University of Nevada, Reno

### Mule Deer Demographics and Parturition Site Selection: Assessing Responses to Provision of Water

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

By

Anthony P. Bush

Dr. Kelley M. Stewart/Thesis Advisor

May 2015



### THE GRADUATE SCHOOL

We recommend that the thesis prepared under our supervision by

### **ANTHONY PAUL BUSH**

Entitled

### Mule Deer Demographics And Parturition Site Selection: Assessing Responses To Provision Of Water

be accepted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Kelley M. Stewart, Ph.D., Advisor

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

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

Scott Bassett, Ph.D., Graduate School Representative

David W. Zeh, Ph. D., Dean, Graduate School

May, 2015

#### THESIS ABSTRACT

Providing permanent sources of water to benefit wildlife where this resource is limited has been a common management tactic since the 1940s. Effects of water provisioning on vital rates, corresponding life-history characteristics, and resulting population dynamics have been difficult to quantify. I used a population of mule deer (*Odocoileus hemionus*) in 3 treatment areas with differing levels of permanently available water in Mojave National Preserve, California to investigate population-level responses to provision of water from 2009 to 2014. I investigated the effects of provision of water on pregnancy and fetal rates as well as adult and neonate survival. In addition I investigated the influence of provision of water on parturition sites resource selection patterns. I identified no effect of provision of water on demographic rates. Furthermore, insufficient sample size prevented investigating differences in parturition site resource selection between study areas. I identified a positive effect of body condition, and a negative effect of timing of birth on neonatal survival. Adult survival differed between years, and within years survival differed during the May-June fawning period and was affected by drought conditions. Mule deer in this study system placed parturition sites at higher elevations, and in closer proximity to permanent water sources than random locations, and selected areas with intermediate levels (30-50%) of shrub canopy cover.

#### **THESIS OVERVIEW**

Installation of water developments to benefit wildlife has been practiced widely since the 1940s (Bleich et al. 2005). In the deserts of the western United States, where water is often a limiting factor, mangers have focused much of their efforts and funding on developing water sources for wildlife (Krausman et al. 2006, Simpson et al. 2011). Despite the widespread use of developed water in wildlife management and its acceptance as an effective strategy of maintaining biodiversity in arid environments, very few studies have shown the specific population-level effects (i.e. improved survival or reproduction, etc.) of providing water for wildlife (Cain et al. 2008, Simpson et al. 2011).

Several studies have attempted to quantify the effects of providing water but were unable to find unequivocal evidence because of insufficient duration of studies, periods of drought, abnormally wet years, or issues with experimental design (Krausman and Etchberger 1995, Broyles and Cutler 1999, Dolan 2006, Cain et al. 2008). Lack of information on population-level responses to provisioning of water, and corresponding effects on fitness, have led many investigators to conclude that there is a genuine need for more experimental research to evaluate the influence and effects of water developments on wild populations (Rosenstock et al. 1999, Simpson et al. 2011). Specifically, further research is needed regarding effects of water provisioning on population performance, and changes in distribution or habitat use by wildlife in response to that management action (Rosenstock et al. 1999, Simpson et al. 2011).

Mule deer (Odocoileus hemionus) are widely distributed across the western United

States and have the ability to adapt to extreme temperature and precipitation gradients (Wallmo 1978). In deserts, often characterized by low habitat productivity, deer require large geographic areas to meet energetic demands (Marshal et al. 2006). Lack of ephemeral water and low levels of preformed water in forage during the hot-dry season can cause deer to further expand their home ranges and daily movements to include permanent water sources (Hervert and Krausman 1986, Rautenstrach and Krausman 1989, Marshal et al. 2006). Normal activities for deer, such as movements between bedding and feeding or watering locations can use 25-50% more energy compared to basal metabolic levels (Short 1981). Therefore, in arid areas in which water availability is limited, deer that must travel greater distances to meet their water requirements may have fewer resources to allocate to body condition, growth, and reproduction (Urness 1981, Parker et al. 1984). As a result, reduced nutritional condition of adult female deer may make them more susceptible to predation (Unsworth et al. 1999). Additionally, increases in home range size and movements may also increase the risk of mortality as the animal moves away from cover and is exposed to predators for greater amounts of time. Therefore, individuals with greater access to perennially available water may have higher survival rates because of better body condition and reduced exposure to predation.

Ungulates are characterized by high and relatively stable adult survival and fecundity rates, while neonate survival and recruitment are typically low and extremely variable (Gaillard et al. 1998, 2000). If provision of water was affecting a population, those effects would be expected to be reflected most strongly in fetal rates, and survival and recruitment of young (Gaillard et al. 1998, Monteith et al. 2014).

Survival and recruitment of neonates may also be related to availability of water. The

condition of females during the last trimester, as well as during lactation can have a substantial impact on survival of neonates (Armstrong 1950, Cook et al. 2004). Mule deer in the eastern Mojave Desert of California give birth during the dry season when pre-formed water and nutritional content of forage are at their lowest (Wallmo 1978, Bowyer 1991). Additionally, females with dependent offspring have greater water demands resulting from lactation (Hazam and Krausman 1988). If there is limited water available, individuals may need to expand their home ranges, using up energy reserves, and as a result may be in poorer condition as they approach parturition, a situation potentially exacerbated by a decline in body condition associated with gestation and lactation (Verme and Ullrey 1984, Wakeling and Bender 2003, Hoenes 2008).

In times of water stress ungulates have been shown to switch their diet to forage that is of poorer nutritional quality but higher in water content (deVos and Miller 2005, Hervert et al. 2005), which would presumably have a negative effect on body condition. Poor body condition of the mother often results in lower birth weights (Parker et al. 2009) and increased mortality rate of neonates (Miller and Broughton 1974, Thorne et al. 1976). Further, growth rates of neonates are directly dependent on the amount and quality of milk the mother can produce (Robbins and Robbins 1979, Cook et al. 2004, Tollefson 2007), and neonates that do not receive adequate milk and grow poorly are often more susceptible to predation (Gerhart et al. 1996, Mackie et al. 1998, Cook et al. 2004). Additionally, females in poor condition may not provide sufficient maternal care to neonates (Langenau and Lerg 1976, Rachlow and Bowyer 1994). Thus, the amount of water available to the adult female may influence the survival of the neonate.

Selection of suitable parturition sites may have a significant influence on the successful rearing of young. Neonatal deer are restricted in their movements for the first few weeks of life and are highly susceptible to predators during this period (Kie and White 1985, Bowyer 1987, Gaillard et al 2000, Raithel et al. 2007, Grovenburg et al 2011). It is therefore essential that females select parturition-sites that provide characteristics to minimize predation, such as greater concealment cover, more rugged terrain, or a combination of these characteristics and other factors that can influence predation rates (Bowyer 1987, Farmer et al. 2006, Van Moorter et al. 2000). Parturition sites must also provide a suitable microclimate to prevent complications with exposure of the neonate, especially in the days immediately following birth (Picton 1984, Bowyer et al. 1998, Barbknecht et al. 2011). Moreover, parturition sites must provide adequate forage and availability of free-standing water to support lactation; the quantity and quality of milk produced is directly related to the amount of quality forage and water available (Hazam and Krausman 1988, Wade and Schneider 1992, Parker et al. 2009). Additionally, the amount and quality of milk produced by the female relates directly to the growth and survival of neonates (Robbins and Robbins 1979, Gerhart et al. 1997, Mackie et al. 1998, Cook et al. 2004). Therefore, selection of parturition sites can have a very direct and sizeable effect on the survival of neonatal mule deer.

In chapter 1, I evaluated survival, pregnancy rates, and fetal rates of adult female mule deer in response to the availability of perennial water in Mojave National Preserve, California, USA from 2009 to 2014. Additionally, I evaluated the effect of provisioning of water on neonatal survival from 2013 to 2014. I hypothesized that adult deer with greater access to permanent water sources would use less energy reserves obtaining this resource, leaving them in better nutritional condition, which would translate to higher levels of investigated demographic rates. Furthermore, I hypothesized that, if adult females are in better nutritional condition in areas with greater access to permanent water, then neonates born in these areas would have higher survival rates. I also evaluated the effects of year, season, age, pregnancy status, and climatic conditions on adult female survival, and the effects of year, timing of birth, relative size, and sex on survival of neonates. I used a z-test for proportions to investigate differences in pregnancy rates, and logistic regression to investigate differences in fetal rates. I used the known fates module in Program MARK to evaluate the relative effects of water provisioning, climatic conditions, and individual characteristics on monthly and annual survival rates of adult female mule deer. I used the nest survival module in Program MARK to evaluate the relative effects of water provisioning, timing of birth, and individual characteristics on daily, weekly, and overall survival of neonatal mule deer to 120 days of age.

In chapter 2, I investigated factors influencing the selection of parturition site of mule deer in Mojave National Preserve, California, USA from 2009 to 2014. I hypothesized that proximity to permanent water sources would be a significant component of parturition-site selection in all treatment areas. Additionally, I hypothesized that in areas with limited water availability selection for water would be necessarily stronger, and that by comparing resource selection between these areas and areas with plentiful water I would be able to identify trade-offs in selection. I hypothesized that factors that ostensibly reduce predation risk (higher elevation, steeper slope, more rugged terrain, shrub and tree cover) would be significant components in selection of parturition-sites. I also hypothesized that habitat characteristics related to forage (shrub cover, higher elevations) would be selected. Lastly, I hypothesized that parturition sites would be placed away from areas of human disturbance (maintained and unmaintained roads). I used resource selection functions in an information theoretic framework to investigate selection and avoidance of habitat characteristics in relation to placement of parturition sites.

### LITERATURE CITED

- Armstrong, R.A. 1950. Fetal development of the northern white-tailed deer (*Odocoileus virginianus borealis* Miller). American Midland Naturalist 43:650-666.
- Barbknecht, A.E., W.S. Fairbanks, J.D. Rogerson, E.J. Maichak, B.M. Scurlock, and L.L. Meadows. 2011. Elk parturition site selection at local and landscape scales. Journal of Wildlife Management 75:646-654.
- Bleich, V.C., J.G. Kie, E.R. Loft, T.R. Stephenson, M.W. Oehler Sr., and A.L. Medina.
  2005. Managing rangelands for wildlife. Pages 74-94 *in* N.J. Silvy , editor. The
  Wildlife Techniques Manual: Management, Seventh Edition, Vol 2. John Hopkins
  University Press, Baltimore, Maryland, USA.
- Bowyer, R.T. 1987. Coyote group size relative to predation on mule deer. Mammalia 51:515-526.
- Bowyer, R.T. 1991. Timing of parturition and lactation in southern mule deer. Journal of Mammalogy 72:138-145.
- Bowyer, R.T., J.G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415-425.

- Broyles, B., and T.L. Cutler. 1999. Effect of surface water on desert bighorn sheep in the Cabeza Prieta National Wildlife Refuge, southwestern Arizona. Wildlife Society Bulletin 27:1082-1088.
- Cain, J.W., P.R. Krausman, J.R. Morgart, B.D. Jansen, and M.P. Pepper. 2008. Responses of desert bighorn sheep to removal of water sources. Wildlife Monographs 171:1-32.
- Cook, J.G., et al. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1-61.
- DeVos, J.C., and W.H. Miller. 2005. Habitat use and survival of Sonoran pronghorn in years with above-average rainfall. Wildlife Society Bulletin 33:35-42.
- Dolan, B.F. 2006. Water developments and desert bighorn sheep: implications for conservation. Wildlife Society Bulletin 34:642-646.
- Farmer C.J., D.K. Person, and R.T. Bowyer. 2006. Risk factors and mortality of blacktailed deer in a managed forest landscape. Journal of Wildlife Management 70:1403-1415.
- Gaillard, J.M., M. Festa-Bianchet, and N.G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment and constant adult survival. Trends in Ecology and Evolution 13:58-63.
- Gaillard, J.M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toigo. 2000.
   Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Gerhart, K.L, D.E. Russell, D Van DeWetering, R.G. White, and R.D. Cameron. 1997.

Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactation infertility. Journal of Zoology 242:17-30.

- Grovenburg, T.W., C.C. Swanson, C.N. Jacques, R.W. Klaver, T.J. Brinkman, B.M. Burris, C.S. DePerno, and J.A. Jenks. 2011. Survival of white-tailed deer neonates in Minnesota and South Dakota. Journal of Wildlife Management 75:213-220.
- Hazam, J.E., and P.R. Krausman. 1988. Measuring water consumption of desert mule deer. Journal of Wildlife Management 52:528-534.
- Hervert, J.J., and P.R. Krausman. 1986. Desert mule deer use of water developments in Arizona. Journal of Wildlife Management 50:670-676.
- Hervert, J.J., J.L. Bright, R.S. Henry, L.A. Piest, and M.T. Brown. 2005. Home-range and habitat-use patterns of Sonoran pronghorn in Arizona. Wildlife Society Bulletin 33:8-15.
- Hoenes, B. 2008. Identification of factors limiting desert mule deer populations in the greater San Andres Mountains of southcentral New Mexico. Thesis, New Mexico State University, Las Cruces, New Mexico, USA.
- Kie, J.G., and M. White. 1985. Population-dynamics of white-tailed deer (Odocoileus virginianus) on the Welder Wildlife Refuge, Texas. Southwestern Naturalist 30:105-118.
- Krausman, P.R., and R.C. Etchberger. 1995. Response of desert ungulates to a water project in Arizona. Journal of Wildlife Management 59:292-300.
- Krausman, P.R., S.S. Rosenstock, and J.W. Cain. 2006. Developed waters for wildlife: science, perception, values, and controversy. Wildlife Society Bulletin 34:563-569.

- Mackie, R.J., D.F.P ac, K.L. Hamlin, and G.L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Federal Aid to Wildlife Restoration Report, Project W-120-R, Montana Department of Fish, Wildlife and Parks, Helena, USA.
- Marshal, J.P., V.C. Bleich, P.R. Krausman, M.L. Reed, and N.G. Andrew. 2006. Factors affecting habitat use and distribution of desert mule deer in an arid environment. Wildlife Society Bulletin 34:609-619.
- Miller, F.L., and E. Broughton. 1974. Calf mortality on the calving grounds of Kaminuriak caribou. Canadian Wildlife Service Report Series No. 26.
- Parker, K.L., C.T. Robbins, and T.A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.
- Parker, K.L., P.S. Barboza, and M.P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57-69.
- Picton, H.D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21:869-879.
- Raithel, R.D., M.J. Kauffman, and D.H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795-803.
- Rautenstrauch, K.R., and P.R. Krausman. 1989. Influence of water availability and rainfall on movements of desert mule deer. Journal of Mammalogy 70:197-201.
- Robbins, C.T., and B.L. Robbins. 1979. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. The American Naturalist 114:101-116.

- Rosenstock, S.S., W.B. Ballard, and J.C. deVos. 1999. Viewpoint: benefits and impacts of wildlife water developments. Journal of Range Management 52:302-311.
- Short, H.L. 1981. Nutrition and metabolism. Pp 99-128 in O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.
- Simpson, N.O., K.M. Stewart, and V.C. Bleich. 2011. What have we learned about water developments for wildlife? Not enough! California Fish and Game 97:190-209.
- Thorne, E.T., R.E. Dean, and W.G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. Journal of Wildlife Management 40:330-335.
- Tollefson, T.N. 2007. The influence of summer and autumn forage quality on body condition and reproduction of lactating mule deer and their fawns (*Odocoileus hemionus*). Dissertation. Washington State University, Pullman, USA.
- Unsworth, J.W., D.F. Pac, G.C. White, and R.M. Bartman. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315-326.
- Urness, P.J. 1981. Desert and chaparral habitats part 1: food habits and nutrition. Pages 347-365 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.
- Van Moorter, B., J.M. Gaillard, P.D. McLoughlin, F. Klein, and M.S. Boyce. 2009.
   Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. Oecologia 159:669-678.

Verme, L.J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91-118 in L. K.

Halls, editor. White-tailed deer: ecology and management. The Stackpole Company, Harrisburg, Pennsylvania, USA.

- Wade, G.N., and J.E. Schneider. 1992. Metabolic fuels and reproduction in female mammals. Neuroscience and Biobehavioral Reviews 16:235-272.
- Wakeling, B.F., and L.C. Bender. 2003. Influence of nutrition on mule deer biology and ecology. Pages 93–116 *in* J.C. deVos, Jr., M. R. Conover, and N.E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Press, Logan, Utah, USA.
- Wallmo, O.C. 1978. Mule and black-tailed deer. Pp 31-41, *in* J.L. Schmidt and D.L. Gilbert, editors. Big game of North America: ecology and management. The Stackpole Company, Harrisburg, Pennsylvania, USA.

#### ACKNOWLEDGMENTS

First and foremost I would like to thank my thesis advisor Dr. Kelley Stewart for giving me the opportunity to work on this project and providing constant support and encouragement throughout the past three years. Through her tireless efforts we were able to obtain and manage the requisite funding and support to keep this project moving forward. Dr. Stewart has been an amazing mentor and my staunchest supporter throughout this period and for that I am extremely thankful and humbled.

Another member of my thesis committee, Dr. Vernon Bleich, was absolutely crucial to the success of this project. He has been involved since the project's inception and has spent countless hours working with CDFW to obtain funding and support for the project. I would also like to graciously thank the other members of my advisory committee (J. Sedinger, and S. Bassett) for assistance and guidance through this process.

I would like to thank the efforts of N. Darby and D. Hughson of the National Park Service for their efforts behind the scenes that helped to keep this project running. I thank all the technicians and volunteers (A. Carapucci, M. Blum, D. Walsh, B. Regan, T. Allen, J. Schoener, C. Bleke, J. Merrell, D. Adams, D. Huggins, D. Tupen, and J. Keehn) that braved the heat and mountains of the Mojave Desert with me to collect the data used in this thesis. I thank all the members of the Stewart and Sedinger labs (C. McKee, C. Schroeder, S. Morano, M. Blum, D. Walsh, B. Boan, C. Downs, B. Sedinger, D. Gibson, E. Blomberg, A. Leach, P. Street, T. Rieke, T. Dilts) that have helped me in myriad ways throughout this process. Thank you to all of the family and friends who have stood by me throughout this long period and provided the necessary support and encouragement to see it through.

I would be remiss to not extend my most heartfelt and deepest thanks to J. Keehn who was my rock for the first two and a half years of the project. Without her to support me through hard times, and being an outlet to enjoying life outside of school I would never have reached this point, and for that I will remain eternally grateful.

I would finally like to thank my predecessor on the project, C. McKee, who helped me through the start of my tenure here, came out and volunteered several times to help me hone my field craft, provided an amazing sounding board for ideas, and great conversation on the desert, mule deer, and life in general. And to the next generation of this project, L. Heffelfinger, good luck, and enjoy yourself out there.

