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Research Article

Annual Elk Calf Survival in a Multiple Carnivore System

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ABSTRACT The realized effect of multiple carnivores on juvenile ungulate recruitment may depend on the carnivore assemblage as well as compensation from forage and winter weather severity, which may mediate juvenile vulnerability to predation in ungulates. We used a time-to-event approach to test for the effects of risk factors on annual elk (*Cervus canadensis*) calf survival and to estimate cause-specific mortality rates for 2 elk populations in adjacent study areas in the southern Bitterroot Valley, Montana, USA, during 2011–2014. We captured and radio-tagged 286 elk calves: 226 neonates, and 60 6-month-old calves. Summer survival probability was less variable than winter ($P = 0.12$) and averaged 0.55 (95% CI = 0.47–0.63), whereas winter survival varied more than summer and significantly across study years ($P = 0.003$) and averaged 0.73 (95% CI = 0.64–0.81). During summer, elk calf survival increased with biomass of preferred forage biomass, and was slightly lower following winters with high precipitation; exposure to mountain lion (*Puma concolor*) predation risk was unimportant. In contrast, during winter, we found that exposure to mountain lion predation risk influenced survival, with a weak negative effect of winter precipitation. We found no evidence that forage availability or winter weather severity mediated vulnerability to mountain lion predation risk in summer or winter (e.g., an interaction), indicating that the effect of mountain lion predation was constant regardless of spatial variation in forage or weather. Mountain lions dominated known causes of elk calf mortality in summer and winter, with estimated cause-specific mortality rates of 0.14 (95% CI = 0.09–0.20) and 0.12 (95% CI = 0.07–0.18), respectively. The effect of carnivores on juvenile ungulate recruitment varies across ecological systems depending on relative carnivore densities. Mountain lions may be the most important carnivore for ungulates, especially where grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) are rare or recovering. Finally, managers may need to reduce adult female harvest of elk as carnivores recolonize to balance carnivore and ungulate management objectives, especially in less productive habitats for elk. © 2016 The Wildlife Society.

KEY WORDS black bear, *Canis lupus*, cause-specific mortality, *Cervus canadensis*, forage availability, mountain lion, predation risk, *Puma concolor*, *Ursus americanus*, wolf.

The expansion of large carnivores in North America, including gray wolves (*Canis lupus*; Pletscher et al. 1997), mountain lions (*Puma concolor*; Riley and Malecki 2001), and grizzly bears (*Ursus arctos*; Kendall et al. 2009), has the potential to alter the population productivity of their primary ungulate prey species. Carnivore effects on juvenile survival may be particularly important to understand because predation mortality is expected to be most intense for juvenile ungulates (Linnell et al. 1995), and variation in juvenile survival often has a primary influence on ungulate population trajectories (Gaillard et al. 2000, Raithel et al. 2007). In ungulate populations with low juvenile recruitment, carnivore removal may be used as a management tool to potentially enhance population growth rates, although the efficacy of removal treatments in reversing population declines may depend on the ecological system (Hayes et al. 2003, White et al. 2010, Hurley et al. 2011) and the extent that predation mortality is compensatory or additive for juvenile ungulates (Boertje et al. 2010). The uncertainty in applying carnivore reduction treatments highlights the difficulty that wildlife managers face in balancing carnivore and ungulate management objectives.

The effect of recolonizing carnivores on juvenile ungulate recruitment also depends on the ability of primary productivity (i.e., forage quality and quantity) to compensate

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for increasing predation. For example, Melis et al. (2009) found that carnivore presence reduced roe deer (*Capreolus capreolus*) densities only in areas of low primary productivity across Europe. These results are consistent with elk (*Cervus canadensis*) in different Greater Yellowstone populations, where the impact of carnivores varied between systems (Garrott and White 2005), and interacted with drought conditions to contribute to population declines in migrant elk (Middleton et al. 2013). These climatic or nutritional factors may affect juvenile ungulate survival indirectly via maternal body condition when nutritional resources are insufficient for adult female ungulates to compensate for poor forage quality and quantity in winter and the demands of lactation (Cook et al. 2004). As a result of these carryover effects, juvenile ungulates may have lighter birth mass, later birth date, or slower growth rates over the summer (Thorne et al. 1976, Clutton-Brock et al. 1987, Cook et al. 2004), which may prolong exposure to early mortality sources for juvenile ungulates that use a hiding strategy to avoid predation (Barber-Meyer and Mech 2008, White et al. 2010). Density dependence can also affect juvenile survival through maternal body condition as populations approach nutritional carrying capacity (Bartmann et al. 1992, Pierce et al. 2012), but high predation rates in multiple carnivore systems usually regulate prey populations from experiencing density-dependent mortality (Messier 1994).

Winter weather severity may be an important influence of variation in overwinter survival of juvenile ungulates (Loison and Langvatn 1998, Garrott et al. 2003), and may potentially influence vulnerability to predation (Hebblewhite 2005). During harsh winters, snow conditions (e.g., depth, density, hardness) and colder temperatures may increase ungulate vulnerability to predation by inhibiting movement and increasing energetic demands, which has been documented in elk-wolf dynamics (Smith et al. 2004, Hebblewhite 2005, Garrott et al. 2008). Mountain lions may also benefit from snow conditions that inhibit ungulate movement, and may compete with wolves given their similar selection for juveniles and spatial overlap with wolves when ungulate prey are concentrated on winter range (Husseman et al. 2003, Atwood et al. 2009). Also, summer-autumn nutrition may carry over to influence juvenile vulnerability to predation in winter by affecting body mass, especially as wolves and other coursers may select for prey in poorer body condition (Husseman et al. 2003). Although the effects of early winter precipitation were more important than autumn plant phenology for overwinter survival in mule deer (*Odocoileus hemionus*) fawns (Hurley et al. 2014), winter weather severity and summer-autumn nutrition are confounded in affecting juvenile body mass in winter, and thus overwinter survival, and are difficult to separate in observational studies.

The effects of carnivore mortality on juvenile ungulates are also more complex in multiple carnivore systems where the importance of a particular carnivore species may vary across space and time. For example, ursid predation was found to be the most important mortality source for neonatal elk calves in Idaho (White et al. 2010), Montana (Raithel 2005), and Wyoming (Smith et al. 2006), whereas mountain lions were most important in Oregon (Rearden 2005, Johnson et al. 2013) and Washington (Myers et al. 1998). Barber-Meyer et al. (2008) reported that carnivore mortality on juvenile elk calves increased by 41% in the northern Yellowstone elk herd compared to an earlier study by Singer et al. (1997), which was mainly influenced by a 3-fold increase in grizzly bear density (Schwartz et al. 2006). Wolves receive a disproportionate amount of attention in the public arena, but most studies have reported relatively weak direct mortality effects of wolves on elk calves (Raithel 2005, Barber-Meyer et al. 2008, White et al. 2010). However, the effect of recolonizing wolves on elk calf survival in multiple carnivore systems is unclear because sample sizes of juvenile ungulates remaining by winter are often inadequate in these studies. Thus, it is important to understand cause-specific mortality across seasons by different carnivores in recovering predator-prey systems.

Similar to other harvested ungulate populations across western North America (Noyes et al. 2002, Raithel 2005, White and Garrott 2005), elk populations in the Bitterroot Valley of western Montana, USA, have also experienced recent declines in juvenile recruitment coincident with wolf recolonization (Eacker 2015). Elk trend counts in the Bitterroot Valley indicated that populations increased from around 2,000 elk in the early 1970s to a peak of 8,169 in 2005. However, by 2008, trend counts in the valley had declined by over 25%, and in 2009 calf recruitment reached a historical low of 14 calves/100 adult females, with especially low recruitment at around 8 calves/100 adult females in the West Fork population (Eacker 2015). With restricted elk harvest and overall low elk productivity in this historically premier elk hunting area, the hunting public quickly became focused on recolonizing wolves as the cause of elk declines. However, other factors, such as moderately dense American black bear populations (*Ursus americanus*) and relatively high density of mountain lions, along with recent large-scale wildfire activity and changes in timber management that have affected habitat quality (Proffitt et al. 2016), may also have contributed to declines in elk calf recruitment.

