

University of Nevada, Reno

**Birth Site Selection and Neonate Survival of Mule Deer
in the Blue Mountains of Oregon**

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

by

Danielle R. Walsh

Dr. Kelley M. Stewart/Thesis Advisor

May, 2016



THE GRADUATE SCHOOL

We recommend that the thesis
prepared under our supervision by

DANIELLE R. WALSH

Entitled

**Birth Site Selection And Neonate Survival Of Mule Deer
In The Blue Mountains Of Oregon**

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

MASTER OF SCIENCE

Kelley M. Stewart, Ph.D, Advisor

Elizabeth Leger, Ph.D, Committee Member

Bruce K. Johnson, Ph.D, Committee Member

Scott Bassett, Ph.D, Graduate School Representative

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

May, 2016

ABSTRACT

Mule deer (*Odocoileus hemionus*) populations have been in decline in recent decades for a variety of reasons including habitat loss, disease, and competition. We were interested in what factors influence survival of neonatal mule deer in the Blue Mountains of Oregon. Individuals should select resources to increase fitness; therefore, females should select parturition sites with characteristics that have the potential to increase survival of their neonates. We examined what habitat characteristics females selected at birth sites as well as how those selected characteristics affected neonate survival. Additionally, we were interested in how changes in forage quality, maternal condition, climate, maternal age, and physical characteristics of neonates affected their survival. We conducted our research at Starkey Experimental Forest and Range in northeast, Oregon, primarily in the Main study area. We captured adult females during the winters of 2013-2014 and 2014-2015, and fitted them with GPS collars as well as inserting vaginally implanted transmitters. When parturition occurred in May and June, we located neonates and birth sites. Neonates were fitted with expandable collars so that we could monitor mortality. We measured metatarsus length, chest girth, and weight for adults and neonates. Additionally, we quantified body condition, measured maximum rump fat, and measured the jaw and body length of adults. At birth sites and 2 adjacent random sites, we measured overstory and hiding cover, the number of trees and shrubs, the distance to the nearest transition in vegetation type, and aspect. We determined selection of habitat characteristics at birth sites with resource selection functions using a mixed effects logistic regression. We chose our best model based on Akaike's Information Criterion

corrected for small sample size. Our best model included significant parameters indicating selection for south facing slopes, increased overstory cover, and increased amounts of woody debris. We modeled neonate survival until weaning using the nest survival module in program MARK. We included different age trends to determine how survival changed. Survival from birth to weaning was 0.3169 (SE 0.706) and did not differ between years. Our best model indicated that survival changed daily from birth to day 30 and then began to stabilize and change weekly until weaning. Additionally our best model included a parameter for birth sites located on south facing slopes. Our results indicate that neonates born on south facing slopes have higher survival rates than those born in other locations. South facing slopes in this montane forested ecosystem are warmer and drier, providing a more stable microclimate for neonates who are born with few energy reserves. South facing slopes likely allow neonates to minimize energy use, which may increase their survival. Results from birth site selection analysis indicates that females selected habitat characteristics that increase hiding cover, potentially decreasing mortality by reducing predation events at birth sites. A better understanding of how deer select habitat characteristics to increase survival as well as what factors increase susceptibility to mortality allows for better management of populations. Management strategies that account for factors influencing survival will be better suited to counter population declines across the west.

ACKNOWLEDGMENTS

First, I want to thank Dr. Kelley Stewart for giving me this opportunity. She has been a wonderful mentor and I have learned a lot from her, both about science and life. I have always appreciated her support and encouragement as well as her humoring me every time I have run into her office excited about something.

I also really appreciate all that my technicians, Ben Regan and Travis Allen, did for the project. They experienced every high and low of fieldwork with me and made every day enjoyable. There is nothing quite like the excitement that filled the bunkhouse when the first fawns of the season were caught and I am grateful for having experienced that with them. The quality and quantity of work put in by Ben, Travis was beyond all possible expectations, and I will always appreciate it. I have to thank Brian Dick, Ryan Kennedy, and Dennis Rea, for all of their help with fieldwork but also for stopping every morning for coffee and cookies to discuss the day's plans. They always make me feel at home while I was in the field. Along with that I have to thank Scott Findholt and Bruce Johnson for always being willing to help me at the drop of a hat, or death of a fawn for that matter. Without them we would not have been able to collect such high quality data.

My peers made graduate school an wonderful period of my life. I do not know what I would have done without the encouragement and support of Cynthia Downs, Jen Gansburg, and Jade Keehn. I could not even begin to count the number of coffees drank over discussion of science, our futures, and our current level of exhaustion. I am extremely grateful that they were able to be there for this experience. I thank all of my

lab mates especially Marcus Blum, Levi Heffelfinger, Ben Sedinger, Kira Hefty, and Tony Bush. Everyone was always extremely willing to help and give advice. The unending support of the Stewart lab made coming to work never actually feel like work.

My family has been wonderful through this process with encouragement and support as well as understanding. Fieldwork occasionally kept me from holidays and events, but my family and friends always understood that it was a means to an end. I also appreciate all the times that family and friends let me talk about my research even though they did not always quite understand what I was doing, the willingness to listen will always be remembered.

Last but far from least, I have to thank Scott Carpenter. His encouragement, support, and confidence during these past years has fueled me to do my best. Anytime I have ever waivered he has been there to tell me that I could do it as well as always seeming to know when I just needed to spend some time enjoying nature. He has been there every step of the way on this adventure and I am looking forward to seeing what the next one holds with him.

TABLE OF CONTENTS

Thesis Overview	1
Literature Cited.....	4
¹Chapter 1: Selection of Parturition Sites by Mule Deer in the Blue Mountains	
Ecosystem	9
Abstract.....	10
Introduction.....	11
Materials and Methods.....	13
Results.....	18
Discussion.....	19
Acknowledgements.....	20
References.....	20
Tables.....	26
Figures.....	28
Chapter 2: Neonate survival of Mule Deer: Physical, Environmental, and Behavioral Effects	
Abstract.....	30
Introduction.....	31
Materials and Methods.....	34

¹ 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)

Results.....	41
Discussion.....	43
Acknowledgements.....	47
Literature Cited.....	47
Figure Legend.....	56
Tables.....	57
Figures.....	61
Thesis Summary.....	67
Literature Cited.....	69
Appendix 1.....	71

THESIS OVERVIEW

Life-history theory predicts that large-bodied species with long life spans maintain survival, but under resource limited conditions may trade off current and future reproduction (Stearns 1992, Morano et al. 2013). Population dynamics of large herbivores are especially influenced by juvenile survival and recruitment relative to other demographic parameters (Gaillard et al. 2000). Variation in population numbers often depend on the recruitment of neonates (McCullough 1979). Recruitment generally occurs when an individual enters the breeding population, which occurs after a juvenile has survived its first summer as well as winter, both of which are times of increased mortality (Gaillard et al. 2000). Following parturition, ungulate neonates are vulnerable to mortality because of their limited mobility and dependence on their mother (White et al. 1972). Mortality during the first months of life can be caused by many factors including predation (Cook et al. 1971), starvation or malnutrition (Roffe 1993), abandonment (Langenau and Lerg 1976), trauma (Roffe 1993), or disease (Smith et al. 2014).

Reproduction in large herbivores requires an individual to have energy stores that exceed those required for maintenance and survival (Parker et al. 2009). Energy stores are influenced by past energy expenditure and the ability of an individual to acquire energy from their environment through the selection of necessary resources (Long et al. 2014). Seasonal changes in climate, forage, activity level, reproductive effort, and metabolic rate influence resource use and energy fluctuations (Robbins 1993). Additionally, in highly seasonal environments young must acquire enough resources during the summer to grow and accumulate energy stores to survive their first winter (Tollefson et al. 2011). Energy is acquired from forage ingested by an individual,

therefore higher quality and quantities increase energy accumulation (Robbins 1993). Survival and recruitment may also be influenced by a variety of indirect variables including maternal effects (Bishop et al. 2009), physical characteristics at birth (Carstensen et al. 2009), climate (Garrott et al. 2003, Picton 1984), and forage availability (Tollefson et al. 2011). Indeed, Monteith et al. (2014) reported that when predation was low, maternal condition and birth weight positively affect neonate survival.

Selection of resources by an individual can affect survival by decreasing predator detection (Bowyer et al. 1998), increasing availability of adequate forage (Rearden et al. 2011), and decreasing energy expenditures (Barbknecht et al. 2011). Resource use changes with resource availability, which often varies across seasons (Zengeya et al. 2014). Energy requirements of mule deer (*Odocoileus hemionus*) change during different seasons and life-history events such as mating, gestation, and lactation (Moen 1978). Indeed, Long et al. (2009) found that mule deer selected different habitats during late gestation, the week of parturition, and following parturition when lactation occurred. Female mule deer invest a large amount of energy into reproduction so resource selection should improve fitness through increased survival and recruitment of offspring. Resource selection around the time of parturition is critical to meeting the needs of the female as well as providing cover and protection for vulnerable neonates (Rearden et al. 2011).

Mule deer are a long lived herbivore with both economic and ecological importance. Mule deer have a very large geographic range covering most of North America west of the 100 meridian (Anderson and Wallmo 1984). They are hunted across most of their range, which provides a source of food to many as well as income to private and government agencies. Mule deer often act as keystone species in their environment by

influencing plant growth through browsing (Paige 1992) as well as providing a prey source to a variety of predators (Ballard et al. 2001). Mule deer have adapted to live in a variety of habitat types (Wallmo 1981) but nonetheless have experienced population declines during recent decades (Gill et al. 2001). Reasons for these declines are controversial and encompass many factors including habitat loss, disease, predation, and competition (DeVos et al 2003). Because of these declines, it is important to identify the factors that affect survival and reproduction. This research was designed to gain a better understanding of what variables effect survival and recruitment of mule deer, including birth characteristics of neonates (i.e. weight and birthdate), maternal condition, and environmental characteristics, such as climate. In addition, this project will allow us to gain a better understanding of the resources used and required during parturition as well as the effect of resource limitations during winter. The study was a collaborative effort among the United States Forest Service, Oregon Department of Fish and Wildlife and the University of Nevada, Reno.

In chapter 1, we evaluated what habitat characteristics were selected by parturient females when choosing birth sites at the Starkey Experimental Forest and Range, Oregon, USA during the springs of 2014 and 2015. We hypothesized that females would select sites with increased concealment cover to avoid predation, as well as topography and vegetation characteristics that provided stable thermal environments for newborn deer. We measured habitat characteristics in a 15 meter radius at used sites and 2 corresponding random locations at a distance of 30 to 130 meters from birth sites. We examined the effect of overstory cover, horizontal cover, quantity and height of trees and shrubs, aspect, distance to the edge of open vegetation, and the quantity of woody debris

on selection of birth sites. We used a mixed effects logistic regression to determine differences in habitat characteristics between used sites and random locations with a random effect of maternal female.

In chapter 2, we investigated what factors influenced survival of neonatal mule deer following parturition at the Starkey Experimental Forest and Range, Oregon, USA in 2014 and 2015. We hypothesized that survival would be affected by changes in vegetation and climate because of their effects on energy use and gain. We also hypothesized that maternal characteristics including body condition and age would affect survival because mothers in better condition could put more energy into the growth and development of their neonates as well as produce high quality milk to provision offspring following parturition. Additionally, older females have more experience rearing young so we predicted that they would be more successful during 2014 and 2015. We also hypothesized that physical characteristics at birth could affect the survival of a neonate including the weight, body condition, and birth date. Finally, we hypothesized that the site a maternal female selected for parturition possessed habitat characteristics that could affect survival so we examined how our results from chapter 1 affected neonate survival. We used the nest survival module in program MARK to evaluate neonate survival to 120 days, which is when weaning occurs in mule deer. We determined how survival varies over time at Starkey as well as what influences neonate survival.

LITERATURE CITED

Anderson A.E., and O. C. Wallmo. 1984. *Odocoileus hemionus*. Mammalian Species 219: 1–9.

- Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and Jr. J. C. DeVos. 2001. 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, B. M. Scurlock, and L. L. Meadows. 2011. Elk parturition site selection at local and landscape scales. *Journal of Wildlife Management* 75:646-654.
- 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.
- 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.
- Carstensen, M., G. D. Delgiudice, B. A. Sampson, and D. W. Kuehn. 2009. Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. *Journal of Wildlife Management* 73:175-183.
- Cook, R. S., M. White, D. O. Trainer, and W. C. Glazener. 1971. Mortality of white-tailed deer fawns in south Texas. *Journal of Wildlife Management* 35:47-56.
- 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.
- 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.

- Garrott, R. A., L. Eberhardt, P. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology* 81:33-45.
- Gill, R. B., T. D. I. Beck, C. J. Bishop, D. J. Freddy, N. T. Hobbs, R. H. Kahn, M. W. Miller, T. M. Pojar, and G. C. White. 2001. Declining mule deer populations in Colorado: Reasons and responses. Colorado Division of Wildlife Special Report Number 77:DOW-R-S-77-01, Fort Collins, Colorado.
- Langenau, E. E. 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.
- 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.
- 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.
- McCullough, D.R. 1979. The George Reserve deer herd: population ecology of a K selected species. University of Michigan Press, Ann Arbor, Michigan.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *Journal of Wildlife Management* 42:715-738.
- Morano, S., K. M. Stewart, J. S. Sedinger, C. A. Nicolai, and M. Vavra. 2013. Life - history strategies of North American elk: trade-offs associated with reproduction and survival. *Journal of Mammalogy* 94:162-172.

- 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.
- Paige, K. N. 1992. Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 6:2076-2085.
- 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.
- Rearden, S. N., R. G. Anthony, and B. K. Johnson. 2011. Birth-site selection and predation risk of Rocky Mountain elk. *Journal of Mammalogy* 95:1118-1126.
- Robbins, C. T. 1993. *Wildlife feeding and nutrition*. Second ed. Academic Press, San Diego, California.
- Roffe, T. J. 1993. Perinatal mortality in caribou from the Porcupine herd, Alaska. *Journal of Wildlife Disease* 29:295-303.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, London.
- Tollefson, T. N., L. A. Shipley, W. L. Myers, and N. Dasgupta. 2011. Forage quality's influence on mule deer fawns. *Journal of Wildlife Management* 75:919-928.
- Wallmo, O. C. 1981. *Mule and black-tailed deer of North America*. University of Nebraska Press, Lincoln.
- White, M., F. F. Knowlton and W.C. Glazener. 1972. Effects of dam-newborn fawn behavior on capture and mortality. *Journal of Wildlife Management* 36:897-906.
- Zengeya, F. M., A. Murwira, and M. De Garine-Wichatitsky. 2014. Seasonal habitat

selection and space use by a semi-free range herbivore in a heterogeneous savanna landscape. *Austral Ecology* 39:722-731.

