Carnivore Management and Elk Recruitment

Evaluating Carnivore Harvest as a Tool for Increasing Elk Calf Survival and Recruitment

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Executive Summary

Understanding the effectiveness of carnivore harvest regulations to manipulate carnivore and elk population abundances is a priority for wildlife managers seeking to achieve carnivore and elk population objectives. The purpose of this project was to evaluate the effects of conservative elk harvest and liberal carnivore harvest on carnivore population abundance and elk population dynamics in west-central Montana.

Our first objective was to evaluate the extent to which mountain lion harvest and abundance can be influenced by harvest management prescriptions. In 2012, Montana Fish, Wildlife and Parks (MFWP) implemented liberalized mountain lion harvest regulations designed to reduce mountain lion population abundance to increase elk survival and population abundance in portions of west-central Montana. We used a before-after-control-treatment approach to evaluate the extent to which mountain lion abundance was influenced by these harvest management prescriptions. We estimated mountain lion population abundance in one watershed managed for reduced populations (Bitterroot) and in one watershed managed for stable populations (Upper Clark Fork) before and 4 years after implementation of the new harvest regulations beginning in 2012. The Bitterroot study area included lion management units 250 and 270, and the Upper Clark Fork study area included lion management units 211/216, 210, 212/215. During 2012–2017, management success (percent of the prescribed quota achieved) was high in both the Bitterroot and Upper Clark Fork study areas. The average male and female harvest management success in the Bitterroot study area was 95% and 87%, respectively. The average male and female harvest management success in the Upper Clark Fork area was 82% and 77%, respectively. Mountain lion abundance declined in the Bitterroot study area (i.e., treatment area) from 161 (90% credible interval = 104, 233) in 2012 to 115 (CI = 69, 173) in 2016. The sex ratio of males changed from M:F = 0.50 (CI = 0.33, 0.67) to 0.28 (CI = 0.17, 0.40), which translated into a decline in the abundance of males, and similar abundances of females (before: males = 80 (CI = 52, 116), females = 81 (CI = 52, 117); after: males = 33 (CI = 20, 49), females = 82 (CI = 49, 124). In the Clark Fork study area (i.e., the control area), we found no evidence of changes in overall abundance or sex ratio of males in the population.

Our second objective was to evaluate the extent to which wolf harvest and minimum wolf counts are controlled by harvest management prescriptions. We summarized the wolf harvest regulations, harvest and minimum counts of wolves for west-central Montana. Harvest regulations were liberalized over time during 2009–2012 and have been consistent within west-central Montana since 2013. Since management authority was returned to MFWP in 2011, the total reported wolf harvest in west-central Montana has varied through time and averaged 32.3 wolves per year (SD=9.6). The minimum count of wolves per hunting district has also varied annually and averaged 10.2 (SD=7.2). Within the Bitterroot study area, harvest since 2011 has averaged 1.9 (SD=2.2) in HD 250 and 3.3 (SD=2.6) in HD 270, and estimated minimum counts have averaged 12.7 (SD=6.1) in HD 250 and 16.0 (SD=3.7) in HD 270. Variation in minimum wolf counts was uncorrelated to wolf harvest regulations or harvest at this scale, but changes in harvest regulations annually during 2009-12 prevented a rigorous evaluation of these effects.

Our third objective was to evaluate the extent to which black bear harvest is controlled by harvest management prescriptions. In 2010, black bear harvest regulations were liberalized in the 2 hunting districts within the Bitterroot study area to include an additional 2-week spring season and an additional 10-day archery-only fall season. We used black bear harvest data from 20 districts within west-central Montana during 2001–2017. We found that across west-central Montana, spring black bear harvest increased following implementation of liberalized harvest regulations that allowed for a 2-week spring hunting season extension. On average, the liberalized spring harvest regulation resulted in an additional 3 bears harvested per hunting district. However, we found no evidence that fall black bear harvest increased following implementation of a liberalized fall harvest regulation that allowed for a 2-week archery-only hunting season extension.

Our fourth objective was to evaluate the effects of carnivore harvest regulations on elk calf survival and cause-specific mortality rates. Because previous studies documented mountain lion predation as an important source of calf mortality in this area, we focused on evaluating the effects of the liberalized mountain lion harvest regulations on calf survival and cause-specific mortality. We marked a sample of elk calves in the Bitterroot study area before, during, and after liberalized mountain lion harvest regulations and estimated calf survival to age 1 as well as causes of mortality. We found evidence that liberalized mountain lion harvest regulations were associated with increased summer, winter, and annual elk calf survival during the harvest treatment period, and estimated rates of annual elk calf survival during the period of liberalized regulations nearly doubled as compared to before the liberalized harvest regulations. However, our results also suggest that the initial increases in annual survival during the treatment period were reduced to intermediate levels 4 years after treatment, resulting in annual survival rates that were only about 10 percent higher than pre-treatment-era levels.

Our fifth objective was to evaluate the effectiveness of using mountain lion harvest as a tool for increasing calf recruitment in west-central Montana. To address this objective, we developed an integrated elk population model to estimate and compare recruitment and population growth rate during the 5 years prior to and 5 years following implementation of the liberalized mountain lion harvest regulations. We included data from two elk populations (HD 250 and HD 270) within the Bitterroot study area that was managed for a reduction in the mountain lion population (i.e., treatment area) and two elk populations (HD 210 and HD 216) within the Upper Clark Fork study area that was managed for stable mountain lion populations (i.e., control area). We found evidence that the liberalized mountain lion harvest regulations were associated with short-term increases in elk recruitment and population growth rates within the treatment area, although the effects of the treatment on recruitment declined during the 5 years following treatment. In the Bitterroot treatment area, per capita elk recruitment was roughly stable around an estimated median value of 0.19 (CI = 0.12, 0.27) in the pre-treatment period (2007–2011), increased immediately after treatment (2013) to 0.42 (CI = 0.29, 0.56), and then declined to 0.21 (CI = 0.11, 0.32) in 2017. In contrast, per capita elk recruitment in the Clark Fork control area had similar median values during the pre- (2007–2011: 0.32, CI = 0.21, 0.45) and post-treatment periods (2013–2017: 0.32, CI = 0.22, 0.45). These changes in recruitment corresponded to similar changes in population growth rate, although we note that population growth rates were also subject to variation due to changing elk harvest. Our results indicate that management objectives to increase calf recruitment were achieved through the implementation of liberalized mountain lion harvest regulations, although effects of the treatment on recruitment were strongest immediately following implementation of the treatment and diminished over time.

Our final objective was to estimate the relative effects of factors that wildlife managers have some degree of control over, such as carnivore density, and factors such as weather and landscape attributes that wildlife managers cannot control on elk calf recruitment (i.e., survival to age 1) in west-central Montana. To address this objective, we evaluated the association between elk calf recruitment, weather, and indices of carnivore population abundance using survey data collected from 17 elk hunting districts across west-central Montana from 2004-2017. We found that environmental conditions experienced by the calf during its first summer, and by the female prior to conception when the calf was in-utero, were strongly associated with recruitment rates. Spring precipitation experienced by the calf during its first summer was negatively associated with recruitment. Cold and wet springs may elevate risk of illness, delay green-up and elevate neonatal mortality. Summer precipitation was positively associated with recruitment. We found an interaction between summer precipitation and winter severity such that dry summers interacted with particularly severe winters to diminish calf recruitment. Although we did not find evidence for a main effect of NDVI, we found an interaction between summer NDVI and winter severity during the year a calf was in-utero indicating that poor primary production during summer interacted with severe winters to diminish recruitment. Together these results demonstrate a strong influence of environmental conditions on calf recruitment. Using indices of carnivore populations across the region, we found support for effects of predation on elk calf recruitment that were generally of smaller magnitude than weather effects, but that interacted with weather effects. Indices of carnivore population abundance were likely not accurate or precise enough to detect predation effects at the broader landscape scale of this analysis compared to the more focused analyses described above, therefore these results should be treated with caution.

Together, our results suggest that carnivore harvest management may be an effective tool for increasing elk populations. Our results from west-central Montana indicate that liberalized mountain lion harvest regulations intended to reduce mountain lion populations and increase elk calf survival and recruitment achieved a moderate (i.e., 29%) reduction in mountain lion population abundances within the treatment area that corresponded with short-term increases in elk recruitment and population growth. Elk population demographic responses suggest that the harvest treatment effect was strongest immediately after the mountain lion harvest treatment was implemented and lessened over time as the harvest treatment was reduced. Regional elk recruitment trends were strongly correlated with weather covariates, indicating that weather effects will mediate the effects of manipulations of carnivore densities on elk populations. We recommend that wildlife managers seeking to balance carnivore and ungulate population objectives design rigorous carnivore and ungulate population monitoring programs to assess the effects of harvest management. We recognize that accurately monitoring local densities of carnivores over regional scales may not be possible, so we advise implementation of rigorous monitoring programs within carefully selected, representative areas to facilitate evaluation of the effects of such management actions. Assessing and understanding effects of carnivore harvest management will set realistic expectations regarding the effects of management programs on carnivore and ungulate populations and allow managers to better design programs to meet carnivore and ungulate population objectives.

Section 1 – Introduction and Project Background

Elk (*Cervus canadensis*) are an iconic species throughout the western United States and play a large role across ecological (Kauffman et al. 2010), social (Haggerty and Travis 2006) and economic (US Department of the Interior et al. 2014) landscapes. However, since the early 2000s, declines in elk numbers and recruitment (i.e., calf survival from birth to age 1) in some parts of the western United States resulted in concerns that the recovery of large carnivores such as wolves (*Canis lupus*), mountain lions (*Puma concolor*) and grizzly bears (*Ursus arctos*) has affected elk populations (Bunnell et al. 2002, Griffin et al. 2011*a*). Thus, wildlife managers are increasingly focused on understanding and managing the effects of predation on elk populations. Carnivore recovery is important to elk populations because predation may be a proximate limiting and regulating factor for many elk populations (Messier 1994, Hebblewhite et al. 2002, Garrott et al. 2008*b*). In addition to carnivore recovery, changing elk harvest management prescriptions, shifts in land use, and changing habitat and climatic conditions all contribute to a complex suite of variables with the potential to affect elk population dynamics. Because of this complexity, understanding the effects of predation on elk population dynamics is difficult, and determining appropriate management actions is challenging.

In the western United States, carnivore recovery has had varying effects on elk populations as the effects of carnivore predation are complex and vary across systems with different carnivore-ungulate assemblages (White and Garrott 2005). In some areas, bear predation is an important mortality source for calves (Smith, et al. 2006, Raithel et al. 2007, White et al. 2010, Lukacs et al. 2018), especially in areas where grizzly bear populations have increased over recent decades (Singer et al. 1997, Barber-Meyer et al. 2008). In other systems, mountain lion predation is the primary mortality source for calves (Myers et al. 1998, Johnson et al. 2013, Eacker et al. 2016). Although public attention is often focused on the effects of wolf recovery on ungulate populations, the impacts vary, with relatively minor effects reported in some studies (Vucetich and Peterson 2004, Barber-Meyer et al. 2008, White et al. 2010, Eacker et al. 2016) and larger effects reported in others (Hebblewhite et al. 2002, Garrott et al. 2008). Furthermore, if elk populations are limited by factors such as weather or habitat (Garrott et al. 2003, Griffin et al. 2011, Johnson et al. 2018), or if predation is compensatory with other factors (Singer et al. 2003, Garrott et al. 2008), changes in carnivore populations may or may not result in changes in the key vital rates that drive elk population growth. These results highlight the importance of understanding the uncertainties associated with carnivore predation as managers try to evaluate the efficacy of various management programs.

To achieve ungulate population abundance goals and address concerns regarding effects of predation, wildlife managers may design integrated carnivore-ungulate harvest management programs. When ungulate populations are low, integrated carnivore-ungulate management programs employ a combination of liberalized carnivore and restrictive ungulate harvest regulations to achieve increases in the ungulate population. These differ from predator control programs in which liberalized carnivore harvest regulations are applied without adjusting ungulate harvest regulations and may include a combination of hunters or management actions to achieve carnivore reductions. Multiple factors affect the efficacy of integrated carnivore-ungulate management, including the duration of the carnivore control effort, the magnitude of the carnivore population reduction during treatment, weather conditions during and after treatment (Boertje et al. 1996), and interactions with other predators and prey in the system (Arthur and Prugh 2010, Prugh and Arthur 2015). Therefore, there are important assumptions underlying the prescription of an integrated carnivore-ungulate harvest management program: 1) carnivore harvest will reduce the abundance of the carnivore population, 2) the carnivore population reduction will result in reduction of the total ungulate predation rate (defined as the product of the killing rate and numeric response that translates as mortality rate), and 3) the reduction in total predation rate will result in additive increases in key vital rates that increase the ungulate population growth rate. If all of these assumptions are valid, then integrated carnivore-ungulate harvest management programs may be a useful tool for wildlife managers seeking to increase ungulate population abundances.

Integrated carnivore-ungulate management programs designed to reduce carnivore populations to increase ungulate recruitment and population growth have been implemented in a variety of ecological systems. However, effects of these management programs on ungulate populations are debated and effects vary across ecological systems (Boertje et al. 1996, Hayes et al. 2003, White et al. 2010, Hurley et al. 2011, Keech et al. 2011, Tatman et al. 2018). Multiple, multi-year studies of bear-wolf-moose (*Alces alces*) systems in Alaska found that predation was the dominant factor affecting moose populations, and, in many cases, experimental reductions of predators increased moose populations (see Boertje et al. 2010 for review; but see also Hayes et al. 2003). In the Rocky Mountains, an experimental study in a bear-mountain lion-elk system found that increased bear and mountain lion harvest increased elk calf survival (White et al. 2010), though effects of predator harvest on predator populations was not directly assessed. An experimental study within the Rocky Mountains in a coyote-mountain lion-mule deer system found only short-term, weak responses of mule deer (*Odocoileus hemionus*) survival and population trends following mountain lion reductions (Hurley et al. 2011). These varying results reflect the complex interactions that affect predator-prey dynamics.

In addition to the underlying complexities of predator-prey dynamics, multiple other sources of uncertainty affect the extent to which carnivore harvest regulations influence ungulate population dynamics. First, objectives of the prescribed carnivore harvest may or may not be achievable using hunter harvest (White et al. 2010, Bischof et al. 2012, Tatman et al. 2018). Second, realized carnivore harvest may or may not result in a biologically significant change in carnivore abundance. Moreover, in many previous studies, changes in carnivore harvest and population abundances were often not measured, resulting in a relatively weak experimental design and limited inferences. Third, a change in carnivore abundance (even if harvest is achieved) and the associated predation rate may or may not affect ungulate population growth rate depending on the degree to which predation affects different vital rates as compared to other factors such as weather or habitat productivity (White and Garrott 2005, Melis et al. 2009, Boertje et al. 2010). This is ultimately related to the degree to which predation mortality is compensatory or additive (Singer et al. 1997, Griffin et al. 2011, Brodie et al. 2013). Thus, the efficacy of integrated carnivore-ungulate management varies across systems, making it difficult for wildlife managers to develop and evaluate effective programs to balance carnivore and ungulate populations at desired levels.

Evaluating the effects of integrated carnivore-ungulate management on carnivore and ungulate populations requires estimating important population parameters of both carnivores and ungulates before and after harvest prescriptions are implemented. As such, an initial step in evaluating the efficacy of integrated carnivore-ungulate management is determining if carnivore harvest prescriptions achieve desired carnivore harvest and population management goals. Estimating carnivore population size is challenging, however, because carnivores often occur at low densities, are wide-ranging and difficult to detect, and often violate closure assumptions employed in traditional capture-recapture population estimation. Recent advances in spatial capture-recapture modeling provide an efficient method of estimating carnivore population size (Proffitt et al. 2015, Boulanger et al. 2018, Paterson et al. 2019*a*) that accounts for the shortcomings of capture-recapture methodology by incorporating the spatial organization of individuals through estimation of trap-specific capture probabilities while also accounting for detection. These methodologies allow wildlife managers to monitor carnivore abundances before and after implementing harvest prescriptions and to evaluate if harvest prescriptions meet the carnivore population management objectives.

In addition to monitoring changes in carnivore abundances, managers need to evaluate ungulate population demography pre- and post- harvest treatment to determine if changes in carnivore populations result in changes in ungulate vital rates, and, ultimately, population growth rate and abundance. Survival of prime-aged females and recruitment can both have strong impacts on a population's trajectory (Gaillard et al. 1998, 2000, Eacker et al. 2016). However, while adult female survival is often high and relatively stable (Nelson and Peek 1982, Garrott et al. 2003), juvenile survival tends to be highly variable and consequently may be a more common driver of ungulate population dynamics (Raithel et al. 2007, Harris et al. 2008). Recruitment, which incorporates fecundity and juvenile survival to age l, represents an important demographic parameter that wildlife managers often use to track trends in population growth rates (DeCesare et al. 2012). Although direct assessments of juvenile survival using marked animals offers the most accurate and informative measure of recruitment, such data are difficult and expensive to collect and may not be a feasible option. Age ratios (i.e., number of juveniles per 100 adult females) are a less expensive and less time-intensive alternative that provide an index of recruitment that is often used by managers to monitor populations (Harris et al. 2008). Such extensive spatiotemporal datasets offer the potential for monitoring changes in recruitment and for assessing long-term trends in populations (Harris et al. 2008, DeCesare et al. 2012).

Evaluating the success of a management program in meeting the ungulate population objectives is often achieved through monitoring programs that estimate animal counts and age ratio data (e.g., calf:cow ratios) as an index of juvenile recruitment (e.g., Lukacs et al. 2018). Ungulate population monitoring programs are routinely employed by state wildlife management agencies annually or biannually. However, uncertainty in the relationship between uncorrected count data and true population size (e.g., sightability, Steinhorst and Samuel 1989), and between age ratio data and annual calf survival (Harris et al. 2008), makes the detection of changes in ungulate population size and juvenile recruitment challenging. Recent methodological advances allow for count and age ratio data to be used in integrated population models that partition the variance in observations into variation associated with biological processes and sampling processes to more precisely estimate demographic parameters, and evaluate associated changes in vital rates and abundance (Link and Nichols 1994, Kéry and Schaub 2011, Nilsen and Strand 2018). However, even with new methods available that improve managers' ability to monitor and estimate populations, the uncertainties in the relationship between prescribed carnivore harvest and ungulate population responses make the effectiveness of integrated carnivore-ungulate management programs uncertain.

In west-central Montana, carnivore recovery concurrent with low recruitment and overall declines in elk populations raised public concerns about the effects of increasing carnivore populations on local elk herds (Eacker et al. 2016). In this area, similar to other parts of the western United States, calf recruitment is a primary factor affecting elk population growth (Raithel et al. 2007, Eacker et al. 2016). Recent studies in the Bitterroot Valley have indicated mountain lion predation as the primary source of calf mortality (Eacker et al. 2016, Forzley 2019). In response to these concerns, wildlife managers in Montana Fish, Wildlife and Parks (MFWP) Region 2 implemented an integrated carnivore-ungulate harvest management program designed to increase elk populations through a reduction in carnivore abundance via increased hunter harvest in conjunction with more restrictive elk harvest.

A primary objective of the carnivore harvest management program was to reduce mountain lion populations by approximately 30% over three watersheds within the region that had declining elk recruitment and populations, while maintaining stable mountain lion populations in a fourth watershed where elk populations were stable. Mountain lion populations are resilient to high harvest and capable of recovering quickly following intensive harvest (Ross and Jalkotzy 1992, Robinson and DeSimone 2011). The objective of a 30% reduction therefore represented a short-term strategy for temporarily reducing the mountain lion population to boost elk populations, while conserving the long-term viability of mountain lions in the area. Given social controversy surrounding mountain lion harvest objectives, a targeted reduction of >30% was unlikely to be acceptable (Mitchell et al. 2018*a*). In west-central Montana, the estimated female mountain lion harvest rate averaged 7% prior to treatment during 2004-2010, whereas a female mortality rate of approximately 20% or greater is needed to achieve population reduction (Robinson et al. 2014). Therefore, to temporarily reduce mountain lion populations, the harvest management objective was to achieve a targeted 35% harvest rate on adult female mountain lions for 3 years and maintain male harvest opportunity and harvest rates at levels similar to the historic average. Harvest quotas to achieve the targeted 35% harvest rate were designed based on mountain lion population abundance estimates (Robinson et al. 2015) and achieved via liberalized female harvest quotas and public hunting seasons. Following the treatment, the management objective shifted to maintaining a stable mountain lion population by reducing female harvest rates.

Additionally, black bear (*Ursus americanus*) and wolf harvest regulations were liberalized during this period. The spring black bear hunting season was extended by two weeks. After wolf management returned to the State of Montana and hunting resumed in 2011, MFWP implemented increasingly liberalized wolf hunting regulations over the following 3 years. These changes included adding a trapping season, removing the state-wide quota, extending the season, and increasing bag limits for individual hunters.

These changes in carnivore management in west-central Montana provided a unique opportunity to build on a recently completed elk-carnivore project and conduct a robust before-after-control-impact evaluation of the effects of carnivore management on carnivore and elk populations. We focused on evaluating the efficacy of mountain lion harvest management as a tool for increasing elk calf survival and population growth rates because previous work demonstrated that predation rates on elk calves from black bears and wolves were relatively low, whereas predation from mountain lions was an important factor limiting elk populations (Eacker et al. 2016). During 2011–2014, we evaluated elk calf survival rates, and rates of predation from mountain lions and other large carnivores in the area (Eacker et al. 2016). We also estimated pre-treatment mountain lion density in an area managed for mountain lion reduction (Bitterroot study area) and an area managed for stability (Upper Clark Fork study area). Building from these previous efforts, the purpose of this project was to evaluate elk calf survival, cause-specific mortality, and population growth rates, as well as carnivore densities, to assess the effect of carnivore harvest management on carnivore and elk populations. Specific goals included the following:

1. Evaluate the extent to which mountain lion harvest and density can be controlled by wildlife management prescriptions (liberalized public harvest opportunities).
2. Evaluate the extent to which wolf harvest and minimum wolf counts can be controlled by wildlife management prescriptions (liberalized public harvest opportunities).
3. Evaluate the extent to which black bear harvest is controlled by wildlife management prescriptions (liberalized public harvest opportunities).
4. Evaluate the effects of carnivore harvest regulations on elk calf survival and cause-specific mortality rates.
5. Evaluate the effectiveness of using mountain lion harvest as a tool for increasing elk calf recruitment in west-central Montana.
6. Evaluate the relative effects of factors wildlife managers have some degree of control over in the short term (carnivore density), some degree of influence over in the long term (habitat-related nutritional differences), and factors wildlife managers cannot control (weather, landscape attributes) on elk calf recruitment in west-central Montana.

Section 2 – Study Area

The study area is located in MFWP administrative Region 2 of west-central Montana. The region is 27,324 km^2 and includes 28 elk hunting districts (Figure 2.1). Approximately 62% of the region is public land, the majority of which is managed by the United States Forest Service. Portions of this study were focused in the southern Bitterroot watershed located primarily in Ravalli County (Bitterroot) and the Rock Creek and Flint Creek portions of the Upper Clark Fork watershed located primarily in Granite County (Upper Clark Fork, Figure 2.2). The Bitterroot study area is 3,350 km^2 and includes the East Fork and the West Fork drainages of the Bitterroot River. The East Fork drainage (hunting district [HD] 270) encompasses the annual range of the East Fork elk herd, a portion of which migrate to summer in the Big Hole Valley (HD 334). The West Fork drainage (HD 250) encompasses the primary annual range of the West Fork elk herd. Elevations range from 1200 m to 2600 m, with moderate to steep terrain. Precipitation in the Bitterroot study area ranges annually from 40 cm in the valley bottoms to 88 cm in the mountains, and primarily falls as snow during winter. The Upper Clark Fork study area spans portions of elk HDs 210, 211, 212, 213, 214, 215 and 216. Elevations range from 1095 m to 2753 m, with moderate to steep terrain. Precipitation ranges annually from 31 cm in the valley bottoms to 113 cm in the mountains and primarily falls as snow during winter (Group 2011).

Ungulate species in both study areas include elk, white-tailed deer (*Odocoileus virginianus*), mule deer, bighorn sheep (*Ovis canadensis*) and moose. Large carnivores occurring during this study include gray wolves, mountain lions, and black bears.

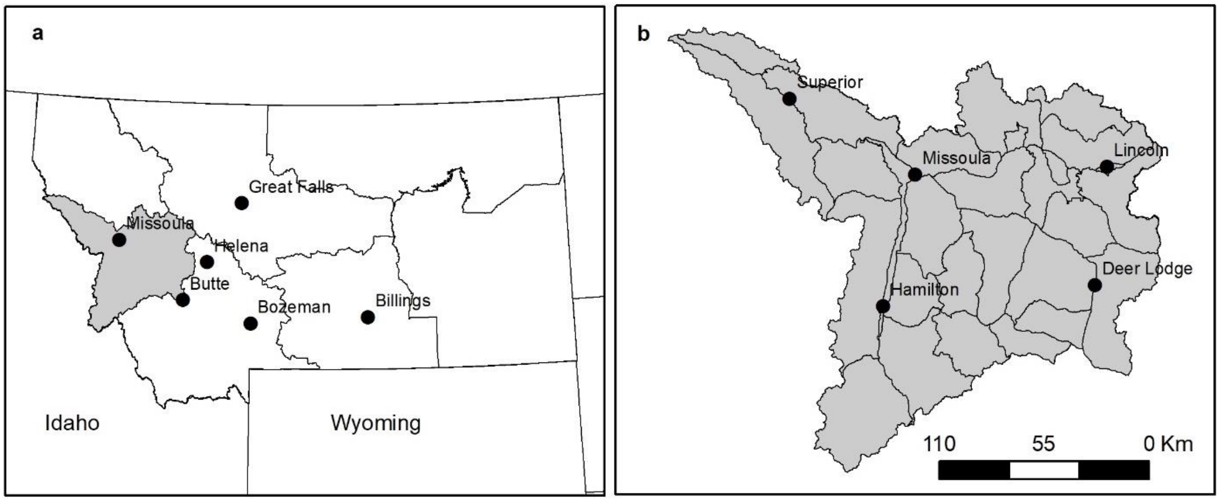


Figure 2.1 *The study area was MFWP Administrative Region 2 in west-central Montana (Panel a, shaded gray). Elk within the study area are managed within 28 different hunting districts (Panel b, black lines).*

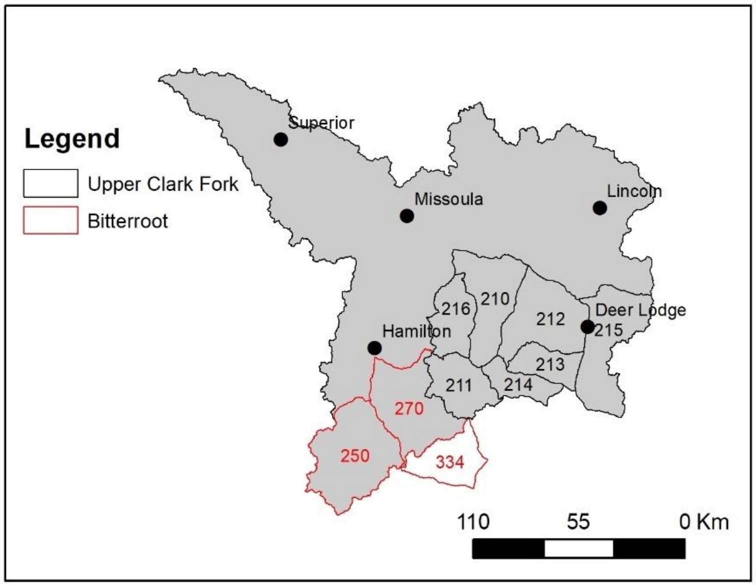


Figure 2.2 *Portions of this study were focused in the southern Bitterroot watershed located primarily in Ravalli County (Bitterroot study area) and the Rock Creek and Flint Creek portions of the Upper Clark Fork watershed located primarily in Granite County (Upper Clark Fork study area). The Bitterroot study area included hunting districts (HD) 250, 270 and 334 (red) and the Upper Clark Fork study area included HD 210, 211, 212, 213, 214, 215 and 216 (black).*

Elk Populations

Two elk populations occupy the Bitterroot study area: the West Fork and the East Fork populations. These two populations are managed within MFWP HDs 250 and 270, respectively. Prior to the 2014 hunting season, the boundary between these two HDs was adjusted to more accurately reflect the range of these elk populations and allow wildlife managers to more precisely manage each population. As a result, HD 250 was reduced in size, while HD 270 expanded. After this adjustment was made, count data was adjusted to reflect the current HD boundaries; however, classification data, including calf recruitment estimates, could only be revised back to 2002. The count data adjusted to reflect the current HD boundaries shows the elk population in HD 250 steadily increased from approximately 330 elk in 1980 to a high of 1,300 in 2005, then declined to 550 observed elk by 2009. Calf recruitment in HD 250 from 1980–2006 fluctuated between 25–45 calves:100 adult females, before declining to 8 calves:100 adult females in 2009. During 2009–2017, the population and recruitment have increased to 850 elk and 29 calves:100 adult females (Figure 2.3). The elk population in HD 270 was stable at about 1,000 from 1980–1998, then steadily increased to a high of 4,400 observed elk in 2013. From 2013–2017, the elk population remained right around 4,000. Calf recruitment was generally between 30–50 calves:100 adult females from 1980–2006, before declining to 15 calves:100 adult females in 2009. Since 2009, calf recruitment has fluctuated between 16-33 calves:100 adult females (Figure 2.3).

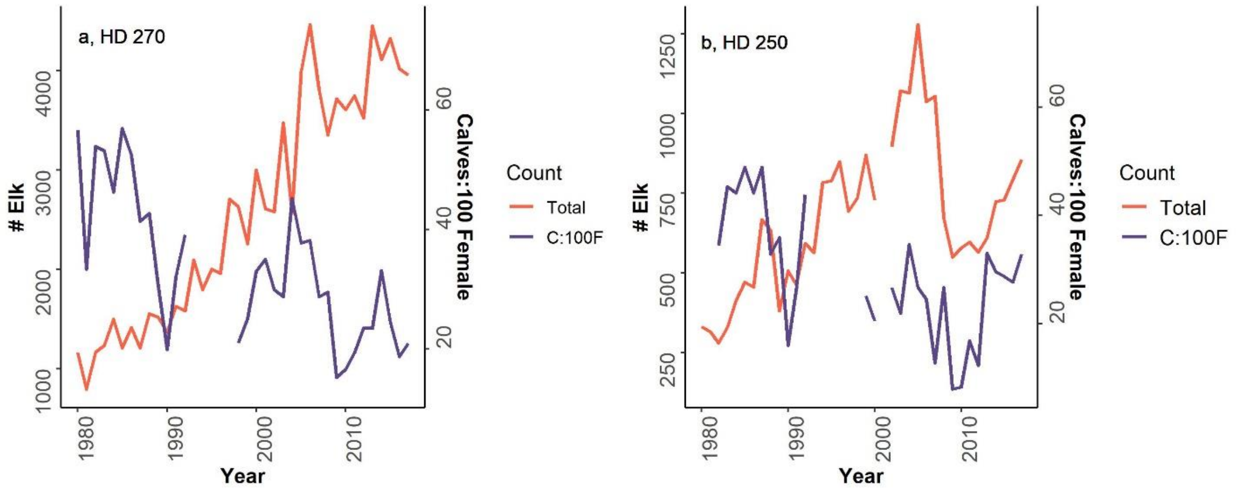


Figure 2.3 *The number of total elk and the calves:100 adult females counted during aerial spring surveys in the (a) HD 270, the East Fork drainage and (b) HD 250, the West Fork drainage from 1980–2017. A boundary change prior to the 2014 season expanded HD 270 and reduced HD 250 and data presented here throughout 1980–2017 are summarized to reflect current boundary definitions.*

Antlerless harvest in HD 250 has been by restricted general license opportunity (e.g. archery, youth, portion of the rifle season with/without a quota) and limited antlerless-only tags (i.e., B-licenses or antlerless permits) since 1980, with license numbers ranging between 100–300 from 1980–2005. From 2008–2010, antlerless harvest in HD 250 was limited to 25–50 antlerless-only tags per year and all general license antlerless opportunity was removed in 2010. Antlerless-only tags were reduced to 0–5 per year during 2011–2013 in response to the declining elk population and were removed altogether from 2014–2017. In addition, antlered bull harvest in HD 250 was restricted to 25–35 limited entry permits during 2011–2017. Antlerless harvest in HD 270 has been on special tag or a combination of special tag and general season quota since 1980. During 1980–2009, the number of special permits fluctuated between 200-500, before being reduced to 20 during 2010–2013. Antlerless tags were increased to 350-450 during 2014–2017. In addition, antlered bull harvest was changed from the general tag to a more restrictive unlimited entry permit during 2012–2017 in response to low bull:cow ratios. In HD 250, annual antlerless harvest averaged 74 from 1980–2003, then increased to 139 during 2004-2010. During 2011–2017, average annual antlerless harvest dropped to 4 as harvest was limited as part of the integrated harvest management program. Antlered bull harvest averaged 108 from 1980–2003, declined to 86 during 2004–2010, and then dropped to 23 during 2011–2017 as harvest was limited. In HD 270, antlerless and antlered harvest averaged 195 and 239 during 1980–2003 and increased to 330 and 253 during 2004–2010. During 2011–2017, average antlerless harvest declined to 102, while antlered bull harvest increased to 285.

