AN ABSTRACT OF THE DISSERTATION OF

Darren A. Clark for the degree of Doctor of Philosophy in Wildlife Science presented on March 18, 2014.
Title: Implications of Cougar Prey Selection and Demography on Population Dynamics
of Elk in Northeast Oregon

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Patricia L. Kennedy

Mule deer (*Odocoileus hemionus hemionus*) and Rocky Mountain elk (*Cervus canadensis nelsoni*; hereafter elk) populations in northeast Oregon have declined in the past 10 to 20 years. Concurrent with these declines, cougar (*Puma concolor*) populations have apparently increased, leading to speculation that predation by cougars may be responsible for declining ungulate populations. However, empirical data on cougar diets, kill rates, and prey selection are lacking to support this speculation. Furthermore, the common assumption that cougar populations have increased in northeast Oregon may not be well founded because cougar populations in other areas within the Pacific Northwest region have declined in recent years. My primary research objectives were to (1) estimate kill rates and prey selection by cougars in northeast Oregon, (2) document causes of mortality and estimate survival rates for cougars, (3) estimate population growth rates of cougars in northeast Oregon and simulate the effects of hypothetical lethal control efforts on the cougar population, and (4) investigate the relative influence of top-down, bottom-up, and climatic factors for limiting population growth rates of elk in northeast Oregon. Results from my research will help guide cougar and elk management in northeast Oregon and provide a framework for assessing relative effects of top-down, bottom-up, and abiotic factors on population growth rates of ungulates in this and other areas.

I implemented a 3-year study in northeast Oregon to investigate diets, kill rates, and prey selection of cougars in a multiple-prey system to better understand mechanisms by which cougars may influence ungulate populations. During my research, 25 adult cougars were captured and fitted with Global Positioning System (GPS) collars to identify kill sites. I monitored predation sequences of these cougars for 7,642 days and

located the remains of 1,213 prey items killed by cougars. Cougars killed ungulates at an average rate of 1.03 per week (95% CI = 0.92 – 1.14); however, ungulate kill rates were variable and influenced by the season and demographic classification of cougars. Cougars killed ungulates 1.55 (95% CI = 1.47 – 1.66) times more frequently during summer (May-Oct) than during winter (Nov-Apr), but killed similar amounts of ungulate biomass (8.05 kg/day; 95% CI = 6.74 – 9.35) throughout the year. Cougars killed ungulates more frequently in summer because juvenile ungulates comprised most of the diet and were smaller on average than ungulate prey killed in winter. Female cougars with kittens killed more frequently (kills/day) than males or solitary females. After accounting for the additional biomass of kittens in cougar family groups, male cougars killed on average more biomass of ungulate prey per day than did females ($R = 0.41$, $P < 0.001$), and female cougars killed more biomass of prey per day as a function of the number and age of their kittens ($R = 0.60$, $P < 0.001$). Patterns of prey selection were influenced by season and demographic classification of cougars. Female cougars selected elk calves during summer and deer fawns during winter. In contrast, male cougars selected elk calves and yearling elk during summer and elk calves during winter. My results strongly supported the hypothesis that cougar predation is influenced by season, gender, and reproductive status of the cougar and these patterns in cougar predation may be generalizable among ecosystems. The observed selection for juvenile elk and deer suggested a possible mechanism by which cougars could negatively affect population growth rates of ungulates.

I investigated survival and documented causes of mortality for radio-collared cougars at 3 study areas in Oregon during 1989 – 2011. Mortality due to hunter harvest was the most common cause of death for cougars in the Catherine Creek study area and the study area combining Wenaha, Sled Springs, and Mt. Emily Wildlife Management Units (WSM study area) in northeast Oregon. In contrast, natural mortality was the most common cause of death for cougars in the Jackson Creek study area in southwest Oregon. Annual survival rates of adult males were lowest at Catherine Creek when it was legal to hunt cougars with dogs ($\hat{S} = 0.57$), but increased following the prohibition of this hunting practice ($\hat{S} = 0.86$). This latter survival rate was similar to those observed at Jackson Creek ($\hat{S} = 0.78$) and WSM ($\hat{S} = 0.82$). Regardless of whether hunting of cougars with

dogs was permitted, annual survival rates of adult females were similar among study areas (Catherine Creek $\hat{S} = 0.86$; WSM $\hat{S} = 0.85$; Jackson Creek $\hat{S} = 0.85$). I did not document an effect of age on cougar survival rates in the Catherine Creek study area, which I attributed to selective harvest of prime-aged, male cougars when it was legal to hunt cougars with dogs. In contrast, I observed an effect of age on annual survival in both the WSM and Jackson Creek study areas. These results indicate that sub-adult males had significantly lower survival rates than sub-adult females, but survival rates of males and females were similar by age 4 or 5 years. My results suggest that survival rates of cougars in areas where hunting cougars with dogs is illegal should be substantially higher than areas where use of dogs is legal.

I used estimates of cougar vital rates from empirical data collected in northeast Oregon to parameterize a Leslie projection matrix model to estimate deterministic and stochastic population growth rates of cougars in northeast Oregon when hunting cougars with dogs was legal (1989 – 1994) and illegal (2002 – 2011). A model cougar population in northeast Oregon that was hunted with dogs increased at a mean stochastic growth rate of 21% per year ($\lambda_S = 1.21$). Similarly, I found that a model cougar population that was subjected to hunting without dogs increased at a rate of 17% per year ($\lambda_S = 1.17$). Given that hunting cougars with dogs typically results in increased harvest and reduced survival rates of cougars, it was unexpected that the cougar population subjected to hunting with dogs was increasing at a faster rate than one that was not hunted with dogs. However, cougar populations in Oregon were subjected to low harvest rates when hunting cougars with dogs was legal and harvest was male biased. This resulted in high survival rates of female cougars and correspondingly high population growth rates.

The Oregon Cougar Management Plan allows the Oregon Department of Fish and Wildlife to administratively reduce cougar populations to benefit ungulate populations, reduce human-cougar conflicts, and limit livestock depredation. Consequently, I was interested in modeling the effects of a hypothetical lethal control effort on a local cougar population. Using empirically-derived vital rates and a deterministic Leslie matrix model, I found that the proportion of the cougar population that would need to be removed annually to achieve a 50% population reduction within 3 years was 28% assuming a closed population, and 48% assuming maximum immigration rates into the

population. Using a stochastic Leslie matrix model, I also determined that the model cougar population would likely return to its pre-removal size in 6 years assuming a closed population, and 2 years assuming maximum immigration rates. These model results indicate that current management practices and harvest regulations, combined with short-term, intensive, and localized population reductions, are unlikely to negatively affect the short-term viability of cougar populations in northeast Oregon. However, at this time, it is not known if intensive lethal control efforts funded by state agencies will be cost-effective (i.e., increased sales of tags to hunt deer and elk will offset the costs of control efforts). Further research is needed to investigate the cost-effectiveness of cougar control efforts in Oregon.

I developed a Leslie matrix population model, parameterized with empirically-derived vital rates for elk in northeast Oregon, to investigate the relative influence on elk population growth rates of (1) survival and pregnancy, and (2) top-down, bottom-up, and climatic variables. I then estimated the effect of varying the strength of top-down factors on growth rates of elk populations. Growth rates of the model elk population were most sensitive to changes in adult female survival, but due to the inherent empirical variation in juvenile survival rates explained the overwhelming majority of variation in model population growth rates ($r^2 = 0.92$). Harvest of female elk had a strong negative effect on model population growth rates of elk ($r^2 = 0.63$). An index of cougar density was inversely related to population growth rates of elk in my model ($r^2 = 0.38$). A delay in mean date of birth was associated with reduced juvenile survival, but this had a minimal effect on population growth rates in my model ($r^2 = 0.06$). Climatic variables, which were used as surrogates for nutritional condition of females, had minimal effects on population growth rates. Likewise, elk density had almost no effect on population growth rates ($r^2 = 0.002$). The results of my model provided a novel finding that cougars can be a strong limiting factor on elk populations. Wildlife managers should consider the potential top-down effects of cougars and other predators as a limiting factor on elk populations.

Implications of Cougar Prey Selection and Demography on Population Dynamics of Elk
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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Darren A. Clark, Author

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This dissertation represents the culmination of my academic training, but is a bittersweet moment in my life given the unfortunate passing of my major professor Dr. Robert G. Anthony. Dr. Anthony served as principal investigator, provided editorial comments on drafts of this dissertation, and served as a mentor during my time at Oregon State University. Bob had the patience, or lack of common sense, to guide me through two graduate degrees at Oregon State University. As I entered graduate school in 2004, I was grateful about the opportunity to work towards my Master's degree. However, I was naïve to the true opportunity presented: the chance to work with one of the premier wildlife ecologists in the world. Over two degree programs, I developed an appreciation for the opportunity I was given and could not imagine a better training as a wildlife ecologist than the one I received from Bob. It was an honor and privilege to be mentored by Bob over the past 10 years and I am extremely grateful for the professional opportunities, mentorship, and friendship provided by Bob. Bob influenced many lives, both personally and professionally, and he is greatly missed by all who had the pleasure of knowing him. Bob was a great scientist and person; I consider myself lucky to have known him.

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CONTRIBUTION OF AUTHORS

Dr. Robert G. Anthony and Dr. Bruce K. Johnson served as co-principal investigators, provided editorial comments, and assisted with study design of Chapters 2 and 3. Greg Davidson assisted with study implementation, data collection, and provided editorial comments for Chapter 2. Dr. DeWaine H. Jackson designed and implemented the Jackson Creek cougar study and provided access to cougar survival data used in Chapter 3 and Appendix F. Dr. Scott L. Findholt collected data on cougar survival at the Wenaha and Sled Springs study areas, which were used in Chapter 3. Mark Henjum and James J. Akenson implemented the Catherine Creek cougar study and provided data used to estimate cougar survival in Chapter 3.

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CHAPTER 1

GENERAL INTRODUCTION

Darren A. Clark

In recent years, many Rocky Mountain elk (*Cervus elaphus nelsoni*; hereafter, elk) populations throughout the western United States have declined (Gratson and Zager 1999, Schommer and Johnson 2003), including elk populations in northeast Oregon (Oregon Department of Fish and Wildlife [ODFW] 2003, 2012). This has been disconcerting because elk provide substantial recreational opportunities, funding resources for state wildlife agencies (Bunnell et al. 2002), and economic benefits to local communities (Bolon 1994, Fried et al. 1995, Brooks et al. 1991). Determining those factors limiting or regulating an elk population is essential for effective management, but elk populations may be influenced by a suite of interacting top-down, bottom-up, and abiotic factors that can be highly variable in space and time.

Bottom-up forces, mediated through nutrition, can limit or regulate ungulate populations (Bishop et al. 2009), typically through density-dependent mechanisms (Fowler 1987). Density-dependent processes generally operate via competition for food, particularly during winter when resources are most limited (Thorne et al. 1976, Houston 1982, Merrill and Boyce 1991). Pregnancy rates and juvenile survival typically decline in high-density elk populations, but adult survival is relatively insensitive to population density (Coughenour and Singer 1996). Juveniles have lower over-winter survival than adults in high-density populations (Sauer and Boyce 1983, Singer et al. 1997) because juveniles are at a competitive disadvantage for limited food resources (Houston 1982, Merrill and Boyce 1991), and they are more affected by adverse climatic conditions (Picton 1984, Singer et al. 1997). Sauer and Boyce (1983) suggested that density-dependent juvenile mortality was a mechanism of population regulation in elk. Nutritionally stressed female elk have reduced pregnancy rates (Trainer 1971, Kohlmann 1999, Cook et al. 2001, 2004, 2103) and give birth to smaller and lighter weight juveniles (Thorne et al. 1976, Keech et al. 2000). Smaller juveniles have lower survival rates than larger juveniles (Whitten et al. 1992, Sams et al. 1996, Singer et al. 1997), and survival of juveniles during the first few months following parturition has been directly linked to maternal body condition (Clutton-Brock et al. 1987, Bartmann et al. 1992, Cameron et al. 1993, Cook et al. 2004).

Predators can influence ungulate population dynamics (Gasaway et al. 1992, Boertje et al. 1996, Kunkel and Pletcher 1999), but predation can occur as a density-

dependent, density-independent, or inversely density-dependent effect (Messier 1994), confounding the net effect of predators on prey populations. The large guild of potential predators on elk [grizzly bears (*Ursus arctos*), black bears (*U. americanus*), gray wolves (*Canis lupus*), coyotes (*C. latrans*), cougars (*Puma concolor*), and bobcats (*Lynx rufus*)] further complicates the potential effect of predators in multiple-predator systems. Predation on elk typically occurs within the juvenile age class (Raedeke et al. 2002, Rearden 2005), and variation in juvenile survival has been identified as a primary determinant of recruitment (White and Garrott 2005, Harris et al. 2008) and population growth rates of elk (Gaillard et al. 1998, 2000, Raithel et al. 2007). Therefore, predation on juveniles may limit or regulate ungulate populations in some systems (Merrill and Boyce 1991, Coughenour and Singer 1996, White et al. 2010). However, predators typically have minimal effects on ungulate populations that are food-limited (Ballard et al. 2001).

Elk populations may be influenced by environmental or density-independent factors, which represent environmental stochasticity that can create substantial variability in population dynamics of ungulates (Raedeke et al. 2002). Furthermore, variation in climate may be the primary factor limiting or regulating some ungulate populations (Hurley et al. 2011). Detrimental environmental conditions can reduce forage production, increase food competition, and negatively affect ungulate populations, especially those at high densities (Sauer and Boyce 1983). In contrast, beneficial climatic conditions may negate density-dependence processes on ungulate populations by providing outstanding forage conditions in some years. Extreme climatic events (i.e., severe droughts or winters) or long-term environmental trends represent density-independent effects, which can influence pregnancy or survival rates of ungulates (Coughenour and Singer 1996, Singer et al. 1997, Garrott et al. 2003). In addition, predators can interact with environmental conditions in complex ways (Merrill and Boyce 1991, Coughenour and Singer 1996), which further complicates the identification of limiting and regulatory processes in ungulate populations.

ODFW and its cooperators have initiated several studies to better understand factors influencing pregnancy rates and survival of juvenile elk. These studies further clarified the importance of nutrition in determining rates of pregnancy and juvenile

survival (Cook et al. 2001, 2004, Noyes et al. 2002). Cougars were the primary source of mortality for free-ranging juvenile elk (> 70% of mortalities) in northeast Oregon, and an index of cougar density was strongly correlated with elk juvenile survival (Rearden 2005; B. Johnson, ODFW, unpublished data) and recruitment (Johnson et al. 2013). Given variation in juvenile survival rate explains most of the variation in population growth rate of elk (Raithel et al. 2007), predation on juvenile elk by cougars may be responsible for ongoing elk population declines in northeast Oregon. However, the link between cougar predation and elk population declines has not been well understood due to a lack of information on cougar abundance, population dynamics, prey selection, and kill rates. In addition, while ODFW has a solid understanding of individual top-down, bottom-up, and nutritional effects on elk pregnancy and juvenile survival rates in northeast Oregon, little is known about the relative effects of each of these factors on population growth rates of elk.

The aim of my research was to provide information on cougar kill rates, prey selection, and population growth rates in northeast Oregon. In addition, I wanted to develop an understanding of effects of intensive lethal control on population dynamics of cougars. Finally, I sought to clarify the relative relationships of top-down, bottom-up, and abiotic factors on population growth rates of elk in northeast Oregon. The objectives of my research were to (1) estimate kill rates and prey selection of cougars in a multiple-prey system (Chapter 2), (2) estimate survival rates of cougars under differing management scenarios (Chapter 3), (3) estimate population growth rates and viability of cougar populations in northeast Oregon (Chapter 4), (4) simulate the effects on cougar populations of intensive lethal control (Chapter 4), and (5) develop a population model for elk, based on field data collected in Oregon that incorporated the effects of top-down, bottom-up, and abiotic factors, and simulate the response of elk populations to varying cougar densities and harvest rates of female elk (Chapter 5). Results from my research will be used to help guide cougar and elk management in Oregon and provide a framework for assessing the relative effects of top-down, bottom-up, and abiotic factors on population growth of ungulates in this and other areas.

My dissertation begins with an analysis of prey use, kill rates, and prey selection by cougars in the Mt. Emily Wildlife Management Unit (WMU) in northeast Oregon.

This analysis further clarifies the effect of season, prey vulnerability, and reproductive status on kill rates, prey use, and prey selection patterns of cougars. In Chapter 3, I estimated survival rates of cougars in 3 study areas in Oregon during 1989 – 2011. These results clarified effects of hunting cougars with dogs on survival rates and documented survival rates where hunting cougars with dogs was prohibited. These results were used in Chapter 4 to investigate population growth rates of cougars in northeast Oregon. Recent studies have indicated that cougar populations may be declining in some areas, and I wanted to determine whether cougar populations in northeast Oregon were declining. I also addressed the potential effects of intensive lethal control of cougars on viability and recovery times of a hypothetical, localized cougar population. This analysis was conducted because ODFW is authorized to lethally remove cougars to benefit declining ungulate populations, reduce livestock depredation, or limit human-cougar conflict. Information regarding effects of intensive lethal control on cougar population dynamics is limited and this analysis clarified those effects. In Chapter 5, I constructed a Leslie matrix population model to assess relative effects of top-down, bottom-up, and abiotic factors on population growth of elk in northeast Oregon. Results from this chapter clarified the importance of cougar predation and hunter harvest on population growth rates of elk. In addition, I simulated effects of a hypothetical reduction of cougar densities on population growth of elk. Results from this chapter will help guide cougar and elk management in northeast Oregon and other areas where cougars are the primary predator of elk. Chapters 2 – 5 of this document were written as standalone manuscripts and have either been submitted (Chapters 2 and 3) or will be submitted (Chapters 4 and 5) to a peer-reviewed scientific journal. Each standalone chapter of my dissertation provides a detailed discussion of results and important implications for conservation and management. In Chapter 6, I provided a brief summary of research findings and their implications for conservation and management.

I have also provided 10 appendices with supplementary information on methods and results that were used in my main dissertation chapters, or that may prove useful for researchers and managers. In Appendix A, I contrasted efficacy of conservation detection dogs and human observers to locate kill sites of cougars based on global positioning system (GPS) location clusters. Estimates of live weights (kg) of prey used

to estimate kill rates (kg prey/day) of cougars in Chapter 2 are provided in Appendix B. In Appendix C, I described the regression model used to distinguish kill sites and non-kill sites of cougars using GPS location data. The methods I used to develop estimates of prey availability are provided in Appendix D. These estimates were used to estimate prey selection by cougars in the Mt. Emily WMU, which was described in Chapter 2. Appendix E provides a graph of dates cougars marked with GPS collars were monitored to assess kill rates and prey use according to the gender and reproductive status of the cougar (described in Chapter 2). In Appendix F, I estimated survival rates of cougar kittens in Oregon. These estimates were used in Chapter 4 to estimate population growth rate of cougars in northeast Oregon. In Appendix G, I estimated age-specific survival rates of female elk in Wenaha and Sled Springs WMUs in northeast Oregon. These estimates were used to parameterize the Leslie matrix model in Chapter 5. In Appendix H, I provided a summary of a pilot study used to assess the efficacy of using baited hair snares to obtain hair samples from cougars. This endeavor was ultimately unsuccessful, and I collaborated with other biologists to utilize conservation detection dogs to collect scat samples from cougars to estimate cougar densities using genetic capture-recapture estimation techniques (Davidson et al. *In Review*). Appendix I presents results from a life-stage simulation analysis to assess the effect of process variance in vital rates of cougars on population growth. Appendix J provides estimates of home-range sizes of GPS collared cougars in the Mt. Emily WMU from 2009 – 2012.

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CHAPTER 2

COUGAR KILL RATES AND PREY SELECTION IN A MULTIPLE PREY SYSTEM
IN NORTHEAST OREGON

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ABSTRACT

It has been suggested that cougars (*Puma concolor*) have contributed to population declines of mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) in northeast Oregon. Little empirical evidence exists to back this suggestion, and the number, species, gender, and age class of ungulates killed by cougars is unknown. We implemented a 3-year study in northeast Oregon to investigate the diet, kill rates, and prey selection of cougars in a multiple prey system to better understand mechanisms by which cougars may influence ungulate populations. We captured and marked 25 adult cougars with Global Positioning System (GPS) collars to identify kill sites. We monitored predation sequences of these cougars for 7,642 days. Through field investigation of kill sites, we located the remains of 1,213 prey items killed by cougars of which 1,158 were ungulates (95.4%). Cougars killed at an average rate of 1.03 ungulates/week (95% CI = 0.92 – 1.14); however, kill rates were variable and influenced by the season and demographic classification of cougars. Cougars killed 1.55 (95% CI = 1.47 – 1.66) times more frequently during summer (May-Oct) than winter (Nov-Apr) but killed similar amounts of ungulate biomass (8.05 kg/day; 95% CI = 6.74 – 9.35) throughout the year. Kill rates were higher in summer because juvenile ungulates comprised most of the diet and were smaller than prey killed in winter. Female cougars with kittens > 6 months old killed more frequently (kills/day) than males, solitary females, and females with kittens < 6 months old. After accounting for the additional biomass of kittens in cougar family groups, male cougars killed more biomass of prey per day than females ($R = 0.41$, $P < 0.001$), and female cougars killed more biomass of prey per day proportional to (or as a function of) the number and age of kittens ($R = 0.60$, $P < 0.001$). We documented patterns in prey selection influenced by season and demographic classification of cougars. Male cougars had stronger selection patterns for elk, and female cougars had stronger selection for deer. Female cougars selected elk calves during summer and deer fawns during winter. In contrast, male cougars selected elk calves and yearling elk during summer and elk calves during winter. Female cougars with kittens > 6 months old demonstrated little selection for any age class or species of prey, and this likely highlighted an opportunistic foraging strategy to maximize energy gains while feeding young. Cougars selected adult male deer during winter but not

during summer but did not select adult elk according to gender. Our results strongly supported the hypothesis that cougar predation is influenced by season and demographic classifications of cougars and our results may be generalizable to other areas. The patterns of selection for juvenile elk and deer suggested a possible mechanism by which cougars could negatively affect ungulate populations. Wildlife managers should consider the potential negative effects of cougars on ungulate populations in areas where juvenile recruitment has been chronically low.

INTRODUCTION

Over the past 2 decades, many Rocky Mountain elk (*Cervus canadensis nelsoni*, hereafter elk) and mule deer (*Odocoileus hemionus*) populations in the western United States have declined (Carpenter 1998, Gill 1999, Gratson and Zager 1999, Washington Department of Fish and Wildlife [WDFW] 2009), and similar declines have been observed for some mule deer and elk populations in northeast Oregon (Oregon Department of Fish and Wildlife [ODFW] 2012). In many areas of northeast Oregon, mule deer and elk populations have declined as much as 50% in the past 10-15 years (ODFW 2003, 2011, 2012). Factors implicated in population declines of mule deer in the western United States include habitat loss (Clements and Young 1997, Gill 1999, Bishop et al. 2009) and degradation (Peek et al. 2001, 2002, ODFW 2011), predation (Ballard et al. 2001, Robinson et al. 2002) competition with elk (Gill 1999), and overharvest (McCorquodale 1999). Mule deer are the primary prey of cougars (*Puma concolor*) throughout western North America (Iriarte et al. 1990, Murphy and Ruth 2010), and cougar populations in Oregon have increased since the mid-1960s from near extirpation to widespread distributions (Keister and Van Dyke 2002, ODFW 2006). Due to the concurrent statewide increase of cougars and decline of some mule deer populations, it has been speculated that cougars may be contributing to the decline of some mule deer populations in Oregon; however, there is scant information on prey use and selection of cougars in Oregon to base management actions that might address this potential relationship (Nowak 1999, ODFW 2011).

During the past 10-15 years in much of northeast Oregon, calf to cow ratios at the end of winter were below the level of recruitment necessary to maintain elk populations (23 calves per 100 cows; ODFW 2003, 2012, Harris et al. 2008). Also, low

pregnancy rates may contribute to inadequate recruitment; however, pregnancy rates of cow elk in northeast Oregon over the past 10-20 years have been ~90% (Johnson et al. 2013a). Despite the relatively low reproductive value of elk calves, variable calf survival explains most of the variation in population growth rates of elk (Raithel et al. 2007). Cougars were identified as the proximate cause of mortality of elk calves in southeast Washington (Myers et al. 1998) and northeast Oregon (Rearden 2005, Griffin et al. 2011). During a 6-yr study in northeast Oregon, annual survival of elk calves ranged from 23-53% annually, and calf survival and recruitment was negatively correlated with an index of cougar density (Rearden 2005, Johnson et al. 2013a). While predation (Kunkel and Pletscher 1999, Johnson et al. 2013a), winter severity (Lubow et al. 2002, Creel and Creel 2009, Johnson et al. 2013a), nutritional deficiencies (Cook et al. 2001, 2004, 2013), and elk density (Fowler 1987, Coughenour and Singer 1996) can all affect recruitment and population dynamics of elk, cougar densities explained the overwhelming majority of variation in calf recruitment in northeast Oregon (Johnson et al. 2013a). Despite this finding, little is known about the age and number of elk killed by individual cougars in northeast Oregon, which makes it difficult to understand and quantify the effect of cougars on elk populations.

Accurate and unbiased estimates of kill rates, prey use, and predator abundance are critical to understanding the link between predator and prey population dynamics (Anderson and Lindzey 2003, Vucetich et al. 2011). Furthermore, ungulate populations in northeast Oregon typically include mule deer, white-tailed deer, and elk, and documenting prey use and selection patterns is important to understanding predator-prey dynamics in multiple prey systems (Robinson et al. 2002). Previous studies that documented cougar predation patterns have often generated contradictory results, but results are starting to align (Knopff et al. 2010, White et al. 2011). Although, it is unknown to what extent patterns of cougar predation may be generalized. The use of kill rates, prey use and selection patterns from other areas may lead to unwarranted conclusions regarding the effect of cougars on ungulates.

We implemented a 3-year study to document kill rates, prey use, and prey selection of a sample of adult cougars in a multiple prey system. Our first objective was to determine if cougar predation patterns can be generalized among study areas, and to do

this we retested the objectives of Knopff et al. (2010) including 1) how frequently do cougars kill ungulates, 2) are there seasonal influences on cougar predation patterns, 3) does gender and reproductive status of females influence predation patterns, and 4) do cougars select vulnerable prey or kill prey at random? Our second objective was to identify mechanisms that may allow cougars to negatively affect ungulate populations that included 1) the composition of species of prey, 2) age and gender of ungulate prey, 3) evidence of prey selection, and 4) evidence of prey switching. While developing a better understanding of cougar predation in Oregon and potential mechanisms by which cougars may affect ungulate populations were the main purposes of our research, this study was not designed to determine if cougars were causing ungulate population declines.

Based largely on the findings of Knopff et al. (2010), we hypothesized cougars would kill more frequently in the summer in response to the ungulate birth pulse, and kill rates and prey use would vary as a function of gender and reproductive status of cougars. We also hypothesized that cougar predation would follow the reproductive vulnerability hypothesis (Lima and Dill 1990), where female ungulates were most vulnerable to predation prior to parturition, males most vulnerable during the rut, and juveniles most vulnerable for the first few months after birth. Given that cougars killed a large percentage of radiocollared elk calves during the first 6 months and fewer calves during months 7 – 12 (Rearden 2005, B. Johnson, ODFW, unpublished data), we hypothesized cougars would select juvenile elk during summer, but switch to alternative prey (i.e., deer) during winter.

METHODS

Study Area

We studied cougar predation in Mt. Emily WMU located in the Blue Mountains of northeast Oregon, USA from 2009-2012 (Fig 2.1). Mt. Emily WMU covers 1,992 km^2 and ranges in elevation from 360—1,850 m. Land ownership was a mixture of private, public, and tribal lands (Confederated Tribes of the Umatilla Indian Reservation; CTUIR). Public lands were managed by U.S. Forest Service (Wallowa-Whitman and Umatilla National Forests) and State of Oregon. Land management practices on private
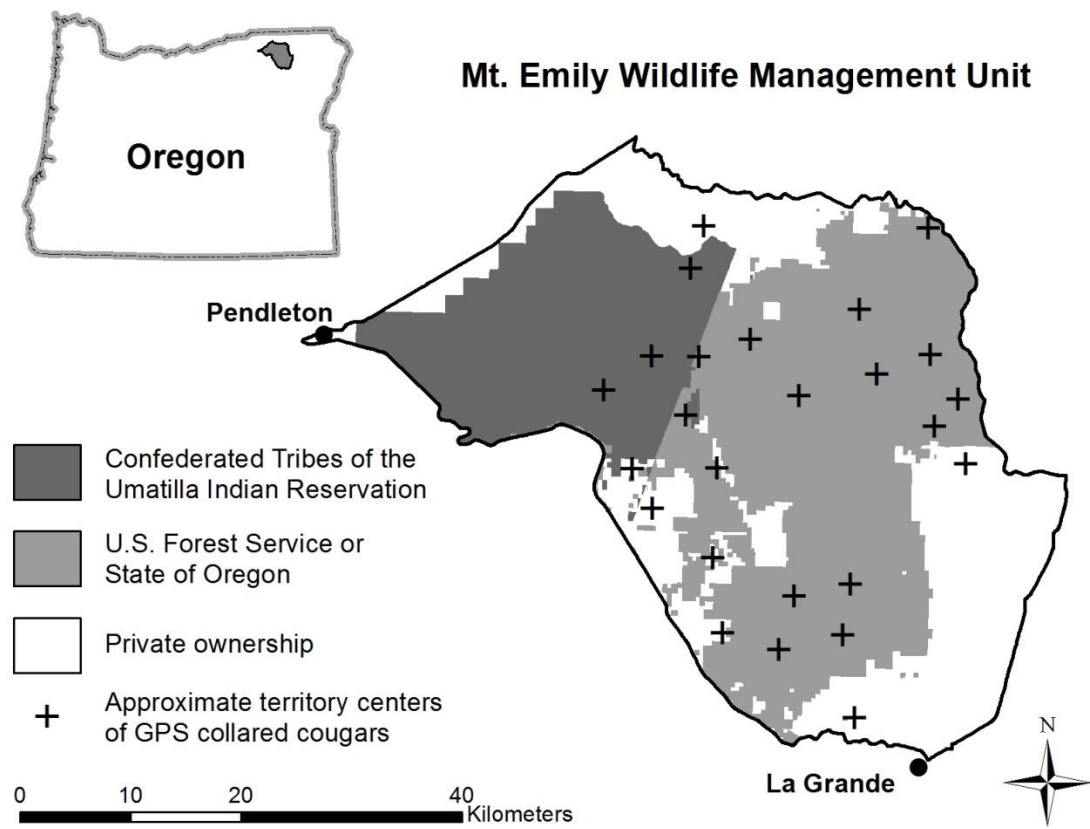
Figure 2.1. Location of the Mt. Emily Wildlife Management Unit in northeast Oregon, USA, and approximate center points of territories of cougars monitored to determine kill rates and prey selection in a multiple prey system from 2009-2012.

lands varied by elevation, with low elevations dominated by commercial agriculture and forested habitats managed as industrial forests or grazing rangelands. Vegetation patterns within the study area were strongly influenced by topography, aspect, and elevation. Low elevation sites on the west side of the study area were dominated by exposed upland slopes and a mixture of hawthorn (*Crataegus columbiana*), willow (*Salix* spp.), and blackberry (*Rubus armeniacus*) in riparian areas. Scattered ponderosa pine (*Pinus posderosa*) and black cottonwood (*Populus trichocarpa*) were found in riparian areas. High elevation sites on the central and eastern side of the study area were dominated by mixed-conifer stands with exposed southern aspects. Common tree species included ponderosa pine, Douglas-fir (*Psuedotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*) and lodgepole pine (*P. contorta*).

Since receiving formal protection in the 1960s, cougar populations in Oregon have increased from isolated populations in northeast and southwest Oregon to widespread distributions throughout the state (Keister and van Dyke 2002, ODFW 2006). Minimum indices of cougar population size generated from population reconstruction indicated that cougar populations in Mt. Emily WMU have remained relatively stable since the late 1980's (B. Johnson, ODFW, unpublished data). Over the past 10-15 years, the minimum number of cougars in the Mt. Emily WMU was between 40 – 55 individuals based only on harvest data (B. Johnson, ODFW, unpublished data). End of winter population estimates (ODFW, unpublished data) indicated mule deer ($n = 4,800$ adults) were the most abundant ungulate available to cougars in our study area followed by elk ($n = 2,850$ adults), and white-tailed deer ($n = 2,500$ adults; *O. virginanus*). Over the past 20 years, elk populations declined 50% (5,500 to 2,850 adults), mule deer populations increased 74% (2700 to 4800 adults), and white-tailed deer increased from extremely low densities to spatially restricted high densities (M. Kirsch, ODFW, pers. comm.).

Approximately 1,700 km^2 (85%) of summer range for deer and elk occurred within Mt. Emily WMU. Defined winter ranges for mule deer and elk covered 595 (30%) and 868 (45%) km^2, respectively of the Mt. Emily WMU (ODFW, unpublished data) and were located at lower elevations on the eastern and western portions of the study area. Elk densities on defined summer and winter ranges averaged 1.7 elk/km^2 and

3.3 elk/km^2, respectively. In contrast, deer densities within defined summer and winter

ranges averaged 4.3 deer/km^2 and 12.3 deer/km^2, respectively. Some mule deer, elk, and

cougars utilized high elevation, exposed, southern aspects during winter outside defined

winter range boundaries. White-tailed deer occurred at relatively high densities on

northwest side of the study area but were relatively rare throughout the remainder of the

study area. Moose (*Alces alces*) occurred at very low numbers (<10; M. Kirsch, ODFW,

pers. comm.). Approximately 500 feral horses (*Equus caballus*) were located on the

CTUIR (C. Scheeler, CTUIR, pers. comm.). An unknown number of domestic livestock

(e.g., cattle and sheep) were present throughout the year on private property and on

grazing allotments managed by the U.S. Forest Service during summer. Black bear

(*Ursus americanus*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*) were common, and

no wolf (*C. lupus*) packs were documented within Mt. Emily WMU during our research.

Cougar Capture and Monitoring

Cougars were captured with use of trained hounds according to procedures

outlined and approved by the Starkey Experimental Forest and Range, Animal Care and

Use Committee (IACUC No. 92-F-0004) and followed the guidelines of the American

Society of Mammalogists for use of wild mammals in research (Sikes et al. 2011). After

being treed, cougars were immobilized with a mixture of Ketamine (200 mg/mL; Fort

Dodge Animal Health, Fort Dodge, IA) and xylazine (20 mg/mL; Rompun$^®$; Bayer, Inc.,

Shawnee Mission, KS, USA) at a dosage of 0.4 mL per 10 kg of body mass and

administered via remote injection from a dart gun. Upon immobilization, cougars were

weighed, gendered, and aged. Whenever possible, we extracted the first premolar of

adult cougars for cementum annuli analysis to determine age (Trainer and Matson 1988).

We also obtained field estimates of cougar age using evidence from tooth wear (Ashman

et al. 1983, Shaw 1986), gum-line recession (Laundré et al. 2000), and pelage spotting

progression (Shaw 1986). Cougars were classified as dependent kittens (< 1 year),

subadults (independent females < 2 years and males < 3 years), and adults (females ≥ 2

years, and males ≥ 3 years). We used a different classification for sub-adult males and

females because males typically did not establish a territory until 3 years of age, and we

did not want to place Global Positioning System (GPS) collars on males that may

disperse from our study area. We marked each adult cougar with a GPS collar (Lotek

4400S or Lotek 7000SA [Lotek Engineering, Newmarket, ON, Canada]) and marked additional adults, sub-adults, and kittens with VHF radiocollars (Telonics MOD-600 [Telonics, Inc., Mesa, AZ, USA]) to monitor survival and aid recapture. We attached 2 permanent, numbered ear tags to uniquely identify each cougar. Prior to release, cougars were administered yohimbine (0.125 mg/kg; Yobine®; Lloyd Laboratories, Shenandoah, IA) as an antagonist for xylazine.

GPS collars were programmed to acquire 6 and 9 locations per day for female and male cougars, respectively (female acquisition schedule: 0300, 0600, 1200, 1800, 2100, 2400 hours; male acquisition schedule: 0130, 0300, 0430, 0600, 1200, 1800, 1930, 2100, 2230, 2400 hours). For unknown reasons, acquisition success of GPS collars placed on males was substantially lower than those on females; consequently, we increased the location acquisition schedule for collars placed on males to improve our ability to locate kills (Knopff et al. 2009). Individual cougars were continuously monitored until their collar failed, the cougar died, or the study ended. We used both ultra-high frequency (UHF) and ARGOS platform GPS collars in our study. We switched to ARGOS platform GPS collars during the later portion of the study to reduce the number of fixed-wing aircraft flights required to download GPS locations from collars. For cougars fitted with UHF GPS collars (Lotek 4400S), we downloaded locations fortnightly via a remote communication link from a fixed-wing aircraft or from the ground. For cougars fitted with ARGOS platform GPS collars (Lotek 7000SA or Lotek SAW), location data were retrieved via a satellite communication link every 5-10 days.

Locating Kill Sites and Identifying Prey Remains

We used an algorithm developed by Knopff et al. (2009) to identify potential predation sites of cougars, which were identified as clusters of GPS locations based on the following criteria: ≥ 2 locations within 200 m occurring within 6 days, with additional locations added if they were obtained within 6 days of the last location included in the cluster. To document predation events, we loaded the geographic coordinates of the geometric center of location clusters onto handheld GPS units (Garmin GPSMap 60csx; Garmin International, Inc., Olathe, KS, USA), hiked to clusters, and systematically searched the area for prey remains. When searching clusters for prey remains, we navigated to the cluster center, hiked along 8 transect lines positioned on cardinal

compass bearings (e.g., N, NE, E) out to 50 m, walked 20 m to the right, then zigzagged back to the cluster center. If additional GPS locations fell outside the 50 m radius, we searched a 25 m radius around each GPS location using the approach outlined above. We also used trained dogs to locate prey remains at location clusters, where a human observer directed the dog to search the area around the cluster using the search pattern outlined above. While detection dogs located kills faster (12 min. vs. 31 min., respectively) and appeared to locate kill remains more frequently than human observers (43% vs. 35%, respectively; Appendix A), detection dogs were not used during the initial portion of the study. After accounting for the probability of a location cluster containing a kill (see below), detection dogs and human observers found kills at similar rates (Appendix A). Consequently, we had no reason to believe that the use or non-use of dogs influenced our results.

Using data collected from GPS collared females monitored during the first year of our study we developed predictive models for both the summer (May – October) and winter (November – April) monitoring periods to eliminate searches at GPS location clusters that had a low probability of having a kill present. Our predictive models were developed using the methodology outlined by Knopff et al. (2009). We developed our own predictive models because we were not certain predictive models developed by Knopff et al. (2009) would generalize among studies. Furthermore, we observed differences in the number of locations observed at GPS location clusters during summer and winter and wanted to develop seasonal models to account for these differences. After the first year of the study, data on location clusters of males was insufficient to develop a predictive model, so we surveyed all location clusters of males for the duration of the study.

After locating prey remains at a location cluster, we used available evidence to determine if a cougar killed the prey item. When there was clear evidence of cougar predation (e.g., bite or claw marks on the hide, puncture marks on the skull or neck), we assigned the carcass as a cougar kill. In the absence of direct evidence of cougar predation, we used cougar sign (i.e., bed sites, scat, tracks, or a cached or covered carcass; Shaw 1977) to determine that a cougar had killed the prey item. If the available evidence indicated the animal was not killed by a cougar (e.g., hunter- or vehicle-killed)

we assigned the remains as a scavenging event. We documented evidence of black bear use and visitation of cougar kills because bears are known to displace cougars from kill sites (Murphy et al. 1998), which could increase kill rates of cougars. We used bear sign (e.g., scat or tracks) combined with disturbance of a kill site (e.g., scattered prey remains) to document visitation of a cougar kill by a black bear.

We determined the species of prey by using skeletal, anatomical, and pelage characteristics (Moore et al. 1974, Verts and Carroway 1998, Jacobson 2004). Ungulate prey was assigned to 1 of 3 age classes: juvenile (< 1 yr), yearling (1 yr), and adult ($\geq$ 2 yr). Age of prey was determined using body size or tooth eruption and wear patterns (Schroeder and Robb 2005). We determined gender of yearling and adult ungulates using presence of antler pedicels. In the event we were unable to determine species, age class, or gender of prey, we recorded these attributes as unknown. We assigned a date to predation events using the date of the first GPS location included in the cluster and assigned each predation event to summer or winter. We selected the summer season to ensure that the following events all occurred: ungulate birth pulse, lack of snowpack throughout the study area, and emergence of black bears from their dens. We assigned an approximate live weight estimate of ungulate prey (Appendix B), because we could not obtain field estimates for individual prey. Weights of yearling and adult deer and elk were determined from deer and elk captured in northeast Oregon (B. Johnson, ODFW, unpublished data). We estimated monthly weights of juvenile prey using a von Bertalanffy growth equation of the form $M(t) = A[1 - 1/3e^{-K(t - I)}]^3$, where $M(t)$ = mass (kg) at age t, A = maximum weight ($t = \infty$), K = growth rate, and I = age in days at inflection point (we used 140 days). We did not calculate separate weights based on gender of prey until they were classified as adults.

Kill Rates

We only used information on cougar killed ungulates to estimate kill rates. We estimated annual kill rates of cougars and compared to published estimates. Gender, age, and reproductive status of cougars can influence kill rates (Ackerman et al. 1986, Anderson and Lindzey 2003, Knopff et al. 2010), and kill rates can vary seasonally (Mattson et al. 2007, Knopff et al. 2010); consequently, we estimated kill rates seasonally for adult males, adult females, adult females with kittens < 6 months old, and adult

females with kittens > 6 months old. We used a ratio estimate (ungulate kills/week) to calculate kill rates because they are more conservative and less biased than other methods (i.e., days between consecutive kills; Hebblewhite et al. 2003), but require longer monitoring intervals to obtain reasonable estimates (Knopff et al. 2009, 2010). We included individual cougars in our analysis if they were monitored ≥ 42 days during a particular season and as part of a particular demographic classification, which removed 28 seasonal monitoring periods of individual cougars. We utilized a 42 day cutoff because this allowed us to retain the majority of our sample, while censoring short monitoring periods that may lead to unreasonable estimates. We determined the reproductive status of female cougars by visiting nursery sites, collaring at least 1 dependent kitten, observing tracks of kittens at kill sites, or visually observing kittens. The reproductive status of females was not monitored daily, and we may have incorrectly classified the reproductive status of females over short time periods (e.g., < 2 weeks). We estimated kill rates as the live weight biomass of prey killed per cougar per unit time (kg/day) to retest the hypothesis that cougar kill rates vary as a function of energetic requirements (Ackerman et al. 1986, Laundré 2005). Kill rates were estimated using the live weight of prey, and we did not apply a correction factor to account for edible biomass of prey, so we overestimated consumption rates of cougars (Knopff et al. 2010). We used a 2-way analysis of variance (ANOVA) and Tukey's honest significance test (HSD) to test for differences in kill rates (ungulates/week and kg prey/day) between demographic classifications of cougars and seasons (Day and Quinn 1989). We regressed kill rates (kg prey/day; dependent variable) on cougar body mass (kg; independent variable) to further test the hypothesis that kill rates were influenced by energetic requirements. To account for additional energetic requirements of females with kittens, we added 15 kg/kitten < 6 months old and 34 kg/kitten > 6 months old to the capture weight of the mother, which represent the median weights of kittens at 6 and 12 months of age, respectively (Laundré and Hernández 2002). We included effect of season and gender in our regression model because these factors may also influence kill rates (Anderson and Lindzey 2003, Knopff et al. 2010).

    To determine factors that may influence monthly variation in kill rates, we calculated inter-kill intervals (IKI) for individual cougars and obtained a monthly average

for all cougars. We used IKIs because they are less biased over short monitoring periods (e.g., days; Hebblewhite et al. 2003). We conducted simultaneous Pearson's correlations between IKIs, the average monthly prey weight, the proportion of juvenile ungulates in the diet, and the proportion of cougar kills visited by black bears in program R using function corr.test in the psych package (R Development Core Team 2011). We utilized a Bonferroni adjustment to correct for multiple comparisons and an alpha of 0.05 to determine significance of correlations. We examined colinearity between explanatory variables prior to analysis and determined that the proportion of juvenile ungulates in the diet and average prey weight were highly correlated ($R^2 = 0.63$). As a result, we only included variables for average prey weight and proportion of cougar kills visited by black bears in our analysis.

Prey Selection

Prey Availability

        We determined proportions of species, gender, and age classes of prey available to cougars within Mt. Emily WMU using population estimates and herd composition data provided by ODFW and CTUIR. We generated seasonal estimates of prey availability that were based on estimates at the start of each season. We calculated mean herd composition values and population estimates for each ungulate species from population surveys conducted by ODFW and CTUIR from 2009 - 2012 to obtain a single estimate of prey availability over the duration of our study. For deer and elk, we utilized separate, but similar approaches to calculate the proportion of individuals within each gender and age class. Additional details can be found in Appendix D.

Prey Selection

        We estimated prey availability at the population level, so we utilized approaches to analyze prey selection by cougars described by Thomas and Taylor (1990). Under Design I, used and available resources are defined at the population level, and individual animals are not identified. Design II compares individual resource use to population level availability. All prey selection analyses were conducted in program R (version 2.14.0; R Development Core Team 2011) using the widesI and widesII functions in the adehabitat package (Calenge 2006).

Design I selection.— We calculated seasonal (summer = May - Oct, winter = Nov - Apr) selection ratios for males, solitary females, females with kittens < 6 months old, and females with kittens > 6 months old. Within each group and season, we pooled kills from individual cougars to define use and compared this to available prey within the study area (i.e., population level). To estimate selection ratios at the population level for each group and season, we used:

$$\hat{w}_i = o_i \, / \, \pi_i$$

where $\hat{w}_i$ is the selection ratio for prey item i, o_i is the proportion of prey item i in the diet, and π_i is the proportion of species i available in the study area (Manly et al. 2002, eq. 4.9). Selection ratios between zero and 1 indicate use lower than available, and > 1 indicate selection.

We conducted 3 separate Design I analyses to assess prey selection at the population level. In the first analysis, we calculated species-specific selection ratios without regard to age or gender of prey. In our second analysis, we calculated genus (i.e., *Odocoileus* or *Cervus*) and age class (i.e., juvenile, yearling, or adult) selection ratios without regard to prey gender. For these analyses, data for cougars was pooled among gender and demographic classifications. We tested the null hypothesis that the 4 demographic classifications of cougars had similar proportions of prey in their diets (χ^2_{L1}; Manly et al. 2002, eq. 4.26) and if any classification of cougar non-randomly used prey (χ^2_{L2}; Manly et al. 2002, eq. 4.27). We compared selection ratios to determine where patterns of selection differed among demographic classifications of cougars. We conducted 1 additional Design I selection analysis (χ^2_L; Manly et al. 2002, eq. 4.11) to determine if cougars seasonally selected for a particular gender of yearling or adult deer or elk. For this analysis, we pooled seasonal data for all cougars to increase sample sizes and decrease Type II errors (Zar 1999).

Design II selection.—We estimated seasonal selection ratios of individual cougars, and individuals needed ≥ 5 predation events as part of a particular demographic classification to be included in the analysis. Female cougars were included in the analysis more than once if they transitioned between reproductive classifications. We estimated individual selection ratios using:

$$\hat{w}_{ij} = u_{ij} \, / \, (\hat{\pi}_i \, u_{+j})$$

where, u_{ij} is the number of prey item i in the diet of cougar j, u_{+j} is the total number of prey in the diet of cougar j, and $\hat{\pi}_{ij}$ is the proportion of available prey that are in category i (Manly et al. 2002, eq. 4.37). We calculated individual selection ratios separately in two analyses according to either the species or genus and age class of prey. The purpose of this analysis was to identify variability in selection ratios among individuals to determine if selection patterns were influenced by definitions of prey availability. We compared the range of individual to population selection ratios to identify the degree of variability among individuals.

RESULTS

We captured 9 adult males and 16 adult females and fitted them with GPS collars. Of the 16 females, 11 transitioned between reproductive classifications at least once. We monitored predation sequences for 7,642 cougar-days ($n = 25$, $\bar{x} = 318 \pm 49$ days/cougar, range = 38 - 850) from April 2009 to April 2012, which represented 20.9 cougar-years. Cougars were monitored more days during the summer (4,286 days, $n = 22$, $\bar{x} = 195 \pm 27$ days/cougar, range = 2 - 184) than the winter (3,356 days, $n = 22$, $\bar{x} = 153 \pm 25$ days/cougar, range = 7 - 181). Female cougars were monitored more days (5,518 days, $n = 16$, $\bar{x} = 368 \pm 67$ days/cougar, range = 59 - 850) than males (2,124 days, $n = 9$, $\bar{x} = 236 \pm 64$ days/cougar, range = 38 - 634). We visited 3,365 GPS location clusters and located the remains of 1,213 prey items at 1,172 clusters. The median number of days between the date a cluster was formed and when it was surveyed was 21 days ($\bar{x} = 28$ days, SD = 25) after kills were made, which resulted in most edible biomass being consumed before kills were documented.

Predictive Model for Determining Presence of a Kill

Our best models for determining the presence or absence of a kill at a GPS location cluster were similar to those of Knopff et al. (2009) but the beta coefficients differed and our model included an interaction term they did not consider (Appendix C). The summer model included parameters for the number of points in the cluster after accounting for fix acquisition success ($\beta = 0.69$), cluster fidelity ($\beta = 0.07$; the number of fixes away from the cluster subtracted from the number of fixes at the cluster), the average distance of all points in the cluster from the cluster center ($\beta = 0.003$), and an interaction term between the number of corrected points and the average distance of

points from the cluster center ($\beta = -0.003$). The winter model included the same parameters as the summer model, but beta coefficients differed (number of points; $\beta = 0.58$, fidelity; $\beta = 0.05$, average distance; $\beta = 0.03$, number of points * average distance; $\beta = -0.004$). We used a probability cutoff level of 0.12 and 0.06 during summer and winter, respectively. These cutoff levels were selected because they allowed > 20% of clusters not to be surveyed, while missing < 1-2% of kills (Appendix C).

Prey Use and Scavenging

Cougars killed a wide range of prey items including ungulates (elk, mule deer, and white-tailed deer), carnivores (badger [*Taxidea taxus*], black bear, cougar, and coyote), small mammals (beaver [*Castor Canadensis*], opossum [*Didelphis virginana*], raccoon [*Procyon lotor*], snowshoe hare [*Lepus americanus*], and woodrat [*Neotoma* spp.]), and birds (dusky grouse [*Dendragapus obscurus*], ruffed grouse [*Bonsana umbellus*], ring-necked pheasant [*Phasianus colchicus*], and turkey [*Meleagris gallopavo*]). Domestic sheep were the only domestic livestock killed by cougars during our study but this was rare (< 0.5% of all kills).

Of the 1,213 cougar kills, 1,158 (95.5%) were deer or elk (Table 2.1). Deer (mule deer and white-tailed deer combined) were the most common ungulate (68.6%) in cougar diets followed by elk (31.4%). The percent of biomass for deer (50.1%) and elk (49.9%) in the diets of cougars were similar. In instances where we were able to distinguish between deer species ($n = 667$), mule deer were the most common species in cougar diets (73.0%). Cougars killed 764 deer during our study, and fawns (46.5%) were the most frequently killed age class, followed by adults (36.1%), yearlings (11.0%), and unknown age deer (6.4%). Adult deer were the most frequently consumed age class of deer according to biomass (60.4%) followed by fawns (18.9%), yearling deer (13.0%), and unknown aged deer (7.7%). Cougars killed 364 elk during our study. Calves (75.3%) were the most frequently killed age class of elk, followed by adults (15.7%), yearlings (8.8%), and unknown age elk (0.2%). Adult elk were the most frequently killed age class according to biomass (42.8%) followed by calves (39.1%) and yearlings (18.1%). Cougar diets differed by gender (Table 2.1) with elk were more common in diets of males than females. The prevalence of deer in diets of solitary females and females with kittens

Table 2.1. Seasonal comparison of cougar diets for adult males, solitary adult females, females with kittens < 6 mo. old, and females with kittens > 6 mo. old. Results were from 1,213 predation events for 25 cougars in northeast Oregon, USA from 2009-2012.

Prey type	Adult male				Adult female no kittens				Adult female with kittens <6 mo. old				Adult female with kittens >6 mo. old			
	Summer		Winter		Summer		Winter		Summer		Winter		Summer		Winter	
	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N
Individual species																
White-tailed deer	11.7	21	11.6	13	6.7	17	20.2	20	18.6	34	6.0	3	18.7	37	25.5	35
Mule deer	17.9	32	32.1	36	42.4	108	62.6	62	43.2	79	74.0	37	38.9	77	40.9	56
Unknown deer[a]	9.5	17	5.4	6	11.0	28	2.0	2	9.3	17	10.0	5	19.7	39	8.8	12
Elk	46.9	84	47.3	53	38.0	97	14.1	14	23.5	43	8.0	4	18.2	36	24.1	33
Other[b]	14.0	25	3.6	4	2.0	5	1.0	1	5.5	10	2.0	1	4.5	9	0.7	1
Condensed ungulate																
Deer	45.5	70	50.9	55	61.2	153	85.7	84	75.1	130	91.8	45	81.0	153	75.7	103
Elk	54.5	84	49.1	53	38.8	97	14.3	14	24.9	43	8.2	4	19.0	36	24.3	33
Ungulates by age class																
Fawn	25.3	39	17.6	19	38.8	97	36.7	36	36.4	63	34.7	17	31.2	59	31.0	39
Yearling deer	2.6	4	6.5	7	5.6	14	8.2	8	9.8	17	4.1	2	11.6	22	10.3	13
Adult deer	15.6	24	17.6	19	14.4	36	33.7	33	28.3	49	46.9	23	32.3	61	33.3	42
Unknown age deer[c]	1.9	3	9.3	10	2.4	6	7.1	7	0.6	1	6.1	3	5.8	11	7.1	9
Calf	39.6	61	16.7	18	36.8	92	9.2	9	23.7	41	2.0	1	14.8	28	11.1	14
Yearling elk	8.4	13	5.6	6	1.2	3	1.0	1	1.2	2	2.0	1	2.1	4	1.6	2
Adult elk	5.8	9	26.9	29	0.8	2	4.1	4	0.0	0	4.1	2	2.1	4	5.6	7

[a] Insufficient prey remains were present to accurately determine species - most (62.7%) of unidentified remains were fawns.
[b] Other prey items included: badger, beaver, black bear, cougar, coyote, domestic sheep, opossum, raccoon, and turkey.
[c] Insufficient evidence was present to accurately assign the prey item to the correct age class.

> 6 months old increased during the winter, and prevalence of deer in the diets of male cougars and female cougars with kittens > 6 mo was similar between seasons.

We documented 50 instances of scavenging by cougars, which represented 4% of all prey remains. Of the 24 cougars monitored 15 (60.0%) scavenged at least once, and males (5 out of 9; 55.6%) and females (10 out of 16; 62.5%) scavenged at similar rates. Most carcasses scavenged by cougars were ungulates (44 of 50; 88%) that were hunter- or vehicle-killed. Cougars also scavenged discarded livestock remains ($n = 4$), illegal bear bait ($n = 1$), and a black bear ($n = 1$). Our results suggested that scavenging was influenced by availability of carcasses to individual cougars. For example, 1 female was responsible for 15 of the 50 instances of scavenging in an area where the remains of slaughtered ungulates and domestic livestock were discarded and vehicle-killed animals from an adjacent highway were present.