We used an observational, comparative approach to investigate the importance of multiple carnivore species for annual elk calf survival over 2 study areas of contrasting forage availability. In summer, we predicted that elk calf mortality risk would decline with increasing forage availability and increase following winters with more severe weather conditions (i.e., greater precipitation, colder temperatures). Following the forage-predation hypothesis (Melis et al. 2009), we also predicted that forage availability would interact with predation risk to stabilize elk calf survival in areas of high predation risk and high forage availability. We also tested the winter weather severity-predation hypothesis, which predicts that predation risk will interact with weather conditions to increase juvenile mortality during winters with more severe weather conditions (Mech et al. 2001). Finally, we expected that wolves would be an important mortality source for elk calves because wolf reestablishment coincided with declines in elk calf recruitment in our study area (Proffitt et al. 2015*b*). However, if wolves had negligible

effects on elk calf survival as in other studies, then we predicted that American black bear predation would be the dominant mortality source on neonatal elk calves <30 days old, and similar to other systems without wolves or grizzly bears, that mountain lion predation would dominate elk calf mortality during the rest of the year (Johnson et al. 2013).

STUDY AREA

We conducted the study from May 2011 to May 2014 in the southern Bitterroot Valley in west-central Montana, USA (46°1′N, −114°10′W). The 2,530-km^2 East Fork area consisted mainly of agricultural lands along the East Fork of the Bitterroot River and elk summer range in the northern Bighole Valley (Fig. 1), which were dominated by open grasslands made up of bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*). The terrain was more moderate than the West Fork and elevation ranged from 1,100 m in the valley bottom to 2,800 m. The 1,437-km^2 West Fork area consisted of more remote, rugged terrain along the West Fork of the Bitterroot River, and was mainly covered in forests of ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) at lower elevations, with subalpine fir (*Abies bifolia*) and lodgepole pine (*Pinus contorta*) at higher elevations. Elevation ranged from 1,200 m in the valley bottom to >3,000 m. The West Fork area experienced greater precipitation and colder temperatures in winter during the study than the East Fork, and winter severity was highest in winter 2011–2012, moderate in 2012–2013, and above average in 2013–2014. Total winter precipitation from December to March averaged 100–241 mm and minimum temperatures ranged from −8.0°C to −7.1°C on elk winter range in the East Fork, whereas in the West Fork total winter precipitation and minimum temperatures ranged from 216–446 mm and −8.2°C to −7.4°C, respectively.

Elk were the most abundant ungulate in the study area, and were sympatric with mule deer, whitetail deer (*O. virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*). Elk population size estimates of adult females and yearlings (both sexes) for the East Fork ranged from 3,281 (95% CI = 2,898–3,746) in 2012 to 3,907 (95% CI = 3,351–4,608) in 2014 (7.4 elk/km^2 and 8.8 elk/km^2 on the 446-km^2 winter range). Population size estimates for the West Fork ranged from 513 (95% CI = 467–576) in 2012 to 602 (95% CI = 528–665) in 2014 (1.7 elk/km^2 and 2.0 elk/km^2 on the 304-km^2 winter range; D. R. Eacker, University of Montana, unpublished data). Hunter harvest of elk mainly focused on adult males in our study area, and harvests averaged <4% ($n = 96.3$) and 1% ($n = 4.7$) per year of the estimated adult female population in the East Fork and West Fork, respectively, during 2011–2014. Elk calf harvest was negligible.

A suite of carnivores occurred in the study area including wolves, coyotes (*Canis latrans*), mountain lions, and American black bears. Gray wolves recolonized the study area in the early 2000s, and their numbers steadily increased until hunting and trapping of wolves was initiated in 2009 (Eacker 2015). Minimum estimates of wolf density in the study area in 2011 were 10.5 wolves/1,000 km^2 in the East

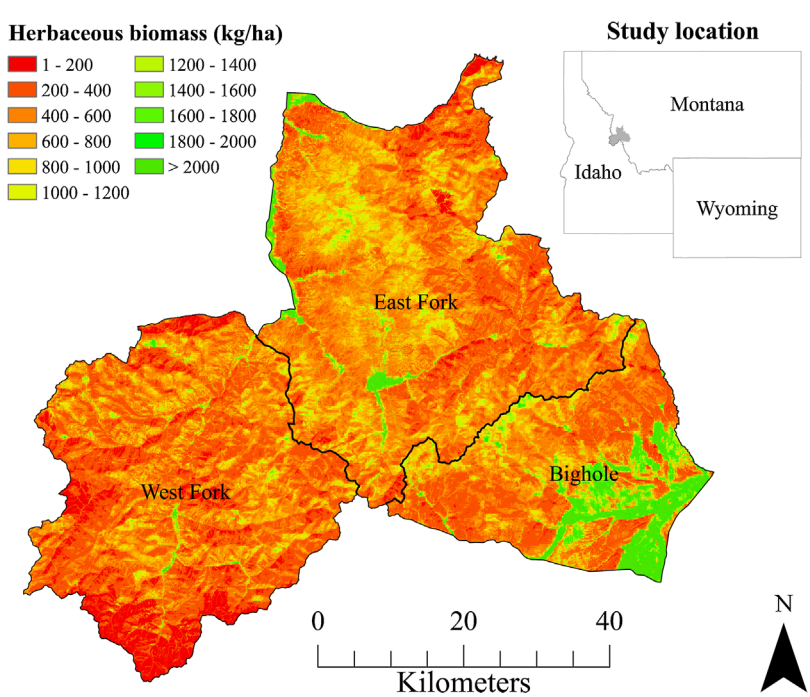

Figure 1. Predicted total herbaceous biomass (kg/ha) in the study area, which included the East and West Forks of the Bitterroot River drainage and the northern Bighole Valley located in west-central Montana, USA. The study area extended into the Bighole to include summer ranges used by migratory East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

Fork and 19.5 wolves/1,000 km^2 in the West Fork (Proffitt et al. 2015*b*). After mountain lion harvest reached a peak in 1998, adult female mountain lion harvest was restricted from 2001 to 2011, and this limited female harvest likely resulted in increasing mountain lion populations. Proffitt et al. (2015*a*) estimated mountain lion population density at 52 mountain lions/1,000 km^2 (95% CI = 34–91) in the East Fork and 45 mountain lions/1,000 km^2 (95% CI = 29–77) in the West Fork in 2012. Black bear population density estimates for the study area were 100 bears/1,000 km^2 (95% CI = 70–120) in the East Fork and 150 bears/1,000 km^2 (95% CI = 130–180) in the West Fork (Mace and Chilton-Radandt 2011). No population estimates were available for coyotes and grizzly bear populations were not present in the area (C. Servheen, U.S. Fish and Wildlife Service, personal communication).

METHODS

Calf Capture, Monitoring, and Mortality Investigation

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

All calves received a radio ear tag transmitter weighing approximately 23 g that was designed to continuously emit a very high-frequency (VHF) signal for 1 year (model 3430, Advanced Telemetry Systems [ATS], Isanti, MN). After experiencing moderate incidence of tag loss in 2011–2012, we switched to an alternative ear tag transmitter in 2012–2013 and 2013–2014 (TW-5, Biotrack, Wareham, Dorset, United Kingdom) that weighed only 1.8 g. All transmitters had a mortality sensor that doubled in pulse rate if the radio tag remained motionless for >4 hours. We monitored VHF radio signals from the ground or aircraft daily from capture through mid-July when the risk of mortality for calves was the highest. During mid-July to late August, as calves became larger and able to escape predation more effectively (Barber-Meyer et al. 2008), we reduced monitoring to 3 times per week. From September through May, we monitored calf signals 2–3 times per week. We relocated individual calves a minimum of 2 times per month from aircraft using telemetry, and recorded location coordinates using global positioning system (GPS) units.