In Montana, state law requires MFWP to manage elk populations within population objectives, as defined by the State Elk Management Plan (Hamlin 2004). During our study, the elk management objectives were to increase the HD 250 population towards its population objective of 1,400 elk and to maintain the HD 270 population at current levels given the population objective of 3,800.

Two elk populations occupy the Upper Clark Fork study area: the HD 216 and HD 210 populations. The Rock Creek elk population in HD 216 has remained relatively stable during 2005–2017, averaging 255 observed elk. The Antelope Hills population in HD 210 increased from 800 to 2000 observed elk during 2005–2011 and remained relatively stable at an average of 1,485 observed elk since 2011. Bull elk harvest is allowed on the general elk license, and antlerless elk harvest is allowed through limited-entry antlerless tags. Antlerless harvest has remained relatively stable in HD 216 and HD 210 averaging 40 and 130 antlerless elk per year during 2011–2017. During the study, the elk management objective was to maintain the HD 216 population at current levels given the population objective of 325 observed elk and reduce the HD 210 population toward the population objective of 850 observed elk.

Section 3 – Mountain Lion Harvest Management and Population Abundance

Introduction

The recovery and recolonization of mountain lions across their historic range has led to concern regarding their potential effects on elk and other ungulate populations (Pletscher et al. 1997, Riley and Malecki 2001, Kendall et al. 2009), and mountain lions have been identified as an important source of mortality for elk calves in many ecosystems in North America (Rearden 2005, Eacker et al. 2016). In February 2012, the Montana Fish and Wildlife Commission adopted mountain lion harvest management regulations for west-central Montana intended to achieve sufficient mountain lion harvests, particularly harvest of females, to decrease the size of some mountain lion populations while also considering broader-scale mountain lion conservation, desired mountain lion hunting opportunity, and the balance of a large carnivore complex with dynamic ungulate populations. The harvest management regulations were designed to reduce mountain lion abundance by 30% across three watersheds in west-central Montana including the Bitterroot study area (treatment area), and manage lion population sizes for stability across one watershed that included the Upper Clark Fork study area (control area, Figure 3.1). In west-central Montana, the estimated female mountain lion harvest rate averaged 7% prior to treatment during 2004–2010, whereas a female mortality rate of approximately 20% or greater is needed to achieve population reduction (Robinson et al. 2014). Therefore, to temporarily reduce mountain lion populations by 30%, the harvest management objective was to achieve a targeted 35% harvest rate on adult female mountain lions for 3-years and maintain male harvest opportunity and harvest rates at levels similar to the historic average. Harvest quotas to achieve the targeted 35% harvest rate were designed based on available mountain lion population abundance estimates (Robinson et al. 2015) as well as social tolerance for harvest levels (Mitchell et al. 2018) and achieved via liberalized harvest quotas and public hunting seasons for mountain lions. Following the 3-year treatment, the management objective was to reduce female harvest rates and manage for stable populations. Due to limited social tolerance for female harvest, the achieved treatment included only 2-years of higher female harvest quota, followed by reduced female harvest quota and increased male harvest quota.

Understanding the effects of mountain lion harvest management on mountain lion populations requires estimating important demographic parameters of mountain lion populations before and after harvest management prescriptions are implemented. Estimating mountain lion population size is challenging though, because mountain lions occur at low densities, are wide ranging and difficult to detect, and often violate closure assumptions employed in traditional capture-recapture population estimation. However, recent advances in spatial capture-recapture modeling provide an efficient method of estimating carnivore population size (Proffitt et al. 2015, Boulanger et al. 2018, Paterson et al. 2019*a*) that accounts for the shortcomings of capture-recapture methodology by incorporating the spatial organization of individuals through estimation of trap-specific capture probabilities while also accounting for detection probability (Efford and Fewster 2013, Efford 2014). These methodologies allow wildlife managers to estimate mountain lion abundances before and after implementing harvest management prescriptions, and to evaluate the effectiveness of these prescriptions on achieving population management objectives.

In this section, our objective was to evaluate the effects of mountain lion harvest management on mountain lion population abundance. We used a before-after-control-impact design to evaluate if harvest management resulted in changes in mountain lion abundance within the Bitterroot treatment (i.e., a watershed managed for mountain lion population reduction) and/or Upper Clark Fork control (i.e., a watershed managed for stable mountain lion populations) areas. Better understanding the extent to which mountain lion harvest and population abundance are controlled by harvest management regulations will improve the ability of wildlife managers to better achieve desired population goals.

Methods

To assess the effects of harvest management on mountain lion abundance, we used spatial capture-recapture modeling to compare mountain lion abundance in a treatment and control area before and after 4 years of increasing quotas in the treatment area (Figure 3.1). We estimated pre- and post-treatment abundance in a portion of the area managed for mountain lion reduction (Bitterroot study area) in 2012 and 2016, respectively. The Bitterroot study area spanned portions of mountain lion management units (LMUs) 250 and 270 and was located within a watershed managed for mountain lion population reduction (i.e., treatment area). We estimated pre- and post-treatment abundance in a portion of the area managed for stability (Upper Clark Fork study area) in 2013 and 2017, respectively. The Upper Clark Fork study area spanned portions of LMUs 210, 211/216, 212/215, and 213/214, and was within a watershed managed for stable mountain lion populations (i.e., control area). Mountain lion management units within these areas have had variable mountain lion harvest quotas, and presumably population sizes, during the past 20 years.

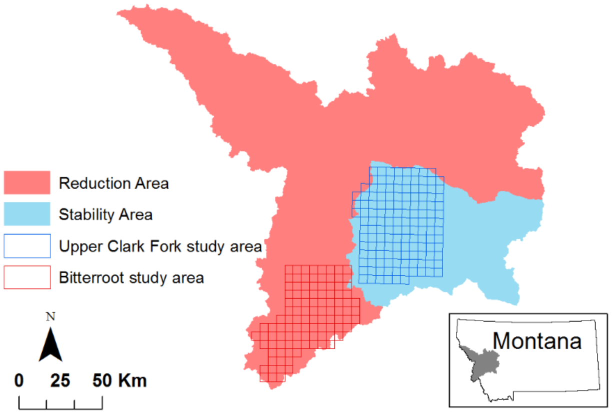


Figure 3.1 *We estimated mountain lion abundance in an area managed for reduced mountain lion populations (Bitterroot study area) and stable mountain lion populations (Upper Clark Fork area) before and after 4-years implementation of harvest management regulations designed to reduce mountain lion populations in three watersheds (shaded red) and maintain stable populations in one watershed (shaded blue) in west-central Montana.*

Mountain lion sampling and genetic analysis

The sampling period was December 1 – April 15. We overlaid a grid of 5 x 5-km cells across each study area (see Figure 3.1). We started searching for mountain lion sign each day in a randomly assigned grid cell. We stratified the starting location of sampling in this manner to ensure sampling was allocated across both the high and low-quality mountain lion habitat within each study area, previously modeled in Robinson et al. 2015. Hound handlers searched for mountain lion tracks and opportunistically collected hair and scat samples. When a fresh track was located, the handler would release trained hounds to locate and tree the mountain lion. Muscle samples were collected from treed animals using biopsy darts fired from a CO2-powered rifle (Palmer Cap-Chur brand). Tracks were inspected to determine if the mountain lion was independent or associated with a family group, and group size was recorded. The estimated age and sex of the animal samples was recorded to determine which member of the group was the mother and/or potential offspring (actual sex and relatedness was determined based on DNA analysis, see below). All field teams used a Global Positioning System (GPS) to record the length (in km) and location of their search effort.

Management removals (e.g. for livestock depredation) and hunter harvest occurred during the sampling period. In Montana, the hide and skull of all harvested mountain lions must be presented to MFWP, and we collected muscle samples from management removals and harvested animals to be included in our dataset. We also used information from the mandatory check to estimate annual harvest of male and female mountain lions within the study areas.

We collared a sample of mountain lions in the Bitterroot and Upper Clark Fork study areas to collect movement data to inform the space use component of the spatial capture-recapture model (see below). We programmed collars to collect 6 locations per day, upload locations daily through the Iridium satellite system, and then drop off the animal after 24 months (Telonics style TGW-4477-4, Telonics telemetry-electronics Consultants, Arizona, USA).

We performed genetic analysis of hair, scat, and muscle samples to identify the sex and individual identity of sampled mountain lions (Russell et al. 2012, Proffitt et al. 2015). We tested the relatedness of any samples that we collected from animals encountered as part of a potential family group. If animals were related based on DNA analyses and field-identified as an adult female and subadult(s) that were traveling together, we censored the subadult(s) consistent with including only the mother. This removed dependent offspring traveling with their mother from the dataset. If animals were related based on DNA and both were field-identified as subadults that were traveling together, we included both subadult siblings in the analysis. This resulted in only independent-aged animals being included in our analysis and estimates of abundance. Complete details of mountain lions sampling and genetic analysis may be found in Proffitt et al. (2015).

Spatial capture-recapture modeling

We developed a multistrata spatial capture-recapture model to estimate the spatial abundance of mountain lions in each of our two study areas during both the pre-treatment and post-treatment sampling periods. There are three main components of our SCR model: a model for the distribution of animal activity centers in space, a model for the probability of encounter given activity centers, and a model for the telemetry information. Previous work in this system (Proffitt et al. 2015) strongly suggested that the abundance of animal activity centers was highly associated with values of a separately estimated mountain lion resource selection function (RSF; Robinson et al. 2015). The first component of our model then expressed the expected number of activity centers in each statespace cell as a function of the RSF value on the log scale:

$$\log\left(\mu(s,\boldsymbol{\beta})\right) = \beta_0 + \beta_{RSF}\text{RSF}(s),$$

where $\mu(s,\beta)$ is the expected number of activity centers in statespace cell s given the covariate value RSF(s) and regression coefficients β_0, β_{RSF}).

We defined our observation process using the bivariate-normal model to define how the probability of detecting individual i in trapping cell *j* on occasion *t* decays with the distance from the location of an individual's activity center (s_i) and the center of a trapping cell (x_j, $\text{d}\left(x_j, s_i\right)$) such that the probability of observation was:

$$p_{i,j,t} = p^0_{ijt}\exp\left(\frac{-1}{2\sigma^2_{\text{sex}}} * \text{d}\left(x_j, s_i\right)^2\right),$$

where p^0_{ijt} was the probability of detection when the distance between an individual's activity center and the trap was zero ($\text{d}(x_j, s_i) = 0$), and σ_{sex} was the sex-specific scale parameter that regulates how the probability of detection declines with distance. We defined p^0_{ijt} on the logit scale:

$$\text{logit}(p^0_{ijt}) = \alpha + \beta_{sex}(\text{Sex}_i) + \beta_{effort} * \log(\text{effort}_{jt})$$

where α was the baseline detection probability, Sex_i is an indicator variable (Female = 0, Male = 1), and $\text{effort}_{j,t}$ is the effort expended in cell *j* during occasion *t*. We set p^0_{ijt} to zero for any trapping cell in which no effort was expended. We included the locations of harvested individuals as if they arose from the detection process; previous work has suggested this introduces negligible bias into estimates (Paterson et al. 2019*b*) and can improve inference in SCR-based estimates of abundance (Proffitt et al. 2015). We then censored these animals from the model for all occasions following harvest to avoid a bias in detection probabilities.

Finally, we defined the telemetry model as a multinomial process where the number of daily locations for animal *i* in any statespace cell given an activity center s_i was governed by an underlying model of space use that shared the space use parameters with the observation model, σ^2_{sex}:

$$\text{m}_i \sim \text{Multinomial}(\text{R}_i, \pi_i)$$

where R_i is the total number of fixes for individual *i*, and π_i is the vector of probabilities defined as:

$$\pi_{i,k} = \frac{\exp\left(\frac{-1}{2\sigma^2_{\text{sex}}} * \text{d}(x_k, s_i)\right)}{\sum_{k=1}^{S} \exp\left(\frac{-1}{2\sigma^2_{\text{sex}}} * \text{d}(x_k, s_i)\right)},$$

where S is the total number of statespace cells in the study area.

One of our key goals was to understand how inferences on abundances changed in the presence of potential underlying variation in baseline detection (α) and space use parameters (σ^2_{sex}). Our multistrata model formulation allowed us to construct four models that allowed different amounts of information to be shared across study areas. We predicted that sharing information across time and space would improve inference, and we tested this prediction by comparing inference from the 4 competing multistrata models. Additional details regarding the modeling approach and goodness of fit may be found in Paterson et al. (2019b).

Results

Mountain lion harvest management quotas and harvest

During the six years of this study (2012–2017), management success (percent of the prescribed quota achieved) was high for both male and female mountain lions. In the Bitterroot treatment area, the average prescribed male and female quota was 3.3 males and 2.9 females per 1000km^2/year during 2012–2017, and the average harvest was 3.0 males and 2.5 females per 1000km^2/year (Table 3.1). The average male and female harvest management success was 92% and 85%, respectively. In the Upper Clark Fork control area, the average prescribed male and female quota was 2.4 males and 0.7 females per 1000km^2/year during 2012–2017, and the average harvest was 1.9 males and 0.5 females per 1000km^2/year (Table 3.1). The average male and female harvest management success was 79% and 70%, respectively.

Table 3.1 *The male and female mountain lion harvest quotas and achieved harvest for the Bitterroot and the Upper Clark Fork study areas in west-central Montana during 2006–2017. The Bitterroot study area included lion management units 250 and 270 and was managed for mountain lion population reduction during 2012–2013 (treatment area), and the Upper Clark Fork study area included lion management units 211/216, 210, 212/215, and 213/214 and was managed for stable mountain lion population abundance (control area). The male and female harvest quota (number per 1000 km^2) is reported for comparison because the area of the Bitterroot and Upper Clark Fork study areas differed. Values indicated with an * indicate total quota (male and female quota), rather than male quota.*

Prescription Type	Study area	Year	Male quota	Male harvest	Female quota	Female harvest	Male quota per 1000 km^2	Male harvest per 1000 km^2	Female quota per 1000 km^2	Female harvest per 1000 km^2
Treatment	Bitterroot	2006	7	8	0	0	2.10	2.40	0.00	0.00
Treatment	Bitterroot	2007	7	6	0	0	2.10	1.80	0.00	0.00
Treatment	Bitterroot	2008	7	2	0	0	2.10	0.60	0.00	0.00
Treatment	Bitterroot	2009	20*	7	2	1	6.00*	2.10	0.60	0.30
Treatment	Bitterroot	2010	30*	11	4	2	9.00*	3.30	1.20	0.60
Treatment	Bitterroot	2011	40*	10	6	6	11.99*	3.00	1.80	1.80
Treatment	Bitterroot	2012	14	12	14	15	4.20	3.60	4.20	4.50
Treatment	Bitterroot	2013	8	10	12	11	2.40	3.00	3.60	3.30
Treatment	Bitterroot	2014	10	8	7	6	3.00	2.40	2.10	1.80
Treatment	Bitterroot	2015	11	11	8	3	3.30	3.30	2.40	0.90
Treatment	Bitterroot	2016	11	7	8	8	3.30	2.10	2.40	2.40
Treatment	Bitterroot	2017	11	11	8	7	3.30	3.30	2.40	2.10
Control	Clark Fork	2006	9	4	0	0	1.31	0.58	0.00	0.00
Control	Clark Fork	2007	7	5	0	0	1.02	0.73	0.00	0.00
Control	Clark Fork	2008	7	3	0	0	1.02	0.44	0.00	0.00
Control	Clark Fork	2009	7	6	0	0	1.02	0.87	0.00	0.00
Control	Clark Fork	2010	20*	8	8	2	2.91*	1.16	1.16	0.29
Control	Clark Fork	2011	20*	9	8	2	2.91*	1.31	1.16	0.29
Control	Clark Fork	2012	20	13	3	3	2.91	1.89	0.44	0.44
Control	Clark Fork	2013	16	14	4	3	2.33	2.03	0.58	0.44
Control	Clark Fork	2014	16	13	6	4	2.33	1.89	0.87	0.58
Control	Clark Fork	2015	16	15	5	4	2.33	2.18	0.73	0.58
Control	Clark Fork	2016	16	10	5	4	2.33	1.45	0.73	0.58
Control	Clark Fork	2017	16	13	5	1	2.33	1.89	0.73	0.15

Mountain lion SCR models

We evaluated four separate spatial capture-recapture models that shared different amounts of information about baseline probabilities of detection and sex-specific space use across the study areas (Table 3.2).

Table 3.2 *Competing multistrata spatial capture-recapture models estimating mountain lion spatial abundances within the Bitterroot and Upper Clark Fork study areas in west-central Montana during two time periods corresponding to different mountain lion harvest management prescriptions. Competing models shared different combinations of information on baseline detection probability and sex-specific space use across study areas and time periods.*

MODEL	MODEL DESCRIPTION
1	Baseline detection shared within study areas only; Sex-specific space use shared within study areas only
2	Baseline detection shared within study areas only; Sex-specific space use shared across study areas
3	Baseline detection shared across study areas; Sex-specific space use shared within study areas only
4	Baseline detection shared across study areas; Sex-specific space use shared across study areas

Across all models, the 90% credible intervals for the β_{RSF} coefficient were positive (Figure 3.2). For example, the estimates from Model 1 predict that abundance of activity centers in the Bitterroot study area in 2012 increases from 0.20 (90% credible interval: 0.06, 0.35) for a statespace cell with an underlying RSF value of 0.05 (the median RSF value) to 1.80 (1.12, 2.36) for a cell with a value of 0.35 (90% quantile RSF value).

We found no evidence that males had a lower overall probability of detection for the Bitterroot (2016) and Upper Clark Fork areas (2013 and 2017), which contrasts with the Bitterroot (2012) where we found strong evidence that males had an overall lower probability of detection. In the Bitterroot in 2012, the probability of detection for 20 km of search effort (approximately the median across all years and study areas) was 0.11 [0.07, 0.15] for females compared to 0.03 [0.01, 0.05] for males (Figure 3.3). The relationship between search effort and detection was broadly consistent across study areas and years (Figure 3.3).

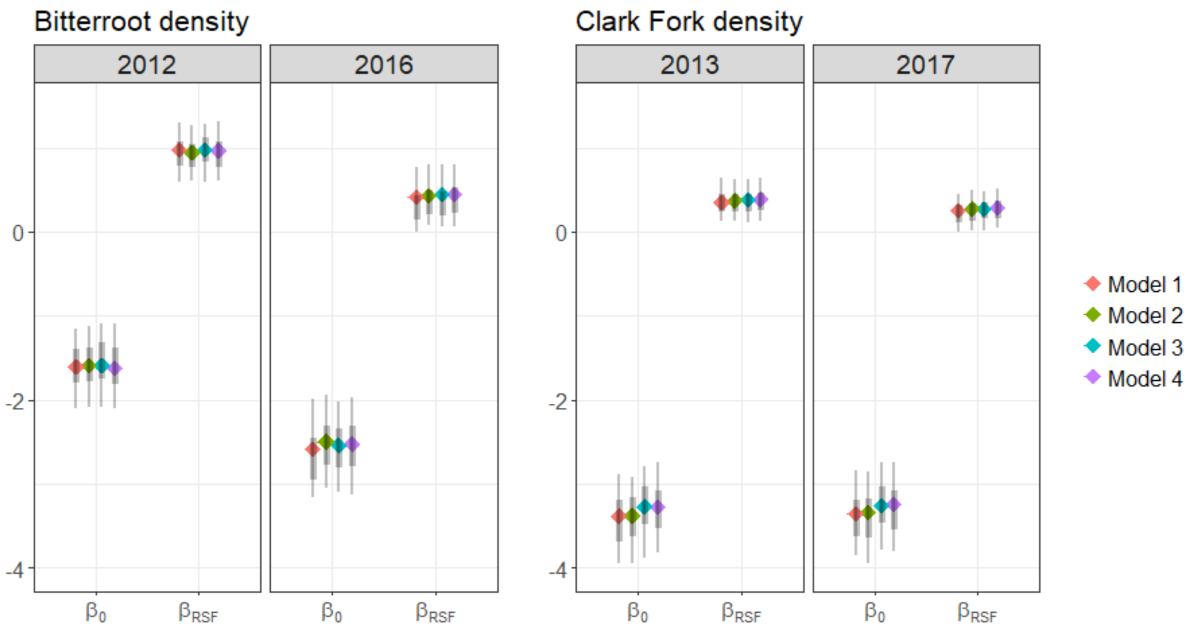


***Figure 3.2** Coefficient estimates (on the log scale) representing the effect of baseline probability of detection (β_o) and mountain lion resource selection function values of each statespace cell (β_{RSF}) on the expected number of mountain lion activity centers for each of four competing spatial capture-recapture models estimating abundance of mountain lions in the Bitterroot and Upper Clark Fork study areas of west-central Montana during 2012—2017. Diamonds represent the mean of the posterior, light gray boxes the 50% credible interval and the whiskers the 90% credible interval.*

For example, Model 1 predicts the probability of detection for females in the Bitterroot (2012) area increased from 0.11 (0.01, 0.15) to 0.28 (0.17, 0.38) as effort increased from 20 km to 100 km. The model-specific probabilities of detection weakly suggest that overall detection in the Upper Clark Fork (e.g., 0.07 [0.04, 0.11] for females with 20 km of effort) is lower than in the Bitterroot (0.11 [0.07, 0.15]), though overlap in the tails of the credible intervals prevents strong inference (Figure 3.3).

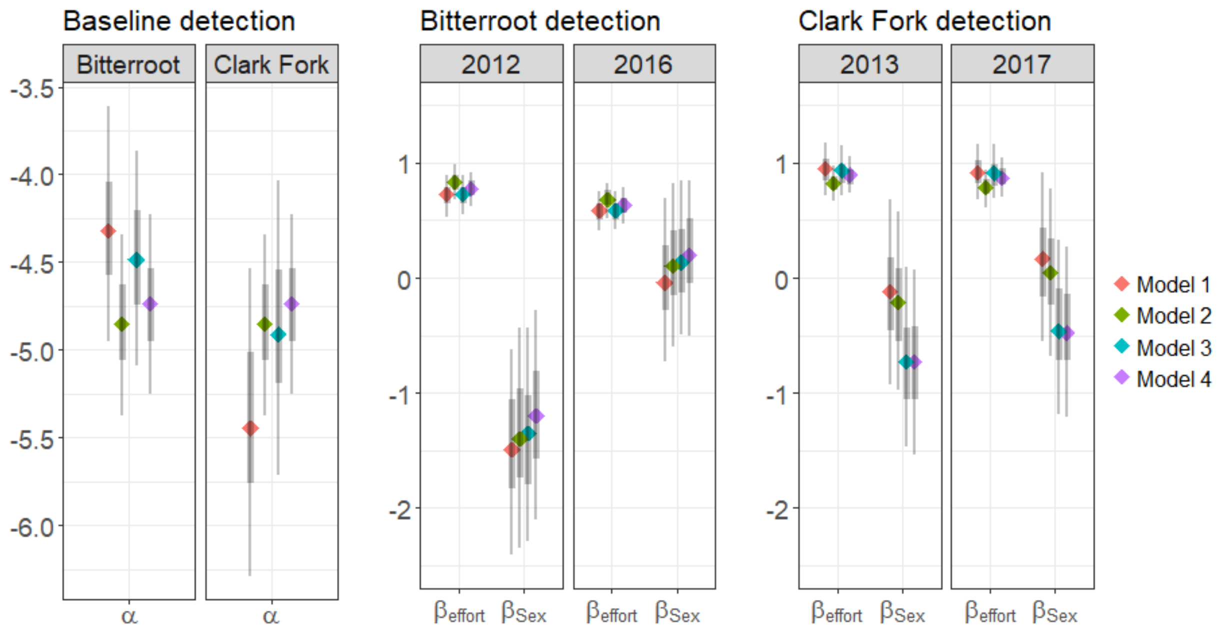


Figure 3.3 *Coefficient estimates (on the log scale) representing the effect of baseline detection probability (α),search effort (β_{effort}), and sex (β_{sex}) on detection probability for each of four competing spatial capture-recapture models estimating abundance of mountain lions in the Bitterroot and Clark Fork study areas of west-central Montana during 2012–2017. Diamonds represent the mean of the posterior, light gray boxes the 50% credible interval and the whiskers the 90% credible interval.*

Estimates of the space-use parameters (σ^2_{sex}) indicated differences among the sexes and four formulations of model structures (Figure 3.4). All models strongly suggest that σ^2_{male} is higher than σ^2_{female} in the Bitterroot (i.e., males use a larger space than females), and that σ^2_{male} is roughly commensurate between the study areas (i.e. male space use is similar between study areas). Only models 1 and 2 separately estimated sex-specific space use for each study area, and the resulting estimates indicated that females in the Upper Clark Fork are using larger areas than females in the Bitterroot and are using areas roughly equal to the size of areas used by males in the Upper Clark Fork (Figure 3.4).

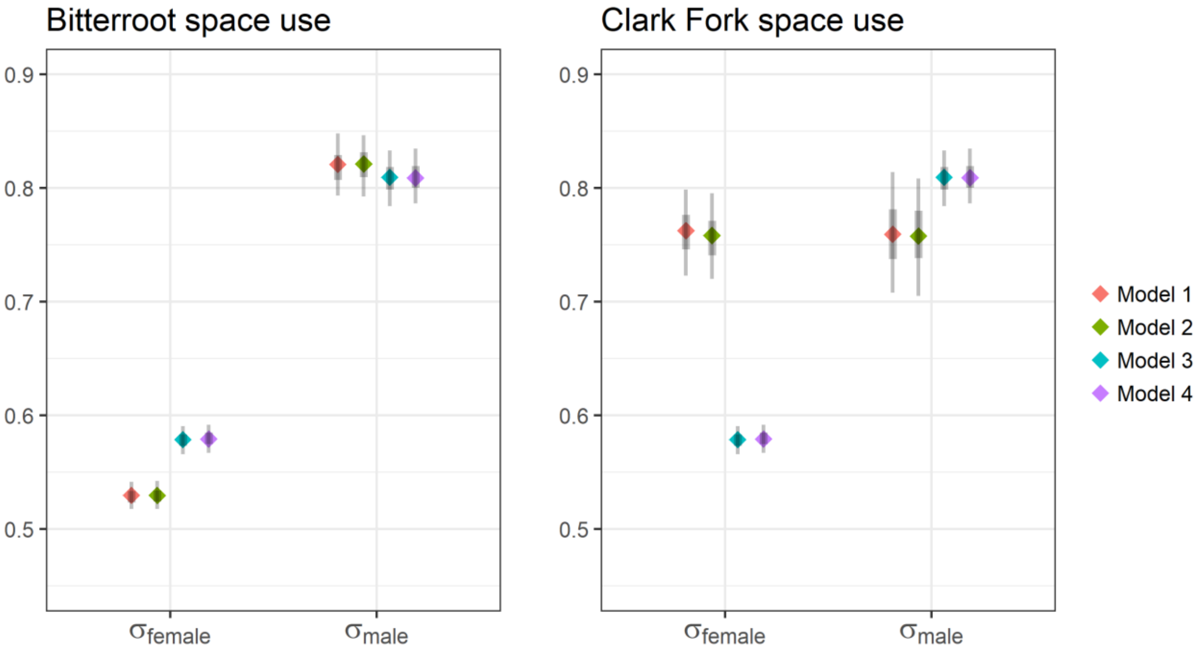


Figure 3.4 *Coefficient estimates representing the effect of distance to an individual's activity center on female (σ_{female}) and male (σ_{male}) mountain lion probability of detection for each of four competing spatial capture-recapture models estimating abundance of mountain lions in the Bitterroot and Upper Clark Fork study areas of west-central Montana during 2012–2017. Diamonds represent the mean of the posterior, light gray boxes the 50% credible interval and the whiskers the 90% credible interval.*

Although the results of the goodness of fit metrics suggest that all models adequately fit the data, the evidence for overall lower estimated probability of detection in the Upper Clark Fork and the differences in sex-specific space use between the study areas from Model 1 suggest that Model 1 is the most appropriate single model from which to make inferences on abundance and density. We selected Model 1 as the most supported model, and report abundance and density estimates from this model below. The resulting mountain lion abundance and density estimates are very similar from all 4 models, and inferences about the effect of the mountain lion harvest treatment on mountain lion abundance and density are not affected by model choice.

Mountain lion sampling

The number of sampling-days, amount of search effort, number of samples included in analysis, and the number of individuals identified varied across the two study areas and two time periods (Table 3.3). The number of individuals identified and the number of spatial captures in each study area and time period, together with previous simulation-based work on the same study design, suggest that each of our four datasets are adequate to produce unbiased spatial capture-recapture abundance estimates (see Paterson et al. 2019*a* for details).

Table 3.3 *The number of sampling-days, search effort (in km), number of male and female samples included in analyses, and the number of individual male and female mountain lions detected in the Bitterroot and Upper Clark Fork study areas in west-central Montana during 2012–2017.*

Study area	Year	Number sampling-days	Search effort (km)	Number of samples		Number of individuals detected	
				Female	Male	Female	Male
Bitterroot	2012	50	8,897	50	28	37	25
Bitterroot	2016	84	14,216	41	33	33	21
Clark Fork	2013	66	12,898	37	23	21	14
Clark Fork	2017	95	10,905	39	27	25	17

Pre- and post-treatment mountain lion population estimates

We used the estimated relationship between the mountain lion RSF and the abundance of activity centers combined with the estimated sex ratios from Model 1 to extract the predicted abundances for each study area (i.e., the trapping grid) and year (Table 3.4). Additionally, we extracted the predicted abundances for each hunting district within each study area and year (Table 3.4). We found that mountain lion abundance declined in the Bitterroot treatment area but not in the Upper Clark Fork control area (Figure 3.5). Our results indicate that overall abundance declined in the Bitterroot study area from 2012 (mean = 161, 90% credible interval: [104, 233]) to 2016 (115 [69, 173]). Additionally, in the Bitterroot study area we found a change in the sex ratio between 2012 (M:F = 0.50 [0.33, 0.67]) and 2016 (M:F = 0.28 [0.17, 0.40]). This translated into a decline in the abundance of males, and similar abundances of females (2012: males = 80 [52, 116], females = 81 [52, 117]; 2016: males = 33 [20, 49], females = 82 [49, 124]).