Kill Rates

We used a subset of 1,099 ungulate kills to calculate kill rates. Annually, cougars killed 1.03 (95% CI = 0.92–1.14) ungulates per week; however, cougars frequently killed at a faster rate. We documented 222 instances where intervals between consecutive kills were ≤ 2 days. Cougars occasionally killed much less frequently, and we documented 33 instances where intervals between consecutive kills were ≥ 21 days. These longer intervals occurred after a cougar killed a large prey item (e.g., adult elk) or scavenged. Kill rates (ungulates/week) of cougars were influenced by gender, reproductive status, and season ($F_{4,57} = 14.51$, $P < 0.001$; Fig. 2.2a). Cougars killed 1.55 (95% C.I. = 1.47-1.66) times more frequently during summer than winter, and female cougars raising kittens > 6 months old killed more frequently than other cougars. We observed substantial monthly variation in kill rates of cougars, as they killed most frequently during the ungulate birth pulse (May-July) and least frequently during winter (December-March). Monthly variation in cougar inter-kill intervals (i.e., days between kills) was best explained by the average weight of prey ($R = 0.92$, $P < 0.001$; Fig 2.3a), and the proportion of cougar kills visited by black bears ($R = -0.72$, $P = 0.02$; Fig 2.3b). Average prey weight was negatively correlated with the proportion of juvenile ungulates in the diet of cougars ($R = -0.80$, $P = 0.002$), indicating that cougars killed most frequently when juvenile ungulates dominated their diets (Table 2.1). The proportion of cougar kills
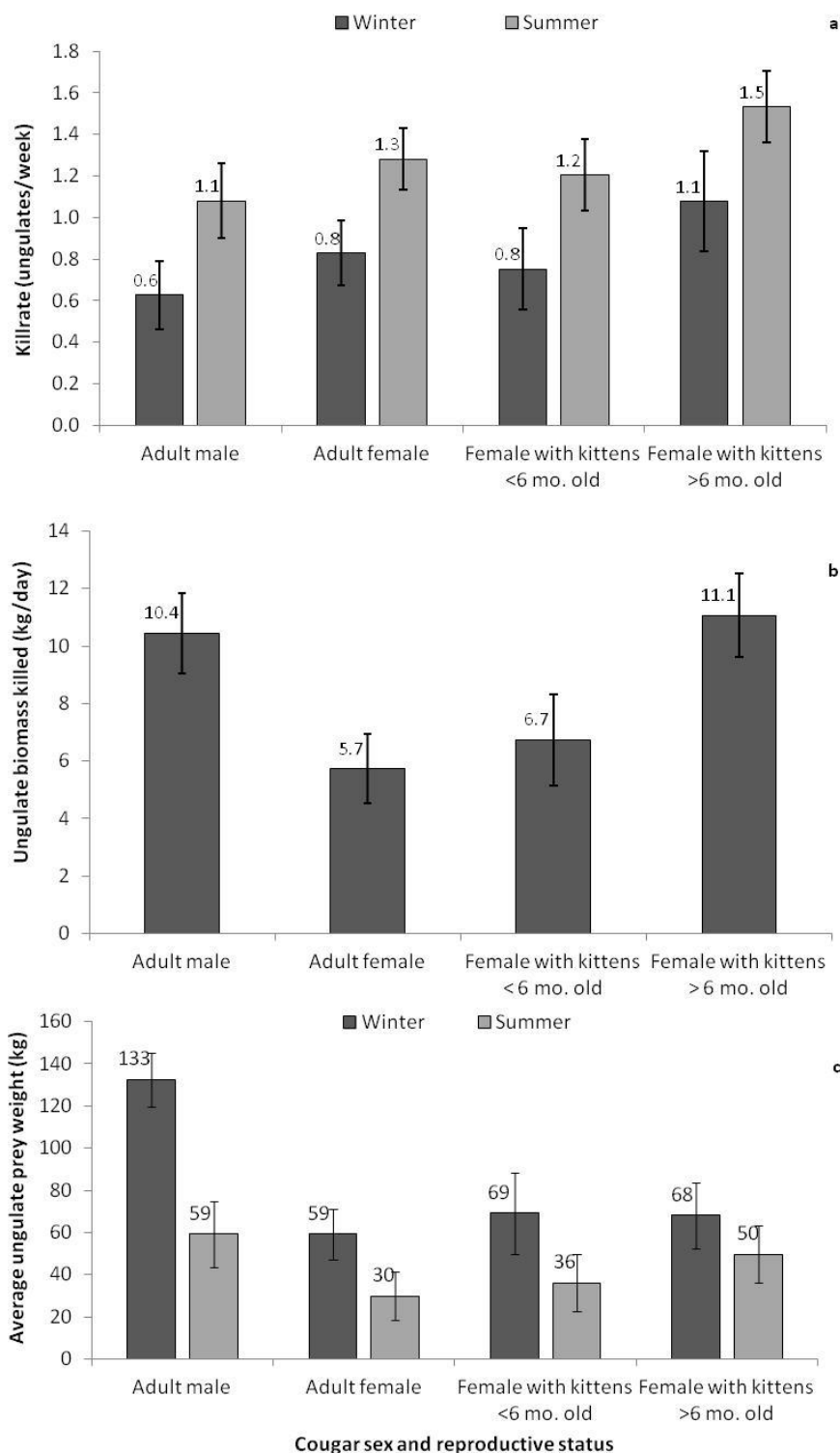
Figure 2.2. Cougar kill rates and associated 95% confidence intervals expressed as (a) frequency, (b) biomass of prey, and (c) average prey size for each of 4 demographic classifications of cougars. Results were from 1,099 consecutive predation events from 21 cougars fitted with Global Positioning System collars in northeast Oregon, USA, from 2009-2012.
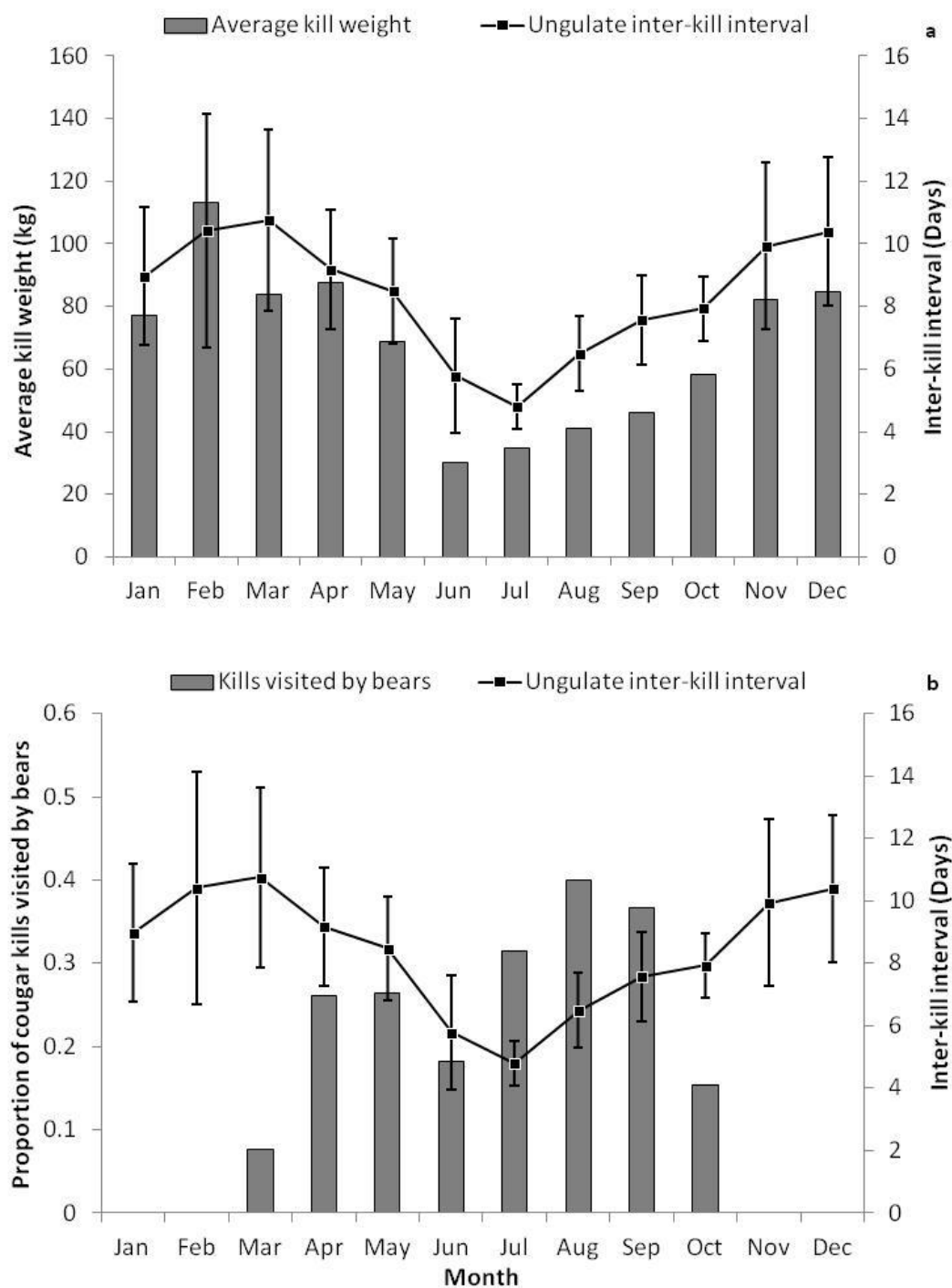
Figure 2.3. The average ungulate inter-kill interval and associated 95% confidence interval in each month versus the (a) average size of prey killed by cougars and (b) proportion of cougar kills visited by black bears in northeast Oregon, USA, from 2009-2012. We derived monthly average prey weights and the proportion of cougar kills visited by black bears using 1,158 ungulate kills where estimated weight and date of death was known. We estimated inter-kill intervals using data from 26 cougars where the date of the previous kill was known.

visited by black bears and average kill weight were correlated (R = -0.70, P = 0.01), suggesting prey size was the primary factor influencing cougar kill rates.

The daily biomass of prey killed by cougars averaged 8.05 kg/day (95% CI = 6.74 – 9.35 kg/day), but varied by gender and reproductive status ($F_{3,58}$ = 15.38, P < 0.001; Fig. 2.2b). Male cougars and females with kittens > 6 months old killed more prey biomass per day than solitary females or females with kittens < 6 months old. The annual live-weight biomass of ungulates killed per cougar averaged approximately 3,800 kg for adult males, 2,100 kg for solitary females, 2,500 kg for females with kittens < 6 months old, and 4,000 kg for females with kittens > 6 months old. While male cougars killed less frequently than female cougars with older kittens (Fig. 2.2a), males killed larger prey ($F_{7,54}$ = 24.78, P < 0.001; Fig. 2.2c), which resulted in males killing similar amounts of biomass per day as females with kittens > 6 months old (Fig. 2.2b).

Our regression model used to explain the effects of cougar biomass on kill rates (kg prey/day) was:

kill rate (kg prey/day) = 3.35 + 0.06 × cougar mass + 3.62 × gender

where, cougar mass is the weight (kg) of cougars after accounting for the age and number of dependent kittens, and gender is an indicator variable (male = 1, female = 0). This model indicated cougar body mass (after accounting for dependent kittens; R = 0.60, P < 0.001) and gender (R = 0.41, P < 0.001) were significant predictors of the biomass of prey (kg) killed per day (R^2 = 0.52; Fig. 2.4). Season was not a significant predictor in our model, indicating cougars killed similar amounts of prey biomass/day annually. Our regression model had a moderate fit to the data (R^2 = 0.52), suggesting that factors other than body mass influenced the amount of biomass killed per day by cougars.
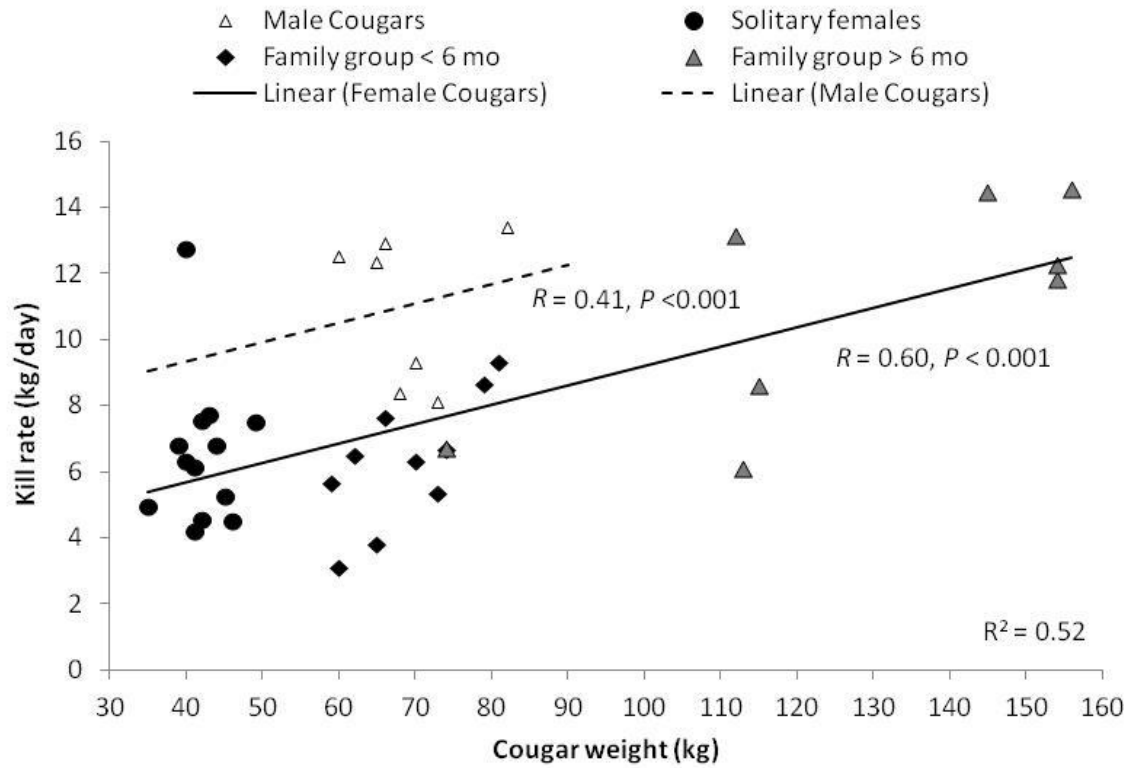
Figure 2.4. Relationship between kill rate (kg prey/day) and cougar body mass accounting for the additional mass of dependent kittens in northeast Oregon, USA, from 2009-2012. Results were from 1,099 predation events from 21 cougars fitted with Global Positioning System collars.

Prey Availability

Mule deer were the most common prey species available to cougars in our study, and the number of elk available to cougars surpassed white-tailed deer during winter (Table 2.2). Juvenile ungulates were the most common prey item available to cougars during summer, and adult deer and elk were the most abundant prey available to cougars during winter (Table 2.3). For deer and elk, percentage of yearling and adult males available to cougars declined in winter, because of legal harvest of males during hunting seasons (Table 2.4).

Prey Selection

Selection by Species of Prey.— We determined the species of 665 cougar-killed ungulates (109 white-tailed deer, 296 mule deer, and 260 elk) during summer. Cougars selected prey by species during summer ($\chi^2_{L2} = 121.87$, $P < 0.001$), and selection varied by gender and reproductive status ($\chi^2_{L1} = 73.16$, $P < 0.001$; Fig. 2.5a). Variability of individual selection ratios for male (Range $w_{ij} = 0.0$ - 2.7) and female cougars (Range $w_{ij} = 0.0 - 3.2$) was greatest for white-tailed deer (Fig. 2.5a), but there was little variability in individual selection ratios for mule deer. We determined the species of 366 ungulates (71 white-tailed deer, 191 mule deer, and 104 elk) killed by cougars during winter. Cougars selected prey by species during winter ($\chi^2_{L2} = 75.45$, $P < 0.001$), selection differed by gender and reproductive status ($\chi^2_{L1} = 61.15$, $P < 0.001$; Fig. 2.5b). The largest amount of variability in selection ratios for individual male cougars was for mule deer (Range $w_{ij} = 0.0 - 1.9$) and white-tailed deer for female cougars (Range $w_{ij} = 0.0 - 2.4$; Fig. 2.5b).

Selection of Deer and Elk by Age Class.— We determined genus and age class of 744 of 766 ungulates killed by cougars during summer. Fawns ($n = 258$; 34.7%) were the most frequently killed prey, followed by elk calves ($n = 222$; 29.8%) and adult deer ($n = 170$; 22.8%). Cougars selected prey by genus and age class of prey during summer ($\chi^2_{L2} = 441.19$, $P < 0.001$), and selection varied according to gender and reproductive status ($\chi^2_{L1} = 101.46$, $P < 0.001$; Fig. 2.6a). The largest amount of variability in selection ratios of individual male cougars occurred among yearling (Range $w_{ij} = 0.0 - 10.1$) and calf (Range $w_{ij} = 1.2 - 5.0$) elk, and the largest amount of variability in selection ratios of female cougars occurred among yearling deer (Range $w_{ij} = 0.0 - 3.9$), elk (Range $w_{ij} =$

Table 2.2. The estimated number and percentage of ungulates available to cougars during summer and winter in the Mt. Emily WMU in northeast Oregon, USA from 2009-2012.

Prey species	Summer[a]		Winter[a]	
	N	%	N	%
White-tailed deer	4,591	24	2,922	24
Mule deer	9,349	49	4,956	42
Elk	5,286	27	3,989	34
Total prey	19,226		11,850	

[a] Summer = May to October, Winter = November to April

Table 2.3. The estimated number and percentage of deer and elk according to age class available to cougars during summer and winter in the Mt. Emily WMU in northeast Oregon, USA from 2009-2012.

Prey species	Age class[a]	Summer[b]		Winter[b]	
		N	%	N	%
Deer[c]	Fawn	6,640	35	1,640	14
	Yearling	1,502	8	1,061	9
	Adult	5,798	30	4,853	42
	Total deer	13,940		7,554	
Elk	Calf	2,000	10	1,000	9
	Yearling	304	2	220	2
	Adult	2,982	15	2,704	24
	Total elk	5,286		3,924	
	Total prey	19,226		11,478	

[a] Fawn and calf = < 1 yr old, Yearling = 1 yr old, Adult = ≥ 2 yr old.
[b] Summer = May to October, Winter = November to April.
[c] The combined populations of mule deer and white-tailed deer.

Table 2.4. The estimated number and percentage of male and female deer and elk by age class available to cougars during summer and winter in the Mt. Emily WMU in northeast Oregon, USA from 2009-2012.

Prey species	Prey item[a]	Summer[b]		Winter[b]	
		N	%	N	%
Deer[c]	Yearling buck	751	50	371	35
	Yearling doe	751	50	690	65
	Adult buck	1372	24	773	16
	Adult doe	4426	76	4080	84
Elk	Yearling bull	152	50	77	35
	Yearling cow	152	50	143	65
	Adult bull	688	23	541	20
	Adult cow	2294	77	2163	80

[a] Yearling = 1 yr old, Adult = ≥ 2 yr old
[b] Summer = May to October, Winter = November to April
[c] Deer is the combined populations of mule deer and white-tailed deer.
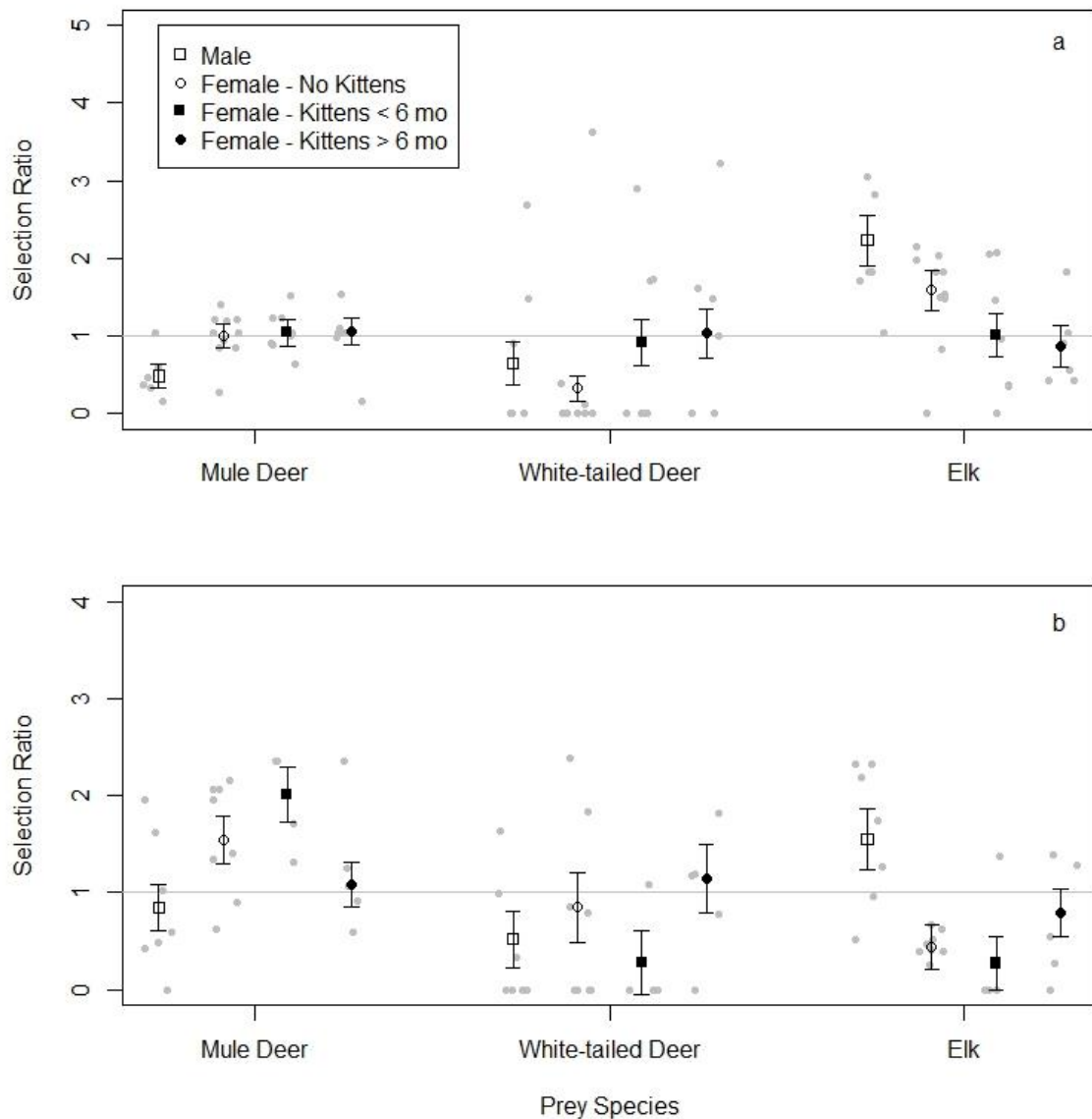
Figure 2.5. Prey selection ratios of cougars with 95% confidence intervals according to the species of prey without regard to the gender or age of prey during (a) summer and (b) winter in northeast Oregon, USA, from 2009-2012. Grey dots represent selection ratios for individual cougars. Population selection ratios were generated by comparing population level use to population level availability (Manly et al. 2002, eq. 4.10), and individual selection ratios were generated by comparing individual use to population level availability (Manly et al. 2002, eq. 4.37). The horizontal grey line represents a selection ratio of 1.0, which indicates use of prey in proportion to availability. Point estimates and associated 95% confidence intervals that are above the grey line indicate selection, while those that are below the grey line indicate prey was killed in lower proportion than available.

Figure 2.6. Prey selection ratios of cougars with 95% confidence intervals according to genus and age class of prey during (a) summer and (b) winter in northeast Oregon, USA, from 2009-2012. Grey dots represent selection ratios for individual cougars. Population selection ratios were generated by comparing population level use to population level availability (Manly et al. 2002, eq. 4.10), and individual selection ratios were generated by comparing individual use to population level availability (Manly et al. 2002, eq. 4.37). The horizontal grey line represents a selection ratio of 1.0, which indicates use of prey in proportion to availability. Point estimates and associated 95% confidence intervals that are above the grey line indicate selection, while those that are below the grey line indicate prey was killed in lower proportion than available.

0.0 – 6.3), and elk calves (Range $w_{ij} = 0.0 – 5.5$; Fig. 2.6a). We determined genus and age class of 352 out of 381 ungulates killed by cougars during winter. Adult deer were the most frequently killed prey ($n = 117$; 33.2%) followed by fawns ($n = 111$; 31.5%). Cougars selected prey by genus and age class of prey during winter ($\chi^2_{L2} = 170.92$, $P < 0.001$), and selection differed by gender and reproductive status ($\chi^2_{L1} = 68.03$, $P < 0.001$; Fig. 2.6b). The largest amount of variability in selection ratios of male cougars during winter was for calf (Range $w_{ij} = 0.7 – 5.4$) and yearling elk (Range $w_{ij} = 0.0 – 6.0$), and the most variability for female cougars was for fawns (Range $w_{ij} = 0.0 – 5.2$), calves (Range $w_{ij} = 0.0 – 4.5$), and yearling elk (Range $w_{ij} = 0.0 – 4.6$; Fig. 2.6b).

Selection of Deer and Elk by Gender.— We determined gender of 29 and 18 yearling deer killed by cougars during summer and winter, respectively. There was no evidence that cougars selected by gender of yearling deer during the summer ($\chi^2_L = 0.87$, $P = 0.35$) or winter ($\chi^2_L = 0.22$, $P = 0.64$; Fig. 2.7a). We determined gender of 108 and 63 adult deer killed by cougars during the summer and winter, respectively. Cougars did not select for either gender of adult deer during summer ($\chi^2_L = 0.57$, $P = 0.45$; Fig. 2.7b), but selected for adult, male deer during winter ($\chi^2_L = 13.30$, $P < 0.001$; $w_i = 1.89$, 95% C.I. = $1.37 – 2.41$) and preyed on adult females proportionally less than their availability ($w_i = 0.73$, 95% C.I. = $0.57 – 0.89$; Fig. 2.7b). Cougars killed a large percentage of adult male deer between August and November (48%), immediately prior to and during the rut, and most adult female deer were preyed on immediately prior to parturition between April and July (51%; Fig. 2.8a). We determined gender of 17 and 8 yearling elk killed by cougars during the summer and winter, respectively. Cougars did not select by gender of yearling elk during the summer ($\chi^2_L = 0.53$, $P = 0.47$) or winter ($\chi^2_L = 0.51$, $P = 0.48$; Fig. 2.7c). We determined the gender of 14 and 39 adult elk killed by cougars during the summer and winter, respectively. There was no evidence cougars selected by gender of adult elk during the summer ($\chi^2_L = 0.02$, $P = 0.88$) or winter ($\chi^2_L = 0.11$, $P = 0.74$; Fig. 2.7d). While we did not observe selection for bull elk, most were killed during or immediately after the rut (Fig. 2.8b), and most (80%) bull elk were killed by male cougars. Sixty-three percent of cow elk killed by cougars were killed prior to parturition between February and May (Fig. 2.8b).
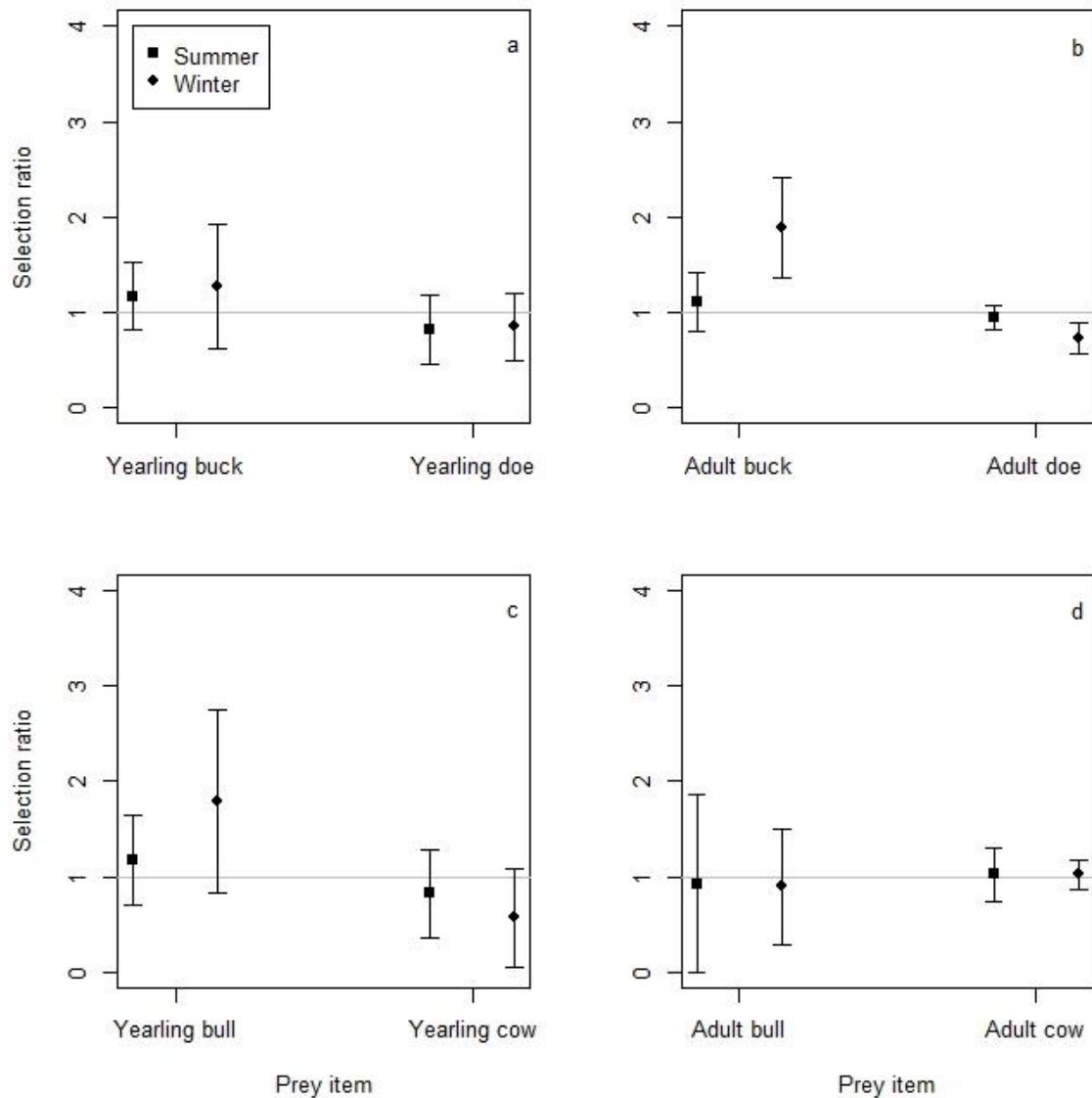
Figure 2.7. Prey selection ratios of cougars with 95% confidence intervals, by season, according to gender of prey for (a) yearling deer, (b) adult deer, (c) yearling elk, and (d) adult elk in northeast Oregon, USA, from 2009-2012. Population selection ratios were generated by comparing population level use to population level availability (Manly et al. 2002, eq. 4.10). The horizontal grey line represents a selection ratio of 1.0, which indicates use of prey in proportion to availability. Point estimates and associated 95% confidence intervals that are above the grey line indicate selection, while those that are below the grey line indicate prey was killed in lower proportion than available.
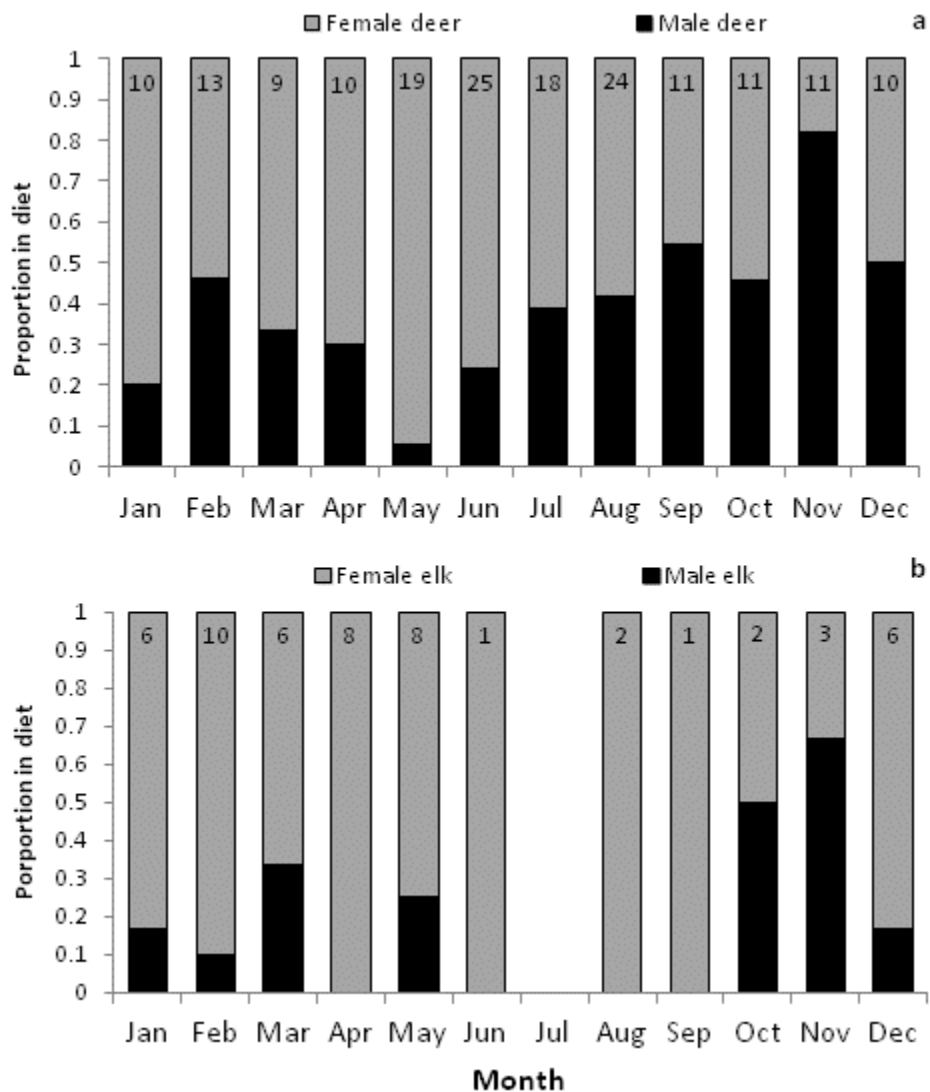
Figure 2.8. Monthly proportions of adult male and female (a) deer and (b) elk in the diets of 26 cougars in northeast Oregon, USA, from 2009-2012. We determined proportions from 234 adult deer and 53 adult elk where we were able to accurately determine the age and gender of prey. The values at the top of the bars indicated the number of individuals that were killed by cougars each month.

DISCUSSION

Kill Rates

The kill rates documented in our study (0.90-1.33 ungulates/week) were at the upper range of published estimates (0.47-1.31 ungulates/week) for cougars in North America (Table 2.5); however, our results were consistent with those from west-central Alberta using identical methodology (Knopff et al. 2010). Given the intensive sampling methods used in our study and by Knopff et al. (2010), we contend kill rates calculated using GPS location clusters provided unbiased estimates. Kill rates estimated from snow-tracking provided seasonal estimates and estimates from VHF telemetry were based on smaller sample sizes; therefore, differences between these estimates and ours were likely attributable to variation in methodology rather than ecological differences. Estimates of kill rates calculated using energetic models (Laundré 2005) were substantially lower than kill rates generated from field sampling of GPS location clusters (Table 2.5), which was not surprising given that energetic models often underestimate kill rates of carnivores (Peterson and Ciucci 2003).

The strong alignment between the our results and those of Knopff et al. (2010) indicated cougar kill rates are influenced by season, demography of cougars, and energetic requirements, and these patterns are generalizable among areas. Cougars should kill more frequently during summer in response to the ungulate birth pulse because cougars increased use of juvenile ungulates (i.e., smaller prey) during summer (this study, Knopff et al. 2010). Cougar kill rates were largely explained by energetic requirements and demography (this study, Knopff et al. 2010, White et al. 2011). Female cougars with kittens have higher kill rates than solitary females due to the greater collective energy requirements of their family group (Ackerman et al. 1986, Anderson and Lindzey 2003, Knopff et al. 2010). In our study and Knopff et al. (2010) increased kill rates for females was not documented until kittens were > 6 months old (Fig. 2.2a and 2b), likely because the energetic burden placed on females with small kittens (< 15 kg) was insufficient to significantly increase kill rates. In addition, females were mostly restricted to nursery sites the first 30 days after kittens were born (D. Clark, OCFWRU, unpublished data), resulting in lower kill rates during this period (summer = 0.99 kills/week, winter = 0.66 kills/week) compared to when kittens were 31-180 days old

Table 2.5. Published estimates of the number of ungulates killed per week by cougars in western North America from 1970-2012.

Source[a]	Study area	Primary prey[b]	Kill rate[c]							Estimation technique[d]	Calculation technique[e]
			UM	UF	ADM	SAM	ADF	SAF	FG		
1	ID	MD, E							1.17	Snow-tracking	Ratio
2	AZ	MD					0.67		1.03	Model (LC-R)	NA
3	UT	MD			0.83		0.44		0.67—2.26	Model (E)	NA
3	UT	MD							1.57	Radiotelemetry	IKI
4	BC	BS, MD							1.67	Radiotelemetry	IKI
5	WY	E, MD			0.94	0.64	0.64	0.69	0.98	Radiotelemetry	IKI
6	OR	MD, E					1.01		0.88	Radiotelemetry	IKI
7	WY	MD, E			0.91	0.74	1.01	0.97	1.31	Model (LC-G)	Ratio
8	ID	MD			0.37		0.29		0.85	Model (E)	NA
9	AZ	E, MD			0.95	0.88	0.76	1.17		Model (LC-G)	IKI
10	WA	W, MD	0.74	0.91					1.20	Radiotelemetry	IKI
11	ID	MD			0.47		0.49		0.59	Model (LC-R)	Ratio
12[f]	AB	W, MD, E, MO			0.67	0.59	0.80	0.46	0.90—1.30[g]	GPS telemetry	Ratio
13[f]	OR	MD, E, W			0.90		1.03		1.00—1.33[g]	GPS telemetry	Ratio

[a] 1 = Hornocker (1970), 2 = Shaw (1977), 3 = Ackerman et al. (1986), 4 = Harrison (1990), 5 = Murphy (1998), 6 = Nowak (1999), 7 = Anderson and Lindzey (2003), 8 = Laundré (2005), 9 = Mattson et al. (2007), 10 = Cooley et al. (2008), 11 = Laundré (2010), 12 = Knopff et al. (2010), and 13 = this study.

[b] MD = mule deer, W = white-tailed deer, MO = moose, BS = bighorn sheep, E = elk

[c] Kill rate = ungulates/week: UM = unknown age male cougar, UF = unknown age female cougar, ADM = adult male, SAM = sub-adult male, ADF = adult female, SAF = sub-adult female, FG = family group.

[d] Estimates were generated from either direct visitation of kills in the field (snow-tracking, radiotelemetry, GPS), or indirectly with models (E = Energetic, LC-R = radiotelemetry location model, LC-G = GPS location model).

[e] Kill rates were calculated using a ratio estimate or inter-kill interval. NA indicates not applicable.

[f] Females that transitioned between reproductive classifications had more than one kill rate calculated.

[g] Kill rates were calculated separately for females with kittens < 6 months old (lower value) and > 6 months old (upper value).

(summer = 1.36 kills/week, winter = 0.83 kills/week). Male cougars killed ungulates at a similar rate as females, but killed larger prey than females (this study, Knopff et al. 2010), allowing males to kill ~2 times more ungulate biomass per day than solitary females, and 1.5 times more than females with kittens (after accounting for body mass of kittens). This likely occurred because home ranges of male cougars are ~2-3 times larger than those of females (Ross and Jolkotzy 1992, Spreadbury et al. 1996, Logan and Sweanor 2001), which required males to expend additional energy to traverse and defend their home ranges.

We observed relatively minor differences in kill rates expressed as either a frequency or biomass metric compared to those of Knopff et al. (2010). Cougars in west-central Alberta killed larger prey (e.g., moose and feral horses; Knopff et al. 2010) than cougars in our study (e.g., elk and deer), so this may explain why cougars in our study killed more frequently (kills/week) than those in Alberta (Table 2.5). Cougars in our study killed less biomass of prey per day (8.05 kg/prey/day) than cougars in west-central Alberta (9.73 kg/prey/day; Knopff et al. 2010), likely because large prey have a higher percentage of inedible biomass. As prey vulnerability and availability change among different systems there will likely be minimal changes in kill rates (kills/week); however, our results suggest that the biomass of prey killed per day is relatively constant among systems.

Prey Use and Selection

Despite differences in vegetation and predator and prey guilds, the patterns of prey use by cougars we observed largely matched those in west-Central Alberta (Knopff et al. (2010). Our results provided additional support that indicated patterns in prey use by cougars vary seasonally, by the gender and reproductive status of cougars, and follow the reproductive vulnerability hypothesis (Lima and Dill 1990). Combined, these results indicated that cougars disproportionately prey upon vulnerable ungulates (i.e., juvenile ungulates during summer, male ungulates during fall, and female ungulates during winter and late spring), rather than killing prey at random, and this pattern likely holds throughout the geographic range of cougars.

Cougars are strongly dimorphic with males able to effectively capture larger prey due to more physical strength which reduces their risk of injury during prey capture

(Sunquist and Sunquist 1989, Iriarte et al. 1990). Our results confirmed this relationship because male cougars had more elk in their diet (50%) than females (25%), and this pattern was well documented in other systems (Anderson and Lindzey 2003, Knopff et al. 2010, White et al. 2011). Knopff et al. (2010) hypothesized that the increased use of large prey by male cougars may be a mechanism to avoid intraspecific competition with females. Another explanation is that males utilize larger prey to reduce the time spent acquiring, processing, and feeding on prey, thus supporting optimal foraging theory. It also would allow increased time for territorial defense and reproductive opportunities (Mattson et al. 2007). Differences in prey use and selection patterns by female cougars appear to balance increased energetic requirements needed to raise kittens with reducing risk of injury when capturing prey (this study, Knopff et al. 2010). Female cougars with kittens > 6 months old demonstrated minimal patterns in selection of prey suggesting an opportunistic foraging strategy to take advantage of every opportunity to kill prey as encountered (this study, Ross and Jalkotzy 1996, Mattson et al. 2007). In contrast, solitary females had lower energetic burdens than females with kittens; consequently, they took fewer risks and preyed upon smaller, weaker prey (this study, Murphy 1998, Knopff et al. 2010, White et al. 2011).

Cougars showed a strong seasonal pattern in prey use where juvenile ungulates were selected by cougars during the summer (this study, Knopff et al. 2010), and this seasonal pattern can be generalized across systems where there is a defined ungulate birth pulse. Cougars disproportionately preyed upon juvenile ungulates (this study, Hornocker 1970, Ross and Jolkotzy 1996, Knopff et al. 2010) because juveniles present very little risk of injury to cougars (Sunquist and Sunquist 1989) and are more naïve than adults (Geist 1982). Furthermore, the ungulate birth pulse increases the density of juveniles available to cougars which results in increased encounter rates between predators and prey (Holling 1959) and potentially contributes to selection of juvenile ungulates (Knopff et al. 2010).

Our results and those of Knopff et al. (2010) indicated that most adult male elk and deer were killed by cougars during and after the rut, and most adult female elk and deer were killed by cougars immediately prior to parturition, which supported the reproductive vulnerability hypothesis (Lima and Dill 1990). While our general results

indicated an increase in adult male deer and elk being killed during and after the rut, cougars in our study did not select adult elk by gender, which was similar to the findings of Spreadbury (1989) and contradictory to other studies (Hornocker 1970, Kunkel et al. 1999, Anderson and Lindzey 2003). The lack of selection for bull elk by cougars suggested that despite that bull elk may be physically weakened following the rut, their large body size and weaponry (i.e., antlers) presented an extreme risk of injury to cougars (Hornocker 1970, Murphy 1998). We expect the pattern of smaller male ungulates (i.e., deer) being selected by cougars during the fall and winter when they are physically weakened to hold true in other areas. Our results suggested that the reproductive vulnerability hypothesis may not apply to yearling ungulates because yearling ungulates are less likely to engage in breeding activities (Squibb 1985); consequently, yearlings are less likely to be subjected to seasonal variability in vulnerability to predation.

During our study, some cougars selected mule deer during winter but not summer, and white-tailed deer were killed in less than or equal proportion to their availability annually. We hypothesize this was a consequence of variation in prey availability at a localized scale, rather than landscape patterns of selection, because selection ratios are strongly influenced by definitions of availability (Manly et al. 2002). White-tailed deer occurred at relatively high densities on the northwest portion of our study area, while mule deer were distributed in a more uniform manner throughout our study area. These distribution patterns resulted in variable levels of prey availability and subsequently selection for mule deer but not white-tailed deer by cougars. As a result, cougars in our study area may have a greater effect on mule deer than white-tailed deer because mule deer were subjected to predation from the entire cougar population, and white-tailed deer were subjected to predation by a limited number of cougars.

We documented a seasonal shift in selection from elk calves to deer fawns between summer and winter. Selection of elk calves by cougars has been previously documented (Hornocker 1970, Murphy 1998, Nowak 1999, Anderson and Lindzey 2003) and occurred because young calves (< 6 months) have a relatively high energetic reward, lack experience, and present a low risk of injury to cougars during capture (Hornocker 1970, Spreadbury et al. 1986, Murphy 1998). The shift in selection from elk calves to deer fawns represented an optimal foraging strategy that balanced the risk of injury or

ease of capture with energetic reward. In summer, cougars killed fawns in proportion to their availability but selected for calves. Even though both were safe prey to capture calves had a larger energetic reward (18 kg at birth) compared to fawns (3-4 kg at birth). By winter, fawns weighed approximately 30-45 kg, which represented an increased energetic benefit to cougars compared to summer, but less risk of injury than larger elk calves (>80 kg). Carbone et al. (1999) predicted optimal prey size for cougars was 70-165 kg. Our results indicated optimal prey size for female cougars was 20-50 kg; female cougars selected for elk calves during summer (18-50 kg) and fawns during winter (30-45 kg). In contrast, diets of male cougars were dominated by elk and they selected for calf and yearling elk throughout the year, which resulted in larger optimal prey size for males (> 60 kg). The seasonal selection patterns of elk calves by cougars in our study corresponded with patterns of mortality and survival of elk calves in northeast Oregon (Rearden 2005, B. Johnson, ODFW, unpublished data). Monthly survival rates of elk calves in northeast Oregon increased in a log-linear fashion from birth until they plateaued in November (i.e., the first 4-5 months of life). Thereafter, few calves were killed by cougars (Rearden 2005), suggesting calves were experienced or large enough to escape predation by cougars or presented a substantial risk of injury to cougars during capture. By the start of winter, approximately 50% of elk calves had died (Rearden 2005, B. Johnson, ODFW, unpublished data), and their decreased abundance likely reduced encounter rates between cougars and elk calves which may have caused cougars to switch to more abundant alternative prey (i.e., fawns).

For most ungulates, population growth is most sensitive to adult female survival but variation in population growth rates are determined by variation in juvenile survival because adult survival is relatively constant (Gaillard et al. 1998, 2000, Raithel et al. 2007). Survival and recruitment of juvenile elk were negatively correlated with increasing cougar densities (Rearden 2005, Johnson et al. 2013a), and low levels of recruitment may result in population declines (Harris et al. 2008). The strong patterns of selection of juvenile elk by cougars could be a mechanism by which cougars negatively affect elk populations. Our results suggest that predation on adult elk by cougars is unlikely to have a substantial effect on elk populations because very few adult elk were killed by cougars (Table 2.1), and survival rates of female elk in northeast Oregon were

not influenced by cougar density (Appendix G). Selection of fawns by cougars may negatively affect mule deer populations or cougars may influence deer populations by killing a large number of adult deer. Although, previous studies suggest mule deer populations are primarily regulated by climatic and nutritional factors, not predators (Bishop et al. 2009, Hurley et al. 2011) suggesting cougar predation on mule deer is compensatory.

Selection of a secondary prey species by a generalist predator whose numbers are determined by a primary prey species can result in population declines for the secondary prey species or allow predators to maintain secondary prey at low densities (Messier 1994, Sinclair et al. 1998). This phenomenon has been termed apparent competition because the asymmetrical influence of a shared predator on secondary prey can appear as if the two prey populations are in direct competition (Holt 1977, Holt and Lawton 1993). Apparent competition, mediated by cougars, has been suggested in systems with mule deer and mountain caribou (Wittmer et al. 2005), mule deer and bighorn sheep (Johnson et al. 2013b), white-tailed deer and mule deer (Robinson et al. 2002, Cooley et al. 2008), and mule deer and porcupine (Sweitzer et al. 1997) but not deer and elk. Cougar densities are likely determined primarily by the densities of their primary prey (Logan and Sweanor 2001, Laundré et al. 2007, Pierce et al. 2012) and secondarily by territory defense and behavioral mechanisms (Hornocker 1970, Logan and Sweanor 2001) raising the possibility that apparent competition could occur in areas with high deer densities. Since the mid-1990s, mule deer and white-tailed deer populations have increased in the Mt. Emily WMU (ODFW, unpublished data) resulting in relatively dense deer populations (~290 adults/100 km^2). Concurrent with increased deer densities in Mt. Emily WMU since the mid-1990s, the elk population has declined, suggesting that apparent competition between deer and elk, mediated by cougars, could be occurring in the Mt. Emily WMU and presents a possible mechanism by which cougars limit elk but not deer populations.

Potential Sources of Bias

The method we used to locate cougar kills (Knopff et al. 2009) potentially caused us to miss small prey items such as non-ungulate prey, and young fawns and calves immediately following their birth. Approximately half of all calves ($n = 143$; 52%) and

fawns 49% ($n = 180$; 49%) killed by cougars during our study occurred during the birth pulse (i.e., late May - June), and the amount of biomass killed per day per cougar was similar during these months as the remainder of the year, suggesting we located most ungulates killed during summer. Newborn fawns weigh approximately 3-4 kg, which represented about one-half of the biomass killed per day by cougars (Fig. 2.2b). We programmed our GPS collars to acquire 1 location every 3 or 4 hours, raising the possibility that cougars captured and consumed an entire newborn fawn (3-4 kg) before a GPS location cluster was formed, which may have caused us to underestimate predation on newborn fawns. By 1 month of age, fawns weigh approximately 7 kg, which is close to the biomass killed per day by cougars, making it unlikely that cougars could consume an entire carcass before a GPS location cluster was formed. This potential bias would be less evident for newborn elk calves because their birth weight (~18 kg) is greater than the daily biomass killed by cougars. Minimum prey size of cougars during winter was >30 kg making it unlikely that we missed a substantial number of kills at this time of year. Hence, we believe our estimates of kill rates and prey use were not biased.

Scavenging can positively bias kill rates and estimates of prey use if scavenging events are incorrectly documented (Anderson and Lindzey 2003). Given that cougars are subordinate to other large carnivores at kill sites and cougars rarely scavenge kills of smaller predators (Murphy and Ruth 2010), scavenging events are most likely to be incorrectly documented when cougars share kills. We suspect kill-sharing by cougars had a minimal influence on our results because we documented only 2 instances where cougars with overlapping territories utilized the same kill; however, kill sharing may have been underestimated because not all cougars in our study area were marked with GPS collars. Given the low rate of interactions between independent cougars (Logan and Sweanor 2001), we believe this source of bias was minimal in our study. Furthermore, the rate of scavenging in our study (~4%) was similar to other studies (Logan and Sweanor 2001, Bauer et al. 2005, Knopff et al. 2010) suggesting we did not underestimate the degree of scavenging by cougars relative to previous studies, and that our estimates of kill rates and prey use of ungulates were not biased.

Our estimates of prey selection may be biased slightly due to miscalculations in prey availability. If our population estimates or herd composition data were biased, our

estimates of prey availability would also be biased which could affect our results (Manly et al. 2002). Our primary concern with estimating prey availability was accurately estimating deer numbers because they are more difficult to enumerate than elk. To address this concern, we conducted 2 post-hoc analyses where we doubled the size of either the elk or deer population. The general conclusions of selection of elk calves during summer and deer fawns during winter did not change, but the magnitude of selection varied depending on the size of deer and elk populations. When we doubled the size of the deer population, patterns of selection were identical to what we reported but strength of selection for elk calves during summer increased (i.e., selection ratios were larger). When we doubled the size of the elk population, fawns were selected by female cougars during summer and winter. We think it is highly unlikely that the elk population was underestimated by 100% because most elk were enumerated annually at the end of winter on their winter range. Given these findings, we believe our results were robust to inaccuracies in estimates of prey availability; however, we acknowledge this potential bias and patterns of selection of elk calves and deer fawns during summer may be greater than we documented.

MANAGEMENT IMPLICATIONS

Our results align with those of Knopff et al. (2010) and should provide managers with confidence to generalize the underlying mechanisms of cougar predation patterns throughout the geographic range of cougars in western North America. Selective predation on juvenile ungulates by cougars may be a potential mechanism that negatively affects ungulate populations, and managers should investigate the role of predation in ungulate populations that are experiencing low recruitment. Cougar management practices are variable throughout western North America (Cooley et al. 2011) and can significantly affect cougar demography, population structure and size (Robinson et al. 2008, Cooley et al. 2009a,b), which in turn influence the effect of cougar predation on ungulate populations. If predators are the primary factor limiting survival and recruitment of juveniles, manipulating predator populations may be an option to increase ungulate populations; however, there are a multitude of factors that affect growth rates of ungulate populations. We advise managers to carefully consider all factors that may contribute to variability in ungulate populations before embarking on management

actions to reduce cougar populations because predation on juveniles may be largely a compensatory mortality source and other factors may be regulating ungulate populations (Ballard et al. 2001, Bishop et al. 2009, Hurley et al. 2011).

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CHAPTER 3

SURVIVAL RATES OF COUGARS IN OREGON FROM 1989 – 2011: A
RETROSPECTIVE ANALYSIS

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ABSTRACT

Cougar (*Puma concolor*) management practices vary throughout the western United States. Legal hunting methods for cougar range from no hunting to hunting with or without the aid of dogs. Moreover, season lengths and tag allocations available to hunt cougars vary by state. Cougar management in Oregon is unique because hunting cougars with dogs was allowed through the 1994 hunting season, but thereafter Ballot Initiative Measure 18 prohibited the use of dogs to pursue cougars. Since 1995 hunting seasons have become increasingly longer with more tags sold. We investigated survival and documented causes of mortality of radio-collared cougars at 3 study areas in Oregon during 1989 – 2011 under contrasting management strategies. The Catherine Creek (1989 – 1996) and Jackson Creek (1993 – 2002) study areas overlapped the prohibition of hunting cougars with dogs, and the Wenaha, Sled Springs, and Mt. Emily (WSM) study was conducted when hunting cougars with dogs was illegal. Sources of mortality differed among study areas. Hunting mortality was the most common cause of death for sub-adult and adult cougars in Catherine Creek ($n = 19$ of 28 mortalities) and WSM ($n = 24$ of 53 mortalities) study areas in northeast Oregon. In contrast, natural mortality was the most common cause of death of sub-adults and adults at the Jackson Creek ($n = 25$ of 45 mortalities) study area in southwest Oregon, but hunting mortality was most common prior to the passage of Measure 18. We estimated annual survival rates of cougars using known fate models in Program MARK. Annual survival rates of adult males were lowest at Catherine Creek prior to the passage of Measure 18 ($\hat{S} = 0.57$; 95% CI $= 0.39 – 0.73$) and increased after Measure 18 ($\hat{S} = 0.86$; 95% CI $= 0.79 – 0.92$), which were similar to those rates observed at Jackson Creek ($\hat{S} = 0.78$; 95% CI $= 0.65 – 0.88$) and WSM ($\hat{S} = 0.82$; 95% CI $= 0.69 – 0.91$). Sub-adult male survival increased from pre-Measure 18 ($\hat{S} = 0.57$; 95% CI $= 0.39 – 0.73$) to post-Measure 18 ($\hat{S} = 0.86$; 95% CI $= 0.79 – 0.92$) at Catherine Creek, which was greater than survival rates observed at Jackson Creek ($\hat{S} = 0.60$; 95% CI $= 0.42 – 0.75$) and WSM ($\hat{S} = 0.45$; 95% CI $= 0.18 – 0.75$). Regardless of hunting regulations, annual survival rates of adult females was similar among study areas (Catherine Creek [$\hat{S} = 0.86$; 95% CI $= 0.79 – 0.92$]; Jackson Creek [$\hat{S} = 0.85$; 95% CI $= 0.77 – 0.91$]; WSM [$\hat{S} = 0.85$; 95% CI $= 0.76 – 0.90$]), as was sub-adult female survival (Catherine Creek [$\hat{S} = 0.86$; 95% CI $= 0.79 – 0.92$]; Jackson Creek [$\hat{S} = 0.89$; 95% CI $=

0.75 – 0.95]; WSM [$\hat{S}$ = 0.88; 95% CI = 0.72 – 0.96]). We did not document an effect of age on cougar survival at the Catherine Creek study area, which we attributed to selective harvest of prime-aged, male cougars prior to the passage of Measure 18. In contrast, we observed an effect of age on annual survival at both Jackson Creek and WSM, but the patterns in age-specific survival differed slightly between study areas. At both Jackson Creek and WSM, sub-adult males had significantly lower survival than sub-adult females, but survival rates of males and females were similar by age 4 or 5 years. At WSM survival declined for both genders at older ages (8-13 years) but this decline was not observed at Jackson Creek. Managers should understand local sources of mortality when setting harvest regulations because sources of mortality may vary widely within and among jurisdictions, even if management practices are similar. Due to the low success rates of harvesting cougars without dogs, survival rates of cougars in these areas could be substantially higher than areas where use of dogs is legal. This suggests the ability of managers to effectively manipulate survival rates of cougars to meet population management objectives will be dependent on available hunting methods. The effect of increasing age on cougar survival should be considered when using survival rates to estimate population growth rates.

INTRODUCTION

In 1994, Ballot Initiative Measure 18 (hereafter Measure 18) was passed by Oregon voters that prohibited the use of dogs to either pursue or hunt cougars (*Puma concolor*) following the 1994 hunting season. In response to cougar populations increasing statewide post-Measure 18 (Kiester and Van Dyke 2002) and low success rates of hunting cougars without dogs (Oregon Department of Fish and Wildlife [ODFW] 2006), hunting seasons, harvest quotas, and bag limits for cougars have become increasingly liberal in Oregon (Table 3.1). These regulation changes were proposed by ODFW and approved by the Oregon Fish and Wildlife Commission. Immediately following Measure 18 (1995 – 1996), cougar harvest declined dramatically, which occurred because of limited opportunity (i.e., expensive and limited numbers of tags coupled with short hunting seasons using inefficient methods). As tag prices declined and season lengths increased, cougar harvest increased but leveled off in recent years

Table 3.1. Summary of hunting regulations for cougars in Oregon from 1989 to 2011 during our investigation of causes of mortality and survival rates of radiocollared cougars at the Catherine Creek, Jackson Creek, and Wenaha-Sled Springs-Mt. Emily study areas in Oregon, USA.

Year	Regulations	Tag cost
1989 - 1994	Controlled hunting, limited tags with use of dogs during 2-4 month hunting seasons	$ 50.00
1994	Use of dogs to hunt cougars was prohibited starting in 1995	
1995	Controlled hunting, limited tags, 2-4 month hunting season	$ 51.00
1996	General season, unlimited tags, quota on harvest during 2-4 month hunting season	$ 51.00
1997	General season, unlimited tags, quota on harvest during 7 month hunting season	$ 51.00
1998-2000	General season, unlimited tags, quota on harvest during 7 month hunting season	$ 11.00
	Tag included with purchase of Sports Pac[a].	
2001-2010	General season, unlimited tags, quota on harvest during 10 month hunting season	$ 11.50
2001	Second tag available in the Blue Mountain Quota Zone	
2005	Second tag available in all of eastern Oregon	
2010-2011	General season, unlimited tags, quota on harvest	$ 14.50
	Year round hunting statewide, second tag available statewide	

[a] Sports Pac: includes a combination angling and hunting license, black bear tag, cougar tag, elk tag, deer tag, upland game bird and waterfowl validation, spring turkey tag, and angling harvest tag. The cost of this option is similar to purchasing a angling and hunting license, deer and elk tags, upland game bird and waterfowl validation, and angling harvest tag individually, making the black bear, cougar, and turkey tags essentially free.

(ODFW 2006, ODFW 2012). Due to the unique changes in hunting regulations in Oregon compared to most other western states and Canadian provinces (i.e., variation in the use of dogs to hunt cougars; Cooley et al. 2011), we were interested in estimating sources of mortality and survival rates of cougars before and after Measure 18, and compare these estimates to other areas where cougars are hunted to determine if the prohibition of hunting cougars with dogs affected cougar survival.

Hunting regulations are likely to have the greatest effect on survival rates of cougars because harvest is the primary source of mortality in most cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008). In hunted populations, female cougars tend to have higher survival rates than males (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009a,b), likely because males are selectively harvested when dogs are used to hunt cougars (Anderson and Lindzey 2005, Zornes et al. 2006). Gender-biased harvest is less common in areas where hunters are not allowed to use dogs to hunt cougars (Zornes et al. 2006), which could lower survival rates of females and increase those of males compared to populations where males are selectively harvested; however, information to support this prediction is lacking. Support for this prediction could have important implications for cougar management because population growth rates of cougars are most sensitive to changes in female survival (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009a,b).

Adult cougars have greater survival rates than kittens and sub-adults (Ross and Jalkotzy 1992, Beier and Barrett 1993, Logan and Sweanor 2001), but little is known about the effect of increasing age on adult survival. Effect of age on cougar survival has typically been estimated for individual age classes (e.g., juvenile, sub-adult, and adult). This approach assumes cougars have similar survival rates once they reach adulthood; however, mortality rates of most long-lived mammals are lowest at intermediate ages and increase at older ages (Caughley 1966). To our knowledge, estimates of age-specific survival have only been reported for a cougar population in the Greater Yellowstone Ecosystem where older individuals had lower survival rates than prime-aged adults (Ruth et al. 2011). Documenting age-specific effects on survival can allow managers to identify vulnerable life-stages that need protection or those that may be able to withstand additional exploitation or be targeted to reduce populations depending on management

objectives. Furthermore, estimates of age-specific survival will increase reliability of population models used to monitor local cougar populations because the model more accurately reflects reality (Caswell 2001, Morris and Doak 2002).

Cougars have been radiocollared in Oregon since 1989, which provided an opportunity to conduct a retrospective analysis to assess causes of mortality and estimate cougar survival rates. Our objectives were to: 1) document sources of cougar mortality in Oregon across different management regimes and ecosystems, 2) estimate survival rates of cougars pre- and post-Measure 18, and 3) determine effects of age on cougar survival. We predicted legal harvest would be the primary cause of mortality at all study areas as seen in other hunted cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008), but non-hunting, human caused mortality would increase over time as statewide cougar populations increased (Kiester and Van Dyke 2002, ODFW 2006) because human-cougar conflict usually increase as cougar populations increase (Beier 1991) or in response to changing attitudes and decreased tolerance of large carnivores over time (Wolch et al. 1997, Schwartz et al. 2003). In response to selective harvest of males when using dogs to hunt cougars (i.e., pre-Measure 18) and non-selective harvest using opportunistic hunting strategies (i.e., post-Measure 18; ODFW 2006, Zornes et al. 2006), we predicted male survival would increase and female survival decrease post-Measure 18. Due to male biased dispersal patterns, we predicted sub-adult males would have lower survival than adults (Ross and Jalkotzy 1992, Beier and Barrett 1993, Logan and Sweanor 2001) regardless of hunting regulations. Finally, we predicted survival would increase with age, peak at prime-ages, and decline at older ages. This pattern is seen in most long-lived mammals (Caughley 1966) and has also been documented in cougars (Ruth et al. 2011).

