OREGON DEPARTMENT OF FISH & WILDLIFE

Wolf Literature Review and Research Recommendations

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Wolves in Oregon: Literature Review and Research Recommendations
EXECUTIVE SUMMARY

1.   Introduction

The Wolf Conservation and Management Plan directs the Oregon Department of Fish and Wildlife to conduct relevant research to understand the effects of wolf re-establishment and to inform conservation and management actions. Also, the vested interests of hunters and conservationists compel the Department to investigate the potential effects of wolves on elk and deer populations. Research directions identified in this document are specific to wolf-ungulate and wolf-predator interactions and are pertinent to Oregon's unique characteristics.

2.   Identified Research Needs: Wolf-Ungulate-Cougar Interactions

Cougars are a major limiting factor of elk recruitment in NE Oregon and may be implicated in mule deer declines. Whether wolves will add to elk and deer mortality or replace cougar-caused mortalities is unknown. Wolf-cougar competition could ameliorate some of the predatory pressure experienced by elk and mule deer. Wolf predation risk could also cause ungulates to utilize landscapes in new ways that reduce access to high-quality forage or increase cougar predation risk. Answers to four questions will help resolve these uncertainties:

*   **What are wolf prey preferences in areas with variable prey availability?** Understanding wolf prey selection across the broad range of prey species and abundance in NE Oregon may have useful application to other regions in the state and could aid in forecasting potential effects of wolves on elk and deer.

*   **Will wolves displace cougars or influence their abundance?** This question is directly relevant to understanding if wolves add to or abate the currently high cougar predation on elk and deer in some Wildlife Management Units (WMUs). The Department has pre-wolf information on cougars in four NE Oregon WMUs against which any changes in cougar habitat selection, productivity, predation, and abundance can be measured.

*   **Will elk respond to wolf re-establishment by altering their habitat use?** Elk habitat resource selection models for the Blue Mountains Region were developed prior to wolf re-establishment. Comparison of this model to elk habitat utilization following the re-establishment of wolves may identify any changes in elk preferences and inform future management decisions. Any shifts in elk distribution to areas with higher cougar predation risk could result in additive mortality after wolf re-establishment.

*   **What level of predator densities can ungulates endure?** Continued monitoring of elk and deer populations is critical for detecting any measurable changes in population trends or elk calf and deer fawn recruitment. Pre-wolf survival and mortality causes for female elk and mule deer, as well as elk calves (available for some NE Oregon WMUs) can be compared to post-wolf information. Understanding how varying ratios of predators and prey affect ungulate populations will help guide future carnivore, deer, and elk management.

3. Oregon's Unique Local Characteristics Relevant to Wolf-System Dynamics

NE Oregon is dissimilar from other areas where wolves have recolonized in that:

*   **Cougar predation is significant.** Unlike in the Northern Rocky Mountains (NRM), cougar predation appears to be the primary limiting factor of elk calf recruitment and thus, elk population growth; black bears contribute marginally to calf mortality. Similarly, cougar predation on adult female mule deer, concurrent with coyote predation on fawns, reduced forage availability, and harsh climate conditions, could be contributing to mule deer declines.

*   **Oregon has different compositions of predators and prey.** In particular, deer (mule deer and white-tailed deer) are generally more abundant than elk in NE Oregon, so wolf prey preferences may differ from those documented in elk-dominated study areas. Also, grizzly and black bears are significant predators of elk calves in the NRM, but in Oregon grizzly bears are not present and black bears are not a major cause of elk calf mortality.

*   **Comparatively, Oregon has a less severe climate.** In contrast to the NRM, Oregon has milder winters and drier summers. Oregon's climate provides higher forage growth and less snow accumulation that may buffer

herds from additional losses to wolves. Ungulates are more vulnerable to wolf predation during severe winters and this is exacerbated by low pregnancy rates due to climate stress or reduced forage availability.

- **Harvest of antlerless deer and elk was minimal prior to and during wolf re-establishment.** Research in the NRM showed that high antlerless harvests preceding and concurrent with wolf recovery contributed significantly to elk declines. However, in NE Oregon, harvests of antlerless deer and elk were relatively low immediately prior to and during wolf re-establishment.

4. Research Highlights from the Northern Rocky Mountain Region

Managers can benefit from the wealth of information obtained since the recovery of wolves in the NRM. General findings most relevant to Oregon's research needs are discussed below.

- Wolf recovery in the NRM has primarily occurred in areas where elk are more abundant than other ungulates. In elk-dominated landscapes, elk were generally the preferred prey year-round.

- Where elk declines occurred, they were predicated on unique combinations of factors such as severe drought and winters, reduced forage, harvest by humans, and altered fire regimes and timber management, some or all of which acted in concert with bear (grizzly and black bear) and wolf predation.

- Varying levels of predator densities influenced prey species' abundances differently. Areas with the most severe elk declines had the highest predator densities (wolves, black bears, grizzlies, or combinations thereof), while some prey population levels remained stable or increased where these predator densities were lower.

- Whether wolf-caused ungulate mortality adds to or replaces other mortality factors is variable. Wolf predation may replace mortality resulting from nutrition or climate stress, human harvest, and predation from other carnivores. In some areas, wolves may have added to deer and elk mortality, resulting in prey declines.

- Wolf prey selection is influenced by prey species' abundance, vulnerability, and energetic value. Wolves' diets may diversify as preferred prey species decline in abundance, allowing packs to persist under reduced prey abundance. Less abundant sympatric prey species may be disproportionately affected by wolves.

- Competition with wolves has caused demonstrable declines in coyotes. Reductions in coyote densities significantly reduced predatory pressure on pronghorn fawns and small mammals.

- Competition between cougars and wolves caused shifts in cougar habitat selection and diet, avoidance of wolves, increased malnutrition, and decreased survival rates and population size. The long-term effects of competition between these carnivores are unknown because most studies were short-term.

- In response to wolf predation risk, elk typically selected areas that afforded greater security, but had lower forage quality. Elk also shifted to more structurally complex landscapes, but in doing so, increased cougar predation. Some portions of elk herds changed migration patterns and seasonal home ranges.

- Predation risk was demonstrated to increase elk vigilance with corresponding decreases in foraging rate, nutrition, and reproductive output. Those that dispute this note that elk can consume food while scanning for predators and that in some areas elk body condition and pregnancy rates remained unchanged since wolf re-establishment.

5. Summary

The broad amount of information from the NRM provides insight into potential effects of wolf re-establishment in Oregon. However, several factors set NE Oregon apart from other areas where wolves have recolonized. Thus, managers may benefit from research that directly pertains to local wolf effects in order to adequately address management concerns.

In addition to research of wolf-ungulate-cougar dynamics, it may be useful for the Department to explore methods for estimating wolf populations and collaborative opportunities to investigate wolf-livestock interactions.

Scientific study of wolves' influence on wildlife and livestock will help meet the Department's research objectives as indicated in the Wolf Conservation and Management Plan, as well as provide much needed information for the future management of wolves and other wildlife in the state.

Wolves in Oregon: Literature Review & Research Recommendations

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1.   Introduction

In 1999, after nearly 60 years since wolves were extirpated from Oregon, the first known wolf (*Canis lupus*) dispersed from neighboring populations in Idaho to northeastern Oregon (Oregon Department of Fish and Wildlife 2010). Since then, other dispersal, pack establishment, and reproduction events have occurred. As of January 2013, the Oregon Department of Fish and Wildlife (ODFW) has documented a minimum population of 53 wolves (22 adults, 25 pups, 6 unknown age) in 7 packs (≥ 4 wolves) and 2 groups (< 4 wolves) in NE Oregon. Oregon's wolf population is expected to increase in areas with adequate prey and habitat (Oregon Department of Fish and Wildlife 2010), prompting public interest in the potential influence of wolves on ungulate populations and hunting opportunities.

The primary ungulate species recreationally harvested in NE Oregon are Rocky Mountain elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus ochrourus)*. Though deer (both species combined) in this region outnumber elk by a minimum ratio of 2:1 (V. Coggins and M. Kirsch, ODFW, personal communication), elk have drawn considerable attention. Declining elk populations trends, decreased calf recruitment, and significant cougar predation effects (Oregon Department of Fish and Wildlife 2003a, Rearden 2005, Johnson et al. 2013a, B. K. Johnson, ODFW, unpublished data) have been documented in parts of this region. Mule deer have also experienced population declines throughout the Intermountain West and Oregon is no exception (Oregon Department of Fish and Wildlife 2003b); decreasing habitat quality and quantity, periodic severe winters, and predation may have contributed to decreasing population trends (Bishop et al. 2009, Hurley et al. 2011, Oregon Department of Fish and Wildlife 2011). White-tailed deer have become established and are abundant in some parts of NE Oregon. Changes in cougar (*Puma concolor*) management, including the elimination of bounties and the prohibition of hunting with the aid of trailing hounds (Legislative Measure 18, 1994), are correlated with a considerable increase in the abundance of this predator since the 1960s (Oregon Department of Fish and Wildlife 2006). Stakeholder attitudes include concerns that the re-establishment of wolves to this current system will negatively affect elk and mule deer populations.

Throughout western North America as wolves have recolonized, a variety of ungulate population responses have been documented that are predicated on the unique characteristics of each region, such as predator and prey compositions and ratios, climatic variation, primary productivity, harvest by humans, timber management, and fire disturbance (Kunkel and Pletscher 1999, Vucetich et al. 2005, Barber-Meyer et al. 2008, Idaho Department of Fish and Game 2010, White et al. 2010, Griffin et al. 2011, Vucetich et al. 2011, Eisenberg 2012, Middleton 2012, Brodie et al. In press). This body of knowledge helps to comprehend the relative contribution of factors which limit ungulate population growth. Factors that apply downward pressure on populations through the removal of individuals, often as a result of predation or harvest by humans, are termed "top-down" factors. Factors related to ungulates' ability to meet nutritional requirements for reproduction and survival are "bottom-up" in nature and include the influence of herbivore density, climate, and habitat conditions on forage availability and ultimately ungulate body condition. Prior research provides some insight into ungulate responses that could be expected in NE Oregon as wolves re-establish. However, NE Oregon differs considerably from areas such as the Rocky Mountains and Great Lakes states where prior research has been conducted. For instance, the importance of cougar predation on ungulate populations, differing predator and prey assemblages, milder winter conditions, and greater forage availability, as well as lower harvests of antlerless deer and elk immediately prior to and during early wolf re-establishment, set NE Oregon apart from earlier study sites.

ODFW's Wolf Conservation and Management Plan (2010, hereinafter referred to as 'Wolf Plan') calls for appropriate long-term research to understand the influence of wolves on wild ungulates (p. 85). The purpose of this literature review is to 1) summarize the current understanding of NE Oregon's elk and mule deer population dynamics; 2) review the available literature pertaining to systems with multiple predators and prey in western North America and the applicability of this knowledge base to NE Oregon; and 3) identify appropriate research approaches to understand the ecological influences of re-established wolves in Oregon. Interactions between wolves and livestock, as well as methods for estimating wolf populations are also topics that warrant further review and investigation, but are beyond the scope of this document.

2.   NE Oregon Elk Population Status

Intensive research efforts have sought to understand declines or, in some cases, plateaus in NE Oregon's elk populations. Elk populations have steadily decreased in several NE Wildlife Management Units (WMUs) over the past 30 years (Oregon Department of Fish and Wildlife 2003a). Declines ranging from 23 to 70% have occurred since population highs in the 1980s in the Chesnimnus, Sled Springs, Walla Walla, Mt. Emily, Keating, Snake River, Lookout Mountain, and Wenaha WMUs. However, three units (Imnaha, Catherine Creek and Pine Creek WMUs) have experienced increases of 32-95% between the 1980s and 2010 (Fig. 1, ODFW, unpublished data). Survival of prime-age adult cow elk is high (>80%; B. K. Johnson, ODFW, unpublished data), elk pregnancy rates exceed 90%, and body condition of cow elk in the region has been the highest in the state (Oregon Department of Fish and Wildlife 2003a). Still, calf recruitment has decreased (Oregon Department of Fish and Wildlife 2003a). Recruitment averaged 47 calves:100 cows during 1946-1984 and is now 50% lower at about 20 calves:100 cows (Oregon Department of Fish and Wildlife 2003a, ODFW, unpublished data).

