

SPATIOTEMPORAL COVARIATES, INDIVIDUAL CHARACTERISTICS, AND
MOUNTAIN LION HARVEST AS POTENTIAL SOURCES OF VARIATION IN ELK
CALF SURVIVAL

by

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ABSTRACT

To understand the efficacy of increasing the harvest of large carnivores for increasing elk calf survival, we compared calf survival data collected from two elk herds before, during, and after a mountain lion harvest treatment which consisted of increases in prescribed mountain lion harvest quotas. We collected survival data from 534 radio-tagged elk calves in both the East Fork and West Fork herds of the upper Bitterroot Valley of west-central Montana. We used these data and time-to-event analyses to estimate the annual rates of survival and cause-specific mortality for elk calves in the study, as well as estimate the relationships between elk calf survival and several factors previously related to variation in annual elk calf survival. Average annual rates of survival for female calves before the mountain lion harvest treatment (pre-treatment era) were 0.38 (95% CI = 0.00-0.54) in the West Fork herd, and 0.37 (95% CI = 0.09-0.65) in the East Fork herd. Annual rates of survival for female calves during the harvest treatment (during-treatment era) were 0.65 (95% CI = 0.47-0.83) in the West Fork herd and 0.65 (95% CI = 0.46-0.87) in the East Fork herd. Annual rates of survival for female calves 4-5 years post-harvest treatment (post-treatment era) were 0.46 (95% CI = 0.31-0.61) in the West Fork herd and 0.47 (95% CI = 0.32-0.62) in the East Fork herd. Survival of male calves followed a similar pattern. Rates of mountain lion predation were highest in the pre-treatment era, moderate in the during-treatment era, and lowest in the post-treatment era. However, decreased rates of mountain lion predation following mountain lion harvest treatment coincided with increased probability of non-predation related mortality, and short-term changes in annual elk calf survival. Our results suggest that mountain lion harvest management prescriptions designed to achieve moderate, short-term reductions in mountain lion population abundance may be effective in allowing for short-term increases in elk calf recruitment and may be an effective management tool to increase calf recruitment.

SPATIOTEMPORAL COVARIATES, INDIVIDUAL CHARACTERISTICS, AND
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CALF SURVIVAL

Introduction

Elk (*Cervus canadensis*) are an important game species in North America that provide economic value to communities in the western United States through both consumptive and non-consumptive use (Duffield and Holliman 1988, Bolon 1994, Boyle and Roach 1998, Fried et al. 2006, Donovan and Champ 2009). Elk also have a significant ecological role, as they modify vegetation, compete with other ungulates for forage, and serve as prey for recovering carnivore and scavenger populations (Riggs et al. 2000, Smith et al. 2003, Beck and Peek 2005). Following the re-introduction of grey wolves (*Canis lupus*), and the restoration of mountain lions (*Puma concolor*) and grizzly bears (*Ursus arctos*) into their historic ranges, carnivore populations steadily increased in western North America during the last two decades (Pletscher et al. 1997, Riley and Malecki 2001, Kendall et al. 2009). Increases in carnivore populations have coincided with declines in the abundance and recruitment of elk and other ungulates in some areas, which has presented challenges to wildlife managers seeking to simultaneously achieve management objectives for elk and carnivore populations (Smith et al. 2003, Batastini 2005, Hamlin et al. 2009, Boertje et al. 2010, Hazen 2012).

Numerous studies of elk population dynamics have focused on understanding which environmental factors affect those vital rates that are most likely to impact the

population's growth rate (Nelson and Peek 1982, Raithel et al. 2007, Eacker et al. 2017). Sensitivity analyses of the vital rates of elk and other ungulate populations demonstrate that changes in adult female survival rate have the potential to strongly impact population growth rate (Nelson and Peek 1982, Gaillard et al. 1998). However, previous studies of adult female elk indicate that adult survival rates are demographically buffered against environmental variability such that they tend to be high and constant across a range of conditions (Raithel et al. 2007, Garrott et al. 2008, Brodie et al. 2013). In contrast, estimated annual variation in calf survival rates tends to be high enough to exert important changes in realized population growth rates and to affect elk population dynamics (Raithel et al. 2007, Garrott et al. 2008, Griffin et al. 2011).

Annual variation in calf survival rates may be influenced by individual characteristics of elk calves, as well as variation in the vegetation communities and environmental conditions experienced by calves and their mothers. Previous research provides many examples of individual characteristics of calves influencing the probability of survival. For example, research in Yellowstone National Park and in Oregon demonstrates that a calf's survival rate declined as its birth date deviated further from the median (Singer et al. 1997, Rearden 2005, Barber-Meyer 2008). Other individual characteristics such as sex and birth weight may also be related to calf survival. Survival rates are generally higher for female calves than for males and for calves with higher birth mass than for lighter calves (Albon et al. 1987, Singer et al. 1997, Cook et al. 2004, Griffin 2011, Eacker et al. 2016).

In addition to the individual characteristics of elk calves, variability in primary productivity, forage conditions, and weather conditions experienced by a calf and its mother, during both the pre- and post-natal periods, may influence the survival of elk calves. For example, favorable forage conditions during the pre-natal period, which can lead to increased maternal investment during gestation, are positively related to calf survival and body condition (Singer et al. 1997, Smith et al. 1997, Cook et al. 2004, Lubow and Smith 2004). Likewise, forage conditions in the weeks immediately following parturition can also be important for calf body condition and survival. Specifically, a mother's ability to maintain body condition can be affected by forage, which can in turn affect her level of maternal investment during lactation (Robbins et al. 1981, Smith et al. 1997). As calves wean, variability in forage conditions and calf body condition during the late summer and fall, immediately preceding their first winter, can affect overwinter calf survival (Cook et al. 2004, Lubow and Smith 2004). Indeed, primary production and favorable forage conditions are positively related to neonate survival across multiple ungulate species and ecosystems (Bishop et al. 2000, Melis et al. 2009). Climatic factors, such as seasonality and variation in weather can also influence the survival of elk calves. In some systems, the severity of winter conditions experienced by calves are negatively related to calf nutritional status and survival probability (Singer et al. 1997, Garrott et al. 2008, Eacker et al. 2016). Similarly, previous research has shown a negative relationship between calf survival rate and the severity of the winter immediately preceding parturition, possibly because mothers have poorer pre-natal body condition after harsher winters (Singer et al. 1997, Lubow and Smith 2004).

In addition to variation in maternal investment during the pre- and post-natal periods and environmental conditions experienced by elk calves, calves also face multiple mortality sources that include predation by a diversity of carnivores (Miller et al. 1998, Cook et al. 2004, Rearden 2005, Barber-Meyer et al. 2008, White et al. 2010). The primary predator of elk calves varies depending on the composition of the carnivore community in the study system and elk-calf development stage. For example, in the northern range of Yellowstone National Park grizzly bears are the primary predator of calves during the spring and early summer despite the presence of grey wolves, black bears and mountain lions (Singer et al. 1997, Barber-Meyer 2008). In other systems without recovered grizzly bear populations, the primary predators of calves have been reported to be black bears (Smith and Anderson 1996, Harris 2006, White et al. 2010, Tatman et al. 2018), mountain lions (Rearden 2005, Eacker et al. 2016), or coyotes (Bender et al. 2002). The primary species of predator might depend on the presence or absence of other large carnivore species, as well as the abundance and diversity of other prey species (Griffin et al. 2011), which suggests that large carnivores compete to consume elk calves and other resources. Indeed, recent work in the Greater Yellowstone Ecosystem suggests that mountain lions and wolves compete for the ability to consume local elk herds (Elbroch et al. 2018). This system of competition suggests functional redundancy in elk calf predators such that if one species of primary predator is absent, another large carnivore will emerge as the primary predator of calves (Errington 1967, Ellis-Felege 2012). If predation is largely compensatory, the removal of all carnivores from a system would result in high rates of elk calf mortality from environmental factors

such as winter severity related to starvation or malnutrition (Garrott et al. 2008).

However, in systems where predation on elk calves is mostly, or even partially additive, the removal of large carnivores can result in higher calf survival rates.

In systems where calf mortality is driven by predation, the primary predator of calves can also vary depending on the time of year (Smith and Anderson 1996, Barber-Meyer 2008, Eacker et al. 2016). Coyotes and bears kill elk calves almost exclusively during the neonatal period, likely because of their limited ability to capture calves once they are larger and more mobile (Matson 1996, Seward 2003, Raithel 2005, Barber-Meyer 2008, Eacker et al. 2016, Tatman et al. 2018). Indeed, even in areas with high densities of grizzly or black bears, most bear predation on elk calves occurs in the 2 months after calves are born (Smith and Anderson 1996; Griffin et al. 2011; Eacker et al. 2016). Conversely, mountain lions and wolves kill calves throughout the year due to their ability to capture larger and more mobile calves (Griffin et al. 2011, Eacker et al. 2016). The complexity of predation on elk calves in multi-predator systems when combined with spatio-temporal variation in environmental conditions and variation in key attributes of individual calves cause the rates of elk calf survival to be highly variable among years and locations. Variability in both summer and winter calf survival is high enough to exert important changes in realized population growth rates and to affect elk population dynamics. However, disentangling the relative influence of the diverse factors related to this variability in elk calf survival can be difficult (Raithel et al. 2007, Eacker et al. 2017).