METHODS

Study Areas

We investigated cougar survival and causes of mortality at 3 study areas in Oregon between 1989 and 2011 (Fig. 3.1). Cougars were radiocollared at the Catherine Creek Wildlife Management Unit (WMU) from 1989-1996, the Jackson Creek study area (Dixon and Evans Creek WMUs) from 1993-2002, and 3 contiguous WMUs in northeast
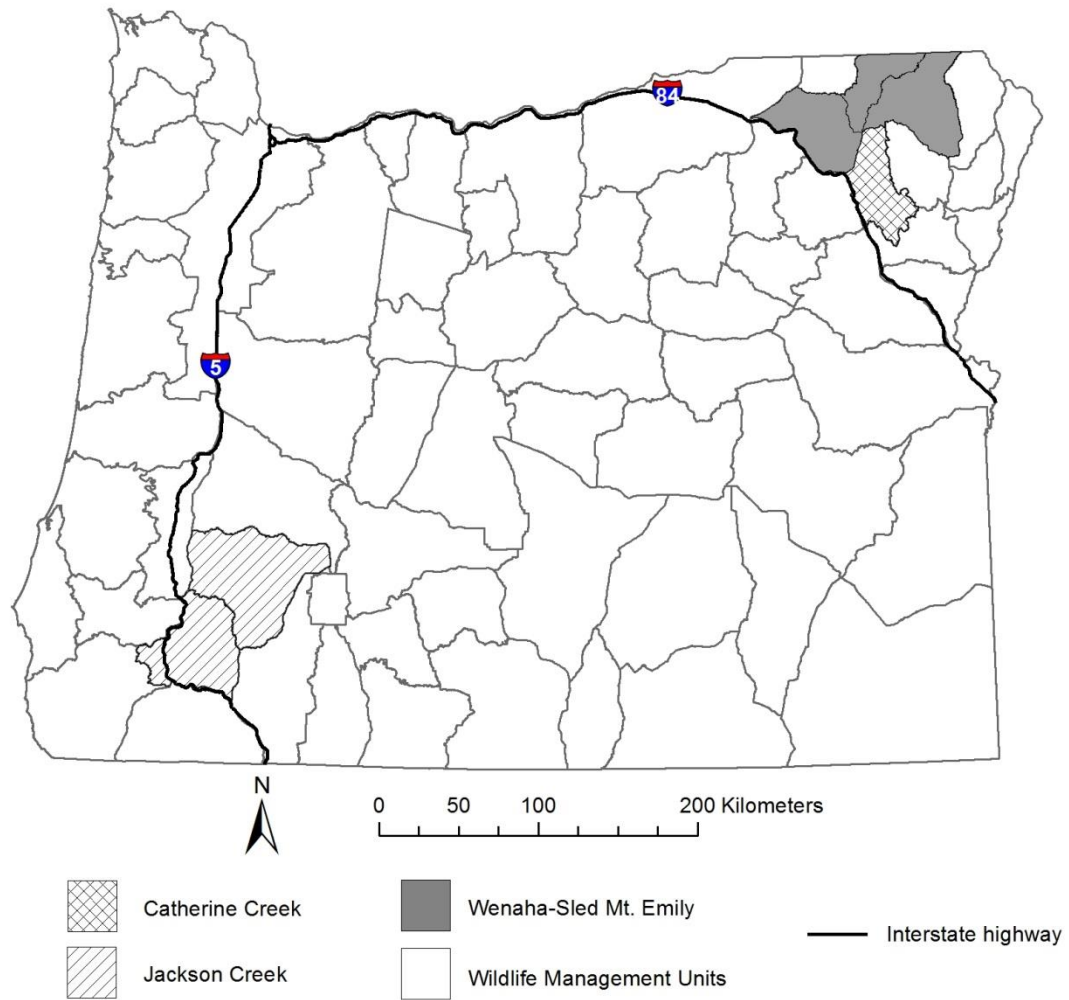
Figure 3.1. Locations of study areas where survival rates and causes of mortality of cougars were estimated from 1989 – 2011 in Oregon, USA. The Catherine Creek study was conducted from 1989 – 1996, the Jackson Creek study was conducted from 1993 – 2002, and the Wenaha-Sled Springs-Mt. Emily study was conducted from 2002 – 2011.

Table 3.2. Summary description of study areas in Oregon, USA where survival rates and sources of mortality of cougars were monitored from 1989 - 2011.

	Study Area				
	Catherine Creek		Jackson Creek		WSM[a]
Area (km^2)	1700		6700		5350
Dates	1989 - 1994	1995 - 1996	1993 - 1994	1995 - 2002	2002 - 2011
Use of dogs to hunt cougars	Yes	No	Yes	No	No
Primary mortality source					
Females	Harvest[b]	Natural	Harvest	Natural[c]	Harvest
Males	Harvest	NA	Harvest	Natural	Harvest
Secondary mortality source					
Females	Natural	Harvest	NA	Other[d]	Other/Natural[e]
Males	Other/Natural	NA	NA	Other	Other

[a] WSM = Wenaha, Sled Springs, and Mt. Emily Wildlife Management Units.

[b] Harvest mortality includes cougars that were legally harvested during sanctioned hunting seasons.

[c] Natural sources of mortality include: cougar predation, disease, parasites, and injuries.

[d] Other sources of mortality include: vehicle killed, poaching, administrative removals and trapping.

[e] Both sources of mortality were equal.

Oregon (Wenaha, Sled Springs, and Mt. Emily; hereafter WSM) from 2002-2011. The ability to hunt cougars with dogs varied over the time periods of the studies (Table 3.2). The Catherine Creek and Jackson Creek studies overlapped the prohibition of dogs to hunt cougars, which allowed us to directly test for an effect of this change in management on cougar survival. The post-Measure 18 portion of the Jackson Creek study was primarily conducted when cougar hunting seasons were limited to 4 – 7 months. In contrast, the WSM study was conducted when hunting seasons had increased to 10 – 12 months. This allowed us to compare survival rates among studies and qualitatively assess the effect of increasing season length on cougar survival.

Mule deer (*Odocoileus hemionus hemionus*), Rocky Mountain elk (*Cervus canadensis nelsoni*), and white-tailed deer (*O. virginianus ochrourus*) were the primary prey species available to cougars at Catherine Creek and WSM. Black-tailed deer (*O. hemionus columbianus*) and Roosevelt elk (*C. canadensis roosevelti*) were the primary prey species available to cougars at Jackson Creek. Other large and medium-sized carnivores present within all study areas included black bear (*Ursus americanus*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*). At the time of our studies, no wolf (*C. lupus*) packs were documented in any of the study areas. Vegetation patterns at study areas in northeast Oregon were strongly influenced by topography, elevation, and aspect. South-facing slopes were dominated by herbaceous vegetation and north-facing slopes were dominated by mixed-conifer stands (Franklin and Dyrness 1973). Common tree species at Catherine Creek and WSM included ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Psuedotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*) and lodgepole pine (*P. contorta*). In contrast, vegetation patterns at Jackson Creek were more homogenous, and most areas were either mixed-conifer or deciduous dominated forest stands (Franklin and Dyrness 1973). Common tree species within the Jackson Creek study area included ponderosa pine, sugar pine (*P. lambertiana*), Douglas-fir, white fir (*A. concolor*), mountain hemlock (*Tsuga mertensiana*), Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), and Pacific madrone (*Arbutus menziesii*).

Cougar Capture and Monitoring

All cougar capture and handling procedures were outlined and approved by ODFW's wildlife veterinarian, the Starkey Experimental Forest and Range, Animal Care

and Use Committee (IACUC No. 92-F-0004), and followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). Cougar capture was dependent upon suitable tracking conditions (i.e., recent snowfall) and restricted to winter months (November – April). Each winter over the course of our studies, we searched for recently made cougar tracks (i.e., within the past 24 hours) along roads within study areas. We did not selectively pursue cougars and dogs were allowed to follow tracks from any sub-adult or adult. Our sampling scheme should have resulted in a representative sample assuming no gender or age class behavior bias in avoidance of roads we used to locate tracks. After being treed, cougars were immobilized with a mixture of Ketamine (200 mg/mL; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine (20 mg/mL; Rompun®; Bayer, Inc., Shawnee Mission, KS, USA) or medetomidine (20 mg/mL; Domitor ®; Pfizer Animal Health, New York, NY, USA) at a dosage of 0.4 mL per 10 kg of body mass, administered via remote injection from a dart gun. Upon immobilization, cougars were weighed, gender determined, and aged. Whenever possible, we extracted the first premolar of cougars to determine age from cementum annuli analysis (Trainer and Matson 1988). We also obtained field estimates of cougar age using evidence from tooth wear (Ashman et al. 1983, Shaw 1986), gum-line recession (Laundré et al. 2000), and pelage spotting progression (Shaw 1986). We marked sub-adult and adult cougars with a VHF (Telonics MOD-500 or MOD-600 [Telonics, Inc., Mesa, AZ, USA]) or GPS radiocollar (Lotek 4400S or Lotek 7000SA [Lotek Engineering, Newmarket, ON, Canada]) containing mortality sensors. We attached 2 permanent, numbered ear tags or tattooed 1 ear to uniquely identify each cougar. Prior to release, cougars were administered yohimbine (0.125 mg/kg; Yobine®; Lloyd Laboratories, Shenandoah, IA) as an antagonist for xylazine.

We monitored fates of individual cougars via radiotelemetry signals from the ground and fixed-wing aircraft. Frequency of aerial surveys varied by study, but typically occurred at least once every month. During each survey, we recorded fates (live or dead) and approximate location of cougars. We were interested in estimating annual survival rates of cougars and attempted to confirm fates of individual cougars at the end of each calendar year. Cougars not located during telemetry flights were recorded as missing. If the fate of an individual was not determined at the end of the year and in

subsequent flights, the cougar was right-censored from the analysis. If the mortality sensor indicated the cougar died, we located the carcass as soon as possible to determine cause of death. If cause of death could not be determined in the field, we submitted the cougar carcass for necropsy at the Veterinary Diagnostic Lab at Oregon State University, College of Veterinary Medicine (Corvallis, OR, USA) or United States Fish and Wildlife Service Forensic Laboratory (Ashland, OR, USA). ODFW required that harvested cougars be checked at a local ODFW office within 72 hours of harvest where the gender, age, approximate harvest location, and date of death were recorded.

Causes of Mortality

For the purposes of our analyses, we pooled causes of mortality into 3 classes: 1) hunter harvest, 2) non-hunting human caused mortality (e.g., administrative removal, vehicle killed cougars, illegal harvest), and 3) natural mortality. We divided Catherine Creek and Jackson Creek into 2 time periods, pre- and post-Measure 18, to account for any changes in sources of mortality related to changes in management. Preliminary analysis indicated frequencies of each cause of mortality were similar between age classes (i.e., sub-adult and adult). Consequently, we pooled data at each study area for each management system (i.e., pre- versus post-Measure 18) to increase sample sizes and reduce Type II errors (Zar 1998). Individuals that died of unknown causes were censored from this analysis. We examined frequencies of mortality causes between study areas and management system separately for each gender using a Pearson's Chi-square test (R Development Core Team 2011), and determined significance using an alpha of 0.05.

Survival Analysis

We estimated annual survival rates ($\hat{S}$) of cougars in program MARK using known-fate models for radiocollared individuals (White and Burnham 1999). We used a modified Kaplan-Meier (1958) estimator that allowed for staggered data entry and censoring of individuals (Pollock et al. 1989). We used Akaike's Information Criteria corrected for small sample sizes (AIC_c) to rank candidate models (Burnham and Anderson 2002). We used the difference between AIC_c of the best model and the *i*th model (ΔAIC_c) to identify closely competing models ($\Delta AIC_c \leq 2.0$; Burnham and Anderson 2002). We used Akaike weights to evaluate the relative support for each candidate model (Burnham and Anderson 2002). To determine significance of the effect

of various factors in the model, we evaluated whether regression coefficients (β) and their associated 95% confidence interval overlapped 0 according to the methods described by Anthony et al. (2006).

We determined fates of individual cougars annually. Individuals were included in the dataset each year they were radiocollared and censored during any year where they were not monitored the entire calendar year. We conducted a separate survival analysis for each study area because minimal overlap existed in timing of each study. We developed a set of candidate models based on biologically plausible hypotheses to test for differences in survival among gender, age, and time (Table 3.3). We used previously outlined approaches when building and naming our candidate model set (Lebreton et al. 1992, White and Burnham 1999). We tested for differences in survival rates between gender because previous studies have indicated females have higher survival than males (Logan and Sweanor 2001, Lambert et al. 2006, Robinson et al. 2008). We investigated models that incorporated 5 temporal effects on cougar survival including constant (.), time varying (t), linear (T), log-linear (lnT), and quadratic (TT) trends (Table 3.3). We tested for these temporal effects because they would account for any undocumented temporal or environmental variation that may influence cougar survival. We modeled additive (+) and interactive (×) combinations of gender and time when appropriate. For example, if the linear trend (T) model ranked higher than the constant survival (.) model, the linear trend was modeled as an interactive and additive effect with gender. We also investigated 2 temporal models that directly tested for an effect of changes in management (i.e., pre- versus post-Measure 18; Table 3.3) on survival rates at the Catherine Creek and Jackson Creek study areas. Harvest of cougars with the use of dogs was male biased compared to harvest without the use of dogs (ODFW 2006, Zornes et al. 2006), so we tested a model that indicated female survival would be constant pre- and post-Measure 18, but male survival would differ. We also tested a model that indicated male and female survival would increase post-Measure 18.

Ages of individual cougars were determined at either time of capture or death and ages in subsequent or previous years were extrapolated from this point. We treated age as a continuous, age-specific covariate and considered 3 separate functional relationships

Table 3.3. Description of biologically plausible hypotheses and models used to test for management, temporal, gender, and age effects on cougar survival at the Catherine Creek, Jackson Creek, and Wenaha-Sled Springs-Mt. Emily study areas in Oregon, USA.

Hypothesis description[a]	Model notation
Temporal effects	
1. Survival rates constant	S (.)
2. Survival rates differ among years	S (t)
3. Survival rates follow a linear trend over time	S (T)
4. Survival rates follow a log-linear trend over time	S (lnT)
5. Survival rates follow a quadratic trend over time	S (TT)
6. Female survival equal to male survival following prohibition of hunting cougars with dogs, but different than male survival when hunting cougars with dogs was legal.	$S(Female(.)=MalePost(.) \neq MalePre(.))$[b]
7. Male and female survival differed before and after the prohibition of hunting cougars with dogs.	S (Gender + Pre(.)≠Post(.))[b]
Group effects	
8. Survival differs by gender	S (Gender)[c]
Age effects[d]	
9. Linear effect of age on cougar survival	S (Age)
10. Log-linear effect of age on cougar survival	S (lnAge)
11. Quadratic effect of age on cougar survival	$S (Age^2)$

[a] We considered models that included all possible combinations of group and temporal effects when appropriate.

[b] Models only considered at Catherine Creek and Jackson Creek study areas.

[c] Gender was modeled as an additive or interactive effect with the best temporal model.

[d] Age was modeled as an additive and interactive relationship with gender.

to test for an effect of age on cougar survival: linear (Age), log-linear (lnAge), and quadratic (Age^2; Table 3.3) and considered additive (+) and interactive (×) relationships between gender and age. The linear and log-linear trends in age-specific survival would identify effect of increasing age on cougar survival, and a quadratic model would also account for effect of old age, if any, on survival.   We modeled age as constant effect over time but allowed ages of individual cougars to change each year. Where age was not determined for a cougar ($n = 1$ at Catherine Creek; $n = 1$ at Jackson Creek), we assigned the individual an age that was equal to the mean age of radiocollared cougars during the year they were first captured. This should have minimal effects on results because the mean of the observed covariate values will not change (i.e., the estimated effect is the same) but the variance will be slightly smaller (Cooch and White 2013). Survival of cougars varies by age (Robinson et al. 2008, Ruth et al. 2011); consequently, we used our best model that included effect of age (yrs) to develop estimates of mean sub-adult (1 yr) and adult ($\geq$ 2 yrs) survival to compare to published literature. Adult survival was estimated by calculating gender specific survival rates based on mean age of adult cougars ([yrs] Catherine Creek, male = 4.25, female = 4.77; Jackson Creek, male = 5.7, female = 5.4; WSM, male = 6.04, female = 4.85) included in the analysis at each study area. Mean ages were calculated with a weighted mean based on number of encounter occasions that individuals of a particular gender and age were monitored.

RESULTS

Cougar Monitoring

On average, we monitored fates of 19 (range = 9 – 26; Table 3.4), 22 (range = 9 – 35; Table 3.5), and 25 (range = 15 – 31; Table 3.6) cougars annually at Catherine Creek, Jackson Creek, and WSM, respectively. We monitored 58 cougars (male = 21, female = 37) at Catherine Creek, 79 cougars at Jackson Creek (male = 37, female = 42), and 97 cougars (male = 40, female = 59) at WSM. At Catherine Creek and Jackson Creek study areas, sub-adults (1 year old) were most frequently monitored (Fig. 3.2a and b). In contrast, 4-year-old cougars were most frequently monitored at WSM (Fig. 3.2c). This may suggest our sample of cougars at WSM was not representative of the population (i.e., sub-adults were under sampled), which should have minimal effects on age-specific

Table 3.4. Number of radiocollared cougars monitored and causes of mortality sorted by year and gender at Catherine Creek study area in Oregon, USA from 1989 - 1996. During the pre-Measure 18 years, cougars were hunted with the use of dogs and during the post-Measure 18 years cougars were hunted without the use of dogs.

	Year															Post-Measure 18				Pre-Measure 18 Total		Post-Measure 18 Total	
	Pre-Measure 18																						
	1989		1990		1991		1992		1993		1994		1995		1996								
Fate	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂		
Monitored	7	2	15	7	16	3	16	4	18	7	19	7	11	3	8	4	91	30	19	7		
Mortalities																						
Natural[a]	0	0	0	0	1	1	2	0	0	0	0	0	1	0	0	0	3	1	1	0		
Harvest[b]	1	0	4	4	1	0	0	0	1	4	1	2	0	0	1	0	8	10	1	0		
Other[c]	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0		
Unknown[d]	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1		
Total	1	0	4	4	2	1	2	2	1	4	2	2	1	0	1	1	12	13	2	1		

[a] Natural mortality included cougar predation, disease, parasites, and injuries.

[b] Harvest mortality included legal harvest and associated wounding loss.

[c] Other mortality included poaching, vehicle killed individuals, trapping, and administrative removals.

[d] Unknown mortality was assigned to cougars where cause of death could not be determined.

Table 3.5. Number of radiocollared cougars monitored and causes of mortality sorted by year and gender at Jackson Creek study area from 1993 – 2002, in Oregon, USA. During the pre-Measure 18 years, cougars were hunted with the use of dogs and during the post-Measure 18 years cougars were hunted without dogs.

	Year																				Pre-Measure 18		Post-Measure 18	
	Pre-Measure 18				Post-Measure 18																Total		Total	
	93		94		95		96		97		98		99		00		01		02					
Fate	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Monitored	4	4	7	5	9	3	11	7	10	7	15	11	17	15	19	12	24	11	21	11	11	9	126	77
Mortalities																								
Natural[a]	0	0	0	0	0	0	2	1	0	1	0	0	0	3	2	4	6	2	2	2	0	0	12	13
Harvest[b]	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	2	1	2
Other[c]	0	0	0	0	1	0	1	2	0	1	1	1	0	0	0	0	0	1	1	2	0	0	4	7
Unknown[d]	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1
Total	0	1	1	2	1	0	3	3	0	2	1	2	1	4	2	5	7	3	3	4	1	3	18	23

[a] Natural mortality included cougar predation, disease, parasites, and injuries.

[b] Harvest mortality included legal harvest and associated wounding loss.

[c] Other mortality included poaching, vehicle killed individuals, trapping, and administrative removals.

[d] Unknown mortality was assigned to cougars where cause of death could not be determined.

Table 3.6. Number of radiocollared cougars monitored and causes of mortality sorted by year and gender at Wenaha-Sled-Springs-Mt. Emily study area in Oregon, USA from 2002 – 2011. During all years cougars were hunted without dogs.

| | Year | | | | | | | | | | | | | | | | | | | | Total | |
| | 02 | | 03 | | 04 | | 05 | | 06 | | 07 | | 08 | | 09 | | 10 | | 11 | | | |
Fate	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Monitored	11	4	18	7	20	6	17	6	17	10	17	11	18	13	23	8	15	5	13	8	169	78
Mortalities																						
Natural[a]	0	0	0	0	4	0	1	1	0	0	0	0	1	2	1	0	0	0	1	1	8	4
Harvest[b]	2	1	2	2	1	1	1	0	2	1	2	1	0	2	2	0	2	1	1	0	15	9
Other[c]	1	1	1	0	1	0	0	0	0	2	1	0	0	1	1	1	1	1	2	1	8	7
Unknown[d]	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Total	3	2	3	2	6	2	2	1	2	3	3	1	1	5	4	2	3	2	4	2	31	22

[a] Natural mortality included cougar predation, disease, parasites, and injuries.

[b] Harvest mortality included legal harvest and associated wounding loss.

[c] Other mortality included poaching, vehicle killed individuals, trapping, and administrative removals.

[d] Unknown mortality was assigned to cougars where cause of death could not be determined.
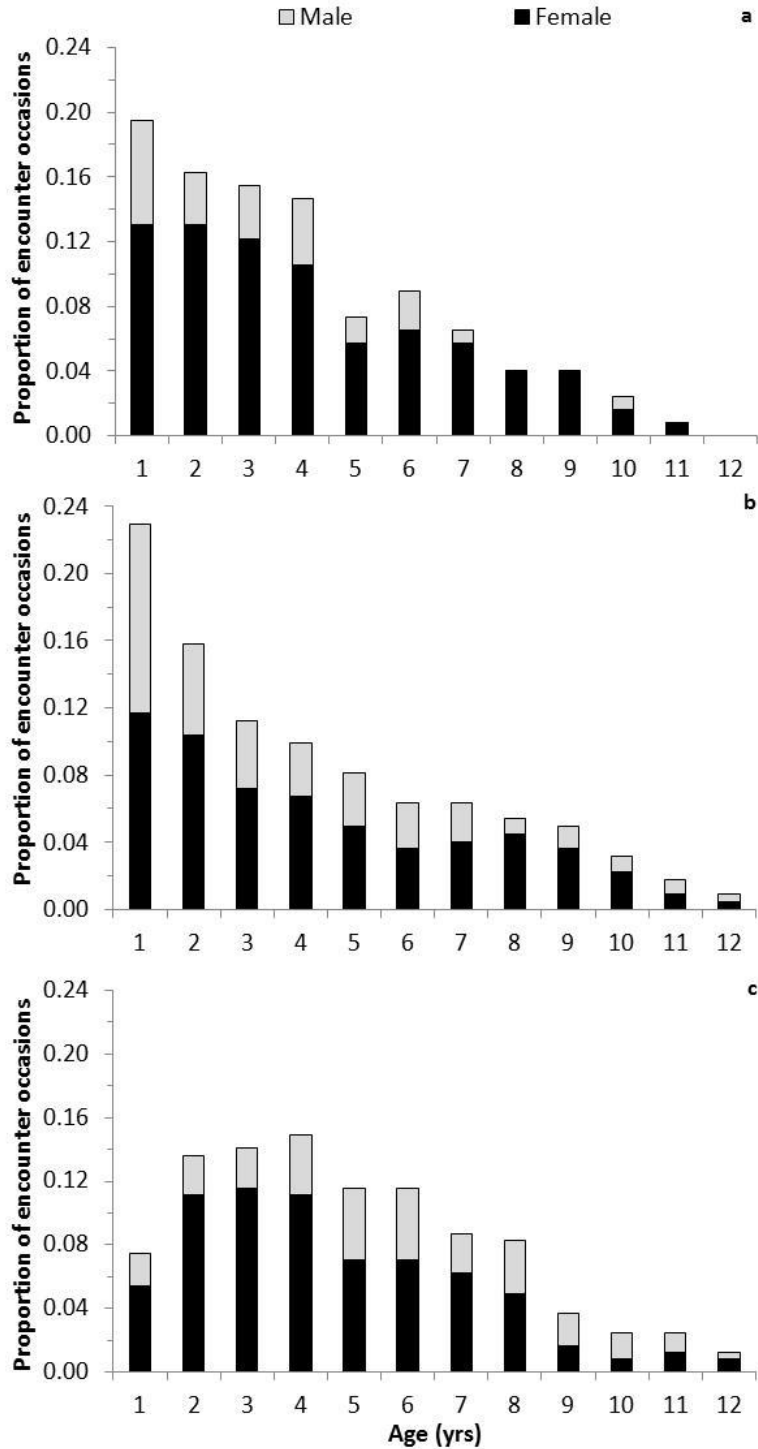
Figure 3.2. Distribution of the proportion of encounter histories, sorted by age and gender, used to estimate survival of cougars at the (a) Catherine Creek, (b) Jackson Creek, and (c) Wenaha-Sled Springs-Mt. Emily study areas. A total of 147, 223, and 247 year and age specific encounter occasions were included in the analysis of survival at Catherine Creek, Jackson Creek, and Wenaha-Sled Springs-Mt. Emily study areas, respectively.

survival estimates so long as sampled individuals were representative of their age class; however, reduced sample sizes for individual ages will increase sample variance.

Causes of Mortality

Frequency of hunting, natural, and non-hunting, human caused mortality varied among study areas and according to management practices (i.e., pre- versus post-Measure 18) for both males ($\chi^2_8 = 26.34$, $P = 0.001$; Fig. 3.3a) and females ($\chi^2_8 = 19.05$, $P = 0.01$; Fig. 3.3b). Hunting mortality was extremely limited at Jackson Creek, but was the only source of mortality documented pre-Measure 18 (Fig. 3.3a and b). In contrast, hunter harvest was the primary source of mortality at Catherine Creek pre- and post-Measure 18 and at WSM. Natural mortalities occurred much more frequently at Jackson Creek following Measure 18 than were observed prior to Measure 18 and at WSM and Catherine Creek pre- or post-Measure 18 (Fig. 3.3a and b). Natural mortalities at Jackson Creek were associated with disease or parasites ($n = 15$), cougar predation ($n = 6$), injuries ($n = 3$), and unknown natural causes ($n = 1$). Natural mortalities at Catherine Creek were associated with injuries ($n = 2$), cougar predation ($n = 2$), and unknown natural causes ($n = 1$). At WSM causes of natural mortalities included unknown natural causes ($n = 7$), disease or parasites ($n = 2$), injury ($n = 2$), and cougar predation ($n = 1$). Frequency of non-hunting, human-caused mortality was lowest at Catherine Creek and greatest at WSM (Fig. 3.3a and b).

Survival

Catherine Creek.—The best model used to estimate cougar survival at the Catherine Creek study area was S(Female(.)=MalePost(.)≠MalePre(.)) (Table 3.7). Interpretation of this model was survival was independent of age, males ($\hat{S} = 0.57$, 95% CI = 0.39 – 0.73) had lower survival rates than females pre-Measure 18 ($\hat{\beta} = -1.58$, 95% CI = -0.69 – -2.48) but equal survival rates to females ($\hat{S} = 0.86$, 95% CI = 0.79 – 0.92) post-Measure 18 (1995-1996; Fig. 3.4). No evidence for effect of age existed on cougar survival (Fig. 3.5a), because the best model that included age [S(Female(.)=MalePost(.)≠MalePre(.) + Age)] had a $\Delta AIC_c > 2.0$ (Table 3.7), and the regression coefficient for the effect of age in this model was centered near and broadly overlapped 0 ($\hat{\beta} = -0.01$, 95% CI = -0.17 – 0.14).
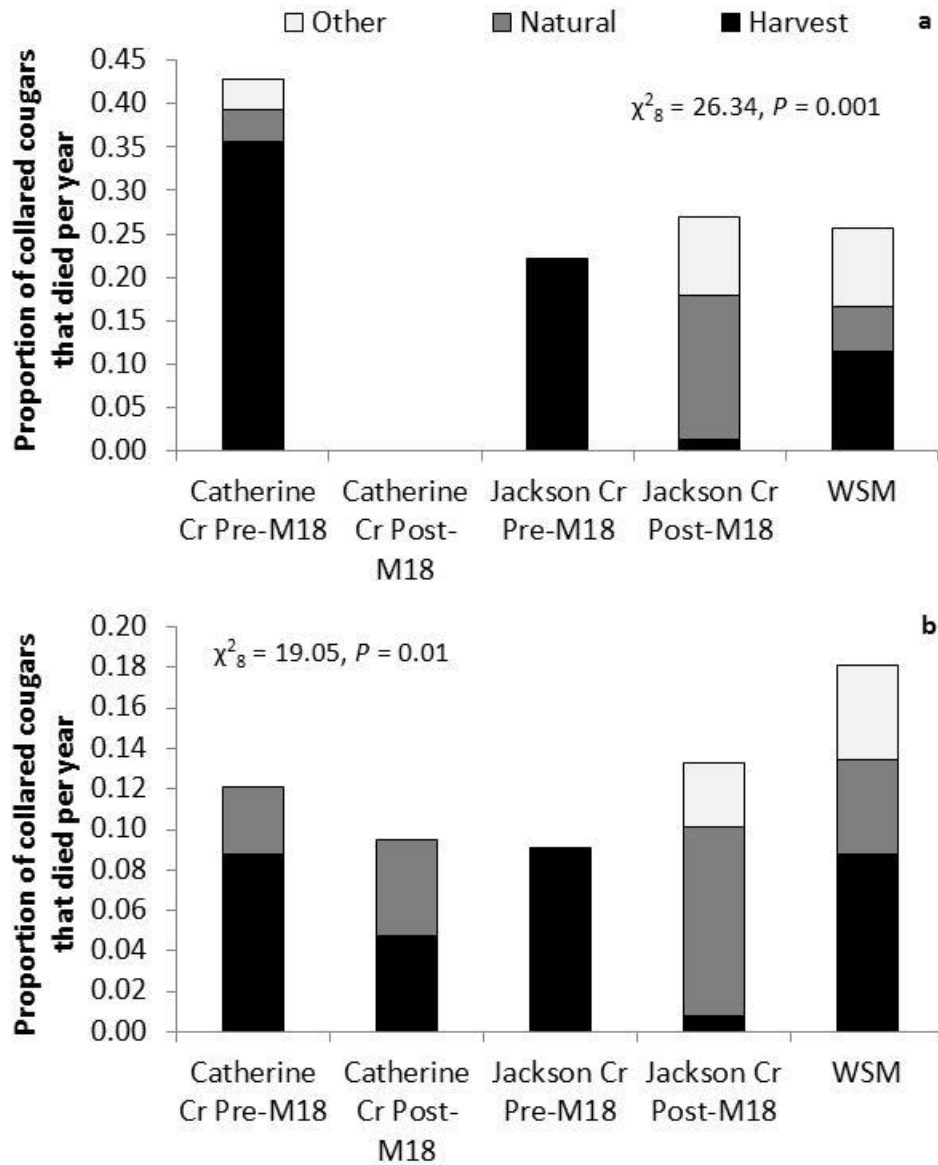
Figure 3.3. The average annual proportion of radiocollared cougar mortalities that were attributable to harvest, natural, or other causes for (a) male and (b) female cougars at the Catherine Creek, Jackson Creek, and Wenaha-Sled Springs-Mt. Emily (WSM) study areas in Oregon, USA. Harvest included cougars that were killed during legal hunting seasons by hunters. Natural mortality included injuries, disease, intraspecific strife, and unknown natural mortality. Other sources of mortality included administrative removals, illegal kills, vehicle killed cougars, and trapping. On average, 5, 4, 5, 10, and 8 males were monitored annually at Catherine Creek pre- and post-Measure 18, Jackson Creek pre- and post-Measure, and WSM, respectively. 15, 10, 6, 16, and, 17 females were monitored annually at Catherine Creek pre- and post-Measure 18, Jackson Creek pre- and post-Measure, and WSM, respectively.

Table 3.7. Model selection results for cougar survival at the Catherine Creek study area in northeast Oregon, USA. Cougars were monitored from 1989 - 1996. Models are ranked according to Akaike's Information Criteria corrected for small sample sizes (AIC_c).

Model[a]	AIC_c	ΔAIC_c	w_i[b]	Likelihood	K[c]
S(Female(.)=MalePost(.)≠MalePre(.))	138.80	0.00	0.27	1.00	2
S(Gender + T)	139.96	1.16	0.15	0.56	3
S(Gender)	140.41	1.60	0.12	0.45	2
S(Female(.)=MalePost(.)≠MalePre(.) + Age)	140.85	2.05	0.10	0.36	3
S(Female(.)=MalePost(.)≠MalePre(.) + lnAge)	140.86	2.06	0.10	0.36	3
S(Gender + Pre(.)≠Post(.))	140.89	2.09	0.10	0.35	3
S(Female(.)=MalePost(.)≠MalePre(.) × Age)	141.91	3.11	0.06	0.21	4
S(Female(.)=MalePost(.)≠MalePre(.) × lnAge)	142.46	3.66	0.04	0.16	4
S(Female(.)=MalePost(.)≠MalePre(.) + Age^2)	142.91	4.11	0.04	0.13	4
S(Female(.)=MalePost(.)≠MalePre(.) × Age^2)	144.92	6.12	0.01	0.05	6
S(T)	148.19	9.39	0.00	0.01	2
S(.)	148.47	9.67	0.00	0.01	1
S(lnT)	148.91	10.11	0.00	0.00	2
S(TT)	150.19	11.39	0.00	0.00	3
S(t)	154.07	15.27	0.00	0.00	8
S(Gender × t)	156.82	18.02	0.00	0.00	16

[a] Temporal effects include time varying (t), linear trend (T), log-linear trend (lnT), quadratic trend (TT). Management effects include male survival different before and after the passage of Measure 18, but female survival equal (Female(.)=MalePost(.)≠MalePre(.)) and male and female survival differs pre- and post-Measure 18 (Gender + Pre(.)≠Post(.)). Effect of age includes linear (Age), log-linear (lnAge), and quadratic (Age^2) relationships.
[b] Akaike weight.
[c] No. parameters in model.
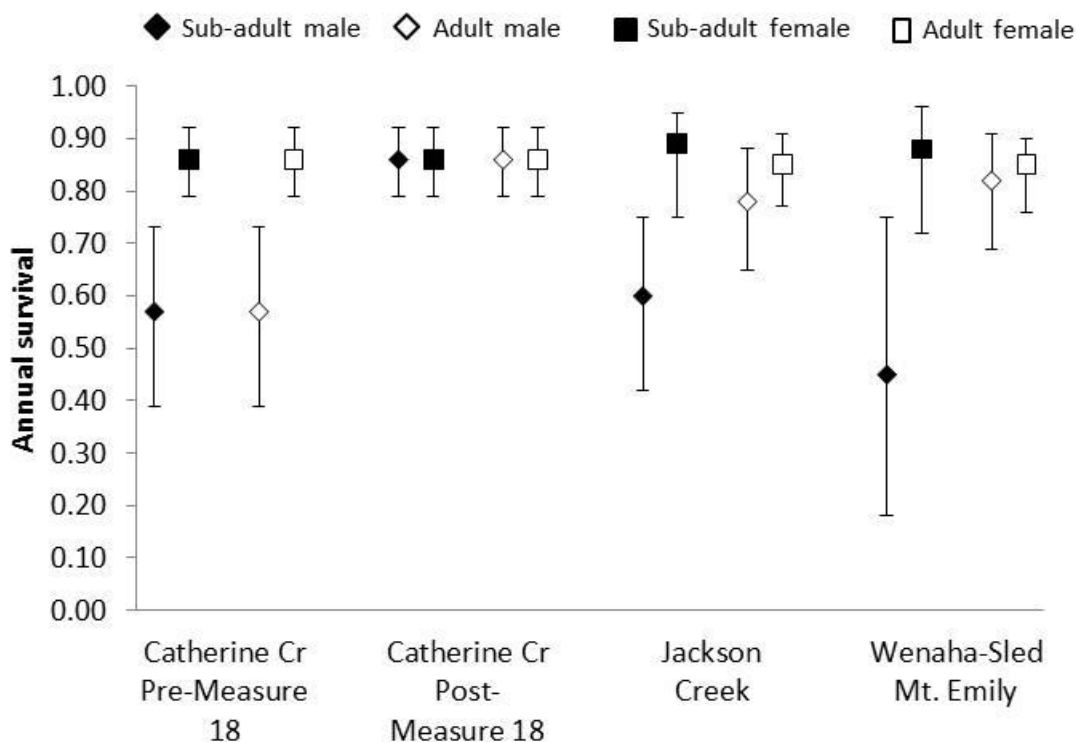
Figure 3.4. Estimated annual survival rates and 95% confidence intervals of sub-adult, and adult male and female cougars at the Catherine Creek, Jackson Creek, and Wenaha-Sled Springs-Mt. Emily (WSM) study areas in Oregon, USA from 1989 - 2011. Cougars were monitored from 1989 – 1996, 1993 – 2002, and 2002 – 2011 at Catherine Creek, Jackson Creek, and WSM, respectively. Adult males were monitored a total of 20, 60, and 70 radio-years at Catherine Creek, Jackson Creek, and WSM, respectively. Sub-adult males were monitored a total of 8, 25, and 5 radio-years at Catherine Creek, Jackson Creek, and WSM, respectively. Females were monitored a total of 79, 111, and 154 radio-years at Catherine Creek, Jackson Creek, and WSM, respectively. Sub-adult females were monitored a total of 16, 26, and 13 radio-years at Catherine Creek, Jackson Creek, and WSM, respectively.
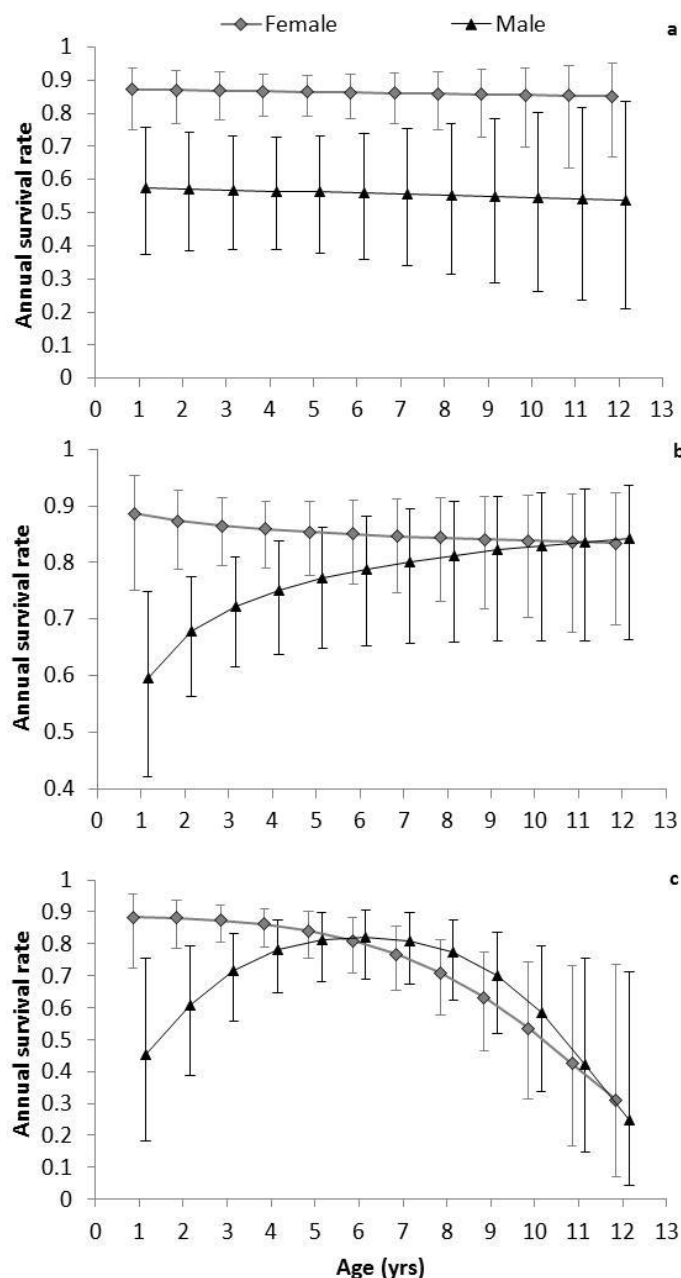
Figure 3.5. Gender- and age-specific survival estimates and 95% confidence intervals of cougars at (a) Catherine Creek, (b) Jackson Creek, and (c) Wenaha-Sled Springs-Mt. Emily study areas in Oregon, USA. Cougars were monitored from 1989-1996 at Catherine Creek, from 1993 – 2002 at Jackson Creek, and from 2002 – 2011 at Wenaha-Sled-Mt. Emily. Estimates were generated using the best ranked model that included effect of age, which was S(Female(.)=MalePost(.)≠MalePre(.) + Age), S(Gender × lnAge), and S(Gender × Age^2) for Catherine Creek, Jackson Creek, and Wenaha-Sled-Mt. Emily, respectively. The displayed estimate of age specific survival for male cougars at Catherine Creek represent survival rates prior to the passage of Measure 18 (1989 – 1994), and survival rates following Measure 18 (1995 – 1996) were identical to females.

Table 3.8. Model selection results for cougar survival at the Jackson Creek study area in southwest Oregon, USA. Cougars were monitored from 1993 - 2002. Models are ranked according to Akaike's Information Criteria corrected for small sample sizes (AIC_c).

Model[a]	AIC_c	ΔAIC_c	w_i[b]	Likelihood	K[c]
S(Gender)	218.72	0.00	0.20	1.00	2
S(Gender × lnAge)	219.11	0.39	0.16	0.82	4
S(Gender + Age^2)	219.23	0.51	0.16	0.77	4
S(Gender + lnAge)	219.74	1.02	0.12	0.60	3
S(Gender × Age)	220.00	1.28	0.11	0.53	4
S(Gender × Age^2)	220.03	1.32	0.10	0.52	6
S(Gender + Age)	220.67	1.95	0.08	0.38	3
S(Gender + Pre(.)≠Post(.))	222.58	3.87	0.03	0.14	4
S(.)	223.96	5.24	0.01	0.07	1
S(T)	224.67	5.95	0.01	0.05	2
S(lnT)	225.09	6.38	0.01	0.04	2
S(FemalePre(.)=MalePost(.)≠MalePre(.))	225.36	6.64	0.00	0.04	2
S(TT)	226.17	7.45	0.00	0.02	3
S(t)	235.27	16.55	0.00	0.00	10
S(Gender × t)	239.54	20.82	0.00	0.00	20

[a] Temporal effects include time varying (t), linear trend (T), log-linear trend (lnT), quadratic trend (TT). Management effects include male survival different before and after the passage of Measure 18, but female survival equal (Female(.)=MalePost(.)≠MalePre(.)) and male and female survival differs pre- and post-Measure 18 (Gender + Pre(.)≠Post(.)). Effect of age includes linear (Age), log-linear (lnAge), and quadratic (Age^2) relationships.
[b] Akaike weight.
[c] No. parameters in model.

Jackson Creek.— The best model that included an effect of age was S(Gender × lnAge; Table 3.8) and this model was used to estimate age specific survival rates of cougars. A strong effect of gender existed on survival rates ($\hat{\beta} = 1.66$, 95% CI = 0.48 – 2.84), but coefficients for lnAge ($\hat{\beta} = 0.52$, 95% CI = -0.05 – 1.08) and the interaction between gender and lnAge ($\hat{\beta} = -0.69$, 95% CI = -1.53 – 0.14) narrowly overlapped 0, which suggested a marginal effect of age on survival. Sub-adult males had lower annual survival ($\hat{S} = 0.60$, 95% CI = 0.42 – 0.75) than adult males ($\hat{S} = 0.78$, 95% CI = 0.65 – 0.88; Fig. 3.4). In contrast, sub-adult females ($\hat{S} = 0.89$, 95% CI = 0.75 – 0.95) and adult females ($\hat{S} = 0.85$, 95% CI = 0.77 – 0.91) had similar survival (Fig. 3.4). Survival varied by age (yrs) with female survival declining slightly with increasing age, male survival increasing with age, but female survival was higher than male survival at younger ages (Fig. 3.5b). We found no evidence that survival was influenced by hunting regulations because models that included this effect had a $\Delta AIC_c \geq 3.8$ (Table 3.8).

Wenaha-Sled Mt. Emily.— Our best model was S(Gender × Age^2) (Table 3.9), which indicated survival differed by gender and age. This model indicated sub-adult males had lower survival ($\hat{S} = 0.45$, 95% CI = 0.18 – 0.75) than adult males ($\hat{S} = 0.82$, 95% CI = 0.69 – 0.91; Fig. 3.4). In contrast, sub-adult females ($\hat{S} = 0.88$, 95% CI = 0.72 – 0.96) and adult females ($\hat{S} = 0.85$, 95% CI = 0.76 – 0.90) had similar survival rates (Fig. 3.4). Cougar survival followed a quadratic trend with age, and the relationship differed for males and females. Females had higher survival than males at younger ages, but males had similar survival by 4-6 yrs, and survival declined at older ages for both genders (Fig. 3.5c). Some of the regression coefficients for the effect of age (female $\hat{\beta} = 0.84$, 95% CI = 0.13 – 1.55, male $\hat{\beta} = -0.79$, 95% CI = -1.70 – 0.13) and age squared (female $\hat{\beta} = -0.07$, 95% CI = -0.13 – -0.01, male $\hat{\beta} = 0.05$, 95% CI = -0.03 – 0.12) narrowly overlapped 0; however, including effect of age substantially improved model fit which indicated age explained some variation in cougar survival (Table 3.9).

DISCUSSION

Causes of Mortalities

With the exception of Jackson Creek following the passage of Measure 18, legal harvest was the greatest cause of mortality of radio-collared cougars, which was also

Table 3.9. Model selection results for cougar survival at the Wenaha-Sled Springs-Mt. Emily study area in northeast Oregon, USA. Cougars were monitored from 2002 - 2011. Models are ranked according to Akaike's Information Criteria corrected for small sample sizes (AIC_c).

Model[a]	AIC_c	ΔAIC_c	w_i[b]	Likelihood	K[c]
$S(\text{Gender} \times \text{Age}^2)$	250.03	0.00	0.48	1.00	6
$S(\text{Gender} + \text{Age}^2)$	251.43	1.40	0.24	0.50	4
$S(\text{Gender} \times \text{Age})$	252.93	2.89	0.11	0.24	4
$S(\text{Gender} \times \text{lnAge})$	253.81	3.77	0.07	0.15	4
$S(\text{Gender} + \text{Age})$	254.15	4.12	0.06	0.13	3
$S(\text{Gender} + \text{lnAge})$	256.90	6.87	0.02	0.03	3
$S(\text{Gender})$	257.93	7.89	0.01	0.02	2
$S(.)$	258.87	8.84	0.01	0.01	1
$\{S(TT)\}$	260.24	10.21	0.00	0.01	3
$\{S(lnT)\}$	260.68	10.65	0.00	0.00	2
$\{S(T)\}$	260.91	10.87	0.00	0.00	2
$S(t)$	273.37	23.34	0.00	0.00	10
$S(\text{Gender} \times t)$	289.14	39.11	0.00	0.00	20

[a] Temporal effects include time varying (t), linear trend (T), log-linear trend (lnT), quadratic trend (TT). Effect of age includes linear (Age), log-linear (lnAge), and quadratic (Age^2) relationships.
[b] Akaike weight.
[b] No. parameters in model.

observed in other hunted cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008). Hunting cougars with dogs greatly increased mortality of male cougars where male harvest was more than 2 times greater compared to when hunting with dogs was prohibited (Fig. 3.3). This was expected since hunting with dogs is more effective and selective than hunting without dogs (Anderson and Linzey 2005, Zornes et al. 2006). Harvest mortality of females was relatively consistent across studies, which was likely a consequence of avoidance of females by hunters pre-Measure 18 and non-selective, inefficient harvest post-Measure 18 (ODFW 2006). We attributed lower harvest rates at Jackson Creek after passage of Measure 18 compared to WSM to differences in habitat. Dense, contiguous forest cover is the dominant vegetative cover in southwest Oregon, and vegetative cover in northeast Oregon is strongly influenced by topography, elevation, and aspect, with substantially more open land cover (Franklin and Dyrness 1973). The increased visibility afforded hunters in northeast Oregon likely allowed hunters to more effectively locate and harvest cougars compared to southwest Oregon. Additionally, we speculate differences in harvest rates at Jackson Creek and WSM could be related to refinements in hunting methods (i.e., predator calling, snow tracking) over time.

The relatively high levels of natural mortality at Jackson Creek following the passage of Measure 18 were unexpected because natural mortality has only been documented as the primary cause of mortality in unhunted cougar populations, where intraspecific strife and aggression was the primary cause of mortality (Hemeker et al. 1984, Beier and Barrett 1993, Logan and Sweanor 2001). Surprisingly, intraspecific strife and aggression was not the most common cause of natural mortality at Jackson Creek, except for sub-adult males (3 of 6 mortalities). While we were unable to determine exact cause of death for most natural mortalities ($n = 12$; 48%) in Jackson Creek, most cougars dying of natural causes ($n = 11$) were infected with a stomach nematode (*Cylicospirura* spp.). These nematodes cause intestinal lesions and parasite load ranged from minimal to extreme (1 – 562 worms/cougar; Ferguson et al. 2011). The clinical effect of *Cylicospirura* was undetermined; however, extreme levels of infestation may reduce fitness of cougars by negatively affecting their ability to hunt large prey (Ferguson et al. 2011). The life history of this nematode is not well known, but because

cougars are obligate carnivores, we speculate the parasite is transmitted via prey to predator. Few cougars were infected with *Cylicospirura* in WSM, and no infections were documented during the Catherine Creek study or in 39 necropsied cougars harvested in northeast Oregon from 1976 – 1978 (Rausch et al. 1983). These findings suggest this parasite and possibly the host may be relatively new to cougar populations in Oregon.

Human-cougar conflicts typically increase as cougar populations or development within cougar habitat increases (Beier 1991); however, based on population reconstruction estimates (ODFW, unpublished data), cougar populations in our study areas have remained relatively stable since the late 1980's. Alternatively, attitudes towards large predators change over time (Wolch et al. 1997, Schwartz et al. 2003), and we speculate increased non-hunting, human caused mortality was associated with a decreased tolerance of cougars by humans. Increased development in rural areas which may increase encounter rates between cougars, humans and livestock, is an additional explanation for increased non-hunting, human caused mortality. Cougars monitored during our studies primarily occupied wildlands (i.e., national forest or industrial timber lands), and rarely used areas near human development. Therefore, increased human development likely did not contribute to increased non-hunting, human caused mortality during our studies.

Survival

We expected male cougars to have lower survival when hunting cougars with dogs was legal given harvest is gender biased using this method (Anderson and Lindzey 2005, Zornes et al. 2006). Prior to Measure 18, approximately 36% of radiocollared male cougars were harvested annually at Catherine Creek, but none were harvested post-Measure 18, and this substantial change in harvest rates increased survival rates. In contrast, approximately 23% and 2% of collared male cougars were harvested annually at Jackson Creek pre- and post-Measure 18, respectively. However, natural and other sources of mortality increased post-Measure 18, which negated any potential increase in survival rates attributable to decreased harvest mortality. Male survival prior to Measure 18 at Catherine Creek ($\hat{S} = 0.57$) was at the upper range of values reported in other areas where hunting cougars with dogs was legal (Table 3.10). Hunting opportunity during the Catherine Creek study was conservative (10 tags issued annually), season lengths short

Table 3.10. Summary of gender-specific point estimates of sub-adult and adult cougar survival under various hunting regulations in the western United States during 1988 - 2011.

	Survival rate				Management		
	Sub-adult		Adult				
State	Male	Female	Male	Female	Hunted	Dogs allowed	Source
Arizona	NA	NA	0.12 - 1.00	0.00 - 0.81	Yes	Yes	Cunningham et al. 2009[a]
Montana	NA	NA	0.29	0.65	Yes	Yes	Ruth 2004
New Mexico	0.56	0.88	0.91	0.82	No	NA	Logan and Sweanor 2001
Oregon	0.56	0.86	0.56	0.86	Yes	Yes	This study - Catherine Creek
	0.86	0.86	0.86	0.86	Yes	No	This study - Catherine Creek
	0.60	0.89	0.78	0.85	Yes	Yes[b]	This study - Jackson Creek
	0.45	0.88	0.82	0.84	Yes	No	This study – Wenaha, Sled-Springs, Mt. Emily
Utah	NA	NA	NA	0.71	Yes	Yes	Lindzey et al. 1988
Washington	0.34	0.34	0.33	0.77	Yes	Yes	Lambert et al. 2006
	0.63	0.59	0.34	0.67 - 0.73[c]	Yes	Yes	Robinson et al. 2008
	0.51	0.76	0.64	0.87	Yes	No	Cooley et al. 2009a
	0.54	1.00	0.45	0.66	Yes	Yes	Cooley et al. 2009b

[a] Range of annual survival estimates.

[b] Hunting cougars with dogs was legal during the first 2 years of the study, and illegal the last 8 years of the study. No differences in survival were observed between changes in hunting regulations.

[c] Lower estimate is for females > 6 years old. Upper estimate is for females 4 - 6 years old.

(1-31 December), and access limited. The study area was adjacent to the Eagle Cap Wilderness reducing vehicle access. We contend limited hunting opportunity and access resulted in male survival greater than previously observed in studies where the use of dogs to hunt cougars was legal (Table 3.10). Our estimates of adult male survival under an opportunistic hunting regime ($\hat{S} = 0.78 - 0.86$) were substantially higher than reported in populations where hunting with dogs was allowed but lower than unhunted populations (Table 3.10). We contend the non-selective and inefficient nature of cougar harvest without the use of dogs (ODFW 2006, Zornes et al. 2006) explained why male cougars in our studies had greater survival rates than in areas where cougars are hunted cougars with dogs (Table 3.10). Consequently, managers should expect to observe reduced survival rates of adult male cougars in areas where it is legal to hunt cougars with dogs.

While adult male survival should be greater in areas where dogs are not allowed to hunt cougars, this conclusion does not apply to sub-adult males because we documented a general trend of declining sub-adult male survival across studies, and our survival rates were similar to those in other hunted populations (Table 3.10), and this was related to male biased dispersal patterns (Sweanor et al. 2000, Logan and Sweanor 2001, Thompson and Jenks 2010). Dispersing sub-adults have higher movement rates than adults (Sweanor et al. 2000, Logan and Sweanor 2001), increasing probabilities of being opportunistically harvested, encountering adult males (Logan and Sweanor 2001), humans (Aune 1991), and livestock (Cunningham et al. 1995, Torres et al. 1996), all of which increase their risk of death (ODFW 2006). For these reasons, we expect sub-adult male survival to be lower than adult male survival regardless of management type.

Given the non-selective nature of hunting cougars without dogs (Zornes et al. 2006), we hypothesized that survival rates of female cougars may decline following the passage of Measure 18 (i.e., non-selective harvest would increase the number of females harvested). Despite increased hunting opportunity (i.e., tags and season lengths) post-Measure 18, hunter success rates were sufficiently low (1-2% annually; ODFW, unpublished data) that harvest rates (Fig. 3.3b) and survival rates (Fig. 3.4) of females, regardless of age, did not differ across studies. Survival rates of adult female cougars in our study areas (0.84 – 0.86) were greater than those observed in hunted populations in Utah, Montana, Arizona, and Washington (Table 3.10) where hunting cougars with dogs

was legal, and similar to those reported for females in an unhunted population in New Mexico (Table 3.10). These comparisons indicated effect of harvest on survival rates of female cougars is dependent on hunting method and intensity as regulated by quota or permit systems. For example, the level of female harvest mortality at our studies when the use of dogs was legal (0.09) and illegal (0.01 – 0.09) was minimal compared to other hunted populations (e.g, 0.15; Robinson et al. 2008, 0.16; Cooley et al. 2009b) where harvest was sufficiently high to negatively affect female survival. We conclude that hunting cougars with dogs has a greater potential to reduce survival rates of female cougars compared to areas where cougar hunting is opportunistic; however, conservative tag allocation programs in areas where hunting cougars with dogs is legal, such as those observed at Catherine Creek, can still result in relatively high survival of females.

In hunted cougar populations, human-caused mortality was the primary cause of death (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008), but in unhunted populations, natural mortalities were most common (Hemker et al. 1984, Beier and Barrett 1993, Logan and Sweanor 2001). Based on these findings, Quigley and Hornocker (2010; p. 66) suggested "the inverse relationship between human-caused and natural mortality suggests a compensatory mechanism in which human-caused mortality is replacing natural mortality in human-impacted ecosystems". While our study was not designed to assess the additive or compensatory nature of human caused mortality on cougar survival, the general patterns in causes of mortality and survival we documented provided additional insight into this issue. We agree with Quigley and Hornocker (2010) that human-caused mortality was partially compensatory, at least at low levels of harvest observed in our study (Fig. 3.3). In areas with low levels of human-caused mortality (e.g., Jackson Creek), natural mortality was greatest, and despite higher levels of human-caused mortality at other study areas, overall survival rates were relatively consistent across studies. Furthermore, we agree with Cooley et al. (2009b) that harvest mortality can be additive in heavily hunted populations and survival rates of adult males in Catherine Creek (i.e., high harvest rates) supported their assertion. We contend human-caused mortality is largely compensatory up to some level, after which, it is additive. Additional research is needed to clarify the inflection point where harvest transitions between being additive or compensatory mortality.

Prior to our research, Ruth et al. (2011) was the only study to estimate age-specific survival rates of cougars, but many studies documented differential survival rates of sub-adults and adults (Anderson et al. 1992, Logan and Sweanor 2001, Lambert et al. 2006). Our results were similar to those reported by Ruth et al. (2011), but included an interactive effect between age and gender as opposed to an additive effect of gender. The interactive effect we documented substantiated females have greater survival rates than males at younger ages (1 – 3 yrs), but survival rates of prime-age (4 – 8 yrs) cougars were similar regardless of gender in lightly hunted populations. Male biased dispersal in cougars (Sweanor et al. 2000, Logan and Sweanor 2001, Thompson and Jenks 2010) likely explains the difference in survival between males and females at younger ages. By the time most males establish a territory (3 – 4 yrs; Logan and Sweanor 2001) survival rates of males in lightly hunted populations were similar to females, which support the conclusion that lower survival rates of males at younger ages are attributable to increased mortality factors encountered during dispersal. We did not to observe any effect of age on cougar survival at Catherine Creek, but male cougars in this study area were subjected to higher harvest levels than Jackson Creek and WSM. Mean age of all male cougars harvested at Catherine Creek was 5.7 years pre-Measure 18 ($n = 10$; 1989 – 1994) and 3.9 years post-Measure 18 ($n = 46$; 1995 – 2011), which suggested hunters using dogs disproportionately harvested older males (ODFW, unpublished data). Selective hunting pressure lowered survival rates of adult male cougars, causing their survival rates to be similar to sub-adults. This type of selective harvest may eliminate effect of age on survival in other hunted populations where prime-age individuals are selectively harvested.

General life history patterns for long-lived mammals indicate older individuals should have lower survival rates than prime-aged individuals (Caughley 1966); consequently, the decline in survival rates of older individuals at WSM was expected but it was surprising this pattern was not observed at Jackson Creek. We conducted a post hoc analysis of cougar survival where we pooled data from Jackson Creek and WSM to estimate effect of age on cougar survival. The best model from this analysis was $S(Gender \times Age^2)$, and results were similar to those observed at WSM (Fig. 3.6c). As a result, we concluded our sample size was inadequate to estimate effect of old age on

survival at the Jackson Creek study area. Not accounting for an effect of age-specific survival could have important implications for managers if survival rates are used to parameterize models to estimate population growth rates and size. In cases where older adults have lower survival, treating adults in an identical manner will cause survival rates of individuals with higher reproductive values to be lower than expected (i.e., older individuals will lower the mean survival rate), which will contribute to conservative estimates of population growth (Morris and Doak 2002). Ideally, modeling efforts should consider age-specific effects on adult survival to improve reliability of population models (Caswell 2001, Morris and Doak 2002). Because acquiring a sufficient sample of individuals to estimate age-specific survival may be logistically or financially challenging, estimating survival for multiple age classes (e.g., Robinson et al. 2008) may provide the best alternative.