Table 3.4 *Predicted male and female mountain lion abundance (N), density (animals per 100km^2), and 90% credible intervals (LCI, UCI) of total, male, and female mountain lions within the trapping grid and hunting districts in the Bitterroot and Upper Clark Fork study areas during 2012–2017.*

Study Area	Year	Inference	Group	N	90%LCI	90%UCI	Density	90%LCI	90%UCI
Bitterroot	2012	trapping grid	Total	161	104	233	6.13	3.96	8.88
Bitterroot	2012	trapping grid	Males	80	52	116	3.05	1.98	4.42
Bitterroot	2012	trapping grid	Females	81	52	117	3.09	1.98	4.46
Bitterroot	2012	HD 250	Total	79	49	117	4.32	2.68	6.39
Bitterroot	2012	HD 250	Males	39	24	58	2.13	1.31	3.17
Bitterroot	2012	HD 250	Females	40	25	59	2.19	1.37	3.22
Bitterroot	2012	HD 270	Total	80	52	116	5.31	3.45	7.70
Bitterroot	2012	HD 270	Males	40	26	58	2.65	1.73	3.85
Bitterroot	2012	HD 270	Females	40	26	58	2.65	1.73	3.85
Bitterroot	2016	trapping grid	Total	115	69	173	4.38	2.63	6.59
Bitterroot	2016	trapping grid	Males	33	20	49	1.26	0.76	1.87
Bitterroot	2016	trapping grid	Females	82	49	124	3.12	1.87	4.72
Bitterroot	2016	HD 250	Total	65	35	104	3.55	1.91	5.68
Bitterroot	2016	HD 250	Males	19	10	30	1.04	0.55	1.64
Bitterroot	2016	HD 250	Females	46	25	74	2.51	1.37	4.04
Bitterroot	2016	HD 270	Total	60	35	92	3.98	2.32	6.10
Bitterroot	2016	HD 270	Males	17	10	26	1.13	0.66	1.73
Bitterroot	2016	HD 270	Females	43	25	66	2.85	1.66	4.38
Clark Fork	2013	trapping grid	Total	57	37	85	1.68	1.09	2.50
Clark Fork	2013	trapping grid	Males	24	16	36	0.71	0.47	1.06
Clark Fork	2013	trapping grid	Females	33	21	49	0.97	0.62	1.44
Clark Fork	2017	trapping grid	Total	72	47	105	2.12	1.38	3.09
Clark Fork	2017	trapping grid	Males	28	18	41	0.82	0.53	1.21
Clark Fork	2017	trapping grid	Females	44	29	64	1.30	0.85	1.88

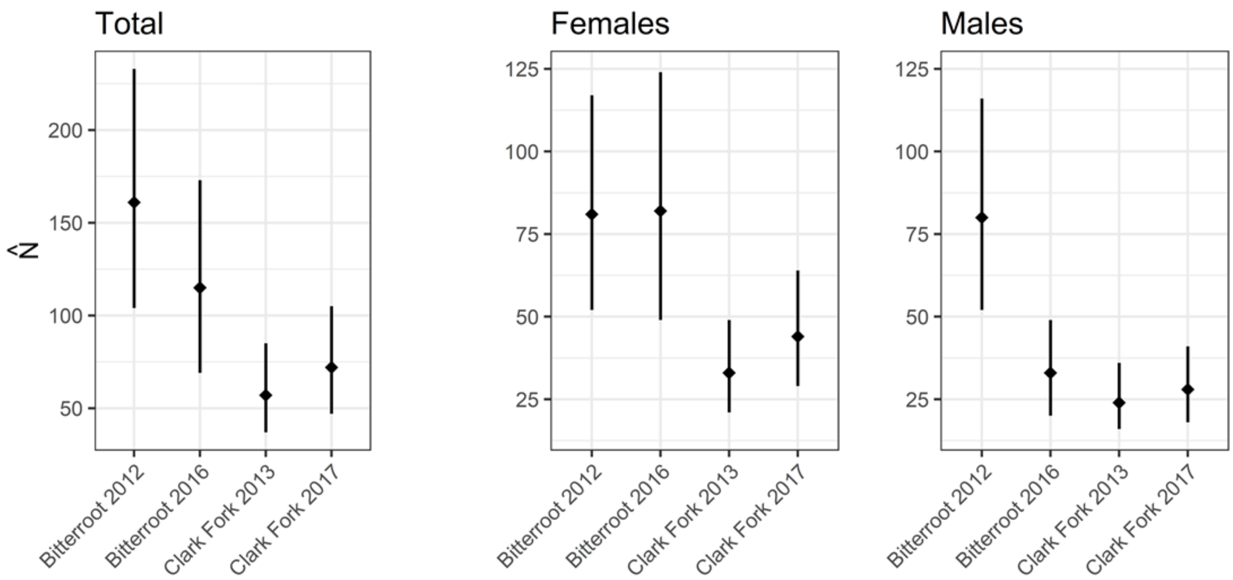


Figure 3.5 *The total, female, and male mountain lion abundance within the Bitterroot and Upper Clark Fork study areas of west-central Montana during 2012-2017 predicted from the most supported spatial capture-recapture model (Model 1). Diamonds represent the mean of the posterior and the whiskers represent the 90% credible interval.*

In the Upper Clark Fork study area, we found evidence for an increase in overall abundance between 2013 (57 [37, 85]) and 2017 (72, [47, 105]). However, we found no meaningful change in the sex ratio between the 2013 (M:F = 0.42 [0.26, 0.58]) and 2017 (0.39 [0.25, 0.54]), resulting in estimated abundances of male and female animals between the two time periods of 2013: males = 24 [16, 36], females = 33 [21, 49]; 2017: males = 28 [18, 41], females = 44 [29, 64] (Figure 3.5).

In addition to overall changes in mountain lion abundance in the Bitterroot study area driven by a decline in the number of males from 2012 to 2016, our results also suggest the relationship between RSF values and mountain lion abundance differed between 2012 and 2016 for the Bitterroot study area (Figure 3.6). This difference results in predicting a different spatial arrangement of mountain lions in the Bitterroot study area in 2012 and 2016. We found a more positive association between RSF values and abundance of activity centers for the 2012 Bitterroot that strongly predicted high mountain lion abundances in the subset of areas with the highest habitat quality (i.e., statespace cells with high RSF values), in contrast with the more moderate relationship for the 2016 Bitterroot (Figure 3.6). This change in relationship suggests that the difference in Bitterroot mountain lion abundance between the two years arose primarily from a decline in abundance in areas with the highest habitat quality (Figure 3.6). This contrasts the results from the Upper Clark Fork study area, where a similar estimated relationship between RSF values and abundance of activity centers yields roughly similar maps of abundance and comparatively minor differences in abundance between years (Figure 3.6).

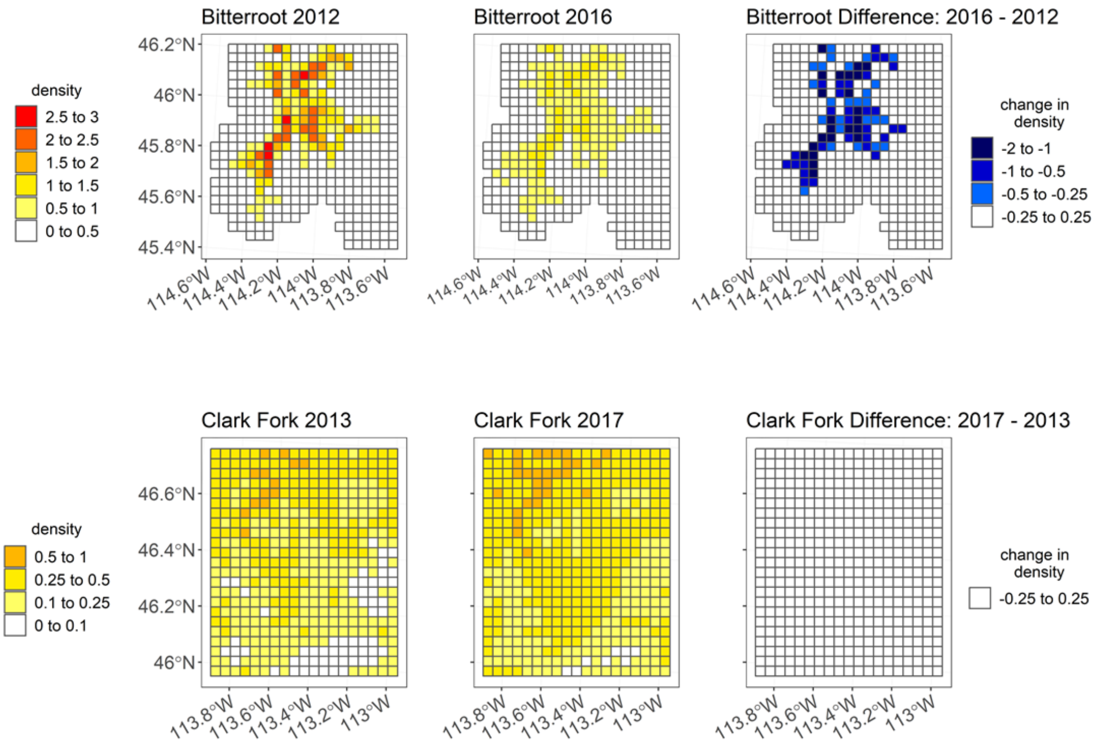


***Figure 3.6** The predicted density (number per 4 km^2) and change in density (number per 4 km^2) of mountain lions pre- (2012, 2013) and post- (2016, 2017) harvest management the Bitterroot and Upper Clark Fork study areas of west-central Montana estimated from the most supported spatial capture-recapture model.*

Discussion

We found that the mountain lion harvest regulations implemented in west-central Montana in 2012 achieved the management objective of moderately reducing mountain lion population abundance within the treatment area. Using a DNA based spatial capture-recapture approach to estimate annual mountain lion population abundance before and 4 years after the harvest regulations were implemented, we were able to quantify the effects of the harvest regulations on population abundance. We estimated a 29% reduction in the mountain lion population within the treatment area (comparing abundance prior to and after the treatment), with the greatest reductions occurring for males (59% reduction in estimated number of males in 2016 versus 2012). Four years after implementation of the harvest regulations, a robust mountain lion population persisted within the treatment area in spite of the achieved reduction. Following implementation of the harvest regulations, we estimated mountain lion density in the two hunting districts within the treatment area at 3.6 and 4.0 mountain lions per 100 km^2, indicating long-term mountain lion conservation goals were achieved and a relatively high-density population persisted.

The mountain lion harvest regulations (i.e., number of quotas in each year) for the two hunting districts in the Bitterroot study area during the first 2 years of treatment equated to a prescribed female harvest rate of 5.3% and 4.5% in the first and second year, respectively (i.e., female quota of 14 and 12 females per 3,335 km^2, or 4.2 and 3.6 females per 1000/km^2 with 80 estimated females between the two hunting districts), and a prescribed total harvest rate of 17.6% and 12.6% in the first and second year, respectively (i.e., total quota of 28 and 20 animals per 3,335 km^2 equating to 8.4 and 6.0 animals per 1000/km^2 with 159 estimated animals between the two hunting districts). While short-term increases in the female and male harvest during 2012–2014 likely contributed to the overall population reductions, the male harvest during the period between our two population estimates (2012–2016) was greater than the female harvest likely contributing to the greater reduction in the male segment of the population and changes in sex ratio.

Population estimates for elusive carnivore species such as mountain lions are necessary to inform management and conservation decisions, and the methodology presented here improves the ability to monitor carnivore populations. Two advancements to previous SCR population estimation approaches are highlighted here: 1) the integration of collar location and recapture data to estimate space use parameters (Paterson et al. 2019*a*), and 2) sharing of information across years and study areas using a multistrata modeling approach. Both of these advancements are aimed at improving the precision of population abundance estimates. Additionally, recent simulation-based approaches to validation of SCR population estimates have been developed and indicate that given the capture-recapture data available in each of our 4 study area-years, our estimates of population abundance are unbiased (Paterson et al. 2019*a*). These recent advances towards improving precision and detecting bias in SCR population estimates increases the applicability of the SCR modeling approach and confidence in model-based population estimates generated from robust datasets such as ours (Paterson et al. 2019*a*).

Section 4 – Wolf Harvest Management and Population Abundance

Introduction

Wolves emigrating from Canada expanded their distribution into northwestern Montana in the 1980s. In 1995–1996, federal reintroduction efforts in Yellowstone National Park and the central Idaho wilderness areas established wolf populations that later expanded their distribution into west-central and southwest Montana. As wolf populations became established in the region, concern regarding the potential effects of wolves on elk abundance and recruitment increased. Between 2008 and 2011, wolves in Montana were federally delisted, relisted, and then delisted again (Hanuska-Brown et al. 2011). This process resulted in a Montana wolf hunting season in 2009, no hunting season in 2010, and hunting seasons from 2011 through the present. Since 2011, wolves in Montana are subject to state management authority guided by the Montana Wolf Conservation and Management Plan.

Since management authority returned to MFWP in 2011, wolf harvest limits and hunting season dates have been liberalized across west-central Montana, and the use of specific trapping methods has been approved. West-central Montana currently has 5 wolf management units (WMUs) that each allow an 11-day archery-only season during early September, a 7-month hunting season during mid-September–mid-March, and a 2.5-month trapping season from mid-December–late February. In 2011, wolf hunting was allowed with quotas established for each WMU. Beginning in 2012, the wolf trapping season was added, with no WMU-specific quota limits. Instead, harvest regulations are based on combined hunting and trapping bag limits of wolves per person. In 2012, wolf harvest regulations limited each person to harvesting a maximum of 3 wolves. In 2013 until present, wolf harvest regulations limited each person to harvesting a maximum of 5 wolves.

Our objectives are to summarize wolf harvest in west-central Montana. We also summarized the estimated minimum wolf population count and harvest for the Bitterroot study area that formed the focal area of our overall project.

Methods

Hunters and trappers are required to report all harvested wolves to MFWP, and we used these harvest data from 2009–2017 to track the number and location of wolves harvested annually. Based on the reported harvest location, we assigned harvested wolves to hunt districts to capture spatial variation in harvest. MFWP used a combination of radio-collaring efforts, direct observational counts, remote cameras, and track surveys to annually track the wolf population, document pack size and breeding pair status of known packs and determine pack territories. We used these data to estimate the minimum count of wolves in each west-central Montana hunting district on December 31st of each year (Coltrane et al. 2016). We assigned wolves to hunting districts by intersecting their estimated home ranges with the hunting district boundaries, and summing the total minimum count of all wolves in each pack whose home range included a portion of the hunting district, with hunting districts being defined based on the current boundary.

Results

The total reported wolf harvest in west-central Montana has varied through time and averaged 54.4 wolves per year (SD=11.8) since management authority was returned to MFWP in 2011 (Figure 4.1). The reported harvest per hunting district has also varied annually during 2009–2017 (Figure 4.2). The minimum counts of wolves per hunting district has varied annually (Figure 4.3) and averaged 10.2 (SD=7.2) wolves since 2011.

Within the Bitterroot study area, harvest within HD 270 and HD 250 has varied annually (Figure 4.4) and since 2011 has averaged 3.1 (SD=2.9) in HD 250 and 5.6 (SD=4.8) in HD 270. Wolves from the central Idaho experimental population expanded into study area in 2001, and the populations increased until 2011 (Figure 4.4). Since 2011, estimated minimum counts in the Bitterroot have averaged 12.7 (SD=6.1) in HD 250 and 16.0 (SD=3.7) in HD 270.

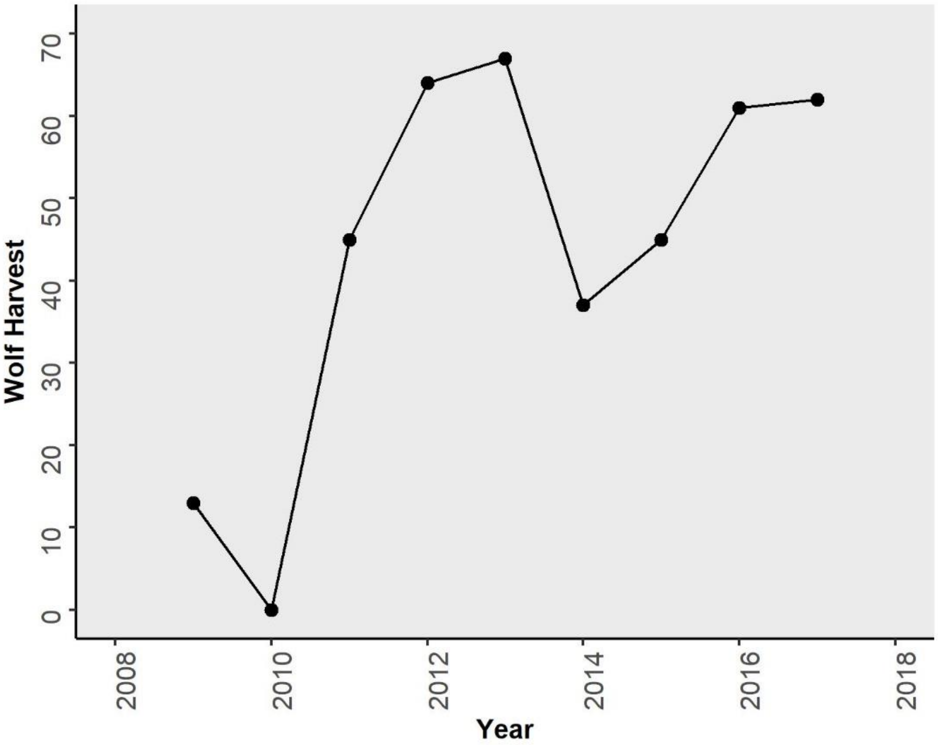


Figure 4.1 *The total reported wolf harvest in west-central Montana during 2009–2017. There was no hunting season in 2010 and wolf management authority was returned to MFWP in 2011.*

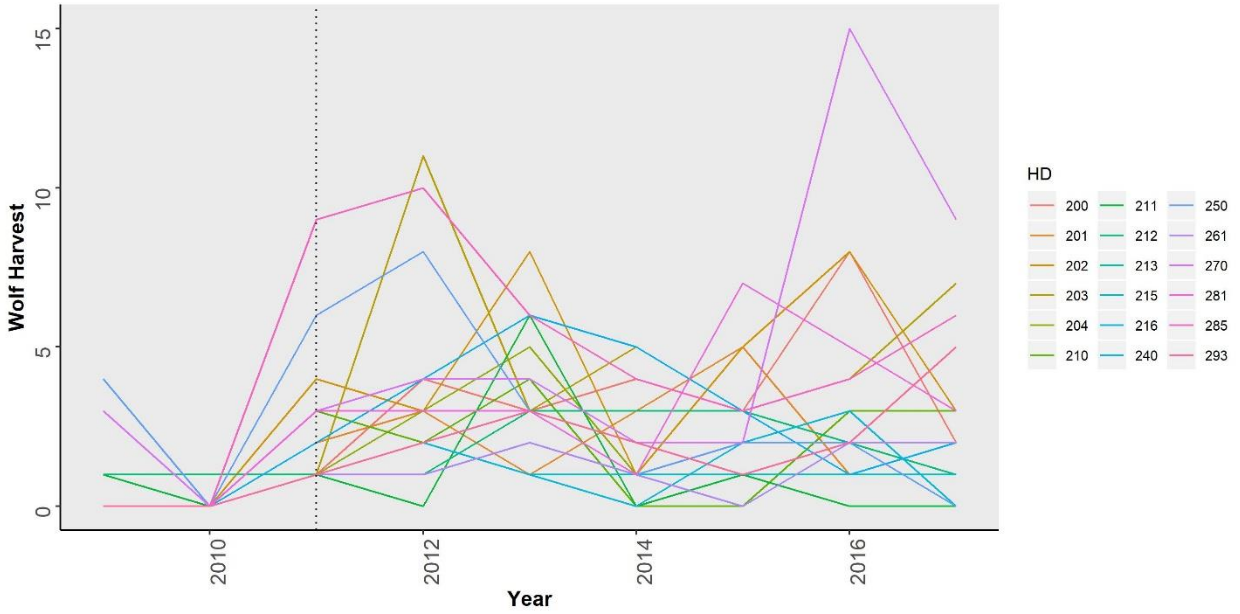


Figure 4.2 *The reported wolf harvest in west-central Montana by hunting district during 2009–2017. There was no hunting season in 2010. The vertical dashed line represents when wolf management authority was returned to MFWP in 2011.*

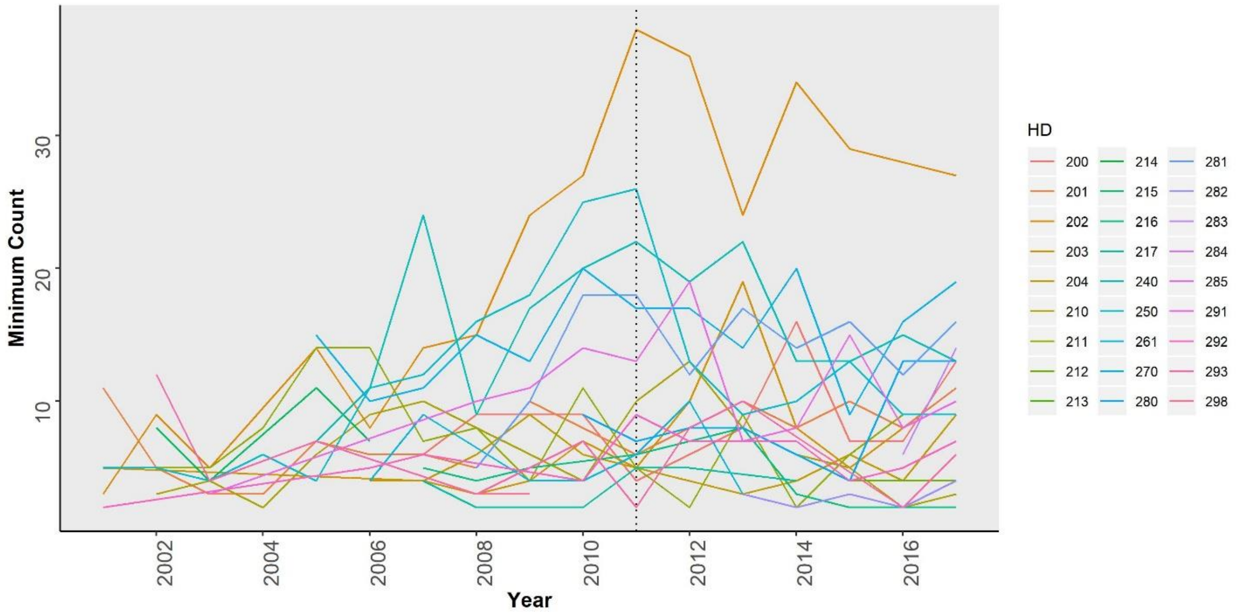


Figure 4.3 *The estimated minimum count of wolves in west-central Montana by hunting district during 2001–2017. The vertical dashed line represents when wolf management authority was returned to MFWP in 2011.*

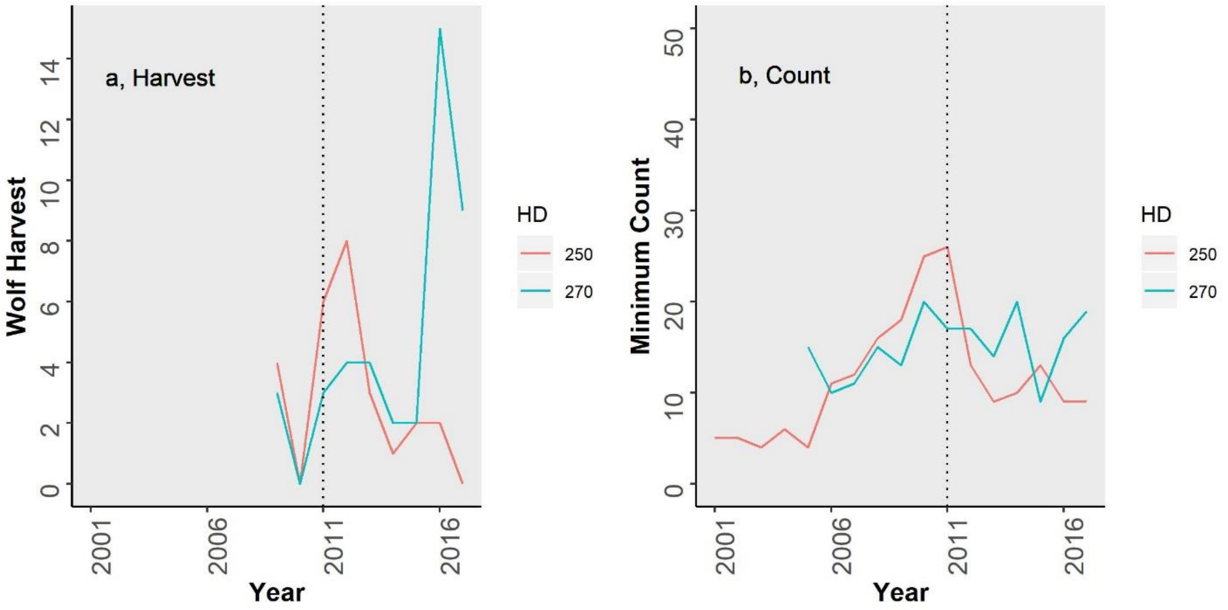


Figure 4.4 *The reported hunter harvest (Panel a) and estimated minimum count (Panel b) of wolves in HD 270 and HD 250 during 2001–2017. A boundary change prior to the 2014 season expanded HD 270 and reduced HD 250. The vertical dashed line represents when wolf management authority was returned to MFWP in 2011.*

Discussion

Since management authority for wolves was returned to MFWP in 2011, harvest across the west-central Montana region and across hunting districts within west-central Montana has varied annually. An adequate sample of harvest data under different regulation types is not available to compare to the effects of the harvest regulations on wolf harvest. Additionally, because information on wolf population size are limited to minimum counts, our inference as to the effects of harvest regulations on population size in west-central Montana is limited. Within the Bitterroot study area, the minimum estimate of wolf abundance has stabilized since the implementation of the 2013 harvest regulations; however, this weak association is insufficient to draw broad inferences as to the effects of wolf harvest regulations on harvest and population abundance.

Previous research has found wolf harvest to be correlated to local wolf population size, such that larger populations create more exposure to hunting and trapping (Robichaud and Boyce 2010, Gude et al. 2012). Absent extensive efforts to reduce or eradicate populations, wolf populations throughout their range tend to exhibit high population growth rates when suitable prey bases are available (Ballard et al. 1987, Pletscher et al. 1997, Hayes and and Harestad 2000, Fuller et al. 2003), and we expect the same is true across west-central Montana where common prey including white-tailed deer, mule deer and elk exist. Even in areas where wolves are exposed to human harvest, wolf population growth rates often remain high due to high levels of recruitment, primarily from reproduction and dispersal (Gude et al. 2012, Jimenez et al. 2017).

Section 5 – Black Bear Harvest Management

West-central Montana has healthy populations of black bears. Black bear populations across the region are estimated from a predictive density model developed by MFWP in 2011. According to the model, the West Fork area (HD 250) has an estimated density of 15 black bears/100 km^2, while the East Fork area (HD 270) has an estimated density of 10 black bears/100 km^2 (Mace and Chilton-Radandt 2011). There is an either-sex hunting season during both spring and fall in both areas. All harvested bears must be reported to MFWP, but there is no quota on either sex in either season.

Prior to 2010, black bear harvest regulations across most of the region allowed for a 6-week spring hunting season (approximately April 15–May 31) and a 10-week fall season (approximately September 15–November 30). In 2010, black bear harvest regulations throughout the region were liberalized to include an additional 2 weeks of archery-only hunting during the first 2 weeks of September. Also, during 2010–2014, spring harvest regulations were liberalized to extend the spring season by approximately 2 weeks to end on June 15. These liberalized spring harvest regulations were first implemented in portions of bear management unit (BMU) 216 and 240 in 2010, expanded to most of the region in 2012, and expanded to the entire region in 2014. Our objective was to determine if the liberalized black bear harvest regulations were associated with increased harvest levels in west-central Montana.

Methods

We used a generalized linear model to determine if black bear harvest increased following implementation of liberalized regulations. We used MFWP harvest data from the west-central Montana study area (Figure 2.1b) during 2001–2017 to estimate and compare the number of bears harvested in each hunting district before and after liberalized harvest regulations were implemented. Because harvest regulations sometimes varied within BMUs, with different regulations being applied to the geographical areas corresponding to deer and elk hunting districts (HDs), we defined the spring and fall black bear harvest regulation and estimated the spring and fall harvest per HD within west-central Montana. If a HD had less than 5 years of spring or fall reported harvest, we censored the HD from analyses.

To evaluate the effects of the fall harvest regulation on fall harvest, we first categorized the fall regulation type for each HD-year as liberalized (included the 2-week early September archery only season) or standard (no 2-week early September archery only season). All hunters are required to report harvested black bears to MFWP, and we used these harvest data to estimate the number of black bears harvested in each hunting district each fall. We used a generalized linear model to relate the fall harvest of black bears in district *d* in year *t* ($\text{Harvest}_{d,t}$) to the fall regulation type:

$$\mu_{d,t} = \alpha + \beta_{regulation} * \text{regulation type}_{d,t} + \partial_d,$$
$$\partial_d \sim Normal(0, \sigma_\partial^2)$$
$$\text{Harvest}_{d,t} \sim Normal\left(\mu_{d,t}, \sigma^2\right),$$

where α is the overall mean harvest in the standard regulation period, $\beta_{regulation}$ is the change harvest from standard to liberalized regulations, regulation $\text{type}_{d,t}$ takes a value of 0 for standard regulations and 1 for liberalized regulations, and ∂_d is a random effect for district. This modeling approach allowed for differences in the overall harvest per HD and differences in the amount of data per HD to be properly accounted for in the evaluation.

To evaluate the effects of the spring harvest regulation on spring harvest, we first categorized the spring regulation type for each HD-year as liberalized (included the 2-week spring season extension) or standard (no 2-week season extension). In spring 2010, liberalized spring harvest regulations were implemented in the HD 270 and HD 250 portions of BMU 216 and BMU 240. In spring 2012, liberalized spring harvest regulations were applied to all portions of BMU 216, BMU 240, BMU 280 and BMU 290. In spring 2014, liberalized spring harvest regulations were expanded to also include BMU 200 and be uniform across all west-central Montana. We used MFWP harvest data to estimate the number of black bears harvested in each hunting district each spring. We assessed the relationship between harvest and regulation type using the same model structure as above, where fall harvest and regulation type were replaced by spring values.

Results

We included 20 HDs in our spring black bear harvest analysis, and each HD had 11–17 years of data. Spring harvest varied across the 20 HDs (Figure 5.1a) and was higher when the liberalized spring harvest regulation was implemented as compared to the standard regulation. Across all HDs, the mean spring bear harvest per HD with the standard regulation was 5.4 (SD=4.9) and the mean harvest per HD with the liberalized regulation was 7.9 (SD=6.3). After accounting for the random effect of HD, the generalized linear model predicted that on average, spring harvest increased by 3.0 bears ($\hat{\beta}_{\text{regulation}}$ = 3.0, 95% CI = 2.2, 3.8) when the spring harvest regulations changed from standard to liberalized.

We included 25 HDs in our fall black bear harvest analysis, and each HD had 9–17 years of data. Fall harvest varied across the 25 HDs (Figure 5.1b) and was similar during implementation of both the standard and liberalized fall harvest regulation. Across all HDs, the mean fall bear harvest per HD with the standard regulation was 6.7 (SD=6.1) and the mean harvest per HD with the liberalized regulation was 6.3 (SD=5.8). After accounting for the random effect of HD, the generalized linear model predicted that the liberalized regulation had no effect on fall harvest as compared to the standard regulation ($\hat{\beta}_{\text{regulation}}$ = -0.6, 95% CI = -1.3, 0.1).

