THE BITTERROOT ELK STUDY

Evaluating bottom-up and top-down effects on elk survival and recruitment in the southern Bitterroot Valley, Montana

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Executive Summary

Elk (*Cervus elaphus*) populations in the Bitterroot Valley in west-central Montana steadily increased throughout the 1980s – early 2000s. Changes in management objectives and harvest levels, increasing and expanding carnivore communities, and large-scale changes in fire activity, timber harvest and land use coincided with changes in overall elk population size and calf recruitment trends from 2000 – 2010. From 2005 – 2009, elk population counts in the 6 Bitterroot Valley hunting districts declined by 25%, and calf recruitment reached a historic low. Low recruitment and elk population declines raised concerns that an increasing carnivore populations, and in particular, increasing wolf populations, may be reducing elk populations and hunting opportunities in the Bitterroot Valley. With a goal of better understanding the causes of declining elk numbers and calf recruitment, Montana Fish, Wildlife and Parks (MFWP) and the University of Montana initiated a research project in 2011 designed to evaluate factors affecting elk survival and calf recruitment in the Bitterroot Valley. The purpose of the project was to evaluate bottom-up habitat and top-down predation factors, as well as weather, that may affect elk vital rates and population dynamics.

Archive photo of a mature bull harvested in the Bitterroot Valley.

The study area included the West Fork of the Bitterroot (Hunting District [HD] 250), an area that experienced severe declines in elk numbers and recruitment, and the East Fork of the Bitterroot (HD 270), an area that experienced relatively stable elk numbers and only moderate declines in recruitment. The West Fork area is more forested and mountainous, while the East Fork area contains a mosaic of lower elevation grasslands and higher elevation forested areas. Both areas support mountain lion (*Puma concolor*), black bear (*Ursus americanus*), coyote (*canis latrans)* and wolf (*Canis lupus*) populations.

From 2011 – 2014, we sampled and radiocollared 120 adult female elk to collect information about elk movements, and estimated adult female survival and cause-specific mortality rates. In the East Fork, elk were primarily migratory (78%), but in the West Fork only 32% of elk were migratory. Mean adult female survival from February 2011 through February 2014 was 0.90 (95% confidence interval [CI] = 0.83, 0.94) in both the West Fork and East Fork. Adult female survival was lower in winter than in summer, and 77% of all adult female mortalities occurred between March and May. Of the 13 adult female mortalities that occurred, 5 were due to predation (3 killed by mountain lions, 2 by wolves); 4 were due to natural, non-predation causes; 1 was due to a vehicle collision; and 3 died from unknown causes. Winter survival rate was lower than summer survival rate, and 77% of all adult elk mortalities occurred between March and May.

To better understand the factors affecting calf elk recruitment (i.e. survival to age 1), we radiotagged 226 neonatal and 60 6-month-old calf elk to estimate calf survival and cause-specific mortality rates. Mean annual survival for calf elk throughout the study area was 0.41 (95% CI = 0.33, 0.48). The summer calf elk survival rate was 0.55 (95% CI = 0.47, 0.63), and was lower for calves born later in the calving period. Overwinter survival rate was 0.74 (95% CI = 0.64,0.81), and was unrelated to birth weight or date. Calves born in the East Fork had a higher survival rate (0.47, 95% CI = 0.36, 0.56) than calf elk born in the West Fork (0.32, 95% CI = 0.22, 0.43). Overall, female calf elk survived at a higher rate (0.50, 95% CI = 0.39, 0.60) than males (0.32, 95% CI = 0.22,0.43). Despite the recent recolonization of the study area by wolves, mountain lions caused more elk calf mortality than wolves in summer and winter. These results are broadly consistent with the relative densities of mountain lions and wolves in our study area.

To evaluate the effects of habitat on elk populations, we first developed a spatial modeling approach to estimate landscape-level nutritional resources for elk. Second, we tested the effects of nutritional resources on elk body condition and pregnancy rates. We measured the available biomass, phenology, and digestibility of forage plant species and then used this information together with spatial data on landscape attributes to estimate forage quality at the landscape-scale. We then tested for the effect of East Fork and West Fork summer range forage quality on the body condition and pregnancy rates of elk during fall in the East Fork and West Fork. We found forage quality varied across landcover types and between East Fork and West Fork summer ranges as a function of differences in landcover and recent fire history. These differences in nutritional resources resulted in differences in elk body fat levels and pregnancy rate, with average pregnancy rates of 89% (95% CI 0.81, 0.98) for East Fork elk exposed to higher forage quality and 72% (95% CI = 0.61, 0.83) for West Fork elk exposed to lower forage quality. Our results suggest that the nutritional resources, or forage quality, on summer range limited West Fork elk pregnancy rate and calf production. These nutritional limitations may predispose the West Fork population to be more sensitive to the effects of harvest, predation, weather events or other factors.

Because multiple factors such as pregnancy rates, calf survival and adult survival interact to drive elk population trajectories, predicting the effectiveness of various management actions at increasing elk survival and recruitment is challenging. To address this challenge, we developed a Bayesian integrated population model to 1) estimate East Fork and West Fork elk population growth rate, 2) investigate the relative importance of different vital rates on elk population dynamics, and 3) simulate the effects of various hypothetical management scenarios on elk population growth rate. We estimated that the mean population growth rate (λ) for the East Fork population ($\lambda = 1.06$, 95% Bayesian Credibilty Interval [BCI] = 1.02, 1.10) was about 3% higher than the West Fork population ($\lambda = 1.03$, 95% BCI = 0.99, 1.07). The East Fork population was increasing during all study years except 2010 – 2011 when the growth rate was near stable at 0.99 (95% BCI = 0.88, 1.10). The West Fork population was stable during 2010 – 2011 (1.00, 95% BCI = 0.87, 1.11), declined in 2011 – 2012 (0.95, 95% BCI = 0.87, 1.05), and increased during the latter half of the study.

Our analysis of the relative importance of different vital rates on population growth rate revealed that in the East Fork population, the most important vital rates were first adult female survival (measured by the slope [β] of the regression of population growth rate on each vital rate, and the amount of variation in population growth rate explained by each vital rate [R^2]; $\beta = 0.87$, $R^2 = 0.43$), followed by calf survival ($\beta = 0.35$, $R^2 = 0.38$), then pregnancy ($\beta = 0.17$, $R^2 = 0.06$). Similarly, in the West Fork, adult female survival ($\beta = 0.89$, $R^2 = 0.56$) was the most important, followed by calf survival ($\beta = 0.33$, $R^2 = 0.33$) and pregnancy ($\beta = 0.12$, $R^2 = 0.06$). After decomposing annual calf survival into seasonal components, our analysis also revealed substantive differences in the relative importance of summer and winter calf survival on λ. In the East Fork, summer and winter calf survival contributed more or less similarly to λ (summer = 0.26, SE = 0.02, $R^2 = 0.20$; winter = 0.22, SE = 0.01, $R^2 = 0.19$), but in the West Fork, summer calf survival was more than twice as important (summer = 0.23, SE = 0.01, $R^2 = 0.23$; winter = 0.15, SE = 0.01, $R^2 = 0.11$) as winter calf survival. The relative magnitude of the differences in adult female and calf survival also varied between populations. In the East Fork, adult female survival was only about 5% more important than calf survival, whereas in the West Fork, adult female survival explained about 23% more of the variance in population growth rate compared to calf survival, highlighting an important population difference.

Our population modeling suggests that management actions aimed at increasing adult survival would have the greatest impact on population growth rate, especially for the more nutritionally limited West Fork population. However, it may be more difficult for managers to make changes in adult survival compared to calf survival, because nearly half of adult mortality was due to causes beyond management control, and because adult female survival varied little. Instead, focusing management actions on increasing calf survival may result in similar increases in population growth rate compared to adult survival, and be more practical to achieve because calf survival was largely driven by predation. Calf survival was most affected by mountain lion predation, and therefore management actions aimed at reducing mountain lion densities to increase calf survival may result in increasing population growth rate. Although adult survival and calf survival were predicted to be more influential on population growth than pregnancy rates in both populations, our simulations support the potential to achieve moderate increases in elk productivity from habitat treatments that improve forage for elk and result in higher pregnancy rates for adult females.

Calf survival was largely driven by mountain lion predation, indicating that management actions aimed at reducing mountain lions densities may result in higher calf survival, thus increasing population growth rates. Overall, the annual rate of predation-caused mortality for elk calves was 0.28 (95% CI = 0.22, 0.35), and mountain lion caused mortality (CIF = 0.20, 95% CI = 0.14, 0.27) dominated over wolf caused mortality (CIF = 0.03, 95% CI = 0.01, 0.07) and black bear caused mortality (CIF = 0.05, 95% CI = 0.02, 0.10). Given the strong effect of predation on elk calf survival and the strong effect of calf survival on elk population growth rate, reducing the level of predation on calf elk is predicted to increase calf survival to age 1 and increase elk population growth rate. Although our results regarding the important impacts of carnivores on elk populations through effects on calf survival are generally consistent with previous carnivore-elk studies conducted in the Greater Yellowstone Area (GYA) of southwest Montana, our results differ in that the primary predator of elk in the Bitterroot Valley was mountain lion, rather than wolves or bears. Together, the GYA and Bitterroot elk studies highlight that carnivores have an important impact on elk populations, but that carnivore communities and the relative effects of different carnivore species on elk populations vary across ecosystems.

Section 1 – Introduction

Background

The factors affecting elk (*Cervus elaphus*) populations throughout Montana have been the subject of numerous research efforts over the past several decades. Elk populations in and around the Greater Yellowstone Area (GYA) in particular have been the basis for several intensive research projects (White and Garrott 2005, Garrott et al. 2008, Hamlin and Cunningham 2009). These efforts have been especially informative towards better understanding the responses of elk populations to factors such as the restoration of wolves (*Canis lupus*) *to* Yellowstone National Park (YNP) in the mid-1990s, increasing wolf and grizzly bear populations throughout the GYA in the early-mid 2000s, and variable environmental conditions. The combination of increasing predation on elk calves by grizzly bear (*Ursus arctos horribilis)* and wolves was found to have a strong influence on calf elk recruitment in the GYA (Hamlin and Cunningham 2009), and in some populations the effect of wolves on adult elk survival approached and, in some cases, surpassed that of human harvest (White and Garrott 2005). However, collectively the GYA studies also suggested that the effects of carnivores on elk populations differed substantially across GYA elk populations, making it difficult to generalize the effects of wolf restoration on elk populations.

These GYA elk studies produced valuable information on a range of factors contributing to elk population trajectories and provided the first information in Montana regarding effects of restored wolves on elk populations. In particular, these projects have drawn on large-scale and long-term data sets to assess the roles of predation, harvest and climate on elk survival and recruitment. However, the applicability of these studies to other ecosystems with different habitat and carnivore communities was unknown. The Bitterroot elk study was designed to evaluate the effects of carnivores, as well as bottom-up factors such as weather and forage quality, on elk populations in the southern Bitterroot Valley. Together with the GYA studies, a comparative carnivore-elk study in the Bitterroot Valley improves our understanding of the effects of carnivores on elk populations.

Adult female elk grazing along the West Fork of the Bitterroot River.

The Bitterroot Valley in west-central Montana has historically been a premier elk hunting destination. The Bitterroot Valley elk population increased from just over 2,000 elk in the early 1970s until it reached a peak of 8,169 in 2005, exceeding elk population objectives in several hunting districts (MFWP 2004). The State of Montana Elk Management Plan (MFWP 2004) defines a range of elk population sizes, called elk objective numbers, for each hunting district that are compatible with other land uses and meet the current and future demand for elk hunting opportunity. The current Elk Management Plan was developed in 2004 following public input and comment, and guides the management of elk population sizes throughout Montana. The increase in Bitterroot Valley elk numbers positively impacted the local and state economies (U. S. Fish and Wildlife Service 2011), but was perceived to be causing increasing levels of elk related property damage throughout the Valley. In response to increasing elk populations throughout the late 1990's and early 2000's, management regulations were implemented to increase female harvest and decrease or maintain elk populations towards objective population sizes. By 2008, elk populations in the Bitterroot Valley had declined by over 25%, and in 2009 valley-wide calf recruitment reached an historic low of 14 calves per 100 cows. As a result, managers reduced adult female hunting opportunities in portions of the Bitterroot Valley to maintain or increase elk populations in areas that dropped below objective population sizes. Despite reductions in elk harvest, continued low calf recruitment kept elk populations from increasing, particularly in the West Fork area of the Bitterroot Valley.

At the same time that elk hunting regulations were liberalized in the early to mid-2000's, the carnivore community in the Bitterroot Valley increased in number and complexity. Wolves recolonized the area in the latter half of the 1990s, and minimum population counts in some portions of the Bitterroot Valley (e.g., the southern Bitterroot) increased more than 5-fold from 2001-2007. In addition to black bear (*Ursus americanus*) populations, a 90% reduction in mountain lion (*Felis concolor*) harvest from 1998 to 2003 likely resulted in increasing mountain lion populations throughout the Bitterroot Valley (Robinson et al. 2014). Moreover, the concurrence of declining elk numbers and recruitment, together with the recovery of wolves, encouraged public perception that wolf predation was largely responsible for elk population declines. As wildlife managers developed strategies aimed at increasing elk recruitment and populations, the need for information on factors contributing to low recruitment and declining populations became increasingly acute.

Understanding factors that drive elk population dynamics is important for wildlife managers developing strategies to maintain elk populations within objective population levels. A critical issue for many wildlife managers trying to increase ungulate population trends is whether to invest in enhancing habitat to improve nutritional resources or trying to manage large carnivores to reduce predation, and how these factors affect the level of sustainable harvest. Hunter harvest and predation are the two primary top-down factors affecting elk population dynamics, with the former being the primary management tool employed to affect population size. However, understanding how bottom-up habitat and nutritional condition affect ungulate populations is critical for guiding management actions, particularly in areas experiencing high carnivore densities and declining ungulate population trends. While the focus of public opinion often centers on management of carnivores, the efficacy of carnivore management in low productivity environments may be limited as bottom-up factors such as habitat and nutrition may drive population dynamics. Furthermore, top-down factors such as predation and harvest and bottom-up factors such as habitat and nutrition can have varying effects on different segments of an elk population. Adult female elk survival tends to be high and stable, with top-down drivers acting as the primary cause of mortality (Brodie et al. 2013). In contrast, calf survival and recruitment are highly variable (Gaillard 1998, 2000; Raithel et al. 2007) and can be susceptible to both top-down and bottom-up influences such as predation, maternal body condition, calf birth weight and timing, and winter severity. With the ability to influence only certain aspects of population dynamics, managers require information on the relative influence of the various factors that affect elk survival and recruitment.

Adult female survival is an important driver of elk population dynamics (Nelson and Peek 1982, Garrott et al. 2003). Adult female harvest can dramatically affect population trends and is a tool used by wildlife managers to reduce populations from levels that are ecologically or socially unsustainable (Haggerty and Travis 2006). The expansion of large carnivores such as gray wolves (Pletscher et al. 1997) and mountain lions (Riley and Malecki 2001), also has the potential to affect adult female survival in the region. If high levels of female harvest overlap with high levels of predation, elk populations may be vulnerable to declines (Eberhardt et al. 2007).

Harvest and predation may also affect recruitment of calves into the population through direct mortality. However, unlike adult survival that is robust to all but the most severe environmental conditions, calves are vulnerable to varying climactic and habitat conditions (Garrott et al. 2003). Additionally, nutritional limitation may affect recruitment through reduced pregnancy rates, birth weights, juvenile growth rates, and overwinter survival (Saether 1997, Eberhardt 2002, Cook et al. 2013). Environmental or human-induced changes have the potential to alter habitat on a landscape level, affecting the nutritional productivity of an area. The Bitterroot Valley has experienced substantial changes

An elk herd during spring aerial surveys in the southern Bitterroot Valley.

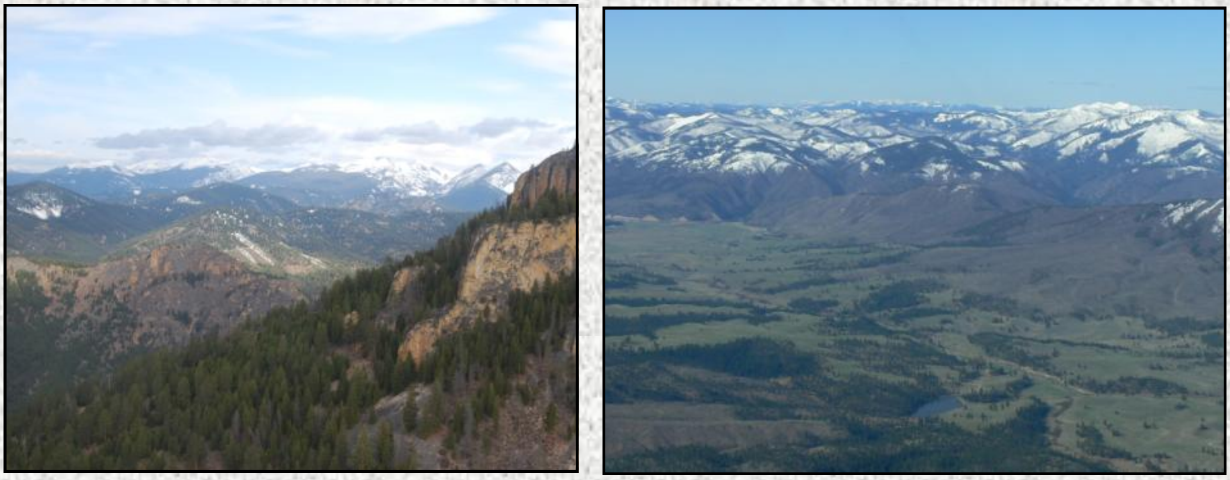
in wildfire activity, forest management, and land use practices over the past several decades; the combination of which may have altered the nutritional carrying capacity in portions of the valley.

Elk habitat quality is determined by a combination of forage quality, quantity, and availability in relation to security (i.e., minimizing mortality risk) on summer and winter ranges (Irwin and Peek 1983, Frair et al. 2005). Throughout the northern Rockies, habitats that meet all elk life history requirements generally include a patchwork of multi-stage forests and open grass and shrub lands (Lyon and Jensen 1980, Skovlin et al. 2002). Historically, wildfires played an important role in the maintenance of forest habitat types with frequent, mosaic-style burns providing multi-succession forests that increased foraging opportunities without sacrificing security (Lyon et al. 2000, Singer et al. 2004). As fire management practices fluctuated throughout the 1900s, periods of fire suppression or exclusion likely contributed to the maturation and homogenization of forest structure and the accumulation of fuels associated with increasing understory density and deadfall (Baker 1992, Calkin et al. 2005). This buildup of fuels combined with warmer and drier conditions have contributed to a shift from smaller, more consistent fires to larger, more sporadic and more intense burns throughout the western US (Bessie and Johnson 1995, Miller et al. 2009, U. S. Forest Service 2013*a*). In the 120 years prior to 1999, a total of 3,035 km^2 burned on the entire Bitterroot National Forest. Since 2000, nearly 5,060 km^2 have burned within the Valley (Gibson et al. 2005, U. S. Forest Service 2013*a*). This increase in fire activity may affect the matrix of forage and security important to elk. Larger and more severe burns can affect the regeneration process, including increased shrub and sapling density, and decreased density and diversity of vascular plants (Turner et al. 1997). Furthermore, the proliferation of intense, large-scale fires can lead to loss of security habitat and thermal cover, stunt the recovery of nutritionally important grasses and forbs, and increase the potential for post-disturbance encroachment of invasive plant species that may be less palatable to elk (Lyon et al. 2000).

Wildfire burning in the West Fork of the Bitterroot.

In addition to fire, timber harvest may have an important landscape-level impact on elk habitat. The effect of timber harvest on elk habitat is dependent on multiple factors, such as the type and size of harvest and the location of harvest (e.g., elevation, slope, etc.; Irwin and Peek 1983). Timber harvest strategies that include moderate levels of harvest on a consistent basis have the potential to create multi-stage forest structures and increase the quality and quantity of forage (Visscher and Merrill 2009). Conversely, sporadic, large-scale timber harvests may lead to loss of security habitat and thermal cover, as well as long-term declines in forage quality and quantity resulting from loss of understory regeneration associated with homogenous forest structures (Lyon and Jensen 1980, Visscher and Merrill 2009). Roads associated with timber harvest also contribute to post-disturbance encroachment of invasive plant species and increased access for hunters, leading to reduced nutritional resources for elk and increased vulnerability to harvest (D'Antonio and Vitousek 1992, Hayes et al. 2002, Frair et al. 2008). Timber harvest on public lands in the Bitterroot Valley decreased 70% during 1980-2013 (U. S. Forest Service 2013*b*). The combination of severe large-scale fires with reduced timber harvest could potentially have contributed to an alteration in elk habitat quality associated with the loss of multi-stage forest structure.

Elk are an iconic species throughout the western United States and beyond. As human populations continue to expand, elk populations will be managed in the context of changing habitat quality and quantity, and evolving social and economic values. Because the factors contributing to fluctuations in elk populations and recruitment are complex, determining appropriate management actions is challenging. Changes in multiple factors affecting elk survival have occurred during a relatively short and recent time period, and human constituencies can argue with equal standing for widely divergent, if not opposing, management solutions. If predation from wolves, black bears, or mountain lions is the predominant source of elk mortality, liberalized carnivore harvests may be effective at increasing elk populations. Additionally, understanding if predation is dominated by one carnivore species can also help target carnivore harvest management. However, there is uncertainty in the efficacy of carnivore management to increase ungulate populations (e.g., Hurley et al. 2011). If nutritional resources are limiting elk survival and productivity,



The West Fork of the Bitterroot River (HD 250; left) is characterized by heavily forested, rugged terrain, while the East Fork of the Bitterroot (HD 270; right) has more moderate terrain and mixed habitat types.

collaborative efforts with land management agencies to improve habitat may be an effective strategy towards increasing elk populations.

The objectives of this project were to comprehensively evaluate factors affecting elk survival, recruitment and population growth of the East Fork and West Fork elk populations in the southern Bitterroot Valley in order and provide recommendations for management strategies to increase elk survival, recruitment and population growth. Specifically, our objectives were:

1) To assess the health of the elk populations by evaluating adult female elk body condition, pregnancy rates, and disease exposure rates.

2) To evaluate elk diet and forage quality, and relate forage quality to adult female body condition and pregnancy rates.

3) To evaluate elk movement behaviors including migration, distributions across public and private lands, and interchange with adjacent elk populations in Montana and Idaho.

4) To estimate adult female elk survival rates and adult female cause-specific mortality rates.

5) To estimate calf elk survival to age 1 (i.e., recruitment rate) and calf cause-specific mortality rates.

6) To integrate vital rate information into a population model to determine the relative importance of different vital rates in affecting East Fork and West Fork elk population growth rate.

7) To use the population model to predict elk population size under different simulated elk management and harvest management scenarios.

Section 2 – Southern Bitterroot Study Area

The 3,350 km^2 study area is located in the southern end of the Bitterroot Valley in western Montana. This area was selected because the West Fork area experienced severe declines in elk calf recruitment while comparatively the East Fork area experienced only moderate calf recruitment declines. The core of the study area is located within the West Fork hunting district (HD 250) and East Fork hunting district (HD 270), as well as portions of the upper Big Hole Valley in HD 334 (Figure 2.1). The administrative boundaries of the HD 250 and HD 270 units changed in 2015 (Figure 2.1), and in this report we define the West Fork and East Fork areas according to the revised 2015 administrative boundaries. The area is surrounded by the Selway-Bitterroot Wilderness to the west, the Salmon River watershed to the south, the Big Hole Valley to the southeast, and the Sapphire and Anaconda Mountains to the east.

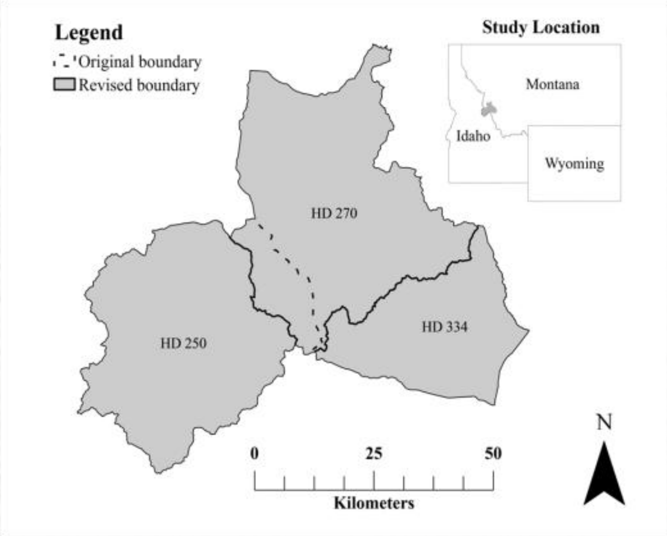


Figure 2.1 The study area was located in the southern Bitterroot watershed and encompassed the West Fork (HD 250) and the East Fork (HD 270) of the Bitterroot River, and portions of the upper Big Hole watershed (HD 334).