Selection of Parturition Sites by Mule Deer in the Blue Mountains

Ecosystem

Danielle R. Walsh, Kelley M. Stewart, Mike J. Wisdom, Mary M. Rowland, Bruce K. Johnson, Darren A. Clark

*D. R. Walsh and K. M. Stewart Natural Resources and Environmental Science,
University of Nevada Reno, Reno, NV, 89557, USA.*

*M. J. Wisdom and M. M. Rowland, U. S. Forestry and Range Sciences Laboratory, 1401
Gekeler Lane, La Grande, OR 97850, USA.*

*B. K. Johnson, and D. A. Clark, Oregon Department of Fish and Wildlife, Forestry and
Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA.*

Abstract

Survival of juveniles in ungulate species often influences population dynamics. Mule deer (*Odocoileus hemionus*) neonates are the most susceptible portion of the population to predation following parturition. Neonates are most vulnerable to mortality following birth because of their limited mobility, lack of energy reserves, and dependence on their mother. Thus, parturient females should select birth sites that increase the likelihood of survival by neonates. We studied birth site selection by mule deer (*Odocoileus hemionus*) at Starkey Experimental Forest and Range, Oregon, during May and June of 2014 and 2015. We located 29 birth sites and determined what habitat characteristics were selected by females compared with two corresponding random locations at a distance of 30 to 130m. We used resource selection functions in a use-availability design to examine selection of birth sites. We created models using a mixed effects logistic regression with the female as the random effect. We used Akaike's Information Criterion adjusted for small sample size (AICc) to evaluate model support. We model averaged the top models with ΔAICc values under 2 to minimize the effect of uninformative parameters. Our best model showed significant selection of birth sites with increased canopy cover, woody debris, and placement on south facing slopes. South facing slopes are typically warmer and xeric, affecting the plant species present. Woody debris increases hiding cover for neonates while canopy cover can influence microsite temperatures as well as provide pockets of light, which increase camouflage of neonates. Parturient mule deer in the Blue Mountains select parturition locations which can deter predation events and reduce the use of the minimal energy reserves of neonates.

Introduction

Individuals select resources to maximize fitness, therefore selection of birth sites is especially important because it directly affects survival of the offspring and fitness of the mother (Fretwell and Lucas 1969, Northrup et al. 2013). Birth sites must provide high quality and quantities of forage for parturient females and provide hiding cover to increase safety of offspring (Rearden et al. 2011). Precociousness of the neonate as well as where it lies on the hider-follower continuum determines the amount of time spent at a birth site, and therefore selection of a birth site (Lent 1974, Ralls et al. 1987, Barbknecht et al. 2011). Ungulate species employ different extents of the hider and follower strategies, creating a continuum instead of a dichotomy, considering variation seen among species as well as populations (Lent 1974, Barbknecht et al. 2011). For example, Caribou (*Rangifer tarandus*), as a follower species, have young that leave the area with their mothers soon after birth (Lent 1974, Pinard et al. 2012). In comparison, mule deer (*Odocoileus hemionus*) may remain at a birth site for 6 hours or more (Johnstone-Yellin et al. 2006) and elk (*Cervus elaphus*) may remain at a site for up to a day (Harper et al. 1967, Barbknecht et al. 2011). While deer and elk may leave a birth site soon after parturition, they remain in the vicinity for multiple days, with neonates continuing to hide unless being fed (Huegel et al. 1985, Vore and Schmidt 2001). Variation among those strategies likely influences the habitat characteristics selected for when choosing parturition sites.

Previous work on birth site selection by ungulates indicates the importance of a site for providing cover for predator avoidance (Bergerud et al. 1984, Barbknecht et al.

2011, Pinard et al. 2012, Roberts and Rubenstein 2014), a stable microclimate for the neonate (Bowyer et al. 1998, Barbknecht et al. 2011), and forage for maternal females (Bowyer et al. 1999). Horizontal and vertical cover both influence predator avoidance by concealing the location of a neonate from predators (Barbknecht et al. 2011), as well as creating pockets of light that aid in the camouflage of the neonate (Bowyer et al. 1999). For ungulates that use the hiding strategy, cover enables the female to move from the birth site out into the open, luring predators away from their concealed young (Lent 1974). Cover also creates a stable microclimate, which is important for neonates who are born with minimal fat reserves and therefore have more difficulty thermoregulating (Robbins 1993, Bowyer 1998). Forage at a birth site supplies maternal females with the nutrients required for the production of milk (Miller 1977, Wade and Schneider 1992). Females that remain at a birth site for extended periods require high quality forage at the birth site to produce milk rich in fat, increasing the likelihood of neonatal survival (Tollefson et al. 2010).

Mule deer produce precocial young with limited energy reserves and high metabolisms (Robbins 1993). Female mule deer move neonates as quickly as 6 hours after birth when mobility is still somewhat limited, but remain in the local vicinity of the birth site for up to a week (Johnstone-Yellin et al. 2006). The short period of time that mule deer remain at the birth site suggests that the provision of adequate forage does not specifically influence selection of the birth site, but rather the likelihood of the neonate surviving in the hours following parturition when they are most vulnerable to predation (Rearden et al. 2011). Nevertheless, forage in the general vicinity is likely to be important for provisioning the offspring over that first week of life. We hypothesized that

heterogeneous cover availability and topography would affect selection of birth sites by mule deer. We predicted that mule deer would select sites with more concealment cover to avoid predation on neonates. In addition, if microclimate is a factor in the selection of birth sites, sites that adequately provide for thermoregulation and energy needs compared to surrounding areas should influence selection.

Materials and Methods

Study Area

Our research was located on the Starkey Experimental Forest and Range (hereafter Starkey), located in north east Oregon, about 65 km from La Grande. Starkey is surrounded by a 2.4m high fence, which prevents the movement of ungulates in and out of the surrounding area. Starkey is divided into multiple study areas, totaling approximately 101.25km². Our research took place in the Main study area, which is approximately 77.6 km². This area provides adequate space for large ungulates to move naturally within their home ranges (McCullough 1979, Stewart et al. 2006). White-tail deer (*Odocoileus virginianus*) and rocky mountain elk (*Cervus canadensis*) are also present within Starkey, along with a suite of predators including black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and mountain lions (*Puma concolor*) (Stewart et al. 2006). Cattle grazed within the Starkey boundary during the summer but were not present during spring when mule deer gave birth. The habitat within Starkey is similar to the surrounding area with conifer forests, shrublands, grasslands, and moderately sloping uplands dissected by drainages (Rowland et al. 1997, Johnson et al.

2000, Stewart et al 2002).

Animal Capture and Handling

We captured adult female mule deer over 2 consecutive winter field seasons, 2013 to 2014 and 2014 to 2015. We captured individuals using baited panel traps (Rowland et al. 1997) and a drop net (Ramsey 1968). We fitted all captured adults with GPS radio collars (4400 and 4500 Series, Lotek Wireless Inc., Newmarket, Ontario, Canada) and determined pregnancy status using a portable ultrasound (Ibex Pro, E. I. Medical Imaging, Loveland, CO). We inserted vaginal implant transmitters (VIT; M3930L, Advanced Telemetry Solutions [ATS], Isanti, MN) in pregnant deer. VITs contained both a temperature and light sensitive switch, which when activated following expulsion from the body, doubled the pulse rate of the transmitted radio signal. The Institutional Animal Care and Use Committee (IACUC) at the University of Nevada, Reno (protocol 00565) and the Starkey in-house IACUC approved all animal handling. All methods were in concordance with guidelines established by the American Society of Mammalogists for care and use of wild mammals in research (Sikes 2011).

We monitored VITs daily during May and June to determine when parturition occurred. We also monitored females that were wearing functioning VHF collars from previous years as part of a larger study. When females expelled VITs or showed behaviors indicative of the presence of a neonate, we searched the area to locate neonates and parturition sites. We used GPS locations from collars collected during the winter of 2014 and into 2015 to identify additional birth sites that were not located the previous

summer. We did this by going to the GPS locations collected during the days previous to our discovery of a neonate and determined if any were clearly used birth sites. We identified birth sites based on characteristics that indicated parturition had occurred, including the presence of a neonate or VIT, blood, placenta, large quantities of insect activity, a moist area, fecal pellets, tracks, smashed vegetation, or licked ground. Generally birth sites were oval shaped and larger than a typical deer bed.

Habitat Data Collection

We found 29 mule deer birth sites during the summers of 2014 ($n = 13$) and 2015 ($n = 16$) and recorded their Universal Transverse Mercator (UTM) coordinates. We used ArcGIS (ArcGIS 10.2; Environmental Systems Research Institute [ESRI], Redlands, CA) to generate 2 random points between 30 and 130m from each used birth site for comparison of used and random habitat characteristics. Random points represented locations with habitat characteristics that were available for selection by a parturient female. The distance between random and birth sites prevented overlap in measurements and was a reasonable distance for comparison, representing an area that a female may have selected to give birth.

We quantified habitat characteristics at used and random sites to determine what characteristics parturient mule deer selected. Because females move neonates within hours of birth we did not believe nutritional quality of the vegetation available for consumption by an adult would influence selection of birth sites, therefore we did not sample vegetation or determine the nutritional quantity of individual plant species present at a site.

Nevertheless, vegetation quality in the surrounding area likely influenced selection at a larger scale. Within a 15 m radius of each birth site we determined the number of trees taller and shorter than 2 m, the number of shrubs taller or shorter than 1 m, and visually estimated the percent of woody debris present. We determined the percent of overstory cover directly above birth and random sites by calculating the mean of 4 densitometer readings facing the 4 cardinal directions (Lemmon 1957). Ungulate species have been documented distracting predators away from neonates; therefore, we measured the distance to the nearest transition zone between dense and open vegetation, which represented the distance a female would need to move to be clearly visible to a predator (Severinghaus and Cheatum 1956, Altmann 1963, Lent 1974). We measured the distance to the edge of vegetation transition with a meter tape when it was within 100 m of a site, and used a vegetation layer in ArcGIS to determine the edge when it was farther (LANDFIRE 2015). At the birth site, we estimated horizontal cover using a cover-pole (Griffith and Youtie 1988). Cover-poles were 2 meters in height and divided into 8 sections of 25 cm lengths. We placed the cover pole at the center of a site and determined the percentage of obscured area in each of the eight sections from a distance of 15 meters. We averaged the percentage covered across readings from each of the four cardinal directions. Additionally, we averaged readings for the lowest 5 sections (1.25 m), representing the amount of cover that would conceal a standing adult female. We used a 10 m² pixel digital elevation model (DEM) maintained by the Oregon Department of Fish and Wildlife and the United States Forest Service (Rowland et al. 1998) to determine the aspect of all locations in ArcGIS. Because aspect is circular data we transformed it using the sine and cosine functions to more easily interpret selection for east to west facing

slopes (sine) and north to south facing slopes (cosine) (Zar 1999).

Statistics

We created resource selection functions (RSFs) with a use-availability design to determine habitat selection by parturient females (Manly et al. 2002, Johnson et al. 2006, Beyer et al. 2010, Long et al. 2014). We conducted a mixed-effects logistic regression with a random effect of individual and a response variable of used (1) or random (0) locations, to model our RSFs using the lme4 package in Program R v. 3.1.2 (Gilles et al. 2006, Bolker et al. 2009, Zuur et al. 2009, R Development Core Team 2011, Long et al. 2014). We modeled all appropriate habitat characteristics as a quadratic to determine if there was a non-linear affect (Neter et al. 1996), but none were significant. We standardized all variables to unit variance prior to analysis, which allowed for direct comparison of parameter estimates (Neter et al. 1996, Long et al. 2014, Stewart et al. 2015). We tested for collinearity and exchanged highly correlated variables to determine which resulted in the best model, removing the variable with the least amount of influence on our models (Long et al. 2014, Stewart et al. 2015). We used the “MuMIn” package in R v3.1.2 to run all possible models (R Development Core Team 2011). This package sorted all models based on Akaike’s Information Criterion corrected for small sample size (AICc), AICc weights, and delta (Δ) values. We averaged top models with Δ AICc value < 2 , to reduce the effect of uninformative parameters (Burnham and Anderson 2002, Arnold 2010, Blum et al. 2015). In general, positive standardized parameter estimates indicate selection for a habitat characteristic while negative values indicate avoidance, with the exception of distance to

the edge of a vegetation transition, which when negative indicates selection of a location closer than expected, while a positive value indicates a location farther from expected (Stewart et al. 2002, Long et al. 2014). Negative values for cosine of aspect represent selection for south facing slopes while positive values represent selection for north facing slopes. Negative values for sine of aspect represent selection for west facing slopes and positive values represent selection for east facing slopes (Zar 1999).

Results

We captured and processed 28 mule deer over the course of two winters. We captured 22 individuals between December 4th 2013 and February 21nd 2014. We recaptured and processed 13 individuals as well as 6 new individuals between November 18th, 2014 and February 9th 2015. We included 29 birth sites in our analysis (Table 1). There were 5 competitive models of resource selection (Δ AICc < 2, Table 2). All competitive models included canopy cover, cosine of aspect, and percent of woody debris. Additionally, the 2nd and 5th models included distance to edge, the 3rd and 5th included shrubs less than 1 meter tall, and the 4th included sine of aspect (Table 2). After averaging our top models, our results indicated selection for canopy cover ($\beta = 0.7525$ SE = 0.3073), percent of woody debris ($\beta = 0.9358$ SE = 0.4690), and cosine of aspect ($\beta = -0.5794$ SE = 0.2878) (Fig. 1). All other parameters were not significant with 95% confidence intervals overlapping 0. Parameter estimates indicate strong selection for birth sites with increased woody debris and canopy cover as well as south facing slopes (Figs. 1 & 2).