We attempted to investigate mortalities within 24 hours of detecting a mortality signal. We searched each mortality site to document signs of predation including tracks, signs of struggle, and any carnivore scat or hair samples present (Smith et al. 2006). We performed a field necropsy on each carcass by examining the locations and measurements of canine puncture wounds, claw or bite marks on the hide, cracked or chewed bones, and consumption patterns. We did not classify a mortality event as predation if there was any possibility that the calf died of non-predation causes, which was differentiated from predation by the absence of internal hemorrhaging when enough of the carcass remained to make a determination. When possible, we extracted genetic samples from carnivore hair and scat collected at calf mortality sites and submitted them to the United States Forest Service, Wildlife Genetics Laboratory, Rocky Mountain Research Station (RMRS; Missoula, Montana) for identification of carnivore species using DNA. We classified calf fates as live, dead, or unknown fate, and concluded calf monitoring on 30 May 2014.

Calf Survival and Risk Factors

We used an age-based timescale for neonatal elk calves with birth date as the origin and left-truncated individuals based on their age at capture (Fieberg and DelGiudice 2009). We estimated age at capture using morphometrics recorded at capture following Johnson (1951). The survival origin for calves caught during winter was 26 November and we left-truncated these individuals until capture. We removed any calves that died or may have possibly died because of capture (i.e., neonates that died within 24 hr and 6-month-old calves that died within 2 weeks of capture). We right censored any calves that may have permanently emigrated or experienced radio-transmitter failure, and thus, were never heard again; physically lost radio-tags; and all surviving calves after 1 year of age. Calves that had radio tag-related failures or permanently emigrated were censored on the day following the date they were last heard live.

We considered internal and external risk factors to explain the overall risk of mortality to elk calves in summer-autumn (summer; 0–180 days) and winter-spring (winter; 181–365 days) seasons. We defined internal risk factors as effects that were due to biological characteristics of the calf (e.g., mass, sex), and defined external risk factors as abiotic effects (e.g., forage, weather). For summer analysis, we divided the time period into 3 intervals that coincided with different calf development phases: early hiding phase (0–14 days) when calves are most vulnerable, when they join nursery herds (15–18 days) and are less vulnerable to mortality, and when they continue to grow larger (>28 days; White et al. 2010).

We regressed calf mass at capture (nearest 0.01 kg) on age at capture separately for each sex, and used the estimated regression coefficients to predict birth mass following Smith et al. (1997). We imputed the mean sex-specific birth mass for calves that did not have birth mass records. We estimated birth dates by subtracting estimated age at capture from capture dates, and formatted birth dates using Julian days across capture years (Smith et al. 1997). In summer, we considered the effects of sex, birth mass, and birth date based on previous elk calf studies (Griffin et al. 2011). In winter, we considered only sex as an internal risk factor, and did not

consider the effects of birth mass or birth date because these covariates were not available for 6-month-old calves.

We used calf relocations to estimate exposure to external risk factors that may explain elk calf survival. We buffered each calf location with a 500-m radius using the package rgeos in program R (Bivand and Rundel 2014), and then randomly sampled 100 points for each calf with replacement within buffered calf locations for each time interval. We used a 500-m buffer to maintain consistency with previous studies (White et al. 2010), and because of our limited ability to assess telemetry error (183 m, 95% CI $\pm$58 m, $n = 39$) by comparing mortality signals located from ground and air, which comprised <2% of our aerial locations. We extracted covariate values for randomly generated points within each spatial layer in ArcGIS 10.2 (Environmental Systems Research Institute, Inc., Redlands, CA) using the RMRS Raster Utility (Hogland and Anderson 2014).

To model the effect of forage availability on elk calf survival, we used predictions of late-summer, total herbaceous (i.e., graminoid and forb) biomass (kg/ha) of plant species in the diet of elk (i.e., forage) from a landscape-scale, spatial forage model (Hebblewhite et al. 2008, Proffitt et al. 2016). We predicted total herbaceous forage biomass from a suite of land cover (e.g., coniferous forest, grassland) and topographical (e.g., elevation, slope) covariates derived from remote-sensing using generalized linear modeling (sensu Hebblewhite et al. 2008). We focused on herbaceous instead of shrub biomass because previous studies reported that predicting shrub biomass was challenging, and, because shrub biomass did not explain differences in forage quality for elk (Hebblewhite et al. 2008). We were able to test effects of summer forage only on summer calf survival, and not winter survival because we did not know the summer locations of elk calves that were captured as 6-month-olds.

Predation risk is strongly influenced by a predator's resource selection and spatial distribution (Lima and Dill 1990, Hebblewhite et al. 2005). We used spatial models of predation risk for wolves and mountain lions derived from resource selection function (RSF; Manly et al. 2002) models developed specifically for our study area in summer and winter seasons. Our approach assumed that general patterns of resource selection are correlated with predation risk (Hebblewhite and Merrill 2007). We did not include a black bear predation risk covariate because the spatial data were unavailable, and because bear predation risk was restricted to the first 30 days of life. We developed wolf resource selection models using study area-specific wolf GPS and VHF data collected from 2000 to 2013 on 20 wolves (Eacker 2015). The top wolf models for summer and winter validated well against data withheld to measure predictive ability (k-folds cross validation $r_s = 0.77$). For mountain lion predation risk (Fig. 2), we used a similar approach to validate a broader-scale mountain lion RSF previously developed by Robinson et al. (2015), and validated the RSF with study area-specific mountain lion harvest data. We mapped spatial wolf and mountain lion predation risk and forage availability in ArcGIS 10.2 at a 30-m^2 pixel resolution.

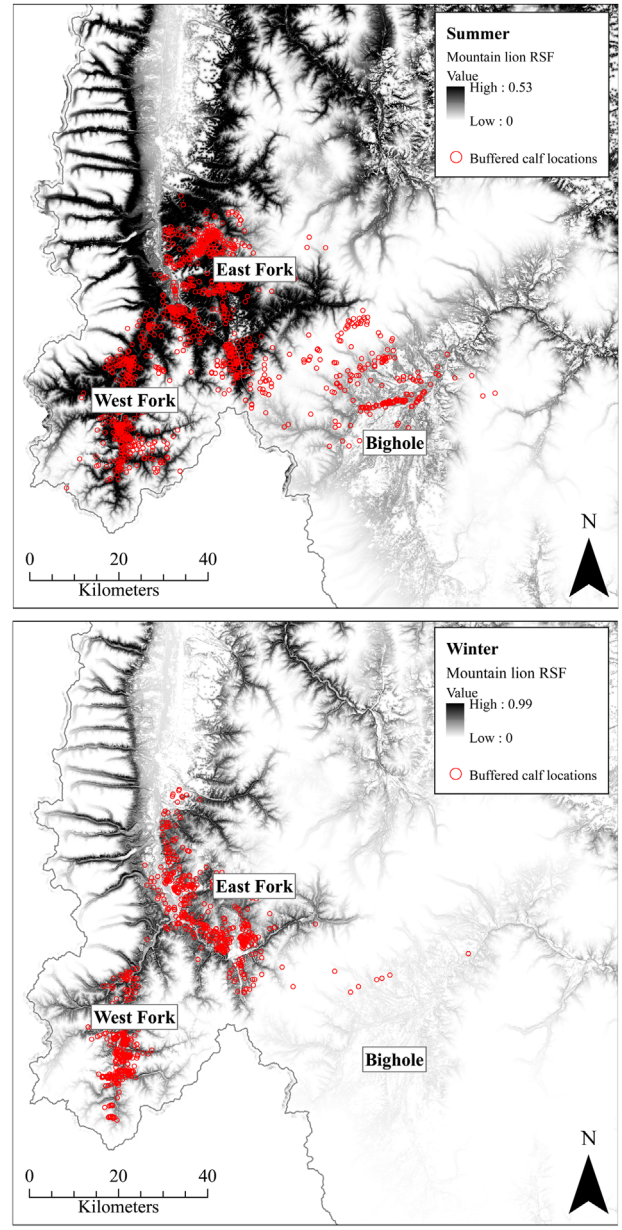

Figure 2. Predicted probability of use for mountain lions across the East Fork and West Fork study areas based on resource selection functions (RSFs). We used season-specific mountain lion RSFs to estimate summer and winter mountain lion predation risk exposure for elk calves in the southern Bitterroot and northern Bighole Valley, Montana, USA.