The West Fork area encompasses the headwaters of the West Fork of the Bitterroot River and is 1,437 km^2. The area consists of rugged terrain, with elevations ranging from just over 1,200 m in the valley bottom to over 3,000 m along the Bitterroot crest. The majority of the area is heavily forested, with lower elevation riparian grasslands and higher elevation alpine terrain. Public lands, primarily owned by the U. S. Forest Service, comprise over 95% of the area. Private lands, comprising less than 5% of the district, are primarily located along the river bottoms of the

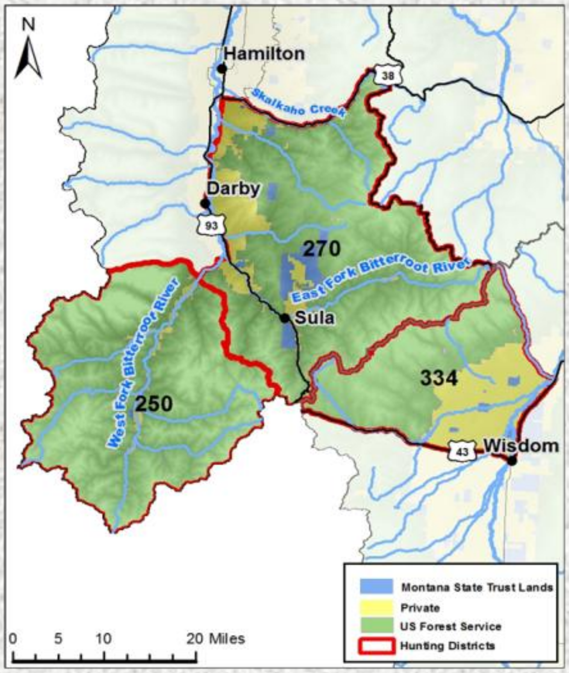


Figure 2.2 Land ownership in the southern Bitterroot Valley study area.

West Fork and Nez Perce Fork of the Bitterroot River (Figure 2.2). Public access via roads is highest along river and creek bottoms, and becomes sparse at higher elevations and in the upper portion of the West Fork. Given the heavily timbered public lands and relatively limited access to large portions of the area, elk security is considered good in this area.

The East Fork area encompasses the headwaters of the East Fork of the Bitterroot River and is 1,719 km^2. The area consists of moderate terrain, with elevations ranging from 1,100 m to just under 2,800 m along the Continental Divide. The area is a mix of open grasslands, mid-elevation rolling hills, and heavily timbered slopes merging into sub-alpine and alpine areas along the Continental Divide. Public lands in the East Fork are a combination of U.S. Forest Service and state trust lands administered by the Montana Department of Natural Resources and Conservation. Private lands account for roughly 18% of the district and are concentrated in the northwestern portion of the area along the main stem of the Bitterroot River and Rye Creek, the Bitterroot River corridor, and the French Basin area in the southern portion of the study area (Figure 2.2). The northern portion of the study area is heavily roaded and the southern portion contains larger blocks of roadless areas, including portions of the Anaconda-Pintler Wilderness.

The West Fork and East Fork areas have experienced variable fire activity. In the West Fork, 194 km^2 burned in the fires of 2000 and 142 km^2 burned in 2011 – 2013 (Figure 2.3). In the East Fork, 809 km^2 burned in the fires of 2000, with little large-scale fire activity since. Timber harvest on the Bitterroot National Forest has declined from a mean of 32.5 million board feet of timber cut per year throughout the 1980s, to 9.5 million board feet per year in the 1990s, down to 7.8 million board feet per year in the 2000s (USFS 2013*b*;).

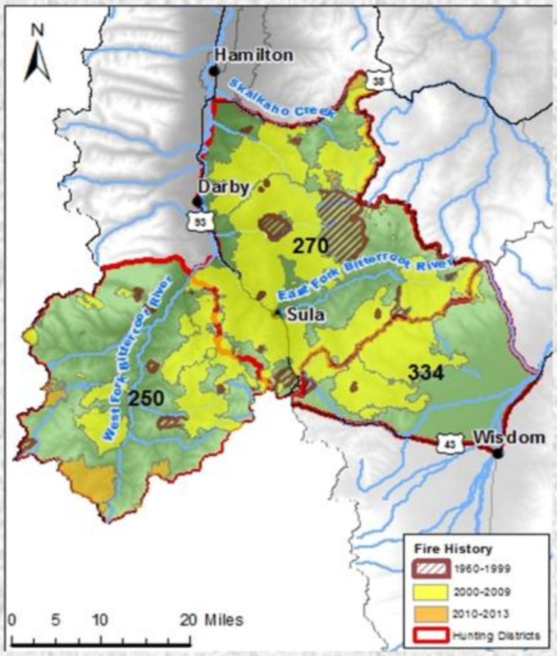


Figure 2.3 Wildfire distributions within the southern Bitterroot Valley study area since 1960. Large scale fires during the 2000's have affected elk habitat through altering forest structure, forage availability, security habitat and thermal cover over large portions of the Bitterroot Valley.

Elk trends and recruitment

MFWP wildlife biologists conduct aerial elk surveys as part of a statewide survey and inventory program to monitor trends in elk populations and calf elk recruitment. In the Bitterroot Valley, elk surveys are conducted annually each spring (late March – early April) from an airplane flying at low elevation. These elk surveys cover the range of the entire elk population, and the number of elk is counted. Additionally, during the survey, elk are classified as adult male, adult females, or calves (i.e, 9–10 month old). Even though surveys cover the entire elk range, surveys do not result in 100% of the elk being counted. Elk counts represent indices of elk population trends, and the number of calves per 100 adult females represents an index of calf elk recruitment.

The West Fork elk population was stable from the mid-1960s through the early 1980s, with annual counts ranging from 264 to 612 (Figure 2.4). Based on the old hunting district boundaries in place at the time, elk numbers steadily increased between 1983 and 2000, reaching a high of 1,914 in 2005. By 2009, the elk population declined to a 20-year low of 744. Mean recruitment, measured as the number of calves per 100 adult female elk during late winter/early spring (e.g., April), was 40 calves:100 cows during 1971 – 2005, then declined to an all time low of 9 calves:100 cows in 2009. Recruitment increased to 33 and 29 calves:100 cows in 2013 and 2014. Trends and recruitment based on the revised and current hunting district boundaries are similar (Figure 2.5).

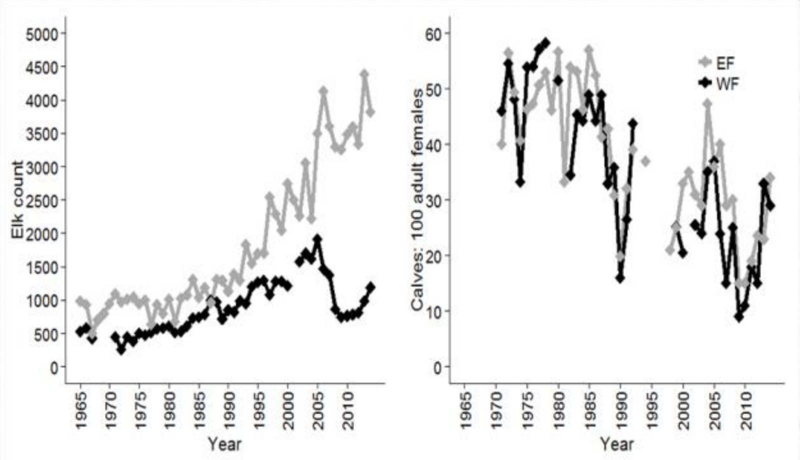


Figure 2.4 Annual elk counts and recruitment from aerial spring surveys in the West Fork (WF, black) and East Fork (EF, gray) areas during 1965 – 2014.

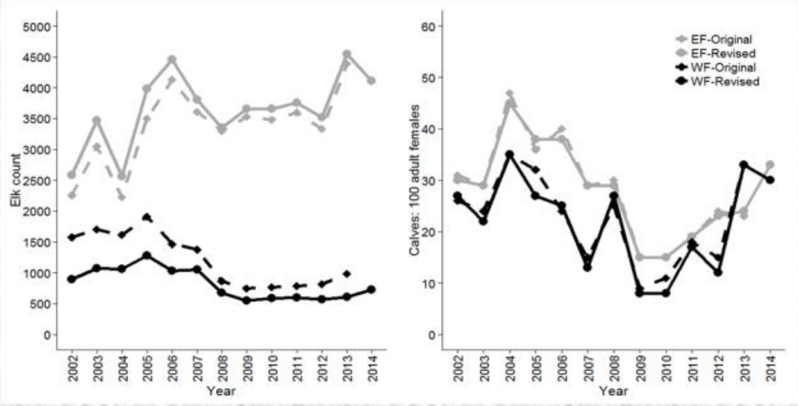


Figure 2.5 Annual elk counts and recruitment from aerial spring surveys in the West Fork (WF) and East Fork (EF) areas during 2002 – 2014. The solid lines represent data for the original West Fork and East Fork hunting district boundaries and the dashed lines represent the data summarized according to the revised hunting district boundaries that were implemented in 2014.

The East Fork elk population was stable from 1966 – 1987, with annual counts ranging from 500 - 1,000 (Figure 2.4). Based on the hunting district boundaries in place at the time, counts steadily increased from between 1998 and 2013, reaching a high of 4,000 elk in 2013. Mean recruitment was 45 calves:100 cows from 1971 – 1992. By 2009, calf recruitment had declined to 15 calves:100 cows. Recruitment increased to

23 and 34 calves:100 cows in 2013 and 2014. Trends and recruitment based on the revised and current hunting district boundaries are similar (Figure 2.5).

Elk hunting regulations and harvest

Elk hunting regulations and harvest management is guided by the State of Montana Elk Management Plan (MFWP 2004). The management plan defines harvest management regulations designed to increase or decrease elk populations towards the population objective levels. Elk population objectives during our study for the West Fork were 2,000 elk, with 10 bulls per 100 adult females and 25 calves per 100 adult females. Elk population objectives during our study for the East Fork were 3,000 elk, with 15 bulls per 100 adult females and 25 calves per 100 adult females.

A harvested bull and white-tail buck at the Darby hunter check station.

In 2004, MFWP instituted a brow-tined bull or antlerless elk season with an antlerless quota for the last 9 days of rifle season. This season structure was in place through the 2007 hunting season in the West Fork and the 2009 season in the East Fork. As a result, antlerless harvest estimates doubled from 2002–2003 and peaked in 2007 (Figure 2.6). Beginning in 2008 in the West Fork and 2010 in the East Fork, antlerless harvest was by limited permit only. By 2011, antlerless harvest declined to 5 in the West Fork and 92 in the East Fork.

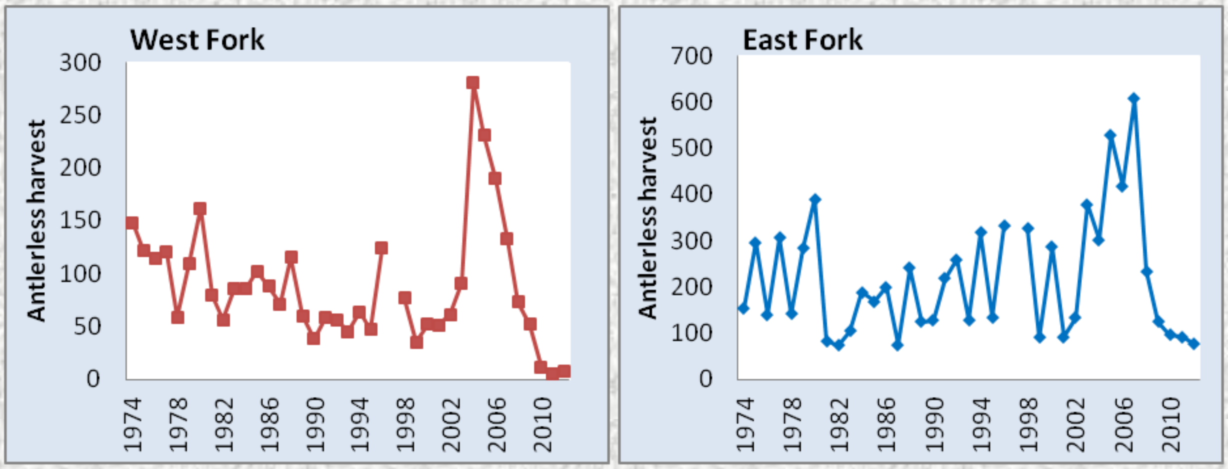


Figure 2.6 Antlerless elk harvest in the West Fork (HD 250) and East Fork (HD270) of the Bitterroot Valley during 1974 – 2013.

Black bear population size and management

We estimated black bear population size based on a population estimation model developed in Montana (Mace and Chilton-Radandt 2011). Mace and Chilton-Radant (2011) developed a predictive model of black bear density in Montana based on mark-resighting data collected at 11 monitoring sites across Montana. Black bear population estimates were then extrapolated to other areas across the state based on habitat and landscape covariates including precipitation and road density. Their model estimated black bear densities were 15 bears/100km^2 (90% CI = 13 - 18) in the West Fork area and 10 bears/100km^2 (90% CI = 7 - 12) in the East Fork area (Mace and Chilton-Radandt 2011). This translates to 216 black bears in the West Fork (90% CI = 187 – 259) and 172 (90% CI = 120 – 206) black bears in the East Fork. During 2000 – 2009, mean black bear harvest was 9 bears per year in the West Fork and 12 bears per year in the East Fork. In 2010, the spring bear season was extended 2 weeks from 31 May to 15 June in BMUs 240 and 216 to increase hunter opportunity and black bear harvest. Mean annual harvest from 2010 to 2013 increased to 13 bears in the West Fork and 16 bears in the East Fork, representing 6.0% and 9.3% of the estimated population, respectively.

Mountain lion population size and management

During the late 1980s through the late 1990s, MFWP implemented mountain lion harvest management regulations in the Bitterroot Valley designed to reduce mountain lion populations with a goal of reducing predation on prey species and address record numbers of human-lion interactions. The number of harvested mountain lions increased until 1998, when it reached a high of 51 mountain lions across the West Fork and East Fork areas (Figure 2.7). From 2001 – 2011, MFWP reduced mountain lion harvest limits and reduced the allowable number of female mountain lions harvested in the West Fork and East Fork to 3 or less females (combined harvest in West Fork and East Fork). Because mountain lion populations increase quickly when female harvest is low and female survival is high (Robinson et al. 2008, Cooley et al. 2011, Robinson and DeSimone 2011), limited female harvest during 2001 – 2011 likely resulted in an increasing mountain lion populations.

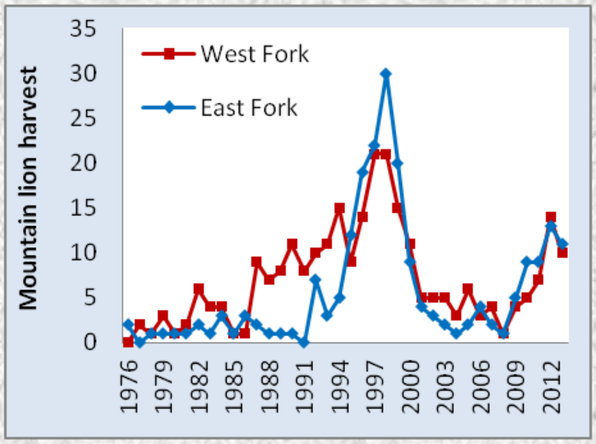


Figure 2.7 Annual mountain lion harvest in the West Fork (HD 250) and East Fork (HD 270) of the Bitterroot Valley during 1976 – 2013.

A female mountain lion in the East Fork of the Bitterroot (HD 270).

Likely due to low female harvest during the previous decade, mountain lion populations in the Bitterroot Valley were perceived to have reached high densities by 2011—2012. In 2012, the West Fork area median mountain lion density was estimated at 4.5 mountain lions/100km^2 (95% CI = 2.9, 7.7) and the East Fork area mountain lion density was estimated at 5.2 mountain lions/100km^2 (95% CI = 3.4, 9.1, Proffitt et al. 2015). Accordingly, in 2012, MFWP implemented mountain lion harvest management regulations designed to achieve levels of female harvest that would reduce mountain lion populations within the Bitterroot watershed by up to 30% over a 3 year period. During 2012 – 2013, mean annual harvest in the West Fork was 12 and in the East Fork was 12, representing 18.5% and 13.5% of the estimated population, respectively. The mean annual female harvest in the West Fork was 7.5 and in the East Fork was 6.5, representing 11.5% and 7.3% of the estimated population, respectively.

Wolf population and management

In 2000, MFWP counted a minimum of 7 wolves in the entire Bitterroot Valley, and the minimum estimated population increased to a high of 74 in 2011 (Figure 2.8). In 2011, there was a minimum of 28 wolves in the West Fork (19.5 wolves/1000km^2) and 18 wolves in the East Fork (10.5 wolves/1000km^2). Between 2008 and 2011, wolves were delisted, relisted, and then delisted again (Hanuska-Brown et al. 2011). This process resulted in a Montana wolf hunting season in 2009, no hunting season in 2010, and then wolf hunting seasons from 2011 through the present. Since MFWP most recently regained wolf management authority in 2011, wolf harvest limits and hunting season dates have been expanded, and the use of specific trapping methods has been approved. In 2012, harvest increased to a high of 8 wolves in the West Fork and 4 wolves in the East Fork 2012 (Figure 2.8), representing 28.6% and 22.2% of the minimum population count, respectively.

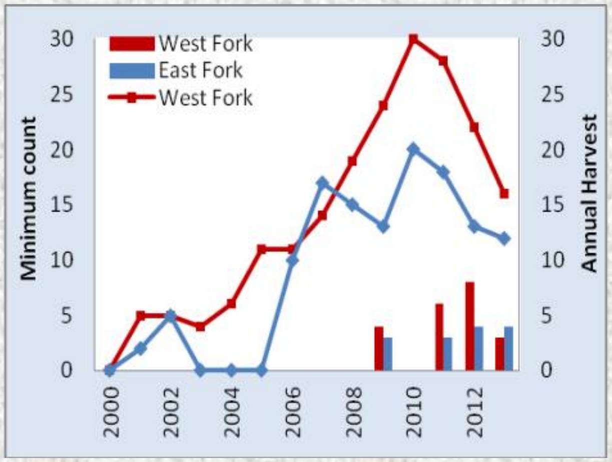


Figure 2.8 Annual minimum wolf count (lines) and wolf harvest (bars in the West Fork (HD 250) and East Fork (HD 270) of the Bitterroot Valley during 2000 – 2013.

Section 3 – Elk Distribution and Movements

Seasonal distributions and migratory behaviors of elk are of increasing interest because of consequences for both game damage issues and hunter access to elk during the fall hunting seasons. Seasonal patterns of habitat use and migration may be strongly influenced by human activity, predation, and changes in habitat types, quality and quantity (Burcham et al. 1999, Proffitt et al. 2010, Cleveland et al. 2012, Middleton et al. 2013). Migratory behavior may affect both survival and reproduction, and is generally linked to either securing access to high quality forage or to reducing exposure to mortality threats (Fryxell and Sinclair 1988, Boyce 1991, Hebblewhite and Merrill 2011). Prevalence, timing, duration, and distance of migration can be affected by variable habitat quality and risk associated with predation and human harvest (Middleton et al. 2013).

Historically, elk within the southern Bitterroot Valley were thought to employ migratory behaviors ranging from nonmigratory (i.e., resident), to long distance annual migrations into the upper East Fork or the Pintlers to the east, the Big Hole to the south, and Idaho to the west. Recently, there have been perceived shifts in fall and winter elk distributions and migratory behavior. Increased use of private lands by big game species is a growing challenge in wildlife management because wildlife managers lose an important tool in managing populations at objective levels if private landowners do not allow hunting (Haggerty and Travis 2006). A better understanding of seasonal elk distributions and migratory behaviors will be an important component as managers strive to find a balance between concerns of private land owners and hunters, and manage elk within population objective levels.

Elk winter range along the East Fork of the Bitterroot River.

We had 3 goals related to evaluating elk movements and distributions. First, our goal was to delineate seasonal elk distributions. Accurate delineation of elk summer and winter ranges is useful in ensuring summer and winter elk habitat management goals are directed to areas currently used by elk. Second, our goal was to summarize elk migratory behaviors. Migratory behaviors are of interest because loss of migratory behaviors may indicate elk distributions are shifting towards establishing resident populations, and having unknown consequences on elk nutritional ecology or on levels of private property damage. Third, our goal was to summarize elk distributions across public and private lands to estimate the availability of elk on public lands during the hunting season.

Methods

Elk collaring and monitoring

We deployed 122 store-on-board, global positioning system (GPS) collars (Lotek Wireless Inc. model 3300L, New Market, Ontario, Canada). Two of the 122 collar deployments were recaptures of previously collared elk, equating to 122 collar deployments on 120 individual, adult female elk. We fit each collar with a timed drop off mechanism set to release after 52 weeks, at which time we retrieved the collars and downloaded the data. We programmed collars to record between 12 and 48 GPS locations per day. Collars emitted a very high frequency (VHF) radio signal allowing them to be monitored from the ground or air. Fix success was >90% and any elk with collars that failed to release were recaptured and had collars manually removed. Location data retrieved from GPS collars resulted in 2,000 to over 17,000 locations per animal per year.

Adult female elk released after being sampled and fitted with a GPS and VHF radio collar.

Seasonal elk distributions

To delineate seasonal elk distributions, we pooled all location data from West Fork and East Fork elk and used a 95% kernel density estimator with reference bandwidth to delineate the seasonal range. We partitioned the data into 5 seasons to address both ecological and management components: spring, summer, archery hunting season, rifle hunting season and winter. We defined archery and rifle seasons according to the annual Montana general elk archery and rifle season dates, where the 6-week archery season starts on the 1st Saturday in

September and the 5-week rifle season starts 5 weeks prior to the Sunday after Thanksgiving. We defined spring as 1 March through 31 May; summer as 1 July until 1 week prior to the opening of archery season; winter as 1 week after the close of rifle season through the end of February. We did not use data from June to avoid primary calving periods and spring migrations.

Elk movements and migrations

We classified elk migration behaviors as migratory, mixed-migrants, resident, nomadic, or disperser based on the timing and distance of movements and the degree of overlap between seasonal home ranges, using methods adapted from Bunnefeld et al. (2011). These methods use GPS collar data to determine if an animal has defined seasonal ranges (i.e., summer and winter), if those seasonal ranges are spatially and temporally discrete, and if the animal moves between ranges within specified time frames. Additionally, this analysis determines the start and end dates of seasonal migrations, duration of migration and distance between seasonal ranges based on the distance and timing of movements away from a seasonal range centroid (Bunnefeld et al. 2011). Based on these parameters, elk classified as migratory established distinct summer and winter ranges which did not overlap, while resident animals used the same ranges during both summer and winter. We considered elk classified as mixed-migrant migratory elk for the purposes of this report. Elk classified as nomadic left the winter range, but then never established a summer or new winter pattern of movement. Elk classified as dispersers left the winter range, established a summer range, but moved to a different winter range the following winter.

Results

Winter range

We identified 2 distinct winter ranges in the West Fork: the upper and lower West Fork (Figure 3.1). Since 2009, elk numbers on the lower West Fork winter range are only 7 –20 elk (MFWP, unpublished aerial survey data). This range consists primarily of private land along the West Fork of the Bitterroot and the Nez Perce Fork, and contains a mix of open fields and the adjoining timbered benches. Winter range in the upper West Fork has 300 - 500 elk and is comprised of a combination of private and public lands along the West Fork of the Bitterroot River,

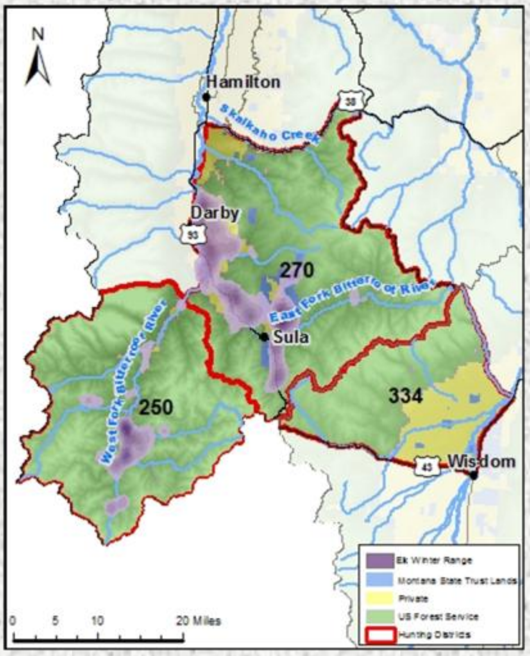


Figure 3.1 Elk winter ranges in the West Fork and East Fork of the Bitterroot Valley during 2011—2013.

adjacent timbered benches, and low to mid elevation ridges and slopes. Collared elk wintering in the West Fork used public lands 81% of the time.