Discussion

Our results indicated that mule deer selected for more woody debris and overstory cover at birth sites, supporting our hypothesis that concealment cover would be important in selection of birth sites. Both of those habitat characteristics have the ability to camouflage neonates, potentially decreasing the likelihood of predation. Overstory cover creates pockets of light and shadows, which in combination with the pelage, size, and lack of smell of a newly born neonate, can make detection by predators difficult (Bowyer et al. 1999). Woody debris, such as downed logs and stumps, also allows for camouflage as well as hiding cover.

We also predicted that the microclimate would affect selection of the birth site. Overstory cover and a south facing slopes, two of the habitat characteristics significant in our best model, affect microclimates by creating pockets of light and shade. In addition, this heterogeneity in exposure to solar radiation means a neonate has the ability to move a very short distance, potentially as small as inches, to accommodate thermoregulatory needs by moving into or out of direct sunlight (Bowyer et al. 1999). Neonates are born with minimal energy reserves so the ability to regulate temperature by physically moving locations to take advantage of solar radiation or shade is important in limiting energy use (Bowyer et al. 1998). South facing slopes in northern latitudes are exposed to solar radiation for longer periods than north facing slopes. This increased exposure increases the rate of snowmelt in the spring as well as increasing the timing of green-up, creating a more xeric environment with different vegetation types (Holland and Steyn 1975). These warmer and drier slopes would therefore be ideal for location of birth sites in the spring

and early summer because they provide more stable microclimates. In ungulate species, the days immediately following birth are when mortality is generally the highest and most variable (Gaillard et al. 2000). By selecting birth sites on south facing slopes and with appropriate cover, parturient females likely selected for temperature regulation and concealment from predators, potentially improving the likelihood of neonate survival.

Acknowledgements– We appreciate the assistance of T. Allen, B. L. Dick, S. L. Findholt, R. Kennedy, B. Regan, and D. Rea for their support and field assistance on the project. M. R. Blum and T. S. Dilts provided valuable GIS and statistical assistance. We would also like to thank C. Borum, and B. Naylor for technical assistance. This research was funded by the Oregon Department of Fish and Wildlife and USFS Federal Aid for Wildlife Restoration W-87-R with in-kind support from the U. S. D. A. Forest Service.

References

- Altmann, M. 1963. Naturalistic studies of maternal care in moose and elk. – In: Reingold, H. L. (ed.), *Maternal behavior in mammals*. Wiley, pp. 233-253.
- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike' information criterion. – *J. Wildl. Manage.* 74: 1175-1178.
- Barbknecht, A. E. et al. 2011. Elk parturition site selection at local and landscape scales.– *J. Wildl. Manage.* 75:646-654.
- Bergerud, A. T. et al. 1984. Antipredator tactics of calving caribou: dispersion in mountains. –*Can. J. Zool.* 65:1566-1575.

- Beyer, H. L. et al. 2010. The interpretation of habitat preference metrics under use-availability designs. – *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365: 2245-2254.
- Blum, M. E. et al. 2015. Effects of large-scale gold mining on migratory behavior of a large herbivore. – *Ecosphere* 6: 74.
- Bolker, B. M. et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. – *Trends Ecol. Evol.* 24: 127-135.
- Bowyer, R. T. et al. 1998. Habitat selection by neonatal Black-tailed deer: Climate, Forage, or risk of predation? – *J. Mammal.* 79: 415-425.
- Bowyer, R. T. et al. 1999. Birth-site selection by Alaskan moose: strategies for coping with a risky environment. – *J. Mammal.* 80: 1070-1083.
- Burnham, K. P. and Anderson, D. R. 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*, second ed. – Springer.
- Cook, R. S. et al. 1971. Mortality of white-tailed deer fawns in south Texas. – *J. Wildl. Manage.* 35: 47-56.
- Fretwell, S. D. and Lucas, H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. – *Acta Biotheor.* 19: 16-36.
- Gaillard, J.M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – *Annu. Rev. Ecol. Syst.* 31: 367-393.
- Gillies, C. S. et al. 2006. Application of random effects to the study of resource selection by animals. – *J. Anim. Ecol.* 75: 887-898
- Griffith, B. and Youtie, B. A. 1988. Two devices for estimating foliage density and deer hiding cover. – *Wildl. Soc. Bull.* 16: 206-210.
- Harper, J. A. et al. 1967. The status and ecology of the Roosevelt elk in California. *Wildl.*

Monogr. 16.

Holland, P. G. and Steyn, D. G. 1975. Vegetational Responses to latitudinal Variations in Slope Angle and Aspect. – *J. Biogeogr.* 2: 179-183.

Huegel, C. N. et al. 1985. Use of doe behavior to capture white-tailed deer fawns. – *Wildl. Soc. Bull.* 13: 287-289.

Johnson, B. K. et al. 2000. Resource selection and spatial separation of mule deer and elk during spring. – *J. Wildl. Manage.* 64: 685-697.

Johnson, C. J. et al. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. – *J. Wildl. Manage.* 70: 347-357.

Johnstone-Yellin, T. L. et al. 2006. Effectiveness of Vaginal Implant Transmitters for locating Neonatal mule deer fawns. – *Wildl. Soc. Bull* 34: 338-344.

LANDFIRE. 2015. National Existing Vegetation Type Layers. U.S. Department of Interior, Geological Survey. <http://gisdata.usgs.net/website/landfire/>.

Lemmon, P.E. 1957. A new instrument for measuring forest overstory density. – *J. For.* 55: 667-668.

Lent, P. C. 1974. Mother-infant relationships in ungulates. – In: Geist, V. and Warner F. (ed.), *The behavior of ungulates and its relation to management*. International Union for the Conservation of Nature, pp 14–55.

Long, R. A. et al. 2014. Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. – *Ecol. Monogr.* 84: 513-532.

Manly, B. F. J. et al. 2002. *Resource selection by animals: statistical analysis and design for field studies*. Second ed. – Kluwer.

- McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a K selected species. – Univ. of Michigan Press.
- Millar, J. S. 1977. Adaptive features of mammalian reproduction. – *Evolution* 31: 370–386.
- Neter, J. M. et al. 1996. Applied linear statistical models, 4th edition. – McGraw-Hill.
- Northrup, J. M. et al. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. – *Ecology* 94: 1456-1463.
- Pinard, V. et al. 2012. Calving Rate, Calf Survival Rate, and Habitat Selection of Forest-Dwelling Caribou in a Highly Managed Landscape. – *J. Wildl. Manage.* 76: 189-199.
- R. Development Core Team. 2011. R Development Core Team, R: a Language and Environment for Statistical Computing. – R Foundation for Statistical Computing.
- Ralls, K. et al. 1987. Mother-young relationships in captive ungulates: spatial and temporal patterns. – *Zoo Biol.* 6: 11–20.
- Ramsey, C. W. 1968. A drop-net deer trap. – *J. Wildl. Manage.* 32:187-190.
- Rearden, S. N. et al. 2011. Birth-site selection and predation risk of Rocky Mountain elk. – *J. Mammal.* 92:1118-1126.
- Robbins, C. T. 1993. Wildlife feeding and nutrition. Second edition. – Academic Press.
- Roberts, B. A. and Rubenstein, D. I. 2014. Maternal tactics for mitigating predation risk during the postpartum period in Thomson's gazelle. – *Behaviour* 151: 1229–1248.
- Roffe, T. J. 1993. Perinatal mortality in caribou from the Porcupine herd, Alaska. – *J. Wildl. Dis.* 29: 295-303.
- Rowland, M. M. et al. 1997. The Starkey project: history, facilities, and data collection

- methods for ungulate research. U.S. Department of Agriculture Forest Service
Technical Report PNW-GTR-396: 1–62.
- Severinghaus, C. W. and Cheatum, E. L. 1956. Life and times of the white-tailed deer. In:
Tayler, W. P. (ed.), The deer of North America. Stackpole Co. and Wildl.
Manage. Inst., pp. 57-186.
- Sikes, R. S., et al. 2011. Guidelines of the American Society of Mammalogists for the use
of wild mammals in research. – J.Mammal. 92: 235-253.
- Smith, J. B. et al. 2014. Disease and Predation: Sorting out Causes of Bighorn Sheep
(*Ovis Canadensis*) Decline. – PLoS ONE 9.
- Stewart, K. M. et al. 2002. Temporal spatial distributions of elk, mule deer, and cattle:
resource partitioning and competitive displacement. – J. Mammal. 83: 229-244.
- Stewart, K. M. et al. 2006. Herbivore optimization by North American elk: Consequences
for theory and management. – Wildl.Monogr. 167: 1-24.
- Stewart, K. M. et al. 2015. Sexual segregation in North American elk: the role of density
dependence. –Ecol. Evol. 5: 709-721.
- Tollefson, T. N. et al. 2010. Influence of summer and autumn Nutrition on body
Condition and Reproduction in lactating Mule Deer. – J. Wildl. Manage. 74: 974-
986.
- Vore, J. M. and Schmidt, E. M. 2001. Movements of female elk during calving season in
northwest Montana. –Wildl. Soc. Bull. 29: 720-725.
- Wade, G. N. and Schneider, J. E. 1992. Metabolic fuels and reproduction in female
mammals. – Neurosci. Biobehav. Rev. 16: 235–272.
- Zar, J. H. 1999. Biostatistical Analysis. 4th ed. – Prentice-Hall.

Zuur, A. F. et al. 2009. *Mixed Effect Models and Extensions in Ecology with R.* –
Springer-Verlag.

Table 1. Descriptive statistics of habitat variables at used birth sites and random locations in our resource selection functions from Starkey Experimental Forest and Range, OR, USA, 2014 - 2015.

Variable	Birth Sites (<i>n</i> = 29)				Random Sites (<i>n</i> = 58)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
% Woody Debris	10.10	12.86	0	45	2.84	5.44	0	35
Shrubs < 1m	219.72	378.77	0	1953	189.67	334.77	0	1632
Shrubs >1m	11.52	36.29	0	191	9.81	34.98	0	212
Trees < 2m	65.14	82.89	0	408	46.31	58.07	0	228
Trees > 2m	112.45	135.45	3	663	66.10	82.47	0	384
Canopy Cover (%)	61.11	26.86	2.9	100	35.83	32.34	0	97.1
Dist to Edge (m)	22.40	23.29	0	93	13.88	27.12	0	143
Cover Pole (Sections 1-5,%)	57.99	29.92	3	100	36.54	31.76	0	100
Sine of Aspect	-0.16	0.73	-1.00	0.99	0.14	0.74	-1.00	1.00
Cosine of Aspect	-0.33	0.61	-0.99	0.95	0.11	0.66	-1.00	1.00

Table 2. Top models ($\Delta \text{AICc} < 2$) in our resource selection function for birth site selection ($n = 29$) at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015.

Model	DF	logLik	AICc	ΔAICc	ω_i
Int + Canopy + Cosine Aspect + %Debris	5	-41.978	94.70	0.00	0.0898
Int + Canopy + Cosine Aspect + %Debris + Dist to Edge	6	-41.140	95.33	0.63	0.0655
Int + Canopy + Cosine Aspect + %Debris + Shrubs <1m	6	-41.300	95.65	0.95	0.0558
Int + Canopy + Cosine Aspect + %Debris + Sin of Aspect	6	-41.526	96.10	1.40	0.0445
Int + Canopy + Cosine Aspect + %Debris + Dist to Edge + Shrubs <1m	7	-40.478	96.37	1.68	0.0389

Figure 1. Standardized parameter estimates obtained from our resource selection functions for birth site selection at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015. Parameters represent habitat characteristics within a 15 meter radius of a birth site ($n = 29$) compared with random sites ($n = 58$). Error bars represent 95% confidence intervals and values that overlap 0 are non-significant. Estimates > 0 represent selection for a resource while estimates < 0 represent avoidance. For sine aspect values < 0 represents east facing slopes and values > 0 indicate west facing slopes. Estimates of cosine aspect > 0 represent selection for north facing slopes and < 0 south facing slopes.