### **TABLE OF CONTENTS**

<sup>1</sup> Chapter 1: Provisioning Water for Wildlife: Assessing Population-level	
Demographic Effects on Mule Deer in Mojave National Preserve, CA.	1
Abstract	2
Introduction	3
Materials and Methods	5
Results	17
Discussion	21
Acknowledgements	24
Literature Cited	25
Tables	38
Figures	44

## Chapter 2: Selection of Parturition Sites by Mule Deer in the Southeastern Mojave

Desert: Responses to Water Provisioning	53
Abstract	54
Introduction	55
Study Area	57
Methods	59
Results	64

<sup>&</sup>lt;sup>1</sup> This thesis is composed in accordance to the University of Nevada, Reno's Alternative Formatting for Thesis or Dissertation, in which the following two chapters are being published concurrently with the submission of this thesis

# TABLE OF CONTENTS (Continued)

Discussion	66
Management Implications	69
Acknowledgements	69
Literature Cited	.70
Tables	.80
Figures	. 84
Thesis Summary	88
Literature Cited	91
Photographs	94

Anthony P. Bush, Kelley M. Stewart, Vernon C. Bleich, James S. Sedinger, Neal W. Darby, Debra Hughson

Provisioning water for wildlife: Assessing demographics of mule deer in Mojave National Preserve, CA.

Anthony P. Bush, Kelley M. Stewart, Vernon C. Bleich, James S. Sedinger

Department of Natural Resources and Environmental Science

University of Nevada, Reno

1664 N. Virginia Street

Reno, Nevada 89557, USA

Email: abush@cabnr.unr.edu

Phone: 775-233-8649

Fax: 775-784-4583

Neal W. Darby, and Debra L. Hughson, National Park Service, 2701 Barstow Road, Barstow, California 92311, USA.

#### ABSTRACT

Providing permanent sources of water to benefit wildlife where this resource was thought to be limited has been a common management tactic since the 1940s. Effects of water provisioning on vital rates, corresponding life-history characteristics, and resulting population dynamics have been difficult to quantify. We used a population of mule deer (Odocoileus hemionus) in 3 treatment areas with differing levels of permanently available water in Mojave National Preserve, California to investigate population-level responses of provision of water from 2009 to 2014. We hypothesized that pregnancy and fetal rates would be higher in areas greater availability of water. Additionally, we hypothesized that survival rates for both adults and neonates would be higher in areas with more sources of permanent water. We used a z-test for proportions to investigate differences in pregnancy rates, and logistic regression to investigate differences in fetal rates, between treatment areas. Pregnancy and fetal rates did not significantly differ between treatment areas. We assessed survival patterns of adults using the known fates module in program MARK based on 132 radiocollared adult female deer from 2009 to 2014, and neonatal survival patterns using the nest survival module in Program MARK, based on 46 radiocollared neonates from 2013 to 2014. We observed no support for a difference in adult survival between treatment areas. Adult survival varied among years and survival rates during the fawning period (May-June) varied within years and were affected by drought conditions. We identified no support for variation in survival of neonates among treatment areas. Survival of neonates was substantially lower in the first week of life than in subsequent weeks, and survival was positively influenced by relative body condition as well as being born earlier in the season.

#### INTRODUCTION

Provisioning water for the benefit of wildlife in arid regions has been a common practice of management agencies since the 1940s (Bleich et al. 2005). This practice is believed to increase the population densities and distributions of species in areas where free-standing water is limited. Suggested negative effects of providing water to wildlife, including poor water quality, increased predation levels, entrapment, and competitive exclusion have not been supported (Andrew et al. 2001; Rosenstock et al. 2001; Bleich et al. 2006; Marshal et al. 2006a; Simpson et al. 2011). Nonetheless, positive benefits to wild populations have not been unequivocally demonstrated either (Brown 1998; Bleich et al. 2005; Simpson et al. 2011). Previous attempts to quantify the population level effects of providing water to wildlife have been unsuccessful because of a variety of factors including confounding climatic conditions, insufficient duration of study, lag effects, and issues with study design (Krausman and Etchberger 1995; Broyles and Cutler 1999; Marshal et al. 2006b; Cain et al. 2008). Lack of information on population level responses of provisioning water and corresponding effects on fitness have led many investigators to conclude that there is a genuine need for more experimental research to evaluate the influence and effects of water developments on wild populations (Rosenstock et al. 1999; Simpson et al. 2011).

In the arid southwest, high ambient temperatures and limited precipitation limit habitat productivity (Rautenstrauch and Krausman 1989; Marshal et al. 2005a, 2005b), and low levels of pre-formed water in forage, especially during the hot or dry months, increases the need for freestanding water (Hazam and Krausman 1988). In times of water scarcity, ungulates have been shown to expand home ranges and increase daily movements to obtain sufficient amounts of water (Hervert and Krausman 1986; Rautenstrach and Krausman 1989; Marshal et al. 2006a), leaving fewer resources to allocate to growth, body condition, and reproduction (Urness 1981; Parker et al. 1984). Water requirements are highest for female ungulates with dependent young during lactation (Hazam and Krausman 1988). The amount of free-standing water and quality forage available to females during this period directly affects the quantity and quality of milk produced (Parker et al. 2009). Moreover, the amount and quality of milk directly influences the growth rate and survival of neonates (Robbins and Robbins 1979; Gerhart et al. 1997; Mackie et al. 1998; Cook et al. 2004). While reduced nutritional condition may negatively affect adult female ungulates by making them more susceptible to predation or disease (Unsworth et al. 1999), it may also impact neonate survival because of reduced milk production (Parker et al 2009) and parental care (Rachlow and Bowyer 1994; Langenau and Lerg 1976).

We used mule deer (*Odocoileus hemionus*), a widely distributed ungulate, to investigate the population-level responses to provisioning of water. Mule deer are highly adaptable and use habitats along extreme temperature and precipitation gradients from northern boreal forests to the arid deserts of North America (Wallmo 1981; Heffelfinger 2006). Nevertheless, mule deer populations have been in decline throughout the western United States for several decades (Workman and Low 1976; Bleich and Taylor 1998; Unsworth et al. 1999; Bishop et al. 2009). Mule deer, like many ungulate species, are characterized by high and relatively stable adult survival rates, while survival and recruitment of neonates is usually low and extremely variable among years (Connelly 1981; Gaillard et al 1998, 2000). Thus, juvenile survival and recruitment often have the greatest effect on population dynamics of ungulates (Gaillard et al. 1998). A better understanding of how provisioning of water affects survival and productivity would provide valuable insight into the management of desert ungulates, such as mule deer, and the implementation of water management projects throughout the arid southwest.

Our objective was to assess the population level effects of supplementing permanent free-standing water sources in an arid system. We investigated the relative influence of the amount of available water on pregnancy rates, fetal rates, and survival of adults and neonates in a population of mule deer in the Mojave Desert of California. Additionally, we investigated the effect of environmental and climatic conditions on those demographic parameters. Lastly, we examined the relative effect of greater access to permanent sources of water on body condition and the subsequent effects of body condition on key demographic traits. We hypothesized that individuals with greater access to perennial water sources would be of better body condition, have higher adult and juvenile survival rates, and higher reproductive output (i.e. higher pregnancy and fetal rates). We used traditional statistical methods to investigate the effect of water provisioning on pregnancy and fetal rates. We used an information theoretic approach to examine the effect of availability of water on survival rates of adults and juveniles.

#### **MATERIALS AND METHODS**

*Study Area.*—We studied a population of mule deer in Mojave National Preserve (hereafter Mojave) located in San Bernardino County, California USA (35° 00' N 115° 28' W) from January 2009 to November 2014. Mojave is nearly 650,000 hectares (ha), and in general is bounded on the east by the Nevada-California border, to the north by

Interstate Highway 15, and the south by Interstate Highway 40 (Figure 1). Elevations range from 270 meters (m) to 2,417 m (Thorne et al 1981). The area is characterized by rugged mountain ranges separated by extensive bajadas and playas in the valley floors (McKee et al. *In Review*). Vegetation assemblages representative of three (Great Basin, Mojave, and Sonoran) of the four major desert ecosystems found in North America are present creating heterogeneity across the landscape (National Park Service 2015).

The climate in Mojave is representative of other areas within the arid southwestern United States with high summer temperatures and limited annual precipitation. Temperature and precipitation patterns differ greatly by elevation with mean maximum temperatures of 40.5°C and 19°C at low elevations and 33°C and 13°C at mid to upper elevations for summer and winter respectively (United States Geological Survey 2015). Precipitation in Mojave is bi-modal with peaks during the winter and summer seasons. At low elevations mean annual precipitation is 8.5 centimeters (cm), while mid to upper elevations receive an average of 27 cm of precipitation annually (1958-2011 Providence Mountains State Recreational Area [SRA], southern Mojave Preserve). Seasons were delineated using a climograph (Stewart et al. 2002) of historical temperature and precipitation data obtained from Providence Mountains SRA from 1958-2011 (McKee et al. In Review). This location is at similar elevation (1300 m) and proximate to the study areas and, therefore, should have representative weather phenomena associated with it. We identified seasons as: winter (cool, wet) December-March; spring (warm, dry) April-June; summer (hot, wet) July-September; autumn (cool, dry) October-November (Mckee et al. In Review).

Vegetation communities in Mojave vary by elevation and associated temperature and precipitation levels. Lower elevations are dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) communities with limited amounts of grasses and forbs (Thorne et al. 1981). Mid-elevations below 1,600 m are characterized by cholla cactus (*Opuntia* spp.), barrel cactus (*Ferocactus* spp.), Spanish bayonet (*Yucca* spp.), blackbrush (*Coleogyne ramosissima*), and Joshua tree woodlands (*Yucca brevifolia*), while elevations above 1,600 m are dominated by Great Basin sagebrush (*Artemisia tridentata*), juniper (*Juniperus* spp.), and pinyon pine (*Pinus monophylla.*; Thorne et al. 1981).

Our study area was delineated into three areas with different levels of water availability. The reference area (Cima Dome), encompassing 40,407 ha, had an elevation range of 1,000-1,900 meters (m). This area had 7 permanent water sources that have been continuously available to wildlife for decades. The 39,304 ha water-provided treatment area (Midhills) ranged in elevation from 1,100-2,300 m and had a total of 23 perennial water sources (12 historic livestock wells were reactivated in September 2008). The water-limited treatment area (New York Mountains) was 27,304 ha in size with an elevation range of 1,000-2,300 m and had only 3 available water sources from 2009-2012, and 4 available water sources from 2013-2014. The additional water source was only included in analyses for 2013-2014. Study area boundaries used in these analyses are modified slightly from those described by McKee et al. (*In Review*) to encompass the home ranges of all individuals used in these analyses, several of which extended beyond the previously delineated boundaries. During the duration of the study a limited number of individuals (n = 4) moved between study areas but in all cases the individual returned to the original study area within a few days to weeks.

Animal Capture and Handling Procedures.—During the early spring of each year (2009-2014), we captured adult female mule deer using a helicopter and net-gun (Krausman et al. 1985; McKee et al. In Review). We captured only 1 individual from each social group to ensure independence of samples. Deer were transported to a central processing station where we fitted Global Positioning System (GPS) store-on-board radiocollars (Sirtrack, Havelock North, New Zealand; Advanced Telemetry Systems, Isanti, MN, USA) to each individual. Collars were equipped with a mortality sensor, a timed remote release set to approximately 1 year after deployment, and were programmed to collect 1 location every 90 minutes. Body mass of each deer was measured to the nearest 0.1 kg using a hanging scale (Pesola Scales, Baar, Switzerland) and morphometric measurements (total body length, chest girth, metatarsus length, jaw length) were collected. Prior to release each individual was uniquely marked with eartags. We used ultrasonography to determine nutritional condition of each individual. We measured the level of subcutaneous fat accumulation at its thickest point (to the nearest 0.1 cm), immediately craniad to the cranial process of the tuber ischium (MAXFAT; Stephenson et al. 2002).

We monitored adult survival monthly by fixed wing aircraft and opportunistically by ground crews in Mojave throughout the year. Signal status (live, mortality) was recorded and all mortality signals were investigated by a ground crew. When possible, a field necropsy was performed to assess cause-specific mortality (Wade and Browns 1985). Individuals who died <2 weeks post-capture were censured from survival analyses because we could not eliminate the possibility of capture-related effects.

During most years, we assessed pregnancy status and fetal rates via ultrasonography (Stephenson et al. 1995), with the exception of 2010 and 2012 when pregnancy was assessed using Pregnancy Specific Protein B (PSPB; Sasser et al. 1986) and fetal rates were not recorded. To assess pregnancy status and number of fetuses present, the left-caudal abdomen of each individual was shaved behind the last rib and lubricant was applied to facilitate transabdominal scanning using a 3-MHz transducer (Stephenson et al. 1995). During 2013-2014 adult females that were pregnant were outfitted with a Vaginal Implant Transmitter (VIT) equipped with both temperature and photo sensors (M3930L, Advanced Telemetry Systems, Isanti, MN, USA). Vaginal implant transmitters have previously been shown to have no effect on female survival or cause any complications with reproductive or birthing processes (Carstensen et al. 2003; Johnstone-Yellin et al. 2006; Bishop et al. 2007). We inserted VITs using a technique similar to the methods described in Bishop et al. (2007). The VITs used in this study were structurally within the same specifications as described in Bishop et al. (2011), but were modified by programming such that if temperature stayed above 34°C and the environment was dark the device remained at a constant 40 pulses-per-minute (ppm), while temperatures less than 30°C and lit conditions resulted in a pulse rate of 80 ppm. Once light reached the photo-sensor the pulse rate would not reset without the combination of both temperature and darkness (i.e. ambient temperature alone would not re-set the device). The VITs used incorporated Precise Event Timing (PET) coding which indicated the amount of time elapsed since the photo sensors had been activated in 30

minute increments out to approximately 5 days. Data from VITs were sent via binary coding from the device once every minute after activation, and signals could be received with handheld telemetry equipment (Advanced Telemetry Systems, Isanti, MN, USA).

Females outfitted with VITs were monitored every 1-3 days from May 1<sup>st</sup> until parturition with most individuals checked daily. Once an expelled VIT was detected, a note was made of the amount of time that had elapsed since expulsion. Technicians then approached to within 50 m of the bedded female and, once she left, systematically searched the area for neonates. Search times were limited to 30 minutes to reduce the amount of disturbance to the female (Livezey 1990). If neonates could not be located in the allotted time, technicians returned the next day and attempted the process again. In addition to fawns captured from radiocollared individuals, we also captured neonates either by observing the behavior of unmarked females with young-at-heel (Carstensen et al. 2003), or opportunistically locating neonates while observing other radiocollared individuals.

In 2013, we also checked for the presence of neonates with 2 pregnant deer that were radiocollared but did not receive a VIT, and 13 others with active collars from the previous year whose pregnancy status was unknown. In 2014 we captured one pregnant deer whose birth canal was too narrow for the VIT applicator and thus did not receive a VIT. In each of those instances technicians approached to within 50 meters from the bed sites of these individuals every 1-3 days without being detected and once the female had left the area, systematically searched the area around the bed-site for neonates.

Once located, fawns were captured by hand and blindfolded. Body mass was obtained by placing the fawn in a pillow case and weighing them to the nearest 0.1 kg

using a spring scale (Pesola Scales, Baar, Switzerland). Chest girth and metatarsus length were measured to the nearest 0.1 cm using a tape measure, and new hoof growth was measured to the nearest 0.01 mm using digital calipers. We recorded sex, presence and status of umbilicus, GPS location at capture site, handling time, and microsite vegetation characteristics. We checked each neonate for any signs of dehydration or deformities, and noted if the individual had fled or struggled upon approach or capture. Each neonate received an expandable very high frequency (VHF) radiocollar equipped with a mortality sensor set to 6 hours (M4210; Advanced Telemetry Systems, Isanti, MN, USA) and was subsequently released.

To reduce the probability of handling-induced abandonment of neonates, we employed several tactics to limit disturbance and reduce the transmission of human scent. To the best of our ability, we ensured that we did not approach parturition sites within the first 3 hours post-birth to reduce the possibility of interrupting the critical bonding and imprinting period between mother and neonate(s) (Livezey 1990). All VHF collars were kept in a scent free bag with local vegetation included for at least one week prior to deployment to limit non-native scents (Livezey 1990). Technicians wore nitrile gloves during all handling procedures, and field clothes of the individual handling the neonate, as well as the blindfold and weighing bag used during processing, were all washed in scent removing detergent after every use. Just prior to release all neonates were doused with water at ambient temperature to help reduce the transmission of human scent as well as to help cool the animals.

Ages of neonates from females equipped with VITs during 2014 were obtained from PET coding data (Advanced Telemetry Systems, Isanti, MN, USA). For 2013 neonates and all neonates associated with unmarked females we determined the age of individuals <2days old by appearance and condition of hooves, presence and condition of umbilicus, and behavior (Haugen and Speake 1958). Neonates 2 days of age or older were aged by using body mass in a regression formula created with 24 known age neonates in this study (Age = -5.14 + 2.02\*Mass, R<sup>2</sup> =0.62). We attempted to use hoof growth to estimate age as described in Sams et al. (1996) but we were not confident that measurements were sufficiently consistent among field crews.

Status of neonates (live or dead) was monitored by ground crews every 1-3 days, with most individuals checked daily until 10 weeks-of-age and monthly by fixed wing aircraft thereafter until collars fell off or a mortality event was detected. When a mortality signal was heard, ground crews investigated, performed a field necropsy when possible, and attempted to identify cause-specific mortality (Wade and Browns 1985).

Capture and handling procedures complied with those developed by the California Department of Fish and Wildlife. All procedures, were approved by the Institutional Animal Care and Use Committee at the University of Nevada, Reno (IACUC: 00058), and were in accordance with guidelines established by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011).

*Statistical Analyses.*—We obtained annual and seasonal precipitation and temperature data from a Meso West weather station (University of Utah, Salt Lake City, UT, USA) located in the Mid Hills area of Mojave. Daily average temperature (°C) and amount of precipitation (cm) was calculated over each 24 hour daily cycle. We then used those data to calculate seasonal and annual average temperatures and total precipitation accumulation. Palmer Drought Severity Index (PDSI; Palmer 1965), which incorporates

precipitation and temperature data to assess relative wetness or dryness, was used to identify monthly, seasonal, and annual drought conditions (National Climatic Data Center 2015). These environmental variables were then related to adult and neonate survival.