Due to the high spatiotemporal variability of elk calf survival, as well as the complex interactions between the several large carnivore species that can be primary predators of elk calves, the efficacy of management actions designed to increase elk calf survival by removing or reducing populations of their primary predator is uncertain (Ballard and Miller 1990, Gasaway et al. 1992, Boertje et al. 2010). Due to functional redundancy, carnivore management programs may be less effective in areas that support multiple species of large carnivores, and the removal of the primary elk calf predator could result in higher rates of mortality due from other predators (Errington 1967, Griffin et al. 2011). Likewise, predation might not be the primary factor influencing calf survival. If so, carnivore management programs might not be an effective means of altering calf survival.

In response to declining ungulate populations in west-central Montana, Montana Fish, Wildlife, and Parks (MFWP) initiated a study of survival and cause-specific mortality of elk calves in two herds in the upper Bitterroot Valley during 2011-2014. Annual rates of calf survival in the two herds averaged 0.41 (range = 0.32 to 0.45) across the three years of study, and mountain lions were identified as the primary predator of elk calves (Eacker et al. 2016). Midway through the study, MFWP implemented a mountain lion harvest treatment designed to moderately reduce mountain lion populations across the Bitterroot watershed. The increased harvest quotas for mountain lions in the Bitterroot watershed were designed to be of relatively short duration and achieve a moderate 30% reduction in mountain lion population abundance. At the same time, the

spring black bear harvest season was extended two-weeks and wolf harvest was liberalized.

Our goal was to evaluate if elk calf survival rates or mountain-lion predation rates differed before, during or after the mountain lion harvest treatment was implemented. We monitored elk calf survival and cause specific mortality before, during, and 4-years after the mountain lion harvest treatment was implemented for two elk herds within the treatment area. The realized harvest of female and male mountain lions in the Upper Bitterroot increased following the implementation of liberalized harvest opportunity (Table 1). There are multiple alternate possibilities regarding the response of elk calf survival in the upper Bitterroot to increased mountain lion harvest. Given that mountain lion predation was an important source of mortality during the pre-treatment era, the mountain lion harvest treatment could coincide with decreased mountain lion predation on elk calves in the upper Bitterroot, and lead to overall higher rates of annual survival (Eacker et al. 2016). However, it is also possible that, if the mountain lion harvest treatment did successfully reduce rates of mountain lion predation on elk calves in the upper Bitterroot Valley, we would see compensatory increases in the rates of mortality from other sources and no change in overall survival.

Study Area

The southern Bitterroot Valley study area, located in west-central Montana is 3,350 km² (Proffitt et al. 2016) and includes the East Fork (hunting district [HD] 270) and the West Fork (HD 250) drainages of the Bitterroot River. The East Fork drainage

encompasses the annual range of the East Fork elk herd that has a migratory component, which summers in the Big Hole Valley (HD 334). The West Fork drainage encompasses the annual range of the West Fork elk herd.

The East Fork encompasses 1,719 km², ranges in elevation from 1,100 to 2,800 m, has areas that have high densities of roads, and 18% of the area is private lands. The East Fork drainage contains modest terrain characterized by heavy agricultural use and open grasslands that give-way to heavily timbered slopes, sub-alpine terrain, and finally alpine terrain (Proffitt et al. 2016). The West Fork drainage encompasses 1,437 km², has elevations that range from 1,200 to 3000 m, is dominated by public land (95%), and has high road densities at lower elevations but few roads at higher elevations. The West Fork contains rugged terrain, and consists mostly of forested areas, and some riparian areas and grasslands at lower elevations. Dominant species at lower elevations of both areas are Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), elk sedge (*Carex geyeri*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii*) (Proffitt et al. 2016). Higher elevations are mostly characterized by subalpine mesic spruce-fir forests, and dominated by lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*), and subalpine fir (*Abies lasiocarpa*). The area in the Big Hole Valley occupied by migratory elk in the East Fork herd differs in terrain and vegetation from the East Fork and West Fork drainages, and is mostly above >2,000 m of elevation (Murray et al. 2018). The Big Hole Valley is considered a high elevation sagebrush basin with meandering riparian areas. Agriculture is dominant in the Big Hole Valley, and the area is highly productive (Liknes 1981). In addition to elk, other ungulates native to the study

area include mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*). The study area's suite of carnivores includes mountain lions, grey wolves, and black bears.

Methods

To understand changes in the annual rates of elk calf survival and cause-specific mortality in the Bitterroot study area before, during, and 4-years after the mountain lion harvest treatment, we compiled and compared data on calf survival and cause of death collected from three periods. We considered calves radio-tagged in 2011-2012 and monitored in 2011-2013 as having occurred in the pre-treatment era, as these data were collected entirely before or just a few months after the increased harvest of mountain lions. We considered calves radio-tagged in 2013 and monitored from 2013-2014 as having occurred in the during-treatment period, as these data overlapped entirely with the increased mountain lion harvest treatment. We radio-tagged calves in 2016 and 2017 and monitored these calves during 2016-2018 to estimate post-treatment calf survival and cause of death. 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 several years after increased mountain lion harvest. 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. Ground crews attempted to locate neonates by watching for behavioral indications from adult females and/or by searching areas on foot. Helicopter crews attempted to spot neonates from the air. From 2011-2012, each captured calf was outfitted with an ATS (model 3430, Advanced Telemetry Systems Inc., Isanti, MN) VHF ear-tag radio-transmitter weighing 23 g. After significant amounts of tag-loss in 2011-2012, calves in all other years of the study were outfitted with TW-5 VHF ear-tag radio transmitters (Biotrack, Wareham, Dorset, United Kingdom) that weighed only 1.8 g. Both brands of ear-tags were designed to sense periods of inactivity >4 hours and increase the signal pulse rate (mortality mode) if such a period occurred. For each calf, we recorded calf sex, measured body mass, right hind-leg length, chest girth, the lengths of the outside edge of both the left and right incisors of each calf, and recorded the dampness of the calf, calf mobility, hoof condition, and development of dew claws. We combined these characteristics with the aging techniques used by Eacker et al. (2016) to obtain an estimate of calf age at capture as well as estimates of 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 during which calves were either chemically immobilized or net-gunned from a helicopter depending on the terrain.

Calf Monitoring

Using a combination of ground and aerial telemetry, we monitored the telemetry signals of calves to determine survival status from the day after capture to 30 May of the following year. We monitored each surviving calf every day from its date of capture to 31 August and 3 to 4 times per week thereafter. We used aerial telemetry from fixed-wing aircraft to obtain weekly locations of each calf from date of capture through 31 August. We did not locate calves from 31 August to the end of November to avoid disturbing elk and hunters during hunting seasons. After hunting seasons ended near the end of November, we located calves monthly until 30 May. We used calf locations in conjunction with mountain lion and wolf resource selection functions (RSF) to construct covariates potentially related to spatial variation in mortality risk (see below).

Investigation of Calf Mortality

When we detected a radio signal that was in mortality mode, we used telemetry to locate the radio-tag and then performed a mortality investigation and necropsy on the calf. 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, Washington Department of Fish and Wildlife 2013, Government of Alberta 2018). For the two years of post-treatment data collection, we swabbed areas that were likely to contain predator saliva, such as sites of subcutaneous hemorrhaging, for DNA analysis to determine predator species identity. Likewise, for all years of data collection, we submitted carnivore scat and hair collected during mortality

investigations for DNA analysis to determine predator species identity. We delivered all saliva, hair, and scat samples to the USFS Rocky Mountain Research Station (Missoula, MT) for analysis. Using inferences from our field necropsies 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. Data for each calf that left the study area or whose ear-tags became detached (e.g., while crossing under a fence) were right censored one day after the calf was last known to be alive.

Cumulative Incidence Functions

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). To estimate CIFs for each potential cause of elk calf mortality, we used the R software platform (R Core Team 2018) and the *WILDI* package (Sargeant 2011). CIF estimates represented the cumulative probability of mortality from each potential cause over the first year (365 days) of a calf's lifetime. CIFs were advantageous as they accounted for uneven sample sizes throughout the sampling period due to staggered entry and estimated risk from more than one potential source of mortality (Heisey and Patterson 2006).