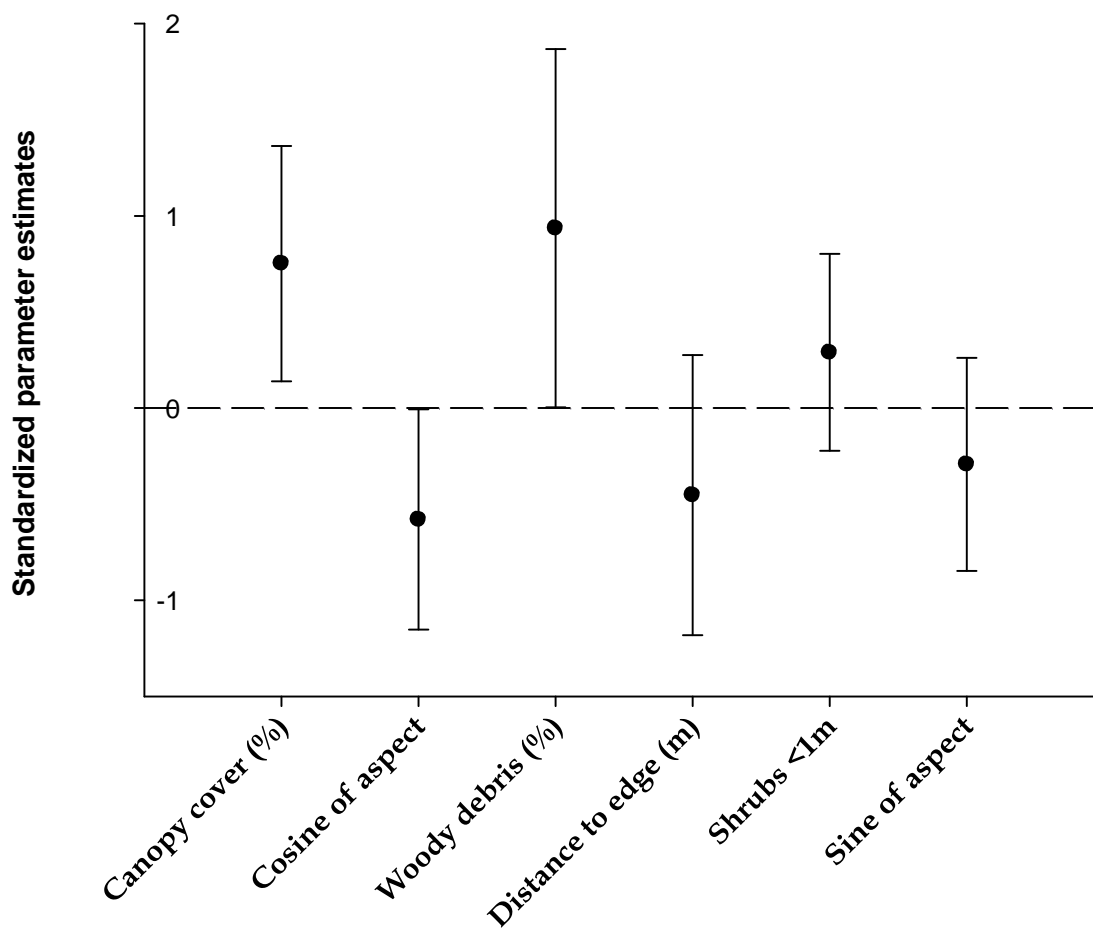
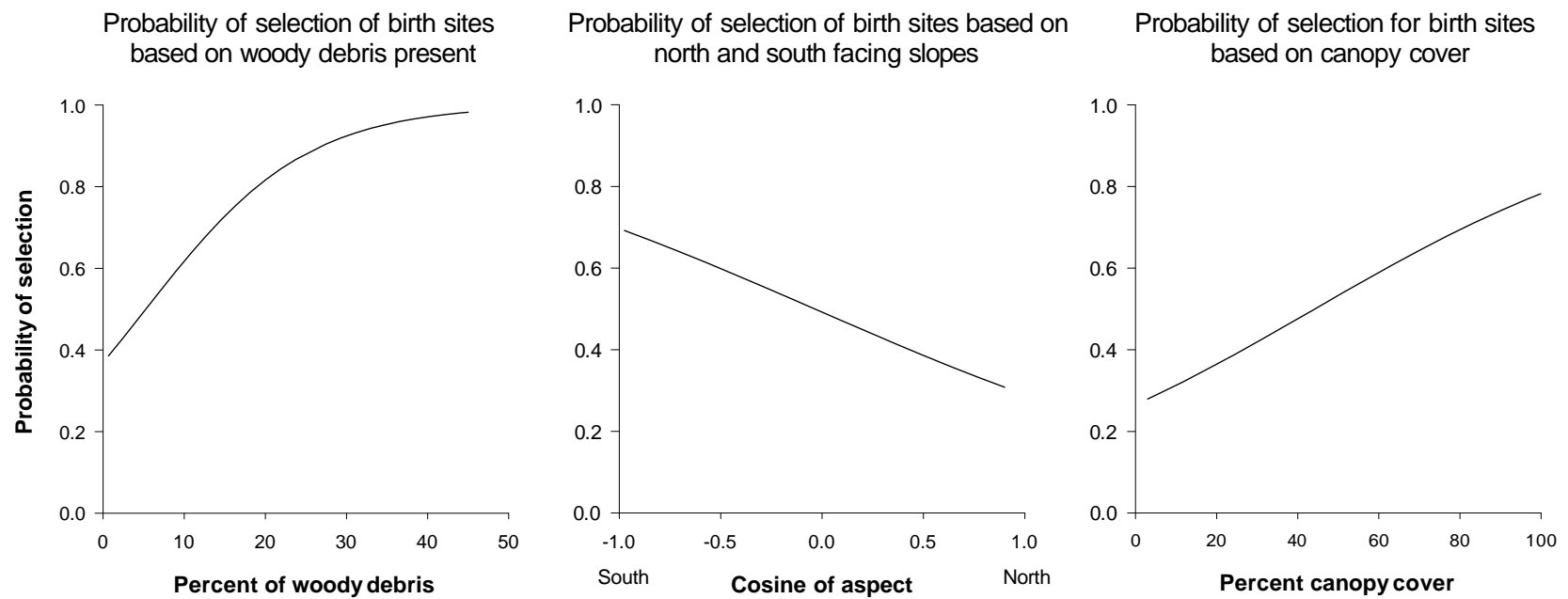


Figure 2. Estimates of probability of selection for the percent of woody debris, cosine aspect (south to north facing slopes), and percent canopy cover by adult mule deer at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015. Parameter estimates were back transformed using the logit-link function to generate effect plots.



Department of Natural Resources and Environmental Science
University of Nevada, Reno
1664 N. Virginia Street Reno, Nevada 89557, USA
dwalsh@cabnr.unr.edu

Neonate Survival of Mule Deer

Neonate survival of mule deer: physical, environmental, and behavioral effects

Danielle R. Walsh*, Kelley M. Stewart, Mike J. Wisdom, Mary M. Rowland, Bruce K. Johnson, Darren A. Clark

Natural Resources and Environmental Science, University of Nevada Reno, Reno, NV, 89557, USA.(DRW, KMS)

U. S. Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA.(MJW, MMR)

Oregon Department of Fish and Wildlife, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA.(BKJ, DAC)

ABSTRACT

Population dynamics of large herbivores are influenced by juvenile survival and recruitment. Juvenile mortality is generally highest between birth and weaning, with causes including predation, disease, and malnutrition. Underlying factors can influence these proximate causes, increasing susceptibility of neonates to mortality. We were interested in how maternal characteristics, climate, changes in spring greenup, physical characteristics at birth, and habitat characteristics at birth sites affected survival of neonatal mule deer (*Odocoileus hemionus*) at the Starkey Experimental Forest and

Range, Oregon, USA. We estimated neonate survival from birth to 120 days, during 2014 and 2015. We used the nest survival module in program MARK to estimate survival, because it allowed for variation in monitoring of individuals. Changes in neonate survival were best represented by daily variation for the first 30 days of life and weekly thereafter, plateauing on day 120 at about a 99% daily survival rate. Birth sites on south facing slopes had a drastic effect on neonatal survival, with a survival rate difference on day one of life of 12.2% between birth sites located on directly south compared with north facing slopes. South facing slopes at Starkey are warmer and drier than north facing slopes, causing difference in vegetation available to deer as well as potentially creating a suitable thermal environment. No other models were competitive indicating that the birth site selected by a maternal female greatly influenced survival of her neonate compared to other factors.

mule deer, *Odocoileus hemionus*, neonate, survival

*Correspondent: Danielle R. Walsh

INTRODUCTION

Mule deer (*Odocoileus hemionus*) are a generalist species inhabiting most of the western United States throughout a variety of habitats (Wallmo 1981), but populations have been declining during recent decades (Bleich and Taylor 1998; Unsworth et al. 1999; Bishop et al. 2009). Reasons for population declines have included habitat loss and fragmentation, disease, predation, competition, and weather severity (Anthony 1976; Bishop et al. 2009;

Dulberger et al. 2010; Hurley et al. 2011). In ungulate populations, adult survival is generally high and stable while juvenile survival is more variable (Gaillard et al. 1998). Although predation is normally identified as the leading cause of juvenile mortality in mule deer populations (Bishop et al. 2009; Monteith et al. 2014; Shallow et al. 2015), effects of climate (Anthony 1976), maternal characteristics (Monteith et al. 2014), forage quality (Bishop et al. 2009), physical characteristics (Carstensen et al. 2009), and behavior (Lent 1974) also may increase susceptibility to mortality.

Changes in female body condition are influenced by winter severity (Mautz 1978), quality and quantities of forage (Tollefson et al. 2010), and provision of young to weaning the previous year (Morano et al. 2013). The third trimester of pregnancy and lactation are the most energetically demanding periods for female ungulates, coupling physical condition and reproduction (Parker et al. 2009). Thus, physical condition of females can affect the likelihood of pregnancy (Morano et al. 2013), fetal counts (Monteith et al. 2010), and ability to carry a fetus to term (Russell et al. 1998). Additionally, body condition of the mother can affect physical characteristics of neonates at birth and the quality of milk a female can produce during lactation (Landete-Castellejos et al. 2005). Birth characteristics, such as weight and sex, have previously been shown to affect neonatal survival in elk (Bender et al. 2002), moose (Keech et al. 2000), reindeer (Bårdsen et al. 2014), white-tail deer (Carstensen et al. 2009), and mule deer (Monteith et al. 2014). Birth characteristics can also have long-term effects on growth (Albon et al. 1987), recruitment (Clutton-Brock et al. 1987), and reproduction (Green and Rothstein 1993).

Energy expenditure and depletion of energy stores can lead to mortality when

energy requirements are not maintained above survival thresholds (Parker. et al. 2009). Fluctuations in temperature and precipitation can shift individuals out of thermal neutral zones, requiring the use of energy for thermoregulation. Parker (1989) reported that energy costs for black-tailed deer (*Odocoileus hemionus columbianus*) increased by 28% after 5 hours in rainfall during cool summer temperatures. Therefore, neonates born with minimal energy reserves are particularly susceptible to mortality when a variable climate requires increased energy use. Females may use previous experience to fulfill their needs and those of their offspring through selection of resources (Gillingham and Bunnell 1989). Experience and knowledge of the landscape differ among individuals creating the potential for variation in survival within a population. Maternal knowledge and experience should increase their survival and that of their neonates to increase fitness.

We were interested in what factors affect survival of neonatal mule deer in northeast, Oregon. We tested multiple hypotheses for what factors affect neonatal survival in mule deer based on changes in vegetation, climate, maternal effects, physical characteristics at birth, and characteristics of birth sites selected by maternal females. Because thermoregulation is costly for neonates born with limited energy reserves, we hypothesized that daily temperature and precipitation may affect survival of neonates by increasing thermoregulatory costs. Lactation requires large energy expenditure by females therefore we hypothesize parturition will occur during spring green-up and before the fastest rate of change in vegetation to take advantage of the highest quality and quantities of forage, allowing females to produce high quality milk for neonates. Because variation among maternal females can cause variation in survival we hypothesized that mature females with more experience as well as better body condition would produce

neonates with higher survival rates. Because they have more time to grow and obtain energy stores before autumn, we hypothesized that neonates born earlier, with larger bodies and in better condition would have higher survival rates. Finally, we hypothesized that characteristics of birth sites selected by maternal females will increase neonatal survival, in turn increasing maternal fitness.

MATERIALS AND METHODS

Study Area.—We conducted our research from 2013 to 2015 at Starkey Experimental Forest and Range (hereafter Starkey), located approximately 65 km west of La Grande, OR. Starkey is located in the Blue Mountains ecoregion and elevations range from 1,120 to 1,500 m (Rowland et al. 1997). Starkey supports a mosaic of forests and grasslands dominated by ponderosa pine (*Pinus ponderosa*), douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*) and lodgepole pine (*Pinus contorta*) communities on moderately sloping uplands dissected by drainages (Rowland et al. 1997, Stewart et al. 2002; Long et al. 2009). Along with mule deer, rocky mountain elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) are present within Starkey (Rowland et al. 1997). Predators at Starkey include black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and mountain lions (*Puma concolor*) (Stewart et al. 2006). Cattle are grazed within Starkey beginning June 15th to October 15th each year (Long et al. 2009).

Research has been ongoing at Starkey since 1989 with yearly captures of both mule deer and elk, creating large, long-term data sets for two ungulate species (Rowland et al. 1997). Starkey is surrounded by a 2.4m fence, and additional fencing divides Starkey into multiple study areas and prevents immigration and emigration of large herbivores (Rowland et al. 1997). We conducted the majority of our research in the Main

study area (77.6 km²) with the addition of Barn Pasture (0.489 km²) during the winter (Fig. 1). During winter, some deer have the ability to enter barn pasture from the main study area, where supplemental food is provided in the form of ad libitum alfalfa hay and pellets (15% crude protein, 3.2% crude fat, NCASI HE 7-95 Elk feed, CHS Inc. Sioux Falls, SD; Rowland et al. 1997). Other individuals remain in the Main study area and did not receive supplemental feeding. During the spring deer return to the Main study area where they are no longer supplementally fed (Rowland et al. 1997). This treatment was designed to create variation among individuals in body condition, which was incorporated into our analysis.

Animal capture and handling.—We captured adult mule deer using panel traps (Rowland et al. 1997) and drop-nets (Ramsey 1968) baited with hay from November to February during the winters of 2013 to 2014 and 2014 to 2015. We captured 22 female deer (≥ 1.5 years old) during the first winter and recaptured 13 the second year, with the addition of 6 new individuals. After capturing individuals we fitted them with Lotek GPS collars (4400 and 4500 Series, Lotek Wireless Inc., Newmarket, Ontario, Canada), assessed pregnancy status using a portable ultrasound (Ibex Pro, E. I. Medical Imaging, Loveland, CO; Stephenson et al. 1995), and inserted vaginal implant transmitters (VIT; M3930L, Advanced Telemetry Solutions [ATS], Isanti, MN) to monitor for parturition. Each VIT had a light and temperature sensor, that when activated, increased the pulse rate of the VHF signal with an alternating binary code representing the length of time since expulsion, indicating that parturition occurred (Advanced Telemetry Solutions [ATS], Isanti, MN). Individuals wearing working collars that were captured the year before our research, or individuals not recaptured the second year, were monitored daily

for parturition along with new individuals.

Following capture, we measured body mass, metatarsus length, chest girth, jaw length, and total body length of all individuals. Additionally, we assigned body condition scores to each individual using palpation, and we measured depth of rump fat using ultrasonography as a quantitative value for body condition (Cook et al. 2007). We determined the age of each individual as a juvenile (\approx 6 months old), yearling (\approx 1.5 years old), or adult (2.5+ years old). Individuals were marked with unique metal strap tags placed in each ear, which were used as identification markers during recaptures (Rowland et al. 1997).

During May and June of 2014 and 2015, we captured neonates between 0 to 4 days old with most individuals caught during their first day of life (0.574 ± 0.853). After the 5th day of life, neonates were more mobile and became difficult to capture. Each neonate received an expandable very high frequency (VHF) radio collar with a mortality sensor (M4210; Advanced Telemetry Solutions, Isanti, MN, USA). Upon capture we determined the sex, and evaluated condition of umbilical cord and hoof growth as a sign of age (Haugen and Speake 1958), and measured the metatarsus, chest girth, and weight. We initially attempted to use hoof growth as described by Haugen and Speake (1958) to estimate age but a distinct hoof growth line was not always obvious, so we were not confident using the measurement as a predictor of age. We knew the ages of some individuals based on the time a VIT was expelled or the state of a neonate when it was found (wet or dry umbilical cord, white hooves, etc.) We regressed body mass against known ages of neonates and applied the slope to predict unknown ages using mass at capture (Monteith et al. 2014).