We used data from spatial climate models (www.prism.oregonstate.edu, accessed 27 May 2016) to derive winter weather covariates for calf survival models. We did not explicitly consider summer weather variables because we expected our forage biomass model would account for these variables. We derived annually varying, population-level weather covariates by summing the total precipitation (mm) and averaging minimum temperatures (C°) over winter. We mapped all winter weather covariates in ArcGIS 10.2 at a 4-km^2 pixel resolution.

We interpolated missing values of external risk covariates using the median values for each individual, which had no effect on our results (D. R. Eacker, unpublished data). In

summary, we considered the effects of 3 internal covariates (i.e., sex, birth mass, birth date) and 6 external covariates (i.e., wolf predation risk, mountain lion predation risk, preferred forage biomass, winter precipitation, temperature) on elk calf survival.

Statistical Analysis

We tested for effects of risk factors on annual juvenile elk calf survival using continuous, time-to-event survival modeling. We used the Andersen–Gill (A-G) formulation of the Cox proportional hazards model (Cox 1972), based on counting process theory (Andersen and Gill 1982, Therneau and Grambsch 2000) to accommodate time-dependent covariates in summer and winter survival models. The A-G proportional hazards model is parameterized in terms of the hazard ratio (HR), which is used to compare hazards among categorical variables and to estimate the effect of covariates on the baseline hazard rate. A hazard ratio of 1 indicates no difference among categorical levels or no effect of a covariate on the hazard of mortality, whereas a HR of <1 or >1 indicates a decreasing or increasing mortality hazard, respectively. The model is considered semi-parametric because parameters are estimated from a partial likelihood, but the baseline hazard cancels out in the estimation of the HR, and thus no assumptions are made about the distribution of mortality times.

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

We used Akaike's Information Criterion with an adjustment for sample size (AIC_c) to select the most parsimonious summer and winter elk calf survival models (Burnham and Anderson 2002). We first conducted univariate analysis to limit the number of candidate variables in our models in attempt to have $\geq$20 deaths/parameter within each season (Hosmer et al. 2008), which required using a cutoff of $P < 0.05$ for variable inclusion. After our univariate analysis, we constructed interaction terms to test for a predation risk $\times$ forage interaction in summer and a predation risk $\times$ weather severity interaction in winter. We initially considered interactions for mountain lion and wolf predation risk within each season, but we did not test for an interaction when the main effects of either covariate were insignificant. We predicted that forage availability would interact with predation risk in summer to reduce mortality risk (HR < 1), or alternatively, that the effect of predation risk on elk calf survival may not depend on forage availability (HR $= 1$). In winter, the effect of predation risk on elk calf survival may be enhanced by increasing winter weather severity (HR > 1) or predation risk may have similar effects on calf survival regardless of winter weather severity (HR $= 1$).

We restricted our model selection to a limited set of nested models based on these a priori hypotheses. We used model-averaged risk ratios and their unconditional standard errors across all models with $\Delta AIC_c < 2$ if 1 model was not clearly supported (Burnham and Anderson 2002). We standardized all continuous covariates by subtracting their mean and dividing by 2 times their standard deviation (Gelman 2008). We also screened covariates for collinearity and included only covariates with a correlation coefficient $< |0.5|$ (Hosmer et al. 2008). We estimated survivorship curves for categorical explanatory variables using a generalized Kaplan–Meier (KM) estimator and tested for significant differences among factors using log-rank tests (Pollock et al. 1989). We report 95% confidence intervals for KM survival estimates on the complementary log-log scale, which has improved coverage near the boundary (i.e., 0 or 1) compared to other methods that rely on truncation (Choudhury 2002). We performed all statistical analyses in program R (R version 3.1.2, www.R-project.org, accessed 10 Apr 2015). We estimated KM survival rates and A-G model coefficients using the R base package survival (Therneau 2015) and conducted model selection using the R package AICcmodavg (Mazerolle 2015).

Cause-Specific Mortality

We estimated cause-specific mortality rates using cumulative incidence functions (CIFs; Heisey and Patterson 2006) to determine the relative importance of mortality sources for elk calf survival in the study system. Cumulative incidence functions account for competing risks of mortality, which occur when an individual is subjected to multiple potential mortality sources, and the occurrence of one mortality event type precludes the occurrence of another. Cumulative incidence functions are also directly interpretable as the probability of death from a cause in a specified time interval (Heisey and Patterson 2006). We categorized mortality sources for elk calves as bear; mountain lion; wolf; unknown; natural, non-predation; and human-related. For our computation of CIFs, we modified the SPLUS code provided in Heisey and Patterson (2006) to estimate confidence intervals on the complementary log-log scale (R code provided in Supplementary Materials S1, available online in Supporting Information). We estimated smoothed functions of the instantaneous cause-specific hazards using the R package bshazard (Rebora et al. 2014).

To assess whether or not unknown mortalities were related to any known mortality sources, we used the data augmentation method in a competing risks framework to decompose summer and winter baseline hazards into their component cause-specific hazards (Lunn and McNeil 1995). The method uses Cox regression to exploit the additivity of hazards by duplicating the data k times based on the number of mortality sources and assigning an indicator variable to

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

Elk calf summary	2011–2012	2012–2013	2013–2014	Total
Period				
Summer	66	76	84	226
Winter[a]	31	29	0	60
Total	97	105	84	286
Capture areas				
East Fork	58	69	56	183
West Fork	39	36	28	103
Sex				
Female	45	52	36	133
Male	51	53	48	152
Unknown	1	0	0	1

[a] Elk calves were not captured during the last winter (2013–2014) because of adequate sample sizes at the beginning of the monitoring period.

each mortality source (Lunn and McNeil 1995). We focused on testing for overlap of unknowns with black bear, mountain lion, and wolf mortality in summer, and mountain lion and wolf mortality in winter. Within each season, we conducted a univariate analysis for each primary mortality source with each mortality identified as the sole cause of death to evaluate whether 95% confidence intervals overlapped between risk sets. In this test, the amount of overlap in 95% confidence intervals for hazard ratios among known and unknown mortality sources indicates similarity among mortality hazards (Murray et al. 2010).

RESULTS

Elk Calf Capture and Relocation

We captured 226 neonatal and 60 6-month-old elk calves for a total of 286 calves throughout both East Fork and West Fork study areas (Table 1). Sex ratio of captured elk calves was not different from parity at 0.9:1 females to males ($n = 285$, $P = 0.26$); we could not record the sex of 1 calf because of an aggressive mother. We consistently caught more calves in the East Fork than in the West Fork, which was expected because elk are more abundant in the East Fork area. We captured similar numbers of each sex of calf during each season and year, and did not capture calves during the last winter (2013–2014) because we had sufficient sample sizes remaining after summer (Table 1). We found no significant evidence of study area, sex, or year effects on birth date, birth mass, or age at capture that would lead us to suspect systematic biases in survival (Eacker 2015). We used an average of 6.5 ± 3.26 (SD; $n = 464$) and 8.4 ± 5.69 (SD; $n = 1{,}045$) locations/calf in summer and winter seasons, respectively (see Eacker 2015 for relocation summaries), to derive external risk covariates for elk calves.

Elk Calf Survival Modeling

After removing 5 calves from our summer survival dataset (1 calf with unknown sex, 1 mortality signal detected in an inaccessible area, and 3 capture-related mortalities), we had a sample of 221 calves, of which we right censored 63 that lost ear tags and 7 with unknown fates. Although censoring rates were relatively high early in the study, we found no strong evidence of informative censoring related to ear tag loss (Eacker 2015). The 90-day KM estimate of calf survival was 0.68 (95% CI = 0.59–0.75; Table 2). The KM estimate of summer (180 day) survival rate was 0.55 (95% CI = 0.47–0.63; Table 2). Female calf survival was almost 20% higher on average than male survival ($P = 0.04$), with respective summer survival rates of 0.65 (95% CI = 0.53–0.74) and 0.46 (95% CI = 0.33–0.59; Table 2). Elk calf summer survival was 0.59 (95% CI = 0.47–0.69) in the East Fork compared to 0.49 (95% CI = 0.35–0.61) in the West Fork area ($P = 0.13$). Elk calf survival rate did not vary significantly from year to year in summer ($P = 0.12$; Fig. 3).

