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LINKING THE EFFECTS OF RISK FACTORS ON ANNUAL CALF SURVIVAL TO ELK POPULATION DYNAMICS IN THE BITTERROOT VALLEY, MONTANA

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LINKING THE EFFECTS OF RISK FACTORS ON ANNUAL CALF SURVIVAL TO ELK POPULATION DYNAMICS IN THE BITTERROOT VALLEY, MONTANA

By

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B.S. University of Montana, Missoula, Montana, 2009

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Linking the Effects of Risk Factors on Annual Calf Survival to Elk Population Dynamics in the Bitterroot Valley, Montana

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ABSTRACT

The recolonization of gray wolves (*Canis lupus*) in multiple carnivore systems has been correlated with declining recruitment of juvenile ungulates, but the importance of wolves relative to other established carnivores is uncertain. The realized effect of carnivores may depend on compensation from forage and winter weather severity, which may mediate juvenile vulnerability to predation. Also, in high predation systems, the importance of juvenile recruitment may be reduced for ungulate population dynamics. We first tested for the effects of risk factors on annual elk (*Cervus elaphus*) calf survival and estimated cause-specific mortality rates. Secondly, we investigated the relative importance of different vital rates, including juvenile survival, on elk population dynamics using Bayesian integrated population modeling. Summer survival probability was less variable and averaged 0.55 (95% CI = 0.47, 0.63), while winter survival varied significantly across study years (*P* = 0.002) and averaged 0.73 (95% CI = 0.64, 0.81). Mountain lions (*Felis concolor*) dominated elk calf mortality in summer and winter, with estimated cause-specific mortality rates of 0.14 (95% CI = 0.09, 0.20) and 0.12 (95% CI = 0.07, 0.18), respectively, compared to only 0.01 (95% CI = 0.002, 0.05) and 0.03 (95% CI = 0.01, 0.07) caused by wolves, demonstrating that despite wolves recolonizing in this system, mountain lions were the leading cause of mortality. We found that elk calf survival increased in areas of high forage biomass in summer, and decreased strongly with increasing predation risk from mountain lions, but only in winter (Hazard Ratio = 2.84, 95% CI = 1.37, 5.88, *P* = 0.005). We found no evidence that forage availability or winter weather severity mediated vulnerability to mountain lion predation risk, indicating that the effects of mountain lion predation were relatively constant. Bayesian integrated population models revealed that on average adult female survival explained more of the variation in population growth rate than elk calf survival, while pregnancy rates were less important for population growth. By decomposing annual calf survival, we found that the summer and winter survival periods were nearly equivalent in importance for elk population dynamics in one population. The importance of carnivores for juvenile ungulate recruitment varies across ecological systems depending on relative carnivore densities, and mountain lions may be the most important carnivore for ungulates in more settings than anticipated. Given the high importance of adult female survival for elk population growth rates in systems with established carnivore populations, managers may need to reduce adult female harvest as carnivores recolonize, especially in areas with less productive habitat for elk.
ACKNOWLEDGEMENTS

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# TABLE OF CONTENTS

ABSTRACT ........................................................................................................ iii
ACKNOWLEDGEMENTS ................................................................................ iv
TABLE OF CONTENTS .................................................................................. vii
LIST OF TABLES ............................................................................................... ix
LIST OF FIGURES ........................................................................................... xii

CHAPTER 1. INTRODUCTION AND OVERVIEW ............................................. 1
  THESIS FORMAT .......................................................................................... 5
  LITERATURE CITED ..................................................................................... 5
  FIGURES .......................................................................................................... 9

CHAPTER 2. LANDSCAPE-LEVEL EFFECTS OF RISK FACTORS FOR ANNUAL
ELK CALF SURVIVAL IN A MULTIPLE CARNIVORE SYSTEM ..................... 11
  KEYWORDS ................................................................................................. 11
  INTRODUCTION ......................................................................................... 11
  STUDY AREA .............................................................................................. 14
  METHODS ..................................................................................................... 15
    Calf capture, monitoring, and mortality investigation ................................... 15
    Calf survival and risk factors ....................................................................... 16
    Statistical Analysis ....................................................................................... 20
    Cause-specific mortality ............................................................................. 22
  RESULTS ....................................................................................................... 23
    Elk calf captures, birth attributes, and relocations ...................................... 23
    Covariate correlations ............................................................................... 25
    Elk calf survival modeling ......................................................................... 25
    Cause-specific mortality ............................................................................. 28
  DISCUSSION ................................................................................................. 30
  MANAGEMENT IMPLICATIONS .................................................................... 37
  LITERATURE CITED ..................................................................................... 37
  TABLES .......................................................................................................... 47
  FIGURES .......................................................................................................... 54
APPENDIX 2. .................................................................................................... 58
  2-A. Competing risk analysis of tag loss ....................................................... 58
  2-B. Elk calf relocation summary ................................................................... 63
  2-C. Estimating elk calf age at capture, birth mass, and birth date ............... 65
  2-D. Wolf resource selection functions ....................................................... 72
  2-E. R code for cumulative incidence functions ......................................... 82

CHAPTER 3. ASSESSING THE IMPORTANCE OF DEMOGRAPHIC PARAMETERS
FOR POPULATION DYNAMICS USING BAYESIAN INTEGRATED POPULATION
MODELING ....................................................................................................... 84
  KEYWORDS ................................................................................................. 84
  INTRODUCTION .......................................................................................... 84
  METHODS ..................................................................................................... 88
1. Elk populations ........................................................................................................... 88
2. Data sources .................................................................................................................. 89
3. Integrated population modeling approach ..................................................................... 90
4. Model formulation and parameterization ..................................................................... 91
5. Bayesian life-stage simulation analysis ......................................................................... 96
6. Model implementation ................................................................................................. 97

RESULTS .......................................................................................................................... 98
1. Parameter estimates ..................................................................................................... 98
2. Sensitivity analysis ....................................................................................................... 100

DISCUSSION .................................................................................................................... 102

LITERATURE CITED ....................................................................................................... 111

TABLES ............................................................................................................................. 122

FIGURES .......................................................................................................................... 125

APPENDIX 3 ....................................................................................................................... 131
3-A. JAGS code for base integrated population model ..................................................... 131
3-B. JAGS code for sensitivity integrated population model ........................................... 134
3-C. Bayesian life-stage simulation analysis with count data ........................................... 139
3-D. Bayesian life-stage simulation analysis based on Raithel et al (2007) ..................... 142
3-E. Harvest and vital rate simulations using integrated population models ................. 144
3-F. JAGS code for projection integrated population model ......................................... 171
LIST OF TABLES

Table 2-1. Number of elk calves captured by period, capture area, and sex in the southern Bitterroot Valley, MT, USA, 2011–2014. .................................47

Table 2-2. Kaplan-Meier survival estimates (S) in summer and winter with 95% log-log confidence intervals (CI) and minimum and maximum number of individuals at risk (n) for elk calves by study area and overall in the southern Bitterroot Valley, Montana, USA, 2011–2014. 48

Table 2-3 Sequential base model selection of A-G proportional hazards models showing the number of model parameters (k), model deviance (Dev), ΔAICc, and model weights (w) for winter elk calf survival in the southern Bitterroot Valley, Montana, USA, 2011–2014. The nested model risk factors were sequentially removed until the ΔAICc increased with variable removal. Year is abbreviated (Yr)...........................49

Table 2-4. Model-averaged coefficients, unconditional standard errors, and 95% confidence intervals for Andersen-Gill proportional hazards models that include the effects of sex (male as reference group), forage availability (F), mountain lion (L) and wolf predation risk (W), and the interaction between predation risk and forage availability on summer survival of for elk calves in the southern Bitterroot Valley, Montana, USA, 2011–2014. ................................................50

Table 2-5. Sequential base model selection of A-G proportional hazards models showing the number of model parameters (k), model deviance (Dev), ΔAICc, and model weights (w) for winter elk calf survival in the southern Bitterroot Valley, Montana, USA, 2011–2014. The nested
model risk covariates and factors were sequentially removed until the ΔAICc increased with variable removal. Abbreviations are estimated birth date (Date), birth mass (Mass), and year (Yr).

Table 2-6. Top two winter Andersen-Gill proportional hazards models showing number of model parameters (k), model deviance (Dev), ΔAICc, model weights (w), standardized coefficient estimates, and 95% confidence intervals (CI) for hazard ratios for elk calves in the southern Bitterroot Valley, Montana, USA, 2011–2014. The final model consisted of only year (Yr; reference = 2011–12) and mountain lion predation risk (L), while the next closest model included winter severity index (WSI).

Table 2-7. Cumulative incidence functions (CIF) in summer and winter for 5 mortality sources (k) with 95% log-log confidence intervals (CI) and raw counts (n) for 110 confirmed elk calf mortalities calves by study area and overall in the southern Bitterroot Valley, Montana, USA, 2011–2014. 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.

Table 3-1. Number of years (n) of aerial count, telemetry, and pregnancy data for elk populations in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. The minimum and maximum numbers of calves and adult females that were radio-marked for telemetry and pregnancy testing are given in parentheses.
Table 3-2. Estimates of calf survival ($\Phi_c$), adult female survival ($\Phi_{af}$) and pregnancy rates ($P_{af}$), and population growth rates ($\lambda_t$) with posterior standard deviations (in parentheses) for elk populations in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Estimates are given by population for different models with likelihoods based on aerial count data only, vital rate data only (survival and pregnancy), and all data integrated into a single model.

Table 3-3. Mean estimates and analytical component elasticities for annual elk calf survival ($\Phi_c$), summer and winter calf survival, adult female survival ($\Phi_{af}$) and pregnancy rate ($P_{af}$) with posterior standard deviations (SD) in Bayesian Life-stage Simulation Analysis for elk populations in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Coefficient estimates from simple linear regressions of asymptotic population growth rates ($\lambda_{asy}$) against each vital rate are given with standard errors (SE). The model intercept ($\beta_0$) provides an estimate of $\lambda$ when the vital rate is zero, and the slope ($\beta_1$) predicts the increase in $\lambda$ with a one unit increase in each vital rate. The coefficient of determination ($R^2$) estimates the proportion of the variation in $\lambda$ explained by each vital rate.
LIST OF FIGURES

Figure 1-1. Population trend counts (left) and number of yearlings per 100 adult females (right) from fixed-wing surveys in the southern Bitterroot Valley, Montana, USA, 2002–2010. Note that the trend counts and yearling/100 adult female ratios reflect the study area boundary changes that occurred later in 2013 (see also Figure 3-E.1 on page 161). .................................................................9

Figure 1-2. Annual minimum wolf count (lines) and wolf harvest (bars) in the East Fork and West fork study areas in the southern Bitterroot Valley, Montana, USA, 2000–2013...............10

Figure 2-1. Predicted total herbaceous biomass (kg/ha) in the study area, which included the East and West Forks of the Bitterroot River drainage and the northern Bighole Valley located in west-central Montana, USA. The study area extended into the Bighole to include summer ranges used by migratory East Fork elk. The East Fork and Bighole areas are dominated by agriculture and are mainly open grasslands, while the West Fork area is more forested, rugged terrain..............54

Figure 2-2. Predicted relocation probability for mountain lions based on resource selection functions (RSF) across the East Fork and West Fork study areas in the southern Bitterroot Valley and northern Bighole Valley, MT. Season-specific mountain lion RSFs were used to estimate summer (top) and winter (bottom) mountain lion predation risk exposure for elk calves. Elk calf locations were buffered with a 500 m radius and are shown as red circles.............................................55

Figure 2-3. Kaplan-Meier (KM) annual survivorship curves for elk calves for 3 biological years in the southern Bitterroot Valley, Montana, USA, 2011–2014. The KM survivorship graph shows
that interannual variation in elk calf survival increases after about 90 days since birth (vertical dotted line). 

Figure 2-4. Smoothed instantaneous mortality hazards (i.e. mortality rate per day) for elk calves for different mortality sources in the southern Bitterroot Valley, Montana, USA, 2011–2014. 

Figure 3-1. Directed acyclic graph of the integrated population model structure used to make joint inference into demographic parameters. The arrows show the direction of stochastic dependencies between estimated parameters (circles) and data (boxes) in the model. The nodes in the model are: survival data ($Y_S$); pregnancy data ($Y_P$); aerial count data for yearlings ($C_y$) and adult females ($C_{af}$); variance of yearling ($\sigma_{cy}^2$) and adult female ($\sigma_{caf}^2$) count data; calf survival ($\Phi_c$); Weibull shape ($p$) and hazard ($h$); adult female survival ($\Phi_{af}$) and pregnancy rate ($P_{af}$); and population size of yearlings ($N_y$) and adult females ($N_{af}$). Prior distributions and covariates are not included in the graph. 

Figure 3-2. Elk population size (combined yearling and adult female) in the East Fork (left) and West Fork (right) study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Blue lines and gray shading represent the mean and 95% credible intervals of population sizes in Bayesian integrated population models and black lines represent raw aerial count data. 

Figure 3-3. Relative standard deviations calculated from residuals of parameter estimates from models using count (blue) and vital rate data only (green) compared to models integrating all data (compared to the baseline) for elk populations in the East Fork (left) and West Fork (right)
study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Relative standard deviations are compared to the combined (vital + count) models; for example, the SD in calf survival estimated from the count only model was 0.14 higher than the count + vital rate model (reference category) in the East Fork.

Figure 3-4. Elk calf recruitment measured as the number of yearlings (~0.9 months old) per 100 adult female ratios in the East Fork (left) and West Fork (right) study areas in the southern Bitterroot Valley, Montana, USA, biological years 2010–2014. Lines are shown for age ratios based on raw aerial count data (Raw), models including only count data (Count), models including only vital rate data (Vital), and models integrating both count and vital rate data (All).

Figure 3-5. Scatterplots of mean vital rate and asymptotic population growth rate ($\lambda_{asy}$) 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 elk calf survival, and adult female survival and pregnancy rate with solid lines for the East Fork (EF) and broken lines for the West Fork (WF).

Figure 3-6. Scatterplots of mean vital rate and asymptotic population growth rate ($\lambda_{asy}$) 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 (EF) and broken lines for the West Fork (WF).
CHAPTER 1. INTRODUCTION AND OVERVIEW

For nearly 70 years, wildlife managers and the hunting public were able to harvest ungulates with minimal concern for large carnivores, which were largely extirpated or reduced in abundance throughout much of their historic range in the lower 48 United States. However, over the last two decades, the expansion of grizzly bear (*Ursus arctos*), mountain lion (*Puma concolor*), and gray wolf (*Canis lupus*) populations throughout portions of western North America has coincided with declines in recruitment and abundance in some elk (*Cervus elaphus*) populations, creating a highly polarized debate between public sectors over large carnivore management. Although recent studies have highlighted the importance of ursid (Barber-Meyer et al. 2008, White et al. 2010) and mountain lion predation (Rearden 2005, Johnson et al. 2013) for elk calf recruitment, the public arena continues to focus mainly on the potential impacts of one recolonizing carnivore—the wolf (Treves et al 2013). Along with the public’s obsession for wolves, strong effects of wolf predation on elk populations were documented in the Greater Yellowstone Ecosystem (Hamlin and Cunningham 2009) and in the Ya Ha Tinda near Banff National Park (Hebblewhite and Merrill 2011). Accordingly, wildlife managers and the scientific community in general expected recolonizing wolves to have strong effects on elk productivity outside of these systems as well. However, despite the strong potential for wolves to alter elk populations dynamics, many of the elk populations experiencing wolf recolonization already had established large carnivore populations, and besides these predation effects, declines in elk productivity may also have resulted from changes in forage or habitat-related factors (Cook et al. 2004; White et al. 2010; Middleton et al. 2013).
Regardless of the myriad of potential causes of declines in elk productivity, wildlife managers are generally constrained to increasing ungulate populations by reducing harvest of ungulates, manipulating large carnivore populations through harvest (Hayes et al. 2003; Boertje et al. 2010; Hurley et al. 2011), and/or manipulating elk nutritional status through habitat improvements (Bishop et al. 2009). Therefore, understanding the relative importance of these top-down and bottom-up factors in driving elk population dynamics is a critical first step in guiding efforts to reverse population declines. From an intuitive standpoint, research has shown that predation is most intense for juvenile ungulates (Linnell et al. 1995), and thus, increases in large carnivore abundance may be a primary driver of recent declines in elk productivity. However, the effect of predation has also been shown to depend on forage conditions (i.e., quality and quantity), which may mediate vulnerability to predation in juvenile ungulates (Melis et al. 2009, Middleton et al. 2013). With these potentially interacting top-down and bottom-up factors to consider, managers generally need information on both predation (i.e., cause-specific mortality) and nutritional factors (i.e., forage, body condition) before implementing measures to manipulate ungulate populations towards objective.

Similar to other harvested ungulate populations across the West, elk populations in the southern Bitterroot Valley of west-central Montana have also experienced recent declines in juvenile recruitment coincident with the recolonization of wolves. After a 35-year period of steady increase in population trend counts recorded annually by Montana Fish, Wildlife and Parks (MFWP), elk populations reached a peak in 2005–2006 at around 5,500 elk including both the East Fork (EF) and West Fork (WF) elk populations in the southern Bitterroot Valley (Fig. 1-1). In response to increasing elk populations prior to 2005–2006, managers applied a more liberal elk harvest to bring elk populations towards management objective. However, elk calf
recruitment and population trend counts continued to decline after increasing harvest, especially in the WF, and by 2009, recruitment had reached a valley-wide historic low of 14 yearlings/100 adult females and overall trend counts in the valley had declined by over 25% (see Fig. 1-1). Despite efforts to reverse declines by restricting elk harvest, elk recruitment and trend counts did not rebound, and elk population growth may have been limited by continued low calf recruitment. With restricted elk harvest and overall low elk productivity in this historically premier elk hunting area, the public quickly became focused on recolonizing wolves as the cause of elk declines, and shortly after this time a headline from a local newspaper read, “What’s eating these elk? Folks in the Bitterroot know the answer is wolves. State biologists aren’t so sure (Sakariassen 2012).”

Along with moderately dense populations of black bears ([*Ursus americanus*]; estimates ranged from 10–15 bears/100-km²; Mace and Chilton-Radant 2011), wolves recolonized the southern Bitterroot Valley in the late 1990s and have been monitored on an annual basis by MFWP. After a small founder population recolonized the area (see Fig. 1-2), wolves continued to expand their populations and reached densities in the range of 10–20 wolves/1000-km² (MFWP, unpublished data). While the expansion of wolf populations in the valley appeared to be correlated with the decline of southern Bitterroot elk populations, mountain lions received little attention. This is also despite a decade-long period of limited female mountain lion harvest beginning in 2001 that may have resulted in higher densities of mountain lions during the time wolves were recolonizing the area. Besides the strong potential for increasing large carnivore densities to limit elk population growth, recent changes in habitat such as a 70% decrease of timber harvest on public lands since 1980 (U.S. Forest Service 2013b) and several large-scale wildfires may have altered forage conditions for elk in the southern Bitterroot Valley. Without
explicit information about the drivers of fluctuations in elk populations that were correlated with multiple landscape-level factors, wildlife managers were unable to provide the public with concrete answers and generate a science-driven, defensible strategy to reverse declines in elk productivity.

However, in the winter of 2010–11, MFWP and the University of Montana, along with many committed stakeholders and volunteers, initiated the Bitterroot Elk Ecology Project as a three-year study to investigate the importance of top-down and bottom-up factors affecting elk population dynamics in the southern Bitterroot Valley, MT. The study was intended to reduce uncertainty in managing carnivore and elk populations in the region by providing the best possible science. Besides the annual monitoring of elk population trends conducted by MFWP, the project collected data on elk calf and adult female survival, pregnancy rates, habitat use and selection, habitat productivity, and large carnivore densities.

I used these data collected by our research team to address a subset of the questions for this project that I developed into two thesis chapters. My primary thesis Chapters 2 and 3 represent a two-stage approach to understanding the population dynamics of southern Bitterroot elk. First, in Chapter 2, I investigated cause-specific mortality and risk factors driving annual elk calf survival. Then in Chapter 3, I used a Bayesian integrated population modeling framework to estimate demographic rates, determine the relative importance of vital rates for overall elk population dynamics, and simulate elk population dynamics under different harvest management scenarios (Appendix 3-E). For the annual elk calf survival analysis, I used landscape-level spatial layers of forage availability and wolf predation risk that were developed by Kelly Proffitt and Mark Hebblewhite, and mountain lion predation risk layers that were authored by Hugh Robinson. I provide basic descriptions of the wolf RSF analysis in Appendix 2-D of the thesis,
which was provided by the previously mentioned authors. Additional details about the forage and mountain lion predation risk models can be found in Proffitt et al. (2015)—a study of the landscape-level effects of forage on elk nutritional ecology, and Robinson et al. (2015)—a statewide estimation of mountain lion populations in Montana based on resource selection function (RSF) models.

**THESIS FORMAT**

For consistency, the following thesis chapters are formatted for Journal of Wildlife Management, and both Chapters 2 and 3 are in review by specific peer-reviewed scientific journals. Currently, Chapter 2 is in review by Journal of Wildlife Management, while a reformatted version of Chapter 3 is in review by Ecological Applications. The following chapters represent the combined efforts of resource managers, stakeholders, researchers, field technicians, and individuals in the community that came together to initiate and follow through on this project, and it is only in this context that I refer to these manuscripts as “my” thesis work; therefore, I use the collective “we” throughout the Thesis.

**LITERATURE CITED**


Mace, R. D., and T. Chilton-Radant. 2011. Black bear harvest, research and management in Montana, MT Fish, Wildlife and Parks, Wildlife Division Helena, MT, USA.


Sakariassen, A. 2012. What’s eating these elk? Folks in the Bitterroot know the answer is wolves. State Biologists aren’t so sure. Missoula Independent. 26 January 2012; Features.


FIGURES

Figure 1-1. Population trend counts (left) and number of yearlings per 100 adult females (right) from fixed-wing surveys in the southern Bitterroot Valley, Montana, USA, 2002–2010. Note that the trend counts and yearling/100 adult female ratios reflect the study area boundary changes that occurred later in 2013 (see also Figure 3-E.1 on page 161).
Figure 1-2. Annual minimum wolf count (lines) and wolf harvest (bars) in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA, 2000–2013.
CHAPTER 2. LANDSCAPE-LEVEL EFFECTS OF RISK FACTORS FOR ANNUAL ELK CALF SURVIVAL IN A MULTIPLE CARNIVORE SYSTEM


INTRODUCTION

The expansion of large carnivores in North America including gray wolves (*Canis lupus*; Pletscher et al. 1997), mountain lions (*Puma concolor*; Riley and Malecki 2001) and grizzly bears (*Ursus arctos*; Kendall et al. 2009), has the potential to dramatically alter the population dynamics of their primary ungulate prey species. Carnivore effects on juvenile survival may be particularly important to understand because the high variability of juvenile survival may strongly influence ungulate population trajectories (Gaillard 1998, 2000; Raithel et al. 2007) and because predation mortality is expected to be most intense for juveniles (Linnell et al. 1995). 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 carnivore and ungulate population objectives.

The effect of carnivore mortality 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 recolonizing 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 analysis found that mountain lion-caused mortality on elk calves declined significantly in systems with sympatric gray wolves (Griffin et al. 2011), suggesting that wolves may have important indirect effects on juvenile survival through interspecific competition with other carnivores. Thus, it will be important to understand cause-specific mortality by different carnivores in recovering predator-prey systems.

Besides the complexity of carnivores recolonizing into multiple carnivore systems, the primary productivity of the landscape may determine the extent that carnivore mortality is compensatory for juvenile ungulates with climatic or nutritional factors (Tveraa et al. 2003; Bishop et al. 2009). For example, Melis et al. (2009) found that carnivore presence only reduced roe deer (Capreolus capreolus) densities in areas of low primary productivity. These results are consistent with different Greater Yellowstone elk populations, where the impact of carnivores varied between systems (Garrott and White 2005), and interacted with drought conditions to contribute to population declines in migrant elk (Middleton et al. 2013). The availability of quality forage during spring and summer may limit maternal body condition of adult female ungulates (Cook et al. 2004), and as a result, juvenile ungulates may be born lighter or develop slower and remain in the vulnerable hiding phase for longer durations (Mathisen et al. 2003). This may cause prolonged exposure to predation during early development and increased exposure to additive mortality sources in summer (White et al. 2010). Although density-
dependence can also result in compensatory mortality from predation as populations approach nutritional carrying capacity (Bartmann et al. 1992; Pierce et al. 2012), high predation rates in multiple carnivore systems usually limit prey populations from experiencing density-dependent mortality (Messier 1994).

The importance of carnivore mortality for juvenile ungulates has largely focused on the neonatal survival period (Linnell et al. 1995; Griffin et al. 2011), but the winter period may supplant summer in importance due to greater interannual variation in winter survival compared to summer, which has been observed in mule deer (*Odocoileus hemionus*) populations (Hurley et al. 2011). Interannual variation in overwinter survival of juveniles may be amplified if the effect of carnivore mortality depends on winter weather severity, such that juvenile ungulates become more vulnerable to predation during winters with deeper snow and colder temperatures, resulting in higher levels of additive mortality (Smith et al. 2004; Hebblewhite 2005; Garrott et al. 2008). Alternatively, if carnivores prey mainly on weak individuals regardless of winter severity (Husseman et al. 2003), predation mortality may be more compensatory and have less influence on juvenile survival in winter. Recolonizing gray 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). Regardless of whether compensatory mortality is driven by forage or winter severity, both may ameliorate the effects of recolonizing carnivores on juvenile survival.

We used an observational, comparative approach to investigate the importance of multiple carnivore species for annual elk calf survival over a gradient of primary productivity (i.e., forage availability), and to test for compensation with forage availability and winter weather severity. In
summer, we predicted that elk calf mortality would become more compensatory with increasing forage availability, resulting in elk calf survival stabilizing in areas of high predation risk with high forage availability (Melis et al. 2009). If predation risk reduced elk calf survival regardless of forage availability, then this may indicate that predation mortality is more additive to elk calf survival in summer (Linnell et al. 1995). We also tested the winter severity-predation hypothesis, which predicts that predation mortality will interact with winter severity to increase mortality risk during winters with greater precipitation and colder temperatures, resulting in increasingly additive predation mortality. We expected that wolves would be an important mortality source for elk calves because wolf reestablishment coincided with declines in elk calf recruitment in our study area (see Chapter 1). However, if wolves had negligible effects on elk calf survival, then we predicted that black bear (*U. americanus*) predation would be the dominant mortality source on neonatal elk calves <30 days old, and similar to other systems without wolves, that mountain lion predation would dominate elk calf mortality (Johnson et al. 2013).

**STUDY AREA**

Our study area was located in the southern Bitterroot Valley in west-central Montana, USA, and included elk summer and winter ranges in two contrasting study areas, the East Fork (EF) and West Fork (WF) of the Bitterroot River drainage (Fig. 2-1). We predicted that heterogeneity in topography, land cover, and human land use would result in variable exposure to forage availability and predation risk for elk calves across the study area (Hebblewhite et al. 2005, Murray et al. 2010, White et al. 2010). The 1,719-km² EF area is dominated by agriculture and is mainly open grasslands composed of bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*). In contrast, the 1,437-km² WF area is more remote, rugged terrain that is mainly covered in forests of Ponderosa pine (*Pinus ponderosa*) and Douglas fir
(Pseudotsuga menziesii) at lower elevations, with Subalpine fir (Abies bifolia) and Lodgepole pine (Pinus contorta) at higher elevations. Elevation ranged from 1,000 m–3,100 m. The study area accumulates deep snow pack at high elevations and experiences variable and intense winter weather severity. Elk in the study area are sympatric with mule deer, whitetail deer (O. virginianus), bighorn sheep (Ovis canadensis) and moose (Alces alces), along with a suite of carnivores including wolves, coyotes (Canis latrans), mountain lions, and black bears.

METHODS

Calf Capture, Monitoring, and Mortality Investigation

For 3 biological years from 2011 to 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 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 2011–12 and in summer of 2012 –13 (see Appendix 2-A), we switched to an alternative ear tag transmitter in winter of 2012–13 and in 2013–14 that weighed only 1.5–1.8 g.
(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. We relocated individual calves a minimum of 2 times per month from aircraft using telemetry, and recorded location coordinates using a Global Positioning System (GPS) unit.

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 any 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 (RMRS), Missoula, MT. We classified calf fates as live, dead or unknown fate, and concluded calf monitoring on 30 May, 2014.