We identified 3 winter ranges in the East Fork: the area from Rye Creek north in the northwestern end, the East Fork corridor along the west central edge, and the French Basin/ Highway 93 South area at the southwestern end (Figure 3.1). The Rye Creek north area winters 1,300 – 1,700 elk and consists almost exclusively of private lands along the river bottom and adjacent open hillsides (MFWP, unpublished aerial survey data). The East Fork corridor has 50 – 400 wintering elk, and consists of a mix of private lands along the river bottom at the northern end, and primarily public lands on higher elevation open slopes and ridges towards the south. The French Basin/Highway 93 south area has 1,200 – 1,800 wintering elk, and consists primarily of private land. Combined, collared elk wintering in the East Fork used public lands 44% of the time.

Migration and summer range

West Fork spring migration start dates ranged from 24 May – 29 June. Start dates for fall migration ranged from 29 July – 11 November (Table 3.1). The mean migration distance among West Fork elk was 12.0 km (95% CI = 10.7 – 13.2). Mean time spent on summer range was 52.7 days (95% CI = 47.2 – 58.1).

Forty-nine percent of West Fork elk were classified as resident (n = 20), 32% (n = 13) as migratory, 17% (n = 7) as nomadic and 2% (n = 1) as dispersers. The majority of migratory elk wintered in the upper West Fork. Resident elk in the West Fork remained on or adjacent to winter ranges throughout the summer (Figure 3.2). Migratory elk in the lower West Fork moved from the lower West Fork and Nez Perce Fork bottoms to summer ranges in the upper tributaries in the northeastern portion of the West Fork watershed. One animal from this area moved northwest over the Bitterroot divide to the head of a tributary of the Selway River in Idaho. Migratory elk in the upper West Fork primarily moved to summer ranges at the heads of West Fork tributaries in the eastern and southwestern portions of the watershed. One elk moved west over Nez Perce Pass to a summer range in Idaho. Nomadic elk in the West Fork used similar habitat as both resident and migratory elk, but lacked the seasonal

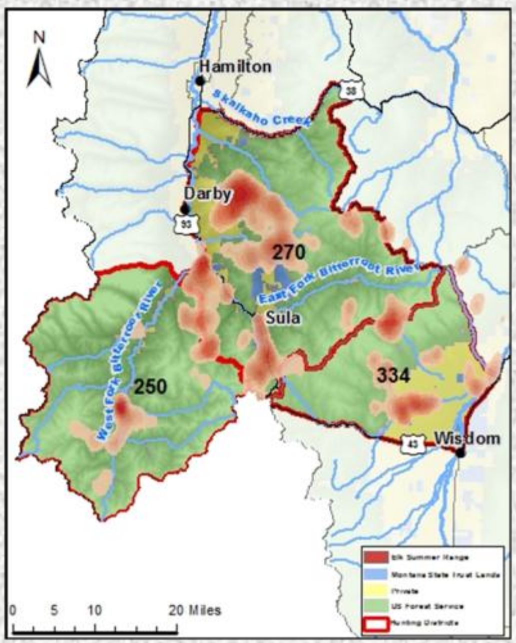


Figure 3.2 Elk summer ranges in the West and East Forks of the Bitterroot Valley and the Big Hole Valley during 2011 – 2013.

Table 3.1: Median start and end dates for spring and fall migrations of 59 radiocollared migratory adult female elk in the West Fork and East Fork of the Bitterroot Valley during 2011 – 2013.

Area	Year	n	Spring Start	Spring End	Fall Start	Fall End
West Fork	2011	5	6/13/2011	7/1/2011	8/24/2011	9/23/2011
	2012	5	5/30/2012	6/23/2012	8/24/2012	9/23/2012
	2013	3	6/29/2013	7/29/2013	9/9/2013	9/18/2013
East Fork	2011	21	5/17/2011	6/3/2011	10/16/2011	11/2/2011
	2012	12	4/28/2012	5/16/2012	9/26/2012	9/29/2012
	2013	13	5/6/2013	5/19/2013	10/13/2013	10/25/2013

fidelity to any particular summer or winter ranges. The one dispersing elk in the West Fork moved from the upper West Fork her first winter to the lower West Fork her second winter a winter, indicating some interchange between these areas.

East Fork spring migration start dates ranged from 8 April - 29 June. Start dates for fall migration ranged from 29 July - 12 December. The mean migration distance among East Fork elk was 20.6 km (95% CI = 16.9 – 24.2). Mean time spent on summer range was 138.3 days (95% CI = 136.2 – 140.5). Seventy-eight percent of East Fork elk were classified as migratory (n = 46), 15% (n = 9) as resident, 5% (n = 3) as nomadic, and <2% (n = 1) as dispersers. Migratory elk that wintered in the Rye Creek area migrated to several summer ranges: 68% (n = 13) moved east and south to the upper tributaries of Rye Creek, 21% (n = 4) moved south into tributaries of the East Fork, and 1 animal moved over the continental divide into the Big Hole Valley in HD 334 (Figure 3.2). Migratory elk that wintered in the East Fork corridor moved in equal numbers either south to the southern portion of the Bitterroot divide towards Lost Trail Pass (n = 2) or south and east over into the Big Hole (n = 2). Migratory elk that had winter ranges in the French Basin area migrated to several summer ranges: 27% (n = 6) moved south and east into summer ranges in the upper tributaries of the East Fork, 18% (n = 4) moved farther south and west along the Bitterroot divide towards Lost Trail pass, and 55% (n = 12) moved southeast into the Big Hole (Figure 3.2). The nomadic collared elk in the East Fork also overlapped with both resident and migratory elk, but again showed little to no seasonal fidelity to specific summer or winter ranges. The one dispersing elk in the East Fork migrated from the

East Fork elk summer range in the Big Hole Valley.

French Basin winter range to a summer range in the Big Hole, but then moved into the Salmon River watershed in Idaho the following winter.

Seasonal use of public and private lands

West Fork elk primarily used public lands throughout the year. Seventy-two to 84% of all elk locations during the summer, archery, and rifle seasons occurred on public land (Figure 3.3). East Fork elk summer locations were primarily on public lands (87%, Figure 3.3). At the start of the archery season, there was a pronounced shift in elk distribution with elk using public lands 56% and 54% of the time during archery and rifle seasons respectively.

Figure 3.3 Percentage of elk locations on public lands during spring, summer, archery hunting season, rifle hunting season and winter in the West Fork and East Fork of the Bitterroot Valley.

Discussion

Elk in the West Fork of the Bitterroot showed less migratory and more resident behaviors than East Fork elk. Migration distances in the West Fork were shorter than in the East Fork. West Fork elk moved to summer range later in the spring and departed summer range earlier in the fall than East Fork elk, and overall spent 60% less time on summer range than East Fork elk. Shifts in seasonal habitat use and migration have generally been attributed to animals attempting to gain access to higher quality forage while avoiding areas of increased mortality risks (Fryxell and Sinclair 1988, Boyce 1991, Middleton et al. 2013, Mysterud 2013). West Fork summer ranges tend to be higher elevation, montane habitats. The area received minimal hunting pressure since 2010 (25 brow-tine bull permits and 5 antlerless licenses for the entire HD, and <1,700 hunter days/year). Accordingly, seasonal habitat use and migratory patterns may be related more to habitat or predator avoidance than avoidance of human hunting pressure. A smaller proportion of migratory elk, combined with less time spent on higher elevation and drier summer ranges, may simply be a factor of shorter snow-free period associated with higher elevations, or may be related to the availability of forage resources.

The East Fork area experienced higher hunter pressure in the fall (almost an order of magnitude higher at 15,000 – 22,000 hunter days/year). Elk that used summer ranges in the Big Hole and around the Continental Divide migrated back to East Fork winter ranges in late October through late November, whereas elk using summer ranges in the Rye Creek north area migrated in mid-August through early September. While differences in productivity of these two summer ranges may have accounted for some of the differences in the timing of fall migration, the disparity in road access and hunting pressure between winter and summer ranges among these areas are also likely important. Summer ranges in the Big Hole and Continental Divide areas had few roads and difficult terrain at higher elevations, and limited public access on lower elevation private lands. East Fork winter ranges of these animals, along with several of the primary migratory routes, included areas of increased road densities and higher levels of public access. Conversely, summer ranges in the Rye Creek north area had more road access and increased hunting pressure, while winter ranges of these animals were largely inaccessible to hunting.

Section 4 – Elk Body Condition, Pregnancy, and Disease Exposure

The nutritional condition of adult female elk, and their potential effects on survival and reproductive performance have become recognized as important factors affecting elk populations (Cook et al. 2013). These factors are important for wildlife managers to consider when evaluating potential effects of habitat treatments, harvest management regulations, and predation. Poor nutritional condition can influence adult overwinter survival, but also may affect reproductive factors such as timing of birth, calf weight at birth, and juvenile survival (Gaillard et al. 2000, Cook et al. 2013). Additionally, females in poorer body condition may have lower pregnancy rates (Cook et al. 2004, Cook et al. 2013). Recent work suggests that nutritional resources during summer influence ungulate reproduction and survival (Cook et al. 2013, Monteith et al. 2013). During summer, female ungulates require sufficient high quality forage to compensate for lower forage quantity and quality during winter, recover the energetic costs of lactation, and build body reserves to survive and maintain pregnancy during the winter (Cook et al. 2004). These important relationships between elk body condition and reproductive performance highlight the need to evaluate body condition of West Fork and East Fork elk, and to improve our understanding of the relationship between elk body condition and summer nutritional resources (see Section 5).

Adult female elk in the West Fork of the Bitterroot.

Our goal was to test the underlying hypothesis that adult female elk in the West Fork area are in poor nutritional condition, and these effects may limit calf production. Variation in recruitment of calf elk into the population can be introduced at several critical stages, including pregnancy rate and intra-uterine survival, as well as neonatal and overwinter survival. Factors such as nutrition, population density, weather, age structure of females, and interactions among these factors may affect calf production (i.e., pregnancy rate and intra-uterine survival). Pregnancy rates and intra-uterine survival are expected to reflect bottom-up effects of density dependence or environmental conditions (Cook et al. 2004), and may or may not also reflect indirect top-down effects of predation risk (Creel et al. 2007; White et al. 2011; Middleton et al. 2013*a,b*). In elk, pregnancy rates decline as a function of body fat (Cook et al. 2004). In captive elk, individuals with body fat levels below 10% begin to experience declines in pregnancy rates; at body fat levels of or below 5%, pregnancy rates declined to 0 (Cook et al. 2004). Thus, pregnancy rate may vary annually with the availability and quality of nutritional resources. Additionally, density-dependent reductions in per-capita nutritional resources have the potential to reduce body condition and consequently pregnancy rates (Kie and White 1985, Stewart et al. 2005).

To evaluate the hypothesis that elk in the West Fork population may be in poorer nutritional condition and have limited calf production, compared to the East Fork population, we estimated the percent ingesta-free body fat and pregnancy rate. Body fat levels integrate energy intake and expenditures and represent a direct measurement of nutritional condition. To evaluate calf production, we estimated pregnancy of adult female elk from blood serum proteins (Noyes et a. 1997). Next, we compared body fat and pregnancy rate of West Fork elk to comparable data collected from the East Fork as well as 8 other elk populations in Montana. Nutritional condition information has been collected across southwest Montana elk populations as part of ongoing efforts to assess the overall nutritional status and health of elk populations across the state.

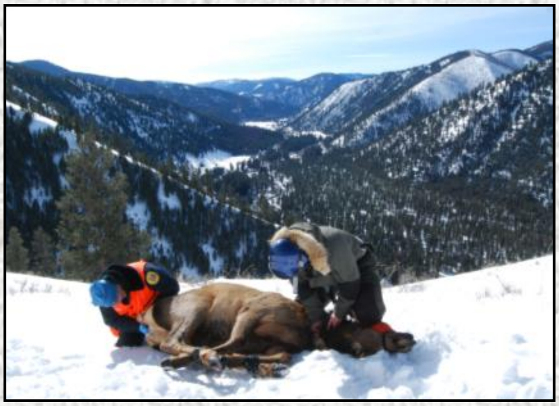
A collared adult female elk is recaptured by netgunning from a helicopter.

Lastly, we estimated levels of disease exposure in the West Fork and East Fork elk populations to assess the overall population health and confirm that disease effects unrelated to nutritional resources were not limiting elk body condition or calf production rates. In addition to nutritional condition and pregnancy rates, disease may affect the overall health and productivity of elk population. MFWP conducts a disease surveillance program across Montana based on screening blood serum collected from captured animals for antibodies indicating exposure to various pathogens. Disease sampling within the Bitterroot Valley has been limited during the past decades, and levels of elk exposure to diseases were unknown.

Methods

Elk capture and sampling

We captured adult female elk by helicopter netgunning and darting following approved MTFWP animal capture protocols and University of Montana Institutional Animal Care and Use Protocols



An adult female elk being sampled and fitted with a GPS/VHF collar in the West Fork of the Bitterroot.

(Protocol 027-11MHWB-042611). We aged elk by tooth eruption and wear patterns (Hamlin et al. 2000). We estimated levels of ingesta-free body fat (IFBF) using a portable ultrasound machine following methods of Cook et al. (2004, 2010). We sampled elk from the East Fork and West Fork populations during both the late fall (early December) and late winter (February), allowing us to detect any over winter variations in population-level body condition or pregnancy rates due to diminishing forage or overwinter fetal mortality. We determined the lactation status of elk captured in the late fall, but were unable to estimate lactation status of elk captured in late winter because lactation declines over winter. Non-lactating elk included elk that were not pregnant the previous year and elk that had lactated an unknown portion of the season due to losing calves. Because fat accretion of lactating and non-lactating female varies substantially and that non-lactating females may be less sensitive to their nutritional environment, we compared only body fat levels from lactating elk during fall. During winter, when we were unable to determine lactation status, we included all animals in our analyses.

We collected a blood sample to determine pregnancy status (Noyes et al. 1997) and screen for exposure to a suite of common diseases previously known to occur in Montana. These included brucellosis (*Brucella abortus),* para-influenza 3, infectious bovine rhinotracheitis, bovine respiratory syncytial virus, bovine viral diarrhea, and leptospirosis (*Leptospira*).

We first tested for effects of population (East Fork or West Fork) and year (2012, 2103) on fall IFBF while controlling for lactation status (yes, no) using a linear model (i.e., ANOVA). We fit all potential combinations of variables (from the full factorial down) and selected the top model explaining IFBF using Akaike Information Criteria (AIC_c) corrected for small sample sizes (Burnham and Anderson 2002). Next, we tested for effects of IFBF, population and year on pregnancy rate using a logistic regression model (Hosmer and Lemeshow 2000). We did not consider season (early, late winter) nor lactation status in the analysis of pregnancy rates because lactation status was unknown in late-winter samples. We fit models with the main effect of IFBF, population and year, and all possible 2 and 3-way interactions and selected the top model explaining variation in pregnancy using AIC_c.

Results

Elk body fat

We captured, sampled and collared a total of 120 individual adult female elk during 2011 – 2013. We recaptured 2 of these elk to remove collars, for a total of 122 capture events. In winter (February) 2011, we captured 44 elk. In 2012 and 2013, we captured 20 elk in late fall (November) and 20 elk in winter (February). Mean age in the West Fork was 6.6 (n = 52, 95% CI = 5.7 – 7.4) and mean age in the East Fork was 5.8 (n = 68, 95% CI = 5.1 – 6.6).

Winter body fat was lower in the West Fork than in the East Fork, although the difference was only statistically significant during 2011 (Figure 4.1). Overall mean winter body fat was 6.4 % (n = 34, 95% CI = 5.7 – 7.1) in the West Fork and 7.1 % (n = 47, 95% CI = 6.6 – 7.7) in the East Fork. As compared to other elk populations from southwestern Montana in this same time period, winter body fat levels in the West Fork and East Fork populations were the lowest observed (Figure 4.2).

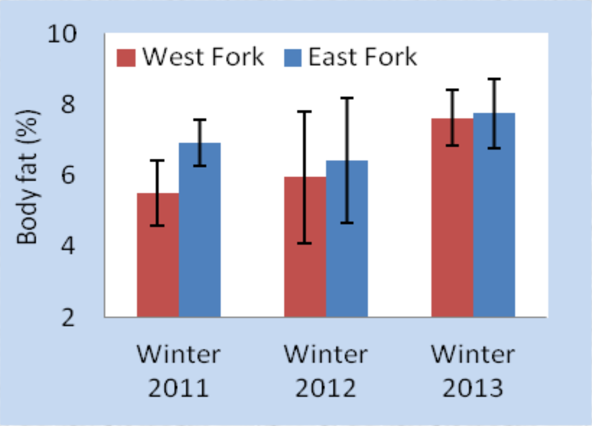


Figure 4.1 Late winter mean body fat of elk captured in the southern portion of the Bitterroot Valley during 2011 – 2013. Error bars represent the 95% confidence interval.

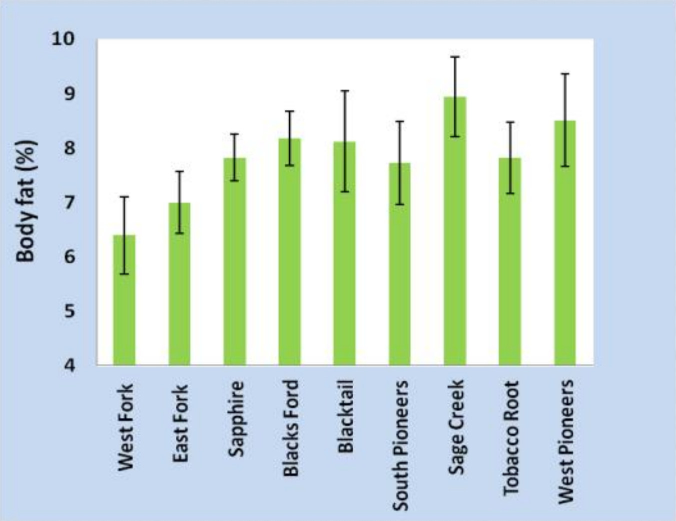


Figure 4.2 Late winter body fat (bars) and pregnancy rates (squares) for elk sampled in the West Fork (2011 – 2013, n= 35), the East Fork (2011 – 2013, n = 43), the northern Sapphire Mountains (2013, n = 42), Blacks Ford (2014, n = 41), Blacktail (2011, n = 32), the South Pioneers (2013, n = 25), Sage Creek (2012, n = 30), the Tobacco Root Mountains (2014, n = 20), and the West Pioneers (2013, n = 25) in Montana.

Fall body fat of lactating elk in the West Fork was lower than lactating elk in the East Fork (Figure 4.3). The top model explaining variation in fall body fat included population, lactation status, and year, and all interactions ($F_{7,29} = 5.86$, $p = 0.0003$, $R^2_{adj} = 0.49$). West Fork elk, on average, had 2.4% lower IFBF ($\beta_{WF} = -2.41$, $p = 0.046$) than East Fork elk. Lactation reduced body fat on average by 2.0 % ($\beta_{Status} = -2.00$, $p = 0.101$). In 2013, all elk had 1.0% higher body fat ($\beta_{2013} = 1.06$, $p = 0.454$), and non-lactating West Fork elk had 4.6% higher body fat ($\beta_{WF*2013} = 4.59$, $p = 0.015$) than non-lactating West Fork elk. Fall body fat of lactating elk was higher in the East Fork than in the West Fork in both 2012 and 2013 (i.e., there was no significant interaction between Population×Status, *p* = 0.410). The interaction between population, lactation status and year was marginally significant, indicating a difference in IFBF for lactating and non-lactating for elk in the West Fork in 2013 where West Fork elk that were lactating had 4.3% lower IFBF in 2013 ($\beta_{WF*2013*Status}$= - 4.27, *p* = 0.120). Fall body fat data from other populations in Montana was not available for comparisons.

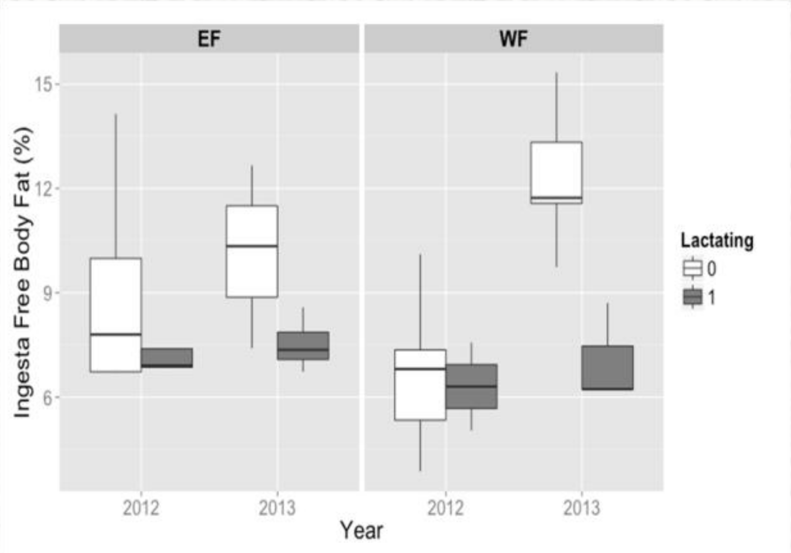


Figure 4.3 Nutritional consequences of differential forage quality available to elk in the East Fork (EF) and West Fork (WF) populations during 2012–2013 showing the estimated fall body fat (%) of lactating (Yes = 1) and non-lactating (No = 0) individuals.

Pregnancy rate

Overall, East Fork elk pregnancy rate was higher than West Fork pregnancy rate in 2011, 2012 and 2013, averaging 89% (95% CI 0.81 – 0.98) for East Fork and 72% (95% CI = 0.61 – 0.83) in the West Fork (Figure 4.4). The top model explaining pregnancy rate was a function of population and body fat. Based on the top model, pregnancy rate increased most strongly as a

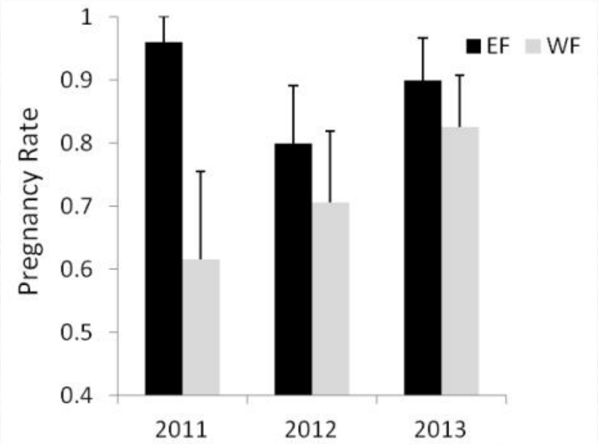


Figure 4.4 The mean pregnancy rates of West Fork (WF) and East Fork (EF) elk during winter 2011, 2012, and 2013. Error bars represent ±1 standard error.

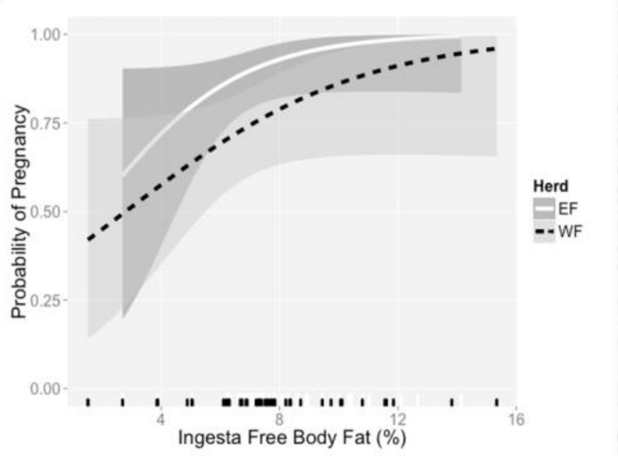


Figure 4.5 The probability of pregnancy and 95% confidence interval (shaded) as a function of percentage ingesta free body fat during winter in the East Fork (EF) and West Fork (WF) populations.

function of body fat (Figure 4.5). For every increase of one percentage point of body fat, the odds of becoming pregnant increased by 1.34 (β= 0.30, z-value = 2.45, *p* = 0.01). However, overall pregnancy rates were lower in the West Fork compared to the East Fork (β= -1.03, z-value = -1.96, *p* = 0.05), indicating an additive reduction in pregnancy rates in the West Fork over and above the effects of IFBF. At a body fat of 8%, West Fork elk had a lower probability of being pregnant (0.78) compared to East Fork elk (0.89). We found no evidence of overwinter pregnancy loss (Figure 4.6).