Our univariate analysis revealed that sex (HR = 1.62), forage availability (HR = 0.20), mountain lion predation risk (HR = 1.72), and previous winter precipitation (HR = 1.68) were most strongly related to summer calf survival, whereas birth mass, birth date, previous minimum temperature, and wolf predation risk were marginal or unrelated to summer calf survival (Table 3). The top summer model included the main effects of sex and forage availability, but we report model-averaged coefficient estimates because of model selection uncertainty (Table 4). After controlling for the effect of sex, our summer survival model revealed that forage availability had a strong, positive effect on elk calf survival (HR = 0.23, 95% CI = 0.08–0.70, $P = 0.009$), with the unstandardized coefficient estimate predicting elk calf mortality risk to decrease by 12.7% for every 100 kg/ha increase in forage availability. We found no support for the main effects of wolf predation risk ($P = 0.65$) or the interaction of mountain lion predation risk and forage in summer ($P = 0.17$). Although elk calf mortality risk increased moderately with greater mountain lion predation risk in summer (HR = 1.72, 95% CI = 1.03–2.87, $P = 0.04$),

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

			East Fork			West Fork			Overall		
Period	Year	n	S	95% CI lower	95% CI upper	S	95% CI lower	95% CI upper	S	95% CI lower	95% CI upper
Summer	2011–2012	19–62	0.65	0.47	0.78	0.45	0.19	0.68	0.59	0.44	0.71
	2012–2013	21–75	0.59	0.42	0.73	0.30	0.11	0.52	0.49	0.35	0.62
	2013–2014	10–82	0.56	0.34	0.74	0.59	0.34	0.78	0.57	0.40	0.71
Winter	2011–2012	18–41	0.71	0.43	0.87	0.40	0.18	0.61	0.54	0.36	0.69
	2012–2013	35–42	0.76	0.55	0.89	1.00	NA[a]	NA	0.85	0.70	0.93
	2013–2014	31–39	0.92	0.71	0.98	0.59	0.31	0.79	0.79	0.63	0.89

[a] NA = not applicable; 95% CIs were not estimable because no mortality events occurred in the West Fork during the 2012–2013 winter.

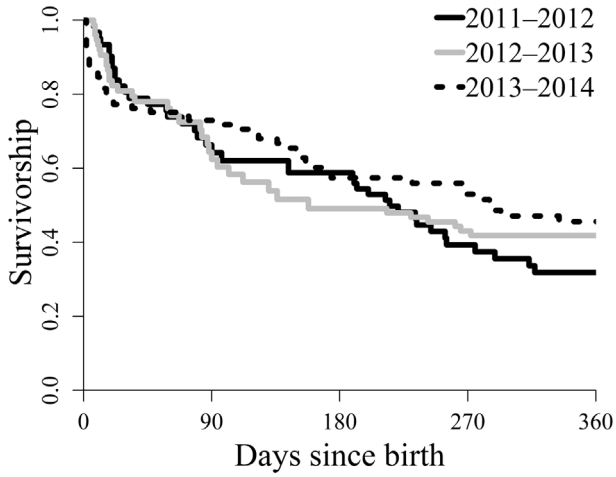

Figure 3. Kaplan–Meier (KM) annual survivorship curves for elk calves for 3 biological years in the southern Bitterroot Valley, Montana, USA, 2011–2014. The KM survivorship graph shows that interannual variation in elk calf survival increases after 90 days since birth.

the effect of mountain lion predation became insignificant ($P = 0.31$) by including forage in the model, reflecting a low level of collinearity from negative correlation among the 2 covariates ($r = -0.40$).

After removing 2 capture-related mortalities from our winter survival dataset, we had a sample of 124 calves, of which we right censored 34 that lost ear tags. The KM estimate of winter survival was 0.73 (95% CI = 0.64–0.81; Table 2). Female calf survival was 0.78 (95% CI = 0.65–0.87) compared to 0.69 (95% CI = 0.55–0.79) for males in winter ($P = 0.24$). We found marginal evidence that elk calf survival was higher in the East Fork (0.80, 95% CI = 0.68–0.88) compared to the West Fork (0.65, 95% CI = 0.49–0.76) during winter ($P = 0.10$). In contrast to summer, elk calf survival rate varied significantly from year to year in winter ($P = 0.007$; Table 2).

Our univariate analysis revealed that mountain lion predation risk (HR = 2.90), wolf predation risk (HR = 3.22), and total winter precipitation (HR = 1.95) were most strongly related to winter calf survival, whereas sex and minimum temperature were unrelated to winter calf survival (Table 3). We dropped wolf predation risk from consideration in winter because of the strong potential for collinearity with mountain lion risk ($r = 0.62$) and because wolf-caused mortality on elk calves was negligible in winter. Although winter precipitation was included in a model within 2 ΔAIC_c units of the top model, the covariate had no explanatory power ($P = 0.28$) in the presence of mountain lion predation risk. However, we report the 2 top models instead of model averaging in winter because covariate effects were consistent across models and the top models ($\Delta AIC_c < 2$) differed by only 1 parameter (Table 5). Our top winter models revealed a strong, negative effect of mountain lion predation risk on winter elk calf survival (HR = 2.90, 95% CI = 1.38–6.08, $P < 0.005$) and a weak but consistent effect of winter precipitation, but our analysis did not support an interaction between mountain lion predation risk and winter precipitation ($P = 0.18$).

Table 3. Results of univariate tests of significance for explanatory variables considered in Andersen–Gill proportional hazards models for elk calves in summer and winter seasons in the southern Bitterroot Valley, Montana, USA, 2011–2014. In summer survival models, we considered sex (female as reference group), birth mass (mass), birth date (date), previous winter total precipitation ($prec_{(t-1)}$) and temperature ($temp_{(t-1)}$), mountain lion (lion) and wolf predation (wolf) risk, and forage biomass (forage). In winter survival models, we considered sex, mountain lion and wolf predation risk, and total precipitation ($prec_{(t)}$), and minimum temperature ($temp_{(t)}$).

Season	Variable	Estimate	Hazard ratio	95% hazard ratio CI	*P*
Summer	Sex	0.49	1.62	1.03–2.56	0.04
	Mass	0.09	1.10	0.71–1.71	0.68
	Date	0.36	1.44	0.94–2.19	0.09
	$Prec_{(t-1)}$	0.52	1.68	1.12–2.51	0.01
	$Temp_{(t-1)}$	−0.09	0.92	0.59–1.43	0.70
	Lion	0.54	1.72	1.03–2.87	0.04
	Wolf	−0.11	0.89	0.55–1.46	0.65
	Forage	−1.62	0.20	0.06–0.61	<0.005
Winter	Sex	0.42	1.52	0.73–3.15	0.36
	Lion	1.06	2.90	1.38–6.08	<0.005
	Wolf	1.17	3.22	1.42–7.30	0.005
	$Prec_{(t)}$	0.67	1.95	1.01–3.78	0.05
	$Temp_{(t)}$	0.65	1.91	0.89–4.07	0.10

Cause-Specific Mortality

Upon detecting a mortality signal, we located and investigated the fate of each calf as soon as possible (median investigation time each year was 0 days). We estimated cause-specific mortality rates with a sample of 221 calves in summer and 124 calves in winter. We investigated 110 mortalities (Table 6). We estimated annual cause-specific mortality rates (CIF) of 0.20 for mountain lion predation; 0.05 for black bear predation; 0.03 for wolf predation; 0.26 for unknown causes; 0.04 for natural, non-predation (e.g., drowning, pneumonia); and 0.02 for human-related mortality (e.g., fence entanglement, hunter harvest; Table 6).

