twins likely maximizes individual fitness of mule
deer (Johnstone-Yellin et al. 2009). We were, however, unable to infer twinning rates at capture to survival and subsequent recruitment into the breeding population of those young. Effects of the provisioning of water on demography of mule deer in a water-limited environment may be better manifested through its influence on survival and recruitment of juveniles among our 3 study areas.

We found little support for effects of climatic conditions on survival of adult females in Mojave. Although our results included a positive effect of total accumulation of precipitation from the previous summer in our top suite of models (Table 3), the confidence intervals for this effect overlapped 0. Additionally, effects of temperature and drought were inconclusive. Survival of adult female mule deer, however, is generally robust to climatic fluctuations and variation in adult survival may be only manifested during extremely poor years (i.e., low rainfall and high temperatures; Gaillard et al. 2000). There was little variation in both temperature and drought among all years and seasons of our study, which likely limited our ability to detect a relationship between those climatic variables and survival.

We did not detect a strong relationship between body condition and survival of adult female mule deer in Mojave but enhanced body condition has been linked to increased survival of females (Bishop et al. 2009). We did, however, identify a relationship between fetal rates and survival in our top model of survival, although the effect of that parameter was not significant. Those results suggest that females carrying twins at capture had higher survival. The inclusion of the parameter related to fetal rates in our top model may be indicative of the importance of individual condition of females on monthly survival in Mojave (i.e., some females may be better equipped to reproduce
and survive than others). Nonetheless, mule deer are a long-lived species and females recruit few off-spring over a lifetime (Anderson 1981; Gaillard et al. 2000). Although body condition of mule deer fluctuates in response to resource conditions on the landscape (Fox and Krausman 1994; Marshal et al. 2008), survival of adult females is relatively insensitive to changes in those conditions (Gaillard et al. 2000). Accordingly, population dynamics of mule deer in Mojave may be better understood through evaluation of birth rates and juvenile recruitment (Bishop et al. 2009; Gaillard et al. 2000; Johnstone-Yellin et al. 2009).

We exercise caution in the interpretation of the negative effect of proximity to water in spring and the positive effect of proximity to maintained roads in autumn in our top model of survival. Both of those results were detected in the shortest seasons of the year and the effect of proximity to maintained roads is counterintuitive to expectations. During spring, when abundance and quality of vegetation in desert ecosystems are at their maximum (Marshal et al. 2005a, 2005b), our top model of survival suggested that deer closer to permanent sources of water had a lower probability of survival. We would expect that mule deer would be least constrained by the acquisition of free-water during this period. Thus, it is not surprising that deer would venture further from water sources and proximity to water is not likely the proximate cause of reduced survival for deer in those areas. Additionally, hunting season of adult males occurs during the autumn. A popular strategy for hunting activity in the area is traveling by vehicle along roads, near which Mojave personnel have documented illegal harvest of female mule deer (N. Darby, unpublished data). Consequently, proximity to roads during the autumn is a risky strategy for either sex of mule deer. Given the relatively small temporal scale of the
effect of proximity to water and maintained roads (i.e., 2 months) on survival of mule deer, we suspect those effects to be an artifact of small sample sizes. The relationship between survival and use of water and roads is in need of further evaluation.