We searched for and handled all neonates as quickly as possible before returning them to their original location to reduce the amount of disturbance to the female and her young (Livezey 1990). All individuals handling neonates wore gloves and washed all clothing and handling gear in scent-free detergent to minimize handling as a cause of abandonment. The Institutional Animal Care and Use Committee (IACUC) at the University of Nevada, Reno (protocol 00565) and the Starkey in-house IACUC approved all animal handling. All methods were in concordance with guidelines established by the American Society of Mammalogists for care and use of wild mammals in research (Sikes 2011).

We monitored survival of neonates daily for the first two months and weekly thereafter. When mortality occurred, we located the carcass as quickly as possible and determined the cause of mortality when identifiable. When a carcass was fresh, we collected tissue sample or removed the entire carcass for transport to the Oregon State University Veterinary Diagnostic Laboratory to determine the cause of mortality via necropsy.

MODEL PARAMETERS.—We compiled values for climate and vegetation attributes to determine their effect on neonate survival (Table 1). We obtained values for daily precipitation from the National Atmospheric Deposition Program (2015) collected from a weather station (OR 18) located at Starkey. Also from the Starkey weather station, we obtained temperature data recorded every half hour using a HOBO temperature logger (Onset Computer Corporation, Bourne, MA, USA). We used the temperature data to determine mean daily temperatures for inclusion in our models.

We used 8-day composite normalized difference vegetation index (NDVI) values

generated from MODIS satellite imagery to determine the start date and the peak of vegetation green-up during the spring (Climate Engine 2015; Bischof et al. 2012; Hird and McDermid 2009). The dates used to represent an NDVI composite are the date at which the composite began, i.e. day 1 of 8. We determined the NDVI value for every pixel in Starkey from February to August. Because we were interested in changes in understory vegetation quality, we eliminated pixels that were comprised mostly of dense tree stands or open grassy areas (> 30%). After identifying 38 appropriate 500 m pixels, we averaged the composite values for each 8-day period and determined when values began to increase during the spring as well as decrease, representing the start and peak of spring green-up (Hird and McDermid 2009). We determined the instantaneous rate of green-up (IRG) during the spring by calculating the first derivative of our NDVI values (Bischof et al. 2012). We quantified the peak IRG for both years, representing when the greatest rate of change to vegetation greenness occurred (Bischof et al. 2012). To determine how changes in vegetation affected each neonate, we calculated the difference in days between the birth of a neonate and the beginning of spring green-up, the peak of green-up, and the peak of IRG for each year (Table 1).

Our previous analysis determined that female mule deer selected increased overstory cover, south facing slopes, and woody debris at birth sites (see Chapter 1). We included these values in our survival analysis to determine if habitat characteristics selected for birth sites affected survival of neonates (Table 1). We calculated ingesta free body fat (IFBF) from body condition scores and rump fat thickness for adult females using equations developed by Cook et al (2010; Table 1). Because we collected the measurements for calculating IFBF over a 4 month period, we wanted to determine if

there was a relationship between IFBF and the date measurements were taken. We used linear regression to address this separately for supplementally fed and not fed individuals because the rate of change in condition likely differed as a function of supplemental feeding over winter (Neter et al. 1996). Neither regression was significant, however, so in our models we added a categorical variable representing supplemental feeding in case it affected neonate survival. Additionally we included IFBF based on measurements collected during capture.

During initial capture at Starkey during winter, the age of an individual is determined (i.e., 6 months old, 1.5 years, 2.5+ years; Rowland et al. 1997). This classification has been used during all past capture years at Starkey. We tabulated the minimum age of maternal females at parturition based on their age when first captured at Starkey. Thus, individuals initially captured as adults were given the age of 2.5 years, although they may have been older. Young of the year or 1-year old individuals were aged as such. Recaptured individuals that were identified by ear tags were aged based on age at initial capture plus time between captures. For example, an individual first captured at 1 year of age, then recaptured 5 years later in this study was aged as a 6-year old. Individuals aged at 2.5 at initial capture and recaptured after 5 years were aged as 7.5 years of age, as a minimum age. Individuals captured as adults may have been older but we could not accurately determine their known ages. The use of minimum ages in our analysis was conservative because we did not have a complete knowledge of all adult ages.

While handling neonates we measured body mass, metatarsus length, chest girth. We used metatarsus length and chest girth to do a principle components analysis (PCA)

representing a metric of body size for a neonate. We used linear regression of the PC scores (X) against body mass (Y) and used the residuals as an index of body condition at birth (Neter et al. 1996). Individuals in better condition for their size had positive residuals, while those in poorer condition had negative residuals. We used both the PCA results and regression residuals in our survival models to determine which had a stronger influence on survival (Table 1). We standardized birth dates to the mean birth date of neonates and included them in our models to determine if the timing of birth affected survival. We included sex in our models to determine if survival differed between male and female neonates.

STATISTICAL ANALYSIS.—We used the nest-success module in Program MARK (Version 8.0; White and Burnham 1999) to estimate daily survival rates of neonates. This method allowed us to account for daily monitoring of survival of individuals for the first two months and weekly monitoring thereafter (Dinsmore et al. 2002; Hupp et al 2008; Blomberg et al. 2014). We modeled daily changes in neonatal survival for the first 120 days of life, ensuring we determined survival to weaning (Short 1981). We standardized to unit variance all parameters before inclusion in survival models (Neter et al. 1996). To determine how survival of neonates changed over the 120 days we modeled different age trends, which allowed survival to vary across different lengths of time (daily, weekly, monthly) and in different combinations (daily for 30 days and then weekly for 90 days; Monteith et al. 2014). We retained our best age trend in all subsequent models and determined the influence of individual covariates on daily survival of neonates. Highly correlated variables were not used within the same model (> 0.70). We chose our best model based on Akaike's Information Criterion corrected for small sample size (AICc),

Δ AICc values, and AIC weights (Burnham and Anderson 2002, Arnold 2010). We used AICc values to determine which age trend best represented the changes in neonate survival. We considered a parameter significant when 95% confidence intervals did not overlap 0.

RESULTS

Mean monthly temperature from May to October was between 9.75 and 20.98 °C for both years (Fig. 2). Mean precipitation from May to October was between 0.25 and 3.81mm (Fig. 2). NDVI values indicated that green-up began the week of March 6th for both years but during 2014 the peak was June 26th and in 2015 the peak was May 25th (Fig.3). Peak IRG in 2014 occurred April 15th and in 2015, May 17th (Fig. 3). During 2014 neonates were born a mean 25.54 ($SD = 5.72$) days before the peak of NDVI and 46.46 ($SD = 5.72$) days after the IRG peak. In 2015 neonates were born 11.14 ($SD = 7.57$) days after the peak of NDVI and 15.14 ($SD = 7.57$) days after the IRG peak.

In 2014 we captured 14 female and 12 male neonates and in 2015 we captured 11 females and 10 males. Over the course of the study, we captured 17 singletons, 13 sets of twins, and one set of triplets. We determined unknown birth dates of neonates using the slope of the relationship ($P = <0.0001$, $R^2 = 0.717$) between 37 known birth dates and weights, resulting in a mean birth date of May 31st ($SD = 5.7$ days) in 2014 and June 5th ($SD = 8.44$ days) in 2015. IFBF values and mean minimum ages of maternal females were similar between years (Table 2). During the first winter 6 out of 16 maternal females received supplemental food and during the second year 5 out of 16 females were fed.

The first principle component for neonate body size (PC1) explained 87% of the

variation. Because the variables associated with PC1 loaded similarly in the first eigenvector, we used PC1 scores in further analysis as an index of body size. Mean PC1 scores were lower but not significantly ($P = 0.112$) in 2014 then 2015 at -0.28 ($SD = 1.34$) and 0.34 ($SD = 1.27$), indicating somewhat smaller body sizes in 2014 (Table 2). We used residuals from the regression analysis of body mass and PC1 ($R^2 = 0.655$, $P < 0.001$) as an index of body condition in further analysis. During 2014 the mean body condition of neonates was lower than expected for a given body size while in 2015 neonates were generally in better condition for their size (Table 2).

SURVIVAL MODELS.—We modeled the effect of year on neonatal survival but it was not significant, with an AICc value lower than our null model (null = 338.95, year = 337.08), therefore all models thereafter combined the data from both years. Our best age trend representing daily changes in survival of neonates allowed survival to vary for the first 30 days and then remained constant per week for the remaining 90 days (Table 3). After including all of our parameters with an additive effect of our best age trend (daily variation for 30 days, weekly variation thereafter), only one had a lower AICc value than the age trend itself, our age trend and south aspect (Table 3; Table 4). No other models were competitive (Table 3). Our best model predicted that neonates in our population had a survival rate of 96.6% on their first day of life, and on day 30 the survival rate had reached about 99% (Fig. 4). Differences in selection of aspect (north to south facing slopes) at a birth site had a significant influence on the survival of a neonate, with survival of neonates born on directly north facing slopes predicted to be 85.7% at birth and reaching 97.9% on day 120 (Fig. 5). In comparison, survival rates of neonates born on directly south facing slope were 98.3% the day they were born and had reached 99.8%

on day 120 (Fig. 5). Overall survival across the duration of the first 120 days of the life of neonates was 31.69% (± 70.6).

CAUSES OF MORTALITY.—We observed 31 mortalities of neonates over the 2 years.

Predation was the leading cause of mortality of neonates for both years ($n = 19$) followed by disease ($n = 5$). Coyotes followed by members of the family Felidae (mountain lions and bobcats) were the leading predators of neonates in our study (Fig.6). We observed one occurrence of starvation following an apparent maternal abandonment. Mortality from trauma occurred both years, with the occurrence in 2014 likely from an elk stepping on the neonate based on necropsy results and evidence at the site. We were able to identify the cause of 4 out of 5 disease related mortalities that occurred during our study: one instance of *Clostridium sp.*, one of *Pasteurella sp.* bacteria, and 2 cases of pleuropneumonia. We observed 4 mortalities where the cause was undetermined because the remains of the neonate were not with the radio collar.

DISCUSSION

Our results indicated that neonate survival for this population changed daily during the first 30 days and then began to plateau weekly thereafter. Those first 30 days were when the most mortality occurred likely because individuals were particularly susceptible to predation, which is similar to what other research has indicated (Steigers and Flinders 1980; Pojar and Bowden 2004; Bishop et al. 2009; Johnstone-Yellin et al. 2009).

Neonates born on south facing slopes had higher survival, supporting our hypothesis that selection of birth sites improved survival. Our survival rate at weaning was lower than that found in other studies (Hamlin et al. 1984; Bishop et al. 2009; Johnstone-Yellin et al. 2009). However, directly comparing survival rates does not consider causes of mortality

and variation between populations. Indeed, Monteith et al. (2014) observed differences in survival within a single mule deer population with lower survival rates on the west side of the Sierra crest (0.13 SE = 0.092) compared to the east (1.44 SE = 0.11) where different factors were found to affect survival.

Prolonged growing seasons allow young an extended period to acquire resources, in turn increasing body stores and increasing over winter survival and recruitment. High quality and quantities of forage occur with increased precipitation and mild temperatures, which are ideal for plant growth (Van Soest 1994). We predicted that precipitation, temperature, and changes in vegetation would affect neonatal survival but our models did not support that hypothesis. We observed a large difference in timing of vegetation change among years relative to birth dates of neonates but this difference did not influence survival.

We observed no indication that physical characteristics of neonates at birth affected their survival. Previous research has shown that birth dates of neonates (Adams et al. 1995; Smith and Anderson 1998; Keech et al. 2000), birth weights (Keech et al. 2000; Carstensen et al. 2009; Monteith et al. 2014), and sex (Smith and Anderson 1998; Bishop et al. 2009) affect survival however, none of those variables entered our best model. Verme (1963) showed that white-tailed deer neonates born with smaller birth weights had a higher rate of weight gain during the first 28 days of life compared to those born with higher birth weights and that weight differences were non-existent after that period. This suggests that neonates born with low birth weights may have the ability to catch up following birth if high qualities and quantities of forage are available, making birth masses unimportant to survival after a certain amount of time. If this observation is

correct, the relationship between birth characteristics and survival should become weaker with time. Indeed, Monteith et al. (2014) reported that birth mass was most influential on mule deer neonate survival during the first 3 weeks of life.

We conducted our research during 2 years of mild temperatures and quantities of precipitation at our study area. Mild winters generally require lower energy expenditures by parturient females allowing them to enter spring in better body condition than following a harsh winter (Mautz 1978, Schwartz et al. 1988). The lack of change in IFBF during winter illustrates that winter climate did not greatly affect neither the fed or unfed females in our population. During future research, it would be beneficial to measure body condition of individuals multiple times throughout winter. Those data would increase the understanding of how winter affects female condition entering spring as well as neonate survival.

Females that are in good condition are more likely to give birth to larger neonates in generally better body condition (Keech 2000). If the energy reserves of females are not entirely depleted entering spring, changes in vegetation quality may play a lesser role in the survival of neonates because energy demands on females are lower. Therefore, neonates in our population may have had higher survival rates because they were born in generally better condition. Additionally, mothers had the ability to produce high quality milk because they had not depleted all of their fat stores and high quality vegetation was readily available before parturition.