MANAGEMENT IMPLICATIONS

Our results indicated that despite similar management practices, sources of cougar mortality may vary among populations. Natural mortality is likely to be greater in systems with low harvest rates compared to those with high harvest rates, which suggests harvest mortality is at least partially compensatory. Our results suggest opportunistic hunting methods can provide high levels of recreation while allowing high survival rates of cougars. Consequently, in systems where hunting cougars with dogs is illegal managers may have difficulty utilizing hunters to manipulate cougar survival to meet population management objectives. Our results also indicated conservative harvest of cougars with dogs (i.e., limited tag numbers) can result in high survival rates of cougars, particularly females, suggesting hunting cougars with dogs may be compatible with maintaining cougar populations. With the option to hunt cougars with dogs, managers can differentially affect survival rates of male and female cougars (Lambert et al. 2006, Cooley et al. 2009a,b, this study) to meet population management objectives. However, managers must clearly define population objectives for cougars when providing hunting opportunities with dogs because excessive harvest can result in additive mortality (Cooley et al. 2009b) and population declines (Lambert et al. 2006). Natural mortality is effectively impossible to detect without intensive radio-collaring programs, which are not logistically feasible across large spatial scales. Consequently, we recommend managers

assess population health through mandatory checks of harvested animals to monitor for diseases and parasites. In areas where disease and parasite infections are detected, managers should consider radio-collaring cougars to determine if disease and parasites are negatively affecting survival. Our results corroborated observations by Ruth et al. (2011) of an effect of age (yrs) on cougar survival. We encourage future investigations of cougar survival test for an effect of age-specific survival. However, inadequate sample sizes may limit the ability of researchers to estimate age-specific survival, and we suggest at a minimum, survival is estimated for multiple age-classes (e.g., Robinson et al. 2008) to account for the effect of increasing age on cougar survival. Managers may consider using our age-specific survival estimates from WSM to parameterize population models to assess potential effects of changes in hunting regulations (i.e., use of dogs versus opportunistic methods); however, we urge managers to use these estimates with caution because other factors (i.e., prey density, habitat, and carnivore guilds) may influence cougar survival rates.

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CHAPTER 4

GROWTH RATES OF COUGAR POPULATIONS AND SIMULATED
POPULATION RESPONSES TO DENSITY REDUCTION UNDER VARIABLE
IMMIGRATION AND EMIGRATION

Darren A. Clark

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ABSTRACT

Cougar (*Puma concolor*) populations are thought to be increasing in much of western North America; however, empirical data to support this claim are sparse, and cougar populations in some areas may be declining. While most state agencies in western North America allow the use of trained hounds to pursue and hunt cougars, Oregon is 1 of 2 western states where cougars can be hunted, but use of dogs is not permitted. Given the unique management system for cougars in Oregon (year-round harvest permitted, but not using dogs), I was interested in estimating the population growth rate of cougars in northeast Oregon. I used empirical estimates of cougar vital rates to parameterize a Leslie matrix projection model to estimate deterministic and stochastic population growth rates of cougars in northeast Oregon, both when hunting cougars with dogs was legal (1989 – 1994) and illegal (2002 – 2011). Model cougar populations in northeast Oregon that were hunted with dogs increased at a deterministic growth rate (λ_D) of 1.18 and a mean stochastic growth rate (λ_S) of 1.21. Similarly, I found that model cougar populations subjected to hunting without dogs increased at a rate of 17% per year under both the deterministic ($\lambda_D = 1.17$) and stochastic ($\lambda_S = 1.17$) population models. Given that hunting cougars with dogs typically results in increased harvest and reduced survival rates of cougars, it was unexpected that the cougar population subjected to hunting with dogs was increasing at a faster rate than one that was not hunted with dogs. However, cougar populations in Oregon were subjected to low harvest rates when hunting cougars with dogs was legal and harvest was male biased. This resulted in high survival rates of female cougars and correspondingly high population growth rates. To create a model cougar population with a growth rate of 1.0 (i.e., stationary population), I found that mean annual survival rates of both genders and all age classes of cougars could be reduced an additional 12% compared to current survival estimates. The Oregon Cougar Management Plan allows the Oregon Department of Fish and Wildlife to administratively reduce cougar populations to benefit ungulate populations, reduce human-cougar conflicts, and limit livestock depredation. Consequently, I was interested in determining the percentage of a local cougar population that needed to be removed annually to achieve a 50% population reduction over 3 years, and the length of time required for the model population to recover from this reduction.

Because dispersal is an important factor influencing population growth rates and re-population of areas with low densities, I incorporated simulated immigration and emigration rates into my models. Using a deterministic Leslie matrix model, I found that 28% of a model cougar population would need to be removed annually to achieve a 50% population reduction after 3 years assuming a closed population and 48% of the population would need to be removed annually assuming maximum immigration rates. Using a stochastic Leslie matrix, I also estimated that a model cougar population would return to the pre-removal population size in 6 years assuming a closed population and in 2 years assuming a maximum number of immigrants. These model results suggest that current management practices combined with short-term, intensive, and localized population reductions are unlikely to negatively affect the short-term viability of cougar populations in northeast Oregon. However, at this time, it is not known if intensive lethal control efforts funded by state agencies will be cost-effective (i.e., increased sales of tags to hunt deer and elk will offset the costs of control efforts). Further research is needed to investigate the cost-effectiveness of cougar control efforts in Oregon.

INTRODUCTION

Cougars (*Puma concolor*) are currently hunted in 13 states and 2 Canadian provinces in western North America, but are not subjected to hunting in California. All but 2 other western states (Oregon and Washington) allow hunting of cougars with dogs. Harvest strategies and season lengths vary among states and provinces, but in most areas harvest is managed through limited entry or quota-based systems during a 4 – 9 month hunting season (Anderson et al. 2009, Cooley et al. 2011). The method of using dogs to pursue or hunt cougars was prohibited in Oregon following the 1994 hunting season after the public voted to prohibit the practice through Ballot Initiative Measure 18 (hereafter, Measure 18). Since Measure 18 was passed and in response to increasing cougar populations (Kiester and Van Dyke 2002), hunting seasons have been steadily extended, tag prices have been reduced, and cougar hunting is currently legal year-round in Oregon (Chapter 3). These changes were proposed by the Oregon Department of Fish and Wildlife (ODFW) and approved by the Oregon Fish and Wildlife Commission. Hunting has been the primary source of mortality for cougar populations in Oregon (Chapter 3) and other states (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al.

2008). Given the high degree of variability in cougar management practices among states, it is likely that population dynamics will also vary. Cougar populations exhibit strong regional source-sink dynamics (Sweanor et al. 2000, Robinson et al. 2008), so estimating population growth rates is critical for understanding local population dynamics and implementing effective management at local, state, and regional scales.

Hunting cougars with dogs is a more effective method than opportunistic hunting (Anderson and Lindzey 2005, Zornes et al. 2006), which is currently the only method permitted for hunting cougars in Oregon (ODFW 2006). Despite the low success rate of hunting cougars without dogs, cougar harvest in northeast Oregon has steadily increased since the mid-1990's (ODFW 2006), but has leveled off at all-time highs in recent years (ODFW 2012). Increased harvest may be a reflection of increasing cougar populations in Oregon since the early 1990's (Kiester and van Dyke 2002, ODFW 2006); however, the recent stabilization of harvest rates (ODFW 2012) may indicate that cougar populations have reached a threshold for ecological carrying capacity based on availability of prey (Logan and Sweanor 2001, Pierce et al. 2012) or territorial mechanisms (Hornocker 1970, Logan and Sweanor 2001). Alternatively, increased harvest rates may be the result of unsustainable harvest levels (Lambert et al. 2006), and immigration from less exploited populations may be necessary to maintain heavily-exploited local populations (Robinson et al. 2008, Cooley et al. 2009a,b). Given that cougar populations in Oregon have successfully recovered from near extirpation in the early 20th Century (Kiester and Van Dyke 2002, ODFW 2006), understanding the effect of hunting on population growth is critical for preventing future conservation concerns for the species. Furthermore, understanding population dynamics of cougar populations are critical for effective management of both cougars and populations of their prey (Anderson and Lindzey 2003, Vucetich et al. 2011).

ODFW is authorized to reduce human-cougar conflict, livestock depredation, and benefit native ungulate populations through the use of lethal removal of cougars in localized areas (hereafter, target area; ODFW 2006). Target areas are typically conducted on the scale of a Wildlife Management Unit (WMU; ~ 1,000 – 2,500 km^2), and reductions of cougar populations typically occur for 3 consecutive years with a goal of increasing adult female mortality to 40-45% of total cougar mortality (ODFW 2006),

which should result in a 50-60% decline in the population (Anderson and Lindzey 2005). Since the implementation of the Oregon Cougar Management Plan in 2006, ODFW has completed cougar removal on 1 target area and is currently implementing removal on 2 additional target areas in northeast Oregon to benefit declining populations of Rocky Mountain elk (*Cervus canadensis nelsoni*) (ODFW 2003, 2006, 2012). The effect of intensive, lethal management actions on the viability of local cougar populations is not well understood. Furthermore, it is unknown how quickly cougar populations are likely to recover to previous densities, and recovery times would influence the longevity of effects from cougar removals on ungulate populations, if any.

Estimation of cougar population size and composition before, during, and after management actions is an ideal approach to document effects of management; however, traditional methods to estimate cougar densities are costly, time consuming, and produce imprecise estimates (Choate et al. 2006). As a result, few studies have directly investigated the effect of population manipulations on population dynamics of cougars, but results were relatively consistent across studies. In New Mexico, an unhunted cougar population recovered from a 47% reduction in population size in 2-3 years (Logan and Sweanor 2001). Similarly, a hunted cougar population in Utah recovered to its initial size in 1-2 years following a 27% reduction in population size (Lindzey et al. 1992). Following a 66% reduction in population size, a hunted cougar population in Wyoming recovered to 79% of the pretreatment population size in 3 years (Anderson and Lindzey 2005). In contrast, another hunted cougar population in Utah that was reduced by more than 60% recovered to just 52% of its original size 3 years after intensive harvest was reduced (Stoner et al. 2006). Estimates of population size and composition of cougars before and after target areas were treated were not available to directly assess the effects of lethal control efforts in northeast Oregon, so I used available information on vital rates to simulate the response of a hypothetical cougar population to lethal control.

I used empirically-derived estimates of survival (Chapter 3), litter size (R. Green, ODFW, unpublished data), and simulated immigration and emigration rates to develop a Leslie matrix population model. My objectives were to: (1) use a deterministic model to estimate sensitivity and elasticity values of vital rates used in my model, (2) estimate stochastic population growth rates of cougars in northeast Oregon before and after the

implementation of Measure 18, (3) determine a rate of cougar exploitation that would result in an approximately stable population (i.e., $0.995 \leq \lambda < 1.005$), (4) determine the level of mortality required to reduce a hypothetical cougar population by 50% over 3 years, which is the common objective of cougar removal efforts conducted by ODFW in target areas (ODFW 2006), and (5) simulate the recovery time of a hypothetical cougar population following a 50% reduction in population size.

METHODS

Study Area

I used annual survival estimates of radio-collared cougars in the Catherine Creek WMU in northeast Oregon from 1989-1994 to simulate population growth rates pre-Measure 18 (Catherine Creek), and annual survival rates of cougars monitored in the Wenaha, Sled Springs, and Mt. Emily (WSM) WMUs in northeast Oregon from 2002-2011 to simulate population growth rates post-Measure 18 (Chapter 3). The survival estimates used in my analysis were obtained from radio-collared cougars that occupied quality deer (*Odocoileus* spp.) and elk habitat (i.e., forested land away from the wildland-urban interface) within the Umatilla and Wallowa-Whitman National Forests or within corporate timber lands. These survival rates may not be applicable to lower quality deer and elk habitat in agriculture-dominated lands or near the wildland-urban interface. Survival rates were estimated in habitat representative of the Blue Mountains, so my results should be widely applicable in the Blue Mountains region and other areas with a similar management systems and habitats.

Mule deer (*O. hemionus hemionus*), Rocky Mountain elk, and white-tailed deer (*O. virginianus*) were common in northeast Oregon. Black bear (*Ursus americanus*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*) were common carnivore species. At the time and place that survival rates of cougars were estimated, no gray wolf (*C. lupus*) packs were present. Vegetation patterns were strongly influenced by topography, aspect, and elevation. South-facing slopes were dominated by herbaceous vegetation and north-facing slopes were dominated by mixed-conifer forests. Common tree species in the Blue Mountains included ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*) and lodgepole pine (*P. contorta*).

Vital Rates

I obtained age- and sex-specific survival rates of cougars (S_{xs}) in northeast Oregon (Chapter 3, Appendix F) pre-Measure 18 (Catherine Creek; Table 4.1) and post-Measure 18 (WSM; Table 4.2). The oldest cougar included in this survival analysis was 13 years; consequently, I assumed longevity of cougars to be 13 years. I obtained estimates of age-specific litter sizes from placental scar counts of 627 known-age cougars harvested throughout Oregon, whose ages ranged from 2 to 18 years (R. Green, ODFW, unpublished data). I pooled data for cougars aged ≥ 10 years into 1 group ($n = 39$) due to small sample sizes in older age classes. The smallest sample was for 9-year-old females ($n = 29$) and the largest was for 3-year-olds ($n = 127$). Maternity was the mean number of kittens of each sex (m_{xm}, m_{xf}) produced annually by a mother of age x. I calculated maternity rates by multiplying the average litter size of females at age x by the sex ratio (0.5; Logan and Sweanor 2001) and then divided by the average successful interbirth interval in years (IBI; the time elapsed between consecutive successfully raised litters). I relied on published IBI estimates (17.4 - 19.4 months; Ross and Jalkotzy 1992, Logan and Sweanor 2001) to arrive at an estimated average IBI of 18 months (Lambert et al. 2006, Robinson et al. 2008), which matched the minimal information on IBIs available for northeast Oregon. I assumed females would not give birth until they were 2 years old, because most females give birth to their first litter at 2 years (Logan and Sweanor 2001). My estimate of mean litter size across all ages was 2.81 kittens, but average litter size varied with age from 2.61 to 3.15 kittens (Tables 4.1 and 4.2). I defined age-specific fecundity rates for each gender of kitten as $F_{xs} = m_{xs} \times S_{x-1f}$, where m_{xs} is the age (x) specific maternity rate for kittens of gender s, and S_{x-1f} is the annual survival rate of females of age x - 1.

Table 4.1. Age-specific annual survival and litter size estimates of cougars used to parameterize a Leslie projection matrix model to simulate population growth rates of cougars in northeast Oregon, USA when hunting cougars with trained dogs was legal (1989 – 1994)[a]. Survival estimates were generated during 1989-1994 in the Catherine Creek Wildlife Management Unit.

| Age | Male cougars | | Female cougars | | | |
	Survival	SD	Survival	SD	Litter size[b]	SD
0	0.66	0.11	0.66	0.11	NA	NA
1	0.57	0.09	0.86	0.03	NA	NA
2	0.57	0.09	0.86	0.03	2.61	0.78
3	0.57	0.09	0.86	0.03	2.62	0.76
4	0.57	0.09	0.86	0.03	2.81	0.69
5	0.57	0.09	0.86	0.03	3.00	0.79
6	0.57	0.09	0.86	0.03	2.88	0.93
7	0.57	0.09	0.86	0.03	3.05	0.97
8	0.57	0.09	0.86	0.03	2.72	0.81
9	0.57	0.09	0.86	0.03	2.85	0.78
10	0.57	0.09	0.86	0.03	3.15	0.90
11	0.57	0.09	0.86	0.03	3.15	0.90
12	0.57	0.09	0.86	0.03	3.15	0.90
13[c]	0.00	0.00	0.00	0.00	0.00	0.00

[a] Estimates of survival from the Catherine Creek WMU during 1989-1994 were used to simulate population growth rates pre-Measure 18 (Chapter 3, Appendix F).
[b] Litter size estimates were obtained from placental scar counts of female cougars harvested throughout Oregon (R. Green, ODFW, unpublished data).
[c] I assumed all cougars would die at age 13. These individuals had a survival rate of zero and, because they died, were not capable of reproducing.

Table 4.2. Age-specific annual survival and litter size estimates of cougars used to parameterize a Leslie projection matrix to simulate population growth rates of cougars in northeast Oregon, USA when hunting cougars with trained dogs was illegal (1995-present)[a]. Survival estimates were generated during 2002-2011 in the combined Wenaha-Sled Springs-Mt. Emily Wildlife Management Units.

| Age | Male cougars | | Female cougars | | | |
	Survival	SD	Survival	SD	Litter size[b]	SD
0	0.66	0.11	0.66	0.11	NA	NA
1	0.45	0.17	0.88	0.06	NA	NA
2	0.61	0.11	0.88	0.04	2.61	0.78
3	0.72	0.07	0.87	0.03	2.62	0.76
4	0.78	0.06	0.86	0.03	2.81	0.69
5	0.81	0.05	0.84	0.04	3.00	0.79
6	0.82	0.05	0.81	0.04	2.88	0.93
7	0.81	0.06	0.77	0.05	3.05	0.97
8	0.77	0.06	0.71	0.06	2.72	0.81
9	0.70	0.08	0.63	0.08	2.85	0.78
10	0.58	0.13	0.54	0.12	3.15	0.90
11	0.42	0.18	0.42	0.16	3.15	0.90
12	0.25	0.19	0.31	0.20	3.15	0.90
13[c]	0.00	0.00	0.00	0.00	0.00	0.00

[a] Estimates of survival from the Wenaha, Sled-Springs, and Mt. Emily (WSM) WMUs from 2002-2011 were used to simulate population growth rates post-Measure 18 (Chapter 3, Appendix F).
[b] Litter size estimates were obtained from placental scar counts of female cougars harvested throughout Oregon (R. Green, ODFW, unpublished data).
[c] I assumed all cougars would die at age 13. These individuals had a survival rate of zero and, because they died, were not capable of reproducing.

Sensitivity and Elasticity Analysis

For both the WSM and Catherine Creek study areas, I constructed separate deterministic, post-breeding, birth-pulse, single-sex, age-classified Leslie matrices. I created all matrices and conducted all analyses in MatLab (version 8.0.0.783, MathWorks, Natick, MA, USA). I used the eigenall.m function (Morris and Doak 2002; p. 223) to obtain the stable age distribution, sensitivity values, and elasticity values. The stable age distribution represented the dominant right eigenvector of my dual-sex Leslie matrix. I calculated sensitivity values (S_{ij}) using:

$$S_{ij} = \frac{v_i w_j}{\sum_{k=1}^{s} v_k w_k} \quad ,$$

where v_i is the reproductive value of individuals in class i and w_j is the fraction of individuals in class j in the stable distribution vector $\mathbf{w}$ (Morris and Doak 2002; eq. 7.10). I determined the relative effect of each vital rate (r_i) on λ by calculating elasticity (Er_i) values using:

$$Er_i = \frac{r_i}{\lambda_1} \frac{\partial \lambda_1}{\partial r_i} \quad ,$$

where λ_1 is the deterministic growth rate, r_i is the vital rate, and $\partial \lambda_1 / \partial r_i$ is the sensitivity of λ_1 to r_i (Morris and Doak 2002; eq. 9.2).

Stochastic Population Modeling

I constructed a post-breeding, birth-pulse, dual-sex, age-classified Leslie projection matrix to calculate stochastic population growth rates of cougars in northeast Oregon pre-Measure 18 (Catherine Creek) and post-Measure 18 (WSM). Survival of cougars differed by gender (Tables 4.1 and 4.2), which necessitated the use of a dual-sex Leslie matrix (Caswell 2001; p. 571). The resulting population matrix consisted of 28 classifications of cougars (14 female, 14 male). I assumed that (1) there was no temporal correlation in vital rates, (2) vital rates among sexes and age classes were uncorrelated within years, (3) no catastrophes or bonanzas (i.e., exceptionally bad or good years) occurred, (4) the population was geographically closed, (5) there was no spatial structure in the population, (6) and the population was not subjected to density-dependent effects. To project the population over time, my model took the form of $\mathbf{n}(t) = \mathbf{L} \times \mathbf{n}(t-1)$, where

n is the vector of population size, *t* is time in years, and *L* is a Leslie matrix[a]. I determined the starting size of the model cougar population in a hypothetical WMU by multiplying the approximate size of a WMU in northeast Oregon (~1,800 km^2) by the density of cougars estimated in the Mt. Emily WMU (5.14 cougars/100 km^2; Davidson et al. *In Review*), which resulted in a starting population size of 93 cougars. I determined the initial population vector (*n*(0)) by proportionally distributing the total cougar population (*n* = 93) according to the stable age distribution calculated from a deterministic Leslie matrix.

I incorporated stochasticity in my model by randomly generating survival (S_x) and litter size elements of *L* from a normal distribution at each time step (Tables 4.1 and 4.2). I constrained litter sizes between 0.0 and 4.0 and survival between 0.0 and 1.0 because these represented biologically realistic values. I estimated stochastic population growth (λ_S) by conducting 5,000 simulations of population growth over 5 years and calculated the mean population growth rate across all simulations. I used a 5-year projection interval because projecting populations for many years (> 10) into the future is often unrealistic and unreliable (Morris and Doak 2002). In addition, cougar management practices have changed substantially over time in Oregon (Chapter 3) and additional management changes may alter vital rates, which would limit the utility of my results.

Simulating the effects of control efforts on cougars

To simulate the effects of lethal control and account for immigration into the target area (i.e., population control area), I modified my Leslie matrix to include 2 populations. The first population represented the population subjected to control efforts (i.e., 1,800 km^2 – the approximate size of a WMU in the Blue Mountains of Oregon), and the second population represented the surrounding population (i.e., 177,405 km^2 – an area approximately equal to 70% of the state of Oregon). The spatial extent of the surrounding population was based on the maximum recorded dispersal distances of sub-adult male cougars (239 km; Sweanor et al. 2000). I used vital rate estimates from the WSM study area (Table 4.2) to parameterize my Leslie matrix model because these vital rates were calculated under current management practices in Oregon. The resulting

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[a] Bold notations using capital letters reference matrices while bold notations with lower case letters reference vectors.

population matrix consisted of 28 classifications of cougars in each population (14 male, 14 female), or a total of 56 classifications. I assumed mean vital rates and associated variances would be identical for the 2 populations; however, vital rates between populations were uncorrelated within a year. I used a dual-population Leslie matrix because I wanted to investigate the effects of immigration on population growth following a population reduction at a localized scale. Using this approach, growth rates of each population can be calculated independently, or movement can be incorporated between populations by specifying the probability that an individual in a particular age class survives the year and disperses to the adjacent population.

Estimating Movement Rates.—Immigration and emigration are important demographic parameters that strongly influence population growth rates. In addition, the number of immigrants that arrive in a localized area will be dependent on the size of the local and surrounding population. To account for the influence of immigration and emigration on the local cougar population, I simulated dispersal of sub-adult cougars to estimate rates of movement into and out of the area where cougar populations were reduced. I used a spatial simulation to calculate movement rates using published estimates of dispersal distances of sub-adult cougars (Sweanor et al. 2000). I first created a circle with an area of 1,800 km^2, which represented the hypothetical area where lethal control of cougars would occur (i.e., target area). This area was buffered by 239 km, which was the maximum dispersal distance of sub-adult male cougars (Sweanor et al. 2000). The resulting area of 177,405 km^2 was the area that contained the population surrounding the target area. I assumed 70% of this area was habitat suitable for cougars, resulting in 124,184 km^2 of habitat occupied by cougars surrounding the target area. Assuming a density of 5.14 cougars/100 km^2 (Davidson et al. *In Review*), approximately 6,384 cougars (all age classes including kittens) occupied the area within 239 km of the target area (i.e., the exterior population).

Cougar dispersal is typically restricted to sub-adults (Sweanor et al. 2000, Logan and Sweanor 2001, Thompson and Jenks 2010); therefore, I simulated dispersal rates for sub-adult cougars and assumed adult cougars would maintain their existing territories because adult cougars rarely disperse and are not nomadic (Logan and Sweanor 2001). I defined sub-adult cougars as 1- and 2-year old males and 1-year old females. Using a

stable age distribution, I estimated that there were 696 1-year old males, 270 2-year old males, and 696 1-year old females in the exterior population. Sub-adult male cougars almost exclusively disperse from their natal territories (Logan and Sweanor 2001, Thompson and Jenks 2010), so I assumed all 1- and 2-year old males would disperse from their natal territories. In contrast, female cougars display high levels of philopatry (40 – 67%; Logan and Sweanor 2001, Thompson and Jenks 2010), so I assumed that 60% of sub-adult females would disperse. Of the 696 1-year old females in the exterior population, 418 would disperse from their natal territories.

For each sub-adult cougar in the exterior population, I randomly generated a single data point outside, but within 239 km of the target area in ArcGIS (Version 10.1, ESRI, Redlands, CA, USA), which represented the starting point of dispersal. For each starting point, I generated 100 random dispersal paths by selecting a random bearing from a uniform distribution (0 - 359°) and a random dispersal distance from a normal distribution with a mean of 161 km ($\pm$ 63 SD) and 13 km ($\pm$ 20 SD) for male and female sub-adults, respectively (Sweanor et al. 2000). I simulated dispersal paths using correlated random walks with the movement.simplecrw function in the Geospatial Modeling Environment (version 0.7.2, Spatial Ecology LLC).

I calculated immigration rates for the model population (i.e., movement from the exterior to the target area population) using 2 metrics. The first was the proportion of simulated dispersal paths ($\pm$ SD) that terminated within the target area boundary, which represented the minimum immigration rate. The second was the proportion of simulated dispersal paths ($\pm$ SD) that crossed the target area, which represented the maximum immigration rate. I conducted an identical analysis for sub-adult cougars within the target area to estimate emigration rates; however, I only calculated the proportion of simulated dispersal paths ($\pm$ SD) that terminated outside the boundary of the target area because all sub-adults crossed the target area boundary.

Sustainable exploitation rate.—Approximately 74% of mortality of female cougars in northeast Oregon under current management strategies was attributable to humans (i.e., hunting, damage complaints; Chapter 3), resulting in an exploitation rate of approximately 13% (e.g., for the current annual mortality rate of 0.18, 74% of this mortality was human caused, $0.18 \times 0.74 = 0.13$). I used annual survival rates of cougars

from WSM (Table 4.2) to parameterize a dual-sex, dual-population, deterministic Leslie projection matrix to estimate the level of mortality a cougar population could sustain before λ (annual rate of population change) was < 1.0, which represented a stable population with no increase or decrease in abundance. I simulated the effect of removing between 1-50% of the population, and for each percentage removal I calculated the deterministic population growth rate and which level of removal resulted in $\lambda_D = 1.0$. I assumed mortality would be proportionally distributed among age classes (i.e., mortality would not be selective). I conducted 3 sets of simulations where I assumed the target area population was closed, the population was subjected to minimum immigration rates, or the population was subjected to maximum immigration rates. I summed the current human-caused exploitation rate of 13% (Chapter 3) with the level of additional population removal (i.e., 1-50%) to obtain an exploitation rate required to obtain a stable population ($\lambda_D = 1.0$). I also calculated the reduction in annual survival rates compared to current survival rates that would be required to obtain a stable cougar population in the model. For each simulation, my starting population (initial population vector; $n(0)$ was 93 individuals distributed proportionally among sex- and age-classes according to a stable age distribution. I assumed litter sizes and annual survival would not be influenced by increased exploitation rates during the short period of removal and simulations (i.e., no density-dependent effects).

Mortality required to reduce a local population in half.— To determine the level of lethal control required to reduce a local cougar population ($n = 93$) by 50% over 3 years, I used a dual-sex, dual-population, deterministic Leslie projection matrix parameterized with mean vital rate values measured at the WSM study area (Table 4.2). I simulated the effect of annually removing 1-50% of the cougar population within the target area for 3 consecutive years. I used this time frame because ODFW typically conducts administrative removals of cougars for 3 years (ODFW 2006). During control efforts I assumed a constant percentage of the population would be removed annually across the three years. I calculated the number of individuals removed at each time step by multiplying the percentage of the population removed by the number of individuals remaining in the population. This value was converted to a proportion and subtracted from the mean annual survival rate of each sex and age class of cougar prior to projecting

the population size at time $t + 1$. I took this approach because I assumed cougars would be removed as encountered, resulting in a proportional distribution of mortality among each sex and age class.

For each level of population removal (i.e., 1-50%), I calculated the number of individuals removed each year, the number of individuals in the population after 3 years, and determined the level of removal that resulted in 46 individuals (half the starting population) remaining in the population. I calculated these metrics for 3 sets of simulations to generate a reasonable range of values upon which to base management actions. For comparison purposes, the first set of simulations assumed that the populations being subjected to removal were geographically closed (i.e., no immigration or emigration). In the second and third set of analyses, immigration rates (i.e., movement from the exterior population to the target area population) were equal to the minimum and maximum rates for sub-adults, respectively. Mean immigration rates were calculated for each sex using the methodology outlined above, where I randomly simulated dispersal paths of sub-adult male and female cougars in the surrounding population. Under the second and third simulations, emigration rates were equal to the mean calculated during simulations of dispersal based on the specified conditions for each simulation.

Calculating recovery time of reduced populations.—Approximately 46 cougars remained within a 1,800 km^2 area of habitat following a 50% reduction in cougar population size. I assumed mortality during removal efforts would be proportionally distributed among sex and age classes because cougars would be removed as encountered. Consequently, I determined the initial population vector (n(0)) following the conclusion of removal efforts by proportionally distributing 46 cougars according to the stable age distribution.

I used a stochastic, dual-sex, dual-population Leslie matrix to calculate the mean number of years required for the population to increase from 46 to 93 individuals. I conducted 3 sets of simulations, where mean immigration and emigration rates varied. I ran the first set of simulations for comparison purposes under the unrealistic assumption that the target area was geographically closed (i.e., no immigration or emigration). For the second and third sets of simulations, I used either the mean immigration rates equal to the minimum estimate (second set of simulations) or the maximum estimate (third set of simulations). I incorporated stochasticity into both immigration and emigration rates by

randomly drawing rates from a normal distribution at each time step. I incorporated immigration and emigration into my model by modifying matrix elements for survival rates of sub-adults to account for dispersal. The proportion of individuals dispersing into the target area was calculated by multiplying the annual survival rate by the probability of immigration, $S_{xs} \times I_{xs}$, where S_{xs} and I_{xs} are the survival and immigration rates of a cougar of age x and sex s, respectively. The proportion of individuals remaining in the exterior population was equal to the product of age specific survival (S_{xs}) and the probability of not immigrating into the target area ($1 - I_{xs}$). Emigration from the target area was modeled in an identical manner except the probabilities of emigrating (E_{xs}) and not emigrating ($1 - E_{xs}$) were substituted for immigration rates (I_{xs})

To estimate recovery times of the model cougar population in the target area, I conducted 1,000 simulations of population growth over 10 years. Once simulated populations reached 93 individuals (i.e., the pre-removal population size), simulations concluded and the number of years since the start of the simulation was recorded. At each time step, I determined the proportion of simulated populations that had recovered to create a cumulative distribution function (CDF). CDFs are typically used to calculate the probability that a population will reach an extinction threshold within a specified time period (Morris and Doak 2002); however, a CDF can be applied to any population threshold and is relevant to population recovery times. I repeated this process 100 times and calculated the mean CDF to determine the cumulative probability of recovery over time (yrs) for each immigration scenario (i.e., closed population, minimum immigration, and maximum immigration). I also recorded the mean population growth rate and population size at each time step.

RESULTS

Population Growth

Pre-Measure 18— According to the stable age distribution, most of the model population consisted of kittens and sub-adults, and males made up a smaller proportion of the population than females (Fig. 4.1a). This was expected because of the empirical finding that females had higher survival rates than males at younger ages (Table 4.1), allowing more females to persist in the model population. Elasticity values were greatest for female kittens and sub-adults, indicating that these individuals had the largest effect on

the growth rate of the model population (Table 4.3). Elasticity values declined considerably for older (> 4-years-old) individuals in the population. Fecundity of individual age classes contributed relatively little to population growth compared to survival rates; however, elasticity values summed across all ages indicated fecundity was somewhat important to population growth (0.24). The summed value of all elasticity values was > 1 because elasticity values for fecundity rates included the product of survival and maternity. The estimated stochastic population growth rate (λ_S) of a model cougar population pre-Measure 18 in the Catherine Creek WMU was 1.21. Both the male (λ_{SMale} = 1.22) and female ($\lambda_{SFemale}$ = 1.20) portions of the model population increased at similar rates. Less than 1% of the annual estimates of population growth over 5 years (i.e., 25,000 calculations of lambda) resulted in a population growth rate < 1.0 (Fig. 4.2a), and all model populations had increased a by minimum of 60 individuals from the starting population size of 93 individuals after 5 years (Fig. 4.2b).

Post-Measure 18— Based on the assumption of a stable age distribution, most of the model population consisted of kittens and sub-adults, and there were fewer adult males in the population than adult females (Fig. 4.1b), as was the case in the pre-Measure 18 model. This was expected because empirical estimates indicated female cougars had higher survival rates than males at younger ages (Table 4.2) allowing more females to persist in the population. Elasticity values were greatest for female kittens and sub-adults, indicating these individuals had the largest effect on growth rate of the model population (Table 4.4). Fecundity of individual age classes contributed relatively little to model population growth compared to survival rates; however, elasticity values summed across all ages indicated fecundity was relatively important to population growth (0.26). The summed value of all elasticity values was > 1 because elasticity values for fecundity rates included the product of survival and maternity. The mean stochastic population growth rate (λ_S) of a model cougar population in northeast Oregon post-Measure 18 was 1.17. None of the 5,000 simulations of population growth over 5 years (i.e., 25,000 calculations of lambda) resulted in λ < 1.0 (Fig. 4.3a) or a population that declined from the starting population size (Fig. 4.3b). Both the male (λ_{SMale} = 1.17) and female ($\lambda_{SFemale}$ = 1.17) portions of the model population increased at similar rates.
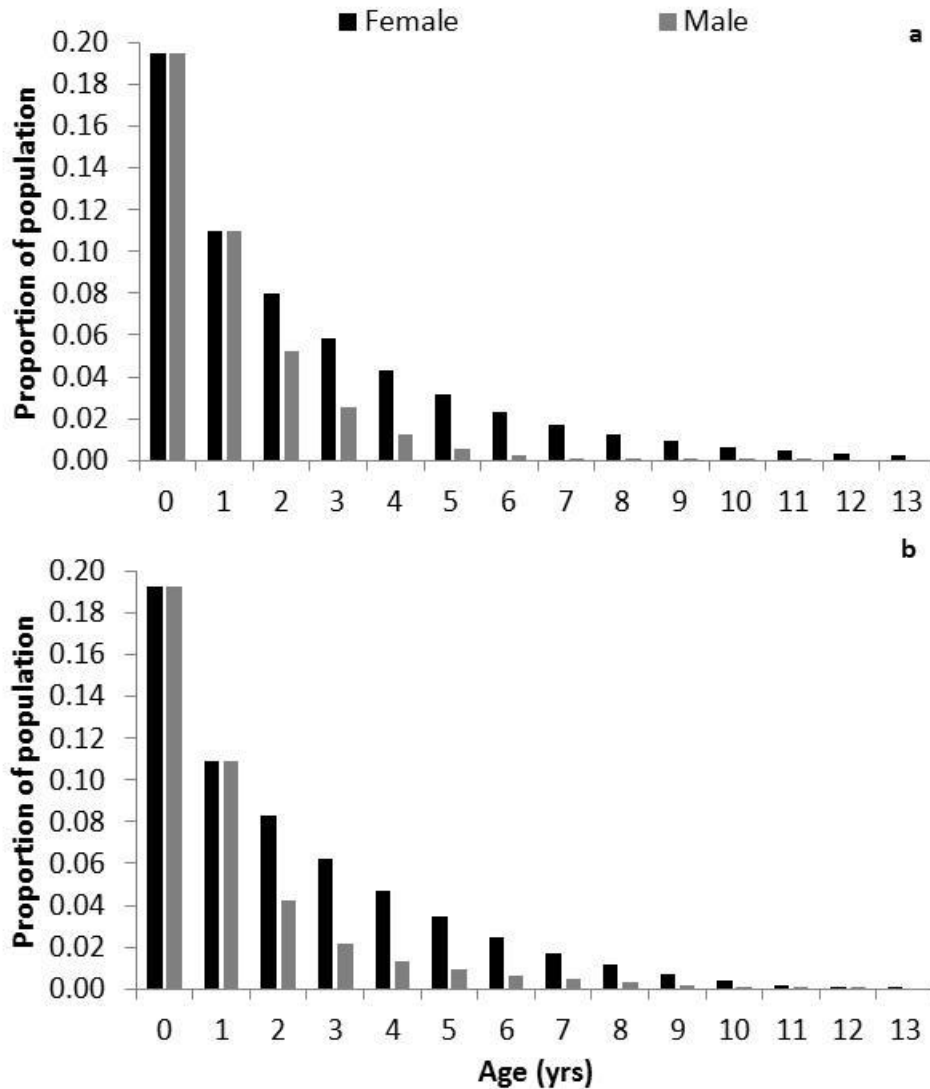
Figure 4.1. A stable age distribution of cougars in northeast Oregon, USA, when hunting cougars with dogs was (a) legal and (b) illegal. The stable age distribution was estimated from a deterministic Leslie matrix using previously estimated vital rates. Survival rates during the time period when hunting cougars with dogs was legal were estimated from 1989 – 1994 in the Catherine Creek Wildlife Management Unit. Survival rates during the time period when hunting cougars with dogs was illegal were estimated from 2002 – 2011 in the Wenaha, Sled Springs, and Mt. Emily Wildlife Management Units. Fecundity rates for both analyses were estimated from placental scar counts of harvested cougars in Oregon.
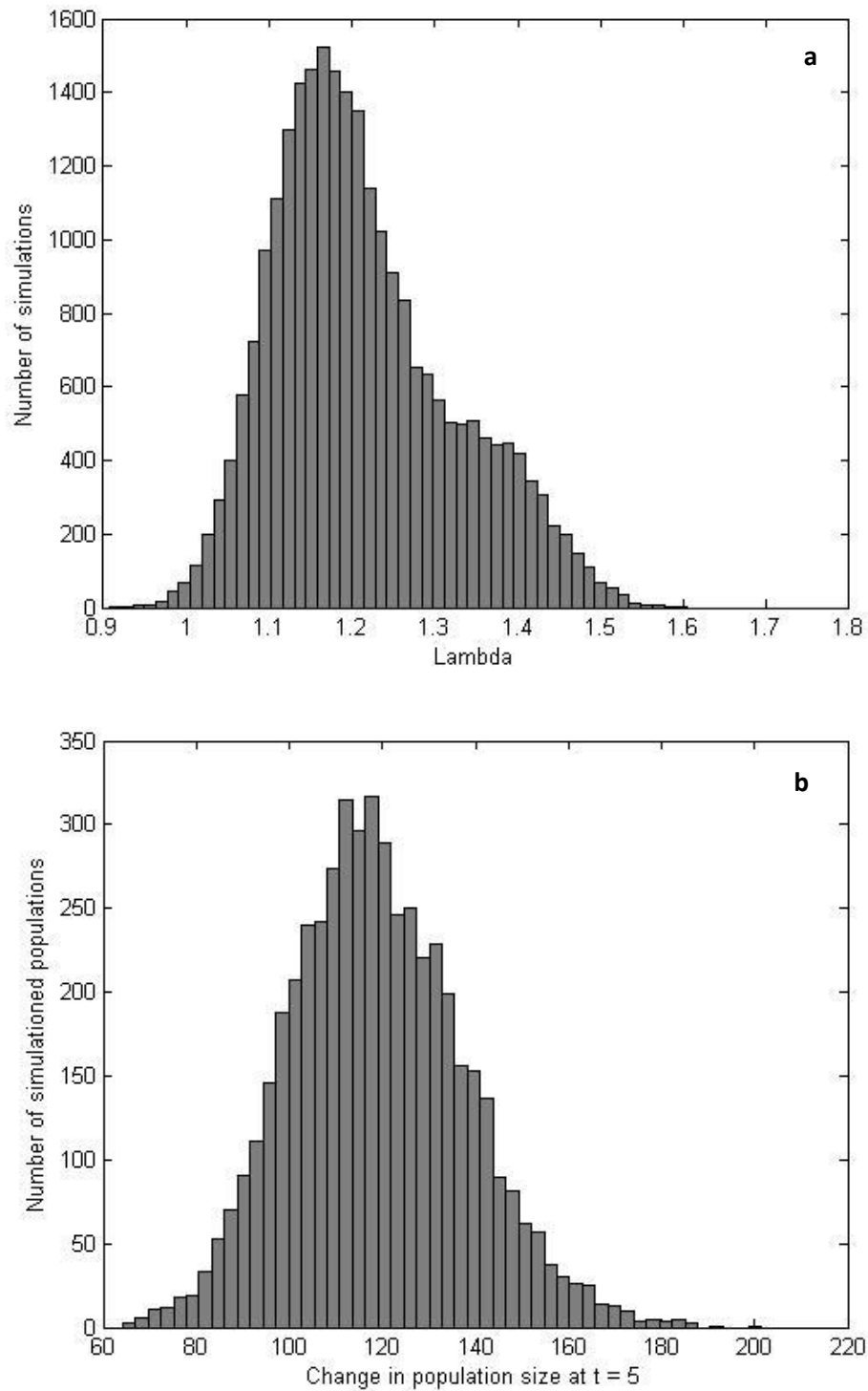
Figure 4.2. Histograms of (a) population growth rates and (b) change in population size from initial population size for 5,000 simulations of population growth over 5 years for a cougar population in northeast Oregon, USA, that was subjected to hunting with the use of dogs.
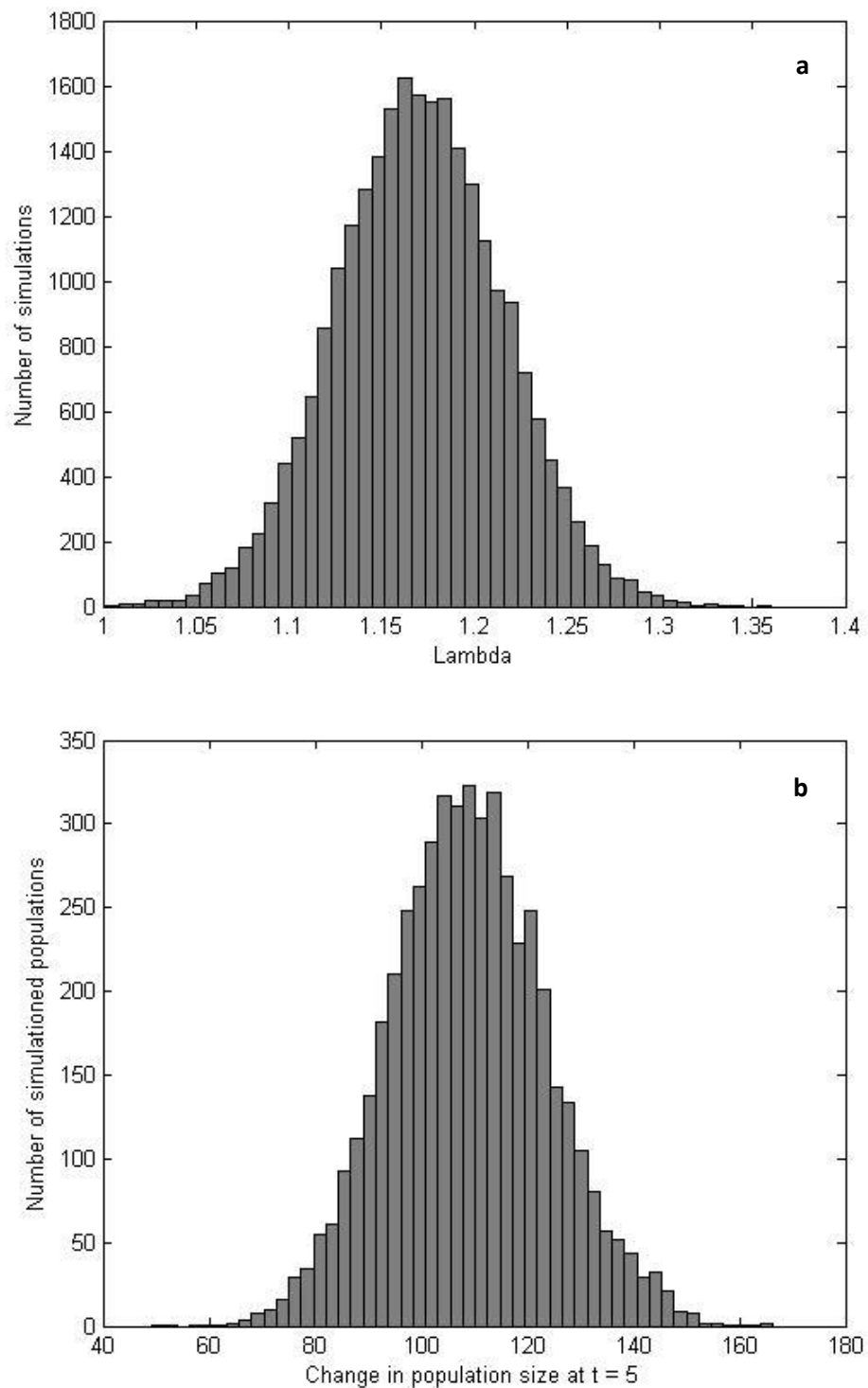
Figure 4.3. Histograms of (a) population growth rates and (b) change in population size from initial population size for 5,000 simulations of population growth over 5 years for a cougar population in northeast Oregon, USA, that was subjected to hunting but dogs were not allowed to pursue or hunt cougars.

Table 4.3. Estimated sensitivity and elasticity values for survival and maternity rates of female cougars in northeast Oregon, USA when hunting cougars with trained dogs was legal at Catherine Creek Wildlife Management Unit. Estimates were calculated using a single sex, birth pulse, deterministic Leslie matrix.

Age	Sensitivity		Elasticity	
	Survival	Maternity	Survival	Maternity
0	0.32	0.00	0.27	0.00
1	0.25	0.00	0.21	0.00
2	0.18	0.07	0.16	0.06
3	0.14	0.05	0.12	0.05
4	0.10	0.04	0.08	0.04
5	0.07	0.03	0.06	0.02
6	0.05	0.02	0.04	0.02
7	0.03	0.02	0.03	0.01
8	0.02	0.01	0.02	0.01
9	0.01	0.01	0.01	0.01
10	0.01	0.01	0.01	0.01
11	0.00	0.00	0.00	0.00
12	0.00	0.00	0.00	0.00
13	0.00	0.00	0.00	0.00

Table 4.4. Estimated sensitivity and elasticity values for survival and maternity rates of female cougars in northeast Oregon, USA when hunting cougars with trained dogs was illegal at Wenaha, Sled-Springs, and Mt. Emily Wildlife Management Units. Estimates were calculated using a single sex, birth pulse, deterministic Leslie matrix.

Age	Sensitivity		Elasticity	
	Survival	Maternity	Survival	Maternity
0	0.35	0.00	0.30	0.00
1	0.26	0.00	0.23	0.00
2	0.19	0.09	0.16	0.07
3	0.14	0.06	0.12	0.06
4	0.09	0.05	0.08	0.04
5	0.06	0.04	0.05	0.03
6	0.04	0.03	0.03	0.02
7	0.02	0.02	0.02	0.02
8	0.01	0.01	0.01	0.01
9	0.01	0.01	0.00	0.01
10	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	0.00
12	0.00	0.00	0.00	0.00
13	0.00	0.00	0.00	0.00

Simulating the effects of cougar control efforts

Estimating Movement Rates.—I calculated immigration rates as the proportion of the sub-adults in the population surrounding the target area that would establish a territory in the target area, based on simulations of cougar movements. My estimates of minimum immigration rates were 0.0091 (± 0.0004 SD) for 1-year-old males, 0.0092 (± 0.0007 SD) for 2-year-old males, and 0.0037 (± 0.0001 SD) for 1-year-old females. Maximum immigration rates were estimated to be 0.0405 (± 0.0183 SD) for 1-year-old males, 0.0163 (± 0.0099 SD) for 2-year-old males, and 0.0061 (± 0.0054 SD) for 1-year-old females. Assuming the mean minimum immigration rate, 3-4 1-year-old males, 2-3 2-year-old males, and 2-3 1-year-old females survived the year, immigrated, and established a territory in the target area annually. In contrast, 12-13 1-year old males, 3-4 2-year old males, and 3-4 1-year old females survived, immigrated, and established a territory in the target area annually under the mean maximum immigration rate.

I calculated emigration rates as the proportion of the sub-adult population within the target area that dispersed to the surrounding population. I estimated emigration rates were equal to 0.9863 (± 0.0039 SE) for 1-year old males, 0.9800 (± 0.0080 SE) for 2-year old males, and 0.2845 (± 0.0081 SE) for 1-year old females. These estimates would result in 2-3 1-year old males, 1-2 2-year old males, and 1-2 1-year old females that survived the year, leaving the target area and established a territory outside the target area the first year after removal efforts concluded. The number of emigrants increased in subsequent years as the population recovered and more sub-adults were available to disperse.

Sustainable exploitation rate.—Assuming a closed population, an additional 13% of the population, above the current exploitation rate of 13%, needed to be removed annually to create a stable model population with $\lambda = 1.0$. At estimated minimum and maximum rates of immigration, an additional 18% and 26% of the population, respectively, needed to be removed annually to maintain a stable model cougar population ($\lambda = 1.0$). Cougar populations in northeast Oregon are being exploited at a rate of approximately 13% annually (Chapter 3). When combined with my estimates of additional mortality required to maintain a stable population, I found that model cougar populations should be able to sustain exploitation rates between 26% (closed population) and 39% (maximum

immigration) annually.   To maintain a stable model cougar population in northeast Oregon, mean survival rates had to be reduced by 0.12, 0.17, and 0.27 assuming a closed population, a population with minimum immigration rates, and a population with maximum immigration rates, respectively (Table 4.5). If these exploitation rates were being applied across a large area, the exploitation rate for a closed population (26%) would be most appropriate because the number of immigrants available to disperse into the target area would be greatly reduced.

Mortality required for a 50% population reduction.—Assuming a localized model cougar population was geographically closed during control efforts, an additional 27 – 28% (40% total removal when current exploitation rates [13%] were included) of the cougar population within a target area would need to be removed annually to achieve a 50% population reduction in 3 years (i.e., ~ 46 individuals remaining; Fig. 4.4). To achieve this, an additional, 23, 18, and 15 cougars had to be removed in years 1, 2, and 3, respectively. This required that λ be reduced from 1.17 to 0.79 – 0.80 for 3 consecutive years. Reductions in population size (i.e., $\lambda < 1.0$) during the first year of removals were not realized until an additional 14% (~ 12 individuals; 13% existing removals plus an additional 14% for a total exploitation rate of 27%) of the model population was removed.

For a model population with minimum and maximum rates of immigration, an additional 36 – 37% or 47 - 48% (49 - 60% total removal when current exploitation rates [13%] are included) of the cougar population would need to be removed annually to achieve a 50% reduction over 3 years, respectively (Fig. 4.4). Under a minimum rate of immigration, an additional 31, 23, and 18 cougars had to be removed in years 1, 2, and 3, respectively. In contrast, under a maximum rate of immigration, an additional 40, 28, and 22 cougars had to be removed in years 1, 2, and 3, respectively. Reductions in population size during the first year of removals were not realized until an additional 19 or 27% (~ 16 or 23 individuals) of the population was removed for model populations with minimum and maximum rates of immigration, respectively.

Table 4.5. Gender and age-specific survival rates of cougars in northeast Oregon, USA required to lower population growth rates (λ_D) from 1.17 under current management practices to a stable population ($\lambda_D = 1.00$) assuming varying levels of immigration.

	Female cougars				Male cougars			
	Current	Survival for immigration rate			Current	Survival for immigration rate		
Age	survival	None	Minimum	Maximum	survival	None	Minimum	Maximum
0	0.66	0.54	0.49	0.39	0.66	0.54	0.49	0.39
1	0.88	0.76	0.71	0.61	0.45	0.33	0.28	0.18
2	0.88	0.76	0.71	0.61	0.61	0.49	0.44	0.34
3	0.87	0.75	0.70	0.60	0.72	0.60	0.55	0.45
4	0.86	0.74	0.69	0.59	0.78	0.66	0.61	0.51
5	0.84	0.72	0.67	0.57	0.81	0.69	0.64	0.54
6	0.81	0.69	0.64	0.54	0.82	0.70	0.65	0.55
7	0.77	0.65	0.60	0.50	0.81	0.69	0.64	0.54
8	0.71	0.59	0.54	0.44	0.77	0.65	0.60	0.50
9	0.63	0.51	0.46	0.36	0.70	0.58	0.53	0.43
10	0.54	0.42	0.37	0.27	0.57	0.45	0.40	0.30
11	0.42	0.30	0.25	0.15	0.42	0.30	0.25	0.15
12	0.31	0.19	0.14	0.04	0.25	0.13	0.08	0.00
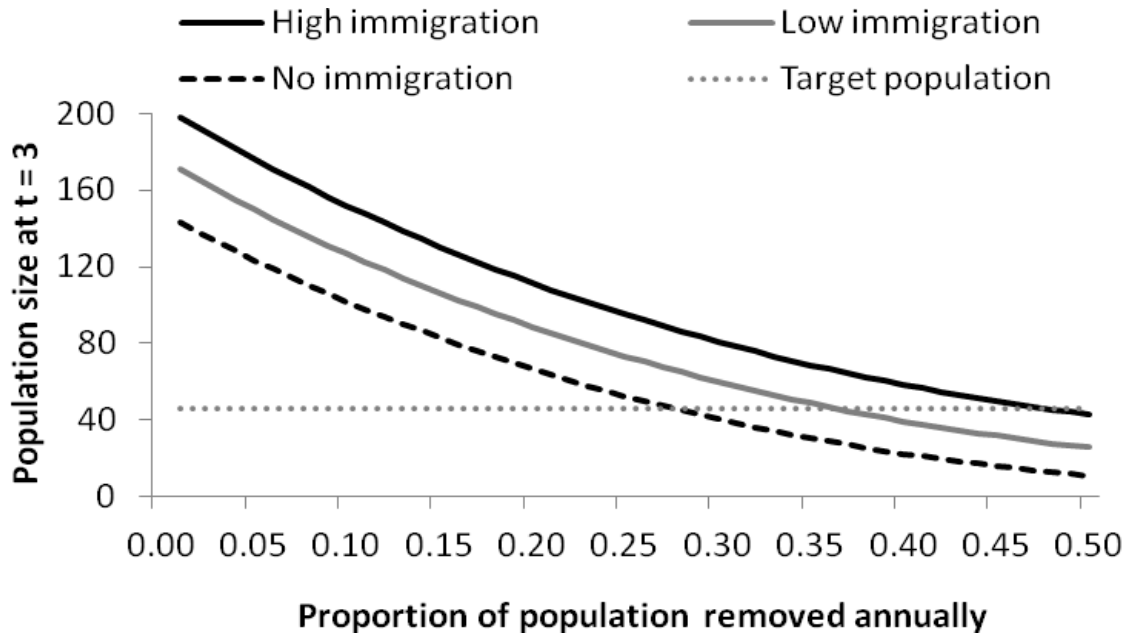
Figure 4.4. The estimated size of a hypothetical cougar population in northeast Oregon, USA, during the third year of lethal control efforts. Three separate simulations were conducted where it was assumed the population was geographically closed or subjected to a minimum or maximum level of immigration. Estimates were generated using a deterministic Leslie matrix where the proportion of the population removed annually was allowed to vary between 0.00 and 0.50. All simulations had a starting population of 93 individuals and estimated population sizes represent the population size after 3 years of removals. Population sizes that were greater than 93 individuals had increased since the implementation of control efforts because lethal control was not sufficient to reduce population size. The dashed, horizontal line represented the number of cougars that would be in the population ($n = 46$) if the population was reduced by 50%.

Recovery time of reduced populations.—Assuming a closed population and a return to the current exploitation rates of 13% following a 50% reduction of population size, the time to population recovery (i.e., all simulated populations reached 93 individuals) for a model cougar population was 5-6 years; however, there was a small probability (0.002) of recovery in as few as 3 years (Fig. 4.5). In contrast, simulations that included immigration had substantially faster recovery times. Assuming minimum immigration rates, there was a 60% probability the model population recovered in 1 year and 100% probability of recovery in 4-5 years (Fig. 4.5). Assuming maximum immigration rates, there was a 90% probability the model population recovered in 1 year and a 98% and 100% probability of recovery by years 2 and 3, respectively (Fig. 4.5).