Elk calf mortality risk was highest over the first 30 days of life in summer when 46.3% (Fig. 4) of summer mortality occurred. The mortality hazard from black bears exceeded that from mountain lions until around 20 days after birth (Fig. 4), with mountain lion predation dominating summer calf mortality thereafter. Mountain lion-caused mortality was relatively constant over the summer period (Fig. 4). The 3 wolf-caused mortality events in summer occurred within the first 90 days of life (Fig. 4). We estimated a summer cause-specific mortality rate (CIF) of 0.14 for mountain lion predation; 0.05 for black bear predation; 0.01 for wolf predation; 0.19 for unknown causes; 0.04 for natural, non-predation; and 0.01 for human-related mortality (Table 6).

Our exploratory analysis of unknown mortality for elk calves in summer revealed distinct hazard ratios between black bear, unknown, and wolf-caused mortality (bear: HR = 0.90, 95% CI = 0.48–1.66; unknown: HR = 2.65, 95% CI = 1.68–4.18; wolf: HR = 0.20, 95% CI = 0.06–0.63), whereas the mountain lion mortality hazard ratio was similar to unknown mortality and slightly overlapped bear mortality hazard (mountain lion: HR = 2.59, 95%

Table 4. Model-averaged coefficients, unconditional standard errors, and 95% confidence intervals for Andersen–Gill proportional hazards models that include the effects of forage biomass (forage), sex (female as reference group), previous winter total precipitation ($prec_{(t-1)}$), and mountain lion predation risk (lion) on summer survival for elk calves in the southern Bitterroot Valley, Montana, USA, 2011–2014.

Model parameter	Estimate[a]	Unconditional SE	CI	Hazard ratio	Relative importance	*P*
Forage	−1.47	0.58	−2.62 to −0.32	0.23	1.00	0.01
Sex	0.46	0.23	0.002 to 0.92	1.58	1.00	0.05
$Prec_{(t-1)}$	0.35	0.21	−0.07 to 0.77	1.42	0.56	0.11
Mountain lion	0.21	0.27	−0.31 to 0.73	1.24	0.34	0.42

[a] Effect sizes have been standardized on 2 standard deviations following Gelman (2008).

Table 5. Top 2 winter Andersen–Gill proportional hazards models showing number of model parameters (*K*), model deviance (Dev), difference in Akaike's Information Criterion with an adjustment for sample size (ΔAIC_c), model weights (w_i), standardized coefficient estimates, and 95% confidence intervals (CI) for hazard ratios for elk calves in the southern Bitterroot Valley, Montana, USA, 2011–2014. The final model consisted of only mountain lion predation risk (lion), whereas the next closest model included total winter precipitation ($prec_{(t)}$).

Model parameter	*K*	Dev	ΔAIC_c	w_i	Estimate	Hazard ratio	95% hazard ratio CI	*P*
Lion	1	−133.09	0.00	0.56	1.06	2.90	1.38–6.08	0.005
Lion	2	−132.51	0.87	0.36	0.92	2.50	1.15–5.45	0.02
$Prec_{(t)}$					0.38	1.47	0.73–3.00	0.28

Table 6. Cumulative incidence functions (CIF) in summer and winter for 5 mortality sources with 95% log-log confidence intervals (CI) and raw counts (*n*) for 110 confirmed elk calf mortalities calves by study area and overall in the southern Bitterroot Valley, Montana, USA, 2011–2014. We pooled CIFs over study years, and collapsed natural, non-predation (drowning, starvation), and human-related mortality (fence entanglement, hunter harvest) categories into a single category (other) for presentation.

	East Fork				West Fork				Overall			
Period	*n*	CIF	95% CI lower	95% CI upper	*n*	CIF	95% CI lower	95% CI upper	*n*	CIF	95% CI lower	95% CI upper
Summer												
Bear	7	0.045	0.016	0.100	5	0.068	0.025	0.141	12	0.053	0.024	0.098
Lion	14	0.107	0.055	0.178	13	0.198	0.106	0.310	27	0.137	0.086	0.200
Wolf	2	0.015	0.001	0.065	1	0.014	0.001	0.103	3	0.014	0.002	0.055
Unknown	19	0.200	0.135	0.275	10	0.164	0.081	0.272	29	0.191	0.136	0.254
Other	6	0.046	0.015	0.102	3	0.073	0.041	0.117	9	0.052	0.021	0.103
Winter												
Lion	4	0.062	0.020	0.139	9	0.187	0.095	0.303	13	0.116	0.065	0.183
Wolf	1	0.014	0.001	0.068	2	0.041	0.007	0.125	3	0.026	0.007	0.067
Unknown	7	0.109	0.048	0.198	6	0.124	0.050	0.233	13	0.116	0.065	0.183
Other	1	0.014	NA[a]	NA	0	NA	NA	NA	1	0.008	NA	NA

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

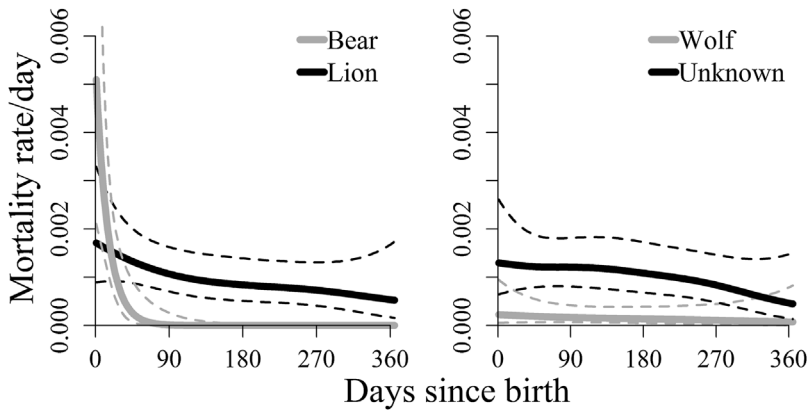

Figure 4. Smoothed instantaneous mortality hazards (i.e., mortality rate/day) for elk calves for different mortality sources in the southern Bitterroot Valley, Montana, USA, 2011–2014.

CI = 1.63–4.11). This suggested that unknown mortality hazard may be a composite of primarily mountain lion-caused mortality, and bear mortality to a lesser extent (i.e., 95% CIs between bear and unknown hazard ratios nearly overlapped). Therefore, we decided not to pool unknown mortality with any specific summer mortality source.

Elk calf mortality risk peaked early in winter when precipitation was greatest, and then, declined to low levels by late spring (Fig. 4). Mountain lions maintained a consistent hazard for elk calves over the winter, whereas wolf-caused mortality was minimal and relatively constant (Fig. 4). We estimated a winter cause-specific rate of 0.12 for mountain lion predation; 0.03 for wolf predation; 0.12 for unknown causes; and 0.01 for natural, non-predation mortality (Table 6).

Our exploratory analysis of unknown mortality for elk calves in winter revealed distinct hazard ratios between unknown and wolf-caused mortality (unknown: HR = 2.65, 95% CI = 1.68–4.18; wolf: HR = 0.45, 95% CI = 0.14–1.47), but the mountain lion mortality hazard ratio was similar to unknown mortality (mountain lion: HR = 3.07, 95% CI = 1.49–6.33). This suggested that unknown mortality hazard was comprised primarily of mountain lion-caused mortality, and wolf mortality to a lesser extent (i.e., 95% CIs between unknown and wolf hazard ratios nearly overlapped). Nonetheless, we decided not to pool unknown mortality with any specific winter mortality source.

DISCUSSION

Few studies have documented strong effects of mountain lion predation on elk calves in a system with recolonizing wolves, and our study highlights the variability in the importance of carnivores across different ecosystems. Our cause-specific mortality analysis revealed that mountain lions dominated calf mortality over the first year of life, with wolves being essentially inconsequential as a mortality source, even during winter when their selection for elk calves is well documented in other systems (Mech et al. 2001, Smith et al. 2004, Metz et al. 2012). Consistently, our results indicated that spatial mountain lion predation risk was the strongest predictor of calf mortality risk in winter. We attribute the dominance of mountain lions for annual elk calf survival to differences in relative carnivore densities in our study system. Mountain lion density in our study areas was among the highest reported in western North America, at about 46 and 54 individuals/1,000 km^2 in the East Fork and West Fork areas, respectively (Proffitt et al. 2015*a*). Considering that wolves were estimated to be at around 2–5 times lower density than mountain lions in the study area (10–20 wolves/1,000 km^2, Proffitt et al. 2015*b*), the strength of mountain lion predation and minimal effect of wolves on elk calf survival is consistent with the differential densities of these 2 carnivores in our system. This emphasizes that density alone may be sufficient to explain the relative importance of different carnivore species on ungulates in multiple carnivore systems.