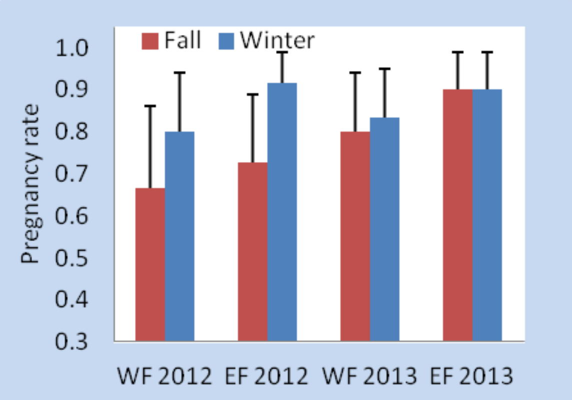


Figure 4.6 Fall and winter estimates of West Fork (WF) and East Fork (EF) pregnancy rates 2012 – 2013. Error bars represent ±1 standard error.

Disease exposure

We obtained and processed viable blood samples from 119 individual elk. Serologic evidence for *Brucella abortus* exposure was not detected in any of the elk sampled. The proportion of elk that tested seropositive for exposure to *Leptospira spp*. varied annually from 0% to 78% (Table 4.1). Levels of disease exposure were similar to levels observed in other wild elk in western and southwestern Montana (K. Proffitt, unpublished data).

Table 4.1. Annual exposure levels to *Brucella abortus (Brucella)*, *Leptospira* (*Leptospira spp.*), Para-infleunza 3 (PI3), Infectious bovine rhinotracheitis (IBR), Bovine respiratory syncytial virus (BRSV), Bovine viral diarrhea (BVD) as determined by serologic testing of elk in the southern Bitterroot Valley during 2011 – 2013.

Year		Brucella	Lepto	PI3	IBR	BRSV	BVD
2011	Sample Size	41	41	41	41	41	41
	# Exposed	0	32	22	2	1	0
	% Exposed	0	78.0	53.7	4.9	2.4	0
2012	Sample Size	39	39	39	39	39	39
	# Exposed	0	10	24	0	4	2
	% Exposed	0	25.6	61.5	0	10.3	5.1
2013	Sample Size	39	39	39	39	39	39
	# Exposed	0	0	10	6	2	1
	% Exposed	0	0	25.6	15.4	5.1	2.6

Discussion

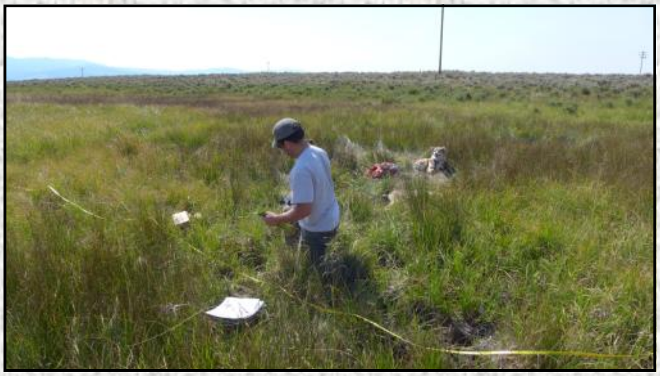
We found support for our predictions that West Fork elk had lower nutritional condition, which resulted in lower pregnancy rates as compared to the East Fork population. Our results support the previously documented relationship between body fat and pregnancy rate (Cook et al. 2013), and provide the first estimates linking observed levels of body fat and pregnancy rate for free-ranging elk in Montana. Although measurements from only 2 populations reported here do not alone establish a universal body fat– pregnancy rate relationship, these results will begin to establish a quantitative measure of adult female elk body condition needed to maximize pregnancy rate and calf production. Beyond body fat effects on pregnancy, our results also suggest underlying differences in the probability of pregnancy given comparable body fat between the two populations. These results are similar to a regional analysis of body fat – pregnancy relationships for 21 elk populations across 4 ecoregions that also documented variability in the probability of pregnancy given body fat (Cook et al. 2013). Although these results could be interpreted as evidence for predation risk effects on elk pregnancy rate (Creel et al. 2007, but see White et al. 2011, Boonstra 2013), this is unlikely given that density of the primary elk predator in this system, mountain lions, is higher in the East Fork area than the West Fork area (Eacker 2015, Proffitt et al. 2015) and that overwinter declines in pregnancy rate were not observed. A more likely explanation is that the reduced probability of pregnancy in the West Fork represents a reproductive pause in response to chronically inadequate nutrition resources (Cameron 1994, Stewart et al. 2005, Festa-Bianchet and Cote 2008, Cook et al. 2013). Such reproductive pauses in response to nutritional stress may enhance long-term reproductive performance in ungulates (Testa 2004).

Our results are consistent with recent studies linking fall body condition and pregnancy rates (Cook et al. 2013), and highlights the role of bottom-up processes in limiting ungulate vital rates and population performance. While the effects of predation on ungulate populations has been broadly studied and discussed, nutritional limitations play a less evident role in the relationship between predator and prey. Nutritional limitations on elk summer range that limit elk body condition, pregnancy rates and calf production may predispose populations to be more sensitive to the effects of predation. These bottom-up effects and the interaction with predation are elemental in understanding the relative role of top-down and bottom-up factors affecting ungulate populations (Melis et al. 2009, Andren and Liburg 2015).

The poor physical condition and low pregnancy rates of West Fork elk suggests that summer nutritional resources may be inadequate and that West Fork elk may be nutritionally limited. Building from these results, Section 5 evaluates summer range forage quality in the West Fork and East Fork, and evaluates potential linkages between elk forage quality and body condition. Poor physical condition and low pregnancy rates have also been identified as a density dependent response in populations that are at or near carrying capacity (Saether 1998, Bowyer et al. 2014), however, our results are unlikely to reflect density-dependent responses given elk populations are lower now than they were a decade ago. Finally, age-dependent differences between East Fork and West Fork elk may also contribute to the nutritional differences we report here of lower body fat and pregnancy rates in the West Fork. However, we detected no differences in mean age of adult female elk in this study. Therefore, we interpret our results as providing evidence of poorer nutritional resource availability in the West Fork relative to the East Fork. In the next section, we test this underlying mechanism for these nutritional differences.

Section 5 – Effects of Forage on Elk Nutritional Ecology

Recent work suggests that ungulate nutritional requirements during summer are important in influencing ungulate reproduction and survival (Cook et al. 2013, Monteith et al. 2013), highlighting the need to improve our understanding of forage quality and quantity during the summer growing season. Female ungulates require sufficient biomass of high quality forage during summer to make up for seasonally poor forage quality during winter, recover the costs of lactation, build body reserves to survive and maintain pregnancy during the winter (Cook et al. 2004). However, the abundance of forage for ungulates is only one component of understanding their nutritional landscape. Forage quality declines with increasing forage biomass as the growing season progresses due to the growth of plant lignins, hemicellulose and cellulose (Van Soest 1982, Parker et al. 2009). Thus, the highest forage quality available to ungulates is usually when plants first emerge in spring, resulting in a phenological 'greenwave' that is a driving mechanism for ungulate resource selection and migration (Fryxell and Sinclair 1988). This trade-off between forage quantity and quality means that estimates of both forage quality and quantity during late summer are required to estimate nutritional resources to understand the consequences of nutrition to ungulates.



Field crews collecting plant biomass and species composition data in the Big Hole (above) and the East Fork of the Bitterroot (below).

Our goals were to first develop a spatial model of landscape-level nutritional resources (hereafter forage quality), for elk. Our second goal was to then test the consequences of forage quality to elk body condition and pregnancy rates that we reported in Section 4. In Section 4, we reported lower body condition and pregnancy rate of West Fork elk as compared to East Fork elk. Here, we test whether landscape-scale differences in forage quality are consistent with our observations that suggested nutritional limitations in the West Fork. We predicted differences in summer range forage quality based on the composition of landcover and recent fire activity, and we predicted that elk on the lower forage quality summer range would have lower measures of body condition and lower pregnancy rates. We also tested the hypothesis that phenological differences between the study areas may drive the nutritional differences.

Methods

We used a combined ground and remote-sensing based approach to develop a landscape-scale late-summer elk forage quality model (Figure 5.1). First, we used a ground-based approach to measure available biomass of plants and plant phenology during July – August 2012 and 2013. Second, we measured summer and winter diet composition using fecal plant fragment analysis. Next, we filtered total available biomass to include only important elk forage species identified in diet analysis. Because nutrition depends on both forage availability and digestibility, we sampled forage plants in different phenological stages to estimate phenological stage-specific digestibility. We combined phenophase-specific forage digestibility and available forage biomass availability to develop a landscape nutrition model of late summer forage quality, measured as grams of digestible forage biomass per m^2. Finally, we tested for the effect of summer East Fork and West Fork forage quality on East Fork and West Fork elk fall body condition and pregnancy rate.

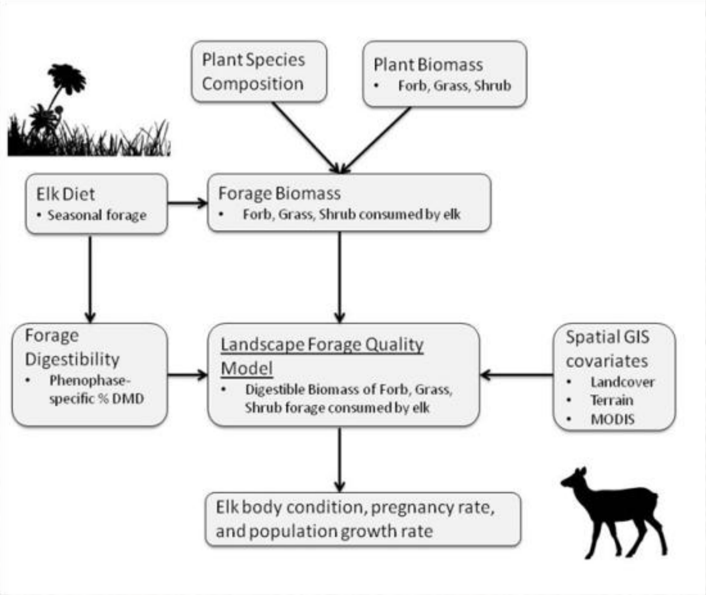


Figure 5.1 Conceptual figure of the landscape forage quality model developed for elk in 2012–2013.

Elk diet

We collected pellet samples to estimate seasonal diet using fecal plant fragment analysis in both the East Fork and West Fork. Fecal plant fragment analyses were performed by the Wildlife Habitat Nutrition Lab (Washington State University, Pullman, WA) at the 'B'-level (e.g., 6-12 species/sample) of resolution with 100 views/sample. Each sample constituted a composite of 10 - 20 individual pellets selected at random from ten pellet groups within a 2 - 5 ha area. A total of 7 samples (3 - 4 in each study area) were collected in spring (May - June), summer (July), late summer (August - September), and winter (December - March). We ranked the top plant species consumed in the diet of elk during the summer growing season (May – September) and winter (December – March) using the species that constituted 95% of the total diet, which resulted in 22 species in both summer and winter. These 22 summer species and 22 winter species constituted our list of summer and winter forage species. To test for differences in forage plants between the East Fork and the West Fork in the different seasons we used multivariate statistical analysis based on the percent occurrence of each species in the diet.

Forage biomass

We sampled plant biomass and species composition at sampling sites randomly positioned within 8 landcover types including wet forests not recently burned (i.e. burned more than 15 years prior), wet forests burned 0-5 years prior, wet forests burned 6-15 years prior, dry forests not recently burned, dry forests burned 0-5 years prior, dry forests burned 6-15 years prior, grasslands, and shrublands. Wet forests included subalpine and alpine forests dominated by *Pinus contorta* and *Abies lasiocarpa*. Dry forests included mixed conifer forests dominated by *Pinus ponderosa* and *Pseudotsuga menziesii*.

At each sampling site, we established a 40 m transect along the contour of the slope. At the 0m, 10m, 20m, 30m, and 40 m mark on the transect, we recorded species composition and percent cover within a 1 m2 quadrant. At the 0m, 20m, and 40m quadrat, we established a 0.5 m2 clip plot and clipped all of the graminoids, forbs, and shrubs within the clip plot. We dried samples at 50°C in a drying oven for 48 hours and measured dry plant biomass weight. Based on the percent cover of graminoids, forbs and shrub cover within the clip plot, we allocated species-specific dry biomass proportional to cover. We then summed the estimated biomass of important forage species in the elk diet to estimate biomass of forage species (in g/m2) at each sampling site.

Field crews collecting species composition and plant phenology data in the East Fork of the Bitterroot Valley.

Plant digestibility and phenology

To estimate the digestibility of plants consumed by elk, we estimated the phenophase-specific percent dry matter digestibility (DMD) of forage species and monitored phenology of forage species in each study area (Mould and Robbins 1982, Van Soest 1982, Cook 2002). We collected representative samples of forage plants during each major phenological stage (newly emergent, flowering, fruiting, mature and cured) to represent DMD changes over time within a season. DMD was determined using sequential detergent fiber analysis at the Wildlife Habitat Nutrition Laboratory (Washington State University, Pullman, WA). We sampled the most

Developing a landscape forage quality model

We developed a landscape forage quality model that predicted the digestible forage biomass during late summer. To do this, we first estimated the biomass (g/m^2) of forage species available to elk from our biomass sampling plots. Second, we estimated the phenological stage frequency distribution for each forage plant species and the DMD of each forage species in each phenophase. We combined the phenological stage and DMD data to estimate the weighted average forage quality of each forage species, measured in dry matter digestibility. We then calculated digestible biomass by multiplying the weighted average DMD per species by biomass of the species to estimate the total biomass of digestible forage per unit area (i.e. forage quality).

We developed generalized linear models with the Poisson link function for forb, graminoid, and shrub forage quality as a function of spatial covariates. We evaluated 10 standardized spatial covariates that were known based on previous studies to have strong influence on forage biomass and quality: vegetation cover class, elevation, slope, aspect, canopy cover, compound topography index (CTI), hillshade, enhanced vegetation index (EVI) and the leaf area index (LAI; both measured from the MODIS (Moderate Resolution Infrared Spectroscopy NASA Satellite, Huete et al. 2002), and sampling season. In particular, the time-varying remotely sensed vegetation indices of the EVI and LAI are known to be strongly predictive of plant phenology, biomass and quality (Pettorelli et al. 2013).

Linking landscape models of forage quality to ungulate responses

We used elk Global Positioning System (GPS) location data collected from collared adult female elk to estimate seasonal ranges for East Fork and West Fork elk populations (see Section 3), then compared nutritional exposure within seasonal-ranges to elk body condition (measured as IFBF, see Section 4) and pregnancy rates. We used location data collected from July 8 – August 31 to estimate a population-level summer range for each population and data collected from January 1 – March 31 to estimate a population-level winter range for each population. We used these seasonal ranges to estimate nutritional exposure of each elk population and season. This allowed us to compare seasonal population-level forage quality to test for differences in forage quality available to elk in each population and season.

Results

Elk diet

We processed 55 composite samples of elk diet. Elk summer diet included 72 species and was twice as diverse as the winter diet that included only 34 species (Table 5.1). Despite overall forage class composition similarity, there were important differences in species

Table 5.1 Elk diet composition during early summer and late summer (Summer) and winter combined for the East Fork and West Fork showing rank in each season, total % of the species in the seasonal diet, and cumulative % of the seasonal diet.

	Summer			Winter		
Species	**Rank**	**%**	**Cum.%**	**Rank**	**%**	**Cum.%**
Carex spp.	1	21.4	24.8	1	29.1	29.1
Poa spp.	2	10.0	36.4	2	12.0	41.1
Lupinus spp.	3	9.7	47.6	18	0.4	93.4
Agropyron/Pseudoroegneria	4	7.4	56.3	4	10.4	62.1
Mahonia repens leaf	5	4.9	62.0	5	6.5	68.6
Balsamorhiza sagittata	6	4.8	67.5	8	3.0	80.9
Pinus contorta	7	4.1	72.2	9	2.7	83.6
Shepherdia / Elaeagnus	8	2.4	75.1	---	---	---
Salix spp. stem	9	1.9	77.3	31	0.5	
Composite hair	10	1.9	79.5	---	---	---
Festuca altaica/campestris	11	1.9	81.7	3	10.6	51.7
Stipa spp.	12	1.6	83.6	10	2.1	85.7
Festuca idahoensis	13	1.5	85.3	6	5.2	73.8
Xerophyllum tenax	14	1.4	86.9	---	---	---
Bromus spp.	15	1.4	88.5	12	1.7	89.1
Achillea millefolium	16	1.1	89.8	---	---	---
Equisetum spp.	17	1.0	91.0	13	1.3	90.4
Vaccinium spp. stem	18	1.0	92.1	33	0.5	
Juncus spp.	19	0.8	93.1	22	0.4	95.1
Symphoricarpos occidentalis	20	0.7	93.8	32	0.5	
Chamerion (Epilobium) angustifolium	21	0.6	94.6	---	---	---
Astragalus spp.	22	0.5	95.2	---	---	---
Linnaea borealis	57	0.01	95.2	7	4.2	78.0
Phleum alpinum	44	0.03	95.2	11	1.8	87.4
Danthonia spp.	42	0.03	95.3	14	0.9	91.3
Festuca rubra	29	0.3	95.6	15	0.9	92.1
Antennaria parvifolia	32	0.1	95.7	16	0.4	92.6
Centaurea maculosa	45	0.03	95.7	17	0.4	93.0
Phlox spp.	26	0.4	96.1	19	0.4	93.9

Table 5.2. The mean biomass of summer and winter forb, graminoid, and shrub forage species for elk in different landcover types.

Landcover	Summer Forage Species			Winter Forage Species		
	Forb biomass (g/m^2)	Graminoid biomass (g/m^2)	Shrub biomass (g/m^2)	Forb biomass (g/m^2)	Graminoid biomass (g/m^2)	Shrub biomass (g/m^2)
Shrubland	4.7	16.2	0.7	4.6	20.4	0.1
Grassland	7.8	30.8	10.5	5.1	35.4	1.5
Wet Forest - Burn Age 1–5	11.2	2.1	2.6	0.0	2.1	0.0
Wet Forest - Burn Age 6–15	22.1	18.3	22.4	3.1	19.7	0.2
Wet Forest - Burn Age > 15	22.8	9.4	20.7	2.4	10.0	0.6
Dry Forest - Burn Age 1–5	6.6	7.2	2.0	1.2	7.4	0.9
Dry Forest - Burn Age 6–15	20.7	16.3	16.4	6.0	16.4	1.4
Dry Forest - Burn Age > 15	12.3	15.2	9.5	8.1	15.6	1.6
Average	14.4	17.7	13.2	4.4	19.7	0.9

prevalent 16 forage plant species and used literature values from previous studies for remaining forage species to estimate phenophase-specific DMD of species in the summer and winter elk diets.

To estimate phenology of each forage species in each study area, we repeat sampled 29 phenology plots monthly from April – October in 2012 and 2013. We measured plant species composition and phenological stage within 10 permanently marked 1 m^2 quadrats along the transect. We estimated the frequency distribution of each forage species in each phenophase between July 8 and August 31, corresponding to the same period as forage biomass estimation.

We tested for differences in DMD between the East Fork and West Fork in two ways. First, we tested for differences in DMD of plant samples within forage classes (forb, graminoid and shrub), phenological phase (1 – 5), and between the East Fork and West Fork study areas using a linear model (ANOVA). This tested for differences between study areas in DMD of the plant samples controlling for species and phenological class; i.e., whether forage quality per se differed between study areas. Second, we tested for differences in the plant phenology (measured using an ordinal phenology score from 1=new to 5=cured) of our ground phenology plots between the East Fork and West Fork as a function of area, elevation, aspect and canopy cover class (open, closed), and month. We tested for differences in the overall phenology score of all elk forage plants using a general linear model (ANOVA) because phenological scores were approximately normally distributed. This tested for landscape-scale differences in phenology between study areas, i.e., whether the availability of forage quality differed between study areas.

composition in East Fork and West Fork elk diet. The largest between group differences in diet at the plant species level occurred in winter. West Fork winter diet included more *Linnaea borealis*, *Carex spp*., *Phleum alpinum*, and *Danthonia spp*.. In contrast, East Fork winter diet included more *Festuca altaica/campestris*, *Muhlenbergia cuspidat*a and *Agropyron pseudoroegneria*. In spring, elk in the East Fork consumed more *Agropyron*, *Balsomorhiza*, *Festuca spp.*, and *Mahonia repens* (leaf), while consuming less *Carex spp.*, *Pinus* and *Poa* than West Fork elk (Figure 5.2), and these differences continued in summer. By late summer, West Fork elk consumed more cured *Balsamorhiza*, whereas East Fork elk consumed double the *Lupinus* in July- September, and 8% *Xerophyllum* compared to 0% in the West Fork.

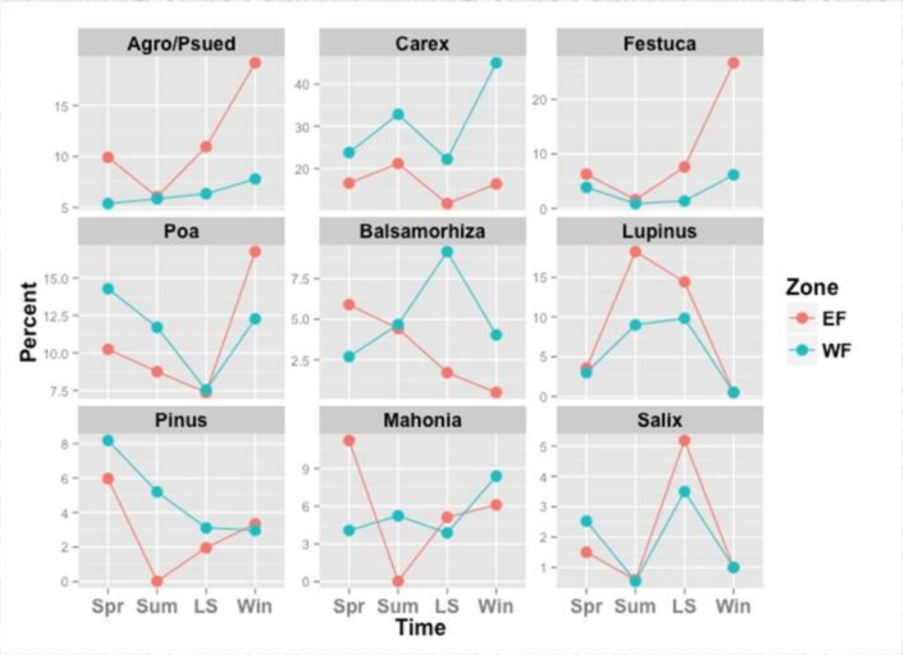


Figure 5.2 Forage plant species composition in the diet of elk in the East Fork (EF) and West Fork (WF), as a function of phenological period during the growing season (Spring – Spr, Summer – Sum, Late Summer – LS), and Winter (Win).

Elk forage biomass, digestibility, and phenology

We sampled vegetation at a total of 235 sites during 8 July – 31 August, 2012-2013. The biomass of summer and winter forage forbs was highest in the wet forests burned more than 6-15 years prior (Table 5.2). The biomass of summer and winter forage graminoids was highest in the grasslands. The biomass of summer forage shrubs was highest in wet forests burned 6 - 15 years prior. Forage abundance in both the wet forest and dry forest cover class decreased 0-5 years post fire, reached a peak 6-15 years post fire, then slowly decline more than 15 years post fire. Forage shrub biomass was low within the shrubland landcover class because this cover class was primarily sagebrush-steppe and contained little of the shrub species that elk consume. The biomass of winter forage shrubs was low across all cover classes.

We collected an average of 6.4 DMD samples/species/phenophase from 16 species in 5 phenological classes (e.g., ~ 502 samples). DMD varied across species and phenophases and was higher in forb and shrub species as compared to graminoid species (Table 5.3). Early phenological phases always had higher DMD ($F_{phase} = 26.5$, $p<0.00005$). For our first analysis of differences in DMD, the top model explaining DMD did not contain any effect of study area indicating no species-specific differences in DMD between plants collected in the East Fork and West Fork.