The mean model population size for simulations that included immigration surpassed the recovery goal (i.e., 93 individuals) within 2 or 3 years after conclusion of lethal control. In contrast, mean model population size in a closed population did not surpass the recovery goal until 6 years after population reduction (Fig. 4.6) but such a situation was highly unrealistic in northeast Oregon because cougar populations are not isolated. This difference occurred because immigrants greatly outnumbered emigrants in open populations during the first year after removal efforts. In the first year after removal efforts, the mean population growth rate was 1.68 and 1.82, for populations that included minimum and maximum levels of immigration, respectively, while the closed population growth rate was 1.17 (Fig. 4.7). The first year after removals, the population within the target area increased sufficiently that the number of immigrants and emigrants became approximately equal. This effectively negated the benefit of immigration in subsequent years, and the population growth rates of open and closed populations were similar. As immigration increased, the estimated proportion of sub-adult males in the population increased, and the estimated proportion of sub-adult females declined slightly (Fig. 4.8).
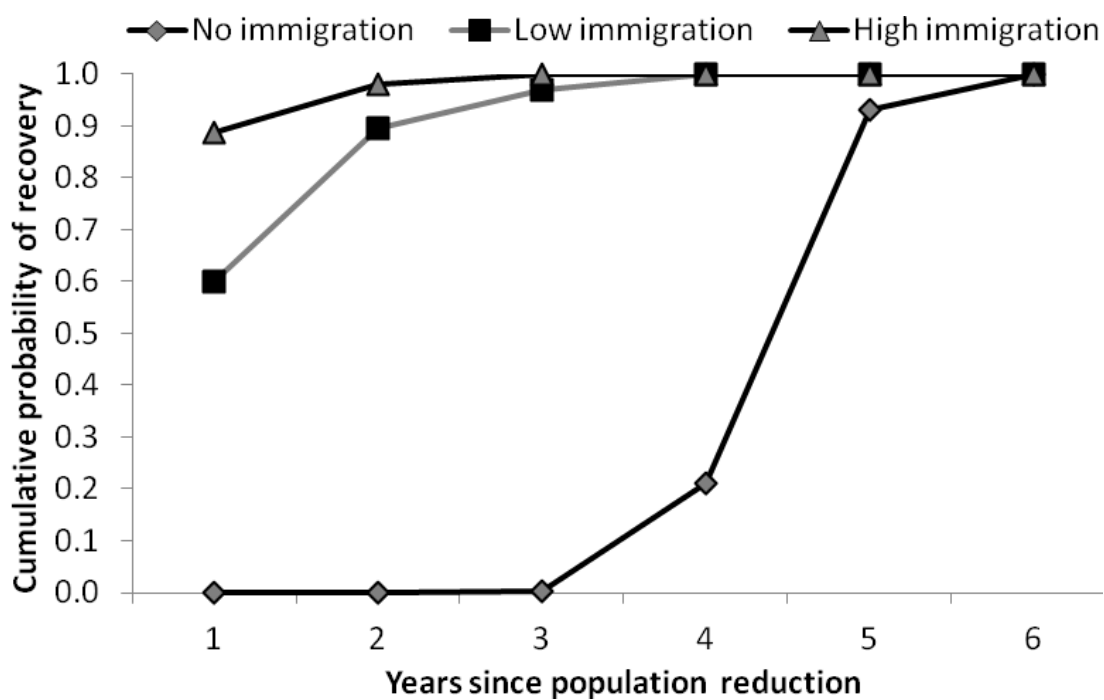
Figure 4.5. Mean cumulative distribution functions of recovery times of hypothetical cougar populations in northeast Oregon, USA following a 50% population reduction. Three separate simulations were conducted where it was assumed the population was geographically closed or subjected to a minimum or maximum level of immigration.
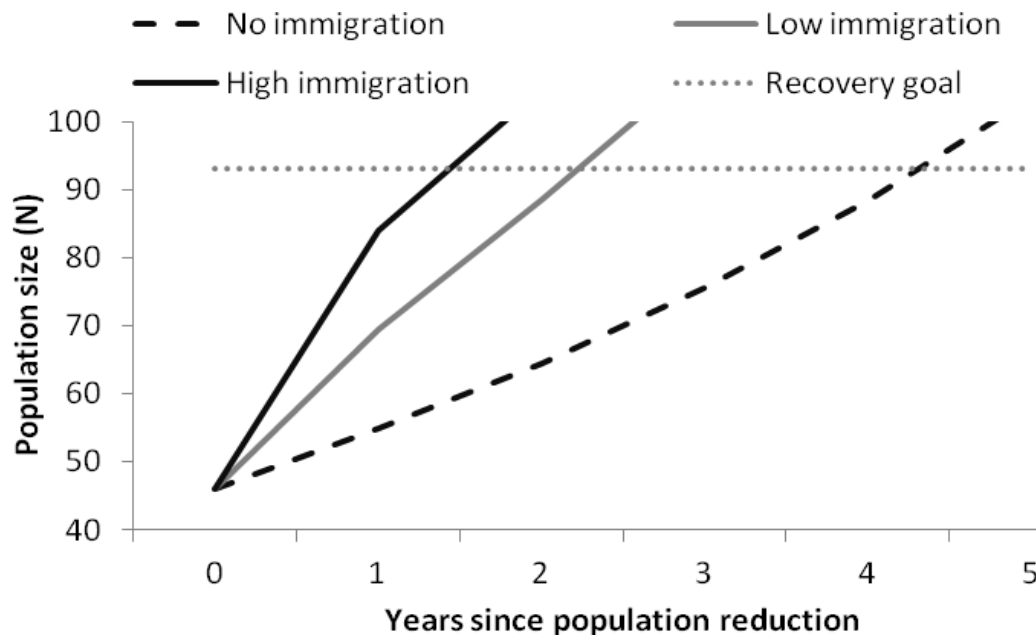
Figure 4.6. Mean population sizes of a hypothetical cougar population in northeast Oregon, USA 1 – 5 years following a 50% population reduction. Three separate simulations were conducted where it was assumed the population was geographically closed or subjected to a minimum or maximum level of immigration. The dashed horizontal line represented the number of cougars that were in the population prior to being subjected to a population reduction.
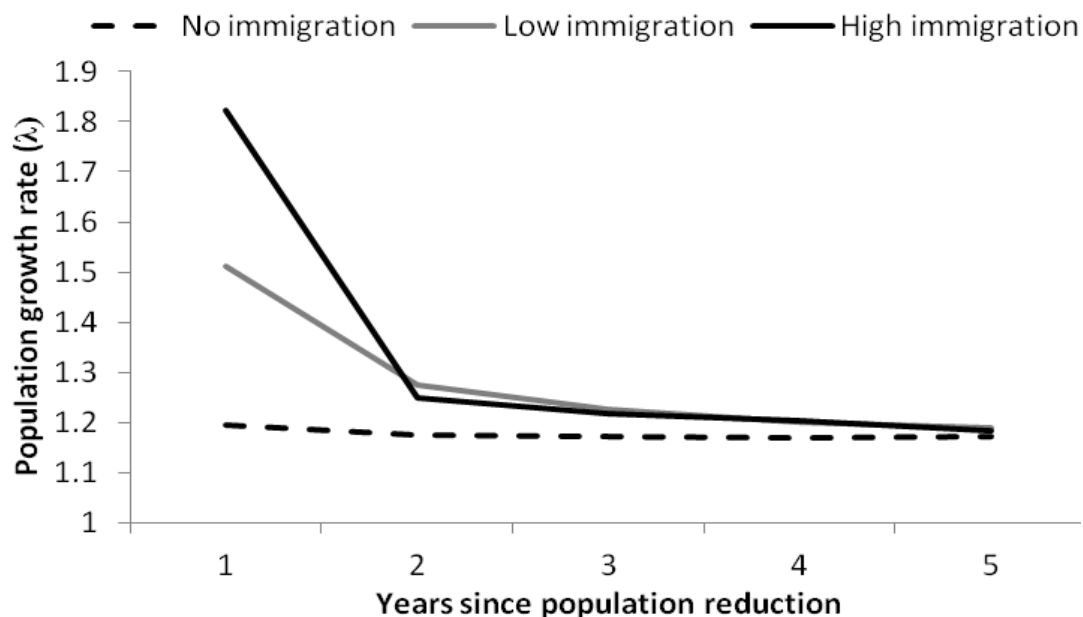
Figure 4.7. The estimated mean stochastic population growth rates of a hypothetical cougar population in northeast Oregon, USA during the 5 years following a 50% population reduction. Three separate simulations were conducted where it was assumed the population was geographically closed or subjected to a minimum or maximum level of immigration.
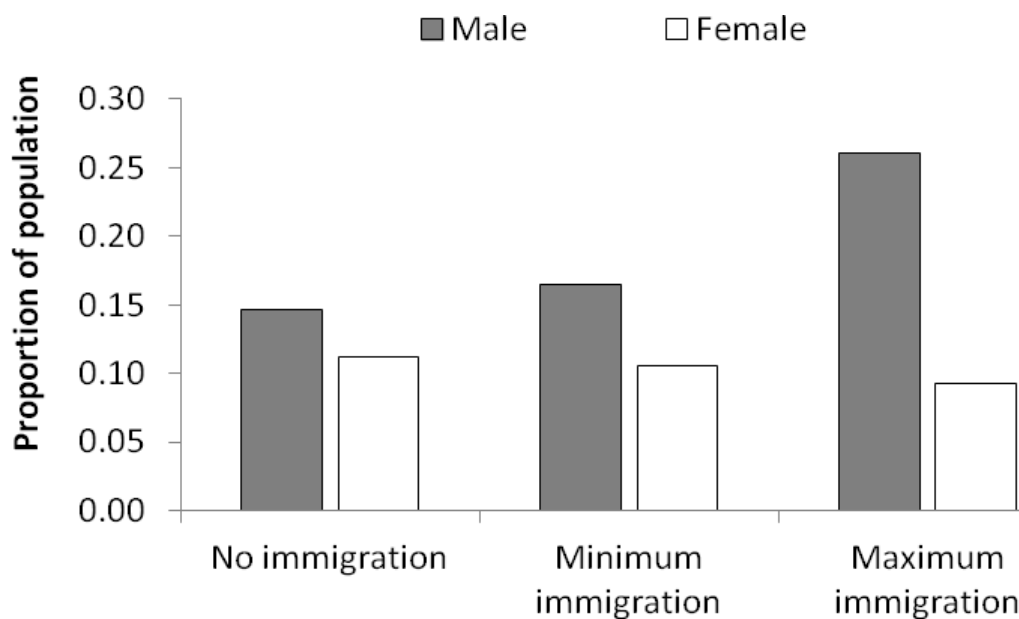
Figure 4.8. The estimated proportion of male and female sub-adults in a hypothetical cougar population one year after being subjected to a 50% reduction in population size. Three separate simulations were conducted where it was assumed the population was geographically closed or subjected to a minimum or maximum level of immigration.

DISCUSSION

Population Growth and Sensitivity

My simulation results indicated model cougar populations in northeast Oregon increased at a substantial rate (17-21% per year) pre- and post-Measure 18. During the Catherine Creek study, cougar populations were likely recovering from historic population lows (Kiester and Van Dyke 2002, ODFW 2006), which caused ODFW to manage for increasing cougar populations while providing minimal recreational hunting opportunities to reduce livestock damage (ODFW 2006). Therefore, the population growth rates I estimated pre-Measure 18 are likely a realistic approximation of observed growth rates. In contrast, survival rates from cougars used to populate my model post-Measure 18 were obtained from cougars occupying high quality habitat in northeast Oregon, which likely resulted in overly optimistic population growth rates. Cougars that utilized the wildland-urban interface or agricultural dominated lands, which likely have lower survival due to increased human conflict, insufficient habitat requirements, or reduced prey abundance, were not monitored post-Measure 18. I contend these areas of sub-optimal habitat likely served as population sinks, while the quality habitat within my study areas served as sources, allowing the overall cougar population in northeast Oregon to remain relatively stable. Further research is needed to clarify this relationship.

Cougar management practices differ throughout western North America (Cooley et al. 2011) and are likely to have a profound effect on population growth rates of cougars, because harvest is the primary source of mortality in hunted populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Chapter 3). However, given the difficulty in generating reliable estimates of cougar population growth, determining the effect of varying management practices on cougar populations has been difficult. Previous research has indicated hunting can result in excessive exploitation of cougars and subsequent population declines (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009a,b). My simulation results indicated hunted cougar populations in northeast Oregon pre- and post-Measure 18 were not declining, and that hunting is compatible with cougar conservation. The differences in findings between my study and previous research can be attributed to variability in hunting methods and exploitation rates. From 1989 – 1994, 10 cougar tags were issued annually within the Catherine Creek WMU, and

the hunting season lasted from 1 – 31 December. This level of hunting pressure was minimal compared to that of declining populations in Washington. While the number of tags issued was not specified by Lambert et al. (2006), legal hunting seasons occurred from 1 August to 31 March. Robinson et al. (2008) indicated that cougar harvest in Washington was managed under a quota based system, with a total of 38 cougars or 15 females harvested causing the season to end. Cougar populations that were declining in Washington were subjected to intensive hunting by dogs, which results in greater exploitation rates than opportunistic hunting (Anderson and Lindzey 2005, Zornes et al. 2006, Chapter 3), which has been used in Oregon post-Measure 18. Despite yearlong hunting seasons, and an unlimited number of tags being issued, cougar harvest success rates are sufficiently low (~1%; ODFW 2012) that opportunistic hunting methods result in low levels of cougar exploitation (Chapter 3). This comparison of results among studies suggests minimal harvest of cougars, either through the use of controlled tag numbers and hunting with tags or unlimited opportunistic hunting, can have minimal effects on population growth of cougars (this study), but excessive harvest can be detrimental to population growth (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009a,b).

My estimate of population growth rates in northeast Oregon indicated model cougar populations were increasing; consequently, improvements in survival are not necessary to maintain this population. In fact, cougar populations in northeast Oregon could sustain additional mortality and maintain relative stability over time. To maintain a stable model cougar population in northeast Oregon post-Measure 18 (i.e., $\lambda = 1.0$), survival rates of cougars could be reduced by as much as of 12% across all age classes (Table 4.5). This level of mortality is unlikely to occur given the extremely low success rate of hunting cougars without dogs (Anderson and Lindzey 2005, Zornes et al. 2006); therefore, the current system of hunting cougars in Oregon is unlikely to threaten the short- or long-term viability of cougar populations. Furthermore, opportunistic hunting methods are an ineffective management tool to manipulate cougar survival to meet population management objectives of cougars. Hunting cougars with dogs is likely the only method available to effectively manipulate cougar survival to result in negative population growth rates (Lambert et al. 2006, Robinson et al. 2008, Cooley et al.

2009a,b); however, hunting of cougars with dogs can result in increasing population growth rates of cougars if tag numbers are limited (this study).

I found population growth of cougars was most sensitive to changes in survival of females, similar to other cougar populations (Lambert et al. 2006, Robinson et al. 2008, Cooley at al. 2009a,b). This was expected because population growth is most sensitive to female survival for most long-lived species of mammals (Raithel et al. 2007) and other taxa (Crouse et al. 1987, Pfister 1998, Sæther and Bakke 2000). Given the high sensitivity of population growth to adult female survival, mangers should consider protection of female cougars during hunting seasons in areas where cougar populations may be declining. In contrast, additional mortality of female cougars would be the quickest way to manipulate population growth rates of cougars to meet management objectives. My life stage simulation analysis (Appendix I) suggests variation in inter-birth intervals (IBI) and kitten survival explain a large amount of variability (20 and 45% respectively) in population growth rates. Managers should consider the importance of these parameters when identifying factors that may be limiting or preventing recovery of cougar populations.

Assumptions and potential biases.—Any biases in vital rates used in my model will translate into biased population growth rates, particularly if biases exist for vital rates that have a large effect on population growth. My results from a life stage simulation analysis (Appendix I) suggest that estimates of IBI, kitten survival, and prime-age (3-9 yr) female survival have the greatest effect on population growth rates. My estimates of prime-age female survival are likely unbiased because they covered several consecutive years and were obtained from large sample sizes. Estimates of IBI's used in my analysis were drawn from the literature but also matched well with the observed values in northeast Oregon. There was some potential for estimates of kitten survival to be positively biased because my sample of kittens mostly included older individuals (> 5 months; Appendix F) and a large proportion of kitten mortality may occur at young ages (1-2 mo.; Logan and Sweanor 2001). To test the relative effect of overestimating kitten survival on my results, I conduct a post-hoc analysis where I set mean kitten survival to 0.33, rather than 0.66. This resulted in a mean population growth rate of 1.05, which was substantially lower than my estimated growth rate of 1.17, but still greater than 1.00. Therefore, I

conclude that my estimate of population growth may be positively biased based on overestimation of kitten survival; however, cougar populations in northeast Oregon are likely to serve as a source population regardless of this potential bias.

I assumed vital rates were uncorrelated among age classes within or among years, and I did not include catastrophes or bonanzas in my model. These effects typically increase variation in annual population growth, resulting in reduced long-term population growth rates (Morris and Doak 2002). The degree of correlation among vital rates in my study was likely minimal because harvest was the primary source of mortality (Chapter 3), and cougar harvest was a relatively random event given the opportunistic nature of hunting cougars without dogs. Vital rates and population growth of cougars typically respond slowly to changing prey densities (Logan and Sweanor 2001, Pierce et al. 2012). Therefore, catastrophes and bonanzas were unlikely to occur and exclusion of these rare occurrences had minimal influence on my results.

Finally, I assumed my population was geographically closed and density dependent mechanisms were not occurring. Obviously, these are biologically unrealistic expectations because these factors likely affect wild populations. The effect of density-dependence on population growth is not well understood for cougars, but is most likely to operate via decreased maternity rates (Thompson 2009), which has minimal influence on population growth (Appendix I). Cougar densities in northeast Oregon were relatively high compared to other populations (5 cougars/100 km^2; Davidson et al. *In Review*), so it was likely that any potential density-dependent effects that occur in cougar populations were likely operating at the time vital rates used in my models were estimated. Therefore, my estimates of population growth may underestimate population growth rates for low density populations. High densities may also result in an increased dispersal of sub-adult males and reduced philopatry in females (Thompson 2009). However, for simplicity and because I had limited information on local dispersal of sub-adult cougars, I assumed my population was geographically closed. Increased dispersal should reduce population growth rates. Therefore, my estimates of population growth may be greater than observed population growth. This is likely particularly true of my estimates of population growth post-Measure 18. Based on minimum population estimates from population reconstruction, cougar densities in northeast Oregon have remained relatively

stable over the past 10-15 years (B. Johnson, ODFW, unpublished data). Therefore, I believe the observed population growth rate of cougars post-Measure 18 is closer to 1.0 than 1.17, and excess cougars are dispersing to surrounding areas.

Effects of Simulated Control Efforts on Cougar Populations

My simulation results confirmed cougar populations are able to sustain relatively high levels of exploitation without substantial negative effects to population growth over time. Model cougar populations in northeast Oregon are capable of high intrinsic growth rates (17-21% annually). Therefore, extensive efforts will be required to reduce cougar populations at a localized scale. To maintain a stable model cougar population in northeast Oregon post-Measure 18 (i.e., $\lambda = 1.0$), survival rates of cougars could be reduced by as much as of 12% across all age classes (Table 4.5). Immigration from surrounding populations will further influence the ability of managers to reduce cougar populations at a local scale. Depending on the level of immigration, 41 - 61% of the population (no vs. maximum immigration) would need to be removed annually over 3 years to reduce a model population by 50%. My simulated levels of removal corresponded well with estimates of control required to greatly reduce cougar population size in field studies. Experimental removals of >40% of the population annually over 3-5 years resulted in 50-60% declines in other cougar populations (Anderson and Lindzey 2005, Stoner et al. 2006). While hunting cougars with dogs can be highly effective, a large portion of the removal needs to be conducted in the first year of any removal effort. For example, in my simulations if 26-39% (no vs. high immigration) of a population is not removed during the first year of control efforts, population growth will be ≥ 1.0, eliminating the potential benefit of removal efforts. This was not surprising given cougar populations sustained harvest rates of 20-30% in field settings (Ashman et al. 1983, Ross and Jalkotzy 1992).

My modeling results also indicated that as immigration rates increased following population reductions, the proportion of sub-adult males in the recovering population increased. During recovery, sub-adult males made up approximately 15% of the model population assuming the population is geographically closed and increased to 26% of the model population under maximum immigration rates. This occurred because cougar dispersal is male biased (Sweanor et al. 2000, Logan and Sweanor 2001, Thompson and

Jenks 2010); consequently, a larger number of male cougars arrived following control efforts. Increased numbers of sub-adult males in heavily hunted cougar populations has been previously documented (Anderson and Lindzey 2005, Robinson et al. 2008), and they are more likely to engage in livestock depredation (Cunningham et al. 1995, Torres et al. 1996) and conflict with humans (Beier 1991). Changes in the composition of the cougar population also can have important implications for ungulate populations because prey use and selection patterns vary according to gender, age-class, and reproductive status of cougars (Knopff et al. 2009, White et al. 2011, Chapter 2).

The level of removal I simulated that was necessary to reduce the local population by 50% may be excessive if cougar removal is selective. Local (i.e., the size of a typical WMU in Oregon) cougar populations in northeast Oregon would not be at risk of extirpation in the short-term (5-10 years) following a 50% population reduction. With a closed population and 13% exploitation rates following control efforts (i.e., the current exploitation rate in northeast Oregon), all simulated populations had recovered within 5-6 years. When immigration and emigration were incorporated into my model, the population recovered to the pre-removal population size in 2 - 3 years depending on the level of immigration. I suspect that as the area encompassed by removal efforts increases in size, recovery times will increase because the absolute number of immigrants arriving in the area will be small compared to the existing population so the effect of immigration will be reduced and population growth will occur primarily from *in situ* reproduction. Increasing the area of lethal control will likely reduce the absolute number of females immigrating into the control area, because their mean dispersal distances are relatively short (13 km; Sweanor et al. 2000). Given females provided the greatest contribution to population growth (Lambert et al. 2006, Robinson et al. 2008, this study); reduction of the absolute number of female immigrants should slow population recovery.

The recovery times of simulated populations I observed were similar to those where populations were experimentally reduced in field studies. Following a 47% reduction of an unhunted cougar population in New Mexico, the adult portion of the population recovered in 2 – 3 years (Logan and Sweanor 2001). A population in Utah recovered in 2 years following a 27% reduction in population size over a 1 year period (Lindzey et al. 1992), and a population in Wyoming that was reduced by 66% recovered

to approximately 79% of the pretreatment size in 3 years (Anderson and Lindzey 2005). My estimated recovery times were extremely similar to those of an unhunted population (Logan and Sweanor 2001), which was not surprising given that survival rates of cougars between my study and theirs were relatively similar (Chapter 3). In contrast, a cougar population in southern Utah had not recovered from a >60% population reduction 3-4 years after an intensive harvest (>40% of the population removed annually) had ended (Stoner et al. 2006). I suspect recovery times of a reduced cougar population in northeast Oregon will be shorter than those observed by Stoner et al. (2006) because exploitation rates are currently ~13% (Chapter 3), which is less than they reported during their recovery phase (~20% of the population removed annually).

Recovery times of my simulated populations were most influenced by immigrants from the surrounding population and secondarily by *in situ* reproduction, which was also observed during experimental density reductions in field studies (Lindzey et al. 1992, Logan and Sweanor 2001, Anderson and Lindzey 2005). The ability of cougar populations to recover from intensive population reductions was not surprising because cougars were heavily persecuted in North America during the early 20th century and have subsequently recovered from population lows and local extirpations throughout most of western North America (Riley and Malecki 2001). Cougars disperse long distances to colonize available habitat (Sweanor et al. 2000, Stoner et al. 2008, Thompson and Jenks 2010), which allows immigrating sub-adults to greatly increase local population growth rates in the short-term. Furthermore, the reproductive capacity of cougars is relatively great compared to other large mammals, because litter sizes are moderately large (~2 - 3 kittens; Ross and Jalkotzy 1992, Spreadbury et al. 1996, Logan and Sweanor 2001), females reproduce for the first time at 18-24 months of age, gestation lengths are short (~90 days; Logan and Sweanor 2001), and cougars can reproduce throughout the year (Ross and Jalkotzy 1992, Logan and Sweanor 2001). The high reproductive potential of cougars combined with their ability to disperse large distances likely accounts for their ability to rapidly recover from natural catastrophic events or intensive control efforts.

I urge caution in using my results as absolute rates of recovery because additional confounding factors may be present in recovering populations. Following a reduction in density, local populations may have increased fecundity or increased levels of philopatry

(Logan and Sweanor 2001) allowing the local population to increase at a faster rate than I predicted. However, it is unlikely that fecundity rates in Oregon will increase following a population reduction because the litter sizes we used in my models ($\bar{x} = 2.81$) are consistent with those observed in the literature (2.6 – 3.1 kittens per litter; Ruth 2004, Logan and Sweanor 2001, Spreadbury et al. 1996), and the survival rates of kittens in Oregon (0.66; Appendix F) were some of the highest reported for hunted populations (0.42; DeSimone and Semmens 2005, 0.57; Lambert et al. 2006, 0.59; Robinson et al. 2008) and similar to an unhunted population (0.66; Logan and Sweanor 2001). Furthermore, fecundity rates have a relatively small influence on population growth rates (summed elasticity values = 0.26) suggesting population growth would not be influenced substantially even if fecundity rates increased. An additional confounding factor is that an insufficient number of males may be available to successfully breed females following a reduction in cougar density, resulting in reduced fecundity rates and population growth. However, this seems unlikely because dispersal in cougars is male biased (Sweanor et al. 2000, Logan and Sweanor 2001, Thompson and Jenks 2010), so a large number of males should arrive on the study area and be available to sire litters.

Assumptions and potential biases.—I assumed mortality from removals would be proportionally distributed according to age and gender of populations, which should occur if cougars were removed as encountered. Female cougars have the largest influence on population growth rates, so if females are selectively removed, total removal efforts may be lower than I documented. Second, I used a deterministic Leslie matrix to estimate the level of removal required to reduce a local cougar population. Deterministic models typically provide an optimistic view of population growth rates (Morris and Doak 2002); consequently, my estimates of mortality required to reduce a cougar population may be biased high because the growth rates may be lower than I estimated. Regardless, even if local control efforts result in a > 50% reduction in cougar populations, my results indicated that populations are resilient and will rapidly recover from population declines with minimal risk of local extirpation.

My model assumed dispersing individuals would be equally likely to arrive from all directions and adjacent habitat consisted of quality habitat (i.e., no spatial structure). While this may be the case for some cougar populations where habitat is extensive and

contiguous in all directions, it is unlikely for populations where barriers to dispersal exist or adjacent habitat is of lower quality. Interstate highways appear to provide a moderate barrier to movement of cougars (D. Clark, OCFWRU, unpublished data), as do non-forested habitats (Anderson et al. 2004, Stoner et al. 2008) and potentially major rivers (Wheeler and Waller 2012). Consequently, recovery times of isolated cougar populations and those in areas that are adjacent to potential barriers will be more similar to that of a closed population (4-5 years) because fewer dispersing individuals will re-populate the area. Finally, my model assumed that population growth rates of adjacent populations from where dispersing individuals would arrive would be similar to those I observed. This assumption was likely true for female cougars because they will be dispersing from adjacent areas (Sweanor et al. 2000, Logan and Sweanor 2001) and subjected to similar management practices and thus population growth rates. In contrast, male cougars disperse long distances and are likely dispersing from areas or states where management practices may be different. This potential reduction in the number of male immigrants may cause recovery times to be longer than I predicted.

MANAGEMENT IMPLICATIONS

My simulation results indicated that hunting cougars without the use of dogs is an ineffective method to manipulate cougar population size to meet population management objectives. Restoration of the ability to hunt cougars with dogs would allow managers to more effectively manage cougar populations by manipulating hunter numbers and harvest quotas to affect population growth and meet management objectives. This would also allow more flexible management of prey populations by allowing effective manipulation of cougar populations to benefit ungulates. A system of unlimited numbers of hunters that are unable to utilize dogs to hunt cougars combined with a restrictive tag-allocation program to allow hunting with dogs would provide maximum recreational opportunities and an effective tool for meeting management objectives for both cougars and their prey. My simulation results indicated that model cougar populations are able to sustain 26 – 39% removal annually; consequently, local managers should be able to use a quota based system to prevent excessive harvest of cougars. This requires knowledge of local sources of mortality and quality estimates of population size, which are difficult to estimate, so a

conservative approach is recommended when applying quota based systems to prevent over-exploitation of local cougar populations.

My simulation results indicated cougar populations are highly resilient and substantial efforts are required to reduce a local population particularly when immigration occurs. Local managers should carefully monitor lethal control to ensure efforts are sufficient to meet the objectives of removal and also not excessive where the viability of the local population is threatened. They should also realize that intensive lethal control is likely to result in an increase in the number of sub-adult males in the population due to the male biased dispersal patterns (Sweanor et al. 2000). Where intensive control of cougars is used to benefit ungulate populations, the intensity of control should be reduced and control efforts terminated once population objectives for ungulates have been obtained. Managers should adapt their approaches when implementing lethal control efforts of cougars depending on their objectives. For example, most cougar removal efforts in Oregon have been conducted to benefit declining elk populations that are experiencing low levels of calf recruitment. In northeast Oregon, the majority of calf mortality attributable to cougars occurred between May and October (Rearden 2005, Chapter 2). Elk utilize specific habitats to give birth (Rearden et al. 2011, Barbknecht et al. 2011) and raise their calves during the months immediately following parturition (Kuck et al. 1982, McCoquodale et al. 1986, Unsworth et al. 1998). Consequently, managers should identify calving areas and focus lethal control of cougars in these areas to maximize benefits to elk calf survival and minimize any negative effects on cougar populations. In contrast, cougars in northeast Oregon killed mule deer throughout the year and selected fawns during winter (Chapter 2). Mule deer in most of northeast Oregon are fairly evenly distributed throughout most Wildlife Management Units; consequently, control efforts may need to be conducted across a larger spatial extent to benefit mule deer (but see Hurley et al. 2012).

My simulation results indicated that intensive localized reductions of cougar populations will not negatively affect long-term population viability. Given that female cougars provide the greatest contribution to population growth and disperse relatively short distances (Sweanor et al. 2000), managers may consider increasing the spatial extent of their removal efforts and focus removal efforts towards females to increase the

length of time it takes for a local population to recover from intensive lethal control. This would provide 2 potential benefits: 1) *in situ* reproduction would be reduced, and 2) the absolute number of sub-adult females arriving in the control area would be reduced.

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CHAPTER 5

DYNAMICS OF ELK POPULATIONS IN NORTHEAST OREGON: INFLUENCE OF
COUGAR PREDATION, FEMALE HARVEST, AND NUTRITION MEDIATED BY
CLIMATE

Darren A. Clark

ABSTRACT

Many Rocky Mountain elk (*Cervus canadensis nelsoni*, hereafter elk) populations in northeast Oregon have declined in recent years, and chronically low recruitment of juvenile elk appears correlated with these declines. Recruitment of juvenile elk in northeast Oregon is influenced by several top-down, bottom-up, and climatic factors; however, the relative influence of each of these factors on growth rates of elk populations is unknown. I developed a Leslie matrix model parameterized with vital rates from elk populations in northeast Oregon, to investigate the relative influence of (1) survival and pregnancy rates and (2) top-down, bottom-up, and climatic variables on population growth rates of elk. I then estimated the effect of varying top-down factors on growth rates of elk populations. Population growth rates of modeled elk populations were most sensitive to changes in adult female survival, but empirically-derived variation in juvenile survival rates explained the overwhelming majority of variation in growth rates of the model elk population ($r^2 = 0.92$). Observed variation in survival and pregnancy rates of prime-age females (3-13 years) explained almost none of the variation in growth rates of the model population ($r^2 = 0.02$ and 0.01, respectively). Dynamics of the model population of elk in northeast Oregon were influenced by a suite of factors, but harvest of female elk had the strongest negative effect on model population growth rates of elk ($r^2 = 0.63$). Cougar density was inversely related to population model growth rates of elk ($r^2 = 0.38$), which suggested that top-down forces had a large effect on population dynamics of elk in northeast Oregon. A delay in mean juvenile birth dates reduced juvenile survival, but this had a minimal effect on population growth rates from the model ($r^2 = 0.06$). August precipitation ($r^2 = 0.07$) and winter severity ($r^2 = 0.01$), which were used as surrogates for nutritional condition of females, also had minimal effects on population growth rates from the model. Likewise, elk density had almost no effect on model population growth rates ($r^2 = 0.002$). August precipitation, winter severity, and elk density all were associated with negative effects on pregnancy rates. Given that pregnancy rates had minimal effects on population growth in the model, it was not surprising that these variables had little influence on population growth rates. The proportion of female elk that were lactating in the fall had a strong, positive association with population growth rates from the model ($r^2 = 0.53$). This was surprising because

increased lactation rates should reduce pregnancy rates; however, this relationship described indirectly the effect of juvenile survival through 6 months on population growth rates of elk. The results of my model identified factors limiting population growth rates of elk and provided a framework to evaluate the effects of reducing cougar populations in an adaptive management scenario. Field validation of my model is needed, but ongoing research, my model, and published literature suggest that cougar predation is likely the primary factor limiting recruitment and population growth of elk in northeast Oregon.

INTRODUCTION

Many Rocky Mountain elk (*Cervus canadensis nelsoni*, hereafter elk) populations in western North America have declined in recent years (Gratson and Zager 1999, Schommer and Johnson 2003), including populations in some Wildlife Management Units (WMU) in northeast Oregon (Oregon Department of Fish and Wildlife [ODFW] 2003, 2012). This has been disconcerting because elk provide substantial recreational opportunities, funding resources for state wildlife agencies (Bunnell et al. 2002), and economic benefits to local communities (Bolon 1994, Fried et al. 1995, Brooks et al. 1991). Determining factors that are limiting or regulating elk populations are essential for effective management, but elk population dynamics may be influenced by a suite of interacting top-down, bottom-up, and abiotic factors that can be highly variable in space and time. As a result, identifying variables that limit or regulate elk populations can be difficult.

Bottom-up forces, mediated through nutrition, primarily limit ungulate populations through density-dependent mechanisms (Fowler 1987). Density-dependent processes generally operate via food competition; particularly during winter when resources are most limited (Thorne et al. 1976, Houston 1982, Merrill and Boyce 1991). The effects of over-winter undernutrition are manifest through reduced pregnancy rates and juvenile survival rates because adult survival appears to be relatively insensitive to population density (Coughenour and Singer 1996). Reduced physical condition of female elk was correlated with low pregnancy rates (Trainer 1971, Kohlmann 1999, Cook et al. 2001, 2004, 2013). Survival of juveniles was linked to female body condition (Clutton-Brock et al. 1987, Bartmann et al. 1992, Cameron et al. 1993, Cook et al. 2004) because

nutritionally stressed females give birth to lighter weight juveniles (Thorne et al. 1976, Keech et al. 2000), which have lower survival than heavier juveniles (Whitten et al. 1992, Sams et al. 1996, Singer et al. 1997). Juveniles have lower survival than adults in high-density populations (Sauer and Boyce 1983, Singer et al. 1997) because juveniles are at a competitive disadvantage with adults for limited food resources (Houston 1982, Merrill and Boyce 1991), and due to their smaller body size they are more affected by adverse climatic conditions than adults (Picton 1984, Singer et al. 1997). Sauer and Boyce (1983) suggested that density-dependent juvenile mortality was a mechanism of population regulation in elk.

Predators influence ungulate population dynamics in some species and areas (Gasaway et al. 1992, Boertje et al. 1996, Kunkel and Pletcher 1999) but predation can act in a density-dependent, density-independent, or inversely density-dependent manner (Messier 1994), confounding the net effect of predators on prey populations. The large guild of potential predators on elk [grizzly bears (*Ursus arctos*), black bears (*U. americanus*), gray wolves (*Canis lupus*), coyotes (*C. latrans*), cougars (*Puma concolor*), and bobcats (*Lynx rufus*)] further complicates the potential effect of predators in multiple-predator systems. Predation on elk typically occurs within the juvenile age class (Raedeke et al. 2002, Rearden 2005), and juvenile survival and recruitment was influenced by predator densities (Rearden 2005, Johnson et al. 2013). Juvenile survival has been identified as a primary determinant of recruitment in ungulate populations (White and Garrott 2005, Harris et al. 2008), and recruitment can be an important factor in population growth rates of elk (Gaillard et al. 1998, 2000, Harris et al. 2008). Therefore, predation on juveniles may limit or regulate ungulate populations in some systems (Merrill and Boyce 1991, Coughenour and Singer 1996, White et al. 2010).

Elk populations may be influenced by environmental or density-independent factors, which represent environmental stochasticity that can create substantial variability in population dynamics of ungulates (Raedeke et al. 2002). Detrimental environmental conditions can reduce forage production, increase food competition and negatively affect ungulate populations, especially those at high densities (Sauer and Boyce 1983). In contrast, beneficial climatic conditions may negate density-dependence processes on ungulate populations by providing outstanding forage conditions in some years. Extreme

climatic events (i.e., severe droughts or winter) or long-term environmental trends are density-independent affects, which can influence pregnancy or survival rates of ungulates (Coughenour and Singer 1996, Singer et al. 1997, Garrott et al. 2003). In addition, predators can interact with environmental conditions in complex ways (Merrill and Boyce 1991, Coughenour and Singer 1996), which further complicates the identification of limiting and regulatory processes in ungulate populations.

For long-lived mammals, such as elk, minimal changes in female survival had a greater influence on population growth than large changes in other vital rates (Pfister 1998, Morris and Doak 2002, Raithel et al. 2007); however, survival of female ungulates tends to be relatively high and stable (Brodie et al. 2013), and this lack of process variation causes female survival to contribute little to variation in population growth (Gaillard et al. 1998, 2000, Raithel et al. 2007). Anthropogenic disturbance, particularly hunting, is the primary way large variations in survival of female elk occur (Brodie et al. 2013), and wildlife managers typically manipulate ungulate populations through harvest of adult females because of their large effect on population growth (Morris and Doak 2002). Harvest can be a substantial and largely additive source of mortality source for female elk (Brodie et al. 2013); consequently, excessive harvest of females may be a factor contributing to population declines or preventing recovery of elk populations.

In northeast Oregon, trends in juvenile recruitment typically tracked elk population size, but some populations remained relatively stable despite declining juvenile recruitment (ODFW 2003, 2012, Johnson et al. 2013). Recruitment of juvenile elk was a complicated process influenced by cougar density, lactation status of female elk in fall, elk density, August precipitation, and an interaction between elk density and cougar density (Johnson et al. 2013). Nutrition, manifested through physical condition of females, provides the foundation for pregnancy rates of elk and can also effect juvenile survival (Cook et al. 2001, 2004, Noyes et al. 2002). Variation in cougar densities explained most of the variation in annual juvenile survival (Rearden 2005, B. Johnson, ODFW, unpublished data) and recruitment (Johnson et al. 2013) in northeast Oregon. These findings suggest that both nutrition and predation influenced recruitment of elk in northeast Oregon, but the relative influence of each of these effects on population growth is not well understood.

To better understand the relative influence of predation and nutrition, mediated by climate, on ungulate population growth, I explored these processes in more detail using vital rate information collected from elk populations in northeast Oregon. My objectives were to 1) estimate population growth rates of elk in northeast Oregon in the absence of female harvest, 2) determine the relative effect of survival and pregnancy rates on population growth, 3) determine the relative effect of cougars, climatic variables, elk density, and legal harvest on population growth rates of elk, and 4) quantify the effect of cougar density reductions on elk populations. Results from this study will guide elk management throughout northeast Oregon and provide a framework for assessing the effects of various factors on elk populations in other areas.

METHODS

Study Area

All vital rates used to parameterize my population model were collected within the Blue Mountains of Oregon; consequently, this effort should be most applicable to elk populations throughout the Blue Mountains and other areas with similar habitat, climate, and predator guilds. Mule deer (*Odocoileus hemionus hemionus*), Rocky Mountain elk, and white-tailed deer (*O. viginianus*) were the primary ungulate species that occurred in the Blue Mountains. Small, localized populations of bighorn sheep (*Ovis canadensis canadensis*), mountain goats (*Oreamnos americanus*), and moose (*Alces alces*) were also present. Cougar, black bear, coyote, and bobcat were common large and medium-sized carnivores within the Blue Mountains. At the time and place vital rates were estimated, no wolf packs were present. Vegetation patterns were influenced by topography, aspect, and elevation. South-facing slopes were dominated by herbaceous vegetation, and north-facing slopes were dominated by mixed-conifer forests. As elevation increased, vegetative composition changed in response to more mesic conditions. Common tree species included ponderosa pine (*Pinus posderosa*), Douglas fir (*Psuedotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*) and lodgepole pine (*P. contorta*). Deciduous forests were uncommon in northeast Oregon. Low elevation sites in large valleys were dominated by agriculture, livestock, and human development (Franklin and Dyrness 1973). Elevation ranged from 400 to 3,000 m, and climate was characterized by

cold, moist winters and hot, dry summers. Precipitation declined in a north to south gradient due to the influence of the Columbia River (Heyerdahl et al. 2002).

Data Acquisition and Summary

Reproductive tracts of female elk (n = 8,385) were collected from 1977 to 2004 during hunts that occurred in November or December in northeast Oregon (see Johnson et al. 2013 for additional details). Johnson et al. (2013) estimated mean pregnancy rates and factors that influence pregnancy for elk aged 3 – 13 years (n = 6,897), and I used these estimates in my model. I estimated mean pregnancy rates of female elk aged 1 – 2 (n = 925 and 1055, for 1 and 2 year olds, respectively) and $\geq$ 14 years directly from reproductive tracts of females harvested from 1977 to 2004 (ODFW, unpublished data). There were fewer females $\geq$ 14 years in the sample (n = 533), and estimation of age-specific pregnancy rates for older females was limited by sample size. Consequently I pooled data for females aged 14 – 16 (n = 327), 17 – 19 (n = 160), and 20 – 22 (n = 46) years to estimate mean pregnancy rates. No harvested females $\geq$ 23 years were pregnant, so I assumed elk $\geq$ 23 years old were senescent. Mean pregnancy rates for females aged 3 – 13 years were greater than elk aged 1 – 2 and $\geq$ 14 years (Table 5.1). Maternity (M_x) represented the mean number of juveniles of each gender produced by a mother of age x. I calculated maternity rates by multiplying age-specific pregnancy rates (P_x) by the expected sex ratio at birth (0.5; B. Johnson, ODFW, unpublished data). Elk can produce twins, but this was a rare occurrence (Kittams 1953, Flook 1970, Houston 1982); therefore, I assumed litter size was equal to 1.0.

Estimates of juvenile survival were obtained from fates of 460 radiocollared juveniles monitored from 2002 – 2007 in the Wenaha and Sled Springs WMUs in northeast Oregon. Annual survival of juveniles was constant among years and between genders (Rearden 2005, B. Johnson, ODFW, unpublished data; Table 5.1). I obtained age-specific survival rates of female elk $\geq$ 2 years from a sample of radiocollared elk in northeast Oregon (Appendix G). Survival rates of female elk declined with increasing age (Table 5.1). No females > 25 years old were harvested in Oregon from 1977 - 2004 (ODFW, unpublished data); consequently, I assumed longevity of elk to be 25 years.

I obtained annual survival estimates of male elk from the Blue Mountains of Washington (McCorquodale et al. 2011) because published estimates of survival of male

Table 5.1. Age-specific annual survival and pregnancy rates of elk used to populate a Leslie projection matrix to simulate population growth rates of elk in northeast Oregon, USA.

Age	Male[a]		Female			
	Survival	SD	Survival[b]	SD	Pregnancy[c]	SD
0[d]	0.32	***[e]	0.32	***[e]	NA	NA
1	0.92	0.06	0.92	0.06	0.21	0.16
2	0.91	0.04	0.98	0.01	0.78	0.17
3	0.91	0.04	0.97	0.01	0.90	***[e]
4	0.91	0.04	0.97	0.02	0.90	***[e]
5	0.91	0.04	0.96	0.02	0.90	***[e]
6	0.91	0.04	0.96	0.02	0.90	***[e]
7	0.91	0.04	0.95	0.02	0.91	***[e]
8	0.91	0.04	0.94	0.02	0.91	***[e]
9	0.91	0.04	0.93	0.02	0.91	***[e]
10	0.91	0.04	0.92	0.02	0.91	***[e]
11	0.91	0.04	0.91	0.02	0.92	***[e]
12	0.91	0.04	0.90	0.02	0.92	***[e]
13	0.91	0.04	0.89	0.02	0.92	***[e]
14	0.91	0.04	0.87	0.03	0.65	0.23
15	0.91	0.04	0.85	0.04	0.65	0.23
16	0.91	0.04	0.83	0.05	0.65	0.23
17	0.91	0.04	0.81	0.06	0.41	0.24
18	0.91	0.04	0.78	0.08	0.41	0.24
19	0.91	0.04	0.75	0.10	0.41	0.24
20	0.91	0.04	0.72	0.11	0.07	0.06
21	0.91	0.04	0.69	0.13	0.07	0.06
22	0.91	0.04	0.66	0.15	0.07	0.06
23	0.91	0.04	0.62	0.17	0.00	0.00
24	0.91	0.04	0.57	0.19	0.00	0.00
25	0.00	0.00	0.00	0.00	0.00	0.00

[a] Survival rates of yearling and adult male elk were obtained from McCorquodale et al. (2011) and adjusted to account for harvest. Harvest of male elk was included separately in the population model.
[b] Survival rates of yearling and adult female elk were obtained from Rearden (2005) and Appendix G.

Table 5.1. Continued…

[c] Pregnancy rates for female elk aged 1 - 2 and $\geq$ 14 years were obtained from female elk harvested between 1964 - 2008 (ODFW, unpublished data). Pregnancy rates for female elk aged 3 - 13 were obtained from Johnson et al. (2013) using the following equation: 1.87 - 1.11*LactationStatus + 15.52*CougarIndex - 0.11*ElkDensity$_{(t-1)}$ + 0.02*AugPPT - 0.08*WinterSeverityIndex$_{(t-1)}$. Covariates were held at their mean value except age was allowed to vary.

[d] Monthly survival rates of juvenile elk were estimated for juvenile elk at the Sled Springs and Wenaha Wildlife Management Units in northeast Oregon using the following equation: S = -4.31 + 0.31*Area + 0.90*ln(Age) - 0.02*BirthDate - 0.24*CougarIndex (B. Johnson, ODFW, unpublished data). Covariates were held at their mean value except age was allowed to vary. Annual survival rates were obtained by taking the product of monthly survival rates.

[e] Estimates of standard deviation are not provided because stochasticity was incorporated in the population model by randomly drawing beta coefficients from a normal distribution.

elk in the Blue Mountains of Oregon were not available. Survival of male elk in the Blue Mountains of Washington and Oregon should be similar because habitat, climate, predator guilds, and hunting regulations (i.e., high harvest of yearling males, limited harvest of adult males) were similar. Survival rates reported by McCorquodale et al. (2011) included harvest mortality. To estimate natural survival rates, which were used in my population model, I multiplied the proportion of mortalities attributable to harvest and associated wounding loss (0.86 and 0.47 for yearling and adult males, respectively; McCorqoudale et al. 2011) by the mortality rate (0.59 and 0.16 for yearling and adult males, respectively) to calculate the mortality rate attributable to harvest. This value was added to the reported survival rate to obtain an estimate of natural survival, and this conversion assumed harvested individuals would have survived the year. Natural survival for yearling males was 0.92 (SD = 0.06) and for males ≥ 2 years was 0.91 (SD = 0.04). I did not have reliable survival estimates for yearling females in northeast Oregon; consequently, I assumed yearling females would have a natural survival rate similar to yearling males (0.92).

Deterministic Population Growth and Elasticity Analysis

I used mean vital rates of female elk in northeast Oregon (Table 5.1) to create an age based, post-breeding, birth pulse, Leslie matrix that consisted of 26 classifications of female elk (0 – 25 years of age). I created all matrices and conducted all analyses in MATLAB (version 8.0.0.783, MathWorks, Natick, MA, USA). I used the eigenall.m function (Morris and Doak 2002; p. 223) to calculate deterministic population growth (λ_D) and the stable age distribution. Lambda was calculated from the dominant eigenvalue, and the stable age distribution was calculated from the dominant right eigenvector of the Leslie matrix.

I used the MATLAB code Limitsens.m (Morris and Doak 2002; p. 346 – 348) to conduct a life stage simulation analysis to determine the relative effect of vital rates on population growth of elk. For each vital rate in the model, I specified the mean, minimum, and maximum plausible values (Table 5.2). I calculated deterministic elasticities for each vital rate using the mean vital rates and estimated mean elasticity values within 1,000 replicate matrices generated by independently selecting vital rates from a uniform probability distribution (Morris and Doak 2002). Mean elasticity values

Table 5.2. Mean, minimum, and maximum vital rates of female elk used to parameterize a Leslie matrix model to conduct a life stage simulation analysis and calculate the effect of variation in vital rates on sensitivity and elasticity of vital rates on population growth rates.

	Pregnancy			Survival		
Age	Mean	Minimum	Maximum	Mean	Minimum	Maximum
0	---	---	---	0.31	0.10	0.60
1	0.21	0.00	0.40	0.92	0.75	0.95
2	0.78	0.50	0.90	0.98	0.95	0.99
3	0.88	0.80	0.99	0.97	0.95	0.99
4	0.88	0.80	0.99	0.97	0.95	0.99
5	0.88	0.80	0.99	0.96	0.95	0.99
6	0.88	0.80	0.99	0.96	0.95	0.99
7	0.89	0.80	0.99	0.95	0.95	0.99
8	0.89	0.80	0.99	0.94	0.95	0.98
9	0.89	0.80	0.99	0.93	0.95	0.98
10	0.90	0.80	0.99	0.92	0.95	0.97
11	0.90	0.80	0.99	0.91	0.95	0.96
12	0.90	0.80	0.99	0.90	0.95	0.95
13	0.90	0.80	0.99	0.89	0.83	0.94
14	0.65	0.40	0.80	0.87	0.80	0.93
15	0.65	0.40	0.80	0.85	0.80	0.92
16	0.65	0.40	0.80	0.83	0.75	0.90
17	0.41	0.20	0.55	0.81	0.70	0.85
18	0.41	0.20	0.55	0.78	0.70	0.85
19	0.41	0.20	0.55	0.75	0.65	0.80
20	0.07	0.01	0.10	0.72	0.63	0.78
21	0.07	0.01	0.10	0.69	0.55	0.75
22	0.07	0.01	0.10	0.66	0.50	0.73
23	0.00	0.00	0.00	0.62	0.45	0.70
24	0.00	0.00	0.00	0.59	0.40	0.65

and associated confidence intervals were estimated by randomly varying a single vital rate across its range of potential values while holding other vital rates at their mean over 1,000 replicate matrices. I regressed λ on each vital rate and calculated the correlation coefficient (r) and the coefficient of determination (r^2) to estimate proportion of total variance in λ attributable to variance in each vital rate. I summed elasticity values for survival and pregnancy rates of prime-aged (3 – 13 years) and senescent ($\geq$ 14 years) females to reduce total number of vital rates from 51 to 9 and simplify interpretation of results. I also calculated the maximum possible λ value and largest proportional change in λ when individual vital rates were set to their maximum value.

Stochastic Population Growth

I created an age based, post-breeding, birth pulse, Leslie matrix to estimate stochastic population growth rates of elk in northeast Oregon. The resulting matrix consisted of 52 classifications of elk (26 classifications of males and females from 0 – 25 years of age). Male elk are disproportionally harvested, and number of elk available for harvest is a critical concern for wildlife managers. Survival of elk differed by gender (Table 5.1), which necessitated the use of a dual sex Leslie matrix (Caswell 2001; p. 571). When implementing my model, I assumed that 1) vital rates among sexes and age classes were uncorrelated within and among years, 2) no catastrophes or bonanzas (i.e., exceptionally bad or good years) occurred, 3) the population was geographically closed, 4) there was no spatial structure in the population, 5) density-dependence would operate via a negative effect on pregnancy rates (see description of vital rates below), and 6) female elk were not harvested until management objectives were reached. To project the population over time, my model took the form of $n(t) = L \times n(t-1)$, where n is the vector of population size, t is time in years, and L is a Leslie matrix[2]. I assumed the starting population size of a hypothetical elk population in northeast Oregon immediately following parturition was 2,000 individuals and the management objective was 5,000 individuals. I determined the initial population vector [$n(0)$] by proportionally distributing the starting elk population ($n = 2,000$) according to a stable age distribution.

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[2] Bold notations using capital letters reference matrices while bold notations with lower case letters reference vectors.

Environmental stochasticity was incorporated into the model by randomly generating vital rates from a normal distribution with predefined means and standard deviations at each time step. Pregnancy rates of female elk aged $1 - 2$ and ≥ 14 years were randomly generated using predefined values (Table 5.1). For female elk aged $3 -$ 13 years, I estimated age-specific pregnancy rates (P_x) at each time step using the following equation from Johnson et al. (2013):

$$P_x = -1.87 - 1.11 \times Lact + 15.52 \times Cougar - 0.11 \times ElkDen_{(t-1)} + 0.03 \times Age + 0.02 \times AugPPT$$
$$- 0.08 \times WSI_{(t-1)}$$

where Lact was lactation status (i.e., proportion of females with a calf at heel in the fall), Cougar was an index of minimum sub-adult and adult cougar density (cougars/km^2), ElkDen$_{(t-1)}$ was previous year elk density (elk/km^2), Age was female age in years, AugPPT was August precipitation (mm), and WSI$_{(t-1)}$ was an index of previous year winter severity (WSI = standardized winter precipitation − standardized temperature; Johnson et al. 2013). August precipitation and previous year winter severity index represented a positive effect on nutritional status from fall green up and a negative carry over effect of severe winters on nutrition, respectively (Johnson et al. 2013). For each year of the simulation, lactation status was directly estimated by dividing the number of juveniles born to females aged 3-13 that survived 6 months by the number of females aged $3 - 13$. Previous year elk density was updated at each time step by calculating size of the simulated population in year $t - 1$. Values for cougar density, August precipitation, and WSI$_{(t-1)}$ were randomly drawn at each time step from a normal distribution to simulate environmental variability (Table 5.3), and I assumed covariate values were uncorrelated among years. Pregnancy rates were constrained between $0.0 - 1.0$ because values outside this range were biologically impossible.

Age-specific survival rates of female and male elk ≥ 1 year were randomly drawn from a normal distribution at each time step (Table 5.1) because I had no evidence to suggest that survival rates of adult elk were influenced by any covariates that I investigated (Appendix G). Annual estimates of juvenile survival, which were used in the Leslie matrix, were calculated as the product of monthly survival estimates from birth to 12 months. Monthly survival rates of juvenile elk of age x (mo) were generated using the following equation (B. Johnson, ODFW, unpublished data):

$$S_{jx} = -4.31 + 0.32 \times \text{Area} + 0.90 \times \ln(x) - 0.02 \times \text{BirthDate} - 0.24 \times \text{Cougar}$$

where Area was an indicator variable for study area [Sled Springs (1) or Wenaha (0)], $\ln(x)$ was the natural log of age in months, BirthDate was the birth date of juvenile elk (Julian date), and Cougar was an index of minimum sub-adult and adult cougar density (cougars/100 km^2). For all simulations, Area was equal to 0.5, which represented the median survival between Sled Springs and Wenaha WMUs (B. Johnson, ODFW, unpublished data). Values for BirthDate and Cougar were randomly drawn from a normal distribution at each time step (Table 5.4), and I assumed covariate values were uncorrelated among years. Survival rates were constrained between 0.0 – 1.0 because this was the range of biologically plausible values.

Incorporating harvest.—Mean survival rates of male elk used to parameterize the Leslie matrix represented natural survival (i.e., no hunting mortality). Use of natural survival rates for male elk was unrealistic because they are legally hunted annually throughout northeast Oregon. Based on harvest and population reconstruction data, yearling (i.e., spikes) and adult males in northeast Oregon had annual survival rates of 0.40 and 0.81 (ODFW, unpublished data), respectively. To account for harvest, I determined number of tags that should be issued annually by calculating number of males expected to survive if no harvest occurred. This was done by multiplying number of males at the start of the biological year (i.e., June) by the expected survival rate that included harvest (0.40 and 0.81 for yearling and adult males, respectively). This value was subtracted from the number of males in the population at the start of the year to determine the number of males expected to die from all causes. I multiplied expected number of elk that would die annually by the percentage of mortality attributable to harvest (0.86 and 0.47 for yearling and adult males, respectively; McCorqoudale et al. 2011) to determine number of yearling and adult males expected to be removed by humans each year. I divided this value by mean harvest success rate to determine number of tags issued annually.

Once I determined number of tags issued, I randomly generated a natural survival rate (Table 5.1) and a harvest success rate (0.13 ± 0.05 and 0.56 ± 0.12; yearling and adult males, respectively) from normal distributions. Harvest success rate was multiplied by number of tags issued to calculate number of elk harvested. I assumed harvest would be proportionally distributed among adult male elk according to age (i.e., no selective

Table 5.3. Estimated coefficients, mean covariate values, and standard deviation of covariate values used to simulate pregnancy rates of female elk aged 3 - 13 years in northeast Oregon, USA.

Variable	Coefficient	Mean covariate value	SD mean value
Intercept	1.866	NA	NA
Lactation Status (proportion of females lactating)	-1.108	0.45[a]	***[b]
Cougar Index (cougars/km^2)	15.522	0.287	0.007
Elk density$_{(t - 1)}$ (elk/km^2)	-0.112	2.000[a]	***[b]
Age (yrs)	0.029	Actual age[c]	***[c]
August Precipitation (mm)	0.022	21.615	21.475
Winter Severity Index$_{(t - 1)}$	0.079	-0.100	1.339

[a] Values were used during the first year of the simulation. In subsequent years, these values were directly calculated using results from the current year (lactation status) and previous year (elk density) of the simulation.
[b] No estimates of standard deviation provided because the data were directly derived from simulation results and were not randomly generated at each time step.
[c] Age specific estimates of female elk aged 3 - 13 years were estimated separately. There was no standard deviation associated with age.

Table 5.4. Estimated coefficients, mean covariate values, and standard deviation of covariate values used to simulate survival of juvenile elk in northeast Oregon, USA.

Variable	Coefficient	Mean covariate value	SD mean value
Intercept	4.314	NA	NA
Study area	0.310	0.500[a]	***[a]
lnAge (mo)[b]	0.901	Actual age[c]	***[c]
Birth date (Julian date)[d]	-0.019	146.738	3.750
Cougar Index (cougars/100 km^2)	-0.243	2.871	0.693
Capture Age (days)[e]	0.076	0.000	0.000

[a] Maintained at a constant value of 0.5 for all simulations to represent the mean study area effect on juvenile survival.

[b] The product of monthly survival rate estimates was used to calculate annual survival estimates. Annual survival estimates were constrained to occur between 0 and 1.

[c] Monthly, age-specific, survival estimates were calculated separately. There was no standard deviation associated with age.

[d] Birth date was constrained to occur between 138 and 160. While juvenile elk were born before and after these dates, this variable represents the mean birth date and these are a reasonable range of values.

[e] Capture age was a nuisance parameter used to account for the fact all juvenile elk were not monitored from birth. I was interested in annual survival from birth, so this variable was set to 0 in all simulations.

harvest). The following equation was used to adjust age-specific survival rates to account for harvest:

$$S_{xmharv} = ((N_{xm} - N_{xharv}) / N_{xm}) \times S_{xm},$$

where N_{xm} was number of males in age class x, N_{xharv} was the number of males of age x harvested, S_{xm} was a randomly generated survival rate of male elk of age x prior to accounting for harvest, and S_{xmharv} was survival rate of male elk of age x after accounting for harvest.

Given that most elk populations in northeast Oregon are currently below management objectives set by ODFW (ODFW 2012), I assumed harvest of female elk would not occur until populations had met or surpassed management objectives. Once the population reached the specified management objective (5,000 individuals), I determined number of tags issued for females by calculating number of females in excess of the management objective and divided this value by the expected success rate of female harvest (34.6%). After number of tags was determined, I used the approach outlined above for male elk to adjust survival rates of females.

Effect of Covariates on Population Growth Rates.—To estimate effect of each covariate in the population model that influenced either pregnancy (e.g., lactation status, winter severity) or survival rates (e.g., cougar density, juvenile birth date), I conducted 5,000 simulations of population growth over 10 years and recorded λ and the associated value of the covariate at each time step. After conclusion of the simulations, I obtained 50,000 randomly generated covariate values and associated λ values. To determine the relative effect of each covariate on population growth, I regressed λ on the simulated covariate value. The estimated effect and relative influence of the variable on λ was represented by the regression equation, correlation coefficient, and coefficient of determination (r^2).

Cougar Predation and Female Elk Harvest

To determine effect of increasing harvest of females on population growth rates, I conducted 5,000 stochastic simulations of population growth over 10 years. At each time step, covariates used to determine survival and pregnancy rates were randomly generated. Furthermore, I randomly generated number of tags issued for females from a normal distribution at each time step. At the conclusion of the simulations, I regressed λ on the proportion of females harvested to determine relative influence of harvest on population

growth rates. I also determined combinations of proportion of females harvested and cougar densities that resulted in a stable elk population ($0.995 \leq \lambda < 1.005$). To determine the combined effect of increasing cougar densities and harvest of females, I conducted a simulation where I allowed cougar density and female harvest to systematically vary while holding other covariates at their mean. For each value of the cougar density index from 1.0 - 6.0 cougars/100 km^2, at intervals of 0.01, I allowed the number of female tags issued to vary between 0 and 500 (which represented 0.00 to 0.18 of the total female elk population to be harvested in a single year) at intervals of 10 tags. For each combination of cougar density and female harvest, I calculated λ to determine combinations of harvest and cougar density that resulted in a declining ($\lambda < 0.995$), stable ($0.995 \leq \lambda < 1.005$), or increasing ($\lambda \geq 1.005$) elk population.

Cougar Removal and Population Growth of Elk

The Oregon Fish and Wildlife Commission authorized ODFW to implement lethal control of cougars to benefit elk populations within individual WMUs (ODFW 2006). At the time of this authorization potential benefits of control efforts on elk populations was not well understood; consequently, estimation of population growth before, during, and after cougar control is critical to understanding the potential benefit of cougar removals on elk populations. In Chapter 4, I simulated the response of cougar populations to control efforts. Here, I use this information to model the effect of cougar removal on population dynamics of elk.

I conducted 2 separate simulations to estimate effect of cougar removal on elk population growth. For both simulations, I used the stochastic population model described above. In the first simulation, mean cougar density was set to 2.87 cougars/100 km^2, which was the mean density observed at the Sled Springs and Wenaha WMUs from 2002 - 2007. For the second simulation, I set the mean cougar density to 4.00 cougars/100 km^2, which was at the upper range of density estimates observed at the Wenaha and Sled Springs WMUs. For each simulation, I conducted 4 separate sets of analyses, where there was no cougar removal conducted (i.e., control), cougar removal was conducted and the cougar population recovered assuming a closed population, or removal occurred with either minimum or maximum immigration rates (i.e., treatments; see Chapter 4). For each set of simulations, I conducted 5,000 projections of population

growth over 10 years. During all years, mean covariate values and vital rates, except cougar density, were randomly generated to incorporate environmental stochasticity. During the first year of the simulation, cougar densities were randomly generated from a normal distribution. During the years of cougar density reduction (years 2 – 4) and subsequent recovery (variable according to immigration rates of cougars, see Chapter 4), cougar density was not allowed to vary, but set to a static density (Table 5.5). Following recovery of the cougar population, cougar density was allowed to stochastically vary at each time step according to a predefined mean and standard deviation. After simulations were completed, I calculated the mean λ and population size at each time step to compare the effect of cougar removal efforts on elk populations.

RESULTS

Population Growth and Sensitivity

In the absence of female harvest the deterministic population growth rate of a model elk population in northeast Oregon was 1.03, and mean annual stochastic population growth rate was 1.04 with a range of 0.92 – 1.18 (Fig. 5.1a). Assuming a starting population of 2,000 individuals and no harvest of female elk, mean population size after 10 years was 2,900 and ranged from approximately 2,180 to 3,780 individuals (Fig. 5.1b). The mean juvenile to adult female ratio at the end of each biological year was 0.23 (range = 0.07 – 0.44; Fig. 5.2a) while mean adult male to female ratio was 0.22 (range = 0.08 – 0.37; Fig. 5.2b).