Mild climate, minimal energy stress on females, and no effect of physical characteristics at birth, suggest that differences in neonatal survival at Starkey result from individual variation in behavior. Previous research has suggested the older females are

more successful at raising neonates because they have access to high quality habitat and are more experienced at avoiding predators (Guinness et al. 1978; Ozoga et al. 1982; Ozoga and Verme 1986; Mech and McRoberts 1990). Because we only knew the minimum age of females, the effect of age and experience on neonatal survival likely was conservative in our models. Selection of a birth site by a female was important with southern aspect having a drastic improvement on survival of neonates. South facing slopes generally are warmer and drier than north facing slopes at the latitude of our study site, providing different vegetation types (Holland and Steyn 1975). South facing slopes also experience increased solar radiation compared to north facing slopes so snowmelt and spring green-up occur earlier (Holland and Steyn 1975). If mothers and neonates remained near a birth site during the first 30 days following parturition, use of south facing slopes could occur for an extended period compared to other birth site characteristics. If south facing slopes have increased concealment cover, then they have the potential to decrease predation events, the leading cause of mortality in our population. Long et al. (2009) determined that female mule deer at Starkey selected south facing slopes with increase amounts of canopy cover prior to parturition. Following parturition selection of resources by females changed (Long et al. 2009). However, because lactating females may not return to nurse their offspring for up to 12 hours, maternal selection cannot be assumed to match neonate habitat selection (Johnstone-Yellin et al. 2006). Bowyer et al. (1998) observed that neonatal black-tailed deer selected hiding locations on south facing slopes, likely because slopes provided favorable thermal environments. If south facing slopes increase the probability of a mule deer neonate surviving, then neonates should continue to use south facing slopes similar to black-tailed

neonates (Bowyer et al. 1998). Long et al. (2009) also demonstrated that movement of females dropped drastically the week of and the weeks following parturition, indicating that mothers and neonates were not moving far from birth sites. If female movement is limited following parturition, neonate movement would also be limited if not more so, making it plausible that habitat surrounding a birth site would be used for an extended amount of time.

Understanding how environmental, behavioral, and physical factors work together to effect each other and survival is fundamental to understanding population dynamics. Mortality of neonates in a population may not change drastically among years but the underlying cause has the ability to change. We must have a strong understanding of these underlying causes if we want to manage for healthy, sustainable populations of mule deer.

ACKNOWLEDGMENTS

We thank T. Allen, B. L. Dick, S. L. Findholt, R. Kennedy, B. Regan, and D. Rea for daily field support and assistance, without which we would never have caught a fawn or adult. T. E. Dilts, L. J. Heffelfinger, B. S. Sedinger, and K. Shoemaker provided essential statistical assistance for which we are very appreciative. We also appreciate the support of C. Borum, and B. Naylor. Funding for this project was from Oregon Department of Fish and Wildlife and USFS Federal Aid for Wildlife Restoration W-87-R with in kind support from the U. S. D. A. Forest Service.

LITERATURE CITED

ADAMS, L. G., F. J. SINGER, AND B. W. DALE. 1995. Caribou calf mortality in Denali

- National Park, Alaska. *Journal of Wildlife Management* 59:584-594.
- ALBON, S. D., T. H. CLUTTON-BROCK, AND F. E. GUINNESS. 1987. Early development and population dynamics in red deer. II. density-independent effects and cohort variation. *Journal of Animal Ecology* 56:69-81.
- ANTHONY, R. G. 1976. Influence of drought on diets and numbers of desert deer. *Journal of Wildlife Management* 40:140-144.
- ARNOLD, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175-1178.
- BÅRDSSEN, B. J., M. W. NÆSS, T. TVERAA, K. LANGELAND, AND P. FAUCHALD. 2014. Risk-sensitive reproductive allocation: fitness consequences of body mass losses in two contrasting environments. *Ecology and Evolution* 4:1030-1038.
- BENDER, L. C., E. CARLSON, S. M. SCHMITT, AND J. B. HAUFLER. 2002. Production and survival of elk (*Cervus elaphus*) calves in Michigan. *American Midland Naturalist*. 148:163-171.
- BISCHOF, R., L. E. LOE, E. L. MEISINGSET, B. ZIMMERMANN, B. VAN MOORTER, AND A. MYSTERUD. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? *The American Naturalist* 180:407-424.
- 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.
- 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.

- 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., J. G. KIE, AND V. VAN BALLEMBERGHE. 1998. Habitat selection by neonatal Black-tailed deer: climate, forage, or risk of predation? *Journal of Mammalogy* 79:415-425.
- BURNHAM, K. P. AND ANDERSON, D. R. 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. 2nd ed. Springer. New York.
- CARSTENSEN, M., G. D. DELGIUDICE, B. A. SAMPSON, AND D. W. KUEHN. 2009. Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. *Journal of Wildlife Management* 73:175-183.
- CLIMATE ENGINE. 2015. Desert Research Institute and University of Idaho. <http://climateengine.org>.
- CLUTTON-BROCK, T. H., M. MAJOR, S. D. ALBON, AND F. E. GUINNESS. 1987. Early development and population dynamics in red deer. I. density-dependent juvenile survival. *Journal of Animal Ecology* 56:53-67.
- COOK, R. C., ET AL. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. *Journal of Wildlife Management* 74:880-896.
- 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.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for

- modeling avian nest survival. *Ecology* 83:3476-3488.
- DULBERGER, J., N. T. HOBBS, H. M. SWANSON, C. J. BISHOP, AND M. W. MILLER. 2010. Estimating chronic wasting disease effects on mule deer recruitment and population growth. *Journal of Wildlife Diseases* 46:1086-1095.
- GAILLARD, J. M., M. FESTA-BIANCHET, AND N. G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58-63.
- GILLINGHAM, M. P. AND F. L. BUNNELL. 1989. Effects of learning on food selection and searching behavior of deer. *Canadian Journal of Zoology* 67:24-32.
- GREEN, W. C. H., AND A. ROTHSTEIN. 1993. Persistent influences of birth date on dominance, growth and reproductive success in bison. *Journal of Zoology* 230:177-186.
- GUINNESS, F. E., T. H. CLUTTON-BROCK, AND S. D. ALBON. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). *Journal of Animal Ecology* 47:817-832.
- HAUGEN, A. O. AND D. W. SPEAKE. 1958. Determining age of young fawn white-tailed deer. *Journal of Wildlife Management* 22:319-321.
- HAMLIN, K. L., S. J. RILEY, D. PYRAH, A. R. DOOD, AND R. J. MACKIE. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *Journal of Wildlife Management* 48:489-499.
- HIRD, J. N., AND G. J. MCDERMID. 2009. Noise reduction of NDVI time series: an empirical comparison of selected techniques. *Remote Sensing of Environment* 113:248-258.

- HOLLAND, P. G. AND STEYN, D. G. 1975. Vegetational responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography* 2:179-183.
- 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.
- JOHNSTONE-YELLIN, T. L., L. A. SHIPLEY, AND W. L. MYERS. 2006. Effectiveness of vaginal implant transmitters for locating neonatal mule deer fawns. *Wildlife Society Bulletin* 34:338-344.
- JOHNSTONE-YELLIN, T. L., L. A. SHIPLEY, W. L. MYERS, AND H. S. ROBINSON. 2009. To twin or not to twin? Trade-offs in litter size and fawn survival in mule deer. *Journal of Mammalogy* 90:453-460.
- KEECH, M. A., R. T. BOWYER, J. M. VERHOEF, R. D. BOERTJE, B. W. DALE, AND T. R. STEPHENSON. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management* 64:450-462.
- LANDETE-CASTILLEJOS, T., A. GARCIA, F. R. LOPEZ-SERRANO, AND L. GALLEGO. 2005. Maternal quality and differences in milk production and composition for male and female Iberian red deer calves (*Cervus elaphus hispanicus*). *Behavioral Ecology and Sociobiology* 57:267-274.
- LENT, P. C. 1974. Mother-infant relationships in ungulates. Pp. 14-55 In *The behavior of ungulates and its relation to management* (V. Geist and F. Warner, eds.). International Union for the Conservation of Nature. Morges, Switzerland.

- LIVEZEY, K. B. 1990. Toward the reduction of marking-induced abandonment in newborn ungulates. *Wildlife Society Bulletin* 18:193-203.
- 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.
- MAUTZ, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. *Wildlife Society Bulletin* 6:88-90.
- MECH, L. D. AND R. E. MCROBERTS. 1990. Survival of white-tailed deer fawns in relation to maternal age. *Journal of Mammalogy* 71:465-467.
- MONTEITH, K. L., V. C. BLEICH, T. R. STEPHENSON, AND 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.
- 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.
- MORANO, S., K. M. STEWART, J. S. SEDINGER, C. A. NICOLAI, AND M. VAVRA. 2013. Life-history strategies of North American elk: trade-offs associated with reproduction and survival. *Journal of Mammalogy* 94:162-172.
- NATIONAL ATMOSPHERIC DEPOSITION PROGRAM. 2015. NADP Program Office, Illinois State Water Survey, University of Illinois, Champaign, IL.

- NETER, J., M. H. KUTNER, C. J. NACHTSHEIM, AND W. WASSERMAN. 1996. Applied linear statistical models. 4th ed. Irwin. Chicago, Illinois.
- OZOGA, J. J., L. J. VERME, AND C. S. BIENZ. 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. *Journal of Wildlife Management* 46:1-11.
- OZOGA, J. J., AND L. J. VERME. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. *Journal of Wildlife Management* 50:480-486.
- PARKER, K. L. 1989. Effects of heat, cold, and rain on black-tailed deer. *Canadian Journal of Zoology* 66:2475-2483.
- PARKER, K. L., P. S. BARBOZA, AND M. P. GILLINGHAM. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23:57-69.
- POJAR, T. M., AND D. C. BOWDEN. 2004. Neonatal mule deer fawn survival in west-central Colorado. *Journal of Wildlife Management* 68:550-560.
- RAMSEY, C. W. 1968. A drop-net deer trap. *Journal of Wildlife Management* 32:187-190.
- ROWLAND, M. M., L. D. BRYANT, B. K. JOHNSON, J. H. NOYES, M. J. WISDOM, AND J. W. THOMAS. 1997. The Starkey project: history, facilities, and data collection methods for ungulate research. U.S. Department of Agriculture Forest Service, Technical Report PNW-GTR-396:1-62.
- RUSSELL, D. E., K. L. GERHART, R. G. WHITE, AND D. VAN DE WETERING. 1998. Detection of early pregnancy in caribou: evidence for embryonic mortality. *Journal of Wildlife Management* 62:1066-1075.
- SCHWARTZ, C. C., W. L. REGELIN, AND A. W. FRANZMANN. 1988. Estimates of

- digestibility of birch, willow, and aspen mixtures in moose. *Journal of Wildlife Management* 52:33-37.
- SHALLOW, J. R. T., M. A. HURLEY, K. L. MONTEITH, AND R. T. BOWYER. 2015. Cascading effects of habitat on maternal condition and life-history characteristics of neonatal mule deer. *Journal of Mammalogy* 96:194-205.
- SHORT, H. L. 1981. Nutrition and metabolism. Pp. 99-127 in *Mule and black-tailed deer of North America* (O. C. Wallmo, ed.). University of Nebraska Press. Lincoln.
- 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, B. L., AND S. H. ANDERSON. 1998. Juvenile survival and population regulation of the Jackson elk herd. *Journal of Wildlife Management* 62: 1036-1045.
- STEIGERS, W. D., JR., AND FLINDERS, J. T. 1980. Mortality and movements of mule deer fawns in Washington. *Journal of Wildlife Management* 44:381-388.
- 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. Temporal spatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* 83:229-244.

- STEWART, K. M., R. T. BOWYER, R. W. RUESS, B. L. DICK, AND J. G. KIE. 2006. Herbivore optimization by North American elk: consequences for theory and management. *Wildlife Monographs* 167:1-24.
- 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., 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.
- 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 SOEST, P. J. 1994. *Nutritional ecology of the ruminant*. Cornell University. Ithaca, New York.
- VERME, J. L. 1963. Effect of nutrition on growth of white-tailed deer fawns. *Transactions of North American Wildlife and Natural Resource Conference* 28:431-443.
- WALLMO, O. C. 1981. *Mule and black-tailed deer of North America*. University of Nebraska Press. Lincoln, Nebraska.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–138.

FIGURE LEGEND

Fig. 1.—Starkey Experimental Forest and Range in northeast, OR, USA. Our research was conducted in Main study area and Barn Pasture.

Fig. 2.—Mean temperature and precipitation from May to October in a) 2014 b) and 2015 at Starkey Experimental Forest and Range, OR, USA.

Fig. 3.—NDVI and IRG values in a) 2014 and b) 2015 representing changes in forage quality and the rate of change at Starkey Experimental Forest and Range, OR, USA.

NDVI values were generated from satellite imagery and represent changes in vegetation greenness. IRG values were calculated by taking the first derivative of NDVI values. IRG values above 0 indicate that NDVI values are increasing, while NDVI values below 0 indicate that NDVI values are decreasing.

Fig. 4.—Daily neonate survival rate for 120 days with associated 95% confidence intervals at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015.

Fig. 5.—Effect of cosine of aspect at the birth site of an individual on daily neonatal survival rate with two standard deviations at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015. Top most dashed line represents a slope facing directly south, while the bottom most dashed line represents a slope facing directly north.

Fig. 6.—The number of predation events on neonatal mule deer at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015.

Table 1.—Parameter, unit, and definition of all variables used in survival models for 47 neonates at Starkey Experimental Forest and Range, OR, USA, during 2014 and 2015.

Parameter	Unit	Definition
Maternal age	Year	Age of parturient female
Precipitation	mm	Daily accumulated precipitation
Temperature	°C	Daily mean temperature
IFBF	%	Ingesta free body fat at the time a female was handled
Fed	Yes/No	Whether a female was supplementally fed the winter before parturition
NDVI Start	Day	Difference between birth dates of neonates and the start of spring green-up
NDVI Peak	Day	Difference between birth dates of neonates and the peak of spring green-up
IRG Peak	Day	Difference between birth dates of neonates the peak of IRG
Woody debris	%	Woody debris at birth sites of neonates
Canopy Cover	%	Canopy cover above the birth site of neonates
Cosine Aspect	◦	Aspect of slope at birth sites of neonates, negative values indicate south facing slopes while positive indicate north facing slopes
Birth Date	Day	Birth date of neonatal mule deer
Sex	M/F	Sex of neonate
PC1	-	First principle component determined using a neonate's chest girth, metatarsus length, and body length
Residuals	-	Residuals from linear regression determining relationship between size of neonates (PC1) and mass
Age Trend	-	How survival varies between birth and 120 days indicated by combinations of time periods (Daily, Weekly, Monthly). Values following time periods in models (30,60,90,120) represent final day of survival time period.

Table 2.—Descriptive statistics of parameters used in neonate survival models for 2014 and 2015 at Starkey Experimental Forest and Range, OR, USA. Data are from 47 neonates and 32 adults, 11 adults had neonates captured both years.