Within the southern Bitterroot Valley, including the HD 270 and HD 250 focal areas of this overall research project, reported black bear harvest varied by hunting district and by season (Figure 5.2). After liberalized spring harvest regulations, spring harvest increased in both HD 270 and HD 250. The mean spring harvest in HD 270 increased from 4.1 (SD=2.2) during 2001–2009 to 8.6 (SD=2.5) during 2010–2017. The mean spring harvest in HD 250 increased from 3.5 (SD=1.9) during 2001–2009 to 6.6 (SD=3.3) during 2010–2017. In contrast to increases in spring black bear harvest, fall black bear harvest was similar before and after the 10-day extension to the fall hunting season. The mean fall harvest in HD 270 was 8.3 (SD=2.7) during 2001–2009 and 9.6 (SD = 3.0) during 2010–2017. The mean fall harvest in HD 250 was 5.4 (SD=2.7) during 2001–2009 and 3.1 (SD=1.9) during 2010–2017.

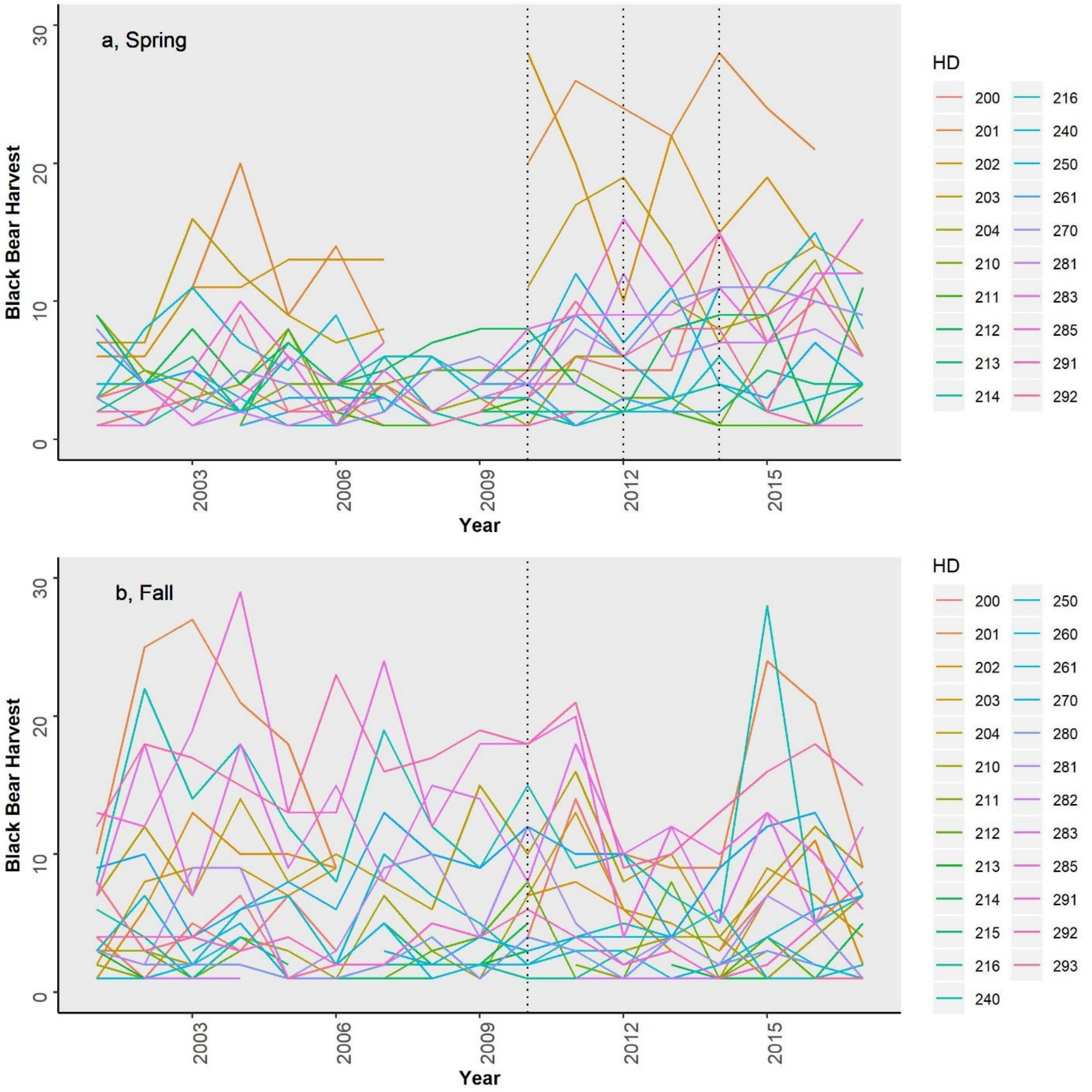


__Figure 5.1__ The spring (a) and fall (b) black bear harvest in west-central Montana hunting districts from 2001–2017. Spring black bear harvest regulations were liberalized in hunting districts 2010, 2012 and 2014 to include a 2-week hunting season extension (denoted with vertical dashed lines). Fall black bear harvest regulations were liberalized in 2010 to include a 2-week archery-only season extension (denoted with vertical dashed line).

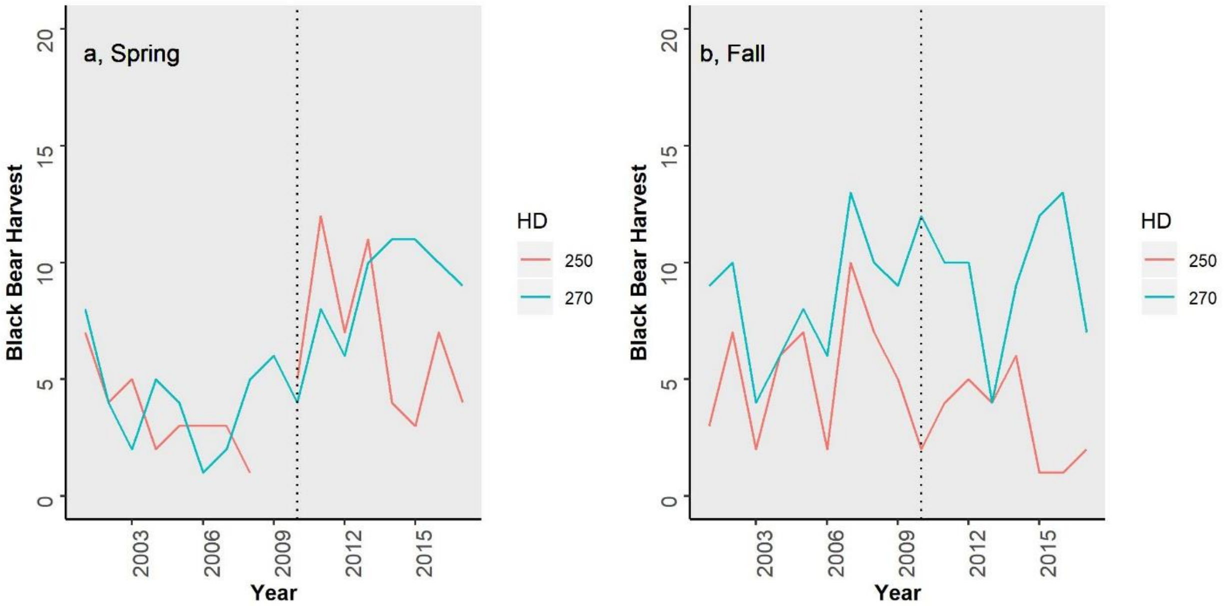


Figure 5.2 *The spring (a) and fall (b) black bear harvest in HD 270 (blue line) and HD 250 (red line) from 2001–2017. In HD 270 and HD 250, black bear harvest regulations were liberalized in 2010 to include a 2-week spring hunting season extension and a 2-week fall archery-only season extension (denoted with vertical dashed line).*

Discussion

We found that across west-central Montana, spring black bear harvest increased following implementation of liberalized harvest regulations that allowed for a 2-week spring hunting season extension. On average, the liberalized spring harvest regulation resulted in an additional 3 bears harvested per hunting district. However, we found no evidence that fall black bear harvest increased following implementation of a liberalized fall harvest regulation that allowed for a 2-week archery-only hunting season extension. These results suggest that the timing and/or method of take associated with the fall harvest regulation change was not effective in increasing black bear harvest. These results also suggest that extending the spring rifle season may be a more effective black bear harvest management tool than extending the fall archery season if the goal is to increase harvest. Spring black bear hunting may be more popular than fall black bear hunting for various reasons, including that fall bear hunting may be more opportunistic (i.e., people are hunting deer or elk, and will harvest a bear if the opportunity presents itself), versus in the spring, when there are fewer hunting opportunities, and people are more likely to specifically target black bears.

We found that within our focal study area, both HD250 and HD270 had higher spring black bear harvest after spring harvest regulations were liberalized. However, neither area had higher harvest after the fall harvest regulations were liberalized, and HD 250 had some evidence that harvest declined. If fall bear hunting is more opportunistic, the decline in fall bear harvest in HD 250 may be partially explained by the substantial reduction in elk and deer hunting opportunity available beginning in 2011, thus reducing the number of hunters in the area. This highlights that expectations for achieving fall bear harvest, even with liberalized regulations, should be moderated to account for levels of deer and elk hunting opportunity in the area.

Section 6 – Elk Calf Survival and Cause-Specific Mortality in the Bitterroot Study Area

Introduction

Studies of elk population dynamics have focused on understanding which vital rates are most likely to impact the population growth rate (Nelson and Peek 1982, Gaillard et al. 1998*b*, Eacker et al. 2017). From this work, we know that annual variation in elk calf survival rates tends to be high enough to exert important influence on the population growth rate (Garrott et al. 2008, Griffin et al. 2011). This high variation in elk calf survival rates may be influenced by characteristics of individual calves, as well as variation in forage and environmental conditions in the pre- and post-natal periods. Further, elk calves are vulnerable to multiple mortality sources, including predation by mountain lions (White et al. 2010, Eacker et al. 2016), black and grizzly bears (Barber-Meyer et al. 2008), wolves (Council 1997), and coyotes. Due to the number of factors related to elk calf survival, and the variability in mortality causes across populations, questions still exist regarding the relative importance of various factors influencing elk calf survival in any given population.

Elk populations experienced declines across much of west-central Montana during 2007–2011, and low calf recruitment and population declines in the southern Bitterroot Valley were particularly concerning. In response, MFWP initiated a study in the Bitterroot study area during 2011 to estimate elk calf survival and mortality causes, and evaluate factors related to variation in annual elk calf survival. Annual rates of calf survival in the East Fork and West Fork elk populations averaged 0.41 (range = 0.32 to 0.45) across the three years of study, and mountain lions were identified as the primary source of elk calf mortality (Eacker et al. 2016). Analysis of the elk population dynamics in the Bitterroot study area during the same time period indicated that elk calf survival was influencing population growth rates, and that increasing elk calf survival would likely have positive effects on elk population growth rates (Eacker et al. 2017).

In efforts to reduce the impacts of carnivores on ungulate populations in west-central Montana, including the Bitterroot study area, MFWP liberalized harvest regulations for mountain lions, wolves, and black bears. However, the efficacy of management actions designed to increase elk calf survival by reducing populations of their primary predator are unknown (Ballard and Miller 1990, Gasaway et al. 1992, Boertje et al. 2010). In the Bitterroot study area, the primary predator of elk calves was mountain lions. In winter 2012–2013, MFWP liberalized mountain lion harvest regulations within the Bitterroot study area to reduce the mountain lion population by 30%. This situation, combined with the information regarding calf survival and mortality sources prior to and during the mountain lion harvest treatment, provided a unique opportunity to quantify possible changes in elk calf survival and cause-specific mortality before, during, and after the liberalized carnivore harvest management prescriptions (*see Sections 3–5*).

Our primary objective in this section is to evaluate if elk calf survival rates, or rates of predation from mountain lions, black bears or wolves, differed before, during, or after the liberalized carnivore harvest management. Our secondary objective was to understand the environmental factors and individual characteristics related to elk calf survival in the Bitterroot study area.

Methods

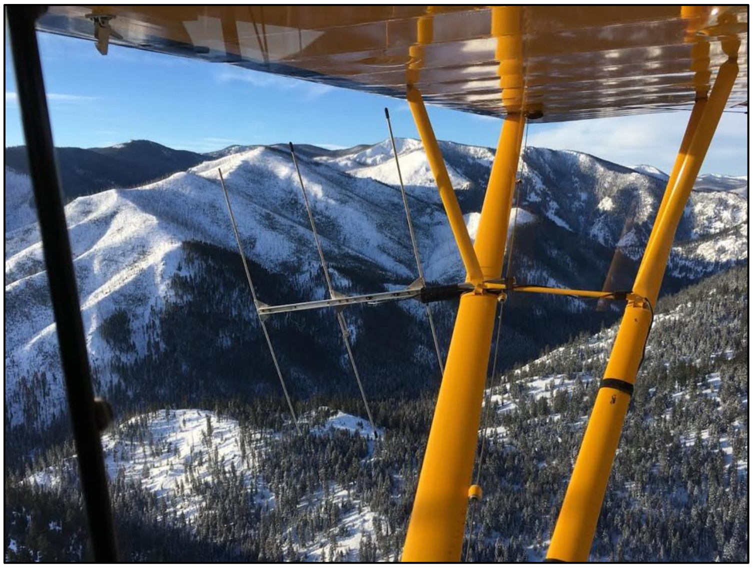
We compared elk calf survival and cause-specific mortality in the Bitterroot study area before, during, and after the mountain lion harvest regulations were liberalized (see Section 3). We focused on evaluating the effects of the mountain lion harvest regulations because earlier studies concluded mountain lion predation was an important factor for calf survival (Eacker et al. 2016). Liberalized mountain lion harvest regulations were implemented in December of 2012 and lasted for two years, after which mountain lion harvest quotas were reduced. Therefore, we included calves radio-tagged in the spring and fall of 2011 and monitored during 2011–2012 in the pre-treatment era; calves tagged the spring and fall of 2012 in the pre-treatment era for their first summer and the during-treatment era for their first winter; calves radio-tagged in the spring and fall of 2013 and monitored during 2013–2014 in the during-treatment era, and calves radio-tagged in 2016 and 2017 and monitored during 2016–2018 in the after-treatment era. During each era, we monitored calf survival and cause of mortality. We compared survival and cause-specific mortality across the three treatment eras to understand changes in the survival and cause-specific mortality of elk calves prior to, during, and after the mountain lion harvest treatment. Additionally, we evaluated relationships between calf survival and other potentially important covariates, as described below.

Calf capture and sampling

During all three treatment eras, we captured neonate elk calves during an approximately 2-week period near the end of May each year following approved animal care protocols (MSU IACUC#2016-06, UM IACUC# 027-11MHWB-042611). We used ground and helicopter crews to search for female elk that showed signs of having recently given birth and for calves already on the ground. Ground crews attempted to locate neonates directly and by watching for behavioral indications from adult females and/or by searching areas on foot. Each calf was outfitted with a very high frequency (VHF) ear-tag radio-transmitter designed to send a mortality signal after hours of inactivity. For each calf we recorded sex and several morphometric measurements which were used to obtain an estimate of age at capture as well as birth mass. To maintain adequate sample sizes for the winter monitoring period, we radio-tagged additional calves most years between 30 November and 5 January via either chemical immobilization or net-gunning from a helicopter.

Calf monitoring

We monitored calves using a combination of ground and aerial telemetry to determine survival status from the day after capture to 30 May of the following year. We monitored all calves daily from date of capture to 31 August and 2–4 times per week thereafter. We used aerial telemetry from fixed-wing aircraft to obtain periodic calf locations. We used calf locations in conjunction with mountain lion and wolf resource selection functions (RSF) to estimate spatial variation in mortality risk (see below).



Investigation of calf mortality

When we detected a mortality signal, we located the ear-tag transmitter within 12–24 hours when possible. If the mortality signal was associated with an actual mortality (i.e., vs. a dropped tag), we performed a detailed mortality investigation. We used characteristics such as consumption pattern, location and presence of claw marks, location and presence of subcutaneous hemorrhaging, width and presence of bite marks, and general characteristics of the kill site to assign causation to each mortality event (Wade and Bowns 2010). We submitted carnivore scat and hair collected during mortality investigations for DNA analysis to determine predator species identity (USFS Rocky Mountain Research Center, Missoula, MT). Using inferences from our field mortality investigations and the results of the DNA-based predator identification, we classified each mortality source as mountain lion, wolf, black bear, unknown predator, non-predation, or unknown cause.

Cause-specific mortality and survival analyses

After classifying the cause of each calf mortality, we used cumulative incidence functions (CIFs) to quantify possible changes in calf mortality from each potential cause between the three treatment eras (Heisey and Patterson 2006, Eacker et al. 2016). CIF estimates represented the cumulative probability of mortality from each potential cause over the first year (365 days) of a calf's lifetime. We used Cox-Proportional Hazards models (Cox 1972) to estimate and compare survival rates in the pre-, during-, and post-treatment eras, and to evaluate support for covariates potentially associated with variation in survival for all tagged calves during all years of data collection. We estimated summer and winter survival separately because we expected seasonal differences in risk factors. We used each calf's birthdate as the origin and estimated mortality risk from age 0 to 180 days for summer models, and 26 November as the origin and estimated mortality risk for the subsequent 185 days for winter models.

We evaluated a suite of risk factors potentially affecting calf survival. Risk factors included characteristics of the calf such as sex, birth mass, birth date, population and treatment era, as well as environmental conditions and mountain lion and wolf risk within the individual calf's seasonal range. Treatment era was a three-level factor variable that indicated whether a calf was monitored in the pre-, during, or post-treatment era. Environmental conditions included a metric of winter severity and three normalized difference vegetation index (NDVI) metrics representing growing season conditions and were estimated for each individual's seasonal range. Risk was estimated from previously published mountain lion and wolf resource selection functions (RSF, Robinson et al. 2015*a*). For models of summer survival, risk factors included sex, birth mass, birthdate, population (East Fork or West Fork), a Big Hole Valley identifier (a two-level factor describing whether a calf was born, tagged, and summered in the Big Hole Valley), treatment era, mountain lion and wolf risk, and NDVI. For models of winter survival, risk factors included sex, population (East Fork and West Fork), treatment era, mountain lion and wolf risk, and winter severity. Additional details regarding analysis are found in Eacker et al. (2016) and Forzley (2019).

Results

Calf captures, monitoring, and mortality investigations

During the pre-treatment era, we radio-tagged 142 calves in the spring (2011–2012 = 66, 2012–2013 = 76) and 31 calves at the start of winter of 2011–2012 for a total pre-treatment sample size of 173 calves. In the during-treatment era, we radio-tagged 84 calves in the spring of 2013 and 29 calves in the winter of 2012–2013 for a total during-treatment sample size of 113 calves. During the two post-treatment years, we radio-tagged 183 calves in the spring (2016–2017 = 81, 2017–2018 = 102) and 65 calves at the start of winter (2016–2017 = 40, 2017–2018 = 25) for a total post-treatment sample size of 248 calves. We maintained a small sample of calves tagged in the Big Hole Valley throughout the study (*n* = 16, 13, and 31 in the pre-, during, and post-treatment eras, respectively). The total sample size was 534 radio-tagged elk calves.

The sex ratios for our treatment era-specific sample of calves were relatively balanced (*n* = 83 females, 90 males; 53 females and 59 males; and 134 females and 113 males in the pre-, during, and post-treatment eras, respectively; 2 calves were of unknown sex). Average estimated birth mass in the pre-, during, and post-treatment eras, respectively was 13.40 kg (SE = 0.20), 14.30 kg (SE = 0.36), and 13.20 (SE = 0.14) for females and 14.90 kg (SE = 0.21), 14.20 kg (SE = 0.30), and 14.50 (SE = 0.13) for male calves. We recorded 19,323 calf survival monitoring observations in the pre-treatment era (*n* = 15,708 live, 75 = dead, and 3,540 = not heard), 20,644 observations in the during-treatment era (*n* = 12,076 live, 35 = dead, and 8,533 = not heard), and 25,185 observations in the post-treatment era (*n* = 19,419 live, 87 = dead, 5,679 = not heard). We obtained 1,834 calf locations in the pre-treatment era, 919 in the during-treatment era, and 1,514 locations in the post-treatment era.

Cause-specific mortality and cumulative incidence functions

We removed records for 10 of the 534 radio-tagged calves from analyses due to mortality within 24 hours of capture (*n* = 6), unknown sex (*n* = 2), or mortality signals detected in inaccessible areas (*n* = 2). We censored data for 192 radio-tagged calves that lost their tag, had tag failures, or left the study area on the day after their last observation (i.e., right censored and still used information prior to tag loss, failure, or emigration). We estimated cause-specific mortality using data from 197 mortalities: 75 in the pre-treatment era, 35 in the during-treatment era, and 87 in the post-treatment era (Table 6.1). We documented 158 calves survived to 1 year of age.

Table 6.1 *Number of calves that died from mountain lion predation, natural (non-predation related) causes, black bear predation, wolf predation, unknown predator, unknown cause or other causes by elk population and treatment era during pre-treatment, during-treatment, and post-treatment eras.*

Population	Cause of mortality	Pre-	During-	Post-	Total
East Fork	Mountain lion	11	7	13	31
	Non-predation	3	1	9	13
	Black bear	6	1	1	8
	Wolf	3	0	3	6
	Unknown predator	3	3	3	9
	Unknown cause	13	7	28	48
	Other	2	1	0	3
West Fork	Mountain lion	16	6	6	28
	Non-predation	2	1	8	11
	Black bear	3	2	4	9
	Wolf	3	0	3	6
	Unknown predator	5	3	1	9
	Unknown cause	5	3	8	16
	Other	0	0	0	0

Estimated CIFs indicated that mountain lion predation in the East Fork was the highest source of known mortality in the pre-treatment (0.16, 95% CI = 0.09–0.24, Figure 6.1) and during-treatment (0.12, 95% CI = 0.04–0.18) eras. However, while mountain lion predation remained an important factor in the post-treatment era (mortality rate = 0.11, 95% CI = 0.03–

0.16), non-predation rates increased compared to the pre- (0.03, 95% CI = 0.00–0.07) and during-treatment (0.02, 95% CI = -0.01–0.05) eras.

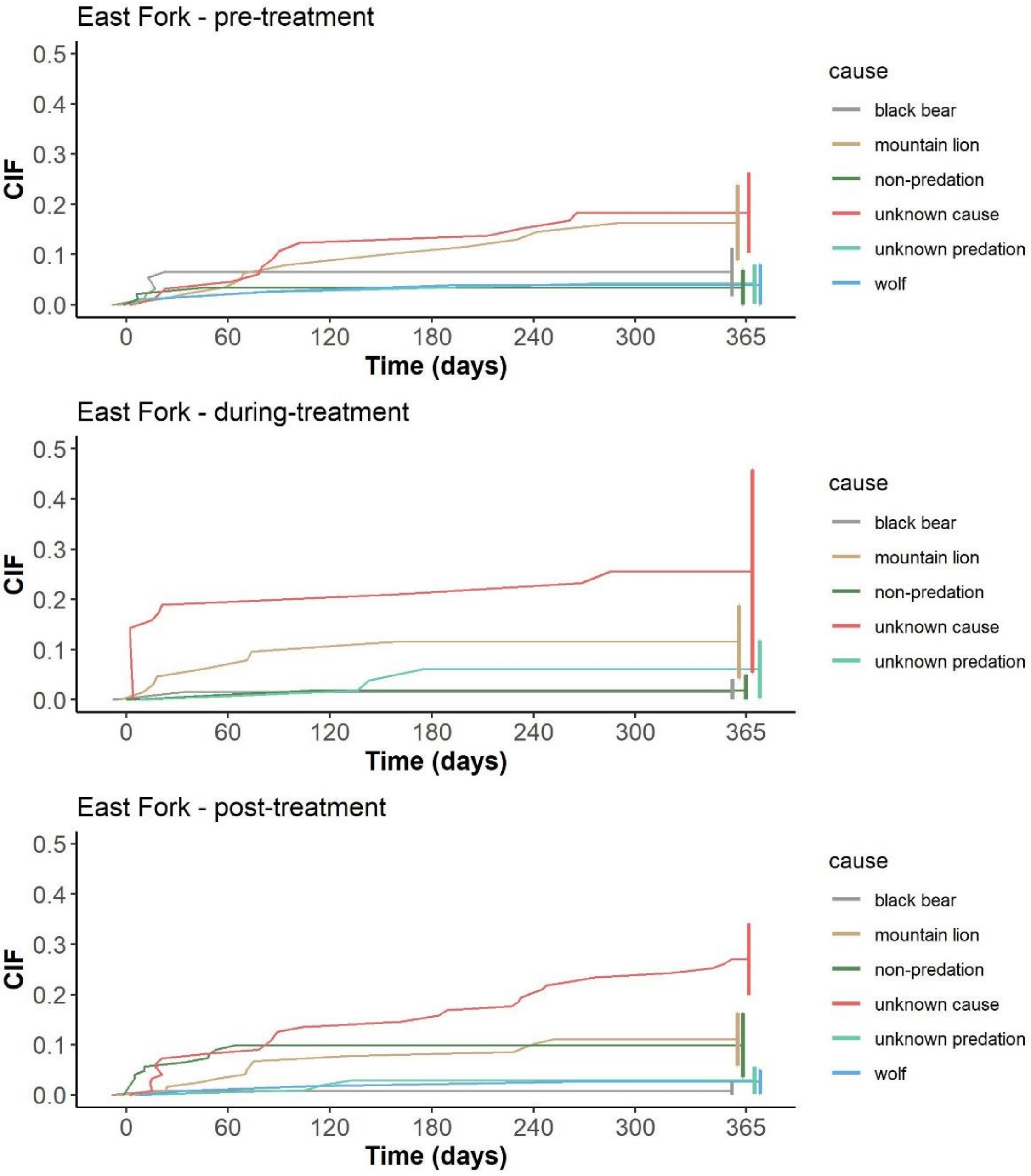


Figure 6.1 *Cumulative Incidence Functions (CIF) showing the cumulative probability of calf mortality (y-axis) from 0 to 365 days after birth in the East Fork from black bear predation, mountain lion predation, natural, non-predation related causes, unknown causes, unknown predators, and wolf predation in the Bitterroot study area, during pre-treatment, during-treatment, and post-treatment eras. Vertical bars show 95% confidence intervals for the cumulative probability of mortality from each cause at the end of one year.*

In the West Fork, estimated CIFs indicated that mountain lion predation was the largest known cause of mortality in both the pre- (0.35, 95% CI = 0.22–0.48) and during-treatment eras (0.24, 95% CI = 0.09–0.38). However, in the post-treatment era, non-predation was the highest source of known mortality (0.42, 95% CI = 0.02–0.81; Fig. 7.2), and cumulative mortality rates for mountain lion predation were relatively low (0.05, 95% CI = 0.00–0.10).

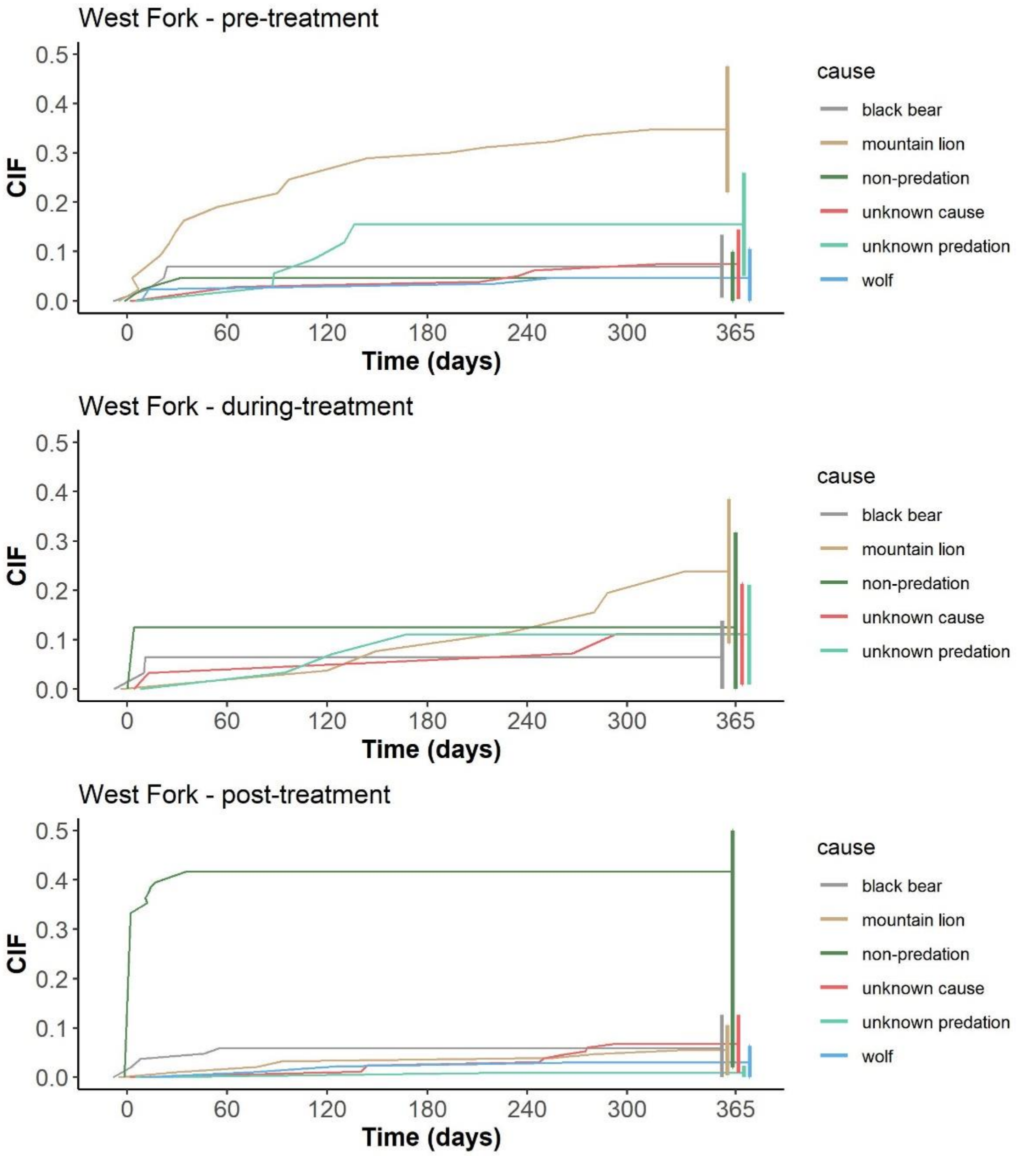


Figure 6.2 *Cumulative Incidence Functions (CIF) showing the cumulative probability of calf mortality (y-axis) from 0 to 365 days after birth in the West Fork from black bear predation, mountain lion predation, natural, non-predation related causes, unknown causes, unknown predators, and wolf predation, by treatment era, in the Bitterroot study area during pre-treatment, during-treatment, and post-treatment eras. Vertical bars show 95% confidence intervals for the cumulative probability of mortality from each cause at the end of one year.*

Elk calf mortality rate was highest during the first 90 days of the summer season and remained relatively constant across fall and winter. Annual probabilities of black bear and wolf predation were low in all three treatment eras for both populations. Mortality due to black bears and non-predation only occurred during the summer season, whereas mortality from mountain lions, wolves, and unknown causes occurred throughout the year. The cumulative annual probability of non-predation mortality increased in the post-treatment era in both populations. CIFs related to the annual probability of unknown cause mortality was high for both populations during all three treatment eras (Figure 6.1; Figure 6.2). The shapes of the curves for the cumulative annual probability of unknown cause and unknown predator mortalities were not similar to any single source of known cause mortality and appeared to be a combination of mortality from multiple sources. For example, in some cases, CIFs related to unknown cause and unknown predator mortality were steep during the early summer months (i.e., similar to black bear and non-predation mortality), but also persisted through winter and the following spring (i.e., similar to mountain lion and wolf mortality).