**Calf Survival and Risk Factors**
We used an age-based time scale for neonatal elk calves with birth date as the origin and left-truncated individuals based on their estimated age at capture, which allowed us to separate time-varying risk factors and age-cohort effects (Fieberg and DelGuidice 2009). Age at capture was estimated using morphometrics recorded at capture following Johnson (1951). The survival origin for calves caught during winter was 26 November and these individuals were left-truncated until capture. 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 considered internal and external risk factors to explain the overall risk of mortality to elk calves in summer (0–180 days) and winter (181–365 days). Internal risk factors were defined as effects that were due to biological characteristics of the calf such as sex, whereas external risk factors were defined as environmental or abiotic effects (e.g., forage or weather). For our summer analysis, we divided the time period into 3 intervals that coincided with different calf development phases (Barber-Meyer et al. 2008, White et al. 2010). Elk calves are most vulnerable to mortality during the early hiding phase (0–14 days), and become less vulnerable as they join nursery herds (15–28 days) and continue to grow larger over the latter part of the summer (>28 days). The winter period was divided into 6 monthly intervals with the number of calendar days in each month defining the time intervals. We grouped the months of November and December together since there was only a maximum of 5 days of risk in November.
**Internal risk factors.** — We regressed calf mass (nearest 0.01 kg) at capture on estimated age at capture separately for each sex, and used the estimated 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). In summer, we considered the effects of sex, birth mass, and birth date based on their on their importance in previous elk calf studies (Raithel 2005; Smith et al. 2006; Barber-Meyer et al. 2008). 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 our sample of 6-month-old calves. In both seasons we tested for study area and year (i.e., unexplained interannual variation) effects on elk calf survival.

**External risk factors.** — We used calf relocation data to estimate exposure to external risk factors that may explain elk calf survival. Following methods used by White et al. (2010), we buffered each calf location with a 500-m radius using the package *rgeos* in program R (Bivand and Rundel 2014), and then randomly sampled 100 points for each calf with replacement within buffered calf locations for each time interval. We projected all spatial layers into the North American Datum of 1983 (NAD83) and sampled the randomly generated points within each spatial layer in ArcGIS 10.2 using the RMRS Raster Utility (Hogland and Anderson 2014).

To model the effect spatial forage availability on elk calf survival, we used predictions of late-summer, total herbaceous (i.e., graminoid and forb) biomass (kg/ha) from a landscape-scale forage model (see Hebblewhite et al. 2008 for the general approach and Proffitt et al. 2015 for more details). We predicted total herbaceous biomass from a suite of landcover (e.g., shrubland, grassland) and topographical (e.g., elevation, slope) covariates derived from remote-sensing
methods (*sensu* Hebblewhite et al. 2008) that were modeled using generalized linear regression with log link function. The observed biomass values at ground-sampled plots were used as the response to predict biomass and were compared to predicted values to assess model accuracy. The final model predictions represented the availability of preferred herbaceous plant species for elk calves during the peak of the growing season.

In general, predation risk is strongly influenced by a predator’s resource selection and spatial distribution (Lima and Dill 1990; Hebblewhite et al. 2005). We used spatial models of predation risk for wolves and mountain lions derived from resource selection function (RSF; Manly et al. 2002) models developed specifically for our study area in summer and winter seasons. We did not include a black bear predation risk covariate because the spatial data was not available, and because bear predation risk was restricted to the first 30 days of life (see results). Wolf resource selection models were developed using study-area specific wolf GPS and VHF data collected from 2000–2013 on 20 wolves (Appendix 3-D). The top wolf models for summer and winter validated well against data withheld to measure predictive ability (k-folds cross validation $r_s = 0.77$). For mountain lion predation risk (Fig 2-2), a similar approach was used to validate a broader-scale mountain lion RSF previously developed by Robinson et al. (2015), and validated with study area-specific mountain lion harvest data. The top mountain lion RSF model validated well in our study area (see Robinson et al. 2015). Spatial wolf and mountain lion predation risk, as well as forage availability, were mapped in ArcGIS 10.2 at a 30-m² pixel resolution.

We used data from spatial climate models (PRISM Climate Group, Oregon State University, www.prism.oregonstate.edu, accessed 4 Apr 2015) to derive winter weather covariates. We used mean monthly-varying estimates of precipitation (mm of combined rain and snowmelt) and temperature ($\degree C$) from December to May to construct a winter severity index by multiplying
monthly precipitation by the negative monthly minimum temperature value. All winter weather covariates were mapped in ArcGIS 10.2 at a 4-km² pixel resolution.

**Statistical Analysis**

We tested for effects of risk factors and covariates on annual juvenile elk calf survival using continuous, time-to-event survival modeling. We used the Andersen-Gill (A-G) formulation of the Cox proportional hazards model (Cox 1972), based on counting process theory (Andersen et al. 1982; Therneau and Grambsch 2000), to examine the effect of time-varying covariates in summer and winter survival models. The A-G proportional hazards 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. The model is considered semi-parametric because parameters are estimated from a partial likelihood, but the baseline hazard cancels out, and thus no assumptions are made about the distribution of the baseline hazard.

The A-G model assumptions are that censoring is independent of survival (i.e., non-informative), individual fates are mutually independent, covariates vary linearly with the log hazard, and that hazards ratios between groups are proportional and remain constant over time for covariates (Hosmer et al. 2008). We used a correlation test between the scaled Schoenfeld residuals and log-transformed survival times to test for non-proportionality in PH models (Therneau and Grambsch 2000). Proportional hazards tests were conducted for all models but not reported unless we detected significant violations of the assumption. We also tested for model
outliers by assessing the scaled-score residuals for each subject with respect to the covariates as well as the likelihood displacement versus Martingale residuals (Hosmer et al. 2008).

We used a two-stage model selection approach based on Akaike's Information Criterion with an adjustment for sample size (AICc) to select the most parsimonious summer and winter elk calf survival models (Burnham and Anderson 2002). First, we used sequential model selection (Arnold 2010) to select base models for each season from a set of internal risk factors (see Internal Risk Factors above). After assessing the main effects of forage availability, mountain lion and wolf predation risk, and winter severity index for elk calf survival, we again used AICc to select the most parsimonious seasonal models from a candidate list that included a predation risk × forage availability interaction in summer and predation risk × weather interaction in winter. We constructed interactions terms for both mountain lion and wolf predation risk within each season. If forage availability interacted significantly with predation risk in summer to reduce mortality risk ($\beta < 0$), then this would indicate that high predation risk is compensated for by higher forage availability; alternatively, the effect of predation risk on elk calf survival may not depend on forage availability ($\beta = 0$). In winter, the effect of predation risk on elk calf survival may be enhanced by increasing winter weather severity ($\beta > 0$) or predation risk may have similar effects on calf survival regardless of winter severity ($\beta = 0$).

We restricted our model selection to a limited set of nested models based on these a priori hypotheses. We used model-averaged risk ratios and their unconditional standard errors if one model was not clearly supported within a given season (Burnham and Anderson 2002). Before assessing the effect of covariates and factors 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). For descriptive purposes, we estimated survivorship curves for categorical explanatory variables using the Generalized Kaplan-Meier (KM) estimator and compared their significance using log-rank tests (Pollock et al. 1989). We report 95% CIs for survival and hazard ratio estimates on the log hazard scale, which has improved coverage near the boundary (i.e., 0 or 1) compared to other methods that rely on truncation (Chourdhury 2002). 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 A-G model coefficients using the R base package survival (Therneau 2015) and conducted model selection using the R package MuMIn (Barton 2015).

Cause-Specific Mortality

We estimated 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 elk calf survival in the study system. 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. We categorized mortality sources for elk calves as bear; mountain lion; wolf; unknown; natural, non-predation; and human-related. For our computation of CIFs, we modified the SPLPLUS code provided in Heisey and Patterson (2006) to estimate confidence intervals (CI) on the log hazard scale (R code provided in Appendix 2-E). Smoothed functions of the instantaneous cause-specific hazards were estimated using the R package bshazard (Rebora et al. 2014).

We applied the data augmentation method in a competing risks framework to decompose summer and winter baseline hazards into their component cause-specific hazards (Lunn and
McNeil 1995), which allowed us to assess whether or not unknown mortalities were related to any known mortality sources (Murray et al. 2010). The method uses Cox regression (Cox 1972) to exploit the “additivity of hazards” by duplicating the data $k$ times based on the number of mortality sources and assigning an indicator variable to each mortality source (Lunn and McNeil 1995). We were primarily concerned with bear, mountain lion, and wolf mortality hazards in summer, and mountain lion and wolf mortality hazards in winter. Within each season, we conducted a univariate analysis for each primary mortality source with each mortality identified as the sole cause of death to evaluate whether 95% CI’s overlapped between risk sets. In this test, the amount of overlap in 95% CI’s for hazard ratios among known and unknown mortality sources indicates similarity among mortality hazards (see Murray et al. 2010).

RESULTS

Elk Calf Captures, Birth Attributes, and Relocations

We captured 226 neonatal and 60 6-month-old elk calves for a total of 286 calves throughout the EF and WF study areas. Sex ratio of captured elk calves was not different from parity at 0.9:1 females to males ($n = 285, P = 0.26$); we could not determine the sex of one calf. We consistently caught more calves in the EF than in the WF, which was expected since elk are more abundant in the EF study area (see Chapter 1, Fig. 1-1). 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 (see Table 2-1).

We estimated birth masses for 212 neonatal elk calves, and imputed the overall mean estimated birth mass ($\bar{x} = 14.13$ 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 \((F_{1, 207} = 4.93, P = 0.0275)\), 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 \((\bar{x} = 14.57 \text{ kg}, \ SD = 3.18, n = 118)\) had heavier \((0.99 \text{ kg})\) birth mass than females \((\bar{x} = 13.58 \text{ kg}, \ SD = 3.12, n = 94)\). Estimated birth masses did not vary by any 2-way interactions of sex, study area or year.

Male calves had slightly higher growth rates \((\text{male capture mass} = 14.56 \text{ kg} + 1.33 \times \text{age at capture})\) than females \((\text{female capture mass} = 13.58 \text{ kg} + 1.22 \times \text{age at capture})\). However, the interaction of sex and age at capture was not significant in our growth rate prediction model \((\beta_{\text{sex} \times \text{age at capture}} = 0.12, \ SE = 0.27, P = 0.67)\), 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 at capture.

We estimated ages of calves at capture from the Johnson method \(\text{(see Appendix 2-C)}\), which ranged from 0 to 6 days, with a mean of 3.73 days \((SD = 1.65, n = 226)\). 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 \((\text{median} = 30 \text{ May})\). 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 EF \((\bar{x}_{\text{female}} = 7.68, \ SD = 3.16; \bar{x}_{\text{male}} = 7.19, \ SD = 2.82)\), and male births occurring about 1 day later on average than females in the WF \((\bar{x}_{\text{female}} = 8.58, \ SD = 3.25; \bar{x}_{\text{male}} = 9.63, \ SD = 3.63)\). The interaction of study area and year resulted from calves being born about 3.5 days later on average in the WF \((\bar{x}_{2011} = 10.86, \ SD = 3.57)\) than in the EF \((\bar{x}_{2011} = 7.56, \ SD = 3.14)\) in 2011–12, with smaller differences in mean birth dates between study areas during 2012–13 \((\bar{x}_{\text{WF}} = 9.14, \ SD = 2.65; \bar{x}_{\text{EF}} = 8.21, \ SD = 3.08)\) and 2013–14 \((\bar{x}_{\text{WF}} = 8.04, \ SD = 3.64; \bar{x}_{\text{EF}} = 7.14, \ SD = 2.65)\).
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.

We used an average of 6.54 (SD = 3.26, \( n = 464 \)) and 8.36 (SD = 5.69, \( n = 1,045 \)) locations per calf in summer and winter seasons, respectively, to derive external risk covariates for our elk calf survival analysis (see Appendix 2-B for additional relocation summary).

**Covariate Correlations**

In summer, we found a very weak, positive correlation between estimated birth mass and birth date (\( R = 0.05 \)). Among our spatial covariates considered in the summer, we found a weak, positive association between wolf and mountain lion predation risk (\( R = 0.30 \)), and wolf and mountain lion predation risk had weak to moderate, negative correlations with forage availability (wolf: \( R = -0.12 \); mountain lion: \( R = -0.38 \)).

In winter, we found a moderate, negative correlation between mean monthly precipitation and minimum temperature (\( R = -0.42 \)), but these weather covariates were not correlated with mountain lion (precipitation: \( R = 0.07 \), temperature: \( R = -0.004 \)) or wolf predation risk (precipitation: \( R = 0.14 \), temperature: \( R = 0.09 \)). Mountain lion and wolf predation risk were strongly correlated in winter (\( R = 0.65 \), see Winter survival below).

**Elk Calf Survival Modeling**

*Summer survival.* — After removing two 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 right 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 (Appendix 2-A). The 90-day KM estimate of calf survival was 0.68 (95% CI = 0.59, 0.75, Table 2-2). The KM estimate of summer (180 day) survival rate was 0.55 (95% CI = 0.47, 0.63; Table 2-2). 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 (95% CI = 0.33, 0.59, Table 2). Elk calf survival was 0.59 (95% CI = 0.47, 0.69) in the EF compared to 0.49 (95% CI = 0.35, 0.61) in the WF area ($P = 0.13$). Elk calf survival rate did not vary significantly from year-to-year in the summer ($P = 0.12$; Fig. 3, Table 2-2).

With relatively constant summer survival rates across study areas and years, the most parsimonious summer base model included only sex and birth date (Table 2-3). 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 ($\chi^2_1 = 2.37, P = 0.12$), and thus, only sex was retained in the summer base model. Birth mass did not influence summer elk calf survival ($P = 0.68$).

The top summer model included the main effects of sex and forage availability, but we report model-averaged coefficient estimates because of model selection uncertainty (Table 2-4). After controlling for the effect of sex, our summer survival model revealed that forage availability had a strong, positive effect on elk calf survival (HR = 0.23, 95% CI = 0.08, 0.70, $P = 0.009$), with the unstandardized coefficient estimate predicting elk calf mortality risk to decrease by 11.4% for every 100 kg/ha increase in forage availability. However, the effect of forage availability was insignificant without including migratory calves that summered in the Bighole Valley ($P = 0.28$), where high calf survival may have also resulted from lower exposure to predation risk. We found no support for the main effects of wolf predation risk ($P = 0.65$) or the interaction of predation
risk and forage availability in summer (mountain lion × forage: $P = 0.17$; wolf × forage: $P = 0.15$). Although elk calf mortality risk increased marginally with greater mountain lion predation risk in summer ($HR = 1.55$, 95% CI = 0.94, 2.58, $P = 0.09$), the effect of mountain lion predation became insignificant ($P = 0.55$) by including forage availability in the model, reflecting a low level of collinearity from the negative correlation between the two covariates.

Winter survival. — After removing one calf from our winter survival dataset because of the uncertainty in the 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 survival (181–365 days) was 0.73 (95% CI = 0.64, 0.81, Table 2-2). Female calf survival was 0.78 (95% CI = 0.65, 0.87) compared to 0.69 (95% CI = 0.55, 0.79) for males in winter ($P = 0.24$). We found marginal evidence that elk calf survival was higher in the EF ($\hat{S} = 0.80$, 95% CI = 0.68, 0.88) compared to the WF ($\hat{S} = 0.65$, 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 ($P = 0.002$; see Table 2-2).

Although we found marginal evidence that winter survival rates varied by study area, the most parsimonious base model for winter calf survival included only a year effect (Table 2-5). Likelihood ratio tests confirmed that neither sex ($\chi^2_1 = 1.83$, $P = 0.18$) nor study area ($\chi^2_1 = 2.00$, $P = 0.16$) contributed significantly to the model. We did not consider wolf predation risk in winter because of the strong potential for collinearly with mountain lion risk ($R = 0.65$) and because wolf-caused mortality on elk calf calves was negligible in winter. The correlation
between mountain lion and wolf predation risk in winter is expected as ungulate prey become concentrated on winter range from deep snow and carnivore habitat selection overlaps (e.g., Atwood et al. 2009).

Although winter severity was included in a model within 2 ΔAICc units of the top model, the covariate added no explanatory power ($P = 0.96$) and only mountain lion risk and year effects were retained in the top models (Table 2-6). We report the two top models instead of model averaging because covariate effects were consistent. After controlling for the effect of year, our winter model revealed a strong, negative effect of mountain lion predation risk on winter elk calf survival ($HR = 2.84$, 95% CI = 1.37, 5.88, $P = 0.005$). We found no support for an interaction between mountain lion predation risk and winter severity ($P = 0.18$), and no effect of any winter weather covariates that we estimated (minimum temperature: $P = 0.46$; precipitation: $P = 0.33$). This lack of winter weather effects may have resulted from the coarse scale that winter weather covariates were derived at (4-km$^2$), or the effect of winter weather may operate at the population scale rather than at the individual level in affecting juvenile survival, which may explain that strong support for a year effect that accounts for unexplained interannual variation in survival.

**Cause-specific Mortality**

Upon detecting a mortality signal, we located and investigated the fate of each calf as soon as possible ($\bar{x} = 1.98$ [SD = 7.67] days in 2011–12; $\bar{x} = 1.06$ [SD = 4.71] days in 2012–13; and $\bar{x} = 0.74$ [SD = 1.72] days in 2013–14); 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 2-7).

Summer cause-specific mortality. — Elk calf mortality risk was highest over the first 30 days of life in summer when a large proportion (46.3%, Fig. 2-4) of summer mortality occurred. The mortality hazard from black bears exceeded mountain lions until around 20 days after birth (Fig. 2-4), with mountain lion predation dominating summer calf mortality thereafter. Mountain lion-caused mortality was relatively constant over the summer period (Fig. 2-4). The three 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 (see Table 2-7).

Our exploratory analysis of unknown mortality for elk calves in summer revealed distinct hazard ratios between bear, unknown and wolf-caused mortality (bear: HR = 0.90 (0.48, 1.66) (95% CI); unknown: HR = 2.65 (1.68, 4.18); wolf: HR = 0.20 (0.06, 0.63), while the mountain lion mortality hazard ratio was similar to unknown mortality and slightly overlapped bear mortality hazard (mountain lion: HR = 2.59 (1.63, 4.11)). This 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), and thus, we decided not to pool unknown mortality with any specific summer mortality source.
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 (Fig. 2-4). Mountain lions maintained a consistent hazard for elk calves over the winter, while wolf-caused mortality was minimal (Fig. 2-4). 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, 0.18) for unknown causes; and 0.01 (95% CI not estimable) for human-related mortality (Table 2-7).

Our exploratory analysis of unknown mortality for elk calves in winter revealed distinct hazard ratios between unknown and wolf-caused mortality (unknown: HR = 2.65 (1.68, 4.18) (95% CI); wolf: HR = 0.45 (0.14, 1.47)), but the mountain lion mortality hazard ratio was similar to unknown mortality (mountain lion: HR = 3.07 (1.49, 6.33)). This 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), and thus, we decided not to pool unknown mortality with any specific winter mortality source.

**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 results indicated that spatial mountain lion predation risk was the strongest predictor of calf mortality risk in winter, while wolf predation risk had negligible effects in any season. Consistently, 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 non-invasive, 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 EF and WF 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$^2$, MFWP, unpublished data), 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.

Despite the importance of mountain lions to cause-specific mortality of elk calves, as well as the importance of exposure of elk calves to spatial mountain lion predation risk in winter, we found no effect of spatial variation in mountain lion predation risk during summer. This was initially puzzling, but a post hoc analysis of risk factors using just elk calves killed by mountain lions during summer confirmed that even for those calves killed by mountain lions, mortality risk was not correlated with their predation risk during summer (the $P$-value for the HR for mountain predation risk in subset analyzed = 0.12). This suggests that because mortality risk for elk calves was uniformly high from mountain lions across most of the study area during summer (Fig. 2-2), there was insufficient spatial variation in mountain lion predation risk across individuals to explain elk calf mortality events. In winter, we found a strong effect of mountain lion predation risk on elk calf mortality risk, which resulted from the wider spatial variation in exposure of
individuals to mountain lions as compared to summer (Fig. 2-2). This could be because of the wider dispersion of elk during summer on summer ranges. Moreover, we note that the diversity of mortality causes was higher during summer when black bear mortality peaked, as well as death from other causes such as entanglement in fences, starvation, disease and abandonment. These results are similar to the many other studies showing a variety of mortality causes during summer (e.g., Griffin et al. 2011) that we take to suggest that summer mortality may not be as influenced by spatial risk factors as during winter when carnivores and ungulates concentrate on low elevation winter range. Thus, understanding the relative importance of spatial risk factors from different carnivores may be most important during winter.

In the Northern Range in 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 (Garrott et al. 2005) 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 as well. With the recolonization of wolves in many regions, and the public furor and fanfare surrounding it (Treves et al. 2013), the
effects of mountain lions 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).

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). The importance of sex-biased mortality may depend on the hunting behavior of the dominant predator in the system, with areas dominated by ambushing carnivores (e.g., lynx [*Lynx lynx*], Mathisen et al. 2003) having greater consequences for juvenile males compared to carnivores using other hunting modes (e.g., coursing). However, 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 this uncertainty due to unknown mortalities, synthesizing data to test this hypothesis seems warranted given the observed variation across systems.
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 latent 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 EF than the WF that we attributed to misplacement of ear tags by less experienced capture crews in the EF (see Appendix 2-A). 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 were unable to pool with any specific mortality source. However, it is possible that our mortality classifications may have been more conservative than some studies due to our strict classification of mortality causation.

Our results generally supported the positive effects of higher forage availability for summer elk calf survival (Cook et al. 2004), but this effect was driven by migratory calves that summered in a high-elevation, agricultural valley with high forage availability and low mountain lion (and wolf) predation risk. Without including these migratory elk calves, the effect of forage availability on summer survival was attenuated and insignificant for resident elk calves. Therefore, we interpret the summer forage effect as a landscape-level scale effect of migration, which indeed did result in higher survival for those elk calves that were born on migratory summer range. Hebblewhite and Merrill (2011) documented similar spatial risk trade-offs for migratory elk herds in the Ya Ha Tinda in Alberta, Canada, with migrants tracking the summer green-up to access high quality forage at the cost of higher exposure to predation risk, which resulted in lower adult female and calf survival compared to resident elk. Migratory portions of the EF elk herd may also trade-off exposure to higher predation risk during migration, but, in
contrast to migratory Ya Ha Tinda elk herds, they have the benefit of higher calf survival over
summer from abundant and safe foraging conditions. Thus, migratory elk herds that summer in
the Bighole Valley may be an important component of sustaining juvenile recruitment in the EF
elk population.

Regardless of the specific migration strategy, we found no strong evidence that higher forage
availability compensated for the negative effects of mountain lion predation risk on elk calf
survival, which, along with early mortality from black bears (White et al. 2010), may indicate
that mountain lions are an additive mortality source for neonatal elk calves in our study system.
The compensatory effects of forage availability may be accentuated in systems with lower
carnivore densities, where climatic and bottom-up nutritional factors may explain more of the
demographic variation in ungulate populations (see Wilmers et al. 2006). For instance, Raithel
(2005) found that spring weather explained neonatal elk calf survival during a period of
experimental increases in hunter harvest of mountain lions in the study area, and reported
considerably higher levels of natural, non-predation mortality (i.e. starvation, disease) and
interannual variation in neonatal survival compared to our study. Consistently, Barber-Meyer et
al. (2008) documented much lower incidence of natural, non-predation mortality and variation in
neonatal elk calf survival in Yellowstone National Park over a decade after wolves recovered
compared to an earlier elk calf study that occurred during a period of lower carnivore densities
(Singer et al. 1997). Also, Melis et al. (2009) detected a signal of compensation with primary
productivity in roe deer populations in Europe that have carnivores present, but presumably at
lower densities due to the early stages of carnivore recolonization in the region. Thus, in systems
where early predation mortality does not overwhelm nutritional factors, the mediating effects of
climate on the spatial and temporal availability of forage (Pettorelli et al. 2007) may determine
the extent that predation mortality in neonates is compensatory through bottom-up nutritional factors (Tverra et al. 2003; Griffin et al. 2011).

Although high carnivore density may limit the importance of nutritional factors on neonatal survival, the effects of forage availability on juvenile survival has been strongly linked to the carryover effects of summer-autumn nutrition on overwinter survival of juvenile ungulates (Bishop et al. 2009; Hurley et al. 2011). In a feeding experiment of elk, for instance, Cook et al. (2004) found that body mass of elk calves at the onset of winter significantly explained overwinter survival probability. Although we found no effect of forage availability on elk calf survival in winter \( (P = 0.58) \), our measure of forage on winter range was based on the average late-summer forage availability over the study period, and we could not account for the body condition of calves entering winter. In a study of mule deer fawn survival across Idaho, Hurley et al. (2014) found that autumn plant phenology was more variable and twice as important compared to spring phenology for fawn nutrition, which had a pronounced effect on body mass that explained variation in winter fawn survival. Also, Bishop et al. (2009) found in Colorado that supplemental feeding during winter of mule deer fawns and adult females had little effect on neonatal survival, but significantly reduced starvation and predation mortality by coyotes and mountain lions of ≥6-month-old fawns during winter. Similarly, we also found that elk calves with higher forage biomass during winter also experienced higher survival in an additive fashion with increased mountain lion predation risk. This suggests that access to forage biomass is also important during winter to offset overwintering costs, perhaps for the same reasons as Bishop et al. (2009) and others. However, we found no significant interaction of predation risk and winter severity on elk calf survival during winter, but documented significant interannual variation in overwinter survival that was unexplained by our spatial risk covariates. Hurley et al. (2011)
found similar results in Idaho that greater precipitation in winter did not strongly effect winter survival of mule deer fawns, but found support for the carryover effects of summer precipitation and fawn body mass. Therefore, the interplay of variable summer-autumn forage conditions and, to a lesser extent, winter precipitation may mediate juvenile vulnerability to predation mortality and drive the higher interannual variability observed in winter survival rates compared to summer (Unsworth et al. 1999; Bishop et al. 2009; Hurley et al. 2011).

**MANAGEMENT IMPLICATIONS**

Understanding the potential role of recolonizing carnivores in driving declines in juvenile ungulate recruitment generally necessitates 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. Decomposing the effects of predation risk, juvenile nutritional status, and winter weather severity will be important for predicting juvenile survival, which could help reduce uncertainty in setting ungulate harvest levels. Reducing adult female harvest may be initially necessary as carnivores recover to allow time to identify the most effective management strategy to balance ungulate and carnivore population objectives. As carnivore recolonization continues, managers may need a more aggressive policy towards habitat (e.g. logging, prescribed burns) or carnivore management for ungulates 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 in providing baseline data to generate predictions and to test the effectiveness of different management strategies.

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**TABLES**

Table 2-1. Number of elk calves captured by period, capture area, and sex in the southern Bitterroot Valley, Montana, USA, 2011–2014.

<table>
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<tr>
<th></th>
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<tbody>
<tr>
<td>Period</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>66</td>
<td>76</td>
<td>84</td>
<td>226</td>
</tr>
<tr>
<td>Winter</td>
<td>31</td>
<td>29</td>
<td>0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>60</td>
</tr>
<tr>
<td>Total</td>
<td>97</td>
<td>105</td>
<td>84</td>
<td>286</td>
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<table>
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<td>East Fork</td>
<td>58</td>
<td>69</td>
<td>56</td>
<td>183</td>
</tr>
<tr>
<td>West Fork</td>
<td>39</td>
<td>36</td>
<td>28</td>
<td>103</td>
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<table>
<thead>
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<tbody>
<tr>
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<td>52</td>
<td>36</td>
<td>133</td>
</tr>
<tr>
<td>Male</td>
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<td>53</td>
<td>48</td>
<td>152</td>
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<tr>
<td>Unknown</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
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</tbody>
</table>

<sup>a</sup>Elk calves were not captured during the last winter (2013–14) due to adequate sample sizes at the beginning of the monitoring period.
Table 2-2. Kaplan-Meier survival estimates ($\hat{S}$) in summer and winter with 95% log-log confidence intervals (CI) and minimum and maximum number of individuals at risk (n) for elk calves by study area and overall in the southern Bitterroot Valley, Montana, USA, 2011–2014.

<table>
<thead>
<tr>
<th>Period</th>
<th>Year</th>
<th>n</th>
<th>$\hat{S}$</th>
<th>95% CI lower</th>
<th>95% CI upper</th>
<th>$\hat{S}$</th>
<th>95% CI lower</th>
<th>95% CI upper</th>
<th>$\hat{S}$</th>
<th>95% CI lower</th>
<th>95% CI upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>2011–12</td>
<td>19–62</td>
<td>0.65</td>
<td>0.47</td>
<td>0.78</td>
<td>0.45</td>
<td>0.19</td>
<td>0.68</td>
<td>0.59</td>
<td>0.44</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>2012–13</td>
<td>21–75</td>
<td>0.59</td>
<td>0.42</td>
<td>0.73</td>
<td>0.30</td>
<td>0.11</td>
<td>0.52</td>
<td>0.49</td>
<td>0.35</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>2013–14</td>
<td>10–82</td>
<td>0.56</td>
<td>0.34</td>
<td>0.74</td>
<td>0.59</td>
<td>0.34</td>
<td>0.78</td>
<td>0.57</td>
<td>0.40</td>
<td>0.71</td>
</tr>
<tr>
<td>Winter</td>
<td>2011–12</td>
<td>18–41</td>
<td>0.71</td>
<td>0.43</td>
<td>0.87</td>
<td>0.40</td>
<td>0.18</td>
<td>0.61</td>
<td>0.54</td>
<td>0.36</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>2012–13</td>
<td>35–42</td>
<td>0.76</td>
<td>0.55</td>
<td>0.89</td>
<td>1.00</td>
<td>NA\textsuperscript{a}</td>
<td>NA</td>
<td>0.85</td>
<td>0.70</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>2013–14</td>
<td>31–39</td>
<td>0.92</td>
<td>0.71</td>
<td>0.98</td>
<td>0.59</td>
<td>0.31</td>
<td>0.79</td>
<td>0.79</td>
<td>0.63</td>
<td>0.89</td>
</tr>
</tbody>
</table>

\textsuperscript{a}NA = not applicable; 95% CIs were not estimable due no mortality events occurring in the West Fork during the 2012–13 winter.
Table 2-3. Sequential base model selection of A-G proportional hazards models showing the number of model parameters ($k$), model deviance (Dev), $\Delta$AICc, and model weights ($w$) for summer elk calf survival in the southern Bitterroot Valley, Montana, USA, 2011–2014. The nested model risk covariates and factors were sequentially removed until the $\Delta$AICc increased with variable removal. Abbreviations are estimated birth date (Date), birth mass (Mass), and year (Yr).