Cook et al. (2004) demonstrated that elk calf over-winter survival was positively related to calf body mass at the start of winter which was in turn mediated by calf birth date and summer-autumn nutrition. In this study, calves were fed rations that simulated extremely harsh winter conditions; these artificial conditions were more severe than those typically endured in NE Oregon. As expected, calves steadily lost weight over the experimental winter and only calves in the best body condition at winter's onset had enough residual body mass to ensure survival to the end of the experiment. Extrapolation of these results suggests that during less severe winters (typical of NE Oregon), calves should lose weight at a slower rate and indeed, empirical evidence demonstrated that radio-collared calf elk survived through winters in NE Oregon to a greater degree than observed in the experimental manipulation. Therefore, calf nutrition and body condition have less support as primary explanatory factors for low calf recruitment in the region.

Johnson et al. (2013a) examined a number of abiotic, top-down, and bottom-up factors that may limit elk calf recruitment and determined that cougar density was the most important covariate linked to calf over-winter survival. Bottom-up (elk density) and density-independent factors (summer precipitation), became increasingly important limiters of calf recruitment when cougar densities were low (Johnson et al. 2013a). Lending support to evidence that cougars are limiting calf recruitment in NE Oregon is the finding that cougar predation was the most important cause of calf mortality (78%) between 2002-2007 in the Wenaha and Sled Springs WMUs (Rearden 2005, B. K. Johnson, ODFW, unpublished data, Griffin et al. 2011). Similarly, cougars were the primary source of mortality for elk calves in the Blue Mountains of SE Washington (Myers et al. 1999). Further, a study conducted in the Mt. Emily WMU demonstrated that year-round, cougars preferentially preyed upon elk calves in greater proportion than their availability (D. Clark, unpublished data, Oregon State University). Recent estimates suggest that densities of cougars in NE Oregon between 2002-2012 were some of the highest documented (Findholt and Johnson In prep, G. Davidson, ODFW, unpublished data) and have increased by 69% between 1994

and 2003 in the Blue Mountain region (Oregon Department of Fish and Wildlife 2006). When cougar densities were reduced in the Heppner WMU, calf recruitment noticeably increased (Kirsch et al. 2009).

Compared to cougars, black bears (*Ursus americanus*) were less important predators of elk calves (causing < 15% of calf mortality) in NE Oregon (Rearden 2005, B. K. Johnson, ODFW, unpublished data , Rearden et al. 2011), despite the relatively high abundance of bears in the region (Oregon Department of Fish and Wildlife 2012). Stable isotope analysis of bear bone specimens collected between 1890-1931showed bears primarily used non-terrestrial sources of protein, such as salmon (Hilderbrand et al. 1996). This could suggest that, historically, in comparison to cougars, bears may have been a less significant predator of elk calves. However, Bull et al. (2001) found that neonate ungulates were seasonally important to black bears in the spring in NE Oregon, though their methodology (scat analysis) was unable to ascertain if neonates were scavenged or preyed upon.

In order to begin to understand the potential influence of wolf re-establishment on NE Oregon elk populations, it is important to synthesize research findings from other states and provinces where wolves have re-established. Perhaps most useful to Oregon wildlife managers is information that pertains to the significant factor that limits elk populations in NE Oregon: low calf recruitment as a result of cougar predation of calves.

3.   NE Oregon Deer Population Status

The factors impacting NE Oregon's mule deer are less definitive, though declines in habitat productivity, periodic severe winters and droughts, illegal harvest, and predation are likely operating in concert to hinder population growth (Oregon Department of Fish and Wildlife 2003b;2011). Mule deer populations in nearly all NE Oregon WMUs have declined by up to 55% in the past five years (ODFW, unpublished data). Average fawn recruitment has decreased by up to 45% in the last five years in comparison to 1999-2005 averages in the Wenaha, Sled Springs, Chesnimnus, Snake River, Minam, Imnaha, Starkey, Catherine Creek, Mt. Emily, Ukiah, and Walla Walla WMUs (ODFW, unpublished data, Oregon Department of Fish and Wildlife 2011).

Cougars were the primary cause of mortality for adult mule deer in some parts of NE Oregon (Mathews and Coggins 1997, Edelmann 2003) and coyotes have been shown to limit fawn recruitment in other regions of the state (Trainer et al. 1981). Oregon's Mule Deer Initiative aims to ameliorate causes that may be limiting mule deer populations (Oregon Department of Fish and Wildlife 2011). In 2006-2008, the Department increased the removal of cougars from one NE Oregon WMU (Heppner); the level of cougar reduction achieved had no measurable impact on the unit's mule deer population (Oregon Department of Fish and Wildlife 2011). Coyote predation of fawns was also suspected to limit recruitment and experimental coyote removal was initiated in 2010 in the Heppner WMU (Oregon Department of Fish and Wildlife 2011). To date, no mule deer population increases have been observed, though fewer cougar removals occurred during the period of coyote culling (M. Kirsch and S. Cherry, ODFW, personal communication). In other western states research suggests that nutrition and climate, rather than predation, are responsible for mule deer population recruitment and growth (Bishop et al. 2009, Hurley et al. 2011).

Over the past several decades, white-tailed deer have increased in abundance from previously low densities in NE Oregon and appear to be persisting in riparian areas and landscapes with gentle terrain (M. Kirsch, P. Matthews, and V. Coggins, ODFW, personal communication). Population indicators are not routinely measured for white-tailed deer and while this species provides some hunting opportunities in NE Oregon, little emphasis is placed on their management.

Research pertaining to the influence of wolves on deer in western North America is sparse, as most investigations in this region have occurred in areas where elk were the dominant ungulate and wolves preferentially selected elk. The most pertinent available information is that which elucidates the role of wolves in suppressing other large predators, as well as smaller mesopredators (e.g. coyotes) that may limit ungulate recruitment. Prior and ongoing inquiries into the function of wolves in other multi-prey systems like Oregon's are most useful in understanding how this predator will influence elk, mule deer, and white-tailed deer in the northeastern part of the state.

4.   Literature Review

Much effort has been dedicated to predict and understand the influence of re-established wolves on ungulate populations, particularly in the Rocky Mountain states and provinces. Prior to the reintroduction of wolves to Yellowstone National Park (YNP), scientists developed models which forecasted 5-20% declines for elk in the Greater Yellowstone Ecosystem (GYE) and that the population would be maintained at this lower equilibrium over the next 100 years (Boyce and Gaillard 1992, Wright et al. 2006). These models performed well in predicting the actual elk declines that occurred through 2005, but underestimated the number of wolves the area could support (Varley and Boyce 2006) and continued elk declines after 2005 (Yellowstone Center for Resources 2011). Along Montana's eastern front of the Rocky Mountains, mule deer were more abundant than elk and were projected to be impacted more by wolf recovery than elk, though this modeling effort was influenced by inputs of larger mule deer predation rates (Vales and Peek 1995).

Research regarding the influence of wolves on ungulates can be organized into three broad areas in which wolf recovery was demonstrated to: 1) add to ungulate mortality; 2) replace another form of ungulate mortality; and/or 3) cause indirect or fear-mediated effects on ungulate populations. Within each study's context, the interplay of bottom-up and top-down forces is a key consideration and underpins the interpretation of findings.

4.1.   Top-down and Bottom-up Regulation

Several meta- and retrospective analyses have shown that ungulate populations are moderated by a combination of top-down and bottom-up factors, including predation, harvest by humans, primary productivity, and climatic conditions (Crête 1999, Melis et al. 2009, Griffin et al. 2011, Johnson et al. 2013a, Brodie et al. In press). In some instances, non-predation related mechanisms, such as high levels of harvest by humans, extreme summer or winter weather, or habitat changes may be the ultimate driver of ungulate declines (Vucetich et al. 2005, White and Garrott 2005, Wright et al. 2006, Middleton 2012, Brodie et al. In press). See Table 1 for a summary of top-down and bottom-up interactions acting on elk populations in the Northern Rocky Mountains.

For example, central Idaho elk population declines were precipitated by decreased browse productivity resulting from decades of fire suppression and reductions in timber harvest, as well as extreme winter conditions in the mid-1990s (Idaho Department of Fish and Game 2006, White et al. 2010). These declines were exacerbated by bear and wolf predation and elk populations have not recovered to previous levels as a result of ongoing predation (Idaho Department of Fish and Game 2006, White et al. 2010). A similar situation appears to have occurred in the Bitterroot Valley, Montana, where prior to wolf re-establishment in 2002, elk population declines appear to have been initiated by a combination of high antlerless harvests, habitat factors resulting in poor elk body condition and low pregnancy rates (<70%), and a growing cougar population (Hamlin and Cunningham 2009, K. Proffitt, Montana Fish, Wildlife, and Parks [MFWP], personal communication). Research is ongoing in the Bitterroot Valley to elucidate mechanisms driving this population trend. As in central Idaho, it is possible that elk

populations continue to suffer from the combination of these pre-existing factors and wolf predation after 2002 (K. Proffitt, MFWP, personal communication).

Ungulate abundance may be restricted as a result of the interplay between top-down and bottom-up factors, such as predation combined with low vegetative productivity and/or harsh climate conditions (Hebblewhite 2005, Melis et al. 2009, Brodie et al. In press).   For example, the combination of high predator:elk ratios and winter severity lowered elk calf survival in Montana (Hamlin and Cunningham 2009) and elk population growth rate in Banff National Park (BNP) (Hebblewhite et al. 2002, Hebblewhite 2005).   These results may be an artifact of the increased vulnerability of ungulates to predation when escape is hindered by deep snow and/or animals experience decreased fitness due to climate-related energy loss and food stress. In support of this explanation, White et al. (2009b) documented that after wolf recovery, elk were rarely found in historic Yellowstone winter ranges that accumulated the most snow (e.g. the Gibbon River drainage) because those areas conferred the greatest vulnerability to predation by wolves. A similar interaction between snow depth and harvest by humans was apparent in the northern range of YNP. During heavy snow years, elk moved to lower elevations outside the park where they were more vulnerable to recreational hunting (White and Garrott 2005).

Study of elk declines in the migratory portion of Yellowstone's Absaroka elk herd provides another example of the synergistic effects of climate and predation (Middleton 2012). Though migratory elk were exposed to four times as many predators (wolves and grizzly bears) as non-migratory elk, Middleton (2012) highlights that severe drought conditions in combination with predation effects were responsible. Low pregnancy rates in the migratory segment were linked to dry, hot spring and summer conditions that caused a 40% reduction in the duration of spring green-up on summer range when compared to the resident portion of the herd (Middleton 2012). Over time poor recruitment caused the age of migratory cows to be skewed to older and less productive age classes, which likely further depressed reproduction in this portion of the herd (Middleton 2012).

Climate can also buffer ungulates against predation. For instance, in YNP increased spring temperatures and precipitation were associated with increased summer elk calf survival in the presence of a full suite of predators (Griffin et al. 2011). Conceivably, spring climate conditions resulting in better summer forage quality could augment calf survival. Additionally, favorable spring conditions could alter the spatio-temporal availability of forage in a manner that draws elk away from areas of higher predation risk (Griffin et al. 2011).