Survival of prime-age females (3 – 13 yrs) had the highest elasticity (0.61) among vital rates in the transition matrix of mean vital rates, followed by survival of juveniles (0.12), yearlings (0.12), 2-yr olds (0.12), and prime-age female pregnancy (0.10); all the remaining vital rates had elasticities ≤ 0.03 (Fig 5.3a). Mean elasticities of 1,000 matrix replicates ranked vital rates in the same order; however, mean simulated point estimates for juvenile, yearling, and 2-year old survival and prime-aged fecundity were slightly lower than deterministic estimates (Fig. 5.3a). Variation in juvenile survival explained the majority of variation in modeled λ estimates ($r^2 = 0.92$; Fig. 5.3b). Variation in pregnancy ($r^2 = 0.01$) and survival ($r^2 = 0.04$) of prime-age females explained little variation in model population growth, and other vital rates explained almost no variation

Table 5.5. Estimates of cougar densities before, during, and after removal efforts used to simulate effect of hypothetical reductions in cougar populations to benefit elk populations in northeast Oregon, USA.

Scenario	Year	No cougar removal	Cougar immigration rate following removal		
			None	Low	High
Low density cougar population	1	2.87 ± 0.69[a]	2.87 ± 0.69	2.87 ± 0.69	2.87 ± 0.69
	2	2.87 ± 0.69	2.22	2.04	1.94
	3	2.87 ± 0.69	1.76	1.64	1.54
	4	2.87 ± 0.69	1.44	1.44	1.44
	6	2.87 ± 0.69	1.70	2.08	2.59
	7	2.87 ± 0.69	1.98	2.75	2.87 ± 0.69
	8	2.87 ± 0.69	2.31	2.87 ± 0.69	2.87 ± 0.69
	9	2.87 ± 0.69	2.72	2.87 ± 0.69	2.87 ± 0.69
	10	2.87 ± 0.69	2.87 ± 0.69	2.87 ± 0.69	2.87 ± 0.69
High density cougar population	1	4.00 ± 0.69[b]	4.00 ± 0.69	4.00 ± 0.69	4.00 ± 0.69
	2	4.00 ± 0.69	2.86	2.63	2.51
	3	4.00 ± 0.69	2.27	2.11	1.99
	4	4.00 ± 0.69	1.85	1.85	1.85
	6	4.00 ± 0.69	2.19	2.69	3.34
	7	4.00 ± 0.69	2.55	3.54	4.00 ± 0.69
	8	4.00 ± 0.69	2.98	4.00 ± 0.69	4.00 ± 0.69
	9	4.00 ± 0.69	3.50	4.00 ± 0.69	4.00 ± 0.69
	10	4.00 ± 0.69	4.00 ± 0.69	4.00 ± 0.69	4.00 ± 0.69

[a] Cougar densities during these years were randomly generated from a normal distribution with a mean of 2.87 and a standard deviation of 0.69

[b] Cougar densities during these years were randomly generated from a normal distribution with a mean of 4.00 and a standard deviation of 0.69
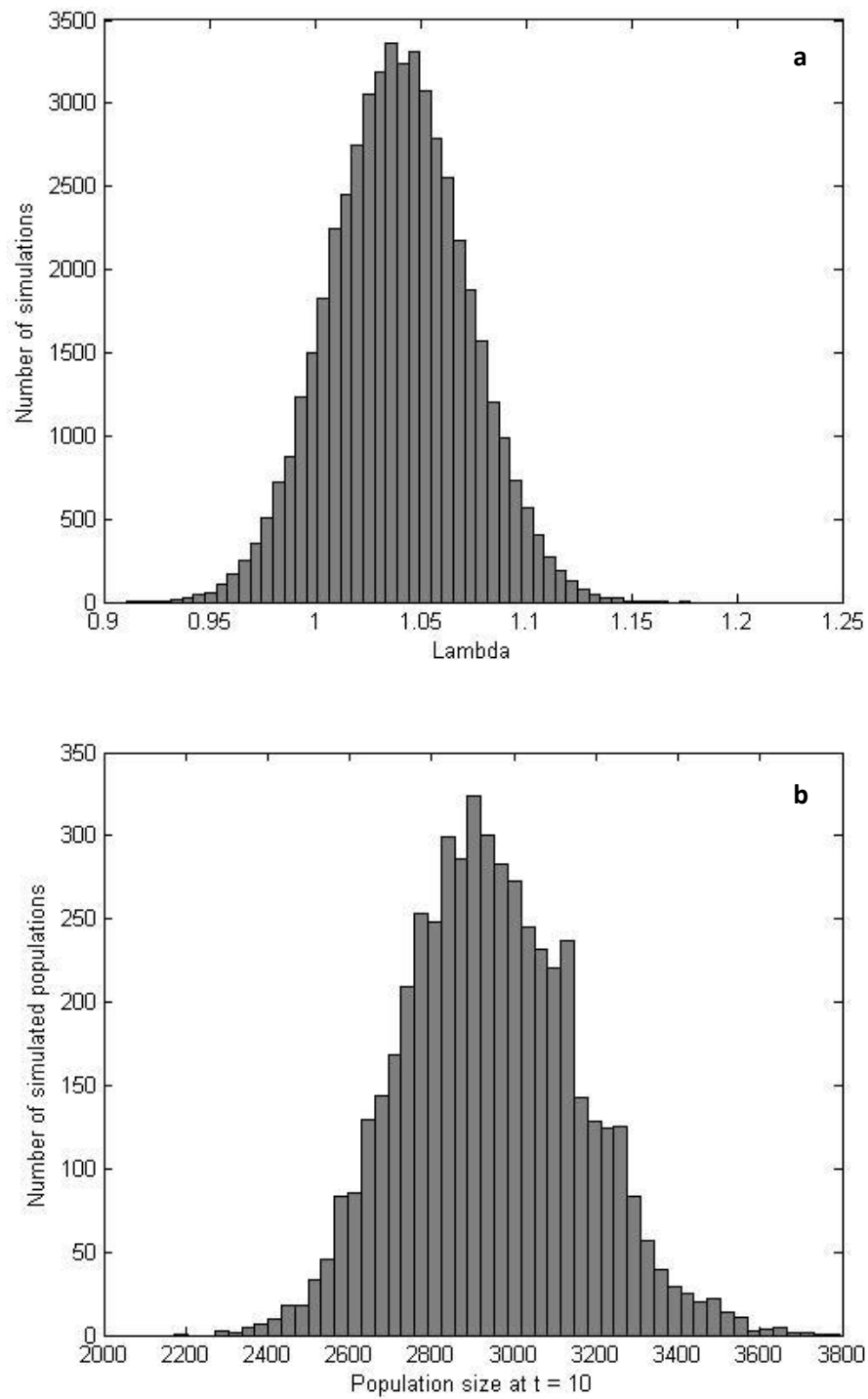
Figure 5.1. Distribution of (a) year-specific population growth rates and (b) population size after 10 years for 5,000 simulated elk populations using vital rate information estimated in the Blue Mountains of Oregon, USA.
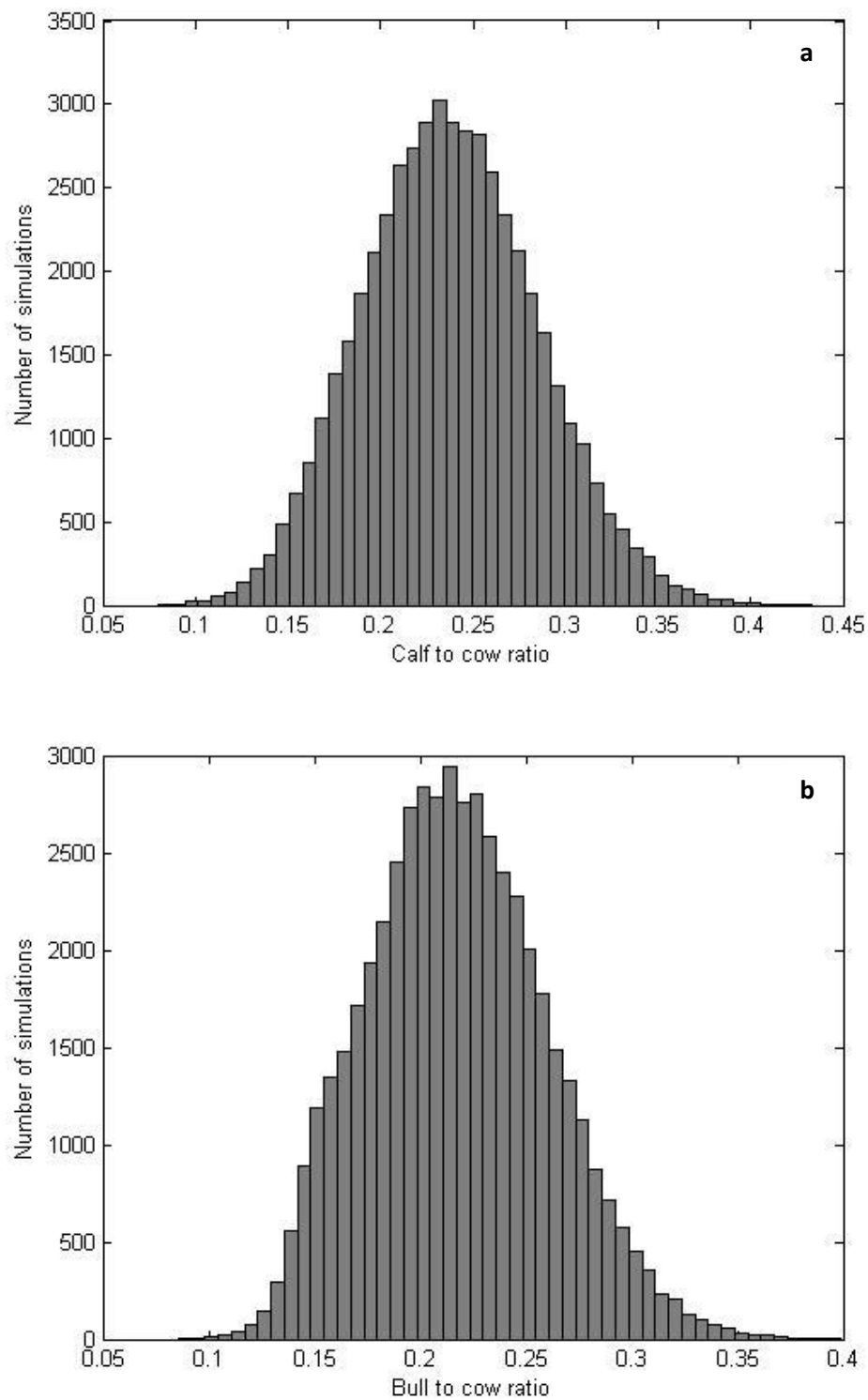
Figure 5.2. Distribution of (a) juvenile to adult female ratios and (b) bull to cow ratios from 5,000 simulated elk populations over 10 years using vital rate information estimated in the Blue Mountains of Oregon, USA.
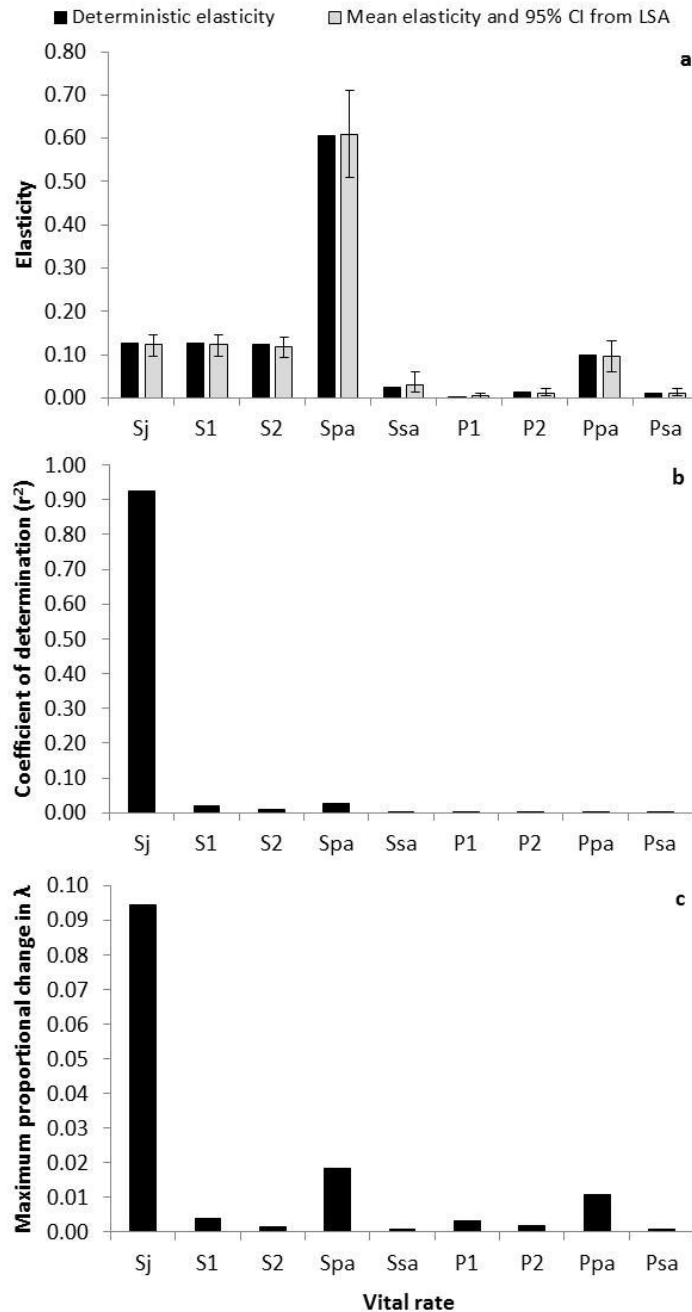
Figure 5.3. Elasticities of vital rates of elk calculated from a Leslie matrix model using mean vital rates in a deterministic matrix and mean elasticities and their 95% confidence intervals from 1,000 matrix replicates in an life-state simulation analysis (LSA; a). The (b) variation in population growth rate explained by variation in each vital rate (r^2), and (c) the maximum proportional change in population growth rates for each vital rate in LSA. Vital rate notations are: juvenile survival (Sj), yearling survival (S1), 2-yr old survival (S2), prime-age (3-13 yrs) female survival (Spa), senescent female survival (Ssa), yearling pregnancy (P1), 2-yr old pregnancy (P2), prime-age pregnancy (Ppa), and senescent fecundity (Psa).

(Fig 5.3b). The maximum λ value obtained when setting juvenile survival at the maximum value (0.60) was 1.13, which increased λ by 9.5 compared to the mean value (Fig. 5.3c). In contrast, the maximum λ obtained when prime-age female survival was set to the maximum value was 1.06 compared to the mean estimate of 1.04. Setting any of the remaining parameters to their maximum resulted in insignificant changes in λ (< 0.01).

Effect of Covariates on Population Growth of Elk

My simulation results indicated the index of minimum cougar density had a relatively strong, negative ($r = -0.62$) effect on population growth rates of elk ($r^2 = 0.38$; Fig. 5.4a) through negative effects on juvenile survival. As mean birth date of juvenile elk increased, model population growth rates declined ($r = -0.24$; Fig. 5.4b), but this had a minimal effect on population growth ($r^2 = 0.06$). Model estimates of λ was positively influenced by August precipitation ($r = 0.26$; Fig. 5.4c) and negatively influenced by $WSI_{(t-1)}$ ($r = -0.10$; Fig. 5.4d); however, both August precipitation ($r^2 = 0.07$) and $WSI_{(t-1)}$ ($r^2 = 0.01$) explained little variation in population growth rates of elk. Previous year elk density was negatively correlated with model population growth rates ($r = -0.04$) but explained almost none of the variation ($r^2 = 0.002$; Fig 5.4e). Model population growth rates were strongly and positively associated ($r = 0.73$) with lactation status ($r^2 = 0.53$; Fig. 5.4f), which was counterintuitive because increasing lactation status had a negative effect on pregnancy rates. However, lactation status was a surrogate of juvenile survival through 6 months, and lactation status described indirectly the effect of juvenile survival through 6 months on population growth. Female harvest had a strong ($r = -0.79$) negative effect on model population growth of elk ($r^2 = 0.63$; Fig. 5.5a). To maintain an elk population (i.e., $0.995 \geq \lambda < 1.005$), the proportion of females that can be harvested decreased as cougar density increased ($r^2 = 0.63$; Fig. 5.5b). High rates of female harvest coupled with high density cougar populations resulted in model population growth rates substantially < 1.0 (Fig. 5.5c), and at cougar densities $\geq 4.2/100$ km^2, cougars caused model elk populations to decline even in the absence of female harvest (Fig. 5.5c).
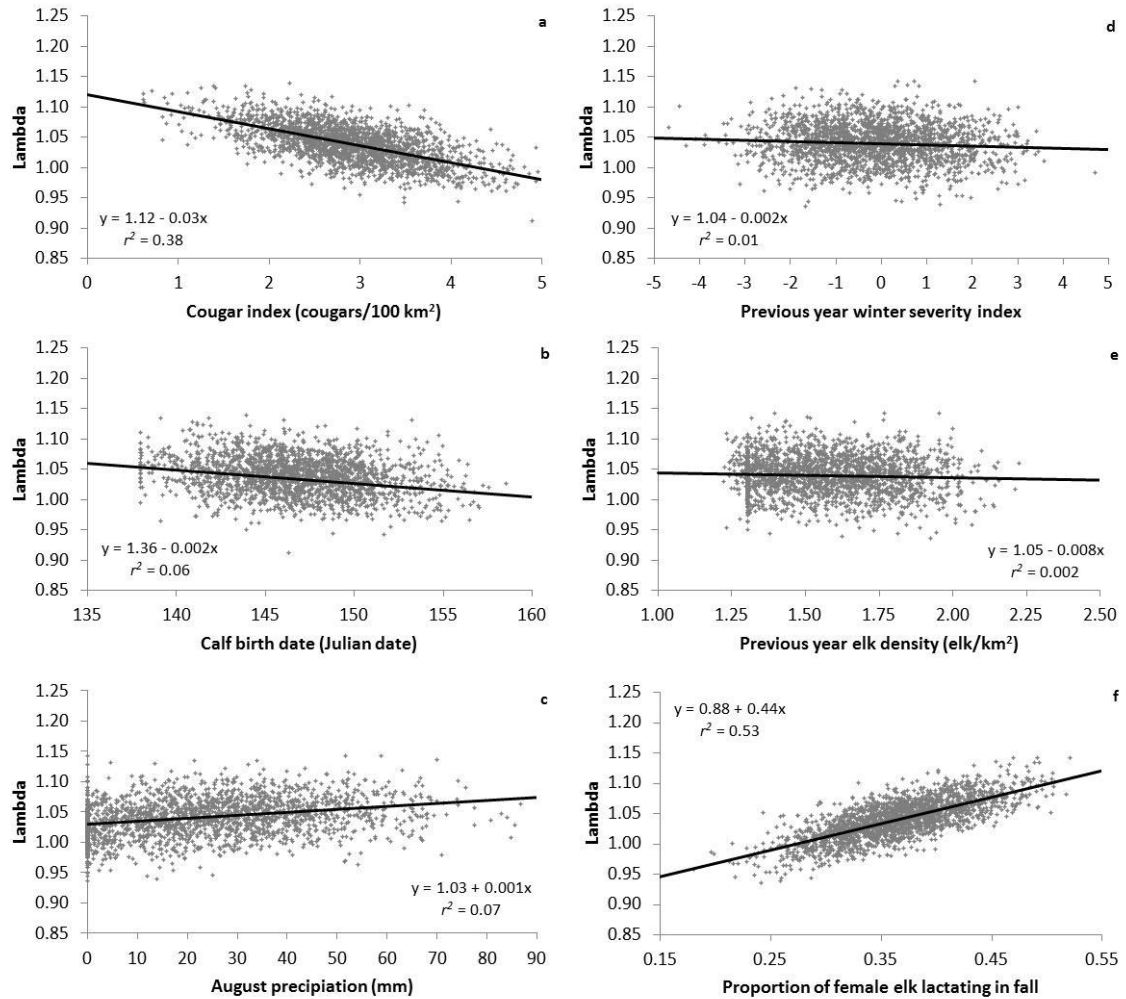
Figure 5.4. The estimated effect of (a) increasing cougar densities, (b) calf birth date, (c) August precipitation (mm), (d) previous year winter severity index, (e) previous year elk density, and (f) proportion of female elk lactating during fall on population growth rates of elk in northeast Oregon. Regression equations and the amount of variability explained by each variable were estimated from 5,000 estimates of population growth rates over 10 years using vital rates of elk estimated in the Blue Mountains of Oregon, USA. Values from 2,000 out of 50,000 simulations are shown on figures.
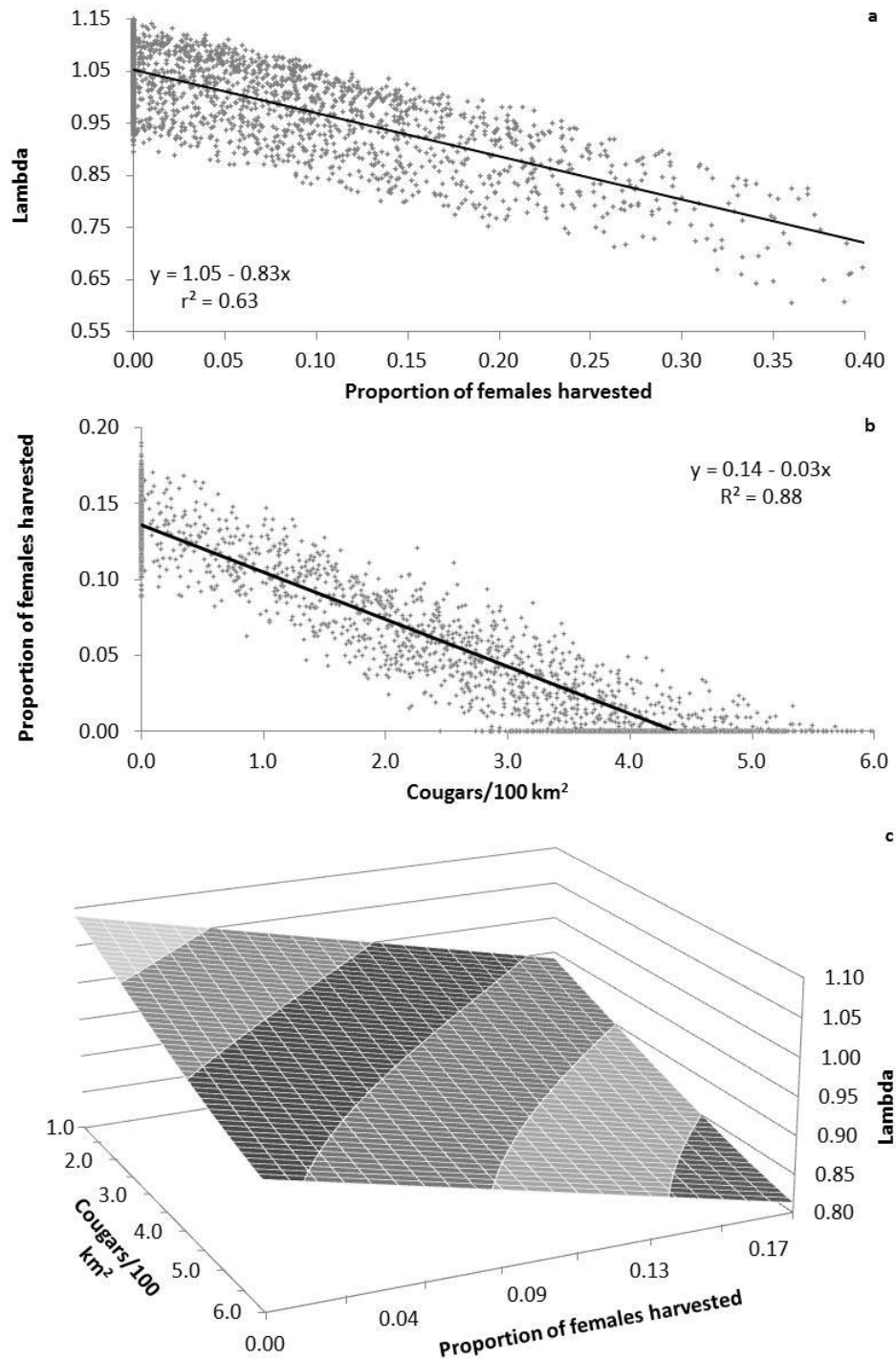
Figure 5.5. The estimated effect of (a) increased adult female harvest on population growth rates of elk, (b) combinations of female harvest and cougar density that resulted in a stationary ($0.995 \leq \lambda < 1.005$) elk population, and (c) the estimated mean effect of cougar density and female harvest on population growth rates of elk. Results were generated from 5,000 stochastic simulations over 10 years using vital rates of elk estimated in the Blue Mountains of Oregon, USA.

Effect of Cougar Removal on Elk Population Growth

Prior to reductions in cougar densities, model elk populations increased at a rate of approximately 3% and 0% annually with mean cougar densities of 2.87 and 4.00 cougars/100 km^2, respectively. Reductions in cougar densities had a positive effect on model population growth rates of elk during the years of cougar removal and subsequent recovery (Fig. 5.6a and 5.6c); however, this effect on growth rate was transient and lasted a few years after removal. The relative benefit of cougar reductions were greater for model elk populations where mean cougar densities were 4.00 cougars/100 km^2 (0.073 increase in lambda during year 4) than where cougar densities were 2.87 cougars/100 km^2 (0.035 increase in lambda during year 4). Cougar removal resulted in substantially more elk in the model population after 10 years compared to when cougars were not lethally controlled (Fig. 5.6b and 5.6d). At a mean density of 2.87 cougars/100 km^2 before and after removal efforts, between 320 (high immigration of cougars following removals) to 475 (no immigration of cougars following removals) more elk were present in the model population by year 10 compared to model populations where cougar removal did not occur. Assuming a mean density of 4.00 cougars/100 km^2 before and after removal efforts, between 480 (high immigration of cougars following removals) to 720 (no immigration of cougars following removals) more elk were present in the model population by year 10 compared to model populations where cougar removal did not occur. Furthermore, at densities of 4.00 cougars/100 km^2, model elk populations declined after 10 years if reductions in cougar density did not occur. Reductions in densities of cougars allowed increased juvenile survival and recruitment in my model, which resulted in more prime-age females in the population than in populations where lethal control of cougars did not occur. This provided a lasting benefit to elk population growth rates (i.e., years 8 – 10; Fig 5.6a and 5.6c) in my model, because prime-age females have higher pregnancy and fecundity rates than older females, which allowed higher maternity rates for the entire population, and more juveniles born annually.

DISCUSSION

My modeling efforts indicated elk population growth was most sensitive to adult female survival; however, this vital rate is relatively constant over time and explains little variation in population growth rates. In contrast, juvenile survival, which is highly
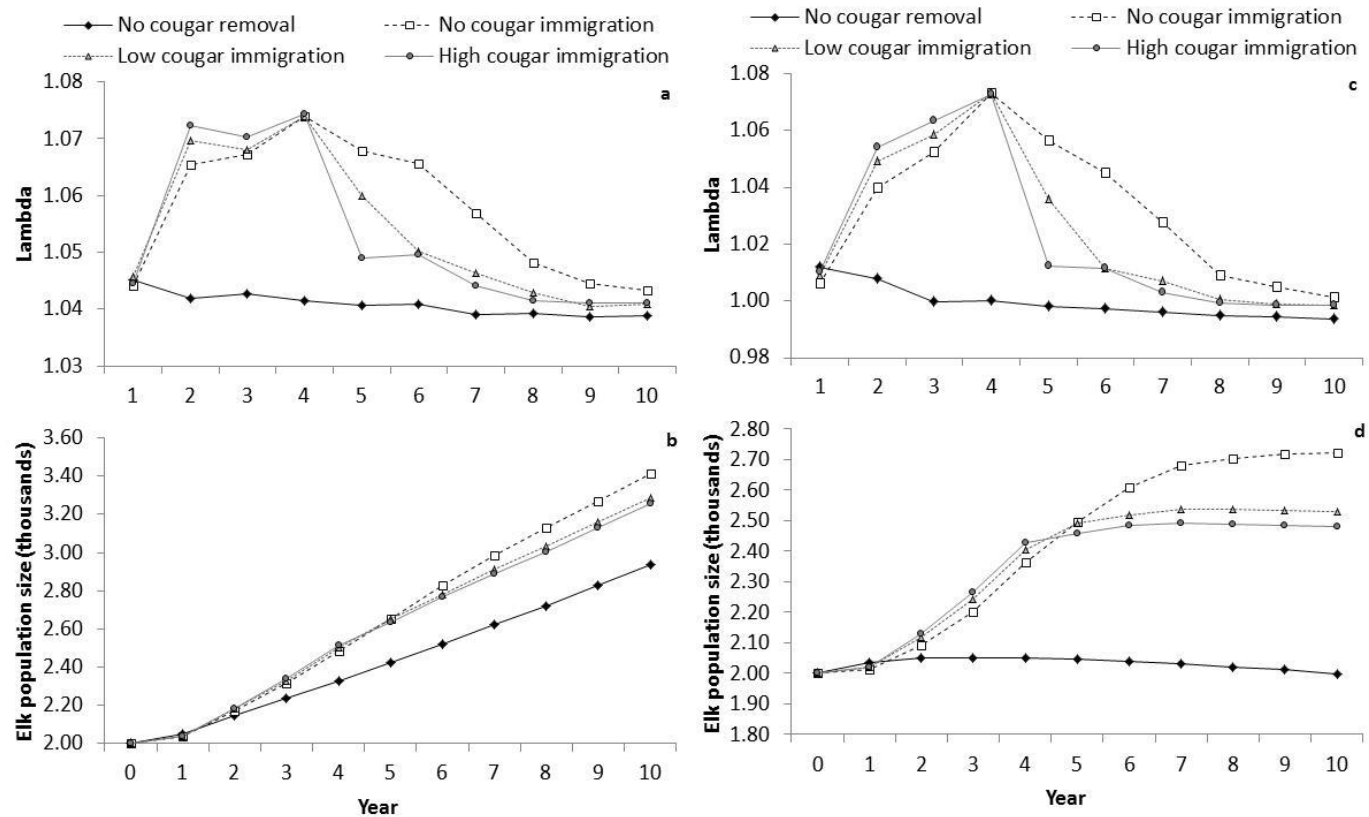
Figure 5.6. The estimated effect of a hypothetical removal of cougars on (a) population growth rates of elk and (b) population size of elk assuming a mean cougar density of 2.87 cougars/100 km^2, and the estimated effect of a hypothetical removal of cougars on (c) population growth rates of elk and (d) population size of elk assuming a mean cougar density of 4.00 cougars/100 km^2. Removal of cougars began in year 2 and concluded in year 4 when cougar densities had been reduced by 50%. Mean cougar densities were randomly generated from a normal distribution at each time step, except for simulations where cougar densities were reduced and densities were determined according to results from Chapter 4. For each cougar removal scenario, 5,000 stochastic simulations of population growth were conducted over 10 years using vital rates of elk estimated in the Blue Mountains of Oregon, USA. Results represent the mean population growth rate and population size at each time step across simulations.

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variable over time, explained the overwhelming majority of variation in model population growth. Pregnancy rates of elk tend to be relatively invariable and have low sensitivity values. Consequently, they explained almost none of the variation in population growth rates of elk in my simulation analyses. Harvest induces variation in survival rates of adult female elk, a vital rate with high sensitivity. My model indicated minimal harvest (5% of females harvested annually) can result in negative population growth rates of elk. Harvest had the greatest effect on population growth rates of elk in my model. Variation in juvenile survival was primarily influenced by an index of cougar density (Rearden 2005, B. Johnson, ODFW, unpublished data). Juvenile survival explained the majority of variation in population growth of elk in my model; consequently, increasing cougar densities had a negative effect on population growth of elk. In the absence of female harvest, cougar density was the primary determinant of population growth of elk in my model. The large effect of cougars on juvenile survival and subsequent population growth of elk was also demonstrated by effect of lactation status on population growth. Lactation status was a surrogate of juvenile survival through 6 months (Johnson et al. 2013) and cougar densities were strongly correlated with juvenile survival through 6 months (Rearden 2005, B. Johnson, ODFW, unpublished data). Nutritional effects were indirectly incorporated in my model through effects of climatic variables on pregnancy rates (Johnson et al. 2013). Pregnancy rates explained little variation in population growth rates. Therefore, it was not surprising that nutritional effects, mediated by climate, had little influence on population growth rates of elk in my model.

Relative Influence of Vital Rates on Population Growth

In most long-lived animals, population growth was most sensitive to survival of adult females (Crouse et al. 1987, Pfister 1998, Sæther and Bakke 2000) and elk follow a similar pattern (Raithel et al. 2007, this study). Despite the high sensitivity of population growth to prime-age female survival, annual survival rates of female elk are relatively invariable among years (Brodie et al. 2013), and this lack of process variance caused female survival to contribute little to annual variation in λ (Raithel et al. 2007, this study). Natural selection should minimize variation in vital rates with high elasticity (Galliard et al. 1998, Pfister 1998), and female ungulates can utilize bet-hedging strategies to influence their survival (Albon et al. 1983, Gaillard and Yoccoz 2003). In contrast,

juvenile ungulates, which are dependent on their mothers for the first year of life, are unable to do so. This results in high process variance in juvenile survival, which explained the overwhelming majority of variation in λ in my model ($r^2 = 0.92$). Given the higher elasticity of adult female survival, the magnitude of change in calf survival would need to be approximately 6 times greater than that of female survival to have a similar effect on λ. While this would appear unlikely, variation in juvenile survival can be an order of magnitude greater than that of adult females (Raithel et al. 2007, this study). As long as anthropogenic factors (e.g., hunting) do not reduce vital rates with low process variance (i.e., adult female survival; Brodie et al. 2013), juvenile survival should govern population growth of elk (Raithel et al. 2007, this study). In addition, pregnancy rates of prime-age females (3-13 years) are relatively invariable and elasticity values are low compared to other vital rates, causing variation in pregnancy rates to have minimal effects on population growth. Furthermore, the product of pregnancy rates and survival are used to estimate maternity rates, further reducing the importance of pregnancy rates because they do not appear as an individual term in the model.

Effect of Top-Down, Bottom-Up, and Abiotic Factors on Elk Populations

My simulation results indicated a negative effect ($r = -0.62$) of increasing cougar densities on elk population growth ($r^2 = 0.38$), and to my knowledge, this study was the first to document such an effect. The negative effect of cougars on elk population growth was also demonstrated indirectly by the positive ($r = 0.73$) effect of lactation status of female elk in late fall on population growth rates ($r^2 = 0.53$). In my model, lactation status served as a surrogate of juvenile survival through 6 months. Cougars were the primary source of mortality of juvenile elk through 6 months in northeast Oregon, and monthly survival rates of juvenile elk increased with age from birth to 6 months, and plateaued at 7 to 8 months of age (Rearden 2005, B. Johnson, ODFW, unpublished data). By 7 months of age, juvenile elk are likely large enough to present a substantial risk of injury to cougars and have better escape tactics, so cougars switch to alternative, smaller prey (i.e., deer fawns) during winter (Chapter 2). In areas with low juvenile survival and recruitment, additional factors that may decrease survival of juveniles [e.g., winter severity (Picton 1984, Singer et al. 1997), wolf predation (Griffin et al. 2011)] should be

carefully monitored because further reductions in juvenile survival could negatively affect elk populations.

Surprisingly, I found a negative effect of cougars on elk population growth because relatively stable or increasing cougar populations were apparently not capable of preventing elk populations from increasing in Idaho (Hornocker 1970), Utah (Lindzey et al. 1994) or the northern Yellowstone ecosystem (Murphy 1998). However, cougars were responsible for very little mortality of radiocollared juvenile elk in these studies (4%, Smith and Anderson 1998; 0%, Singer et al. 1997; 2-4%; Barber-Meyer et al. 2008), and densities of cougars in these systems ($0.3 – 2.6$ cougars/100 km^2; Seidensticker et al. 1973, Lindzey et al. 1994, Murphy 1998) were well below the density of cougars required to reduce elk populations that I observed (≥ 4.2 cougars/100 km^2). In contrast, cougar predation in Blue Mountains of Oregon and Washington appears to be a significant mortality source of juvenile elk (42%; Myers et al. 1999, 70%; Rearden 2005, B. Johnson, ODFW, unpublished data). Cougars displayed a strong pattern of selection for juvenile elk during the summer (May – October; Chapter 2), and this contributed to low annual survival of juveniles (Rearden 2005, B. Johnson, ODFW, unpublished data) and reduced recruitment (Johnson et al. 2013). Annual indices of cougar density (i.e., the minimum number of sub-adult and adults) in the Sled Springs and Wenaha Wildlife Management Units in northeast Oregon ranged from $1.7 – 4.2$ cougars/100 km^2 from $2002 – 2007$ (B. Johnson, ODFW, unpublished data). Using genetic mark-recapture techniques, mean cougar densities in the Mt. Emily Wildlife Management Unit in northeast Oregon were estimated to be ~5.0 cougars/100 km^2 (95% CI = $3.2 – 7.7$; Davidson et al. *In Review*), but this estimate was not directly comparable to those used in my model because it likely included some, but not all, dependent kittens (Davidson et al. *In Review*). Dependent kittens (< 1 year) typically make up approximately 30% of resident cougar populations (Chapter 4). Using these estimates, sub-adult and adult cougar densities in the Mt. Emily WMU likely ranged from $2.2 – 5.4$ cougars/100 km^2, which provides additional evidence that cougars can reach densities at which they can negatively affect recruitment in elk populations.

Harvest of female elk negatively ($r = -0.57$) affected population growth rates of elk in my model ($r^2 = 0.63$), which was expected because population growth of elk was

most sensitive to survival of prime-age females (Raithel et al. 2007, this study). Harvest increased variability in female survival (Brodie et al. 2013), which is a vital rate that was likely evolutionarily constrained to have minimal variability (Pfister 1998). Increased process variance attributable to harvest resulted in female survival having a larger effect on λ. Harvest of female elk in most WMUs in northeast Oregon has been extremely limited (e.g., agricultural damage hunts) or eliminated during the past 10 to 15 years in response to declining elk populations (ODFW 2003, 2012). Despite reductions in female harvest, a post-hoc analysis of population growth of elk in northeast Oregon that included harvest mortality in survival rates of female elk (Appendix G) indicated minimal harvest (4% mortality rate) of female elk can slow or prevent recovery of elk populations (3% decline in λ). This occurred because harvest of females is largely an additive mortality source (Brodie et al. 2013). Cougar populations in Oregon have steadily increased since the 1990's (Kiester and Van Dyke 2002, ODFW 2006), and many elk populations have declined, which created speculation that cougars were solely responsible for declines in elk populations. While my study could not directly address the causes for historic declines in elk populations, I speculate that female harvest combined with increasing cougar populations were responsible for elk population declines is supported by my analysis. My results indicated harvest of female elk was not compatible with maintenance of elk populations in areas of extremely high cougar densities (> 4.2 cougars/100 km^2), and even moderate cougar densities ($2.5 – 3.5$ cougars/100 km^2) combined with minimal harvest (5% of the females harvested annually) resulted in population declines in my simulations. Combinations of harvest and cougar densities that resulted in negative population growth rates of elk were likely common as cougar populations recovered because harvest of female elk continued well into the 21st century in some WMUs (ODFW 2003, 2012).

Mean birth date of juveniles was negatively correlated ($r = -0.24$) with population growth rates of elk because juveniles born later had lower survival than those born early (Rearden 2005, B. Johnson, ODFW, unpublished data); however, this relationship had a minimal effect on population growth rates in my model ($r^2 = 0.06$). Birth dates of juvenile ungulates are governed by conception dates (Raedeke et al. 2002), and insufficient numbers of mature males (>3 years) results in an asynchronous pattern of

conception dates which resulted in later mean birth dates of juveniles (Noyes et al. 1996, 2002). Based on these findings, most state wildlife agencies manage elk populations to have sufficient numbers of mature males (>15 adult males per 100 adult females) in the population to ensure synchronous conception dates and early birth dates of juveniles. Nutritional deficiencies also can result in females entering the breeding season in poor body condition, which can result in asynchronous conception dates and later born juveniles (Noyes et al. 2002, Cook et al. 2004). Body condition scores of female elk in northeast Oregon were extremely high (B. Johnson, ODFW, unpublished data). As a result, pregnancy rates were high (89%), most juveniles were born early during the birth pulse, and juvenile survival was not affected by female body condition (Rearden 2005, B. Johnson, ODFW, unpublished data). Therefore, inadequate numbers of mature males and nutritional deficiencies of female elk were unlikely to cause late born juveniles and negative effects on population growth in northeast Oregon.

Climatic variables are often used as a surrogate of available forage conditions and nutritional effects on elk. In Oregon, August precipitation and an index of winter severity were used as surrogates for summer and winter nutritional condition of females, respectively (Johnson et al. 2013). August precipitation best explained percent ingesta-free body fat of female elk (Johnson et al. 2013), which was a strong determinant of pregnancy rates (Cook et al. 2001, 2004), and winter severity represented potential nutritional deficiencies that carried over through summer (Johnson et al. 2013). In addition, lactation places an energetic burden on female elk that can reduce pregnancy rates (Cook et al. 2001, 2004). Increased August precipitation stimulates new growth of vegetation during fall, which may allow lactating females to acquire sufficient forage resources to increase body condition and become pregnant, but most females will become pregnant regardless of new vegetation growth during fall (79%; Johnson et al. 2013). Furthermore, high lactation rates in fall indicated a substantial number of juveniles survived 6 months, which was an extremely strong predictor of juvenile survival and population growth; therefore, any negative effects to population growths rates attributable to high lactation rates are offset by high juvenile survival. Severe winters negatively affect ungulate populations by reducing physical condition of females, which can reduce pregnancy or survival rates of juveniles and adults (Merril and Boyce 1991, Coughenour

and Singer 1996, Singer et al. 1997). Body condition scores and pregnancy rates of female elk during early spring in northeast Oregon were some of the highest in the state (B. Johnson, ODFW, unpublished data). Furthermore, during 7 years of monitoring radiocollared juvenile and adult elk in northeast Oregon, no juvenile or adult female elk died from malnutrition during winter (Appendix G; B. Johnson, ODFW, unpublished data). This indicated winters in northeast Oregon were not severe enough to negatively affect pregnancy or survival rates of elk as seen in other areas (Coughenour and Singer 1996, Loison and Lagvatn 1998, Garrott et al. 2003) or winter ranges in Oregon were sufficient to meet habitat requirements of elk (Thomas et al. 1988). Most elk populations in northeast Oregon are currently below ecological carrying capacity; however, as elk populations recover, the effects of winter severity may increase as elk compete for any limited food resources (Sauer and Boyce 1983).

There was minimal evidence that density-dependent mechanisms were negatively effecting simulated elk populations in my analysis. This likely occurred because most elk populations in northeast Oregon are currently below management objectives and ecological carrying capacities (ODFW 2003, 2012). Density-dependent processes have negatively affected elk populations through competition with other elk (Houston 1982, Merrill and Boyce 1991) by reducing pregnancy rates (Thorne et al. 1976, Houston 1982, Merrill and Boyce 1991) or juvenile survival (Clutton-Brock et al. 1987, Singer et al. 1997). Density-dependent effects in elk populations are most likely observed through effects on juvenile rather than adult elk (Coughenour and Singer 1996); however, my population model included the effect of density-dependence (i.e., previous year elk density) on pregnancy rates but not juvenile survival. The estimates of juvenile survival used in my model were estimated from relatively low density elk populations; therefore, density-dependence did not affect juvenile survival. As elk populations in northeast Oregon increase, revisions to juvenile survival to incorporate density-dependence may be necessary to better reflect current conditions.

Wolves recently recolonized much of northeast Oregon, and the addition of another large carnivore will likely alter elk population dynamics, because prey use of wolves will likely differ from that of cougars (Kunkel et al. 1999), wolf predation can interact with climatic variables (Mech and Peterson 2003), wolves may alter resource use

and distributions of elk (Fortin et al. 2005), and the degree to which wolf predation is compensatory to other mortality sources varies among systems (Mech and Peterson 2003). Furthermore, the extent to which wolf predation influences prey use, densities, and space use of cougars is largely unknown (Ruth and Murphy 2010).

Effects of Cougar Control Efforts on Elk Populations

At high densities (> 4.0 cougars/100 km^2), cougars are capable of reducing elk populations in my model, and recovery is likely to occur only through reduction of cougar populations. In contrast, model elk populations were able to increase by 4% annually at a mean cougar density of 2.87 cougars/100 km^2, which suggested that populations can recover without lethal control of cougars, but the rate of recovery during the years that cougars are removed would be greater. My simulation results indicated reductions of cougar densities were the fastest way to generate increases in elk populations, so long as harvest of female elk has been eliminated. This occurred because cougars were the primary factor limiting juvenile survival (Rearden 2005, B. Johnson, ODFW, unpublished data), and variation in juvenile survival had the greatest influence on population growth rates of elk (Raithel et al. 2007, this study). Removal of cougars had 2 primary benefits for elk populations: 1) increased juvenile survival resulting in increased recruitment, and 2) this increased the number of prime-aged females in the population allowing more calves to be born annually in subsequent years. Increased juvenile survival provided a short-term (3 – 6 years) benefit because juvenile survival declined as cougar populations recovered. However, the increased number of prime-age females in the population provided a lasting, but minimal, benefit because a greater number of calves were born in subsequent years. I suspect that ungulate populations in other areas will also respond positively to reductions in predator densities so long as the population is not food limited and predators are responsible for the majority of juvenile mortality (White et al. 2010). In Idaho, survival of juvenile elk increased following reductions of black bear and cougar densities. While most of the increase was attributable to reductions in black bear densities because they were the primary predator of juvenile elk, there was a measurable effect of reduced cougar densities on juvenile survival (White et al. 2010). Despite these findings, factors that influence elk recruitment can vary spatially (White et al. 2010); therefore, manipulations of predator populations

may not benefit elk in all areas. Ungulate populations that are food limited do not respond well to reductions in predator densities (Ballard et al. 2001) because nutritional (Bishop et al. 2009) or climatic (Hurley et al. 2011) factors are limiting or regulating population growth to a greater extent.

Cougar removal efforts conducted in Oregon during recent years provides some evidence that cougar removals may benefit elk populations. During administrative removals of cougars conducted in the Heppner WMU from July 2006 to June 2009, an average of 26 cougars was removed by hunters and administrative actions annually (total removal = 78). Based on population reconstruction estimates, this reduced the cougar population by approximately 50%. In the 3 years prior to cougars being removed, age ratios averaged 17:100 (range 16 – 18:100). After the first year of cougar removals, the age ratio was 15:100 but increased to 29:100 by the third year of cougar removal and have averaged 29:100 (range 25 – 33:100) during the 4 years after removal efforts concluded. In contrast, recruitment of juvenile elk at 2 additional areas where cougars have been removed (Ukiah and Wenaha WMUs) has not increased substantially following lethal control of cougars, but removal efforts are ongoing. A short term increase in recruitment (~15:100 to 25:100) was observed at Wenaha WMU during the first two years cougars were removed, but declined to pretreatment levels in subsequent years (~15:100). This potentially occurred because removal efforts have not been consistent, allowing cougar populations to recover to pretreatment densities. Recruitment of juveniles at Ukiah WMU has remained relatively constant during cougar removals (range 15-20:100), suggesting cougar removals did not affect recruitment. However, elk from several WMUs utilize winter range habitat in Ukiah WMU, which may dilute the ability to detect changes in age ratios in response to cougar removals.

Elk provide substantial recreational and economic benefits throughout their geographic range (Brooks et al. 1991, Bolon 1994, Fried et al. 1995, Bunnell et al. 2002); therefore, it is appealing to have larger elk populations to allow increased hunting and recreational opportunities. However, removal of predators to increase ungulate populations can have profound, direct and indirect effects on local ecosystems. Intensive lethal management of cougars can result in an influx of sub-adult males in the population (Stoner et al. 2006, Robinson et al. 2008, Chapter 4), which could affect predator-prey

dynamics (Knopff et al. 2010), or increase livestock depredation and human-cougar conflicts (Aune 1991, Cunningham et al. 1995, Torres et al. 1996). Reductions or extirpations of top carnivore populations also can influence densities of mesopredators, which can generate cascading trophic effects in ecosystems (Crooks and Soulé 1999, Ritchie and Johnson 2009). Elk populations relieved from predation pressure may alter their behavior or obtain high densities, resulting in impacts to vegetation, which can have cascading effects throughout local ecosystems (Ripple et al. 2001, Ripple and Beschta 2003, 2012, Fortin et al. 2005). Furthermore, as elk populations increase, crop damage and human conflict may increase, and alleviation of these concerns is often completed through expensive short-term solutions (i.e., fencing or supplemental feeding programs) or through reduction of elk herds via increased harvest (Toweill and Thomas 2002).

MANAGEMENT IMPLICATIONS

In the absence of female harvest, growth rates of elk populations in my model were governed by juvenile survival. For populations below management objectives where juvenile survival, measured by juvenile to adult female ratios, is chronically low, managers should identify factors contributing to reduced juvenile survival and direct management actions to increase juvenile survival. Management actions directed at increasing pregnancy rates are unlikely to benefit elk populations because pregnancy rates had little influence on population growth in my model. My simulation results indicated the two factors under direct manipulation of wildlife managers (female harvest and cougar densities) had the greatest effect on elk population growth. For elk populations that are declining or currently below management objectives, managers should eliminate or greatly reduce harvest of females. In contrast, for elk populations above management objectives or ecological carrying capacities, managers should increase female harvest because this is the quickest way to reduce elk populations. Given that cougar populations were extremely resilient to population perturbations (Chapter 4), implementation of lethal control is likely to have minimal effects on cougar populations over the long-term, but may provide the only option to increase elk populations. In situations where cougar densities are relatively high (> 3.5 cougars/100 km^2), juvenile survival is low, and elk populations are well below management objectives, lethal control of cougars may be used to increase elk populations. At relatively low cougar densities ($<$

2.5 cougars/100 km^2) elk populations are expected to increase by at least 4% annually in my model, and the costs of cougar control efforts may outweigh the potential benefits to the elk population. Therefore, managers should consider allowing elk populations to naturally recover in these situations. The effect of top-down forces of cougars on juvenile survival may not translate well to other areas where cougar densities may be lower or where bears or wolves are the primary mortality source of juvenile elk because bears primarily prey upon neonates (< 1 month) and wolves prey on juveniles primarily during winter. Furthermore, the effects of top-down factors on elk populations will likely vary as a function of predator and prey densities, and composition of the predator guild (Vucetich et al. 2011).

While my simulation results indicated top-down forces can have a substantial influence on elk populations, the importance of habitat and nutrition for elk populations should not be underestimated or ignored. Nutrition, which is determined by habitat conditions, provides the foundation of productivity in elk populations (Cook et al. 2013). Substantial effort, planning, and resources were invested to protect, enhance, and manage public lands to provide suitable habitat conditions for elk throughout the Intermountain West. These efforts likely reduced the importance of nutritional effects in my analysis. Consequently, managers should continue to protect and manage public and private lands to ensure sufficient and suitable habitat conditions for elk. This will allow existing distributions and populations of elk to be maintained, ensure an adequate forage base for long-term productivity, and reduce conflicts with private land-owners.

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CHAPTER 6

SUMMARY AND MANAGEMENT IMPLICATIONS

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SUMMARY

Rocky Mountain elk (*Cervus canadensis nelsoni*; hereafter, elk) populations in many areas of the western United States have declined in recent years. Two hypotheses proposed for the cause of declining elk populations include overabundance of elk, resulting in density-dependent effects and long-term declines in productivity (Riggs et al. 2000), and reductions in habitat quantity and quality, resulting in reduced pregnancy rates and survival due to nutritional deficiencies (Cook et al. 2001, 2004, 2013). Recovery of large carnivores, including cougars (*Puma concolor*), from near extirpation is another explanation for declining elk populations (Hebblewhite et al. 2002, White and Garrott 2005, Barber-Meyer et al. 2008, White et al. 2010). Disentangling the individual effects of various top-down, bottom-up, and abiotic factors on elk populations can be difficult due to their interactive and synergistic effects. Cougars are thought to be contributing to ongoing elk population declines in northeast Oregon through predation on juvenile elk (Rearden 2005, Johnson et al. 2013). Despite this implication, little is known about cougar predation patterns and demography in Oregon. My dissertation provided insight on cougar ecology in Oregon through estimation of predation rates and prey selection (Chapter 2), survival rates in relation to hunting regulations (Chapter 3), population growth rates under varying management prescriptions (Chapter 4), and effects of intensive lethal control on population dynamics of cougars (Chapter 4). I also was able to determine the relative influence of top-down, bottom-up, and abiotic factors on population growth rates of elk in Oregon (Chapter 5). My results provided additional insight into factors influencing population dynamics of elk, contributed to the understanding of cougar ecology and population dynamics, and will help guide cougar and elk management. Below, I provide a brief description of each chapter of my dissertation and highlight important findings that will help managers more effectively manage predator and prey populations.

To effectively assess predator and prey dynamics, accurate and unbiased estimates of kill rates, prey use, and predator abundance must be developed (Anderson and Lindzey 2003, Vucetich et al. 2011). Due to their large home ranges, solitary nature, and relatively low population densities, cougars are very difficult to study, and information on cougar predation patterns is limited, particularly in multiple-prey systems.

To develop a better understanding of cougar predation patterns and identify mechanisms by which cougars may limit ungulate populations in northeast Oregon, I implemented a 3-year study to document cougar kill rates and prey selection through the use of global positioning system (GPS) technology (Chapter 2). In addition, I wanted to determine the degree to which cougar predation patterns may be generalized across the species range. To do so, I tested hypotheses that cougar kill rates are influenced by season, gender, and reproductive status, and that cougars non-randomly select prey according to the reproductive vulnerability hypothesis (Lima and Dill 1990).

My results indicated that cougar kill rates and prey use are influenced by season, gender, reproductive status of females, and the energetic requirements of the individual; these results support the reproductive vulnerability hypothesis. Based on the close alignment of my results and those in obtained in west-central Alberta (Knopff et al. 2010), I suggest that these patterns are generalizable across the geographic range of cougars. Cougars should kill more frequently (ungulates/week) during summer when prey use is dominated by juvenile ungulates (i.e., smaller prey; Chapter 2, Knopff et al. 2010). Cougar kill rates (kg prey/day) were largely explained by energetic requirements, which are driven by gender and demography (Chapter 2, Knopff et al. 2010, White et al. 2011). Male cougars killed ungulates at a similar rate as females (ungulates/week), but killed larger prey than females (Chapter 2, Knopff et al. 2010), allowing males to kill about twice as much ungulate biomass per day on average, compared to solitary females. Female cougars with kittens kill more ungulate biomass per day than do solitary females, due to the greater collective energy requirements of their family group (Ackerman et al. 1986, Anderson and Lindzey 2003, Knopff et al. 2010). Differences among ecosystems in the average size of available prey will likely cause some variation in the number of ungulates killed per week by cougars (i.e., cougars killing smaller prey will kill more frequently); however, my results suggest that biomass of prey killed per day should be relatively constant. Prey use by cougars should also follow generalizable patterns that are explained by relative prey vulnerability, which changes over the course of the year. Cougars should disproportionately prey upon small, naïve, juvenile ungulates during summer, physically weakened male ungulates during fall, and female ungulates, burdened by large fetuses, during winter and late spring. The use of a particular species

of prey is likely to be strongly influenced by relative prey availability within an ecosystem, but the general pattern of cougars preying upon vulnerable prey should hold true across the species' range.

Cougars in my study area demonstrated strong selection for juvenile elk during summer and juvenile deer during winter. Variation in ungulate population growth rates appears to be determined primarily by variation in juvenile survival (Chapter 5, Raithel et al. 2007). Therefore, cougars are most likely to affect deer and elk populations through selective predation on juveniles. However, previous research suggests that mule deer populations are limited primarily by climatic and nutritional factors, not predators (Bishop et al. 2009, Hurley et al. 2011). Apparent competition can occur when a generalist predator selects a secondary prey species whose numbers are associated with the abundance of a primary prey species. Generalist predators whose numbers are determined by primary prey densities but selectively prey upon secondary prey may cause population declines for the secondary prey species, or maintain the secondary prey at low densities (Messier 1994, Sinclair et al. 1998). Cougar densities are determined primarily by the densities of their primary prey (Logan and Sweanor 2001, Laundré et al. 2007, Pierce et al. 2012) and secondarily by territory defense and behavioral mechanisms (Hornocker 1970, Logan and Sweanor 2001). In my study, deer dominated cougar diets, suggesting that deer serve as the primary prey of cougars in northeast Oregon, but elk calves were a secondary prey species that was selected by cougars. This raises the possibility that selective predation on elk calves by cougars may limit elk populations in northeast Oregon.

Hunting regulations likely have the greatest effect on survival rates of cougars because hunter harvest is the primary source of mortality in most cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008). Cougar hunting throughout their geographic range is typically conducted using trained dogs, which are used to pursue and tree cougars (Cooley et al. 2011). This type of hunting is highly effective, but also results in selective harvest of adult males (ODFW 2006, Zornes et al. 2006). In 1994, Ballot Initiative Measure 18 (hereafter Measure 18) was passed by Oregon voters, which prohibited the use of dogs to either pursue or hunt cougars following the 1994 hunting season. This resulted in a novel set of hunting regulations

with potentially important implications for cougar survival rates because hunting cougars without dogs is less effective and selective than when dogs are used (ODFW 2006, Zornes et al. 2006). Fortuitously, cougars have been radio-collared in Oregon since 1989, which provided an opportunity to conduct a retrospective analysis to assess causes of mortality and estimate cougar survival rates under different hunting regulations (Chapter 3).

Survival rates of adult male cougars increased following prohibition of the use of dogs to hunt cougars. This occurred because harvest of cougars tended to be male-biased when dogs were used (ODFW 2006, Zornes et al. 2006). Survival rates of subadult male cougars were low regardless of hunting regulations. I attributed this to male-biased dispersal patterns in cougars (Sweanor et al. 2000, Logan and Sweanor 2001), which increases the risk of mortality in younger males while dispersing. Survival rates of female cougars were similar regardless of hunting regulations (i.e., use or non-use of dogs), which I attributed to avoidance of harvesting females when use of dogs was legal, and extremely low harvest rates when use of dogs was illegal. The survival rates I documented in my study were some of the highest ever reported for cougars and similar to those of unhunted populations (Logan and Sweanor 2001), suggesting that current harvest pressure (use of dogs not allowed) has minimal effects on cougar survival. My results indicated that human-caused mortality was largely compensatory in cougars. I reached this conclusion because natural mortality rates increased as human-caused mortality rates decreased and survival rates were similar across varying harvest rates. However, harvest may become an additive mortality source, particularly for females, at harvest rates greater than I observed in my study (e.g., Cooley et al. 2009).

I documented a strong effect of age on survival rates of cougars in lightly hunted populations. Female cougars had substantially greater survival rates than males at younger ages $(1 - 3$ yrs), but males had similar survival rates to females at intermediate ages $(4 - 8$ yrs). The lower survival rate of males at younger ages was a consequence of male biased dispersal patterns in cougars (Sweanor et al. 2000, Logan and Sweanor 2001). I found some evidence of senescence in cougars because survival rates of older individuals declined at one of my study areas. This pattern was expected because in most long-lived mammals older individuals have higher mortality rates (Caughley 1966). I did

not observe an effect of age on survival at the Catherine Creek study area. Cougars during the Catherine Creek study were subjected to hunting with dogs, which is a highly effective and selective (i.e., male-biased) hunting method (Anderson and Lindzey 2003). This selective hunting pressure reduced survival rates of prime-aged males so they were similar to sub-adult males, which eliminated the effect of age on cougar survival.