Previous work evaluating landscape ruggedness of ungulates inhabiting a desert ecosystem have identified preferences by those animals for heterogeneity in terrain (Bleich et al. 1997; Fox and Krausman 1994; Ordway and Krausman 1986; Sanchez-Rojas and Gallina 2000), a relationship that was also exhibited by mule deer in Mojave (McKee 2012). A preference for rugged terrain could represent a predator avoidance strategy, in which mule deer seek out areas that allow for long-distance detection of danger and rapid escape (Connolly 1981; Geist 1998). Although mule deer in Mojave preferentially selected areas of increased ruggedness (McKee 2012), we identified a negative relationship between increased ruggedness and probability of survival of females during the autumn, winter, and spring. Coyotes (Canis latrans) have been identified as a primary predator of juvenile mule deer (Bishop et al. 2009; Connolly 1981; Hurley et al. 2011) and are more abundant in areas of decreased ruggedness (Bleich et al. 1997). Mule deer will move to areas of more rugged habitat in response to risk of predation by coyotes (Lingle 2002). Movement to rugged habitat could increase the exposure of individuals to risk of predation by mountain lions (Beier et al. 1995; Murphy and Ruth 2009; Pierce et al. 2004), a primary predator of adult mule deer (Connolly 1981; Hurley et al. 2011). We acknowledge, however, that we were unable to detect a relationship between female survival and terrain ruggedness during the summer, a critical period of juvenile vulnerability (Bishop et al. 2009; Gaillard et al. 2000; Hurley et al. 2011; Johnstone-Yellin et al. 2009). Additionally, selection of habitats with a
higher risk of predation is contrary to expectations of species that exhibit life-history strategies consistent with strong density dependence (Gaillard et al. 2000). Continued monitoring of mule deer in Mojave will yield a better understanding of the relationship between ruggedness and adult female survival.

Monthly and annual probabilities of survival of adult females in all 3 study areas of Mojave were generally high and consistent with other populations of mule deer (Bender et al. 2007; Bishop et al. 2005; Bishop et al. 2009; Hurley et al. 2011; Lukacs et al. 2009). Interestingly, we were unable to differentiate patterns of survival between our 2 treatment areas but we identified significantly higher survival in the control study area. The configuration of the landscape comprising the control area of Mojave consists of gentle slopes with a dense vertical vegetation structure and few rugged ranges. Consequently, the region may not be conducive to the stalk and ambush behavior of mountain lions (Beier et al. 1995; Murphy and Ruth 2009; Pierce et al. 2004). We suspect that higher survival of adult female mule deer in the control area is a result of a reduction in predation risk. This hypothesis requires further study on predator abundance and distributions in Mojave.

We did not identify variation in either monthly or annual estimates of survival, indicating constant survival of mule deer during our study. Those results may be due to short monitoring intervals of individuals, limiting our ability to detect variation, or, more likely, sample size. Nonetheless, mature female ungulates generally exhibit little temporal variation in survival (Gaillard et al. 2000), although evaluation of survival does provide insight into the dynamics of the population as a whole (Bender et al. 2007; Lukacs et al. 2009). Identification of variation in parameters related to recruitment of
neonates is likely a better indicator of population performance when adult survival is high (Gaillard et al. 2000). Therefore, we may better understand the effects of manipulation of water sources on mule deer by evaluating variation birth rates and survival of juveniles among our 3 study areas.

The influence of water developments on body condition and demographic traits of adult female mule deer in Mojave remains largely unknown. Because survival of mule deer in Mojave was high and stable during our study, parameters related to recruitment of young may be more variable and provide a better perspective of the overall importance of development of water sources. Our results, however, describe findings from phase 1 of a 10 year study. During phase 2, water catchments in the water-limited area will be reinstituted, which will likely provide further insight into life history strategies of those mule deer and improve our likelihood of detecting effects of water developments on adult females. Although not novel, we were able to identify a link between precipitation and body fat, and body fat and fetal rates, and an indication of an overall effect of female condition on survival. The description of baseline information related to those components of demography provides an understanding of the general dynamics of a formerly unstudied population of desert-dwelling herbivores.

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Table 1. Description, abbreviation (Abbr), and effect category of parameters investigated in models of survival for mule deer in Mojave National Preserve, California, USA where the effects of permanent water provisioning on demography of mule deer were investigated, 2008-2011.