Summer and Winter Calf Survival Estimation

We used Cox-Proportional Hazards models (Lee 1992) 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 (2011-14 and 2016-18). To evaluate competing models of calf survival, we used the R software platform (R Core Team 2018) and the *survival* package (Therneau 2018). The results of the modeling provided hazard ratios (HR) for each covariate: ratios greater than one indicated that the daily risk of mortality increased as the covariate value increased. We modeled data for summer and winter separately because we expected seasonal differences in risk factors. As in Eacker et al. (2016), we used each calf's birthdate as the origin and estimated mortality risk from age 0 to 180 days for summer models, and we used 26 November as the origin and estimated mortality risk for the subsequent 185 days for winter models.

We evaluated a suite of internal and external risk factors potentially affecting calf survival (Appendix A). Internal risk factors included the biological characteristics of calves as well as each calf's herd and treatment era values. External risk factors were descriptors of environmental conditions that could possibly explain annual variation in calf survival. For summer models, internal risk factors included sex, birth mass, birthdate, herd identifier (East Fork or West Fork), and a Big Hole Valley identifier (a two-level factor describing whether or not a calf was tagged in the Big Hole Valley). For models of winter survival, we used calf sex and elk herd (East Fork and West Fork) as internal descriptors of calf survival.

Based on previous assessments of elk calf survival, we predicted that birth mass would be positively related to summer calf survival, later-borne calves would be more susceptible to predation, and that female calves would have higher rates of survival than male calves (Cook et al. 2004, Barber-Meyer 2006, White et al. 2010, Griffin et al. 2011).

We predicted that calves tagged in the migratory Big Hole population would survive at higher rates than calves tagged in the East Fork and West Fork herds based on the results of previous analyses of calf survival in the area (Eacker et al. 2016). Further, we predicted that calves that spent the neonatal period (their most vulnerable stage of development) in the Big Hole Valley would have higher survival rates because they were exposed to higher estimates of primary production, and lower predicted probability of large carnivore activity than calves tagged in the East Fork and West Fork.

For our summer and winter analyses, we included the following external risk factors: predicted mountain lion and wolf activity RSF values in the estimated home range of each calf, winter severity, and three NDVI (normalized difference vegetation index) metrics. We predicted that the mountain lion RSF covariate would be closely related to elk calf survival, with calves occupying seasonal ranges with higher mountain lion RSF values having higher probability of dying. Likewise, previous research has found late-summer NDVI to be important to body condition of calves and their mothers (Cook et al. 2004), and we predicted that late-summer NDVI would be positively related to both summer and winter survival. Previous analyses of calf survival in the upper Bitterroot indicated that winter precipitation was negatively associated with both summer and winter calf survival (Eacker et al. 2016). Thus, we predicted that winter severity would be negatively related to calf survival.

Lastly, we included a three-level factor variable that indicated whether a calf was studied in the pre-, during, or post-treatment era. Depending on how mountain lion predation and overall elk calf survival changed during each of the three treatment eras, it

is possible that the mountain lion harvest treatment resulted in decreased predation of elk calves by mountain lions, and overall increases in estimates of summer, winter, and annual elk calf survival in the during- and post-treatment eras. Alternatively, any potential decreases in mountain lion predation may coincide with compensatory increases in mortality from other causes, and no difference in survival between the three treatment eras.

Model Selection

We evaluated competing models of survival in each season using four model-selection steps and then evaluated several possible interactions of interest. First, because of possible correlations between competing NDVI metrics, we compared support from the data for each NDVI covariate and retained the best-supported version for the next model-selection step. In the second step, we compared all possible combinations of our full suite of external risk covariates and the NDVI covariate retained from step one, without including any internal risk covariates. We retained all external risk covariates included in models within 4 AIC_c (corrected Akaike information criterion) units of the best-supported model and removed models that contained uninformative external risk parameters from further consideration (Burnham and Anderson 2002, Arnold 2010). In our third model-selection step, we separately compared all possible combinations of our internal risk covariates, without including any external risk covariates, and retained all internal risk covariates included in models within 4 AIC_c of the best-supported model and again removed uninformative parameters. In our final model-selection step, we compared

all-possible combinations of the internal and external risk covariates retained from steps two and three.

We also evaluated models that included interactions between treatment era and each of the external covariates in our final model-selection step to evaluate whether or not possible associations between covariates and calf survival might have changed between treatment eras. Additionally, we evaluated a model that included an interaction between the treatment-era covariate and the herd identifier (East Fork vs. West Fork) to evaluate the possibility that treatment-era differences in survival rates might have differed by herd. Once we identified a best-approximating model for summer and winter data, we used it along with relevant covariate values to predict calf survival rates for each season for covariate conditions realized during each era, e.g., pre-, during-, and post-treatment eras. To test the assumption that the relative hazard functions for different groups are constant over time, i.e., hazard functions are proportional over time, we examined the scaled Schoenfeld residuals for each covariate over time and checked whether any followed a non-random pattern through time using the *survival* package (Therneau 2018) in R (R Core Team 2018).

Annual Calf Survival Estimation

We used the best-approximating model for each season to estimate summer and winter survival rates and multiplied the two seasonal rates together and obtained measures of uncertainty for each of the annual estimates using the delta method (Seber 1982). To account for possible temporal variation in covariates (NDVI covariates and winter severity) between treatment eras, we estimated annual survival rates for each herd

in each treatment era using herd- and treatment-era specific means for each of the relevant temporal covariates. To account for possible variation in covariates that varied spatially, we estimated annual survival rates for each herd and treatment-era combination for high (95th percentile), average, and low (2.5th percentile) values of each RSF covariate found to be important in our best-supported model. By accounting for variation in the most relevant spatial and temporal covariates, at values specific to each elk herd and treatment era, we were able to estimate annual rates of survival for conditions experienced on average by calves in each herd and treatment-era combination .

Results

Calf Captures, Monitoring, and Mortality Investigations

During the two pre-treatment years, we radio-tagged 142 calves in the spring (2011-2012 = 66, 2012-2013 = 76) and 60 calves at the start of winter (2011-2012 = 31, 2012-2013 = 29, $n_{pre-treatment} = 202$). In the one during-treatment year, we radio-tagged 84 calves in the spring and added no calves at the start of winter ($n_{during-treatment} = 84$). 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, $n_{post-treatment} = 248$). The total sample size for all three treatment eras was 534 radio-tagged elk calves. We radio-tagged more calves in the East Fork than the West Fork during all treatment eras and maintained a small sample of calves tagged in the Big Hole Valley throughout the study ($n = 16, 13, \text{ and } 31$ in the pre-, during, and post-treatment eras, respectively).

The era-specific samples were relatively balanced by sex ($n = 97$ females, 104 males; 36 females and 48 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 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 estimated 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 ($n = 2$). Due to high rates of tag loss, and because 23 calves left the study area, fates were unknown for 169 radio-tagged calves. 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 2). Of 524 elk calves, 158 calves were known to have survived to 1-year of age. Estimated CIFs indicated that mountain lion predation decreased during the during- and post-treatment eras in the East Fork during all three treatment eras (Fig. 1) and cumulative mortality rates for non-

predation and mountain lions were similar in the post-treatment era. In the West Fork, estimated CIFs indicated that mountain lion predation was the largest known cause of mortality in both the pre- and during-treatment eras, whereas non-predation was the greatest in the post-treatment era (Fig. 2). The cumulative probability of non-predation mortality increased in the post-treatment era in both herds. Annual probabilities of black bear and wolf predation were low in all three treatment eras for both herds. CIFs related to the annual probability of unknown cause mortality were high for both herds during all three treatment eras (Figure 1; Figure 2).

The rate of mortality for elk calves was highest during the first 90 days of the summer season and remained relatively constant across fall and winter. 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 CIF curves for 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, CIF curves related to unknown cause and unknown predator mortality were steep during the early summer months (i.e., similar to patterns 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 best-supported survival model for summer contained five covariates: calf sex, the Big Hole indicator, treatment era, the mountain lion RSF covariate, and the

interaction between treatment era and the mountain lion RSF covariate (Appendix B).

This model met the assumptions associated with proportional hazards modeling, and the relative hazards for different strata were constant and proportional over time. Our best-supported summer model indicated that male calves had a higher daily risk of dying than did females (HR = 1.63, 95% CI = 1.17-2.32). The model also indicated that the daily risk of mortality in the pre- and post-treatment eras was higher for elk calves that tended to occupy locations with higher mountain lion RSF values (HR = 16.77, 95% CI = 1.23-226.97, Fig. 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 (0.327, 95% CI = 0.29-0.35) were all relatively high and similar 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 (Fig. 3).