Cause-specific mortality was dominated by mountain lions year-round in contrast with recent studies in the Greater Yellowstone Ecosystem but comparable to other systems across western North America. In the Northern Range of Yellowstone National Park, where wolves were about 4–5 times more abundant than mountain lions, Barber-Meyer et al. (2008) documented that wolf predation accounted for 14–17% of all elk calf mortality, whereas mountain lion predation was minimal. Another elk calf survival study in Wyoming concluded that low amounts of wolf-caused mortality were related to low wolf densities in the study area, whereas neonatal mortality rates increased over time with increasing grizzly bear density (Smith et al. 2006). In our study system and most other parts of the Rocky Mountains where livestock production is a dominant land use (Garrott et al. 2005), wolves may be held at lower densities because of mortality from livestock conflict and human harvest (i.e., hunting and trapping). Additionally, a decade-long period of reduced mountain lion harvest in western Montana (2001–2011; Montana Fish Wildlife and Parks, unpublished data) combined with a diverse ungulate prey base may have resulted in high densities of mountain lions. Similar reductions in mountain lion harvests, for a variety of reasons (i.e., hunting bans in California, restrictions to hunting seasons in Washington), have occurred across the western United States, and might contribute to increased importance of mountain lions as ungulate predators (Johnson et al. 2013). Although coyotes were a cause of mortality for neonate elk calves in 8 of 12 studies synthesized by Griffin et al. (2011), we did not detect any coyote-caused mortality of elk calves in our study. Perhaps the high densities of mountain lions (Proffitt et al. 2015*a*) or abundant small-mammal or lagomorph densities (as the case with mule deer; Hurley et al. 2011), lead to minimal coyote predation on elk calves in our study area. Although black bear predation was important especially during the first 20 days of our study, it was lower (CIF = 0.05) than most other studies synthesized by Griffin et al. (2011) where cause-specific mortality rates ranged from 0.10 to 0.30. Thus, black bear predation was not as important in our study area, even without grizzly bears present. With the recolonization of wolves in many regions, and the public furor and fanfare surrounding it (Treves et al. 2013), the effects of mountain lions on ungulate populations may be overlooked. Combined with our results, there is growing evidence suggesting that mountain lions may be the most important carnivore for ungulates in more settings than anticipated, especially where grizzly bears and wolves are absent, such as California, Oregon, and much of Washington (Myers et al. 1998, Rearden 2005, Johnson et al. 2013).

Despite the importance of exposure of elk calves to spatial mountain lion predation risk in winter, we found no effect of spatial variation in mountain lion predation risk during summer. This was initially puzzling, but a post-hoc analysis of risk factors with mountain lion-caused mortality as the only mortality source during summer (all others censored) confirmed that even for just those calves killed by mountain lions, mortality risk was not correlated with their predation risk during summer ($P = 0.12$). This suggests that during summer, mortality risk for elk calves was high regardless of spatial risk factors. That is, elk calves died everywhere.

Summer exposure to predation risk by mountain lions was also more uniform and high across individuals compared to winter (Fig. 2), when there was wider spatial variation in exposure of individuals to low and high mountain lion predation risk. This could be because of the wider dispersion of elk during summer on summer ranges or the wider dispersion of mountain lions during summer. Moreover, we note that the diversity of mortality causes was higher during summer when black bear mortality peaked along with death from other causes (e.g., entanglement in fences, starvation, disease, abandonment). These results are similar to other studies reporting a variety of mortality causes during summer (Griffin et al. 2011), and those reporting fewer spatial predictors of risk during summer (White et al. 2010). Therefore, summer mortality may not be as influenced by spatial risk factors as during winter when carnivores and ungulates concentrate on low elevation winter range.

The most consistent weather effect on survival was the effects of winter precipitation on the following summer survival rates, and, during winter itself. Summer survival was lower following winters with heavier precipitation (snowfall), consistent with previous studies (Mech et al. 2001, Evans et al. 2006), suggesting a mechanism of maternal effects translating to reduced viability of calves following birth and potentially lower birth weights. However, there was no evident relationship between birth mass and previous winter precipitation (D. R. Eacker, unpublished data). There were also no differences in birth mass of West Fork and East Fork calves that would suggest carryover winter effects that were herd specific (D. R. Eacker, unpublished data). Therefore, the mechanism of reduced summer survival following higher winter precipitation in our study could be through maternal body condition itself and enhanced lactation during summer (Cook et al. 2013). Regardless, other studies have reported carryover effects of winter on juvenile neonate survival in the wild (Portier et al. 1998, Proffitt et al. 2014, Shallow et al. 2015) and in captivity (Cook et al. 2004). And in a broad synthesis of 2,000 elk calves across 12 studies, Griffin et al. (2011) reported a longer carryover effect of previous summer's precipitation on juvenile survival the following summer, also hypothesized to be via overwinter maternal effects. This interpretation was also supported by the direct negative effects of winter severity on overwinter elk calf survival. Although the effect was not statistically strong in our study, previous juvenile winter survival studies report that increasing winter snow precipitation decreases winter survival of ungulates (Bishop et al. 2009, Hurley et al. 2014).

Our results also supported the positive effects of higher forage availability for summer elk calf survival (Cook et al. 2004, 2013) consistent with the bottom-up effects in Proffitt et al. (2016) in our same study area. Proffitt et al. (2016) extended the forage biomass model used here to estimate forage quality (i.e., digestible energy) and showed that the West Fork herd had lower summer exposure to forage biomass, forage quality, and, therefore, had resultant lower ingesta free body fat and pregnancy rates. In contrast, the East Fork had higher forage biomass and quality, higher body fat and higher pregnancy rates. In fact, in comparison to results of Cook et al. (2013), our West Fork population had marginal nutritional availability in comparison to 13 other populations across the western United States. Thus, the strong effect of summer forage on summer elk calf survival is also consistent with nutritional limitation in the West Fork, which may render West Fork calves more vulnerable to mountain lion predation year-round.

The well-known benefits of ungulate migration (Hebblewhite et al. 2008) for gaining access to high-quality forage also likely contributed to the importance of forage during summer. In the East Fork, the higher forage biomass was also driven by migratory calves that summered in a high-elevation, agricultural valley with high forage availability and low mountain lion (and wolf) predation risk. Without including these migratory elk calves, the effect of forage availability on summer survival was attenuated and insignificant for resident elk calves in a post-hoc analysis ($P = 0.28$). Therefore, we interpret the summer forage effect as a landscape-level scale effect of migration (Hebblewhite et al. 2008), which resulted in higher survival for those elk calves that were born on migratory summer range. Hebblewhite and Merrill (2007) documented similar spatial risk trade-offs for migratory elk herds in the Ya Ha Tinda in Alberta, Canada, with migrants tracking the summer green-up to access high-quality forage at the cost of higher exposure to predation risk, which resulted in lower adult female and calf survival compared to resident elk. Migratory portions of the East Fork elk herd may also trade-off exposure to higher predation risk during migration, but, in contrast to migratory Ya Ha Tinda elk herds, their summer ranges on agricultural lands benefitted from reduced predation risk and enhanced forage. Thus, migratory elk herds that summer in the Bighole Valley may be an important component of sustaining juvenile recruitment in the elk population in East Fork. However, given the potential effects of climate change reducing the duration of the growing season even at high elevations such as observed in Yellowstone (Middleton et al. 2013), the bottom-up benefits of migration may not continue in the future.