We used GPS location data from radiocollared deer (2009-2014) to calculate individual home ranges of adult deer using ArcGIS 10.1(Environmental Systems Research Institute [ESRI], Redlands, California, USA). Location data were visually evaluated to identify major outliers and locations outside of the designated study area which were subsequently removed (Moen et al. 1997; McKee et al. In Review). Using the corrected shape files from ArcGIS we then created 2-dimensional 95% (home range) and 50% (core area of use) fixed-kernel density estimates (kde), which we used as a metric to estimate utilization distributions (UD; Seaman and Powell 1996; McKee et al. In Review) using the Geospatial Modeling Environment (0.7.3.0; Beyer 2012). We used least-squares cross-validation as a smoothing parameter (h) for kernel density estimates (Seaman and Powell 1996; Seaman et al 1999). Annual and seasonal UDs were created for all adult individuals in the study. Area (ha) of the home range and core area of use, along with the distance (m) from the centroid of each to the nearest perennial water source were calculated in ArcGIS (Environmental Systems Research Institute [ESRI], Redlands, California, USA). We used these values as covariates in survival analyses for adult deer.

We created a single metric of body size for each individual adult and neonate using principal components analyses (PCA; SAS 9.4, SAS Institute, Cary, NC, USA). For adult deer we used total body length, chest girth, and metatarsus length in the PCA analysis, while for neonates we used chest girth and metatarsus length. We obtained an index of body condition using the residual values obtained by regressing body mass against the results of the principal component analysis (PCA) of morphometric measurements (PROC REG; SAS 9.4, SAS Institute, Cary, NC, USA). Residual values that were above the predicted line indicated that individual was in better condition than expected for a given body size, while those below the predicted line were considered to be in poorer condition. Neonates have no subcutaneous fat and very limited visceral fat, additionally there is no rumen fill and the nutrients obtained from milk are used almost exclusively for growth (Short et al. 1981; Parker et al. 2009). Therefore the relative body condition of neonates is a comparison of lean body mass in relation to structural size.

For neonates, we calculated relative birth date as the difference between the date of birth of the individual and the median date of the fawning period for 2009-2014. We converted relative birth dates to standard normal variables before conducting survival analyses (Zar 2010). In addition, we included sex as an individual covariate in survival analyses. Additional individual covariates used for adults were age class (young, medium, old), pregnancy status (pregnant, not pregnant), and fetal count.

To investigate differences in pregnancy rates between treatments we used a z-test for proportions (Zar 2010). Because nearly all mule deer females become pregnant variation in number of fetuses is more indicative of changes in reproduction among treatments and we used logistic regression framework to investigate differences in fetal rates between treatments (PROC GLM, SAS 9.4, SAS Institute, Cary, NC, USA), where a 0 indicated the female was carrying a single offspring and a 1 indicated 2 fetuses. We used the Hosmer and Lemeshow test to assess goodness-of-fit of the logistic regression (Zar 2010). We used the known-fates module in Program MARK (Version 8.0; Cooch and White 2015) to estimate monthly survival rates for adult female mule deer using a staggered entry design (Pollock et al. 1989). We used a sequential model building procedure (Blomberg et al. 2013) to examine biological effects while reducing the overall number of models we considered. First, we modeled effects of temporal variables month, year, season, and combinations of month or season on adult survival. We then tested spatial models that incorporated delineation between treatment groups (water-provided, water-limited, reference) using the best supported temporal model. The best supported spatial or temporal model was then used for all further analyses investigating the influence of climatic patterns, as well as landscape and individual covariates, on the monthly survival rates of adult mule deer.

We used the nest-survival module in Program MARK (Version 8.0; Cooch and White 2015; White and Burnham 1999) to estimate daily survival rates of neonates. Nestsurvival models have been shown to be very effective for analyzing telemetry data in which individuals were monitored at irregular intervals (Dinsmore et al. 2002; Hupp et al. 2008; Blomberg et al. 2014). We used day as our occasion and modelled survival out to 120 days at which point juveniles had shed their spotted pelage, were completely weaned, and move around freely with their mothers (Dixon 1934; Short 1964; Knipe 1977; Heffelfinger 2003). After 120 days, young have a survival rate similar to that of adults (Heffelfinger 2006). We again employed the sequential model building procedure in MARK beginning with several time varying models. We allowed each daily (1-120), weekly (1-17), monthly (1-4), and yearly (1-2) survival rate to vary in separate models. Additionally, we tried several different combinations of those temporal delineations, as well as trends on weekly and monthly survival and quadratic effects. We tested spatial models delineating between treatment groups (water-provided, water-limited, reference) using the best supported temporal model, and then used the best supported spatial or temporal model to test the influence of individual covariates on daily survival of neonates.

We employed an information theoretic approach to model selection (Burnham and Anderson 2002). For all adult and neonate survival models we calculated Akaike Information Criterion adjusted for small sample size (AIC<sub>c</sub>; Akaike 1973),  $\Delta$ AIC<sub>c</sub>, and Akaike weights ( $w_i$ ; Burnham and Anderson 2002) to evaluate candidate models of survival (Anderson et al. 2000; Burnham and Anderson 2001). The model with the lowest AIC<sub>c</sub> value was considered the most parsimonious (Burnham and Anderson 2002), and we used model averaging to obtain survival rates in Program MARK (Cooch and White 2015). We calculated annual survival estimates for adult deer by multiplying the associated monthly estimates together and using bootstrapping to obtain standard errors. Weekly survival rates for neonates were obtained by raising the daily survival rates to the 7<sup>th</sup> power and standard errors were obtained using the delta method (Cooch and White 2015; Powell 2007). We then calculated model averaged parameter estimates and associated 85% confidence intervals based on unconditional standard errors (Arnold 2010; Buckland et al. 1997). We determined model-averaged parameter estimates to be significant if the 95% confidence intervals did not overlap zero.

#### RESULTS

We captured and radiocollared 132 individual adult female deer from 2009 to 2014, with most collars remaining on individuals for 10-12 months. We classified mortalities as vehicle, mountain lion predation, labor dystocia, or undetermined. We observed 25 mortality events of which 8 were confirmed mountain lion predation events, 2 individuals were hit by vehicles, 1 female died of complications of birthing (labor dystocia), and in 14 instances we were unable to identify the cause of death (Fig. 2).

The overall pregnancy rate in Mojave from 2009 to 2014 was 0.96 and overall fetal rate from the years 2009, 2011, and 2013-2014 was 1.61 fetus per female. Pregnancy rates did not significantly differ between the water-limited (0.93, n = 40) and water provided (0.96, n = 56) study areas (Z = 0.389, P = 0.35). Pregnancy rates also did not differ between the reference area (1.0, n = 41) and the water-provided area (Z = 0.50, P = 0.31), or between the water-limited and reference areas (Z = 1.18, P = 0.12). The logistic regression model of fetal rates by study area was 58% concordant and results of the Hosmer and Lemeshow goodness-of-fit test were non-significant ( $\chi^2$  (7, n=83) = 7.44, P = 0.38), indicating a logistic fit to the data. We observed no effect of study area on fetal rates between the water-limited area and reference area (Wald  $\chi^2$  (1, n = 83) 0.0078, P = 0.93), or water-provided area (Wald  $\chi^2$  (1, n = 83) 0.0083, P = 0.93).

We captured A total of 46 mule deer neonates from 2013-2014 from the waterlimited (n = 15), water-provided (n = 14), and reference (n = 17) areas. In 2013 we captured 24 neonates from deer with VITs (n = 12), with radiocollars only (n = 9), and from non-collared individuals (n = 3). In 2014, we captured 22 neonates from deer with VITs (n = 18) and from non-collared individuals (n = 4). Successful VIT retention (i.e. device was retained to parturition and located within close proximity to the birth-site) was 69% for 2013 and 82% for 2014. Of neonates captured, 57% (26 of 46) were  $\leq$ 2 days old, while all captured individuals were caught in the first week post-partum. Mortalities of neonates were classified as non-predation (i.e. abandonment or disease), coyote predation, felid predation, mother deceased, stillborn, or undetermined. We investigated 34 mortality events of which 3 were identified as non-predation, 6 mortalities were caused by coyote predation, 5 were identified as felid predation, 4 individuals were stillborn (one of which was severely deformed), and 2 occasions occurred where the mother was killed prior to the neonates death, and 14 cases were classified as undetermined (Fig 2).

In the principal component analysis (PCA) for adult deer the first principal component (PC1) explained 55% of the variation in body size. Because the eigenvector associated with PC1 loaded similarly (0.55-0.61) across all body size metrics, we used PC1 in all further analyses as an index of body size. Residuals of the regression analysis of body mass and PC1 ( $R^2$ =0.36, P < 0.0001) were used as a metric of body condition in further analyses. For neonates, the first principal component explained 85% of the variation in body size and eigenvectors loaded similarly (0.70-0.71) therefore, we used these values in our regression analysis ( $R^2$ =0.62, P < 0.0001) and residuals of the regression were used as a metric of relative body condition for neonates in all further analyses.

Effect of study area of adult survival was not supported in our analyses ( $\Delta AICc =$  17.04). Nevertheless, we used this model for comparison of the average monthly survival rate between study areas over the duration of the study. The average monthly survival of

adults by study areas were: water-provided 0.988 (SE = 0.005, n = 53), water-limited 0.983 (SE = 0.005, n = 37), and 0.987 (SE = 0.003, n = 42) in the reference area. Mean annual survival rate of adult females in Mojave, assessed using monthly estimates from the null model raised to the  $12^{\text{th}}$  power, was 0.85 (SE = 0.022, *n* = 132). Models including complete time variation (i.e. all 71 monthly survivals estimated individually) did not converge and were removed from the analysis. We observed no support for either body condition or the size of the core area of use on adult survival. Two models received equal support for estimating monthly adult survival, both included additive effects of year, fawning period, and drought severity during the fawning period, while one included distance to nearest perennial water source (AIC<sub>c</sub> = 432.36,  $w_i$  = 0.247; Table 3). Three other models also were competitive ( $\Delta AIC_c \leq 2$ ) therefore the top 5 models were used for model averaging of parameter estimates (Table 3). Results of model averaging (Table 4) indicated that 2009 ( $\beta = -1.37$ , SE = 0.81), 2010 ( $\beta = -2.36$ , SE = 0.78), 2011 ( $\beta = -1.35$ , SE = 0.88), 2012 ( $\beta$  = -2.48, SE = 0.81), and 2013 ( $\beta$  = -1.62, SE = 0.79) all had significantly lower survival rates then 2014 (Figure 3). Additionally survival was lower, within years, during the fawning period (May-June;  $\beta = -0.71$ , SE = 0.44), and was positively affected by reduced drought severity (CurrentPDSI;  $\beta = 0.65$ , SE = 0.35). All top models included differences in survival by year, as well as, differences in survival during the fawning period within years (May-Jun; Figure 4). We observed a positive, significant effect of PDSI on survival during the fawning season (Figure 5). Most of the competitive models included PDSI values from the current season with the exception of one that had the previous season's PDSI value (i.e. winter PDSI value applied to fawning period). This result most likely resulted from fact that PDSI values are cumulative;

therefore, drier winters would lead to drier fawning seasons and vice versa. Although size of the home range and distance to water were present in three of the competing models, the confidence intervals of the beta estimates overlapped zero (Table 4).

All top models of neonate survival contained a positive trend of survival across weeks, as well as an effect of relative body size and timing of birth on survival (Table 5). The best performing survival model for neonates that included an effect of study area was not competitive with our top models ( $\Delta AIC_c = 19.97$ ). Conversely, models allowing full time variation, as well as all models containing a combination of weekly survival for the early weeks and monthly or constant survival for the later periods did not converge and were removed. One competitive model included a positive quadratic effect of week on neonate survival. Four models were competitive ( $\Delta AIC_c \leq 2$ ) with our top model and we used model averaging in Program MARK to obtain survival rates (Table 5). We estimated neonate survival through 120 days to be 0.20 (SE = 0.004) with substantially lower weekly survival during the first week (0.72 SE = 0.10) then in later weeks (0.99weeks 14-17; Figure 6). Results of model averaging of parameter estimates indicated a significant positive relationship between relative body size and survival ( $\beta = 1.03$ , SE = 0.45; Table 6, Figure 7) and a significant negative relationship between survival and timing of birth ( $\beta = -0.52$ , SE = 0.22, Figure 8). The cumulative effects of relative size and timing of birth on daily neonatal survival result in substantially lower survival of smaller neonates that are born later (Figure 9).

## DISCUSSION

Although we observed no direct effect of provision of water on neonate survival, we identified significant effects of timing of birth and relative body condition in neonates. Neonates born earlier in the fawning period survived better than those born later, and neonates in better relative condition survived better than those in poorer relative condition. Additionally, we found that timing of birth mitigates much of the effects of poor body condition. Previous research has shown that females that are in better physical condition give birth earlier than those of poorer condition (McGinnis and Downing 1977; Robinette et al. 1977; McCullough 1979). Growth rates of neonates are directly related to milk quality and quantity, with those not receiving adequate amounts of milk often having reduced growth and higher susceptibility to predation (Robbins and Robbins 1979; Mackie et al. 1998; Cook et al. 2004; Tollefson 2007). Additionally, neonates born to females in poorer body condition are often born later and at lower birth weights (Julander et al 1961; Verme 1962; McCollough 1979), which can increase early mortality (Holl et al. 1979). Furthermore, quality of forage and the amount of pre-formed water in forage are highest in the early spring and decline thereafter until summer rains arrive (Marshal et al. 2005b). Thus, a female may be able to obtain sufficient nutrition through diet to adequately provision a neonate born in poor condition and allow that individual to recover, or catch up, from a bad start, while this would become increasingly less probable as range conditions (e.g. forage availability) decline. The positive effects of timing of birth and relative condition are likely due to neonates being born to females in better condition, as well as during times when range conditions are optimal, and therefore

females were better able to provide a sufficient amount and quality of milk to successfully rear young.

We were unable to identify an effect of treatment area on neonatal survival during our study. Neonate survival rate for Mojave through the first 4 months of life (0.20) was lower than the average across the Intermountain West for 6 month survival (0.44) and for annual survival (0.29; Forrester and Wittmer 2013). During the survival period we used in our models (May-August), Mojave was experiencing extreme drought (PDSI  $\leq$  -4.0; Palmer 1965) for both 2013 (PDSI -5.2) and 2014 (PDSI -4.4), which may have contributed to the lower survival rates we observed. Moreover, southern mule deer in California give birth to young during the dry season, nearly two months before the summer rains arrive, when forage quality and pre-formed water in forage are at their lowest (Wallmo 1978; Bowyer 1991), which likely exacerbated the effects of the drought. Drought conditions, which reduce ephemeral water sources and decrease the quality and quantity of available food, have previously been shown to cause lower survival rates of neonates in desert deer populations (Taylor and Hahn 1947; Carroll and Brown 1977).

The amount of available water had no effect on pregnancy rates during our study. A high and relatively stable pregnancy rate is common in mule deer populations across the Intermountain West (Hurley et al. 2011; Bender et al 2012; Freeman et al 2014; Monteith et al. 2014), therefore it is not surprising that this demographic parameter was not strongly affected by provision of water. Our hypothesis that the amount of permanent water available would increase fetal rates was also not supported. Possibly that vital rate is more strongly affected by other factors such as quantity and quality of available forage, which may not differ significantly among our treatment areas.

We observed no support for a treatment area effect on adult survival; however, the monthly survival rate was lowest in in the water-limited area (0.983) and highest in the water-provided area (0.988). Annual survival rates for Mojave (0.85) were consistent with the average survival of adult female mule deer across the Intermountain West (0.84; Forrester and Wittmer 2013). Survival differed among years and survival during the fawning period was lower than during other periods of the year, with an additional negative effect of drought severity on survival during this time period. In years when drought severity was high, adult females had lower survival during May and June then the rest of the year. Poorer range conditions during drought years may have resulted in more time spent obtaining adequate resources including forage and water then would be necessary during wet years, increasing exposure to predation events. Lack of variation observed in adult female survival between treatment groups is not entirely surprising, though, as this vital rate is commonly the last to be effected when resources are limiting (Gaillard et al 1998, 2000; Eberhardt 2002; Monteith et al 2014). Therefore, we would expect, if provision of water was positively affecting populations, to see the benefits reflected more strongly in fetal rates, and survival and recruitment of young (Gaillard et al 1998; Monteith et al 2014).

Water is an important and often limiting resource, in arid environments (Rosenstock et al. 1999; Morgart et al. 2005; Cain et al. 2006). Negative effects of drought conditions on survival of adult females during the critical fawning period, as well as the possible negative effects of drought conditions on neonate survival described here, may increase if the projected effects of climate change come to fruition. Droughts are expected to increase in intensity and duration as climate changes in the future (IPCC 2013; Diffenbaugh et al. 2015). If these phenomena occur it will likely further reduce the amount of naturally occurring free-standing water sources. Ungulate populations have been shown to be dependent on permanent water sources during hot-dry periods (Bleich et al. 1997; Rosenstock et al. 1999; Morgart et al. 2005) and further reduction of available water sources resulting from a combination of climate change and anthropogenic uses could make provisioning of water essential for the persistence of many species inhabiting arid regions (Longshore et al. 2009). More information is likely needed to fully understand the population level benefits of providing water to wild populations, and therefore, how best to manage wildlife habitat in arid regions.

## ACKNOWLEDGMENTS

We gratefully acknowledge financial and technical support from the National Park Service, California Department of Fish and Wildlife, Safari Club International Foundation, University of Nevada, Reno, Golden Gate Chapter of Safari Club International, California Deer Association, Nevada Department of Wildlife, Nevada Wildlife Record Book Foundation, and the Boone and Crockett club. This research was supported by a Hatch Grant from the Agricultural Experiment Station at the University of Nevada, Reno. We received invaluable assistance and expertise in handling animals from B. Gonzalez, B.M. Pierce, L. Konde. We thank C. McKee for his assistance with field methodologies and for collecting some of the data used herein. We thank technicians A. Carapucci, J. Schoener, C. Bleke, M. Blum, D. Walsh, B. Regan, T. Allen, and numerous volunteers who helped collect the data used in this manuscript. We graciously thank D. Gibson, B. Sedinger, and A. Leach for their statistical assistance.