Our analysis of differences in East Fork and West Fork plant phenology also revealed no differences between areas in the landscape-scale availability of forage quality over time. The top model did not contain an effect of study area, and plant phenology was predictably affected by month (increasing phenophase of $\beta = 0.57$ per month, $p<0.00005$), elevation (decreasing phenophase of $\beta = -0.3$ per 1000 feet of elevation gain, $p=0.0005$), was earlier in open canopied habitats ($\beta = 0.6$, $p = 0.00001$), was delayed in north aspects ($\beta = -0.47$, $p = 0.004$), and was earlier in 2013 ($\beta = -0.8$, $p < 0.00001$). Therefore we interpret there to be no difference in plant phenology that would influence forage quality between our two study areas.

Table 5.3. The average percent dry matter digestibility (DMD) of forb, graminoid and shrub forage species in the diet of elk phenological growth stage. Phenological stages were defined as newly emergent, flowering, fruiting, mature, and cured.

	New	Flowering	Fruiting	Mature	Cured	Average
Forb	63.49	64.38	56.15	55.93	39.44	59.51
Graminoid	32.85	32.79	29.72	30.46	23.97	27.55
Shrub	65.85	63.26	61.80	58.46	50.93	61.88

Landscape forage quality model

Despite no support for differences in East Fork and West Fork DMD or phenology, forage quality (measured as grams of digestible forage biomass per m_2) varied across landcover types throughout the study area and between study areas as a function of differences in landcover (Table 5.4). On average, summer herbaceous forage quality was highest in wet forests burned 6-15 years prior and grasslands. Summer shrub forage quality was highest in the forests burned 6-15 years prior, and wet forests burned more than 15 years prior. Winter herbaceous forage quality was highest in grasslands and shrublands, and winter

Table 5.4. The summer and winter forage quality, measured as grams of digestible matter per m^2, by landcover type in the East Fork (EF) and West Fork (WF) seasonal elk ranges.

Cover Type	Forb		Graminoid		Shrub	
	EF	WF	EF	WF	EF	WF
			Summer			
Grassland	3.8	2.9	11.4	4.7	14.1	5.9
Shrubland	3.1	-	12.0	-	0.0	-
Dry Forest - Burn Age 0–5	-	4.9	-	2.9	-	3.8
Dry Forest - Burn Age 6–15	5.0	7.8	8.2	2.5	14.7	9.7
Dry Forest - Burn Age > 15	12.4	1.8	5.4	5.1	9.3	4.8
Wet Forest - Burn Age 0–5	-	5.3	-	1.2	-	2.1
Wet Forest - Burn Age 6–15	11.0	-	5.8	-	13.1	-
Wet Forest - Burn Age > 15	5.4	13.3	3.4	0.7	14.3	10.0
			Winter			
Grassland	2.1	2.9	9.9	3.9	4.9	2.3
Shrubland	2.5	-	10.9	-	0.0	-
Dry Forest - Burn Age 0–5	-	5.0	-	2.7	-	0.7
Dry Forest - Burn Age 6–15	3.9	1.5	6.7	2.0	2.8	3.0
Dry Forest - Burn Age > 15	9.7	1.3	4.4	3.9	1.8	1.2
Wet Forest - Burn Age 0–5	-	0.0	-	1.0	-	0.0
Wet Forest - Burn Age 6–15	3.2	-	4.8	-	1.0	-
Wet Forest - Burn Age > 15	1.6	0.0	2.6	0.3	0.3	0.0

shrub forage quality was highest in grasslands. Within landcover classes, graminoid and shrub forage quality was higher in the East Fork than the West Fork.

The best models of summer forb, graminoid, and shrub forage quality explained 24%, 36% and 19%, respectively, of the variation in forage quality (Figure 5.3). Overall, landcover type was a strong predictor of forage quality (Table 5.5). The best models of winter forb, graminoid, and shrub forage quality explained 29%, 40% and 14%, respectively, of the variation in forage quality. Again, landcover type was a strong predictor of forage quality across all plant classes (Table 5.5).

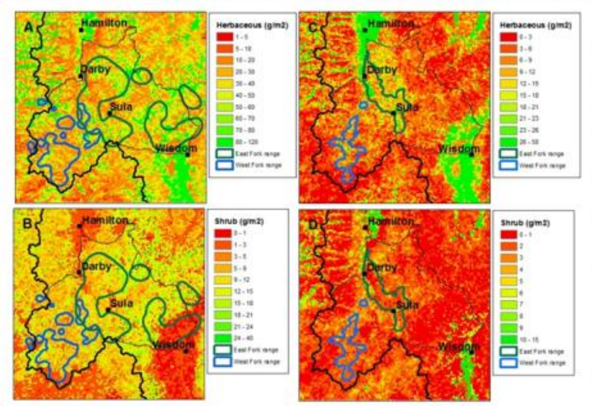


Figure 5.3 The estimated summer (Panel A, B) and winter (Panel C, D) herbaceous and shrub forage quality (in grams of digestible matter per m^2) in the East Fork and West Fork elk seasonal ranges as predicted from top ranked summer and winter landscape forage quality models.

Table 5.5 Standardized coefficient estimates for top models explaining the variation in summer and winter forb, graminoid, and shrub forage quality available to elk in the southern Bitterroot Valley of western Montana during 2012–2013. Boldfaced values denote a value with a confidence interval that does not include 0.

	Summer			Winter		
	Forb	Graminoid	Shrub	Forb	Graminoid	Shrub
(Intercept)	**1.28**	**1.38**	**0.02**	**0.39**	**1.09**	**-2.00**
EVI	**0.32**	**0.34**	**0.06**	**-**	**0.37**	**0.79**
LAI	0.06	**-0.75**	**0.11**	-0.21	**-1.01**	**0.21**
Wet Forest[1] - Burn Age 1–5	-0.08	**-1.50**	**-2.16**	-1.83	**-1.38**	-0.45
Wet Forest - Burn Age 6–15	**0.26**	**0.81**	**0.33**	-0.21	**0.86**	0.08
Dry Forest - Burn Age > 15	-0.07	**0.31**	**-0.62**	**1.02**	**0.39**	0.48
Dry Forest - Burn Age 1–5	**-0.77**	**-0.54**	**-2.29**	-0.17	-0.36	0.51
Dry Forest - Burn Age 6–15	**0.72**	**0.61**	-0.15	**1.19**	**0.69**	0.90
Shrubland	**-0.51**	0.24	**-3.06**	**0.58**	**0.33**	-1.42
Grassland	-0.10	**0.67**	-0.05	**0.44**	**0.78**	**0.90**
CTI	**-0.18**	**0.27**	**-**	**-0.43**	**0.26**	**-0.28**
Aspect South	**-**	**-0.42**	**2.16**	**-0.61**	**-0.46**	**0.51**
Elevation	**0.55**	**-0.20**	**-**	**0.29**	**-0.17**	**-0.35**
Hillshade	**0.16**	**-**	0.05	**-**	**-**	**-**
Season	**0.58**	**0.24**	**-**	**0.44**	**0.30**	**-**
Slope	**0.19**	**0.21**	**-0.21**	**0.19**	**0.21**	**0.41**
Canopy Cover	**-0.12**	-0.08	**0.25**	**-0.48**	-0.08	**-**
Aspect North	**-0.39**	**-0.49**	**2.37**	**-1.07**	**-0.57**	**-**

[1] The base landcover type was Wet Forest – Burn Age >15 years.

Table 5.6. The percentage of the East Fork (EF) and West Fork (WF) seasonal elk ranges comprised of each landcover type in the southern Bitterroot Valley of western Montana, 2012–2013.

Cover Type	Summer range		Winter range	
	EF	WF	EF	WF
Shrubland	9.6	< 1	2.8	< 1
Grassland	26.9	21.5	54.6	30.8
Wet Forest - Burn Age 0–5	2.5	5.7	0.0	0.8
Wet Forest - Burn Age 6–15	18.5	5.5	2.3	1.2
WetForest - No recent burn	15.9	16.6	0.2	4.8
Dry Forest - Burn Age 0–5	2.9	8.5	0.1	3.5
Dry Forest - Burn Age 6–15	15.9	10.4	25.8	11.3
DryForest - No recent burn	8.0	31.7	14.2	47.6

Linking landscape models of forage quality to elk nutritional ecology

We collected summer range location data from 60 elk in the East Fork and 44 elk in the West Fork. The East Fork summer range was 1,441 km^2 and the West Fork summer range was 519 km^2. A greater proportion of the East Fork summer range was comprised of forests burned 6 – 15 years prior, and a greater proportion of the West Fork range was comprised of recently burned forests, or forests not burned within 15 years (Table 5.6). The East Fork summer range had higher mean forb, graminoid and shrub forage quality (32.9, 9.4 and 8.9 g/m^2, respectively) than the West Fork summer range (26.0, 5.6 and 8.4 g/m^2), and the difference in forage quality was greatest for forbs and graminoids.

We collected winter range location data from 66 elk in the East Fork and 50 elk in the West Fork. The East Fork winter range was comprised of a higher proportion of grasslands and forests burned 6- 15 years prior, and the West Fork winter range was comprised of a higher proportion of forests not burned within the past 15 years (Table 5.6). The East Fork winter range had higher forb, graminoid and shrub forage quality (2.9, 22.0 and 2.4 g/m^2, respectively) than the West Fork winter range (1.6, 7.5 and 2.1 g/m^2), and the difference in forage quality was greatest for graminoids. The mean winter graminoid forage quality was 22.0 g/m^2 in the East Fork as compared to only 7.5 g/m^2 in the West Fork.

A collared adult female elk in the West Fork of the Bitterroot.

The differences in West Fork and East Fork summer range forage quality corresponded to lower fall body condition of lactating West Fork elk, as compared to East Fork elk and to lower West Fork elk pregnancy rate (see Section 4). Differences in winter range forage quality corresponded to lower overall body condition and pregnancy rate in the West Fork, as compared to the East Fork.

Elk on winter range in the upper West Fork of the Bitterroot.

Discussion

The West Fork elk population was exposed to lower summer range forage quality and had lower body fat entering winter than the East Fork, resulting in lower pregnancy rates in the West Fork as compared to the East Fork population. Although our results are consistent with recent studies linking summer range nutrition, ungulate fall body condition, and pregnancy rates (Cook et al. 2013), our results show that the greatest differences in West Fork and East Fork elk exposure to forage quality occurred during winter, highlighting the variability in winter range nutritional resources within two geographically nearby areas. Nutritional conditions on winter range may affect changes in rate of body fat depletion overwinter and the probability of overwinter survival (Cook et al. 2004). Additionally, adult female elk may produce more robust calves if they enter spring in better condition with more energy available to support the increasing costs of pregnancy and the initial stages of lactation (Cook 2002). The effects of these differences in winter nutrition on elk body condition are difficult to assess, as comparisons of winter body fat data are affected by summer nutritional condition and the proportion of the population that lactated during the summer and fall (Cook et al. 2004, Cook et al. 2013). Our winter body fat data suggest that elk in the West Fork were in poor nutritional condition (see Section 4). While this is in part due to the poorer forage quality available on their summer range, the poor forage quality on winter range likely resulted in greater declines in body fat as compared with elk wintering in areas of higher winter forage quality. Therefore, while summer nutrition may affect ungulate population dynamics through effects on pregnancy rate and overwinter survival rate, it is important to also recognize that winter nutrition may affect population dynamics through effects on calf birth weight and neonate survival the following spring, or on overwinter adult survival during the current winter.

Summer range forage quality is the result of forage species availability, abundance, and digestibility. The differences in summer range forage quality were likely less related to overall differences in summer diet, plant digestibility, or phenology, and more likely related to species abundance due to recent fire history that affected landcover composition of the two summer ranges (Turner et al. 1994, Kie et al. 2003, Fisher and Wilkinson 2005). For example, we found no intrinsic differences in forage quality between plants that might have arisen because of soil differences, nor differences in plant phenology that might provide a longer growing season to one population. Although both areas have experienced significant wildfire activity, a higher proportion of the East Fork summer range was burned within the past 6 – 15 years, the period during

An adult female elk after being outfitted with a GPS/VHF collar.

which forage biomass and quality was highest. The West Fork summer range experienced more fire activity during the past 0 – 5 years, and these were high severity fires resulting in little vegetation regrowth. The effects of wildfire have landscape-scale effects on ungulate forage and potentially ungulate productivity (Turner et al. 1994, Romme et al. 2011). The large-scale wildfires within our study area that occurred in 2000, 2007, 2011 and 2013 likely resulted in short term declines in ungulate forage quality, followed by a period of increasing forage quantity and quality largely due to changes in landcover composition.

Understanding the relative effects of bottom-up and top-down factors on ungulate populations will be crucial to developing appropriate management strategies to maintain ungulate populations within management objectives. Wildlife managers should identify ungulate populations that are nutritionally limited and be aware that these populations may be more impacted by predation or harvest than more productive populations. Managers may consider applying conservative ungulate harvest prescriptions, together with liberal carnivore management prescriptions in these areas. Habitat treatments that increase forage quality on summer ranges may benefit ungulate populations. In our study area, on average wildfire in both low elevation dry forests and higher elevation wet forests produced similar increases in forage quality. However, forage quality also varied with elevation and aspect so the actual effects of wildfire may depend on fire placement on the landscape. Maintaining a mosaic of fire history and distribution will likely most benefit ungulate species, as composition-induced changes in forage quality may initially decrease post fire, reach a peak 6 – 15 years post fire, then decrease as the forest ages.

Section 6 – Adult Female Elk Survival

Adult female survival is an important vital rate for ungulate populations due to its important effect on population growth rate (Nelson and Peek 1982; Gaillard et al. 1998, 2000), and small changes in adult female survival can have disproportionately large effects on population trajectories. The high sensitivity of population growth rate to adult female survival occurs because adult female survival determines the number of adult females in the population available to reproduce the following year. Adult female survival is generally high and constant in most wild ungulate populations (Gaillard et al. 2000). The low variation in adult female survival in ungulates is consistent with the life history of most long-lived mammals, where vital rates with high sensitivity for population growth rate are canalized against environmental variability (Gaillard and Yoccoz 2003). However, when adult female survival becomes more variable due to anthropogenic and/or predation factors, for instance, it can be the primary driver of declines in ungulate populations (e.g., Owen-Smith and Mason 2005, Hebblewhite et al. 2007, DeCesare et al. 2012).

Capture helicopter gets into position to netgun an elk.

In harvested ungulate populations, human harvest is often a primary source of variation in adult female survival (Vucetich et al. 2005; White and Garrott 2005; Webb et al. 2011), and the importance of managing adult female harvest to affect ungulate population growth is well-established among wildlife managers (Brodie et al. 2013). Because non-human-related mortality is generally low for adult female ungulates, it is sometimes difficult to detect differences in adult female survival among populations or estimate effects of other risk factors that may explain differential survival among individuals. However, risk factors have been identified for adult females in some ungulates, such as significantly lower survival for adult female moose (*Alces alces*) with calves compared to females that forego reproduction (Testa 2004). Also, Brodie et al. (2013), using data from 2,746 radio-collared adult female elk,

Elk on winter range in the East Fork of the Bitterroot Valley.

found that the negative effects of very high winter precipitation on adult female survival were intensified in elk populations with sympatric wolves. Understanding these risk factors affecting adult female survival rates is useful in predicting survival for adult female ungulates, especially in harvested populations where managers are attempting to balance carnivore and ungulate population objectives.

We tested for any differences in adult female survival between the East Fork and West Fork elk populations. We hypothesized that if the West Fork had both lower forage quality and higher wolf densities, then adult female survival in the West Fork would be lower than the East Fork. We also predicted that adult female survival probability would be lower for older-aged compared to prime-aged elk age (Raithel et al. 2007). Although we could not assess whether a female had a calf or not (e.g., Testa 2004, Hebblewhite 2006), we did determine pregnancy status for adult female elk and predicted that pregnancy would result in lower adult female survival due to higher nutritional demands compared to females that were not pregnant (Cook et al. 2004). Along with our survival analysis, we examined any important differences between East Fork and West Fork in terms of cause-specific mortality. Based on previous studies of wolf-elk dynamics, we initially expected wolf-caused mortality to be the leading non-human cause of death for adult female elk based on other systems such as the Greater Yellowstone Ecosystem (GYE; Garrott et al. 2008) and Banff National Park in Canada (Hebblewhite and Merrill 2011).

Methods

Survival

We equipped each adult female elk with a radio-collar that triggered a mortality sensor if the collar was stationary for more than 6 hours (see Section 3 for capture details). We monitored adult female elk radio signals 1 – 3 times per week via ground and aerial telemetry from Feb 2011 through March 2014. We used a biological timescale to estimate adult female survival rates with the median estimated calf birth date (30 May, day 1) and the earliest winter capture date (28 Nov, day 180) defining the beginning of summer and winter seasons, respectively. Thus, adult female elk entered into the study during a given winter season based on their capture date (i.e., left-staggered entry), and were censored on the day after they were last heard live if they experienced radio-collar failure or permanently emigrated from the study area (DeCesare et al. 2016). Elk were right censored at the end of the survival period if they survived. Most individuals were monitored for 12 months, however some individuals were monitored for longer (24 – 36 months) because their collars failed to release on schedule (see results). Because we used a biological timescale, most adult female elk were present in at least two biological years because capture occurred in winter (December or February) and elk entered into the following biological year if they survived until summer (May 30). We classified adult female elk fates as either live, dead or unknown fate.

We used the Kaplan-Meier (KM) estimator and log-rank tests to provide basic survival estimates and compare survival across age groups, pregnancy status, populations and years (Pollock et al. 1989). The log-rank test is similar to a chi-square test, where the observed and expected numbers of failures are formally compared between groups (i.e., the test estimates *P*-values). We report 95% confidence intervals (CI) for survival estimates and compared survival across groups with log-rank tests using the R base package survival (Therneau 2015).

For our survival comparisons, we treated year as a categorical variable. We considered the effect of age based on dentition characteristics recorded at capture, but because of the uncertainty in aging elk from tooth eruption and wear patterns (Hamlin et al. 2000), we categorized adult female elk as either prime (2 – 9 years old) or older (10 and older) based on Raithel et al. (2007).

Cause-specific mortality

We determined the cause and timing of mortality based on factors such as presence of carnivore tracks and scat (species and number of individuals at the scene and surrounding area), location and types of wounds to the animal (location, depth and size of bite and claw marks), signs of struggle, severity and timing of injuries (pre- or post-mortem based on subcutaneous hemorrhaging), patterns of consumption, presence and patterns of carcass caching, and signs of scavenging (Smith et al. 2006; Barber-Meyer et al. 2008). Carnivore hair and scat sample were identified to species using DNA analysis at the United States Forest Service (USFS) Rocky Mountain Research Station, Missoula, MT. We also documented photographic evidence at each mortality location.

Characteristics such as signs of injury (upper left), presence of predator scat (upper right), body condition at the time of death (lower left) and signs of predation (lower right) were among the information used to determine cause of death.

We categorized mortality sources for adult female elk as mountain lion; wolf; unknown; natural, non-predation (e.g., starvation, disease); and human-related (e.g., hunter harvest, vehicle collision, fence entanglement). We only classified a mortality event to a specific cause if the confidence level was certain, which meant that evidence was sufficiently clear and unambiguous as to the source of mortality. If the confidence level was only probable (suggestive of a cause of death, but insufficient to assign a cause beyond a reasonable doubt) or lower, we classified the mortality as unknown. We then estimated annual cause-specific mortality rates using cumulative incidence functions ([CIFs]; Heisey and Patterson 2006) to determine the relative importance of recolonizing wolves and other mortality sources for adult female elk survival. CIFs account for competing risks of mortality, which occur when an individual is subjected to multiple potential mortality sources, and the occurrence of one mortality event type precludes the occurrence of another. For more details see Eacker (2015).

Results

Adult female survival

We captured a total of 122 adult female elk in our survival analysis. Adult female elk collars were programmed to drop off after 365 days, but due to collar release device failure, 14 elk remained on air for two calendar years and four elk remained on air for three calendar years. The annual survival rate for adult female elk was 0.90 (95% CI = 0.83, 0.94). Adult female survival was nearly identical between populations at 0.903 (95% CI = 0.81, 0.95) in the East Fork and 0.898 (95% CI = 0.79, 0.95) in the West Fork (*P* = 0.84). We found that adult female survival was marginally higher in summer compared to winter (*P* = 0.08), with survival rates of 0.97 (95% CI = 0.92, 0.99) in summer and 0.93 (95% CI = 0.87, 0.96) in winter. Annual adult female survival was highest in 2012 – 2013 at 0.96 (95% CI = 0.83, 0.99) and lowest in 2011 – 12 at 0.90 (95% CI = 0.76, 0.96, Table 6.1), but, as expected, survival did not vary significantly across years (*P* = 0.50).

Our results supported the general predictions of declining survival with senescence in ungulates, as we found moderate evidence that prime-aged adult female elk had higher survival than old-aged individuals (*P* = 0.04), which resulted from a 14.6% higher survival probability in prime-aged (*S* = 0.92, 95% CI = 0.85, 0.96) compared to older-aged elk (*S* = 0.78, 95% CI = 0.55, 0.90). The effect of age was mainly attributable to differences in winter survival of adult female

Table 6.1. Kaplan-Meier estimates of annual survival probability (*S*) with 95% confidence intervals (lower confidence interval = LCI; upper confidence interval = UCI) by population and pooled, and the minimum and maximum number of individuals at risk (*n*) for adult female elk in the southern Bitter-root Valley, MT, 2010 – 2014.

		East Fork			West Fork			Pooled		
Year	*n*	$\hat{S}$	LCI	UCI	$\hat{S}$	LCI	UCI	$\hat{S}$	LCI	UCI
2010–11	(39–43)	0.90	0.72	0.97	0.92	0.57	0.99	0.91	0.77	0.96
2011–12	(35–53)	0.89	0.68	0.96	0.94	0.65	0.99	0.90	0.76	0.96
2012–13	(44–45)	1.00[a]			0.92	0.71	0.98	0.96	0.83	0.99
2013–14	(20–43)	0.95	0.69	0.99	0.88	0.57	0.97	0.91	0.72	0.97

[a] No adult female elk mortalities occurred in the East Fork during 2012–13; therefore confidence intervals could not be estimated.

elk (*P* = 0.07), with older-aged mortality events concentrated in late winter (days 290 – 350; Figure 6.1), while age effects were insignificant in summer (*P* = 0.47).

Adult female cause-specific mortality

We investigated a total of 13 mortalities. We estimated an annual cause-specific mortality rate to 365 days of 0.02 (95% CI = 0.006, 0.06) for mountain lion predation; 0.01 (95% CI = 0.002, 0.06) for wolf predation; 0.02 (95% CI = 0. 005, 0.07) for unknown causes; 0.03 (95% CI = 0.001, 0.07) for natural, non-predation (e.g., starvation, disease); and 0.01 (95% CI = 0.001, 0.05) for human-related mortality (i.e., vehicle collision). None of our radio-collared adult female elk died from hunter harvest.

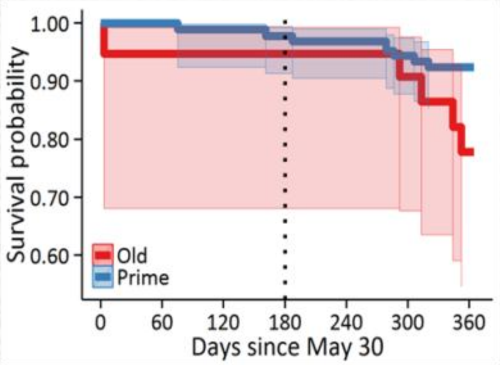


Figure 6.1. Kaplan-Meier survival curves with 95% confidence intervals by age group for adult female elk in the southern Bitterroot Valley, MT, 2010 – 2014. Note that the y-axis ranges from

In the East Fork, we were able to attribute 5 out of the 7 mortalities to a specific cause (i.e., cause of death was certain), with annual mortality rates of 0.01 (95% CI = 0.001, 0.07; *n* = 1) for mountain lion predation, 0.01 (95% CI = 0.001, 0.06; *n* = 1) for wolf predation, 0.02 for unknown mortalities (95% CI not estimable; *n* = 1), 0.04 for natural, non-predation mortalities (95% CI = 0.01, 0.10; *n* = 3), and 0.02 (95% CI = 0.001, 0.08; *n* = 1) for human-caused mortality (see Figure 6.2). In the West Fork, we were able to attribute 4 out of the 6 mortalities to specific causes, with annual mortality rates of 0.03 (95% CI = 0.006, 0.092; *n* = 2) for mountain lion predation, 0.02 (95% CI = 0.002, 0.09; *n* = 1) for wolf predation, 0.03 (95% CI = 0.006, 0.10; *n* = 2) for unknown mortalities, and 0.02 (95% CI not estimable; *n* = 1) for natural, non-predation mortalities (Figure 6.2).