The daily risk of mortality for calves tagged in the Big Hole was approximately half that of calves tagged in the East Fork or West Fork (HR = 0.47, 95 % CI = 0.19–1.12). When estimated at herd-specific average values for the risk factors in our best-supported summer model, summer survival rates in the East Fork herd were estimated as 0.57 (0.45-0.72), 0.67 (0.45-0.72), and 0.66 (0.56-0.78) for females and 0.40 (0.28-0.57),

0.52 (0.38-0.69), and 0.51 (0.39-0.66) for males, during the pre-, during, and post-treatment eras respectively. Summer survival rates in the West Fork herd were estimated as 0.50 (0.39-0.65), 0.70 (0.59-0.85), and 0.60 (0.50-0.72) for females and 0.32 (0.22-0.48), 0.56 (0.42-0.74) and 0.43 (0.32-0.58) for males, in the pre-, during-, and post-treatment eras respectively. Summer survival rates in the Big Hole sub-unit of the East Fork herd were estimated as 0.73 (0.54-0.98), 0.85 (0.72-1.00), and 0.79 (0.63-0.98) for females and 0.59 (0.36-0.97), 0.76 (0.58-1.00) and 0.68 (0.47-0.97) for males, in the pre-, during-, and post-treatment eras respectively.

Winter Calf Survival

Our best-supported model for winter survival contained four covariates: mountain lion RSF, previous late-summer NDVI, treatment era, and the interaction between treatment era and mountain lion RSF (Appendix B). In all three treatment eras, calves that tended to occupy sites with higher mountain lion RSF values had a higher daily mortality risk in winter (HR = 3.39, 95% CI = 2.31-181.78, Fig. 6). Indeed, 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 (Fig. 4). Late-summer NDVI was positively related to the daily risk of winter mortality for calves (HR = 2.67, 1.26 – 5.67). When estimated at herd-specific averages of the risk factors included in our best-supported winter model, average winter survival rates were 0.72 (0.62-0.84), 0.95 (0.87-1.00), and 0.77 (0.70-0.85) for East Fork calves and 0.74 (0.64-0.87), 0.93 (0.85-1.00), and 0.78 (0.71-0.85) for West Fork calves in the pre-, during, and post-treatment eras, respectively.

Annual Calf Survival

Based on our best-supported summer and winter models, variation in annual survival was related to treatment era, calf sex, spatial variation in the mountain lion RSF covariate, and temporal variation in the post-natal late-summer NDVI conditions between the three treatment eras. Annual survival was consistently higher for females than males and similar between herds, and across values of mountain lion RSF that were specific to each herd (Table 3). At mean values of the mountain lion RSF covariate, point estimates of annual survival rates based on treatment-era averages for late-summer NDVI were lowest in the pre-treatment era, highest in the during-treatment era, and intermediate in the post-treatment era (Table 3).

Discussion

Our analysis of annual elk calf survival represents a unique opportunity to understand the factors related to annual elk calf survival, as well as the efficacy of mountain lion harvest management regulations aimed at increasing elk calf survival. Our

data collected from over 500 radio-tagged elk calves and five years represents an unprecedented sample of annual calf survival and cause-specific mortality data, and few studies have evaluated the annual survival of elk calves across both summer and winter (Griffin et al. 2011). Moreover, few studies have evaluated annual elk calf survival pre-, during-, and post- increased carnivore harvest. Our sampling design provides a unique opportunity to evaluate the effects of mountain lion harvest management on calf mortality sources and annual survival rates, and provide insights regarding relationships between carnivore harvest and calf survival. Our data suggest that the mountain lion harvest treatment in the study area was related to increased summer, winter, and annual elk calf survival during the mountain lion harvest treatment, and intermediate elk calf survival 4 years after the mountain lion harvest treatment. Although overlapping confidence intervals between the survival rates associated with the calves in each of the three treatment eras slightly restricts our inference, the treatment era covariate was well supported throughout model selection, and our best supported summer and winter calf survival models both included the effects of treatment era. Estimates of annual elk calf survival in the during-treatment era suggested that estimated calf survival rates may have doubled following 1-2 years of increased mountain lion harvest. The initial increase in elk calf survival during the mountain lion harvest treatment may have been related to a coinciding decline in the probability of mountain lion predation for calves in both the East Fork and West Fork herds. However, the initial increases in annual survival in the during-treatment era were intermediate several years later, and 4-years post-treatment declined to levels only about 10 percent higher than in the pre-treatment era. These

intermediate rates of annual calf survival in the post-treatment era were possibly due to compensatory increases in the probability of non-predation mortality for elk calves in both herds, which partially offset decreased rates of mountain lion predation in the post-treatment era.

Previous research has identified several different causes of summer non-predation mortality of elk calves such as, disease, drowning, malnutrition, and abandonment (Raithel 2005, Barber-Meyer et al. 2008, Tatman et al. 2018). In our sample of calves that died to non-predation mortality, two calves died from drowning, but we found no evidence during field necropsies to suggest that the other non-predation mortalities were related to starvation, disease, or abandonment. Regardless, decreased rates of mountain lion predation in the post-treatment era were partially offset by increases in the probability of non-predation mortality, which could suggest that mountain lion predation in the area is partially compensatory. Despite this, a 10 percent increase in the annual survival rate of elk calves in the post-treatment era would likely have net positive effects on elk calf recruitment and population growth rates (Raithel et al. 2007). However, it is important to note that in each era, there were enough mortalities that could not be assigned to a specific cause because of our conservative mortality cause classification criteria that our ability to disentangle the relative influence of each carnivore species on elk calf survival in the upper Bitterroot Valley is restricted.

In addition to increased rates of non-predation mortality in the post-treatment era, intermediate rates of survival in the post-treatment era may have been related to recovery in area mountain lion populations following the short-term mountain lion harvest

treatment. Juvenile mountain lions have been shown to disperse long distances before establishing a home range (Beier 1995, Thompson and Jenks 2005). Perhaps areas vacated during the mountain lion harvest treatment by hunter harvest in the study area were recolonized by dispersing juveniles from adjacent populations in the post-treatment era. Further, previous research indicates that mountain lion populations exhibit source-sink dynamics, such that regular movement between adjacent populations could result in rapid recovery of populations following harvest (Andreasen et al. 2012). Given that areas adjacent to the upper Bitterroot were not included in the mountain lion harvest treatment, and the propensity for immigration between adjacent mountain lion populations, it is possible that intermediate rates of annual calf survival in the post-treatment era were a result of mountain lion populations being at or near levels comparable to the pre-treatment era.

Although our data suggest that elk calf survival increased during the mountain lion harvest treatment, the level of uncertainty in our estimates of the probability of mountain lion predation and the relatively high rates of unknown cause mortality in each treatment era prevent us from confidently relating the mountain lion harvest treatment to increases in elk calf survival. The mountain lion harvest treatment also coincided with increases in the allowable harvest of black bears and wolves in the upper Bitterroot Valley, and our results are not certain enough to disentangle the relative influence of each on elk calf survival. There was considerable overlap in the confidence intervals associated with the rates of mountain lion predation before, during, and after the mountain lion harvest treatment. Further, although we saw consistently low rates of black

bear and wolf predation throughout the study, rates of unknown cause mortality were high enough to restrict our ability to precisely understand the relative influence of each carnivore on changes to elk calf survival.

We found that the most important factors affecting elk calf survival were treatment era, spatial variation in the mountain lion RSF covariate and sex in the summer, and treatment era, the mountain lion RSF covariate, sex, and late-summer NDVI in the winter. For all but one of the summer, winter, and treatment era combinations, 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 calves having higher values of the mountain lion predation risk covariate were more likely to die, but not necessarily due to mountain lion predation. 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 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 hypothesize that the positive relationship between summer elk calf survival and the mountain lion RSF covariate in the during-treatment era was possibly related to either: 1) smaller sample sizes during that treatment era (>50% fewer calves than the other two treatment eras) or, 2) behavioral

differences in female elk and calves during that treatment era related to lower rates of mountain lion predation and higher overall rates of summer survival. Perhaps due to the initial success of the increased mountain lion harvest at reducing mountain lion predation and increasing summer calf survival, adult females and calves during that treatment era occupied favorable habitat that they otherwise would have avoided due to potential mountain lion predation.

Individual characteristics of elk calves have been related to calf survival in several studies. For calves in our sample, summer survival varied by calf sex, and female calves survived at a higher rate than male calves during both treatment eras, supporting our predictions about calf sex. Neonate males in many ungulate species have been shown to survive at lower rates than females, and previous studies of elk calf survival have documented similar results (Fisher 1930, Franzmann & Schwartz 1986, Mahoney et al. 1990, Linnell et al. 1995, Aanes and Andersen 1996, Smith and Anderson 1996). These differences in survival between male and female neonate ungulates are possibly related to male neonates exhibiting riskier behavior than females (Aanes and Andersen 1996). Indeed, previous research found that male white-tailed deer fawns were more active than female fawns, which was possibly associated with higher rates of mortality and predation (Jackson et al. 1972, Schwede et al. 1992). We did not find evidence to suggest that winter survival varied by calf sex, and the effects of sex were limited to summer survival.

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. Cook et

al. (2004) showed that higher calf body mass and more favorable calf body condition was related to increased winter calf survival. Likewise, we speculated that increases in late-summer NDVI during the neonatal summer would lead to higher winter calf body mass and higher survival during the following winter. Our data did not support this prediction, and in fact, we found the opposite relationship between winter calf survival and late-summer NDVI. In our five 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. Regardless, we did not find any evidence to support the predicted positive relationship between primary productivity in the late summer and elk calf survival (Melis et al. 2009).