Lastly, it has been demonstrated that cervid recovery after bottom-up limitations subside can be attenuated by the effects of predation. For instance, in the California Sierra Mountains, mule deer populations were depressed as a result of a severe and prolonged drought (Pierce et al. 2012). However, once the drought abated, mule deer populations remained below carrying capacity as a result of predation by cougars (Pierce et al. 2012). Also, in the Clearwater region of Idaho, elk herds were believed to be at carrying capacity and calf-recruitment was thought to be limited by elk density. However, the herds showed no response after managers increased antlerless hunts to reduce density-dependent limits; thus, predation was then suspected to limit calf-recruitment (White et al. 2010). Similarly, the Green River elk herd in Washington was considered to be limited by an over-abundance of elk, yet elk numbers declined substantially after cow harvest was increased. Further research revealed that cougar predation was limiting calf-recruitment and a subsequent reduction in the cougar population allowed calf:cow ratios to rebound (D. Vales, Muckleshoot Indian Tribe, personal communication). In another example in a portion of BNP where wolf predation was relatively low, elk population growth was linked to density dependence and recreational harvest (Hebblewhite et al. 2002).

4.2.   Additive Mortality versus Compensatory Mortality – Multi-Predator Systems and Ungulate Survival

When a new mortality agent is introduced to an ecosystem, it can either add to or replace a portion of previously existing mortality causes. Likewise, an increase in an existing mortality factor can contribute to an overall increase in fatalities within a population or it can result in a corresponding decrease in fatalities caused by other mortality factor(s). The new or increased cause of mortality is considered additive when the proportion of all other mortality factors remains constant and the combination of all mortality factors contributes to decreased survival of the population. Conversely, when an increase or introduction of a new mortality agent occurs in conjunction with an equivalent decrease of another mortality factor, this is considered compensatory mortality. In the case of compensatory mortality, survival of individuals within the population remains unchanged because overall, no increase in fatalities takes place.

4.2.1.   Influence of Multiple Predators and Predator:Prey Ratios

The influence of multiple predators on ungulate survival varies contextually, depending on the composition and densities of both the ungulate prey base and predators present. A meta-analysis of data obtained from 12 elk populations compared summer neonate survival (first 93 days of life) in systems with three (cougars, black bear, and coyotes), four (addition of wolves), and five (addition of grizzly bears) predators (Griffin et al. 2011). When a system included an additional predator, the neonate mortality caused by the new predator nearly replaced mortality caused by other pre-existing predator(s) (compensatory mortality).   The only exceptions to this were ecosystems with grizzly bears: this carnivore caused an overall increase in neonate mortality rates (additive). In comparison to three predator systems, four predator systems had low wolf predation (<5%), slightly more black bear predation, less cougar predation, and similar coyote predation of elk calves (Griffin et al. 2011). While neonate survival was lower in four versus three predator systems, decreases in cougar predation partially negated the addition of wolf-caused mortality and increases in mortality caused by black bears. The decrease in cougar predation could be explained by the fact that cougars tend to avoid wolves and are generally subordinate when they must compete with wolves for resources (see section 4.3.3., Kunkel et al. 1999, Ruth 2004a, Akenson et al. 2005, Kortello et al. 2007).

It is important to note that Griffin et al. (2011) did not assess whether mortality caused by any predator was compensatory to other non-predation mortality factors. Several studies have highlighted that wolves, owing to their coursing hunting style, select physically disadvantaged and older- or younger-aged prey that might otherwise succumb to severe winter or summer drought conditions (Husseman et al. 2003, Vucetich et al. 2005, Atwood et al. 2007, Barber-Meyer et al. 2008, Metz et al. 2012). This concept of compensatory mortality is supported by data documenting reductions in mortalities caused by nutritional deficiencies where wolves were present. For instance in the northern range of YNP some elk calf mortality shifted from winter malnutrition during pre-wolf years to predation after wolves re-established (Barber-Meyer et al. 2008).   A similar result was uncovered in the Madison Headwaters herd (YNP); before wolves returned, severe winters resulted in a large rate of elk starvation, but once wolves returned they imparted the majority of mortality during harsh winters (Garrott et al. 2009b).

Grizzly and black bears were found to be the most impactful predator of elk calves in YNP (Barber-Meyer et al. 2008). Grizzly bear recovery was concurrent with wolf re-establishment in the GYE (Haroldson 2011) and this predator appeared to be a significant contributor to elk declines (Barber-Meyer et al. 2008). Temporally, bears prey on elk calves earliest of all predators in the ecosystem, thus Barber-Meyer et al. (2008) concluded that wolves' relatively late predation (after calves reach 35 days old) may be additive when compared with pre-wolf conditions.

Similarly, in Glacier National Park (GNP) it was determined that the recovery of wolves added to cervid mortality where cougars, grizzly, and black bears were also present (Kunkel and Pletscher 1999). Here, cougars were the primary predator of both female elk and white-tailed deer. Humans and wolves were the second most important predators of elk, and white-tailed deer, respectively (Kunkel and Pletscher 1999). According to the authors, predation resulted in additive mortality because any annual increase in a particular mortality factor for an ungulate species had a corresponding decrease in that species' annual survival.

Despite the fact that certain predators may add to ungulate mortality, predator reduction has varying results in augmenting prey populations. Predator manipulation studies have shown that experimental decreases in cougars and coyotes did not significantly increase mule deer and elk populations (White et al. 2010, Hurley et al. 2011). Rather, climate and primary productivity were found to regulate mule deer increases (Hurley et al. 2011) and bear harvest and habitat structure were most critical to elk calf survival (White et al. 2010). Increased cougar harvest in one WMU in NE Oregon did result in a noticeable increase in calf recruitment, however mule deer population metrics remained unchanged, indicating that different mechanisms may be limiting mule deer (Kirsch et al. 2009). In SE Oregon, culling of coyotes was followed by a decrease in mule deer fawn mortality, but the targeted herd's population size did not increase overall (Trainer et al. 1981). Similar coyote removal efforts in NE Oregon did not produce demonstrable improvements in fawn recruitment (S. Cherry, ODFW, personal communication).

Many studies are unable to analyze the impact of varying degrees of predator:prey ratios due to lack of predator density information. Where this information is available, it has been shown that the ratio of predators to available prey was important in gauging the impact of predation on ungulate populations.   In Montana, Idaho, and the GYE, areas that experienced the most severe elk declines had the highest predator densities of wolves alone (Idaho Department of Fish and Game 2010), bears alone (White et al. 2010), or wolves and grizzly bears combined (Barber-Meyer et al. 2008, Hamlin et al. 2009). Varying levels of predator densities influence prey species differently; local context also influences the degree of susceptibility of prey species to various predator densities. For example, in British Columbia, moose recruitment was negatively impacted when wolf density exceeded 8 wolves/1000 km^2, but recruitment of sympatric caribou was limited at lower wolf densities (>6.5 wolves/1000 km^2) (Bergerud and Elliot 1986). Hamlin et al. (2009) found that when either wolf, grizzly bear, or combinations of these two predators numbered less than 5 per 1000 elk, elk populations in Montana could sustain both predation and hunter harvest. Lower wolf-grizzly densities occurred in areas where wolves were not protected and were removed as a result of agricultural damage or sport hunting (Hamlin et al. 2009). However, it is noteworthy that cougar densities and their relative impact on elk were unknown for the reported areas (R. Garrott, University of Montana, personal communication). Cougar, coyote, and black bear densities were thus assumed to be constant across all elk herds and were not included in the aforementioned ratio (Hamlin et al. 2009).

4.2.2.   Influence of Recreational Harvest

Some have argued that wolf-caused mortality is compensatory to harvest by humans (Vucetich et al. 2005, Varley and Boyce 2006). Vucetich et al. (2005) modeled elk population growth rate prior to the return of wolves in the northern range of YNP (1961-1995). When the best model developed for the pre-wolf situation was projected onto elk populations in the post-wolf era (1995-2004), they found that 64% of elk decline after wolves returned was explained by hunter harvest, climate, and density dependent factors. Models which incorporated wolf predation were five times less effective in explaining elk declines. Further, the authors demonstrated that harvest by humans, in particular late-season (January-February) harvests of antlerless elk, were 'super-additive': for every 1% increase in harvest rate, the elk population growth rate declined by 1.5% (Vucetich et al. 2005). Models for this same herd developed by Varley and Boyce (2006) also showed that hunting in the absence of wolf predation

resulted in a smaller elk herd than wolves in the absence of hunter harvests. This was explained in part by the difference in age-sex classes selected by hunters and wolves; hunters typically select prime-age individuals while wolves tend to select age classes with low reproductive value that are most likely to succumb to predation or other climate-related stressors (very old or young elk) (Wright et al. 2006).

White and Garrott (2005) also considered wolf predation and harvest by hunters to have combined additive effects in Yellowstone's northern range because survival of adult cow elk was lower during years when both of these mortality factors were in operation versus years before wolves were restored and when human removal of elk was low (1969-1975). These authors suggested the combination of wolves and hunters led to recent population declines and also note that the continued high harvest rates of the most reproductive segment of the population was significantly instrumental in reducing elk population growth between 1995-2002.

This conclusion is disputed by others, however. Hamlin et al. (2009) point out that after 2004, late season harvests of antlerless elk were further reduced on Yellowstone's northern range with no corresponding increase in elk numbers. Furthermore, these opponents of Vucetich et al.'s (2005) findings note that predation by grizzly bears, a significant contributor to elk calf mortality, was omitted from Vucetich et al.'s (2005) analysis. In 2005-2006 wolf kills exceeded hunters' harvest of adult female elk (Hamlin et al. 2009), causing some to suggest that wolf predation will become the most important variable defining elk population size in the future (White and Garrott 2005).

Survival models that incorporated 45 elk populations in western North America also demonstrate the relative importance of hunter harvest and predation (Brodie et al. In press). Models for adult female elk survival incorporated the presence/absence of cougars and wolves, as well as environmental and habitat variables. When harvest mortality was excluded from analysis, elk survival was most influenced by the presence of wolves, winter precipitation, and the interaction between these two terms. In this harvest-free analysis, all predation was additive, with the impact of wolf-induced mortality (significantly additive) exceeding that of cougar-caused fatalities (not additive). Paradoxically, there was only a 1.6% decrease in adult female elk survival between populations exposed to both wolf and cougar predation and those without either carnivore. However, when harvest by humans was considered, harvest was the only mortality factor that was additive and it had stronger effects on survival than any individual carnivore or all carnivores combined (Brodie et al. In press). The difference in age classes selected by wolves and hunters was invoked to explain the considerable harvest impacts uncovered by this study.

4.2.3.   Influence of Multiple Prey Species

In multi-prey systems, wolf prey selection is believed to be influenced by prey species' abundance, vulnerability to predation, and potential energetic value (biomass), as well as wolf preferences (Murdoch 1969, Garrott et al. 2007). Prey vulnerability is determined by the size, age, or physical condition of animals, but also by their behavioral response to predation. For instance, animals that flee when attacked may become entrapped by environmental features versus those that are more prone to remain stationary and aggressively stand down wolf attacks (Garrott et al. 2009a).

Where alternative prey are available, the prey-switching capabilities of generalist carnivores may insulate them from fluctuations in the abundance of their staple prey and allow them to persist at high densities (Glen and Dickman 2005, Garrott et al. 2009a). In this manner, predators may continue to drive staple prey species down, particularly during low points in prey abundance due to human management or environmental or density-dependent conditions. For example, in BNP, up to one third of wolf diets consisted of alternative ungulate prey

during a period of increasing wolf populations and decreasing primary prey (elk) (Kortello et al. 2007). Also, Garrott et al. (2009a) predicted that bison in the Madison Headwaters (YNP) could sustain wolf populations as elk abundance in the Headwaters decreases, potentially to the extent that this herd is restricted to refugia or is extirpated. Contrast this to Isle Royale National Park (IRNP) where the primary available prey were moose and a predator-prey cycle was documented: as wolves increased in abundance, moose decreased until wolf populations dropped sufficiently for moose populations to rebound (Post et al. 2002). With the abundance of alternative prey in NE Oregon, high densities of wolves may be sustained by more abundant deer, despite wolves' general preference for elk documented elsewhere (Smith 2005, Kortello et al. 2007, Metz et al. 2012). If elk decline, but wolf population size and diet remain constant, elk would be disproportionately affected by wolf predation.