*a We report only the top four models here ($\Delta$AICc <4).

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model</th>
<th>$k$</th>
<th>Dev</th>
<th>$\Delta$AICc</th>
<th>$w$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Sex + Date</td>
<td>2</td>
<td>-396.34</td>
<td>0.00</td>
<td>0.35</td>
</tr>
<tr>
<td>2</td>
<td>Sex + Date + Yr</td>
<td>4</td>
<td>-394.39</td>
<td>0.23</td>
<td>0.31</td>
</tr>
<tr>
<td>3</td>
<td>Sex + Date + Yr + Study area</td>
<td>5</td>
<td>-393.66</td>
<td>0.87</td>
<td>0.23</td>
</tr>
<tr>
<td>4</td>
<td>Sex + Date + Yr + Study area + Mass</td>
<td>6</td>
<td>-393.66</td>
<td>2.97</td>
<td>0.08</td>
</tr>
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</table>
Table 2-4. Model-averaged coefficients, unconditional standard errors, and 95% confidence intervals for Andersen-Gill proportional hazards models that include the effects of sex (male as reference group), forage availability (F), mountain lion (L) and wolf predation risk (W), and the interaction between predation risk and forage availability on summer survival of for elk calves in the southern Bitterroot Valley, Montana, USA, 2011–2014.

<table>
<thead>
<tr>
<th>Model parameter</th>
<th>Estimatea</th>
<th>Unconditional SE</th>
<th>Confidence interval</th>
<th>Hazard ratio</th>
<th>Relative importance</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>-1.39</td>
<td>0.61</td>
<td>(-2.58, -0.20)</td>
<td>0.25</td>
<td>1.00</td>
<td>0.02</td>
</tr>
<tr>
<td>Sex</td>
<td>0.43</td>
<td>0.23</td>
<td>(-0.03, 0.89)</td>
<td>1.54</td>
<td>0.85</td>
<td>0.06</td>
</tr>
<tr>
<td>L</td>
<td>-0.08</td>
<td>0.37</td>
<td>(-0.37, 1.07)</td>
<td>1.41</td>
<td>0.28</td>
<td>0.35</td>
</tr>
<tr>
<td>W</td>
<td>0.35</td>
<td>0.26</td>
<td>(-0.68, 0.52)</td>
<td>0.93</td>
<td>0.28</td>
<td>0.80</td>
</tr>
<tr>
<td>L × F</td>
<td>1.90</td>
<td>1.38</td>
<td>(-0.80, 4.59)</td>
<td>6.67</td>
<td>0.14</td>
<td>0.17</td>
</tr>
<tr>
<td>W × F</td>
<td>1.42</td>
<td>0.88</td>
<td>(-0.31, 3.15)</td>
<td>4.12</td>
<td>0.15</td>
<td>0.11</td>
</tr>
</tbody>
</table>

a Effect sizes have been standardized on two standard deviations following Gelman (2008).
Table 2-5. Sequential base model selection of A-G proportional hazards models showing the number of model parameters ($k$), model deviance (Dev), $\Delta$AICc, and model weights ($w$) for winter elk calf survival in the southern Bitterroot Valley, Montana, USA, 2011–2014. The nested model risk covariates and factors were sequentially removed until the $\Delta$AICc increased with variable removal. Abbreviations are estimated birth date (Date), birth mass (Mass), and year (Yr).

<table>
<thead>
<tr>
<th>Model rank</th>
<th>Model$^a$</th>
<th>$k$</th>
<th>Dev</th>
<th>$\Delta$AICc</th>
<th>$w$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Yr</td>
<td>2</td>
<td>-132.26</td>
<td>0.00</td>
<td>0.35</td>
</tr>
<tr>
<td>2</td>
<td>Yr + Study area</td>
<td>3</td>
<td>-131.38</td>
<td>0.33</td>
<td>0.30</td>
</tr>
<tr>
<td>3</td>
<td>Yr + Study area + Sex</td>
<td>4</td>
<td>-130.46</td>
<td>0.63</td>
<td>0.25</td>
</tr>
<tr>
<td>4</td>
<td>Yr + Study area + Sex + Study area × Sex</td>
<td>5</td>
<td>-130.44</td>
<td>2.75</td>
<td>0.09</td>
</tr>
</tbody>
</table>

$^a$We report only the top four models here ($\Delta$AICc <4).
Table 2-6. Top two winter Andersen-Gill proportional hazards models showing number of model parameters (k), model deviance (Dev), ΔAICc, model weights (w), standardized coefficient estimates, and 95% confidence intervals (CI) for hazard ratios for elk calves in the southern Bitterroot Valley, Montana, USA, 2011–2014. The final model consisted of only year (Yr; reference = 2011–12) and mountain lion predation risk (L), while the next closest model included winter severity index (WSI).

<table>
<thead>
<tr>
<th>Model parameter</th>
<th>k</th>
<th>Dev</th>
<th>ΔAICc</th>
<th>w</th>
<th>Coefficient estimate</th>
<th>Hazard ratio</th>
<th>95% Hazard ratio CI</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>3</td>
<td>-120.40</td>
<td>0.00</td>
<td>0.50</td>
<td>1.04</td>
<td>2.84</td>
<td>(1.37, 5.88)</td>
<td>0.005</td>
</tr>
<tr>
<td>Yr: 2012–13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-1.63</td>
<td>0.20</td>
<td>(0.07, 0.54)</td>
<td>0.002</td>
</tr>
<tr>
<td>Yr: 2013–14</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-1.67</td>
<td>0.19</td>
<td>(0.08, 0.47)</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

| L               | 4 | -120.08 | 1.38  | 0.25 | 1.04 | 2.84         | (1.36, 5.90) | 0.005|
| Yr: 2012–13     |   |       |       |     | -1.63 | 0.20         | (0.07, 0.55) | 0.002|
| Yr: 2013–14     |   |       |       |     | -1.82 | 0.16         | (0.06, 0.43) | <0.001|
| WSI             |   |       |       |     | 0.43  | 1.53         | (0.55, 4.25) | 0.41 |
Table 2-7. Cumulative incidence functions (CIF) in summer and winter for 5 mortality sources \((k)\) with 95\% log-log confidence intervals (CI) and raw counts \((n)\) for 110 confirmed elk calf mortalities calves by study area and overall in the southern Bitterroot Valley, Montana, USA, 2011–2014. 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.

<table>
<thead>
<tr>
<th>Period</th>
<th>East Fork</th>
<th>West Fork</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n)</td>
<td>CIF</td>
<td>95% CI lower</td>
</tr>
<tr>
<td><strong>Summer</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bear</td>
<td>7</td>
<td>0.045</td>
<td>0.016</td>
</tr>
<tr>
<td>Mountain Lion</td>
<td>14</td>
<td>0.107</td>
<td>0.055</td>
</tr>
<tr>
<td>Wolf</td>
<td>2</td>
<td>0.015</td>
<td>0.001</td>
</tr>
<tr>
<td>Unknown</td>
<td>19</td>
<td>0.201</td>
<td>0.135</td>
</tr>
<tr>
<td>Other</td>
<td>6</td>
<td>0.046</td>
<td>0.015</td>
</tr>
<tr>
<td><strong>Winter</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mountain Lion</td>
<td>4</td>
<td>0.062</td>
<td>0.020</td>
</tr>
<tr>
<td>Wolf</td>
<td>1</td>
<td>0.014</td>
<td>0.001</td>
</tr>
<tr>
<td>Unknown</td>
<td>7</td>
<td>0.109</td>
<td>0.048</td>
</tr>
<tr>
<td>Other</td>
<td>1</td>
<td>0.014</td>
<td>NA(^a)</td>
</tr>
</tbody>
</table>

\(^a\) 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.
FIGURES

Figure 2-1. Predicted total herbaceous biomass (kg/ha) in the study area, which included the East and West Forks of the Bitterroot River drainage and the northern Bighole Valley located in west-central Montana, USA. The study area extended into the Bighole to include summer ranges used by migratory East Fork elk. The East Fork and Bighole areas are dominated by agriculture and are mainly open grasslands, while the West Fork area is more forested, rugged terrain.
Figure 2-2. Predicted relocation probability for mountain lions based on resource selection functions (RSF) across the East Fork and West Fork study areas in the southern Bitterroot Valley and northern Bighole Valley, Montana, USA. Season-specific mountain lion RSFs were used to estimate summer (top) and winter (bottom) mountain lion predation risk exposure for elk calves. Elk calf locations were buffered with a 500 m radius and are shown as red circles.
Figure 2-3. Kaplan-Meier (KM) annual survivorship curves for elk calves for 3 biological years in the southern Bitterroot Valley, Montana, USA, 2011–2014. The KM survivorship graph shows that interannual variation in elk calf survival increases after about 90 days since birth (vertical dotted line).
Figure 2-4. Smoothed instantaneous mortality hazards (i.e. mortality rate per day) for elk calves for different mortality sources in the southern Bitterroot Valley, Montana, USA, 2011–2014.
APPENDIX 2
Appendix 2-A. Competing risk analysis of tag loss: testing for potential effects of tag loss on survival estimates

INTRODUCTION
Informative censoring occurs when a censoring event is non-random and associated with a latent mortality event. During the Bitterroot elk study, we experienced high-enough levels of tag loss, especially during the first half of the study, to warrant investigating whether tag loss might have been non-random. An example provided by Murray (2006) is when a wolf is censored in a telemetry study due to a putative collar failure, when in reality, the collar failure occurred from a transmitter being destroyed after the individual was illegally killed. These types of informative censoring events can introduce positive bias into survival estimates and potentially alter inferences into the effects of covariates on survival probability (Collett 2003; Murray 2006). While no definitive method is available to test for informative censoring, there are methods that allow for increased confidence that the results of a study are not biased from informative censoring. In the wolf example, finding that the proximately to private land significantly explained censoring events land may provide suggestive evidence of informative censoring. In the case of tag loss, if there were some covariates correlated with individuals that lost tags, this may also suggest informative censoring. We consider the possibly of informative censoring here for our elk calf survival dataset as a precautionary and necessary step in providing reliable inference into survival estimates and the effect of risk covariates. We also conducted sensitivity analyses to evaluate potential effects of tag loss on survival rates (Murray 2006).

METHODS
We captured and radio-tagged elk with two different brands of ear tags; for the first half of the study (i.e., biological year of 2011–12 and summer of 2012–13), we deployed ATS ear tags. For the second half of the study (i.e., winter of 2012–13, and biological year of 2013–14), we deployed Biotrack ear tags (see Chapter 2). We estimated the incidence of tag loss for these two brands using cumulative incidence functions [CIFs] as described in Heisey and Patterson (2006). In a competing risks framework, we tested treated tag loss as a competing risk for elk calves and modeled the effect of risk covariates using Cox proportional hazards [PH] regression (Broström 2012). Since we had no a-priori hypotheses to test concerning the effect of risk covariates or factors on the incidence of tag loss, we considered the main effects of sex and study area for both summer and winter risk models. We also applied another method of testing for possible informative censoring is based on a sensitivity analysis, where survival rates are estimated under two scenarios: (1) censored individuals are assumed to have died at the censoring time, and (2) censored individuals are assumed to have survived beyond the longest survival time of all subjects (Murray 2006). If the survival estimates obtained under normal censoring procedures differ markedly from either altered dataset, then censoring may be informative (Allison 1995, Murray 2006). We compared these survival estimates using a Kaplan-Meier (KM) estimator (Pollock et al. 1989). For all tag loss analyses, we used the same risk set as described in Chapter 2, which included 224 calves in summer and 125 calves in winter, and an annual risk set of 283 elk calves.
RESULTS
The overall cumulative incidence of tag loss was 0.34 (95% CI = 0.27, 0.40). Tag loss rates were significantly higher for calves equipped with ATS brand ear tags (CIF = 0.46, 95% CI = 0.38, 0.54) compared to Biotrack ear tags (CIF = 0.13, 95% CI = 0.07, 0.21) as 95% confidence intervals failed to overlap. Overall, female calves had higher rates of tag loss (CIF = 0.40, 95% CI = 0.31, 0.49) than males (CIF = 0.26, 95% CI = 0.18, 0.36), but this difference was not significant (P = 0.35). The overall incidence of tag loss was significantly higher (P = 0.02) in the East Fork (EF, CIF = 0.39, 95% CI = 0.31, 0.48) compared to the West Fork (WF) study area (CIF = 0.22, 95% CI = 0.14, 0.32). Tag loss rates were significantly higher (P <0.001) in summer (CIF = 0.28, 95% CI = 0.21, 0.35) compared to winter (CIF = 0.17, 95% CI = 0.11, 0.25), which likely resulted from using ATS ear tags with lower retention rates for two summers and only one winter, while Biotrack ear tags were deployed for one summer and two winters.

As expected, summer tag loss rates varied significantly across years (P <0.001), and were highest in the summer of 2011–12 (CIF = 0.44, 95% CI = 0.31, 0.55; ATS tags) and for those deployed in spring 2012–13 (CIF = 0.35, 95% CI = 0.24, 0.46; ATS tags), and were considerably lower during the summer of 2013–14 (CIF = 0.11, 95% CI = 0.05, 0.18; Biotrack tags). Female calves had higher incidence of tag loss during summer (CIF = 0.34, 95% CI = 0.25, 0.44) compared to male calves (0.22, 95% CI = 0.14, 0.31), but this difference was not significant (P = 0.47). Also, tag loss rates were marginally higher (P = 0.10) in the East Fork study area during summer (CIF = 0.32, 95% CI = 0.24, 0.41) compared to the West Fork (CIF = 0.18, 95% CI = 0.18, 0.39).

Tag loss rates in winter followed a similar pattern as summer with significant variation among years (P = 0.006), with rates of 0.20 (95% CI = 0.10, 0.33) in 2011-12 (ATS), 0.29 (95% CI = 0.16, 0.43) in 2012–13 (mix of both ATS and Biotrack ear tags), and 0.03 (95% CI = 0.002, 0.13) in 2013–14 (Biotrack tags). Female calves had higher tag loss rates during winter (CIF = 0.20, 95% CI = 0.11, 0.31) compared to males (CIF = 0.15, 95% CI = 0.07, 0.25) but this difference was not statistically significant (P = 0.66). Tag loss rates were higher but not statistically different (P = 0.25) for calves in the EF area in winter (CIF = 0.22, 95% CI = 0.13, 0.32) compared to the WF (CIF = 0.12, 95% CI = 0.05, 0.22).

The simulation of completely informative censoring where all individuals censored from tag loss were treated as mortalities resulted in KM survival rates of 0.25 (95% CI = 0.19, 0.31) for summer and 0.47 (95% CI = 0.37, 0.56) for winter. Conversely, simulating all individuals that were censored from tag loss surviving until the longest observed survival time for summer (180 days) and winter (185 days) resulted in survival rates of 0.61 (95% CI = 0.53, 0.68) for summer and 0.76 (95% CI = 0.67, 0.83) for winter. Compared to the seasonal survival rates from our normally censored data, the extreme informative censoring survival estimates did not fall within the 95% confidence interval for summer (0.47, 0.63) or winter (0.65, 0.81) survival estimates, but the completely non-informative survival estimates were captured in the confidence intervals.

DISCUSSION
The relatively high incidences of tag loss that occurred during the first two years of our elk calf survival study are likely due to simple causes. During the first half of the study,
we used ATS ear tags (model 3430, Advanced Telemetry System), which had a relatively long antennae compared to the Biotrack ear tags (TW-5, Biotrack Ltd., Wareham, Dorset, United Kingdom) that were deployed during the second winter (2012–13) and for the remainder of the study. The Biotrack ear tags were produced so that the transmitter would be balanced in the ear (see Fig. 2-A.1). We noticed that the ATS ear tags would leave large holes in the ears of calves that were found dead, presumably from spinning around, and the radio signal from these tags would be more difficult to hear if the antennae was facing downward.

The overall difference in ear tag loss incidences between study areas may also be due to simple causes. Since it was more difficult to spot elk calves in the West Fork area due to dense forests, we mainly caught calves using aerial methods. The helicopter capture crews operating in the WF generally had a larger percentage of highly-trained personnel with extensive experience capturing calves, and despite the low-quality design of the ATS tags, these highly-trained individuals may have placed the ear tag farther down into the cartilage of the ear, allowing the tag to be retained longer. In contrast, we relied on a larger amount of volunteer help in the EF area, especially during the first year of the study, which included many individuals with no previous capture experience. Consequently, more of the ear tags in the East Fork area may have been placed too high in the ear, resulting in low retention rates. Given that our sample sizes were larger in East Fork, it is unlikely that these differences in censoring affected our inferences related to survival estimates and risk factors.

Although there appeared to be higher tag loss incidences in females compared to males, this difference was not significant and was likely due to random chance. A chi-squared test confirmed that the observed tag loss among males and females across study years was homogenously distributed ($\chi^2 = 1.78, P = 0.41$). We feel confident that any differences in tag loss among sexes did not affect our result that males were at higher risk of mortality than females, especially given that a greater reduction in female sample size from losing ear tags would cause each female mortality to have a larger effect on survival probability than male mortalities.

While censoring has the potential to be informative in both wildlife and medical studies (Collett 2003; Murray 2006), we feel confident from our analysis that our censoring due to tag loss was not due to latent or unobservable mortality events. Furthermore, we agree with Murray (2006) that censoring rates should always be reported in telemetry studies and that it is important to consider the range of survival probabilities under worst and best-case scenarios. The issue of censoring due to tag loss in wildlife telemetry studies, especially for juvenile ungulates, is more a problem of engineering and properly training personnel before the start of the study. Considering the importance of survival estimates from radio telemetry studies, we recommend using Biotrack over ATS ear tags in juvenile ungulate studies and spending extra time to train volunteer personnel in the proper placement of ear tags.

**LITERATURE CITED**


FIGURES

Figure 2-A.1. Diagram of modified ear tag transmitter provided to Biotrack Ltd., Wareham, Dorset, United Kingdom, that was deployed on elk calves during the winter of 2012–13 and the biological year of 2013–14.
Appendix 2-B. Elk calf telemetry relocation summary

**Table 2-B.1.** Telemetry location summary for 224 elk calves by study area and sex from aerial relocations, and capture and mortality locations during summer in the southern Bitterroot Valley, Montana, USA, 2011–2014. The summary includes mean number of locations/calf ($\bar{x}$), standard deviations (SD), and number of locations ($n$).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Sex</th>
<th>Year</th>
<th>$\bar{x}$</th>
<th>SD</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Fork</td>
<td>Female</td>
<td>2011–12</td>
<td>7.57</td>
<td>3.59</td>
<td>159</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>6.59</td>
<td>4.13</td>
<td>178</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>7.19</td>
<td>2.10</td>
<td>187</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>2011–12</td>
<td>5.39</td>
<td>3.60</td>
<td>124</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>7.12</td>
<td>4.12</td>
<td>185</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>6.90</td>
<td>2.35</td>
<td>207</td>
</tr>
<tr>
<td>West Fork</td>
<td>Female</td>
<td>2011–12</td>
<td>7.56</td>
<td>3.54</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>6.56</td>
<td>3.28</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>6.60</td>
<td>1.78</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>2011–12</td>
<td>5.58</td>
<td>3.53</td>
<td>67</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>4.62</td>
<td>3.10</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>5.78</td>
<td>2.05</td>
<td>104</td>
</tr>
</tbody>
</table>
Table 2-B.2. Location summary for 125 elk calves by study area and sex from aerial relocations, and capture and mortality locations during winter in the southern Bitterroot Valley, Montana, USA, 2011–2014. The summary includes mean number of locations/calf ($\bar{x}$), standard deviations (SD), and number of locations ($n$).

<table>
<thead>
<tr>
<th>Study area</th>
<th>Sex</th>
<th>Year</th>
<th>$\bar{x}$</th>
<th>SD</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Fork</td>
<td>Female</td>
<td>2011–12</td>
<td>5.30</td>
<td>3.30</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>10.64</td>
<td>7.81</td>
<td>149</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>8.70</td>
<td>0.82</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>2011–12</td>
<td>5.18</td>
<td>2.75</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>10.07</td>
<td>8.10</td>
<td>141</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>7.93</td>
<td>1.82</td>
<td>111</td>
</tr>
<tr>
<td>West Fork</td>
<td>Female</td>
<td>2011–12</td>
<td>4.55</td>
<td>1.91</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>15.82</td>
<td>5.08</td>
<td>174</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>8.33</td>
<td>2.58</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>2011–12</td>
<td>3.90</td>
<td>2.13</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2012–13</td>
<td>16.00</td>
<td>5.10</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2013–14</td>
<td>6.00</td>
<td>2.06</td>
<td>54</td>
</tr>
</tbody>
</table>
Appendix 2-C. Estimating elk calf age at capture, birth mass, and birth date

BACKGROUND
The purpose of this aging analysis was to estimate the age (in days) of calves at capture. The age at capture was used in our age-based survival analysis (Chapter 2), and allowed us to directly estimate the importance of time-dependent risk factors (e.g. forage quality, winter severity) for elk calf survival. The age-based timescale also allowed time-dependent risk factors to vary within risk sets, which is necessary to avoid confounding their effect with the baseline hazard such as in a study-based timescale (Fieberg and DelGuidice 2009). The age-based method of handling the time origin treats the effect of age non-parametrically, where calves enter at their age at capture (or time since birth) and exit at death or censoring event (Fieberg and DelGuidice 2009; Griffin et al. 2011). The design is a left-staggered entry with right-censoring. Other possibilities of timescale include: a study-based model, where individuals enter at the calendar time since the first capture of the year; a recurrent model that uses a consistent annual date to reset the clock; and days since capture.

METHODS
The two methods used to age elk calves at capture are a quantitative method developed by Montgomery (2005) and a categorical technique by Johnson (1951). Montgomery (2005) does not recommend using her technique on wild elk calves because it was developed from measurements taken on captive elk calves involved in feeding experiments, and as a result, significant differences in daily weight gains may occur between captive and wild elk calves. In practice, researchers still rely on the Johnson (1951) methods because the age at capture is greatly overestimated using the Montgomery model in wild elk populations. However, there are some drawbacks to using the Johnson method because the categorical system was developed without knowing the actual ages of the elk calves (i.e. response variable), and thus, the aging criteria includes subjective judgment (although the researchers were expert elk biologists). Furthermore, Johnson (1951) included incisor measurements as an aging criteria, but does not specify whether he measured the middle or outside of the incisor. Montgomery (2005) uses the outside incisor measurement in her model, but does compare the middle incisor measurements to the range of incisor values reported by Johnson (1951).

Due to uncertainty in aging methods, we recorded measurements on elk calves during capture to apply both the Montgomery and Johnson aging techniques. To determine our final estimates of age at capture for elk, we compared our field capture estimates with estimates from the Johnson method based solely on incisor measurements, the Johnson method (except moisture on hair), and the Montgomery method. Because newborn (day 0) calves could be clearly identified in the field, we thought it reasonable to retain these estimates for our final aging determination. We compared the mean age at capture estimates from our field estimates to each of these aging methods. Finally, we regressed the mass at capture (kg) on the estimated ages at capture to estimate daily rates of mass gain (see Chapter 2 results, Calf Capture and Birth Attributes).

Outside incisor measurements. — We did not record the outside incisor measurements of calves captured in 2011 and 2012, but we did record the inside and middle incisor measurements. To predict the outside incisor measurements for 2011 and
2012 calves, we recorded all incisor measurements in 2013 (i.e. inside, middle and outside). The inside measurements were often 0.0 mm, which was not useful for prediction. We fit two regressions of outside vs. middle incisor lengths separately for measurements taken on the left and right incisors. The following prediction equations were estimated for the left (equation 1) and right (equation 2) outside incisors:

- Left outside incisor = 1.9869 + 0.6607*left middle incisor
- Right outside incisor = 2.1327 + 0.6448*right middle incisor

The regression of the left outside incisor on the left middle incisor was highly significant ($F_{1,79} = 205.4, P < 0.0001$), and the left middle incisor explained 72.2% of the variation in left outside incisor. The regression of the right outside incisor on the right middle incisor was also highly significant ($F_{1,80} = 212, P < 0.0001$), and the right middle incisor explained 72.6% of the variation in right outside incisor. We detected no departures from normality in the residuals of either regression, and both regressions had similar strong, positive linear associations (see Fig. 2-C.1). Therefore, we used the predicted outside incisor lengths in the Montgomery and Johnson aging procedures for calves captured in 2011 and 2012, and used field measurements for calves in 2013. Finally, the left and right outside incisor values were averaged for the analysis.

**Field age estimates.** — We recorded field estimates of age at capture for 65.5% of calves; therefore, it was not possible to compare all individual field estimates to each aging technique. We searched all of the estimated age records and capture notes for any evidence that a calf was born on day 0.

**Johnson incisor age estimates.** — Montgomery (2005) reported age estimates from the Johnson technique in her comparison study by using only the outside incisor measurements for the aging criteria to provide a single day estimate. Following Montgomery (2005), we used the outside incisor measurements recorded at capture to classify elk calves into the aging categories according to the Johnson method (see dentition, Table 2-C.1). Using these incisor measurement categories, we divided each measurement range by the number of ages included in the category. For example, the age category 0-1 for dentition ranged from 0 to 3.18 mm, so by dividing 3.18 by 2, we get age 0 calves ranging from 0 to 1.59 mm and age 1 calves ranging from 1.59 to 3.18 mm. Elk calves 8 days and older were classified into a single category with incisors ranging from 9.50 to 15.9 mm.

**Johnson categorical age estimates.** — The Johnson method uses a categorical system to classify elk calves into age ranges in days of 0-1, 2-4, 5-7, 8+ using different morphometric characteristics recorded at capture. Although Johnson (1951) provides age classifications for the criteria of capture weight (lbs), total length (in), tail length (in), hind foot (in) and ear length (in), the ranges of these variables have a high degree of overlap among the different age categories, and thus, are not helpful in estimating elk calf age at capture. A few other problems are apparent with this technique: 1) the age categories only give age ranges and the authors do not provide a protocol to determine a single estimate of age at capture (i.e. 1 instead of 0-1 ), 2) some categories only distinguish between 0-1 and 2-8+, whereas others include more age bins, 3) only two of the categories are quantitative measurements (dentition and navel diameter), and 4) the age range determinations may not agree within individuals.

Researchers have used a simple scoring technique to deal with these inconsistencies in applying the Johnson method (Mark Hurley, *pers. comm.*) and to minimize subjective
classifications. We also used a scoring technique that allowed age at capture estimates for individuals that did not have records for every category. Out of the seven categories considered, one calf had the following classification results: 2-4, 5-7, 5-7, NA, 0-1, 2-4, 5-8+. This resulted in the following vector: \{2, 3, 4, 5, 6, 7, 5, 6, 7, 0, 1, 2, 4, 5, 6, 7, 8\}, and mean and median age at capture estimates of 4.5 and 5, respectively. We consider estimated of both the mean and median age estimate.

Johnson categorical age estimates. — The Montgomery model uses the variables mass (kg) at capture, tooth (cm), tooth^2 (cm^2), hoofline (cm), and sex (1 for males, 0 otherwise). Equation 3 gives the coefficient estimates for the fixed effects in the Montgomery model:

\[
\text{Age at Capture} = -10.95 + 0.59*\text{mass} + 2.16*\text{tooth} + 5.24*\text{tooth}^2 + 1.95*\text{hoofline} + -0.84*\text{sex}
\] (3)

The model included mixed-effects, where repeated measures on individual calves required estimating a random intercept and slope.

RESULTS
The estimated age at capture for field estimates ranged from 0-5 days with a mean age of 2.14 days \((n = 149)\) for field estimates; Johnson incisor estimates ranged from 0-7 days with a mean age of 2.85 days \((n = 222)\); Johnson categorical mean estimates ranged from 1-6 days with a mean age of 3.88 days \((n = 225)\); Johnson categorical median estimates ranged from 0-6 days with a mean age of 3.85 days \((n = 225)\), and the Montgomery estimates ranged from -1 to 46 with a mean of 15.32 \((n = 208)\); (see Fig 2-C.2a-d.).