Summer calf survival

Our modeling of summer calf survival yielded considerable model-selection uncertainty among several well supported models explaining variation in survival associated with different combinations of covariates. Due to this model-selection uncertainty, we used model averaging to estimate summer elk calf survival based on all covariates in our final model selection step. Calf sex was our best-supported covariate affecting elk calf survival in summer. Model averaged coefficients indicated that male calves had a higher daily risk of dying than females during summer (HR = 1.68, 95% CI = 1.70–2.37). The daily risk of mortality in the pre- and post-treatment eras was higher for elk calves that occupied areas of higher mountain lion RSF values (Hazard Ratio [HR] = 17.25, 95% CI = 1.00–297.32, Figure 6.3). The mean value of the mountain lion RSF covariate for calves that died during the summer during the pre- and post-treatment eras (0.35, 95% CI = 0.33–0.37) was higher than the mean for calves that survived (0.31, 95% CI = 0.30–0.32). Further, that pattern held true regardless of the cause of death: mean values of the summer mountain lion RSF covariate for calves that died due to mountain lions (0.36, 95% CI = 0.34–0.39), wolves (0.37, 95% CI = 0.33–0.41), black bears (0.38, 95% CI = 0.35–0.41), non-predation (0.35, 95% CI = 0.32–0.39), and unknown causes (0.33, 95% CI = 0.29-0.35) were all similarly high compared to values for calves that survived. In contrast to results for the pre- and post-treatment eras, the relationship between summer calf survival and mountain lion RSF was positive in the during-treatment era (Figure 6.3). The mountain lion RSF covariate varied between the East Fork and West Fork elk populations, and the model averaged coefficient indicated that the strength of the relationship was weaker in the West Fork (0.67, 95% CI = 0.21–2.20).

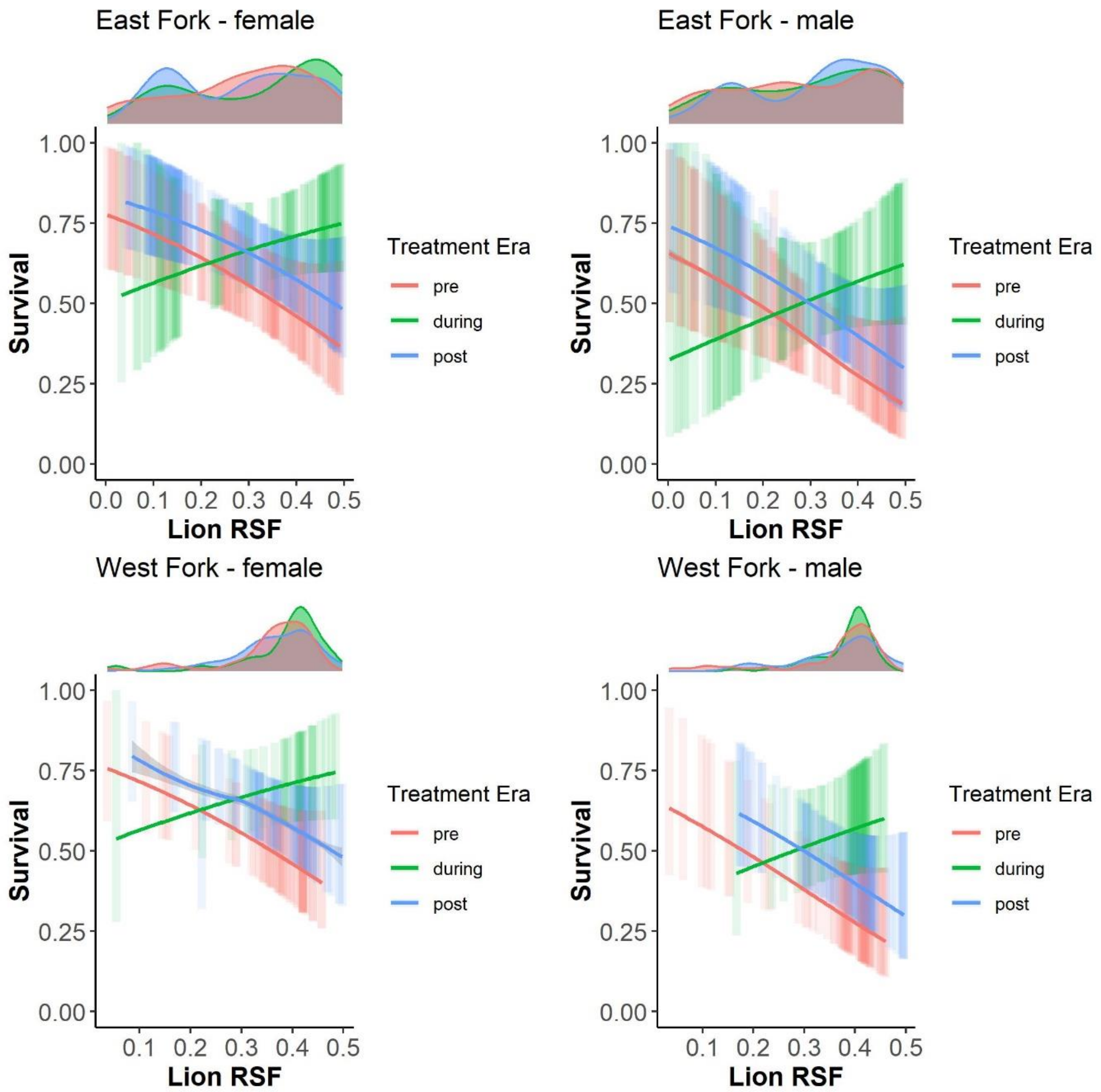


Figure 6.3 *Estimated relationship between elk calf summer survival rate and mountain lion RSF values in the area used by a calf in the Bitterroot study area. Data were collected before, during, and after the liberalized carnivore harvest management prescriptions and relationships were estimated using our best-supported summer proportional hazards model. Distributions of observed lion RSF values for calves in each herd and treatment era are provided at the top of each plot.*

Summer survival rates estimated using model averaged predictions in the East Fork population were estimated as 0.57 (0.45–0.72), 0.69 (0.56–0.85), and 0.62 (0.52–0.74) for females and 0.39 (0.27–0.57), 0.55 (0.39–0.76), and 0.44 (0.33–0.61) for males, during the pre-, during, and post-treatment eras respectively. Summer survival rates in the West Fork population were estimated as 0.53 (0.39–0.73), 0.72 (0.58–0.90), and 0.70 (0.59–0.83) for females and 0.35 (0.21–0.57), 0.58 (0.41–0.83) and 0.55 (0.42–0.72) for males, in the pre-, during-, and post-treatment eras respectively. We found that the daily risk of mortality for calves tagged in the Big Hole was lower than that of calves tagged in the East Fork or West Fork (HR = 0.65, 95 % CI = 0.24–1.77). Summer survival rates in the Big Hole sub-unit of the East Fork population were estimated as 0.66 (0.43–0.99), 0.81 (0.64–1.00), and 0.79 (0.62–1.00) for females and 0.50 (0.23–1.00), 0.70 (0.47–1.00) and 0.67 (0.62–0.97) for males, in the pre-, during-, and post-treatment eras respectively.

Winter calf survival

Our best-supported model for winter survival contained three covariates: treatment era, mountain lion RSF, and the interaction between treatment era and mountain lion RSF. In all three treatment eras, model averaged coefficients indicated that calves that occupied areas with higher mountain lion RSF values had a higher daily mortality risk in winter (HR = 8.55, 95% CI = 1.03-71.02, Fig. 7.4). The mean value of the mountain lion RSF covariate for calves that died during the winter (0.32, 95% CI = 0.30–0.34) was higher than the mean value for calves that survived (0.28, 95% CI = 0.27–0.28). However, winter mountain lion RSF scores were higher for all calves that died, regardless of the cause of death: mean values of the winter mountain lion RSF covariate for calves that died due to mountain lions (0.35, 95% CI = 0.32–0.38), wolves (0.34, 95% CI = 0.29–0.39), or unknown causes (0.31, 95% CI = 0.28–0.33) were all relatively high and similar. The interaction between the mountain lion RSF covariate and treatment era indicated that the relationship between winter calf survival and mountain lion RSF covariate was negative in all three treatment eras (Figure 6.4).

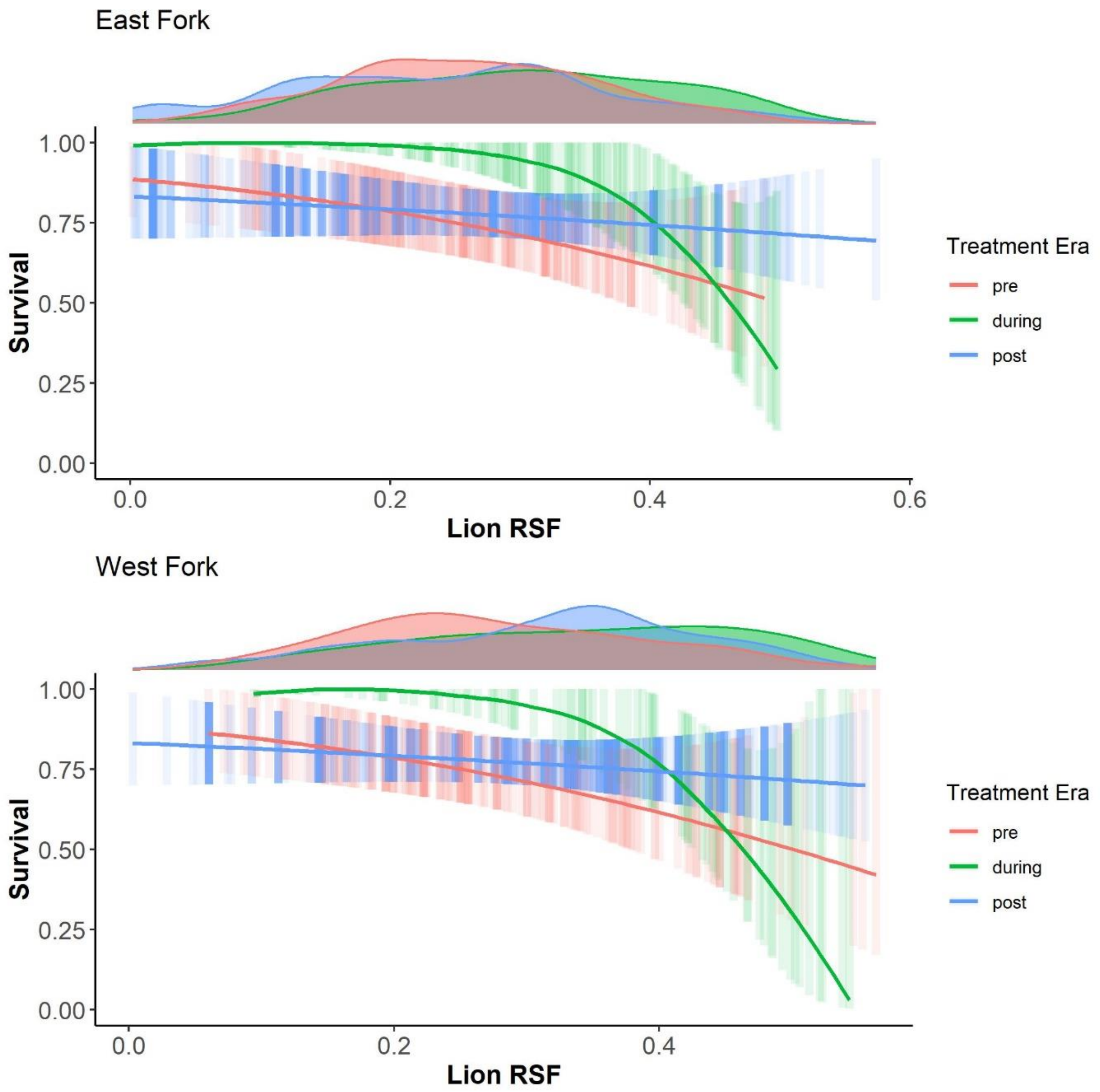


Figure 6.4 *Estimated relationship between elk calf winter survival rate and mountain lion RSF values in the area used by a calf in the Bitterroot study area, Montana, USA. Data were collected before, during, and after the liberalized mountain lion harvest management regulations, and relationships were estimated using our best-supported winter proportional hazards model. Distributions of observed lion RSF values for calves in each herd and treatment era are provided at the top of each plot.*

Treatment era was included in all but two of our best-supported winter models. Predicted winter survival rates obtained from model-averaging for each treatment era using era- and population-specific values of mountain lion RSF were 0.53 (0.37–0.76), 0.81 (0.72–0.91), and 0.78 (0.70–0.87) for East Fork calves and 0.56 (0.39–0.78), 0.84 (0.75–0.94), and 0.79 (0.71–0.89) for West Fork calves in the pre-, during, and post-treatment eras, respectively.

Annual survival rates

Based on model averaged coefficients from our best-supported summer and winter models, variation in annual survival was related to treatment era, calf sex, and spatial variation in the mountain lion RSF covariate. Annual survival was consistently higher for females than males and similar between populations, and across values of mountain lion RSF that were specific to each population (Table 6.2). At mean values of the mountain lion RSF covariate, point estimates of annual survival rates were lowest in the pre-treatment era, highest in the during-treatment era, and intermediate in the post-treatment era (Table 6.2).

Table 6.2 *East Fork and West Fork annual calf survival rates and 95% confidence intervals for the pre-treatment, during-treatment, and post-treatment eras at mean values of the mountain lion RSF covariate, specific to each sex, population, and treatment era in the Bitterroot study area.*

Population	**Sex**	**Era**	**Annual Survival**
East Fork	Male	Pre	0.21 (0.05–0.36)
		During	0.44 (0.21–0.68)
		Post	0.34 (0.13–0.56)
East Fork	Female	Pre	0.30 (0.11–0.48)
		During	0.55 (0.30–0.82)
		Post	0.49 (0.24–0.73)
West Fork	Male	Pre	0.18 (0.03–0.34)
		During	0.48 (0.24–0.74)
		Post	0.43 (0.20–0.67)
West Fork	Female	Pre	0.29 (0.10–0.47)
		During	0.59 (0.32–0.85)
		Post	0.55 (0.30–0.81)

Discussion

Our analysis of annual elk calf survival offers an opportunity to understand the effects of mountain lion harvest management regulations on elk calf survival, while controlling for potential confounding variables. Our estimates of elk calf survival provide evidence that liberalized mountain lion harvest regulations were associated with increased summer, winter, and annual elk calf survival during the harvest treatment period, and estimated rates of annual elk calf survival during the period of liberalized regulations nearly doubled as compared to before the liberalized harvest regulations. However, our results also suggest that the initial increases in annual survival in the during-treatment period were reduced to intermediate levels 4 years after treatment, resulting in annual survival rates that were only about 10 percent higher than pre-treatment-era levels. These findings echo results of previous studies that link carnivore harvest treatments to increased rates of elk calf survival (White et al. 2010) and results of other studies that demonstrated a return to pre-predator-control conditions after liberalized harvest regulations are discontinued (Council 1997, Hayes et al. 2003).

Although overlapping confidence intervals between the survival rates associated with the calves in each of the 3 treatment eras weakens our inference, the inclusion of the treatment-era covariate was well-supported by model selection, and several well-supported summer and winter calf survival models included the effects of a short-lived treatment-era response. Therefore, our modeling of elk calf survival data suggests that the mountain lion harvest treatment, designed to achieve only a moderate reduction in mountain lion population abundance (see Section 3), did coincide with short-term increases in elk calf survival rate. This initial increase in elk calf survival during the mountain lion harvest treatment, coinciding with a decline in the estimated probability of mountain lion predation for calves in both the East Fork and West Fork populations, could lead to the assumption that decreased rates of mountain lion predation were related to the harvest treatment and subsequently resulted in higher rates of elk calf survival. However, the high numbers of calves that died from unknown causes throughout the study must be addressed.

The probability of calves dying from unknown causes was high throughout all 3 treatment eras in both elk populations. In many cases, unknown cause mortality was the most common mortality category for a given population and treatment era combination. In an attempt to better understand potential sources of these unknown-case mortalities, we compared the CIF curves and timing of unknown cause mortalities with those of all other known sources of mortality. However, both the shape the CIF curves and the fact that the probability of unknown cause mortality remained relatively consistent throughout the year indicated that the unknown cause mortalities may have been a combination of several mortality sources, and made it difficult to determine if any particular mortality sources were more or less likely to contribute to unknown cause mortalities. During the mountain lion harvest treatment specifically, the estimated rates of unknown cause mortality for both elk populations were higher than rates for any other mortality source. Therefore, the high number and ambiguous nature of the unknown cause mortalities makes it difficult to know for certain that mountain lion predation did in fact decrease during the harvest treatment.

Despite the frequency with which calves were assigned to the unknown cause mortality category and our inability to conclusively relate the harvest treatment to decreased rates of mountain lion predation and short-term increases in elk calf survival, there were some noteworthy changes in the known rates of cause-specific mortality between the 3 treatment eras. As previously stated, rates of mountain lion predation decreased during the mountain lion harvest treatment and remained relatively low through the post-treatment era. These decreased rates of mountain lion predation coincided with increases in the probability of non-predation mortality, as well as intermediate rates of annual survival, for elk calves in both populations during the post-treatment era. While we can only speculate due to the high rates of unknown cause mortality, we can cautiously hypothesize that this sustained period of decreased mountain lion predation resulted in compensatory increases in non-predation mortality, and intermediate rates of survival, for elk calves in both populations. If so, this would suggest that mountain lion predation in the area is partially compensatory. However, this hypothesis assumes that 1) non-predation mortality and mountain lion predation are equally represented in the unknown cause mortalities or 2) that none of the unknown cause mortalities can be attributed to non-predation mortality or mountain lion predation. Despite changes in the rates of mountain lion predation and non-predation mortality, there were no notable changes in the probability of mortality from other sources, such as wolves and black bears, before, during, or after the mountain lion harvest treatment.

In addition to the treatment era covariate, spatial measures of predation risk by mountain lions were strongly predictive of the risk of calf mortality. In all but one of the combinations of season and treatment era (during-treatment/summer), as calves spent more time in areas of higher predicted mountain lion activity (i.e., as values of the mountain lion predation RSF covariate increased), their daily risk of mortality increased. However, exploratory analysis revealed that while calves that had higher values of the mountain lion predation risk covariate were more likely to die, they were not necessarily killed by mountain lions. It is possible that black bears, wolves, and mountain lions all congregated in elk calving grounds during the neonatal period and exhibited similar patterns of space use during early summer when calves were most vulnerable to predation. Likewise, most carnivores tend to follow the prey towards lower elevations in the winter (Houston 1978, Beschta and Ripple 2007), which may increase the probability of wolf and mountain lion ranges overlapping with the home ranges of elk calves during winter. This may have resulted in the mountain lion predation risk covariate acting as a predictor of mortality from all possible sources, not just mountain lion predation.

We included NDVI covariates as predictors of variation in forage conditions and annual productivity related to maternal and calf body condition and found none of the predicted positive relationships between NDVI covariates and elk calf survival. In our 5-year monitoring effort, a relatively short time period to try to capture annual variation in vital rates associated with climate variation, we found a negative relationship between late-summer NDVI during the post-natal period and winter calf survival. We hypothesize that our data may not have spanned a long enough time period to capture sufficient variability in late-summer NDVI and survival needed to evaluate these relationships, resulting in the unexpected negative relationship between winter calf survival and late-summer NDVI. It’s also possible that NDVI was a poor surrogate for elk nutrition in the study area.

Section 7 – Effects of Carnivore Management on Elk Population Growth

Introduction

Understanding the effects of carnivore management on ungulate populations requires estimating important demographic parameters of the ungulate population before and after carnivore harvest management prescriptions are implemented to determine if changes in carnivore populations result in changes in recruitment or population growth rate. If ungulate populations are limited by factors such as weather or habitat (Garrott et al. 2003, Griffin et al. 2011, Johnson et al. 2019), or if predation is compensatory with other factors (Singer et al. 2003, Garrott et al. 2008), changes in carnivore populations may or may not result in changes in ungulate populations.

Ungulate population monitoring programs are routinely employed by state wildlife management agencies annually or biannually; however, uncertainty in the relationship between uncorrected count data and true population size, and between age ratio data (i.e., number of calves: 100 adult female) and annual calf survival, makes the detection of changes in ungulate population size and juvenile recruitment challenging. Recent methodological advances allow for count and age ratio data to be used in integrated population models that partition the variance in observations into variation associated with biological processes and sampling error to more precisely estimate demographic parameters, and evaluate associated changes in ungulate vital rates (Link et al. 2003, Kéry and Schaub 2011, Nilsen and Strand 2018). However, even with new methods available that improve managers ability to monitor and estimate populations (see Section 8, Paterson et al. 2019*b*), the uncertainties in the relationship between carnivore harvest management regulations and ungulate population responses make the effects of carnivore management uncertain.

Our goal was to evaluate the efficacy of the liberalized mountain lion harvest management as a tool for increasing elk calf recruitment and population growth rates by evaluating changes in elk recruitment and population growth rate before and after implementation of liberalized mountain lion harvest regulations. We developed an integrated elk population model to estimate calf recruitment and population growth rate of two elk populations within the area managed for mountain lion population reduction (i.e., treatment area) and two elk populations within the area managed for stable mountain lion populations (i.e., control area). The primary goal of this model was to assess the strength of evidence for a difference in calf recruitment during the pre- and post-mountain lion harvest treatment periods for elk populations in the treatment and control areas, while accounting for annual environmental variations. We compared trends in calf recruitment and elk population growth rate during the 5-years pre- (2006–2011) and post- (2013–2017) mountain lion harvest treatment to evaluate if the mountain lion harvest management was associated with population-level changes in elk recruitment and growth rates.

Methods

The study was conducted in two areas within west-central Montana: the southern Bitterroot watershed located primarily in Ravalli County (Bitterroot study area) and the Rock Creek and Flint Creek portions of the Upper Clark Fork watershed located primarily in Granite County (Upper Clark Fork study area, Figure 7.1). The Bitterroot study area was located within a watershed managed for mountain lion population reduction (i.e., treatment area), and included the: HD 250 and HD 270 elk populations (*see Section 2*). The Upper Clark Fork study area was within a watershed managed for stable mountain lion populations (i.e., control area), and included the HD 216 and HD 210 elk populations (*see Section 2*).

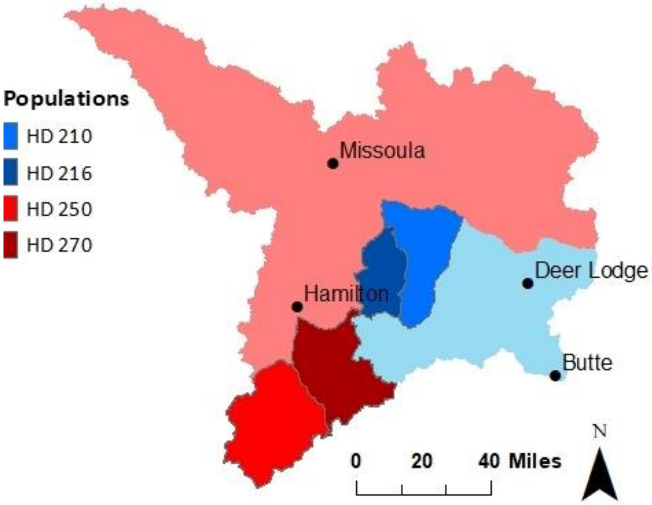


Figure 7.1 *Study area in west-central Montana. Three watersheds within the study area (Bitterroot, Blackfoot, Lower Clark Fork, shades of red) were managed for mountain lion population reduction and one watershed (Upper Clark Fork, shades of blue) was managed for stable mountain lion populations. The two focal elk populations within the Bitterroot watershed included HD 250 (West Fork) and HD 270 (East Fork) and the two focal elk populations within the Upper Clark Fork watershed included HD 210 and HD 216.*

Population model description

To assess changes in the population dynamics of the 4 elk populations within the Bitterroot treatment and Upper Clark Fork control areas, we used an integrated population modeling approach that modeled two separated processes: 1) a model for the biological processes of survival, per-capita recruitment and harvest, and 2) the observation process that gives rise to the observed counts and age ratios (see Paterson et al. 2019*b* for details).

We defined the annual population cycle from the birth pulse (in May-June) to the following spring (March-April) when calves recruit to the population as 1-year-olds. The population cycle can be represented as an age-structured matrix model, where the expected number of calves (N_{c}), adult females (N_{af}) and adult males ($N_{\mathrm{adult.m}}$) in year t and district u is given as:

$$E\left\{\begin{matrix} N_{t,u}^{\mathrm{c}} \\ N_{t,u}^{\mathrm{af}} \\ N_{t,u}^{\mathrm{am}} \end{matrix}\right\} = \left\{\begin{matrix} \tau N_{t-1,u}^{\mathrm{af}} - \ h_{t,u}^{\mathrm{c}} \\ \phi_a\left(\delta N_{t-1,u}^{\mathrm{c}} + N_{t-1,u}^{\mathrm{af}} - h_{t,u}^{\mathrm{af}}\right) \\ \phi_a\left((1-\delta)N_{t-1,u}^{\mathrm{c}} + N_{t-1,u}^{\mathrm{am}} - h_{t,u}^{\mathrm{am}}\right) \end{matrix}\right\}$$

where the vital rates that connect the population size across years are apparent adult survival (ϕ_a), the proportion of calves that were female (δ, here assumed to be equal to 0.5), and the per capita recruitment rate (τ), and h^{c}, h^{af}, and h^{am} are age/sex specific harvest. Here we assumed the survival of all age/sex classes other than calves was the same through time. Per capita recruitment is the product of a series of vital rates, including the probability of conception, in-utero survival to birth, and then calf survival from birth to census the next spring.

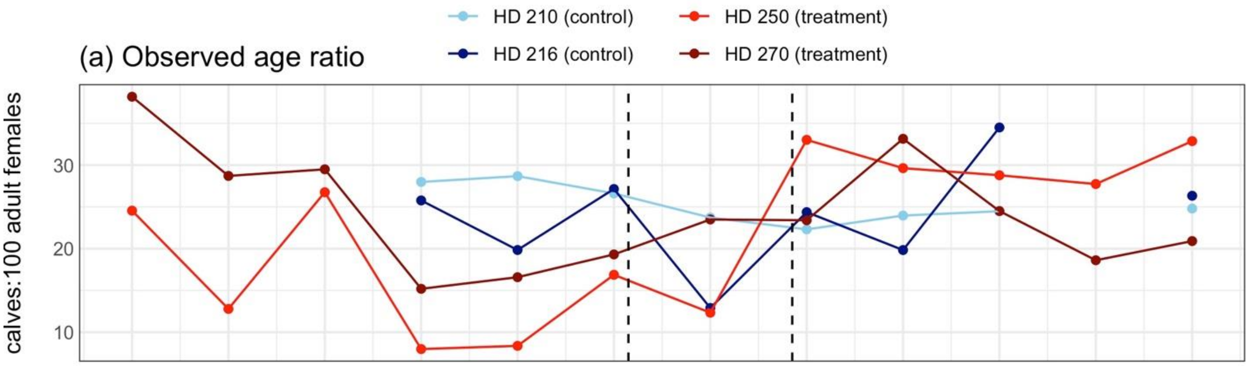
Although our primary goal was to assess the strength of evidence for changing trends in per capita recruitment rates in the treatment and control areas before and after the mountain lion harvest treatment, we also needed to account for potentially confounding environmental factors that may influence recruitment. Therefore, we developed annual environmental covariates for each of the 4 hunting districts to index summer growing season and precipitation, winter severity, and predation risk.

Results

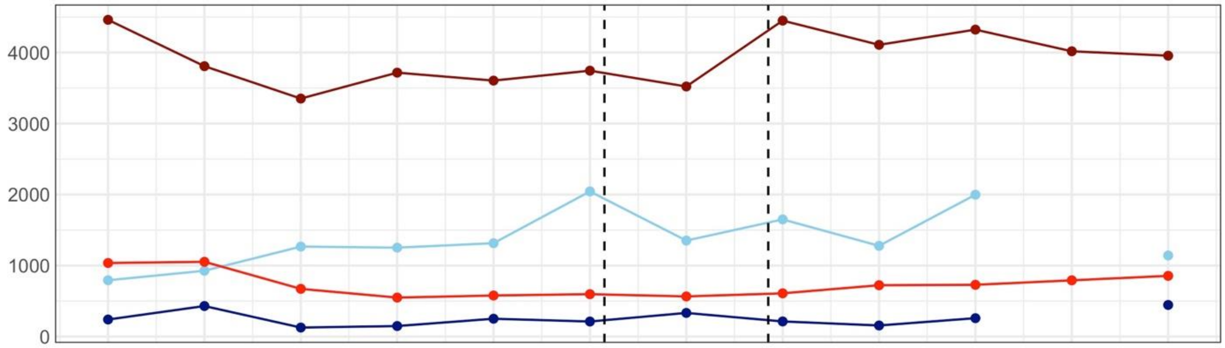
Elk data and environmental variation

We found among-hunting district variation in elk population counts during the study. In the control area, HD 210 had a mean count of 1,365 elk (SD = 393) over the duration of the study with a mild, apparent increase over time, and HD 216 had a mean count of 256 elk (SD = 107) with an approximately stable count over time (Figure 7.2). In the treatment area, both HD 250 (mean = 730, SD = 175) and HD 270 (mean = 3,922, SD = 363) displayed an initial decrease in counts of elk, followed by a slow, apparent increase over time (Figure 7.2). Observed age ratios displayed a similar degree of variation. In the control area there was no obvious trend in age ratios, and the mean was roughly the same between HD 210 (mean = 25.3, SD = 2.2) and HD 216 (mean = 23.8, SD = 6.4), although HD 216 showed more among-year variation (Figure 7.2). In the treatment area, observed age ratios initially decreased in both populations and reached a minimum in 2009 before subsequently increasing (HD 250 mean = 21.8, SD = 9.5; HD 270 mean = 24.3, SD = 6.9; Figure 7.2). Values of our environmental covariates displayed no strong temporal trend (Figure 7.3). There was no obvious difference in the median and range of covariate values for any district between the pre-treatment and post-treatment periods (Figure 7.3).