The availability of staple prey that is sympatric with rarer species may also be detrimental for the scarcer species (Sinclair et al. 1988, Johnson et al. 2013b). With the availability of moose (*Alces alces*, staple prey), wolf populations in British Columbia are thought to exist at higher densities than would be supported by more predator-sensitive caribou (*Rangifer tarandus caribou*, secondary prey); consequently, caribou declines have ensued (Bergerud and Elliot 1986, Wittmer et al. 2005). Hebblewhite et al. (2007) modeled the effects of high wolf densities sustained by focal prey (elk) in BNP and determined that even with moderate caribou predation rates, wolves could drive the park's extremely small population of caribou to extinction. Alternatively, as found by Kunkel and Pletscher (1999) in northwest Montana, the presence of abundant staple prey (deer) may have diluted the predatory effects of wolves, and thereby buffered a scarcer species (moose) from predation. Though current models of wolf-prey dynamics in YNP do not predict significant impacts to alternative prey, such as bison, mule deer, and moose, these models were based on diet studies during the first 10 years of wolf reestablishment before significant elk declines occurred; as of 2005 wolves almost exclusively preyed on elk (~90% of wolf diets) (Varley and Boyce 2006). Indeed, increased selection for bison has been noted in some parts of YNP (Garrott et al. 2007) and a study of year-round predation by wolves showed a slightly more diversified summer diet (Metz et al. 2012).

4.3.   Carnivore Interactions

Interactions between carnivores are highly relevant to the discussion of additive and compensatory ungulate mortality. Dominant carnivores may exclude or reduce the abundance of other predators through interference competition, such as direct killing, aggressive interactions, territorial marking, as well as exploitive competition in which carnivores compete for prey or other resources (Crabtree and Sheldon 1999, Crooks and Soule 1999, O'Neill 2002, Glen and Dickman 2005, Berger and Gese 2007, Ritchie and Johnson 2009). High dietary overlap between carnivores can be detrimental for subordinate predators and may lead to malnourishment, as well as antagonistic encounters and intraguild predation as competitors pursue the same prey (Donadio and Buskirk 2006, Ruth and Murphy 2010). These interactions are heightened as competitors converge when shared prey is scarce (Begon et al. 1996, Donadio and Buskirk 2006, Glen et al. 2007).

4.3.1.   Wolf-Coyote Interactions

Top-order predators, like wolves, can shape ecosystems by competing with mesopredators, such as coyotes. When apex predators are removed from an ecosystem, mesopredators may be freed from exploitive and/or interference competition, resulting in an increase in the abundance of mesopredators (Rayner et al. 2007, Trewby et al. 2008). This phenomenon, termed 'mesopredator release' (Soulé et al. 1988, Ritchie and Johnson 2009), can have negative impacts for mesopredator prey (Soulé et al. 1988, Crooks and Soule 1999, Rayner et al. 2007, Berger et al. 2008). The return of top-order predators can reverse the impacts of mesopredator release and relieve

the predatory pressure experienced by mesopredator prey (Berger et al. 2008, Letnic and Dworjanyn 2011, Miller et al. 2012).

It has been shown that wolves can have demonstrable impacts on coyotes where they overlap. For instance, within eight years of wolf recolonization of IRNP, coyotes were completely eliminated from the island due to competitive interactions (Krefting 1969). Emerging research in western North America has also documented the suppressive effects of wolves on coyotes. Studies in the GYE show that coyote densities were significantly lower in the presence of reintroduced wolves and transient coyotes dispersed out of sites where wolves were abundant (Berger and Gese 2007). Within the first two years of reintroduction, wolves killed 23-33% of coyotes located in core wolf use areas (Crabtree and Sheldon 1999). The number of coyote packs and pack size were also reduced (Crabtree and Sheldon 1999). In the years since wolf reintroduction, coyotes appear to have learned behaviors to reduce aggressive encounters with wolves (Merkle et al. 2009). The original decrease in the number of coyote packs returned to the pre-wolf average, but pack size remained smaller, indicating that the overall coyote population is less than during the pre-wolf period (Hebblewhite and Smith 2009). While coyotes in the GYE now have access to increased wolf-killed carrion (Wilmers et al. 2003), interference and exploitation competition between the two canids reduces the full effect of the subsidy provided by wolves (Arjo and Pletscher 1999, Switalski 2003, Merkle et al. 2009).

Whether reduced coyote populations ultimately relieve the predatory pressure experienced by prey has only begun to be examined. For example, in the GYE, pronghorn antelope fawn survival rates were four times higher at sites with greater wolf densities and lower coyote densities (Berger et al. 2008). Additionally, over a 3-year study in Grand Teton National Park, areas within 3 km of a newly established wolf den showed significantly less coyote activity and greater abundances of small mammal prey when compared with areas 9-15 km from the den site (Miller et al. 2012).

4.3.2.   Wolf-Bear Interactions

A summary of wolf-grizzly bear interactions in BNP pointed to the likelihood that wolves successfully compete with grizzly bears for possession of carcasses, with the exception of groups of wolves numbering less than four (Hebblewhite and Smith 2009). However, the opposite has been observed in YNP, where grizzly bear densities are 2.5 times higher and average bear body size is greater; there, grizzly bears prevailed in the majority (85%) of competitive encounters at carcasses (Hebblewhite and Smith 2009).

More relevant to Oregon, smaller black bears were observed to be subordinate to wolves at carcasses in YNP (Ballard et al. 2003). Wolves are also known to kill black bears and, in some cases, wolves have dug into winter dens to kill bears (Horejsi et al. 1984, Paquet and Carbyn 1986). Bears have initiated interactions with wolves (Hayes and Mossop 1987) and wolves are occasionally killed by bears, but this has had minimal impacts on wolf populations (Jimenez et al. 2008).

Dietary overlap between wolves and black bears is probably less significant given that ungulates are typically only important in spring bear diets as neonates; bears' nutritional requirements are met through invertebrates and plant matter during the remainder of the non-hibernation period (Bull et al. 2001). Scavenging of wolf-killed carcasses may become an added source of protein for bears (bears scavenged a high degree of cougar-killed prey in NE Oregon; D. Clark, Oregon State University, unpublished data) and this could lead to competitive interactions between wolves and bears at kill sites.

4.3.3.   Wolf-Cougar Interactions

Studies of the influence of wolf re-establishment on cougars have documented the more easily detected interference competition between the two carnivores, as wolves appropriate or scavenge cougar kills and are implicated in direct killings of cougars (Kunkel et al. 1999, Ruth 2004a, Akenson et al. 2005, Kortello et al. 2007). Exploitative mechanisms in the form of dietary competition may only become evident with declining ungulate abundances and differences in prey assemblages moderated by varying habitat, climatic conditions, human harvest, and predation rates (Kunkel et al. 1999, Ruth 2004a). Because wolves are socially cooperative, they tend to dominate in interactions with solitary cougars despite the similar body mass of the two carnivores (Palomares and Caro 1999, Donadio and Buskirk 2006). Subordinate cougars may decline numerically as a result of lethal interactions or nutritional stress due to relinquishing kills, or they may avoid wolves on both wide-scale and fine resolution landscape levels (Riley et al. 2004, Alexander et al. 2006). Documented wolf-cougar interactions are summarized in Table 2.

4.3.3.a. Interspecific Killings and Aggressive Interference

Wolf-killed cougars have been documented in a number of locations. In YNP, Ruth (2004a) discovered that 23% of cougar mortalities were attributed to wolves. Cougars killed by wolves have also been documented in GNP (Boyd and Neale 1992, Kunkel et al. 1999, Ruth 2004b) and BNP (Kortello et al. 2007). Wolves also demonstrated non-lethal aggressive behavior towards cougars. For instance, cougars have been chased and treed by wolves (Ruth 2004b, Akenson et al. 2005). Observations of cougars killing wolves are rare (Ruth 2004a, Jimenez et al. 2008) and cougars only prevailed in interactions involving solitary wolves (Ruth and Murphy 2010).

4.3.3.b. Dietary Overlap and Usurping or Scavenging of Kills

Studies conducted to assess overlap in the diets of cougars and wolves are restricted to the winter season since logistics complicate quantifying wolf predation events during other times of the year. However, because spatial overlap between the two carnivores is typically highest during this season as both predators follow ungulates to their winter ranges (Ruth 2004b, Alexander et al. 2006), winter diets may be the most demonstrative of competition. At the prey species level, winter dietary overlap between these carnivores tends to be high (≥90%, Ruth and Murphy 2010; see Table 2.).

Ruth (2004a) compared cougar diets before and after YNP's wolf reintroduction and revealed few differences, however this research concluded at the onset of dramatic elk declines (Yellowstone Center for Resources 2011). At the time of their study, Kunkel et al. (1999) did not note any changes in cougar prey selection after wolves recolonized and prey availability was declining in GNP; they speculated this was because there was still adequate prey biomass for both carnivores. In contrast to Yellowstone and Glacier National Parks, interference and exploitation competition with wolves apparently altered cougars' diets in BNP (Kortello et al. 2007). As the primary prey (elk) in the study area declined, cougars trained their diets on mule deer and bighorn sheep, while wolves continued to specialize in elk (Kortello et al. 2007).

Wolves and cougars utilize disparate hunting strategies (coursing and pack hunting versus stalking and solitary ambushes). Thus, it follows that in order to balance the nutritional benefits with the energy demands and risks associated with each hunting tactic, the two carnivores should exhibit different prey preferences. When chasing a group of ungulates, wolves often subdue the least fit individual and wolves' cooperative hunting method facilitates the attainment of large prey (Peterson and Ciucci 2003). Conversely, cougars are expected to select smaller ungulates since they must kill without the aid of conspecifics. Because cougars ambush prey, they should

not select for any particular prey fitness level (Sunquist and Sunquist 1989).

In general, the concept of prey partitioning is borne out in field studies comparing the diets of cougars and wolves, though diet separation based on prey species, sex, age, and fitness is not universal (see Table 3 for a summary of diet comparisons from available studies). For instance, in the Madison Range, Montana, wolves were seven times more likely to prey upon nutritionally disadvantaged elk than cougars (Atwood et al. 2007). Wolves also selected larger prey than cougars; wolves were more likely to choose elk and male ungulates (Atwood et al. 2007). However, the potential for competitive interactions remained in that both carnivores preferentially selected male elk more, female elk less, and elk calves equivalent to their respective availabilities in the study area (Atwood et al. 2007).

In GNP, the opposite of theorized prey partitioning was observed: wolves and cougars both preferentially selected white-tailed deer in greater proportion than this species' abundance on the landscape (Kunkel et al. 1999, Ruth 2004b). This study did not find any significant difference in the nutritional fitness of deer selected by either predator (both killed vulnerable prey). Though cougars selected more fawns and wolves consumed more young elk (<3 years old), the age distributions of male and female deer and elk killed by each predator were not statistically different. Both carnivores preyed upon the same sex distribution of deer, however, cougars selected male elk more than wolves (Kunkel et al. 1999, Ruth 2004b).

In the Salmon River Mountains of Idaho, both cougars and wolves specialized in elk prey overall and selected for equivalent age classes of elk (Husseman et al. 2003). Both carnivores preyed upon elk calves in greater proportion than they were available in the study area and avoided cow elk (Husseman et al. 2003). However, in this study, wolves selected mule deer fawns more than cougars. As expected, wolf prey was in poorer condition (based on marrow fat) than cougar prey and notably, wolves were twice as likely to prey on male ungulates as cougars (Husseman et al. 2003).