The Montgomery aging method clearly provided unrealistic estimates of age at capture, while estimates from the Johnson categorical mean and median were very close. Although the incisor age at capture from the Johnson incisor method was closest to the field estimates, we had little confidence in this comparison due to the large percentage of calves that did not have field estimates of age at capture.

For consistency with other published studies (Griffin et al. 2011), we used the mean Johnson categorical estimates for our final age at capture estimates. Also, we retained the field age at capture estimate for calves that were determined to be 0-days-old (i.e. newly born), because of they were estimated with high confidence due to the wetness of the calf just following the parturition event.

DISCUSSION
Aging juvenile ungulates from characteristics recorded at capture involves some level of uncertainty, and will continue to until a large enough dataset is assembled to build an accurate, wild-based prediction equation. We found that the simple scoring system applied to the Johnson (1951) aging categorical aging criteria provided reasonable estimates of age at capture for use in our age-based survival models and reduced subjectivity in estimating age at capture for elk calves. It is unclear why Montgomery (2005) built an aging model that allows for negative estimates of age, as a Poisson or another statistical distribution for discrete count data could have been used avoided this problem. Despite this issue, we commend the author for the effort spent on this prediction problem, and we think it could provide a valuable methodology for further development of elk calf aging models, especially if the original data was made available.
**TABLES**
Table 2-C.1. The lower and upper ranges of outside incisor length (mm) bins used to estimate age at capture for elk calves.

<table>
<thead>
<tr>
<th>Age (in days) at capture</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.00</td>
<td>1.59</td>
</tr>
<tr>
<td>1</td>
<td>1.59</td>
<td>3.18</td>
</tr>
<tr>
<td>2</td>
<td>3.18</td>
<td>4.29</td>
</tr>
<tr>
<td>3</td>
<td>4.29</td>
<td>5.40</td>
</tr>
<tr>
<td>4</td>
<td>5.40</td>
<td>6.35</td>
</tr>
<tr>
<td>5</td>
<td>6.35</td>
<td>7.40</td>
</tr>
<tr>
<td>6</td>
<td>7.40</td>
<td>8.45</td>
</tr>
<tr>
<td>7</td>
<td>8.45</td>
<td>9.50</td>
</tr>
<tr>
<td>8+</td>
<td>9.50</td>
<td>15.9</td>
</tr>
</tbody>
</table>
FIGURES
Figure 2-C.1. Simple linear regressions of outside incisor length on middle incisor length for the left incisor (left) and the right incisor (right).
Figure 2-C.2. Histograms of the estimated incisor age at capture (a), mean age at capture (b), median age at capture (c), and Montgomery age at capture (d).
Appendix 2-D. Modeling wolf resource selection and predation risk for elk in the southern Bitterroot Valley, MT

Mark Hebblewhite, Kelly Proffitt, and Liz Bradley

INTRODUCTION

Ungulates must balance obtaining high quality forage with the risk of being killed by predators. There have been many recent studies of the effects of predation risk on large herbivore spatial ecology, survival, and reproduction (Hebblewhite and Merrill 2008; Middleton et al. 2013; DeCesare et al. 2014). Yet few have examined consequences of spatial variation in predation risk from a juvenile ungulate perspective. Predation is especially important for neonatal juvenile survival during summer, and we may expect that risk-forage trade-offs may be heightened for juveniles and their mothers during summer (Griffin et al. 2011). As part of the Bitterroot elk project, we discovered high mountain lion predation on juvenile elk year round, and a surprisingly lower than expected wolf predation risk. Understanding whether calf exposure to differential predation risk by different predators may help us understand if there is any spatial compensation occurring where by avoiding wolf predation risk, juvenile elk may inadvertently expose themselves to higher predation risk by mountain lions.

Here, our objective was to develop a wolf resource selection function (RFS) model for the southern Bitterroot Valley, MT. The purpose of developing this wolf RSF was to understand wolf predation risk effects on calf survival and adult female resource selection in conjunction with mountain lion resource selection and forage availability. Here, we make the assumption for both wolf and mountain lion that predation risk is proportional to the relative probability of use at a fairly broad landscape scale. This necessarily ignores finer-scale predation risk dynamics such as spatio-temporal avoidance, fine-scale spatial refugia, or patch depression. Nonetheless, previous studies have demonstrated that a significant portion of predation risk is attributable to resource selection by the predator (Hebblewhite and Merrill 2008; Kauffman et al. 2007), bolstering these simplifying assumptions. Previous studies have provided coarse, landscape-level, second-order resource selection models for gray wolves at the scale of Idaho, Montana and Wyoming (Oakleaf et al. 2005), and second-order RSF models for mountain lions at the scale of Montana (Robinson et al. 2015). Here, we develop an intermediate spatial scale wolf RSF model intermediate in scale between the second and third order scale as an index of landscape-scale predation risk. Because predation risk is strongly seasonal, we develop summer and winter RSF models.

METHODS

Wolf Collaring and Telemetry Data

We deployed 4 GPS collars on wolves from August 2008 – 2014; two GPS 7000SW-Argos and two GPS 7000 iridium (LOTEK, Aurora, ON, Canada). GPS iridium collars were programmed to take 1 location every 2 hours, and uploaded data daily to a LOTEK server. GPS 7000-Argos GPS collars were programmed to take 1 location every 3 hours and GPS location data were transmitted to Argos satellites during a 6-hour period once every 10 to 14 days. GPS collars collected an average of 2799 locations/wolf, duration of
358 days/collar. GPS fix success (≥ 2D or greater) was 97.6% for the 2 GPS Iridium collars, and 62% for the two GPS-Argos collars. Overall GPS fix rates were 80.1%.

We captured and radiocollared a total of 34 wolves with VHF collars in 10 wolf packs from 2006 – 2014; on average, we radiocollared 3.7 wolves/pack. Wolves were radiocollared an average of 479 days (range 4 – 1350 days). We obtained a total of 559 VHF locations (95% aerial) from these 34 wolves, with each wolf having 15 locations and each pack an average of 55.9 locations/pack.

**Wolf Resource Selection Function Modeling**

I used the common used-availability RSF design to estimate mixed-effects models (Manly et al. 2002), comparing landscape covariates at wolf GPS locations (used) and random (available) locations with a logistic model. We used a hybrid availability sampling design to estimate landscape-level availability in two seasons, winter (November – April) and summer (May to October). First, for every wolf GPS location, I generated 2 random locations based on random draws from the empirical wolf step-length and turning angle distribution for all 4 GPS collared wolves. This is akin to a matched-case sampling design, but, instead of pairing at the individual wolf ID level, which yields inferences valid only along the movement path of the wolf, I only considered pairing within the individual wolf with a random intercept. This allows availability to be sampled with a movement-based algorithm (always recommended), but yields inferences to the wolf pack territory scale, the appropriate scale of predation risk to an elk in our study area. Availability sampling was conducted with Geospatial Modeling Environment (Beyer et al. 2011) and ArcGIS 10.1 (ESRI Redlands, CA).

We extended the used-available RSF model to include a random intercept for each individual wolf following:

\[
\text{Logit}(y_{ijk}) = \gamma_{00} + \zeta_j^{(\text{wolf})} + X\beta + \epsilon_{ijk}
\]  

(1)

where \(\hat{w}^*(x)\) is the relative probability of use as a function of covariates \(x_n\), \(X\beta\) is the vector of the coefficients \(\hat{\gamma}_1 + \hat{\gamma}_2 + \ldots + \hat{\gamma}_n\) estimated from fixed-effects logistic regression, \(\gamma_{00}\) is the fixed-effect intercept, \(\zeta_j^{(\text{wolf})}\) is the random variation in the intercept at the wolf level, and \(\epsilon_{ijk}\) is unexplained residual variation (Manly et al. 2002). All analyses were conducted in R 3.1.2 (R Core Team 2015), with the package lme4 being used for mixed-effects modeling.

Model selection was conducted by first screening individual covariates for collinearity (using \(r=0.5\)) and confounding by examining coefficient stability. We also examined biologically meaningful interactions (i.e., interaction between distance to motorized roads in open and closed habitats), as well as potential quadratic non-linear forms for continuous covariates. We then used AIC to conduct model selection (forwards and backwards) on the fixed-effects of all covariates. Once the final model structure was determined, we added the random effect for individual wolf, and re-examined model structure. We evaluated models using a combination of internal and external model goodness of fit and cross-validation. We tested GOF using the Hosmer-Lemeshow Goodness of Fit Statistic, as well as the Receiver Operating Curve (ROC) score to gauge predictive performance. We also used k-folds cross validation across 5 subsamples of each seasonal model to evaluate model fit; both across the entire model, and then between each individual wolf to evaluate predictive performance between individuals.
Finally, we conducted two types of external model validation. First, we tested the predictive performance of the top seasonal RSF models using the withheld VHF telemetry data from the same 4 packs and 6 others that were not used to develop the model. Last, we validated the model against the previously developed Oakleaf et al. (2005) model.

**Covariates**

We developed a suite of spatial GIS-based covariates based on previous wolf resource selection studies in the Northern Rockies (Hebblewhite et al. 2005; Hebblewhite and Merrill 2008; Bergman et al. 2009; Kauffman et al. 2007). We developed a suite of covariates that reflected variation in topographic, human, landfeature, landcover and vegetation productivity (summarized in Proffitt et al. 2015). We developed elevation, slope and aspect as topographic covariates. Aspect was transformed to be an index of solar radiation from low (-1, NE aspects) to high (1, SW aspects).

We also developed indices of human activity using distance to all roads (including closed roads), and just to motorized roads. Because previous studies showed distance to forest edges and water were important, we developed a distance to forest cover and distance to water covariate. For all distance to variables, we considered that the effects of these covariates were more likely to attenuate in a non-linear fashion (e.g., Merrill et al. 1999). Therefore, we transformed all distance covariates with an exponential decay of the form $1 - e^{-\alpha d}$ where $d$ is the distance in kilometers and $\alpha$ is the maximum distance at which an effect can be observed (Apps et al. 2004; Whittington et al. 2011). As a result, at very small distances from the feature, the effect of the feature is strong and then decays to 0 at far distances, becoming essentially negligible beyond $\alpha$ km (see supplemental materials). To remain consistent with how beta coefficients for distance covariates are interpreted, we subtracted the transformed covariates from 1 to inverse the covariates such that lower values are associated with short distances (Nielsen et al. 2009). We investigated values for $\alpha$ using AIC; for almost all covariates, effects attenuated greater than 2 km, therefore, we set $\alpha=2$ for all distance covariates. To assist model convergence, all covariates were standardized prior to statistical modeling.

**RESULTS**

The top summer and winter wolf RSF models cross-validated well internally against the data used to develop the model, passed goodness of fit tests, and had adequate measures of predictive performance (Table 2-D.1). In summer, wolf resource selection was function of avoidance of steep slopes, higher elevations, selection for warmer aspects, and areas of close proximity to forest edges and water. The effects of motorized roads on wolf resource selection varied according to whether wolves were in closed cover (forest) or not. In open habitats wolves strongly selected areas far from open motorized roads, and only weakly avoided areas close to motorized roads in forested areas during summer. There was no effect of landcover type during summer, and the strongest covariates, based on standardized coefficients, were avoidance of steep slopes, distance to forests, and distances to motorized roads.

In winter, wolves selected for shallower slopes, but less so than during summer, and did not show any selection for aspects nor elevations. However, landcover was important with wolves showing the strongest selection for forested areas and grasslands, with shrubs and other landcover types subsumed in the intercept. Similar to their patterns of
winter resource selection, wolves showed affinity for proximity to forests, but less so than winter, as well as selection for areas closer to water slightly more than during winter. As far motorized roads, wolves preferred to be far from them, but again, not as much as during summer, and similarly showed an interaction with their response dependent on whether they were in closed or open canopies.

**LITERATURE CITED**


**TABLES**

Table 2-D.1. Wolf Resource Selection Function for the southern Bitterroot Valley, MT, 2008–2014, estimated from GPS collared wolves, with standardized coefficients.

<table>
<thead>
<tr>
<th></th>
<th>Summer Wolf RSF</th>
<th>Winter Wolf RSF</th>
</tr>
</thead>
<tbody>
<tr>
<td>N Obs</td>
<td>11536.4</td>
<td>21605.4</td>
</tr>
<tr>
<td>Deviance</td>
<td>14162.6</td>
<td>27128.7</td>
</tr>
<tr>
<td>LL</td>
<td>-7081.3</td>
<td>-13564.4</td>
</tr>
<tr>
<td>kfolds</td>
<td>0.9636</td>
<td>0.9535</td>
</tr>
<tr>
<td>kfolds-wolfID</td>
<td>0.543</td>
<td>0.518</td>
</tr>
<tr>
<td>External k-folds</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ROC</td>
<td>0.77</td>
<td>0.72</td>
</tr>
<tr>
<td>H-L GOF</td>
<td>0.12</td>
<td>0.31</td>
</tr>
</tbody>
</table>

|                  | Estimate        | Std. Error      | Pr(>|z|) | Estimate        | Std. Error      | Pr(>|z|) |
|------------------|-----------------|-----------------|---------|-----------------|-----------------|---------|
| Intercept        | -0.711          | 0.0321          | < 2e-16 *** | -0.814          | 0.0563          | < 2e-16 *** |
| slopes           | -0.481          | 0.0249          | < 2e-16 *** | -0.265          | 0.0157          | < 2e-16 *** |
| aspect3s         | 0.047           | 0.0205          | 0.023218 * | N/A             |                 |         |
| elevs            | -0.059          | 0.0210          | 0.004776 ** | N/A             |                 |         |
| Forest Cover     | N/A             |                 |         | 0.245           | 0.0824          | 0.0029 ** |
| Grasslands       | N/A             | 0.150           | 0.0630   | 0.0169 *        |                 |         |
| dist_forest2s    | -0.250          | 0.0335          | 7.87e-14 *** | -0.101          | 0.0183          | 3.37e-08 *** |
| dist_mot_road2s  | 0.235           | 0.0275          | < 2e-16 *** | 0.113           | 0.0298          | 0.00015 *** |
| dist_water2s     | -0.072          | 0.0203          | 0.0004 *** | -0.119          | 0.0150          | 1.92e-15 *** |
| dist_mot_roadXforests | -27.043       | 4.0970          | 4.09e-11 *** | -11.075         | 6.2663          | 0.077171 . |
FIGURES
Figure 2-D.1. Southern Bitterroot Valley wolf GPS data used to develop seasonal resource selection functions from 2008–2014. GPS data by pack and VHF telemetry location data used to validate models are shown.
Figure 2-D.2. Summer wolf resource selection as a function of continuous landcover, anthropogenic and topographic covariates in the southern Bitterroot Valley, MT, 2008–2014. Distance to variables were transformed to be between 0 (close) and 1 (far), and for distance to motorized roads, the significant interaction between whether the wolf was in closed forest cover (blue) or not (red) reveals stronger effects of motorized roads on wolves in open cover.
Figure 2-D.3. Winter wolf resource selection as a function of continuous covariates in the southern Bitterroot Valley, MT, 2008–2014. Distance to variables were transformed to be between 0 (close) and 1 (far), and for distance to motorized roads, the significant interaction between whether the wolf was in closed forest cover (blue) or not (red) reveals stronger effects of motorized roads on wolves in open cover, but not as strong as in summer.
Figure 2-D.4. Wolf resource selection represented as a relative probability during summer and winter in the southern Bitterroot Valley, MT, 2008–2014. The relative probability in 10 ranked categories ranging from low (dark green) to high (red) are shown.
Appendix 2-E. R code for cumulative incidence functions

# Heisey and Patterson (2006) cumulative incidence function (CIF)
# estimator with log-log confidence intervals
# load R base package survival
library(survival)

# Create function "cause.survival"
"cause.survival" = function(table, p)
{
    assign("p", p)
    # Create tables to hold the results of Generalized Kaplan Meier survival estimates for all events and for cause specific event
temp.all <- summary(survfit(Surv(enter, exit, event) ~ 1, conf.type="log-log", data = table))
temp.s <- summary(survfit(Surv(enter, exit, cause == p) ~ 1, conf.type="log-log", data = table))

    # Combine the two tables so survival of all events can be combined with those of the cause-specific events
s.df <- data.frame(time = temp.s$time, n.event = temp.s$n.event, n.risk = temp.s$n.risk, survival = temp.s$surv)
all.df <- data.frame(time = temp.all$time, n.event = temp.all$n.event, n.risk = temp.all$n.risk, survival = temp.all$surv)
all.s.df <- merge(all.df, s.df, by.x = "time", by.y = "time", all.x = T, suffixes = c(".all", ".s"))
    assign("n", all.s.df)
    x <- length(n[,1])

    # Create temporary placeholders for the calculation of the mortality rate and the cause-specific cumulative incidence function.
tmp.string <- numeric(x)
tmp.string2 <- numeric(x)
t <- 1

    # Cycle through the records of the table, including all events to calculate mortality rate and CIF
while(t <= x) {
    tmp.string[1] <- n$n.event.s[1]/n$n.risk.s[1]
    if (t == 1) tmp.string[t] <- NA else tmp.string[t] <- (n$survival.all[t-1] * n$n.event.s[t])/(n$n.risk.s[t])
    if(is.na(tmp.string[t])) tmp.string2[t] <- NA else tmp.string2[t] <- sum(tmp.string[1:t], na.rm = T)
    t = t + 1
}
MORT <- data.frame(mort.rate = tmp.string)
CIF2 <- data.frame(CIF = tmp.string2)
CIF.s.all <- chind(all.s.df, MORT, CIF2)

# Calculate the variance, standard error, and the log-log confidence Intervals around CIF
SE <- numeric(x)
totvar.t <- numeric(x)

    # Reset all temporary variables
    t <- 1
    j <- 1
    Ij <- 0
cumvar.p1 <- 0
cumvar.p2 <- 0
cumvar.p3 <- 0

    # Loop for the total number of records
while (t <= x) {
    It <- CIF.s.all$CIF[t]
    if(is.na(It)) {
        CIF.s.all$cumvar[t] <- "NA"
CIF.s.all$StdErr[t] <- "NA"
CIF.s.all$CI.l[t] <- "NA"
CIF.s.all$CI.u[t] <- "NA"
t = t + 1

else
{
  while (j < t)
  {
    if(is.na(CIF.s.all$CIF[j]))
      Ij <- Ij
    else
      Ij <- CIF.s.all$CIF[j]
    cumvar.p1 <- cumvar.p1 + (It - Ij)^2 *
      (CIF.s.all$n.event.all[j]/(CIF.s.all$n.risk.all[j] * (CIF.s.all$n.risk.all[j] -
        CIF.s.all$n.event.all[j])))
    if(!is.na(CIF.s.all$CIF[j]))
      {
        if(j == 1)
          Sj3 <- 1
        else
          Sj3 <- CIF.s.all$survival.all[j-1]
        Ijc <- CIF.s.all$CIF[j]
        cumvar.p3 <- cumvar.p3 + (It - Ijc)*(Sj3)*(CIF.s.all$n.event.all[j] /
          (CIF.s.all$n.risk.all[j])^2)
      }
    j <- j + 1
  }
  if (t == 1)
    Sj2 <- 1
  else
    Sj2 <- CIF.s.all$survival.all[t-1]
  cumvar.p2 <- (Sj2)^2 * (((CIF.s.all$n.event.all[t])*(CIF.s.all$n.risk.all[t] -
        CIF.s.all$n.event.all[t]))/(CIF.s.all$n.risk.all[t])^3) + cumvar.p2
#Total all three components of the variance equation to get the #final variance,
#generate std. err and confidence intervals
#Assign all results to the output table
totvar.t[t] <- cumvar.p1 + cumvar.p2 - (2 * cumvar.p3)
CIF.s.all$cumvar[t] <- totvar.t[t]
SE[t] <- sqrt(totvar.t[t])
CIF.s.all$StdErr[t] <- SE[t]
#Calculate confidence intervals on log-log scale
CIF.s.all$CI.l[t] <- CIF.s.all$CIF[t]^((exp((-1.96 *
    SE[t])/(CIF.s.all$CIF[t]*log(CIF.s.all$CIF[t]))))
CIF.s.all$CI.u[t] <- CIF.s.all$CIF[t]^((exp((1.96 *
    SE[t])/(CIF.s.all$CIF[t]*log(CIF.s.all$CIF[t]))))
t = t + 1
j <- 1
}
cumvar.p1 <- 0
cumvar.p3 <- 0
Ij <- 0
It <- 0

} #Variance calculations end here
return(CIF.s.all)

} #End of CIF estimation

########################################################

83
CHAPTER 3. ASSESSING THE IMPORTANCE OF DEMOGRAPHIC PARAMETERS FOR POPULATION DYNAMICS USING BAYESIAN INTEGRATED POPULATION MODELING

KEYWORDS: Bayesian state-space models, *Cervus elaphus*, elk, life-stage simulation analysis, pregnancy, recruitment, survival, ungulate, vital rates

INTRODUCTION

To efficiently respond to changing conditions that may alter population dynamics such as carnivore recolonization (Pletscher et al. 1997; Riley and Malecki 2001; Kendall et al. 2009), climate change (Gaillard et al. 2013; Zimova et al. 2014), or habitat degradation (DeCesare et al. 2012), managers must be able to identify the demographic processes (e.g., juvenile vs. adult survival, fecundity) that have the greatest influence on population growth rate ($\lambda$) and assess the likelihood of management actions being successful (Mills 2013). This is irrespective of whether species are endangered and declining, invasive, irruptive or otherwise considered a pest, or in the case of harvested species where harvest can have great economic value (Mills 2013). Matrix modeling frameworks are fundamental to assessing population dynamics (Caswell 2001), and make use of analytical sensitivities and simulation methods to target key vital rates and prioritize management actions (Heppell et al. 1994; Buenau and Gerber 2004). These methods have proven to be invaluable for guiding conservation and wildlife management efforts to recover declining species such as Loggerhead turtles (*Caretta caretta*) (Crouse et al. 1987; Crowder et al. 1994) and endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) (Johnson et al. 2010).

The Loggerhead turtle is a classic example of the non-intuitive inferences that can arise from sensitivity analyses, where, in this particular case, the public and managers were convinced that
increasing survival of eggs and hatchlings would reverse the declining trend in turtle populations (Mills 2013). However, a sensitivity analysis by Crouse et al. (1987) revealed that the key to increasing $\lambda$ in turtles was protecting large juveniles, which, incidentally, were experiencing high mortality rates from becoming entangled in shrimp nets.

A primary tool for assessing population dynamics using matrix models has become life-stage simulations analysis (LSA; Wisdom and Mills 1997; Wisdom et al. 2000), which combines both analytical and simulation techniques to determine the importance of vital rates in affecting $\lambda$. LSA approaches are advantageous over deterministic matrix-population model approaches because they explicitly incorporate the variability in each vital rate, instead of relying on theoretical sensitivity from a deterministic matrix model (Wisdom et al. 2000). Indeed, often the vital rate that has the most theoretical sensitivity also displays the least variation in the wild, which evolutionary biologists have recognized as a form of evolutionary canalization (Gaillard and Yoccoz 2003). LSA repeatedly simulates population growth rates using random Monte Carlo draws of vital rates from sampling distributions (e.g., beta distribution) that are based on the mean and process variances of each vital rate (Mills and Lindberg 2002). By regressing $\lambda$ on each vital rate, the analysis provides an estimate of the amount of variation in $\lambda$ explained by each vital rate ($R^2$) and the rate of change in $\lambda$ as a function of each vital rate (i.e., the slope or partial derivative). An important result of LSA is that vital rates with high process variance will have a relatively large influence on the population trajectory despite having lower sensitivity, because high variation in a vital rate will translate to greater variation in $\lambda$, dampening population growth over time (Mills et al. 1999; Wisdom et al. 2000; Coulson et al. 2005).

Recently, the use of integrated population models (IPMs), also known as hierarchical or state-space models, have become more common in assessing population dynamics (King et al. 2010).
2008; Johnson et al. 2010; Abadi et al. 2010a) because of their ability to overcome many of the limitations imposed by traditional demographic analyses. In contrast to traditional methods, IPMs estimate demographic parameters in a single, comprehensive model to make joint inference about population processes (Schaub and Abadi 2011). The benefits to this approach are that parameter estimates become more precise, variance-covariance relationships are accounted for among demographic parameters, and that latent or unobserved parameters are estimable in some cases (Besbeas et al. 2002; Tavecchia et al. 2009). The hierarchical nature of IPM’s also allow separation of the sampling and process mechanisms underlying population dynamics (Schaub and Abadi 2011). While methods exist to maximize joint likelihoods using frequentist methods (Besbeas et al. 2002), Bayesian IPMs are more flexible because they can interpolate parameter estimates in years with missing data, homogenize error structures across different data types, and simultaneously model the effect of covariates on demographic parameters (Brooks et al. 2004; Schaub and Abadi 2011; Hobbs and Hooten 2015). For example, Abadi et al. (2010b) used Bayesian IPMs to analyze population dynamics for little owls (Athene noctua), and found that by having the flexibility to model immigration as a parameter rather than a derived quantity, they could estimate the effect of vole abundance on immigration rate. Also, from a practical standpoint, Bayesian approaches to IPMs are easier to implement than maximum likelihood approaches, and a number of tools are now available that provide broad accessibility for practicing ecologists (Kéry and Schaub 2012; Hobbs and Hooten 2015).

Given the flexibility of this powerful statistical method, Bayesian IPMs are useful in applied conservation settings (Schaub et al. 2007; King et al. 2008; Ballie et al. 2009) where data is often limited and is usually expensive to collect. For example, Lukacs et al. (2009) demonstrated the ability of IPMs to inform harvest management of mule deer (Odocoileus hemionus) in Colorado,
USA, by modeling correlations among fawn survival rates across deer management units to predict fawn survival in units without concurrent estimates. Also, Johnson et al. (2010) applied Bayesian state-space models to sparse data from different sources for populations of endangered Sierra Nevada bighorn sheep. They found that the improved precision on estimates of λ from their IPM provided a clear signal that one population was declining, whereas estimates of λ from count data alone was too imprecise to determine if the population was in decline. IPMs may be particularly useful in carnivore-ungulate management where managers must decide how to best manipulate populations to achieve conservation objectives, which are often contentious issues in the public arena (Treves et al. 2013).

Despite the advances of Bayesian IPM methods, few have applied such models to determine the most important vital rates driving population dynamics (e.g., variation in λ) from a sensitivity perspective. We used a Bayesian IPM approach to conduct a Bayesian LSA to determine the drivers of population dynamics for elk (Cervus elaphus) in two populations in the southern Bitterroot Valley, MT, USA. Recent declines in elk recruitment across the West (Lukacs et al. in review) and in the study area (Chapter 1) coincident with carnivore recolonization has prompted questions about whether the drivers of ungulate population dynamics might differ under high predation. Our objectives were to i) estimate demographic parameters for elk in two populations using an IPM approach, ii) compare demographic parameter estimates across populations and data types, iii) conduct a Bayesian LSA analysis to determine the relative importance of vital rates for λ in the two populations, and iv) illustrate the consequences of different management scenarios by projecting population size into the future under different combinations of harvest and vital harvest (see Appendix 3-E).
Following the prevailing paradigm of large herbivore population ecology, we hypothesized that calf survival would be most important vital rate in affecting $\lambda$ (Gaillard et al. 2000). However, in contrast to Raithel et al. (2007) who found that neonatal elk calf survival was the most important vital rate in affecting $\lambda$, we predicted that overwinter calf survival would be more important than neonatal survival for $\lambda$ if overwinter survival experienced greater interannual variability (see Chapter 2; and also Unsworth 1999; Hurley et al. 2011). In multiple carnivore systems, neonatal ungulates experience high predation rates that generally overwhelm nutritional or climate effects (Linnell et al. 1995; Raithel 2005). As a result, annual variation in juvenile survival may be driven more by summer-autumn forage (Portier et al. 1998; Cook et al. 2004; Hurley et al. 2014) and winter snow accumulation that affect juvenile survival and vulnerability to predation during winter (Smith et al. 2004; Garrott et al. 2008). Thus, variation in neonate survival during summer might be lower than during winter in ungulate populations experiencing high predation. Alternatively, if either of our populations was declining rapidly, we might predict that in contrast to the prevailing paradigm of calf survival being the most important, adult female survival might be the primary driver of population dynamics (Johnson et al. 2010; Hebblewhite et al. 2007).