## LITERATURE CITED

- AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. Pp. 267-281 in Second International Symposium on Information Theory (B.N. Petrov and F. Csaki, eds). Akademiai Kiado, Budapest.
- ANDERSON, D. R., K. P. BURNHAM, and W. L. THOMPSON. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.
- ANDREW, N. G., V. C. BLEICH, A. D. MORRISON, L. M. LESICKA, and P. J. COOLEY.
  2001. Wildlife mortalities associated with artificial water sources. Wildlife
  Society Bulletin 29:275-280.
- ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175-1178.
- BENDER, L. C., L. A. LOMAS, and T. KAMIENSKI. 2007. Habitat effects on condition of doe mule deer in arid mixed wood land-grassland. Rangeland Ecology and Management 60:277-284.
- BEYER, H. L. 2012.Geospatial Modelling Environment (Version 0.7.3.0). <a href="http://www.spatialecology.com/gme">http://www.spatialecology.com/gme</a>.
- BISHOP, C. J., D. J. FREDDY, G. C. WHITE, B. E. WATKINS, T. S. STEPHENSON, and L. L. WOLFE. 2007. Using vaginal-implant transmitters to aid in capture of mule deer neonates. Journal of Wildlife Management 71:945-954.
- BISHOP, C. J., G. C. WHITE, D. J. FREDDY, B. E. WATKINS, and T. R. STEPHENSON. 2009. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172:1-28.

- BISHOP, C. J., C. R. ANDERSON JR., D. P. WALSH, E. J. BERGMAN, P. KUECHLE, and J. ROTH. 2011. Effectiveness of a redesigned vaginal implant transmitter in mule deer. Journal of Wildlife Management 75:1797-1806.
- BLEICH, V. C. 2005. In my opinion: politics, promises, and illogical legislation confound wildlife conservation. Wildlife Society Bulletin 33:66-73.
- BLEICH, V. C., and T. J. TAYLOR. 1998. Survivorship and cause-specific mortality in five populations of mule deer. Great Basin Naturalist 58:265-272.
- BLEICH, V. C., R. T. BOWYER, and J. D. WEHAUSEN. 1997. Sexual segregation in mountain sheep: Resources or predation? Wildlife Monographs 132:1-50
- BLEICH, V. C., N. G. ANDREW, M. J. MARTIN, G. P. MULCAHY, A. M. PAULI, and S. S. ROSENSTOCK. 2006. Quality of water available to wildlife in desert environments: comparisons among anthropogenic and natural sources. Wildlife Society Bulletin 34:627-632.
- BLOMBERG, E. J., J. S. SEDINGER, D. V. NONNE, and M. T. ATAMIAN. 2013. Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. Journal of Avian Biology 44:149-158.
- BLOMBERG, E. J., J. S. SEDINGER, D. GIBSON, P. S. COATES, M. L. CASAZZA. 2014. Carryover effects and climatic conditions influence the post fledging survival of greater sage-grouse. Ecology and Evolution 4:4488-4499.
- BOWYER, R. T. 1991. Timing of parturition and lactation in southern mule deer. Journal of Mammalogy 72:138-145.
- BROWN, D. E. 1998. Water for wildlife: belief before science. Pp. 9-16 in Environmental,

economical and legal issues related to rangeland water developments. (J.M. Feller and D.S. Strouse, eds). Arizona State University College of Law, Temple, USA.

- BROYLES, B., and T. L. CUTLER. 1999. Effect of surface water on desert bighorn sheep in the Cabeza Prieta National Wildlife Refuge, southwestern Arizona. Wildlife Society Bulletin 27:1082-1088.
- BUCKLAND, S. T., K. P. BURNHAM, and N. H. AUGUSTIN. 1997. Model selection: an integral part of inference. Biometrics 53:603-618.
- BURNHAM, K. P., and D. R. ANDERSON. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28:111-119.
- BURNHAM, K. P., and D. R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, New York, USA.
- CAIN, J. W., P. R. KRAUSMAN, S. S. ROSENSTOCK, and J. C. TURNER. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. Wildlife Society Bulletin 34:570-581.
- CAIN, J. W., P. R. KRAUSMAN, J. R. MORGART, B. D. JANSEN, and M. P. PEPPER. 2008. Responses of desert bighorn sheep to removal of water sources. Wildlife Monographs 171:1-32.
- CARROLL, B. K., and D. L. BROWN. 1977. Factors affecting survival in southern-central Texas. Journal of Wildlife Management 41:63-69.
- CARSTENSEN, M., G. D. DELGUIDICE, and B. A. SAMPSON. 2003. Using doe behavior and vaginal-implant transmitters to capture neonate white-tailed deer in north-central Minnesota. Wildlife Society Bulletin 31:634-641.

- CLUTTON-BROCK, T. H., S. D. ALBON, and F. E. GUINESS. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337:260-262.
- CONNOLLY, G. E. 1981. Limiting factors and population regulation. Pp. 245-285 in Mule and black-tailed deer of North America (O. C. Wallmo, ed.). University of Nebraska Press, Lincoln, USA.
- COOCH, E. G., and G. C. WHITE, eds. 2015. Program MARK: a gentle introduction. 14th ed. http://www.phidot.org/software/mark/docs/book/ Accessed 15 February 2015.
- COOK, J. G., et al. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1-61.
- COOK, R. C., T. R. STEPHENSON, W. L. MYERS, J. G. COOK, and L. A. SHIPLEY. 2007. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934-1943.
- DEVOS, J. C., and W. H. MILLER. 2005. Habitat use and survival of Sonoran pronghorn in years with above-average rainfall. Wildlife Society Bulletin 33:35-42.
- DIFFENBAUGH, N. S., D. L. SWAIN, and D. TOUMA. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Science 112:3931-3936.
- DINSMORE, S. J., G. C. WHITE, and F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476-3488.
- DIXON, J. S. 1934. A study of the life history and food habits of the mule deer in California. California Fish and Game 20:1-142.
- EBERHARDT, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841-2854.

- FORRESTER, T. D., and H. U. WITTMER. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. Mammal Review 43:292-308.
- FREEMAN, E. D., R. T. LARSEN, M. E. PETERSON, C. R. ANDERSON JR., K. R. HERSEY, and B. R. MCMILLAN. 2014. Effects of male-biased harvest on mule deer: implications for rates of pregnancy, synchrony, and timing of parturition. Wildlife Society Bulletin 38:806-811.
- GAILLARD, J. M., M. FESTA-BIANCHET, and N. G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment and constant adult survival. Trends in Ecology and Evolution 13:58-63.
- GAILLARD, J. M., M. FESTA-BIANCHET, N. G. YOCCOZ, A. LOISON, and C. TOIGO. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.
- GERHART, K. L, D. E. RUSSELL, D. VAN DEWETERING, R. G. WHITE, and R. D. CAMERON. 1997. Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactation infertility. Journal of Zoology 242:17-30.
- HAUGEN, A. O. and D. W. SPEAKE. 1958. Determining age of young fawn white-tailed deer. Journal of Wildlife Management 22:319-321.
- HAZAM, J. E., and P. R. KRAUSMAN. 1988. Measuring water consumption of desert mule deer. Journal of Wildlife Management 52:528-534.
- HEFFELFINGER, J. R. 2006. Deer of the southwest: a complete guide to the natural history, biology, and management of southwestern mule deer and white-tailed deer. Texas A&M University Press, College Station.

- HERVERT, J. J., and P. R. KRAUSMAN. 1986. Desert mule deer use of water developments in Arizona. Journal of Wildlife Management 50:670-676.
- HOLL, S. A., H. SALWASSER, and B. BROWNING. 1979. The diet composition and energy reserves of California mule deer during pregnancy. California Fish and Game 65:68-79.
- HUPP, J. W., J. A. SCHMUTZ, and C. R. ELY. 2008. Seasonal survival of radiomarked emperor geese in western Alaska. Journal of Wildlife Management 72:1584-1595.
- HURLEY, M. A., et al. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1-33.
- IPCC. 2013. Summary for policymakers. Climate Change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change, (Stocker, T.F. et al. eds.) Cambridge University Press, Cambridge, UK.
- JOHNSTONE-YELLIN, T. L., L. A. SHIPLEY, and W. L. MEYERS. 2006. Effectiveness of vaginal implant transmitters for locating neonatal mule deer fawns. Wildlife Society Bulletin 34:338-344.
- JULANDER, O., W. L. ROBINETTE, D. A. JONES. 1961. Relation of summer range condition to mule deer herd productivity. Journal of Wildlife Management 25:54-60.
- KNIPE, T. 1977. The Arizona whitetail deer. Special Report No. 6. Arizona Game and Fish Department, Phoenix. 108 Pp.

KRAUSMAN, P. R., and R. C. ETCHBERGER. 1995. Response of desert ungulates to a water

project in Arizona. Journal of Wildlife Management 59:292-300.

- KRAUSMAN P. R., HERVERT J. J., and ORDWAY L. L. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.
- LANGENAU, E. E. JR., and J. M. LERG. 1976. The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. Applied Animal Ethology 2:207-223.
- LESLIE, D. M. JR., and C. L. DOUGLAS. 1979. Desert bighorn sheep of the River Mountains, Nevada. Wildlife Monographs 66:3-56.
- LIVEZEY, K. B. 1990. Toward the reduction of marking-induced abandonment in newborn ungulates. Wildlife Society Bulletin 18:193-203.
- LONGSHORE, K. M., C. LOWREY, and D. B. THOMPSON. 2009. Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73:280-286.
- LOUDON, A. S. I. 1985. Lactation and neonatal survival of mammals. Symposium of the Zoological Society of London 54:183-207.
- MACKIE, R. J., D. F. PAC, K. L. HAMLIN, and G. L. DUSEK. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Federal Aid to Wildlife Restoration Report, Project W-120-R, Montana Fish, Wildlife and Parks, Wildlife Division, Helena, USA.
- MARSHAL, J. P., P. R. KRAUSMAN, and V. C. BLEICH. 2005a. Dynamics of mule deer forage in the Sonoran Desert. Journal of Arid Environments 60:593-609.

MARSHAL, J. P., P. R. KRAUSMAN, and V. C. BLEICH. 2005b. Rainfall, temperature, and

forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology and Management 58:360-365.

- MARSHAL, J. P., L. M. LESICKA, V. C. BLEICH, P. R. KRAUSMAN, G. P. MULCAHY, and N. G. ANDREW. 2006a. Demography of desert mule deer in southeastern California. California Fish and Game 92:55-66.
- MARSHAL, J. P., V. C. BLEICH, P. R. KRAUSMAN, M. L. REED, and N. G. ANDREW. 2006b. Factors affecting habitat use and distribution of desert mule deer in an arid environment. Wildlife Society Bulletin 34:609-619.
- MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. The University of Michigan Press, Ann Arbor, Michigan, USA.
- MCGINNIS, B. S., and R. L. DOWNING. 1977. Factors affecting the peak of white-tailed deer fawning in Virginia. Journal of Wildlife Management 41:715-719.
- MCKEE, C. J., K. M. STEWART, J. S. SEDINGER, A. P. BUSH, N. W. DARBY, D. L. HUGHSON, and V. C. BLEICH. *In review*. Spatial distribution and resource selection by mule deer in an arid environment: responses to provision of water. Journal of Arid Environments.
- MOEN R. A., PASTOR J., and COHEN Y. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 61:530-539.
- MONTEITH, K. L., V. C. BLEICH, T. R. STEPHENSON, B. M. PIERCE, M. M. CONNER, J. G. KIE, and R. T. BOWYER. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-62.

MORGART, J. R., J. J. HERVERT, P. R. KRAUSMAN, J. L. BRIGHT, and R. S. HENRY. 2005.

Sonoran pronghorn use of anthropogenic and natural water sources. Wildlife Society Bulletin 33:51-60.

- NATIONAL CLIMATIC DATA CENTER. 2015. Climatological Rankings. <a href="http://www.ncdc.noaa.gov/temp-and-precip/climatological-rankings/index.php">http://www.ncdc.noaa.gov/temp-and-precip/climatological-rankings/index.php</a> >. Accessed 15 January 2015.
- NATIONAL PARK SERVICE. 2015. Nature and Science of Mojave National Preserve. <a href="http://www.nps.gov/moja/naturescience/index.htm">http://www.nps.gov/moja/naturescience/index.htm</a>. Accessed 31 March 2015.
- PALMER, W. C. 1965. Meteorological drought: Report 45. U.S. Department of Commerce, Washington, D.C., USA.
- PARKER, K. L., C. T. ROBBINS, and T. A. HANLEY. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.
- PARKER, K. L., P. S. BARBOZA, and M. P. GILLINGHAM. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57-69.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, and P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.
- POWELL, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. The Condor 109:949-954.
- RACHLOW, J. L., and R. T. BOWYER. 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? Journal of Mammalogy 75:328-337.
- RAUTENSTRAUCH, K. R., and P. R. KRAUSMAN. 1989. Influence of water availability and rainfall on movements of desert mule deer. Journal of Mammalogy 70:197-201.

- ROBINETTE, W. L., N. V. HANCOCK, and D. A. JONES. 1977. The Oak Creek mule deer herd in Utah. Utah State Division of Wildlife Resources Publication 77-15:1-148.
- ROBBINS, C. T., and B. L. ROBBINS. 1979. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. The American Naturalist 114:101-116.
- ROSENSTOCK, S. S., W. B. BALLARD, and J. C. DEVOS. 1999. Viewpoint: benefits and impacts of wildlife water developments. Journal of Range Management 52:302-311.
- ROSENSTOCK, S. S., J. J. HERVERT, V. C. BLEICH, and P. R. KRAUSMAN. 2001. Muddying the water with poor science: a reply to Broyles and Cutler. Wildlife Society Bulletin 29:734-738.
- SAMS, M. G., R. L. LOCHMILLER, E. C. HELLGREN, W. D. WARDE, and L. W. VARNER. 1996. Morphometric predictors of neonatal age for white-tailed deer. Wildlife Society Bulletin 24:53-57.
- SASSER, R. G., C. A. RUDER, K. A. IVANI, J. E. BUTLER, and W. C. HAMILTON. 1986. Detection of pregnancy by radioimmunoassay of a novel pregnancy-specific protein in serum of cows and profile of serum concentrations during gestation. Biology of Reproduction 35:936–942.
- SEAMAN, D. E., and R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home-range analysis. Ecology 77:2075-2085.
- SEAMAN, D. E., J. T. MILLSPAUGH, B. T. KEROHAN, G. C. BRUNDIGE, K. T. RAEDEKE, and R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

- SHORT, H. L. 1964. Post-natal stomach development of white-tailed deer. Journal of Wildlife Management 28:445-458.
- SIKES R. S., W. L GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.
- SIMPSON, N. O., K. M. STEWART, and V. C. BLEICH. 2011. What have we learned about water developments for wildlife? Not enough! California Fish and Game 97:190-209.
- STEPHENSON, T. R., J. W. TESTA, G. P. ADAMS, R. G. SASSER, C. C. SCHWARTZ, and K. J. HUNDERTMARK. 1995. Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. Alces 31:167-172
- STEWART, K. M., R. T. BOWYER, J. G. KIE, N. J. CIMON, and B. K. JOHNSON. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229-244.
- TAYLOR, W. P., and H. C. HAHN. 1947. Die-offs among the white-tailed deer in the Edwards Plateau of Texas. Journal of Wildlife Management 11:317-323.
- THORNE, R. F., B. A. PRIGGE, and J. HENRICKSON. 1981. A flora of the higher ranges and the Kelso Dunes of the eastern Mojave Desert in California. ALISO 10:71-186.
- TOLLEFSON, T. N. 2007. The influence of summer and autumn forage quality on body condition and reproduction of lactating mule deer and their fawns (*Odocoileus hemionus*). Dissertation. Washington State University, Pullman, Washington, USA.

- UNITED STATES GEOLOGICAL SURVEY. 2015. Climate history of the Mojave Desert region. <a href="http://mojave.usgs.gov/climate-history/">http://mojave.usgs.gov/climate-history/</a>. Accessed 23 March 2015.
- UNSWORTH, J. W., D. F. PAC, G. C. WHITE, and R. M. BARTMAN. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315-326.
- URNESS, P. J. 1981. Desert and chaparral habitats part 1: food habits and nutrition. Pp.347-365 in Mule and Black-Tailed Deer of North America (O. C. Wallmo, ed.).University of Nebraska Press, Lincoln, USA.
- VERME, L. J. 1962. Mortality of white-tailed deer fawns in relation to nutrition. Proceedings of the National White-Tailed Deer Disease Symposium 1:15-38.
- WADE, D. A., and J. E. BROWNS. 1985. Procedures for evaluating predation on livestock and wildlife. Texas Agriculture Extension Service Bulletin B-1429, College Station, Texas, USA.
- WALLMO, O. C. 1978. Mule and Black-tailed deer. Pp. 31-41 in Big game of North America: ecology and management (J.L. Schmidt and D.L. Gilbert eds.). The Stackpole Company, Harrisburg, Pennsylvania, 494 pp.
- WALLMO, O. C. 1981. Mule and black-tailed deer distribution and habitats. Pp. 1-26 in Mule and Black-tailed Deer of North America. (O. C. Wallmo, ed.). University of Nebraska Press, Lincoln, USA.
- WHITE, G. C., and K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.
- WORKMAN, G. W., and J. B. LOW, eds. 1976. Mule deer decline in the west: a symposium. Utah State University, Logan, USA.

ZAR, J. H. 2010. Biostatistical Analysis. Fifth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA. **Table 1**. Abbreviation, definition, and effect category of parameters investigated in models of adult survival for 132 mule deer inMojave National Preserve, CA, USA, 2009-2014.

Abbreviation	Definition		
YEAR	Year of the study (2009-2013 relative to 2014)	Group	
SEASON	Survival rates delineated by season	Group	
FAWNING	May and June survivals differ from rest of the year	Group	
H2O	Standardized distance to water from centroid of home range to nearest perennial water	Covariate	
HR	Standardized size of home range	Covariate	
CORE	Standardized size of core area of use	Covariate	
H2OC	Standardized distance to water from centroid of core area of use to nearest perennial water	Covariate	
PR	Pregnancy Status (pregnant, not pregnant)	Covariate	
FE	Fetus number (How many fetuses the female was carrying)	Covariate	
RESID	Residuals from PCA-Mass linear regression (relative condition of individuals)	Covariate	
PDSI	Palmer Drought Severity Index included for all months	Group	
CurrentPDSI	Average Palmer Drought Severity index for current Spring season included on May-June survival	Group	
PrevPDSI	Average Palmer Drought Severity Index for the previous Winter season applied to May-June survival	Group	
PrevPrecip	Amount of precipitation (cm) during previous Winter on May-June survival	Group	

**Table 2**. Abbreviation, definition, and effect category of parameters investigated in models of juvenile survival for 46 mule deer inMojave National Preserve, CA, USA, 2013-2014.