Limitations of our study are related to the relatively short time-period during which we hoped to capture variation in annual elk calf survival related to variation in related abiotic and biotic conditions, as well as high rates of unknown cause and unknown predator mortality. Research such as ours, which directly estimated the survival of marked elk calves over a relatively short 5-year time-period, may not be the most effective way to gain an understanding of the environmental factors related to elk calf survival. Our sample of calf survival data is unprecedented, and represents survival data from >500 calves over a five-year period. We monitored calves year-round, recorded

thousands of calf locations, and coupled our survival data with advanced spatial and temporal covariates. However, even with all of this information, we were unable to detect meaningful relationships between calf survival and bottom-up covariates shown to be relevant in other systems. Perhaps these relationships do not exist, but what is more likely is that our data do not cover an adequate time-period. As an alternative, it may be helpful for researchers to focus on relating annual indices of recruitment that are routinely collected by management agencies, such as cow-to-calf ratios, to variation in spatiotemporal covariates over longer time-periods. By doing so, they may capture more annual variation in calf recruitment resulting from variation in the spatiotemporal factors related to calf survival. Further, our study experienced high rates of unknown cause mortality, and the probability of calves dying from unknown causes was high in both herds, throughout all three treatment eras. In many cases, unknown cause mortality was the highest source of mortality for a given herd and treatment era combination, and the CIF curves indicated that the unknown cause mortality may have been a combination of mortality from several sources. This restricts strong inference about how the probability of mortality from various causes varied before, during, and after the mountain lion harvest treatment.

Despite the uncertainty related to our analyses of potential survival covariates and cause-specific mortality, our proportional hazards analysis indicated that summer, winter, and annual elk survival increased immediately following the mountain lion harvest treatment in the upper Bitterroot. However, several years after the mountain lion harvest treatment, annual calf survival fell to intermediate levels. Our mountain lion RSF

covariate, calf sex, and late-summer NDVI were all related to variation in calf survival, and the effects of each remained mostly the same throughout both treatment eras. There is evidence to suggest that the mountain lion harvest treatment resulted in decreased mountain lion predation, coinciding with increased non-predation mortality and short-term overall changes in annual survival. However, high rates of mortality due to unknown causes, as well as high uncertainty related to our estimates of cause-specific mortality, make it difficult to disentangle the relative influence of the mountain lion harvest treatment from increases to the allowable harvest of black bears and wolves.

Management Implications

In our west-central Montana study area, the prescribed harvest regulations of the primary elk calf predator, mountain lions, did coincide with short-term increases in elk calf survival. However, 4-5 years later calf survival rates were intermediate. Thus, the prescribed harvest were successful in providing a short-term increase in calf survival but may not result in long-term increases in calf survival. The modest long-term effects of increasing the harvest of mountain lions on elk calf survival were possibly a result of mountain lion predation being partially compensatory, such that sustained periods of decreased mountain lion predation resulted in increases in the probability of mortality from other causes. This highlights the idea that strategies aimed to influence the top-down effects on elk calf survival may not account for other factors outside the control of wildlife managers, and may not be sustainable for long-term goals. Despite this, the mountain lion harvest treatment was designed to provide short-term relief for area elk

populations, and our work suggests that similar mountain lion harvest treatments may be a favorable option for wildlife managers when considering strategies to provide short-term relief for ungulate recruitment.

Table 1. The male and female mountain lion harvest prescribed quotas and achieved harvest for the Upper Bitterroot study area in west-central Montana during 2012–2017, including the number of female licenses per 1000 square kilometers. The Bitterroot study area included lion management units 250 and 270 and was managed for mountain lion population reduction (treatment), with the goal of increasing elk calf recruitment and survival.

Year	Male quota	Female quota	Male harvest	Female harvest	Female licenses per 1000 km ²
2009	- ¹	2	7	1	0.60
2010	-	4	11	3	1.20
2011	-	6	10	6	1.80
2012	14	14	12	15	4.20
2013	8	12	10	11	3.60
2014	10	7	8	6	2.10
2015	11	8	11	4	2.40
2016	11	8	8	8	2.40
2017	11	8	11	7	2.40

¹ During 2009-2011, there was no male subquota, only a female subquota and total harvest quota.

Table 2. Number of calves that died from black bear predation, mountain lion predation, wolf predation, non-predation, unknown predator, and unknown cause, by elk herd and treatment era, in the upper Bitterroot Valley, Montana, USA, during pre-treatment, during-treatment, and post-treatment eras.

Herd	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

Figure 1. Cumulative Incidence Functions (CIF) showing the cumulative probability of calf mortality (y-axis) from 0 to 365 days after parturition in the East Fork herd from mountain lions, black bears, wolves, non-predation, unknown causes, and unknown predators in the upper Bitterroot Valley, Montana, USA, 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.

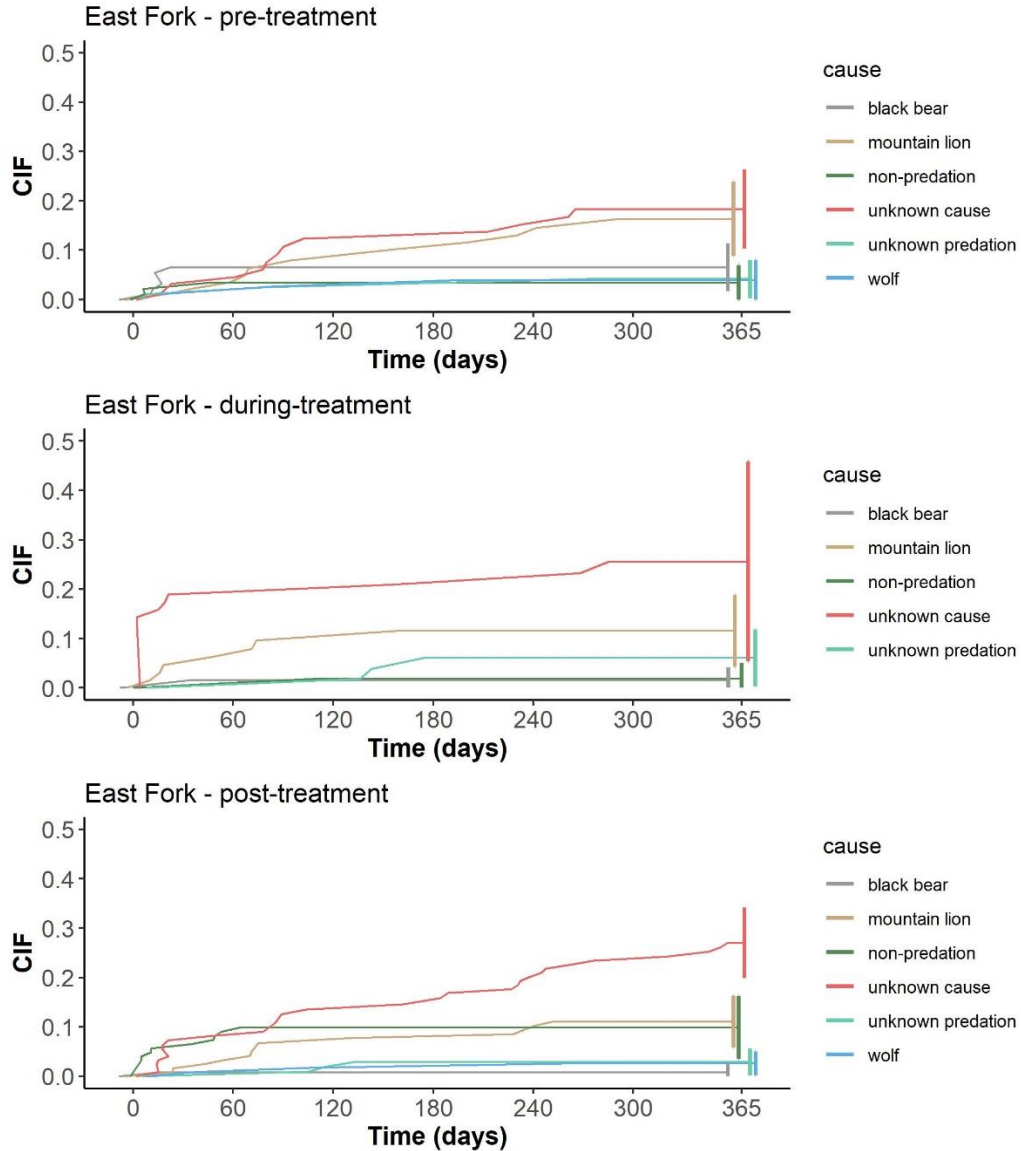


Figure 2. Cumulative Incidence Functions (CIF) showing the cumulative probability of calf mortality (y-axis) from 0 to 365 days after parturition in the West Fork from mountain lions, black bears, wolves, non-predation, unknown causes, and unknown predators, by treatment era, in the upper Bitterroot Valley, Montana, USA, 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.