<table>
<thead>
<tr>
<th>Model Parameter</th>
<th>Abbr</th>
<th>Description</th>
<th>Effect Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>AREA</td>
<td>Study area</td>
<td>Group</td>
</tr>
<tr>
<td>Body Condition</td>
<td>BF</td>
<td>Ingesta-free body fat (%)</td>
<td>Covariate</td>
</tr>
<tr>
<td>Control Area</td>
<td>CA</td>
<td>Control area</td>
<td>Group</td>
</tr>
<tr>
<td>Fetal Rate</td>
<td>FR</td>
<td>Fetal count at capture</td>
<td>Covariate</td>
</tr>
<tr>
<td>Water</td>
<td>H2O</td>
<td>Distance to nearest source of water (m)</td>
<td>Covariate†</td>
</tr>
<tr>
<td>Precipitation</td>
<td>PREC</td>
<td>Precipitation from previous summer (cm)</td>
<td>Group</td>
</tr>
<tr>
<td>Maintained Roads</td>
<td>RDS</td>
<td>Distance to nearest maintained road (m)</td>
<td>Covariate†</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>RUG</td>
<td>Vector ruggedness metric (0 to 1)</td>
<td>Covariate†</td>
</tr>
</tbody>
</table>

†Parameter evaluated as a time-varying individual covariate
Table 2. Candidate models of monthly survival of 78 mule deer in Mojave National Preserve, California, USA, 2008-2011.

Models were analyzed using Program MARK (version 6.1, Cooch and White 2009) and evaluated using differences in Akaike’s Information Criterion values ($\Delta AIC_c$) and model support ($w_i$). Provided are the top 2 models of survival ($w_i = 0.129$) and all models containing an additional parameter ($k$) but occur $\leq 2$ $AIC_c$ units of the top model. Certain effects were only detectable during specific seasons and are indicated in parenthesis of the model description: spring (sp), summer (su), autumn (a), winter (w). See Table 1 for parameter descriptions.

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA + FR (sp, su, a) + RUG (a, w, sp) + H2O (sp) + RDS (a)</td>
<td>6</td>
<td>146.39</td>
<td>0.00</td>
<td>0.070</td>
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<tr>
<td>CA + FR (sp, su, a) + RUG (a, w, sp) + RDS (a)</td>
<td>5</td>
<td>146.72</td>
<td>0.33</td>
<td>0.059</td>
</tr>
<tr>
<td>CA + FR (sp, su, a) + RUG (a, w, sp) + RDS (a) + RUG*H2O (sp)</td>
<td>7</td>
<td>147.43</td>
<td>1.04</td>
<td>0.042</td>
</tr>
<tr>
<td>CA + PREC (a, w) + FR (sp, su, a) + RUG (a, w, sp) + H2O (sp) + RDS (a)</td>
<td>7</td>
<td>147.49</td>
<td>1.10</td>
<td>0.040</td>
</tr>
<tr>
<td>CA + PREC (a, w) + FR (sp, su, a) + RUG (a, w, sp) + H2O (sp, a) + RDS (a)</td>
<td>7</td>
<td>147.74</td>
<td>1.35</td>
<td>0.036</td>
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<tr>
<td>CA + FR (sp, su, a) + RUG (a, w, sp) + H2O (sp) + RDS (a) + BF (w)</td>
<td>7</td>
<td>147.95</td>
<td>1.57</td>
<td>0.032</td>
</tr>
<tr>
<td>CA + FR (sp, su, a) + RUG (a, w, sp) + H2O (sp) + RDS (a) + BF (w, sp)</td>
<td>7</td>
<td>148.27</td>
<td>1.88</td>
<td>0.027</td>
</tr>
<tr>
<td>Description</td>
<td>DF</td>
<td>SS</td>
<td>MS</td>
<td>P</td>
</tr>
<tr>
<td>----------------------------------------------------------------------------</td>
<td>----</td>
<td>-----</td>
<td>-----</td>
<td>----</td>
</tr>
<tr>
<td>CA + FR (sp,su,a) + RUG (a,w,sp) + H2O (sp) + RDS (a) + SU</td>
<td>7</td>
<td>148.29</td>
<td>1.91</td>
<td>0.027</td>
</tr>
<tr>
<td>CA + FR (sp,su,a) + RUG (a,w,sp) + H2O (sp) + RDS (a) + BF</td>
<td>7</td>
<td>148.36</td>
<td>1.97</td>
<td>0.026</td>
</tr>
<tr>
<td>AREA + PREC (a,w) + FR (sp,su,a) + RDS (a) + RUG (a) + H2O (sp)</td>
<td>8</td>
<td>149.59</td>
<td>3.20</td>
<td>0.014</td>
</tr>
<tr>
<td>NULL MODEL (.)</td>
<td>1</td>
<td>151.86</td>
<td>5.47</td>
<td>0.005</td>
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</table>
Table 3. Parameter estimates ($\beta_i$), standard errors (SE), and 95% confidence intervals from best competing model of monthly survival for 78 mule deer in Mojave National Preserve, California, USA, 2008-2011 (see Table 2). The top model included positive effects of the study control area, fetal rates, and proximity to maintained roads, as well as negative effects of ruggedness, and proximity to water. See Table 1 for parameter descriptions.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\beta_i$</th>
<th>SE</th>
<th>lower</th>
<th>upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>INT†</td>
<td>4.32</td>
<td>0.33</td>
<td>3.68</td>
<td>4.97</td>
</tr>
<tr>
<td>CA</td>
<td>1.78</td>
<td>1.07</td>
<td>-0.31</td>
<td>3.87</td>
</tr>
<tr>
<td>FR</td>
<td>0.5</td>
<td>0.32</td>
<td>-0.12</td>
<td>1.12</td>
</tr>
<tr>
<td>RUG</td>
<td>-0.81</td>
<td>0.4</td>
<td>-1.58</td>
<td>-0.04</td>
</tr>
<tr>
<td>H2O</td>
<td>1.13</td>
<td>0.65</td>
<td>-0.15</td>
<td>2.42</td>
</tr>
<tr>
<td>RDS</td>
<td>-1.09</td>
<td>0.53</td>
<td>-2.13</td>
<td>-0.06</td>
</tr>
</tbody>
</table>