Abbreviation	Definition	Effect Type	
TREND	Trend on daily survival rates delineated by week (1-17)	Group	
DAY	Standardized difference between date of birth and median date of fawning	Covariate	
RESID	Residuals of PCA-Mass linear regression (relative size of the fawn)	Covariate	
QUAD	Quadratic effect on daily survival rates	Group	
YEAR	Study year (2013, 2014)	Group	
SEX	Sex of the fawn	Group	

**Table 3**. Candidate models used to estimate monthly survival of 132 adult female deer in Mojave National Preserve, CA, USA, 2009-2014. Number of parameters (K), Akaike's Information Criterion adjusted for small sample size (AIC<sub>c</sub>),  $\Delta$ AIC<sub>c</sub>, and model weight (W<sub>i</sub>) See Table 1 for parameter descriptions.

Model Rank	<sup>1</sup> Model	К	AICc	Δ AICc	Wi
1	YEAR + FAWNING + CurrentPDSI + H2O	9	432.36	0.00	0.247
2	YEAR + FAWNING + CurrentPDSI	8	432.36	0.00	0.247
3	YEAR + FAWNING + PrevPDSI	8	433.66	1.30	0.129
4	YEAR + FAWNING + CurrentPDSI + H2O + HR	10	434.09	1.73	0.104
5	YEAR + FAWNING + CurrentPDSI + HR	9	434.24	1.88	0.097
6	YEAR + FAWNING + CurrentPDSI + H2O + RESID	10	434.37	2.01	0.091
7	YEAR + FAWNING	7	436.66	4.29	0.029
8	YEAR + FAWNING + RESID	8	438.54	6.18	0.011
9	YEAR + PrevPRECIP	7	439.17	6.81	0.008
10	YEAR + PDSI	7	440.55	8.19	0.004

<sup>1</sup>See Table 1 for descriptions

**Table 4**. Model averaged parameter estimates ( $\beta$ ), standard errors (SE), and 95% confidence intervals from monthly survival analysis of 132 adult female mule deer in Mojave National Preserve, CA, USA, 2009-2014. See Table 1 for parameter descriptions.

Parameter	β	SE	85% CI		
	۲		Lower	Upper	
INT	6.02	0.78	4.90	7.13	
2009 <sup>1</sup>	-1.37	0.81	-2.53	-0.21	
2010 <sup>1</sup>	-2.36	0.84	-3.57	-1.15	
2011 <sup>1</sup>	-1.35	0.88	-2.62	-0.08	
2012 <sup>1</sup>	-2.48	0.81	-3.64	-1.32	
2013 <sup>1</sup>	-1.62	0.79	-2.75	-0.49	
May-Jun	-0.71	0.44	-1.35	-0.08	
CurrentPDSI	0.65	0.35	0.15	1.15	
H2O	0.01	0.01	-0.01	0.03	
PrevPDSI	0.16	0.39	-0.40	0.71	
HR	0.02	0.09	-0.11	0.14	

<sup>1</sup>Relative to 2014 survival; See Table 1 for descriptions

**Table 5**. Candidate models used to estimate daily survival of 46 neonate mule deer in Mojave National Preserve, CA, USA, 2013-2014. Number of parameters (K), Akaike's Information Criterion adjusted for small sample size (AIC<sub>c</sub>),  $\Delta$ AIC<sub>c</sub>, and model weight (W<sub>i</sub>) See Table 2 for parameter descriptions.

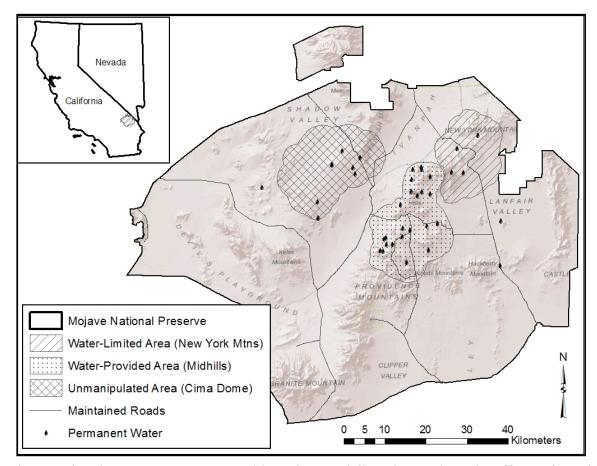
Model Rank	<sup>1</sup> Model	К	AICc	Δ AICc	Wi
1	TREND + DAY + RESID	4	257.09	0.00	0.289
2	TREND + QUAD + DAY + RESID	5	257.83	0.74	0.200
3	TREND + YEAR + DAY + RESID	5	258.21	1.12	0.165
4	TREND + DAY + RESID + SEX	5	258.82	1.73	0.122
5	TREND + QUAD + YEAR + DAY + RESID	6	259.28	2.20	0.096
6	TREND + DAY	3	260.22	3.14	0.060
7	TREND + QUAD + DAY	4	261.49	4.40	0.032
8	TREND + RESID	3	261.96	4.87	0.025
9	TREND + QUAD	3	265.44	8.35	0.004
10	TREND	2	266.34	9.25	0.003

<sup>1</sup>See Table 2 for descriptions

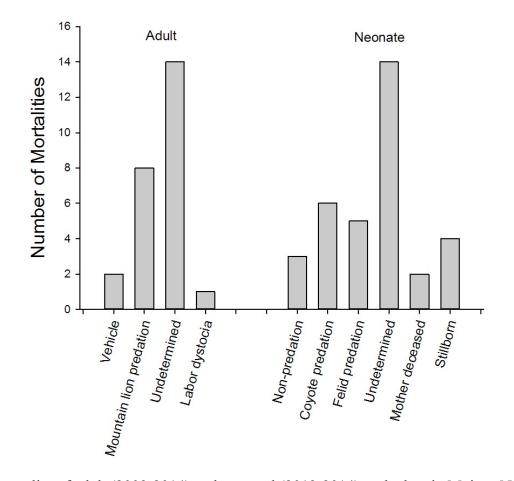
<sup>1</sup> Parameter	β SE		85% CI		
			Lower	Upper	
INT	2.81	0.66	1.86	3.76	
TREND	0.17	0.21	-0.12	0.47	
DAY	-0.52	0.22	-0.83	-0.20	
RESID	1.03	0.45	0.38	1.67	
QUAD	0.01	0.01	-0.01	0.03	
SEX	-0.03	0.16	-0.27	0.20	
YEAR	0.08	0.23	-0.25	0.41	

**Table 6**. Model averaged parameter estimates ( $\beta$ ), standard errors (SE), and 95% confidence intervals from daily survival analysis of 46 juvenile mule deer in Mojave National Preserve, CA, USA, 2013-2014. See Table 2 for parameter descriptions.

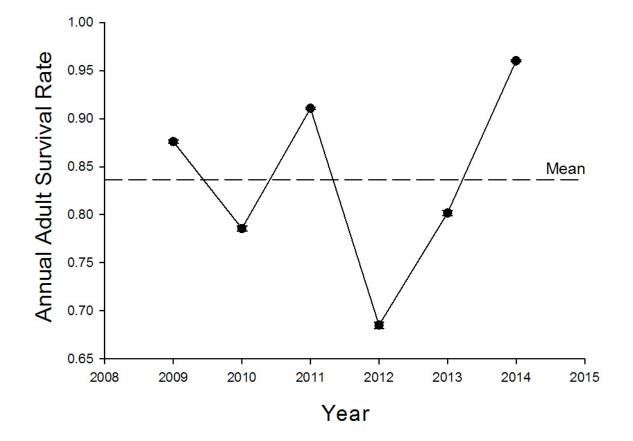
<sup>1</sup>See Table 2 for descriptions



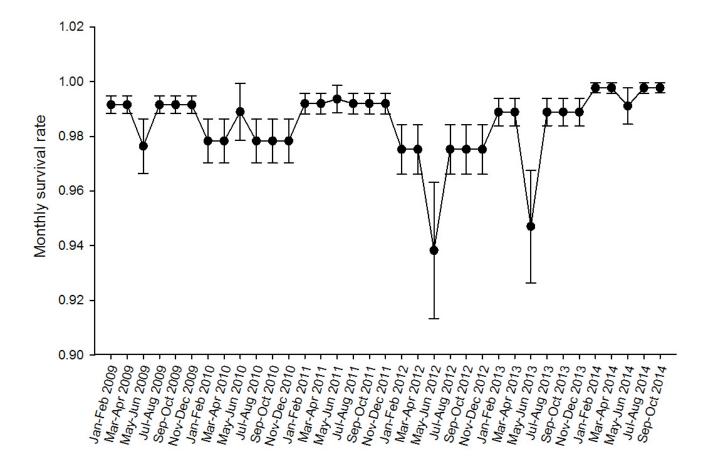
**Figure 1.** Map of Mojave National Preserve, CA, USA, with study area delineations, where the effects of provision of water were investigated, 2009-2014. Inset map shows location relative to Nevada and California. Note: although boundaries for the water-provided and water-limited were close the topography of that separation prevented movement of radio collared deer between areas.



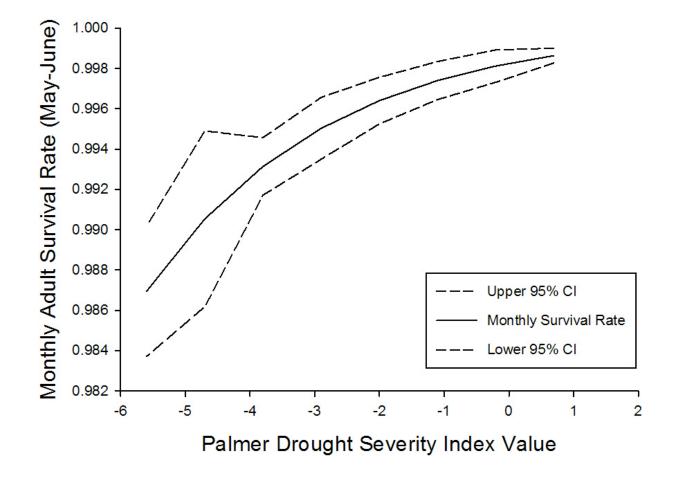
**Figure 2.** Cause specific mortality of adult (2009-2014) and neonatal (2013-2014) mule deer in Mojave National Preserve CA, USA.



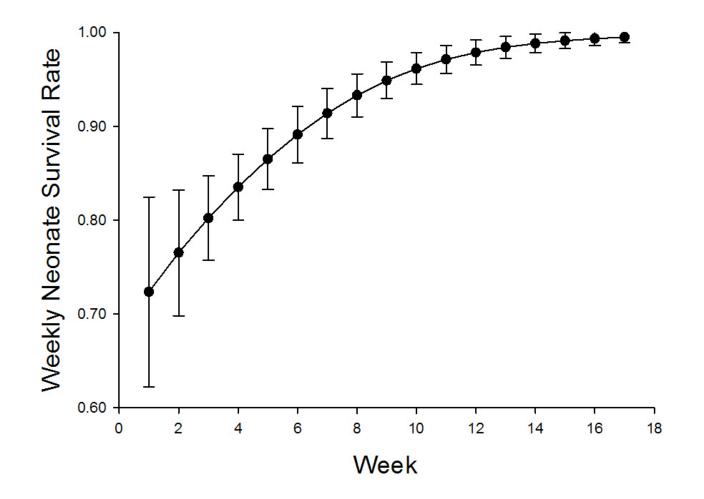
**Figure 3.** Annual adult female mule deer survival rates and 95% confidence intervals in Mojave National Preserve, CA, USA 2009-2014.



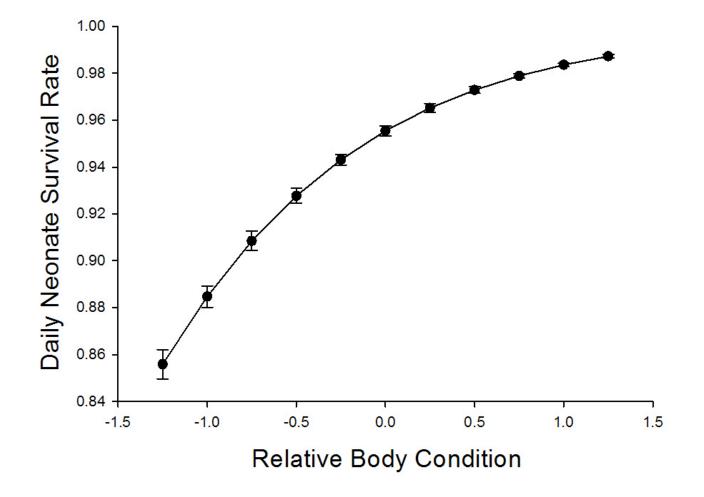
**Figure 4.** Model averaged monthly survival rates and 95% confidence intervals for adult female mule deer in Mojave National Preserve, CA, USA, 2009-2014.



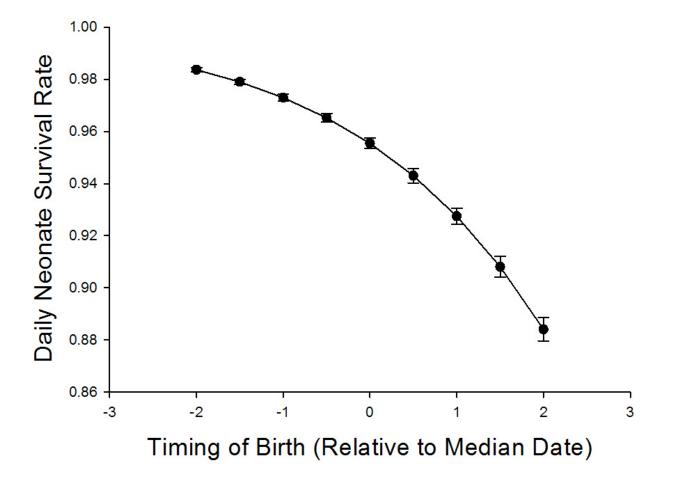
**Figure 5.** Effect of Palmer Drought Severity Index (PDSI) levels during the fawning period (May-June) on monthly survival (with 95% confidence interval) of adult female mule deer in Mojave National Preserve, CA, USA 2009-2014.



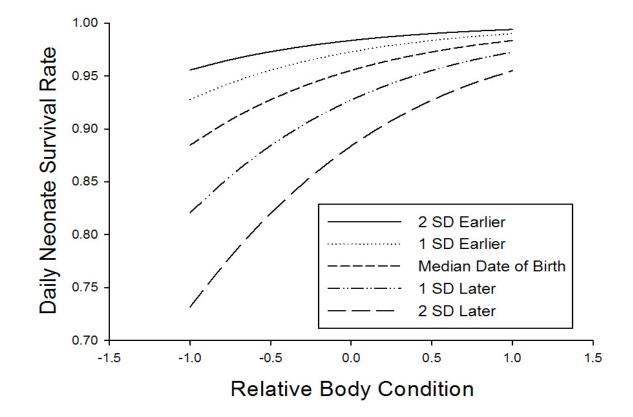
**Figure 6.** Daily fawn survival rate, delineated by week, to 120 days with associated 95% confidence intervals in Mojave National Preserve, CA, USA, 2013-2014.



**Figure 7.** Effect of standardized relative body condition of neonates on daily survival rate with 95% confidence interval for mule deer in Mojave National Preserve, CA, USA 2013-2014.



**Figure 8.** Effect of timing of birth relative the median date of parturition (standardized) on daily survival rate with 95% confidence intervals for neonatal mule deer in Mojave National Preserve, CA, USA 2013-2014.



**Figure 9.** Combined effects of relative body condition and timing of birth relative to median parturition date on neonatal mule deer survival in Mojave National Preserve, CA, USA 2013-2014. Each line indicates a different timing of birth with the center line representing individuals born on the median date of fawning, while lines above or below this represent 1-2 standard deviations away from the median date.

Anthony P. Bush University of Nevada, Reno 1664 N. Virginia Street Reno, Nevada 89557 (775)233-8649 abush@cabnr.unr.edu

RH: Bush et al. · Parturition Site Selection by Mule Deer in Mojave Desert Selection of Parturition Sites by Mule Deer in the Southeastern Mojave Desert: Responses to Water Provisioning

Anthony P. Bush, Department of Natural Resources and Environmental Science,

University of Nevada, Reno 1664 N. Virginia Street, Reno, Nevada, 89557, USA.

- Kelley M. Stewart, Department of Natural Resources and Environmental Science, University of Nevada, Reno 1664 N. Virginia Street, Reno, Nevada, 89557, USA.
- James S. Sedinger, Department of Natural Resources and Environmental Science, University of Nevada, Reno 1664 N. Virginia Street, Reno, Nevada, 89557, USA.
- Vernon C. Bleich, Department of Natural Resources and Environmental Science, University of Nevada, Reno 1664 N. Virginia Street, Reno, Nevada, 89557, USA.
- Neal W. Darby, National Park Service, 2701 Barstow Road, Barstow, California 92311, USA.
- Debra L. Hughson, National Park Service, 2701 Barstow Road, Barstow, California 92311, USA.

## ABSTRACT

Population-level effects of provisioning water to wildlife have not been unequivocally demonstrated, despite being commonly practiced since the 1940s. Declines in mule deer populations in recent decades are ostensibly a result of low recruitment rates, and therefore it is important to understand habitat characteristics that are most important to successful recruitment of young. Our objectives were to identify those landscape-level resources that are important in selection of parturition sites. We used parturition sites that we verified (n = 26) by direct observation and those estimated by changes in movement patterns (n = 76) to investigate the effect of differing levels of water provisioning on selection of parturition sites in a population of mule deer (Odocoileus hemionus) in Mojave National Preserve, California, USA from 2009 to 2014. We hypothesized that selection of resources associated with parturition sites would differ relative to availability of water. Further we hypothesized that proximity to water would be selected more strongly in a water-limited area compared to two others where that resource was more plentiful. We used resource selection functions (RSFs) in an information theoretic framework to identify differences in habitat selection between areas with relatively more or less available water sources at 35 and 100 meter spatial extents. We observed no support for a difference in resource selection relative to availability of water. Nevertheless, we observed selection for proximity to water, higher elevations, avoidance of roads, 40-50% shrub canopy cover at both spatial extents, and selection for 30-40% shrub canopy cover at the 100 m spatial extent. We identified several factors related to selection of parturition sites that can be used by managers to protect, or improve, habitat crucial to successful recruitment of mule deer in desert systems.