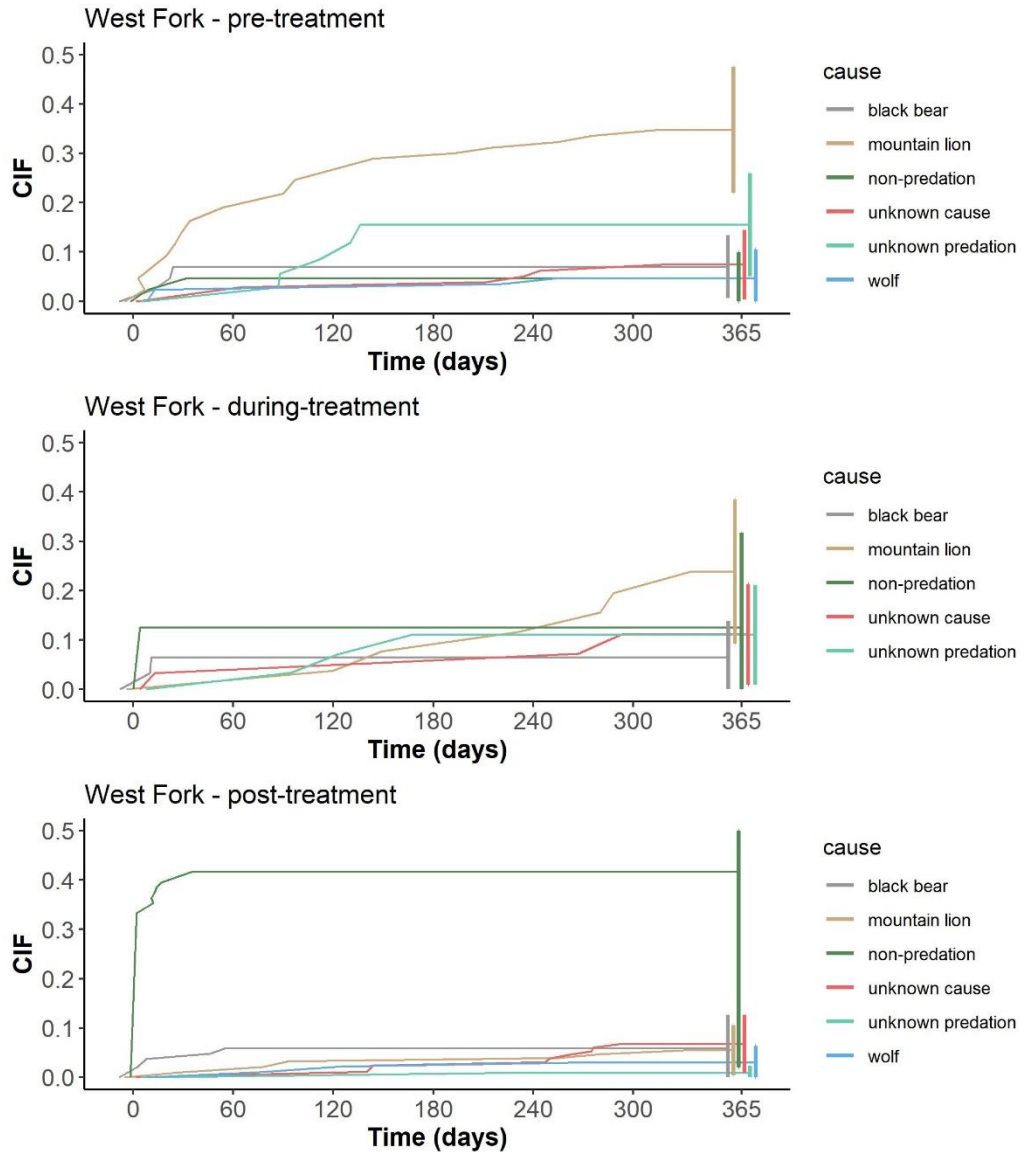


Figure 3. Estimated relationship between elk calf summer survival rate and mountain lion RSF values in the area used by a calf in the upper Bitterroot Valley, Montana, USA. Data were collected before, during, and after the mountain lion harvest treatment in the area, and relationships were estimated 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.

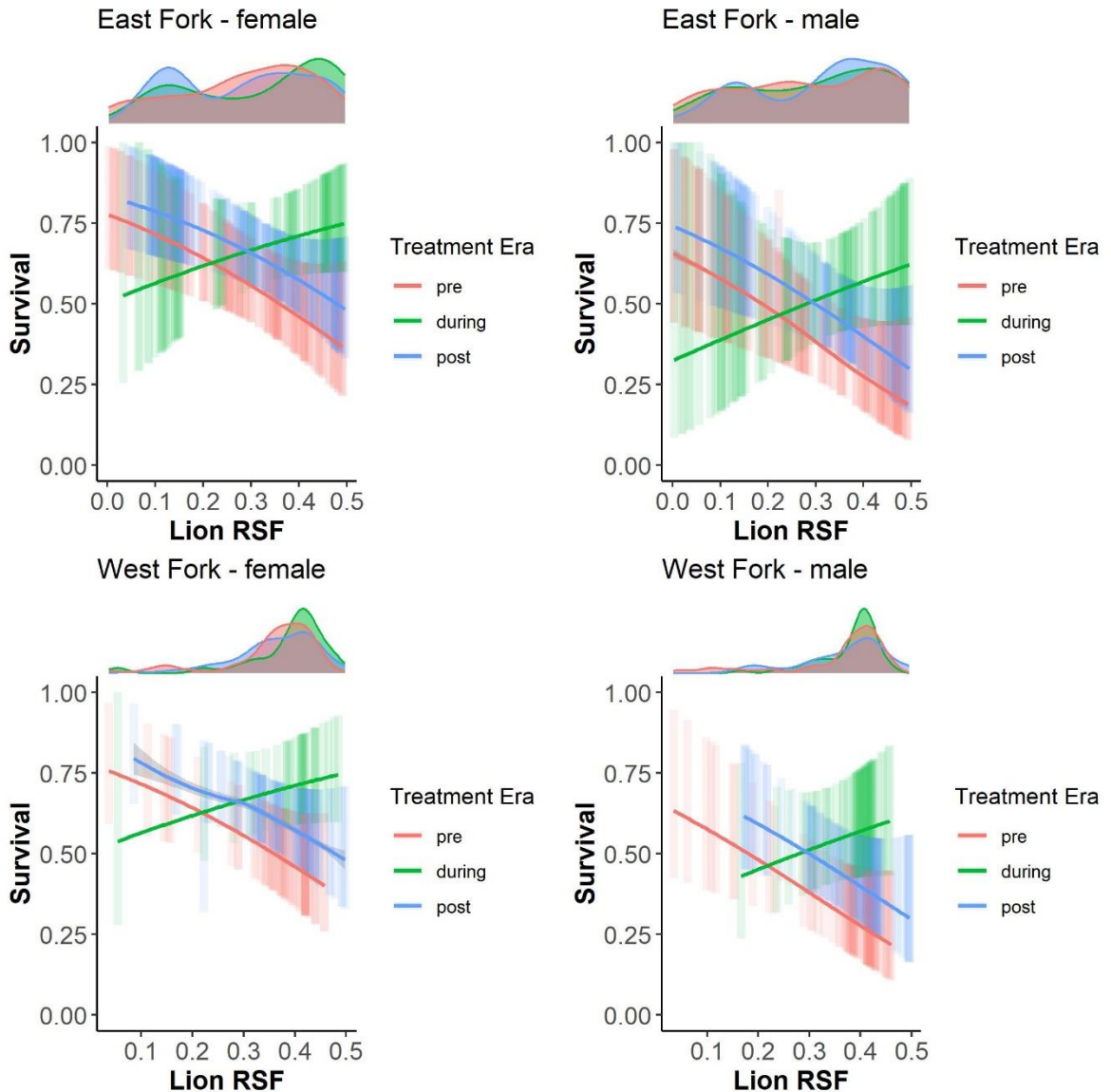


Figure 4. Estimated relationship between elk calf winter survival rate and mountain lion RSF values in the area used by a calf in the upper Bitterroot Valley, Montana, USA. Data were collected before, during, and after the mountain lion harvest treatment in the area, and relationships were estimated 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.