†Intercept of top ranked model
FIGURE LEGENDS

Figure 1. Location of control and treatment areas in Mojave National Preserve, southwestern California, USA, where the effects of permanent water provisioning on demography of mule deer was investigated, 2008-2011.

Figure 2. Annual temperature and precipitation pattern used to delineate seasons in Mojave National Preserve, California, USA, 2008-2011. Winter was identified as December-March, spring as April-May, summer as June-September, and autumn as October-November. Gradient-filled circles identify mid-winter (February) and mid-summer (August) precipitation peaks, exhibiting a distinct bi-modal pattern of annual precipitation. Climatological data were collected at Mitchell Caverns in central Mojave National Preserve from 1958-1996.

Figure 3. Relationship between ingesta-free body fat (Cook et al. 2007) and precipitation accumulation from previous year for mule deer in Mojave National Preserve, California, USA where the effects of permanent water provisioning on demography of mule deer were investigated, 2008-2011. We evaluated body fat of 16 animals captured in 2008, 28 animals in 2009, and 32 animals in 2011. A significant relationship between body fat and total precipitation from previous year was detected ($r^2 = 0.70; F_{1,66} = 27.31, P < 0.001$). Estimated depositions of body fat ($\bar{x} \pm SE; previous year’s rainfall in parenthesis) of mule deer captured in 2008 was $6.76 \pm 0.26\%$ (19.05
cm), 2.91 ± 0.38% (16.21 cm) for mule deer captured in 2009, and 4.97 ± 0.31% (19.38 cm) for mule deer captured in 2011.

**Figure 4.** Relative probability of monthly survival ($S$) of mule deer ($n = 78$), while holding other model parameters constant (see Table 3), for influence of terrain ruggedness in Mojave National Preserve, California, USA, 2008-2011. We detected a significant and negative effect of increased terrain ruggedness on monthly survival during the autumn, winter, and spring ($\beta_i = -0.81$, 95% CI= -1.58– -1.04). Solid curve represents the relationship between monthly survival and terrain ruggedness, while dashed line represents cumulative effect of ruggedness on autumn, winter, and spring survival.

**Figure 5.** Monthly patterns of survival ($S$) for mule deer in Mojave National Preserve, California, USA during June through May, 2008-2011. Solid curve represents survival patterns in the study control area ($n = 23$). Dashed curve represents survival patterns exhibited by mule deer for both the water-provided treatment area ($n = 37$) and the water-limited treatment area ($n = 15$).