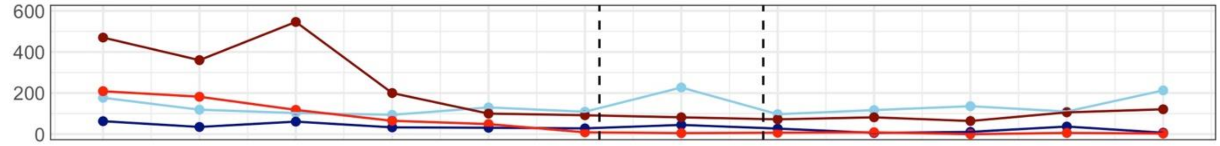
(a) Observed age ratio



(b) Total count of elk



(c) Antlerless harvest



(d) Antlered harvest

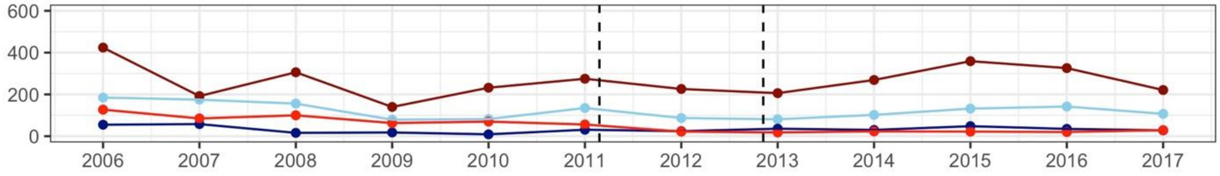


Figure 7.2 *Summary of 2006–2017 (a) observed age ratio (calves:100 adult females), (b) count, (c) antlerless and (d) antlered harvest data for each of the four elk populations included in the elk population model. The HD 210 and HD 216 elk populations are located within the Upper Clark Fork control study area and the HD 250 and 270 elk populations are located within the Bitterroot study area treated with a mountain lion harvest management prescription designed to reduce mountain lion populations. The vertical dashed black lines separate the pre-treatment era (2007-2011) from the post-treatment area (2013-2017).*

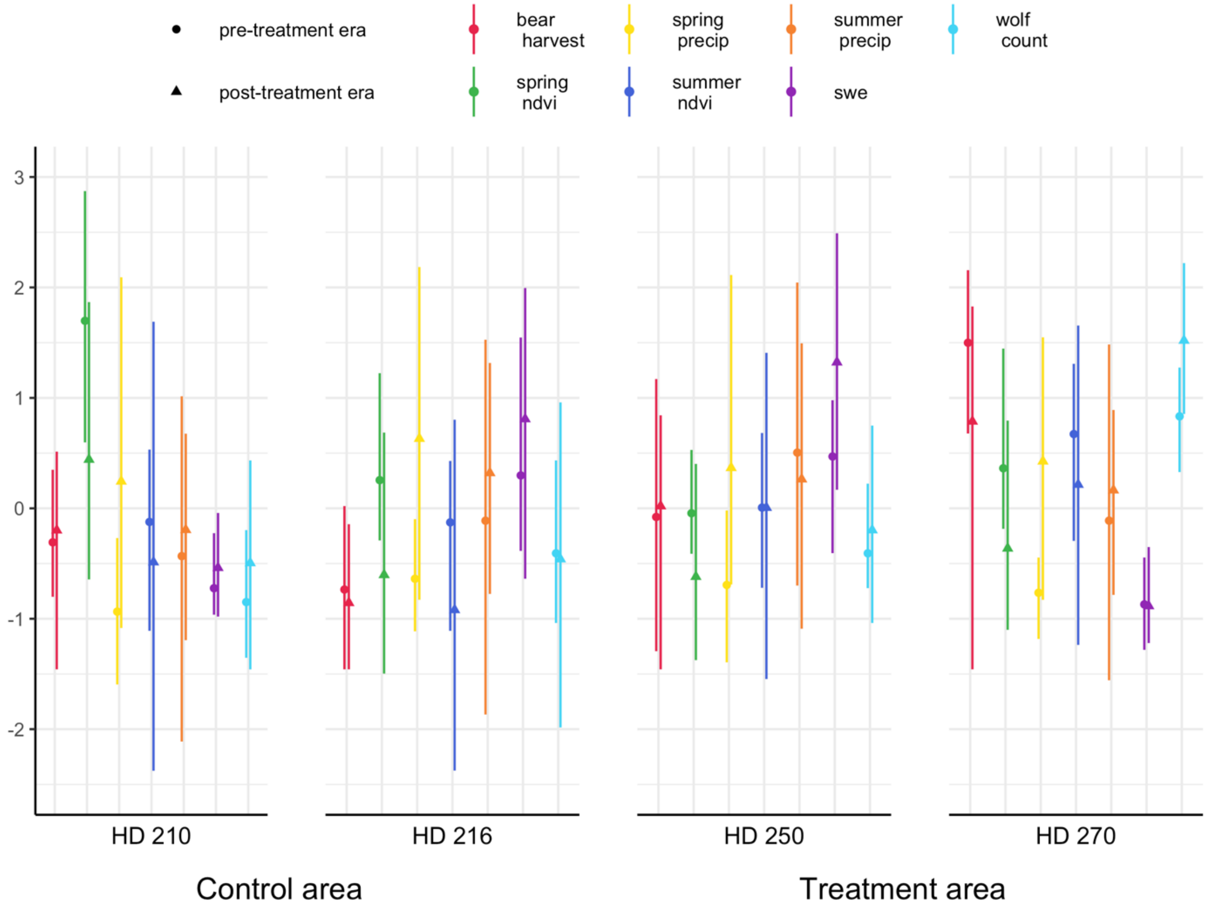


Figure 7.3 *The median (circle = pre-treatment, triangle=post-treatment) and range (minimum to maximum, thin line) of values for covariates in the elk population model explaining variation in calf recruitment during the pre-treatment (2007–2011) and post-treatment (2013–2017) periods for four elk populations in west-central Montana. The HD 210 and HD 216 elk populations are located within the Upper Clark Fork control study area and the HD 250 and 270 elk populations are located within the Bitterroot study area treated with a mountain lion harvest management prescription designed to reduce mountain lion populations. The y-axis represents standardized covariate values. In all cases, environmental variation is similar within units before and after the treatment period.*

Elk population models

We found strong evidence for the association of several environmental covariates with per capita calf recruitment rates (Figure 7.4). We estimated regression coefficients of these covariates from scaled data using the logit link. To help interpret the effects of these covariates on recruitment, we compared median recruitment (i.e., the median value of all estimated recruitment) to estimated recruitment at 1 standard deviation above or below the average of a given covariate. We emphasize that there was significant temporal and spatial variation in environmental covariates, and this is a significant reduction of the variation used to aid interpretation only. The median estimated recruitment rate across time and area from our model was 0.24 (90% CI = 0.23, 0.26). The magnitude of bear harvest (an index of bear population abundance) had a negative relationship with recruitment, opposite to that expected if bear harvest enhanced elk recruitment (and, we acknowledge, may be indicative of a potentially spurious correlation). The estimated bear harvest effect on the standardized scale was -0.26 (SD = 0.08), corresponding to recruitment declining from 0.24 for the average bear harvest of 18 to 0.20 (CI = 0.17, 0.22) for a bear harvest one standard deviation above the average (corresponding to a total of 30 bears harvested). Cumulative snow water equivalent in the previous year (SWE) had a negative relationship with recruitment as expected. SWE in the previous year had an estimated effect on the standardized scale of -0.30 (SD = 0.07), such that per capita recruitment declined from the overall median recruitment at the average SWE of 12.5 m to 0.19 (CI = 0.17, 0.22) at one standard deviation of SWE above the average (corresponding to 21.2 m). No relationship with recruitment was found for snow water equivalent in the current year. Summer precipitation in the current year had a large, positive association with per capita recruitment as predicted, with an estimated effect on the standardized scale of 0.24 (SD = 0.09). This corresponded to an increase in recruitment from the overall median at the average value of cumulative summer precipitation of 14 cm to 0.29 (CI = 0.26, 0.33) at one standard deviation of summer precipitation above the average (corresponding to 17 cm).

Additionally, we found strong evidence for a positive association with summer precipitation in the previous year with an estimated effect on the standardized scale of 0.17 (SD = 0.07). This corresponded to an increase in recruitment from the overall mean at the average value of summer precipitation of 12.5 m to 0.27 (CI = 0.24, 0.31) at one standard deviation above the average summer precipitation (corresponding to 17 cm). We found comparatively weak or no evidence for an association between recruitment and wolf counts, spring time-integrated NDVI, summer time-integrated NDVI, spring cumulative precipitation, or the lagged versions of summer time-integrated NDVI. We found no evidence for an association between recruitment and the size of the population in the previous year. Finally, we found no association between per capita calf recruitment rates and the latent size of the population.

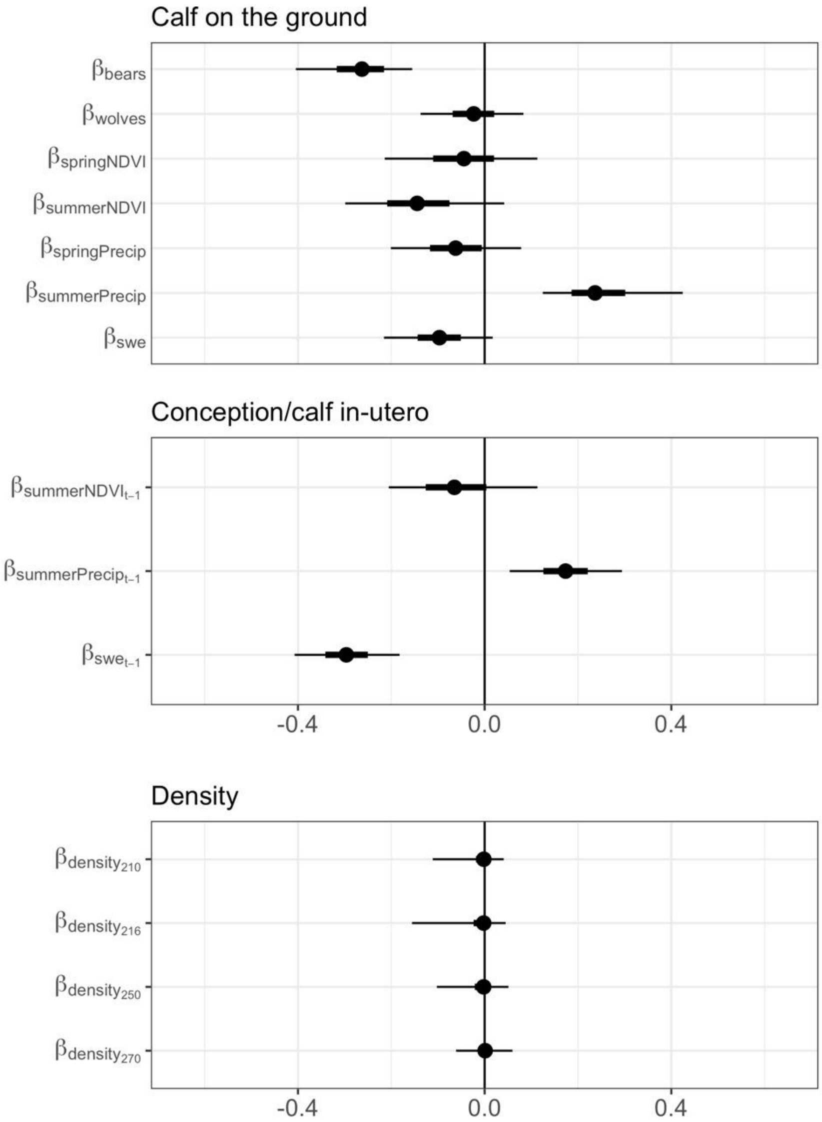


Figure 7.4 *Estimated regression coefficients for covariates explaining variation in calf recruitment rate for four elk populations in west-central Montana. The x-axis represents the standardized coefficient values with 0 denoted with a vertical line. Circles denote the median estimated effect, the thick line denotes the 50% highest posterior density interval (HPDI), and the thin line represents the 90% HPDI. The top panel represents covariate values during the summer or winter the calf was on the ground (i.e. following parturition), the middle panel represents covariate values that were lagged by one year and correspond to the year of conception and in-utero growth (i.e. prior to parturition), and the bottom panel represents the estimated relationship with the latent size (density) of the population.*

Pre- and post-treatment elk vital rates

We first predicted the relationship for the trends in recruitment rate in the control and treatment area by holding environmental covariates to their median values within each area using the estimated intercept and slope terms from the linear trend component of the model. These results represent a prediction of what would have happened under median environmental conditions in each area across all years (Figure 7.5). We found essentially no evidence for a declining trend in per capita recruitment in the control area during the pre-treatment period (for example, in 2007 we estimated a median = 0.40, CI = 0.23, 0.58 compared to a median in 2011: 0.26, CI = 0.12, 0.39).The uncertainty in these estimates as well as the estimated slope term ($\beta_{\text{pre,control}}$ = -0.15, CI = -0.40, 0.09) suggested an overall stable recruitment rate. Similarly, during the post-treatment period we estimated a roughly stable (if slightly higher) per capita recruitment rate (for example, in 2013 we estimated a median = 0.40, CI = 0.26, 0.58; compared to a median in 2017 of 0.25, CI = 0.14, 0.40; $\beta_{\text{post,control}}$ = -0.17, CI = -0.36, 0.02).

In contrast, we found strong evidence for a difference in temporal trends in recruitment in the treatment area. During the pre-treatment period, we estimated roughly stable per capita recruitment rates (for example, in 2007 we estimated a median of 0.21, CI = 0.12, 0.33 and a median of 0.17, CI = 0.08, 0.26 in 2011; $\beta_{\text{pre,treatment}}$ = -0.06, CI = -0.28, 0.13); whereas we found strong evidence for an initial increase in recruitment in 2013 (median = 0.42, CI = 0.29, 0.56) followed by a steady decline ($\beta_{\text{post,treatment}}$ = -0.24, CI = -0.40, -0.09) to 2017 (median = 0.21, CI = 0.11, 0.32), such that per capita recruitment rates were essentially the same in 2017 as in 2007.

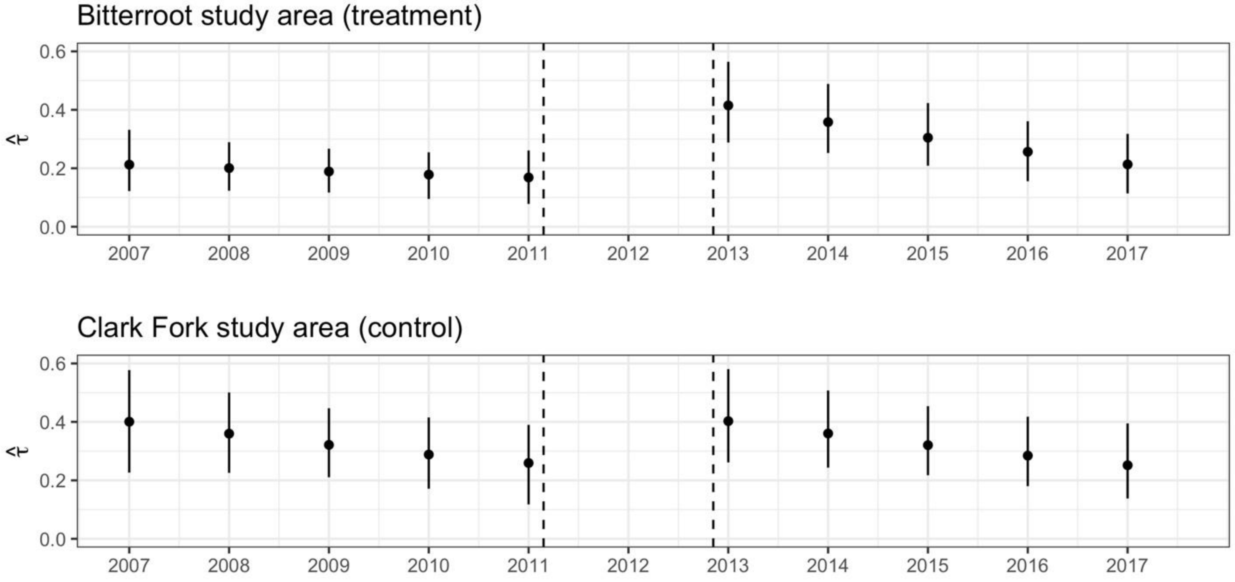


Figure 7.5 *The trends in mean calf recruitment rate in the Bitterroot and Upper Clark Fork study areas during the 5-year pre-treatment (2007–2011) and post-treatment (2013–2017) periods predicted by holding all population model covariates to their median values within each area. The thin lines represent the 90% highest posterior density interval.*

Our second approach to interpreting model results regarding changes in per capita recruitment rates was to compare estimated median values of recruitment during the pre- and post-treatment periods for both areas at the hunting district level , i.e., values that incorporate the linear trend as well as observed environmental variation (Figure 7.6). In the control area, we found that the median recruitment rates were nearly identical during the pre- (HD 210: median = 0.27, CI = 0.23, 0.31; HD 216: median = 0.28, CI = 0.21, 0.35) and post-treatment periods (HD 210: median = 0.26, CI = 0.23, 0.38; HD 216: median = 0.23, CI = 0.19, 0.28). For the treatment area, we found strong evidence that the median recruitment in HD 250 increased in the post-treatment period (median = 0.33, CI = 0.29, 0.38) relative to the pre-treatment period (median = 0.15, CI = 0.12, 0.18) and evidence of an increase in HD 270 (pre-treatment: median = 0.21, CI = 0.20, 0.23; post-treatment: median = 0.28, CI = 0.27, 0.30).

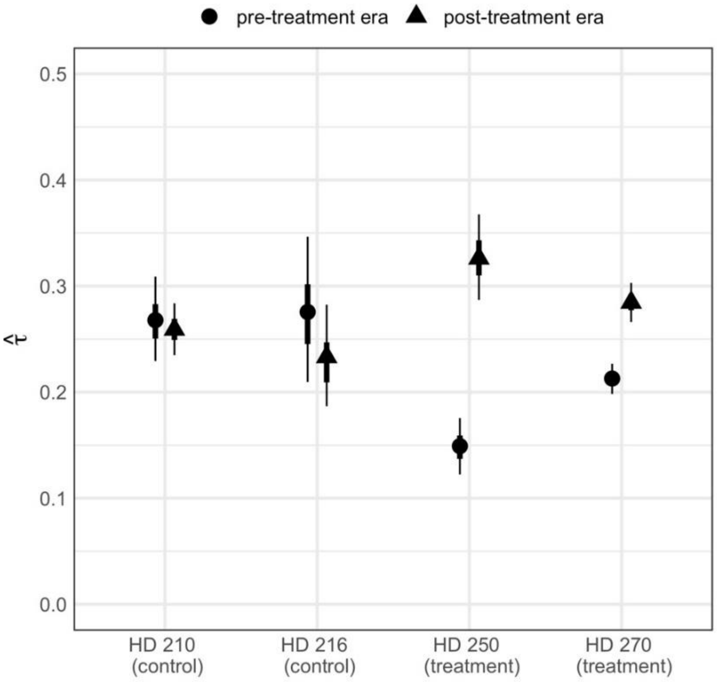


Figure 7.6 *The predicted mean calf recruitment rate for each of the 4 elk populations during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017) given the observed annual covariate conditions. The thick line denotes the 50% highest posterior density interval (HPDI) and the thin line represents the 90% HPDI.*

As expected, these post-treatment increases in recruitment in the treatment areas corresponded to increases in population growth rate. Population growth rates were roughly similar in the control area during both phases, in a pattern similar to that for recruitment rates (Figure 7.7). However, we note that the estimated growth rates were influenced by changes in harvest in both areas through time. To aid the interpretation of the relationship between recruitment rates and growth rates, we first predicted λ for each treatment area given the scenario of no harvest in the previous fall and with the observed environmental variation. For example, in the Bitterroot area, we treated hunting districts 250 and 270 as a single population, and then used the approximate posterior distribution of estimated λ to predict what λ would have been had total harvest been zero in the previous year (Figure 7.8). In the treatment area, pre-treatment elk populations were declining (growth rates less than 1) from 2006–2008, and slightly increasing from 2009–2010 (e.g., 2010: $\hat{\lambda} = 1.07$, CI = 1.04, 1.10). In a pattern similar to estimates of recruitment, estimated population growth rates jumped substantially at the beginning of the post-treatment phase ($\hat{\lambda} = 1.17$, CI = 1.13, 1.20) prior to declining to 1.06 (CI = 1.04, 1.09) by 2017. In contrast, we found no evidence of a pattern in population growth rates in the control area, with population growth rates ranging from 0.87 (CI = 0.78, 0.94) in 2015 to 1.12 (CI = 1.08, 1.17) in 2014.

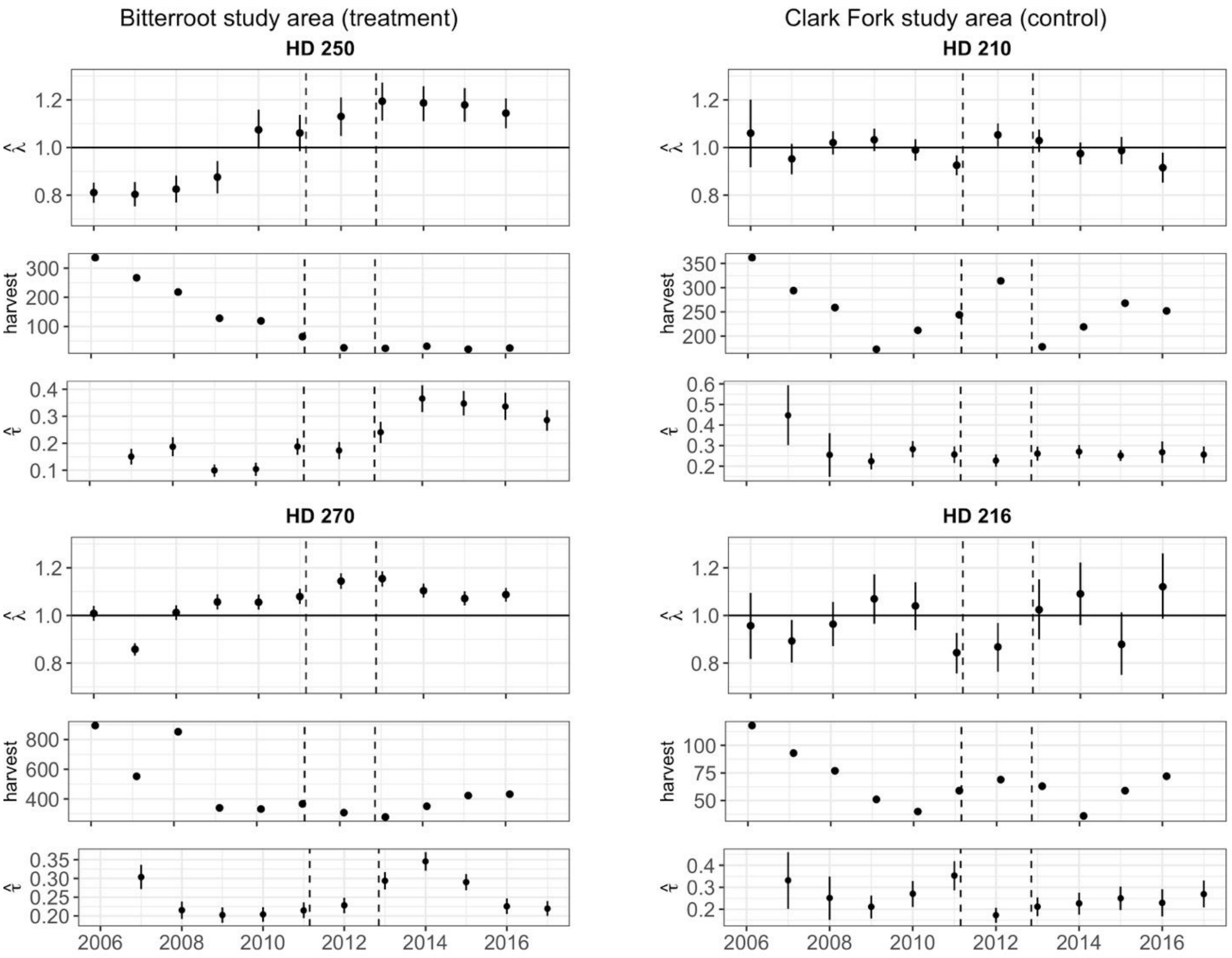


Figure 7.7 *The estimated population growth rates (λ), total harvest, and recruitment rates (τ) for each of the four elk populations in the Bitterroot and Upper Clark Fork study areas during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017). Population growth rates are the aggregated result of variation in harvest and recruitment rates. The dot indicates the mean value and the thin line the 90% highest density posterior interval.*

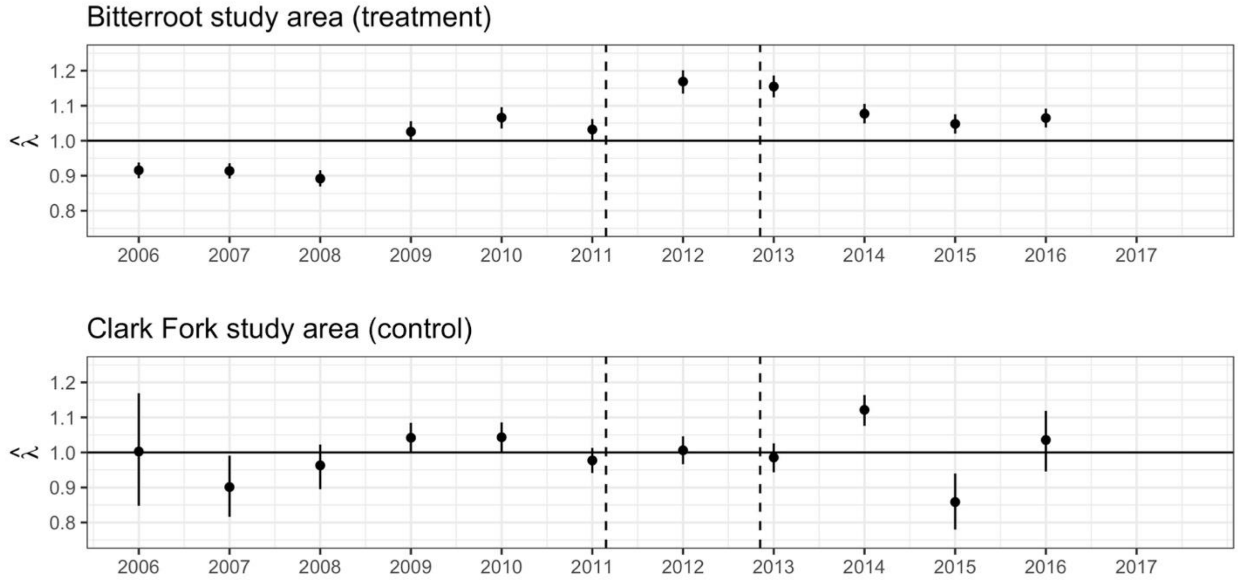


Figure 7.8 *The predicted population growth rates (λ) for the Bitterroot and Upper Clark Fork study areas during the 5-years pre-treatment (2007–2011) and post-treatment (2013–2017) assuming no harvest the previous year. Elk populations were aggregated within each area, then lambda was estimated as if there were no harvest in the previous year. The dot indicates the mean value and the thin line the 90% highest density posterior interval.*

Additionally, we used a second approach to understand variation in population growth rates, similar to that for recruitment rates, by comparing estimated median values of λ (incorporating observed environmental variation) during the pre- and post- treatment periods for both areas at the level of the hunting district (Figure 7.9). Similar to recruitment rates, in the control area we found that median population growth rates were nearly identical in the pre- (HD 210: median = 1.01, CI = 0.97, 1.04; HD 216: median = 0.98, CI = 0.92, 1.05) and post-treatment phases (HD 210: median = 0.99, CI = 0.96, 1.03; HD 216: median = 1.00, CI = 0.91, 1.09). In contrast, we found strong evidence that median population growth rates in the treatment area were higher during the post-treatment period in both HD 250 (post-treatment median = 1.17, CI = 1.13, 1.21; pre-treatment median = 0.84, CI = 0.80, 0.87), and in HD 270 (post-treatment: median = 1.11, CI = 1.08, 1.13; pre-treatment: median = 1.02, CI = 1.00, 1.04).

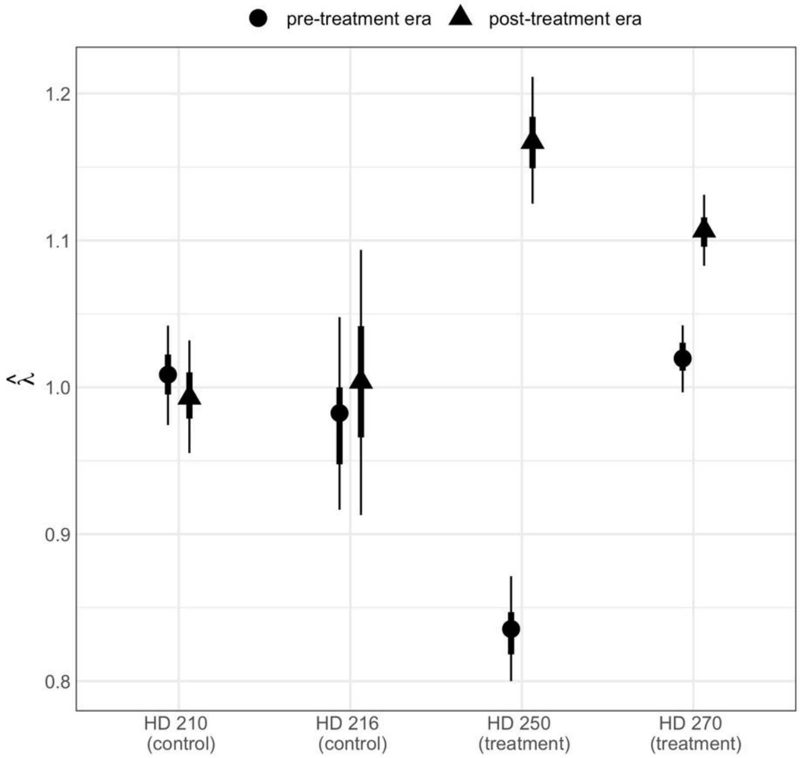


Figure 7.9 *The predicted mean population growth rate for each of the four elk populations in the Bitterroot and Upper Clark Fork study areas during the 5 years pre-treatment (2007–2011) and post-treatment (2013–2017) given the observed annual covariate conditions. The thick line denotes the 50% highest posterior density interval (HPDI) and the thin line represents the 90% HPDI.*

Discussion

Our analytical methodologies allowed for a quantitative evaluation of effects of the liberalized mountain lion harvest regulations on elk populations in west-central Montana. We found evidence that the liberalized mountain lion harvest regulations were associated with short-term increases in elk recruitment and population growth rates. Elk populations within the treatment area showed an increase in recruitment rate following implementation of the mountain lion harvest treatment, although the effects of the treatment declined during the 5-years following treatment. Our results indicate that management objectives to increase calf recruitment were achieved, although effects of the treatment on recruitment were strongest immediately following implementation of the treatment and diminished over time.

Our results contribute to the broader body of literature regarding the effects of carnivore management on ungulate populations. Effects of carnivore management vary widely across studies, likely due to variability in the magnitude of carnivore harvest or removals, unique combinations of factors limiting the ungulate population under consideration, and post-treatment monitoring approaches used to draw inference. In this case, there was strong prior evidence that mountain lion predation was a proximate limiting factor on elk calf recruitment (Eacker et al. 2016) and that elk calf recruitment was an important driver of elk population growth rate in this system (Eacker et al. 2017). Therefore, we expected that reductions in mountain lion population abundance would result in increased calf recruitment and ultimately population growth rates. Our work here supports the conclusion that calf recruitment increased following the mountain lion harvest treatment.

We found that although calf recruitment increased following liberalized mountain lion harvest regulations, the effects of the mountain lion harvest on recruitment were short-term. Calf recruitment is well documented to respond to annual variability in weather and growing season conditions (Paterson et al. 2019b); however, even after accounting for annual variations using a population modeling approach, our dataset showed that recruitment increased following treatment. After the initial increase in recruitment immediately after the harvest treatment, calf recruitment declined during the 5 years following treatment to similar rates as pre-treatment. These short-term effects are not unexpected, and are similar to the observed short-term effects of increased mountain lion harvest on elk calf survival within this study area which suggested elk calf survival was lowest pre-harvest treatment, highest in the first year post-treatment, and at intermediate levels 4 years post treatment (*see Section 6*). Similarly, only short-term effects of mountain lion reductions on mule deer populations were observed in Idaho (Hurley et al. 2011). Mountain lion populations are capable of rapid growth following reductions in harvest (Ross and Jalkotzy 1992), and populations likely rebound to pre-treatment levels following reductions in harvest. Thus, only short-term effects on prey populations should be expected given a short-term mountain lion harvest treatment. In this case, the intent and outcome (see Section 3) of the mountain lion harvest treatment was a moderate reduction in the mountain lion population that allowed for short-term releases in the elk populations. Our results suggest that these goals were indeed achieved.