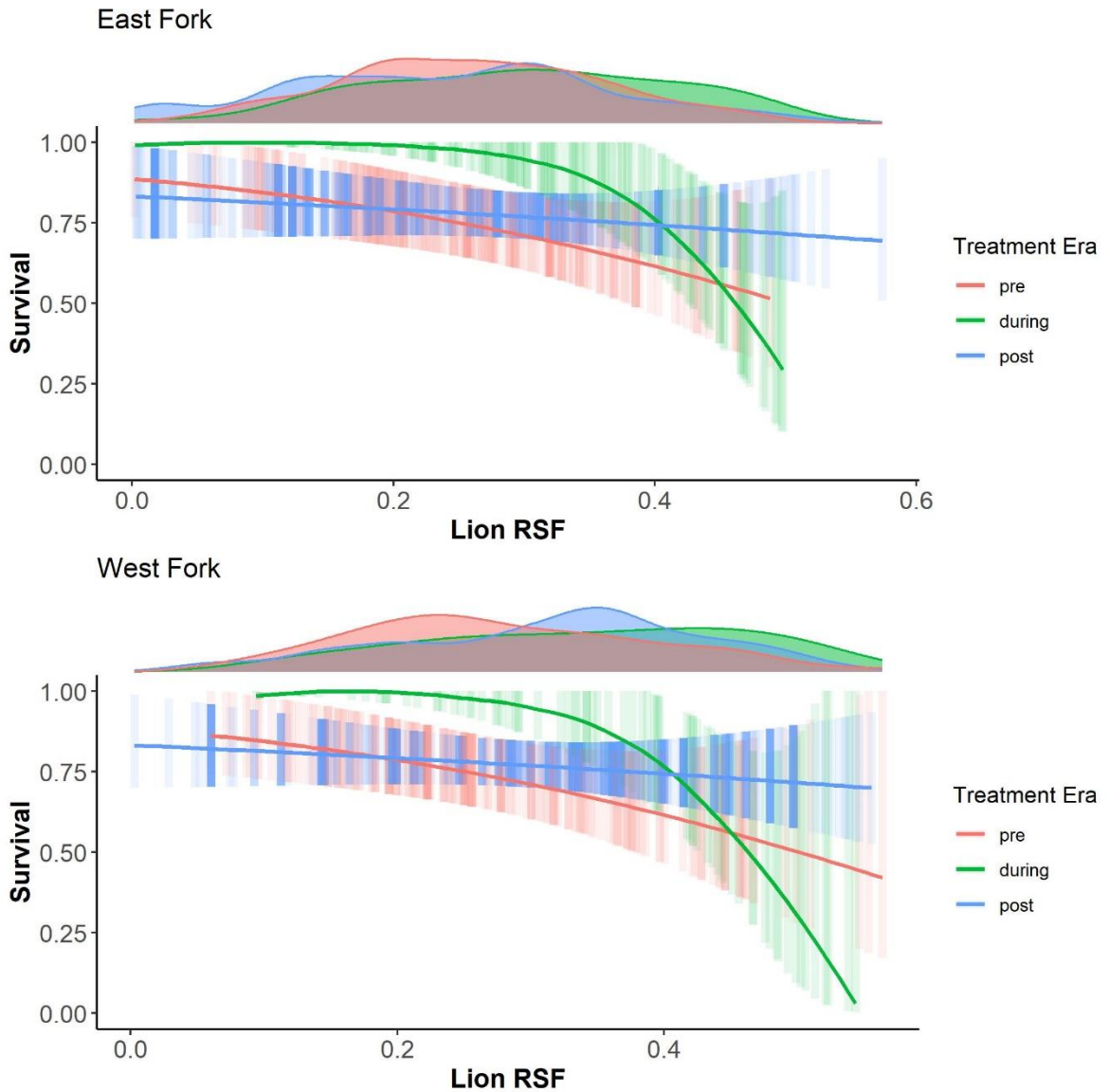


Table 3. East Fork and West Fork herd annual calf survival rates and 95% confidence intervals, for the pre-treatment, during-treatment, and post-treatment eras at mean values of the mountain lion RSF covariate, specific to each sex, herd, and treatment era in the Bitterroot Valley, Montana, USA.

Herd	Sex	Era	Annual Survival
East Fork	Male	Pre	0.25 (0.13 - 0.42)
		During	0.52 (0.25 - 0.80)
		Post	0.34 (0.10 - 0.60)
East Fork	Female	Pre	0.37 (0.09 - 0.65)
		During	0.66 (0.46 - 0.87)
		Post	0.47 (0.32 - 0.62)
Herd	Sex	Era	Survival - Mean
West Fork	Male	Pre	0.24 (0.00 - 0.54)
		During	0.52 (0.26 - 0.78)
		Post	0.33 (0.10 - 0.56)
West Fork	Female	Pre	0.38 (0.17 - 0.58)
		During	0.65 (0.47 - 0.83)
		Post	0.46 (0.31 - 0.61)

APPENDICES

APPENDIX A

PROPORTIONAL HAZARDS INTERNAL AND EXTERNAL RISK FACTORS

We evaluated a suite of internal and external risk factors potentially affecting calf survival. Internal risk factors included the biological characteristics of calves as well as each calf's herd and treatment era values. External risk factors were descriptors of environmental conditions that could possibly explain annual variation in calf survival.

Internal Risk Factors

Big Hole Valley identifier

Due to biotic and abiotic differences in the features of the Big Hole Valley, the range of values for some external risk factors were much different for calves tagged and monitored in the Big Hole Valley when compared to values for calves tagged in East Fork or West Fork. For example, estimated NDVI (Normalized Vegetation Difference, see below) values from calf summer ranges in the Big Hole were much higher than the East Fork and West Fork, likely due to the heavy amount of irrigation in the high elevation grasslands and agricultural areas of the Big Hole Valley. Additionally, estimated RSF values for both wolves and mountain lions (see below) were much lower in the Big Hole Valley when compared to values for the East Fork and West Fork drainages. To account for these differences in the values of some spatial and temporal covariates, we modeled summer survival data for Big Hole calves separately. For summer analyses, we included an indicator variable for calves tagged in the Big Hole Valley. We did not use the Big Hole indicator covariate for winter because calves tagged in that area

migrated to the East Fork drainage each fall, and we considered them to be part of the East Fork herd during winter.

Calf birthdate

To estimate calf birthdate we subtracted the calf's estimated age at capture from the date of capture. We used birthdate only in our analyses of summer calf survival, as we did not have information on birth mass for calves marked when they were ~6-months old.

Calf birth mass

To calculate birth mass, we used linear regression to model the relationship between calf mass at capture and calf age at capture. (Smith 1997, Eacker et al. 2016). We estimated each calf's birth mass with sex-specific linear regression models of the relationship between calf body mass and age at capture, and predicted mass at age 0 days (Smith 1997, Eacker et al. 2016). We only used birth mass for summer survival analyses as we did not have information on calf age or birth mass for calves marked when they were ~6-months old.

External Risk Factors

Mountain lion and wolf resource selection (RSF) covariates

We estimated mountain lion and wolf RSF covariates using published equations for mountain lion (Robinson et al. 2015, Eacker et al. 2016) and wolf (Eacker 2015, unpublished data) RSFs for summer and winter that were developed using species-specific telemetry studies in western Montana. We used locations obtained from aerial telemetry to estimate home ranges for each calf following the methods of White et al.

(2010) and Eacker et al. (2016), which we used to extract average mountain lion and wolf RSF values for each calf using R package *raster* (Hijmans et al. 2018). Calves received higher scores for a species-specific RSF covariate if they spent more time in areas of higher predicted mountain lion or wolf activity. We used the same spatial distribution of species-specific RSF values for all three treatment eras, i.e., we assumed that a given predator's relative probability of space use remained consistent even if its era-specific density changed.

Spring-of-parturition integrated NDVI, late-summer integrated NDVI, and growing-season integrated NDVI

We used three NDVI metrics as possible descriptors of forage conditions and productivity that might be related to maternal and calf body condition and subsequently to calf survival: spring-of-parturition integrated NDVI, late-summer integrated NDVI, and growing-season integrated NDVI. Each NDVI value was estimated as the integrated value from the baseline value at the start of the growing season during spring (May-June), late-summer (July-September) or growing season (May-September) for the summer range of each elk herd (Pettorelli et al. 2006). By removing the baseline NDVI values from our estimates of integrated NDVI for each part of the study area, we partially accounted for variation in substrate and canopy cover between areas and estimated seasonal changes in NDVI related to primary productivity (Rundquist 2002, Pettoelli et al. 2006). For our summer survival model, we included spring-of-parturition NDVI, growing-season NDVI from the pre-natal summer, and late-summer NDVI from the pre-natal late-summer. Spring-of-parturition NDVI might capture variation in maternal body

condition immediately before, during, and after parturition, expressed as variation in maternal investment during lactation (Robbins et al. 1981, McCorquodale et al. 1986). We incorporated previous-growing-season integrated NDVI and late-summer integrated NDVI from the pre-natal summer to capture possible variation in pre-natal maternal body condition, expressed as variation in maternal investment during gestation (Thorne et al. 1976, Cook et al. 2004). For our winter models, we included spring-of-parturition integrated NDVI, coupled with integrated NDVI values from the neonate (post-natal) growing-season and late-summer because variation in forage abundance and productivity during the neonate spring, summer, and fall, might be related to calf body condition at the beginning of winter and thus related to winter survival rates (Cook et al. 2004, Melis et al. 2009).