## INTRODUCTION

In recent decades mule deer (*Odocoileus hemionus*) populations have experienced periodic declines across the western United States (Unsworth et al 1999, Monteith et al. 2014). Causes of the declines remain unclear (deVos et al. 2003, Connelly et al. 2012), but likely include loss or fragmentation of habitat, reduced forage quality, predation, disease, interspecific competition, and climate change (deVos et al 2003, Bishop et al. 2009, Hurley et al. 2011). Throughout the range of the species, mule deer populations maintain high and relatively stable adult female survival (Forrester and Wittmer 2013) and pregnancy rates (Hurley et al. 2011, Bender et al 2012, Freeman et al 2014, Monteith et al. 2014). Fetal rates in captive (Robinette et al. 1973, Tollefson et al. 2010), and free-ranging (Monteith et al. 2010) populations, however, are positively associated with the nutritional status of the female. Because adult survival is often high with little variability, fluctuations in mule deer populations are generally most strongly influenced by survival and recruitment of young (Connelly 1981, Unsworth et al. 1999, Gaillard et al 1998, 2000, Forrester and Wittmer 2013).

Selection of suitable parturition sites may have a significant effect on the successful rearing of young. During the first few weeks of life, movements of neonatal mule deer are highly restricted and, thus, those neonates are particularly vulnerable to predation (Bowyer et al. 1998, Gaillard et al. 2000, Raithel et al. 2007, Grovenburg et al 2011). Parturition sites must, therefore, provide some means of predator avoidance either through concealment (Van Moorter et al. 2009), more rugged terrain (Bowyer 1987, Farmer et al. 2006), or a combination of these and other factors. Parturition sites must also provide a suitable microclimate (to prevent exposure) for the neonate, especially in

the hours or days immediately following birth (Picton 1984, Bowyer et al. 1998, Barbknecht et al. 2011).

While predator avoidance is a major factor in selection of parturition sites, other attributes, such as forage quality and access to free-standing water, also are crucially important. The amount and quality of milk produced by the female is directly related to the growth rate and survival of her offspring (Robbins and Robbins 1979, Gerhart et al. 1997, Mackie et al. 1998, Cook et al. 2004). Moreover, water and nutritional demands of females are highest during lactation, and quality and quantity of milk produced is directly dependent on forage quality and availability of water (Hazam and Krausman 1988, Wade and Schneider 1992, Parker et al. 2009). In addition to reduced milk production, neonatal survival can be reduced because nutritionally stressed females can decrease parental care (Langenau and Lerg 1976, Rachlow and Bowyer 1994). Therefore, females must select parturition sites with forage and water availabilities that are commensurate with successful rearing of young.

The use of vaginal implant transmitters (VITs) allows investigators to accurately identify parturition sites. Many previous studies used the location of neonates as a proxy for the true birthing site because of the inherent difficulty in locating the actual site (Barbknecht et al. 2011). Because the female selects the parturition location, and the neonate—at least, to some degree—,selects the bedding location, there may be biases associated with these data (Van Moorter et al 2009, Svartholm 2010, Barbknecht et al. 2011). Vaginal implant transmitters also eliminate biases present in studies that rely on visual survey techniques in locating neonates, whereby, ease of location in some habitats may cause those habitats to be over represented in the data (Barbknecht et al. 2011).

We investigated resource selection of parturition sites for 102 mule deer between 3 treatment areas with differing levels of permanent water available in Mojave National Preserve, California from 2009 to 2014. Our objective was to identify those landscapelevel factors important in choosing parturition sites. We hypothesized that selection of resources associated with parturition sites would differ between treatment areas in relation to availability of water. Further we hypothesized that proximity to water would be more important in the water-limited treatment area, when compared to the other areas in which that resource was more plentiful. Additionally, we hypothesized that resources associated with reduced predation (elevation, ruggedness, cover), nutritional condition (water and forage), and exposure of neonates (hiding cover and thermal refugia) would be important factors in selection of parturition sites.

### **STUDY AREA**

Mojave National Preserve (hereafter Mojave), located in San Bernardino County, California USA (35° 00' N 115° 28' W), is nearly 650,000 hectares (ha) and is bounded to the east by the Nevada-California border, to the north by Interstate Highway 15, and to the south by Interstate Highway 40 (Figure 1). The area is characterized by precipitous, rocky mountain ranges, rising to as high as 2,417 meters (m), separated by expansive bajadas and playas in the valley floors at elevations as low as 270 m (Thorne et al. 1981). The area is dominated by Mojave Desert vegetation assemblages, but remnant pockets of Great Basin vegetation and the presence of Sonoran Desert vegetation in the transition zones creates a highly heterogeneous landscape (National Park Service 2015). Precipitation patterns vary by elevation, with lower elevations receiving 8.5 centimeters (cm) of precipitation and mid-to-upper elevations receiving as much as 27 cm annually (1958-2011 Providence Mountains State Recreation Area, southern Mojave Preserve; McKee et al. *In Review*). The precipitation pattern for this area is bi-modal with peaks during the winter and summer months (McKee et al. *In Review*). The proportion of precipitation occurring during each season, however, has varied by year: 2009 had precipitation evenly distributed between the two seasons, during 2010-2011 the majority of precipitation occurred in winter, and from 2012 to 2014 the majority of precipitation occurred during summer. Average temperatures also vary by elevation; mean maximum temperatures in summer are 40.5°C at low elevations, and 33°C at mid-to-upper elevations, while mean maximum temperatures in winter are 19°C and 13°C for low and mid-to-upper elevations, respectively (United States Geological Survey 2015). Seasons were previously delineated using a climograph (Stewart et al. 2002) as: winter (December-March), Spring (April-June), Summer (July-September), and Autumn (October-November; McKee et al. *In Review*).

Low elevations in the Mojave are characterized by white bursage (*Ambrosia dumosa*) and creosote bush (*Larrea tridentata*) with very limited herbaceous plants in the understory (Thorne et al. 1981). At mid-elevations ( $\leq 1600$  m), Joshua Tree (*Yucca brevifolia*) woodlands, and shrublands dominated by blackbrush (*Coleogyne ramosissima*), cholla (*Opuntia* spp.), barrel cactus (*Ferocactus* spp.), and Spanish bayonet (*Yucca spp.*) are dominant (Thorne et al. 1981). Vegetation assemblages at elevations above 1600 m are characterized by pinyon pine (*Pinus Monophylla*), live oak (*Quercus* spp.) and juniper (*Juniperus* spp.) woodlands and shrublands dominated by Great Basin sagebrush (*Artemisia tridentata*), desert almond (*Prunus fasiculata*), and bitterbrush (*Purshia* spp.; Thorne et al. 1981).

We established 3 separate treatment areas of roughly equal size and similar elevations, each having differing levels of permanently available water sources (Figure 1). The water-provided treatment (Midhills) had 23 perennial springs and catchments, of which 12 were historic cattle wells that were restored in September of 2008 (McKee et al. In Review). The water-limited treatment (New York Mountains) had 3 water sources (2009-2012) with an additional catchment constructed in early 2013 and included in analyses for 2013-2014. In addition, one natural spring in the water-limited area was fenced off prior to the start of the study to prevent mule deer use while allowing use by other species (McKee et al. In Review). The reference area (Cima Dome) had 7 perennial water sources (4 historic cattle wells, 3 natural springs) which have never been deactivated and have remained continuously available to wildlife. The treatment areas used in this study are an augmentation of those used in Mckee et al. (In Review). Home ranges of several individuals that were added to the study (2012-2014) were partially outside of the previously delineated boundaries and therefore the boundaries were expanded to fully include those other individuals. From 2009 to 2014 a limited number of individuals (n = 4) moved between study areas but in all cases returned to their original study area within a few days to weeks.

#### **METHODS**

### **Animal Capture and Handling**

Adult female mule deer were captured using a net-gun and helicopter (Krausman et al. 1985, McKee et al. *In Review*) during the late winter or early spring (2009-2014) and transported to a central processing station. To ensure independence of samples, only 1

adult female from each social group was captured. We outfitted each individual with a global positioning system (GPS) store-on-board radiocollar (Sirtrack, Havelock North, New Zealand; Advanced Telemetry Systems, Isanti, Minnesota, USA). Collars were programmed to collect 1 location every 1.5 hours and to remotely release approximately one year after deployment (McKee et al. *In Review*). We used ultrasonography during most years to assess pregnancy status (Stephenson et al. 1995, Monteith et al. 2014). We used Pregnancy Specific Protein B (PSPB) levels to assess pregnancy in 2010 and 2012 (Sasser et al. 1986), because we were unable to use ultrasonography those years.

In 2013 and 2014 we outfitted pregnant females with a vaginal implant transmitter (VIT; M3930L, Advanced Telemetry Systems, Isanti, Minnesota, USA). The use of VITs has been shown to have no negative effect on adult survival, neonate survival, or to impede the birthing process (Carstensen et al. 2003, Johnstone-Yellin et al. 2006, Bishop et al. 2007). Methods for VIT deployment were consistent with those used by Bishop et al. (2011). During May and June of 2013-2014, parturition status of deer with VITs was monitored every 1-3 days and most individuals were monitored daily. After parturition occurred, field crews located the VIT and searched for evidence of a birth-site such as disturbed soil, crushed fecal pellets, moist soil, odor, and presence of insects (Barbkneckt et al 2011). We collected GPS location data for all located parturition sites.

Capture and handling procedures were compliant with those developed by California Department of Fish and Wildlife. All procedures were approved by the Institutional Animal Care and Use Committee at the University of Nevada, Reno (IACUC: 00058), and were in accordance with guidelines established by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011).

### **Statistical Analyses**

Movement data were used to estimate parturition sites for all deer radiocollared from 2009 to 2012. Deer greatly reduce movements immediately after giving birth (Bertrand et al. 1996, Bowyer et al. 1999, Vore and Schmidt 2001, Carstensen et al. 2003, Ciuti et al. 2006, Long et al. 2009). We used timing of reduced movement rates (m/hour) obtained from GPS collar data to estimate the date of parturition (Long et al. 2009). Although movement rates have been used to estimate timing of parturition (Bertrand et al. 1996, Bowyer et al. 1999, Long et al. 2009), to our knowledge no study has used movement rates to estimate the location of parturition sites. When movement rates dropped to  $\leq 30$  m per hour, averaged over a 24 hour period, and stayed at that level for multiple days ( $\geq 2$ ) we considered parturition to have occurred. Once timing of parturition for an individual was identified, we uploaded the location data (including the day before and a few days after the initial drop in movement rate) into ArcGIS (10.2; Environmental Systems Research Institute [ESRI], Redlands, California, USA). We identified the initial clustering of points and eliminated all the points leading into and out of the cluster. We then created a polygon around all the points in the cluster and the centroid of the polygon was used as an estimate for the actual parturition site. We then used all located (n = 26)and estimated (n = 76) parturition site locations to investigate selection of parturition sites. We performed the same estimation process on the 26 known locations, to identify the amount of error associated with the process we used for estimating parturition sites. Mean error associated with our estimation process was 34.7 m (median 19.2 m), therefore, the smallest spatial scale we investigated was 35 m. To ensure our analyses encompassed

habitat characteristics associated with placement of parturition sites, we also investigated selection at the 100 m scale to determine if any significant discrepancies were present.

We assessed parturition site resource selection at the landscape scale (Barbknecht et al. 2011). For each used parturition location we created 3 random locations within the same treatment area to quantify habitat available to females for parturition. We used GIS coverages to extract vegetation and physical characteristics for each parturition and random sites. We obtained distance values from all parturition site locations to the nearest maintained road, 4x4 road, and perennial water source. As distance values were taken from the centroid (i.e. not from the outer edge of the spatial extent) to the resource, distance variables were the same at both spatial extents. We assigned values at each spatial extent for elevation, ruggedness (vector ruggedness metric VRM; Sappington et al. 2007), northness (aspect transformed by cosine function), and westness (aspect transformed by the sine function) which we calculated from a digital elevation model (DEM; United States Geological Survey 2015; Table 1). We included percent canopy cover of shrubs and trees obtained from the LANDFIRE project (LANDFIRE 2006), however, herbaceous cover was extremely variable and specific to a particular year, thus we did not include those data in the analysis. Shrub and tree canopy cover provide hiding cover and thermal refugia for neonates and adults, as well as sources of forage for the female (Parker and Robbins 1984, deVos et al. 2003). Shrub canopy cover values used were 10-20%, 21-30%, 31-40%, 41-50% and because of limited occurrences, we grouped all other values as 51-80%. We investigated selection of tree canopy cover values of 10-20% and 21-50%. We used landcover data obtained from the United States Geological Survey (USGS) to assign vegetation type data to each point (Thomas et al. 2002, McKee

et al. In Review). Vegetation types used were blackbrush shrubland, sagebrush shrubland, Mojave yucca shrubland, Joshua tree woodland, and pinyon-juniper woodland (McKee et al. In Review). The Hackberry Complex fire of 2005 burned large portions of Great Basin sagebrush shrubland and pinyon-juniper woodland and created large expanses of sparsely vegetated habitat in one of our treatment areas. Post-fire, native species such as globemallow (Sphaeralcea spp.), bitterbrush (Purshia tridentata), and desert almond (Prunus fasiculata) dominated the landscape. Therefore, we included the burn area as a separate vegetation type in our resource selection analyses (McKee et al. *In Review*). We used blackbrush shrubland as the basis for comparison of use among vegetation types because it was found in all three study areas and use was similar to availability (Long et al. 2009, McKee et al. In Review). We assessed collinearity among variables using a correlation matrix (PROC CORR; SAS Institute, Cary, NC; Stewart et al. 2002, Long et al. 2014, McKee et al. *In Review*). None of the variables used was highly correlated with any other (all  $|r| \le 0.60$ ) and all predictor variables were retained. Prior to analysis all covariates were converted to standard normal variables (Zar 2010).

We used RSFs to quantify the relative influence of all factors on parturition-site selection in a use-availability framework (Manly et al. 2002; Barbknecht et al. 2011, McKee et al. *In Review*). We created models at the landscape scale and used an information theoretic approach to model selection (Burnham and Anderson 2002). We used Akaike's Information Criterion adjusted for small sample size (AIC<sub>c</sub>) to evaluate relative model support (Anderson et al. 2000; Burnham and Anderson 2002). We used the dredge tool to test all possible models, and then selected those models that were competitive with our top model ( $\Delta$ AICc < 2) and used model averaging to obtain

parameter estimates, standard errors, and 95% confidence intervals for all parameter estimates. All analyses were performed using the glm and MuMIn packages in Program R (v3.1.1; R Development Core Team 2011). Model averaged parameter estimates were considered significantly different from 0 if 95% confidence intervals did not overlap 0 (Burnham and Anderson 2002). We classified variables as selected when parameter estimates were positive, and avoided when parameter estimates were negative. Conversely, with distance variables a negative value indicates that the individual was a lesser distance from the feature (e.g., water source), while a positive value indicated that deer were further away (Stewart et al. 2002, McKee et al. *In Review*). In all figures and tables we report a selection coefficient wherein we switched the sign on distance variables for ease of interpretation (McKee et al. *In Review*).

# RESULTS

We evaluated resource selection patterns for 102 parturition sites from 2009 to 2014 from the water-provided (n = 41), water-limited (n = 21), and reference (n = 40) treatment areas. The median date of fawning during this period was 2 June. The fawning period showed a high level of synchrony with 51% of births occurring within a 15 day period (May 26-June 9) and 90% of births occurring within a 35 day period (May 16-June 19; Figure 2).

Our attempts to model selection at the 35 m spatial extent with a separation by treatment group did not converge, so treatment area delineations were not included in any subsequent modeling. At the 35 m spatial extent there were 4 competitive ( $\Delta AIC_c < 2$ ) models of resource selection (Table 2). None of the top models included support for

vegetation type (i.e. sagebrush shrubland, Joshua tree woodland etc.) affecting parturition site selection. All competitive models included shrub canopy cover (Shrub), elevation, distance to maintained roads (Dist rds), distance to unmaintained roads (Dist 4x4), and distance to perennial water source (Dist H<sub>2</sub>O). Additionally, 3 competitive models included tree canopy cover (Tree), one model included ruggedness (VRM), and one model indicated support for westness (sin\_aspect). Results of model averaging of parameter estimates using our top models indicated selection for shrub canopy cover of 40-50% ( $\beta = 1.73$  SE 0.54), higher elevations ( $\beta = 1.01$  SE 0.20), closer proximity to maintained roads ( $\beta = 0.65$  SE 0.22), closer proximity to water ( $\beta = 0.81$  SE 0.23), and avoidance of areas in close proximity to unmaintained roads ( $\beta = -0.43$  SE 0.15; Figure 3). All other parameter estimates had 95% confidence intervals that overlapped zero (Table 3).

Attempts to model parturition site selection separately by treatment group at the 100 m spatial extent did not converge, so treatment area delineations were not included subsequent modeling. We observed 7 competitive ( $\Delta AIC_c < 2$ ) models of resource selection at the 100 m spatial extent (Table 2), which were similar to those at the 35 m. None of our top models included support for an effect of vegetation type on selection for parturition sites. All top models included elevation, distance to maintained and unmaintained roads, and distance to water. All but one of the top models included shrub canopy cover, and 5 of the 7 models included tree canopy cover. Additionally, we observed some support for northness (2 models), slope, and ruggedness (present in one model each). Model averaged parameter estimates indicated selection for 30-40% ( $\beta$  = 0.84 SE 0.38), as well as, 40-50% ( $\beta$  = 1.03 SE 0.52) shrub canopy cover (Table 4,

Figure 4). We observed similar levels of selection for distance to water ( $\beta = 0.90$  SE 0.22), distance to maintained roads ( $\beta = 0.62$  SE 0.20), and elevation ( $\beta = 1.08$  SE 0.19), as well as similar level of avoidance of unmaintained roads ( $\beta = -0.54$  SE 0.15), as seen at the 35 m spatial extent (Figure 4). All other parameters were not significant; their 95% confidence intervals overlapped zero (Table 4).

### DISCUSSION

At both spatial extents we identified selection of higher elevations, supporting our hypothesis. Selection for higher elevation sites may result from multiple factors. Use of higher elevations allows individuals to escape extreme temperatures encountered at lower elevations during summer, which would reduce the energetic costs of thermoregulation (Cain et al. 2006) and reduce water loss (Cain et al. 2008). Higher elevations, especially in arid regions, often have forage of higher quality likely a result of the synergistic effects of more annual precipitation and reduced heat stress on plants (Festa-Bianchet 1988, Albon and Lanvatn 1992). Additionally, observed use of higher elevations for parturition sites from this study could be related to predator avoidance. Coyotes (Canis latrans) are the primary predator of mule deer neonates in many areas (Ballard et al. 2001), covote predation is often higher in gentle rolling terrain or low on slopes (Lingle 2002), and presence of covotes was nearly absent in the higher, rugged areas selected by female mountain sheep (Ovis canadensis nelsoni) in our study area (Bleich et al. 1997). Thus, choosing birthing locations at higher elevations may help reduce predation on neonates. Surprisingly, we did not observe selection for steeper slopes, or greater ruggedness, because covotes have been shown to rarely use these types of areas as well (Riley and

Dood 1984, Lingle 2002). Lack of selection for steeper slopes could possibly result from the propensity of mountain lions (*Puma concolor*), the primary predator of adult mule deer, to use habitats with steeper slopes, and areas of steeper slope often correspondingly have a higher degree of ruggedness (Logan and Irwin 1985, Berger 1991, Laing and Lindzey 1991).