Since the arrival of Europeans in North America, large carnivores, including cougars, were extensively persecuted, often through government assistance. This relentless persecution resulted in profound reductions in the ranges of large carnivores, plus local or regional extirpations of many, including cougars (Laliberte and Ripple 2004). In Oregon, cougars were classified as an unprotected predator from the 1800's until 1967, and there were no restrictions on methods used to kill cougars or number of cougars that could be harvested (ODFW 2006). In 1967, fewer than 200 cougars remained in Oregon, which resulted in cougars receiving formal protection as a game animal in 1968 (ODFW 2006). This distinction allowed ODFW to manage cougar populations through restrictions on harvest rates, and strict harvest regulations allowed cougar populations to increase to approximately 3,000 individuals by 1994 (Kiester and van Dyke 2002). In 1994, Oregon voters passed Measure 18, which prohibited use of dogs to pursue cougars. Since that time, cougar populations are thought to have continued to increase (Kiester and van Dyke 2002), despite record harvest of cougars in recent years (ODFW 2012). Recently, however, it has been discovered that cougar populations in some portions of their geographic range are declining (Lambert et al. 2006), apparently in response to excessive harvest (Robinson et al. 2008, Cooley et al. 2009a,b). This is disconcerting given the recovery of cougars from near extirpation throughout their geographic range. To determine whether cougar populations in northeast Oregon were declining in response to record harvest rates, I used survival rates of cougars to parameterize a Leslie population matrix model to estimate population growth rates of cougars (Chapter 4). My simulation results indicated that despite record harvest in recent years under regulations that prohibit the hunting cougars with dogs (ODFW 2006, 2012) cougar populations in Oregon were increasing, and likely serve as a source population for surrounding areas. This suggests that current hunting methods are not negatively effecting the size of cougar populations in Oregon, and managers will not

be able to utilize hunters to manipulate cougar population size for meeting management objectives.

ODFW is authorized to reduce cougar populations through administrative actions to benefit declining ungulate populations (ODFW 2006). When reducing cougar populations, ODFW conducts removals over 3 consecutive years with a goal of increasing adult female mortality to 40-45% of total cougar mortality (ODFW 2006), which should result in a 50-60% decline in the population (Anderson and Lindzey 2005). However, it is unknown whether this level of removal is insufficient, adequate, or excessive for achieving desired population reduction levels (i.e., 50% reduction). Furthermore, little is known about the effects of intensive lethal control on cougar population viability and population recovery times. To determine the effort required to reduce a cougar population by 50% and assess the effect of intensive lethal control on cougar populations, I ran population simulations using varying immigration and emigration rates (Chapter 4). My simulation results indicated intensive removal efforts (40 – 60% of the population removed annually) are required to reduce a cougar population by 50% over 3 years. This level of removal was necessary because cougar populations are capable of increasing rapidly due to *in situ* reproduction, and high immigration rates from surrounding populations. Given high intrinsic growth rates and immigration from surrounding populations, my simulation results indicated local cougar populations subjected to intensive control efforts had no risk of becoming locally extirpated in response to intensive short-term population reductions. Following a 50% population reduction, model cougar populations were able to recover to pre-treatment densities within 2 – 6 years, depending on the level of immigration from surrounding populations. The results from my simulations corresponded well with experimental reductions of cougar populations in empirical field studies (e.g., Logan and Sweanor 2001, Anderson and Lindzey 2005, Stoner et al. 2006).

Elk populations are influenced by a suite of interacting top-down, bottom-up, and abiotic factors (Sauer and Boyce 1983, Fowler 1987, Gasaway et al. 1992, Coughenour and Singer 1996). To assess the relative effects of top-down, bottom-up, and abiotic factors on elk population growth rates, I used data collected during field studies in northeast Oregon to parameterize a Leslie matrix model (Chapter 5). I found variation in

juvenile survival explained the overwhelming majority of variation in population growth rates of a model elk population, despite population growth being most sensitive to adult female survival. This occurred because adult female survival was relatively invariable and contributed little to variance to population growth. However, harvest of female elk introduced additional variation in survival rates, which resulted in a large, negative effect on population growth rates.

An index of cougar density had a strong, negative association with population growth rate of elk in my model. The apparent negative effect of cougar predation on the elk population was manifested through reductions in juvenile survival (Rearden 2005; B. Johnson, ODFW, unpublished data), despite increased cougar densities being positively associated with pregnancy rates of elk (Johnson et al. 2013). These findings suggest that cougars were the primary determinant of population growth rate of elk in northeast Oregon. This was surprising because relatively stable or increasing cougar populations were apparently not capable of preventing elk populations from increasing in Idaho (Hornocker 1970), Utah (Lindzey et al. 1994), or the northern Yellowstone ecosystem (Murphy 1998). However, densities of cougars (Davidson et al. *In Review*) and juvenile elk mortality rates attributed to cougars (Rearden 2005; B. Johnson, ODFW, unpublished data) in Oregon were substantially greater than observed in other areas. Therefore, cougars are only likely to negatively affect elk populations when cougars occur at high densities and selectively prey upon juvenile elk.

Mean birth date of juvenile elk was negatively correlated with population growth rates of elk in my model because juveniles born later in the calving period had lower survival than those born early (Rearden 2005; B. Johnson, ODFW, unpublished data); however, this relationship had a minimal effect on population growth rates. The effect of juvenile birth date was minimal in my analysis because elk populations in Oregon are managed to include sufficient numbers of mature bulls (>10-15 per 100 females) to ensure synchronous conception and early birth dates for juveniles (Noyes et al. 1996, 2002, ODFW 2003). In addition, body condition scores of female elk entering the breeding season in northeast Oregon have been extremely high (B. Johnson, ODFW, unpublished data), which allows females to be bred during their first estrous cycle and allowing earlier mean birth dates of juveniles (Noyes et al. 2002, Cook et al. 2004).

In my analysis, August precipitation and an index of winter severity were used as surrogates for summer and winter nutritional condition of females, respectively (Johnson et al. 2013). August precipitation best explained percent ingesta-free body fat of female elk (Johnson et al. 2013), which was a strong determinant of pregnancy rates (Cook et al. 2001, 2004), and winter severity represented potential nutritional deficiencies that carried over through summer (Johnson et al. 2013). Both of these factors negatively affect pregnancy rates, which have low elasticities and minimal variation over time, so they contribute little to variation in population growth rates in my model. Increased August precipitation stimulates new growth of vegetation during fall, which may allow lactating females to ingest sufficient forage resources to increase body condition and become pregnant. But most females will become pregnant regardless of availability of new vegetation growth during fall (79%; Johnson et al. 2013), which minimized the effect of August precipitation in my analysis. Severe winters negatively affect ungulate populations by reducing the physical condition of females, which can reduce pregnancy rates or survival rates of juveniles and adults (Merril and Boyce 1991, Coughenour and Singer 1996, Singer et al. 1997). Body condition scores and pregnancy rates of female elk during early spring in northeast Oregon were some of the highest in the state (B. Johnson, ODFW, unpublished data). This indicated that winters in northeast Oregon were not severe enough to negatively affect pregnancy or survival rates of elk, as has been seen in other areas (Coughenour and Singer 1996, Loison and Lagvatn 1998, Garrott et al. 2003), or that winter ranges in Oregon were sufficient to meet nutritional requirements of elk (Thomas et al. 1988).

There was minimal evidence that density-dependent mechanisms were negatively affecting elk populations in my model. This likely was the case because most elk populations in northeast Oregon are currently below management objectives and estimated ecological carrying capacities (ODFW 2003, 2012). Density-dependent effects in elk populations are most likely observed through effects on juvenile rather than adult elk (Coughenour and Singer 1996); however, my population model included the effect of density-dependence (i.e., previous year elk density) on pregnancy rates, but not juvenile survival. The estimates of juvenile survival used in my model were measured from relatively low-density elk populations. As elk populations in northeast Oregon increase,

revisions in juvenile survival to incorporate density-dependence may be necessary to better reflect current conditions.

My simulation results indicated that, in the absence of female harvest, elk populations in northeast Oregon should be expected to increase in association with low to moderate cougar densities (< 4.00 cougars/100 km^2); however, cougars are likely to cause elk populations to decline at high densities (> 4.00 cougars/100 km^2). Therefore, the relative benefit to elk populations of cougar reductions was greater where cougar densities were high. Removal of cougars had 2 primary benefits for elk populations: (1) increased juvenile survival resulting in increased recruitment, and (2) increased recruitment resulting in higher numbers of prime-aged females in the population, allowing more calves to be born annually in subsequent years. Increased juvenile survival provided a short-term (3 – 6 years) benefit because juvenile survival declined as cougar populations recovered. However, the increased number of prime-age female elk in the population provided a lasting, but minimal, benefit because a greater number of calves were born in subsequent years. Despite these findings, factors that influence elk recruitment can vary spatially (White et al. 2010); therefore, manipulations of predator populations may not benefit elk in all areas. Ungulate populations that are food-limited do not respond well to reductions in predator densities (Ballard et al. 2001) because nutritional (Bishop et al. 2009) or climatic (Hurley et al. 2011) factors are limiting population growth rates to a greater extent.

MANAGEMENT IMPLICATIONS

In the absence of female harvest, growth rates of elk populations in my model were governed primarily by juvenile survival. For populations below management objectives where juvenile survival, measured by juvenile to adult female ratios, is chronically low, managers should identify factors contributing to reduced juvenile survival and implement management actions to increase juvenile survival. Unless pregnancy rates are chronically low, management actions (e.g., habitat improvements) directed at increasing pregnancy rates are unlikely to benefit elk populations because pregnancy rates had little influence on population growth rates in my model. Harvest of adult females increases variation in survival, a vital rate with high elasticity, and can cause substantial declines in population growth rate of elk. For elk populations that are

declining or currently below management objectives, managers should eliminate or greatly reduce harvest of females. In contrast, for elk populations above management objectives or ecological carrying capacities, managers should increase female harvest because this is the quickest way to reduce elk populations.

While my simulation results indicated top-down forces were the primary factor influencing population dynamics of elk, the importance of adequate habitat and nutrition for elk populations should not be underestimated or ignored. Nutrition, which is determined by habitat conditions, provides the foundation of productivity in elk populations (Cook et al. 2013). Substantial effort, planning, and resources were invested to protect, enhance, and manage public lands to provide suitable habitat conditions for elk and other ungulates throughout the Intermountain West. These efforts likely reduced the importance of nutritional effects on population dynamics of elk in my analyses. Managers should continue to protect and manage public and private lands to ensure sufficient and suitable habitat conditions for native taxa and maintain existing ecosystem processes. This will allow existing distributions and populations of ungulates to be maintained, ensure an adequate forage base for long-term productivity, and reduce conflicts with private land-owners.

The effect on elk of top-down forces from cougar predation may not translate well to areas where bears or wolves are the primary source of mortality for juvenile elk because bears primarily prey upon neonates (< 1 month) and wolves prey on juveniles primarily during winter. In contrast, cougars prey on juvenile elk throughout the year, which may cause them to have a greater effect on elk populations than other predators. Furthermore, the effects of top-down factors on elk populations will likely vary as a function of predator and prey densities, and composition of the predator guild.

Cougar management practices are variable throughout western North America and can significantly affect cougar demography, population structure, and population size (Robinson et al. 2008, Cooley et al. 2009a,b; Chapters 3 and 4), which in turn can influence the effects of cougars on ungulate populations. Selective predation of juvenile elk appears to be the primary factor limiting elk populations in northeast Oregon, particularly when cougars are at high densities. Managers should strongly consider the negative effects of cougar predation on elk populations in areas with high cougar

densities. In situations where cougar densities are relatively high (> 3.5 cougars/100 km^2), juvenile elk survival is low, and elk populations are well below management objectives, lethal control of cougars may be the best option for increasing elk populations. At relatively low cougar densities (< 2.5 cougars/100 km^2) elk populations are expected to increase by at least 4% annually in my model, and costs of cougar control efforts may outweigh the potential benefits to the elk population. Furthermore, managers should carefully consider the consequences of manipulating cougar population structure and size prior to embarking on predator removal efforts to benefit ungulate populations. If predators are the primary factor limiting survival and recruitment of juveniles in other populations, manipulating predator populations may be an option to increase ungulate populations; however, there are a multitude of factors that affect growth rates of ungulate populations. I advise managers to carefully consider all factors that may contribute to variability in ungulate populations before embarking on management actions to reduce predator populations because predation on juveniles may be largely a source of compensatory mortality and other factors may be limiting ungulate populations (Ballard et al. 2001, Bishop et al. 2009, Hurley et al. 2011).

Opportunistic hunting methods (i.e., hunting without dogs) can provide high levels of recreation while allowing high survival and population growth rates of cougars. Consequently, in systems where hunting cougars with dogs is illegal, managers may have difficulty utilizing hunters to manipulate cougar survival and population size to meet management objectives. Conservative harvest of cougars with dogs (i.e., limited tag numbers) can result in high survival and population growth of cougars, suggesting hunting cougars with dogs can be compatible with maintaining cougar populations. With the option to hunt cougars with dogs, managers can affect survival rates of male and female cougars differentially (Lambert et al. 2006, Cooley et al. 2009a,b, Chapter 3) to meet population management objectives. Restoration of the ability to hunt cougars with dogs would allow managers to more effectively manage cougar populations by manipulating hunter numbers and harvest quotas to affect population growth and meet management objectives. This would also allow more flexible management of prey populations by allowing effective manipulation of cougar populations to benefit ungulates. A system of unlimited numbers of hunters that hunt cougars without the use

of dogs, combined with a restrictive tag-allocation program to allow hunting with dogs, would provide maximum recreational opportunities and an effective tool for meeting management objectives for both cougars and their prey. However, managers must clearly define population objectives for cougars when providing hunting opportunities with dogs, because excessive harvest can result in additive mortality (Cooley et al. 2009b) and population declines (Lambert et al. 2006).

My results indicated cougar populations are able to sustain 26 – 39% removal annually; consequently, local managers should be able to use a quota-based system to prevent excessive harvest of cougars. This requires knowledge of local sources of mortality and quality estimates of population size, which are difficult to obtain, so a conservative approach is recommended when applying quota-based systems to prevent over-exploitation of local cougar populations. Given high intrinsic growth rates and immigration from surrounding populations, substantial efforts are required to reduce local cougar populations. Local managers should carefully monitor lethal control efforts to ensure they are sufficient to meet the objectives of removal and also not so excessive that the viability of the local population is threatened. However, my results indicate that cougar populations are highly resilient and can recover quickly from excessive exploitation, allowing a margin of error for managers when manipulating cougar populations. Managers should also realize that intensive lethal control is likely to result in an increase in the number of sub-adult males in the population due to male-biased dispersal patterns (Sweanor et al. 2000), which could result in increased livestock depredation and human-cougar conflict. Furthermore, reductions of large carnivore populations to increase ungulate populations may result in unexpected ecological effects (e.g., trophic cascades). Where intensive control of cougars is used to benefit ungulate populations, intensity of control should be reduced or control efforts terminated once population objectives for ungulates have been attained.

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APPENDICES

Appendix A. Comparison of using Conservation Detection Dogs versus Human Observers to Locate Prey Remains at Cougar Kill Sites in northeast Oregon, USA.

INTRODUCTION

Investigation of kill sites of large carnivores is extremely labor intensive. Consequently, methods that can reduce the effort required to locate kill sites of large carnivores can be invaluable. Prior to the advent of Global Positioning System (GPS) collars, intensive snow-tracking of cougars was required to document kill sites. GPS collars allow researchers to obtain large, continuous location information on individual animals. Anderson and Lindzey (2003) pioneered a technique to locate potential kill sites of cougars from GPS location data. This technique was further refined by Knopff et al. (2009) who developed a predictive model to distinguish between kill sites and non-kill sties. While these efforts have made it possible to identify and discriminate potential kill sites, intensive labor efforts are required to actively search potential kill sites for prey remains.

The use of conservation detection dogs in wildlife studies has increased rapidly in recent years. Detection dogs are typically used to locate scat from wildlife (Long et al. 2007a,b , MacKay et al. 2008) but have also been used to locate live animals (Cablk et al. 2006, Stevenson et al. 2010) and bird and bat fatalities under wind turbines (Arnett 2006, Paula et al. 2011). Detection dogs are selected for their high drive and search ability, and are trained using techniques developed for drug, bomb, and search and rescue dogs. Due to their high drive, mobility, and highly sensitive olfactory system (Syrotuck 1972), detection dogs can efficiently cover larger, remote areas with difficult terrain more quickly than human observers. Consequently, the use of detection dogs to locate remains of cougar killed prey could decrease labor and increase the accuracy of predation results. To my knowledge, detection dogs have not been utilized to locate kill sites of large predators and their ability to locate kill compared to human observers is not well known. My objectives were to compare: 1) average search times of potential cougar kill sites, 2) the percentage of known cougar kills assigned to a species, age-class, and gender, and 3) the percentage of potential kills sites where a kill was located based on the probability the kill site should contain a kill for human observers and detection dog teams.

METHODS

Location of Cougar Kill Sites

Identification of potential kill sites of cougars from GPS location data are described by Knopff et al. (2009) and in Chapter 2 of this document. To document predation events, the geographic coordinates of the geometric center of GPS location clusters were loaded onto handheld GPS units (Garmin GPSMap 60csx; Garmin International, Inc., Olathe, KS, USA), field crews hiked to clusters, and systematically searched the area for prey remains. Methods for locating cougar kill sites and determining species, age class, and gender of prey remains are described in Chapter 2 of this document.

Metrics of Comparing Detection Dogs and Human Observers

I calculated 3 metrics by which to compare the ability of detection dogs and human observers at locating cougar kill sites. Under the first metric, I compared average search times of human observers and detection dogs at sites where kills were located and where they were not located. For the second metric, I calculated the percentage of kills assigned to a 1) a species, 2) an age-class, and 3) gender for yearling and adult ungulates. I calculated this metric because remains of prey at cougar kill sites were typically scattered, and unique identifying features of prey may not be able to be determined if specific remains are not located. Detection dogs, because they use scent rather than sight, may be able to locate additional prey remains that will more accurately describe the prey item in question. For the final metric, I used information from potential predation sites created by female cougars. For each potential predation site, I assigned a probability of a kill site containing a kill (methods for calculating kill site probabilities are described in Appendix C). I then created 5 bins based on the probability of the cluster containing a kill (e.g., 0.00 – 0.19, 0.20 – 0.39, etc…) and then determined the number of clusters searched within each bin and the number of kills located within each bin by detection dogs and human observers. This was conducted separately for potential predation sites in the summer (May – Oct) and winter (Nov – Apr). Given the descriptive nature of these metrics, I did not conduct any statistical analysis to determine differences between detection dogs and human observers. Rather, I provide summary statistics to contrast between detection dogs and human observers.

RESULTS

Detection dogs were able to locate kill sites of cougars on average 11.6 minutes faster than human observers and were able to search non-kill sites on average 21.4 minutes faster than human observers (Table A.1). During the course of the cougar predation study, 3,365 potential predation sites were searched, of which, prey remains were located at 1,172 and were not located at 2,193. Given the average difference in search times between detection dogs and human observers, if detection dogs would have been utilized during the entire study a total of 1,008 hours of search time (126 days of labor assuming 8 hour days) could have been saved.

Detection dog teams were able to assign known kills to species 96.2% (282 of 293 kills) of the time compared to 87.4% (806 of 922 kills) of kills located by human observers. While this may suggest detection dogs increased the ability to distinguish species of cougar kills, caution is needed when interpreting this result because the dog handlers were the 2 most experienced personnel on the research project and may have been better at using available evidence to distinguish the species of prey. Human observers were able to accurately assign ungulate kills to an age-class 95.1% (834 of 877 kills) of the time compared to 96.8% (272 of 281 kills) for detection dog teams, suggesting no difference between survey methods. Detection dog teams were able to assign 62.7% (79 of 126 kills) of yearling and adult cougar killed ungulates to a gender compared to 64.4% (217 of 337) for human observers, which suggested no difference between survey methods.

During summer, detection dogs appeared to do a slightly better job at locating kills at potential predation sites with a low probability of containing a kill; however, human observers appeared to do a slightly better job at locating kills at potential kill sites with a high probability of containing a kill (Table A.2). The number of potential kill sites that had an intermediate probability (0.40 – 0.79) of being surveyed by detection dogs was limited ($n = 31$); consequently, it is difficult to determine if differences are attributable to small sample sizes or an actual difference between detection dogs and human observers. During winter, detection dogs and human observers located kills at similar rates regardless of the probability the potential kill site contained a kill (Table A.3).

Table A.1. Comparison of average search times of human observers and detection dogs at potential kill sites of cougars in northeast Oregon, USA.

Survey Method	Kill Site	Average search time (min)	SE
Human	Yes	15.7	0.97
	No	39.6	0.51
Detection dog	Yes	4.1	0.39
	No	18.2	0.43

Table A.2. Comparison of the percentage of potential predation sites of cougars that contained a kill based on the probability the predation site should contain a kill for human observers and detection dogs during summer (May - October).

Observer	Probability of kill	No. of clusters surveyed	No. of kills located	% of clusters with kills
Human	0.00 - 0.19	625	67	10.7
	0.20 - 0.39	239	89	37.2
	0.40 - 0.59	110	59	53.6
	0.60 - 0.79	66	47	71.2
	0.80 - 1.00	347	305	87.9
	Total	1387	567	40.9
Detection dog	0.00 - 0.19	87	7	8.0
	0.20 - 0.39	26	12	46.2
	0.40 - 0.59	18	11	61.1
	0.60 - 0.79	13	7	53.8
	0.80 - 1.00	70	55	78.6
	Total	214	92	43.0

Table A.3. Comparison of the percentage of potential predation sites of cougars that contained a kill based on the probability the predation site should contain a kill for human observers and detection dogs during winter (Nov - Apr).

Observer	Probability of kill	No. of clusters surveyed	No. of kills located	% of clusters with kills
Human	0.00 - 0.19	378	30	7.9
	0.20 - 0.39	42	17	40.5
	0.40 - 0.59	17	11	64.7
	0.60 - 0.79	12	10	83.3
	0.80 - 1.00	124	117	94.4
	Total	573	185	32.3
Detection dog	0.00 - 0.19	102	8	7.8
	0.20 - 0.39	16	7	43.8
	0.40 - 0.59	4	2	50.0
	0.60 - 0.79	9	9	100.0
	0.80 - 1.00	60	57	95.0
	Total	191	83	43.5

DISCUSSION

I documented no evidence that detection dogs located kill sites at a lower frequency than human observers, which suggested use of detection dogs did not influence the results of research to document kill rates and prey selection of cougars (Chapter 2). Furthermore, these results suggested that detection dogs did not provide any substantial benefit in the ability to locate kill sites of cougars from GPS location clusters. The main benefit of detection dogs was that they were able to locate kills and search non-kill sites substantially faster than human observers. One additional benefit of detection dogs was their ability to locate kill sites during winter. Human observers were limited to visual searches of potential kill sites. Consequently, human observers were unable to search potential kill sites following recent snowfall and kill sites could only be searched after snow had melted. In contrast, detection dogs were able to locate kills buried under $1 - 2$ feet of snow.

While detection dogs located cougar kills faster and at a similar success rate as human observers, it is unlikely that detection dogs will be useful on future research projects investigating kill sites of large carnivores. During this study, the project able to purchase 2 detection dogs from PackLeader LLC (Gig Harbor, WA) for $5,000 each; however, this was not a common practice. Most detection dogs are leased to research projects after personnel have received handler training, or detection dogs and handlers are provided for specific research projects. The long-term nature of predation studies will likely make it cost prohibitive to use detection dogs to locate kill sites of large carnivores. Detection dogs are typically leased at a cost of $500 – 750 dollars per week and handler expenses (e.g., salary, per diem, and housing) are not included in the cost of leasing dogs. Consequently, the lease of 2 detection dogs for 1 year would cost approximately $52,000 - 78,000 before handler expenses are included. As a result, it is cost ineffective to utilize detection dogs for long-term research of large predator kill sites because the only benefit of using detection dogs was faster search times at kill sites, and the cost of 2 dogs outweighs the amount of time saved using detection dogs (~1,000 hours of search time over 3 years or $15,000 if technicians were paid $15 per hour).

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Appendix B. Weights (kg) of ungulates used to calculate kill rate (kg/day) and prey composition (biomass) of cougars in northeast Oregon, USA, from 2009-2012.

Age and gender of prey	Species			
	Mule deer[a]	White-tailed deer[b]	Unknown deer[c]	Elk[a]
Adult male	75	68	72	315
Adult female	65	59	62	217
Yearling (12-23 mo.)	50	45	48	179
Juvenile[d] (11 mo.)	44	40	42	138
Juvenile (10 mo.)	41	37	39	129
Juvenile (9 mo.)	38	35	36	119
Juvenile (8mo.)	35	31	33	109
Juvenile (7 mo.)	31	28	30	98
Juvenile (6 mo.)	27	24	26	87
Juvenile (5 mo.)	13	21	22	75
Juvenile (4 mo.)	19	17	18	62
Juvenile (3 mo.)	14	13	14	50
Juvenile (2 mo.)	10	9	10	39
Juvenile (1 mo.)	7	6	6	28
Juvenile (0 mo.)	4	3	4	18
Adult - Unk Gender[e]	70	64	67	266
Yearling/Adult[f]	58	52	55	198

[a] Estimates of adult and yearling weights were obtained from capture data from northeast Oregon (ODFW; unpublished data). Cow elk weight estimates were obtained from capture data from northeast Oregon (ODFW; unpublished data), bulls were assumed to be 1.45 times larger than females (Hudson et al. 2002).
[b] We calculated white-tailed deer weights by assuming they weighed approximately 90% of the weight of a similar aged mule deer.
[c] Average of mule deer and white-tailed deer estimates.
[d] Median, monthly weights of juvenile age classes were obtained from a von Bertanlanffy growth equation of the form $M(t) = A[1 -1/3e^{-K(t-I)}]^3$, where $M(t) =$ mass (kg) at age t, $A =$ max. weight (adult female), $K =$ growth rate (we used 0.0049 for deer and 0.0042 for elk), and $I =$ age at inflection point (140 days).
[e] Calculated using the average of adult male and female weights for each species.
[f] Calculated using the average of yearling female and adult female weights for each species.

Appendix C: Development of a Predictive Model to Identify Predation Sites of Female Cougars from Global Positioning System Location Data.

INTRODUCTION

Calculating unbiased and precise estimates of prey use (Robinson et al. 2002) and kill rates (Sand et al. 2008) of predators are critical to understanding predator prey dynamics (Anderson and Lindzey 2003). Past efforts to document predation patterns of large carnivores have primarily focused on snow-tracking or intensive monitoring of individual animals marked with VHF radiocollars. Radiotelemetry efforts are extremely labor intensive and often greatly restricts the sample of individual animals that can be monitored; however, this method allows year round monitoring of individual animals.

Recent advances in Global Positioning Systems (GPS) radiotelemetry have allowed researchers to efficiently obtain a large number of location information from multiple animals. Large carnivores often take substantial amount of time consuming the large prey items that they kill; consequently, individuals wearing GPS collars typically have a large number of locations at kill sites. Anderson and Lindzey (2003) developed a technique for identifying potential kill sites of cougars from GPS location clusters. At this point in time, GPS collars stored location information directly on the collar and did not allow researchers to visit potential kill sites until collars were retrieved. Since that time, remote download capabilities have allowed researchers to frequently obtain GPS location data and investigate potential kill sites shortly after they were created. Despite this advancement which allowed researchers to investigate kill sites in a timely manner, many potential kill sites did not actually contain a kill and field crews spent a substantial amount of time searching potential kill sites. To reduce the amount of time spent searching for kill sites, Knopff et al. (2009) developed a predictive model to identify cougar kill sites from GPS location cluster data. I conducted a similar study to Knopff et al. (2009); however, given that my prey system was substantially different from that in Alberta, Canada, I wanted to develop my own predictive model using GPS location data from collared cougars in northeast Oregon. My primary objective was to develop a predictive model to identify kill sites of cougars in northeast Oregon to eliminate field searches of potential predation sites that had a low probability of containing a kill.

METHODS

Locating Kill Sites and Identifying Prey Remains

I used an algorithm developed by Knopff et al. (2009) to identify potential predation sites of cougars in the Mt. Emily Wildlife Management Unit (WMU) in northeast Oregon (see Chapter 2 for study area description). Potential predation sites were identified as clusters of GPS locations based on the following criteria: ≥ 2 locations within 200 m occurring within 6 days of each other with additional locations added to the cluster if they were obtained within 6 days of the last location that was included in the cluster. To document predation events, I loaded the geographic coordinates of the geometric center of location clusters onto handheld GPS units (Garmin GPSMap 60csx; Garmin International, Inc., Olathe, KS, USA), hiked to clusters, and systematically searched the area for prey remains. After locating prey remains at a location cluster, I used available evidence to determine if the cougar had killed the prey item in question, and species, age class, and gender of prey (see Chapter 2 for additional methods). In the event I was unable to determine species, age class, or sex of prey, I recorded these attributes as unknown. I assigned a date to predation events using date of the first GPS location that was included in the cluster and assigned each predation event to summer (May – October) or winter (November – April). I selected the summer season to ensure that the following events all occurred: ungulate birth pulse, lack of snowpack throughout the study area, and emergence of black bears from their dens.

Development of a Predictive Model

My primary objective with developing a predictive model to identify cougar kills from GPS location clusters was to reduce the number of GPS location clusters that needed to be searched by field crews. Therefore, I developed predictive models following the first year I monitored cougars; however, my sample of males was small and I continued to monitor all clusters created by male cougars for the duration of the study, and only developed a predictive model for female cougars. I did not combine GPS location cluster data for male and female cougars because it was apparent attributes associated with GPS location clusters created by male cougars were different than those created by females. After initial monitoring of cougars, I noted that characteristics of clusters during summer (May – Oct) and winter (Nov – Apr) appeared to differ, which

was likely a function of increased prey size during winter (Chapter 2). Consequently, I developed a separate model for female cougars for each season.

I used logistic regression (Hosmer and Lemeshow 2000) to model presence or absence of a cougar kill at a GPS location cluster. GPS location clusters where a cougar killed ungulate was located were coded as kills (1) and those where nothing was located or non-ungulate prey was located were coded as a non-kill (0). Non-ungulate prey was coded as a non-kill because this type of predation event was rare and I was primarily interested in documenting kill rates and prey use of ungulate prey by cougars (Chapter 2). When developing the model, I censored GPS location clusters that were created immediately after capture (i.e., recovery areas) and those associated with nursery sites where females had kittens.

I developed a candidate set of models based on attributes of GPS location clusters that included: 1) corrected points (CP) – the number of locations obtained at the cluster divided by the fix rate success, 2) fidelity (FID) – the number of locations in the cluster minus the number of fixes away from the cluster, 3) average distance (AD) – the mean distance from locations in the cluster to the cluster center, 4) binary day period (BiDAY) – equal to 1 if > 24 hours were spent at the cluster and equal to 0 if < 24 hours were spent at the cluster, and 5) day period (DP) – the number of 24 hour periods with at least one location at the cluster. When developing the candidate model set, I used the following guidelines: 1) corrected points must be included in the model, 2) models would either include binary day period or day period, not both, and 3) an interaction term between corrected points and average distance would be considered, but no additional interaction terms would be modeled. I used Akaike's Information Criteria corrected for small sample sizes (AIC_c) to rank candidate models (Burnham and Anderson 2002). I used the difference between AIC_c of the best model and the ith model (ΔAIC_c) to identify closely competing models ($\Delta AIC_c \leq 2.0$; Burnham and Anderson 2002), but I used the best ranked model to distinguish between kills and non-kills.

Selection of Probability Cutoff

Many GPS location clusters that are created from location data of GPS collared cougars do not contain a kill and are associated with other activities (i.e., resting) (Knopff et al. 2009). Consequently, a large number of potential kill sites will not contain a kill

and substantial effort is required to search non-kill sites. I determined that it would be acceptable to miss ≤ 2% of cougar kills. To select an appropriate probability cutoff point at which to not search clusters with a probability below the cutoff, I determined at which probability level would result in ≤ 2% of kills being missed by calculating this value from the data used to create the initial model. This required assigning each GPS location cluster a probability of containing a kill, then determine at which probability 2% of kills would be missed. I also calculated the percentage of kills that would be missed and percentage of clusters removed under 3 arbitrary cutoff levels (e.g., 0.05, 0.10, and 0.15).

Field Validation of Models

Following creation of seasonal predictive models and associated probability level cutoffs, I began to collect data at low probability GPS location clusters to validate the predictive model. After GPS location data were processed and potential predation sites were identified, I randomly selected 1 cougar to search all GPS location clusters rather than just those clusters that had a probability above the cutoff level. This allowed independent evaluation of the predictive model to determine if a substantial number of kills would be missed over the course of the study. In addition to searching low probability clusters for a randomly selected female, I also opportunistically searched low probability clusters. This typically occurred when hiking into a high probability cluster and I was in the general area of a low probability cluster and stopped to search the cluster on my way to the high probability cluster. Finally, some GPS location clusters that were assigned a probability below the cutoff level were searched because based on a visual inspection of GPS locations it appeared a kill might be present at the site. This was a relatively rare occurrence; however, because I wanted to reduce the number of cougar kills that were undetected, I searched these clusters anyway.

To assess the predictive ability of the model, I calculated the number of kills that were located at GPS location clusters where the probability of detecting a kill was below the selected cutoff point. I was not concerned with validating the model where the GPS location cluster was assigned a value above the cutoff point because all clusters were searched anyway.

RESULTS

Seasonal Models

During summer, the best logistic regression model that differentiated between kill sites and non-kill sites of cougars included terms for the number of locations in the cluster (adjusted for fix success), fidelity to the cluster, average distance of locations from the geometric center, and an interaction between number of locations and average distance (Table C.1). The probability of finding a kill increased with the number of points in the cluster, fidelity at the cluster and the average distance of the cluster (Table C.2). The interaction term in the model indicated the probability of the GPS location cluster containing a kill was greater at location clusters with more locations that were close to the geometric center.

During winter, the best logistic regression model that differentiated between kill sites and non-kill sites of cougars included terms for the number of locations in the cluster (adjusted for fix success), fidelity to the cluster, average distance of locations from the geometric center, and an interaction between number of locations and average distance (Table C.3). The probability of finding a kill at a location cluster increased with the number of points in the cluster, fidelity at the cluster and the average distance of the cluster (Table C.4). The interaction term in the model indicated the probability of the GPS location cluster containing a kill was greater at location clusters with more locations that were close to the geometric center. The winter model was extremely similar to the summer model because the estimated effect of coefficients in the model was in the same direction; however, the size of the beta coefficient and significance of each effect varied between models.

Selection of Cutoff Points

During summer, a probability cutoff of 0.115 would allow approximately 20% of clusters to not be surveyed, while still being able to miss approximately 2% of ungulate kills (Table C.5). During winter, a probability cutoff of 0.06 would result in 31.3% of clusters not being searched and 0.0% of kills being missed by field crews (Table C.5). To reach the acceptable level of 2% of ungulate kills being missed due to not surveying clusters, a probability cutoff of 0.09 could be applied which would result in 42.9% of clusters being removed; however, this resulted in 6 scavenging events being missed.

Table C.1. Model selection results for logistic regression models that were used to identify kill sites of female cougars from Global Positioning System location data during summer (May – Oct) in northeast Oregon, USA.

Model	AIC	ΔAIC[a]	W_i[b]	Likelihood	K[c]
CP[d] + FID[e] + AD[f] + CP*AD[g]	395.62	0.00	0.30	1.00	4
BiDay[h] + CP + FID + AD + CP*AD	396.76	1.14	0.17	0.57	5
CP + FID + AD	397.12	1.50	0.14	0.47	3
DP[i] + CP + FID + AD + CP*AD	397.56	1.94	0.11	0.38	5
BiDay + CP + FID + AD	397.69	2.07	0.11	0.36	4
DP + CP + FID + AD	399.02	3.40	0.05	0.18	4
CP + FID	400.03	4.41	0.03	0.11	2
DP + CP + AD + CP*AD	400.58	4.96	0.03	0.08	4
BiDay + CP + FID	400.68	5.06	0.02	0.08	3
DP + CP + FID	401.84	6.22	0.01	0.04	3
DP + CP + AD	402.58	6.96	0.01	0.03	3
CP + AD + CP*AD	403.96	8.34	0.00	0.02	3
BiDay + CP + AD + CP*AD	404.61	8.99	0.00	0.01	4
CP + AD	406.01	10.39	0.00	0.01	2
BiDay + CP + AD	407.12	11.50	0.00	0.00	3
DP + CP	407.93	12.31	0.00	0.00	2
BiDay + CP	413.64	18.02	0.00	0.00	2
CP	413.86	18.24	0.00	0.00	1

[a] Difference in AIC between the best model and the current model.

[b] Akaike weight

[c] No. of parameters in the model

[d] Corrected points: the number of fixes divided by the proportion of successful fixes
[e] Fidelity: the number of fixes away cluster subtracted from the number of fixes at the cluster

[f] Average Distance: average distance of all points at the cluster from the cluster center

[g] Interaction between corrected points and average distance

[h] Binary Day: binary variable indicating 1-day or >1-day period spent at the cluster
[i] Day period: the number of 24-hour periods where at least one location was in the cluster

Table C.2. Estimated coefficient values for the best ranked logistic regression model used to identify kill sites of female cougars from Global Positioning System location data during summer (May – Oct) in northeast Oregon, USA.

Parameter	β	SE	p
Intercept	-3.453	0.459	< 0.001
CP[a]	0.691	0.110	< 0.001
FID[b]	0.073	0.025	0.003
AD[c]	0.003	0.008	0.710
CP*AD[d]	-0.003	0.002	0.058

[a] Corrected points: the number of fixes divided by the proportion of successful fixes
[b] Fidelity: the number of fixes away cluster subtracted from the number of fixes at the cluster
[c] Average Distance: average distance of all points at the cluster from the cluster center

[d] Interaction between corrected points and average distance

Table C.3. Model selection results for logistic regression models that were used to identify kill sites of female cougars from Global Positioning System location data during winter (Nov - Apr) in northeast Oregon, USA.

Model	AIC	ΔAIC[a]	W_i[b]	Likelihood	K[c]
CP[d] + FID[e] + AD[f] + CP*AD[g]	217.76	0.00	0.14	1.00	4
CP + AD + CP*AD	218.03	0.27	0.13	0.87	3
BiDay[h] + CP + FID + AD + CP*AD	218.57	0.81	0.10	0.67	5
BiDay + CP + FID	219.02	1.26	0.08	0.53	3
CP	219.10	1.34	0.07	0.51	1
CP + FID	219.37	1.61	0.06	0.45	2
DP[i] + CP + FID + AD + CP*AD	219.49	1.73	0.06	0.42	5
DP + CP + AD + CP*AD	219.49	1.73	0.06	0.42	4
BiDay + CP + AD + CP*AD	220.03	2.27	0.05	0.32	4
BiDay + CP + FID + AD	220.21	2.45	0.04	0.29	4
CP + FID + AD	220.28	2.52	0.04	0.28	3
CP + AD	220.62	2.86	0.03	0.24	2
DP + CP	220.85	3.09	0.03	0.21	2
DP + CP + FID	220.89	3.13	0.03	0.21	3
BiDay + CP	220.94	3.18	0.03	0.20	2
DP + CP + FID + AD	221.86	4.10	0.02	0.13	4
DP + CP + AD	222.16	4.40	0.02	0.11	3
BiDay + CP + AD	222.56	4.80	0.01	0.09	3

[a] Difference in AIC between the best model and the current model.

[b] Akaike weight

[c] No. of parameters in the model

[d] Corrected points: the number of fixes divided by the proportion of successful fixes

[e] Fidelity: the number of fixes away cluster subtracted from the number of fixes at the cluster

[f] Average Distance: average distance of all points at the cluster from the cluster center

[g] Interaction between corrected points and average distance

[h] Binary Day: binary variable indicating 1-day or >1-day period spent at the cluster

[i] Day period: the number of 24-hour periods where at least one location was in the cluster

Table C.4. Estimated coefficient values for the best ranked logistic regression model used to identify kill sites of female cougars from Global Positioning System location data during winter (Nov – Apr) in northeast Oregon, USA.

Parameter	β	SE	p
Intercept	-4.868	0.724	< 0.001
CP[a]	0.577	0.128	< 0.001
FID[b]	0.046	0.033	0.162
AD[c]	0.027	0.012	0.022
CP*AD[d]	-0.004	0.002	0.033

[a] Corrected points: the number of fixes divided by the proportion of successful fixes

[b] Fidelity: the number of fixes away cluster subtracted from the number of fixes at the cluster

[c] Average Distance: average distance of all points at the cluster from the cluster center

[d] Interaction between corrected points and average distance

Table C.5. Comparison of various probability level cutoffs to the optimal cutoff level used to distinguish between kill sites and non-kill sites of cougars at GPS location clusters during summer and winter in northeast Oregon, USA.

Probability level cutoff	Summer		Winter	
	% kills missed	% clusters removed	% kills missed	% clusters removed
0.050	0.0	2.2	0.0	23.2
0.060	NA[a]	NA[a]	0.0	31.3
0.100	1.1	11.2	3.0	48.4
0.115	2.1	20.2	NA[a]	NA[a]
0.150	7.4	40.9	6.9	65.3

[a] This probability cutoff level was not applied to the season because it was the optimum cutoff level for the other season.

Consequently, I took a conservative approach and applied a cutoff level of 0.06 because this allowed scavenging events to be detected while also documenting all kills made during winter. In both seasons, I could have applied a more aggressive cutoff level, which would have substantially reduced survey effort; however, as more aggressive cutoff levels are applied, a rapidly increasing number of kills would be missed (Table C.5). When applying my predictive model to clusters generated in subsequent seasons, I used a cutoff level of 0.115 and 0.06 during summer and winter, respectively.

Model Validation

After creation of a summer model to predict the presence of a kill at a GPS location cluster created by a cougar, a total of 68 clusters with a probability of containing a kill < 0.115 were searched. Prey remains were located at 8 of these clusters (11.7%); however, 4 of these clusters where kills were located would have been searched anyway based on a cluster of GPS locations in a centralized area. The fidelity term in the predictive model often caused clusters with a tight group of points to be given a low probability if 1 or 2 points were included in the cluster within 6 days of the tight cluster of points being created. I visually inspected clusters and associated locations in ArcGIS to ensure that low probability clusters that might contain a kill were also searched. Based on this, prey remains would have been located at 5.9% of clusters that were assigned a low probability of containing a kill. This was worse than expected based on my probability cutoff of 0.115, which was expected to result in only 2.1% of kills being missed (Table C.5). All kills that were missed were fawns. Based on the fact that there were 156 low probability clusters created by female cougars that were not searched, I likely would have missed approximately 9 fawns being killed by cougars during summer. I found a total of 219 fawns killed by female cougars during the course of the study (Chapter 2); consequently, I likely underestimated the percentage of fawns killed by female cougars by 4% (i.e., 219 out of 228 kills = 96% of fawns located).

After creation of a winter model to predict the presence of a kill at a GPS location cluster created by a cougar, a total of 43 clusters with a probability of containing a kill < 0.06 were searched. Kills were located at 2 of these clusters, suggesting 4.7% of kills were not located during the winter. This was surprising given that we should not have missed any kills based on a probability cutoff of 0.06 (Table C.5). However, 1 of these

kills would have been located because the female cougar was coming and going to the kill from a nursery site. The fidelity term in the model indicated many locations were away from the GPS location cluster, which caused the probability of a kill to decline. After accounting for this kill, only 1 kill would have been missed during the winter, which would result in 2.3% of kills being missed, and was close to the percentage of kills I was willing to miss. The remaining low probability cluster that contained a kill would likely not have been searched given the probability cutoff level I used. Although this cluster was in an area of several consecutive low probability GPS location clusters, the area was searched anyway and a kill was located.

DISCUSSION

My results highlight the benefit of using a predictive model to distinguish between kill sites and non-kill sites of cougars. The predictive model allowed between 20 – 30% of all GPS location clusters to be censored and not searched while missing 2 – 6% of known kills. The summer model performed worse than the winter model, but this was mostly attributable to missing newborn fawns during summer. Fawns weigh approximately 3 – 7 kg the first 2 months of life (Appendix B) and my model was designed to locate prey items > 8 kg (Knopff et al. 2009). Consequently, it was not surprising that I potentially missed fawns during the summer months. Despite this potential bias in kill rate and prey use estimates of female cougars, this bias was minimal because I still located approximately 96% of cougar killed fawns. This was similar to the results of Knopff et al. (2009) who found that field searches of potential kill sites could be reduced by as much as 25%, while sill locating >95% of all cougar kills.

The 2 seasonal models I developed included identical parameters (Tables C.1 and C.3) suggesting the same factors influence the probability of a GPS location cluster containing a kill. While the parameters in the model were the same, the values of estimated coefficients changed between seasons. One of the biggest changes between seasons was that during winter, more GPS locations needed to be included in the GPS location cluster for the kill site to be determined a kill. This was expected, because average prey size of cougars was greater during winter (Chapter 2), and handling times should be longer with larger prey (Knopff et al. 2009) resulting in an increased number of points in the GPS location cluster. Applying a separate model during winter allowed

many of the location clusters that contained 2 – 3 locations to be given a low probability of containing a kill and not be searched. This allowed approximately 10% more of the clusters to be censored during winter versus summer and highlights the benefit of creating seasonal models to predict presence of a kill, because prey use patterns may change over time resulting in different handling times between seasons.

I applied the Knopff et al. (2009) predictive model to the data set that I used to create a predictive model during the summer. When applying my initial probability cutoff level of 0.115, I found that I would miss approximately 13% of known kills and would miss 31% of known kills when applying the optimal cutoff level specified by Knopff et al. (2009) of 0.22. To ensure that only 2% of kills were missed, a cutoff level of 0.07 would need to be used during summer on my data set while running the Knopff et al. (2009) model, which would result in 14% of the clusters being removed by the probability cutoff level. Similar results were obtained when applying the Knopff et al. (2009) model to the data set used to create the predictive model I used during winter. While using my cutoff level of 0.06, only 2.9% of kills was missed, the model only censored 6.2% of the clusters. When applying the optimal cutoff level of 0.22 specified by Knopff et al. (2009) approximately 24% of kills were missed. When applied to their own data, the Knopff et al. (2009) model was able to reduce field visitation of clusters by approximately 25% while still locating > 95% of cougar kills. My findings suggest that predictive models developed in 1 landscape may not be broadly applicable to another landscape. While the parameters used to develop models were identical and reflected cougar behavior while at a kill site, other factors are likely not accounted for in the model. The average prey size killed by cougars in this study (Chapter 2) was smaller than those in Alberta, Canada (Knopff et al. 2010). Consequently, prey use patterns may have a profound impact on predictive models used to identify kill sites because handling times, and subsequently cougar behavior, likely vary as prey use patterns change. I suggest that future investigations of cougar prey use attempting to distinguish kill sites from GPS location clusters develop their own predictive model using preliminary data from their study area.

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Appendix D. Methods to Estimate the Number of Ungulates Available to Cougars in the Mt. Emily Wildlife Management Unit in northeast Oregon, USA.

DEER

I used end of winter herd composition data to determine the proportion of yearling, adult male, and adult female deer in the population at the start of summer. I then multiplied the total population size (4,800 mule deer, 2,500 white-tailed deer) by the proportion of the population that was adult females (mule deer = 0.632, white-tailed deer = 0.557) to calculate the number of adult females at the start of summer. To determine number of yearling and adult male deer in the population at the start of summer, I multiplied the adjusted end of winter buck to doe (31 bucks per 100 does for both species) and fawn to doe ratios (mule deer = 27.25 fawns per 100 does, white-tailed deer = 48.5 fawns per 100 does) by the number of adult females. I used a fecundity estimate of 1.5 fawns per adult doe to determine the number of fawns born at the start of the summer.

To determine the number of yearling and adult female deer at the start of winter, I multiplied a 6-mo survival rate for each age class by the number of individuals in the population during the summer. I obtained the 6-mo survival rate (0.922) of deer by taking the square root of the annual survival rates (0.85) of deer from published estimates (White et al. 1987, Unsworth et al. 1999, Bishop et al. 2005) because I did not have survival data for deer in northeast Oregon. I multiplied the end of hunting season buck to doe (mule deer = 18 bucks per 100 does, white-tailed deer = 21 bucks per 100 does) and fawn to doe ratios (mule deer = 32 fawns per 100 does, white-tailed deer = 58 fawns per 100 does) by the number of females at the start of winter to estimate the number of bucks and fawns in the population at the start of winter.

ELK

I multiplied the reported elk population estimate (2,850) by proportion of the surveyed population that was adult females (0.805) to calculate the number of adult females in the population at the start of summer. I multiplied the adjusted bull to cow (30 bulls per 100 cows) and the calf to cow ratio (13.25 calves per 100 cows) at the end of winter by the number of cow elk to determine the number of yearling and bull elk in the population at the start of summer. I multiplied the number of adult cow elk by the

pregnancy rate of 0.872, which was the average pregnancy rate of cow elk in northeast Oregon from 2002—2008 (B. Johnson, ODFW, unpublished data) to estimate the number of calves born into the population at the start of summer.

To determine number of calf, cow, and yearling elk at the start of winter, I multiplied the 6-mo survival estimate for calf, yearling, and cow elk by the number of elk in each age class at the start of summer. I assumed an annual survival rate of 0.89 for cow elk (6-mo survival = 0.943; ODFW, unpublished data) and 0.88 for yearling elk (6-mo survival = 0.938; Raithel et al. 2007). For elk calves, I used a 6-mo survival rate of 0.50 (Rearden 2005). To determine the number of adult bull elk in the winter population, I multiplied the adjusted end of winter bull to cow ratio (25 bulls per 100 cows) by the number of cow elk in the winter population. To account for legal hunting mortality of yearling male elk, prior to the start of winter, I assumed the ratio of yearling male to females would be 35:65.

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Appendix E.1. Graph of dates individual female cougars were monitored to determine predation rates and diet composition in northeast Oregon, USA from April 2009 through August 2011. Data is sorted by year and month. Blank cells indicate the cougar was not monitored during the particular month.

Cougar ID	2009									2010												2011							
	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A
C143										N[a]	N	N	N	N	Y[b]	Y	Y												
C145																							Y	Y	Y				
C146	O[c]	O	O	N	N	N	Y	N	N	N	N	Y	Y	Y	Y	Y	Y	Y	O	O									
C147	O	O	O	O	O	O	O	O	O	N	N	N	N	Y	Y	Y	Y	Y	Y	O	O	O	O	O	O	O	O	O	O
C149	O	O	O	O	O	O	N	N	N	N	N	N	N	N	N	Y	Y	Y	Y	Y	Y	O	O	O	O	O	O	O	
C150	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N													
C155		N	N	N	N	N	N																						
C158	N	N	N	N	N	N	Y	Y	Y	Y	Y	Y	O	O	O	O	O	O	O	O	O	O	O	O					
C160																									N	N	N	N	Y
C161									N	N	N																		
C163											N	N	N	N	N	N	Y	Y	Y										
C167													N	Y	Y	Y	Y	Y	Y	Y	O	O	O	O	O	O	O	O	O
C176													N	N	N	N	Y	Y	N	N		N[a]	Y	Y	Y	Y	Y	Y	
C187																				O	O	N	N	N	N	Y	Y	Y	
C193																							N	N	Y	N	N	N	N

[a] N: Indicates a female cougar that did not have dependent kittens present at the time of monitoring.

[b] Y: Indicates a female cougar that had kittens less than 6 months old present at the time of monitoring.

[c] O: Indicates a female cougar that had kittens greater than 6 months old present at the time of monitoring.

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Appendix E.2. Graph of dates individual male cougars were monitored to determine predation rates and diet composition in northeast Oregon, USA from April 2009 through August 2011. Data is sorted by year and month. Blank cells indicate the cougar was not monitored during the particular month.

Cougar ID	2009					2010												2011												2012		
	A	M	J	…	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
C156	X	X																														
C157	X	X																														
C162						X	X	X	X	X	X	X	X	X	X																	
C164							X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X		X	X		X	X	X
C166								X	X	X	X	X	X	X	X	X	X	X	X	X	X											
C192																	X	X	X	X	X	X	X	X	X	X	X					
C194																						X	X	X	X	X	X	X	X	X	X	X
C197																							X	X								
C201																												X	X	X	X	X

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Appendix F. Survival rates of cougar kittens in Oregon, USA.

INTRODUCTION

Population modeling is frequently used to estimate cougar (*Puma concolor*) population size and growth rates across regional scales. Age-specific survival estimates can profoundly improve the reliability of population models because increased variability incorporated in the model more accurately reflects population growth rates (Caswell 2001, Morris and Doak 2002). Adult cougars have greater survival rates than kittens and sub-adults (Ross and Jalkotzy 1992, Beier and Barrett 1993, Logan and Sweanor 2001), but reliable estimates of kitten survival are sparse because it is difficult to radiocollar a large number of kittens. My objective was to estimate survival rates of kittens to use in a Leslie matrix model to estimate population growth rates of cougars (Chapter 4).

METHODS

Cougar Capture and Monitoring

I investigated survival and assessed causes of mortality of cougar kittens at 3 study areas in Oregon between 1989 and 2011 (see Chapter 3 for study area descriptions). Cougar kittens were radiocollared at the Catherine Creek Wildlife Management Unit (WMU) from 1989-1996, the Jackson Creek study area from 1993-2002, and 3 contiguous WMUs in northeast Oregon (Wenaha, Sled Springs, and Mt. Emily; hereafter WSM) from 2002-2011. All cougar capture and handling procedures were outlined and approved by ODFW's wildlife veterinary, the Starkey Experimental Forest and Range, Animal Care and Use Committee (IACUC No. 92-F-0004), and followed guidelines of the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2011). Capture methods for kittens > 15 kg are outlined in Chapter 3 of this document. Cougar kittens were opportunistically captured at young ages (< 6 weeks) at nursery sites. When kittens were captured at nursery sites, they were physically restrained and fitted with an expandable very high frequency (VHF) radiocollar.

Fates of individual cougars were determined via radiotelemetry signals from the ground and fixed-wing aircraft. Frequency of aerial surveys varied by study, but typically occurred at least once every month. During each survey, the fates (live or dead) and approximate location of cougars were recorded. Cougars not located during telemetry flights were recorded as missing. If the fate of an individual was not

determined in subsequent flights, the cougar was right-censored from the data set. If the mortality sensor indicated the cougar died, the carcass was located as soon as possible to determine cause of death.

Survival Analysis

I estimated annual survival rates ($\hat{S}$) of cougars in program MARK using procedures for model development and selection outlined in Chapter 3. Most kittens (65%) were radiocollared at Jackson Creek, and number of kittens radiocollared in any 1 year was relatively small (e.g., < 10). Consequently, I pooled data from all study areas and years into 1 encounter history. Individuals were entered into the dataset according to their age (mo) at capture, and I estimated monthly survival rates of kittens from birth until age 1. I tested for differences in survival between genders and investigated constant (.), time varying (moAge), linear (Age), log-linear (lnAge), and quadratic (Age^2) relationships between kitten age (mo) and survival. I investigated additive (+) and interactive (*) relationships between sex and age when appropriate. To estimate annual survival rates of kittens, I calculated the product of age-specific (i.e., monthly) survival rates from 1 month to 12 months of age. The fates of cougar kittens from the same litter are likely dependent (Ruth et al. 2011), so I estimated an overdispersion parameter ($\hat{c}$) using the median $\hat{c}$ estimation technique in Program MARK. If my estimate of $\hat{c}$ was > 1.2 (Bishop et al. 2008) I adjusted $\hat{c}$ in Program MARK and used quasi-AIC$_c$ (QAIC$_c$) to rank my candidate model set (Burnham and Anderson 2002).

RESULTS

Monitoring and Causes of Mortality

The majority of kittens were monitored at the Jackson Creek study area ($n = 47$; 65%) followed by Catherine Creek ($n = 17$; 8%) and WSM ($n = 8$; 5%), and the sample of radiocollared kittens included more females ($n = 42$; 58%) than males ($n = 30$; 42%). Individual kittens were monitored a total of 432 months. Mean age of kittens at capture was 5.9 ($\pm$ 0.3 SE) months, and individuals were monitored an average of 6.0 ($\pm$ 0.3 SE) months. Nine (3 females, 6 males) kittens died before they were 1 year of age. Causes of mortality for kittens included natural causes ($n = 8$) and wounding loss ($n = 1$). Natural causes of mortality included infanticide ($n = 5$), injuries ($n = 2$), and disease ($n = 1$).

Survival

My estimate of the overdispersion parameter, $\hat{c}$, was 1.68, which indicated a small lack of independence in the data set; consequently, we used $QAIC_c$ to rank our candidate set of models for kittens. The best survival model for kittens was S(Age) (Table F.1), which indicated survival increased in a linear manner with age ($\hat{\beta} = 0.22$, 95% CI = -0.06 – 0.51; Fig. F.1) and resulted in an annual survival estimate of 0.66 (95% CI = 0.42 – 0.84; Fig. F.1). The estimated effect of age on kitten survival appeared to be a log-linear trend because Program MARK constrains parameter estimates between 0 and 1. The estimated effect of age on kitten survival was weak because the beta coefficient slightly overlapped 0. This marginal relationship was likely attributable to few young cougars (i.e., < 3 months old) included in our sample. The majority of our candidate model set was considered competing with our best model (Table F.1); however, most of these models included a variation in the effect of age on kitten survival (e.g., Age^2 and lnAge models), or they included an effect of sex where the beta coefficient broadly overlapped 0. No evidence existed for differences in survival between male and female kittens as all models that included gender were ranked below S(.), and confidence intervals for the effect of gender broadly overlapped 0, so models that included an effect of gender were not considered further. The second ranked model indicated no effect of age on survival (S(.)) (Table F.1), resulting in an annual survival estimate of 0.78 (95% CI = 0.62 – 0.88), which was slightly higher but within the 95% confidence intervals of the estimate from the best model. The best model was only slightly better than the model for no effect of age with an Akaike weight of 0.17 versus 0.14.

Table F.1. Model selection results for cougar kitten survival (S) in Oregon, USA. Models are ranked according to quasi-Akaike's Information Criteria corrected for small sample sizes ($QAIC_c$).

Model[a]	$QAIC_c$	$\Delta QAIC_c$	w_i[b]	Likelihood	K[c]
S(Age)	53.69	0.00	0.17	1.00	2
S(.)	54.02	0.33	0.14	0.85	1
S(Sex + Age)	54.28	0.59	0.12	0.74	3
S(lnAge)	54.37	0.68	0.12	0.71	2
S(Sex)	54.49	0.81	0.11	0.67	2
S(Sex + lnAge)	54.97	1.29	0.09	0.53	3
S(Age^2)	55.32	1.63	0.07	0.44	3
S(Sex * Age)	55.55	1.86	0.07	0.39	4
S(Sex + Age^2)	55.88	2.19	0.06	0.33	4
S(Sex * lnAge)	56.51	2.82	0.04	0.24	4
S(Sex * Age^2)	58.94	5.25	0.01	0.07	6
S(Sex + moAge)	66.02	12.33	0.00	0.00	13
S(Sex * moAge)	86.23	32.54	0.00	0.00	24

[a] Model notation: Age = survival follows a linear trend based on kitten age, . = constant survival across all months, Sex = gender of kitten, lnAge = survival follows a log-linear trend based on kitten age, Age^2 = survival follows a quadratic trend based on kitten age, moAge = survival varies by age (mo) of kitten.
[b] Akaike weight.
[c] No. parameters in model.