**Figure 6.** Annual estimates of survival ($S$) for mule deer in 3 study areas of Mojave National Preserve, California, USA where the effects of permanent water provisioning on demography of mule deer were investigated, 2008-2011. Sample size ($n$) indicated above survival estimates in figure.
Figure 1

Mojave National Preserve, California, USA

Legend
- Mojave Boundary
- Control Area (Cima Dome)
- Water-Provided Area (Mid Hills)
- Water-Limited Area (New York Mts.)
- Maintained Roads
- Water Catchment
- Permanent Spring

0 5 10 20 30 40 km
Figure 2

Mojave National Preserve, 1958-1996

Total Precipitation (mm)

Maximum Temperature (°C)

- JAN
- FEB
- MAR
- DEC
- NOV
- OCT
- APR
- MAY
- JUN
- JUL
- SEP
- AUG

0 10 15 20 25 30 35
10 20 30 40 50

Figure 2
Figure 3
Figure 4
Figure 5

Probability of Monthly Survival (S)

Month

Control Area

Treatment Areas
Figure 6
THESIS SUMMARY

Effects of water developments on spatial patterns and population performance of ungulates inhabiting a desert ecosystem still remains largely unknown. Our findings of constricted distributions by mule deer and the overall importance of free-water in patterns of resource selection support our original predictions of changes in special patterns in response to the provision of water. Nevertheless, those results have undoubtedly been confounded by landscape-level disturbance caused by a large wildfire. Indeed, we encountered many of the same issues as our predecessors investigating the utility of water provisioning for desert ungulates (Broyles and Cutler 1999, Marshal et al. 2006, Cain et al. 2008). Attributing our findings in movement and selection exclusively to improved density and distribution of permanent sources of water would be a misleading interpretation of the results from our research. Wildfire often promotes the regeneration of forage of high nutritional quality to ungulates in fire-adapted ecosystems (Ruthven et al. 2000, Holl et al. 2004, Bleich et al. 2008, Long et al. 2008, Meek et al. 2008). The relationship between wildfire and habitat productivity for ungulates appears to also be true in a desert system where historical fire regimes were likely infrequent. Additional research characterizing the quality of vegetation communities following wildfire in Mojave National Preserve, California would provide insight into the relationship between wildfire disturbance and habitat productivity, and the effects of that relationship on use of permanent water by mule deer.

We identified a link between precipitation and body fat of mule deer, and body fat and fetal rates, and an indication of an overall effect of female condition on survival.
Indeed, precipitation appears to be a vital climatic component driving those traits of demography and its importance is manifested through fluctuations in quantity and availability of forage (Marshal et al. 2005b;a, Esparza-Carlos et al. 2011). As climatic conditions become more stochastic due to future changes in global climate (Longshore et al. 2009), the preservation and provisioning of water in desert environments will likely become necessary to augment variability in natural precipitation.

We did not detect improvements in body condition, fetal rates, or survival of mule deer in response to water-provisioning. We were also unable to infer those fetal rates at capture to subsequent recruitment of young into the breeding population. Mature female ungulates generally exhibit little temporal variation in survival (Gaillard et al. 2000), which is a relationship that appears to be true in our 3 study areas. Identification of variation in parameters related to recruitment of neonates is likely a better indicator of population performance when adult survival is high (Gaillard et al. 2000). Therefore, the effects of manipulation of water sources on mule deer may be better understood by evaluating parameters related to juvenile recruitment.

The findings presented in this thesis are from phase 1 of a 2 phase study conducted over 10 years. During phase 2, water catchments of the water-limited study area will be reinstituted, which will likely provide further insight into life-history strategies of mule deer in Mojave National Preserve and improve our likelihood of detecting effects of water developments on population performance. This information related to space use and population performance relative to provisioning of water and wildfire, nonetheless, provide a better understanding of the general dynamics of a formerly unstudied population of desert-dwelling herbivore.
LITERATURE CITED