METHODS

Elk Populations

We analyzed demographic data for two harvested elk populations in the East Fork (EF) and West Fork (WF) drainages of the Bitterroot River in west-central Montana, USA. We assumed independent dynamics between the EF and WF elk because little to no adult female movement occurs between populations (K. Proffitt, Montana Fish, Wildlife, and Parks [MFWP], unpublished data). After a steady 35-year increase in elk trend counts, elk populations in the
southern Bitterroot Valley reached a peak at around 5,500 elk in 2005–2006. In response to increasing elk populations, managers applied a more liberal elk harvest to bring elk populations towards management objective. However, elk population trend counts and calf recruitment continued to decline after increasing harvest, and by 2009, trend counts in the valley had declined by over 25% and recruitment reached a historic low of 14 calves/100 adult females, with especially low recruitment in the WF population at around 8 calves/100 adult females (see Chapter 1). Most of the harvest focused on adult males in our study, and adult female harvests averaged less than 4% and 1% per year in the EF and WF respectively (i.e., mean adult female harvest was 4.6 elk in the WF and 92.2 elk in the EF during 2010–2014) of the estimated adult female population. We discuss the integration of harvest into the population model below in Data Sources.

Data Sources

Aerial count data ($y_c$). — Elk count data was collected annually by MFWP from fixed-wing aircraft (typically a Piper Super Cub) from 1965 to present. We used a subset of this data from that overlapped with years that survival and pregnancy data were collected (Table 3-1). The aerial counts were conducted from late March to early May of each year before elk migrated to summer range (pre-birth pulse). The calving period for Rocky Mountain elk generally occurs around late May to early June of each year with adult females rarely giving birth to more than one offspring (Johnson 1951, Flook 1970). 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 ($\sim$0.9 years old during surveys; $C_y$) and adult females ($> 1.9$ years; $C_{af}$). We could not separate observation error from variation in count data due to immigration and emigration without correcting for
sightability (e.g., Samuel et al. 1987), and thus, we were unable to estimate immigration rate as a latent parameter from combining our count and vital rate data (Abadi et al. 2010b).

*Survival data* ($y_s$). — We captured and radio-marked elk calves and adult females to estimate survival and reproduction. To maintain an adequate sample of radio-marked calves, we captured them just after birth as neonates and as 6-month-olds during winter (see Chapter 2 for details). Adult female elk were captured and radio-collared with Global Positioning System (GPS) collars during the late-fall (November-December) and late-winter (February). We captured and handled all elk in compliance with requirements of the Institutional Animal Care and Use Committee for the University of Montana-Missoula (Protocol 027-11MHWB-042611).

We monitored all radio signals by ground or aircraft daily from the beginning of calf capture (late-May) 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 all signals 2–3 times per week. Besides estimating survival, we also recorded cause-specific mortality data for elk (Chapter 2), which allowed us to estimate mortality due to human harvest. None of our radio-marked adult females and only one calf elk died of human harvest during the monitoring period (2010–2014), thus losses due to human harvest were captured in our survival estimate given that our sample of radio-marked elk were available for harvest in the study area.

*Pregnancy data* ($y_p$). — We collected a blood sample during capture of adult female elk in the EF and WF herds to estimate pregnancy status based on pregnancy-specific protein-B levels (Noyes et al. 1997).

**Integrated Population Modeling Approach**
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 (or state) process for a given population (see Schaub and Abadi 2011). The observation models are used to estimate demographic parameters that appear in the process model, which is the set of difference equations that describe annual change in population abundance with changes in age or stage-specific vital rates (Caswell 2001). The integrated model combines information about the population from multiple sources including count data collected annually from aerial surveys and vital rate data collected from radio-telemetered individuals (Fig. 3-1).

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 (Chapter 2) defining the start of the annual intervals. Because only yearling and adult female elk were identified in pre-birth trend counts, the biological process model can be represented by a $2 \times 2$ Lefkovitch matrix (Caswell 2001) that describes the expected number of elk in each stage at time $t+1$ as a function of the matrix of vital rates and the vector of stage-specific abundances at time $t$:

$$
\begin{bmatrix}
N_y \\
N_{af}
\end{bmatrix}_{t+1} = \begin{bmatrix}
0 & P_{af} \phi_c \\
R \phi_y & \phi_{af}
\end{bmatrix}
\begin{bmatrix}
N_y \\
N_{af}
\end{bmatrix}_t
$$

(1)

The vital rates that determine the rate of change in our population model are annual calf survival ($\phi_c$), yearling survival ($\phi_y$), adult female survival ($\phi_{af}$) and pregnancy ($P_{af}$), and the proportion of yearlings that are female ($R$), while $N_y$ and $N_{af}$ are the number of yearlings (of both sexes) and adult females, respectively. Adult female fecundity (the number of calves that recruit into the population per adult female) is a product of pregnancy and calf survival rates ($P_{af} \phi_c$); we set yearling fecundity to zero since reproduction does not occur in elk at this age (~0.9 years old). Because yearling counts included both sexes and adult counts were female-only, we adjusted the
contribution of yearlings to the number of adult females at time \( t+1 \) by multiplying by the proportion of yearlings that were female \((R, \text{see below})\). The expected population sizes in year \( t+1 \) from the matrix projections in Equation 1 are a deterministic function of stage-specific vital rates and population sizes in year \( t \), but demographic stochasticity is included in the model by defining the appropriate statistical distributions that generate biological processes (Schaub and Abadi 2011).

**Biological process model.** — We used a Poisson distribution to model the number of yearlings in year \( t+1 \) as a function of calf survival \((\Phi_{c,t})\), pregnancy rate of adult females \((P_{af,t})\) from \( t \) to \( t+1 \), and the number of adult female elk in year \( t \):

\[
N_{y,t+1} \sim \text{Pois}(\Phi_{c,t}P_{af,t}N_{af,t})
\]

We also used a Poisson distribution to model the number of adult female elk in year \( t+1 \) as the sum of the contributions from 1) the yearling survival rate from \( t \) to \( t+1 \) \((\Phi_{y,t})\), mean proportion of yearlings that were female \((R)\), and the number of yearlings in year \( t \), and 2) the adult female survival rate from \( t \) to \( t+1 \) \((\Phi_{af,t})\) and the number of adult female elk in year \( t \):

\[
N_{af,t+1} \sim \text{Pois}(R\Phi_{y,t}N_{y,t} + \Phi_{af,t}N_{af,t})
\]

**Aerial count likelihood functions.** — Because aerial counts were not adjusted for sightability, we assumed that counts of yearlings \((C_y)\) and adult female \((C_{af})\) elk were log-normally distributed as a function of the true number of yearlings \((N_y)\) and adult females \((N_{af})\) in year \( t \):

\[
C_{y,t} \sim \text{log-Norm}(N_{y,t}, \sigma_{cy}^2)
\]

\[
C_{af,t} \sim \text{log-Norm}(N_{af,t}, \sigma_{caf}^2)
\]

This assumed that counts are more often an underestimate of the true mean (i.e., the residual error is right-skewed), but also allowed for the eventual occurrence of double counting due to elk moving between survey days.
Survival likelihood functions for marked animals. — In addition to the indirect information about adult female survival from count data, we used telemetry data from our sample of collared adult female elk to provide direct estimates of survival. We modeled known-fate telemetry data for adult females with a binomial distribution (Schaub and Abadi 2011) to estimate the survival probability of adult females \((\Phi_{af})\) as a function of the number of adult females that survived \((AF_{surv})\) and the total number of adult females collared during the monitoring period \((AF_{collars})\) in year \(t\):

\[
AF_{surv,t} \sim \text{Bin}(\Phi_{af,t}, AF_{collars,t})
\]  

(6)

To estimate the survival of calf elk from birth to the yearling age class, we modeled the failure times for elk calves \((f_i)\) from known-fate telemetry data with a parametric Weibull distribution (Hosmer et al. 2008, Griffin et al. 2011). We adjusted elk calf survival risk sets to account for left-truncation and right-censoring using a staggered-entry design (Pollock et al. 1989). The Weibull distribution is often parameterized as a proportional hazards model that allows the instantaneous hazard of mortality \((h_t)\) to vary over time by including a shape parameter \((p)\). When \(p < 1\) the hazard of mortality decreases over time, and when \(p > 1\) the hazard of mortality increases over time. Although the Weibull model can be parameterized in terms of proportional hazards or accelerated failure time (Hosmer et al. 2008), we parameterized the model in terms of survival probability with the following equation:

\[
\Phi_t = \exp(-ht^p)
\]  

(7)

By solving Equation 7 for the hazard and setting \(t\) to 365 days, we used the Weibull distribution to derive a discrete-time estimate of annual elk calf survival:

\[
f_i \sim \text{Weib}(p, h)
\]  

(8)

\[
h = -\ln(\Phi_{c,t})/365^p
\]  

(9)
From this parameterization of mean calf survival ($\Phi_c$), we estimated an offset by including an indicator variable for study area through a logit link function:

$$\text{logit}(\Phi_c) = \beta_0 + \beta_1(Area_{t,i})$$  \hspace{1cm} (10)

We used this study area factor to combine the calf survival data into a single parametric model, while continuing to model other parameters separately for the two populations. This formulation increased computational efficiency and convergence by estimating a single shape parameter ($p$) in the Weibull survival model.

In a separate IPM, we estimated mean sex-specific calf survival rates for both study areas by including an additional indicator variable for sex in the logit link:

$$\text{logit}(\Phi_c) = \beta_0 + \beta_1(Area_{t,i}) + \beta_2(Sex_{t,i})$$  \hspace{1cm} (11)

Then, after back-transforming logit estimates to mean study area and sex-specific survival probabilities, we derived the mean proportion of yearlings that were female ($R$) for each population as a function of the mean female calf survival rate ($\Phi_{cf}$) divided by the sum of the mean female and male calf survival ($\Phi_{cm}$) rates:

$$R = \Phi_{cf}/(\Phi_{cf} + \Phi_{cm})$$  \hspace{1cm} (12)

Thus, if male and female calf survival rates were equal ($R = 0.5/[0.5 + 0.5]$), the count of yearlings at $t + 1$ would consist of 50% females assuming an equal sex ratio at birth, which is reasonable based on the observed sex ratio being near parity for our sample of radio-marked calves (see Chapter 2 for details).

The change in consecutive counts of yearling elk between years provided an estimate of yearling survival, but yearling survival was biased low in the model using counts without direct survival data available. Therefore, we used a Normal distribution ($\mu, \sigma^2$) truncated at 0 and 1 to
model an informative prior for yearling survival based on the mean (0.883) and process variance (0.004) provided for yearling elk in Raithel et al. (2007):

\[ \Phi_y \sim \text{Norm}(0.883, 0.004)T(0, 1) \]  

(13)

Because an informative prior informed yearling survival, we do not report results of yearling sensitivity.

We used a binomial distribution to estimate pregnancy rates for adult females (\( P_{af} \)) as a function of the number of adult females that were pregnant (\( AF_{preg} \)) and the total number sampled during the monitoring period (\( AF_{sampled} \)) in year \( t \):

\[ AF_{preg,t} \sim \text{Bin}(P_{af,t}, AF_{sampled,t}) \]  

(14)

Although the data sources for adult female survival and pregnancy were not completely independent (i.e., some adult females were sampled in both data sets), we found no evidence that pregnancy status affected adult female survival probability (unpublished data), but others reported differences in survival between adult female ungulates (Moose, \( Alces alces \)) with and without calves (Testa 2004). Therefore, we assumed independence among data sets (Besbeas et al. 2002, Brooks et al. 2004) and defined the component likelihoods for each data type as:

Aerial count: \( L(y_C \mid N_y, N_{af}, \Phi_y, \Phi_{af}) \)  

(15)

Survival: \( L(y_S \mid \Phi_c, \Phi_{af}, p) \)  

(16)

Pregnancy: \( L(y_P \mid P_{af}) \)  

(17)

We then combined independent likelihoods from our different data types to form a joint likelihood for our integrated model:

\[ L(y_C, y_S, y_P \mid N_y, N_{af}, \Phi_c, \Phi_y, \Phi_{af}, P_{af}, p) \]  

(18)

We calculated the annual (\( \lambda_t \)) and geometric mean (\( \lambda_G \)) population growth rates as derived quantities in our model using the following expressions:
\[ \lambda_t = \frac{(N_{y,t+1} + N_{af,t+1})}{(N_{y,t} + N_{af,t})} \]  
\[ \lambda_G = \prod_t \lambda_t^{1/t} \]

**Bayesian Life-Stage Simulation Analysis**

We developed a specific set of IPMs to estimate analytical elasticities (or proportional sensitivities) for each vital rate and conducted LSA (Wisdom and Mills 1997; Wisdom et al. 2000) using a Bayesian approach. We report results here from vital rate-only models for both populations to estimate mean vital rates over the study period, and then, we used these vital rate estimates to simultaneously derive asymptotic population growth rates (\(\lambda_{asy}\)) and component elasticities in the models. We also report confirmatory results of the comparison of sensitivity from integrating both vital rates and counts in Appendix 3-C. The Bayesian approach is similar to traditional LSA where vital rates are sampled from predefined statistical distributions, but instead of retaining every sampled parameter value, the method uses Markov-chain Monte Carlo (MCMC) simulation to retain the most likely parameter values based on the data and any prior information. We thinned MCMC chains to retain 1000 samples of each vital rate and \(\lambda_{asy}\) to include in simple linear regressions as the explanatory and response variables, respectively. The intercept (\(\beta_0\)) in these regressions provided an estimate of \(\lambda\) when the vital rate was at zero, and the slope (\(\beta_1\)) predicted the increase in \(\lambda\) per unit increase in each vital rate. Also, the coefficient of determination (\(R^2\)) was used to estimate the proportion of the variation in \(\lambda\) explained by each vital rate (Wisdom and Mills 1997, Wisdom et al. 2000). These metrics allowed us to compare \(\lambda\) within and across the EF and WF elk populations. For comparison, we also estimated sensitivities by combining vital and count data and by using estimates of process variance based on the values for elk given in Raithel et al. (2007).
Because we monitored elk calf survival on an annual basis, we were able to decompose calf survival into summer and winter components to compare their importance for population dynamics. We performed this by stratifying our annual calf survival model into two separate seasonal observation models, but continued to include both EF and WF calves in the same models with an indicator variable to estimate a study area offset (see Equation 10 above). However, because the winter mortality hazard for calves was relatively constant (Chapter 2), we used an exponential distribution (the equivalent of a Weibull distribution with $p = 1$) to describe winter calf survival and retained the Weibull distribution to describe summer calf survival. After back-transforming logit estimates to seasonal, study area-specific survival probabilities, we derived annual elk calf survival rates by multiplying summer and winter survival rates for each population (JAGS code provided in Appendix 3-A for IPM only and Appendix 3-B for IPM with integrated Bayesian LSA code). This allowed us to simultaneously evaluate the importance of seasonal and annual elk calf survival for population dynamics within the same model.

**Model Implementation**

We estimated marginal distributions for the posterior likelihoods of model parameters using JAGS 3.4.0 (Plummer 2013), which we conducted in program R using the R2jags package (Yu-Sung Su and Yajima 2015). JAGS models are coded in the BUGS language, which provides an accessible interface for ecologists to develop and analyze Bayesian models (Kéry and Schaub 2012). We assessed model convergence by visually examining trace plots and posterior distributions for each parameter, and initiated at least two MCMC chains to assess convergence with the Brooks-Gelman-Rubin statistic (Brooks and Gelman 1998). We increased the burn-in period as necessary for models to converge on stable distributions before retaining samples, and thinned samples to reduce autocorrelation in the chains (Abadi et al. 2010). We achieved
convergence in all models by running 200,000 iterations in 2 parallel chains with the first 150,000 as burn-in, and retained every 10th sample for a total of 10,000 samples.

We specified a prior distribution for parameters estimated in model, and besides the informative prior used for yearling survival, we used vague (or diffuse) priors for all parameters. We initialized population sizes using the counts of each stage class in the first year as the mean of a Normal distribution truncated at the lower bound at 0 with a vague precision (1/σ²) of 10⁻⁴ (Brooks et al. 2004). We also used normal priors with mean 0 and vague precision (10⁻⁴) for parameters estimated on the logit scale. We used uniform distributions spanning from 0 to 1 for parameters estimated on the probability scale. We used a gamma distribution as a prior on the precision of aerial counts with the shape and scale parameters set to 0.001 (Brooks et al. 2004). We specified random initial starting values for all parameters in the model, and used aerial counts as initial starting values for population sizes of yearlings and adult females (Kéry and Schaub 2012). We report 95% credible intervals (CRI) for all parameters and derived quantities.

RESULTS

Parameter Estimates

The integrated model with counts and vital rate data estimated that the geometric mean growth rate (λ_G) for the EF population was about 3% (λ_G = 1.06, 95% CRI = 1.02, 1.10) higher than the WF population (λ_G = 1.03, 95% CRI = 0.99, 1.07). The EF population was increasing during all study years except 2010–11 when the growth rate was near stable at 0.99 (95% CRI = 0.88, 1.10). The WF population was stable during 2010–11 (1.00, 95% CRI = 0.87, 1.11), declined in 2011–12 (0.95, 95% CRI = 0.87, 1.05), and increased during the latter half of the study (Table 2). Total population size estimates for the EF ranged from a low of 3,299 (95% CRI = 2,942–3,674) in 2011–12 to a high of 4,156 (95% CRI = 3,597–4,922) in 2013–14. Total population
size estimates for the WF ranged from a low of 530 (95% CRI = 490–585) in 2012–13 to a high of 635 (95% CRI = 574–702) in 2013–14 (see Fig. 3-2). Estimates of \( \lambda_G \) from count data-only models were near identical to estimates from vital rate-only models in the WF (\( \lambda_G = 1.02, \) 95% CRI = 0.92, 1.14), and both estimates of \( \lambda_G \) were similar but much less precise than estimates from the integrated model (Table 3-2). In contrast to the WF, estimates of \( \lambda_G \) were about 9% higher in the EF elk population based only on vital rate data (\( \lambda_G = 1.11, \) 95% CRI = 1.03, 1.21) compared to estimates from count data only (\( \lambda_G = 1.02, \) 95% CRI = 0.95, 1.08), which may have resulted from underestimating fecundity (both calf survival and pregnancy) or adult female survival from aerial count surveys in the EF.

Consistent with estimates of mean growth rates, we observed closer correspondence between vital rates estimated with only vital rate (survival and pregnancy) data and those estimated from count data in the WF, and more pronounced differences in calf survival and pregnancy estimates in the EF (Table 3-2). Adult female survival rates were estimated much more precisely from count data compared to other vital rates, but tended to be lower in models with that included count data (Table 3-2, Fig. 3-3). Compared to integrated models, estimates from vital rate data were much more similar than estimates from count data-only models (Table 3-2, Fig. 3-3), which suggested that vital rate data had a larger effect on parameter estimates than count data in the integrated models. The discrepancy in calf survival and pregnancy rates among elk populations may reflect the greater variability in counts of yearlings and adult females in the EF (\( \sigma_{Cy} = 0.18, \sigma_{caf} = 0.12 \)) compared to the WF (\( \sigma_{Cy} = 0.14, \sigma_{caf} = 0.07 \)), but within populations, the discrepancy may result from different levels of uncertainty in estimating these vital rates. For instance, only adult female survival had to be estimated to determine the number of adult females in year \( t+1 \) due to yearling survival being modeled with an informative prior, while both calf
survival and pregnancy had to be estimated to determine the number of yearlings in year $t+1$.

Regardless of the potential reasons for differences between specific vital rates from the different models (Table 3-2, Fig. 3-3), models that combined information from vital rates and counts almost always yielded more precise estimates of vital rates, population growth, and population size (Table 2).

Although the degree of concurrence among vital rate and count data depended on the population, we found disagreement in both populations between age ratios (e.g., the ratio of 9-month old ‘yearlings’/100 adult females as a measure of recruitment) derived from estimates that included count data (raw counts, count-only, and integrated models) and those derived only from vital rates. For example, the age ratios from vital rate data estimated 20 yearlings/100 adult females in the WF in 2013, while models using only count data estimated 37 yearling/100 adult females (Fig. 3-3). Similarly, age ratios from vital rate data estimated 46 yearlings/100 adult females in the EF in 2014, while models using count data only estimated 34 yearlings:100 adult females. This difference in recruitment estimates among data sources in the EF translated to large differences in $\lambda$, with estimates from count data indicating a 4% decline during 2013–14 ($\lambda = 0.96, 95\% \text{ CRI} = 0.73, 1.19$), while vital rate data suggested a 20% increase during the same year ($\lambda = 1.20, 95\% \text{ CRI} = 1.04, 1.35$). The estimate of $\lambda$ from the integrated model was more intermediate ($\lambda = 1.08, 95\% \text{ CRI} = 0.98, 1.22$) compared to other models, with differences between the integrated and count data-only models in the EF resulting from 12% higher adult female survival rates on average in the integrated model compared to the count-only model (Table 3-2).

**Sensitivity Analysis**
Bayesian LSA revealed which vital rates had the most impact on $\lambda$ of our two populations. In the EF population, the most important vital rates driving population growth based on the slopes of the regressions of asymptotic population growth rate ($\lambda_{asy}$) on each vital rate and its coefficient of determination ($R^2$), were first adult female survival ($\beta_1 = 0.87$, SE = 0.03, $R^2 = 0.43$, Table 3-3, Fig. 3-4), followed by calf survival ($\beta_1 = 0.35$, SE = 0.01, $R^2 = 0.38$), then pregnancy ($\beta_1 = 0.17$, SE = 0.02, $R^2 = 0.06$). Similarly, in the WF, adult female survival ($\beta_1 = 0.89$, SE = 0.03, $R^2 = 0.56$) was the most important, followed by calf survival ($\beta_1 = 0.33$, SE = 0.02, $R^2 = 0.33$) and pregnancy ($\beta_1 = 0.12$, SE = 0.02, $R^2 = 0.06$). While the slope and coefficient estimates supported the same rankings across populations, the relative magnitude of the differences in adult female and calf survival varied between populations. In the EF, adult female survival was only about 5% more important than calf survival, whereas in the WF, adult female survival explained about 23% more of the variance in $\lambda_{asy}$ compared to calf survival, highlighting an important population difference. Lastly, there were no qualitative differences in the sensitivity of population growth rate to changes in vital rates from either the vital-rate only or integrated sensitivity models (Table 3, see Appendix 3-C), but as expected, calf survival became more important than adult female survival when we used estimates of process variance from Raithel et al. (2007) for each vital rate (see Appendix 3-D).

After decomposing annual calf survival into seasonal components, our analysis also revealed important differences in the relative importance of summer and winter calf survival on $\lambda$. In the EF, summer and winter calf survival contributed more or less similarly to $\lambda$ (summer: $\beta_1 = 0.26$, SE = 0.02, $R^2 = 0.20$; winter: $\beta_1 = 0.22$, SE = 0.01, $R^2 = 0.19$; Table 3-3, Fig. 3-5), but in the WF, summer calf survival was more than twice as important (summer: $\beta_1 = 0.23$, SE = 0.01, $R^2 = 0.23$; winter: $\beta_1 = 0.15$, SE = 0.01, $R^2 = 0.11$) as winter calf survival. Our comparison of
deterministic elasticity confirms results of previous studies showing that deterministic elasticities provide different results that stochastic sensitivity. For example, if we had used only analytical elasticities, we would have concluded that adult female survival was most important, but that pregnancy was the second most important vital rate (Table 3-2).

**DISCUSSION**

Here, we demonstrate novel methodology for applying traditional LSA methods, which have been critically important for conservation and management of imperiled species (Crouse et al. 1987; Wisdom and Mills 1997; Morris and Doak 2002), in Bayesian IPMs to understand the relative importance of vital rates for population dynamics. The use of Bayesian IPMs that combined vital rate and count data improved our ability to understand population dynamics in a variety of ways compared to traditional methods. We found estimates of $\lambda$, vital rates, and population size became more precise by combining multiple data sources and sharing information across parameters. For example, combining count and vital rate data provided more confidence that the EF population was increasing over the study period, while credible intervals around mean $\lambda$ from count only models included 1.0. Importantly, these benefits of improved precision helped us highlight differences in the drivers of two adjacent large herbivore populations. In one population, adult survival was the most important driver of $\lambda$, followed by calf survival, compared to the other population where adult and calf survival were near parity in importance in driving population growth rate. In contrast to the prevailing paradigm, and despite decades of research focusing on neonate survival (0 to 90 days) of large herbivores (Linnell 1995; Griffin et al. 2011), our results demonstrate summer and winter survival can be equally important in driving $\lambda$. This important result supports our predictions that the relative effects of various vital rates on $\lambda$ may vary across systems experiencing different levels of predation.
We combined traditional LSA methods with our Bayesian integrated modeling framework to determine the most important vital rates affecting population dynamics. Almost 20 years ago, Wisdom and Mills (1997) developed LSA as a simulation-based approach to sensitivity analysis that hybridized manual perturbation and analytical sensitivity methods. Because deterministic matrix population model sensitivity approaches rely on theoretical sensitivity from a deterministic matrix model (Wisdom et al. 2000), they do not account for how much variation in a vital rate may actually occur, while simulation methods account for the range of variation in a vital rate by incorporating estimates of process variances from field data (Wisdom et al. 2000). LSA simulates the elasticity and variability of vital rates based on the distributions of observed means and process variances estimated from field data (Mills and Lindberg 2002). The LSA method of randomly simulating vital rate values based on statistical distributions is inherently Bayesian, which, in a similar approach, uses MCMC to sample through and retain the most likely parameter values. The differences we report (Table 3-3) in deterministic elasticity and Bayesian LSA result from this failure of deterministic approaches to account for the variability in different vital rates and are determined only by the mean matrix of vital rates (Caswell 2001), while simulation techniques such as LSA (Bayesian or otherwise) combine both vital rate elasticities and variability into a unified analysis to determine vital rate importance for population dynamics.

We specifically developed an IPM to conduct sensitivity analysis by deriving asymptotic growth rates and elasticities in a single, comprehensive model, which required simple algebra for a $2 \times 2$ matrix to derive dominant eigenvalues ($\lambda$) and component elasticities (see Caswell 2001) needed in Bayesian LSA (Wisdom et al. 2000). Kéry and Schaub (2012) present an approach to estimate the correlation between annual estimates of $\lambda$ and vital rates. However, to our knowledge, this is the first time traditional LSA methods have been combined with Bayesian
IPMs to understand the relative importance of vital rates for population dynamics. We found only one other population dynamics assessment using Bayesian IPMs that used manual perturbation to derive component elasticities (Koons et al. 2015). However, it does not appear that these values were derived using their IPM framework to estimate sensitivities (or proportional elasticities), but rather that mean parameter estimates from top models were used in a deterministic calculations of elasticity by recording the change in population growth with 1%, 5%, or 10% changes in parameter values. The advantages of our Bayesian approach over traditional LSA are that (i) multiple data sources can be used to estimate mean vital rates and process variances, (ii) all quantities of interest including mean vital rates and process variances, \( \lambda \), component elasticities, and the simulated parameter values are estimated simultaneously, (iii) insights into population dynamics will be more precise for species with sparse data (e.g., Johnson et al. 2010, King et al. 2008), and (iv) different mean vital rates and estimates of process variance can easily be simulated with informative priors.

We applied our Bayesian LSA approach to understand the dynamics of our two populations in relation to the dominant paradigm in ungulate ecology, which predicts that juvenile survival will be most important for ungulate population dynamics due to it high process variability, while other vital rates such as adult females survival with high elasticities will be less important because they are canalized against variation (Gaillard et al. 2000). In contrast to these expectations and the species-specific corroboration of this result for elk (Raithel et al. 2007), our results clearly supported adult female survival as the most important vital rate in both populations. In the WF population, adult female survival was almost twice as important in explaining variation in \( \lambda \) as annual calf survival (Table 3), which is consistent with a declining population due to lower adult female survival. For example, adult female survival was most
important to population trajectories of African ungulates in tropical systems with diverse assemblages of large carnivores (Owen-Smith and Mason 2005). In the endangered Sierra Nevada bighorn sheep, the importance of different vital rates varied between populations, with adult female survival more important in declining populations (Johnson et al. 2010). Similarly, Hebblewhite et al. (2007) showed differing importance of adult vs. juvenile survival to λ in a large and stable southern mountain caribou (Rangifer tarandus) population vs. a small and declining population. Thus, while generally accurate across ungulate populations, for some populations vital rate importance will often vary.

These shifts in the importance of different vital rates with differing population trajectories have been previously demonstrated in long-term studies of red deer (Cervus elaphus) released from culling on Rhum (Albon et al. 2000; Coulson et al. 2004). There, the drivers of λ similarly changed following the cessation of culling, where red deer population dynamics that were previously driven by birth rates shifted to adult female winter survival having the largest effect on variation in population growth (Albon et al. 2000; Coulson et al. 2004). In our study, although calf survival was twice as variable compared to adult female survival, both mean calf survival (0.30) and mean pregnancy rates (0.73) were both relatively low in the WF (Raithel et al. 2007), which may have increased the importance of variation in adult female survival relative to fecundity (calf survival and pregnancy) for λ. Our results were similar to most previous analyses of ungulate population dynamics, however, in revealing that variation in pregnancy rates contributed very little to fluctuations in population trajectories (Gaillard et al. 2000; Raithel et al. 2007). Regardless, our results clearly suggest that general paradigm of large herbivore population dynamics may not hold up in multiple carnivore systems with high predation rates, where increased predation mortality reduces survival and dampens variation in λ and vital rates.
(Wilmers et al. 2007), such as in endangered species with declining population size. Because predation mortality is mainly focused on juvenile ungulates (Linnell et al. 1995, Griffin et al. 2011), the dampened variation in juvenile survival, especially in summer, will consequently decrease in importance for population dynamics.