Opportunity for competitive interactions was also high in another Idaho study that noted that wolves and cougars had nearly identical diets. Both selected elk calves, as well as adult elk and deer in proportion to their relative abundances (Akenson et al. 2005). Some prey partitioning according to age class was evident in that wolf diets contained more elk calves and cougar more frequently ate older elk (>9 years), yet overall distributions of elk age classes selected by both predators were not significantly different. There was no difference in the nutritional status of ungulates consumed by either predator (Akenson et al. 2005).

As the more dominant predator, wolves are effective in appropriating cougar-killed prey. Kunkel et al. (1999) noted wolves scavenged 20% of cougar kills, while cougars only visited 3% of wolf-killed carcasses. Wolves usurped and scavenged 12% and 25%, respectively, of cougar kills in BNP (Kortello et al. 2007). This behavior was not reciprocated by cougars (cougars scavenged only 4% of wolf kills) and cougars rarely returned to carcasses once wolves visited them (Kortello et al. 2007). In YNP, Ruth (2004a) observed a lower rate of wolf scavenging of cougar kills (7%) and though in these instances wolves typically claimed the kills for their own, this did not yet translate to an increase in cougar kill rates. No other studies investigated the impact of wolves' preemption of cougar-killed carcasses on cougar kill rates.

4.3.3.c. Habitat Partitioning and Avoidance Behaviors of Cougars

Cougars have been shown to spatially segregate from wolves on multiple landscape scales. At the broadest context, Riley et al. (2004) used the spatial array of historical (1902-1930) statewide bounty payments for both species to represent the distribution of both carnivores in Montana. These records showed that wolves were primarily dispatched along an east-west gradient with the most wolves taken in the eastern prairies and fewer

wolves harvested in the more rugged western terrain. Meanwhile, the inverse was true for cougars. With humans' westward expansion, most low elevation and gentle terrain has been adopted for agricultural purposes and potential conflict with livestock meant that wolves were no longer tolerated where they historically persisted. In consideration of this fact, at the most expansive scale, wolves and cougars must now share mountainous habitats which could give rise to more competitive interactions (Riley et al. 2004).

However, at more discrete levels of spatial analysis, it becomes apparent that cougars and wolves are able to partition habitat in order to reduce potential conflict. For instance, Kortello et al. (2007) found evidence that at a fine scale, cougars avoided areas recently visited by wolves, but a gross-scale home range analysis showed a high degree of spatial overlap between the two predators. Akenson et al. (2005) also observed fine scale avoidance behaviors; radio-marked cougars moved to the perimeter of their home ranges when radio-marked wolves were present in their territories.

In comparison with pre- and post-wolf conditions, it was observed that cougars shifted to more secure refugia with less potential for conflict with wolves. In YNP, cougar refugia were more rugged areas associated with the bottoms of steep river canyons (Buotte et al. 2005, T. Ruth, personal communication). Cougars in YNP also condensed the size of their home ranges after wolves were restored, presumably to avoid interactions (Buotte et al. 2005). In BNP, areas with lower wolf-density and reduced carnivore overlap were associated with human development (Hebblewhite and Smith 2009); cougar shifts to this habitat as a result of increased wolf numbers could lead to more human conflict (T. Ruth, personal communication).

During winter, cougars and wolves were able to maintain distinct use of habitat, despite the fact that their home ranges converge as they seek prey that migrate to lower elevations or areas with milder conditions (Alexander et al. 2006). In BNP and other areas of the Canadian Rocky Mountains, wolves consistently used gentle-sloped valley bottoms associated with high elk densities, while cougars descended from higher elevations as winter progressed and rarely accessed the valley floor, opting instead to remain on the adjacent hillsides (Alexander et al. 2006). Cougar selection for areas with high elk or deer densities varied throughout the winter (Alexander et al. 2006).

In GNP, a high degree of overlap was found between the predators' home ranges and finer-scale spatial segregation between the two competitors was not observed (Ruth 2004b). While overlap of core areas used by each species was low, cougars did not appear to avoid these areas of overlap. On a spatial-temporal basis, there was no trend in the simultaneous distance between cougars and wolves, implying cougars did not avoid wolves with any consistency. Further, Ruth (2004b) noted significant similarities in the habitat characteristics preferred by each predator on a seasonal basis, with the exception that year-round cougars selected areas with steeper topography than wolves.

Winter severity may moderate the degree to which cougars and wolves overlap seasonally; more "open" winters with less snow accumulation allow ungulates to use a broader range of topography while harsh winters force the concentration of ungulates and thus, carnivores (Kunkel et al. 1999). The greater availability of summer habitat afforded the predators added opportunity to separate spatially (Ruth 2004b).

Evaluation of wolf and cougar kill sites also provides evidence for spatial partitioning between the two carnivores. Due to each predator's distinct hunting style, the location of predation events are uniquely characteristic to each predator. In the northern range of YNP, Kauffman et al. (2007) observed that in the winter, wolf hunting grounds were snow-covered, grassy areas of level terrain. Similarly, in the Madison Range, Montana, wolf kill sites were 45 times more likely to occur in open and gentle-sloped riparian habitat which is more suitable for long pursuits (Atwood et al. 2007). By contrast, sites of cougar-kills were located on steeper terrain (>15% slope) and were

more structurally complex which would provide advantages for an ambush predator (Atwood et al. 2007). Similar topographical differences between the predators' kill sites were noted in the Salmon River Mountains, Idaho (Husseman et al. 2003).

In summary, fine-scale differential use of overlapping habitat could alleviate the potential for competitive interactions between cougars and wolves. However, in areas of uniform topography and vegetation density, sympatric cougars and wolves would be expected to have little opportunity to partition habitat or prey. For example, Kunkel et al. (1999) noted that dense vegetation and rugged topography did not preclude wolves' use of available habitat, though it limited their ability to chase prey. Rather, they observed that wolves used ambush-style tactics more akin to cougars. Finally, during winter, cougars experience an increased risk of encounters with wolves on ungulate winter ranges, though cougars are still able to separate from wolves on the basis of topographical roughness. Severe winters which further concentrate ungulates may elevate the chance of interspecific encounters.

4.3.3.d. Impacts on Cougar Survival and Population Size

Although significant competition was noted in the northern range of YNP, cougar survival rates 10 years after wolf reintroduction remained unchanged from the pre-wolf time period (Ruth et al. 2011). Conversely, Kortello et al. (2007) noted depressed cougar survival rates (0.51) in BNP and Akenson et al. (2005) observed decreased cougar populations after the return of wolves in north central Idaho. Ruth (2004b) speculated that the pre-wolf cougar population size would not be supported in the GNP region as prey declines continued. In all study areas where wolves co-existed with cougars, necropsies of dead cougars revealed severe malnourishment (Ruth 2004b, Akenson et al. 2005, Kortello et al. 2007). Orphaning, malnutrition, and wolf-caused mortality of kittens was documented with greater frequency by Ruth et al. (2011) after wolves recolonized the northern range of YNP. Without emigration from nearby source areas, cougar populations may decline as a result of direct wolf-induced mortality, starvation resulting from prey competition, and slowed reproduction and recruitment (Kunkel et al. 1999, Ruth 2004a, Kortello et al. 2007).

4.4.   Indirect Effects of Wolves on Elk

In addition to wolf predation that causes ungulate mortality directly, researchers have documented several 'non-consumptive' or 'indirect effects' of wolves. These effects are a result of formerly naïve ungulates experiencing new fear elicited by the now present risk of wolf predation. In response to wolf predation risk, elk have modified their behavior by changing their selection of habitat, group size, vigilance, movement rates, and migration patterns.

Herbivores must select habitat that maximizes the availability of nutritional resources and favorable climatic conditions, while minimizing the risk of predation. Wolf recovery in western North America has allowed for the study of ungulate responses to the addition of spatially-explicit wolf predation risk. If predation risk causes elk to utilize areas of lesser forage quality for long durations, elk fitness and reproductive potential would be expected to suffer (Creel et al. 2009). Additionally, if elk must divert time from acquiring food in order to allocate more time to scan for predators, they may become nutritionally challenged with similar consequences (Creel et al. 2009).

4.4.1.   Changes in Habitat Selection

Elk in GYE utilized habitat differently after wolves were reintroduced (Creel et al. 2005, Mao et al. 2005). Mao et al. (2005) compared elk habitat selection between pre- and post-wolf periods. In comparison to summer habitat used during the pre-wolf years, elk selected higher elevation areas away from wolf den activity centers. In the

summertime during the post-wolf period, elk avoided open areas and preferred burned areas that offered better forage and possibly the structural complexity of fire debris to defend against wolf attacks. Elk in high-density wolf areas utilized steeper slopes that also may provide an advantage during wolf attacks. After wolf restoration, elk selected more open habitats during the winter, despite the fact that open grasslands were the riskiest areas (i.e. where the most wolf kills occurred, Kauffman et al. 2007). In a broad spatial and temporal context, Mao et al. (2005) did not detect avoidance of wolves on winter range, though in high-density wolf areas, elk utilized zones with less snow accumulation that would facilitate escape from predation. Within winter ranges, the mosaic of open, risky sites and safer areas with denser vegetation appeared to allow elk to respond to predation risk by making short movements to proximal safety zones (Kauffman et al. 2007).

This notion is supported by consideration of elk habitat use on a fine time scale. When elk habitat use was examined on an hourly basis, Creel et al. (2005) demonstrated that elk exchanged open grasslands for conifers when wolves were within about 1 km. When individual animal movements were analyzed, wintering elk showed different travel patterns that depended on wolf distributions (Fortin et al. 2005). In low wolf density areas, elk movements were more likely to terminate in aspen stands (which are preferred for forage) than open or forested areas. Conversely, in high wolf density areas, elk shifted to conifer areas (which may be avoided by wolves, Kunkel and Pletscher 1999) more than open terrain and aspen stands (Fortin et al. 2005). Elk also used aspen stands less than shrub and grassy areas during times of high wolf presence in GNP and Waterton Lakes National Park (WLNP) and elk habitat selection was driven by habitat characteristics including the field of vision provided and availability of clear escape paths (in terms of forest debris) (Eisenberg 2012).

Changes in elk habitat use after exposure to wolf predation were also noticed in the Madison Range, Montana (Atwood et al. 2007, Atwood et al. 2009). Within three years of wolf recolonization of the study area, elk gradually utilized more structurally complex landscapes which may have reduced their vulnerability to wolf predation, but increased their susceptibility to cougars. This is supported by the fact that the proportion of elk in cougar diets increased significantly over the duration of the study. One interesting auxiliary benefit, as hypothesized by Atwood et al. (2009), is that as elk moved into more complex habitat types typically utilized by mule deer and cougars, cougar predation risk experienced by mule deer may have been diluted to the ultimate benefit of mule deer populations.

4.4.2.   Changes in Migratory Behavior and Distribution

In some cases, the pressure of wolves appears to have caused elk to make substantial changes in their use of the landscape. Elk showed decreased faithfulness to their winter ranges between years in the Madison Headwaters area of YNP (Gower et al. 2009b). Some abandoned winter ranges altogether within the Madison-Firehole-Gibbon drainages; approximately 19% of the formerly non-migratory Madison Headwaters herd began migrating elsewhere for winter (Gower et al. 2009b). Elk in this region gradually constricted into the Madison drainage over the duration of wolf recolonization where the deep and wide ice-free Madison River afforded an escape route during wolf attacks (White et al. 2009b). Hamlin and Cunningham (2009) suspected that similar changes in elk migratory behaviors might also explain decreases among wintering Gallatin Canyon herds in YNP. Hebblewhite and Merrill (2007) demonstrated that in comparison to residents, migrating elk in BNP were exposed to nearly twice as much predation risk while traveling to summer range. Large portions of two major elk herds in and near BNP have become non-migratory, preferring the safety of human development where human activity reduced wolf presence and therefore, predation risk (Hebblewhite et al. 2005, Hebblewhite et al. 2006). This was despite the fact that migration afforded higher quality forage (Hebblewhite et al. 2008). It has also been observed that elk have abandoned traditional calving grounds that are near wolf dens (Hamlin and Cunningham 2009). If elk

change their overall use of the landscape in response to wolves, some historic recreational hunting areas may have lower harvest rates (Hamlin and Cunningham 2009).