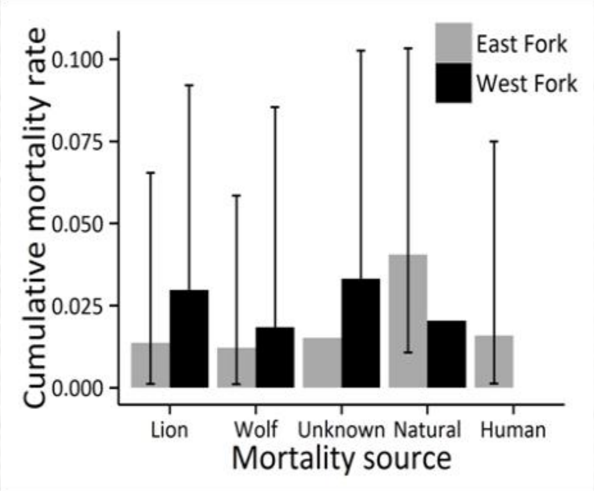


Figure. 6.2. Cumulative cause-specific mortality rates with 95% confidence intervals to 365 days for adult female elk in the East Fork and West Fork elk populations.

Ten out of the 13 documented mortalities occurred in winter between the beginning of March and the middle of May (days 270 – 350; see Figure 6.3). The 4 moralities that occurred outside this timeframe included an adult female elk that died of birthing complications in early June 2013 in the West Fork, and 3 mortalities in the East Fork that included 1 unknown cause, 1 vehicle collision, and 1 natural, non-predation mortality that occurred just after the beginning of winter period.

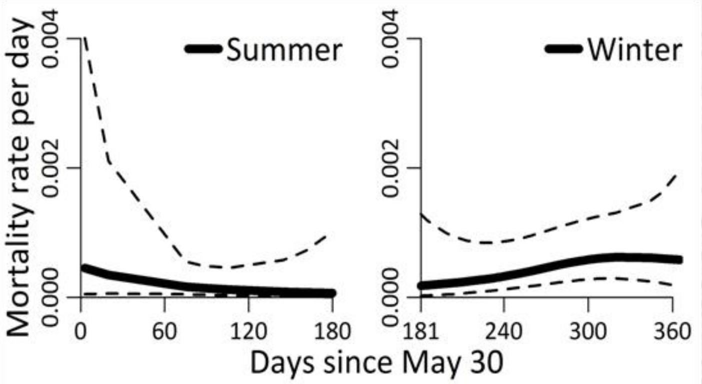


Figure. 6.3. Instantaneous mortality hazard (i.e. mortality rate per day) with 95% confidence intervals for adult female elk in summer (left) and winter (right) seasons in the southern Bitterroot Valley, MT, 2010 – 2014.

Discussion

Effectively managing harvested ungulate populations experiencing declines concurrent with recolonizing carnivores and other bottom-up influences (Section 5) requires understanding the factors affecting adult female survival. Here, we found that adult female survival was high and constant as predicted (Gaillard et al. 2000), and was not different from the average adult female survival rate reported for other harvested elk populations across western North America which ranged from 0.84 – 0.94 in harvested and unharvested populations (Brodie et al. 2013). Although the East Fork and West Fork populations experienced differential declines in elk trends and recruitment, we found that adult female survival was nearly equivalent between the study areas.

However, similar to other elk studies (Kunkel and Pletscher 1999, Garrott et al. 2003), we found that prime-aged (2 – 9) adult female elk survival rates were higher on average than survival for older-aged individuals (≥10 yr old). Raithel et al. (2007) separated older adult female elk into two categories, and estimated survival rates of 0.87 for old-aged (10 – 14 yr old) and 0.72 for senescent (≥15 yr old) adult female elk, whereas our combined estimate of older-aged adult female survival was0.78. Our results highlight that understanding adult female age structure in harvested ungulate populations is important if survival or pregnancy rates decline with senescence (Gaillard et al. 2000, Proffitt et al. 2014). Given this strong evidence for age-dependent survival, the similarity in ages between the West Fork and East Fork populations (see Section 4) suggests that age had little effect on any differences in survival among populations.

A collared adult female elk that died of natural causes (i.e. over-winter mortality).

We expected that wolf-caused mortality might be the leading non-harvest related cause of death for adult female elk based on other systems (Hebblewhite 2006; Garrott et al. 2008), but we found that mortalities were distributed somewhat uniformly across mortality sources. The annual mortality rate for adult female elk from both mountain lions (CIF = 0.021) and wolves (CIF = 0.014) combined in our study was 0.035, while population-averaged estimates from all carnivore mortality sources (not including grizzly bear-caused mortality) averaged less than 0.02 for elk populations across western North America (Brodie et al. 2013). Although estimates were based on small sample sizes, Hamlin and Cunningham (2009) documented annual mortality rates for bear and wolf predation of 0.03 and 0.01, respectively, in the northern Yellowstone elk population, while minimal hunter harvest (0.01) and no mountain lion predation occurred. Hebblewhite (2006) found that wolves were the dominant mortality source for adult female elk near Banff, with estimated mortality rates of 0.06 for wolves and 0.03 from grizzly bears, while the hunter harvest mortality rate was 0.04. Because grizzly bears were not present in our study area and hunter harvest of adult females was minimal, overall mortality rates were slightly lower than those near Banff but similar to northern Yellowstone elk where harvest was restricted as carnivore densities increased (Hamlin and Cunningham 2009).

In harvested ungulate populations with recolonizing or increasing number of carnivores (e.g., Hamlin et al. 2009), managers tend to compensate for increased predation by restricting antlerless elk harvest in efforts to increase adult female survival rates. For instance, despite adult female elk being exposed to both mountain lion and wolf predation in our study area, overall adult female mortality rates were low because minimal antlerless harvest occurred over the study period and non-human-related mortality rates were low. After antlerless elk harvest in the West Fork and East Fork was liberalized in 2004 to reduce elk population sizes toward population objective levels (Montana Statewide Elk Management Plan 2004), managers then restricted antlerless elk harvest in the West Fork (HD 250) in 2008 and in the East Fork (HD 270) in 2010 in response to the continued declines in elk population numbers and calf recruitment. As a result of harvest restrictions, antlerless elk harvest—made up mostly of adult female elk—declined on average by 71% in the East Fork and 83% in the West Fork from 2008 – 2011 compared to 2004 – 2007. This reduction in adult female harvest likely helped stabilize the population and increase calf production during our study period. Given the potential effects of nutrition and predation on elk populations, managers may need to reduce adult female harvest in areas where predator populations are expanding, especially if these coincide with areas of less productive habitat for elk.

Section 7 - Calf Survival

The expansion of large carnivores in North America has the potential to dramatically alter the population dynamics of their primary ungulate prey species. Understanding the effects of carnivore on juvenile survival may be particularly important because the high variability of juvenile survival may strongly influence ungulate population trajectories (Gaillard 1998, 2000; Raithel et al. 2007). In ungulate populations with low juvenile recruitment, carnivore removal may be used as a management tool to enhance population growth rates, although the efficacy of removal treatments in reversing population declines may depend on the ecological system (Hayes et al. 2003; White et al. 2010; Hurley et al. 2011) and the extent that predation mortality is compensatory or additive for juvenile ungulates (Boertje et al. 2010). The uncertainty in the effects of reducing carnivores on ungulate survival highlights the difficulty that wildlife managers face in balancing the conservation and management of carnivore and ungulate populations.

The effect of carnivore predation on juvenile ungulates is more complex in multiple carnivore systems where the importance of a particular carnivore species may vary across space. For example, ursid predation was found to be the most important mortality source for neonatal (<90 days old) elk (*Cervus elaphus*) calves in the Greater Yellowstone Area (Barber-Meyer et al. 2008), Idaho (White et al. 2010), Montana (Raithel 2005), and Wyoming (Smith et al. 2006), while mountain lions were most important for elk calves in Oregon (Rearden 2005, Johnson et al. 2013) and Washington (Myers et al. 1998). Despite receiving a disproportionate amount of attention in the public arena compared to other carnivores, most studies have found only weak direct mortality effects of wolves on elk calves (Raithel 2005; Barber-Meyer et al. 2008; White et al. 2010). However, a recent synthesis across previous studies found that mountain lion-caused mortality on elk calves declined significantly in systems with wolves (Griffin et al. 2011), suggesting that wolves may have important indirect effects on juvenile survival through interspecific competition with other carnivores. Thus, it is important to understand cause-specific mortality by different carnivores in predator-prey systems with recolonizing carnivore species or changing carnivore densities.

A bedded neonate elk calf .

The importance of carnivore predation for juvenile ungulates has largely focused on the neonatal survival period, mainly because predation is expected to be most intense for juveniles during the first 90 days of life (Linnell et al. 1995; Griffin et al. 2011). However, despite high juvenile mortality rates in summer, the winter period may also be important due to greater interannual variation in winter compared to summer survival rates, which has been observed in mule deer (*Odocoileus hemionus*) populations (Hurley et al. 2011). Wolves may have particularly strong interactions with winter severity because wolf predation is expected to mainly occur in winter (Smith et al. 2004; Evans et al. 2006) when wolves strongly select for juvenile ungulates (Huggard 1993; Mech et al. 2001; Metz et al. 2012). Thus, understanding predation effects on annual juvenile survival is critical to resolving uncertainty over the importance of wolves and other carnivores in affecting juvenile recruitment.

We used an observational, comparative approach to investigate the importance of multiple carnivore species for annual elk calf survival. We expected that wolves would be an important mortality source for elk calves because wolf recolonization and population increases coincided with declines in elk calf recruitment in the study area. We also predicted that black bear (*U. americanus*) predation would be the dominant mortality source for neonatal elk calves <30 days old, and similar to other systems without wolves, that mountain lion predation would contribute elk calf mortality throughout the year (Johnson et al. 2013). We considered risk factors to explain the overall risk of mortality to elk calves in summer and winter seasons. In summer, we considered the effects of sex, birth mass, and birth date based on their on their importance in previous elk calf survival studies (Raithel 2005; Smith et al. 2006; Barber-Meyer et al. 2008). We predicted that summer calf survival would increase with higher birth mass (Rearden 2005; Smith et al. 2006; White et al. 2010) and decrease with earlier birth dates (Raithel 2005). In winter, we only considered sex as a risk factor, and did not consider the effects of birth mass or birth date because these individual covariates were not available for calves that entered the sample as 6-month-old calves. We predicted that male elk calves would have lower survival than females in summer due to sex-specific vulnerability to predation (e.g., Mathisen et al. 2003), and that differences in male and female survival would be less pronounced in winter when vulnerability to predation is lower across individuals. In both seasons, we tested for study area and year (i.e., unexplained interannual variation) effects on elk calf survival, and predicted that the West Fork would have lower calf survival than the East Fork given lower recruitment rates. We also predicted that winter survival would be more variable than summer survival (Hurley et al. 2011).

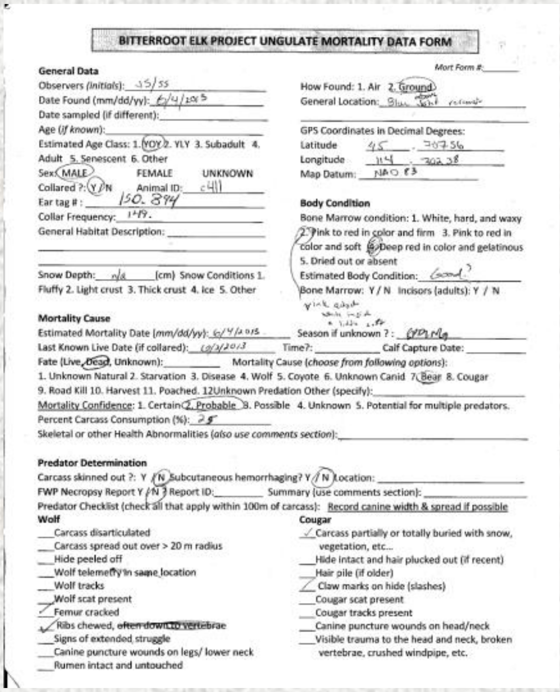

A neonate calf hides in the foreground as a helicopter searches in the background during calf captures in the southern Bitterroot Valley.

METHODS

Calf capture, monitoring, and mortality investigation

For 3 years from 2011 – 2014, we captured elk calves during the neonatal period from 27 May – 16 June and 6-month-old calves from 28 November – 1 December. We used both ground and aerial methods to search for adult female elk showing signs of recent parturition or that had an observable calf. We used a helicopter to assist in spotting and capturing neonatal elk calves during the peak of parturition from 31 May – 6 June and aerial darting or netgunning of 6-month-old calves captured during winter. We applied blindfolds and physically restrained calves with hobbles, wore latex gloves to reduce scent transfer, and attempted to handle calves for <5 minutes to minimize stress. We captured and handled all elk calves in compliance with requirements of the Institutional Animal Care and Use Committee for the University of Montana-Missoula (Protocol 027-11MHWB-042611).

All calves received a radio ear tag transmitter weighing approximately 23 g that was designed to continuously emit a very high-frequency (VHF) signal for 1 year (model 3430, Advanced Telemetry Systems [ATS], Inc., Isanti, MN). After experiencing moderate incidence of tag loss in 2011 – 2012 and in summer of 2012 – 2013, we switched to an alternative ear tag transmitter in winter of 2012 – 2013 and in 2013 – 2014 (TW-5, Biotrack Ltd., Wareham, Dorset, United Kingdom). All transmitters had a mortality sensor that doubled in pulse rate if the radio tag remained motionless for >4 hours. We monitored VHF radio signals from the ground or aircraft daily from capture through mid-July when the risk of mortality for calves was the highest. During mid-July to late August, as calves became larger and able to escape predation more effectively (Barber-Meyer et al. 2008), we reduced monitoring to 3 times per week. From September through May, we monitored calf signals 2 – 3 times per week.



BITTERROOT ELK PROJECT UNGULATE MORTALITY DATA FORM

Mort Form #:

General Data

Observers (Initials): JS/SS
Date Found (mm/dd/yy): 6/4/2013
Date sampled (if different):
Age (if known):
Estimated Age Class: [✓ 1. YOY] 2. YLY 3. Subadult 4. Adult 5. Senescent 6. Other
Sex: [✓ MALE] FEMALE UNKNOWN
Collared ?: [✓ Y] / N Animal ID: c411
Ear tag # : 150.894
Collar Frequency: 149.
General Habitat Description:
Snow Depth: n/a (cm) Snow Conditions 1. Fluffy 2. Light crust 3. Thick crust 4. Ice 5. Other

How Found: 1. Air [✓ 2. Ground]
General Location: [illegible]
GPS Coordinates in Decimal Degrees:
Latitude 45 . 70756
Longitude 114 . 30238
Map Datum: NAD 83

Body Condition

Bone Marrow condition: 1. White, hard, and waxy [✓ 2. Pink to red in color and firm] 3. Pink to red in color and soft [✓ 4. Deep red in color and gelatinous] 5. Dried out or absent
Estimated Body Condition: Good?
Bone Marrow: Y / N Incisors (adults): Y / N

Mortality Cause

Estimated Mortality Date (mm/dd/yy): 6/4/2013 Season if unknown ? : [illegible]
Last Known Live Date (if collared): 6/3/2013 Time?: Calf Capture Date:
Fate (Live, [✓ Dead], Unknown): Mortality Cause (choose from following options):
1. Unknown Natural 2. Starvation 3. Disease 4. Wolf 5. Coyote 6. Unknown Canid [✓ 7. Bear] 8. Cougar 9. Road Kill 10. Harvest 11. Poached. 12Unknown Predation Other (specify):
Mortality Confidence: 1. Certain [✓ 2. Probable] 3. Possible 4. Unknown 5. Potential for multiple predators.
Percent Carcass Consumption (%): 25
Skeletal or other Health Abnormalities (also use comments section):

Predator Determination

Carcass skinned out ?: Y / [✓ N] Subcutaneous hemorrhaging? Y / [✓ N] Location:
FWP Necropsy Report Y / [✓ N] ? Report ID: Summary (use comments section):
Predator Checklist (check all that apply within 100m of carcass): Record canine width & spread if possible

Wolf

- ___Carcass disarticulated
- ___Carcass spread out over > 20 m radius
- ___Hide peeled off
- ___Wolf telemetry in same location
- ___Wolf tracks
- ___Wolf scat present
- ✓ Femur cracked
- ✓ Ribs chewed, ~~often down to vertebrae~~
- ___Signs of extended struggle
- ___Canine puncture wounds on legs/ lower neck
- ___Rumen intact and untouched

Cougar

- ✓ Carcass partially or totally buried with snow, vegetation, etc...
- ___Hide intact and hair plucked out (if recent)
- ___Hair pile (if older)
- ✓ Claw marks on hide (slashes)
- ___Cougar scat present
- ___Cougar tracks present
- ___Canine puncture wounds on head/neck
- ___Visible trauma to the head and neck, broken vertebrae, crushed windpipe, etc.

A project mortality form showing a portion of the detailed notes taken at mortality scenes used to determine cause of mortality.

We attempted to investigate mortality signals within 24 hours of detecting a mortality signal. We searched each mortality site to document signs of predation including tracks, signs of struggle, and any carnivore scat or hair samples present (Smith et al. 2006; Barber-Meyer et al. 2008). We performed a field necropsy on each carcass by examining the locations and measurements of canine puncture wounds, claw or bite marks on the hide, cracked or chewed bones, and consumption patterns. We did not classify a mortality as predation if there was a possibility that the calf died of non-predation causes or was only scavenged upon, which was differentiated from predation by the absence of internal hemorrhaging. When possible, genetic samples were extracted from carnivore hair and scat collected at calf mortality sites and carnivore species were identified using DNA by the U.S. Forest Service, Wildlife Genetics Laboratory, Rocky Mountain Research Station in Missoula, MT. We classified calf fates as live, dead or unknown fate, and concluded calf monitoring on 30 May, 2014.

Once a neonate elk calf is captured, a VHF eartag transmitter is applied and morphometric data is collected.

Calf survival and risk factors

We used an age-based time scale for neonatal elk calves with birth date as the origin. Age at capture was estimated using morphometrics recorded at capture following Johnson (1951, see Eacker 2015 for details). The survival origin for calves caught during winter was 26 Nov. We right censored any calves that may have died due to capture (i.e., neonates that died within 24 hours and 6-month-old calves that died within 2 weeks of capture), may have permanently emigrated or experienced radio transmitter failure, and thus, were never heard again; physically lost radio tags; or survived the monitoring period. Calves dying from capture-related events were censored on the day of death, and calves that had radio tag-related failures or permanently emigrated were censored on the day following the date they were last heard live.

We regressed calf mass at capture on estimated age at capture, and used the estimated sex-specific regression coefficients to predict birth mass following the approach of Smith et al. (1997). We imputed the mean sex-specific birth mass for calves that did not have birth mass records. We estimated birth dates by subtracting estimated age at capture from capture dates, and formatted birth dates using standardized Julian days across capture years (Smith et al. 1997). We treated year as a categorical variable.

Statistical analysis

We tested for effects of risk covariates on annual juvenile elk calf survival using continuous, time-to-event survival Cox-proportional hazards models (Cox 1972; Therneau and Grambsch 2000) to examine the effect of risk covariates in summer (0 – 180 days) and winter (181 – 365 days). The Cox proportional hazards (PH) model is parameterized in terms of the hazard ratio (HR), which is used to compare hazards among categorical variables and to estimate the effect of covariates on the baseline hazard rate. A hazard ratio of 1 indicates no difference among categorical levels or no effect of a covariate on the hazard of mortality, while a HR of <1 or >1 indicates a decreasing or increasing mortality hazard, respectively.

We applied a sequential model selection approach (Arnold 2010) to Akaike's Information Criterion with an adjustment for sample size (AIC_c) to select the most parsimonious summer and winter elk calf survival models (Burnham and Anderson 2002). We assessed the importance of variables in the top models using likelihood ratio tests. Before assessing the effect of risk covariates on elk calf survival, we standardized all continuous covariates by subtracting their mean and dividing by two times their standard deviation (Gelman 2008), allowing covariate effect sizes to be comparable to factors (e.g. sex). We also screened covariates for collinearity and included only covariates with a Pearson's correlation coefficient < |0.6| (Zuur et al. 2007).

We estimated basic survival rates using the Kaplan-Meier (KM) estimator (described in Section 6) and compared their significance across groups using log-rank tests (Pollock et al. 1989). We report 95% confidence intervals (CIs) for survival and hazard ratio estimates. All statistical analyses were performed in program R (R version 3.1.2, www.R-project.org, accessed 10 Apr 2015). We estimated KM survival rates and Cox PH model coefficients using the R base package `survival` (Therneau 2015) and conducted model selection using the R package `MuMIn` (Barton 2015). See Eacker (2015) for detailed description of survival models.

Cause-specific mortality

We estimated cause-specific mortality rates using cumulative incidence functions (CIFs) and smoothed instantaneous hazard rates as described in Section 6. We categorized mortality sources for elk calves as bear; mountain lion; wolf; unknown; natural, non-predation; and human-related. Given moderate incidence of unknown mortality in our study relative to other calf survival studies, we assessed whether or not unknown mortalities were related to any known mortality sources using a competing risks framework to decompose summer and winter baseline hazards into their component cause-specific hazards (see Eacker 2015 for details). We were primarily concerned with the relationship of unknown mortality hazard to bear, mountain lion, and wolf mortality hazards in summer, and mountain lion and wolf mortality hazards in winter to determine if patterns in unknown mortality were similar to those of bear, mountain lion or wolf predation and suggestive of a particular cause.

Black bears, wolves and lions are calf elk predators across the western US

RESULTS

Elk calf captures and birth attributes

We captured 226 neonatal and 60 6-month-old elk calves for a total of 286 calves throughout the East Fork and West Ford study areas. Sex ratio of captured elk calves was not different from parity at 0.9:1 females to males (n = 285, P = 0.26). The sex of one calf was not determined. We consistently caught more calves in the East Fork than in the West Fork, which was expected since elk are more abundant in the East Fork study area (see Section 2). We captured similar numbers of each sex of calf during each season and year, and did not capture calves during the last winter (2013 – 14) due to sufficient sample sizes remaining after summer (Table 7.1).

Table 7.1. Number of elk calves captured by period, capture area, and sex.

Elk calf summary	2011–12	2012–13	2013–14	Total
Period				
Summer	66	76	84	226
Winter	31	29	0[a]	60
Total	97	105	84	286
Capture areas				
East Fork	58	69	56	183
West Fork	39	36	28	103
Sex				
Female	45	52	36	133
Male	51	53	48	152
Unknown	1	0	0	1

We estimated birth masses for 212 neonatal elk calves, and imputed the overall mean estimated birth mass (x = 14.13 kg, SD = 3.22) for 14 calves that did not have capture mass measured. We tested the effect of censoring calves with missing capture masses in summer survival models and found negligible effects on the coefficients estimates and precision. Estimated birth mass differed by sex ($F_{1, 207}$ = 4.93, P = 0.03), but not by study area ($F_{1, 207}$ < 0.0002, P = 0.99) or year ($F_{2, 207}$ = 0.02, P = 0.98). Male calves (x = 14.6 kg, SD = 3.2, n = 118) had heavier (0.99 kg) birth mass than females (x = 13.6 kg, SD = 3.1, n = 94). Estimated birth masses did not vary by any 2-way interactions of sex, study area or year. Male calves had slightly higher growth rates (male capture mass = 14.56 kg + 1.33 × age at capture) than females (female capture mass = 13.58 kg + 1.22 × age at capture). However, the interaction of sex and age at capture was not significant in our growth rate prediction model (β = 0.12, SE = 0.27, P = 0.67), and any true differences in growth rates between sexes were overwhelmed by the large variation in mass at capture over the range of estimated ages.