The elk modeling approach applied in this study also offers a novel approach for advancements and improvements over interpreting monitoring data. The use of a population model allowed for biological inferences that would otherwise have likely been masked by the lack of statistical power induced by not treating observations as a time series of biological processes and the variance associated with the observation process (Paterson et al. 2019*b*). Detecting the effects of carnivore harvest on ungulate populations has been difficult in many systems, and our approach that accounted for the process and observations separately allowed for stronger inference regarding these relationships. Additionally, the modeling approach allowed for the evaluation of the effects of mountain lion harvest management on calf recruitment in two ways: first, by considering the variation in other important covariates during the years of this study, and second, by holding the other covariates constant at their mean values to assess only the effects of harvest management. The process variation associated with other important covariates affecting calf recruitment may mask the carnivore (or carnivore harvest) effects in certain areas or time periods, yet our population modeling methodology accounts for the other covariate effects to evaluate the effect of carnivore harvest during the period that the harvest treatment was implemented. The ability to disentangle the effects of annual variability in covariates affecting calf recruitment and the effects of the harvest treatment provides an important methodological advancement towards better understanding carnivore-ungulate population dynamics.

Section 8 – Factors Affecting Elk Calf Recruitment in West-Central Montana

Introduction

Ungulate population trajectories are driven by vital rates such as survival, reproduction, and recruitment, and effective population management requires information on how each of these rates affect demographic performance (Johnson et al. 2010). Although variation in adult female survival rates has the highest proportional impact on population growth rate, theoretical and empirical work strongly suggest that adult survival rates are buffered against high variation (Pfister 1998, Gaillard and Yoccoz 2003, Jäkäläniemi et al. 2013, Péron et al. 2016). In contrast, juvenile survival has a lower proportional impact on growth rate but much higher spatial and temporal variation, such that it can have a large impact on population growth rates (Gaillard et al. 1998*a*, Raithel et al. 2007, Eacker et al. 2017). Thus, juvenile survival is commonly monitored and used as an index of population performance. However, juvenile survival varies annually, and causes of mortality differ widely across ecosystems (Raithel et al. 2007, White et al. 2010), which makes it difficult to understand and make generalizations about sources of variation in juvenile survival.

Given the practical challenges of long-term studies on individually marked animals, many ungulate populations are routinely monitored and managed using age ratios (e.g., juveniles per 100 adult females) as a proxy for juvenile survival (Raithel et al. 2007, Harris et al. 2008). In contrast to data on individually marked individuals (*see Section 6*), data on age ratios are comparatively easy to acquire and widely applicable to management of multiple species, which has led to routine collection of age ratio data and the development of long-time series of ratios (Caughley 1974, Bender 2006, Harris et al. 2008). However, use of data on age ratios to manage populations has been challenged because they conflate variation in two age classes, and distill complicated population dynamics into a single summary statistic (Caughley 1974, Downing et al. 1977, Bonenfant et al. 2005, Bender 2006). Moreover, the interpretation of age-ratios from harvested populations of ungulates can be further complicated by the timing of surveys. For age-ratio data collected in the spring, the numerator (juveniles) is driven by rates of pregnancy and calf survival from birth to the time of the count, whereas the denominator (counts of adult females) is driven by adult survival and harvest, and change in harvest the previous fall can drive variation in age ratios.

Our goal was to evaluate the sources of variation in elk calf recruitment using a time-series of data on harvested elk populations in west-central Montana and evaluate the relative influence of factors that managers can and cannot control on recruitment. We used a population modeling approach to model per capita elk calf recruitment rates as a separate biological process, and then used regression analysis to assess the evidence for factors affecting elk calf recruitment rates. Importantly, this modeling approach uses data that are already routinely collected by wildlife managers, i.e., the numbers of individuals observed in each class, to make inference about the key vital rate for which age-ratios are a proxy: the per capita recruitment rate that can drive the population dynamics of ungulates.

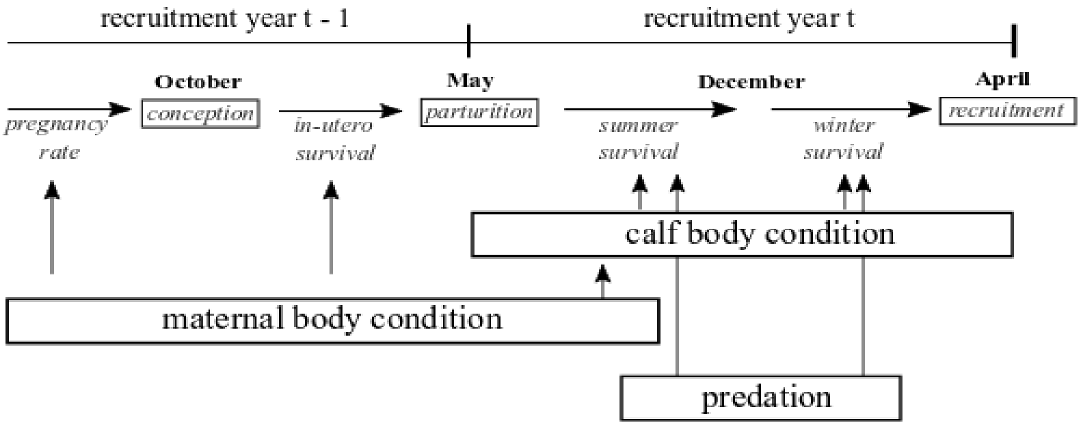


Figure 8.1 *Concept diagram illustrating the progression of events and rates underlying recruitment for spring surveys. The probability that each calf is available to be surveyed during the late spring surveys is the product of pregnancy rates, in-utero survival to parturition, then summer and winter survival, the product of which is the per capita recruitment rate. Each rate is hypothesized to be associated with multiple drivers related to the timing of events.*

The per capita recruitment rate is the result of a series of processes that are potentially affected by environmental conditions and predator pressure (Figure 8.1). Maternal body condition from the summer prior to conception through parturition has been shown to be related to pregnancy rates (Bonenfant et al. 2002, Cook et al. 2004), calf parturition mass (Bender et al. 2002) and neonatal survival during the maternal care period following birth (Griffin et al. 2011). Therefore, we expected per capita recruitment rates to be positively associated with indices of nutrition (year *t*-1), negatively associated with winter severity (year *t*-1), and potentially demonstrate an interaction between nutrition indices and winter severity such that poor summer conditions and severe winter conditions combine to further reduce recruitment (Cook et al. 1996). Environmental conditions experienced after parturition (year *t*) are thought to be related to juvenile survival in its first year, either through direct impact on juvenile nutrition through foraging (Cook et al. 1996) or as mediated through maternal provisioning during the maternal care period (Cook et al. 2004). There is an evolving debate as to whether spring conditions or late summer conditions are more important to juvenile survival (Hurley et al. 2014), and we split indices of the nutritional environment into spring and summer periods to assess the relative importance of these two periods. We expected per capita recruitment rates to be positively associated with indices of nutrition (year *t*). Juvenile survival to recruitment has been shown to be related to winter conditions (Loison and Langvatn 1998) and we expected per capita recruitment rates to be negatively associated with winter severity (year *t*), and interact with nutritional conditions such that the impact of poor nutritional conditions is made worse in severe winters. Predators can have a large impact on juvenile survival (Barber-Meyer et al. 2008, White et al. 2010, Brodie et al. 2013, Eacker et al. 2016), and we expected per capita recruitment rates to be negatively associated with indices of predator abundance.

Methods

Elk count and harvest data

For our analyses of elk recruitment, we used data from 17 hunting districts in west-central Montana (Figure 8.2). These HDs included, but were not limited to, the Bitterroot and Upper Clark Fork study areas. We used annual spring elk count and age/sex classification data collected from fixed wing aircraft. Surveys were conducted annually on the winter range for each district in the late spring prior to the migration to summer range and the birth pulse. Due to logistical limitations, not every district had count and age/sex classification data for each of the 13 years (2004 to 2016), which generated a discontinuous time series for most districts (median number of years = 7, minimum = 6, maximum = 13). In our analysis, we included all hunting districts that had a minimum of 6 years of count data collected during 2004 to 2016. For a small number of district-years a total count was available, but no age/sex classification was reported (*n* = 5). For the population modeling approach, we were able to treat the age/sex classifications in these years as missing data. Moreover, throughout this period there were instances where animals were counted but not classified, resulting in total counts but no classification information.

We aggregated data on the fall elk harvest (calves, adult females and adult males) as estimated by the state wildlife agency. For the population model (see Section 7), we included the number of calves, adult females and adult males harvested.

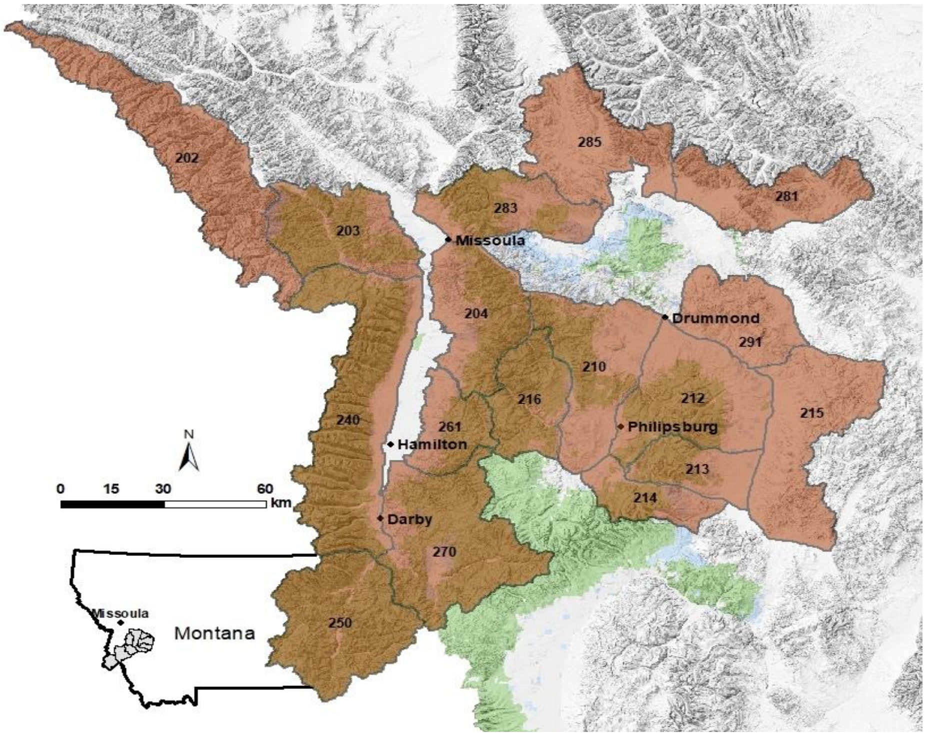


Figure 8.2 *The elk hunting districts in west-central Montana used for analysis. We restricted our analysis to those hunting districts with at least 6 years of data.*

Covariates

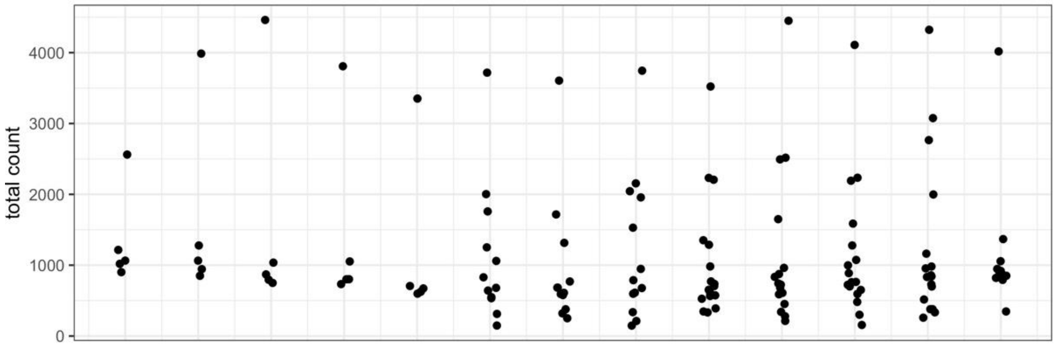
Our primary goal was to assess the strength of evidence for a series of potential sources of variation in the recruitment of elk calves as mediated through maternal body condition, calf body condition and predation risk (Figure 8.1). We developed covariates to index environmental conditions during the summer growing season, winter severity, and predator abundances. We estimated the average cumulative precipitation values within each elk population range over the spring (neonatal period, May–June) and summer periods (juvenile independence period, July–September, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, accessed 11 September 2018). As an index of summer growing season conditions, we estimated the average annual integrated-NDVI values within each elk population range over the spring and summer periods. As an index of winter severity, we used snow-water equivalent (swe), a metric of snowpack density. We estimated the mean cumulative swe for each population range from December 1 to April 31 of each year.

Information on carnivores across all of the hunting districts included in this analysis was available from harvest records (mountain lion and black bears) and annual surveys (wolves). State regulations require that all harvested mountain lions and black bears that are harvested be presented with intact evidence of sex to MFWP staff, and these harvest data were available through all years and for all districts in our study. For both black bears and mountain lions, we used the total harvest in recruitment year *t* as the covariate, e.g., if the recruitment year was 2010 the covariate was the total harvest of each in the fall of 2009 and spring of 2010. End-of-the-year minimum wolf counts (number observed by December 31 of each year) were available as part of the state of Montana’s wolf monitoring program and management plan. We used the number harvested mountain lion and black bear and wolf counts as covariates in the models, hypothesizing that they were an index to the underlying populations.

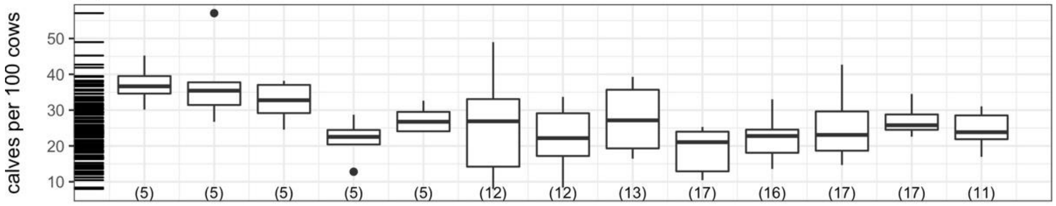
Results

The number of elk counted, observed age ratios, and harvested elk varied considerably among years and hunting districts (Figure 8.3). Antlerless and antlered harvest varied across years and hunting districts in response to changing regulations over the time period of the study. Notably, high harvest in some districts from 2004 to 2007 was followed by reduced harvest.

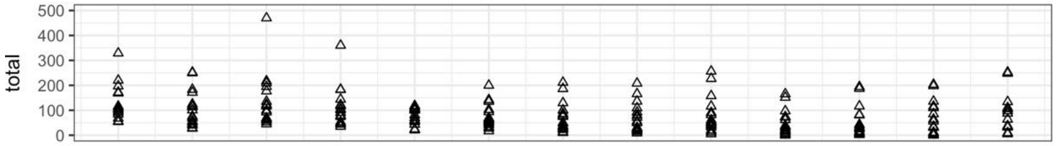
(a) Observed counts



(b) Observed age ratio



(c) Antlerless harvest



(d) Antlered harvest

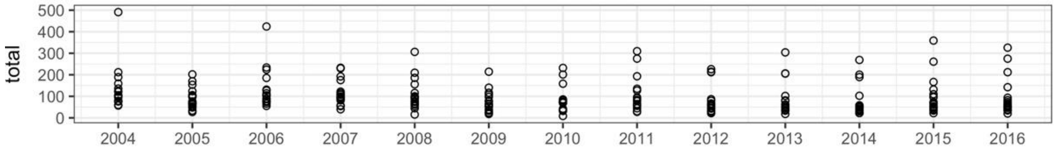


Figure 8.3 *Summary of observed elk count and classification data and estimated antlerless and antlered harvest for the 17 hunting districts included in the elk population model. Both observed counts and age ratios (sample size in parentheses) demonstrated large variation among years and hunting districts. Similarly, antler and antlerless harvest varied through time and district. In panel (a), the observations have been jittered along the x-axis to improve visibility. In panel (b), the y-axis includes a rug that highlights the distribution of the data.*

Sources of variation in recruitment

We found strong evidence for a series of relationships between covariates and recruitment using the population model. For an average year and with all covariates held to their average value (zero for standardized covariates), our model predicted an overall mean recruitment rate of 0.25 (90% CI = [0.21, 0.29]). For each covariate below, we report the estimated effect on the logit scale and then a prediction of how recruitment changed from this overall mean as that covariate increased/decreased one standard deviation from the average value. We found a weak negative association between mountain lion harvest and per capita recruitment rates ($\hat{\beta}_{lions}$ = -0.04 [-0.07, 0]), which corresponded to a decline in per capita recruitment from the overall mean of 0.25 (90% CI = [0.21, 0.29]) at the average lion harvest (4.12 harvested) to 0.24 [0.19, 0.27] at one standard deviation above the average lion harvest (7.88 harvested). Similarly, we found a weak association between black bear harvest and per capita recruitment rates ($\hat{\beta}_{bears}$ = -0.05 [-0.09, 0]), declining from the overall mean (0.25 [0.21, 0.29])) at the average black bear harvest (21.31 harvested) to 0.24 [0.21, 0.28] at one standard deviation above the average black bear harvest (39.17 harvested). However, we found strong evidence for an interaction with cumulative snow water equivalent (swe) ($\hat{\beta}_{bears*swe}$ = -0.11 [-0.16, -0.05]) that became different from zero only at higher bear harvests and more severe winters. At the average black bear harvest, per capita recruitment rates in a mild winter (hereafter defined as the 5th percentile of standardized swe values, swe = -0.95), average winter (swe = 0), or severe winter (hereafter defined by the 95th percentile of swe values, swe = 2.22) showed no meaningful difference. At one standard deviation above the average black bear harvest recruitment in a mild winter was higher than in a mean winter (difference = 0.02 [0.01, 0.04]), and even higher than in a severe winter (difference = 0.07 [0.03, 0.12]). In contrast, we found a weak positive association between wolf counts and recruitment ($\hat{\beta}_{wolves}$ = 0.05 [0, 0.09]), increasing from the overall mean (0.25 [0.21, 0.29]) at the average wolf count (15.99 wolves) to 0.26 [0.22, 0.30] at one standard deviation above the average wolf count (30.49 wolves). However, we also found strong evidence for a negative interaction with cumulative snow water equivalent ($\hat{\beta}_{wolves*swe}$ = -0.06 [-0.11, -0.02]) such that recruitment declined with high wolf counts and increasing winter severity. At one standard deviation above the average wolf count recruitment in a mild winter was higher than in a mean winter (difference = 0.02 [0.01, 0.03]), and even higher than in a severe winter (difference = 0.06 [0.03, 0.09]).

We also found strong evidence for an association between several environmental covariates that corresponded to conditions when the calf is on the ground (year *t)* and per capita recruitment. Cumulative spring precipitation had a negative association with per capita recruitment rates ($\hat{\beta}_{springPrecip}$ = -0.2 [-0.26, -0.14]), declining from the overall mean at the average spring precipitation (0.17 m) to 0.21 [0.18, 0.25] at one standard deviation above the average spring precipitation (0.22 m). In comparison, cumulative summer precipitation had a weaker positive association with recruitment ($\hat{\beta}_{summerPrecip}$ = 0.08 [0.03, 0.13]), increasing from the overall mean at the average summer precipitation (0.15 m) to 0.27 [0.23, 0.31] at one standard deviation above the average summer precipitation (0.19 m), and strong evidence for an interaction with winter severity($\hat{\beta}_{summerPrecip*swe}$ = 0.04 [0, 0.07]) such that low values of summer precipitation combined with winter severity to reduce per capita recruitment. At one standard deviation below the average summer precipitation (0.11 m), recruitment was higher in a mild winter than in an average one (difference = 0.02, [0.01, 0.03]), and even higher than in a severe winter (difference = 0.04, [0.01, 0.07]). Although we found no evidence for a main effect of spring NDVI, we found evidence for an interaction with winter severity ($\hat{\beta}_{springNDVI*swe}$ = 0.05 [0.01, 0.1]. Low values of spring NDVI combined with severe winters were associated with reduced recruitment. At one standard deviation below the average spring NDVI (0.81), recruitment was higher in a mild winter than an average winter (difference = 0.02 [0, 0.03]) and a severe winter (difference = 0.05 [0.01, 0.08]).

Finally, we also found strong evidence for an association between environmental variation during the year in which the calf is in-utero (year *t-1*) and recruitment. We found strong evidence for a negative association with lagged winter severity ($\hat{\beta}_{swe[t-1]}$ = -0.06 [-0.1, -0.01]

(0.25, [0.21, 0.29] at the average swe (8.15 m) to 0.23 [0.20, 0.28] at one standard deviation above the average swe (14.45 m). Although we did not find evidence for a main effect of summer NDVI, we found strong evidence for an interaction with winter severity ($\hat{\beta}_{summerNDVI*swe[t-1]}$ = 0.08 [0.05, 0.12] such that recruitment at low summer NDVI (1 standard deviation below the mean) was higher in a mild winter than a mean winter (difference = 0.03 [0.02, 0.04]), and considerably higher than in a severe winter (difference = 0.08 [0.05, 0.12]).

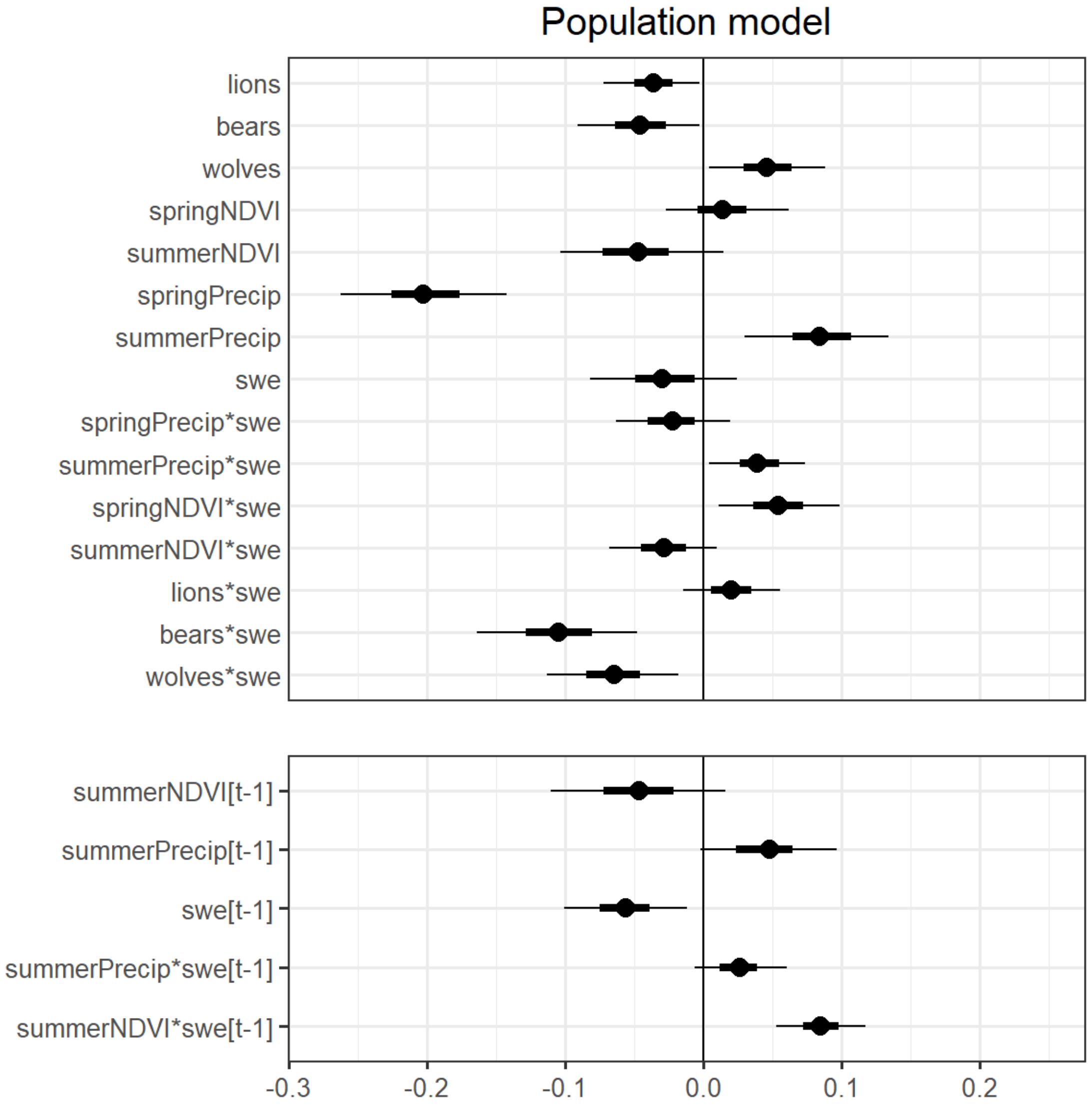


Figure 8.4 *Estimated regression coefficients for standardized covariates representing the effect of each covariate on per capita recruitment. The top panel denotes covariates affecting the calf during its first year of life and the bottom panel denotes covariates affecting the calf through in-utero maternal effects. The black dot denotes the median of the approximate posterior distribution, the heavy black line the 50% highest posterior density interval (HPD) and the light black line the 90% HPD interval.*

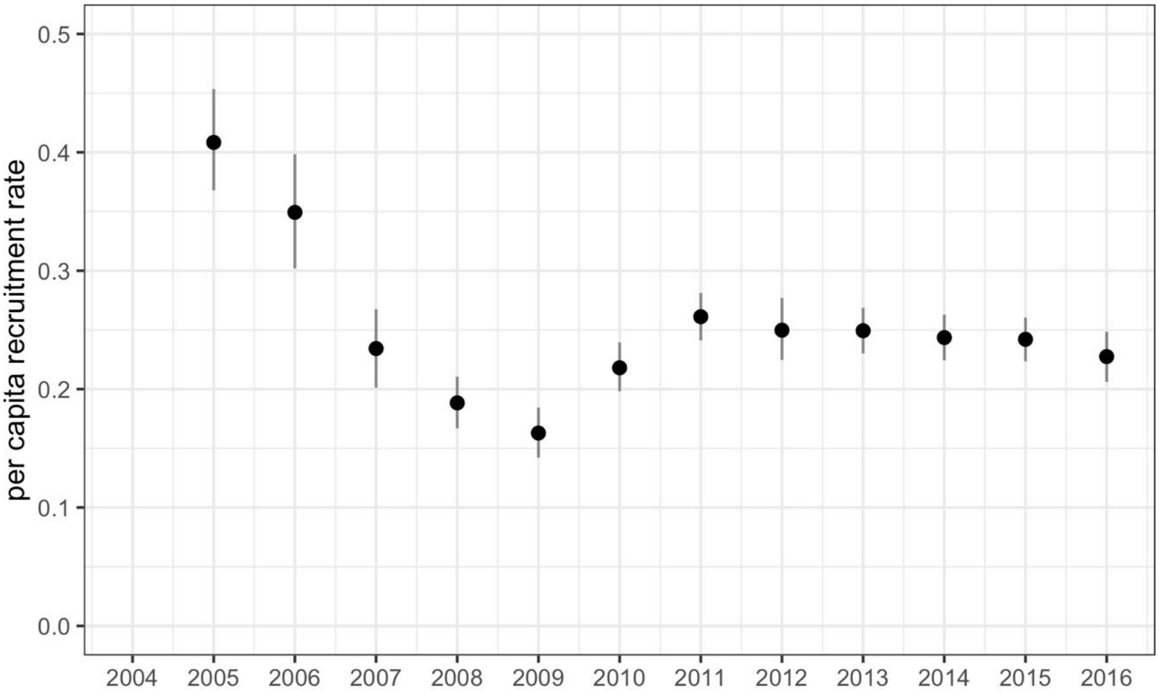


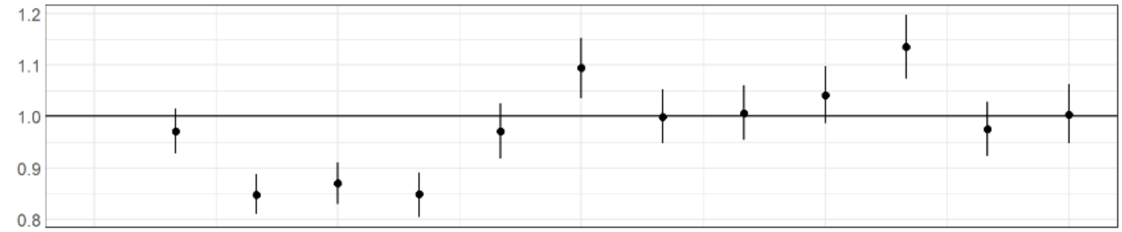
Figure 8.5 *Estimated per capita recruitment rates across hunting districts for each year. The black dot denotes the median of the approximate posterior distribution and the light black line the 90% HPD interval.*

Understanding population dynamics

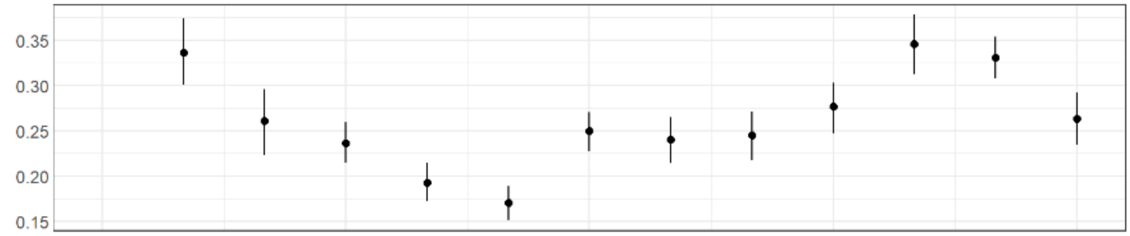
In addition to understanding the sources of variation in per capita recruitment rates (Figure 8.4, Figure 8.5), the population model also allowed deeper insights into population dynamics. By linking the numbers in each age/sex class through time via biological processes (i.e., survival and reproduction), specific numbers, ratios, and population parameters can be estimated that are of direct interest to wildlife management (Figure 8.6).

(a) λ

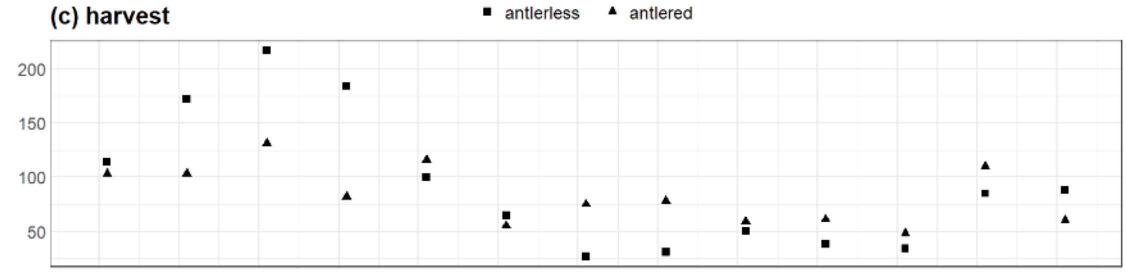
HD 240



(b) per capita recruitment rate



(c) harvest



(d) total size

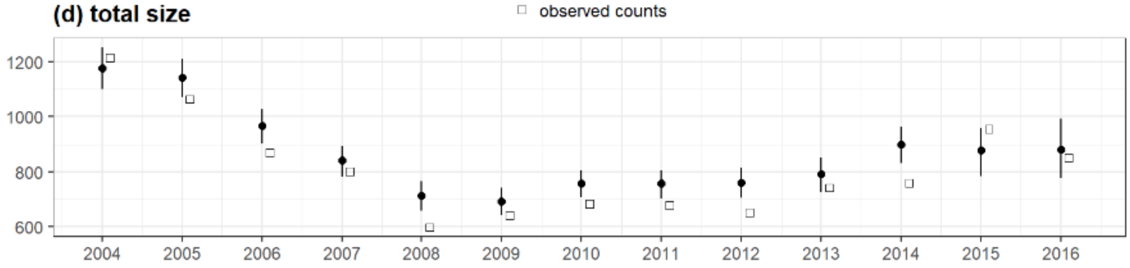


Figure 8.6 *Summary of population model output for an example hunting district (HD 240), including (a) population growth rate, (b) per capita recruitment rate, (c) observed harvest, and (d) predicted/observed total population size. The black dot denotes the median of the approximate posterior distribution and the light black line the 90% HPD interval.*

For example, the estimated sum of all age/sex classes (N_{total}) provided a qualitative way of assessing the accuracy the observation process. If observed counts are markedly different than the predicted number in a population, it indicates a lack of model fit to the observation process. This could simply be a result of poor model performance, or it could indicate issues with the count data itself, such as double counting (in the case of an overestimate), or partial counting (in the case of an underestimate). It could also indicate a lack of fit due to a closure violation, which could indicate immigration/emigration, and help inform how populations are defined in the management process. Moreover, estimated sizes (N_t^{total}) through time also provide insight into population growth rates, $\lambda_t = \frac{N_t^{total}}{N_{t-1}^{total}}$, provided they are a consistent index of the true, unknown population size (Figure 8.6). Where populations are managed using harvest as the primary tool, a comparison of harvest numbers to estimated values of λ through time provides insight into the efficacy of harvest regulations on management objectives indexed by population growth rates.