4.4.3.   Changes in Group Size and Movement Rate

In winter, elk organized into larger groups in response to the presence of wolves and it was speculated that this behavior may dilute the effects of predation and increase the ability of elk to detect wolves (Hebblewhite and Pletscher 2002, Mao 2003, Proffitt et al. 2009). However, this finding was not replicated by Creel and Winnie (2005) who noted that when wolves were present, elk formed small groups regardless of their distance from cover. These authors speculated that disaggregating might reduce overall encounter rates with wolves. Further, Creel and Winnie (2005) contended that large groups of elk were associated with low predation risk that afforded elk the opportunity to forage en masse in open habitats.   Similarly, Proffitt et al. (2009) determined that elk grouping behavior was dependent on habitat type. In sagebrush steppe areas, elk disaggregated and they grouped more in grassland hills. A portion of grouping behavior was attributed to the enhanced forage available in some habitats (Proffitt et al. 2009).

Elk movement rates increased in response to increased predation risk, but this response only occurred when wolves were within 1-5 km (Proffitt et al. 2009, Middleton 2012). Gower et al. (2009b) observed that elk in the Madison Headwaters (YNP) increased their home range size by 53% after wolves were established and they postulated that this was in response to larger movements to avoid imminent predation. Some elk made temporary, but long distance movements (10-15 km) after wolf attacks (Gower et al. 2009b). That elk appear to only respond to wolf presence when they are in close proximity seems to imply that elk experience acute rather than generalized fear of predation.

4.4.4.   Nutrition Costs

Another non-predation impact described in the literature is based on the idea that elk exposed to predation risk should forgo a portion of foraging effort in order to engage in vigilance behaviors. Presumably, this would result in reduced caloric intake and ultimately lower elk fitness levels (Laundré et al. 2001). Wolff and Van Horn (2003) compared the ratio of time spent in foraging and vigilance behaviors for elk herds exposed to wolves (YNP) and those in wolf-free locales (Rocky Mountain National Park and Mammoth Hot Springs); elk that were sympatric with wolves spent more time in vigilant behaviors than those in herds where wolves had not yet recolonized. Within YNP, Laundré et al. (2001) compared areas with and without wolves and determined that cow elk showed higher vigilance levels in the presence of wolves; over time as wolves expanded into new areas, cow elk became more watchful and cows with calves displayed the highest vigilance levels of all animals exposed to wolf predation. In GNP and WLNP, elk vigilance increased correspondingly with wolf density (Eisenberg 2012). In addition to wolf density, several factors impacted elk vigilance in different wolf-elk systems, including elk group size, amount of physical obstructions hindering escape (i.e. forest debris), distance to forest edge, and proximity to roads (Halofsky and Ripple 2008, Liley and Creel 2008, Eisenberg 2012). Further, increased surveillance for predators resulted in less time spent foraging in some studies (Laundré et al. 2001, Childress and Lung 2003, Winnie and Creel 2007).

However, Middleton (2012) and Gower et al. (2009a) noted that pervasive non-specific predation risk did not translate to generalized alertness in elk. Elk did not reduce time spent foraging even when wolves were in close proximity (Middleton 2012). Several researchers advocated that elk are able to scan for predators while chewing (Fortin et al. 2004a, Gower et al. 2009a, Middleton 2012), and Fortin et al. (2004b) demonstrated that elk only

slightly reduce their bite rate when engaged in vigilant behaviors. This was supported by Middleton's (2012) finding that predation risk did not impact spring body fat levels of elk.

Little research has linked the anti-predator behaviors discussed above to reduced fitness and/or reproductive output of ungulates (Lind and Cresswell 2005). Consistent with shifts in elk habitat utilization patterns, diets of adult female elk included greater quantities of less nutritious evergreen shrubs and conifers when elk were presented with the risk of wolf predation (Christianson and Creel 2008). Corroborating this finding is evidence found by chemical analyses of elk urine and fecal matter that pointed to reduced nutrition among elk exposed to wolves (Hernández and Laundré 2005, Christianson and Creel 2010). However, others have not detected changes in nutritional indices for elk (White et al. 2009a) and White et al. (2011) determined that the elk body fat in the northern range of YNP was almost identical between wolf-free and wolf-present time periods. Moreover, the body fat levels were adequate to prevent fitness-induced pregnancy loss (White et al. 2011). It should be noted that this form of indirect nutrition-related effects of wolves on elk continues to be debated. For instance, Creel et al. (2011) raised concerns about the data and methods that White et al. (2011) used to compare elk pregnancy rates and body fat between pre- and post-wolf time frames.

The fact that predation alone cannot fully explain decreased calf recruitment in some elk populations has prompted inquiry into the potential consequences of wolf-induced fear and stress on elk pregnancy rates (Creel et al. 2007, Creel et al. 2009, Hamlin et al. 2009, Creel et al. 2011, White et al. 2011). Creel et al. (2007) documented decreased progesterone in fecal samples of Gallatin Canyon (YNP) elk exposed to chronic predation risk which could indicate reduced pregnancy rates. Further, Creel et al. (2007) demonstrated that progesterone concentrations were predictive of calf recruitment in the next year. Garrott et al. (2009b) also detected decreased pregnancy rates for Madison Headwaters (YNP) elk between 2002-2007 (7 years after wolf reintroduction) based on serum progesterone levels and serum concentrations of pregnancy specific protein B (PSPB) and proposed that lower pregnancy rates could have resulted from either elk anti-predatory behaviors in response to wolf presence or nutritional deficiencies in elk due to prolonged drought in the region.

However, that elk have reduced pregnancy rates when presented with additional predation risk has been disputed. The accuracy of pregnancy determination using fecal progesterone levels has been inconsistent (White et al. 2011). Additionally, no decrease in pregnancy rates, as measured by blood serum concentrations of PSPB, (Hamlin and Cunningham 2009, White et al. 2011) and hunter reports from late cow hunts (Hamlin and Cunningham 2009), have been documented in YNP's northern range elk since wolf reintroduction. Furthermore, the link established between pregnancy rates to the next year's calf recruitment ignored predation costs on calf survival (White et al. 2011) and new information showing that neonate calves comprised the majority of summer wolf diets was not considered (Metz et al. 2012). Lastly, (Hamlin et al. 2009) showed that there was no significant relationship between the pregnancy rates in several YNP herds and the wolf:1000 elk ratio associated with each herd.

Creel et al. (2009) also examined the effect of chronic stress on elk by measuring fecal levels of the stress hormone, glucocorticoid (as measured by fecal glucocorticoid metabolite, fGCM). They found no relationship between early winter mean levels of the stress hormone and exposure to wolf predation and were unable to detect any relationship between fGCM and progesterone or calf recruitment. Thus, the researchers concluded that decreased pregnancy rates were due to nutritional deficiencies rather than chronic stress. However, Boonstra (2012) argued that the Creel et al. (2009) findings actually reject the assertion that elk exposed to wolves are in poorer nutritional condition. Prior research has documented high levels of stress hormones in nutritionally-compromised animals (Dallman et al. 1999, Kitaysky et al. 2007). Thus, if elk have chronically reduced nutrition

in the presence of wolves, they would be expected to have elevated fGCM levels. However, Creel et al. (2009) failed to find abnormally high levels of fGCM in elk exposed to wolves.

5.   Relevance and Applicability of Prior Research to NE Oregon

While there has been considerable wolf-ungulate and a degree of wolf-predator research conducted in the Rocky Mountain provinces and states, NE Oregon is characteristically different and thus, may bear distinct results. The nearly singular importance of cougar predation on elk populations has rarely been documented elsewhere (but see Myers et al. 1999, Vales 2009). Furthermore, the role of alternative prey has been understudied given that available ungulates in other regions are primarily elk and wolves have shown a strong preference for elk (Smith 2005, Metz et al. 2012). Differences in the prevalence of harvests of antlerless deer and elk immediately prior to and during wolf re-establishment also set NE Oregon apart from previous study areas. Lastly, the relatively mild climate in NE Oregon may preclude the demonstrable effects of wolf predation operating in concert with severe winters that has been observed elsewhere.

5.1.   Significance of Cougars in NE Oregon

Unlike other areas in Wyoming, Montana, and Idaho, cougars in NE Oregon were the top predators of elk calves while black bears had a minor influence on elk calf survival (Rearden 2005 B. K. Johnson, ODFW, unpublished data, Rearden et al. 2011). This was also found to be the case in SE Washington (Myers et al. 1999). As wolves re-establish, it is unlikely that cougars' role in NE Oregon ungulate dynamics will be functionally equivalent to that of bears reported in other wolf systems. In YNP, bears (grizzly and black bears combined) consumed 40% of available calves, primarily within the first 12 days of birth during which calves are hidden to avoid detection (Barber-Meyer et al. 2008). Other predators concentrated on this prey type at least one month post-parturition and thus had fewer opportunities to acquire elk calves (Barber-Meyer et al. 2008). In contrast, cougars and bears in NE Oregon each consumed 5% of available elk calves ≤ 12 days old (B. K. Johnson, ODFW, unpublished data), leaving considerably more potential for wolves to take advantage of calves surviving to more mobile stages. Thus, multi-predator-prey systems where bears' headmost predation limits elk calf recruitment may have limited application to NE Oregon.

In NE Oregon for cougars and YNP for wolves, the apex of elk calf predation by both carnivores was during the summer (June-July) and after the peak calving period (late May) (D. Clark, Oregon State Univeristy, unpublished data, Barber-Meyer et al. 2008, Metz et al. 2012). During this time frame, elk calves were 62% and 31% of wolf (YNP) and cougar (Mt. Emily WMU) diets, respectively (Metz et al. 2012, D. Clark, Oregon State University, unpublished data). Cougars selected elk calves in greater proportion to their availability in NE Oregon (D. Clark, Oregon State University, unpublished data), so preferential predation by wolves on calves more than one month old could result in competitive interactions between the two carnivores and/or further depress calf recruitment.

Ongoing research in the Bitterroot Valley, Montana may be highly applicable to NE Oregon ecosystems. This project is assessing calf survival in an area with the same suite of predators (cougar, coyote, black bear, and wolf) (Montana Fish Wildlife and Parks 2012). Also akin to NE Oregon, the primary predators of elk calves are cougars (36%), followed by bears (13%). Wolves are the third most important predator in this ecosystem (8%). Though non-predation factors appear to have contributed to elk declines in the Bitterroot Valley, future findings may shed light on calf survival in NE Oregon where cougars are limiting calf recruitment.

Although it is highly relevant to NE Oregon, there is a dearth of long-term data documenting cougar-wolf interactions and how these interactions play out for ungulate prey. Thus, it is difficult to predict how wolves will

interact with the previously (and currently) numerically dominant cougar in NE Oregon, and what the implications may be for ungulate prey. Nearby source populations of cougars could help to replace cougars lost to competitive interactions with wolves, though changing conditions may support an overall smaller number of cougars in NE Oregon. If competition with wolves leads to sustained declines in cougar populations, it is conceivable that ungulates may experience a reduction in overall predation pressure. However, if wolves usurp cougar kills, cougars may increase their kill rate in order to meet their nutritional requirements, thereby negatively impacting ungulates. Though increased cougar kill rates has not been documented elsewhere, this competitive result has been suggested in the Mt. Emily WMU where cougars killed more frequently as their average prey size decreased in the summer (due to the selection of calves and fawns) and active bears scavenged their kills (D. Clark, Oregon State University, unpublished data). One other result from competition could occur - should wolves specialize and precipitate declines in a specific prey species, cougars may shift their diets as a result, which would transfer a degree of predatory pressure from one ungulate species to another. This outcome was noted in BNP as elk declined (Kortello et al. 2007).