A novel insight from our approach was the equivalent importance of summer and overwinter juvenile survival in driving ungulate population dynamics. Most previous studies addressed only neonatal juvenile ungulate survival (e.g., from 0 to 90 days, Griffin et al. 2011) for two main reasons. Logistically, it was difficult in early studies to monitor juveniles for longer because of technological limitations (e.g., short battery life), and, second, because it was logically assumed that because most mortality occurred during the neonate period, it would be the most important in driving population dynamics (Linnell et al. 1995). Our results clearly show that this logic may be suspect, especially in populations subject to predation. For example, in our study (Chapter 2) we had a sample size of 224 neonatal and 125 6-month-old radio-marked calves, and the observed cause-specific mortality rate (which accounts for differences in sample size) was 45% from birth to 6 months of age, but only 27% from 6–12 months. Our LSA approach, however, showed that despite the greater proportion of mortalities (and a higher cause-specific mortality rate) occurring during summer, overwinter survival was equivalently important in driving dynamics in the EF population. Thus, the high number of summer mortalities in the EF had a disproportionately lower impact on population growth than winter juvenile mortality. This is consistent with summer mortality being more compensatory (Boyce et al. 1999), as many previous studies of neonatal juvenile survival have suggested (Smith et al. 2006; Johnson et al. 2013). Instead, winter juvenile survival may be more additive than assumed for juveniles in some populations.
We were also able to highlight discrepancies in estimates of juvenile recruitment (yearling/100 adult females) as well as precision among different data sources and populations, which has important implications for using count data to assess ungulate population trajectories. Age ratios were always higher from vital rate estimates compared to models using count data. In the WF, estimates from vital rate-only and count data were more consistent as compared to the EF. In the EF, count-only models showed a consistent negative bias in recruitment estimates, potentially resulting from the effects of spatial segregation and group size on detection probabilities, where adult females with calves are in smaller groups with lower detection probabilities compared to females without calves that have higher detection rates (White and Garrott 2005; White et al. 2010). Alternatively, if elk shifted their movements from more open to denser cover in response to recolonization by wolves (Atwood et al. 2009), trend count data may indicate that recruitment is declining while only detection probability has changed. Despite the weaknesses of using age ratios for population assessments (Caughley 1974; Bonenfant et al. 2005), recent studies found that age ratios in elk populations correlate strongly ($R^2 = 0.93$) with summer (0–6 months old) elk calf survival (Harris et al. 2008), and correlate across broad spatial scales with large carnivore community richness, annual variation in forage quality, and quality of winter range (Lukacs et al. *in revision*). However, most age ratio surveys are conducted in mid-winter (Lukacs et al. *in revision*), and thus, may fail to account for late winter mortality in juvenile ungulates. Our previous results (Chapter 2) and other recent ungulate studies (Hurley et al. 2011) found evidence that winter survival of juvenile ungulates may be equally or more important than summer survival to population dynamics due to greater interannual variation in overwinter survival, especially in systems with high predation. Therefore age ratio data collected mid-winter may be a poor predictor of juvenile survival for many large herbivores, and,
especially in populations that experience significant and variable winter predation (such as ours, Chapter 2), mid-winter age ratio data may not accurately predict \( \lambda \).

There are several limitations to our particular application of Bayesian LSA to evaluating population dynamics. Due to the duration of study (3 years), we were unable to estimate temporal process variance for vital rates in our sensitivity analysis, and thus, the parameter space sampled for each vital rate is based on the total observed variation in each vital rate. However, in comparing our estimates of total variance to those reported in Raithel et al. (2007), our estimates were about 16 times less variable for calf survival, 10 times less for adult female survival, and near identical to estimates of variance for pregnancy rates. As a test of potential bias introduced in our results by not explicitly removing sampling variance, we ran our sensitivity analysis based on the proportion of variance attributable to process variance in each vital rate estimated in Raithel et al. (2007), which was 88.3% for calf survival, 54.4% for adult female survival, and 79.3% for prime-aged pregnancy rate. Both this test and our sensitivity models integrating both count and vital rate data failed to produce qualitatively different results from our sensitivity analysis based only on vital rate-only data (Appendix 3-C, D). The considerably larger mean process variability of calf survival and adult female survival in Raithel et al. (2007) may reflect the fact that they included many studies without predation and did not account for winter calf survival (due to inadequate sample sizes), both of which could explain the differences in our results. Also, we were unable to account for transient dynamics in our models that may have resulted from historically higher adult female harvest that occurred in the mid 2000’s, which is an important consideration for population dynamics in harvested ungulate populations (Brodie et al. 2013).
Another limitation our IPM highlighted in our data was the issue of detection in count data. Because our aerial count data was not corrected for sightability, we used the log-Normal distribution to account for the fact that our index of abundance was more likely to underestimate the true population size (Cooper et al. 2003). This approach reduced the influence of annual trend counts on population size estimates over vital rates in our integrated models, which was especially important in the EF (Fig. 3-2), where counts of adult females increased by 31% (813 individuals) between 2012 and 2013, and then, in the following year, declined by 20% (682 individuals). It was unclear what proportion of the variability in aerial counts was due to sightability, observation error or demographic processes such as immigration and emigration (Abadi et al. 2010b; Ahrestani et al. 2013), but our approach of fitting a log-Normal count distribution can accommodate all of these potential mechanisms. As an alternative to directly modeling uncorrected count data, Cooper et al. (2003) demonstrated the utility of IPMs to reconstruct population size and structure by combining sex-specific harvest and age ratio data. We chose not to use this population reconstruction approach because yearling and adult female harvest was negligible over the study period. If harvest was substantial, then population reconstruction could have been an option provided that harvested radio-collared animals were censored from the estimates of survival in the IPM, and harvest estimates could be fed directly into the IPM (Cooper et al. 2003). Regardless, given the potential for biased estimates of population trend, sightability or detection probability should be accounted for when using count or age ratio data in population assessments (Saether et al. 2009; Knape and de Valpine 2012) either using direct estimates of sightability or an approach such as ours that allows population size to be greater than the raw counts.
Despite the potential for Bayesian integrated population models to advance our ability to understand the drivers of population dynamics and extract more information out of limited demographic data, the method has seen very little application in the field of wildlife conservation and management (Schaub and Abadi 2011). Our Bayesian LSA revealed that adult female survival may be more important to population growth than calf survival in systems with high predation rates, and that winter calf survival may be equally as important as summer survival. Further, the ability to integrate multiple data sources allowed us to highlight the need for sightability corrections in aerial count surveys. Given the importance of winter calf survival, aerial surveys may be more effective at tracking population trends if they are conducted in mid-April to May, after the majority of annual mortality has occurred but before animals have migrated to summer ranges.

Besides the importance of our application of Bayesian population assessment to ungulates, the method may prove useful in a broad range of other conservation applications. Because data is most often costly to collect or species may be rare, the use of combining multiple data streams to estimate vital rates in a Bayesian LSA framework provides more accurate and precise population assessment for species with limited data. Because the method directly incorporates traditional population matrix modeling, the framework can be adapted for any stage or age-structured matrix model (Caswell 2001), which makes it broadly applicable to population assessment. Additionally, the Bayesian LSA approach provides a framework to integrate the many existing benefits of IPM’s in addition to our novel contribution of an integrated approach of assessing sensitivity. Regardless of whether species are endangered, invasive, or harvested, the use of IPMs provides a powerful and flexible technique to compare and improve population monitoring techniques, and efficiently respond to changing conditions that may alter population dynamics.
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Table 3-1. Number of years \((n)\) of aerial count, telemetry, and pregnancy data for elk populations in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. The minimum and maximum numbers of calves and adult females that were radio-marked for telemetry and pregnancy testing are given in parentheses.

<table>
<thead>
<tr>
<th>Population</th>
<th>Data years included</th>
<th>Aerial count</th>
<th>Telemetry – adult survival</th>
<th>Telemetry – calf survival</th>
<th>Pregnancy</th>
</tr>
</thead>
</table>
Table 3-2. Estimates of calf survival ($\Phi_c$), adult female survival ($\Phi_{af}$) and pregnancy rates ($P_{af}$), and population growth rates ($\lambda_t$) with posterior standard deviations (in parentheses) for elk populations in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Estimates are given by population for different models with likelihoods based on aerial count data only, vital rate data only (survival and pregnancy), and all data integrated into a single model.

<table>
<thead>
<tr>
<th>Study area and years</th>
<th>Aerial count only</th>
<th>Vital rate only</th>
<th>Integrated model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\Phi_c$</td>
<td>$\Phi_{af}$</td>
<td>$P_{af}$</td>
</tr>
<tr>
<td><strong>East Fork</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2010–11</td>
<td>0.48</td>
<td>0.90</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>(0.22)</td>
<td>(0.07)</td>
<td>(0.23)</td>
</tr>
<tr>
<td>2011–12</td>
<td>0.54</td>
<td>0.86</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>(0.23)</td>
<td>(0.08)</td>
<td>(0.23)</td>
</tr>
<tr>
<td>2012–13</td>
<td>0.58</td>
<td>0.93</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>(0.21)</td>
<td>(0.08)</td>
<td>(0.21)</td>
</tr>
<tr>
<td>2013–14</td>
<td>0.57</td>
<td>0.76</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>(0.21)</td>
<td>(0.11)</td>
<td>(0.21)</td>
</tr>
<tr>
<td><strong>West Fork</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2010–11</td>
<td>0.47</td>
<td>0.87</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>(0.24)</td>
<td>(0.08)</td>
<td>(0.24)</td>
</tr>
<tr>
<td>2011–12</td>
<td>0.43</td>
<td>0.85</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>(0.25)</td>
<td>(0.09)</td>
<td>(0.25)</td>
</tr>
<tr>
<td>2012–13</td>
<td>0.60</td>
<td>0.87</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>(0.21)</td>
<td>(0.08)</td>
<td>(0.21)</td>
</tr>
<tr>
<td>2013–14</td>
<td>0.61</td>
<td>0.89</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>(0.21)</td>
<td>(0.09)</td>
<td>(0.21)</td>
</tr>
</tbody>
</table>

$^a$ These parameters were only informed with count data for certain years, and the low precision of these estimates (i.e., relatively high SD) is present in both the count only and integrated models.
Table 3-3. Mean estimates and analytical component elasticities for annual elk calf survival ($\Phi_c$), summer and winter calf survival, adult female survival ($\Phi_{af}$) and pregnancy rate ($P_{af}$) with posterior standard deviations (SD) in Bayesian Life-stage Simulation Analysis for elk populations in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Coefficient estimates from simple linear regressions of asymptotic population growth rates ($\lambda_{asy}$) against each vital rate are given with standard errors (SE). The model intercept ($\beta_0$) provides an estimate of $\lambda$ when the vital rate is zero, and the slope ($\beta_1$) predicts the increase in $\lambda$ with a one unit increase in each vital rate. The coefficient of determination ($R^2$) estimates the proportion of the variation in $\lambda$ explained by each vital rate.

<table>
<thead>
<tr>
<th>Study area and vital rate</th>
<th>Mean (SD)</th>
<th>Elasticity (SD)</th>
<th>$\beta_0$</th>
<th>$\beta_1$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Fork</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\Phi_c$</td>
<td>0.46 (0.05)</td>
<td>0.07 (0.01)</td>
<td>0.96 (0.01)</td>
<td>0.35 (0.01)</td>
<td>0.38</td>
</tr>
<tr>
<td>summer</td>
<td>0.58 (0.04)</td>
<td>0.12 (0.02)</td>
<td>0.97 (0.01)</td>
<td>0.26 (0.02)</td>
<td>0.20</td>
</tr>
<tr>
<td>winter</td>
<td>0.78 (0.05)</td>
<td>0.21 (0.03)</td>
<td>0.95 (0.01)</td>
<td>0.22 (0.01)</td>
<td>0.19</td>
</tr>
<tr>
<td>$\Phi_{af}$</td>
<td>0.94 (0.02)</td>
<td>0.68 (0.03)</td>
<td>0.31 (0.03)</td>
<td>0.87 (0.03)</td>
<td>0.43</td>
</tr>
<tr>
<td>$P_{af}$</td>
<td>0.89 (0.04)</td>
<td>0.27 (0.03)</td>
<td>0.98 (0.02)</td>
<td>0.17 (0.02)</td>
<td>0.06</td>
</tr>
<tr>
<td>West Fork</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\Phi_c$</td>
<td>0.30 (0.05)</td>
<td>0.04 (0.01)</td>
<td>0.94 (0.005)</td>
<td>0.33 (0.02)</td>
<td>0.33</td>
</tr>
<tr>
<td>summer</td>
<td>0.47 (0.06)</td>
<td>0.10 (0.02)</td>
<td>0.93 (0.01)</td>
<td>0.23 (0.01)</td>
<td>0.23</td>
</tr>
<tr>
<td>winter</td>
<td>0.64 (0.07)</td>
<td>0.18 (0.04)</td>
<td>0.95 (0.01)</td>
<td>0.15 (0.01)</td>
<td>0.11</td>
</tr>
<tr>
<td>$\Phi_{af}$</td>
<td>0.93 (0.03)</td>
<td>0.76 (0.04)</td>
<td>0.21 (0.02)</td>
<td>0.89 (0.03)</td>
<td>0.56</td>
</tr>
<tr>
<td>$P_{af}$</td>
<td>0.73 (0.06)</td>
<td>0.23 (0.04)</td>
<td>0.95 (0.01)</td>
<td>0.12 (0.02)</td>
<td>0.06</td>
</tr>
</tbody>
</table>

$^a$ All regression coefficients were significant at $P < 0.0001$. 

124
FIGURES

Figure 3-1. Directed acyclic graph of the integrated population model structure used to make joint inference into demographic parameters. The arrows show the direction of stochastic dependencies between estimated parameters (circles) and data (boxes) in the model. The nodes in the model are: survival data ($Y_S$); pregnancy data ($Y_p$); aerial count data for yearlings ($C_y$) and adult females ($C_{af}$); variance of yearling ($\sigma_{cy}^2$) and adult female ($\sigma_{caf}^2$) count data; calf survival ($\Phi_c$); Weibull shape ($p$) and hazard ($h$); adult female survival ($\Phi_{af}$) and pregnancy rate ($P_{af}$); and population size of yearlings ($N_y$) and adult females ($N_{af}$). Prior distributions and covariates are not included in the graph.
Figure 3-2. Elk population size (combined yearling and adult female) in the East Fork (left) and West Fork (right) study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Blue lines and gray shading represent the mean and 95% credible intervals of population sizes in Bayesian integrated population models and black lines represent raw aerial count data.
Figure 3-3. Relative standard deviations calculated from residuals of parameter estimates from models using count (blue) and vital rate data only (green) compared to models integrating all data (compared to the baseline) for elk populations in the East Fork (left) and West Fork (right) study areas in the southern Bitterroot Valley, Montana, USA, 2010–2014. Relative standard deviations are compared to the combined (vital + count) models; for example, the SD in calf survival estimated from the count only model was 0.14 higher than the count+vital rate model (reference category) in the East Fork.
Figure 3-4. Elk calf recruitment measured as the number of yearlings (~0.9 months old) per 100 adult female ratios in the East Fork (left) and West Fork (right) study areas in the southern Bitterroot Valley, Montana, USA, 2011–2014. Lines are shown for age ratios based on raw aerial count data (Raw), models including only count data (Count), models including only vital rate data (Vital), and models integrating both count and vital rate data (All).
Figure 3-5. Scatterplots of mean vital rate and asymptotic population growth rate ($\lambda_{asy}$) 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 elk calf survival, and adult female survival and pregnancy rate with solid lines for the East Fork (EF) and broken lines for the West Fork (WF).
Figure 3-6. Scatterplots of mean vital rate and asymptotic population growth rate ($\lambda_{asy}$) 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 (EF) and broken lines for the West Fork (WF).
APPENDIX 3
Appendix 3-A. JAGS code for base integrated population model

##################################################################################################
#Data for Weibull calf model right censoring
data {
  for(t in 2:(nYears-1)){
    for(i in 1:(n.obs[t])){
        one[t,i] <- 1
    }
  }
}
}
model{
#COUNT DATA FOR EF AND WF
#priors for counts observation error
for(t in 1:(nYears)){
  yWF[t] ~ dlnorm(CyWF[t], tauYWF) T(0,)
  afWF[t] ~ dlnorm(CafWF[t], tauAFWF) T(0,)
  CyWF[t] <- log(NyWF[t])
  CafWF[t] <- log(NafWF[t])
}
for(t in 1:(nYears)){
  yEF[t] ~ dlnorm(CyEF[t], tauYEF) T(0,)
  afEF[t] ~ dlnorm(CafEF[t], tauAFEF) T(0,)
  CyEF[t] <- log(NyEF[t])
  CafEF[t] <- log(NafEF[t])
  tauYEF~dgamma(0.001, 0.001)
  tauAFEF~dgamma(0.001, 0.001)
  tauYWF~dgamma(0.001, 0.001)
  tauAFWF~dgamma(0.001, 0.001)
  sigma2YEF<-1/tauYEF
  sigma2AFEF<-1/tauAFEF
  sigma2YWF<-1/tauYWF
  sigma2AFWF<-1/tauAFWF
  sigmaYEF<-sqrt(sigma2YEF)
  sigmaAFEF<-sqrt(sigma2AFEF)
  sigmaYWF<-sqrt(sigma2YWF)
  sigmaAFWF<-sqrt(sigma2AFWF)

  # initial population size (priors) at time 1
  NyWF[1] ~ dnorm(43, 0.0001) T(0,)
  NafWF[1] ~ dnorm(519, 0.0001) T(0,)
  NyEF[1] ~ dnorm(447, 0.0001) T(0,)
  NafEF[1] ~ dnorm(2904, 0.0001) T(0,)

  ### Process model (aka biology)
  for( t in 2:nYears){
    #Process models (i.e. difference equations from matrix math)
    meanNyWF[t] <- ScWF[t-1]*PregWF[t-1]*NafWF[t-1]
    meanNafWF[t] <- (SafWF[t-1]*NafWF[t-1]) + (SyWF*(NyWF[t-1]*R.WF))
    NyWF[t] ~ dpois(meanNyWF[t])
  }
  }
}
}
\[
NafWF[t] \sim \text{dpois}(\text{meanNafWF}[t])
\]

\[
\text{meanNyEF[t]} \leftarrow \text{ScEF}[t-1]*\text{PregEF}[t-1]*\text{NafEF}[t-1] \\
\text{meanNafEF[t]} \leftarrow (\text{SaEF}[t-1]*\text{NafEF}[t-1]) + (\text{SyEF}*(\text{NyEF}[t-1]*\text{R.EF}))
\]

\[
\text{NyEF[t]} \sim \text{dpois}(\text{meanNyEF}[t]) \\
\text{NafEF[t]} \sim \text{dpois}(\text{meanNafEF}[t])
\]

for \(t\) in 1:nYears{
  \[
  \text{Ntot.WF}[t] \leftarrow \text{NyWF}[t] + \text{NafWF}[t] \\
  \text{propY.WF}[t] \leftarrow \text{NyWF}[t]/\text{Ntot.WF}[t] \\
  \text{propAF.WF}[t] \leftarrow \text{NafWF}[t]/\text{Ntot.WF}[t] \\
  \text{Ntot.EF}[t] \leftarrow \text{NyEF}[t] + \text{NafEF}[t] \\
  \text{propY.EF}[t] \leftarrow \text{NyEF}[t]/\text{Ntot.EF}[t] \\
  \text{propAF.EF}[t] \leftarrow \text{NafEF}[t]/\text{Ntot.EF}[t]
  \]
}

##Derive annual growth rates
for \(t\) in 1:(nYears-1){
  \[
  \text{pop.growthWF}[t] \leftarrow ((\text{Ntot.WF}[t+1] + 1)/(\text{Ntot.WF}[t] + 1)) \\
  \text{pop.growthEF}[t] \leftarrow ((\text{Ntot.EF}[t+1] + 1)/(\text{Ntot.EF}[t] + 1))
  \]
}

\[
\text{meanGROWTH.WF} \leftarrow \text{sum(} \text{pop.growthWF}[1:nYears-1] \text{)/(nYears-1)} \\
\text{medianGROWTH.WF} \leftarrow (\text{prod(} \text{pop.growthWF}[1:nYears-1] \text{)})^{(1/(nYears-1))}
\]

\[
\text{meanGROWTH.EF} \leftarrow \text{sum(} \text{pop.growthEF}[1:nYears-1] \text{)/(nYears-1)} \\
\text{medianGROWTH.EF} \leftarrow (\text{prod(} \text{pop.growthEF}[1:nYears-1] \text{)})^{(1/(nYears-1))}
\]

##Survival and pregnancy probabilities and priors
for \(t\) in 1:nYears-1{
  \[
  \text{SafWF}[t] \sim \text{dunif}(0,1) \\
  \text{SafEF}[t] \sim \text{dunif}(0,1) \\
  \text{PregEF}[t] \sim \text{dunif}(0,1) \\
  \text{PregWF}[t] \sim \text{dunif}(0,1)
  \]
}

\[
\text{SyEF} \sim \text{dnorm}(0.883, 238)T(0,1) \\
\text{SyWF} \sim \text{dnorm}(0.883, 238)T(0,1)
\]

# Observation model (aka likelihood)
for \(t\) in 1:nYears-1{
  \[
  \text{femaleSurvivedWF}[t] \sim \text{dbin}( \text{SafWF}[t], \text{NumberOfCollarsAFWF}[t]) \\
  \text{femaleSurvivedEF}[t] \sim \text{dbin}( \text{SafEF}[t], \text{NumberOfCollarsAFEF}[t])
  \]
}

for \(t\) in 2:nYears-1{
  \[
  \text{pregWF}[t] \sim \text{dbin(} \text{PregWF}[t], \text{afCollarsWF}[t]) \\
  \text{pregEF}[t] \sim \text{dbin(} \text{PregEF}[t], \text{afCollarsEF}[t])
  \]
}

# Observation model (aka likelihood)
for \(t\) in 1:nYears-1{
  \[
  \text{femaleSurvivedWF}[t] \sim \text{dbin(} \text{SafWF}[t], \text{NumberOfCollarsAFWF}[t]) \\
  \text{femaleSurvivedEF}[t] \sim \text{dbin(} \text{SafEF}[t], \text{NumberOfCollarsAFEF}[t])
  \]
}

for \(t\) in 2:nYears-1{
  \[
  \text{pregWF}[t] \sim \text{dbin(} \text{PregWF}[t], \text{afCollarsWF}[t]) \\
  \text{pregEF}[t] \sim \text{dbin(} \text{PregEF}[t], \text{afCollarsEF}[t])
  \]
}

##Model for calf survival
for \(t\) in 2:nYears-1{
  \[
  \text{shape} \sim \text{dunif}(0, 2)
  \]
}

##ANNUAL CALF SURVIVAL
for \(t\) in 2:nYears-1{
  \[
  \text{shape} \sim \text{dunif}(0, 2)
  \]
}

##Calculate study area survival rates and overall survival
for \(t\) in 1:nYears-1{
  \[
  \text{ScWF}[t] \leftarrow \exp(\text{lSc}[t])/(1+\exp(-\text{lSc}[t]+\text{Area}[\text{Area}[t,i]]))
  \]
}
ScEF[t] <- exp(lSc[t] + lArea) / (1 + exp(lSc[t] + lArea))
lSc[t] ~ dnorm(0, 0.0001) T(-10, 10)
}
lArea ~ dnorm(0, 0.0001) T(-10, 10)
}
# End model

###
Appendix 3-B. JAGS code for sensitivity integrated population model

# Data for Weibull calf model right censoring - summer and winter
data{
  for(t in 2:(nYears-1)){
    for(i in 1:(n.obsS[t])){
      oneS[t,i] <- 1
    }
  }
  for(t in 2:(nYears-1)){
    for(i in 1:(n.obsW[t])){
      oneW[t,i] <- 1
    }
  }
}
model{
  # COUNT DATA FOR EF AND WF
  # priors for counts observation error
  for(t in 1:(nYears)){
    yWF[t] ~ dlnorm(CyWF[t], tauYWF) T(0,)
    aWF[t] ~ dlnorm(CafWF[t], tauAFWF) T(0,)
    CyWF[t] <- log(NyWF[t])
    CafWF[t] <- log(NafWF[t])
  }
  for(t in 1:(nYears)){
    yEF[t] ~ dlnorm(CyEF[t], tauYEF) T(0,)
    aEF[t] ~ dlnorm(CafEF[t], tauAFEF) T(0,)
    CyEF[t] <- log(NyEF[t])
    CafEF[t] <- log(NafEF[t])
  }
  tauYEF~dgamma(0.001, 0.001)
  tauAFEF~dgamma(0.001, 0.001)
  tauYWF~dgamma(0.001, 0.001)
  tauAFWF~dgamma(0.001, 0.001)
  sigma2YEF<-(1/tauYEF)
  sigma2AFEF<-(1/tauAFEF)
  sigma2YWF<-(1/tauYWF)
  sigma2AFWF<-(1/tauAFWF)
  sigmaYEF<-sqrt(sigma2YEF)
  sigmaAFEF<-sqrt(sigma2AFEF)
  sigmaYWF<-sqrt(sigma2YWF)
  sigmaAFWF<-sqrt(sigma2AFWF)
}

# initial population size (priors) at time 1
NyWF[1] ~ dnorm(43, 0.0001) T(0,)
NafWF[1] ~ dnorm(519, 0.0001) T(0,)
NyEF[1] ~ dnorm(447, 0.0001) T(0,)
NafEF[1] ~ dnorm(2904, 0.0001) T(0,)

### Process model (aka biology)
for( t in 2:nYears){

# Process models (i.e. difference equations from matrix math)

# yearlings and adult females

meanNyWF[t] <- ScWF*PregWF*NafWF[t-1]
meanNafWF[t] <- (SafWF*NafWF[t-1]) + (SyWF*(NyWF[t-1]*R.WF))

NyWF[t] ~ dpois(meanNyWF[t])
NafWF[t] ~ dpois(meanNafWF[t])

meanNyEF[t] <- ScEF*PregEF*NafEF[t-1]
meanNafEF[t] <- (SafEF*NafEF[t-1]) + (SyEF*(NyEF[t-1]*R.EF))

NyEF[t] ~ dpois(meanNyEF[t])
NafEF[t] ~ dpois(meanNafEF[t])

for(t in 1:nYears){
Ntot.WF[t] <- NyWF[t] + NafWF[t]
propY.WF[t]<-NyWF[t]/Ntot.WF[t]
propAF.WF[t]<-NafWF[t]/Ntot.WF[t]
Ntot.EF[t] <- NyEF[t] + NafEF[t]
propY.EF[t]<-NyEF[t]/Ntot.EF[t]
propAF.EF[t]<-NafEF[t]/Ntot.EF[t]
}

## Derive annual growth rates

for(t in 1:(nYears-1)){
pop.growthWF[t]<-((Ntot.WF[t+1] + 1)/(Ntot.WF[t] + 1))
pop.growthEF[t]<-((Ntot.EF[t+1] + 1)/(Ntot.EF[t] + 1))
}

meanGROWTH.WF<- sum(pop.growthWF[1:nYears-1])/(nYears-1)
medianGROWTH.WF<- (prod(pop.growthWF[1:nYears-1]))^(1/(nYears-1))
meanGROWTH.EF<- sum(pop.growthEF[1:nYears-1])/(nYears-1)
medianGROWTH.EF<- (prod(pop.growthEF[1:nYears-1]))^(1/(nYears-1))

## Survival and pregnancy probabilities and priors

for(t in 1:nYears-1){
SafWF~dunif(0,1)
SafEF~dunif(0,1)
PregEF~dunif(0,1)
PregWF~dunif(0,1)
}

SyEF~dnorm(0.883, 238)T(0,1)
SyWF~ dnorm(0.883, 238)T(0,1)

## Observation model (aka likelihood)

for(t in 1:nYears){

femaleSurvivedWF[t] ~ dbin( SafWF, NumberOFCollarsAFWF[t])
femaleSurvivedEF[t] ~ dbin( SafEF, NumberOFCollarsAEWF[t])
}

for(t in 2:nYears){
pregWF[t] ~ dbin(PregWF, afCollarsWF[t])
pregEF[t] ~ dbin(PregEF, afCollarsEF[t])
}

## SUMMER CALF SURVIVAL

for(t in 2:(nYears-1)){

for(i in 1:(n.obsS[t])){
oneS[t,i]~dinterval(yS[t,i], y.censS[t,i])
yS[t,i]~dweib(shapeS, lambdaS[t,i])T(y.entS[t,i], )
}
lambdaS[t,i] <- -log(ScS[t,i])/pow(180, shapeS)
ScS[t,i]<-1/(1+exp(-(1ScS+1AreaS*AreaS[t,i])))
}