Discussion

Our results demonstrate how using a population model developed from routinely collected elk count, classification, and harvest data can provide information regarding not only recruitment, but also estimates of population growth rates. The population modeling approach provided insights regarding factors affecting recruitment that may also inform management decisions. We found that per capita recruitment rates are most strongly associated with spring and summer precipitation, and to a lesser extent associated with indices of winter severity, predator populations, and primary production.

We found that environmental conditions experienced by the calf on the ground (year *t*, related to calf survival) and the female prior to conception and when the calf is in-utero (year *t*-1) were strongly connected to per capita recruitment rates. Contrary to our expectations, cumulative spring precipitation in year *t* was negatively associated with recruitment. A post-hoc analysis of the precipitation signal strongly suggested that these high values of spring precipitation were the result of heavy snow on the summer range, an observation consistent with previous work on elk in this larger system (Lukacs et al. 2018). Cold and wet springs are thought to be a risk factor for elevated neonatal mortality, as environmental conditions interact to predispose neonates to the effects of illness, delayed green-up and increase risk of predation (Adams et al. 1995, Tveraa et al. 2003). Summer precipitation during year *t* and year *t* -1 was strongly, positively associated with recruitment. We also found evidence to support an interaction between summer precipitation values and winter severity in year *t* such that dry summers interacted with particularly severe winters to diminish calf survival in year *t*. Precipitation is known to be directly related to the rate of forage senescence, digestible energy and relative protein content (Onillon et al. 1995, MacKlon et al. 1996, Yang et al. 2001), thought to be key factors in determining the body condition of ungulates headed into winter (Blanchard et al. 2003, Link et al. 2003, Tollefson et al. 2011). Our results are broadly consistent with previous work concluding that body condition during this critical period is a key factor associated with overwinter survival in the case of calves on the ground, and with offspring survival the following spring in the case of pregnant females (Cook et al. 2004). In contrast to previous work that found the relationship between precipitation and recruitment to be relatively minor (Lukacs et al. 2018), we found spring and summer precipitation in year *t* to be major contributors to variation in recruitment. We also attribute the difference to our separation of precipitation into the two critical phases of spring (an index of early growing/environmental conditions) and summer (as an index of forage quality headed into winter). The use of a season-long precipitation metric could conflate variation in these two periods such that only the most extreme combination (e.g., a very wet spring coupled to a dry summer) would be associated with variation in recruitment.

We found mixed evidence for a relationship between primary production (NDVI) and per capita recruitment rates. Although we found no evidence for a direct relationship between NDVI in either in the spring or summer during the year the calf is on the ground and recruitment, we did find evidence for an interaction between spring NDVI and winter severity such that years with combined low spring NDVI and severe winters were associated with diminished recruitment. Moreover, we found an interaction between summer NDVI and winter severity during the year the calf is in-utero (year *t*-1) that suggested that high values of summer NDVI and severe winters reduced recruitment. NDVI is frequently interpreted as an index of forage quality (Pettorelli et al. 2011), though the link between the two is uncertain and can depend on the NDVI metric used (Fryxell 1991, Hebblewhite et al. 2008, Johnson et al. 2018). Spring green-up as indexed by increasing NDVI values has been positively associated with body condition (Hamel et al. 2009), as the greening vegetation has high digestible energy and protein content, and the relative value of this phase of forage quality has been suggested as a driver of spring migrations (Merkle et al. 2016). We used a time-integrated NDVI metric where low values likely corresponded to a delayed start of seasonal plant growth and found the NDVI metric only become meaningful when followed by a severe winter, consistent with other work highlighting the interactive effects of nutrition and winter severity (Singer et al. 1997, Garrott et al. 2003), and broadly suggesting that calves can otherwise make up for a poor start in mild winter conditions. We also found strong evidence that summer NDVI and winter severity in year *t*-1 were related to recruitment through an interaction such that high values of summer NDVI in a severe winter were negatively associated with recruitment. This is not the first study to document a surprising relationship between NDVI and the demographic performance of ungulates (Lukacs et al. 2018), which highlights the care that must be taken in assuming NDVI represents the same thing across a growing season. The relationship between NDVI and forage quality may be fundamentally different in late summer, when the high primary production NDVI represents actually corresponds to diminished digestible energy (Hebblewhite et al. 2008). Alternatively, we speculate that summer NDVI values might be correlated to large scale, long-term weather patterns such that they are serving as a proxy for environmental conditions in the approaching winter. Further work is required to detail the link between NDVI and forage quality as it relates to ungulate nutrition and body condition, and we caution against the assumption that NDVI is a proxy for it.

Predation has been shown to be a major factor influencing juvenile elk survival in individual-based studies that allow for the estimation of cause-specific mortality (Barber-Meyer et al. 2008, Eacker et al. 2016). It is considerably more challenging to assess the effects of predators on vital rates when working at the regional level, considering multiple elk populations, given accurate predator population estimates are difficult to attain and the effects of predation can be complicated by interacting effects with weather and resource limitation. In particular, studies need to be carefully designed when trying to assess how the harvest of predators is related to variation in the vital rates of prey (Boutin 1992). The connection between predator harvest, predator population dynamics and predation risk to ungulates is unclear and has rarely been evaluated (Wolfe et al. 2016). This lack of clarity is worsened where predator harvest regulations are set in response to a combination of social, biological, and political factors (Clark et al. 1996, Bruskotter 2013, Young et al. 2015). Although high harvest with heavy hunting pressure has been implicated in the declines of predator populations (Kolenosky 1986, Allen et al. 2018*a*), harvest numbers have also been positively associated with population sizes of predators (Clark et al. 1996, Bruskotter 2013, Young et al. 2015, Wolfe et al. 2016, Allen et al. 2018). Our results for the association between mountain lion and black bear harvest generally support this latter interpretation, as we found that the magnitude of harvest was negatively associated with per capita recruitment rates. For black bears, predation is thought to occur primarily during the neonate phase in late spring/early summer (Forzley 2019), and high harvest the following fall and spring may serve as a reasonable proxy for the population size of black bears during the birth pulse. On the other hand, we found a weak positive association between minimum wolf counts, ostensibly a more direct index of population size, and recruitment that we interpret as a spatial arrangement of predators on the landscape to take advantage of more productive areas (Fuller and Sievert 2001). That signal was swamped, however, by the interaction between wolf counts and winter severity that suggested high wolf counts interacted with severe winters to reduce recruitment. This result is consistent with prior work in the region (Brodie et al. 2013, but see Garrott et al. 2008), and we speculate that it may reflect an additive effect of predation to nutritional and environmental stress during severe winters. We stress that more work is needed to understand the relationship between minimum wolf counts, wolf abundance and vital rates. More generally, we echo the caution that adequately understanding the connections between predator indices (harvest or counts), predator population dynamics and ungulate vital rates requires carefully designed experiments (Boutin 1992).

Section 9 – Conclusions and Management Recommendations

Understanding the effectiveness of carnivore harvest regulations to manipulate carnivore and ungulate population abundances is a priority for wildlife managers seeking to balance and manage populations to achieve population objectives. We found that liberalized mountain lion harvest regulations to be an effective tool for providing a short-term increase in elk calf recruitment and population growth. In the Bitterroot study area, a two-year mountain lion harvest treatment resulted in an estimated 17.6 and 12.6% mountain lion population harvest rate and 29% reduction in mountain lion population abundance. The harvest treatment corresponded to short-term increases in calf recruitment and elk population growth rates.

Despite the effectiveness of the harvest treatment on decreasing mountain lion abundances and increasing elk calf recruitment, we found no evidence that coinciding liberalized harvest regulations for black bears and wolves influenced elk calf survival or recruitment. Rates of wolf predation on marked calves in the Bitterroot study area remained low throughout all years, despite variation in wolf harvest regulations, realized wolf harvest, and minimum wolf counts. Extended black bear hunting seasons did coincide with increases in the realized harvest of black bears, however, increases to black bear harvest were limited to spring hunting seasons, and we were unable to infer how these increases in harvest related to the underlying black bear populations. Additionally, rates of black bear predation on calves remained relatively low throughout the study, suggesting that liberalized black bear harvest regulations may not have an important effect on calf recruitment in the Bitterroot study area. Although our results fail to show either wolf of black bear predation had a large effect on calf survival, we cannot confidently infer that neither are impacting elk recruitment in the study area. Our estimates of elk calf cause-specific mortality suffered from high rates of unknown-cause mortality, which limits the strength of our inference about the direct effects of wolf and black bear predation on elk calves in the Bitterroot study area (Forzley 2019). If there is a positive association between black bear harvest levels and the underlying black bear population, the increases we saw in black bear harvest may be indicative of a growing black bear population in the area. If so, the negative relationship we found between black bear harvest and elk calf recruitment throughout Region 2 could be the result of increased predation on elk calves by a growing black bear population, leading to decreased elk recruitment in the area. As such, despite having evidence to suggest that the mountain lion harvest treatment was related to increased elk calf survival and recruitment, we cannot infer with confidence whether or not liberalized black bear and wolf harvest regulations were related to any similar changes to elk recruitment.

Despite the uncertainty related to the role of black bears and wolves in elk population dynamics in west-central Montana, we did find that liberalized mountain lion harvest regulations resulted in an increase in elk recruitment. However, the ability to implement carnivore harvest treatments to benefit ungulate populations is challenging given the social dynamics and controversy surrounding carnivore harvest, and public support for carnivore harvest regulations is often unknown or controversial (Decker et al. 2009, Treves 2009, Boertje et al. 2010, Mitchell et al. 2018). Decisions regarding wildlife management and harvest regulations reflect the values of a diversity of stakeholders, as well as scientific information (Riley et al. 2002). In the case of carnivore management to benefit ungulate populations, there are often opposing values between ungulate hunting advocates, carnivore hunting advocates, and anti-carnivore hunting advocates, and these conflicting values challenge wildlife decision makers. In west-central Montana, decision-making regarding setting harvest quotas to achieve moderate mountain lion population reductions was still controversial due to these conflicting values (Mitchell et al. 2018). The mountain lion harvest quotas prescribed to achieve a 30% reduction in mountain lion populations created controversy, with prescribed female harvest quotas being reduced following 2 years of treatment due to these controversies (Mitchell et al. 2018). Montana is a rural state with the majority of residents holding utilitarian-oriented wildlife values (Teel and Manfredo 2010), yet still these harvest management decisions were highly controversial, suggesting the potential to implement such integrated carnivore-ungulate management in other states may be even less palatable. Therefore, while our results demonstrate that carnivore harvest management may be used as a tool for affecting ungulate populations, the social acceptance of such regulations may challenge the implementation of such integrated carnivore-ungulate management programs. To utilize carnivore harvest as a management tool for increasing ungulate populations, it may be more acceptable to consider smaller increases in carnivore harvest rates applied over a longer time period in order to achieve a more sustained and socially acceptable carnivore harvest and slower yet more sustained ungulate population response. However, evaluating the efficacy of these programs would challenge even the most rigorous monitoring programs to detect subtle changes in carnivore or ungulate populations and would fail to advance our understanding of integrated carnivore-ungulate management.

We caution against the generalization that these specific carnivore harvest rates will correspond to these specific changes in ungulate vital rates in other systems, as the complex predator-prey relationships will undoubtedly vary across systems with different carnivore assemblages, prey assemblages, and primary productivity. Additionally, the effects of carnivore harvest treatments on elk population dynamics will be mediated in their effectiveness by weather and other factors outside of management control. However, the analytic tools for monitoring carnivore and ungulate populations presented in Sections 3, and 6─8 are widely applicable, and we recommend intensive pre-treatment and post-treatment monitoring of carnivore and ungulate populations to 1) improve our understanding of carnivore harvest management as a tool for increasing ungulate populations across different ecological systems, 2) provide reference carnivore population information and harvest rate targets for wildlife managers prescribing carnivore harvest to achieve specific ungulate population responses, and 3) quantify the effectiveness (or lack thereof) of integrated carnivore-ungulate management so that decision-makers can use science to inform these controversial harvest management decisions. This type of intensive monitoring would need to be directed at focal areas because the general population monitoring indices routinely applied over the broader region were not as correlated to elk population dynamics.

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Literature Cited

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou Calf Mortality in Denali National Park, Alaska. The Journal of Wildlife Management 59:584–594.

Allen, M. L., A. S. Norton, G. Stauffer, N. M. Roberts, Y. Luo, Q. Li, D. MacFarland, and T. R. Van Deelen. 2018. A Bayesian state-space model using age-at-harvest data for estimating the population of black bears (*Ursus americanus*) in Wisconsin. Scientific Reports 8:1–12.

Andreasen, A. M., K. M. Stewart, W. S. Longland, J. P. Beckmann, and M. L. Forister. 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. Molecular Ecology 21:5689–5701.

Arthur, S. M., and L. R. Prugh. 2010. Predator-mediated indirect effects of snowshoe hares on Dall's sheep in Alaska. The Journal of Wildlife Management 74:1709–1721.

Ballard, W. B., and S. D. Miller. 1990. Effects of reducing brown bear density on moose calf survival in southcentral Alaska. Alces 26:9–13.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife monographs 98:3–54.

Barber-Meyer, S., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1–30.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. The Journal of Wildlife Management 59:228–237.

Bender, L. C. 2006. Uses of herd composition and age ratios in ungulate management. Wildlife Society Bulletin 34:1225–1230.

Bender, L. C., E. Carlson, S. M. Schmitt, and J. B. Haufler. 2002. Production and survival of elk (*Cervus elaphus*) calves in Michigan. American Midland Naturalist 148:163–171.

Beschta, R. L., and W. J. Ripple. 2007. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. Canadian Journal of Forest Research 37:1873–1885.

Bischof, R., E. B. Nilsen, H. Brøseth, P. Männil, J. Ozoliņš, and J. D. C. Linnell. 2012. Implementation uncertainty when using recreational hunting to manage carnivores. Journal of Applied Ecology 49:824–832.

Blanchard, P., M. Festa-Bianchet, J.-M. Gaillard, and J. T. Jorgenson. 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. The Journal of Wildlife Management 67:477–484.

Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. The Journal of Wildlife Management 74:917–928.

Boertje, R. D., P. Valkenburg, and M. E. McNay. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. The Journal of Wildlife Management 60:474–489.

Bonenfant, C., J.-M. Gaillard, F. Klein, and J.-L. Hamann. 2005. Can we use the young: female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. Journal of Applied Ecology 42:361–370.

Bonenfant, C., J.-M. Gaillard, F. Klein, and A. Loison. 2002. Sex-and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. Ecography 25:446–458.

Boulanger, J., S. E. Nielsen, and G. B. Stenhouse. 2018. Using spatial mark-recapture for conservation monitoring of grizzly bear populations in Alberta. Scientific Reports 8:5204.

Boutin, S. 1992. Predation and moose population dynamics: a critique. The Journal of Wildlife Management 56:116–127.

Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, J. Gude, J. Herbert, K. Hersey, M. Hurley, P. Lukacs, S. McCorquodale, E. McIntire, J. Nowak, H. Sawyer, D. Smith, and P. J. White. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology 50:295–305.

Bruskotter, J. T. 2013. The predator pendulum revisited: social conflict over wolves and their management in the western United States. Wildlife Society Bulletin 37:674–679.

Bunnell, S. D., M. L. Wolfe, M. W. Brunson, and D. R. Potter. 2002. Recreational use of elk. Pages 701-748 *in* North American elk. Ecology and Management. Smithsonian Institution Press. Washington, D.C. USA.

Caughley, G. 1974. Interpretation of age ratios. The Journal of Wildlife Management 38:557–562.

Clark, T. W., A. P. Curlee, and R. P. Reading. 1996. Crafting fffective solutions to the large carnivore conservation problem. Conservation Biology 10:940–948.

Coltrane, J., J. Gude, R. Inman, N. Lance, K. Laudon, A. Messer, A. Nelson, T. Parks, M. Ross, T. Smucker, J. Steuber, and J. Vore. 2016. Montana gray wolf conservation and management 2015 Annual Report. Annual Report, Montana Fish, Wildlife and Parks, Helena, MT USA.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. I. M. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. The Journal of Wildlife Management 60:528–541.

Council, N. R. 1997. Wolves, bears, and their prey in Alaska: biological and social challenges in wildlife management. National Academies Press.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society: Series B (Methodological) 34:187–202.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, and others. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068–1083.

Decker, D. J., J. F. Organ, and C. A. Jacobson. 2009. Why should all Americans care about the North American model of wildlife conservation. Pages 32–36 *in*. Transactions of the 74th North American Wildlife and Natural Resources Conference. Volume 74.

Downing, R. L., E. D. Michael, and R. J. Poux Jr. 1977. Accuracy of sex and age ratio counts of white-tailed deer. The Journal of Wildlife Management 41:709–714.

Eacker, D. R., M. Hebblewhite, K. M. Proffitt, B. S. Jimenez, M. S. Mitchell, and H. S. Robinson. 2016. Annual elk calf survival in a multiple carnivore system. The Journal of Wildlife Management 80:1345–1359.

Eacker, D. R., P. M. Lukacs, K. M. Proffitt, and M. Hebblewhite. 2017. Assessing the importance of demographic parameters for population dynamics using Bayesian integrated population modeling. Ecological Applications 27:1280–1293.

Efford, M. G. 2014. Bias from heterogeneous usage of space in spatially explicit capture–recapture analyses. Methods in Ecology and Evolution 5:599–602.

Efford, M. G., and R. M. Fewster. 2013. Estimating population size by spatially explicit capture–recapture. Oikos 122:918–928.

Forzley, M. J. 2019. Spatiotemporal covariates, individual characteristics, and mountain lion harvest as potential sources of variation in elk calf survival. PhD Thesis, Montana State University-Bozeman, College of Letters & Science.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. The American Naturalist 138:478–498.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 *in* L. D. Mech and L. Boitana, editors. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, IL.

Fuller, T. K., and P. R. Sievert. 2001. Carnivore demography and the consequences of changes in prey availability. Conservation Biology Series - Cambridge 163–178.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gaillard, J.-M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294–3306.

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81:33–45.

Garrott, R. A., P. J. White, and J. J. Rotella. 2008*a*. The Madison headwaters elk herd: transitioning from bottom–up regulation to top–down limitation. Pages 489–517 *in*. The Ecology of Large Mammals in Central Yellowstone. Volume 3. Academic Press.

Garrott, R. A., Patrick J. White, F. G. Watson, R. A. Garrott, and P. J. White. 2008*b*. The Ecology of Large Mammals in Central Yellowstone. Elsevier Science & Technology.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:3–59.

Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, and D. H. Jackson. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. Journal of Animal Ecology 80:1246–1257.

Group, P. C. 2011. PRISM climate data. Oregon State University.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the US Northern Rocky Mountains are affected by recruitment and human-caused mortality. The Journal of Wildlife Management 76:108–118.

Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37:816–830.

Hamel, S., M. Garel, M. Festa-Bianchet, J.-M. Gaillard, and S. D. Côté. 2009. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46:582–589.

Hamlin, K. L. 2004. Montana elk management plan. Montana Fish, Wildlife and Parks, Helena, MT, USA.

Hanuska-Brown, L., J. Gude, and N. Lance. 2011. Montana gray wolf conservation and management 2011 Annual Report. Annual Report, Montana Fish, Wildlife and Parks, Helena, MT USA.

Harris, N. C., M. J. Kauffman, and L. S. Mills. 2008. Inferences about ungulate population dynamics derived from age ratios. The Journal of Wildlife Management 72:1143–1151.

Hayes, R. D., R. Farnell, R. M. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildlife Monographs 152:1–35.

Hayes, R. D., and A. S. and Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

Hebblewhite, M., D. H. Pletscher, and P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology 80:789–799.

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

Houston, D. B. 1978. Elk as winter-spring food for carnivores in northern Yellowstone National Park. Journal of Applied Ecology 15:653–661.

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

Jäkäläniemi, A., S. Ramula, and J. Tuomi. 2013. Variability of important vital rates challenges the demographic buffering hypothesis. Evolutionary ecology 27:533–545.

Jimenez, M. D., E. E. Bangs, D. K. Boyd, D. W. Smith, S. A. Becker, D. E. Ausband, S. P. Woodruff, E. H. Bradley, J. Holyan, and K. Laudon. 2017. Wolf dispersal in the Rocky Mountains, Western United States: 1993–2008. The Journal of Wildlife Management 81:581–592.

Johnson, B., D. Jackson, R. C. Cook, D. Clark, P. K. Coe, J. Cook, S. Rearden, S. Findholt, and J. Noyes. 2019. Roles of maternal condition and predation in survival of juvenile Elk in Oregon. Wildlife Monographs 201:3–60.

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

Johnson, H. E., D. D. Gustine, T. S. Golden, L. G. Adams, L. S. Parrett, E. A. Lenart, and P. S. Barboza. 2018. NDVI exhibits mixed success in predicting spatiotemporal variation in caribou summer forage quality and quantity. Ecosphere 9:e02461.

Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91:2742–2755.

Keech, M. A., M. S. Lindberg, R. D. Boertje, P. Valkenburg, B. D. Taras, T. A. Boudreau, and K. B. Beckmen. 2011. Effects of predator treatments, individual traits, and environment on moose survival in Alaska. The Journal of Wildlife Management 75:1361–1380.

Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. The Journal of Wildlife Management 73:3–16.

Kéry, M., and M. Schaub. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.

Kolenosky, G. B. 1986. The effects of hunting on an Ontario black bear population. Bears: Their Biology and Management 6:45–55.

Link, W. A., and J. D. Nichols. 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. Oikos 69:539–544.

Link, W. A., J. A. Royle, and J. S. Hatfield. 2003. Demographic analysis from summaries of an age-structured population. Biometrics 59:778–785.

Loison, A., and R. Langvatn. 1998. Short-and long-term effects of winter and spring weather on growth and survival of red deer in Norway. Oecologia 116:489–500.

Lubow, B. C., and B. L. Smith. 2004. Population dynamics of the Jackson elk herd. The Journal of Wildlife Management 68:810–829.

Lukacs, P. M., M. S. Mitchell, M. Hebblewhite, B. K. Johnson, H. Johnson, M. Kauffman, K. M. Proffitt, P. Zager, J. Brodie, and K. Hersey. 2018. Factors influencing elk recruitment across ecotypes in the Western United States. The Journal of Wildlife Management 82:698–710.

Mace, R. D., and T. Chilton-Radandt. 2011. Black bear harvest research and management in Montana. Federal Aid in Wildlife Restoration, Montana Fish, Wildlife and Parks, Helena, MT USA.

MacKlon, A. E. S., L. A. Mackie-Dawson, C. A. Shand, and A. Sim. 1996. Soil water effects on growth and nutrition in upland pastures. Journal of Range Management 49:251–256.

Melis, C., B. Jędrzejewska, M. Apollonio, K. A. Bartoń, W. Jędrzejewski, J. D. Linnell, I. Kojola, J. Kusak, M. Adamic, and S. Ciuti. 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global ecology and biogeography 18:724–734.

Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society B: Biological Sciences 283:20160456.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488.

Mitchell, M. S., H. Cooley, J. A. Gude, J. Kolbe, J. J. Nowak, K. M. Proffitt, S. N. Sells, and M. Thompson. 2018*a*. Distinguishing values from science in decision making: Setting harvest quotas for mountain lions in Montana. Wildlife Society Bulletin 42:13–21.

Myers, W. L., B. Lyndaker, P. E. Fowler, and W. Moore. 1998. Investigations of calf elk mortalities in southwest Washington. Progress Report, Washington Department of Fish and Wildlife, Olympia, WA, USA.

Nelson, L. J., and J. M. Peek. 1982. Effect of survival and fecundity on rate of increase of elk. The Journal of Wildlife Management 46:535–540.

Nilsen, E. B., and O. Strand. 2018. Integrating data from multiple sources for insights into demographic processes: Simulation studies and proof of concept for hierarchical change-in-ratio models. PloS one 13: e0194566.

Onillon, B., J.-L. Durand, F. Gastal, and R. Tournebize. 1995. Drought effects on growth and carbon partitioning in a tall fescue sward grown at different rates of nitrogen fertilization. European Journal of Agronomy 4:91–99.

Paterson, J. T., K. Proffitt, B. Jimenez, J. Rotella, and R. Garrott. 2019*a*. Simulation-based validation of spatial capture-recapture models: A case study using mountain lions. PloS one 14: e0226492.

Paterson, J. T., K. Proffitt, J. Rotella, and R. Garrott. 2019*b*. An improved understanding of ungulate population dynamics using count data: Insights from western Montana. PloS one 14.

Péron, G., J.-M. Gaillard, C. Barbraud, C. Bonenfant, A. Charmantier, R. Choquet, T. Coulson, V. Grosbois, A. Loison, and G. Marzolin. 2016. Evidence of reduced individual heterogeneity in adult survival of long-lived species. Evolution 70:2909–2914.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jędrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate research 46:15–27.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213–218.

Pletscher, D. H., R. R. Ream, D. K. Boyd, M. W. Fairchild, and K. E. Kunkel. 1997. Population dynamics of a recolonizing wolf population. The Journal of Wildlife Management 459–465.

Proffitt, K. M., J. F. Goldberg, M. Hebblewhite, R. Russell, B. S. Jimenez, H. S. Robinson, K. Pilgrim, and M. K. Schwartz. 2015. Integrating resource selection into spatial capture-recapture models for large carnivores. Ecosphere 6:1-15.

Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. Ecological Applications 26:2156–2174.

Prugh, L. R., and S. M. Arthur. 2015. Optimal predator management for mountain sheep conservation depends on the strength of mesopredator release. Oikos 124:1241–1250.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. The Journal of Wildlife Management 71:795–803.

Rearden, S. N. 2005. Juvenile survival and birth-site selection of Rocky Mountain elk in northeastern Oregon. Thesis, Oregon State University, Corvallis, Oregon, USA

Rich, L. N., R. E. Russell, E. M. Glenn, M. S. Mitchell, J. A. Gude, K. M. Podruzny, C. A. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. The Journal of Wildlife Management 77:1280–1289.

Riley, S. J., D. J. Decker, L. H. Carpenter, J. F. Organ, W. F. Siemer, G. F. Mattfeld, and G. Parsons. 2002. The essence of wildlife management. Wildlife Society Bulletin 30:585–593.

Riley, S. J., and R. A. Malecki. 2001. A landscape analysis of cougar distribution and abundance in Montana, USA. Environmental Management 28:317–323.

Robichaud, C. B., and M. S. Boyce. 2010. Spatial and temporal patterns of wolf harvest on registered traplines in Alberta, Canada. The Journal of Wildlife Management 74:635–643.

Robinson, H., and R. DeSimone. 2011. The Garnet Range mountain lion study: characteristics of a hunted population in west-central Montana. Montana Department of Fish, Wildlife & Parks, Helena, MT 102.

Robinson, H. S., R. DeSimone, C. Hartway, J. A. Gude, M. J. Thompson, M. Mitchell, and M. Hebblewhite. 2014. A test of the compensatory mortality hypothesis in mountain lions: A management experiment in west-central Montana. The Journal of Wildlife Management 78:791–807.

Robinson, H. S., T. Ruth, J. A. Gude, D. Choate, R. DeSimone, M. Hebblewhite, K. Kunkel, M. R. Matchett, M. S. Mitchell, K. Murphy, and J. Williams. 2015. Linking resource selection and mortality modeling for population estimation of mountain lions in Montana. Ecological Modelling 312:11–25.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. The Journal of wildlife management 56:417–426.

Royle, J. A., R. B. Chandler, K. D. Gazenski, and T. A. Graves. 2013. Spatial capture–recapture models for jointly estimating population density and landscape connectivity. Ecology 94:287–294.

Russell, R. E., J. A. Royle, R. Desimone, M. K. Schwartz, V. L. Edwards, K. P. Pilgrim, and K. S. Mckelvey. 2012. Estimating abundance of mountain lions from unstructured spatial sampling. The Journal of Wildlife Management 76:1551–1561.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. The Journal of Wildlife Management 61:12–25.

Singer, F. J., G. Wang, and N. T. Hobbs. 2003. The role of ungulates and large predators on plant communities and ecosystem processes in western national parks. Mammal Community

Dynamics. Management and Conservation in the Coniferous Forests of Western North America 444–486.

Smith, B. L., E. S. Williams, T. L. McFarland, G. Wang, and T. D. Moore. 2006. Neonatal mortality of elk in Wyoming: environmental, population, and predator effects. U.S Department of Interior, U.S. Fish and Wildlife Service, Biological Technical Publication, BTP-R6007-2006, Washington, D.C, USA.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

Tatman, N., S. G. Liley, J. W. Cain, and J. W. Pitman. 2018. Effects of calf predation and nutrition on elk vital rates. The Journal of Wildlife Management 82:1417–1428.

Teel, T., and M. Manfredo. 2010. Understanding the diversity of public interests in wildlife conservation. Conservation Biology 24:128–139.

Thompson, D. J., and J. A. Jenks. 2005. Long-distance dispersal by a subadult male cougar from the Black Hills, South Dakota. The Journal of Wildlife Management 69:818–820.

Tollefson, T. N., L. A. Shipley, W. L. Myers, and N. Dasgupta. 2011. Forage quality’s influence on mule deer fawns. The Journal of Wildlife Management 75:919–928.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46:1350–1356.

Tveraa, T., P. Fauchald, C. Henaug, and N. G. Yoccoz. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. Oecologia 137:370–376.

US Department of the Interior, U. F., Wildlife Service, and U. C. B. US Department of Commerce. 2014. 2011 National survey of fishing, hunting, and wildlife-associated recreation. US Government Printing Office Washington, DC.

Vucetich, J. A., and R. O. Peterson. 2004. The influence of top–down, bottom–up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proceedings of the Royal Society of London. Series B: Biological Sciences 271:183–189.

Wade, D. A., and J. E. Bowns. 2010. Procedures for evaluating predation on livestock and wildlife. AgriLIFE Extension, Texas A & M System.

White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. The Journal of Wildlife Management 74:355–369.

White, P. J., and R. A. Garrott. 2005. Northern Yellowstone elk after wolf restoration. Wildlife Society Bulletin (1973-2006) 33:942–955.

Wolfe, M. L., E. M. Gese, P. Terletzky, D. C. Stoner, and L. M. Aubry. 2016. Evaluation of harvest indices for monitoring cougar survival and abundance. The Journal of Wildlife Management 80:27–36.

Yang, J., J. Zhang, Z. Wang, Q. Zhu, and L. Liu. 2001. Water deficit-induced senescence and its relationship to the remobilization of pre-stored carbon in wheat during grain filling. Agronomy journal 93:196–206.

Young, J. K., Z. Ma, A. Laudati, and J. Berger. 2015. Human–carnivore interactions: Lessons learned from communities in the American west. Human Dimensions of Wildlife 20:349–366.