Ungulates may be affected by other more subtle interactions between wolves and cougars. For instance, if cougars shift their use of habitat to avoid wolves or to seek available prey, ungulate populations may respond at localized levels depending on new patterns of relative predation risk on the landscape. Furthermore, in order to avoid wolf predation, ungulates altered their habitat use (Atwood et al. 2009). In some cases, these prey species began selecting habitats with increased risk of cougar predation (e. g. sites with more vegetation complexity and rugged terrain, Atwood et al. 2007, Atwood et al. 2009). Escape from wolf predation may be negated by an increased risk of cougar predation in this case and the potential for additive ungulate mortality exists if wolf predation remains constant concomitant to elevated cougar predation (Atwood et al. 2007). Additionally, if wolves and cougars partition prey along ungulate sex or age classes allowing cougars' predation rate and population size to remain stable, the combined predation of both predators could impact all classes and the results could be detrimental for ungulates.

Hamlin et al. (2009) observed that predator:prey ratios could be important in forecasting ungulate population dynamics and offered that in Montana, grizzly bear and/or wolf densities over 5 per 1000 elk were correlated with elk population declines; cougar densities were not known and therefore were not incorporated into these estimates. The daily biomass consumed by a single wolf varies seasonally between 4 kg/wolf/day in the summer to 8.5 kg/wolf/day in late winter (Metz et al. 2012); accordingly 5 wolves would consume a total of 20-43 kg of biomass daily. In contrast, individual cougars in NE Oregon consumed an average of 9 kg/day (D. Clark, Oregon State University, unpublished data) and estimated independent adult cougar:elk ratios range from 8-24 cougars:1000 elk (derived from population reconstruction and DNA analyses of scat for three NE Oregon WMUs; G. Davidson, ODFW, unpublished data, Findholt and Johnson In prep). This corresponds to total daily consumption rates ranging from 68-218 kg of biomass/day. Thus, it is not surprising that declines in elk are occurring in these WMUs and throughout the NE Oregon region. It will be important to assess how re-establishing wolves may impact cougar populations as a means to comprehend the combined impact of these predators. For example, if Oregon prey respond to predator:prey ratios as elk did in Montana, managers will need to know if wolf predation is additive to the already high quantity of ungulate biomass consumed by cougars or if wolves will ultimately reduce the abundance of cougars and their total consumption rate.

5.2.   Alternative Prey in NE Oregon

How the availability of alternative prey in NE Oregon will influence wolf prey selection is difficult to predict given that wolf diets can vary based on "… differences in ungulate abundance, body size, anti-predator behaviors and defenses, and vulnerability, as well as variability in wolf preference[s] …" (Garrott et al. 2007 p. 1589).

Wolves do not always align their diets with the most abundant prey. For example, in Alaska, wolves primarily killed caribou even when moose and Dall sheep (*Ovis dalli*) were more abundant (Dale et al. 1995). Few studies report deer as a major dietary component for wolves when elk are also available. However, in Jasper National Park, Carbyn (1974) found that mule deer were the most common prey, comprising about 50% of winter wolf diets, though elk and bighorn sheep (*Ovis canadensis*) were each eight times more abundant during that season. In the summer, elk (presumably calves) became slightly more important than mule deer, but mule deer still were five time less abundant (Carbyn 1974). Carbyn (1983) observed that elk (primary winter prey) were selected in proportion to their abundance in Riding Mountain National Park, Manitoba, while deer were selected more than their abundance would predict, particularly during light snow years. A sharp contrast is noted in most Rocky Mountain sites where winter diets of wolves in elk-dominated landscapes are comprised almost entirely of elk (Hebblewhite et al. 2003, Smith 2005, Kortello et al. 2007, Metz et al. 2012). Deer contributed to a small portion of wolf diets during the spring and summer in YNP (7% and 14%, respectively, Stahler et al. 2006, Metz et al. 2012). Metz et al. (2012) suggested that wolves selected the most vulnerable and/or available prey during each season (e.g. nutritionally compromised male elk in winter and neonates in summer) and that deer were utilized to a lesser degree because their swiftness made them more difficult to attain than elk.

However, in NE Oregon, mule deer and white-tailed deer are predominant. If NE Oregon wolves key in on the most abundant prey, deer may be consumed more than elk, as was observed in GNP (Kunkel et al. 1999). This possibility has several implications. Because white-tailed deer and mule deer partition habitat on the basis of topography, white-tailed deer in characteristic wolf habitat could bear the preponderance of wolf predation, which would offer relief to sympatric elk and mule deer. Alternatively, as discussed earlier, the availability of abundant alternative deer prey could maintain high wolf populations that continue to prey on less abundant ungulate species to some degree; this result could be detrimental for the later species.

The abundance of alternative prey may trigger other outcomes. Deer (mostly mule deer) were the most common prey item of cougars in the Mt. Emily WMU (comprising roughly two-thirds of their diet year-round) and were consumed in proportion to their abundance on the landscape (D. Clark, Oregon State University, unpublished data). Should wolves incorporate mule deer as a major dietary component and cougars continue to consume mule deer as during the pre-wolf timeframe, this species would suffer from additive mortality. Complete additive mortality is not guaranteed since cougars would be required to share their focal prey with another carnivore; the resulting competition could in turn, reduce cougar populations or alter cougar prey selection. However, if wolves perceive elk to be more optimal to attain than deer, cougars and wolves could co-exist with marginal interference.

5.3.   Harvest of Antlerless Deer and Elk in NE Oregon

Hunting of ungulates was not universal in previous study areas, given that many studies occurred in national parks. However, research conducted outside of protected areas has demonstrated a significant contribution of harvest of antlerless elk to elk population dynamics, particularly in advance of and throughout the period of wolf recovery. Knowledge of hunting influences may not offer insight to Oregon managers because harvests of antlerless deer and elk have decreased over the past decade (prior to and concurrent with wolf re-establishment) and in NE Oregon, they occur primarily on private land in response to agricultural damage.

5.4.   Climate Conditions in Oregon

In comparison to the Northern Rocky Mountains, NE Oregon experiences relatively mild winters and higher forage productivity which benefits elk survival. For instance, only 3% of radio-marked adult female elk between 1982-2008 succumbed to climate-related mortality in the winter (Johnson et al. 2013a). These favorable

environmental conditions may somewhat buffer NE Oregon ungulate populations from the additional loss to wolves (Vales and Peek 1995). Severe drought or winter conditions and/or habitat management strategies that reduce forage were concomitant to wolf and bear predation in many areas where elk declines have taken place in the NRM; these conditions resulted in low pregnancy rates and vulnerable prey in winter (Hamlin et al. 2009, White et al. 2010, K. Proffitt, MFWP, personal communication, Middleton 2012). Ungulate winter ranges in the NRM that are wind-swept likely accumulate similar snow depths as those in NE Oregon and may provide an indication of Oregon's future wolf-ungulate dynamics. For instance, the Madison Valley in YNP does not accumulate snow to the extent that elk movements are hindered (Garrott et al. 2009a); the combination of fewer environmental impediments and fewer wolves in this area may be responsible for the continued increase of this herd after wolf reintroduction (Hamlin et al. 2009). Despite Oregon's mild seasonal trends, it is important to note that climate behaves stochastically and it is possible that NE Oregon could also experience extreme conditions that would confer reduced reproduction, calf over-winter survival, and/or increased susceptibility to predation.

6.   Recommended Research Priorities for Oregon

Social, political, and ecological issues pertaining to wolf re-establishment in Oregon have and will continue to pose vexing questions to the Oregon Department of Fish and Wildlife as the wolf population in Oregon expands in number and distribution. Two major public interest groups—hunters and conservationists—are concerned with how the Department will manage wolves and how their interests may be impacted. Consequently, there are compelling reasons for undertaking research on wolves and their effects on wildlife. Oregon's Wolf Plan (Oregon Department of Fish and Wildlife 2010), specifies that relevant research should be undertaken by the Department and, where appropriate, in collaboration with other research institutions, to understand the effects of wolf re-establishment and inform conservation and management actions. Specifically, after review of literature from other areas of wolf re-establishment, it is recommended that the Department investigate possible changes in deer and elk populations as a result of: 1) wolf prey preferences across a variety of ungulate assemblages in NE Oregon; 2) wolf competition with cougars; 3) shifts in ungulate habitat utilization.

Cougars are a major limiting factor of elk recruitment in NE Oregon and may be implicated in mule deer declines. Whether wolves will add to elk and deer mortality or simply replace cougar-caused mortalities is unknown. Wolf-cougar competition could ameliorate some of the predatory pressure experienced by elk and mule deer. Wolf predation risk could cause ungulates to respond such that they utilize landscapes in new ways that reduce access to high-quality forage or increase cougar predation risk. In order to resolve these uncertainties, the following four questions must be addressed:

- **What are wolf prey preferences in areas with variable prey availability?** Understanding wolf prey selection across the broad range of prey species and abundance in NE Oregon may have useful application for other regions in the state and could aid in forecasting potential effects of wolves on elk and deer, as well as competition with other carnivores. Areas within NE Oregon where wolves have re-established vary in terms of prey availability; thus, the region offers an excellent opportunity to compare wolf prey selection across study areas. For example, the Umatilla wolf pack exists in an area dominated by white-tailed deer with fewer mule deer and elk in winter, while the Wenaha wolf pack resides in an area dominated by elk with some mule deer and fewer white-tailed deer, bighorn sheep, mountain goats, and moose. Since few areas in NE Oregon have more elk than mule deer (e.g. Snake River WMU), research from the Northern Rocky Mountains may be less informative for predicting wolf prey preferences. Pursing this question will provide important information about local wolf diets.

- **Will wolves displace cougars or influence their abundance?** This question is directly relevant to understanding if wolves will add to or abate the currently high cougar predation on elk and deer in some WMUs. The Department has multi-faceted pre-wolf information on cougars in the Wenaha, Sled Springs, Catherine Creek, and Mt. Emily WMUs against which any changes in cougar habitat selection, productivity, predation, and abundance can be measured.

- **Will elk respond to wolf re-establishment by altering their habitat use?** Elk habitat resource selection models for the Blue Mountains Region were developed prior to wolf re-establishment in Oregon. Comparison of this model to elk habitat utilization following the re-establishment of wolves will be useful to identify any new elk preferences and inform future management decisions. Because pre-wolf data from radio-marked elk is available in areas where there are now wolf packs, currently and additional GPS-collared elk could be used to contrast elk habitat selection between the two time periods. Any documented shifts of elk to more rugged habitat that is typically associated with cougars could point to higher cougar predation risk and thus, predict additive mortality after wolf re-establishment.

- **Will wolf re-establishment alter ungulate population trends and what level of predator densities can ungulates endure?** Continued monitoring of elk and deer population trends is critical to detect any measurable changes in population estimates, as well as elk calf and deer fawn recruitment. Pre-wolf survival and causes of mortality for adult female elk and mule deer, as well as elk calves are available for several NE Oregon WMUs and can be compared to information collected during wolf re-establishment. Knowledge of both ungulate population trends and predator densities within herd ranges will allow managers to understand how varying predator:prey ratios affect ungulates. Pre-wolf density estimates for cougars and bears are available for some NE Oregon WMUs which can be re-measured or incorporated into current predator estimates. An elk population model is currently under development using recently and locally collected cougar metrics. As wolf data is amassed, the model can be refined to include this additional and potentially important predator. This information will be essential to guide future carnivore, deer, and elk management.