We estimated ages of calves at capture from the Johnson method (see Eacker 2015), which ranged from 0 to 6 days, with a mean of 3.7 days (SD = 1.7, n = 226). Estimated age at capture did not significantly vary by sex, study area, year or any interactions among these variables. Estimated birth dates ranged from 22 May to 11 June (median = 30 May). In our 3-

way ANOVA explaining standardized Julian birth dates, we found significant 2-way interactions among sex and study area ($F_{1, 217}$ = 4.38, P = 0.04) and among study area and year ($F_{2, 217}$ = 2.90, P = 0.06). The interaction of sex and study area resulted from females having a about a 0.5 day later mean birth date than males in the East Fork (x_{female} = 7.7, SD = 3.2; x_{male} = 7.2, SD = 2.8), and male births occurring about 1 day later on average than females in the WF (x_{female} = 8.58, SD = 3.3; x_{male} = 9.6, SD = 3.6). The interaction of study area and year resulted from calves being born about 3.5 days later on average in the West Fork (x_{2011} = 10.9, SD = 3.6) than in the East Fork (x_{2011} =7.6, SD = 3.1) in 2011 – 2012, with smaller differences in mean birth dates between study areas during 2012 – 2013 (x_{WF} = 9.1, SD = 2.7; x_{EF} = 8.2, SD = 3.1) and 2013 – 2014 (x_{WF} = 8.0, SD = 3.6; x_{EF} = 6.6, SD = 2.6). In summer, we found a very weak, positive correlation between estimated birth mass and birth date (R = 0.05). Overall, we found no strong evidence of study area, sex, or year effects on birth date, birth mass, or age at capture that would lead us to suspect consistent biases in survival.

Calf survival

Summer survival

After removing 2 calves from our summer survival dataset (1 calf with unknown sex and 1 calf mortality signal detected in an inaccessible area), we had a total sample of 224 calves, of which we censored 63 that lost ear tags, 7 with unknown fates that may have left the study area or experienced ear tag failures, 2 possible capture-related mortalities (died the same day as capture), and 1 known capture-related mortality. Although censoring rates were relatively high early in the study, we found no strong evidence of bias or informative censoring related to ear tag loss (Eacker 2015). The KM estimate of summer (180 day) survival rate was 0.55 (95% CI = 0.47, 0.63; Table 7.2). Female calf survival was almost 20% higher on average than male survival (P = 0.04), with respective summer survival rates of 0.65 (95% CI = 0.53, 0.74) and 0.46

Table 7.2. Kaplan-Meier estimates of annual survival probability (S) with 95% confidence intervals (lower confidence interval = LCI; upper confidence interval = UCI) by population and pooled, and the minimum and maximum number of elk calves at risk (n) in summer and winter seasons.

			East Fork			West Fork			Pooled		
Period	**Year**	***n***	$\widehat{S}$	**LCI**	**UCI**	$\widehat{S}$	**LCI**	**UCI**	$\widehat{S}$	**LCI**	**UCI**
Summer	2011–12	(19–62)	0.65	0.47	0.78	0.45	0.19	0.68	0.59	0.44	0.71
	2012–13	(21–75)	0.59	0.42	0.73	0.30	0.11	0.52	0.49	0.35	0.62
	2013–14	(10–82)	0.56	0.34	0.74	0.59	0.34	0.78	0.57	0.40	0.71
Winter	2011–12	(18–41)	0.71	0.43	0.87	0.40	0.18	0.61	0.54	0.36	0.69
	2012–13	(35–42)	0.76	0.55	0.89	1.00	NA[a]	NA	0.85	0.70	0.93
	2013–14	(31–39)	0.92	0.71	0.98	0.59	0.31	0.79	0.79	0.63	0.89

[a] NA = not applicable; 95% CIs were not estimable due no mortality events occurring.

(95% CI = 0.33, 0.59, Table 7.2). Elk calf survival was 0.59 (95% CI = 0.47, 0.69) in the East Fork compared to 0.49 (95% CI = 0.35, 0.61) in the West Fork area (*P* = 0.13). Elk calf survival rate did not vary significantly from year-to-year in the summer (*P* = 0.12; Figure 7.1, Table 7.2). With relatively constant summer survival rates across study areas and years, the best model of summer survival included only sex and birth date (Table 7.3). Contrary to the findings of Raithel (2005), we found that elk calf survival decreased marginally with increasing birth date (Hazard Ratio [HR] = 1.06, 95% CI = 0.99, 1.13, *P* = 0.09), but a likelihood ratio test revealed that birth date did not significantly contribute to the model ($\chi^2_1 = 2.37$, *P* = 0.12),

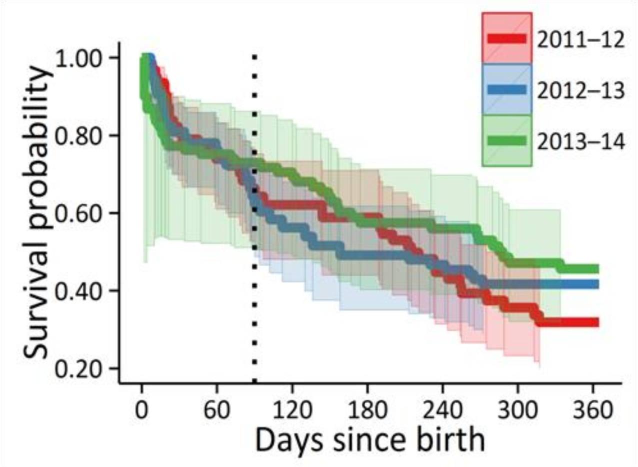


Figure 7.1. Kaplan-Meier survival curves with 95% confidence intervals for 3 biological years for elk calves in the southern Bitterroot Valley, MT, 2011–2014. The KM survivorship graph shows that inter-annual variation in elk calf survival increases after about 90 days since birth (vertical dotted line).

Table 7.3. Sequential base model selection of Cox proportional hazards models showing the number of model parameters (*k*), model deviance (Dev), ΔAIC*c*, and model weights (*w*) for summer and winter elk calf survival. The nested model risk covariates and factors were sequentially removed until the ΔAIC*c* increased with variable removal. Abbreviations are estimated birth date (Date), birth mass (Mass), and year (Yr).

Season	Model rank	Model	*k*	Dev	ΔAIC*c*	*w*
Summer	1	Sex + Date	2	-396.34	0.00	0.35
	2	Sex + Date + Yr	4	-394.39	0.23	0.31
	3	Sex + Date + Yr + Study area	5	-393.66	0.87	0.23
	4	Sex + Date + Yr + Study area + Mass	6	-393.66	2.97	0.08
Winter	1	Yr	2	-132.26	0.00	0.35
	2	Yr + Study area	3	-131.38	0.33	0.30
	3	Yr + Study area + Sex	4	-130.46	0.63	0.25
	4	Yr + Study area + Sex + Study area × Sex	5	-130.44	2.75	0.09

and thus, only sex was retained in the top summer model. Birth mass did not influence summer elk calf survival (*P* = 0.68).

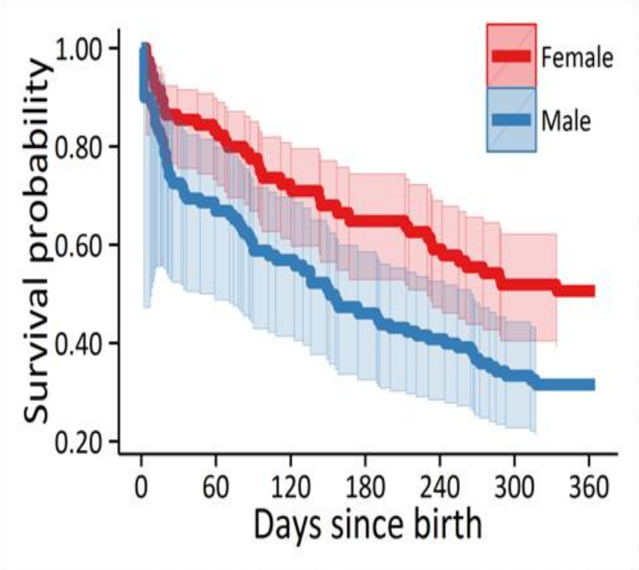


Figure 7.2. Kaplan-Meier survival curves with 95% confidence intervals for female (red) and male (blue) for elk calves in the southern Bitterroot Valley, MT, 2011–2014. Male calves had significantly higher survival than female calves mainly due to differences during summer.

Winter survival

After removing 1 calf from our winter survival dataset because of the uncertainty inthe timing of a possible capture-related mortality event (i.e., died within two weeks of capture and experienced an ear tag malfunction that delayed the mortality investigation), we had a total sample of 125 calves, of which we right censored 21 that lost ear tags, 10 with unknown fates that may have left the study area or experienced ear tag failures, 1 capture-related mortalities, and 2 mortality signals that could not be investigated due to access. The KM estimate of winter (181–365 days) survival was 0.73 (95% CI = 0.64, 0.81, Table 7.2). Winter female calf survival was 0.78 (95% CI = 0.65, 0.87) compared to 0.69 (95% CI = 0.55, 0.79) for males (*P* = 0.24), Figure 7.2). We found marginal evidence that elk calf survival was higher in the East Fork (*S* = 0.80, 95% CI = 0.68, 0.88) compared to the West Fork (*S* = 0.65, 95% CI = 0.49, 0.76) during winter (*P* = 0.10). In contrast to summer, elk calf survival rate varied significantly from year-to-year in winter (*P* = 0.002, Table 7.2). Although we found marginal evidence that winter survival rates varied by study area, the most parsimonious model for winter calf survival included only a year effect (Table 7.3). Likelihood ratio tests confirmed that neither

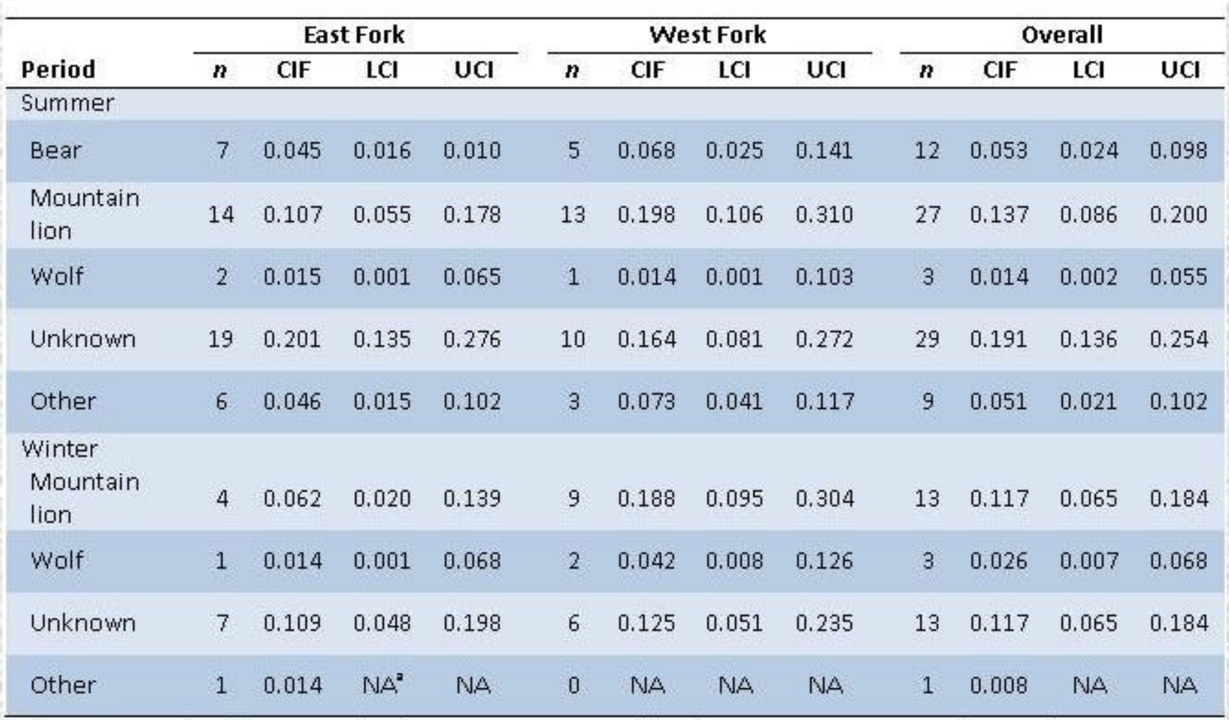
Specific details such as location and types of wounds, patterns of consumption, and whether/ how a carcass is cached can often help distinguish between predation by wolves (above), mountain lion (upper right) or bear (lower right).

sex (χ^2_1 = 1.83, *P* = 0.18) nor study area (χ^2_1 = 2.00, *P* = 0.16) contributed significantly to the model.

Calf cause-specific mortality

Upon detecting a mortality signal, we located and investigated the fate of each calf as soon as possible (*x* = 2.0 [SD = 7.7] days in 2011–2012; *x* = 1.1 [SD = 4.7] days in 2012–2013; and *x* = 0.7 [SD = 1.7] days in 2013–2014); the median investigation time each year was 0 days. We estimated cause-specific mortality rates with a sample of 224 calves in summer and 125 calves in winter. We investigated a total of 110 mortalities. We estimated annual cause-specific mortality rates (CIF) of 0.20 (95% CI = 0.14, 0.27) for mountain lion predation; 0.05 (95% CI = 0.02, 0.10) for bear predation; 0.03 (95% CI = 0.01, 0.07) for wolf predation; 0.26 (95% CI = 0.19, 0.32) for unknown causes; 0.04 (95% CI = 0.01, 0.09) for natural, non-predation (e.g., drowning, pneumonia); and 0.02 (95% CI = 0.003, 0.05) for human-related mortality (e.g., fence entanglement, hunter harvest; see Table 7.4).

Table 7.4. Cumulative incidence functions (CIF) in summer and winter for 5 mortality sources with 95% confidence intervals (lower confidence interval = LCI; upper confidence interval = UCI) by population, and raw counts (n) for 110 confirmed elk calf mortalities. CIFs were pooled over study years, and natural, non-predation (drowning, starvation and human-related mortality (fence entanglement, hunter harvest) categories were collapsed into a single category (other) for presentation.



	East Fork				West Fork				Overall			
Period	***n***	**CIF**	**LCI**	**UCI**	***n***	**CIF**	**LCI**	**UCI**	***n***	**CIF**	**LCI**	**UCI**
Summer												
Bear	7	0.045	0.016	0.010	5	0.068	0.025	0.141	12	0.053	0.024	0.098
Mountain lion	14	0.107	0.055	0.178	13	0.198	0.106	0.310	27	0.137	0.086	0.200
Wolf	2	0.015	0.001	0.065	1	0.014	0.001	0.103	3	0.014	0.002	0.055
Unknown	19	0.201	0.135	0.276	10	0.164	0.081	0.272	29	0.191	0.136	0.254
Other	6	0.046	0.015	0.102	3	0.073	0.041	0.117	9	0.051	0.021	0.102
Winter												
Mountain lion	4	0.062	0.020	0.139	9	0.188	0.095	0.304	13	0.117	0.065	0.184
Wolf	1	0.014	0.001	0.068	2	0.042	0.008	0.126	3	0.026	0.007	0.068
Unknown	7	0.109	0.048	0.198	6	0.125	0.051	0.235	13	0.117	0.065	0.184
Other	1	0.014	NA[a]	NA	0	NA	NA	NA	1	0.008	NA	NA

[a] NA = not applicable; CIFs and 95% CIs were not estimable due no events occurring due to other causes in the West Fork and only a single event (a fence entanglement) due to other causes in the East Fork during winter.

Summary cause-specific mortality

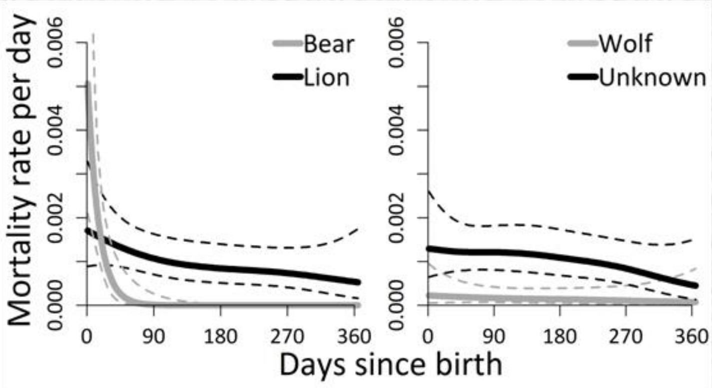


Figure 7.3. Smoothed instantaneous mortality hazards (i.e. mortality rate per day) for elk calves for different mortality sources in the southern Bitterroot Valley, MT, 2011 – 2014.

Elk calf mortality risk was highest over the first 30 days of life, with 46.3% of all summer mortality occurring during this time (Figure 7.3). The mortality hazard from black bears exceeded mountain lions until 20 days after birth (Figure 7.3), and then mountain lion predation dominated summer calf mortality thereafter. Mountain lion-caused mortality was relatively constant over the summer period (Figure 7.3). The 3 wolf-caused mortality events in summer occurred within the first 90 days of life. We estimated a summer cause-specific mortality rate (CIF) of 0.14 (95% CI = 0.09, 0.20) for mountain lion predation; 0.05 (95% CI = 0.02, 0.10) for bear predation; 0.01 (95% CI = 0.002, 0.06) for wolf predation; 0.19 (95% CI = 0.14, 0.25) for unknown causes; 0.04 (95% CI = 0.02, 0.09) for natural, non-predation; and 0.01 (95% CI = 0.001, 0.05) for human-related mortality (Table 7.4). Our exploratory analysis of unknown mortality for elk calves suggested that unknown mortality hazard may be a composite of mainly mountain lion-caused mortality, and bear and wolf mortality to a lesser extent (i.e., 95% CI's between bear and unknown hazard ratios nearly overlapped (see Eacker 2015 for details).

Winter cause-specific mortality

Elk calf mortality risk peaked around late January to February in winter when precipitation was greatest, and then, declined to low levels by late spring (Figure 7.3). Mountain lions maintained a consistent hazard for elk calves over the winter, while wolf-caused mortality was minimal (Figure 7.3). We estimated a winter cause-specific rate of 0.12 (95% CI = 0.07, 0.18) for mountain lion predation; 0.03 (95% CI = 0.01, 0.07) for wolf predation; 0.12 (95% CI = 0.07,

Even with intensive monitoring and extensive efforts, the cause of some mortalities remain unknown, such as this ear and eartag that were found in the top of a spruce tree.

0.18) for unknown causes; and 0.01 (95% CI not estimable) for human-related mortality (Table 7.4). Our exploratory analysis of unknown mortality for elk calves in winter suggested that unknown mortality hazard may be a composite of mainly mountain lion-caused mortality, and wolf mortality to a lesser extent (i.e., 95% CI's between unknown and wolf hazard ratios nearly overlapped).

DISCUSSION

Few studies have documented strong effects of mountain lion predation on elk calves in a system with recolonizing wolves, and our study highlights the variability in the importance of carnivores across different ecological systems. Our cause-specific mortality analysis revealed that mountain lions dominated calf mortality over the first year of life, with wolves being essentially inconsequential as a mortality source, even during winter when their selection for elk calves is well documented in other systems (Mech et al. 2001; Smith et al. 2004; Metz et al. 2012). We attribute the dominance of mountain lions for annual elk calf survival to differences in relative carnivore densities in our study system. After identifying mountain lions as a dominant mortality source for elk calves, we conducted a DNA-based spatial-capture-recapture study of mountain lion density during our calf study. We estimated mountain lion density to be relatively high at about 46 and 54 individuals/1000 km^2 in the East Fork and West Fork areas, respectively (Proffitt et al. 2015). Considering that wolves were estimated to be at around 2–5 times lower density than mountain lions in the study area (10–20 wolves/1000 km^2, see Section 2), the strength of mountain lion predation and minimal effect of wolves on elk calf survival is consistent with the differential densities of these two carnivores in our system. This emphasizes that density alone may be sufficient to explain the relative importance of different carnivore species in multiple carnivore systems.

An 8-month old elk calf killed and cached by a mountain lion in January in the West Fork of the Bitterroot.

A neonate calf in the East Fork of the Bitterroot is just big enough to keep up with the herd.

In the northern range of Yellowstone National Park, where wolves were about 4–5 times more abundant than mountain lions, Barber-Meyer et al. (2008) documented that wolf predation accounted for 14 – 17% of all elk calf mortality, while mountain lion predation was minimal. Another elk calf survival study in Wyoming (Smith et al. 2006) concluded that low amounts of wolf-caused mortality were related to low wolf densities in the study area, while neonatal mortality rates due to bear predation increased over the time with increasing grizzly bear density. In our study system and most other parts of the Rocky Mountains where livestock production is a dominant land use wolves may be held at lower densities due to mortality from livestock conflict and human harvest (i.e. hunting and trapping). Additionally, a decade-long period of reduced mountain lion harvest in western Montana (2000–2010, MFWP unpublished data) combined with a diverse ungulate prey base may have resulted in high densities of mountain lions. Similar declines in mountain lion harvests, for a variety of reasons, have similarly occurred across the western United States. With the recolonization of wolves in many regions, and the public interests surrounding it (Treves et al. 2013), the effects of increasing mountain lion populations on ungulate populations may have been overlooked. Combined with our results, there is growing evidence suggesting that mountain lions may be the most important carnivore for ungulates in more settings than anticipated (Myers et al. 1998; Rearden 2005; Johnson et al. 2013).

A caveat to our results is the high levels of tag loss that occurred during the first year of the study, which has the potential to bias survival estimates when censoring is due to missed mortality events (Murray et al. 2010). We found no evidence of informative censoring due to intrinsic factors (i.e., sex, birth mass), but we did find a significant difference across study areas with higher tag loss rates in the East Fork than the West Fork that we attributed to misplacement of ear tags by less experienced capture crews in the East Fork (see Eacker 2015). Despite high tag loss rates in summer, we were able to maintain adequate sample sizes throughout the study by supplementing our winter sample of calves. Also, we had a relatively high incidence of unknown mortality that we could not successfully pool with any specific mortality source. However, our mortality classifications may have been more conservative than some studies due to our strict classification of mortality causation.

We found a consistent effect of male-biased mortality in summer across study years, which we hypothesize may be due to the consequences of neonatal males exhibiting riskier behavior compared to females in a system dominated by mountain lions, an ambushing predator. For example, Mathisen et al. (2003) found that neonatal semi-domestic reindeer (*Rangifer tarandus*) exhibited marked behavioral differences between male and female calves that were thought to drive differences in vulnerability to predation mortality; male calves were observed farther away from their mothers and exhibited more locomotion. Although our study and others have found a strong signal of male-biased mortality in elk calves (Smith et al. 2006), the direction and strength of this effect seems to vary across study systems (Rearden 2005; White et al. 2010) and environmental conditions (Smith and Anderson 1996). We found from a post hoc competing risks analysis that male-biased calf mortality in summer was mainly due to differences in unknown mortality (*P* = 0.03) rather than mountain lion-caused mortality (*P* = 0.64), but our exploratory analysis of unknown mortality revealed that unknown mortality hazard was most similar to mountain lion hazard in summer. Regardless of the uncertainty due to unknown mortalities, male-biased calf mortality will reduce the recruitment of yearling and adult male elk into the population, and declines in recruitment may lead to declines in adult sex ratios where male-biased juvenile mortality is significant.

Understanding the role of multiple carnivores in driving declines in juvenile ungulate recruitment generally requires estimates of cause-specific mortality. Carnivore density estimates may provide a surrogate to predict the relative importance of carnivores when cause-specific mortality rates are unobtainable. In areas where carnivore populations continue to increase, managers may need a more aggressive policy towards habitat (e.g. logging, prescribed burns) or carnivore management to increase ungulate recruitment in less productive habitats. Management efficiency will gain from aligning treatments with experimental designs that provide strong inference into factors driving ungulate population dynamics. Although observational studies are weaker inferentially, they are valuable in reducing uncertainty in management problems and provide valuable insights into ungulate population dynamics. Given the greater variation observed in winter compared to summer elk calf survival rates, aerial surveys conducted in late spring before migration occurs may provide a more accurate depiction of over-winter calf survival and calf recruitment. For areas that use mid-winter surveys, annual survival estimates may be adjusted to account for variation in winter survival of juveniles.

Section 8 - Population Modeling

Wildlife managers are tasked with developing harvest management regulations that will move elk population sizes towards objectives. Traditionally, managers have mainly relied on harvest estimates and aerial or ground-based count data to monitor elk population trends through time and guide decision-making. While young-to-adult female or age ratios derived from trend count data have been shown to correlate strongly ($R^2 = 0.93$) with summer (0–6 months old) elk calf survival (Harris et al. 2008), there are a number of demographic parameters in age ratio data (e.g., pregnancy, calf survival) that cannot be disentangled without direct estimates of survival and pregnancy. Thus, effective management may require more detailed information to determine the drivers of observed declines in age ratios or trend counts. Given the need for pregnancy and survival rate estimates from radio-marked individuals, an inevitable problem that arises for management is how to combine these different data sources (e.g., count and telemetry data) to estimate population growth rates, understand population dynamics, and predict population size into the future under different harvest scenarios. And thus, addressing these fundamental objectives is essential to successfully manipulating elk population sizes.