##WINTER CALF SURVIVAL
for(t in 2:(nYears-1)){
  for(i in 1:(n.obsW[t])){
    oneW[t,i]~dinterval(yW[t,i], y.censW[t,i])
yW[t,i]~dweib(1, lambdaW[t,i])T(y.entW[t,i], )
    lambdaW[t,i] <- -log(ScW[t,i])/pow(185, 1)
ScW[t,i]<-1/(1+exp(-(1ScW+1AreaW*AreaW[t,i])))
  }
  shapeS ~ dunif(0, 2)
}

##Calculate study area mean survival rates
ScEFS<-exp(lScS+lAreaS)/(1+exp(lScS+lAreaS))
ScWFS<-exp(lScW)/(1+exp(lScW))
ScWF<-ScWFS*ScWFW
ScEF<-ScEFS*ScEFW
ScEFS~dnorm(0, 0.0001)T(-10,10)
ScWFS~dnorm(0, 0.0001)T(-10,10)
ScWF~dnorm(0, 0.0001)T(-10,10)
ScEF~dnorm(0, 0.0001)T(-10,10)

#East Fork sensitivity analysis
Q1EF<- 1
Q2EF<- (-SafEF)
Q3EF<- (-SyEF*R.EF*(ScEF*PregEF))
eig.value1EF<- (-Q2EF + (sqrt((Q2EF^2) - (4*Q1EF*Q3EF))))/(2*Q1EF)
eig.value2EF<- (-Q2EF - (sqrt((Q2EF^2) - (4*Q1EF*Q3EF))))/(2*Q1EF)
Id1EF<-eig.value1EF*Identity
Id2EF<-eig.value2EF*Identity
matEF[1,1]<-0
matEF[1,2]<-(ScEF*PregEF)
matEF[2,1]<-(SyEF*R.EF)
matEF[2,2]<-SafEF
new.mat1EF<-matEF-Id1EF
new.mat2EF<-matEF-Id2EF
eig.vec1EF<- (new.mat1EF[1,1])/(new.mat1EF[1,1])
eig.vec2EF<-eig.vec1EF/sqrt(1 + (eig.vec2EF^2))
eig.vec2EF<-eig.vec2EF/sqrt(1 + (eig.vec2EF^2))
eig.vec3EF<- (new.mat2EF[1,1])/(new.mat2EF[1,1])
eig.vec4EF<-eig.vec3EF/sqrt(1 + (eig.vec4EF^2))
eig.vec4EF<-eig.vec4EF/sqrt(1 + (eig.vec4EF^2))
sensMATEF[1,1]<-eig.vec1EF
sensMATEF[1,2]<-eig.vec3EF
sensMATEF[2,1]<-eig.vect2EF
sensMATEF[2,2]<-eig.vect4EF

inMATEF[1,1]<-sensMATEF[2,2]
inMATEF[1,2]<-(-sensMATEF[1,2])
inMATEF[2,1]<-(-sensMATEF[2,1])
inMATEF[2,2]<-sensMATEF[1,1]

vEF <- 1/((sensMATEF[1,1]*sensMATEF[2,2])-
(sensMATEF[1,2]*sensMATEF[2,1]))*inMATEF
v1EF<-vEF[1,]
w1EF<-sensMATEF[1:2,1]
SSD.EF[1]<-w1EF[1]/(w1EF[1]+w1EF[2])
RV.EF[1]<-v1EF[1]/(v1EF[1])
RV.EF[2]<-v1EF[2]/(v1EF[1])
sensEF[1,1]<-v1EF[1]*w1EF[1]
sensEF[1,2]<-v1EF[1]*w1EF[2]
sensEF[2,1]<-v1EF[2]*w1EF[1]
elasEF<- (matEF/eig.value1EF) * sensEF

#West Fork sensitivity analysis
Q1WF< 1
Q2WF<- (~SafWF)
Q3WF<- (~0.5*SfWF*(ScWF*PregWF))
eig.value1WF<- (~Q2WF^2 + (sqrt((Q2WF^2) - (4*Q1WF*Q3WF))))/(2*Q1WF)
eig.value2WF<- (~Q2WF^2 - (sqrt((Q2WF^2) - (4*Q1WF*Q3WF))))/(2*Q1WF)
Id1WF<-eig.value1WF*Identity
Id2WF<-eig.value2WF*Identity
matWF[1,1]<-0
matWF[1,2]<- (~SfWF*PregWF)
matWF[2,1]<- (~SyWF*R.WF)
matWF[2,2]<- SafWF

new.mat1WF<-matWF-Id1WF
new.mat2WF<-matWF-Id2WF
eig.vec1WF< 1
eig.vec2WF<- (new.mat1WF[1,1])/(-new.mat1WF[1,2])
eig.vec1WF<-eig.vec1WF/sqrt(1 + (eig.vec2WF^2))
eig.vec2WF<-eig.vec2WF/sqrt(1 + (eig.vec2WF^2))
eig.vec3WF<- 1
eig.vec4WF<- (new.mat2WF[1,1])/(-new.mat2WF[1,2])
eig.vec3WF<-eig.vec3WF/sqrt(1 + (eig.vec4WF^2))
eig.vec4WF<-eig.vec4WF/sqrt(1 + (eig.vec4WF^2))
sensMATWF[1,1]<- eig.vec1WF
sensMATWF[1,2]<- eig.vec3WF
sensMATWF[2,1]<- eig.vec2WF
sensMATWF[2,2]<- eig.vec4WF

inMATWF[1,1]<-sensMATWF[2,2]
inMATWF[1,2]<-(-sensMATWF[1,2])
inMATWF[2,1]<-(-sensMATWF[2,1])
inMATWF[2,2]<-sensMATWF[1,1]
vWF <- (1/((sensMATWF[1,1]*sensMATWF[2,2]) - 
(sensMATWF[1,2]*sensMATWF[2,1])))*inMATWF
v1WF <- vWF[1]
wlWF <- sensMATWF[1:2,1]
RV.WF[1] <- v1WF[1]/(v1WF[1])
RV.WF[2] <- v1WF[2]/(v1WF[1])
sensWF[1,1] <- v1WF[1]*wlWF[1]
sensWF[1,2] <- v1WF[1]*wlWF[2]
elasWF <- (matWF/eig.value1WF) * sensWF

# component elasticities
# East fork
cmp.ScEFs <- (sensEF[1,2]*ScEFS)*(ScEFS/eig.value1EF)
cmp.ScEFW <- (sensEF[1,2]*ScEFW)*(ScEFW/eig.value1EF)
cmp.ScEF <- (sensEF[1,2]*ScEF)*(ScEF/eig.value1EF)
cmp.SafEF <- (sensEF[2,2]*SafEF)*(SafEF/eig.value1EF)
cmp.PregEF <- (sensEF[1,2]*PregEF)*(PregEF/eig.value1EF)
cmp.SyEF <- (sensEF[2,1]*SyEF)*(SyEF/eig.value1EF)
cmp.R.EF <- (sensEF[2,1]*R.EF)*(R.EF/eig.value1EF)
# West fork
cmp.ScWFs <- (sensWF[1,2]*ScWFS)*(ScWFS/eig.value1WF)
cmp.ScWFW <- (sensWF[1,2]*ScWFW)*(ScWFW/eig.value1WF)
cmp.ScWF <- (sensWF[1,2]*ScWF)*(ScWF/eig.value1WF)
cmp.SafWF <- (sensWF[2,2]*SafWF)*(SafWF/eig.value1WF)
cmp.PregWF <- (sensWF[1,2]*PregWF)*(PregWF/eig.value1WF)
cmp.SyWF <- (sensWF[2,1]*SyWF)*(SyWF/eig.value1WF)
cmp.R.WF <- (sensWF[2,1]*R.WF)*(R.WF/eig.value1WF)
}

# End model

########################################################################
Appendix 3-C. Bayesian life-stage simulation analysis with count data

TABLES
Table 3-C.1. Mean vital rates, analytical component elasticities, and posterior standard deviations (SD) from sensitivity IPMs that include count data for annual elk calf survival ($\Phi_c$), and adult female survival ($\Phi_{af}$) and pregnancy rate ($P_{af}$) for elk populations in the East and West Fork study areas in the southern Bitterroot Valley, Montana, USA. Coefficient estimates from simple linear regressions of asymptotic population growth rates ($\lambda_{asy}$) against each vital rate are given with standard errors (SE). The model intercept ($\beta_0$) provides an estimate of $\lambda$ when the vital rate is zero, and the slope ($\beta_1$) predicts the increase in $\lambda$ with a one unit increase in each vital rate. The coefficient of determination ($R^2$) estimates the proportion of the variation in $\lambda$ explained by each vital rate.

<table>
<thead>
<tr>
<th>Study area and vital rate</th>
<th>Mean (SD)</th>
<th>Elasticity (SD)</th>
<th>$\beta_0^a$ (SE)</th>
<th>$\beta_1^a$ (SE)</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_{asy}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>East Fork</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\Phi_c$</td>
<td>0.37 (0.05)</td>
<td>0.05 (0.01)</td>
<td>0.98 (0.01)</td>
<td>0.24 (0.01)</td>
<td>0.22</td>
</tr>
<tr>
<td>summer</td>
<td>0.51 (0.05)</td>
<td>0.10 (0.02)</td>
<td>0.99 (0.01)</td>
<td>0.15 (0.01)</td>
<td>0.10</td>
</tr>
<tr>
<td>winter</td>
<td>0.71 (0.06)</td>
<td>0.20 (0.03)</td>
<td>0.99 (0.01)</td>
<td>0.11 (0.01)</td>
<td>0.09</td>
</tr>
<tr>
<td>$\Phi_{af}$</td>
<td>0.92 (0.02)</td>
<td>0.68 (0.04)</td>
<td>0.46 (0.02)</td>
<td>0.66 (0.03)</td>
<td>0.41</td>
</tr>
<tr>
<td>$P_{af}$</td>
<td>0.85 (0.05)</td>
<td>0.28 (0.03)</td>
<td>1.00 (0.01)</td>
<td>0.08 (0.02)</td>
<td>0.02</td>
</tr>
<tr>
<td><strong>West Fork</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\Phi_c$</td>
<td>0.29 (0.04)</td>
<td>0.04 (0.01)</td>
<td>0.97 (0.005)</td>
<td>0.19 (0.02)</td>
<td>0.11</td>
</tr>
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<td>summer</td>
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<td>0.10 (0.02)</td>
<td>0.98 (0.01)</td>
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</tr>
<tr>
<td>winter</td>
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<td>0.18 (0.04)</td>
<td>0.98 (0.01)</td>
<td>0.06 (0.01)</td>
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</tr>
<tr>
<td>$\Phi_{af}$</td>
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<td>0.78 (0.02)</td>
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<tr>
<td>$P_{af}$</td>
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<td>0.23 (0.04)</td>
<td>0.98 (0.01)</td>
<td>0.06 (0.01)</td>
<td>0.02</td>
</tr>
</tbody>
</table>

$^a$All regression coefficients were significant at $P < 0.0001$. 

139
FIGURES
Figure 3-C.1. Scatterplots of mean vital rate and asymptotic population growth rate ($\lambda_{asy}$) values for the East Fork (gray) and West Fork (black) elk populations in Bayesian life-stage simulation analysis with count data included in the model. The graph shows estimated regression lines (slopes) and coefficient of determination ($R^2$) for elk calf survival, and adult female survival and pregnancy rates with solid lines for the East Fork (EF) and broken lines for the West Fork (WF).
Figure 3-C.2. Scatterplots of mean vital rate and asymptotic population growth rate ($\lambda_{asy}$) values for the East Fork (gray) and West Fork (black) elk populations in Bayesian life-stage simulation analysis with count data included in the model. The graph includes estimated regression lines (slopes) and coefficient of determination ($R^2$) for summer and winter elk calf survival for both populations.
Appendix 3-D. Bayesian life-stage simulation analysis based on Raithel et al. (2007)

TABLES
Table 3-D.1. Mean vital rates, analytical component elasticities, and posterior standard deviations (SD) from sensitivity IPMs using count data for annual elk calf survival ($\Phi_c$), and adult female survival ($\Phi_{af}$) and pregnancy rate ($P_{af}$) for elk populations in the East and West Fork study areas in the southern Bitterroot Valley, Montana, USA. Estimates of process variance for vital rates are based on Raithel et al. (2007). Coefficient estimates from simple linear regressions of asymptotic population growth rates ($\lambda_{asy}$) against each vital rate are given with standard errors (SE). The model intercept ($\beta_0$) provides an estimate of $\lambda$ when the vital rate is zero, and the slope ($\beta_1$) predicts the increase in $\lambda$ with a one unit increase in each vital rate. The coefficient of determination ($R^2$) estimates the proportion of the variation in $\lambda$ explained by each vital rate.

<table>
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<th>Study area and vital rate</th>
<th>$\lambda_{asy}$</th>
<th>Mean (SD)</th>
<th>Elasticity (SD)</th>
<th>$\beta_0^a$ (SE)</th>
<th>$\beta_1^a$ (SE)</th>
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<td><strong>East Fork</strong></td>
<td></td>
<td></td>
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<tr>
<td>$\Phi_c$</td>
<td>0.46 (0.20)</td>
<td>0.08 (0.05)</td>
<td>0.95 (0.004)</td>
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<tr>
<td>$\Phi_{af}$</td>
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<td>0.68 (0.09)</td>
<td>0.27 (0.04)</td>
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<td>$P_{af}$</td>
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<td>0.98 (0.04)</td>
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<tr>
<td><strong>West Fork</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0.05 (0.05)</td>
<td>0.94 (0.003)</td>
<td>0.31 (0.01)</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>$\Phi_{af}$</td>
<td>0.92 (0.05)</td>
<td>0.76 (0.10)</td>
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<tr>
<td>$P_{af}$</td>
<td>0.73 (0.07)</td>
<td>0.24 (0.06)</td>
<td>0.92 (0.02)</td>
<td>0.15 (0.03)</td>
<td>0.02</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ All regression coefficients were significant at $P < 0.0001$. 
FIGURES
Figure 3-D.1. Scatterplots of mean vital rate and asymptotic population growth rate ($\lambda_{asy}$) values for the East Fork (gray) and West Fork (black) elk populations in Bayesian life-stage simulation analysis. Estimates of process variance for vital rates are based on Raithel et al. (2007). The graph shows estimated regression lines (slopes) and coefficient of determination ($R^2$) for elk calf survival, and adult female survival and pregnancy rates with solid lines for the East Fork (EF) and broken lines for the West Fork (WF).
Appendix 3-E. Simulations of harvest, calf survival and pregnancy using Bayesian integrated population models (IPMs) for elk populations in the East Fork and West Fork study areas in the southern Bitterroot Valley, Montana, USA

INTRODUCTION
Aerial trend count data are a vital component of monitoring ungulate populations and, combined with harvest data, are used as a basis to set elk harvest regulations in many western states and provinces. In the absence of field estimates of vital rates, aerial trend count and age/sex classification data provide an index of recruitment (juvenile/100 adult females) and adult male productivity (adult males/100 adult females), which are both considered indicators for the ability of ungulate populations to increase in size and/or sustain harvest (Harris et al. 2008, DeCesare et al. 2012). Juvenile-to-adult age ratios of elk derived from mid-winter aerial trend counts correlated strongly ($R^2 = 0.93$) with summer calf survival rates and were found to track long-term population trends well (Harris et al. 2008). However, the relationship between annual elk calf survival and age ratio estimates is unclear because most elk calf survival studies have only focused on summer survival (e.g., Raithel 2005, Barber-Meyer et al. 2008, White et al. 2010) and most ungulate trend surveys are conducted in mid-winter to maximize sightability (Lukacs et al. 2015). We monitored annual calf survival for three years (Chapter 2), which limited our assessment of the correlation between annual survival rates and age ratios. Instead, we used the observed vital rates (i.e., calf survival and pregnancy) and age ratios derived from trend counts to develop simulations that managers could use to evaluate the efficacy of different harvest alternatives in meeting population objectives.

Within our study area, elk populations are managed in three Hunting Districts (HDs). The East Fork (EF) area consists of two HDs, HD 270 in the East Fork of the Bitterroot River drainage and HD 334 in the northern Bighole Valley. Elk counted in HD 270 in mid-April include some migratory elk that may be available for harvest in HD 334 in the fall. The West Fork (WF) area includes only HD 250 (Fig. 3-E.1). In 2004, MFWP instituted a brow-tined or antlerless elk season with an antlerless quota for the last 9 days of rifle season in the HD 250 and HD 270. This hunting season structure was in place through 2007 in HD 250 and 2009 in the HD 270. However, beginning in 2008 in the HD 250 and 2010 in the HD 270, antlerless harvest was by limited permit only, which decreased annual antlerless elk harvests. Beginning in 2011, brow-tined antlered elk were managed on a limited permit system in HD 250, and beginning in 2012 brow-tined antlered elk were managed on an unlimited permit system in HD 270 (if an applicant selected the HD as their top choice). Brow-tined antlered elk have been on a general license in HD 334.

Given recent fluctuations in these elk populations, several competing proposed management objectives are being considered. For example, a potential population objective for the EF is 3800 (range: 3040–4560) total elk with a recruitment range of 20–30 yearling/100 adult female elk. A potential population objective for the West Fork (WF) is 1400 (range: 1120–1680) total elk and a recruitment range of 30–40 yearling/100 adult females. To provide guidance as to the effects of various recruitment and harvest management scenarios, we forecasted elk population size in the EF and WF under different scenarios of harvest, calf survival and pregnancy rates.

METHODS
For our sensitivity analyses in Chapter 2, we modeled elk population dynamics using a female-only process model, and did not include adult males. The rationale for this decision was based on
i) the high uncertainty in the uncorrected aerial counts of adult males, ii) the fact that we did not have radio-collared adult males to estimate survival, and iii) adult males did not affect estimates of asymptotic population growth rate ($\lambda_{asy}$), and thus, were unimportant in our sensitivity analysis. However, to project population size under different harvest scenarios, we needed to include adult male elk in the population model.

**Simulations**

We developed a total of 8 simulations (3 for the EF, 5 for the WF) of antlered and antlerless harvest over a range of calf survival (or age ratios) and pregnancy rates (Table 3-E.1). We projected elk populations 5 years into the future from 2016–2020, and included count, harvest and vital rate data from 2010–2015 (Table 3-E.2; see Data Sources in Chapter 3 for more details).

*Harvest.* — Based on the past 5-year average estimate of harvest, the status quo for harvest was 290 antlered (brow-tined only) and 100 antlerless elk per year in the EF area, and 25 antlered and 0 antlerless elk per year in the WF area (note that between 0–10 antlerless elk were harvested in the WF during 2010–2015). To account for study area boundary changes that occurred in 2013 (see Fig. 3-E.1), we multiplied the harvest estimates by the specific annual percent of change in trend counts for adult female (EF: $\bar{x} = 1.05$, SD = 0.02; WF: $\bar{x} = 0.72$, SD = 0.07) and adult male elk (EF: $\bar{x} = 1.06$, SD = 0.05; WF: $\bar{x} = 0.59$, SD = 0.15) in each population; thus, annual harvest estimates increased in the EF by 5–6% and decreased in the WF by 28–41% due to boundary changes. Additionally, we adjusted EF harvest estimates upward by 10 antlered and 15 antlerless elk to account for migratory elk harvested in HD 334 (see Table 3-E.1 for harvest summary). We varied harvest by 100 (status quo), 200, and 300 antlerless elk in the EF and 0 (status quo), 25, 50, and 75 antlerless elk in WF area. We simulated harvests of 25 (status quo), 50, and 75 antlered elk in the WF.

Antlerless elk were defined as an elk with antlers < 4 inches long as measured from the top of the skull, which includes adult females and male and female juveniles; however, we only considered adult female elk in the antlerless harvest because hunters generally select for prime-aged adult females rather than juvenile elk (Vucetich et al. 2005). This was evidenced by the fact that out of 110 confirmed mortalities from our sample of 286 elk calves in a 3-year study, only 1 mortality was due to hunter harvest (see Chapter 2).

*Calf survival and age ratios.* — 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/100 adult female elk at time $t + 1$:

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

(1)

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 ($\Phi_{af,t}$), pregnancy ($P_{af,t}$), yearling survival ($\Phi_{y,t}$), 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.

*Pregnancy.* — We used the mean observed pregnancy rate in the EF of 0.85 to simulate increased pregnancy rates for the WF elk population. The simulation assessed the ability of the WF population to sustain increased antlerless harvest with compensation from higher pregnancy rates.

**Model Formulation and Parameterization**

We extended our Bayesian integrated population model (IPM) developed in Chapter 3 to include adult males and annual harvest estimates. 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 (rifle) season for elk hunting was from late-October to late-November of each year (see Fig 3-E.2). We deducted annual harvest estimates from the total number of adult male and female elk as a deterministic process. We assumed that hunter harvest was additive to adult males and females (Vucetich et al. 2005). We did not detect any harvest mortality in our collared sample of adult female elk (unpublished data), but we included harvest through a simple annual deduction for simulation purposes.

**Biological process model.** — To include adult male elk in the process model, we used a Poisson distribution to model the number of adult male elk in year $t + 1$ as the sum of the contributions from 1) the yearling survival rate from $t$ to $t + 1$ ($\Phi_{y,t}$), mean proportion of yearlings that were male ($1 - R$), and the number of yearlings in year $t$, and 2) the adult male survival rate from $t$ to $t + 1$ ($\Phi_{am,t}$) and the number of adult male elk minus the number harvested ($H_{am,t}$) in year $t$:

$$N_{am,t+1} \sim \text{Pois}([1-R]\Phi_{y,t}N_{y,t} + \Phi_{am,t}[N_{am,t} - H_{am,t}])$$

A similar process model formulation was used to include harvest of adult female elk:

$$N_{af,t+1} \sim \text{Pois}(R\Phi_{y,t}N_{y,t} + \Phi_{af,t}[N_{af,t} - H_{af,t}])$$

**Aerial count likelihood function.** — We combined aerial counts of male and female adult elk into a single observation model to account for uncertainty in identifying adult male and female elk. This was a concern with our count data since aerial surveys occurred in mid-April to mid-May when adult male elk had dropped their antlers. The combined observation model for adults also helped to account for the fact that estimates of harvest were greater than the uncorrected aerial counts of adult males in some years. Thus, we dealt with sex misclassification and undercounting adult males by combining count observations of adult male and female elk, but we continued to model male and female adult elk in separate process models.

Because aerial counts were not adjusted for sightability, we assumed that counts of adult elk ($C_a$) were log-Normally distributed as a function of the true number of adults ($N_a$) in year $t$:

$$C_{a,t} \sim \log-\text{Norm}(N_{a,t}, \sigma_{ca}^2)$$

**Adult male survival.** — The change in consecutive counts of adult male elk provided an estimate of survival, but adult male survival was biased low without direct telemetry data (unpublished data). Therefore, we used a Normal distribution ($\mu$, $\tau$) truncated at 0 and 1 to model an informative prior for adult male survival using a mean of 0.90 for both populations, and a precision based on the posterior standard deviation (SD) of adult female survival for each population:

$$\Phi_{EF_{am}} \sim \text{Norm}(0.92, 2770)T(0, 1)$$

$$\Phi_{WF_{am}} \sim \text{Norm}(0.91, 977)T(0, 1)$$

We chose 0.91–0.92 for adult male survival because adult male elk generally have high survival rates without harvest mortality. For example, Unsworth et al. (1993) radio-collared 169 adult male elk in northcentral Idaho, USA, and found that only 6 out of 64 (9.4%) mortalities were due to non-harvest mortality sources. We set mean adult male survival 1% higher in EF (0.92) compared to the WF (0.91) based on the observed difference in adult female survival between the two study areas.
Simulation of vital rates. — We modified our base IPM parameterization to project population size into the future based on mean vital rates and process variances (Kéry and Schaub 2012). Because we could not separate process from sampling variance due to the limited duration of our study, we based estimates of process variance on values from 37 elk studies reviewed by Raithel et al. (2007). We formulated the model to loop over data and projection years (2010–2020) and constructed a set of random temporal error terms for each vital rate to share information across years (Abadi et al. 2012). In Bayesian models, this is accomplished by estimating mean vital rates ($\beta_0$) on the logit scale and including random error terms ($\epsilon_t$) with prior distributions that model the process variance (or standard deviation) as a hyperparameter (i.e., a parameter of a prior distribution). For example, calf survival at year $t$ would be modeled as:

$$\text{logit}(\Phi_{c,t}) = \beta_0 + \epsilon_t$$

(7)

$$\epsilon_t \sim \text{Norm}(0, \tau)$$

(8)

$$\tau = 1/(\sigma^2)$$

(9)

$$\sigma \sim \text{Unif}(0, 10)$$

(10)

We simulated calf survival and pregnancy rates using a uniform distributions spanning from 0 to 1 (i.e., a vague prior) for the observation period (2010–2015) and an informative prior for the predictions period (2016–2020). We based informative priors on the Normal distribution truncated at 0 and 1 (similar to Equation 5 and 6), with precision ($\tau$) based on the process variance estimates from Raithel et al. (2007) and means based simulated values. We implemented the simulation IPMs using similar methods as described in Chapter 3. We report posterior standard deviations (SD) and 95% credible intervals for derived and estimated parameters. JAGS code for the projection IPM can be found in Appendix 3-F.

**RESULTS**

With adult males and harvest included in the IPM, the average juvenile to adult female ratio during 2010–15 (i.e., observation period) was 20 yearlings/100 adult females in the WF and 25 yearlings/100 adult females in the EF. These age ratios corresponded to mean observed calf survival rates of 0.31 (SD = 0.04) in the EF and 0.30 (SD = 0.04) in the WF. Adult female survival averaged 0.94 (SD = 0.02) in the EF and 0.93 (SD = 0.02) in the WF. Pregnancy rate averaged 0.85 (SD = 0.05) in the EF and 0.74 (SD = 0.06) in the WF. The average population size over the observation period was 738 yearlings and 3034 adult elk in the EF and 93 yearlings and 463 adult elk in the WF. Population size ranged from a low of 3606 (SD = 122) in 2010 to a high of 4349 (SD = 204) in 2016 in the EF, and similarly, ranged from a low of 575 (SD = 32) in 2010 to a high of 683 (SD = 36) in 2015 in the WF.

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 0.25 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 WF, 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 EF and WF populations.

In simulations for the EF elk population, except for the simulation of 25% calf survival (20 yearlings/100 adult females) and 300 antlerless elk harvested annually (see Table 3-E.4, Fig. 3-
E.4), all scenarios resulted in mean projected population sizes that were above the maximum proposed population objective ($n = 4560$; see Table 3-E.3, Table 3-E.5, Fig. 3-E.3, Fig. 3-E.5); however, the lower 95% credible intervals of most simulations were within the proposed population size objectives. For the EF elk population, mean population growth rates ($\lambda$) over the prediction interval decreased by about 1–2% on average for every additional 100 antlerless elk harvested, and ranged from $\lambda = 1.02$ to $\lambda = 1.13$ under simulations with the lowest (i.e., 0.25; Table 3-E.4, Fig. 3-E.4) and highest (i.e., 0.50; Table 3-E.5, Fig. 3-E.5) calf survival rates, respectively.

In simulations of the WF elk population, only simulations using a calf survival rate of 55% and antlerless harvest of 0–25 resulted in mean projected population sizes that were above the minimum proposed population objective ($n = 1,120$; Table 3-E.9, Fig. 3-E.9), although upper 95% credible intervals of most simulations were in population size objectives when harvest was low (i.e., 0–25 antlerless, 25–50 antlered). For the WF population, mean $\lambda$ over the prediction interval decreased by about 3% on average for every additional 25 antlerless elk and 1–2% on average for every additional 25 antlered elk harvested. Population growth rates ranged from $\lambda = 1.02$ to $\lambda = 1.13$ under simulations with the lowest (i.e., 0.30; Table 3-E.6, Fig. 3-E.6) and highest (i.e., 0.55; Table 3-E.9, Fig. 3-E.9) calf survival rates, respectively. Simulations using pregnancy rates of 85% resulted in similar projected population sizes and yearling/100 adult female ratios as a simulated calf survival rate of 35% (see Table 3-E.8, Table 3-E.10, Fig. 3-E.8, Fig. 3-E.10).

Consistently, projected yearling/100 adult females ratios slightly increased with increasing adult female harvest in the WF (1 yearling/100 adult females for every 25 antlerless elk harvested), reflecting the fact that increased adult female harvest can increase age ratios. However, larger population sizes in the EF buffered yearling/100 adult female ratios from experiencing increases due to antlerless harvest. Precision of projected yearling/100 adult female ratios tended to increase (i.e., posterior standard deviations increased) when vital rates were projected from the observed means and variances rather than simulated from informative priors, which may have reduced uncertainty by sharing information across years.