Though it was beyond the scope of this literature review, it is recommended that the Department explore collaborative opportunities to investigate wolf-livestock interactions. Inquiry into summer livestock predation rates, potential impacts on cattle fitness, and cattle behaviors in response to predation risk could be explored in partnership with US Forest Service, USDA Eastern Oregon Agriculture Research Station, the Washington Department of Fish and Wildlife, and a regional university.

It will be important for the Department to keep current with emerging methods to quantify wolf densities, as well as other carnivores. As wolves expand throughout the state, this information will aid in providing total predator densities necessary to predict ungulate responses and to prompt appropriate management actions to reduce the impact of combinations of carnivores.

7. Conclusion

The broad amount of information from the Northern Rocky Mountains and other areas in North America where wolves are present provides insight into the potential effects of wolf re-establishment in Oregon. Prior literature has covered topics relating to wolves' role within the framework of top-down and bottom-up regulation of ungulates, additive versus compensatory mortality caused by wolves, interactions between wolves and other

carnivores and the implications of carnivore competition, as well as a variety of non-consumptive, or indirect effects of wolves on ungulates.

However, NE Oregon is dissimilar from other areas where wolves have recolonized in that the region has: 1) a primarily cougar-driven elk population dynamic and a declining mule deer population resulting, in part, from cougar predation; 2) different compositions of predators and prey; 3) minimal harvest of antlerless deer and elk in advance of and during wolf re-establishment; and 4) a less severe climate. Thus, it will be important to pursue research that directly pertains to regional wolf effects on ungulates and other predators in order to adequately address the concerns of the Department's constituents. Specifically, it is recommended that the Department initiate inquiry to understand potential changes in deer and elk populations resulting from: 1) wolf prey preferences in a region with variable prey assemblages; 2) wolf competition with cougars; and 3) shifts in ungulate habitat utilization. Scientific study of wolves' influence on wildlife will help meet the Department's research objectives as indicated in the Wolf Plan, as well as provide much needed information for the future management of wolves and other wildlife in the state.

The return of wolves to Oregon offers the opportunity to understand their trophic role in a dramatically different ecosystem than those in which the preponderance of research has occurred. Oregon's research efforts will advance the body of knowledge pertaining to wolves in temperate zones with a unique assemblage of predator and prey species. Moreover, the research questions proposed in this document will provide essential information for the successful management of Oregon's wolves and their prey specific to the local environment.
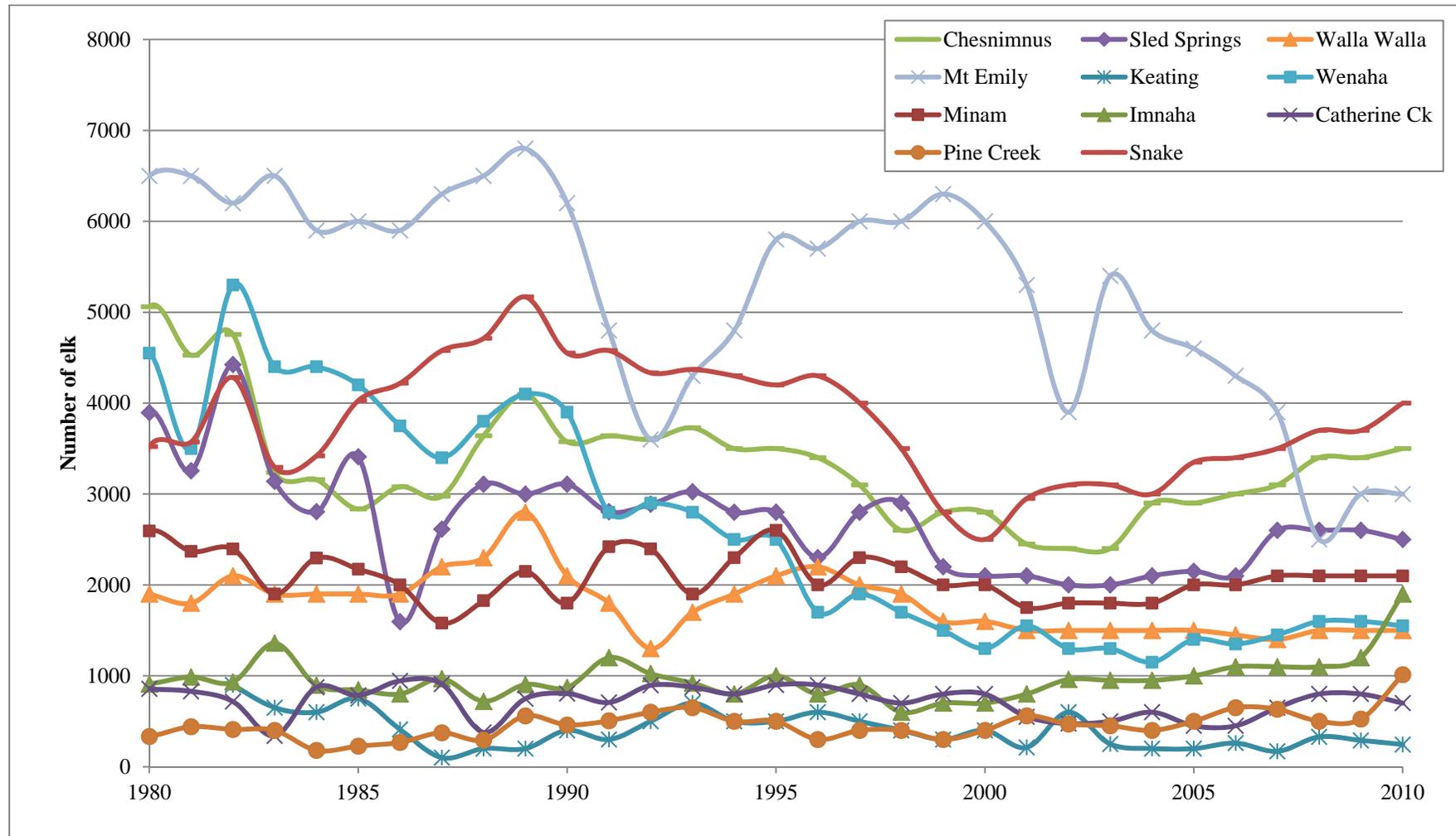
8.   Figures and Tables

Figure 1. Population estimates for NE Oregon elk herds 1980-2012.

Table 1. A summary of top-down and bottom-up factors contributing to elk declines in the Northern Rocky Mountains.

Location	Factors contributing to elk declines				
	High predator:elk ratios[†]	Winter severity	Antlerless harvest	Drought	Habitat management[‡]
1. Clearwater (ID)	✓	✓			✓
2. Bitterroot Valley (MT)	✓		✓		✓
3. Yellowstone Northern Range (WY, MT)	✓	✓	✓	✓	
4. Banff NP (CAN)	✓	✓			
5. Madison-Firehole (WY), Gallatin (MT)	✓	✓			
6. Absaroka, Yellowstone (WY)	✓			✓	

†Predators include wolves, black bears, grizzly bears, or combinations thereof, with the exception of the Bitterroot Valley, where cougars are significant predators of elk calves.
‡Habitat management that resulted in reduced forage availability (e.g. fire suppression or reduced timber harvest)

Citations:
1. Idaho Department of Fish and Game (2006), White et al. (2010)
2. Montana Fish, Wildlife & Parks (K. Proffitt, personal communication)
3. Vucetich et al. (2005), White and Garrott (2005), Varley and Boyce (2006), Barber-Meyer et al. (2008), Hamlin et al. (2009)
4. Hebblewhite et al. (2002), Hebblewhite (2005)
5. Hamlin and Cunningham (2009)
6. Middleton (2012)

Table 2. Summary of competitive interactions between wolves and cougars in the Northern Rocky Mountains.

Location	Interaction observed					Effects on cougars		
	Cougars killed by wolves	Cougar kills usurped/ scavenged by wolves	High diet overlap	Similar prey selectivity	Avoidance/ habitat shift	Starvation	Survival and population	Diet
1. GNP (MT)	✓	✓	✓	✓	NO	✓	No Δ survival	No Δ diet
2. Yellowstone Northern Range (WY, MT)	✓	✓	NR	NR	✓	✓	No Δ survival Population ↓	No Δ diet No Δ kill rate
3. Banff NP (CAN)	✓	✓	✓	✓	✓	✓	Low survival	Diet shift
4. Salmon River Mts. (ID)	✓	NR	✓	✓	NR	NR	NR	NR
5. Taylor Ranch (ID)	NO	✓	✓	✓	✓	✓	Population ↓	Diet shift
6. Madison Range (MT)	NR	NR	NO	✓	NR	NR	NR	Diet shift†

NR = Not measured/reported; NO = Not observed; †Diet shift was due to change in elk habitat selection

Citations:
1. Kunkel et al. (1999), Ruth (2004b)
2. Ruth (2004a), Buotte et al. (2005), T. Ruth (personal communication)
3. Kortello et al. (2007)
4. Husseman et al. (2003)
5. Akenson et al. (2005)
6. Atwood et al. (2007), Atwood et al. (2009)

Table 3. Summary of diets of sympatric cougars and wolves.

Location	Diet similarities	Diet differences
1. GNP (MT)	• Both predators' diets primarily consisted of white-tailed deer (83% of wolf diets; 92% of cougar diets) • Both preferentially selected white-tailed deer more than their availability† • Both selected nutritionally disadvantaged deer† • Both selected similar sex distribution of deer† • Both selected similar age class distribution of male and female deer† • Both selected similar age class distribution male and female elk†	• Wolf diets had more elk than cougar diets (14% of wolf diets; 6% of cougar diets) • Cougar diets had more male elk than wolf diets† • Cougar diets had more fawns than wolf diets • Wolf diets had more young elk (< 3yrs old) than cougar diets
2. Banff NP (CAN)	• Both predators' diets primarily consisted of elk (> 65% of each predator's diet was elk during the initial 2 years of study)	• Wolf diets had more elk than cougar diets (entire study duration)
3. Salmon River Mts. (ID)	• Both predators' diets primarily consisted of elk (73% of cougar diets; 77% of wolf diets) • Both selected similar age class distribution of elk† • Both selected elk calves more than their availability† • Both selected cow elk less than their availability†	• Wolf diets had more mule deer fawns than cougar diets† • Wolf prey was in poorer nutritional condition than cougar prey† • Wolf diets had 2x more adult male ungulates than cougar diets† • Wolf diets had 1.7x more juvenile prey than cougar diets (when adult males are excluded from analysis)†
4. Taylor Ranch (ID)	• Both predators' diets primarily consisted of elk (~70% of each predator diet) • Both selected elk and deer in proportion to their availability† • Both selected elk calves more than their availability† • Both selected nutritionally disadvantaged elk† • Both selected similar age class distribution of elk†	• Wolf diets had 2x more elk calves than cougar diets† • Cougar diets had more older elk (> 9 yrs old) than wolf diets • Cougars had a more diverse diet than wolves
5. Madison Range (MT)	• Both selected male elk more than their availability • Both selected elk calves in proportion to their availability • Both selected female elk less than their availability	• Wolf diet was primarily elk (70% of diet); cougar diet was primarily mule deer (55% of diet) • Wolves selected nutritionally disadvantaged prey 7x more than cougars • Wolf prey size was larger than cougar prey size • Wolf diets had 1.6x more elk than cougar diets • Wolf diets had 2x more male ungulates than cougar diets

†Statistically significant finding. Citations: 1. Kunkel et al. (1999), Ruth (2004b); 2. Kortello et al. (2007); 3. Husseman et al. (2003); 4. Akenson et al. (2005); 5. Atwood et al. (2007)

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