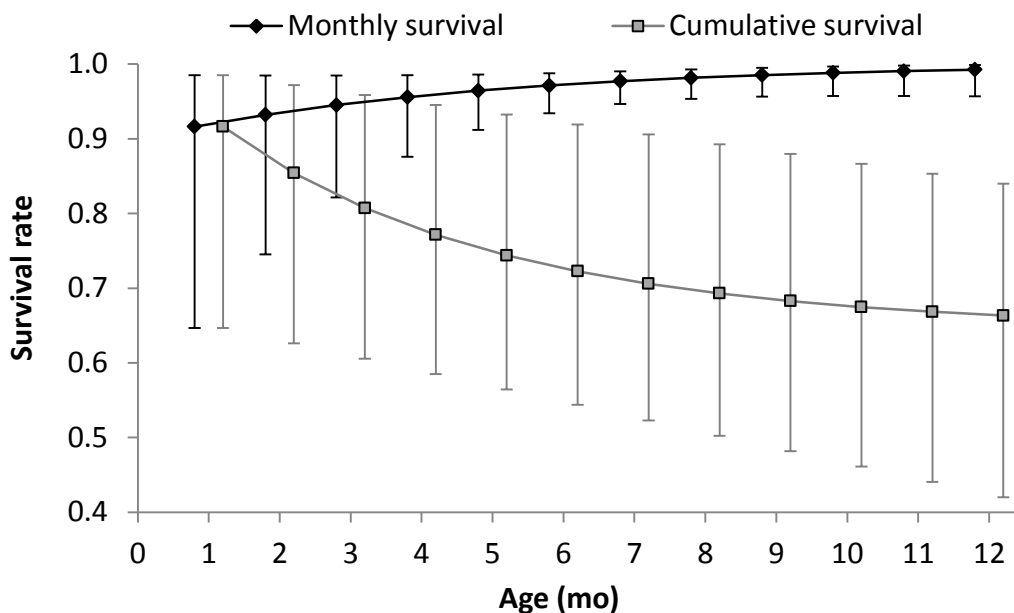Figure F.1. Estimates of monthly survival rates and cumulative survival probabilities and 95% confidence intervals of cougar kittens in Oregon, USA from birth to 12 months of age. To estimate survival rates, I used information from 72 kittens that were radiocollared between 1989 and 2011. Estimates were generated using model S(Age) which indicated survival of kittens increased in a linear manner with age (mo.).

DISCUSSION

In the most comprehensive study of kitten survival ($n = 157$), annual survival rates were estimated to be 0.64 (Logan and Sweanor 2001), which was similar to my estimate of 0.66 (SE = 0.11). My estimated annual survival rate of kittens is slightly higher than those reported in California (0.45 – 0.52; Beier and Barrett 1993), Greater Yellowstone Ecosystem (GYE; 0.50; Ruth 2004), Montana (0.42; DeSimone and Semmens 2005), and Washington (0.57; Lambert et al. 2006, 0.59; Robinson et al. 2008, 0.31 – 0.72; Cooley et al. 2009a, b) but substantially lower than those reported in Alberta (0.98; Ross and Jalkotzy 1992). The latter estimate from Alberta was likely positively biased because age at first monitoring was well into the first year of the kitten's life (6-8 months) and early causes of mortality were likely not accounted for.

The increasing trend of kitten survival with age that I observed was previously documented in New Mexico and the GYE (Logan and Sweanor 2001, Ruth et al. 2011). Nursery sites serve as a center point of activity for mothers, and this area of high activity may attract predators to the nursery site increasing susceptibility of immobile kittens to predation (Logan and Sweanor 2001). Predation risk of kittens likely decreases with age as kittens grow and are better able to escape predators. My results supported this hypothesis because I did not document any kittens being killed by predators after 8 months of age. Kittens may have increased risk of injury associated with navigating rugged terrain early in life, which may contribute to increased mortality (Logan and Sweanor 2001). During this study, 2 kittens died from injuries. These kittens were 6 and 8 months of age and died of a broken leg and natural trauma, respectively.

My estimate of kitten survival may be widely applicable to areas where adult female survival is high even though most of the kittens in my analysis were monitored at Jackson Creek in southwest Oregon. I believe this to be the case because (1) infanticide was the most common cause of death at Jackson Creek, similar to previous studies (Beier and Barrett 1993, Logan and Sweanor 2001, Ruth et al. 2011), and (2) I expect infanticide to be the primary cause of kitten mortality throughout North America, allowing my estimates to be widely applicable so long as female survival is sufficiently high to prevent orphaning of young kittens. Given that harvest of spotted kittens in Oregon is illegal (ODFW 2006), it is unlikely that harvest would have a substantial direct

influence on kitten survival. Harvest of adult females, resulting in the orphaning of kittens can occur, but current survival of adult females in Oregon are some of the highest reported (Chapter 3) suggesting this will not be a significant factor influencing kitten survival.

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Appendix G. Survival Rates of Radiocollared Female Elk in Northeast Oregon, USA from 2002 – 2007.

INTRODUCTION

        Population growth of elk (*Cervus canadensis*) is most sensitive to changes in adult female survival (Raithel et al. 2007); consequently, developing estimates of adult female survival and documenting sources of mortality are critical to understanding population dynamics and implementing effective management of elk populations. Furthermore, estimates of age-specific survival can greatly improve the reliability of population models because the increased variability incorporated in the model more accurately predicts population growth rates (Caswell 2001, Morris and Doak 2002). Patterns in age-specific survival of female ungulates have previously been documented (Loison et al. 1999, Gaillard et al. 2000, Solberg et al. 2000, Festa-Bianchet et al. 2003), so determining the effect of age-specific survival is critical for developing reliable population models. As part of the study to estimate survival of juvenile elk, ODFW placed radiocollars on female elk and monitored fates of individuals annually. My objective was to estimate annual, age-specific survival rates of female elk in northeast Oregon to use in a Leslie projection matrix.

METHODS

Study Area

        Survival of female elk was investigated in the Wenaha and Sled Springs WMUs located in the Blue Mountains of northeast Oregon. Further description of the study area can be found in Chapter 5. Recreational hunting of female elk was limited during the study and was primarily restricted to Sled Springs. Within the areas used by radiocollared female elk, an average of 156 (range = 144 – 176) centerfire rifle hunting tags were issued annually in the Sled Springs and Wenaha WMUs. Additional hunting tags were issued in each unit; however, these tags were issued in areas that were not used by radiocollared elk. No archery tags were issued for female elk in the Wenaha WMU during the course of the study. Approximately 212 any elk and 166 spike male or female elk archery tags were issued annually in the Sled Springs WMU during the course of the study; however, it was unlikely that all of the tag holders hunted in areas that were used by radiocollared elk. Hunting by members of the Nez Pierce tribe was also allowed by

treaty rights, but the number of hunters utilizing the study area on an annual basis was unknown.

Elk Capture and Monitoring

Female elk were captured by ODFW employees according to procedures approved by the Starkey Experimental Forest and Range, Animal Care and use Committee (IACUC No. 92-F-0004) and followed the American Society of Mammalogists guidelines for use of wild mammals in research (Sikes et al. 2011). Female elk were captured between November 2001 and March 2007. Elk were captured from a helicopter and were immobilized with a mixture of carfentanil citrate (3.6 mg) and xylazine hydrochloride (100 mg) administered via a dart gun. Elk were administered naltrexone hydrocholoride (360 mg) and yohimbine hydrochloride (25 mg) as antagonists for carfentanil and xylazine, respectively. Prior to release, elk were administered injections of penicillin, vitamin E/selenium, vitamin B, and 8-way *Clostridium* vaccine. In addition, a canine tooth was extracted from each female the first time they were captured to determine age through cementum annuli analysis (Fancy 1980). Female elk ≥ 2 years old were marked with a very high-frequency (VHF) radiocollar equipped with a mortality sensor.

Fates of individual female elk were monitored from fixed-wing aircraft at least once per month; however, every elk was not located every flight due to inclement weather. During each flight, the fate (live or dead) and approximate location of elk was recorded. I was interested in estimating annual survival rates of elk and attempted to confirm fates of individual elk at the end of each calendar year. If the fate of an individual elk could not be determined at the end of the year and in subsequent flights, the elk was censored from the data set for that year. If the radiocollar indicated the elk was dead (i.e., the pulse rate of the transmitter doubled), field crews located the carcass or remains of the elk as soon as possible to determine the cause of death. Radiocollars from harvested elk were typically returned to a local ODFW office where the date and approximate location of harvest was recorded. In some instances, harvest was determined to be the cause of death because the radiocollar had been cut with a knife and the collar was left in the field.

Survival Analysis

I estimated annual survival rates ($\hat{S}$) of elk in program MARK using known-fate models for radio-marked individuals (White and Burnham 1999). Methods used to develop and select models are described in Chapter 3. I determined fates of individual elk on an annual basis (1 Jan – 31 Dec). Individuals were entered into the dataset the year they were first captured and censored during any year where they were not monitored the entire year. I conducted 2 separate analyses of female survival. In the first analysis, all radio-collared elk were included. To obtain a survival rate in the absence of hunting mortality, I censored elk that were legally killed by hunters, poached, or wounded and not recovered by hunters. I censored individuals from the analysis rather than right censoring data during the year the animal was harvested. Collared elk that were typically recaptured multiple years to assess pregnancy status. In both analyses, elk that died due to handling related mortality were right censored during the year they died.

For each analysis, I modeled survival using a two-step process. First, I developed a set of candidate models based on biologically plausible hypotheses to test for differences in survival between study areas over time. My primary objective with this portion of the analysis was to develop a null model upon which I could model effect of age on female elk survival. I first compared a model that indicated there were differences in survival between study areas S(Area) and a model that indicated survival was similar between study areas S(.). If the model that indicated differences in survival between study areas was ranked higher than the intercept only model, I then modeled all possible additive (+) and interactive (*) combinations of study area and time, including time varying (t), linear (T), log-linear (lnT), and quadratic (TT) trends over time. If the intercept-only model ranked higher than the study area model, I ran all possible time varying models listed above without the effect of study area included in the model. After determining the best model that included temporal or study area effects, I modeled effect of cougar density (cougars/100 km^2) on female elk survival. Cougar densities were estimated annually for each study at the start of each biological year (i.e., 1 June). For further description of the methods used to estimate cougar densities see Johnson et al. (2013). I assumed effect of cougar density would be the same every year (i.e., no temporal variation), so I modeled cougar density as a constant effect over time but

allowed cougar densities at each study area to change each year. Cougar density was added as an additive effect with the best temporal and study area effects model. If the model that included cougar density was ranked lower than the best model, I concluded there was no effect of cougars on female elk survival.

The second step of my analysis was to model effect of age on female survival. I used the best ranked model from the first portion of my analysis and modeled age as an individual covariate, where each elk was assigned an age (yr) each year they were monitored. Ages of individual elk were determined at the time of initial capture and ages in subsequent years were extrapolated from this starting point. I considered 3 separate functional relationships for age: linear (Age), log-linear (lnAge), and quadratic (Age^2). If the base model indicated there were differences in survival between study areas, I considered all possible combinations of additive (+) and interactive (*) relationships between study area and age. I assumed the effect of age would be the same every year (i.e., no temporal variation), so I modeled age as a constant effect over time but allowed ages of individual elk to change each year.

RESULTS

Monitoring and Sources of Mortality

The sample of radiomarked female elk included 46 and 54 at Wenaha and Sled Springs, respectively. After harvest mortality was censored, the sample of radiomarked female elk included 40 and 47 at Wenaha and Sled Springs, respectively. From 2002-2007, 35 female elk died, and more died at Sled Springs ($n = 21$) than at Wenaha ($n = 14$). Cougars were the primary source of mortality ($n = 16$; 46%) overall and at both study areas (Wenaha = 7, Sled Springs = 9). Hunter harvest and associated mortality from animals that were not recovered by hunters (i.e., wounding loss) was the second most common source of mortality ($n = 13$; 37%). Two elk died of natural causes other than predation at Sled Springs, but this type of mortality was not observed at Wenaha. The cause of death could not be determined for the remaining mortalities (Wenaha = 1, Sled Springs = 3).

Survival

All mortality sources.—The best model that did not include an age-specific covariate was S(.) (Table G.1). Interpretation of this model was that annual survival of female elk was

equal between study areas and did not vary with time ($\hat{S}$ = 0.88, 95% CI = 0.84 – 0.92; Fig G.1a). While 3 models were considered competing with model S(.) (i.e., within 2 AICc units), these models were not considered further. The model that included an effect of study area had a beta coefficient that broadly overlapped 0 ($\hat{\beta}$ = 0.38, 95% CI = -0.34 – 1.11), which indicated there was little support for difference in survival between study areas. All models that included a temporal effect on female elk survival [i.e., S(T), S(lnT), and S(TT)] ranked lower than the model that indicated constant survival over time S(.) (Table G.1). Model S(T) was the best ranked temporal effects model, but the 95% confidence interval for beta coefficient for the effect of a linear trend in survival over time broadly overlapped 0 ($\hat{\beta}$ = -0.05, 95% CI = -0.27 – 0.16) indicating no support for this effect. There was no evidence to indicate cougar density had an effect on female elk survival because the model that included an effect of cougars ranked lower than the model the indicated constant survival S(.) (Table G.1).

The best model for the analysis of female survival that included all elk regardless of the source of mortality was S(Age) (Table G.1). Interpretation of this model was that female elk survival declined with increasing age in a linear fashion ($\hat{\beta}$ = -0.09, 95% CI = -0.19 – 0.00; Fig. G.1b); however this effect was marginally supported by the data because the beta coefficient barely overlapped zero. The estimated linear effect of age on elk survival appears to be non-linear when graphed, but this occurs because survival at young ages is approaching 1.0, and Program MARK constrains parameter estimates between 0 and 1. Two other models that included an effect of age (i.e., lnAge and Age^2) were competitive with the best model. The three top models that included the effect of age accounted for 64% of the AIC_c weight, which provided additional support for the effect of age on female survival. I did not consider the competing models further because these models described a similar relationship as the best model, but did not fit the data as well as the best model.

Table G.1. Model selection results for survival of adult female elk in northeast Oregon, USA during 2002 - 2007. Analysis included all elk that were fitted with a VHF radiocollar.

Model	AIC_c	ΔAIC_c[a]	W_i[b]	Likelihood	K[c]
S(Age)	216.49	0.00	0.28	1.00	2
S(Age^2)	217.52	1.03	0.17	0.60	3
S(lnAge)	217.72	1.23	0.15	0.54	2
S(.)	218.15	1.66	0.12	0.44	1
S(Area)	219.09	2.60	0.08	0.27	2
S(T)	219.91	3.42	0.05	0.18	2
S(lnT)	219.95	3.46	0.05	0.18	2
S(Cougar)	219.96	3.48	0.05	0.18	2
S(t)	221.60	5.11	0.02	0.08	6
S(TT)	221.95	5.46	0.02	0.07	3

[a] Difference in AIC_c between the listed model and the model with the lowest AIC_c

[b] Akaike weight of the listed model

[c] No. of parameters in the model
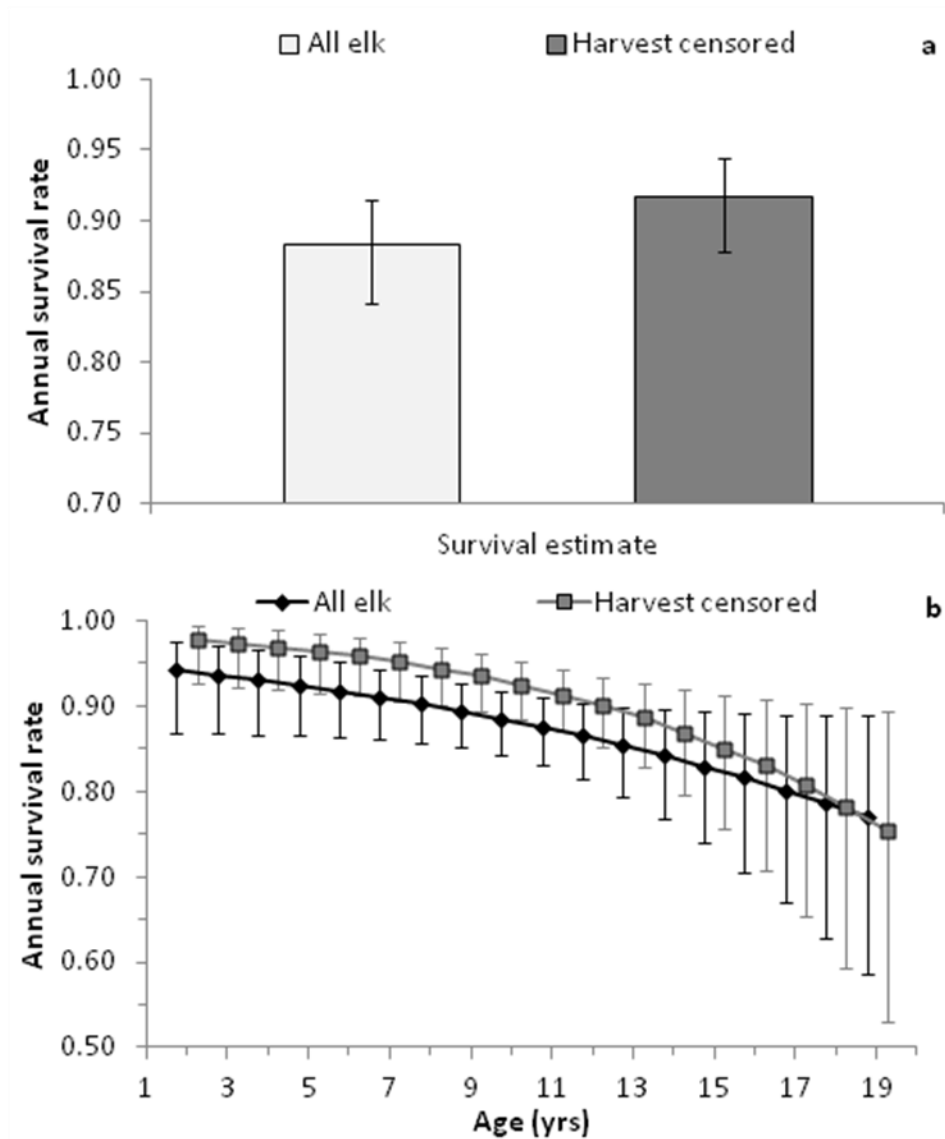
Figure G.1. Annual survival rates of female elk in northeast Oregon, USA (a) without effect of age and (b) with effect of age included. Two separate analyses of survival were conducted. In the first analysis, all radiocollared female elk were included in the analysis, and in the second analysis, elk that were harvested by hunters were censored from the data set. For both analyses, I used model S(.) to estimate survival rates without the effect of age, and model S(Age) to estimate age-specific survival rates.

Hunting mortality censored.—The best model that did not include effect of age on female survival when hunting mortality was censored was S(.) (Table G.2). Interpretation of this model was that annual survival of female elk was equal between study areas and constant over time ($\hat{S}$ = 0.92, 95% CI = 0.88 – 0.94; Fig G.1a). This model was similar to the best model for the analysis where all radiocollared elk were included in the encounter history, but the point estimate of survival was approximately 0.04 greater when hunting mortality was censored. There were 2 models that were considered competing with model S(.) [S(Area) and S(lnT); Table G.2]; however, these models were not considered further because neither the effect of study area nor a temporal effect were well supported by the data. The model that indicated survival differed by study area S(Area) had a beta coefficient that broadly overlapped 0 ($\hat{\beta}$ = 0.56, 95% CI = -0.38 – 1.50), which indicated there was no support for differences in survival between study areas. The best ranked model that included a temporal effect on female survival was S(lnT) which indicated a log-linear trend over time; however this effect was not supported by the data because the 95% confidence interval for beta coefficient broadly overlapped 0 ($\hat{\beta}$ = 0.22, 95% CI = -0.50 – 0.94), and this model was ranked below the model that indicated constant survival S(.) (Table G.2). There was no evidence to indicate cougar density had an effect on female elk survival because the model that included an effect of cougars ranked lower than the model the indicated constant survival S(.) (Table G.2).

The best model in the analysis that censored individuals killed directly or indirectly by hunters was S(Age) (Table G.2). Interpretation of this model was that female survival declined in a linear manner with increasing age ($\hat{\beta}$ = -0.15, 95% CI = -0.27 – -0.03; Fig. G.1b). As explained above, the linear effect of age on elk survival appears to be non-linear when graphed because Program MARK constrains parameter estimates between 0 and 1. The observed effect of age in this analysis was stronger than when all elk were included in the analysis because the beta coefficient for the effect of age did not overlap 0. All models that included an effect of age were competitive with the best model and accounted for 86% of the AIC_c weight, which provided additional support for the effect of age on female elk survival. I did not consider the competing models further because these models described a similar relationship as the best model, but did not fit the data as well.

Table G.2. Model selection results for survival of adult female elk in northeast
Oregon, USA during 2002 - 2007. Female elk that were harvested by hunters were
censored from the analysis.

Model	AIC_c	ΔAIC_c[a]	W_i[b]	Likelihood	K[c]
S(Age)	149.37	0.00	0.44	1.00	2
S(lnAge)	150.85	1.48	0.21	0.48	2
S(Age^2)	151.00	1.64	0.19	0.44	3
S(.)	153.81	4.45	0.05	0.11	1
S(Area)	154.36	4.99	0.04	0.08	2
S(Cougar)	155.31	5.95	0.02	0.05	2
S(lnT)	155.49	6.12	0.02	0.05	2
S(T)	155.69	6.32	0.02	0.04	2
S(TT)	157.42	8.06	0.01	0.02	3
S(t)	159.62	10.26	0.00	0.01	6

[a] Difference in AIC_c between the listed model and the model with the lowest AIC_c

[b] Akaike weight of the listed model

[c] No. of parameters in the model

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Appendix H. Evaluation of the Efficacy of Baited Hair Snares to Obtain Hair Samples from Cougars in the Mt. Emily Wildlife Management Unit in Northeast Oregon.

INTRODUCTION

Cougars (*Puma concolor*) are solitary, long-lived, wide-ranging, and secretive animals (Logan and Sweanor 2001), which makes accurate estimation of their populations difficult (Anderson and Lindzey 2005, Choate et al. 2006). Currently, intensive marking of cougars with radio-collars, in an effort to census the population, is the most effective method for estimating population size (Choate et al. 2006); however, this method is extremely labor intensive and highly invasive to cougars. Mark-recapture population estimators have been used to estimate cougar populations (Anderson and Lindzey 2005) but they are subject to underlying model assumptions, which are typically not met. In particular, the geographic closure assumption is rarely met for wild animal populations (Otis et al. 1978, Seber 1986, Eberhardt 1990), and the equal capture effort and catchability assumption will not be met because cougar capture relies on suitable snow conditions, which are variable in space and time (Anderson and Lindzey 2005, Choate et al. 2006). Additional methods that have been used to estimate or index cougar populations include: road snow track surveys (Van Dyke et al. 1986), aerial snow track surveys (Van Sickle and Lindzey 1991), quadrat sampling track counts (Smallwood and Fitzhugh 1995), catch per unit effort estimators, and hunter harvest indices (Choate et al. 2006). However, most of these methods have proven ineffective or have been biased and/or imprecise.

Non-invasive population estimates are a desirable alternative to invasive methods because they often require reduced labor requirements which make them more cost-effective, and they do not subject animals to undo stress from capture. In particular, DNA-based capture-recapture methods using hair samples have become common for estimating abundance of mammalian predators (Woods et al. 1999, Mowat and Strobeck 2000, Triant et al. 2004, Immell and Anthony 2008). However, these methods are dependent upon obtaining a sufficiently large sample of DNA from individuals, and the success of hair snares to collect cougar hair samples has varied. The National Lynx Survey used scented, barbed rub pads to collect lynx (*Lynx canadensis*) hair, and using this method they collected nearly as many cougar samples as lynx samples (Kendell and

McKelvey 2008). Barbed wire, strung across highway underpasses, successfully obtained hair samples from three of five cougars observed using the underpasses (Clevenger and Waltho 2005). In contrast, hair snares had a low probability of obtaining cougar hair in Yellowstone National Park (Sawaya et al. 2005) and northeast Utah (Choate et al. 2006), or failed to collect hair samples from cougars known to be present (Kendell and McKelvey 2008). Given the mixed success of obtaining hair samples from cougars, I implemented a pilot study using a sample of 25 hair snare stations to obtain hair samples from cougars. The objective of this pilot study was to determine the efficiency of hair snares to obtain a genetic sample from cougars.

METHODS

I conducted this pilot study within the home-ranges of 5 GPS-collared cougars in the Mt. Emily Wildlife Management Unit (WMU; see Chapter 2 for study area description). I followed methods of McDaniel et al. (2000) when constructing hair snares. Each hair snare consisted of a 10x10 cm carpet pad with 9 to 10 barbed nails, which served as a hair snaring device, driven through the back of the carpet pad (Fig. H.1). On each snare I applied a scent lure that consisted of a mixture of beaver (*Castor canadensis*) castoreum and catnip oil mixed in a 1:32 ratio. Propylene glycol and glycerin oil were added to the scent lure to prevent the lure from freezing or drying. I mixed the scent lure with the propylene glycol and glycerin oil in a 6:1:1 ratio, and applied approximately 12 ml of the scent lure to each hair snare.

Within the home-range of 5 GPS-collared cougars, I identified a road that traveled through the individual's home-range. I systematically selected a segment of the road within each GPS collared cougars home-range that did not pass through private property, was at least 5 km long and completely contained within the home-range. I selected road segments within the home-ranges of GPS collared cougars rather than randomly selecting road segments throughout the study area so that I could identify instances where a collared cougar was near a hair snare but did not interact with the snare. After selecting a road segment that ran through the cougars home-range, I then created a transect that was 200 m from the road and ran parallel to the road. Next, I placed a point at the start of the transect line and placed additional points on the transect using a 1 km spacing. This often led to more than 5 points being placed on each transect. Consequently, I randomly

Figure H.1. Scented carpet pad, with barbed nails pushed through the carpet that was used in an attempt to obtain hair samples from cougars in the Mt. Emily Wildlife Management Unit in northeast Oregon, USA.

selected 1 point on the transect line to use as a starting point and selected the 4 closest, adjacent points along the transect line to make up the sample of scent stations within each home-range.

Using a handheld GPS unit, I hiked to the geographic coordinates of each hair snare station. If I discovered that the scent stations were located in open areas, I located the forested area that was closest to the original location and placed the hair snare in the forested area. When I originally established hair snare locations, I avoided placement on private property; consequently, I did not need to move hair snares because they were near human development. At each station, I nailed a hair snare to a tree that was closest to the geographic coordinates of the station. The hair snare was placed 60-66 cm off the ground to facilitate cranial rubbing behavior (Reiger 1979). I also hung an aluminum pie pan from a tree branch near the hair snare (i.e., within 5 m), approximately 1.5 m off the ground, to serve as a visual attractant (Fig. H.2). I cleared the area surrounding the tree of vegetation and cleared the snow of existing tracks so that animals that approached the hair snare would leave an identifiable track. I revisited hair snares 3 times at approximately 2 weeks intervals. Upon each visit I recorded presence of tracks in the area and if hair was present on the snare. Hair snares were replaced with a fresh scent lure each time I revisited them, and I left old scent lures in the area to increase amount of lure present. I used location data from GPS-collared cougars to determine if a cougar was in the vicinity of the hair snare, but did not approach the snare.

Figure H.2. Hair snare station with a baited hair snare attached to a tree with a pie pan dangling from an adjacent tree to serve as a visual attractant. The hair snare is circled in the picture.

RESULTS AND DISCUSSION

I placed 3 sets of 25 scented hair snare stations out for a minimum of 2 weeks per trapping set (Table H.1). I obtained a total of 1,190 trap-nights of data with an average of 47.6 trap-nights per station. During this time, I did not obtain hair samples from any species. On one occasion I observed cougar tracks approaching a hair snare station (Table H.2); however, when the cougar was approximately 5 m from the station, the cougar abruptly turned and traveled away from the station. Bobcat (*Lynx rufus*) tracks were observed within 10 m of hair snare stations on 4 separate occasions, but hair was not obtained on the snare (Table H.2). On 10 occasions, a location from a GPS-collared cougar was obtained within 300 m of a hair snare station (Table H.3). However, there was no evidence (e.g., tracks) that these cougars approached the hair snares in any of these 10 occasions. Results from this study and others (Sawaya et al. 2005, Choate et al. 2006, Kendell and McKelvey 2008) indicated that hair snares, baited with a beaver castoreum and catnip oil mixture are ineffective at attracting and obtaining hair samples from cougars. One alternative to a beaver castoreum and catnip oil scent lure is a pheromone based lure. Pheromone based lures have successfully obtained 10 genetic samples from cougars in an area of extremely low cougar density in Quebec and New Brunswick (M. Gauthier, Envirotel 3000, Inc., Sherbrooke, Quebec, personal communication). However, pheromone lures are expensive ($100 per station per set) and would likely be cost prohibitive to implement on a large scale. For example, to cover 10% of the Mt. Emily WMU with a grid of pheromone based scent stations spaced at 1 km intervals for 3 trapping occasions would cost $60,000 in pheromone lures alone. Furthermore, it is unknown at this time if pheromone lures have an equal probability of attracting female and male cougars, or if they would be biased towards male cougars (M. Gauthier, Envirotel 3000, Inc., Sherbrooke, Quebec, personal communication). Other low cost, commercially available, lures (e.g., Pacific Call[TM], Hawbacker's Lure #1[TM], BB1[TM], and Cat Passion[TM]) were ineffective at attracting lynx (McDaniel et al. 2000), and would also likely be ineffective at attracting cougars. Therefore, it was apparent a cost effective method to obtain hair samples from cougars does not currently exist. Consequently, I did not deploy hair snares on a large spatial scale to estimate the cougar population in the Mt. Emily WMU.

Table H.1. Dates of deployment and retrieval for a sample of 25 hair snares, deployed over 3 trapping occasions in the Mt. Emily Wildlife Management Unit in northeast Oregon.

| Station | Snare Set 1 | | Snare Set 2 | | Snare Set 3 | | Total |
	Deployed	Retrieved	Deployed	Retrieved	Deployed	Retrieved	Trap Days
1852 4-8	12/23/09	1/10/10	1/10/10	1/23/10	1/23/10	2/9/10	49x5 = 245
1854 3-7	12/23/09	1/10/10	1/10/10	1/23/10	1/23/10	2/9/10	49x5 = 245
1848 2-6	12/24/09	1/8/10	1/8/10	1/21/10	1/21/10	2/4/10	43x5 = 215
1853 3-7	12/24/09	1/8/10	1/8/10	1/21/10	1/21/10	2/15/10	54x5 = 270
1846 1-5	12/24/10	1/8/10	1/8/10	1/21/10	1/21/10	2/4/10	43x5 = 215

Table H.2. Tracks observed and hair samples present at 25 hair snare stations deployed over 3 trapping occasions in the Mt. Emily Wildlife Management Unit in northeast Oregon.

	Snare Set 1		Snare Set 2		Snare Set 3	
Station ID	Tracks	Hair Present	Tracks	Hair Present	Tracks	Hair Present
1852-4	---	No	---	No	---	No
1852-5	---	No	---	No	---	No
1852-6	---	No	---	No	---	No
1852-7	---	No	---	No	Bobcat	No
1852-8	---	No	---	No	---	No
1854-3	---	No	---	No	---	No
1854-4	---	No	---	No	---	No
1854-5	---	No	---	No	---	No
1854-6	Bobcat	No	---	No	---	No
1848-2	Bobcat	No	---	No	---	No
1848-3	---	No	---	No	---	No
1848-4	---	No	---	No	---	No
1848-5	Cougar	No	Bobcat	No	---	No
1848-6	---	No	---	No	---	No
1853-3	---	No	---	No	---	No
1853-4	---	No	---	No	---	No
1853-6	---	No	---	No	---	No
1853-7	---	No	---	No	---	No
1846-5	---	No	---	No	---	No
1846-4	---	No	---	No	---	No
1846-3	---	No	---	No	---	No
1846-2	---	No	---	No	---	No
1846-1	---	No	---	No	---	No

Table H.3. Documented instances where a GPS-collared cougar was within 300 m of a hair snare station in the Mt Emily Wildlife Management Unit in northeast Oregon, USA.

Event No.	Station ID	Cougar ID	Date	Distance from Station
1	1854-7	1854	12/29/09	285 m
2	1846-2	1853	1/20/10	244 m
3	1846-3	1853	1/25/10	212 m
4	1846-3	1853	1/20/10	264 m
5	1846-4	1846	1/9/10	177 m
6	1846-5	1846	1/9/10	196 m
7	1846-5	1846	1/10/10	284 m
8	1846-5	1846	1/19/10	54 m
9	1846-5	1846	1/20/10	88 m
10	1846-5	1846	1/21/10	268 m

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Appendix I. Life stage simulation analysis of cougars.

INTRODUCTION

Traditionally, analytical elasticities have been used to identify vital rates that exert the largest influence on population growth rate, λ (Crouse et al. 1987, Heppell et al. 1994, Buenau and Gerber 2004). Despite this paradigm, the overall influence of a vital rate on λ is a function of its elasticity and variability (Wisdom and Mills 1997, Gaillard et al. 1998, Wisdom et al. 2000, Mills et al. 2001). For cougars, it has commonly been found that adult female survival has the greatest effect (i.e., highest elasticity) on λ (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009a,b); however, other vital rates, such as kitten survival, tend to be highly variable (Logan and Sweanor 2001, Lambert et al. 2006, Robinson et al. 2008, Appendix F) and could have a substantial influence on population growth rates. To evaluate the relative influence of cougar vital rates on population growth rate, I conducted a life stage simulation analysis (LSA). LSA incorporate inherent variability into a simulation, under the assumption that observed variation in vital rates is indicative of potential variation in the future (Wisdom and Mills 1997, Wisdom et al. 2000, Mills et al. 2001). LSA allows vital-rate specific coefficient of determination (r^2) to be calculated by regressing λ on each vital rate as other rates change simultaneously. The r^2 represents the proportion of variation in population growth rates attributable to potential variation in that vital rate (Mills and Lindberg 2002). My objectives were to: 1) calculate sensitivity of λ to changes in each vital rate using elasticities, 2) determine amount of variation in λ explained by variation in each vital rate using LSA, and 3) calculate the largest proportional change in λ when individual vital rates were set to their maximum value.

METHODS

I used the MATLAB code Limitsens.m (Morris and Doak 2002; p. 346 – 348) to conduct a life stage simulation analysis to determine the relative effect of vital rates on population growth of cougars. For each vital rate in the model, I specified the mean, minimum, and maximum plausible values (Table I.1). I calculated deterministic elasticities for each vital rate using the mean vital rates and estimated mean elasticity values within 500 replicate matrices generated by independently selecting vital rates from

Table I.1. Mean, minimum, and maximum vital rates of female cougars used to parameterize a Leslie matrix model to conduct a life stage simulation analysis and calculate effect of variation in vital rates on sensitivity and elasticity of vital rates on population growth rates. Inter-birth interval was set to a mean of 18 months, with a minimum and maximum of 12 and 24 months, respectively.

Age class[a]	Litter size			Survival		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Kitten	---	---	---	0.50	0.20	0.80
1	---	---	---	0.88	0.60	0.99
2	2.50	1.00	3.00	0.88	0.70	0.99
Prime Age	3.00	2.00	4.00	0.86	0.70	0.99
Old	1.00	0.00	2.00	0.45	0.10	0.50

[a] Kitten = 0-12 months, 1 = 1-yr old, 2 = 2-yr old, Prime age = 3-9 yrs, Old = > 9 years.

a uniform probability distribution (Morris and Doak 2002). Mean elasticity values and associated confidence intervals were estimated by randomly varying a single vital rate across its range of potential values while holding other vital rates at their mean over 500 replicate matrices. I regressed λ on each vital rate and calculated the coefficient of determination (r^2) to estimate proportion of total variance in λ attributable to variance in each vital rate. I also calculated the maximum possible λ value and the largest proportional change in λ when individual vital rates were set to their maximum value.

RESULTS

Survival of prime-age females (3 – 9 yrs) had the highest elasticity (0.44) among vital rates in the transition matrix of mean vital rates, followed by survival of kittens (0.19), yearlings (0.19), 2-yr olds (0.19), and prime-age female litter size (0.14); all the remaining vital rates had elasticities $\leq$ 0.04 (Fig I.1a). Inter-birth intervals (IBI; the length of time between the birth of dates of successfully raised litters of kittens) had a negative elasticity value (-0.19) because increasing the IBI had a negative effect on λ. Mean elasticities of 500 matrix replicates ranked vital rates in the same order; however, mean simulated point estimates for juvenile, yearling, and 2-year old survival and 2-year old litter size were slightly lower than deterministic estimates (Fig. I.1a). In contrast, mean elasticities from matrix replicates for prime-age female survival and litter size were slightly greater than deterministic point estimates. Variation in kitten survival explained the greatest amount of variation in λ (r^2 = 0.45; Fig. I.1b). Variation in prime-age female survival (r^2 = 0.22) and IBIs (r^2 = 0.20) of prime-age females also explained a large amount of variation in λ, and other vital rates explained almost no variation (i.e., r^2 < 0.10 Fig I.1b). The maximum λ value obtained when setting kitten survival at the maximum value (0.80) was 1.21, which increased λ by 0.095 compared to the mean value (Fig. I.1c). Decreasing the IBI from 18 months to 12 months increased λ by 0.081 units. Increasing prime-age female survival and litter size to their maximum values increased λ by 0.066 and 0.043 units, respectively. Setting any of the remaining parameters to their maximum resulted in insignificant changes in λ ($\leq$ 0.02).

DISCUSSION

Previous studies investigating effect of vital rates on cougar population growth have focused on calculating deterministic elasticities. These studies have consistently
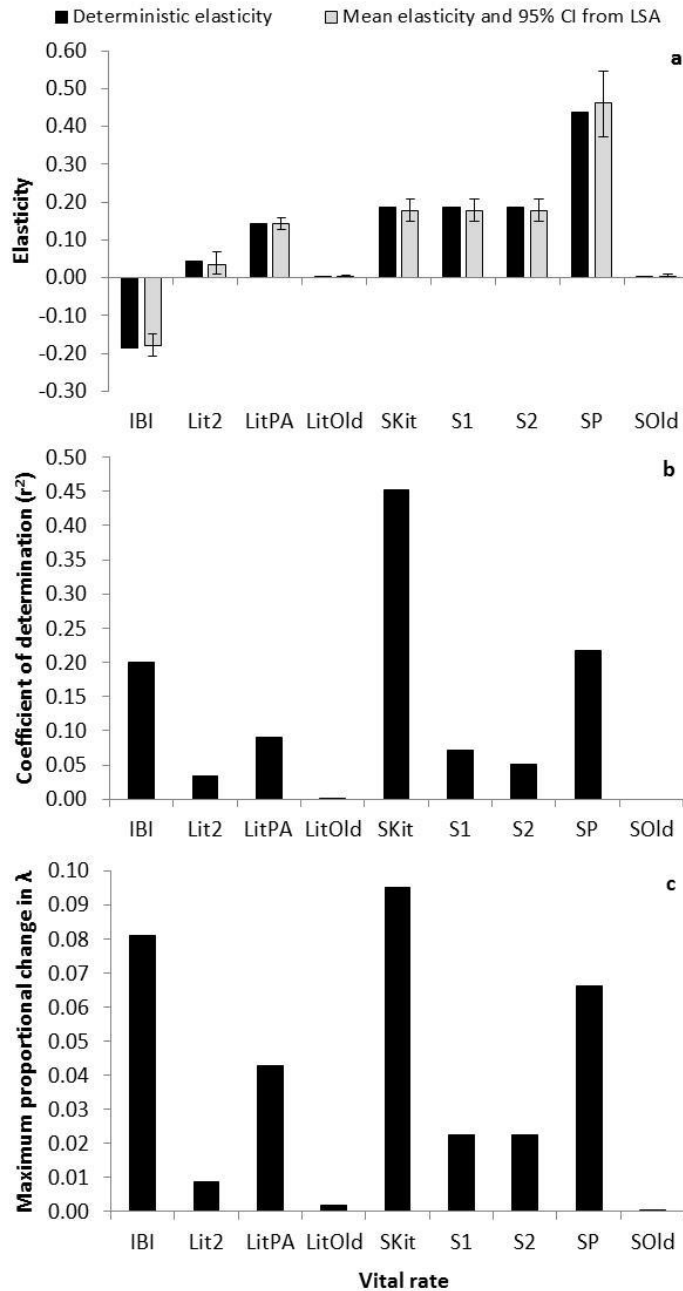
Figure I.1. Elasticities of vital rates of cougars calculated from a Leslie matrix model using mean vital rates in a deterministic matrix and mean elasticities and their 95% confidence intervals from 500 matrix replicates in a life-stage simulation analysis (LSA; a). The (b) variation in population growth rate explained by variation in each viral rate (r^2), and (c) the maximum proportional change in population growth rates for each vital rate in LSA. Vital rate notations are: Inter-birth interval (IBI), litter size of 2 yr old females, litter size of prime-age (3-9 yrs) females (LitPA), litter size of old (10-13 yrs) females (LitOld), survival of kittens (SKit), survival of 1 yr old females (S1), survival of 2 yr old females (S2), survival of prime-age females (SP), and survival of old females (SOld).

found cougar population growth is most influenced by adult female survival (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009a,b). My results support this conclusion; however, the majority of variation in cougar population growth is explained by variation in kitten survival, adult female survival, and the IBI. Kitten survival had a greater effect on population growth because of the large degree of variance in this vital rate compared to that of adult female survival (Table I.1). The pattern of adult female survival having high elasticity and low process variance matches well with observations from other long-lived mammals (Pfister 1998). This is expected because natural selection should minimize variation in vital rates that have high elasticity (Pfister 1998). Cougars have a unique reproductive system compared to most taxa occupying temperate latitudes in that they give birth to young year round (Logan and Sweanor 2001). Furthermore, female cougars frequently leave their offspring unattended while hunting which increases the risk of predation to their young (Logan and Sweanor 2001). This introduces a high level of process variance in kitten survival, and suggests that adult females should make behavioral decisions to minimize variation in their own survival (i.e., use a bet-hedging strategy to ensure they can reproduce at a later date).

Harvest mortality is the primary source of mortality in most hunted cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008, Chapter 3). This type of anthropogenic disturbance increases variation in a vital rate that was likely evolutionarily constrained to have minimal variance. This suggests that harvest of adult females is likely to have a profound effect on population growth rates of cougars. Empirical evidence supports this assertion because high levels of female harvest can result in declining cougar populations (Lambert et al. 2006, Robinson et al. 2008, Cooley et al. 2009 a,b). Therefore, in areas where cougar populations are declining, managers should consider eliminating harvest of females. Alternatively, if managers want to manipulate cougar population size to meet population management objectives, harvest of females will likely be the most effective way to meet objectives. If these actions are insufficient to meet population objectives, managers should focus efforts on altering kitten survival because this vital rate has the greatest effect on variation in population growth.

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Appendix J. Effect of variable age ratios on population growth rates of elk.

INTRODUCTION

End of winter, juvenile to adult female ratios (hereafter age ratios) are commonly used by wildlife managers to assess recruitment, which is the product of fecundity and juvenile survival (White and Garrott 2005). However, the use of age ratios to monitor population trajectory has been questioned. In particular, age ratios have been questioned because they do not indicate which component of the ratio has changed (Caughley 1974). Furthermore, it is commonly assumed the denominator in the ratio (i.e., female survival) is constant over time, which may not be a reasonable assumption in all ungulate populations (McCullough 1994). My objectives were to 1) determine the ability of age ratios to predict population growth rates and trajectory, 2) assess if juvenile or adult survival explain the majority of variation in age ratios, and 3) determine effects of female harvest on age ratios.

METHODS

Ratios of juvenile to adult females (hereafter, age ratios) represent recruitment of juveniles into the adult population and are typically used by managers as an index of population growth of elk. To determine the relative influence of age ratios on population growth rates of elk, I conducted 5,000 stochastic simulations of population growth over 10 years. At each time step and for each simulation, I recorded the end of year age ratio and associated population growth rate and identified age ratios that resulted in decreasing ($\lambda < 0.995$), stable ($0.995 \leq \lambda < 1.005$) or increasing ($\lambda \geq 1.005$) populations. I regressed λ on the age ratio and recorded the correlation coefficient (r) and the coefficient of determination (r^2) to identify the relative influence of recruitment on population growth rates of elk. I also regressed the age ratio on juvenile and prime-age female survival to determine which vital rate explained the majority of variation in age ratios. To determine the effect of female harvest on age ratios, I conducted 5,000 simulations of population growth over 10 years where I randomly generated the number of tags issued for females and harvest success rates from a normal distribution at each time step. At the conclusion of the simulations, I determined combinations of juvenile to adult female ratios and female harvest that resulted in stationary populations ($0.995 \leq \lambda < 1.005$), and then regressed the age ratio against the proportion of females harvested.

RESULTS

There was a positive association ($r = 0.59$) between age ratios and λ, but age ratios explained only a moderate amount of variability in λ ($r^2 = 0.35$; Fig. J.1a), so the predictability of this association was poor. However, changes in age ratios were strongly influenced ($r = 0.97$) by variation in survival of juveniles ($r^2 = 0.94$; Fig. J.1b) but not variation in prime-age female survival ($r^2 < 0.001$; Fig. J.1c). In the absence of female harvest, mean age ratios at the end of winter of 20:100 resulted in $\lambda \approx 1.0$, but there was a substantial amount of variability in ratios that resulted in $\lambda \approx 1.0$ (Fig. J.2a). Stationary populations ($0.995 \leq \lambda < 1.005$) were observed between age ratios of 9-32:100, declining populations ($\lambda < 0.995$) observed at ratios up to 32:100, and increasing populations ($\lambda \geq 1.005$) observed at ratios as small as 9:100 (Fig. J.2b). Harvest of females caused age ratios to increase; however, this association was weakly supported ($r^2 = 0.07$; Fig. J.3a) because of high variability in juvenile survival. As harvest of females increased, juvenile to adult female ratios that resulted in a stable population ($0.995 \leq \lambda < 1.005$) increased in a linear fashion (Fig. J.3b) which indicated that harvest of females requires increased recruitment to maintain populations.
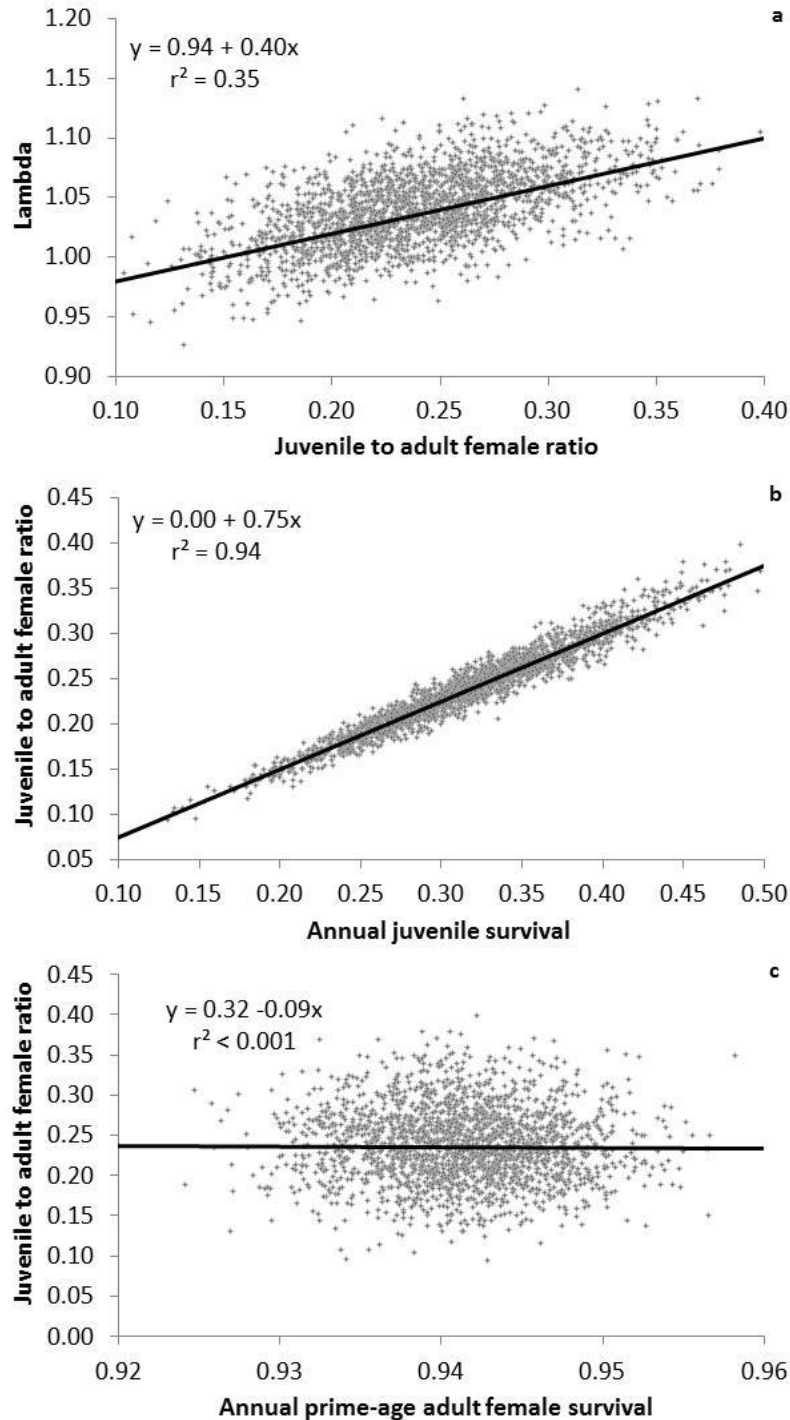
Figure J.1. The (a) ability of juvenile to adult female ratios to reflect changes in population growth rates of elk, and the amount of variability in juvenile to adult female ratios explained by (b) annual juvenile survival, and (c) annual prime-aged female survival. Regression equations were calculated from 5,000 simulations of population growth over 10 years using vital rate information estimated in the Blue Mountains of Oregon, USA. 2,000 out of 50,000 data points are included in the figure.
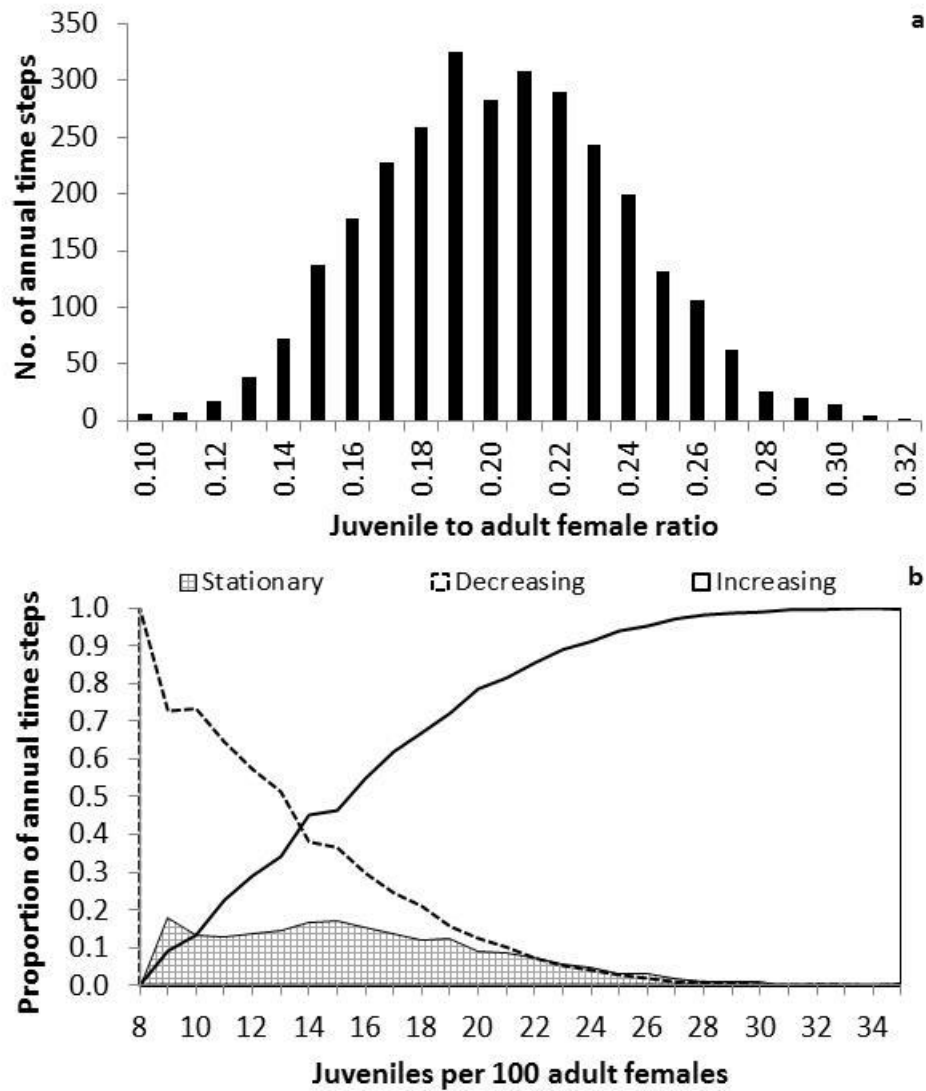
Figure J.2. Distribution of (a) juvenile to adult female ratios that resulted in a stable elk population, and (b) the proportion of simulated populations that resulted in a decreasing ($\lambda < 0.995$), stationary ($0.995 \leq \lambda < 1.005$), or increasing ($\lambda \geq 1.005$) population. Results were generated from 5,000 stochastic simulations of population growth over 10 years using vital rates of elk estimated in the Blue Mountains of Oregon, USA.
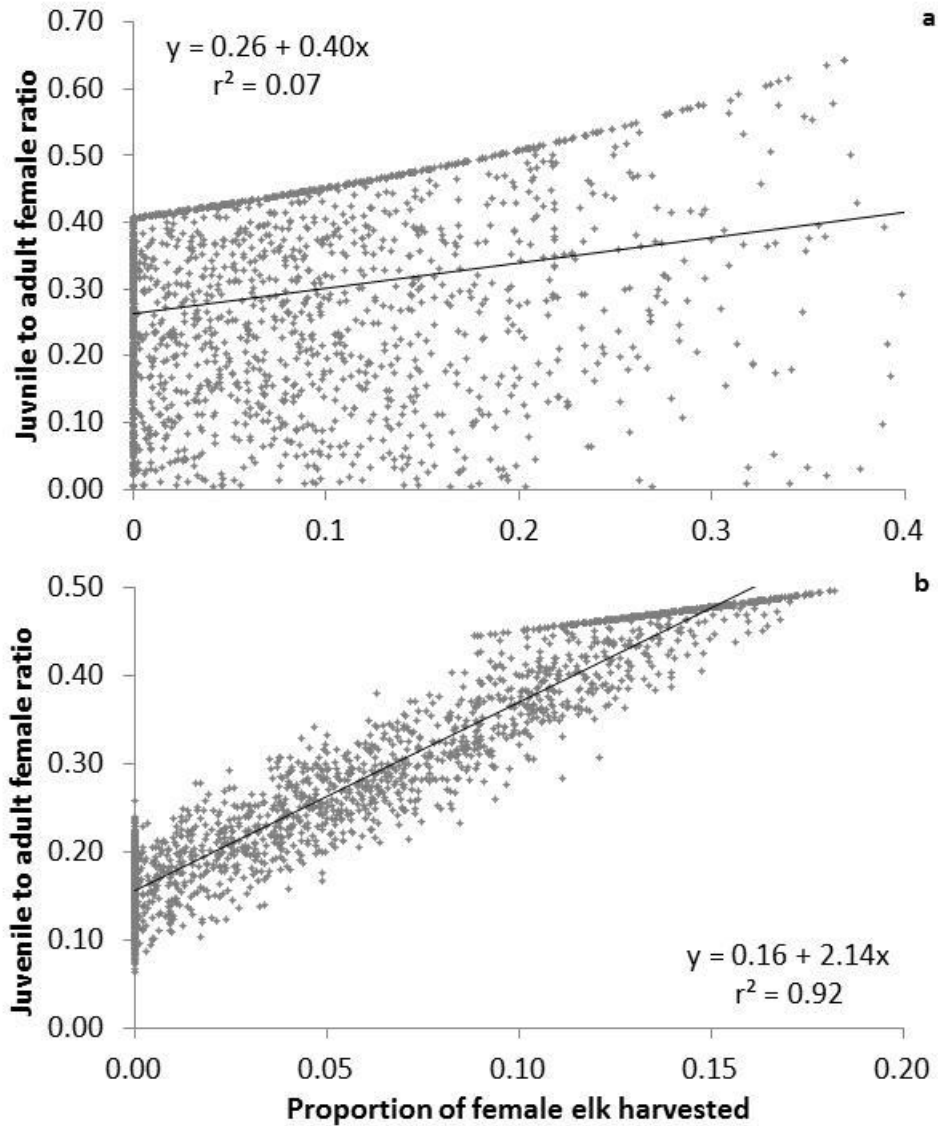
Figure J.3. The estimated effect of (a) increasing harvest on juvenile to adult female ratios, and (b) juvenile to adult female ratios that resulted in a stationary ($0.995 \leq \lambda < 1.005$) elk population under variable adult female harvest. Results were generated from 5,000 stochastic population simulations over 10 years using vital rates of elk estimated in the Blue Mountains of Oregon, USA.

DISCUSSION

Age ratios are commonly used as an index of population growth of ungulates by managers (White and Garrott 2005), but their use has been criticized because changes do not explain which components of the ratio varied or what the trajectory of population might be (Caughley 1974). Furthermore, for age ratios to be useful as a population index, the denominator in the equation should not change, which may not be the case for all species (McCullough 1994), particularly when harvest of adult females is a primary objective. Within most elk populations, survival of adult females is relatively constant (Brodie et al. 2013) and juvenile survival is highly variable (Griffin et al. 2011), which causes the denominator in the age ratio to remain relatively constant and the numerator to vary annually. Consequently, I agree with the conclusions of Harris et al. (2008) that age ratios are a useful metric for assessing relative survival of juvenile elk. The utility of age ratios to monitor juvenile survival in other species will depend largely on annual variation in adult survival. Despite the potential utility to monitor juvenile survival, age ratios were unable to detect declines in juvenile survival until several consecutive years $(3 - 4)$ of substantial declines $(> 25\%)$ occurred (Harris et al. 2008). Consequently, age ratios should be used for coarse scale monitoring, and direct estimation of juvenile survival may be necessary for adequate monitoring of elk populations that are of management concern. Furthermore, age ratios provide no information on the timing or causes of juvenile mortality. Estimating age ratios during the late fall and at the end of winter would help provide insight into the timing (summer versus winter) at which juvenile mortality occurred.

The use of age ratios to determine population growth in my study was questionable because ratios ranging from 9-32:100 resulted in stable populations; increasing populations were observed at ratios as small as 10:100, and declining populations were observed at ratios as large as 32:100. Despite the relative imprecision in the ability of age ratios to detect population trajectories, I contend that age ratios have some utility when used at a coarse scale measure of recruitment. For example, elk populations with chronically low juvenile recruitment $(< 15:100)$ are likely declining, and populations with age ratios $> 25:100$ annually are likely indicative of a relatively stable or

increasing population. For populations with age ratios between 15-24:100, additional monitoring of the population (e.g., independent population estimates) is likely warranted to determine population trajectories. Biases and inaccuracies in age ratios can occur due to observation error (Smith and McDonald 2002, Bender et al. 2003), sightability (Samuel et al. 1987, Noyes et al. 2000), and survey design (Gasaway et al. 1985, Samuel et al. 1992), and these biases will further reduce the utility of age ratios. Harvest rates of female elk can be highly variable (ODFW, unpublished data) and may be dependent on the number of hunters (Bunnell et al. 2002) or weather (Vucetich et al. 2005). Variable harvest will cause variability in the denominator of the age ratio making interpretation of age ratios difficult. Furthermore, any level of harvest will reduce the denominator in the age ratio, which will cause age ratios to increase, resulting in a positively biased estimate.

Given the large degree of variability in age ratios that resulted in decreasing, stable, and increasing populations, I recommend caution when using age ratios as a surrogate of ungulate population growth or declines (see Caughley 1974). Age ratios should be viewed as a coarse scale monitoring tool that may be useful in detecting large changes in juvenile survival and potential negative effects to elk populations. For populations that are of management concern, I recommend managers directly estimate elk populations annually rather than rely on age ratios to monitor populations. Age ratios will likely serve as a suitable monitoring option for elk populations at or above management objectives so long as major changes are not observed in age ratios or population size and age ratios are consistently > 20:100. Harvest of female elk reduces the utility of age ratios to monitor elk populations because harvest increases variability in the denominator of the ratio. Therefore, I recommend that age ratios are not used to monitor ungulate populations subjected to considerable female harvest because estimates of juvenile survival and recruitment will be positively biased and difficult to interpret.

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