The importance of water was strongly demonstrated by significant selection for closer proximity to perennial water sources, a pattern that has been previously shown in mule deer during the fawning period (Bowyer 1984, Hazam and Krausman 1988, McKee et al. *In Review*). We predicted more dense shrub canopy cover would be selected because shrubs provide cover and concealment of neonates, as well as, forage for the mother. We identified significant selection for 30-40% shrub canopy cover at the 35 m spatial extent and for 41-50% at both spatial extents. In addition, a pattern of selection was apparent wherein use relative to availability of shrub canopy cover increased as percent cover increased up to a threshold above which use declined (Figure 3,4). Shrub cover has been shown to be important for neonate crypsis and escape cover (Smith and Lecount 1979, Riley and Dood 1984). The majority of our study area has limited cover of grasses and forbs, leaving shrubs (and trees when present) as the only available cover for concealment and thermal refugia for neonates (Parker and Robbins 1984, Bowyer et al. 1998, deVos et al. 2003).

The quantity, quality, and variety of forage items is one of the most important factors influencing health, survival, and productivity of mule deer in the American southwest (Richardson et al. 2001, Wakeling and Bender 2003), and small differences in forage quality can have significant effects on ungulate growth (White 1983). Nevertheless, succession of habitats to high percentage shrub cover can reduce plant species diversity (Gibbens et al. 1992), and areas of high shrub canopy cover are often composed of older individuals, with little current annual growth resulting in lower nutritional quality (Heffelfinger et al. 2006). At low to medium levels of shrub cover, areas ostensibly with higher proportions of forbs, with smaller and younger shrubs, we observed increasing selection for parturition locations. Those areas would provide adequate hiding cover for neonates while simultaneously having forage of potentially high nutritional value. Similar to our findings, Avey et al. (2003) reported that mule deer in Texas used areas with a mean shrub cover of 37.7%. Similarly, Wiggers and Beasom (1986) reported that mule deer numbers decreased as woody plant cover increased and suggested managing landscapes at 40% canopy cover or less. Our results for tree canopy cover were inconsistent between spatial extents likely a result of limited amount of substantial tree cover in the area, as well as limited sample size.

Results for avoidance of roads was partially supported, deer selected areas further away from unmaintained roads. Surprisingly, parturition sites were located closer to maintained roads than were random points. There is an extremely low density of maintained roads in Mojave (Figure 1), which likely caused that pattern of selection. Parturition sites were located nearly three times further away from maintained then unmaintained roads (Table 1). Deer in our area used areas closer to maintained roads then our random points, however, placement of parturition sites averaged nearly 3 kilometers away from the nearest maintained road, thereby supporting our hypothesis that distance from maintained roads was a factor affecting selection of parturition sites. Selection for proximity to maintained roads likely was a result of the low density and uneven distribution of these roads across study areas.

### MANAGEMENT IMPLICATIONS

Fluctuations in mule deer populations are most often driven by neonate survival or juvenile recruitment. Mortality of neonates often occurs within several days after parturition by way of predation, disease, or malnutrition. Many factors influence survival of neonates during this critical period, including, sufficient concealment and thermal cover for the neonate, and ample access to water and high-quality forage for the mother. Identification of critically important habitat characteristics that are necessary for successful rearing of neonates will allow managers to protect existing birthing habitat and, identify areas where habitat restoration or enhanced management could improve birthing habitats, with the result of improvement of recruitment rates. Our results illustrate the importance of managing for intermediate levels of shrub cover ( $\leq$  50%), perennial water sources, and limited fragmentation by roads when managing specifically for parturition habitat of mule deer occupying arid regions.

## ACKNOWLEDGEMENTS

We gratefully acknowledge financial and technical support from the National Park Service, California Department of Fish and Wildlife (CDFW), Safari Club International Foundation, University of Nevada, Reno, Golden Gate Chapter of Safari Club International, California Deer Association, Nevada Department of Wildlife, Nevada Wildlife Record Book Foundation, and the Boone and Crockett Club. This project was supported by a Hatch Grant from the Agriculture Experiment Station at the University of Nevada, Reno. We received invaluable assistance and expertise in handling animals from CDFW personnel, B. Gonzalez, B.M. Pierce, and L. Konde. We thank C. McKee for his assistance with field methodologies and for collecting some of the data used herein. We also thank technicians A. Carapucci, J. Schoener, C. Bleke, M. Blum, D. Walsh, B. Regan, T. Allen, J. Merrill, D. Adams, D. Huggins and numerous volunteers who helped collect the data used in this manuscript. We gratefully acknowledge the statistical assistance of M. Blum and T. Dilts.

### LITERATURE CITED

- Albon, S.D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502-513.
- Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912-923.
- Avey, J.T., W.B Ballard, M.C. Wallace, M.H. Humphrey, P.K. Krausman, and E.B. Fish.
  2003. Habitat relationships between sympatric mule deer and white-tailed deer in Texas. The Southwestern Naturalist 48:644-653.
- Ballard, W.B., D. Lutz, T.W. Keegan, L.H. Carpenter, and J.C. deVos. 2001. Deerpredator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99-115

Barbknecht, A.E., W.S. Fairbanks, J.D. Rogerson, E.J. Maichak, and L.L. Meadows.

2009. Effectiveness of vaginal-implant transmitters for locating elk parturition sites. Journal of Wildlife Management 73:144-148.

- Barbknecht, A.E., W.S. Fairbanks, J.D. Rogerson, E.J. Maichak, B.M. Scurlock, and L.L. Meadows. 2011. Elk parturition site selection at local and landscape scales. Journal of Wildlife Management 75:646-654.
- Bender, L.C., L.A. Lomas, and T. Kamienski. 2007. Habitat effects on condition of doe mule deer in arid mixed wood land-grassland. Rangeland Ecology and Management 60:277-284.
- Berger, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for bighorn sheep. Animal Behaviour 41:61-77.
- Bertrand, M.R., A.J. DeNicola, S.R. Beissinger, and R.K. Swihart. 1996. Effects of parturition on home ranges and social affiliations of female white-tailed deer. Journal of Wildlife Management 60:899-909.
- Bishop, C.J., D.J. Freddy, G.C. White, B.E. Watkins, T.S. Stephenson, and L.L. Wolfe.
  2007. Using vaginal-implant transmitters to aid in capture of mule deer neonates.
  Journal of Wildlife Management 71:945-954.
- Bishop, C.J., G.C. White, D.J. Freddy, B.E. Watkins, and T.R. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172:1-28.
- Bishop, C.J., C.R. Anderson Jr., D.P. Walsh, E.J. Bergman, P. Kuechle, and J. Roth.2011. Effectiveness of a redesigned vaginal implant transmitter in mule deer.Journal of Wildlife Management 75:1797-1806.

Bowyer, R.T. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy

- Bowyer, R.T., J.G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415-425.
- Bowyer, R.T., V. Van Ballenberghe, J.G. Kie, and J.A.K. Maier. 1999. Birth-site selection by Alaskan moose: strategies for coping with a risky environment. Journal of Mammalogy 80:1070-1083.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Cain, J.W., P.R. Krausman, S.S. Rosenstock, and J.C. Turner. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. Wildlife Society Bulletin 34:570-581.
- Cain, J.W., B.D. Jansen, R.R. Wilson, and P.R. Krausman. 2008. Potential thermoregulatory advantages of shade use by desert bighorn sheep. Journal of Arid Environments 72:1518-1525.
- Carstensen, M., G.D. DelGuidice, and B.A. Sampson. 2003. Using doe behavior and vaginal-implant transmitters to capture neonate white-tailed deer in north-central Minnesota. Wildlife Society Bulletin 31:634-641.
- Ciuti, S., P. Bongi, S. Vassale, and M. Apollonio. 2006. Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. Journal of Zoology 268:97-107.

Connolly, G.E. 1981. Limiting factors and population regulation. Pages 245-285 in O.C.

Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.

- Connelly, J.W., J.H. Gammonley, and J.M. Peek. 2012. Harvest management. Pages 202-231 *in* N.J. Silvy, editor. The wildlife techniques manual: management. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Cook, J.G., et al. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1-61.
- deVos, J.C., Jr., M.R. Conover, and N.E. Headrick. 2003. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State, University, Logan, USA.
- Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580-586.
- Forrester, T.D., and H.U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. Mammal Review 43:292-308.
- Freeman, E.D., R.T. Larsen, M.E. Peterson, C.R. Anderson Jr., K.R. Hersey, and B.R. McMillan. 2014. Effects of male-biased harvest on mule deer: implications for rates of pregnancy, synchrony, and timing of parturition. Wildlife Society Bulletin 38:806-811.
- Gaillard, J.M., M. Festa-Bianchet, and N.G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment and constant adult survival. Trends in Ecology and Evolution 13:58-63.

Gaillard, J.M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toigo. 2000.

Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

- Gibbens, R.P., R.F. Beck, R.P. McNeely, and C.H. Herbel. 1992. Recent rates in mesquite establishment in the northern Chihuahuan Desert. Journal of Range Management 45:585-588.
- Gerhart, K.L, D.E. Russell, D Van DeWetering, R.G. White, and R.D. Cameron. 1997.Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactation infertility.Journal of Zoology 242:17-30.
- Grovenburg, T.W., C.C. Swanson, C.N. Jacques, R.W. Klaver, T.J. Brinkman, B.M. Burris, C.S. DePerno, and J.A. Jenks. 2011. Survival of white-tailed deer neonates in Minnesota and South Dakota. Journal of Wildlife Management 75:213-220.
- Hazam, J.E., and P.R. Krausman. 1988. Measuring water consumption of desert mule deer. Journal of Wildlife Management 52:528-534.
- Heffelfinger, J.R., C. Brewer, C.H. Alcala-Galvan, B. Hale, D.L. Weybright, B.F.
  Wakeling, L.H. Carpenter, and N.L. Dodd. 2006. Habitat guidelines for mule
  deer: southwest deserts ecoregion. Mule Deer Working Group, Western
  Association of Fish and Wildlife Agencies.
- Hurley, M.A., et al. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1-33.
- Johnstone-Yellin, T.L., L.A. Shipley, and W.L. Meyers. 2006. Effectiveness of vaginal implant transmitters for locating neonatal mule deer fawns. Wildlife Society Bulletin 34:338-344.

- Krausman, P.R., J.J. Hervert, and L.L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.
- Laing, S.P., and F.G. Lindzey. 1991. Cougar habitat selection in south-central Utah. Pages 27-37 in C.S. Braun, editor. Proceedings of the mountain lion-human interaction workshop. Colorado Division of Wildlife, Denver, USA.
- Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. Ecology 83:2037-2048.
- LANDFIRE. 2006. National existing vegetation type layer. USDI Geological Survey. <a href="http://gisdata.usgs.net/website/landfire/">http://gisdata.usgs.net/website/landfire/</a> . Accessed 13 Feb 2015.
- Logan, K.A., and L.L. Irwin. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. Wildlife Society Bulletin 13:257-262.
- Long, R.A., J.G. Kie, R.T. Bowyer, and M.A. Hurley. 2009. Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. Wildlife Biology 15:288-298.
- Long, R.A., R.T. Bowyer, W.P Porter, P. Mathewson, K.L. Monteith, and J.G. Kie. 2014. Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. Ecological Monographs 84:513-532.
- Mackie, R.J., D.F.P ac, K.L. Hamlin, and G.L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Federal Aid to Wildlife Restoration Report, Project W-120-R, Montana Fish, Wildlife and Parks, Wildlife Division, Helena, USA.
- Manly, B.F., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson.

2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

- McKee, C.J., K.M. Stewart, J.S. Sedinger, A.P. Bush, N.W. Darby, D.L.
  Hughson, and V.C. Bleich. *In review*. Spatial distribution and resource selection
  by mule deer in an arid environment: responses to provision of water. Journal of
  Arid Environments.
- Monteith, K.L., V.C. Bleich, T.R. Stephenson, B.M. Pierce. 2010. Population dynamics of mule deer in the eastern Sierra Nevada: implications of nutritional condition.California Department of Fish and Game, Bishop, California, USA.
- Monteith, K.L., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, J.G. Kie, and R.T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-62.
- National Park Service. 2015. Nature and science of Mojave National Preserve. <a href="http://www.nps.gov/moja/naturescience/index.htm">http://www.nps.gov/moja/naturescience/index.htm</a>. Accessed 31 Feb 2015.
- Parker, K.L., and C.T. Robbins. 1984. Thermoregulation in mule deer and elk. Canadian Journal of Zoology 62:1409-1422.
- Parker, K.L., P.S. Barboza, and M.P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57-69.
- Picton, H.D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology 21:869-879.
- Richardson, C., R. Cantu, and K. Brown. 2001. Comprehensive wildlife management

guidelines for the Trans-Pecos ecological region. Texas Parks and Wildlife Department, Austin, Texas.

- Riley, S.J., and A.R. Dood. 1984. Summer movements, home range, habitat use, and behavior of mule deer fawns. Journal of Wildlife Management 48:1302-1310.
- Robinette, W.L., C.H. Baer, R.E. Pillmore, C.E. Knittle. 1973. Effects of nutritional change on captive mule deer. Journal of Wildlife Management 37:312-326.
- Robbins, C.T., and B.L. Robbins. 1979. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. The American Naturalist 114:101-116.
- Sappington, J.M., K.M. Longshore, and D.B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419-1426.
- Sasser, R.G., C.A. Ruder, K.A. Ivani, J.E. Butler, and W.C. Hamilton. 1986. Detection of pregnancy by radioimmunoassay of a novel pregnancy-specific protein in serum of cows and profile of serum concentrations during gestation. Biology of Reproduction 35:936–942.
- Sikes R.S., W.L Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.
- Smith, R.H. and A. LeCount.1979. Some factors affecting survival of desert mule deer fawns. Journal of Wildlife Management 43:657-665.

Stephenson, T.R., J.W. Testa, G.P. Adams, R.G. Sasser, C.C. Schwartz, and K.J.

Hundertmark. 1995. Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. Alces 31:167-172.

- Stewart, K.M., R.T. Bowyer, J.G. Kie, N.J. Cimon, and B.K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229-244.
- Thomas, K., J. Franklin, T. Keeler-Wolf and P. Stine. 2002. Central Mojave vegetation map. A digital spatial database (ArcInfo). United States Geological Survey.
- Thorne, R.F., B.A. Prigge, and J. Henrickson. 1981. A flora of the higher ranges and the Kelso Dunes of the eastern Mojave Desert in California. ALISO 10:71-186.
- Tollefson, T.N., L.A. Shipley, W.L. Myers, D.H. Keisler, and N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management 74:974-986.
- United States Geological Survey. 2015. Climate history of the Mojave Desert region. <a href="http://mojave.usgs.gov/climate-history/">http://mojave.usgs.gov/climate-history/</a>. Accessed 23 Mar 2015.
- Unsworth, J.W., D.F. Pac, G.C. White, and R.M. Bartman. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315-326.
- Van Moorter, B., J.M. Gaillard, P.D. McLoughlin, F. Klein, and M.S. Boyce. 2009.
   Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. Oecologia 159:669-678.
- Vore, J.M., and E.M. Schmidt. 2001. Movements of female elk during calving season in northwest Montana. Wildlife Society Bulletin 29: 720-725.
- Wade, G.N., and J.E. Schneider. 1992. Metabolic fuels and reproduction in female mammals. Neuroscience and Biobehavioral Reviews 16:235-272

- Wakeling, B.F., and L.C. Bender. 2003. Influence of nutrition on mule deer biology and ecology. Pages 93–116 *in* J.C. deVos, Jr., M.R. Conover, and N.E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Press, Logan, Utah, USA.
- White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377-384.
- Wiggers, E.P., and S.L. Beasom. 1986. Characterization of sympatric or adjacent habitats of 2 deer species in west Texas. Journal of Wildlife Management 50:129-134.
- Zar, J.H. 2010. Biostatistical Analysis. Fifth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

**Table 1**. Descriptive statistics (Mean  $\pm$  SD) of habitat variables from available (random) and used (mule deer birth site) locations

 for 102 mule deer in 3 study areas within Mojave National Preserve, CA, USA, 2009-2014. Parameters were standardized prior to

 analysis. Note\* distance variables were measured from the parturition site so did not differ with spatial extent.

	35 N	leter	100 N	Vleter
Variable	Available	Locations	Available	Locations
Dist. To water (m)	3383 ± 2176.6	1969 ± 1063.1	3383 ± 2176.6	1969 ± 1063.1
Elevation (m)	1439 ± 173.7	1583 ± 116.5	1440 ± 173.6	1583 ± 115.7
Dist. to maintained roads (m)	4316 ± 3596.9	2953 ± 2436.5	4316 ± 3596.9	2953 ± 2436.5
Dist. to unmaintained roads (m)	898 ± 766.7	1106 ± 607.8	898 ± 766.7	1106 ± 607.8
Slope (%)	14.7 ± 16.4	21.7 ± 14.4	14.8 ± 15.9	22.2 ± 14.1
Vector Ruggedness Index (VRM)	0.002 ± 0.002	0.003 ± 0.002	0.002 ± 0.003	0.003 ± 0.003
Northness aspect (cosine transformation)	0.006 ± 0.123	0.001 ± 0.094	0.005 ± 0.062	0.003 ± 0.047
Westness aspect (sine transformation)	0.003 ± 0.114	0.009 ± 0.105	0.007 ± 0.053	0.007 ± 0.035

<b>Table 2</b> . Ranked top models ( $\Delta AIC_c \le 2$ ) of resource selection functions, at two different spatial scales, for 102 mule deer in
Mojave National Preserve, CA, USA, 2009-2014.