Parameter	2014				2015			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Age of maternal female	6.313	3.22	2	12	6.13	2.83	2	13
IFBF	9.74	2.33	7.31	16.64	10.09	2.33	7.30	16.64
Principle component 1 scores	-0.28	1.34	-3.02	3.12	0.34	1.27	-2.12	2.94
Residuals	-0.04	0.29	-1.10	0.55	0.05	0.29	-0.47	0.42
Birth Date	5/31	5.7	5/23	6/10	6/5	8.44	5/25	6/20
NDVI Start*	86.46	5.72	78.00	96.00	91.14	7.57	80.00	106.00
NDVI Peak*	-25.54	5.72	-34.00	-16.00	11.14	7.57	0.00	26.00
IRG Peak*	46.46	5.72	38.00	56.00	15.14	7.57	4.00	30.00
Woody debris	15.00	13.59	1.00	35.00	6.45	13.00	0.00	45.00
Canopy Cover	66.32	22.70	30.90	100.00	57.61	32.42	2.90	100.00
Cosine Aspect	-0.30	0.64	-0.95	0.95	-0.42	0.54	-0.99	0.42

*In relation to mean neonate birth date

Table 3.—Candidate models used to estimate monthly survival of 47 neonatal mule deer at Starkey Experimental Forest and Range, OR, USA, 2015 - 2015. Age trends represent daily (Daily), weekly (Weekly), and monthly (Monthly) variation in neonatal survival for the first 120 days of life.

Model Rank	Model	K	AICc	Δ AICc	ω_i
1	Age Trend : Daily 30 Weekly 120 + Cosine Aspect	4	317.55	0.00	0.524
2	Age Trend : Daily 30 Weekly 120	3	322.92	5.37	0.036
3	Age Trend : Daily 30 Weekly + Maternal Age	4	322.93	5.38	0.036
4	Age Trend : Daily 30 Weekly 90 Monthly 120	3	323.38	5.83	0.028
5	Age Trend: Daily 30 Weekly 120 + Sibling	4	323.50	5.95	0.027
6	Age Trend : Weekly 120	3	323.56	6.01	0.026
7	Age Trend : Daily 120	3	323.58	6.03	0.026
8	Age Trend : Daily 30 Weekly + Residual	4	323.59	6.05	0.025
9	Age Trend : Daily 60 Weekly 120	3	323.73	6.18	0.024
10	Age Trend : Daily 30 Weekly 60 Monthly 120	3	323.91	6.36	0.022

Table 4.—Top model parameter estimates (β), standard errors (SE), and 95% confidence intervals from survival analysis of 47 neonatal mule deer at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015. Age Trend represents variation in neonatal survival with daily variation during the first 30 days and weekly variation until 120 days.

Parameter	β	SE	95% CI	
			Lower	Upper
Intercept	3.25	0.32	2.61	3.89
Age Trend: Daily 30 Week 120	0.05	0.01	0.02	0.07
Cosine Aspect	-0.64	0.23	-1.09	-0.19

Fig. 1.—Starkey Experimental Forest and Range in northeast, OR, USA. Our research was conducted in Main study area and Barn Pasture.

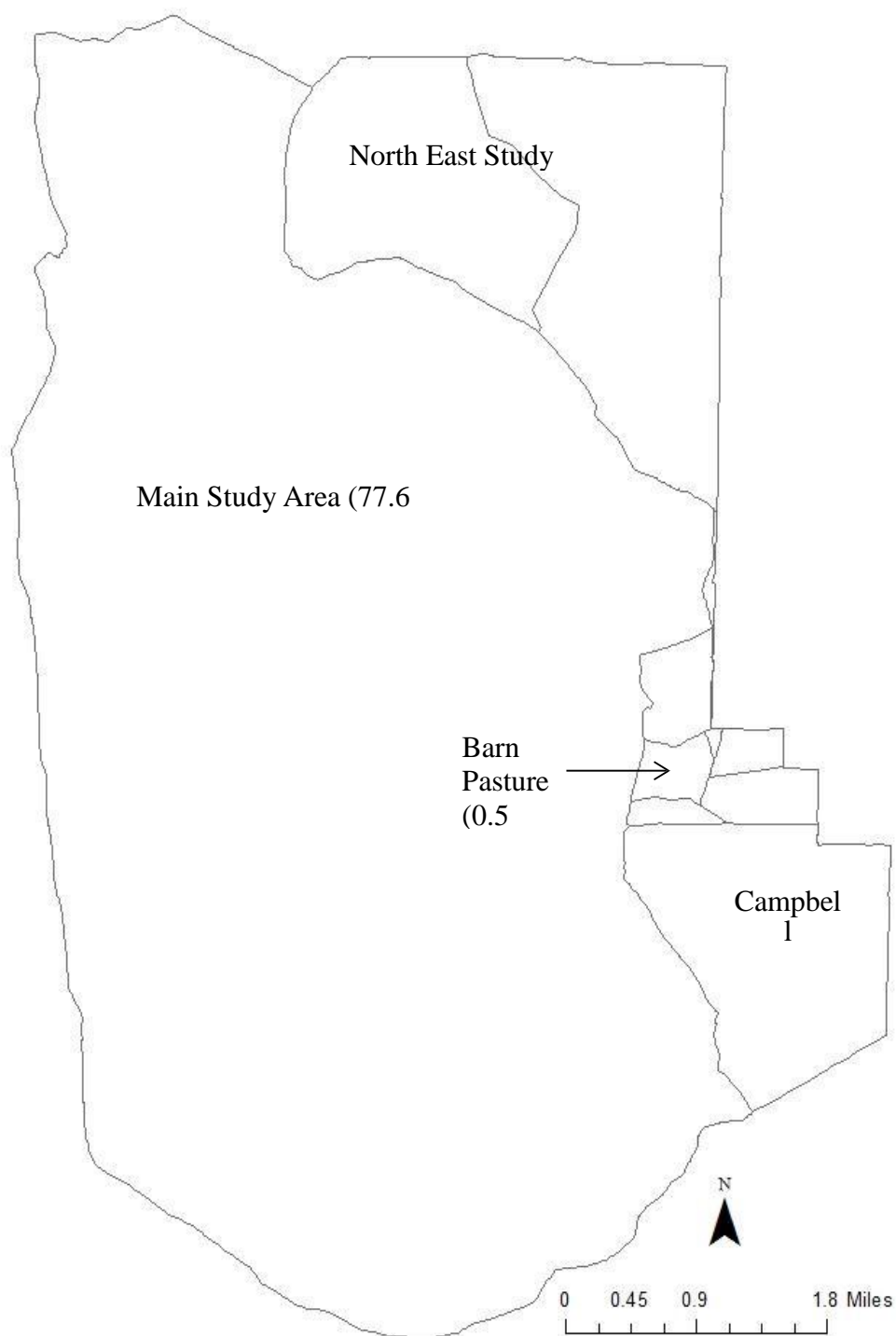


Fig. 2.—Mean temperature and total daily precipitation from May to October in a) 2014 b) and 2015 at Starkey Experimental Forest and Range, OR, USA.

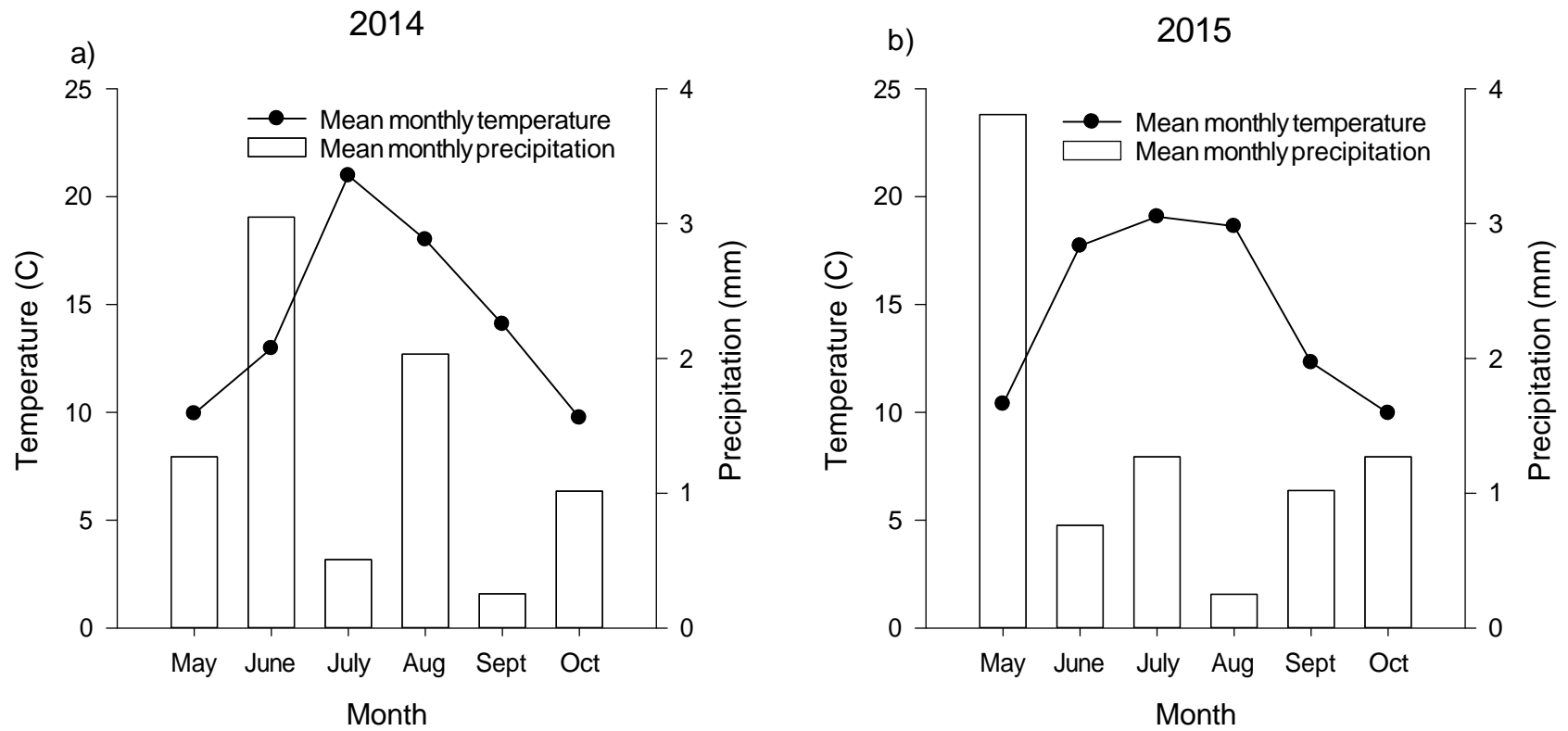


Fig. 3.—NDVI and IRG values in a) 2014 and b) 2015 representing changes in forage quality and the rate of change at Starkey Experimental Forest and Range, OR, USA. NDVI values were generated from satellite imagery and represent changes in vegetation greenness. IRG values were calculated by taking the first derivative of NDVI values. IRG values above 0 indicate that NDVI values are increasing, while NDVI values below 0 indicate that NDVI values are decreasing.

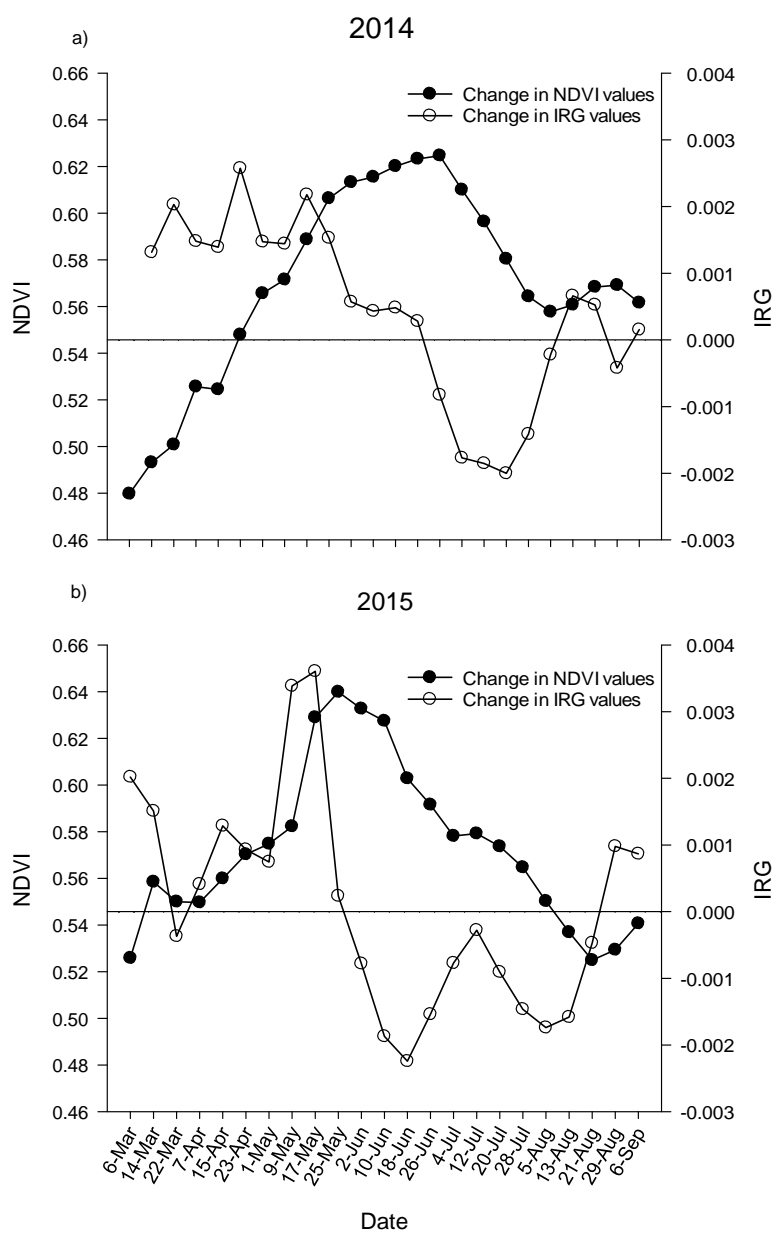


Fig. 4.—Daily neonate survival rate for 120 days with associated 95% confidence intervals at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015.

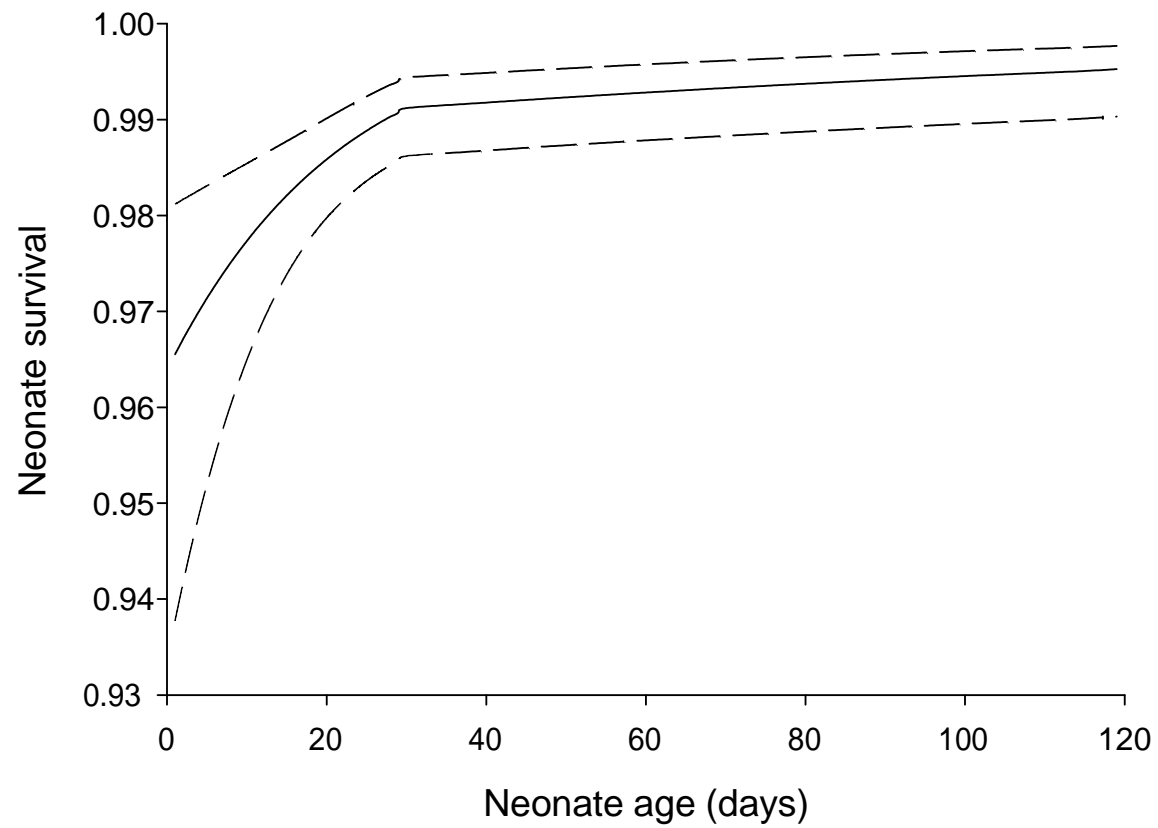


Fig. 5.—Effect of cosine of aspect at the birth site of an individual on daily neonatal survival rate with two standard deviations at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015. Top most dashed line represents a slope facing directly south, while the bottom most dashed line represents a slope facing directly north.

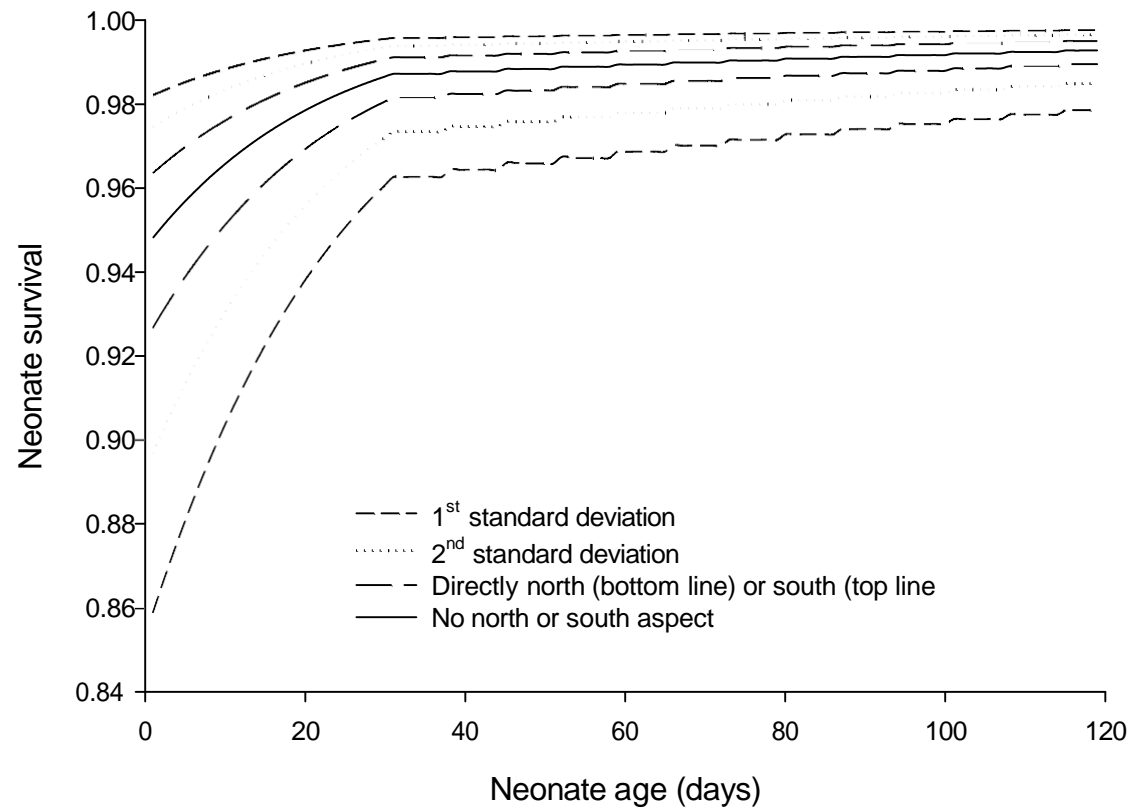
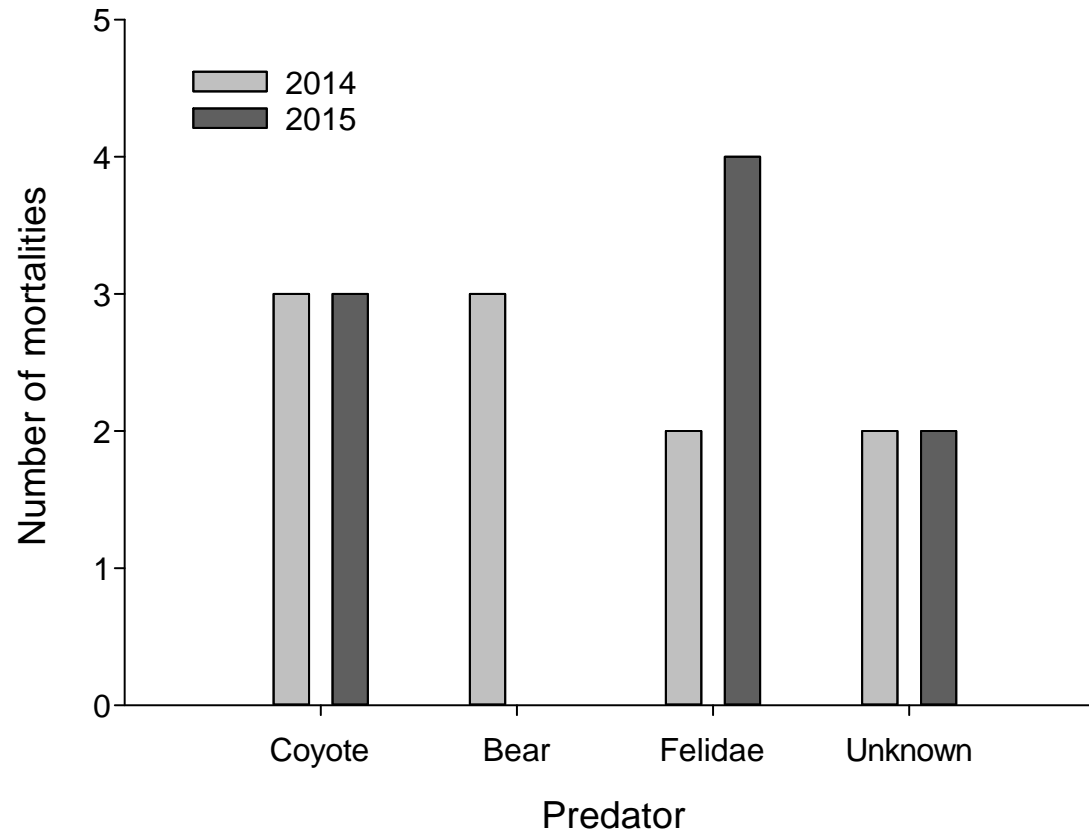


Fig. 6.—The number of predation events on neonatal mule deer at Starkey Experimental Forest and Range, OR, USA, 2014 - 2015.



THESIS SUMMARY

Neonate survival and recruitment influences population dynamics in ungulates because it may vary greatly among years (Gaillard et al. 1998). Changes in population numbers of mule deer have been attributed to neonate mortality in many cases (Gill et al. 2001; Andelt et al. 2004; Wasley 2004; Monteith et al. 2014). Mortality of neonates is highest in the months following parturition (Gaillard et al. 2000). During this period, maternal females are under high energy demands to produce milk and have just finished the huge energy expense of reproduction (Parker et al. 2009). Our research examined what habitat characteristics were important to a female when selecting a parturition site during the springs of 2014 and 2015 at the Starkey Experimental Forest and Range, Oregon. Additionally we examined what factors affect neonate survival from birth to 120 days, when weaning generally occurs in mule deer.

We predicted that maternal females would select birth sites based on habitat characteristics that could increase survival of neonates. Our resource selection functions indicated that maternal females chose birth sites with higher quantities of overstory cover and woody debris compared to available locations. Additionally, females selected birth sites on south facing slopes. These habitat characteristics can increase survival through the camouflage of neonates and the creation of thermal environments that limit energy expenditure from neonates (Bowyer et al. 1998, 1999). Understanding what factors are important to the selection of birth sites in Oregon, allows managers to protect such areas. So that deer can use the most suitable habitat for parturition, managers should conserve south facing slopes with down logs and mature tree canopies.

Habitat characteristics selected at birth sites were not limited to influencing survival of neonates on their date of birth alone. Our neonate survival model generated using program MARK (White and Burnham 1999), indicated that neonates born on south-facing slopes had higher survival to 120 days than those born at birth sites with northern aspects.

We did not find support for effects of changing vegetation, climate, physical condition of maternal females, or birth characteristics in our survival models. This may have been because both winters that occurred during our research were mild with minimal winter precipitation (24.69cm and 28.02cm) and a sum of 31 days with mean daily temperatures under -6°C from November 1st to Feb 28th. During mild winters, females likely minimized energy use and depletion of energy reserves. Monteith et al. (2013) reported that during winter, some females gained fat stores, after entering winter range in relatively poor body condition. If this occurred in our population, females entered spring in better than average condition, allowing them to produce neonates on a higher plane of nutrition compared to other populations. Changes in vegetation quality likely had a lesser effect on females because they were in good condition and already possessed the energy reserves necessary for milk production.

This thesis was based on the first 2 years of an ongoing project at Starkey that will continue to collect demographic and habitat data of mule deer. In the future, multiple measurements of a single female over the course of winter may allow for more insight into how body condition changes during both mild and severe winters. How survival of both neonates and adults change overtime and how factors interact and influence survival will have important consequences for management actions. A better understanding of

population dynamics and habitat use will allow managers to change hunting regulations, restore habitat, and retain habitat important for survival of mule deer in the future.

LITERATURE CITED

- Andelt, W. F., T. M. Pojar, and L. W. Johnson. 2004. Long-term trends in mule deer pregnancy and fetal rates in Colorado. *Journal of Wildlife Management* 68:542-549.
- 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.
- Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with 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.
- Gill, R. B., T. D. I. Beck, C. J. Bishop, D. J. Freddy, N. T. Hobbs, R. H. Kahn, M. W. Miller, T. M. Pojar, and G. C. White. 2001. Declining mule deer populations in Colorado: reasons and responses. Colorado Division of Wildlife Special Report Number, 77:DOW-R-S-77-01, Fort Collins, Colorado.

- Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce, and R. T. Bowyer. 2013. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *Journal of Animal Ecology* 82:377-388.
- 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.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23:57-69.
- Wasley, T. 2004. Mule deer population dynamics: issues and influences. Nevada Department of Wildlife Biological Bulletin No. 14, Reno, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–138

Appendix 1. Descriptive statistics of measurements taken on adults and neonates during 2013 - 2015 at Starkey Experimental Forest and Range, OR, USA.

Measurement	Adults							
	2013-2014 Winter ($n = 25$)				2014-2015 Winter ($n = 15$)			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Max Metatarsus	36.82	1.80	30.5	39	36.83			
	0.98	35.5	38.5					
Chest Girth	100.13	4.62	93.5	113	97.25	4.90	91	106
Weight	57.42	5.91	48	69	59.88	5.24	50.43	66.72
Body length	157.27	7.99	146	169	162.33	6.35	152	172
Jaw length	24.20	1.33	21	26.5	24.93	1.32	22	27
Rump body condition Score	3.80	0.62	3	5	4.40	0.83	2	5
Max Rump Fat*	3.50	1.69	1	6	3.38	1.19	2	5
Measurement	Neonates							
	2014 ($n = 26$)				2015 ($n = 21$)			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Metatarsus	20.91	1.07	19	21.5	21.14	0.88	19.5	22.5
Chest Girth	34.76	1.76	31	36	36.02	2.08	32.5	40.5
Weight	3.65	0.42	2.78	3.88	3.92	0.55	2.75	4.98

*During 2013 - 2014 winter $n = 24$, during 2014 - 2015 winter $n = 13$