**DISCUSSION**

As many western states and provinces face declining elk recruitment in harvested populations coincident with carnivore recolonization, ungulate managers may have to initially reduce adult female harvest, especially in less productive habitats. However, it may be difficult to determine an appropriate level of harvest without reliable demographic data and a framework to project population size under different management alternatives. We demonstrated the utility of Bayesian IPMs to project population size and age ratios for two elk populations under a range of harvest alternatives and vital rate scenarios. Our simulations highlighted that one population had little capacity to sustain harvest (i.e., WF), while another population could likely sustain greater harvest (i.e., EF). The integration of vital rate (i.e., telemetry and pregnancy), aerial trend count and harvest data into a single model provided a flexible and powerful means to reduce uncertainty in harvest outcomes. This predictive approach is broadly applicable, and could be easily integrated into structured decision making frameworks to compare the consequences of different management alternatives. The projection model used here can also be configured to use only aerial count data to estimate recruitment in the model without having to collect more extensive data (e.g., telemetry or blood samples).
While Bayesian IPMs hold tremendous potential to simulate population dynamics for harvest management purposes, the predictions from IPMs, like any model, are only as good as the data feeding into them. For instance, we did not have survival estimates of yearling or adult male survival from radio-collared elk, and thus, we had to rely on the literature to provide prior information for these parameters. Also, our aerial trend counts used in the model were not corrected for sightability, which underestimated true population size. This was particularly evident in counts of adult males that were less than the estimated antlered harvest in some years. While modeling techniques such as using a log-Normal distribution for uncorrected counts or combining adult counts into a single observation model can provide a way forward under these circumstances, they are still imprecise and may not be a viable method for long-term monitoring, especially considering that what appears to be declining trend counts may be related only to changes in sightability or detection.

An additional source of uncertainty is that we used a simple population model that did not incorporate density dependence, which could cause projections of population size into the future to be biased high if population size increased above carrying capacity. Ideally, we would need to collect vital rate data for more years to assess density-dependence. However, we found little evidence for density-dependence in the EF elk population based on a nutritional assessment, but the WF population appeared more nutritionally limited (Proffitt et al. 2015). In the WF, an increase of 25% in mean calf survival rate is predicted to allow for more antlerless harvest and achieve the minimum population objective (i.e., Table 3-E.9, Fig. 3-E.9), but this calf survival rate may not be attainable, if, for example, bottom-up nutritional limitation reduces overwinter calf survival despite efforts to reduce winter mortality sources (i.e., increasing harvest of large carnivores). Therefore, combining carnivore reduction with nutritional treatments such as prescribed burns or logging may be more effective to increase calf survival in less productive habitats. Additionally, not including other factors such as wounding loss or poaching may have biased our projections of elk population size high, but we did not include these parameters because they are typically incorporated subjectively and represent an additional source of error. Despite the inherent assumptions and caveats involved in projecting populations into the future, our illustration of harvest scenarios will hopefully serve as a guideline for harvest planning in our study area, provide a useful example for practitioners, and encourage others to explore Bayesian integrated population modeling as a simulation tool.
LITERATURE CITED


TABLES
Table 3-E.1. Summary of calf survival, pregnancy, and harvest (antlerless and antlered) values used in 8 simulations for elk populations in the East Fork and West Fork study areas of the southern Bitterroot Valley, Montana, USA. Simulations 1–3 used the same harvest numbers but varied calf survival for the East Fork elk population, and simulations 4–8 varied calf survival and pregnancy rates under different antlerless and antlerless harvest prescriptions for the West Fork elk population.

<table>
<thead>
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<th>Simulated parameter</th>
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<td></td>
<td>290</td>
<td>290</td>
<td>290</td>
<td>25</td>
<td>75</td>
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</tbody>
</table>
Table 3-E.2. Summary of aerial trend count and harvest data used in elk harvest simulations including minimum counts of yearlings (Yrl), and adult females (AF) and males (AM); yearling/100 adult female ratios (Yrl/100 AF); and number of antlerless ($H_{af}$) and antlered ($H_{am}$) elk harvested during 2010–2015 in the East Fork (HD 270 and HD 334) and West Fork (HD 250) study areas in the southern Bitterroot Valley, Montana, USA. Aerial trend surveys were conducted annually during mid-April to mid-May, and the general (rifle) season for elk hunting was from late-October to late-November of each year. Both aerial trend count and harvest numbers were adjusted for study area (and hunting district) boundary changes that occurred in 2013.

<table>
<thead>
<tr>
<th>Year</th>
<th>East Fork</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>West Fork</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trend count</td>
<td>Harvest</td>
<td>Trend count</td>
<td>Harvest</td>
<td>Trend count</td>
<td>Harvest</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Yrl</td>
<td>AF</td>
<td>AM</td>
<td>Total</td>
<td>Yrl/100 AF</td>
<td>$H_{af}$</td>
<td>$H_{am}$</td>
<td>Total</td>
<td>Yrl</td>
<td>AF</td>
</tr>
<tr>
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<td>447</td>
<td>2,904</td>
<td>255</td>
<td>3,606</td>
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<td>116</td>
<td>320</td>
<td>436</td>
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</tr>
<tr>
<td>2011</td>
<td>567</td>
<td>2,950</td>
<td>242</td>
<td>3,759</td>
<td>19</td>
<td>113</td>
<td>242</td>
<td>355</td>
<td>82</td>
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</tr>
<tr>
<td>2012</td>
<td>612</td>
<td>2,605</td>
<td>305</td>
<td>3,522</td>
<td>23</td>
<td>96</td>
<td>223</td>
<td>319</td>
<td>56</td>
<td>462</td>
</tr>
<tr>
<td>2013</td>
<td>806</td>
<td>3,418</td>
<td>321</td>
<td>4,545</td>
<td>24</td>
<td>125</td>
<td>303</td>
<td>428</td>
<td>143</td>
<td>433</td>
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<tr>
<td>2014</td>
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<td>2,736</td>
<td>472</td>
<td>4,115</td>
<td>33</td>
<td>86</td>
<td>369</td>
<td>455</td>
<td>147</td>
<td>496</td>
</tr>
<tr>
<td>2015</td>
<td>766</td>
<td>3,126</td>
<td>426</td>
<td>4,318</td>
<td>25</td>
<td>133</td>
<td>462</td>
<td>127</td>
<td>722</td>
<td>29</td>
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</tbody>
</table>
Table 3-E.3. Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) with 95% credible intervals (CRI) from Bayesian integrated population models that simulated harvests of 100 antlerless (i.e., status quo), 200 antlerless, and 300 antlerless elk for the East Fork (EF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data. A potential population objective for the EF is 3800 (range: 3040–4560) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

| Year | 100 Antlerless | | | | 200 Antlerless | | | | 300 Antlerless | | |
|---|---|---|---|---|---|---|---|---|---|---|
|  \( \hat{N} \) | ±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 | 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 3-E.4. Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) from Bayesian integrated population models that simulated harvests of 100 antlerless (i.e., status quo), 200 antlerless, and 300 antlerless elk for the East Fork (EF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) with a simulated calf survival rate of 0.25 (i.e., 20 yearlings/100 adult female elk). A potential population objective for the EF is 3800 (range: 3040–4560) total elk with a recruitment range of 20–30 yearling/100 adult female elk. A potential population objective for the EF is 3800 (range: 3040–4560) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

<table>
<thead>
<tr>
<th>Year</th>
<th>100 Antlerless</th>
<th>200 Antlerless</th>
<th>300 Antlerless</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{N}$</td>
<td>±95% CRI</td>
<td>Yrl/100 AF</td>
</tr>
<tr>
<td>2016</td>
<td>4,718</td>
<td>1,053</td>
<td>24</td>
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<tr>
<td>2017</td>
<td>4,910</td>
<td>1,366</td>
<td>24</td>
</tr>
<tr>
<td>2018</td>
<td>5,113</td>
<td>1,654</td>
<td>24</td>
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<td>2019</td>
<td>5,349</td>
<td>1,928</td>
<td>24</td>
</tr>
<tr>
<td>2020</td>
<td>5,609</td>
<td>2,225</td>
<td>24</td>
</tr>
</tbody>
</table>
Table 3-E.5 Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) from Bayesian integrated population models that simulated harvests of 100 antlerless (i.e., status quo), 200 antlerless, and 300 antlerless elk for the East Fork (EF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) with a simulated calf survival rate of 0.50 (i.e., 40 yearlings/100 adult female elk). A potential population objective for the EF is 3800 (range: 3040–4560) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

| Year | 100 Antlerless | | | 200 Antlerless | | | 300 Antlerless | |
|------|---------------|---|---|---------------|---|---|---------------|---|---|
|      | $\hat{N}$     | ±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 3-E.6. Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, and 50 antlerless, and 75 antlerless elk for the West Fork (WF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data. A potential population objective for the WF is 1400 (range: 1120–1680) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

<table>
<thead>
<tr>
<th>Year</th>
<th>0 Antlerless</th>
<th>25 Antlerless</th>
<th>50 Antlerless</th>
<th>75 Antlerless</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{N}$</td>
<td>±95% CRI</td>
<td>Yrl/100 AF</td>
<td>±95% CRI</td>
</tr>
<tr>
<td>2016</td>
<td>745</td>
<td>117</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td>2017</td>
<td>780</td>
<td>158</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td>2018</td>
<td>817</td>
<td>198</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td>2019</td>
<td>857</td>
<td>239</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td>2020</td>
<td>900</td>
<td>282</td>
<td>22</td>
<td>8</td>
</tr>
</tbody>
</table>
Table 3-E.7. Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) from Bayesian integrated population models that simulated harvests of 25 antlered (i.e., status quo), 50 antlered, 75 antlered elk for the West Fork (WF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data. A potential population objective for the WF is 1400 (range: 1120–1680) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

<table>
<thead>
<tr>
<th>Year</th>
<th>25 Antlered</th>
<th></th>
<th>50 Antlered</th>
<th></th>
<th>75 Antlered</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{N}$</td>
<td>±95% CRI</td>
<td>Yrl/100 AF</td>
<td>±95% CRI</td>
<td>$\hat{N}$</td>
<td>±95% CRI</td>
</tr>
<tr>
<td>2016</td>
<td>745</td>
<td>117</td>
<td>22</td>
<td>8</td>
<td>726</td>
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</tr>
<tr>
<td>2017</td>
<td>780</td>
<td>158</td>
<td>22</td>
<td>8</td>
<td>739</td>
<td>157</td>
</tr>
<tr>
<td>2018</td>
<td>817</td>
<td>198</td>
<td>22</td>
<td>8</td>
<td>758</td>
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</tr>
<tr>
<td>2019</td>
<td>857</td>
<td>239</td>
<td>22</td>
<td>8</td>
<td>782</td>
<td>233</td>
</tr>
<tr>
<td>2020</td>
<td>900</td>
<td>282</td>
<td>22</td>
<td>8</td>
<td>812</td>
<td>273</td>
</tr>
</tbody>
</table>
Table 3-E.8. Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, 50 antlerless, and 75 antlerless elk for the West Fork (WF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) with a simulated calf survival rate of 0.35 (i.e., 25 yearlings/100 adult female elk). A potential population objective for the WF is 1400 (range: 1120–1680) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

<table>
<thead>
<tr>
<th>Year</th>
<th>0 Antlerless</th>
<th>25 Antlerless</th>
<th>50 Antlerless</th>
<th>75 Antlerless</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{N}$</td>
<td>±95% CRI</td>
<td>Yrl/100 AF</td>
<td>±95% CRI</td>
</tr>
<tr>
<td>2016</td>
<td>787</td>
<td>149</td>
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<td>2017</td>
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<td>2019</td>
<td>952</td>
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<td>23</td>
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<tr>
<td>2020</td>
<td>1,013</td>
<td>379</td>
<td>26</td>
<td>23</td>
</tr>
</tbody>
</table>
Table 3-E.9. Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, 50 antlerless, and 75 antlerless elk for the West Fork (WF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) with a simulated calf survival rate of 0.55 (i.e., 40 yearlings/100 adult female elk). A potential population objective for the WF is 1400 (range: 1120–1680) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

<table>
<thead>
<tr>
<th>Year</th>
<th>0 Antlerless</th>
<th></th>
<th></th>
<th>25 Antlerless</th>
<th></th>
<th></th>
<th>50 Antlerless</th>
<th></th>
<th></th>
<th>75 Antlerless</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{N}$ ±95% CRI</td>
<td>Yrl/100 AF</td>
<td>±95% CRI</td>
<td>$\hat{N}$ ±95% CRI</td>
<td>Yrl/100 AF</td>
<td>±95% CRI</td>
<td>$\hat{N}$ ±95% CRI</td>
<td>Yrl/100 AF</td>
<td>±95% CRI</td>
<td>$\hat{N}$ ±95% CRI</td>
<td>Yrl/100 AF</td>
</tr>
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<td>852</td>
<td>161</td>
<td>37</td>
<td>26</td>
<td>833</td>
<td>166</td>
<td>39</td>
<td>27</td>
<td>809</td>
<td>165</td>
<td>41</td>
</tr>
<tr>
<td>2017</td>
<td>962</td>
<td>231</td>
<td>36</td>
<td>25</td>
<td>911</td>
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<td>37</td>
<td>26</td>
<td>857</td>
<td>218</td>
<td>39</td>
</tr>
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<td>292</td>
<td>38</td>
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<td>911</td>
<td>283</td>
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<tr>
<td>2019</td>
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<td>36</td>
<td>25</td>
<td>1,098</td>
<td>360</td>
<td>38</td>
<td>25</td>
<td>965</td>
<td>346</td>
<td>39</td>
</tr>
<tr>
<td>2020</td>
<td>1,384</td>
<td>481</td>
<td>36</td>
<td>25</td>
<td>1,205</td>
<td>448</td>
<td>37</td>
<td>26</td>
<td>1,021</td>
<td>417</td>
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Table 3-E.10. Projections of population size ($\hat{N}$) and yearling/100 adult female ratios (Yrl/100 AF) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, 50 antlerless, and 75 antlerless elk for the West Fork (WF) population in the southern Bitterroot Valley, Montana, USA. Under these simulated harvests, population sizes and yearling/100 adult female ratios were projected into the future 5 years (2016–2020) with a simulated pregnancy rate of 0.85 (i.e., 25 yearlings/100 adult female elk). A potential population objective for the WF is 1400 (range: 1120–1680) total elk with a recruitment range of 20–30 yearling/100 adult female elk.

<table>
<thead>
<tr>
<th>Year</th>
<th>0 Antlerless</th>
<th>25 Antlerless</th>
<th>50 Antlerless</th>
<th>75 Antlerless</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{N}$</td>
<td>±95% CRI</td>
<td>Yrl/100 AF</td>
<td>±95% CRI</td>
</tr>
<tr>
<td>2016</td>
<td>798</td>
<td>111</td>
<td>27</td>
<td>10</td>
</tr>
<tr>
<td>2017</td>
<td>858</td>
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<td>27</td>
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</tr>
<tr>
<td>2018</td>
<td>924</td>
<td>203</td>
<td>27</td>
<td>10</td>
</tr>
<tr>
<td>2019</td>
<td>996</td>
<td>254</td>
<td>27</td>
<td>9</td>
</tr>
<tr>
<td>2020</td>
<td>1,073</td>
<td>313</td>
<td>27</td>
<td>10</td>
</tr>
</tbody>
</table>
Within our study area, elk populations are managed in three Hunting Districts (HDs) in west-central Montana, USA. The East Fork (EF) area consists of two HDs, HD 270 in the East Fork of the Bitterroot River drainage and HD 334 in the northern Bighole Valley. Elk counted in HD 270 in mid-April include some migratory elk that may be available for harvest in HD 334 in the fall. The West Fork (WF) area includes only HD 250. Note that elk harvest estimates used in simulations were adjusted to reflect study area boundary changes that occurred in 2013, when the original boundary (dotted line) between HD 250 and HD 270 was moved southwest to more accurately reflect elk population boundaries (solid line) as determined by Global Positioning System (GPS) data collected from adult female elk.
Figure 3-E.2. We based the annual population cycle of elk on a biological timescale, with the median birth date (May 30) of 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 early fall, while the general (rifle) hunting season for was from late-October to late-November of each year.
Figure 3-E.3. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 100 antlerless (i.e., status quo), 200 antlerless, and 300 antlerless elk for the East Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015. The thick black line and points show aerial trend counts. The thin solid and dotted black lines show the median \(n = 3,800\), and lower \((n = 3,040)\) and upper \((n = 4,560)\) bounds for the East Fork proposed population objective.
Figure 3-E.4. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 100 antlerless (i.e., status quo), 200 antlerless, and 300 antlerless elk for the East Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015, and a simulated calf survival rate of 0.25 for the prediction period. The thick black line and points show aerial trend counts. The thin solid and dotted black lines show the median ($n = 3,800$), and lower ($n = 3,040$) and upper ($n = 4,560$) bounds for the East Fork proposed population objective.
Figure 3-E.5. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 100 antlerless (i.e., status quo), 200 antlerless, and 300 antlerless elk for the East Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015, and a simulated calf survival rate of 0.50 for the prediction period. The thick black line and points show aerial trend counts. The thin solid and dotted black lines show the median ($n = 3,800$), and lower ($n = 3,040$) and upper ($n = 4,560$) bounds for the East Fork proposed population objective.
Figure 3-E.6. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, 50 antlerless, and 75 antlerless elk for the West Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015. The thick black line and points show aerial trend counts. The thin solid and dotted black lines show the median ($n = 1,400$), and lower ($n = 1,120$) and upper ($n = 1,680$) bounds for the West Fork proposed population objective.
Figure 3-E.7. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 25 antlered (i.e., status quo), 50 antlered, and 75 antlered elk for the West Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015. The thick black line and points show aerial trend counts. The thin solid and dotted black lines show the median ($n = 1,400$), and lower ($n = 1,120$) and upper ($n = 1,680$) bounds for the West Fork proposed population objective.
Figure 3-E.8. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, 50 antlerless, and 75 antlerless elk for the West Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015, and a simulated calf survival rate of 0.35 for the prediction period. The thin solid and dotted black lines show the median \( (n = 1,400) \), and lower \( (n = 1,120) \) and upper \( (n = 1,680) \) bounds for the West Fork proposed population objective.
Figure 3-E.9. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, 50 antlerless, and 75 antlerless elk for the West Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015, and a simulated calf survival rate of 0.55 for the prediction period. The thick black line and points show aerial trend counts. The thin solid and dotted black lines show the median ($n = 1,400$), and lower ($n = 1,120$) and upper ($n = 1,680$) bounds for the West Fork proposed population objective.
Figure 3-E.10. Projections of population size with 95% credible intervals (dotted lines) from Bayesian integrated population models that simulated harvests of 0 antlerless (i.e., status quo), 25 antlerless, 50 antlerless, and 75 antlerless elk for the West Fork population in the southern Bitterroot Valley, Montana, USA. Population sizes were projected into the future 5 years (2016–2020) based on observed vital rate and aerial trend count data collected from 2010–2015, and a simulated pregnancy rate of 0.85 for the prediction period. The thick black line and points show aerial trend counts. The thin solid and dotted black lines show the median (n = 1,400), and lower (n =1,120) and upper (n = 1,680) bounds for the West Fork proposed population objective.
Appendix 3-F. JAGS code for projection integrated population model

# JAGS code for Bitterroot Elk Population IPM
#
# Data for weibull calf model right censoring
data {
    for(t in 2:(nYears-2)){
        for(i in 1:(n.obsEF[t])){
            oneEF[t,i] <- 1
        }
    }
    for(t in 2:(nYears-2)){
        for(i in 1:(n.obsWF[t])){
            oneWF[t,i] <- 1
        }
    }
}

model{
    # COUNT DATA FOR EF AND WF
    # priors for counts observation error
    for(t in 1:nYears){
        CtyWF[t] ~ dlnorm(CyWF[t], tauYWF)T(0,)
        CtaWF[t] ~ dlnorm(CaWF[t], tauAWF)T(0,)
        CyWF[t] <- log(NyWF[t])
        CaWF[t] <- log(NaWF[t])
    }
    for(t in 1:(nYears)){
        CtyEF[t] ~ dlnorm(CyEF[t], tauYEF)T(0,)
        CtaEF[t] ~ dlnorm(CaEF[t], tauAEF)T(0,)
        CyEF[t] <- log(NyEF[t])
        CaEF[t] <- log(NaEF[t])
    }
    tauYEF~dgamma(0.001, 0.001)
    tauAEF~dgamma(0.001, 0.001)
    tauYWF~dgamma(0.001, 0.001)
    tauAWF~dgamma(0.001, 0.001)

    sigma2YEF<-(1/tauYEF)
    sigma2AEF<-(1/tauAEF)
    sigma2YWF<-(1/tauYWF)
    sigma2AWF<-(1/tauAWF)
\[
\begin{align*}
\sigma_{YEF} &= \sqrt{\sigma_{2YEF}} \\
\sigma_{AEF} &= \sqrt{\sigma_{2AEF}} \\
\sigma_{YWF} &= \sqrt{\sigma_{2YWF}} \\
\sigma_{AWF} &= \sqrt{\sigma_{2AWF}}
\end{align*}
\]

# initial population size (priors) at time 1
## East fork

\[Ny_{EF1} \sim \text{dnorm}(447, 0.0001) T(0,)
\]

\[Ny_{EF1} <- \text{round}(Ny_{EF1})
\]

\[Na_{EF1} \sim \text{dnorm}(255, 0.0001) T(0,)
\]

\[Na_{EF1} <- \text{round}(Na_{EF1})
\]

\[Na_{EF1} = Na_{EF1} + Na_{EF1}
\]

## West fork

\[Ny_{WF1} \sim \text{dnorm}(43, 0.0001) T(0,)
\]

\[Ny_{WF1} <- \text{round}(Ny_{WF1})
\]

\[Na_{WF1} \sim \text{dnorm}(519, 0.0001) T(0,)
\]

\[Na_{WF1} <- \text{round}(Na_{WF1})
\]

\[Na_{WF1} = Na_{WF1} + Na_{WF1}
\]

##### Process model (aka biology)

Calculate total number of adult females and males at time 1

\[
\begin{align*}
\text{for}(t \text{ in } 2: \text{nYears+t.pred}){ }
\end{align*}
\]

# West Fork process model (i.e. difference equations from matrix math)

\[
\begin{align*}
\text{meanNy}_{WF}[t] &\leftarrow \text{Sc}_{WF}[t-1]*\text{Preg}_{WF}[t-1]*\text{Na}_{WF}[t-1] \\
\text{meanNa}_{WF}[t] &\leftarrow (\text{Sa}_{WF}[t-1]*(\text{Na}_{WF}[t-1]-\text{Ha}_{WF}[t-1])) + (\text{Sy}_{WF}*\text{Ny}_{WF}[t-1]*\text{R}_{WF}) \\
\text{meanNa}_{WF}[t] &\leftarrow (\text{Sa}_{WF}*(\text{Na}_{WF}[t-1]-\text{Ha}_{WF}[t-1])) + (\text{Sy}_{WF}*\text{Ny}_{WF}[t-1]*(1-\text{R}_{WF}))
\end{align*}
\]

\[Ny_{WF}[t] \sim \text{dpois}(\text{ifelse(meanNy}_{WF}[t] <= 0, 1, \text{meanNy}_{WF}[t]))
\]

\[Na_{WF}[t] \sim \text{dpois}(\text{ifelse(meanNa}_{WF}[t] <= 0, 1, \text{meanNa}_{WF}[t]))
\]

\[Na_{WF}[t] \sim \text{dpois}(\text{ifelse(meanNa}_{WF}[t] <= 0, 1, \text{meanNa}_{WF}[t]))
\]

# East Fork process model (i.e. difference equations from matrix math)

\[
\begin{align*}
\text{for}(t \text{ in } 2: \text{nYears+t.pred}){ }
\end{align*}
\]

# #number of calves, adults from yearlings, and adults
meanNyEF[t] <- ScEF[t-1]*PregEF[t-1]*NafEF[t-1]
meanNaEF[t] <- (SafEF[t-1]*(NaEF[t-1]-HamEF[t-1])) + (SyEF*NyEF[t-1]*R.EF)
meanNamEF[t] <- (SamEF*(NamEF[t-1]-HamEF[t-1])) + (SyEF*NyEF[t-1]*(1-R.EF))

#use ifelse statement to prevent 0 or negative values for populations size
NyEF[t] ~ dpois(ifelse(meanNyEF[t] <= 0, 1, meanNyEF[t]))
NaEF[t] ~ dpois(ifelse(meanNaEF[t] <= 0, 1, meanNaEF[t]))
NamEF[t] ~ dpois(ifelse(meanNamEF[t] <= 0, 1, meanNamEF[t]))

for(t in 1:nYears+t.pred){
  Ntot.WF[t] <- NyWF[t] + NaWF[t]
  Ntot.EF[t] <- NyEF[t] + NaEF[t]
  y.100afWF[t]<-(NyWF[t]/NafWF[t])*100
  y.100afEF[t]<-(NyEF[t]/NafEF[t])*100
  am.100afWF[t]<-(NamWF[t]/NafWF[t])*100
  am.100afEF[t]<-(NamEF[t]/NafEF[t])*100
}

##Derive annual growth rates
for(t in 1:(nYears-1+t.pred)){
  pop.growthWF[t]<-((Ntot.WF[t+1] + 1)/(Ntot.WF[t] + 1))
  pop.growthEF[t]<-((Ntot.EF[t+1] + 1)/(Ntot.EF[t] + 1))
}

meanGROWTH.WF<- sum(pop.growthWF[1:nYears+t.pred-1])/(nYears+t.pred-1)
medianGROWTH.WF<- (prod(pop.growthWF[1:nYears+t.pred-1]))^(1/(nYears+t.pred-1))
meanGROWTH.EF<- sum(pop.growthEF[1:nYears+t.pred-1])/(nYears+t.pred-1)
medianGROWTH.EF<- (prod(pop.growthEF[1:nYears+t.pred-1]))^(1/(nYears+t.pred-1))

#Precision of standard deviations of temporal variability
sig.PregEF<-0.035
tau.PregEF <-pow(sig.PregEF, -2)
sig.SafEF<-  0.058
tau.SafEF<-pow(sig.SafEF, -2)
sig.ScEF<-0.196
tau.ScEF<-pow(sig.ScEF, -2)

sig.PregWF<-0.035
tau.PregWF <-pow(sig.PregWF, -2)
sig.SafWF<-  0.058
tau.SafWF<-pow(sig.SafWF, -2)
sig.ScWF<-0.196
tau.ScWF<-pow(sig.ScWF, -2)

#Distribution of error terms (bounded to help with convergence)
1.SafEF~dnorm(0,0.0001)T(-10, 10)
1.ScEF~dnorm(0,0.0001)T(-10, 10)
# Prior for yearling survival
 SyEF ~ dnorm(0.883, 238) T(0, 1)
 SyWF ~ dnorm(0.883, 238) T(0, 1)

# Prior for adult male survival
 SamEF ~ dnorm(0.918, 2770) T(0, 1)
 SamWF ~ dnorm(0.909, 977) T(0, 1)

# Observation aka likelihood

# Adult female survival
for(t in 1:nYears-2){
    femaleSurvivedWF[t] ~ dbin( SafWF[t], NumberOFCollarsAFWF[t])
    femaleSurvivedEF[t] ~ dbin( SafEF[t], NumberOFCollarsAFEWF[t])
}

#Adult female pregnancy
for(t in 2:nYears-2){
    pregWF[t] ~ dbin(PregWF[t], afCollarsWF[t])
   pregEF[t] ~ dbin(PregEF[t], afCollarsEF[t])
}

#Model for annual calf survival

#East Fork CALF SURVIVAL
for(t in 2:(nYears-2)){
    for(i in 1:(n.obsEF[t])){
        oneEF[t,i]~dinterval(yEF[t,i], y.censEF[t,i])
        yEF[t,i]~dweib(shapeEF, lambdaEF[t])T(y.entEF[t,i], )
    }
    lambdaEF[t] <- -log(ScEF[t])/pow(365, shapeEF)
}

#West Fork CALF SURVIVAL
for(t in 2:(nYears-2)){
    for(i in 1:(n.obsWF[t])){
        oneWF[t,i]~dinterval(yWF[t,i], y.censWF[t,i])
        yWF[t,i]~dweib(shapeWF, lambdaWF[t])T(y.entWF[t,i], )
    }
    lambdaWF[t] <- -log(ScWF[t])/pow(365, shapeWF)
}

#Priors for shape parameter
shapeEF ~ dunif(0, 2)
shapeWF ~ dunif(0, 2)

#Derive mean vital rates on probability scale
mSafEF<-exp(l.SafEF)/(1+exp(l.SafEF))
mPregEF<-exp(l.PregEF)/(1+exp(l.PregEF))
mScEF<-exp(l.ScEF)/(1+exp(l.ScEF))
mSafWF<-exp(l.SafWF)/(1+exp(l.SafWF))
mPregWF<-exp(l.PregWF)/(1+exp(l.PregWF))
mScWF<-exp(l.ScWF)/(1+exp(l.ScWF))

#End Model