Model	DF	LogLik	AICc	Δ AICc	W <sub>i</sub>
35 Meter					
Int + Shrub + Elevation + Dist rds + Dist $4x4$ + Dist $H_2O$ + Tree	12	-172.74	370.27	0.00	0.41
Int + Shrub + Elevation + Dist rds + Dist $4x4$ + Sin_aspect + Dist $H_2O$ + Tree	13	-172.28	371.49	1.22	0.22
Int + Shrub + Elevation + Dist rds + Dist $4x4$ + Dist $H_2O$	10	-175.55	371.66	1.38	0.21
Int + Shrub + Elevation + Dist rds + Dist $4x4 + VRM + Dist H_2O + Tree$	13	-172.63	372.20	1.93	0.16
100 Meter					
Int + Shrub + Elevation + Dist rds + Dist $4x4$ + Dist $H_2O$	10	-170.21	360.98	0.00	0.25
Int + Shrub + Elevation + Dist rds + Dist $4x4$ + Dist $H_2O$ + Tree	11	-196.21	361.09	0.11	0.24
Int + Shrub + Elevation + Dist rds + Dist 4x4 + VRM + Dist H <sub>2</sub> O + Tree	12	-168.91	362.62	1.65	0.11
Int + Shrub + Elevation + Dist rds + Dist 4x4 + Slope + Dist H <sub>2</sub> O + Tree	12	-168.95	362.69	1.71	0.11
Int + Shrub + Cos_aspect + Elevation + Dist rds + Dist $4x4$ + Dist $H_2O$	11	-170.04	362.76	1.78	0.10
Int + Elevation + Dist rds + Dist $4x4$ + Dist $H_2O$ + Tree	6	-175.30	362.82	1.84	0.10
Int + Shrub + Cos_aspect + Elevation + Dist rds + Dist $4x4$ + Dist $H_2O$ + Tree	12	-169.07	362.95	1.97	0.09

**Table 3**. Model averaged parameter estimates ( $\beta$ ), standard errors (SE) and 95% confidence intervals from resource selection functions at 35 meter spatial extent for 102 mule deer in Mojave National Preserve, CA, USA, 2009-2014.

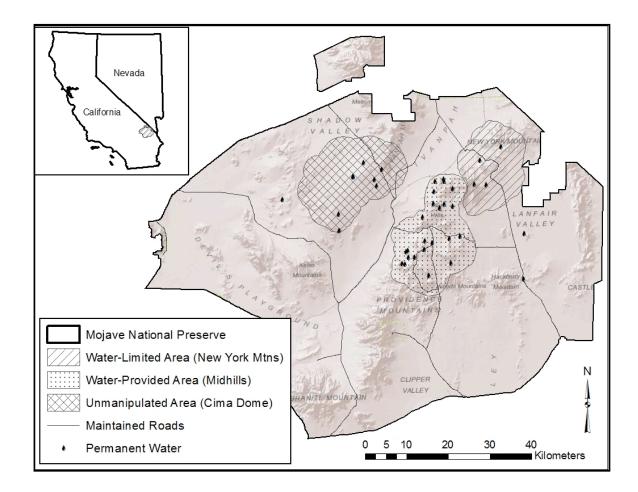
Devementer	0	сг	95%	% CI
Parameter	β	SE	Lower	Upper
Elevation <sup>+</sup>	1.009	0.196	0.624	1.394
Dist. to maintained roads <sup>+</sup>	0.645	0.215	1.067	0.222
Dist. to unmaintained roads <sup>+</sup>	-0.426	0.148	-0.135	-0.717
Dist. to water <sup>+</sup>	0.805	0.227	1.252	0.359
Westness aspect <sup>+</sup>	0.137	0.143	-0.145	0.418
VRM†	0.066	0.145	-0.218	0.351
Shrub Cover (10-20%)	-1.454	0.943	-3.308	0.400
Shrub Cover (20-30%)	0.443	0.47	-0.493	1.379
Shrub Cover (30-40%)	0.562	0.363	-0.151	1.275
Shrub Cover (40-50%)	1.731	0.539	0.671	2.790
Shrub Cover (50-80%)	0.430	0.637	-0.823	1.682
Tree Cover (10-20%)	0.232	0.547	-0.844	1.308
Tree Cover (20-50%)	-2.277	1.200	-4.636	0.082

<sup>+</sup>Parameter z-standardizied prior to model analysis

Parameter	ß	SE	95%	95% CI	
	β	JE	Lower	Upper	
Elevation <sup>+</sup>	1.077	0.192	0.699	1.456	
Dist. to maintained roads <sup>+</sup>	0.616	0.196	1.002	0.229	
Dist. to unmaintained roads +	-0.541	0.153	-0.240	-0.842	
Dist. to water †	0.903	0.217	1.330	0.477	
Northness aspect +	-0.086	0.158	-0.397	0.224	
Slope†	0.107	0.148	-0.184	0.398	
VRM†	0.112	0.145	-0.173	0.396	
Shrub Cover (10-20%)	-0.613	0.669	-1.929	0.702	
Shrub Cover (20-30%)	0.048	0.482	-0.899	0.995	
Shrub Cover (30-40%)	0.836	0.382	0.085	1.587	
Shrub Cover (40-50%)	1.029	0.516	0.015	2.043	
Shrub Cover (50-80%)	-0.860	1.113	-3.048	1.328	
Tree Cover (10-20%)	-0.772	0.508	-1.770	0.226	

**Table 4**. Model averaged parameter estimates ( $\beta$ ), standard errors (SE) and 95% confidence intervals from resource selection functions at 100 meter spatial extent for 102 mule deer in Mojave National Preserve, CA, USA, 2009-2014.

<sup>+</sup>Parameter z-standardizied prior to model analysis



**Figure 1.** Map of Mojave National Preserve, CA, USA, with study area delineations, where the effects of provision of water were investigated, 2009-2014. Inset map shows location relative to Nevada and California. Note: although boundaries for the water-provided and water-limited were close the topography of that separation prevented movement of radio collared deer between areas.

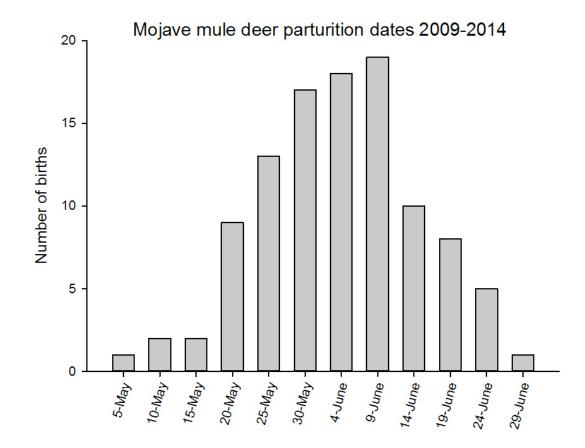
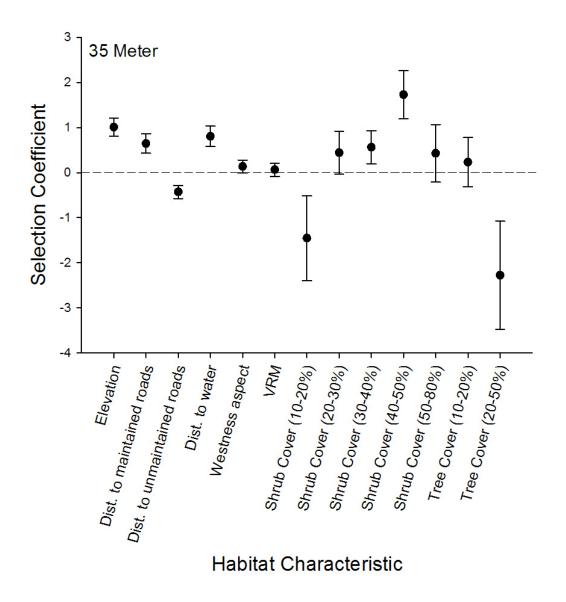
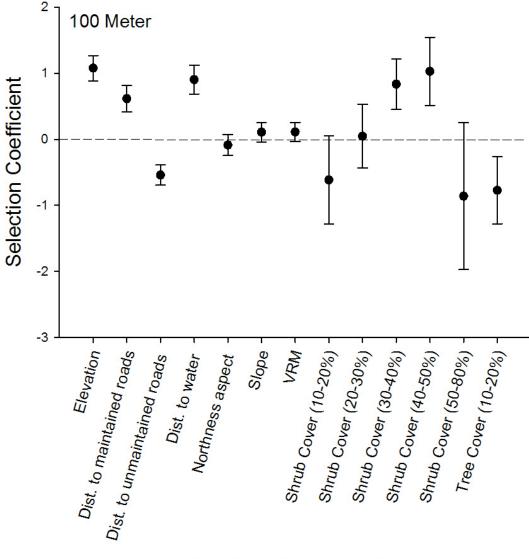


Figure 2. Descriptive statistics of timing of parturition for 102 mule deer in Mojave National Preserve, CA, USA 2009-2014.



**Figure 3.** Selection Index, of 35 meters surrounding parturition site, based on standardized parameter estimates obtained from resource selection functions for mule deer in Mojave National Preserve, CA, USA, 2009-2014. Resource selection functions were derived from generalized linear mixed models fit to used and random locations. Error bars represent 95% confidence intervals.



Habitat Characteristic

**Figure 4.** Selection Index, of 100 meters surrounding parturition site, based on standardized parameter estimates obtained from resource selection functions for mule deer in Mojave National Preserve, CA, USA, 2009-2014. Resource selection functions were derived from generalized linear mixed models fit to used and random locations. Error bars represent 95% confidence intervals.

# THESIS SUMMARY

Water is an essential and often limiting resource in arid environments, especially under drought conditions (Rosenstock et al. 1999, Morgart et al. 2005, Cain et al. 2006). Furthermore, droughts are expected to increase in intensity and duration as climate changes in the future (IPCC 2013, Diffenbaugh et al. 2015). Subsequent reductions in available water sources resulting from a combination of climate change and anthropogenic uses could make provisioning of water essential for the persistence of many species inhabiting arid regions (Longshore et al. 2009). Nevertheless, the effects of provisioning water on demographic rates and selection of resources remain unclear. Indeed, I encountered many of the same confounding factors in investigating the benefits of provision of water as my predecessors (Broyles and Cutler 1999, Marshal et al. 2006, Cain et al. 2008), and obtained similar equivocal results.

I was unable to identify any effect of availability of permanent water sources on any of the demographic rates investigated. High and relatively stable adult female survival and pregnancy rates are common in mule deer populations across the Intermountain West (Gaillard et al 1998, 2000; Eberhardt 2002, Hurley et al. 2011, Bender et al 2007, Freeman et al 2014, Monteith et al. 2014); therefore, it is not surprising that these demographic parameters were not strongly affected by provision of water. I expected to see the benefits of provision of water reflected more strongly in fetal rates, and survival and recruitment of young (Gaillard et al 1998, Monteith et al 2014), but I observed no support for improvement in those vital rates relative to availability of water, during this study. I also observed no support for an effect of availability of water on adult survival. Survival differed among years, and within years during the fawning period, with a significant negative effect of drought severity on survival during this time period. In years when drought severity was high, adult females had lower survival during May and June than the rest of the year. Poorer range conditions during drought years may have resulted in more time spent obtaining adequate resources including forage and water than would be necessary during wet years, increasing exposure to predation events.

Although I observed no direct effect of provision of water on neonate survival, I identified significant effects of timing of birth and relative body condition on survival of neonates. Neonates born earlier in the fawning period survived better than those born later, and neonates in better relative condition survived better than those in poorer relative condition. Additionally, I found that timing of birth mitigates much of the effects of neonates that were born in poor body condition. During the survival period used in my study (May-August), Mojave was experiencing extreme drought (PDSI  $\leq$  -4.0; Palmer 1965) for both 2013 (PDSI = -5.2) and 2014 (PDSI = -4.4), which likely contributed to low neonatal survival rates in all study areas. Forage quality and the amount of preformed water in forage are likely highest early in the fawning period and therefore females that give birth to neonates at this time are likely better able to provide sufficient milk to successfully rear their young. Drought conditions, which reduce ephemeral water sources and decrease the quality and quantity of available food, have previously been shown to result in lower survival rates of neonates in desert deer populations (Taylor and Hahn 1947; Carroll and Brown 1977). Further research on the quantity, quality, and amount of preformed water in forage among these treatment areas would provide a better

understanding of the influence of water availability on mule deer demography, relative to other resources.

The importance of free-standing water was strongly demonstrated by significant selection for placement of parturition sites in proximity to perennial water sources, a pattern that has been previously shown in mule deer during the fawning period (Bowyer 1984, Hazam and Krausman 1988, McKee et al. *In Review*). Identification of critically important habitat characteristics that are necessary for successful rearing of neonates will allow managers to protect existing birthing habitat and identify areas where habitat restoration or enhanced management could improve birthing habitats, with the result of improvement of recruitment rates. My results illustrate the importance of managing for intermediate levels of shrub cover (30-50%), perennial water sources, and limited fragmentation by roads when managing specifically for parturition habitat of mule deer occupying arid regions.

Climatic conditions in Mojave from 2009 to 2014 varied substantially between years with wet years in which most precipitation fell in the winter (2010-2011) and drought years where most precipitation fell in the summer (2012-2014). Investigating demographic rates only during drought years (when importance and dependence on permanent water sources is potentially highest) may provide more insight into the population-level effects of provisioning water. Moreover, the findings presented in this thesis are from phase 1 of a 2 phase experimental study. During phase 2 additional water sources will be developed in the water-limited treatment area, allowing for comparisons within the same population before and after water was provisioned. This will hopefully provide better insight into the effects of providing water to wildlife in arid regions. Nevertheless, the results of this thesis provide a better understanding of the demographics and resource selection patterns of a previously unstudied desert ungulate population.

# LITERATURE CITED

- Bender, L.C., L.A. Lomas, and T. Kamienski. 2007. Habitat effects on condition of doe mule deer in arid mixed wood land-grassland. Rangeland Ecology and Management 60:277-284.
- Bowyer, R.T. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy 65:410-417.
- Broyles, B., and T.L. Cutler. 1999. Effect of surface water on desert bighorn sheep in the Cabeza Prieta National Wildlife Refuge, southwestern Arizona. Wildlife Society Bulletin 27:1082-1088.
- Cain, J.W., P.R. Krausman, S.S. Rosenstock, and J.C. Turner. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. Wildlife Society Bulletin 34:570-581.
- Cain, J.W., P.R. Krausman, J.R. Morgart, B.D. Jansen, and M.P. Pepper. 2008. Responses of desert bighorn sheep to removal of water sources. Wildlife Monographs 171:1-32.
- Carroll, B.K., and D.L. Brown. 1977. Factors affecting survival in Southern-Central Texas. Journal of Wildlife Management 41:63-69.
- Diffenbaugh, N.S., D.L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Science 112:3931-3936.

Eberhardt, L.L. 2002. A paradigm for population analysis of long-lived vertebrates.

Ecology 83:2841-2854.

- Freeman, E.D., R.T. Larsen, M.E. Peterson, C.R. Anderson Jr., K.R. Hersey, and B.R. McMillan. 2014. Effects of male-biased harvest on mule deer: implications for rates of pregnancy, synchrony, and timing of parturition. Wildlife Society Bulletin 38:806-811.
- Gaillard, J.M., M. Festa-Bianchet, and N.G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment and constant adult survival. Trends in Ecology and Evolution 13:58-63.
- Gaillard, J.M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.
- Hazam, J.E., and P.R. Krausman. 1988. Measuring water consumption of desert mule deer. Journal of Wildlife Management 52:528-534.
- Hurley, M.A., et al. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1-33.
- IPCC. 2013. Summary for policymakers. Climate Change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change, (T.F. Stocker, et al. editors.) Cambridge University Press, Cambridge, UK.

Longshore, K. M., C. Lowrey, and D. B. Thompson. 2009. Compensating for

diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73:280-286.

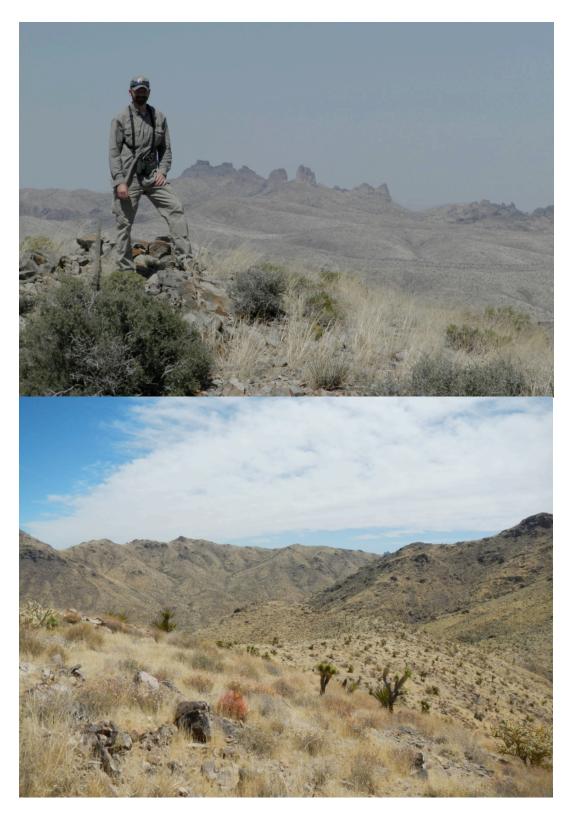
- Marshal, J. P., L. M. Lesicka, V. C. Bleich, P. R. Krausman, G. P. Mulcahy, and N. G. Andrew. 2006. Demography of desert mule deer in southeastern California. California Fish and Game 92:55-66.
- McKee, C.J., K.M. Stewart, J.S. Sedinger, A.P. Bush, N.W. Darby, D.L. Hughson, and V. C. Bleich. *In review*. Spatial distribution and resource selection by mule deer in an arid environment: responses to provision of water. Journal of Arid Environments.
- Monteith, K.L., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, J.G. Kie, and R.T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-62.
- Morgart, J.R., J.J. Hervert, P.R. Krausman, J.L. Bright, and R. S. Henry. 2005. Sonoran pronghorn use of anthropogenic and natural water sources. Wildlife Society Bulletin 33:51-60.
- Palmer, W.C. 1965. Meteorological drought: Report 45. U.S. Department of Commerce, Washington, D.C., USA.
- Rosenstock, S.S., W.B. Ballard, and J.C. deVos. 1999. Viewpoint: benefits and impacts of wildlife water developments. Journal of Range Management 52:302-311.
- Taylor, W.P., and H.C. Hahn. 1947. Die-offs among the white-tailed deer in the Edwards Plateau of Texas. Journal of Wildlife Management 11:317-323.



**Photographs 1**. Neonatal mule deer, Mojave National Preserve, CA. Top: Female with VHF radiocollar installed. Bottom: Male, < 1 day old, just prior to capture and processing



**Photographs 2.** Processing neonates. Top: installing expandable VHF radiocollar. Bottom: measuring new hoof growth (used to estimate age).



**Photographs 3.** New York Mountains, Mojave National Preserve, CA. Top: On top of a mountain with the Castle Peaks in the Background. Bottom: Deep in the wilderness area.