SNODAS-estimated cumulative snow-water equivalent (SWE)

To estimate cumulative SWE values for each winter, we averaged the SWE values across the winter range of both the West Fork herd and the East Fork herd. We then derived our final SWE covariate by summing all of the daily averages of SWE across the winter ranges of each elk herd. For models of summer survival, we used estimates of previous winter severity as a proxy for maternal body condition in the prenatal period, which we predicted to be related to summer calf survival (DeGiudice et al. 1991). For models of winter survival, we used current-winter SWE metrics to evaluate if winter severity in the current year was directly related to winter survival (Garrott et al. 2008).

APPENDIX B

PROPORTIONAL HAZARDS MODEL-SELECTION TABLES

Here we show model selection tables for three rounds of model selection, comparing support for a suite of internal and external risk covariates as possible descriptors of summer and winter calf survival.

Table A1. Model-selection table for the second model-selection step that compares support for competing models that were within 4 AICc (corrected Akaike information criterion) units of the best-supported model containing external risk factors for data from summer and winter. External covariates included in this round of model selection were winter severity, mountain lion RSF (MLR), spring-of-parturition NDVI (PNDVI), late summer NDVI (LS), and wolf RSF (WR). Here we report the number of parameters in each model (k), the likelihood of each model, model weight (w), and the difference in AICc between each model and the best-supported model (ΔAICc). Based on the results of this model selection step, we retained the mountain lion RSF covariate for summer, and the mountain lion RSF and late-summer NDVI covariates for winter.

Model structure	K	Likelihood	w	ΔAICc
Summer – external risk factors				
MLR	1	-780.417	0.387	0.00
MLR + PNDVI	2	-780.328	0.151	1.88
MLR + winter severity	2	-780.39	0.142	2.01
MLR + WR	2	-780.401	0.141	2.03
MLR + PNDVI + WR	3	-780.318	0.054	3.95
MLR + winter severity + PNDVI	3	-780.322	0.054	3.96
MLR + winter severity + WR	3	-780.383	0.050	3.97
Winter – external risk factors				
MLR + LS	2	-318.291	0.590	0.00
MLR + LS + winter severity	3	-318.237	0.210	2.11
MLR + LS + WR	3	-318.271	0.200	2.17

Table A2. Model-selection table for the third model-selection step that compares support for competing models that were within 4 AICc (corrected Akaike information criterion) units of the best-supported model containing internal risk factors for data from summer and winter. Internal covariates included in this round of model selection were the Big Hole indicator covariate (BH), calf sex, birth date (BD), birth mass (BM), elk herd, treatment era (TR), and an interaction between elk herd and treatment era (TR x herd). Here we report the number of parameters in each model (k), the likelihood of each model, model weight (w), and the difference in AICc between each model and the best-supported model (ΔAICc). Based on the results of this model selection step, we retained treatment era, the treatment era by herd interaction, the Big Hole covariate, and calf sex for summer modeling. For winter modeling, we retained calf sex, the treatment era covariate and the treatment era by herd interaction.

Model structure	K	Likelihood	w	ΔAICc
Summer – internal risk factors				
BH + BD + sex	3	-775.08	0.103	0.00
BH + TR + herd + sex + TR x herd	7	-770.85	0.092	0.23
BH + BD + herd + sex	4	-774.28	0.079	0.53
BH + sex	2	-776.42	0.076	0.59
BH + TR + sex	4	-774.32	0.076	0.62
BH + BD + BM + sex	4	-774.49	0.064	0.95
BH + BD + TR + herd + sex + TR x herd	8	-770.20	0.057	1.17
BH + BD + TR + sex	5	-773.67	0.050	1.46
BH + BM + sex	3	-775.84	0.048	1.54
BH + BM + TR + herd + sex + TR x herd	8	-770.38	0.048	1.54
BH + BD + BM + herd + sex	5	-773.73	0.047	1.57
BH + BM + TR + sex	5	-773.82	0.042	1.77
BH + herd + sex	3	-776.05	0.039	1.95
BH + TR + herd + sex	5	-774.06	0.034	2.24
BH + BD + TR + herd + sex	6	-773.06	0.031	2.43
BH + BD + BM + TR + sex	6	-773.13	0.029	2.56
BH + BM + herd + sex	4	-775.50	0.023	2.97
BH + BM + TR + herd + sex	6	-773.58	0.018	3.46
BH + BD + BM + TR + herd + sex	7	-772.53	0.017	3.59
Winter – internal risk factors				
sex	1	-326.29	0.200	0.00
TR	2	-325.31	0.180	0.18
TR + herd + TR x herd	5	-322.09	0.140	0.63
herd	1	-326.73	0.130	0.88
TR + sex	3	-324.77	0.100	1.32
TR + herd + sex + TR x herd	6	-321.38	0.090	1.67
herd + sex	2	-326.27	0.070	2.11
TR + herd	3	-325.29	0.060	2.37
TR + herd + sex	4	-324.76	0.030	3.60

Table A3. Model-selection table for the final model-selection step that compares support for competing models that were within 4 AICc (corrected Akaike information criterion) units of the best-supported model containing internal and external risk factors retained from Tables A1 and A2, for data from summer and winter. Internal and external covariates compared in this model selection step were the Big Hole indicator covariate (BH), calf sex, herd, treatment era (TR), mountain lion RSF (MLR), and late summer NDVI (LS).

Here we report the number of parameters in each model (k), the likelihood of each model, model weight (w), and the difference in AICc between each model and the best-supported model (ΔAIC_c). The best-supported summer proportional hazards model included mountain lion RSF, the Big Hole covariate, calf sex, treatment era, and the treatment era by mountain lion RSF covariate interaction. The best-supported winter proportional hazards model included mountain lion RSF and late-summer NDVI from the previous growing season, treatment era, and the treatment era by mountain lion RSF interaction.

Model structure	K	Likelihood	w	ΔAIC_c
Summer – all risk factors				
BH + MLR + TR + sex + ML x TR	7	-769.09	0.104	0.00
BH + MLR + TR + herd + sex + MLR x TR + TR x herd	10	-765.77	0.093	0.22
MLR + TR + sex + MLR x TR	6	-770.50	0.077	0.60
BH + MLR + TR + herd + sex + TR x herd	8	-768.48	0.062	1.05
MLR + TR + sex	4	-772.92	0.060	1.10
BH + MLR + TR + sex	5	-771.90	0.056	1.22
MLR + TR + herd + sex + MLR + TR x herd	9	-767.46	0.054	1.29
BH + MLR + TR + herd + sex + MLR x TR	8	-768.67	0.051	1.43
MLR + TR + herd + sex + TR x herd	7	-769.90	0.046	1.63
MLR + TR + herd + sex + MLR x TR	7	-770.26	0.032	2.35
MLR + TR + herd + sex + MLR x herd + TR x herd	8	-769.16	0.031	2.39
BH + MLR + TR + herd + sex	6	-771.47	0.029	2.54
BH + MLR + sex	3	-774.74	0.028	2.63
MLR + TR + herd + sex + MLR x TR + MLR x herd	8	-769.28	0.028	2.65
MLR + TR + herd + sex	5	-772.65	0.027	2.72
MLR + TR + herd + sex + MLR x herd	6	-771.78	0.021	3.17
MLR + sex	2	-776.23	0.018	3.52
BH + TR + herd + sex + TR x herd	7	-770.85	0.018	3.53
BH + MLR + herd + sex	4	-774.21	0.016	3.68
BH + sex	2	-776.42	0.015	3.89

BH + TR + sex	4	-774.32	0.015	3.92
Winter – all risk factors				
TR + MLR + LS + TR x MLR	6	-312.882	0.00	0.148
TR + MLR + LS + herd + LS x herd + TR x herd + MLR x TR	10	-307.600	0.28	0.128
TR + MLR + LS + herd + TR x herd + LS x herd	8	-310.682	0.81	0.098
TR + MLR + LS + MLR x TR + LS x TR	8	-310.958	1.36	0.075
MLR + LS	2	-318.291	1.47	0.071
TR + MLR + LS + sex + MLR x TR	7	-312.635	2.06	0.053
TR + MLR + LS + sex + LS x herd + TR x herd	9	-310.172	2.55	0.041
TR + MLR + LS + herd + MLR x TR	7	-312.881	2.56	0.041
TR + MLR + LS + herd + MLR x TR + TR x herd	9	-310.302	2.81	0.036
MLR + LS + sex	3	-317.935	2.97	0.033
TR + MLR + LS + herd + LS x herd + MLR x TR	8	-311.839	3.13	0.031
TR + MLR + LS + herd + TR x herd	7	-313.224	3.24	0.029
TR + MLR + LS + LS x TR	6	-314.655	3.55	0.025
TR + MLR + LS + sex + LS x TR + MLR x TR	9	-310.702	3.61	0.024
MLR + LS + herd	3	-318.28	3.66	0.024

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