



Research Article

Effects of Calf Predation and Nutrition on Elk Vital Rates

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ABSTRACT Demographic data indicated a population of elk (*Cervus canadensis*) in northern New Mexico had reduced juvenile recruitment, resulting in a concern over quality hunting opportunities. Following several years of low calf:female ratios of <25:100, we conducted a 4-year study from 2009–2012 to identify reasons for poor recruitment and evaluated the role of predation and nutrition in limiting productivity. We captured and fixed ear-tag radio transmitters to 245 elk calves (126 males, 119 females) to determine cause-specific mortality and estimate calf survival. During the second half of our study, we implemented a new spring black bear (*Ursus americanus*) season resulting in higher spring black bear harvest and evaluated response in calf survival. We also quantified herd-wide nutritional condition and productivity. We estimated percent ingesta-free body fat (IFBF) and pregnancy rates by sampling 1,808 hunter-harvested female elk from autumn through winter. The primary cause of summer mortality for calves across all years was black bear predation. Estimates for annual calf survival were greater when spring black bear harvest was moderate to high (0.44–0.47) compared to periods with lower bear harvest (0.33–0.35). For every additional bear harvested in spring, radio-tagged elk calves were 2.4% more likely to survive the summer. Across years and age classes $82 \pm 1\%$ (SE) of females were pregnant. Pregnancy rate was greatest for prime-aged (2–14 yr) females ($88 \pm 1\%$). Our herd-wide estimate of IFBF for prime-aged adult female elk was $11.9 \pm 0.19\%$ but varied by pregnancy and lactation status. Our results that black bear predation was the primary cause of summer calf mortality and that adult females were in adequate nutritional condition suggested that black bear predation was limiting population productivity. Additionally, calf survival was higher in drought years, the same years when targeted spring black bear harvest was implemented. Our results demonstrated that productivity could be increased by implementing a spring black bear harvest strategy targeted around calving areas and could be applied in other areas experiencing low elk calf survival. © 2018 The Wildlife Society.

KEY WORDS black bear, *Cervus canadensis*, Cox proportional hazards, elk, juvenile survival, New Mexico, nutrition, predation, *Ursus americanus*.

Effective management of ungulate populations requires an understanding of mechanisms affecting population dynamics. However, this can be challenging given the interactive effects of biotic, abiotic, and anthropogenic factors (Caughley 1977, Gaillard et al. 1998, Mysterud et al. 2002, Owen-Smith et al. 2005, Owen-Smith 2010). Forage quality and quantity are considered bottom-up factors because poor nutrition can affect reproduction, survival, recruitment, and ultimately population growth (McCullough 1979; Parker et al. 1999, 2009). Furthermore, carrying capacity for wild ungulates can vary depending on local climatic conditions and land use patterns. Conversely, predation and hunting are

top-down factors because they result in direct mortality to individuals down the trophic chain (Terborgh et al. 2001, Sinclair et al. 2003, Wittmer et al. 2005, Krebs 2009, Johnson et al. 2013). These limiting factors likely function on a continuum, and the effects of each can vary in space and time; thus, a population is rarely limited completely by either top-down or bottom-up forces (Owen-Smith 2010), creating a dynamic situation where both influences are at play simultaneously and in varying degrees at different times (Kie et al. 2003, Bowyer et al. 2005, Monteith et al. 2014).

Population dynamics of ungulates are largely influenced by adult female survival, but in most cases, juvenile survival has a larger influence on population growth rates because adult female survival is typically high and relatively constant, whereas juvenile survival is much more variable (Gaillard et al. 1998, 2000; Ballard et al. 2001; Raithel et al. 2007; