AN ABSTRACT OF THE THESIS OF

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It is critical for wildlife managers to understand the population dynamics of a harvested species, particularly for ungulates, which are a valuable wildlife resource. Due to concerns that mule deer (*Odocoileus hemionus*) populations in Oregon were declining, more comprehensive data on population vital rates and the factors potentially affecting them were needed by resource managers. To meet this research need, Oregon Department of Fish and Wildlife implemented a seven year study to investigate habitat use and survival of mule deer in eastern Oregon. From 2005-2012, the agency radio-collared 621 mule deer in south-central Oregon in order to gain more comprehensive information about seasonal movement, seasonal and annual survival, and changes in habitat use for the population. I used the radio-telemetry data from this larger study to investigate mule deer survival rates and cause-specific mortality and the effects of deer seasonal distributions, movement behavior, and environmental factors such as annual and climatic variation.

I used known-fate data for 408 adult female radio-collared mule deer to estimate monthly survival rates and to investigate a variety of factors that might affect these rates including seasonal distribution, temporal effects (seasonal, annual, and trends across season and year), movement behavior, and climatic covariates on differing scales. Variation in survival rates for this population of female mule deer in eastern Oregon was best explained by an additive effect of migration behavior, fall migration period, and precipitation levels on individual winter ranges. Survival was significantly higher for migratory deer than residents. Both groups had lower survival during the fall migration

period (Oct-Nov) and a positive linear relationship between survival and winter precipitation in individual winter ranges. Annual survival estimates for migrants ranged from 0.81-0.82, which is similar to other findings, but survival rates for residents (0.76-0.77) were low in comparison to survival rates for adult female mule deer in other parts of their range.

I used a nonparametric cumulative incidence function estimator (NPCIFE) to generate annual cumulative incidence functions separately for males and females due to differing risks associated with each sex. The four competing sources of mortality I included in this analysis for males were legal harvest, illegal harvest, predation, and starvation, disease, vehicle or fence-collision combined as one category (i.e., other). For females in investigated predation, human-associated mortality (vehicle or fence), illegal harvest, and natural causes (starvation and disease). Annual risk functions were pooled across all years of the study to maximize sample size. For males, the cumulative risk was highest for legal harvest (0.249, 95%CI=0.172-0.326), with predation the next highest cause of mortality for this sex (0.104, 95%CI=0.042-0.611). For females, the cumulative risk was highest for predation, (0.044, 95%CI=0.028-0.065) with anthropogenic causes (0.038, 95%CI=0.021-0.054) and illegal harvest (0.031, 95%CI=0.17-0.054) also important sources of mortality.

Higher monthly survival rates of migrants compared to residents (across all months of the biological cycle) suggested that leaving for potentially higher quality summer foraging grounds outweighed the cost of traveling through unfamiliar habitats and energy expenditure from migration. Conversely, it may also imply that the summer ranges for residents had a negative effect on survival due to habitat quality or human disturbance. Both migrants and residents had lower monthly survival during the fall migration period (Oct - Nov). Female mule deer were excluded from the state-managed bow and rifle hunting season during this study, but females may experience the negative effects of human disturbance associated with fall hunting activities. This time of year is also energetically costly for females, being that some may still be nursing, which could have an additive effect to the energy used to migrate or avoid human disturbance. Winter precipitation also had positive effect on survival for both groups, possibly because

increased average winter precipitation resulted in increased winter forage quantity and quality.

My results suggest that female survival rates observed during my study are on the low end of the range reported for this species and may be contributing to population declines of mule deer in Oregon. Annual estimates of male survival were also low, but it is unclear how that might contribute to overall population declines without more information on annual and seasonal variation in male survival. Surprisingly, I observed high levels of illegal harvest on female deer and evidence that female survival during the fall migration period, which overlaps Oregon's legal harvest season, was lower than other times of the year. It is unclear why the fall migration period negatively affects both migrants and resident deer similarly, but future research should attempt to determine the specific factors that are negatively impacting mule deer survival during this time period in south-central Oregon. In addition, as human development in the area continues to grow, it is important to consider migration paths and the habitat quality of both summer and winter ranges. My results suggested that conditions may differ between summer ranges in particular, for residents vs. migrants, and understanding these differences may be the key to increasing survival of female mule deer in Oregon. Sharing information from this study with law enforcement and the general public may be the first step towards increasing awareness of, and thereby reducing, the relatively high levels of illegal harvest I documented for the female population. Future research should focus on investigating the differences in habitat quality for residents versus migrants, the factors that decrease survival during fall migration for both groups, and the social and economic factors that contribute to the illegal harvest of female mule deer in eastern Oregon.

Survival Rates and Cause-Specific Mortality for Mule Deer in South-central Oregon

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Elizabeth M. Mulligan, Author

ACKNOWLEDGEMENTS

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CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

Elizabeth M. Mulligan

BACKGROUND

Mule deer population status

Mule deer (*Odocoileus hemionus*) are native to the western U.S., including Oregon where they occur east of the crest of the Cascade Mountain Range primarily in sagebrush steppe ecosystems (Wallmo 1981). These sagebrush habitats have been lost and degraded due to livestock grazing, fire, recreational activity, and sagebrush removal, which has impacted many wildlife populations, including western mule deer (West 1999). Mule deer populations were believed to have declined across the west through the 1990s (Unsworth et al. 1999) including populations in south-central Oregon (Peek et al. 2002). However, since the 1990s, mean population growth rate estimates from mule deer and black-tailed deer populations (*Odocoileus hemionus columbianus*) across their range showed little evidence of strong annual declines (n=8 populations, λ= 0.99, SE =0.04; Forrester and Wittmer 2013). In contrast, recent data from surveys, including doe:fawn ratios, herd composition, density estimates, and harvest numbers suggest that mule deer populations in Oregon declined from 300,000 individuals in 2001 to 229,326 in 2015, a 24% decline in 15 years (Oregon Department of Fish and Wildlife 2003, unpublished data).

Mule deer population declines in other parts of their western range have been attributed to low annual survival rates of adults and fawns (White & Bartmann 1997, Robinson et al. 2002, Bender et al. 2007, Bishop et al. 2009) and low recruitment rates (Unsworth et al. 1999). However, in general, factors affecting mule deer population are not well understood. Some research has suggested that predation, anthropogenic mortality, and forage quantity and quality are major limiting factors in Oregon, California, and Nevada (Peek et al. 2002, Bleich and Taylor 1998). High levels of winter precipitation (particularly in the form of snow) and low temperatures have been shown to negatively affected survival for adults and fawns in Colorado (Bishop et al. 2005). Conversely, in arid systems like Arizona, and southwestern Texas, drought was associated with a decrease in mule deer abundance (Anthony 1976, Leopold and Krausman 1991). Habitat loss due to increased human development in Oregon (Kline 2012), invasion of exotic species in Nevada (Clements

and Young 1997), and energy development in Wyoming (Sawyer et al. 2006) have also been indirectly related to mule deer population declines.

MULE DEER POPULATION DYNAMICS

The fundamentals required to understand changes in population size include an understanding of the primary population processes (births, deaths, immigration, and emigration) that result in population change (Williams et al. 2002), and the factors that affect these vital rates (Gaillard et al. 1998). For harvested species, the goal is to maintain population abundance at a level in which harvest yield will meet commercial or recreational objectives (Nichols et al. 1995, Hilborn and Walters 1992). This requires understanding how many births and deaths (or the per capita survival rate) are occurring in the population. Survival rates of individuals ultimately correspond to what is happening at the population level (Williams et al. 2002) and are critical for predicting population responses to management.

Mule mule deer have a polygynous mating system (Wallmo 1981), so variation in male survival does not have as much of an influence on population dynamics as variation in female survival (Gaillard et al. 1998). Therefore, fluctuations in adult female survival can have large effects on growth rate of mule deer populations (Robinson et al. 2002) or be an important secondary factor affecting changes in population growth (Bishop et al. 2009). Female adult deer tend to have higher, less variable annual survival rates than males, partly due to selective harvest of males compared to females (Peek et al. 2002), and the increased activity of males during the breeding season which can expose them to additional hazards and leave them with lower energy reserves going into the winter (Connelly 1981). Male mule deer survival rates are not often reported (Forrester and Wittmer 2013), however, estimates for the 2-month hunting season (Oct-Nov) in Montana ranged from 0.60 – 0.72 (Pac and White 2007) and annual adult male survival ranged from 0.52-0.60 in South Dakota (Robling et al. 2014).

Estimates of annual survival rates for adult female mule deer do however vary widely, both temporally and spatially, ranging from 0.853 in Colorado, Idaho, and Montana (Unsworth et al. 1999), to 0.935 in Colorado (Lukacs et al. 2009), and from

0.71 to 0.90 in adjacent populations in southwest Idaho (Bishop et al. 2005). During 3 years in New Mexico, annual female survival rates varied from 0.63 in 2002 to 0.90 and 0.91 in 2003 and 2004, respectively (Bender et al. 2007). Annual and seasonal variation in survival for adult female mule deer has been primarily related to major stochastic environmental events (e.g., severe winter and drought; Gaillard et al. 1998, Unsworth et al. 1999), although also to food availability (Unsworth et al. 1999, Bishop et al. 2005), and predation (White et al. 1987, Unsworth et al. 1999). For example, poor forage quality on home ranges, especially winter ranges (Sawyer et al. 2005), can influence mule deer populations by decreasing body condition, and thereby decreasing annual survival rates (Smith and LeCount 1979, Hoenes and Bender 2012,). Precipitation can be a strong predictor of mule deer survival (Peek et al. 2002), with higher survival associated with increased winter precipitation (Bender et al. 2007). However, severe weather conditions, like drought or increased snow depth, can decrease survival, likely due to increased cost of movement and decreased food availability (Wallmo 1981). A 30-year review of population dynamics of mule deer proposed that weather and forage availability was a limiting factor across many populations in North America (Forrester and Wittmer 2013).

Winter ranges for mule deer are frequently found near human populations, and human activities such as outdoor-related recreation (Rost and Bailey 1979), urban development, and agricultural activities (Thomas and Irby 1991) can have negative impacts on mule deer survival. For example, more human activity occurs in areas adjacent to water sources, especially during warmer months (Hammit et al. 2015), and deer densities have been shown to increase near water during summer as well (Eberhardt et al. 1984). However, deer survival rates are lower for individuals with summer home ranges near water, apparently due to the increased human disturbance (Nicholson et al. 1997).

Movement patterns are components of mule deer behavior and ecology that are integral to understanding vital rates (including survival) and population dynamics (Bolger et al. 2008, Pulliam and Danielson 1991). The movement behavior of mule deer is also highly variable throughout their range (Nicholson et al. 1997, Gruell and Papez 1963), and can be influenced by topographic and vegetative patterns (Eberhardt

et al. 1984, Garrott et al. 1987), water availability (Eberhardt et al. 1984), and precipitation (D'Eon and Serrouya 2005). Some populations migrate from winter to summer ranges (Garrot et al. 1987; Brown 1992), some populations remain resident year-round (Eberhardt et al. 1984), and some populations include both resident and migratory individuals (Brown 1992). It is unknown whether mule deer migratory behavior is consistent from year to year (e.g., do migratory individuals always migrate?), or if there are individual or annual factors that influence whether an individual (or population) migrates or not. In mountainous regions, deer will migrate between low-elevation winter ranges to higher-elevation summer ranges, usually attributed to snow accumulation during winter (forcing deer to move downslope), and increased forage quality upslope after snowmelt (D'Eon and Serrouya 2005, Monteith et al. 2011). For migratory deer summer and winter ranges are often separated by great distances (Sawyer et al. 2005), and migration distance does not appear to vary by sex (Brown 1992). However, the timing of the migration between seasonal ranges can vary between males and females, with females more likely to migrate earlier than males (Kucera 1992).

Migratory deer will choose to avoid human disturbance more than resident deer by utilizing summer and winter ranges farther from anthropogenic activity (Nicholson et al. 1997). In addition, human disturbance (any anthropogenic activity associated with development) can influence migration corridors by encroaching on already tightly bottlenecked areas which are critical for movement between ranges (Sawyer et al. 2005). Migratory behavior can also increase the probability of crossing highways and therefore increase the risk of deer-vehicle collisions (Lloyd and Casey 2005, Jackson and Cupples 2012). Vehicle-related mortality can be partially additive, decreasing survival rates below rates expected from natural mortality alone, particularly for declining populations (Litvaitis and Tash 2008).

Migration behavior can affect survival, but there are associated trade-offs between maximizing foraging benefits while minimizing risks of mortality such as predation or starvation (Nicholson et al. 1997, White et al. 1987). In addition, this trade-off can vary annually, depending on climatic factors (White et al. 1987). For example, in California, female mule deer that migrated had lower survival rates than

non-migratory deer during years with lower precipitation (Nicholson et al. 1997). In addition, predation in some areas has a greater impact on mule deer survival than in others due to movement behavior (deer that moved off seasonal ranges evaded cougar predation; White et al. 1987). Predation risk has been linked to habitat composition, as deer that selected foraging areas that offered more cover had a lower risk of predation than those in open areas (Pierce et al. 2004). Thus, the dynamics of mule deer populations and the factors that affect them are varied and often complex.

Cause-specific mortality

In addition to survival rates that reflect the result of general mortality across designated time intervals, understanding the per day risk of individuals to specific mortality events can be critically important to understanding population dynamics for harvested species (Heisey and Patterson 2006). The influence of anthropogenic (hunting, car collisions, etc.) vs. natural sources of mortality (predation, variation in resources) and how they interact to influence populations (i.e., additively or in a compensatory manner) form the basis for much of the theory and practice associated with game management in North America (Bolen and Robinson 2003). Harvest can be considered compensatory when harvest mortality is substituted for natural mortality that would have occurred without hunting (Anderson and Burnham 1976). In contrast, hunting can be additive when harvest mortality adds to the natural mortality by removing individuals that would have otherwise survived if there was no hunting pressure on the population (Anderson and Burnham 1976). Most wildlife managers allocate hunting tags under the notion that deer have a harvestable surplus, meaning that a similar number of deer harvested each season would have died from other causes if they were not removed by hunters in a similar timeframe (i.e., hunting is "compensatory"; Wallmo 1981). Thus, although it is often difficult to determine whether specific causes of mortality are additive or compensatory, in order to set sustainable harvest levels it is crucial for wildlife managers to understand the relative contribution of hunting and other sources of anthropogenic mortality (i.e., vehicle collisions) to mule deer population dynamics (Bartmann et al. 1992; Bookhout 1994).

Causes of mortality that have been identified at rates high enough to decrease mule deer populations include predation (coyote and cougar), harvest (legal and

illegal), starvation and malnutrition, vehicle collisions, and disease (Bleich and Taylor 1998, Bender et al. 2007). Cougar predation was the leading cause of mortality for a mule deer population in northeastern Oregon (Mathews and Coggins 1997), whereas starvation was the major cause of mortality for female mule deer in New Mexico (Bender et al. 2007). In most cases, there is little support for the additive effect of predation to mule deer population changes (Bartmann et al. 1992, Bishop et al. 2009, Hurley et al. 2011).

MANAGEMENT OF MULE DEER IN OREGON

Declining mule deer populations are of concern in Oregon because they are a valuable wildlife resource at the state, regional, and local level (Oregon Department Fish and Wildlife 2003). Oregon Department of Fish and Wildlife (ODFW) estimated that the annual mule deer harvest generates between $14.9 and $29.8 million for Oregon's economy (Oregon Department of Fish and Wildlife 2003). In addition, state wildlife management agencies are legally responsible for managing wildlife resources for an array of stakeholder interests and ecological functions, such as maintaining biodiversity or conservation of protected species. This management responsibility can become more challenging when wildlife habitat occurs on land that is not managed by the state. Much of the land in south-central Oregon is federally owned, including the Deschutes and Winema-Fremont National Forest administered by USDA Forest Service, and lands administered by the Bureau of Land Management (US Dept. of Interior). Privately owned lands are also interspersed throughout the region. Management goals on federal lands include providing recreational and resource extraction opportunities (i.e. timber harvest – USDA Forest Service; energy development - Bureau of Land Management). However, it is difficult to achieve these goals simultaneously, particularly when human development is increasing across the west (Kline et al. 2004) and can have negative effects on mule deer populations (Sawyer et al. 2005).

ODFW manages their ungulate populations within the context of discretely bounded areas known as Wildlife Management Units (WMUs). WMUs were created in 1958 to facilitate the equal distribution of wildlife harvest levels across the state

(Mace et al. 1995). The boundaries were established prior to the availability of information on animal movements across the landscape, so were set by societal and geographic factors rather than as boundaries that contained discrete populations of managed species (D.H. Jackson, Oregon Department of Fish and Wildlife, personal communication). Typically, mule deer hunting regulations in Oregon are established for each WMU based on the results of the annual herd composition survey, and the annual hunter harvest survey (Oregon Department of Fish and Wildlife 2003). After each hunting season, fall herd composition surveys are conducted to classify deer by sex and age class (Oregon Department of Fish and Wildlife 2003). These surveys are conducted visually by aircraft, vehicle, horseback, or on foot. Deer are counted, sexed, and aged, and the information is used to determine how many bucks and fawns there are per 100 does (Oregon Department of Fish and Wildlife 2003). Post-season buck:doe ratios indicate the number and age classes of bucks available for breeding relative to the number of does, and adult:fawn ratios indicate the number of fawns present per adult in the population before winter (Oregon Department of Fish and Wildlife 2003). Spring herd composition (adult:fawn) surveys are used to index over-winter survival and fawn recruitment. Additionally, after the hunting season, surveys are conducted by contacting hunters (those who bought mule deer tags) by phone to find out how many days they hunted and whether they were successful. This harvest survey information is used to estimate the average number of hunter-days per year, hunter success rates, and the total number of mule deer harvested each year (Oregon Department of Fish and Wildlife 2003). Until recently, these surveys were the only way to estimate the number of deer harvested each year, but in 2012, ODFW implemented mandatory harvest reporting, so all hunters have to report the number of deer they killed each year, and these data will aid in obtaining accurate harvest estimates. However, these methods are generally not explicit enough to accurately model population dynamics because they only measure recruitment (White and Bartmann 1997). For wildlife managers who are using population models to project the following year's harvest, the most sensitive parameter in a population model is adult female survival, so accurate estimates of annual survival rates are required to estimate annual rates of population change (White and Bartmann 1997).

ODFW Mule Deer Research Project

The use of radio telemetry methods for monitoring ungulate populations has allowed biologists to understand and identify herd and sub-population distribution and habitat use, to determine survival rates, and identify specific causes of mortality, thereby providing information necessary for effective game management strategies (e.g., Millspaugh and Marzluff 2001). Radio telemetry techniques offer advances over traditional count or mark-resight or recapture methods by providing information on survival status without being invasive (recaptures are not required) and mortality censors included in the units allow for identification of death events shortly after they occur (Murray 2006). The advance of global positioning system collars (GPS), that allow data to be stored directly in the collars or downloaded from a satellite to a workstation has increased the accuracy of location data (Bowman et al. 2000), the frequency with which locations and live/dead status can be obtained, and decreased personnel expenses required to track animals using traditional radio-transmitter technology (Hebblewhite and Haydon 2010). Using these devices, it is now possible for researchers to study movements and population dynamics of large ungulates at fine temporal or spatial scales.

From 2006 to 2012, Oregon Department of Fish and Wildlife implemented a study to estimate survival and cause-specific mortality, as well as to document habitat selection, movement parameters, and seasonal distribution of mule deer in south-central Oregon. Agency personnel marked 591 mule deer with radio transmitter collars in locations that would reflect exposure to differing risks of mortality (i.e., number of highways traversed during annual movement, predation). In addition, harvest pressure (i.e., percentage of allotted hunting tags sold each year) varied by WMUs, so deer were captured and collared in locations that reflected the range in harvest pressure across the study area. A majority (457) of the deployed collars provided locations based on Global Positioning System and included a mortality sensor to monitor survival and allow evaluation of mortality causes shortly after they occurred.

As a part of this larger study, my research objectives were to estimate survival and cause-specific mortality for this sample of radio-marked mule deer in eastern

Oregon. I used this extensive radio-telemetry dataset to develop a better understanding of mule deer survival, particularly for females, in south-central Oregon, as influenced by seasonal distribution, environmental factors like annual and climatic variation, and movement behavior (Chapter 2). In addition, I determined the net impact of the factors that affect mortality for both male and female mule deer (Chapter 2). This information in turn will better equip biologist and wildlife managers with more accurate population statistics and aid in Oregon's mule deer management decisions (Chapter 3).

LITERATURE CITED

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the Mallard: VI. The effect of exploitation on survival. United States Fish and Wildlife Service Resource Publication 128.

Anthony, R. G. 1976. Influence of drought on diets and numbers of desert deer. Journal of Wildlife Management 40:140–144.

Bartmann R.M., G.C. White, and L.H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:3-39.

Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118–1124.

Bishop C.J., J.W. Unsworth, and E.O. Garton. 2005. Mule deer survival among populations in Southwest Idaho. The Journal of Wildlife Management 69:311-321.

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.

Bolen, E.G., and W.L. Robinson. 2003. Wildlife ecology and management. Fifth edition. Pearson Education Inc., Upper Saddle River, New Jersey, USA.

Bolger D.T., W.D. Newmark, T.A .Morrison, and D.F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates.

Ecology Letters 11:63-77.

Bookhout, T.A., editor. 1994. Research and management techniques for wildlife and habitats. Fifth Edition. The Wildlife Society, Bethesda, Maryland, USA.

Bowman, J.L., Kochanny, C.O., Demarais, S. and Leopold, B.D. 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28:141–145.

Brown, C.G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. The Journal of Wildlife Management 56:246-253.

Bureau of Land Management. 2015 Strategic Plan. United States Department of the Interior p30.

Clements, C.D., J.A. Young. 1997. A viewpoint: rangeland health and mule deer habitat. Journal of Range Management 50:129-138.

Connelly, G. E. 1981. Limiting factors and population regulation. Pages 245-285 in O. C.Wall-mo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

D'Eon, R.G., and R. Serrouya. 2005. Mule deer seasonal movement and multiscale resource selection using global positioning system radio telemetry. American Society of Mammologists 86:736-744.

Eberhardt, L. E., E.E. Hanson, and L.L. Cadwell. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. Journal of Mammalogy 65: 404–409.

Forrester, T.D. and H.U. Whittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer Odeocileus hemionus in North America. Mammal Review 43: 292-308.

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.

Garrott, R. A., G.C. White, R.M. Bartmann, L.H. Carpenter, and A.W. Alldredge. 1987. Movements of female mule deer in northwest Colorado." The Journal of Wildlife Management 51: 634–643.

Gruell, G.E., and N.J. Papez. 1963. Movements of mule deer in northeastern Nevada. Journal of Wildlife Mangement 27:414-423.

Hammitt, W. E., Cole, D. N., & Monz, C. A. 2015. Wildland recreation: ecology and management. John Wiley & Sons, West Sussex, UK

Hebblewhite M., and D.T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B 365:2303–2312

Heisey, D.M., and B.R. Patterson. 2006. A review of method to estimate cause-specific mortality in presence of competing risks. The Journal of Wildlife Management 70:1544-1555.

Hilborn, R. and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty. Chapman Hall. New York.

Hoenes, B.D., and L.C. Bender. 2012. Factors influencing foraging habitats of mule deer, (Odocoileus hemionus) in the San Andres Mountains, New Mexico. The Southwest Naturalist 57:37-379.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1–33.

Jackson, D. H., and J. Cupples. 2012. Mule deer ecology in south central Oregon. Oregon Department of Fish and Wildlife. Annual Project Performance Report.

Kline, D.K., D. L. Azuma, and R.J. Alig. 2004. Population growth, urban expansion and private forestry in western Oregon. Forest Science 50:33-43.

Kline, J.D. 2012. Seasonal neighbors: residential development encroaches on mule deer winter range in central Oregon. Pacific Northwest Research Station, Publication 140, Portland, Oregon, USA.

Kucera, T.E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122-130.

Leopold, B.D. and P.R. Krausman. 1991. Factors influencing desert mule deer distribution and productivity in southwestern Texas. Southwestern Naturalist 36:67–74.

Litvaitis, J.A., and J. P. Tash. 2008. An approach toward understanding wildlife-vehicle collisions. Environmental Management 42:688-697.

Lloyd, J. and A. Casey. 2005. Wildlife hotspots along highways in Northwestern Oregon. Report to Oregon Department of Transportation, Salem, OR, 64 pp.

Lukacs, P.M., G.C. White, B.E. Watkins, R. H. Kahn, B.A. Banulis, A.A. Holland,

J.A. Martens, and J. Vayhinger. 2009. Separating components of variation in survival of mule deer in Colorado. The Journal of Wildlife Management. 73: 817-826.

Mace, R.U., R. Denney, and R. Ingram. 1995. Big game history. Oregon Department Fish and Wildlife, Portland, OR, USA.

Matthews, P. E., and V.L. Coggins. 1997. Movements and mortality of mule deer in the Wallowa Mountains. In Proceedings of the 1997 Deer/Elk Workshop. Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, Arizona, USA pp. 78-88.

Millspaugh, J.J., and J. M. Marzluff. 2001. Radio tracking and animal populations. Academic Press, San Diego, CA. 474pp.

Monteith, K.L., C.B. Vernon, B.M. Stephenson, M.M. Conner, R.W. Klaver, and R.T. Bowyer. 2011. Timing of seasonal migration in mule deerL effects of climate, plant phenology, and life-history characteristics. Ecosphere 2:1-34.

Murray, D.L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70:1530-1543.

Nichols, J. D., F. A. Johnson, and B. K. Williams. 1995. Managing North American waterfowl in the face of uncertainty. Ann. Rev. Ecol. Syst. 26:177-199.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat section and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

Oregon Department of Fish and Wildlife. 2003. Oregon's mule deer management plan. Oregon Department of Fish and Wildlife, Portland, OR, USA.

Oregon Department Fish and Wildlife. 2015. Mule deer population trend in Oregon by Wildlife Management Unit. <http://www.dfw.state.or.us/resources/hunting/big_game/controlled_hunts/docs/hunt_statistics/15/Mule_Deer_10-15_26Jun15.pdf>. Accessed 12 Aug 2015.

Pac, D. F., and G. C. White. 2007. Survival and cause-specific mortality of male mule deer under different hunting regulations in the Bridger Mountains, Montana. Journal of Wildlife Management 71:816–827.

Peek, J.M., B. Dennis, and T. Hershey. 2002. Predicting population trends of mule deer. The Journal of Wildlife Management 66:729-736.

Pierce, B.M., R. T. Bowyer, and V.C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management, 8:533-

541.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist 137:50-66

Robling, K.A., S.L. Griffin, and S.Stolz. 2014. Movement patterns, survival and sightability of mule in central and western South Dakota. South Dakota Department of Game, Fish and Parks, Peirre, South Dakota, USA.

Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian Journal of Zoology 80:556–568.

Rost, G.R. and J.A. Bailey. 1979: Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43: 634-641.

Sawyer, H., F. Lindzey, and D. McWhriter. 2005. Mule deer and pronghorn in western Wyoming.Wildlife Society Bulletin 33:1266-1273.

Sawyer, H., R.M. Nielson, F. Lindzey, L.L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396-403

Smith, R. H., and A. LeCount. 1979. Some factors affecting survival of desert mule deer. Journal of Wildlife Management 43:657–665.

Thomas, T.R. and L.R. Irby. 1991: Winter habitat use by mule deer with access to wheat fields and planted forb grassland. Wildlife Society Bulletin 19: 155-162.

Unsworth, J. W., F.D. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. The Journal of Wildlife Management 63:315–326.

Wallmo, O.C., editor. 1981. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska.

West N.E. 1999. Synecology and disturbance regimes of sagebrush steppe ecosystems. Sagebrush Steppe Ecosystems Symposium, Boise State University, Boise, Idaho.

White, G.C., R.A. Garrot, R.M Bartmann, L.H. Carpenter, and A.W. Alldredge. 1987. Survival of mule deer in northwest Colorado. The Journal of Wildlife Management 51:852-859.

White, G.C., and R. M. Bartmann. 1997. Mule deer management-what should be monitored? Pages 104-118. Proceedings of the 1997 deer/elk workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, N.Y.

CHAPTER 2

SURVIVAL RATES AND CAUSE-SPECIFIC MORTALITY OF MULE DEER IN SOUTH-CENTRAL OREGON.

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INTRODUCTION

It is critical for wildlife managers to understand the population dynamics of a harvested species, particularly for ungulates, which are a valuable economic wildlife resource (Gordon et al. 2004). Besides their social and economic contribution (Oregon Department of Fish and Wildlife 2003) mule deer fulfill an important ecosystem service by directly and indirectly cycling nutrients through browsing and their effect on disturbance regimes (Hobbs et al. 1996). They are also an effective ecological indicator of early and mid-successional habitats because of their specific life stage requirements (Hanley et al. 1996).

Factors that are most commonly attributed to fluctuations in the population size of ungulates are highly variable survival rates for juveniles (1-year old; Gaillard et al. 1998) and fawns (White and Bartmann 1997). In fact, ungulate populations are generally characterized as having high, constant adult female survival rates (Gaillard et al. 1998). However, where survival rates for adult females have been quantified, they can vary temporally and spatially between populations (Nicholson et al. 1997, Unsworth et al. 1999, Bishop et al. 2005), and small changes in adult female survival of mule deer can have major impacts on the overall population growth rate (Morris and Doak 2002). A review of 48 research studies conducted on the population dynamics of mule deer (*Odocoileus hemionus)* and the black-tailed deer subspecies (*Odocoileus hemionus columbianus)* concluded that mule deer populations may rely more on high stable adult survival rates than other ungulate populations to prevent long-term population fluctuations (Forrester and Whittmer 2013). Thus, biotic and abiotic factors that increase variation in adult female survival rates can decrease mule deer population stability (Gaillard et al. 1998). Factors including predation (Zager et al. 2007, Bishop et al. 2009), weather (Monteith et al. 2011), migration behavior (Nicholson et al. 1997), vehicle collisions (Neilsen et al. 2003), and other sources of non-hunting anthropogenic mortality (automobiles, trains, and fences; Zager et al. 2007) have been associated with temporal and spatial variation in mule deer survival rates.

In addition to understanding the probability of surviving over some specified interval of time, understanding the probability of mortality from a particular risk in a population at a particular time (i.e., cause-specific mortality rates; Heisey & Patterson 2006) can be equally important to the understanding and management of ungulate population dynamics. Both sexes of mule deer are at risk from a variety of factors and the probability of mortality during winter, due to predation for example, can be as high as 14% for populations preyed on by cougars (Robinson et al. 2002) or 11% for those preyed on by coyotes (Bishop et al. 2005). Annual mortality risk for adult mule deer from malnutrition (23%; Bender et al. 2007) and harvest (35%; Bishop et al. 2005) can be even higher.

For many ungulate populations, migratory individuals outnumber residents by an order of magnitude in grassland ecosystems around the world (Fryxell et al. 1988). Though the evolutionary reasoning for these life-history trade-offs are not well understood, there are clear costs and benefits to migration behavior (Alerstam et al. 2003). The benefits include seasonal escape from predation or insect harassment (Fryxell et al. 1988) and the advantage of following seasonal food availability (Pettorelli et al. 2005) or other limiting resources (water; Murray 1995). The direct and indirect costs of migration are the physical stress of traveling from one location to the next and the risks of predation or inadvertent injury while traveling through unknown locations (Alerstam et al. 2003). Deer that migrate must travel further distances, and can be exposed to greater risks such as predation or vehicle collisions associated with crossing highways (Nicholson et al. 1997). This evolutionary trade-off is found in mule deer populations across the west that contains both migratory and non-migratory individuals (Garrott et al. 1987, Brown 1992, Nicholson et al. 1997).

Mule deer that migrate generally move from higher-elevation summer ranges to lower-elevation winter ranges, presumably to follow seasonal forage and water availability (Nicholson et al. 1997, D'Eon and Serrouya 2005). However, independent of migration behavior, the location of winter ranges seems to affect mule deer survival (Bishop et al. 2005). The encroaching residential development on lower elevation winter ranges can negatively affect mule deer populations by reducing

available habitat and increasing stress (Kline 2012). Anthropogenic activity in urban areas can also increase the chances of vehicle collisions (Neilsen et al. 2003).

In addition to migration behavior and the location of seasonal ranges, environmental variation can account for variation in survival of wild ungulates (Saether 1997). Seasonal movement of individuals between summer and winter ranges can subject an ungulate population to varying climate or weather stresses during different parts of the annual cycle (Post and Stenseth 1999). In particular, winter precipitation (Bishop et al. 2005), winter severity (DeLgiudice et al. 2012), and midsummer drought (Brown et al. 2006) can be associated with variation in mule deer survival. Climate change has led to increased winter precipitation and a rise in winter temperatures in northern continental areas (Walther 2002). Although there is an increase in snow accumulation, snow melt occurs much earlier than in previous years, leading to a shift in plant emergence and their reproductive performance (Inouye and McGuire 1991, Molau 1997). Due to the shifting phenology of plants, snow accumulation and timing of snow melt influence can have a direct effect on forage availability, growth, and fecundity for northern ungulates (Post and Stenseth 1999). Climate change models for the Pacific Northwest predict drier summers and wetter autumns and winters (Mote and Salathé 2010). Climate models have also predicted an associated wildlife fire risk in the Western United States due to a rise in summer and spring temperatures and earlier spring snowmelt (Westerling et al. 2006). This can have a greater impact on ungulates that rely on seasonal movement for forage opportunities (Post and Stenseth 1999).

My study was designed to gain a better understanding of adult female mule deer survival in south-central Oregon, as influenced by seasonal distribution, environmental factors, and movement behavior. The objectives of my study were 1) to estimate survival rates and the factors associated with variation in survival for adult female mule deer in eastern Oregon using 7 years (2005-2012) of GPS collar data, and 2) to investigate cause-specific mortality of competing risks for both males and female deer during the same time period. Specifically, I investigated the effects of season, year, summer and winter range locations, movement behavior, local weather, and regional climate patterns on adult female survival. I also estimated cause-specific

mortality risks associated with predation, harvest, and other sources of anthropogenic mortality (i.e., vehicle collisions).

STUDY AREA

The study area was located in south-central Oregon near the eastern slopes of the Cascade Range and extended into the High Lava Plains and the Basin and Range provinces (Franklin and Dyrness 1973). The study area primarily included lands under federal ownership administered by the USDA Forest Service and Bureau of Land Management, with private land dispersed throughout. Although plant communities differed across the study area due to longitude, elevation, and soil type (Franklin and Dyrness 1973), vegetation for a large portion of study area was typical of shrub-steppe habitat (low rainfall, natural grassland primary composed of sage brush) with forest habitats at higher elevation. Shrub-steppe habitat is characterized by plant communities which include sagebrush (*Artemisia* sp.), antelope bitterbrush (*Purshia tridentata),* snowbrush (*Ceanothus velutinus*), rabbitbrush (*Chrysothamnus* sp.), fescue (*Festuca* sp.), wheat grass (*Agropyron* sp.), and blue bunch wheatgrass (*Agropyron spicatums*). Forested habitat is characterized by plant communities which include ponderosa pine (*Pinus ponderosa*), western juniper (*Juniperus occidentalis*), douglas fir (*Pseudotsuga menziesi*), quaking aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*).

Oregon Department of Fish and Wildlife (ODFW) manages ungulate populations within the context of discretely bounded areas know as Wildlife Management Units (WMUs). WMUs were created in 1958 to facilitate the equal distribution of wildlife harvest levels across the state (Mace et al. 1995). State administrative boundaries within my study area included Klamath, Lake, and Deschutes counties, and the Fort Rock, Interstate, Klamath Falls, Paulina, Metolius, Silver Lake, Sprague, Upper Deschutes, and Wagontire WMUs (Oregon Department of Fish and Wildlife 2003). The core study area included the Fort Rock, Sprague, Sliver Lake, and portions of Paulina, Wagontire, and Upper Deschutes WMUs (Figure 1). Some mule deer also occupied small areas during the winter in Maury and

Warner WMUs, north-central California, west of the Cascade Mountain crest in McKenzie, Indigo, and Santiam WMUs.

The climate in this region is described as having dry warm summers (average July maximum temperatures of 27 to 31^0C) and cold winters (average minimum January temperatures of -7 to -11^0C) (PRISM Climate Group, http://www.prism.oregonstate.edu/). Annual precipitation ranges from 38cm to 89cm, usually in the form of snow (Franklin and Dyrness 1973), and elevations range from 340m to 3,157m. Soil types varied widely throughout the study area, mostly compromised of pumice and ash, due to the eruption of Mt. Mazama over 8,000 years ago (Franklin and Dyrness 1973).

METHODS

Capture and Handling

A total of 621 mule deer were captured and radio-collared by ODFW research personnel from June 2005 to September 2011. The majority were captured using helicopter net guns (439 deer; 66.4%), with the rest captured using panel or clover traps (Clover 1954), or chemical immobilized using a rifle-fired dart. Seventy-nine deer were captured but released because they had been collared previously during the study or were fawns (only adults were collared). A combination of Telazol (Zoetis Inc., Kalamazoo, MI, USA), Xylazine,(Lloyd Inc., Shenandoah, IA, USA), and Ketamine (Bionichepharma, Galaway, Ireland) was used to chemically immobilize deer with Tolazine used as an antagonist (J. Burco, Oregon Department Fish and Wildlife, personal communication, Monteith et al. 2012). The ODFW Veterinarian supervised capture operations which followed the Guidelines for the Capture, Handling, and Care of Mammals as approved by the American Society of Mammologists (Committee on Acceptable Field Methods 1987). ODFW staff restrained and blindfolded all captured deer to reduce stress and then deer were ear-tagged, sexed, and aged (fawn, yearling, adult), and blood, tissue, and fecal samples were collected.

Research personnel placed radio collars on mule deer captured in 9 Oregon WMUs (Table 1). Female deer were collared with VHF transmitter collars (MOD-

500, Telonics Inc., Mesa, AZ) or Global Positioning System radio collars (GPS), with data either stored-on-board (3300S, LOTEK Engineering Ltd., Newmarket, ON, Canada), or downloaded remotely (4400S, LOTEK Engineering Ltd., Newmarket, ON, Canada). Due to the swelling of the neck during the rut, male deer needed to receive collars that would expand, which were not available in GPS systems during this study. Therefore, males were fitted with VHF transmitters (MOD-500, Telonics Inc., Mesa, AZ) attached to an expanding Kydex collar (Keister et al. 1988). GPS collars obtained location data automatically every 4 hours, which was much more efficient and precise than manual triangulations required for the VHF collars. Therefore, GPS collars were preferred, and female deer were targeted and collared more frequently than males (526 does, 91 bucks). A total of 496 GPS store-on-board (females only), 44 VHF (female), and 81 expanding VHF (male) collars were deployed (see Table 2). A total of 58 deer lost radio collars (i.e., slipped or broken; n=18), experienced collar malfunction or permanent signal loss (n=33), or died (n=7) within the 14-day period between capture and entry into the sample population and were excluded from subsequent analyses.

VHF radio-collared deer were located a minimum of 1-2 times a month using aerial or ground telemetry and their locations recorded using the Universal Transverse Mercator (UTM) coordinate system. Deer wearing VHF collars were monitored for as long as they were alive during the study, which ranged from 2 weeks to 6 years. Ground telemetry included a handheld Yagi antennae or a truck-mounted single Omni antenna, whereas aerial telemetry was conducted from a fixed-wing Cessna aircraft with Yagi antennas attached to both wing struts. During the fall (October-November) and spring (April-June) migration periods, deer with VHF radio-collars were located as frequently as possible (2-4 times per month) to determine movement patterns and to identify critical migration corridors.

GPS radio-collars were programmed to obtain locations every 4 h except during fall and spring migration periods when programmed location frequency was increased to obtain a location every 1.5 h. The comprehensive location data stored on collars became available when the deer died, or once the radio collar automatically detached from the deer 17 months after attachment. All radio collars had a motion-

sensitive sensor that would cause a change in the transmitter's pulse rate if the transmitter was motionless for >4 h. Those signals were considered indicative of mortality and were investigated as soon as possible (usually within 24-72 hours). Mortality investigations included necropsies if the carcass was present, and assignment to one of 8 mortality categories including 1) cougar predation, 2) coyote predation, 3) illegal harvest, 4) harvest, 5) vehicle collision, 6) disease (i.e. adenovirus hemorrhagic disease), 7) other (including fence collisions, malnutrition/starvation, and death during fawning) and 8) unknown. A standardized protocol was developed by ODFW and used to evaluate cause of death for every necropsy. Causes of mortality were ranked as "possible", "probable", or "positive" based on available evidence and only "probable" or "positive" causes were included as specific mortality causes in my analysis. If it appeared predation had occurred, a complete checklist of descriptive indications (i.e. bite marks, scat, tracks) at each site was required for a carcass to be assigned to a potential predator (cougar, bobcat, coyote, bear); otherwise it was classified as scavenged and therefore, predator unknown. After a deer mortality was investigated, the GPS collar was collected and the collar location data were downloaded into a GIS database, ArcMap, (ArcMap Version 10.0, Environmental Systems Research Institute, Inc., Redlands, California, USA).

Covariates and predicted effects on survival

INDIVIDUAL COVARIATES

Temporal variation- I estimated monthly survival rates for adult female mule deer from August 2005 through May 2012. I defined the mule deer annual cycle in terms of their biology with each biological year starting on June 1, when the majority of fawns are born (Speten 2014), and ending 12 months later on May 31. I defined 4 seasons that reflected different stages of the mule deer life cycle: 1) Summer (June 1st- August 30th), 2) Fall (September 1st - November 30th), 3) Winter (December 1st – February 28th), and 4) Spring (March 1st – May 31st). I also identified spring (April & May) and fall (October & November) migration periods, and the hunting season (August - October) as potentially important sources of temporal variation in survival.

Although there is no female mule deer hunting season during this study, I predicted that the disturbance of hunting (hunters on foot, sounds of firearms, increased vehicle use) would negatively affect females by increasing flight response time (Stankowich 2008), decreasing time spent foraging, or increasing interactions with vehicles. I predicted that these yearly and seasonal periods could have either additive effect or interactive effects on survival.

Summer and winter WMU location- I plotted the location data for each individual deer to determine summer (June 1st – August 30th) and winter ranges (December 1st – February 28th). I categorized movements between the ranges as migration routes and did not use these locations to determine either range. I differentiated between ranges and migration routes by examining distances and direction of sequential movements. The beginning of the migration movement was defined by the first movement (>3 km) outside the seasonal ranges without returning, and ended once the individual reached the new seasonal range (Thomas and Irby 1990). Each seasonal range was determined by short movements (<3km within 4 hour period). Once each summer and winter cluster was determined and migration locations were removed, I used spatial statistics in ArcMap (ArcMap Version 10.0, Environmental Systems Research Institute, Inc., Redlands, California, USA) to obtain the mean center of the seasonal range. I considered a deer to be migrating when the direction of its movement was away from the mean center of one seasonal range in the direction of the other mean center seasonal range, outside of the cluster (Brown 1992). I also assigned each seasonal range center a WMU number associated with the WMU where it occurred. If a deer remained in one area all year round then I categorized it as a resident deer and calculated a mean center using all location data. I predicted variation in survival could be explained by variation in summer and winter WMU location.

Herd group- Mule deer herd composition was estimated annually for population trend information and hunting tag allocation by ODFW (Oregon Department Fish and Wildlife 2003). Historically, managers would conduct these counts during the spring (March-April) and fall (November-December) months when some deer were moving between ranges, and therefore, these observations did not

accurately define true range locations, or the complexity associated with migration. A previous analysis, using the same spatial data from the GPS radio-collar information as my study (Cupples and Jackson 2014; Figure 2), was able to identify groups of deer based on fine-scale temporal location data. Mule deer groups, identified as "herds" are now determined by similarities in winter location, angle and distance of travel from winter location, and migration pathways (Jackie Cupples, personal communication, ODFW; Table 3). There is a large amount of variation in wintering range locations of herd groups, the distance they migrate between ranges, and the migration pathways they take each spring and fall. I predicted that variation in survival could be explained by differences in herd groups, which might reflect differences in migration behavior and winter habitat use.

   Proximity to development- I used the Wildland Urban Interface (WUI) geospatial data from Oregon Department Forestry (http://www.oregon.gov/odf/pages/fire/sb360/sb360.aspx) to delineate zones in the study area where human development occurred. This information is used to determine the interface where houses (urban, suburban, and sometimes rural areas) meet with a undeveloped habitats (Radeloff et al. 2005). I used this information as an index of human development in proximity to the seasonal ranges and migration pathways of mule deer. I assigned each individual deer a binary value for each seasonal range depending on whether that range was inside (= "1") or outside (= "0") the WUI. Previous studies have found that human disturbance (i.e. development) has a negative effect on mule deer populations (Nicholson et al. 1997) including my study population (Kline 2012). Thus, I predicted that deer that had ranges inside the WUI would have lower survival than deer that had ranges outside due to higher exposure of human disturbance.

MOVEMENT COVARIATES

Migratory Behavior & Distance Migrated – I considered an individual deer "migratory" if its seasonal ranges did not overlap (Brown 1992), whereas I categorized deer that had both winter and summer ranges in the same location as "resident" deer. If a deer died before I could determine its migratory status, I

categorized it as "unknown", so I had 3 categories associated with migration behavior and 2 dummy variables to code these categories (Migratory: Mig=1 and Unk=0, Unknown: Mig=0 and Unk=1; Resident: Mig=0 and Unk=0). I estimated distance migrated by measuring the distance (miles) between the seasonal range centers following the actual migration path. I predicted that deer that migrated would have lower survival than deer that did not, due to an increase in risk of predation or vehicle collision while moving between ranges. I also predicted the survival rates would decrease as the distance traveled between season ranges increased due to an increase in energy expenditure, risk of predation, or vehicle collision.

Number of highways crossed and number of crossings- Deer-vehicle highway collisions have long been a concern to state agencies nationwide (Romin and Bissonette 1996). The Department of Oregon Transportation describes the state and regional highways in the study area as "a safe and efficient, high-speed, continuous-flow operation" (Oregon Department of Transportation 1999). I used Oregon state highways GIS layer from Oregon Department of Transportation land use development zones (2009) (http://www.oregon.gov/ODOT/TD/TDATA/pages/gis/odotmaps.aspx) to calculate the number of highways a deer crossed during both fall and spring migration (range 0-3) and used those numbers as two continuous covariates in the survival analysis. In some cases, deer would take a different migration path back to its seasonal range. Therefore, the number of highway crossings a deer made during migration was also calculated and used as a continuous variable for the survival analysis (range 0-6). I predicted that survival rates would decrease in association with the number or highways crossed and number of crossings during migration because the risk of collision with a vehicle would be increased the more often a deer crossed a large highway.

ENVIRONMENTAL COVARIATES

Precipitation - Weather information from 2005-2012 was obtained from the PRISM Climate Group website (http://www.prism.oregonstate.edu/). PRISM (Parameter Elevated Regression on Independent Slopes Models) models incorporate aspect, topographic effects, rain shadows, and coastal effects into a raster-based digital map

(4 km² grid cell size) based off of weather station information. I calculated a single winter precipitation value (mm) as an individual covariate by averaging the mean monthly precipitation (mm) for December, January, and February. I did this for two spatial scales: 1) the individual winter range and 2) across the entire WMU assigned to each winter range. The resolution of the PRISM data was similar in size to the winter seasonal ranges, so I used the precipitation value taken at the mean center point of the winter range to determine the winter precipitation at the individual level. Due to the expansive area within each WMU (> 5,000 km²), I used zonal statistic in ArcMap (ArcMap Version 10.0, Environmental Systems Research Institute, Inc., Redlands, California, USA) to calculate the mean winter precipitation across each WMU for each year. I chose two different spatial scales (WMU and individual home range) to be able to detect different weather patterns and variability, while trying to eliminate bias of perceived ecological importance (Levin 1992). Snow levels can make deer more susceptible to predation and starvation, therefore, I predicted that winter survival rates would be negatively affected by higher winter precipitation at the WMU level and individual home range level because increased.

Winter Severity- I used geospatial winter severity data developed by ODFW to index winter range conditions during December through February (Johnson et al. 2012). This index was calculated using total precipitation from December to February and the average monthly minimum temperature and then standardized into a single metric (WSI = standardized precipitation – standardized temperature; Johnson et al. 2012) using PRISM models (PRISM Climate Group 2010). I calculated winter severity at two spatial scales: 1) each individual's winter range and 2) at the WMU scale, following the methods outlined for winter precipitation above. I predicted that survival rates would be negatively affected by higher winter severity at the WMU level and individual home range level due deer becoming more susceptible to predation and starvation as temperatures lower and precipitation increases.

Drought- I used Palmer Drought Severity Index (PDSI; Palmer 1965) data (http://www.wrcc.dri.edu/wwdt/about.html) to compare an index to soil moisture conditions across years on deer summer ranges. This standardized index is widely-used to measure long-term drought intensity, which is based on evaporation, soil

moisture, and temperature on past and current weather patterns (Palmer 1965). PDSI values range from -6 to +6, with negative values indicating drier conditions (Palmer 1965). Ungulate survival was positively related to PDSI in other systems (Lawrence et al. 2004, Brown et al. 2006), suggesting that drought during the summer season can negatively impact female ungulate survival. I used the PDSI for the month of August to determine if summer drought directly influenced summer survival, or if there were lag effects of drought that influenced fall survival at the individual summer range level.

Adult Female Survival Analysis

I generated monthly survival estimates for adult female mule deer using known-fate models, with estimates and model selection statistics generated in Program MARK (White and Burnham 1999). This approach allowed for a staggered entry, and the modeling of temporal variation as well as individually-specific covariates that I predicted would affect survival within a standardized model selection and multi-model inference framework (Murray 2006). Males and females collared with VHF collars were excluded from this analysis due to irregular or sparse signal checks associated with the VHF collars and the small sample sizes available per survival interval (<20). Deer that died within 14 days of capture were also excluded from analyses due to likelihood of capture myopathy (Chalmers and Barrett 1982).

I used an information-theoretic approach to evaluate models using the Akaike Information Criterion (AICc); models within 2 ΔAICc were considered competitive with the top model (Burnham and Anderson 2002). I also examined the 95% confidence intervals for slope coefficients (betas) and used the degree of interval overlap to evaluate the direction and strength of model covariates. I developed an *a priori* model set and used a hierarchical modeling approach to investigate specific covariates and associated hypotheses of interest (Table 4). This approach allowed me to avoid generating a large model set that included every possible combination of covariates, and has been shown to provide model selection results comparable to an "all possible combinations" strategy (Doherty et al. 2010).

I began by building models that examined temporal covariates including year, season, migration period, and hunting season. Retaining the model with the best temporal structure on monthly survival, I then tested the location covariates associated with individuals, including summer and winter WMU location, herd group number, or proximity to human development (winter range present within WUI). The best model from this step was retained, and I added movement parameters, including migration behavior, distance migrated, and number of highway crossed. Finally, using the competitive models from the previous two modeling steps, I tested whether monthly survival was associated with winter precipitation or winter severity at the WMU scale and also at the individual home range scale. The most general model including separate estimates of survival for each month and year [S(t)] and the model with no effects [S(.)] were included for comparison at all modeling stages.

Cause-Specific Mortality Analysis

Both males and females were included in this analysis because precisely timed signal checks to confirm survival were not required as long as deer were checked regularly enough to determine survival and mortality at roughly monthly intervals. The only information needed was sex, entry date (the date the deer was collared), exit date (the date the deer died), and cause of mortality. I also analyzed each sex separately because the competing risks varied by group (i.e., harvest mortality for males only) due to differences in behavior and management objectives. Deer that died within 14 days of capture were excluded from analyses due to likelihood of capture myopathy (Chalmers and Barrett 1982). To determine cause-specific mortality rates (CSM), I used non-parametric cumulative incidence function (CIF) models (Heisey and Patterson 2006) using the *wild1* package (Sargeant 2011) in Program R (R Development Core Team 2014). I also generated a Kaplan-Meier annual survival rate estimate for males using the *wild1* package (Sargeant 2011) in Program R (R Development Core Team 2014).

The causes of mortality were grouped into 4 competing risks for males: harvest (shot within season and claimed with a hunting tag), illegal harvest, (shot outside of the legal hunting season), predation (cougar and coyote combined), and

"other" which grouped other mortality sources that made up a small fraction of the known mortalities for males including disease, starvation/malnutrition and collisions with vehicles or fencing.

The competing risks for females were also grouped into 4 categories: predation, anthropogenic mortality (vehicle collision or fencing entanglement), illegal harvest, and natural mortality (fawning, disease, and starvation/malnutrition). During this study, Oregon did not issue hunting tags for females and very few deer management permits were given to landowners with nuisance deer (i.e., n=1 for deer in this study). Illegal harvest for females was defined as any deer that was found mortality wounded from an arrow or firearm both inside and outside the hunting season. While legal harvest of female mule deer on most state and federal lands in Oregon was not permitted during my study, there is a small possibility that some legal harvest of female deer on tribal lands could have occurred both within Oregon's archery/rifle season, as well as outside this season, so there is a potential that some of the females were unclaimed legal tribal take. However, considering that the locations of these mortalities fell well outside tribal hunting areas (all but 2 were 30+ miles away), it was unlikely these deer represented legal tribal harvest. . Therefore, all female deer that were killed by archery or rifle were considered illegal harvest.

Due to logistical difficulties associated with the location of mortalities (some were in difficult to reach places) and the limited number of personnel available to investigate mortalities, a portion of the carcasses could not be investigated in a timely enough manner to determine cause of death and became categorized as "unknowns". Including unknown mortality in a CSM can be misleading because the category contains multiple competing risks instead of those from a single source (Bishop et al. 2009). However, excluding the deer with unknown sources of mortality can positively bias survival estimates, risk functions, and the distribution of competing risks. For this study I chose to include the unknown sources of mortality as a separate risk, and I assumed that the distribution of unknown mortalities was random relative to the risk categories. Thus, while the mean estimates and distribution of competing risks should be considered "minimums", the relative distribution of mortalities among known risks should be unbiased.

RESULTS

Adult Female Survival Estimates

Out of the 526 collared females, only 408 females met the criteria for the known-fate survival analysis. I excluded 118 deer from the analysis based on collar type (VHF), failure during the data download process, or capture myopathy. Adult female survival (S) was best modeled by the effect of migration behavior (did a deer migrate or not), the additive effect of the fall migration time period (Oct-Nov) and the additive effect of winter precipitation at the level of the individual's winter range [S(MU + FMig + Ipp); Table 5]. Only models including migration behavior had any model weight, and survival was positively influenced by whether a deer migrated ($\hat{\beta}_{migrant}$ = 0.556, SE= 0.252, 95%CI= 0.060 to 1.052) compared to if a deer was resident, and resident deer had higher survival than unknowns ($\hat{\beta}_{unknown}$ = -1.719, SE= 0.325, 95% CI= -2.375 to -1.080). Survival also decreased during fall migration for all deer ($\hat{\beta}_{fall\ migration}$ = -0.413, SE=0.244, 95% CI= -0.892to -0.064) compared to monthly survival during the rest of the biological year (Mar-Sep). Precipitation on an individual's winter range was positively associated with survival ($\hat{\beta}_{Ipp=}$ = 0.014, SE=0.008, 95% CI= -0.002 to 0.031) during winter (Dec - Feb), contrary to predictions (Figure 3). However, the effect of winter precipitation was weak as evidenced by 95% CIs on the covariate coefficient that overlapped zero, albeit slightly (<10% of the interval overlapped zero) (Figure 4). Two other models were competitive (≤ 2 ΔAICc), but model weights were driven primarily by the inclusion of either the migration behavior covariate [migration; Table 5] or the individual winter precipitation covariate [Ipp; Table 5].

I calculated annual survival rates as the product of migratory months (Oct-Nov), winter months (Dec-Feb) and the rest of year (Mar-Sep) associated with a deer's biological year (June – May) from my best survival model including the effect of migration behavior, migration period and winter precipitation (mean value across all deer each year; $S_{MU + FMig + Ipp}$). I used a 1st order Taylor expansion (i.e., the Delta method; Appendix B, Cooch and White 2015) to estimate standard errors for these estimates (e.g., annual survival in 2005 = summer 2005*fall 2005*winter 2006, annual survival in 2006 = summer 2006*fall 2006*winter2007, etc.). For female

migrants, annual survival rates ranged from a low of 0.815 (SE =0.00995) in 2005 to a high of 0.821 (SE=0.00970) in 2010 (Table 6, Figure 5). For female residents, annual survival rates ranged from 0.755 (SE=0.02570) in 2005, to 0.765(SE=0.02488) in 2010 (Table 6, Figure 5).

Cause-specific Mortality Rates

Oregon Department of Fish and Wildlife was able to determine cause of mortality for 124 of 216 radio-collared mule deer that died during the study (both GPS and VHF; 57%, 42 males, 81 females) with the deaths of 94 other deer (43%, 8 males, 84 females) categorized as unknown (Table 7).

I calculated an annual cumulative incidence function separately for each sex (males, n= 50; females n = 166), and all competing risks were higher for males than for females. The cumulative annual risk of harvest was the highest known cause of mortality for males (0.249, 95%CI= 0.172 – 0.326), followed by predation (0.104, 95%CI = 0.042 – 0.166), illegal harvest (0.066, 95% CI=0.023-0.108), and the combined category of other mortality sources (0.061, 95%CI=0.006-0.115) The annual adult male survival rates for the 77 individuals in the CSM analysis was 0.40 (SE=0.015, 95%CI = 0.385-0.415).

The cumulative annual risk of predation was the highest known cause of mortality for females (0.044, 95% CI =0.028 -0.065), followed by human-caused mortality (0.038, 95% CI=0.021-0.054), illegal harvest (0.031, 95%CI=0.017-0.054) and natural mortality (0.007, 95%CI = 0.0002-0.015) (Table 8, Figure 6 & Figure 7).

DISCUSSION

Survival

I observed large differences in monthly survival rates between migratory deer and resident deer: on average, migratory deer had 6% higher annual survival rate compared to residents. Migration behavior represents a trade-off between the benefits of moving to higher quality habitat which can ultimately increase reproductive success, compared to the potentially greater risk of predation or vehicle collision during the migration process (Nicholson et al. 1997). In my study, moving to a

different seasonal range appeared to be worth the risk in terms of increased survival, and was also evident in the high number of migratory deer (n=316) compared to resident deer (n=69) observed in the sample population. Mule deer generally migrate from low elevations to a higher summer elevation for better foraging (D'Eon and Serrouya 2005, Monteith et al. 2011). Mule deer summer ranges offer higher nutritional benefits in terms of quantity and quality than winter ranges at lower elevations (Wallmo et al. 1977) and can be partly responsible for herd productivity (Julander et al. 1961). Historically, it may have been beneficial for some deer to remain on the winter range all year when foraging quality was not significantly better on the summer range (e.g., during drought) making it advantageous for deer not to leave lower elevations for better foraging, hence retaining non-migratory behavior. Average summer precipitation (June-August) was lower in 2008 and higher in 2009, but overall during my study summer rainfall was similar to the long-term average (Figure 8). Other studies have found annual variation in survival associated with drought during the summer months (Lawrence et al. 2004, Brown et al. 2006), but I found no support for an effect of drought on survival, likely because severe drought was not observed during the years of my study. Thus, it is difficult to determine if summer range forage quality influences one migratory strategy over the other in relation to weather patterns.

Human disturbance is difficult to quantify, and the parameter I developed specifically to quantify the effect of human disturbance on individual deer was not strongly supported. However, it may not have accurately represented the effect of development, land conversion, or vehicle traffic on mule deer. The positive effect of migration on survival that I did observe might represent the overall benefit to deer that winter farther away from the summer ranges in the Bend area. Thus, my study suggests there could be a link to lower survival for resident deer that live closer to urban areas. A recent study reported that the substantial increase in human development (resorts, homes, and roads) has led to an increase in habitat loss, disruption of migratory routes, and potentially increasing stress on the mule deer population in the Bend, Oregon area (Kline 2012). The sprawling urbanization could also be linked to a decrease in habitat quality and therefore, lack of sufficient

resources necessary for mule deer to meet their life history needs (i.e., forage, cover, water).

However, over the long-term, survival and reproduction between the two movement groups must ultimately result in benefits from both types of behaviors for mixed strategies to persist in a species or population (Nicholson et al. 1997, Hebblewhite and Merrill 2009). Unfortunately, collars were only worn by deer up to 17 months, so I was unable to determine if migratory strategies changed among individuals. Presumably some environmental factor either during early development of a deer, or annually if an individual can change strategies over time, contributes to whether a deer migrates or not every year. In southern California, during winters with low precipitation (little snow), it was more advantageous to be a resident and conversely, during winters with high precipitation it was beneficial to be a migrant (Nicholson et al. 1997). The increased rate of mortality for migrants during years of high precipitation, or snow depth, was attributed to increased cost of locomotion and decreased access to forage (Nicholson et al. 1997).

In addition to a consistent difference in monthly survival related to migration behavior category, I also observed a difference in monthly survival during the fall migration period (Oct-Nov) consistent with observations for mule deer in southern California (Nicholson et al. 1997). However, the negative effect observed in my study was consistent for both migrants and residents (no support for an interaction), and only occurred during the fall migration period rather than both fall and spring. One explanation could be the overlap of the fall migration period with the annual hunting season, although the model including a specific hunting season affect received little support in my analysis. Although females were not included in the legal harvest season in my study, the increase in human disturbance (increase in vehicle activity, sounds made from firearms, hunters on foot) may have increased the flight response, increasing energy expenditures (Stankowich 2008). The more energy an individual spends fleeing from disturbance, the less energy it has to spend on life history requirements such as foraging and reproductive behavior, which can ultimately decrease survival. The main deer hunting season in Oregon starts at the end of August and runs through October, so it only overlaps the fall migration period (Oct-

Nov) by a month. However, in conjunction with other hunting activities that run through October (upland gamebirds, waterfowl, bear, etc.) human disturbance may be high enough during the onset of migration to affect both resident and migratory deer (Budeau 2010, Oregon Department Fish and Wildlife 2015*a*, *b*).

In addition, a closer look at mortality rate (number of deaths per day on an annual scale) of each competing risk (Figure 9) for all adult females in my study suggests that 3 (predation, human-caused, and illegal harvest) out of the 4 competing risks I estimated have high mortality rates in late October (Julian date 300 = October 27th). Adult females had the highest rate of mortality due to illegal harvest during this time of year. Illegal harvest, coupled with a spike in predation at that same time, may be responsible for the negative effect on survival during the fall migration period. Predation negatively affects deer while they migrate through unfamiliar habitat (Nicholson et al. 1997) but the illegal harvest and human-caused mortality (mainly vehicle collisions) can have an effect on either resident or migratory deer. During this time of year, some females may still be nursing fawns which is an energetic cost due (Wallmo 1981) and could be another factor to why survival is lower for both groups.

Interestingly, the positive relationship I observed between winter survival (Dec-Feb) and precipitation (snow and/or rain) during winter was consistent regardless of migration strategy (i.e., additive) and was contrary to my prediction. At lower elevations (~1525m), annual snowfall averages 33 inches (Franklin and Dryness 1973), which likely is not detrimental to mule deer survival (Hobbs 1989). I did not have a measure of snowfall included in my analysis, but annual winter precipitation during 2005 – 2012 was similar to the long-term average (1970-2004). Average winter temperature for each year was near but often higher than freezing, suggesting that precipitation was mainly in the form of rain and not snow (Figure 10). In New Mexico a positive relationship between adult female survival and total precipitation from January to June was reported (Bender et al. 2007). An increase in precipitation led to better foraging and in turn, to an increase in nutrition, and ultimately increased mule deer survival (Bender et al. 2007). In my study, the winters with the greatest rainfall were 2005/2006 and 2010/2011(PRISM Climate Group 2010; Figure 11). It could be that forage is a limiting factor during winter, and that the

increase in precipitation allowed for more forb and grasses which are preferred by mule deer (Bender 2006). Adult survival in ungulates is the last demographic affected by resource limitations (Gaillard et al. 2000) and therefore it is difficult to observe differences year to year. However, it is apparent that the mean winter precipitation for 2010/2011 was above average compared to the 30-year average (Figure 11). In a shrub-steppe ecosystem, winters with higher precipitation likely result in more productive plant growth due to plants utilizing most of the available water earlier in the year (Mata-González et al. 2014).

Consistent with predictions regarding temporal variation in annual survival of adult females, I found very little support for year to year variation in female survival rates but strong support for variation between migrants and residents. Annual survival rates for females in my study were lower for resident deer (0.755-0.756) than survival rates reported for adult females in other populations (0.85, Unsworth et al, 1999; 0.86, Bleich et al. 2006; 0.81, Bender et al. 2007; 0.91, Bishop et al. 2009). However, the weighted mean annual survival rate for adult females from values reported in the literature (n=21) over 30 years was 0.84 (CV=0.06; Forrester and Wittmer 2013), which was very similar to my annual estimates for migrant deer (0.814-0.821). The mean annual survival estimate for all females ("residents", "migrants", and unknowns) in my study across all years was 0.79 (SE=0.02) which is still slightly lower than other reported studies (Figure 12).

Estimates of adult male annual survival from my study were substantially lower (0.404, 95% CI: 0.375-04.33) than annual estimates reported for adult males in Montana over 5 years (0.522, SD= 0.13); Pac and White 2007). However, male survival in a heavily hunted population, in this same study, reported 0.303 (SE= 0.0780, 95%CI= 0.174-0.473) during the months of October and November (Pac and White 2007). Low annual survival for adult males in harvested populations could reflect the possibility that harvest mortality is additive rather than compensatory and population levels cannot be sustained given current levels of harvest relative to other sources of mortality (Bender et al. 2004). I was unable to look at seasonal survival for males in my study, but harvest can become an additive source of mortality in the early fall, when males are in their best condition and natural mortality is low (Pac and

White 2007). In Washington harvest levels for black-tailed deer and mule deer were additive to the male population and models that assumed that hunting pressure and harvest effort were compensatory may have resulted in an overharvest of the male population (Bender et al. 2004).

The rate of change in population size in ungulates is sensitive to female survival rates (Gaillard et al. 2000), and estimates of fecundity and recruitment and juvenile survival are needed to accurately estimate population growth rates. By using a Leslie matrix model (Leslie 1945), one can estimate annual rate of increase (N_{t+1}/N_t) from a simple 2 age-class model (White and Bartmann 1997) as follows:

$$\lambda = (RS_f + 2S_A)/2$$

where R is the fawn:doe ratio, S_f is overwinter fawn survival rate and S_A is the mean adult female survival rate. During this study, fawn:doe recruitment hovered around 55:100 (Oregon Department Fish and Wildlife 2015) and fawn survival was between 62-70 % ($\bar{x} = 0.66$) (Oregon Department Fish and Wildlife 2015). I used estimates from 2010 for migratory deer (when adult female survival was the highest for both groups) in this equation to get a better understanding of the potential rate of change in this population, assuming the highest survival rates I observed in my study (R $=0.55$ $S_f=0.66$, $S_A= 0.82$: migratory annual survival; Oregon Department Fish and Wildlife 2015c). Given annual adult survival for females of 0.82, and using the simple equation above, I estimated a nearly stable rate of population growth based on λ $=1.0015$. However, using this same equation and only changing the survival estimates for adults to the highest annual survival rate I observed for residents (for the same year: 2010; R $=0.55$ $S_f=0.66$, $S_A= 0.77$: resident annual survival), I found a decrease in the population of 4.85% based on $\lambda =0.9515$. Migratory deer were more common in my study than resident deer, but the overall mean annual survival rate for the entire study population over all years (mean $S_A=0.79$, was <0.82 and resulted in a 2.9% annual decline in the adult female population (i.e., $\lambda =0.9715$) Estimates of average adult female survival in my study (across years) were lower for residents ($\bar{x}$ $=0.75$) and migrants ($\bar{x} =0.81$) when compared to a weighted mean of 0.84 (CV$=0.06$; n=21) (Forrester and Wittmer 2013). The over-winter fawn survival estimates for this population during this study (Oregon Department Fish and Wildlife 2015c), are

comparable to what other studies have found (n=12) of 0.61 (CV=0.31; Forrester and Wittmer 2013), so assuming these rates are reasonably accurate for my population, most of the survival rates I observed for female deer in my study were lower than what is required to maintain stable populations. Lower female mule deer survival (S = 0.72; 95% CI=0.09) has been linked to a 12% decrease in annual population growth rate (λ= 0.88; Robinson et al. 2002) in British Columbia, and a 36% annual rate of decline when female survival (0.63, SE=0.08) and annual recruitment (2/100) was very low in New Mexico (Bender et al 2007). To fully understand the rate of population change in this population, estimates of juvenile survival need to be obtained. Although adult female survival estimates in this population are not as low as these examples, based on the simple two, age-class model above, survival estimates from my study are low enough to negatively influence population growth.

The motivation behind this study was an increasing perception by ODFW that the mule deer population was declining. These results suggest that low male and female survival rates may both be contributing factors to a declining population trend. Very high rates of adult male mortality can impact the population dynamics of ungulates compared to females (McCorquodale 1999). Variation in adult survival has the greatest effect on population growth, which has three times more of an impact than a change in recruitment (Gaillard et al. 1998). However, without additional information, in particular, the carrying-capacity of the landscape and vital rates including fecundity and recruitment, the effect of these estimated survival rates on long-term mule deer population trends can only be hypothesized.

Cause-specific Mortality

Understanding the probability of mortality for each competing risk is an important key to understanding observed survival rates (Heisey and Fuller 1985). Legal harvest was the leading cause of mortality for mule deer males in this study and a male was about twice as likely to die from hunting than from predation by a cougar or coyote. My results are consistent with findings by Pac and White (2007), where harvest was the leading cause of mortality, with predation (coyote and cougar) the next most significant source of mortality for hunted male mule deer in Montana.

Predation was the leading cause of known mortality for female mule deer in my study (4.4%), which is consistent with findings for other mule deer populations (Bleich and Taylor 1998, Robinson et al. 2002). Human-caused (mainly vehicle collision) was second (3.8%), and illegal harvest (3.1%) the third leading cause of mortality for females. This is one of the more surprising findings of my research, since Oregon hunting regulations did not allow for any female harvest during the years of this study (with one exception of a permitted nuisance permit). Competing risks like illegal or illegal harvest are often grouped together with other sources of mortality (often reported as "other) that are not significant enough to stand on their own as separate category (Forrester and Wittmer 2013). Thus, it is unclear how prevalent illegal harvest is for females in other populations, but presumably it is low given it is rarely reported separately. However, a study in Washington on black-tailed deer reported females were twice as likely to die from illegal harvest as legal harvest and males had a 20% probability of being killed from illegal harvest (McCorquodale 1999). So, there are some populations that do experience similar illegal harvest pressure. Malnutrition/disease is typically reported to be the second most prevalent competing risk for adult females in most mule deer populations (Forrester and Wittmer 2013). However, my study suggested mortality from these sources was low and deer in south-central Oregon are more likely to die from a human-caused risk and illegal harvest (second to predation) than other natural causes. This supports the theory that human disturbance has a strong negative effect on survival for the mule deer in my study population.

Unknown-cause mortalities do not contribute any information regarding the distribution of cause-specific mortality in a sample population (Bishop et al. 2009). Generally, they are removed from the analysis or are included under the assumption that known competing risk categories are likely underestimated. In my study, 43% of mortalities were considered of unknown cause, which renders a form of bias in my CIF estimates. I chose to include deer that died from "unknown" causes of mortality by giving them a separate category. I did this so that the overall mortality estimates for males in particular would not be negatively biased and could be compared to the survival estimates from other analyses. Therefore, the cause-specific mortality rates

from this study should be viewed as minimum levels of risk for males (harvest, illegal harvest, predation, and other) and females (predation, human-caused, illegal harvest, and natural) and only suggestive of the relative relationship between the causes of mortality rather than estimates of the actual level of each mortality cause in the population.

LITERATURE CITED

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos, 103: 247–260.

Bender, L. C., G. A. Schirato, R. D. Spencer, K. R. McAllister, and B. L. Murphie. 2004. Survival, cause-specific mortality, and harvesting of male black-tailed deer in Washington. Journal of Wildlife Management 68:870–878.

Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118–1124.

Bishop C.J., J.W. Unsworth, and E.O. Garton. 2005. Mule deer survival among populations in Southwest Idaho. The Journal of Wildlife Management 69:311-321.

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.

Brown, C.G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. The Journal of Wildlife Management 56:246-253.

Brown, D. E., D. Warnecke, T. McKinney, and C. A. Jones. 2006. Effects of midsummer drought on mortality of doe pronghorn (Antilocapra americana). Southwestern Naturalist 51:220–225.

Budeau, D. 2010. Oregon upland game bird hunting season framework. Wildlife Division, Oregon Department of Fish and Wildlife Salem, OR USA.

Bureau of Land Management. 2015 Strategic Plan. United States Department of the Interior p30.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Chalmers, G. A., and M.W. Barrett. 1982. Capture myopathy. Pages 84-94 in G. L. Hoff and J. W. Davis, eds. Noninfectious diseases of wildlife. Iowa State Univ. Press, Ames

Clover, M.R. 1954. A portable trap and catch-net. California Fish and Game 40:367-373.

Committee of acceptable field methods in mammalogy. 1987. Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. Journal of Mammalogy, 68, (supplement) 1-18.

Cooch, E., and G. White. 2015. A gentle introduction to Program Mark:14th edition. <http:// www.phidot.org/software/mark/docs/book/> Accessed 1 May 2015.

Cupples, J.B., D.H. Jackson. 2014. Comparison of mule deer distributions during winter and hunting seasons in south-central Oregon. Wildlife Technical Report. Oregon Department Fish and Wildlife, Portland, OR, USA

D'Eon, R.G., and R. Serrouya. 2005. Mule deer seasonal movement and multiscale resource selection using global positioning system radio telemetry. American Society of Mammologists 86:736-744.

DeLgiudice, G.D., M.R. Riggs, P. Joly and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. The Journal of Wildlife Management 66: 698-717

Doherty, P. F., G. C. White, and K. P. Burnham. 2010. Comparison of model building and selection strategies. Journal of Ornithology 152:317–323.

Forrester, T.D. and H.U. Whittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer Odeocileus hemionus in North America. Mammal Review 43: 292-308.

Franklin, J.F., and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Portland, USA.

Fryxell, J.M., J. Greever, and A.R.E, Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist, 131: 781–798.

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.

Garrott, R. A., G.C. White, R.M. Bartmann, L.H. Carpenter, and A.W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. The Journal of Wildlife Management 51: 634–643.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

Hanley, T. A. 1996. Potential role of deer (Cervidae) as ecological indicators of forest management. Forest Ecology and Management 88:199–204.

Hebblewhite , M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

Heisey, D. M., and T.K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Heisey, D.M., and B.R. Patterson. 2006. A review of method to estimate cause-specific mortality in presence of competing risks. The Journal of Wildlife Management 70:1544-1555.

Hobbs, N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101:3-39

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Inouye, D. W., and A. D. McGuire. 1991. Effects of snowpack on timing and abundance of flowering in *Delphinium nelsonii* (Ranunculaceae): implications for climate change. American Journal of Botany 78:997–1001.

Johnson, B. K., P. K. Coe, and R. L. Green. 2013. Abiotic, bottom-up, and top-down influences on recruitment of Rocky Mountain elk in Oregon: a retrospective analysis. Journal of Wildlife Management 77:102–116.

Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. Journal of Wildlife Management25:54–60.

Keister, G. P, Jr., C. E. Trainer, and M. J. Willis. 1988. A self-adjusting collar for young ungulates. Wildlife Society Bulletin 16: 321-323.

Kline, J.D. 2012. Seasonal neighbors: residential development encroaches on mule deer winter range in central Oregon. Pacific Northwest Research Station, Publication 140, Portland, Oregon, USA.

Lawrence, R.K., S Demarais, R.A. Relyea, S.P. Haskell, W. B. Ballard, and T.L Clark. 2004. Desert mule deer survival in southwest Texas. Journal of Wildlife Management 68*:* 561-569

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Mace, R.U., R. Denney, and R. Ingram. 1995. Big game history. Oregon Department Fish and Wildlife, Portland, OR, USA.

Mata-González, R., T. L. Evans, D. W. Martin, T. McLendon., J. S. Noller, C. Wan, and R. E. Sosebee. 2014. Patterns of Water Use by Great Basin Plant Species Under Summer Watering. Arid Land Research and Management 28:428–446

McCorquodale, S.M. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management 63:861-871.

Molau, U.1997. Phenology and reproductive success in Arctic plants: susceptibility to climate change. Pages 153–170 in W. C. Oechel et al., editors. Global change and Arctic terrestrial ecosystems. Springer-Verlag, Berlin, Germany.

Monteith, K.L., C.B. Vernon, B.M. Stephenson, M.M. Conner, R.W. Klaver, and R.T. Bowyer. 2011. Timing of seasonal migration in mule deer effects of climate, plant phenology, and life-history characteristics. Ecosphere 2:1-34.

Monteith, K. L., K. B. Monteith, J.A. Delger, L.E. Schmitz, T.J. Brinkman, C.S. Deperno, and J.A. Jenks. 2012. Immobilization of white-tailed deer with telazol, ketamine, and xylazine, and evaluation of antagonists. The Journal of Wildlife Management 76:1412-1419.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Mote, P.W., E.P Salathé. 2010. Future climate change in the Pacific Northwest. Climate Change, 102:29-50.

Murray, M. G. (1995). Specific nutrient requirements and migration of wildebeest. In: Serengeti II: Dynamics, Management, and Conservation of an Ecosystem (eds. Sinclair, A.R.E. & Arcese, P.) University of Chicago Press,

Chicago, pp. 231–256.

Murray, D.L. 2006. On improving telemetry-based survival estimation. Journal of
Wildlife Management 70:1530-1543.

Neilsen, C.K., R.G. Anderson, and M.D. Grund. 2003. Landscape Influences on deer-
vehicle accident areas in an urban environment. The Journal of Wildlife
Management. 67:46-51.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat section and survival of
mule deer: tradeoffs associated with migration. Journal of Mammalogy
78:483-504.

Oregon Department of Fish and Wildlife. 2003. Oregon's mule deer management
plan. Oregon Department of Fish and Wildlife, Portland, OR, USA.

Oregon Department of Fish and Wildlife. 2015*a*. Oregon migratory bird regulations.
Oregon Department of Fish and Wildlife, Portland, OR, USA.

Oregon Department of Fish and Wildlife. 2015*b*. Oregon big game regulations.
Oregon Department of Fish and Wildlife, Portland, OR, USA.

Oregon Department Fish and Wildlife. 2015*c*. Mule deer population trend in Oregon
by Wildlife Management Unit. <http://www.dfw.state.or.us/resources/hunting/
big_game/controlled_hunts/docs/hunt_statistics/15/Mule_Deer_10-
15_26Jun15.pdf>. Accessed 12 Aug 2015.

Oregon Department of Transportation. 1999. Oregon Highway Plan. Oregon
Department of Transportation, Salem, OR USA.

Oregon Department of Transportation. 2010. Oregon State Highway System, traffic
map 2010. Oregon Department of Transportation, Salem, OR USA.

Pac, D. F., and G. C. White. 2007. Survival and cause-specific mortality of male mule
deer under different hunting regulations in the Bridger Mountains, Montana.
Journal of Wildlife Management 71:816–827.

Palmer, W. C. 1965. Meteorological drought. Department of Commerce Weather
Bureau Research Paper 45, Washington, D.C., USA.

Pettorelli, N.*,* A. Mysterud, N.G. Yoccoz*,* R. Langvatn, and N.C Stenseth.
2005. Importance of climatological downscaling and plant phenology for red
deer in heterogeneous landscapes*.* Proceedings of the Royal Society of
London B*,* 272: 2357–2364.

Post, P., N.C. Stenseth. 1999. Climate variability, plant phenology, and northern

ungulates. Ecology 80:1322-1339

PRISM Climate Group. 2010. <http://www.prism.oregonstate.edu>.Accessed 18 Jun 2014.

Radeloff, V.C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland-urban interface in the United States. Ecological Applications 15:799–805

Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian Journal of Zoology 80:556–568.

Romin L.A., and Bissonette J.A. 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24:276-83

Saether, B.E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution. 12: 143–149.

Sargeant, G. A. 2011. Using csm to estimate cause-specific mortality from left-truncated data. <http://cran.r.project.org/web/packages/wild1/vignettes/csm.pdf>. Accessed 25 April 2014.

Speten, D. 2014. Assessment of Mule Deer Fawn Survival and Birth Site Habitat Attributes in South-Central Oregon. Oregon State University, Corvallis, Oregon, USA.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Bioloogical Conservation. 141:2159-2173.

Thomas, T.R., Irby, L.R. 1990. Habitat use and movement patterns by migrating mule deer in southeastern Idaho. Northwest Science 64:19-27

Unsworth, J. W., F.D. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. The Journal of Wildlife Management 63:315–326.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal Range Management 30:122-127.

Wallmo, O.C., editor. 1981. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska.

Walther GR, Post E, Convery P, Menzel A, Parmesan C, et al. 2002. Ecological responses to recent climate change. Nature 416:389-9

Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increase Western U.S. forest fire activity. Science. 313: 940–943.

White, G.C., and R. M. Bartmann. 1997. Mule deer management-what should be monitored? Pages 104-118. Proceedings of the 1997 deer/elk workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120-139.

Zager P., G. Pauley, M. Hurley, C. White. 2007. Statewide Ungulate Ecology. Idaho Dept. of Fish and Game, Biose, Idaho, USA.

Figure 1. Location and core study area of the 408 adult female mule deer used in the known fate survival analysis and, 165 adult female and 50 adult male mule deer used in the cause-specific mortality analysis in south-central Oregon, August 2005 to May 2012.
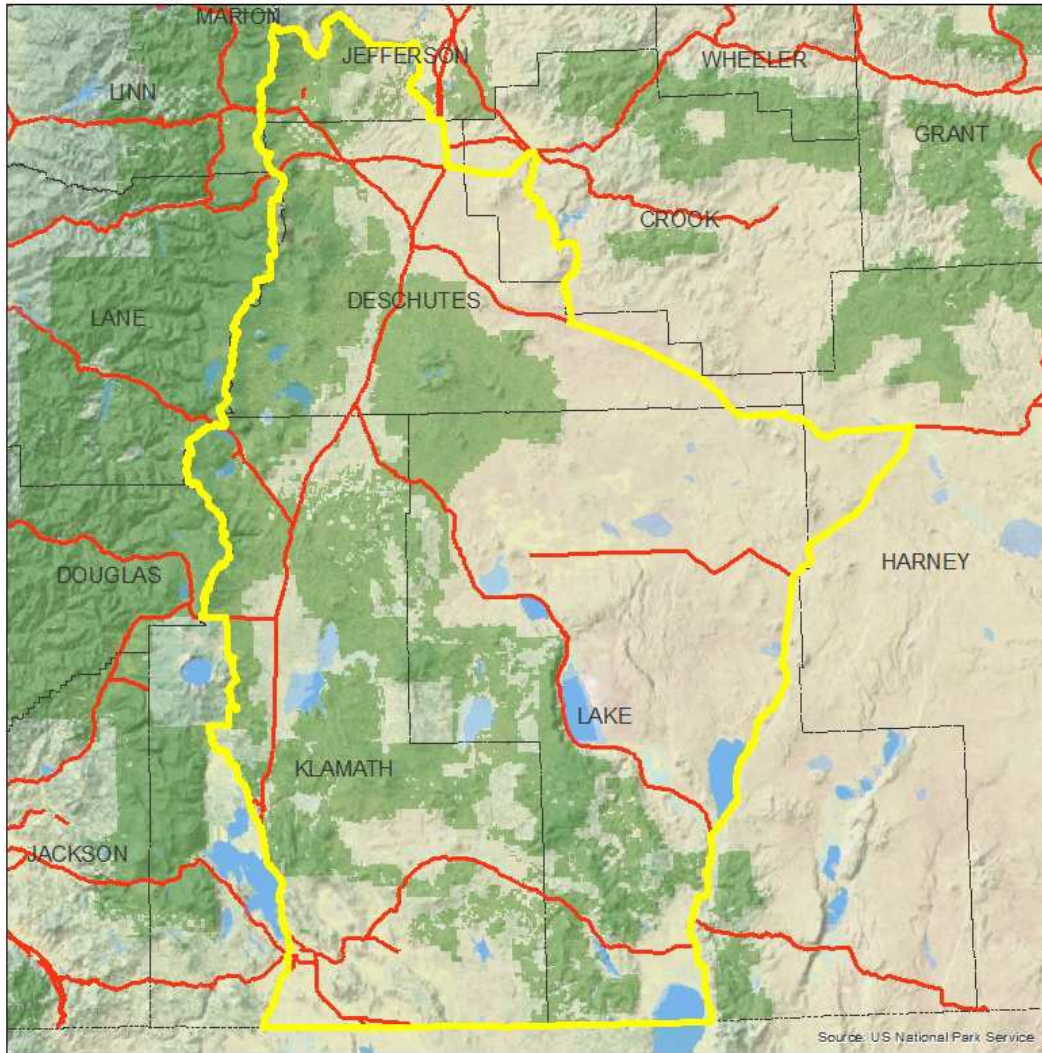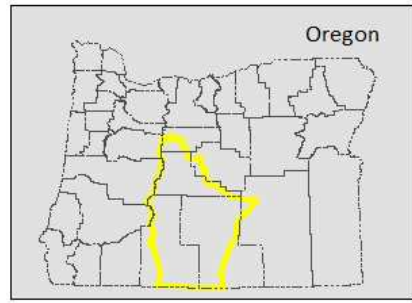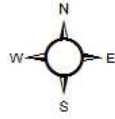
Table 1. Total radio-collars (VHF and GPS) deployed by wildlife management unit (WMU) on adult mule deer (*Odocoileus hemionus*) in south-central Oregon, June 2005 – September 2011.

WMU	Males	Females	Total Radio-Collars Deployed
Sprague	4	14	18
Klamath Falls	0	20	20
Upper Deschutes	7	18	25
Metolius	17	65	82
Paulina	26	110	136
Wagontire	2	41	43
Interstate	1	96	97
Silver Lake	18	86	104
Fort Rock	20	76	96
Total	**95**	**526**	**621**

Table 2. Total number of deer captured and radio-collars deployed (by type) on mule deer (*Odocoileus hemionus*) in south-central Oregon, June 2005 - September 2011.

Capture period	Radio-collar Type				Summary	
	GPS	VHF	Kydex or Expanding VHF	No collar	Total Capture	Total Collars
2005	6	2	6	8	22	14
2006	54	34	22	54	164	110
2007	67	4	18	8	97	89
2008	81	-	7	7	95	88
2009	60	-	11	2	73	71
2010	138	4	11	-	153	153
2011	90	-	6	-	96	96
Total	**496** **(79.9%)**	**44** **(7.1%)**	**81** **(13.0%)**	**79** **(11.2%)**	**700**	**621**

Table 3. Mule deer (*Odocoileus hemionus)* herd number and name determined from GPS-collared individuals using winter location, angle and distance of travel from winter location, and migration pathway from 2005-2012 in south-central Oregon.

Herd Number	Herd Complex
0	Unknown
1	California Clear Lake-Gerber Herd Complex
2	Bly Herd Complex
3	Tucker Hills-Valley Falls Herd Complex
4	North Silver Lake-Paulina Marsh Herd Complex
5	South Silver Lake-Paulina Marsh Herd Complex
6	Summer Lake Complex
7	North Fort Rock Valley-Lava Fields Herd Complex
8	South Fort Rock Valley-Lava Fields Herd Complex
9	Pine Mountain Herd Complex
10	Bear Creek Buttes Herd Complex
11	SE Bend Herd Complex
12	North Wagontire Herd Complex (short distance migrators)
13	North Wagontire Herd Complex (long distance migrators)
14	Metolius-Upper Deschutes Herd Complex (North Squaw Back Ridge area)
15	Metolius-Upper Deschutes Herd Complex (South Squaw Back Ridge area)
16	Metolius-Upper Deschutes Herd Complex (Lake Billy Chinook area)
17	Metolius-Upper Deschutes Herd Complex (Sisters area)
18	Swan Lake Bonanza Herd Complex
19	Goose Lake Valley Herd

Figure 2. Minimum convex polygons of GPS radio collared mule deer (*Odocoileus hemionus*) herds in south-central Oregon from 2005-2012.
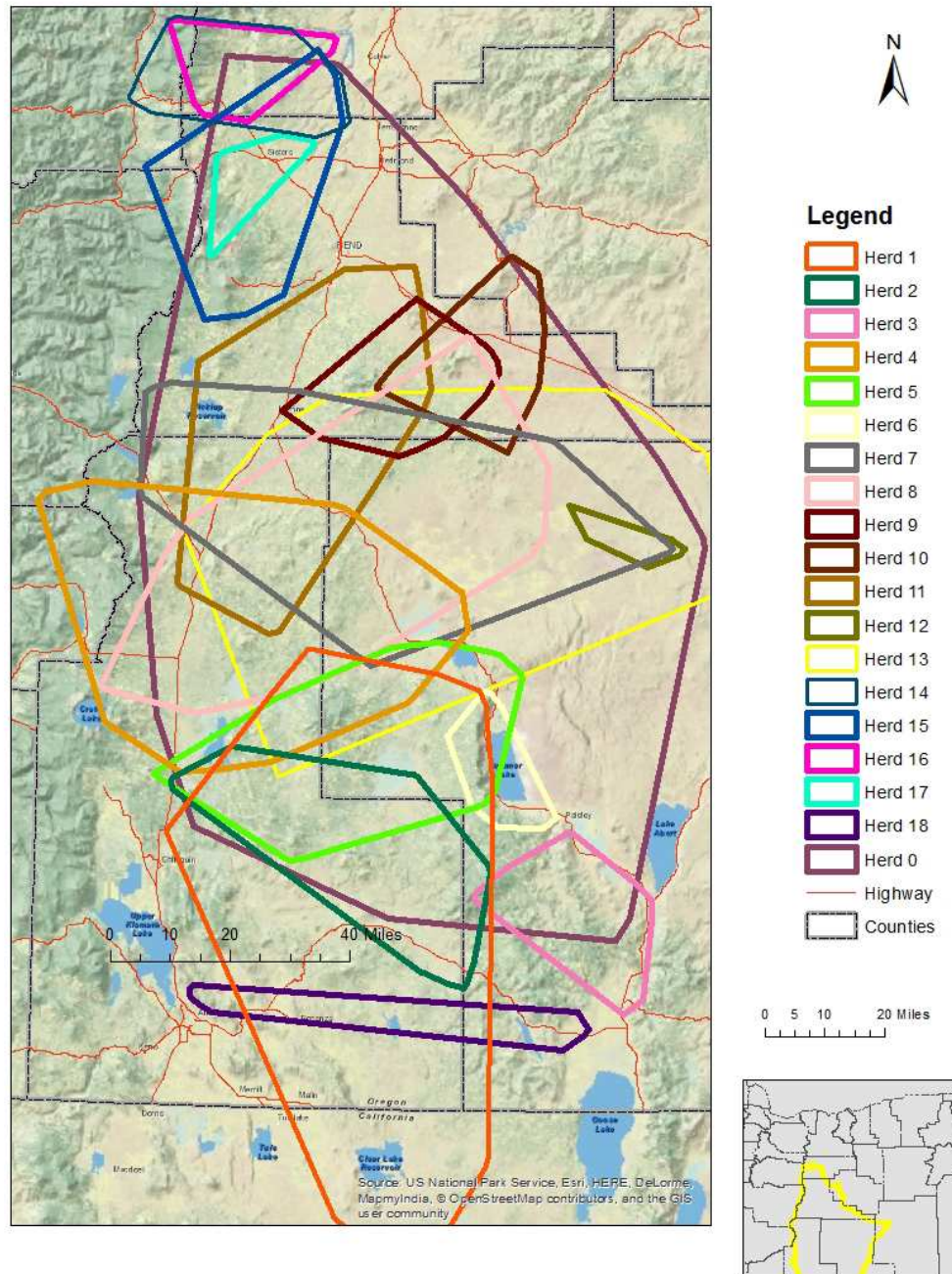
Table 4. Hierarchical modeling framework used to develop an a priori model set for known-fate survival analysis of female mule deer (*Odocoileus hemionus)* in south-central Oregon, 2005-2012. S is the survival rate estimate

Stage	Model Name	Hypothesis	Explanation
1) Time effect	S(t)	βt>0	FULL MODEL: S is fully time-dependent
	S(.)	β.=0	S is fixed through time (.e., monthly intervals)
	S(YR)	βYR>0	S varies annually by biological year (June – May 2005-2012).
	S(T, Ln (T), TT)	βT>0, βln(T)>0, βTT>0	Monthly survival exhibits a linear (T), log-linear (lnT) or quadratic (TT) time trend within years.
	S(SEAS)	βSEAS>0	S varies as a function of season and as interaction and additive effect
	S(YR*SEAS)	βYR*SEAS>0	
	S(YR+SEAS)	βYR+SEAS>0	
	S(YR+t)	βYR+t>0	S varies through an interaction between year and over time
	S(YR*t)	βYR*t>0	
	S(HUNT)	βHUNT<0	S is negatively affected by hunting pressure (August and September)with year as an additive and interaction.
	S(HUNT+YR)	β HUNT+YR<0	
	S(HUNT*YR)	β HUNT*YR<0	
	S(FSprM)	β FSprM<0	S is negatively affected during both migration periods and the interaction and additive (i.e., Fall: Oct-Nov; Spring :Apr-May)
	S(FSprM+YR)	β FSprM+YR <0	
	S(FSprM*YR)	β FSprM*YR <0	
	S(SprM)	β SprM <0	S is negatively affected during the spring migration period only
	S(FMig)	β FMig <0	S is negatively affected during the fall migration period only

2) Individual Covariates	S(sumWMU)	βsumWMU>0	S varies as a function of summer WMU
	S(winWMU)	βwinWMU>0	S varies as a function of winter WMU
	S(H)	βH>0	S varies as a function of herd group
	S(WUI)	βWUI>0	S is negatively affected when ranges fall within the Wildland Urban Interface
3) Movement Parameters	S(MU)	βMU<0	S varies as a function of migratory behavior 3 levels (migrant, resident, unknown), so effect consists of 2 covariates – M=1 for migrant, 0=resident, U=1 for unknown, 1=resident.
	S(D)	βD<0	S is negatively associated with the distance migrated between seasonal ranges
	S(HC)	βHC<0	S is negatively associated with the number of highways crossed during migration
	S(TC)	βTC<0	S is negatively associated with the times highways are crossed during migration
4) Environmental Covariates	S(Wpp)	βWpp<0	S is negatively associated with an increase in winter precipitation at the WMU level
	S(Ipp)	βIpp<0	S is negatively associated with an increase in winter precipitation at the individual winter range level
	S(Iws)	βIws<0	S is negatively associated with an increase in winter severity at the individual winter range level
	S(Wws)	βWws<0	S is negatively associated with an increase in winter severity at the WMU level
	S(Dr)	βDr<0	S is negatively associated with an increase in drought severity during the month of August.

Table 5. Model selection results for all *a priori* models investigating survival probability (S) of radio-marked mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2011, relative to time effects, individual covariates, environmental covariates, and movement behavior. Models are ranked according to Akaike Information Criterion adjusted for small sample sizes (AIC$_c$). Delta AIC$_c$ (ΔAIC$_c$), Akaike weight (w_i), number of parameters (K), and deviance are also listed for each model. Model set also includes the intercept-only (null model) of constant S over time [S(.)] and the most general model with survival variation by season and year.

[S(t)].Model	AICc	ΔAICc	*wi*	K	Deviance
{S(MU+FMig+Ipp)}	1018.84	0	0.31	5	1008.83
{S(MU + Ipp)}	1019.52	0.68	0.22	4	1011.51
{S(MU + FMig)}	1020.22	1.38	0.16	4	1012.21
{S(MU +FSprM)}	1021.33	2.49	0.09	5	1011.31
{S(MU +SprM +Ipp)}	1021.52	2.68	0.08	5	1011.51
{S(MU)}	1022.13	3.29	0.06	3	1016.12
{S(MU* FMig))}	1023.39	4.55	0.03	6	1011.37
{S(MU + SprM)}	1023.94	5.10	0.02	4	1015.93
{S(MU * SprM)}	1025.74	6.90	0.01	6	1013.72
{S(MU* FSprM)}	1026.46	7.62	0.01	9	1008.43
{S(D)}	1060.77	41.93	0	2	1056.77
{S(TC)}	1065.50	46.66	0	2	1061.50
{S(Ipp)}	1066.74	47.90	0	2	1062.74
{S(Ipp + FMig)}	1066.76	47.92	0	3	1060.75
{S(Ipp + SprM)}	1068.74	49.90	0	3	1062.74
{S(H)}	1069.34	50.50	0	20	1029.18
{S(Iws)}	1070.44	51.60	0	2	1066.44
{S(Wpp)}	1070.78	51.94	0	2	1066.77
{S(FMig)}	1070.84	52.00	0	2	1066.83
{S(FSprM)}	1071.60	52.76	0	3	1065.60
{S(HC)}	1072.29	53.45	0	2	1068.28
{S(.) PIM}	1072.32	53.48	0	1	1070.32
{S(WinWMU)}	1072.62	53.78	0	2	1068.62
{S(Dr)}	1073.15	54.31	0	2	1069.15
{S(WUI)}	1073.32	54.48	0	2	1069.31
{S(HUNT)}	1073.83	54.99	0	2	1069.83
{S(SprM) }	1073.93	55.09	0	2	1069.93
{S(SEAS)}	1074.04	55.20	0	4	1066.03
{S(Wws)}	1074.32	55.48	0	2	1070.31

{S(SumWMU)}	1074.32	55.48	0	2	1070.32
{S(YR(lnT))}	1079.33	60.49	0	7	1065.31
{S(YR + FSprM)}	1080.20	61.36	0	9	1062.17
{S(YR)}	1080.79	61.95	0	7	1066.77
{S(YR+HUNT)}	1082.32	63.48	0	8	1066.29
{S(YR + SEAS)}	1082.86	64.02	0	10	1062.82
{S(YR*HUNT)}	1084.24	65.40	0	14	1056.16
{S(YR *FSprM)}	1087.16	68.32	0	20	1047.00
{S(YR +t)}	1089.65	70.81	0	19	1051.50
{S(YR * SEAS)}	1092.17	73.32	0	28	1035.86
{S(t) PIM}	1134.15	115.31	0	82	967.54
{S(YR+t)}	1148.62	129.78	0	89	967.54
{S(YR *t)}	1152.76	133.92	0	91	967.54

[a] Model notation: Winter WMU location (WinWMU); Summer WMU location(SumWMU); Biological year: June – May (YR); Season (SEAS); Migration season (FSprM); Migration season, fall only (FMig); Migration season, spring only (SprM); Hunting Season (HUNT); Migration (M); Distance migrated (D), Highways crossed (HC); Number of times a highways were crossed (TC); Individual home range precipitation (Ipp); WMU precipitation (Wws); Individual home range winter severity (Iws); WMU winter severity (Wws); Drought (Dr).

Figure 3. Seasonal survival rate estimates (S) and 95% confidence intervals for migratory and resident adult female radio-marked mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2012. Estimates were derived from the best approximating known-fate model including the additive effect of migration ("migrants", "residents", and "unknown"), the fall migration time period, individual winter range precipitation (Ipp; December-February, mean across all individuals each year) [S(MU+FMig+Ipp)].
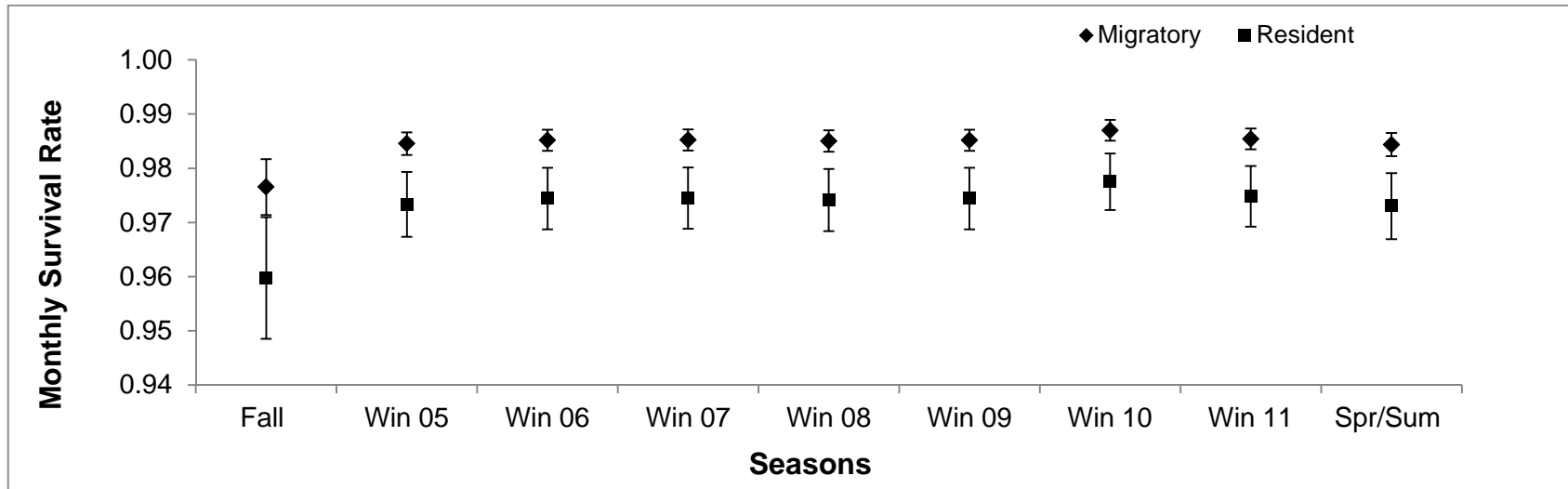
Figure 4. Range of winter precipitation (December-February) and 95% confidence intervals for individual adult female radio-marked mule deer (*Odocoileus hemionus)* winter ranges in south-central Oregon, 2005-2012. Estimates were derived from the best approximating known-fate model including the additive effect of migration (mean across all migration categories, "migrants", "residents", and "unknown"), the fall migration time period and individual winter range precipitation (December-February) [S(MU+FMig + Ipp)].
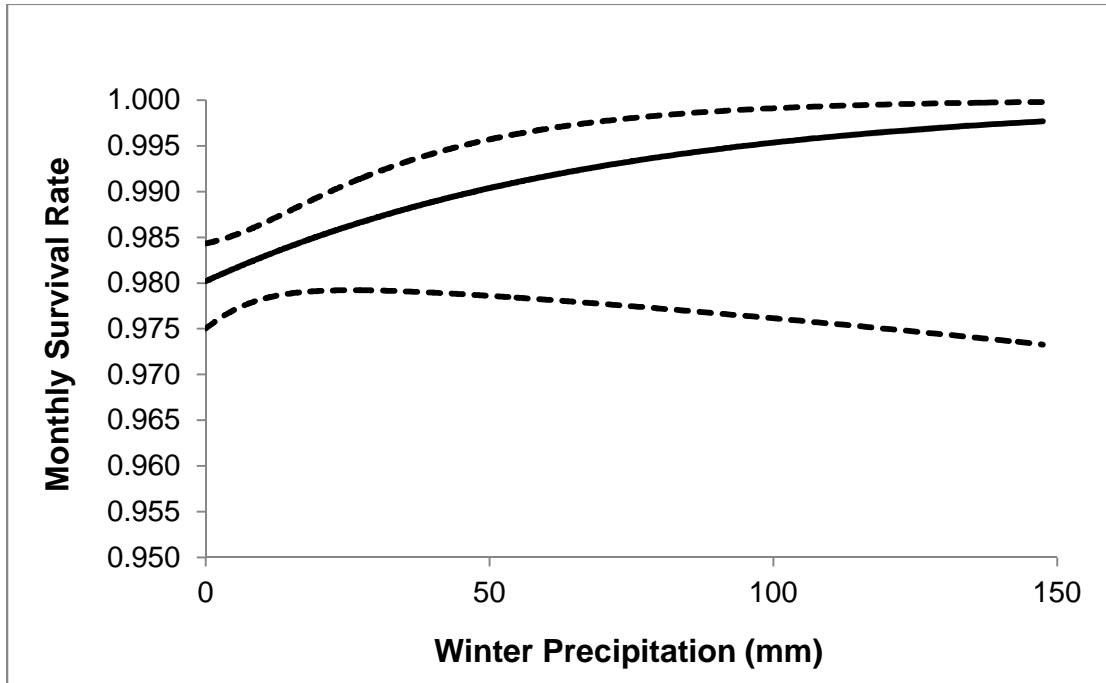
Table 6. Annual survival rate estimates (S) and 95% confidence intervals for migratory and resident adult female radio-marked mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2012. Estimates are based on biological year (June 1 - May 31). Estimates were derived from the best approximating known-fate model including the additive effect of migration (mean across all migration categories, "migrants", "residents", and "unknown"), the fall migration time period, individual winter range precipitation (December-February) [S(MU+FMig+Ipp)].

	Year	Survival	LCL	UCL
Migratory	2005	0.8149	0.7954	0.8344
	2006	0.8165	0.7972	0.8358
	2007	0.8166	0.7973	0.8359
	2008	0.8161	0.7968	0.8354
	2009	0.8165	0.7972	0.8357
	2010	0.8210	0.8020	0.8400
	2011	0.8171	0.7979	0.8363
Resident	2005	0.7553	0.7049	0.8057
	2006	0.7579	0.7080	0.8077
	2007	0.7580	0.7082	0.8078
	2008	0.7572	0.7072	0.8071
	2009	0.7578	0.7079	0.8076
	2010	0.7651	0.7163	0.8139
	2011	0.7588	0.7091	0.8084

Figure 5. Annual survival rate estimates (S) and 95% confidence intervals for migratory and resident adult female radio-marked mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2012. Estimates were derived from the best known-fate model including the additive effect of migration ("migrants", "residents", and "unknown"), the fall migration time period, individual winter range precipitation (December-February; mean across all individuals each year) [S(MU+FMig+Ipp)].
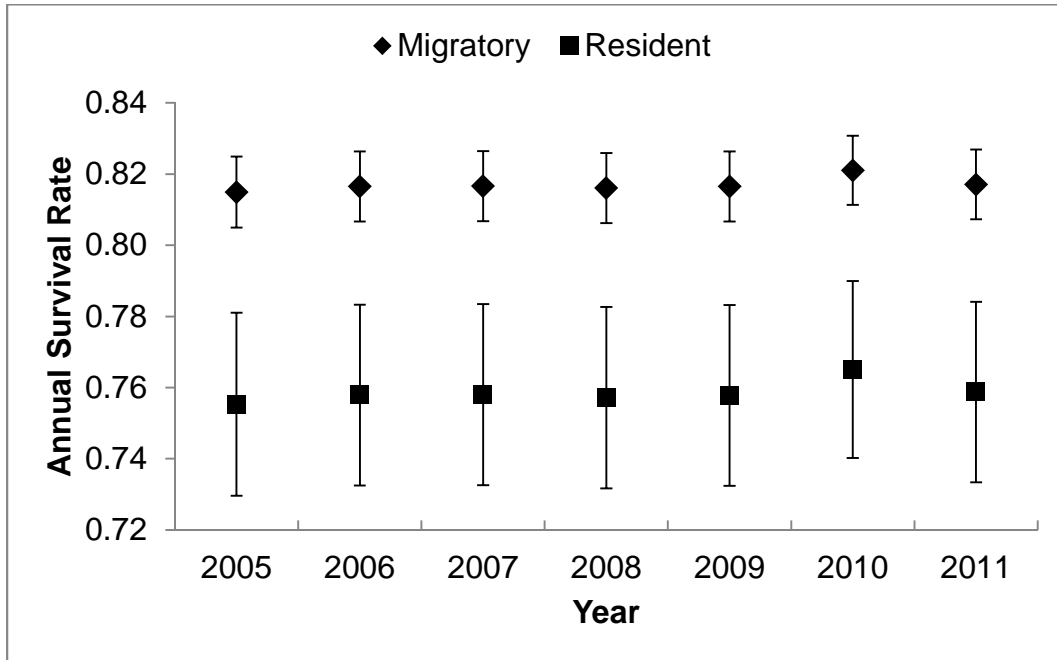
Table 7. Total number (% of total) of mortalities for GPS and VHF radio-collared mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2011. Males and females were assigned to the following categories: Predation, Legal Harvest, Illegal Harvest, Human-caused, and Natural. The "Unknown" category includes the number of deer for which a cause of mortality could not be determined.

		Cause of Mortality					
Sex	Predation	Legal Harvest	Illegal Harvest	Human-caused	Natural	Total Known	Unknown
Female	31 (38%)	1 (1%)	19 (23%)	25 (31%)	5 (6%)	**81**	84
Male	8 (19%)	24 (57%)	6 (14%)	4 (10%)	1 (2%)	**42**	8
Total	**39 (32%)**	**25 (20%)**	**25 (20%)**	**29 (24%)**	**6 (5%)**	**123**	**92**

Table 8. Cumulative incidence functions (CIF's) and 95% confidence limits (LCL,UCL) from a 365 day annual period for male and female radio-collared mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2012. Hazard rate estimates were calculated for the following sources of mortality: predation (cougar and coyote), legal harvest (rifle and archery), illegal harvest, human caused (vehicle or fence), natural (disease, malnutrition, fawning), "other" (males only; human-cause and natural mortality) and unknown (cause of mortality could not be determined).

	Mortality Source	CIF	LCL	UCL
Females	Predation	0.044	0.028	0.065
	Human Caused	0.038	0.021	0.054
	Illegal Harvest	0.031	0.017	0.054
	Natural	0.007	0.0002	0.015
	Unknown	0.130	0.105	0.155
Males	Predation	0.104	0.042	0.166
	Harvest	0.249	0.172	0.326
	Illegal Harvest	0.066	0.023	0.108
	Other	0.061	0.006	0.115
	Unknown	0.116	0.042	0.191

Figure 6. Annual cumulative incidence functions for all competing risks of male radio-marked mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2012. Risk functions are pooled across all years of the study. Days are Julian date.
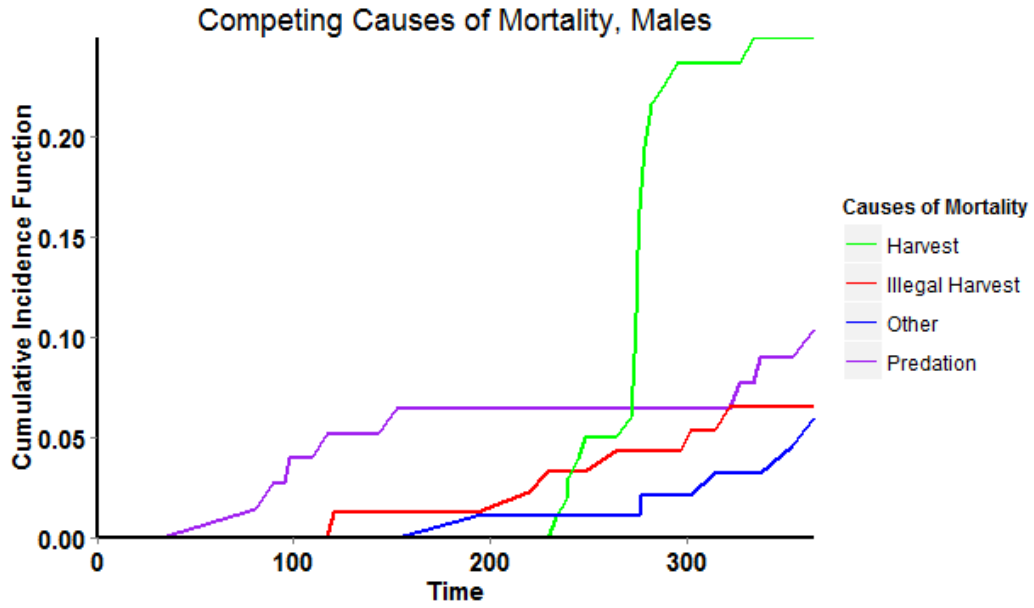
Figure 7. Annual cumulative incidence functions for all competing risks of female radio-marked mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2012. Risk functions are pooled across all years of the study. Days are Julian date.

Figure 8. Average mean monthly precipitation (mm) for June through August in south-central Oregon, 2005-2012. Dashed line represents long-term average (1970-2012) mean month precipitation for June through August in same location. Data from PRISM Climate Group.
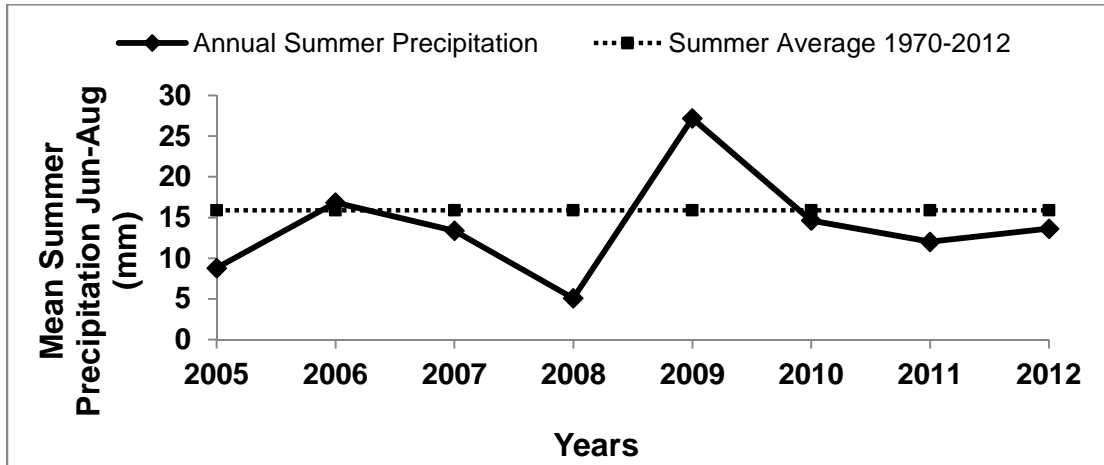
Figure 9. Annual mortality rate for all competing risks of female radio-marked mule deer (*Odocoileus hemionus*) in south-central Oregon, 2005-2012. Risk functions are pooled across all years of the study. Days are Julian date.
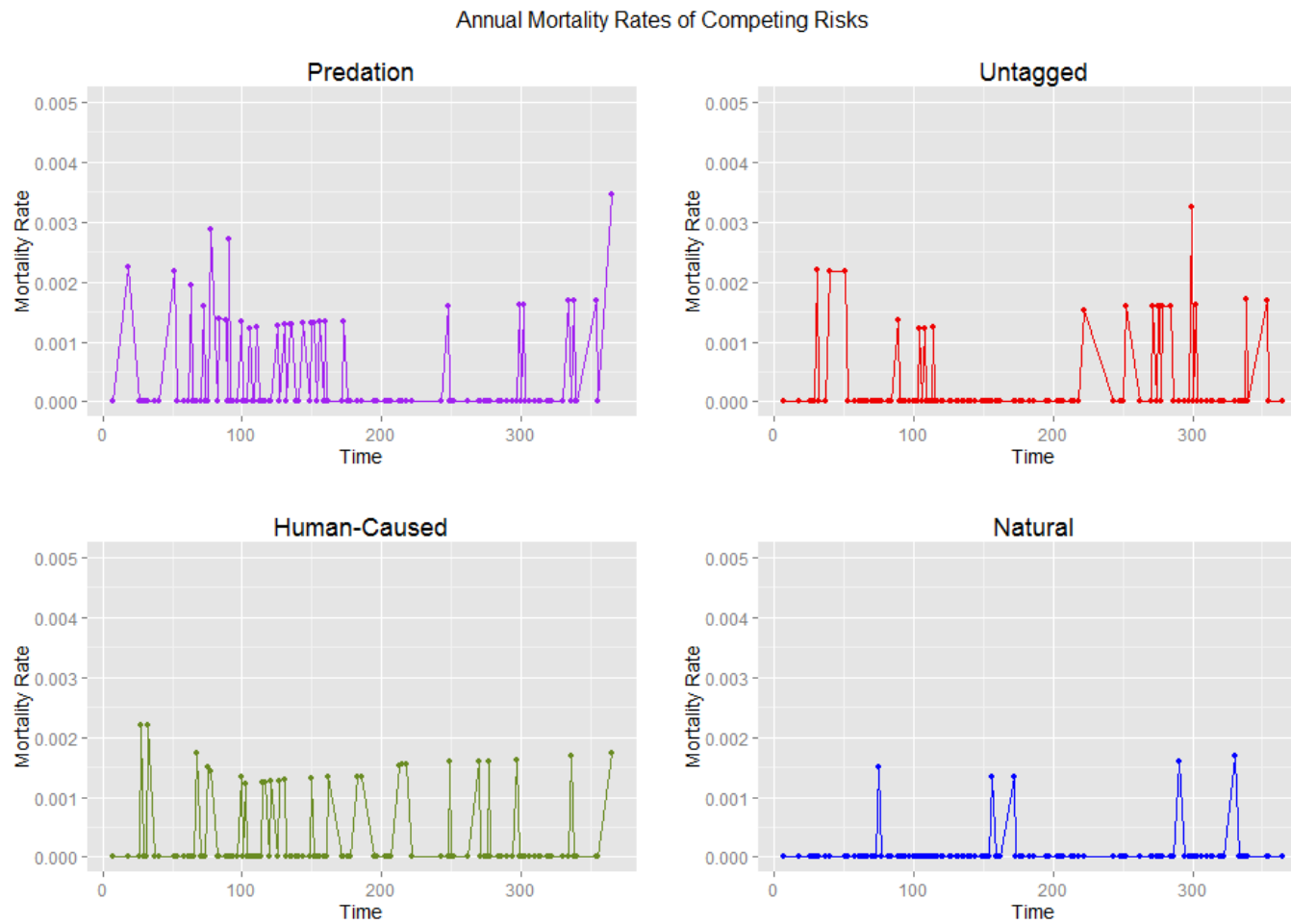
Figure 10. Average winter temperature (C°) for December through February in south-central Oregon from winters 2005 to 2012. Dashed line represents point at which rain becomes snow. Data from PRISM Climate Group.
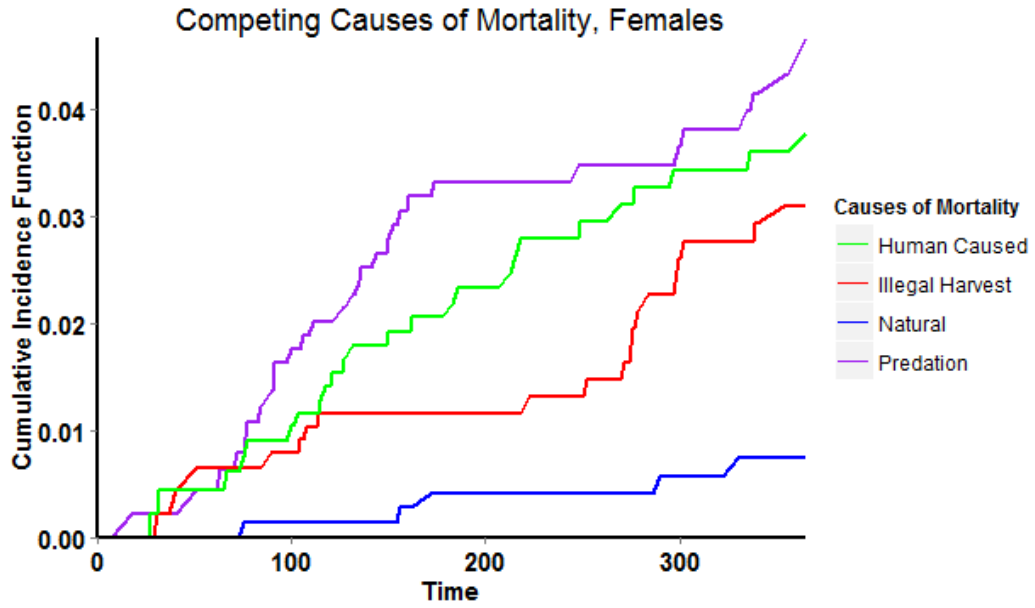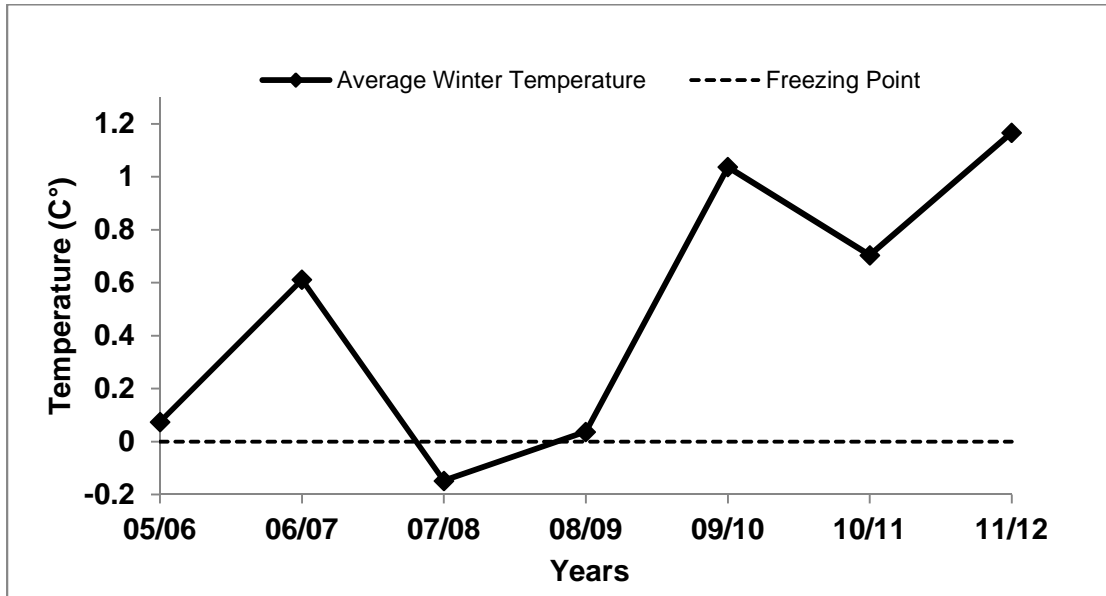
Figure 11. Average mean monthly precipitation (mm) for December through February in south-central Oregon, 2005-2012. Dashed line represents long-term average (1970-2012) mean month precipitation for December through February in same location. Data from PRISM Climate Group.
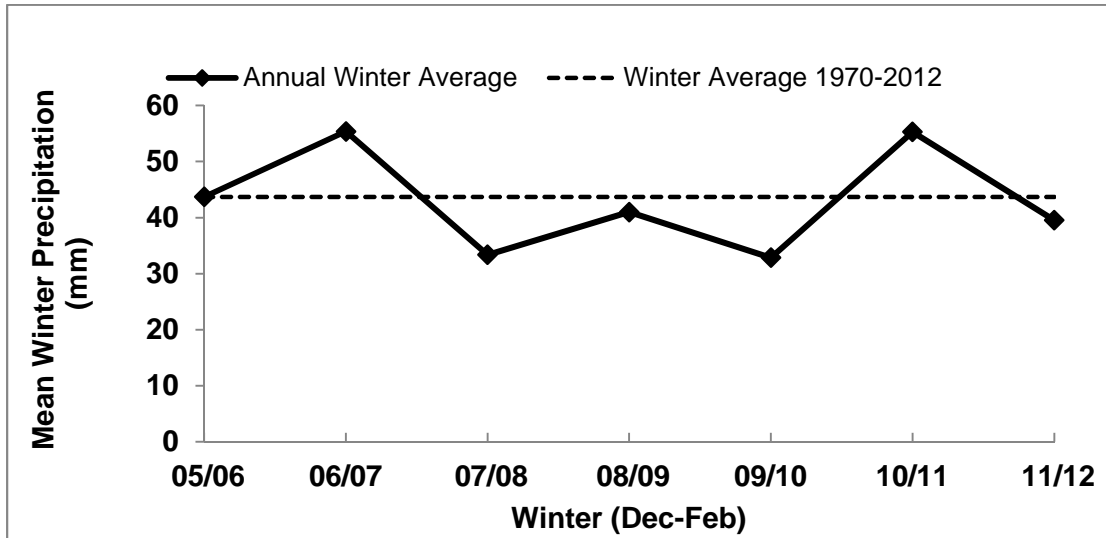
Figure 12. Comparison of annual survival estimates for radio-marked adult female mule deer with standard errors (SE) from across their range.
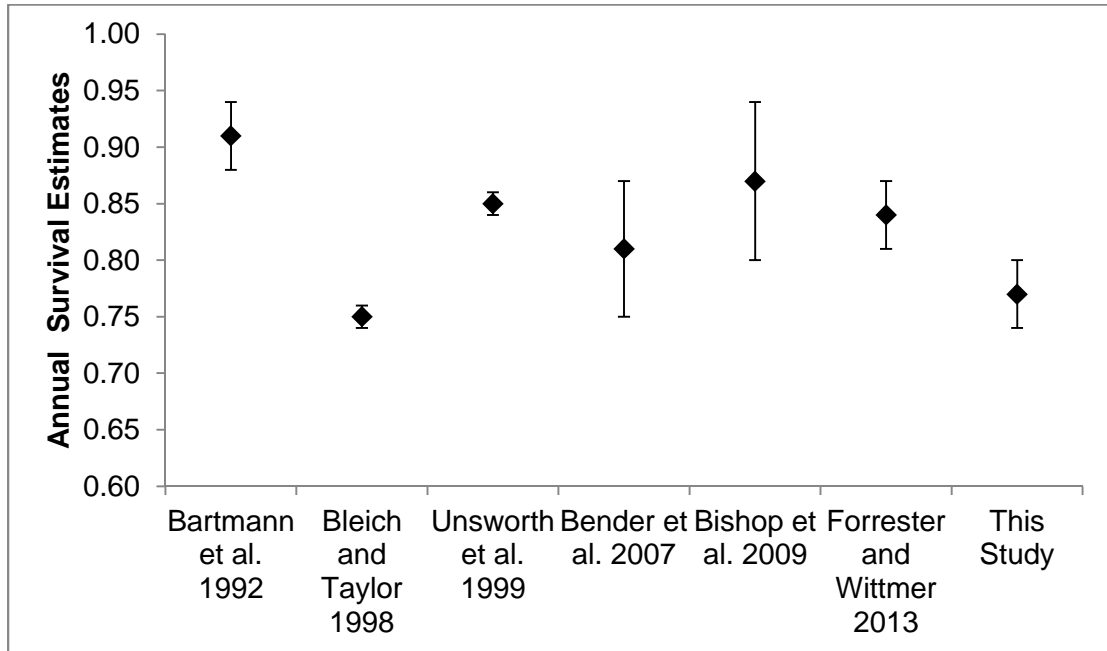
CHAPTER 3

CONCLUSION: SUMMARY AND MANAGEMENT IMPLICATIONS

Elizabeth M. Mulligan

SUMMARY

Mule deer are a valuable economic resource and they provide important ecosystem services within the shrub-steppe and forested landscapes they inhabit (Oregon Department Fish and Wildlife 2003, Hobbs et al. 1996). Mule deer populations declined across the west in the 1990s (Unsworth et al. 1999) including south-central Oregon (Peek et al. 2002), where populations have continued to decline (24% since 2001; Oregon Department Fish and Wildlife 2003). This decline was theorized to stem from major habitat alterations, such as grazing, fire, recreational activity, and sagebrush removal, which have also impacted other western wildlife populations (West 1999). Mule deer population declines in other parts of their western range have been attributed to low annual survival rates of adults and fawns (White & Bartmann 1998, Robinson et al. 2002, Lomas & Bender 2007, Bishop et al. 2009) and low recruitment (Unsworth et al. 1999); however, in general, factors affecting mule deer population declines are not well understood.

Wildlife managers should understand the population dynamics of a harvested population, especially when there is a concern about changes in population size or species distribution. This entails understanding primary processes (births, deaths, immigration, and emigration) and the factors that affect these vital rates (Gillard et al. 1998). Survival rates of individuals are indicative of patterns observed at the population level (Williams et al. 2002); thus relationships observed at the individual level can be used to make population-level predictions. The objectives of my thesis were to estimate monthly survival rates for adult female mule deer and the temporal and spatial patterns of variation in these rates, and to examine cause-specific mortality for both sexes using data collected from radio-collared individuals in south-central Oregon from 2005 – 2012.

Variation in monthly survival rates of adult female mule deer in my study was best explained by migration behavior, the additive effect of the fall migration period, and the additive effect of precipitation on individual winter ranges. Subsequently, deer that migrated had higher average (7%) annual survival than resident deer, supporting the theory that migration in mule deer can be a beneficial life strategy in a mixed population of migrants and residents (Nicholson et al. 1997). However,

survival was also lower for all adult females regardless of migration behavior during the months when fall migration occurred (October and November). This suggests that even though deer that migrate had overall higher survival, activities or environmental conditions that occur during October and November during this study negatively affected both migrant and resident deer alike. Thus, it is not necessarily the process of moving from one location to another that impacts survival, since both groups of deer are equally affected. Even though female deer were not hunted during my study, increased human disturbance associated with hunting season activities which partially overlapped the fall migration period could be responsible for the patterns I observed (Stankowich 2008). Finally, survival increased during the winter months (December-February) in relation to an increase in precipitation. This was contrary to my prediction that increased precipitation would reflect increased snow pack, and therefore, negatively affect adult survival (Nicholson et al. 1997). This is likely due to an increase in foraging quantity or quality as a result of water availability in a semi-arid landscape.

Based on my study, a male mule deer in Oregon was about twice as likely to die from a hunter (0.249; 95%CI=0.172-0.326) than a predator (*Puma concolor* or *Canis latrans)* (0.104, 95%CI=0.042-0.166). Conversely, predation was the highest competing mortality risk for females (0.044; 95%CI=0.028-0.065), and females were almost as likely to die from human-caused (vehicle or fence) (0.038; 95%0.021-0.054) as illegal harvest (0.031; 95%CI=0.017-0.054). Illegal harvest in this study was much higher than has been previously reported for mule deer (Forrester and Wittmer 2013). This competing risk was especially high during the migration period, which could have an additive effect for both migrants and residents, and could explain why both groups are negatively affected during this time of year.

Overall, annual survival estimates for migratory females (S=0.82, 95% CI: 0.80 to 0.84) were within the range of other reported survival estimates or female mule deer; however, survival rates for resident deer in my study (S=0.75, 95%CI: 0.71 – 0.81) were at the lower range of what was previously reported (Table 9). Annual estimates of survival for males in my study (0.404, SE=0.015, 95%CI = 0.375, 0.433) were also low relative to annual estimates reported for male mule deer

in other parts of their range (Table 9). I calculated an estimate of the population growth rate for all females during the study and estimated a 2.9% decline. However, this would result in greater population declines than actually observed between 2001 and 2015 (24%; Oregon Department Fish and Wildlife 2015) if the population experienced an annual rate of decline I estimated (2.9% per year = 34% decline from 2001 to 2015). More rigorous estimates of recruitment, fawn survival, juvenile recruitment, and carrying capacity are necessary to fully understand the annual rates of population change in this mule deer population.

A feedback pattern may be driving mule deer populations in some areas where anthropogenic changes to habitat leads to decreased food resources or changes in predator/prey dynamics (Forrester and Wittmer 2013). This in turn modifies mule deer carrying capacity or predation risk which ultimately increases variance and decreases resilience in mule deer population dynamics (Forrester and Wittmer 2013). Major habitat alterations occurring in this study area could have contributed to a negative feedback as described above. For example, the Bureau of Land Management has both renewable and non-renewable energy projects underway in the study area (Bureau of Land Management 2015). Also, Bend and the surrounding areas have seen a dramatic population increase which has increased development and urban expansion (Kline 2012). As anthropogenic alterations to the landscape continue to occur, it is important for biologists to consider and monitor the potential changes in carrying capacity and subsequent changes in vital rates and population size as necessary resources for mule deer are decreased.

MANAGEMENT IMPLICATIONS:

Migratory female mule deer had higher survival than residents during the 7 years of this study. Social structure of mule deer is driven by female philopatry (Wallmo 1981) and migration paths tend to be passed down through females (Nicholson et al. 1997). Therefore, it is important to maintain these corridors and pathways for future mule deer movements given the current benefits of migration to annual female survival. Conversely, resident deer had lower survival than those deer that wintered in other locations. Other studies in the Bend area have attributed mule deer population

declines to habitat loss due to urban expansion (Kline 2012). Even at low densities, development could negatively affect winter habitat use and migration paths by fencing, collisions with motor vehicles and anthropogenic disturbance. However, there may be some benefit to being a resident during some years with extreme environmental conditions not observed in this study. Regardless, if maintaining or increasing mule deer populations in this part of Oregon is an important objective, then it may be important for future development to consider deer migration routes and winter ranges when expanding urban areas to increase survival rates of resident female mule deer throughout the year.

My research suggests that female mule deer have lower survival during the fall migration period (October and November) and that illegal harvest is a substantial cause of mortality for females. In addition, during the fall migration period there is a steady increase in the daily risk of mortality for female mule deer from both illegal harvest and human-related causes. Thus, female mule deer appear to be at the most risk of mortality during these two months of the year, despite being excluded from the legal hunting season. Although there is no hunting season for females in this population set by the state of Oregon, females can be legally harvested by tribal members on tribal and public lands. Unfortunately we could not distinguish this type of legal harvest from illegal harvest, but if illegal harvest of female mule deer by non-tribal members represents a large part of this category, then increased monitoring and surveillance by law enforcement to decrease illegal harvest may be beneficial, particularly during times of the year when illegal harvest mortality of females is high. Hunter education and awareness is also an important tactic that can be implemented through the annual hunting regulations and hunter education classes. Explaining to the general hunting public, that harvest of female mule deer in this study area has a negative effect on female survival rates, which can ultimately lead to population decline, may urge more ethical hunting practices by those responsible for the illegal harvest. Encouraging hunters to be observant of their surroundings, including other hunters, and report any suspicious activity may also decrease the portion of the illegal harvest observed in this population.

The state agency that manages the mule deer populations (ODFW) does not manage the habitat in which they are found and therefore, strong partnerships with the private and public landowners should be made to meet the wildlife management goals of the species. Sharing habitat requirements, seasonal range locations, and migration paths with city planners and developers would also benefit the overall populations of mule deer. This includes cooperation and sharing information between ODFW and local law enforcement about out of season and illegal harvest. Establishing a long-term environmental monitoring program to provide insight on the effects like climate change habitat fragmentation would aid in the understanding of the population changes observed by wildlife managers. The results of this study can aid wildlife biologists with mule deer population estimates and decision making for habitat management. Understanding mule deer population dynamics is essential for maintaining viable populations, establishing harvest regulations, and preventing unnecessary resource conflicts.

LITERATURE CITED

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.

Buruea of Land Management. 2015. Energy Maps and Reports. Non-Renewable energy projects, Oregon. <http://www.blm.gov/or/energy/files/NonRenewable EnergyProjects_OR-Jan2015.pdf> Accessed 24 September 2015.

Buruea of Land Management. 2015. Energy Maps and Reports. Renewable energy projects, Oregon. < http://www.blm.gov/or/energy/files/RenewableEnergy Projects _OR-Jan2015.pdf> Accessed 24 September 2015> Accessed 24 September 2015.

Forrester, T.D. and H.U. Whittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer Odeocileus hemionus in North America. Mammal Review 43: 292-308.

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.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Kline, J.D. 2012. Seasonal neighbors: residential development encroaches on mule deer winter range in central Oregon. Pacific Northwest Research Station, Publication 140, Portland, Oregon, USA.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat section and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

Oregon Department of Fish and Wildlife. 2003. Oregon's mule deer management plan. Oregon Department of Fish and Wildlife, Portland, OR, USA.

Peek, J.M., B. Dennis, and T. Hershey. 2002. Predicting population trends of mule deer. The Journal of Wildlife Management 66:729-736.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Bioloogical Conservation. 141:2159-2173.

Unsworth, J. W., F.D. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. The Journal of Wildlife Management 63:315–326.

Wallmo, O.C., editor. 1981. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska.

West N.E. 1999. Synecology and disturbance regimes of sagebrush steppe ecosystems. Sagebrush Steppe Ecosystems Symposium, Boise State University, Boise, Idaho.

White, G.C., and R. M. Bartmann. 1997. Mule deer management-what should be monitored? Pages 104-118. Proceedings of the 1997 deer/elk workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, N.Y.

Table 9. Comparison of annual survival estimates for female and male mule deer with standard errors (SE) from across their range.

State	Females (SE)	Males (SE)	Source
CO, ID, MT	0.85 (0.01)	-	Unsworth et al. 1999

NV, CA	0.75 (0.01)	-	Bleich and Taylor 1998
NM	0.81 (0.06)	-	Bender et al. 2007
CO	0.87 (0.07)		Bartmann et al. 1992
CO	0.91 (0.03)	-	Bishop et al. 2009
MT	-	0.522 (SD= 0.13)	Pac and White 2007
OR	0.79 (0.02)	0.40 (0.015)	(this study)

LITERATURE CITED

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos, 103: 247–260.

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the Mallard: VI. The effect of exploitation on survival. United States Fish and Wildlife Service Resource Publication 128.

Anthony, R. G. 1976. Influence of drought on diets and numbers of desert deer. Journal of Wildlife Management 40:140–144.

Bartmann R.M., G.C. White, and L.H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:3-39.

Bender, L. C., G. A. Schirato, R. D. Spencer, K. R. McAllister, and B. L. Murphie. 2004. Survival, cause-specific mortality, and harvesting of male black-tailed deer in Washington. Journal of Wildlife Management 68:870–878.

Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118–1124.

Bishop C.J., J.W. Unsworth, and E.O. Garton. 2005. Mule deer survival among populations in Southwest Idaho. The Journal of Wildlife Management 69:311-321.

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.

Brown, C.G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. The Journal of Wildlife Management 56:246-253.

Brown, D. E., D. Warnecke, T. McKinney, and C. A. Jones. 2006. Effects of midsummer drought on mortality of doe pronghorn (Antilocapra americana). Southwestern Naturalist 51:220–225.

Bolen, E.G., and W.L. Robinson. 2003. Wildlife ecology and management. Fifth edition. Pearson Education Inc., Upper Saddle River, New Jersey, USA.

Bolger D.T., W.D. Newmark, T.A .Morrison, and D.F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63-77.

Bookhout, T.A., editor. 1994. Research and management techniques for wildlife and habitats. Fifth Edition. The Wildlife Society, Bethesda, Maryland, USA.

Bowman, J.L., Kochanny, C.O., Demarais, S. and Leopold, B.D. 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28:141–145.

Budeau, D. 2010. Oregon upland game bird hunting season framework. Wildlife Division, Oregon Department of Fish and Wildlife Salem, OR USA.

Bureau of Land Management. 2015*a*. Strategic Plan. United States Department of the Interior p30.

Buruea of Land Management. 2015*b*. Energy Maps and Reports. Non-Renewable energy projects, Oregon. <http://www.blm.gov/or/energy/files/NonRenewable EnergyProjects_OR-Jan2015.pdf> Accessed 24 September 2015.

Buruea of Land Management. 2015*c*. Energy Maps and Reports. Renewable energy projects, Oregon. < http://www.blm.gov/or/energy/files/RenewableEnergy Projects _OR-Jan2015.pdf> Accessed 24 September 2015> Accessed 24 September 2015.

Chalmers, G. A., and M.W. Barrett. 1982. Capture myopathy. Pages 84-94 in G. L. Hoff and J. W. Davis, eds. Noninfectious diseases of wildlife. Iowa State Univ. Press, Ames.

Clements, C.D., J.A. Young. 1997. A viewpoint: rangeland health and mule deer habitat. Journal of Range Management 50:129-138.

Clover, M.R. 1954. A portable trap and catch-net. California Fish and Game 40:367-373.

Committee of acceptable field methods in mammalogy. 1987. Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. Journal of Mammalogy, 68, (supplement) 1-18.

Connelly, G. E. 1981. Limiting factors and population regulation. Pages 245-285 in O. C.Wall-mo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

Cooch, E., and G. White. 2015. A gentle introduction to Program Mark:14th edition. <http:// www.phidot.org/software/mark/docs/book/> Accessed 1 May 2015.

Cupples, J.B., D.H. Jackson. 2014. Comparison of mule deer distributions during winter and hunting seasons in south-central Oregon. Wildlife Technical Report. Oregon Department Fish and Wildlife, Portland, OR, USA

D'Eon, R.G., and R. Serrouya. 2005. Mule deer seasonal movement and multiscale resource selection using global positioning system radio telemetry. American Society of Mammologists 86:736-744.

DeLgiudice, G.D., M.R. Riggs, P. Joly and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central   Minnesota. The Journal of Wildlife Management 66: 698-717

Doherty, P. F., G. C. White, and K. P. Burnham. 2010. Comparison of model building and selection strategies. Journal of Ornithology 152:317–323.

Eberhardt, L. E., E.E. Hanson, and L.L. Cadwell. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. Journal of Mammalogy 65: 404–409.

Forrester, T.D. and H.U. Whittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer Odeocileus hemionus in North America. Mammal Review 43: 292-308.

Franklin, J.F., and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Portland, USA.

Fryxell, J.M., J. Greever, and A.R.E, Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist, 131: 781–798.

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.

Garrott, R. A., G.C. White, R.M. Bartmann, L.H. Carpenter, and A.W. Alldredge. 1987. Movements of female mule deer in northwest Colorado." The Journal of Wildlife Management 51: 634–643.

Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

Gruell, G.E., and N.J. Papez. 1963. Movements of mule deer in northeastern Nevada. Journal of Wildlife Mangement 27:414-423.

Hammitt, W. E., Cole, D. N., & Monz, C. A. 2015. Wildland recreation: ecology and management. John Wiley & Sons, West Sussex, UK

Hanley, T. A. 1996. Potential role of deer (Cervidae) as ecological indicators of forest management. Forest Ecology and Management 88:199–204.

Hebblewhite , M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

Hebblewhite M., and D.T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B 365:2303–2312.

Heisey, D. M., and T.K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Heisey, D.M., and B.R. Patterson. 2006. A review of method to estimate cause-specific mortality in presence of competing risks. The Journal of Wildlife Management 70:1544-1555.

Hilborn, R. and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty. Chapman Hall. New York.

Hobbs, N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101:3-39

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Hoenes, B.D., and L.C. Bender. 2012. Factors influencing foraging habitats of mule deer, (Odocoileus hemionus) in the San Andres Mountains, New Mexico. The Southwest Naturalist 57:37-379.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1–33.

Inouye, D. W., and A. D. McGuire. 1991. Effects of snowpack on timing and abundance of flowering in Delphinium nelsonii (Ranunculaceae): implications for climate change. American Journal of Botany 78:997–1001.

Jackson, D. H., and J. Cupples. 2012. Mule deer ecology in south central Oregon. Oregon Department of Fish and Wildlife. Annual Project Performance Report.

Johnson, B. K., P. K. Coe, and R. L. Green. 2013. Abiotic, bottom-up, and top-down influences on recruitment of Rocky Mountain elk in Oregon: a retrospective analysis. Journal of Wildlife Management 77:102–116.

Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. Journal of Wildlife

Management25:54–60.

Keister, G. P, Jr., C. E. Trainer, and M. J. Willis. 1988. A self-adjusting collar for young ungulates. Wildlife Society Bulletin 16: 321-323.

Kline, D.K., D. L. Azuma, and R.J. Alig. 2004. Population growth, urban expansion and private forestry in western Oregon. Forest Science 50:33-43.

Kucera, T.E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122-130.

Lawrence, R.K., S Demarais, R.A. Relyea, S.P. Haskell, W. B. Ballard, and T.L Clark. 2004. Desert mule deer survival in southwest Texas. Journal of Wildlife Management 68*:* 561-569

Leopold, B.D. and P.R. Krausman. 1991. Factors influencing desert mule deer distribution and productivity in southwestern Texas. Southwestern Naturalist 36:67–74.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Litvaitis, J.A., and J. P. Tash. 2008. An approach toward understanding wildlife-vehicle collisions. Environmental Management 42:688-697.

Lloyd, J. and A. Casey. 2005. Wildlife hotspots along highways in Northwestern Oregon. Report to Oregon Department of Transportation, Salem, OR, 64 pp.

Lukacs, P.M., G.C. White, B.E. Watkins, R. H. Kahn, B.A. Banulis, A.A. Holland, J.A. Martens, and J. Vayhinger. 2009. Separating components of variation in survival of mule deer in Colorado. The Journal of Wildlife Management. 73: 817-826.

Mace, R.U., R. Denney, and R. Ingram. 1995. Big game history. Oregon Department Fish and Wildlife, Portland, OR, USA.

Mata-González, R., T. L. Evans, D. W. Martin, T. McLendon., J. S. Noller, C. Wan, and R. E. Sosebee. 2014. Patterns of Water Use by Great Basin Plant Species Under Summer Watering. Arid Land Research and Management 28:428–446

Matthews, P. E., and V.L. Coggins. 1997. Movements and mortality of mule deer in the Wallowa Mountains. In Proceedings of the 1997 Deer/Elk Workshop. Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, Arizona,

USA pp. 78-88.

McCorquodale, S.M. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management 63:861-871.

Millspaugh, J.J., and J. M. Marzluff. 2001. Radio tracking and animal populations. Academic Press, San Diego, CA. 474pp.

Molau, U.1997. Phenology and reproductive success in Arctic plants: susceptibility to climate change. Pages 153–170 in W. C. Oechel et al., editors. Global change and Arctic terrestrial ecosystems. Springer-Verlag, Berlin, Germany.

Monteith, K.L., C.B. Vernon, B.M. Stephenson, M.M. Conner, R.W. Klaver, and R.T. Bowyer. 2011. Timing of seasonal migration in mule deerL effects of climate, plant phenology, and life-history characteristics. Ecosphere 2:1-34.

Monteith, K. L., K. B. Monteith, J.A. Delger, L.E. Schmitz, T.J. Brinkman, C.S. Deperno, and J.A. Jenks. 2012. Immobilization of white-tailed deer with telazol, ketamine, and xylazine, and evaluation of antagonists. The Journal of Wildlife Management 76:1412-1419.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Mote, P.W., E.P Salathé. 2010. Future climate change in the Pacific Northwest. Climate Change, 102:29-50.

Murray, M. G. (1995). Specific nutrient requirements and migration of wildebeest. In: Serengeti II: Dynamics, Management, and Conservation of an Ecosystem (eds. Sinclair, A.R.E. & Arcese, P.) University of Chicago Press, Chicago, pp. 231–256.

Murray, D.L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70:1530-1543.

Neilsen, C.K., R.G. Anderson, and M.D. Grund. 2003. Landscape Influences on deer-vehicle accident areas in an urban environment. The Journal of Wildlife Management. 67:46-51.

Nichols, J. D., F. A. Johnson, and B. K. Williams. 1995. Managing North American waterfowl in the face of uncertainty. Ann. Rev. Ecol. Syst. 26:177-199.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat section and survival of

mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

Oregon Department of Fish and Wildlife. 2003. Oregon's mule deer management plan. Oregon Department of Fish and Wildlife, Portland, OR, USA.

Oregon Department of Fish and Wildlife. 2015*a*. Oregon migratory bird regulations. Oregon Department of Fish and Wildlife, Portland, OR, USA.

Oregon Department of Fish and Wildlife. 2015*b*. Oregon big game regulations. Oregon Department of Fish and Wildlife, Portland, OR, USA.

Oregon Department Fish and Wildlife. 2015*c*. Mule deer population trend in Oregon by Wildlife Management Unit. <http://www.dfw.state.or.us/resources/hunting/big_game/controlled_hunts/docs/hunt_statistics/15/Mule_Deer_10-15_26Jun15.pdf>.
Accessed 12 Aug 2015.

Oregon Department of Transportation. 1999. Oregon Highway Plan. Oregon Department of Transportation, Salem, OR USA.

Oregon Department of Transportation. 2010. Oregon State Highway System, traffic map 2010. Oregon Department of Transportation, Salem, OR USA.

Pac, D. F., and G. C. White. 2007. Survival and cause-specific mortality of male mule deer under different hunting regulations in the Bridger Mountains, Montana. Journal of Wildlife Management 71:816–827.

Palmer, W. C. 1965. Meteorological drought. Department of Commerce Weather Bureau Research Paper 45, Washington, D.C., USA.

Peek, J.M., B. Dennis, and T. Hershey. 2002. Predicting population trends of mule deer. The Journal of Wildlife Management 66:729-736.

Pettorelli, N., A. Mysterud, N.G. Yoccoz, R. Langvatn, and N.C Stenseth. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society of London B, 272: 2357–2364.

Pierce, B.M., R. T. Bowyer, and V.C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management, 8:533-541.

Post, P., N.C. Stenseth. 1999. Climate variability, plant phenology, and northern ungulates. Ecology 80:1322-1339

PRISM Climate Group. 2010. <http://www.prism.oregonstate.edu>.Accessed 18 Jun 2014.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist 137:50-66

Radeloff, V.C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland-urban interface in the United States. Ecological Applications 15:799–805

Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian

Journal of Zoology 80:556–568.

Robling, K.A., S.L. Griffin, and S.Stolz. 2014. Movement patterns, survival and sightability of mule in central and western South Dakota. South Dakota Department of Game, Fish and Parks, Peirre, South Dakota, USA.

Romin L.A., and Bissonette J.A. 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24:276-83

Rost, G.R. and J.A. Bailey. 1979: Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43: 634-641.

Saether, B.E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution. 12: 143–149.

Sargeant, G. A. 2011. Using csm to estimate cause-specific mortality from left-truncated data. <http://cran.r.project.org/web/packages/wild1/vignettes/csm.pdf>. Accessed 25 April 2014.

Sawyer, H., F. Lindzey, and D. McWhriter. 2005. Mule deer and pronghorn in western Wyoming.Wildlife Society Bulletin 33:1266-1273.

Sawyer, H., R.M. Nielson, F. Lindzey, L.L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396-403

Smith, R. H., and A. LeCount. 1979. Some factors affecting survival of desert mule deer. Journal of Wildlife Management 43:657–665.

Speten, D. 2014. Assessment of Mule Deer Fawn Survival and Birth Site Habitat Attributes in South-Central Oregon. Oregon State University, Corvallis, Oregon, USA.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Bioloogical Conservation. 141:2159-2173.

Thomas, T.R. and L.R. Irby. 1991: Winter habitat use by mule deer with access to wheat fields and planted forb grassland. Wildlife Society Bulletin 19: 155-162.

Unsworth, J. W., F.D. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. The Journal of Wildlife Management 63:315–326.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal Range Management 30:122-127.

Wallmo, O.C., editor. 1981. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska.

Walther GR, Post E, Convery P, Menzel A, Parmesan C, et al. 2002. Ecological responses to recent climate change. Nature 416:389-9

West N.E. 1999. Synecology and disturbance regimes of sagebrush steppe ecosystems. Sagebrush Steppe Ecosystems Symposium, Boise State University, Boise, Idaho.

Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increase Western U.S. forest fire activity. Science. 313: 940–943.

White, G.C., R.A. Garrot, R.M Bartmann, L.H. Carpenter, and A.W. Alldredge. 1987. Survival of mule deer in northwest Colorado. The Journal of Wildlife Management 51:852-859.

White, G.C., and R. M. Bartmann. 1997. Mule deer management-what should be monitored? Pages 104-118. Proceedings of the 1997 deer/elk workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, N.Y.

Zager P., G. Pauley, M. Hurley, C. White. 2007. Statewide Ungulate Ecology. Idaho Dept. of Fish and Game, Biose, Idaho, USA.