Regardless of the specific migration strategy, we found no evidence that higher forage availability compensated for (i.e., interacted with) the negative effects of mountain lion predation risk on elk calf survival in either season. This suggests that mountain lions are an additive mortality source for neonatal elk calves in our study system, especially during summer. The brief, but intense pulse of black bear predation is also likely additive (White et al. 2010, Griffin et al. 2011), and although we saw minimal wolf predation in general, it was relatively constant, also suggesting little interaction with weather conditions as expected (Evans et al. 2006). Compensatory mortality, in general, whether due to forage or weather, may be reduced in multipredator systems compared to systems with fewer carnivores where climatic and nutritional factors explain more of the demographic variation in ungulate populations (Wilmers et al. 2007). For instance, Raithel (2005) reported that spring weather explained neonatal elk calf survival during a period of experimental increases in hunter harvest of mountain lions in

a nearby Montana study area also without grizzly bears or wolves, and reported considerably higher levels of natural, non-predation mortality (i.e., starvation, disease) and interannual variation in neonatal survival compared to our study. Consistently, Barber-Meyer et al. (2008) documented much lower incidence of natural, non-predation mortality and variation in neonatal elk calf survival in Yellowstone National Park over a decade after wolves recovered compared to an earlier elk calf study that occurred during a period of lower carnivore densities (Singer et al. 1997). Thus, in systems with high levels of predation, there may be fewer opportunities for compensatory mortality to manifest because of interactions amongst carnivore species (Griffin et al. 2011), the early additive pulse of bear predation, and lower density dependence because of strong predator effects in general.

We also found a consistent effect of male-biased mortality in summer across study years, which we hypothesize may be due to the consequences of neonatal males exhibiting riskier behavior compared to females in a system dominated by mountain lions, an ambushing predator. For example, Mathisen et al. (2003) reported that neonatal semi-domestic reindeer (*Rangifer tarandus*) exhibited marked behavioral differences between male and female calves that were thought to influence differences in vulnerability to predation mortality; male calves were observed farther away from their mothers and exihibited more locomotion. Although our study and others have reported a strong signal of male-biased mortality in elk calves (Smith et al. 2006), the direction and strength of this effect seem to vary across study systems (Rearden 2005. White et al. 2010) and environmental conditions (Smith and Anderson 1996). For an example, in a recent syntheses across 12 study areas, there was no consistent effect of sex on neonatal survival (Griffin et al. 2011). The importance of sex-biased mortality may depend on the hunting behavior of the dominant predator in the system, with areas dominated by ambushing carnivores (e.g., lynx [*Lynx lynx*]; Mathisen et al. 2003) having greater consequences for juvenile males compared to carnivores using other hunting modes (e.g., coursing). However, unlike a strong sex effect, we found no effect of birth mass on survival, in contrast to the weak birth mass effect desribed by Griffin et al. (2011) across 12 study areas surrounding ours. The causes of inconsistencies between studies in whether birth mass or sex affect juvenile ungulate survival remain unclear. But at least in our study dominated by mountain lion-caused mortality, male elk calves experienced substantially higher risk (50% higher), which has important implications for harvest of male elk given the focus of hunting on adult male harvest.

With any field-based survival study, there are a number of potential caveats. The first is the high levels of tag loss, especially during the first year of the study, which has the potential to bias survival estimates if censoring is informative (Murray et al. 2010). Following advice from Murray et al. (2010), we tested for and found no evidence of informative censoring due to intrinsic factors (i.e., sex, birth mass). Despite high tag loss rates in summer, we were able to maintain adequate sample sizes throughout the study by supplementing our winter sample of calves. We found no evidence that tag loss represented latent mortality causes. The next potential concern were the unknown mortality events (19%) that we were unable to pool with any specific mortality source. Yet this level of unknown mortality is intermediate compared to other juvenile elk studies (e.g., $\leq$35% of unknown mortalities; Griffin et al. 2011). Regardless, our exploratory tests suggested that unknown mortalities were most similar to mountain lion predation. Nonetheless, we opted to conservatively keep them classified as unknowns.

Another limitation is the growing awareness that opportunistically captured elk calves may not entirely represent the population of newborn elk calves (i.e., day 0–1; Gilbert et al. 2014). Thus, some advocate for the strict use of vaginal implant transmitters (VITs) to circumvent this criticism, which is especially important if nutritionally caused mortalities happen in the first few days following birth, as is expected for elk. However, our mean age at capture was 2.14 days, and no exploratory analyses revealed any differences in mortality risk between ground and aerial captures. Although our study design may have unavoidably missed some nutrition-related mortality in newly born elk calves, we still found evidence of nutritional limitation in the West Fork (Proffitt et al. 2016), which may be the ultimate cause of higher mountain lion-caused mortality rates in that area. Another common concern with survival studies is sample size. Even with 286 calves, we studied approximately 23 elk calves/season/year/study area. To guard against model overfitting in this case, we considered a reduced list of covariates. And yet our results are consistent with recent syntheses across approximately 2,000 elk calves at least for neonatal mortality patterns (Griffin et al. 2011). Lastly, although bear mortality was important during the first 30 days of spring, we did not explicitly test for spatial bear predation risk effects on the risk of mortality. Regardless, despite the challenges of tag loss and unknown mortalities, the leading known cause of death was unequivocally mountain lion predation during both seasons and study areas.

In conclusion, the differences in elk calf survival we observed in our 2 study areas translated to important differences in population dynamics that have consequences for ungulate management and significance beyond our study area. We combined these estimates of season- and area-specific calf survival with adult female survival, pregnancy rates, and population counts into a Bayesian integrated population model (IPM; Besbeas et al. 2002, Lee et al. 2015) for the West Fork and East Fork populations (Eacker 2015). There were few differences between adult female survival ($n = 144$) between the 2 areas; the average rates were 0.903 in the East Fork and 0.898 in the West Fork (Eacker 2015). As previously mentioned, pregnancy rates in the West Fork were lower (0.72, $n = 65$) than the East Fork (0.89, $n = 53$), as predicted by higher forage quantity and quality in the East Fork (Proffitt et al. 2016). Combined, our IPM showed that both populations were stable or slightly declining in 2011 but started to increase in 2012 and

2013 with the increase in calf survival. Sensitivity analyses of factors affecting population growth rate showed annual variation in elk calf survival was nearly as important as adult female survival in our study area (Eacker 2015), and of course was much more variable than adult survival (Gaillard et al. 2000, Raithel et al. 2007). When we considered the separate effects of winter versus summer elk calf survival, in the East Fork, summer and winter survival explained equal amounts of variation in population growth rate, whereas in the West Fork, summer calf survival was 40% more important in driving population growth rate than winter. These results demonstrate that the low annual calf survival rates we observed early in the study were consistent with stable or declining elk populations, and that increasing calf survival increased population trajectories. Second, these population results demonstrated important differences in the relative importance of summer versus winter survival in affecting population growth rate. In the nutritionally limited West Fork, summer survival was 40% more important than winter calf survival. Yet in the more productive East Fork, winter survival, though constituting fewer than 50% of annual mortalities, was equal in importance to summer in driving populations. These results emphasize the equal importance of overwinter survival in driving ungulate dynamics in some populations (Portier et al. 1998, Hurley et al. 2014).

MANAGEMENT IMPLICATIONS

Carnivore density estimates and the number of carnivores may provide a surrogate to predict the relative effect of carnivores on ungulates when cause-specific mortality rates are unobtainable. An important management implication of our work is the unanticipated importance of mountain lion predation in our study area despite the recent recolonization of gray wolves. As wolves recover in the lower 48 United States, our results imply that managers need not necessarily assume their effects will be paramount, compared to burgeoning mountain lion populations. Our results also show that effects of predation may be the strongest in the lower quality habitat, exacerbating declines of ungulate populations. Reversing trends with changing harvest will be difficult, however, because of the general unimportance of human hunting to calf recruitment. Therefore, in declining elk populations with recovering carnivores, reducing adult female harvest may be initially necessary as carnivores recover to allow time to identify the most effective strategy to balance ungulate and carnivore management objectives. As carnivore recovery continues, managers may need to consider a more aggressive policy toward habitat restoration (e.g., logging, prescribed burns) or carnivore management for ungulates in less productive habitats, while developing adaptive management experiments to ensure that management can disentangle the bottom-up and top-down effects on ungulates (Hayes et al. 2003, Bishop et al. 2009, Hurley et al. 2011).

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