Recently, the use of integrated population models (IPMs), also known as hierarchical or state-space models, have become more common in conservation applications (King et al. 2008; Johnson et al. 2010; Abadi et al. 2010a) because of their ability to overcome many of the limitations imposed by traditional demographic analyses. The benefits of this integrated modelling approach are that variance-covariance relationships are accounted for among demographic parameters, parameter estimates become more precise, and that unobserved or latent parameters are estimable in some cases (Besbeas et al. 2002, Tavecchia et al. 2009). More specifically, Bayesian IPMs use a hierarchical approach to assess population dynamics by linking models describing the observation process (empirical data collection) to models describing the biological process for a given population (see Schaub and Abadi 2011). The observation models are used to estimate demographic parameters (i.e. survival rate, pregnancy, etc.) in the process model, which is the set of difference equations that describe annual

Elk counted and classified as part of winter or spring aerial surveys, combined with harvest estimates are primary components of management decisions.

change in population abundance with changes in age or stage-specific vital rates (Caswell 2001). The population model integrates information about the population from multiple data sources including count data collected annually from aerial surveys and vital rate data collected from radio-telemetered individuals.

Despite the advances of Bayesian IPM methods, few have applied such models to determine the most important vital rates driving population growth rate (λ) from a life-stage simulation analysis (LSA) perspective. LSA determines the importance of various vital rates such as adult female survival or calf survival in affecting λ. By regressing λ on each vital rate, the analysis provides an estimate of the amount of variation in λ explained by each vital rate and the rate of change in λ as a function of each vital rate. An important result of LSA is that vital rates with high process variance will have a relatively large influence on the population growth rate because high variation in a vital rate will translate to greater variation in λ, dampening population growth over time (Mills et al. 1999; Wisdom et al. 2000; Coulson et al. 2005).

We used a Bayesian integrated population modelling approach to evaluate the important drivers of population dynamics for East Fork and West Fork elk. Our objectives were to 1) estimate vital rates for the West Fork and East Fork elk populations, 2) evaluate the importance of different drivers of population dynamics for the East Fork and West Fork elk, and 3) forecast the consequences of different harvest management scenarios on elk population size by projecting elk population size into the future under different combinations of vital rates and harvest.

Methods

Data sources

Elk count data were collected annually by MFWP from fixed-wing aircraft and the new hunting district boundaries (Figure 2.1) were used for all population modelling. We used a subset of this data that overlapped with years that elk survival and pregnancy data were collected. The aerial counts were conducted from late March to early May of each year before elk migrated to summer range (pre-birth pulse). We considered juveniles classified as calves in the aerial surveys as the number of yearlings because these elk were nearly 1 year of age. Therefore, the two stages observed during aerial surveys included the number of yearlings (~0.9 years old during surveys) and adult females ($\geq$ 1.9 years). We captured and radio-marked elk calves and adult females to estimate survival and reproduction (see Sections 6–7). We collected a blood sample during capture of adult female elk in the East Fork and West Fork populations to estimate pregnancy status based on pregnancy-specific protein-B levels (Noyes et al. 1997, see Section 4). We used harvest data collected through the MFWP harvest survey program to estimate the annual antlerless and antlered elk harvest during the study period.

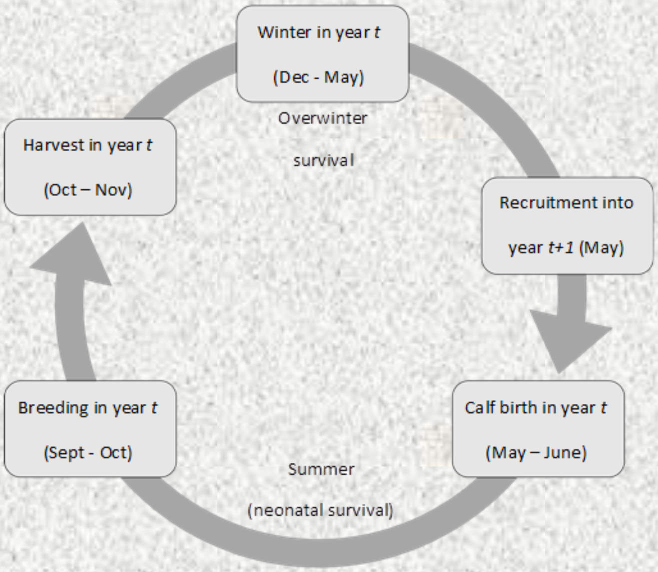


Figure 8.1. We based the annual population cycle on a biological timescale, with the median birth date (May 30) of elk calves observed during the study period defining the start of the annual interval; thus, the summer survival period was from May 30–November 25, while the winter survival period spanned from November 26–May 29. The rut or breeding period for elk occurred in the fall, while the general hunting season for was from late-October to late-November of each year.

Model formulation and parameterization

We based the annual population cycle on a biological timescale, with the median birth date (May 30) of elk calves observed during the study period defining the start of the annual interval. Aerial count surveys of elk were conducted in April to May, while the general elk hunting season was from late-October to late-November of each year (Figure 8.1). We deducted annual harvest estimates from the total number of adult male and female elk as a deterministic process. Density dependence was not included in the model. For details on model formulation and parameterization, see Eacker 2015.

Evaluating harvest management scenarios

To evaluate potential harvest management scenarios, we used the IPM to forecast East Fork and West Fork elk population size during the next 5 years given 2 different levels of calf recruitment and 3 different levels of antlerless elk harvest for a total of 6 simulated scenarios for each of the East Fork and West Fork populations. Under each of these 6 potential harvest management scenarios, we evaluated elk population size relative to potential elk population objectives of 3,800 elk (range 3,040 – 4,560) in the East Fork and 1,400 elk (range 1120 – 1680) in the West Fork population. Additional simulations including simulated adult male elk harvest management are reported in Eacker (2015).

Based on the past 5-year average estimate of harvest, the status quo (i.e. number elk harvested given past harvest regulations) for harvest was 280 antlered and 100 antlerless elk per year in the East Fork area, and 25 antlered and 0 antlerless elk per year in the West Fork area (note that between 0–10 antlerless elk were harvested in the West Fork during 2010–2015). We adjusted East Fork harvest estimates upward by 10 antlered and 15 antlerless elk to account for migratory elk harvested in HD 334 (unpublished data). In the East Fork, we evaluated a simulated calf recruitment (i.e. ratio of yearlings to adult females) of 25 yearlings : 100 adults and 50 yearlings : 100 adults and simulated a harvest of 100 (i.e. status quo), 200, and 300 antlerless elk. In the West Fork, we evaluated a simulated calf recruitment of 25 yearlings : 100 adults and 40 yearlings : 100 adults and simulated a harvest of 0 (i.e., status quo), 25, 50 and 75 antlerless elk.

We used the mean vital rates and number of yearling and adult females estimated from our IPMs to calculate the calf survival rates that corresponded to specific age ratios in our simulations. The following equation was used to predict the expected number of yearlings per 100 adult female elk at time *t* + 1:

$$(N_{y,t+1}/N_{af,t+1}) \times 100 = (\Phi_{c,t}P_{af,t}N_{af,t})/(R\Phi_{y,t}N_{y,t} + \Phi_{af,t}N_{af,t}) \times 100$$

By setting the number of yearlings ($N_{y,t}$) and adult females ($N_{af,\, t}$) at time *t* to the mean number observed over the study period, and holding adult female survival ($\emptyset_{af,\, t}$), pregnancy (P (af,t)), yearling survival ($\emptyset_{Y,\, t}$), and the proportion of yearlings that were female (*R*) at their mean observed rates, we were able to vary calf survival to simulate different age ratios.

Results

We estimated that the mean population growth rate (λ) for the East Fork population (λ = 1.06, 95% Bayesian Credible Interval [BCI] = 1.02, 1.10) was about 3% higher than the West Fork population (λ = 1.03, 95% BCI = 0.99, 1.07). The East Fork population was increasing during all study years except 2010 – 2011 when the growth rate was near stable at 0.99 (95% BCI = 0.88, 1.10). The West Fork population was stable during 2010 – 2011 (1.00, 95% BCI = 0.87, 1.11), declined in 2011 – 2012 (0.95, 95% BCI = 0.87, 1.05), and increased during the latter half of the study.

Life-stage simulation analysis

Bayesian LSA revealed which vital rates had the most important effect on population growth rate (λ). In the East Fork population, the most important vital rates driving λ based on the slopes of the regressions of λ on each vital rate and its coefficient of determination (R^2), were first adult female survival (β = 0.87, SE = 0.03, R^2 = 0.43, Figure 8.2), followed by calf survival (β = 0.35, SE = 0.01, R^2 = 0.38), then pregnancy (β = 0.17, SE = 0.02, R^2 = 0.06). Similarly, in the West Fork, adult female survival (β = 0.89, SE = 0.03, R^2 = 0.56) was the most important vital rate driving λ, followed by calf survival (β = 0.33, SE = 0.02, R^2 = 0.33) and pregnancy (β = 0.12, SE = 0.02, R^2 = 0.06). While the slope and coefficient estimates supported the same rankings of vital rate importance in the East Fork and West Fork populations, the relative magnitude of the differences in the effect of adult female and calf survival on λ varied

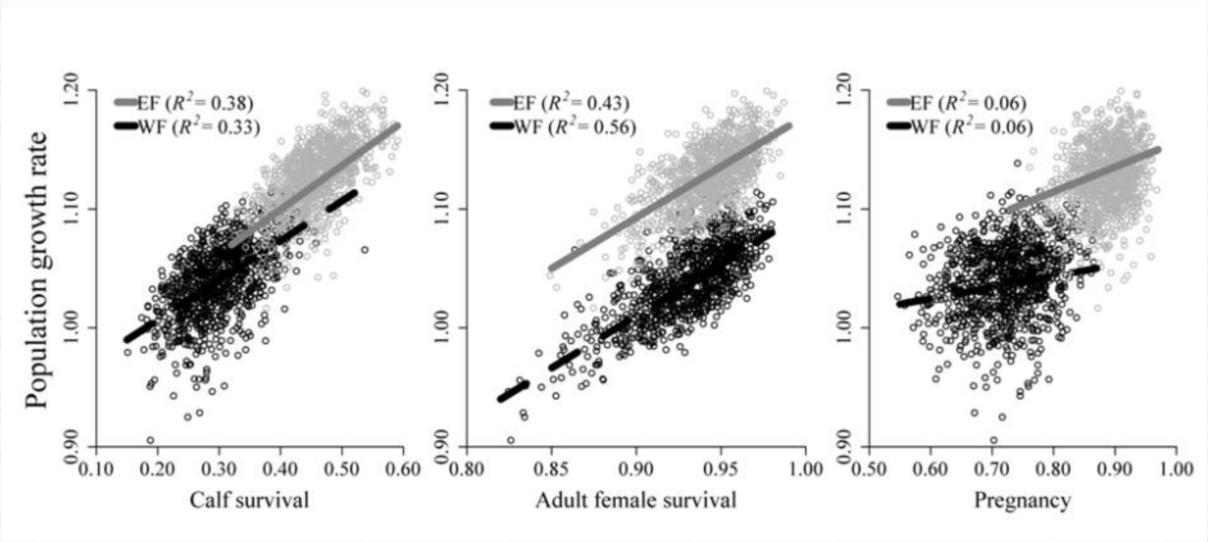


Figure 8.2. Scatterplots of mean vital rate and population growth rate values for the East Fork (gray) and West Fork (black) elk populations in Bayesian life-stage simulation analysis. The graph shows estimated regression lines (slopes) and coefficient of determination (R^2) for annual elk calf survival, adult female survival and pregnancy rate with solid lines for the East Fork (East Fork) and broken lines for the West Fork (West Fork).

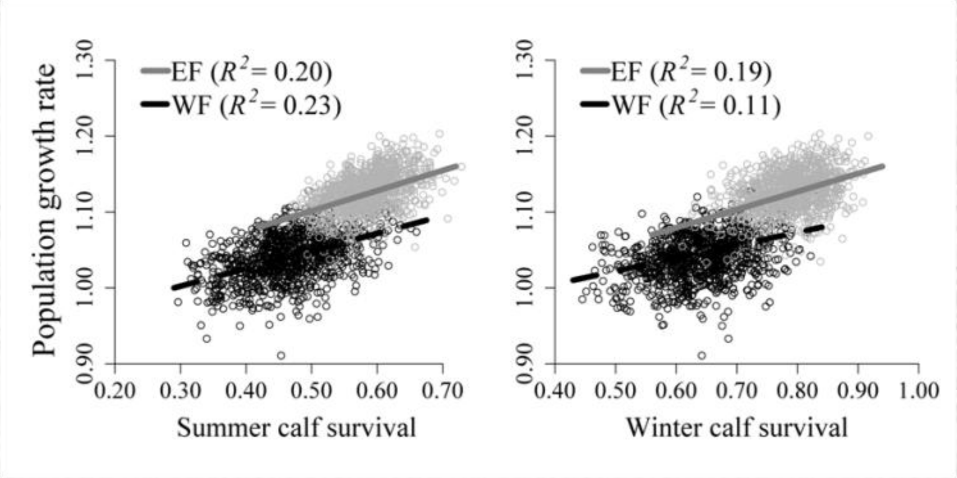


Figure 8.3. Scatterplots of mean vital rate and asymptotic population growth rate values for the East Fork (gray) and West Fork (black) elk populations in Bayesian life-stage simulation analysis. The graph includes estimated regression lines (slopes) and coefficient of determination (R^2) for summer (left) and winter (right) elk calf survival with solid lines for the East Fork (East Fork) and broken lines for the West Fork (West Fork).

between populations. In the East Fork, adult female survival was only about 5% more important than calf survival, whereas in the West Fork, adult female survival explained about 23% more of the variance in λ compared to calf survival, highlighting an important population difference.

After decomposing annual calf survival into seasonal components, our analysis revealed important differences in the relative importance of summer and winter calf survival on λ. In the East Fork, summer and winter calf survival contributed more or less similarly to λ (summer: β = 0.26, SE = 0.02, R^2 = 0.20; winter: β = 0.22, SE = 0.01, R^2 = 0.19; Figure 8.3), but in the West Fork, summer calf survival was more than twice as important in driving λ (summer: β = 0.23, SE = 0.01, R^2 = 0.23; winter: β = 0.15, SE = 0.01, R^2 = 0.11) as winter calf survival.

Har**vest management scenarios**

From our IPM, we estimated that the average juvenile to adult female ratio during the 2010–2015 sampling period was 20 yearlings : 100 adult females in the West Fork and 25 yearlings : 100 adult females in the East Fork. These age ratios corresponded to mean observed calf survival rates of 0.31 (SD = 0.04) in the East Fork and 0.30 (SD = 0.04) in the West Fork. Adult female survival averaged 0.94 (SD = 0.02) in the East Fork and 0.93 (SD = 0.02) in the West Fork. Pregnancy rate averaged 0.85 (SD = 0.05) in the East Fork and 0.74 (SD = 0.06) in the West Fork. The average population size over the observation period was 738 yearlings and 3,034 adult female elk in the East Fork and 93 yearlings and 463 adult female elk in the West Fork. Population size ranged from a low of 3,606 (SD = 122) in 2010 to a high of 4,349 (SD = 204) in 2016 in the East Fork, and similarly, ranged from a low of 575 (SD = 32) in 2010 to a high of 683 (SD = 36) in 2015 in the West Fork. Survival and pregnancy rates reported here differ slightly than those reported in previous sections of this report because the estimates are based on multiple sources of data (i.e., jointly estimated with count, pregnancy and telemetry data), and because Bayesian models inherently incorporate stochasticity in parameter estimates.

We used these mean vital rates and population sizes to calculate the calf survival rates needed to achieve age ratio objectives in the two study areas. We estimated that elk calf survival would have to be 0.31 to have 25 yearlings : 100 adult females and 0.50 to have 40 yearlings : 100 adult female elk in the East Fork area. In the West Fork, elk calf survival would have to be 0.35 to have 25 yearlings : 100 adult females and 0.55 to have 40 yearlings : 100 adult females. We estimated that yearling per adult female elk would increase by 1 for every 1.25% increase in calf survival for both East Fork and West Fork populations.

For the East Fork population, all scenarios resulted in mean projected population sizes that were above the maximum population objective used in simulations (*n* = 4,560; Table 8.1

and Table 8.2); however, the lower 95% credible intervals of most simulations were within the population size objective. For the East Fork elk population, mean population growth rates (λ) over the prediction interval decreased by about 1–2% on average for every additional 100 antlerless elk harvested, and ranged from λ = 1.02 to λ = 1.13 under simulations with the lower (i.e., 0.25) and higher (i.e., 0.50) calf survival rates.

In simulations of the West Fork elk population, none of the simulations of mean projected population sizes were above the minimum population objective used in simulations (*n* = 1,120; Table 8.3 and Table 8.4), although upper 95% credible intervals of most simulations were in population size objectives when harvest was low (i.e., 0 – 25 antlerless elk). For the West Fork population, mean λ's over the prediction interval decreased by about 3% on average for every additional 25 antlerless elk. Population growth rates ranged from λ = 1.02 to λ = 1.13 under simulations with the lowest (i.e., 0.35) and highest (i.e., 0.55) calf survival rates. Consistently, projected yearling : 100 adult females ratios slightly increased with increasing adult female harvest in the West Fork (1 yearling: 100 adult female for 25 antlerless elk), reflecting the fact that increased adult female harvest can increase age ratios. However, larger population sizes in the East Fork buffered yearling: 100 adult female ratios from increases due to antlerless harvest. Precision of projected yearling: 100 adult female ratios tended to decrease (i.e., posterior standard deviations increased) when vital rates were simulated rather than projected from the observed means and variances, which may have resulted from increased uncertainty from using random error terms for vital rates to share information across years.

Table 8.1 Projections of population size (N) and yearling : 100 adult female ratios (Yrl : 100 AF) from Bayesian integrated population model that simulated harvests of 100, 200, and 300 antlerless elk and a calf survival rate of 0.31 (i.e., 25 yearlings : 100 adult female elk) for the East Fork population.

	100 Antlerless				200 Antlerless				300 Antlerless			
Year	$\widehat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\widehat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\widehat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI
2016	4,695	655	26	8	4,599	649	27	8	4,510	657	28	9
2017	4,970	847	26	8	4,760	840	26	8	4,555	837	27	8
2018	5,277	1,069	26	8	4,938	1,042	26	8	4,601	1,018	27	8
2019	5,617	1,305	26	8	5,127	1,274	26	8	4,645	1,221	27	8
2020	5,990	1,572	26	8	5,334	1,523	26	8	4,688	1,441	27	8

Table 8.2 Projections of population size (N) and yearling : 100 adult female ratios (Yrl : 100 AF) from Bayesian integrated population model that simulated harvests of 100, 200, and 300 antlerless elk and a calf survival rate of 0.50 (i.e., 40 yearlings: 100 adult female elk) for the East Fork population.

	100 Antlerless				200 Antlerless				300 Antlerless			
Year	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI
2016	5,459	1,375	41	31	5,355	1,385	42	31	5,263	1,370	43	32
2017	6,212	1,830	29	29	5,964	1,796	39	29	5,761	1,780	40	29
2018	7,097	2,382	39	29	6,689	2,276	40	29	6,335	2,236	40	30
2019	8,113	2,954	39	28	7,505	2,814	39	29	6,964	2,795	40	30
2020	9,264	3,627	39	29	8,427	3,460	39	29	7,670	3,379	40	30

Table 8.3. Projections of population size (N) and yearling: 100 adult female ratios (Yrl: 100 AF) from Bayesian integrated population model that simulated harvests of 0, 25, 50 and 75 antlerless elk and a calf survival rate of 0.35 (i.e., 25 yearlings : 100 adult female elk) for the West Fork population.

	0 Antlerless				25 Antlerless				50 Antlerless				75 Antlerless			
Year	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI
2016	787	149	26	23	765	148	27	24	743	150	28	25	720	148	29	25
2017	837	202	26	22	789	204	27	24	739	193	28	24	688	193	30	26
2018	892	260	26	23	812	247	27	24	732	240	28	25	650	230	30	26
2019	952	325	26	23	837	292	27	24	722	276	28	25	606	261	31	27
2020	1,013	379	26	23	861	344	27	24	710	317	29	25	555	293	32	28

Table 8.4. Projections of population size (N) and yearling : 100 adult female ratios (Yrl : 100 AF) from Bayesian integrated population model that simulated harvests of 0, 25, 50 and 75 antlerless elk and a calf survival rate of 0.55 (i.e., 40 yearlings : 100 adult female elk) for the West Fork population.

	0 Antlerless				25 Antlerless				50 Antlerless				75 Antlerless			
Year	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI	$\hat{N}$	±95% CRI	Yrl: 100 AF	±95% CRI
2016	852	161	37	26	833	166	39	27	809	165	41	29	785	163	43	30
2017	962	231	36	25	911	224	37	26	857	218	39	27	803	210	41	28
2018	1,087	307	36	25	1,000	292	38	26	911	283	39	27	821	266	42	29
2019	1,227	391	36	25	1,098	360	38	25	965	346	39	27	832	319	41	29
2020	1,384	481	36	25	1,205	448	37	26	1,021	417	39	27	841	388	42	29

Section 9 – Conclusions and Management Applications

We found that both habitat and predation affected elk population growth rates in the southern Bitterroot Valley, but the relative strength of top-down and bottom-up effects differed between the East Fork and West Fork populations. Elk population growth rate was most sensitive to changes in adult survival, indicating that increasing antlerless harvest and reducing adult survival rate would strongly affect population growth rate. Additionally, predation of calf elk by mountain lions had a strong effect on elk population growth rate. Our integrated population model provides a tool for managers to simulate the effects of reducing adult survival through increasing antlerless harvest or increasing calf survival through reductions in predation on elk population growth rates. The population modeling tool allows managers to determine what levels of adult survival, calf survival, and pregnancy rates are needed to achieve and maintain a target population size, and will assist managers in developing management regulations to achieve that goal.

Based on the observed vital rate data and population modeling results, we recommend managers trying to increase elk population growth rate employ strategies to increase calf elk survival. Calf survival rates ranged annually from 0.32 – 0.45, and the annual variation in calf survival rate was primarily due to differences in overwinter survival (0.55 – 0.85). West Fork winter calf survival was especially low and variable, ranging annually from 0.40 – 1.00. The level of calf elk predation suggests that management strategies aimed at reducing carnivore densities may result in increasing elk calf survival. Overall, the annual rate of predation-caused mortality for elk calves was 0.28 (95% CI = 0.22, 0.35), and mountain lion caused mortality (CIF = 0.20, 95% CI = 0.14, 0.27) dominated over wolf caused mortality (CIF = 0.03, 95% CI = 0.01, 0.07) and black bear caused mortality (CIF = 0.05, 95% CI = 0.02, 0.10). Given the strong effect of mountain lion predation on elk calf survival and the strong effect of calf survival on elk population growth rate, we predict that reducing the level of mountain lion predation on calf elk will result in increased calf survival and a higher elk population growth rate. However, the efficacy of reducing carnivore populations in efforts to increase calf elk survival is unknown. Additionally, the efficacy of enacting carnivore management in low productivity environments may be more limited as bottom-up nutritional influences also affect population growth rate.

West Fork summer range forage quality limited elk pregnancy rate and calf production, and these nutritional limitations may predispose this elk population to be more sensitive to the effects of harvest, predation, weather or other factors. The low elk body condition and pregnancy rates in the West Fork may indicate insufficient summer forage quality or quantity to support increasing elk populations in this area. However, the recent fire activity in the upper

West Fork area may result in increased forage quality, thus reducing the effects of these nutritional limitations. Maintaining a mosaic of fire history and distribution will likely benefit most ungulate species, as composition-induced changes in forage quality because of fire were the biggest driver of the bottom-up differences we observed.

Declines in the southern Bitterroot elk population and recruitment prompted managers to reduce hunter opportunity and harvest levels for antlered and antlerless elk in portions of the Bitterroot Valley. Managers are now trying to restore elk populations to levels that allow for increased hunter opportunity. To achieve goals of both allowing for hunter opportunity and restoring elk populations to objective levels, managers need to understand not only the factors that affect population dynamics, but also which of these factors are within management control and to what extent. Management actions designed to address a single factor affecting elk population growth rates (i.e., pregnancy rates, adult survival, or juvenile survival) may be insufficient in areas such as the West Fork where each of these rates is low. Instead, an integrated management approach where antlerless harvest remains low, carnivore densities are reduced, and efforts are made to improve habitat quality and quantity, would likely be a more effective way to increase elk population growth rate and achieve and maintain a larger elk population size.

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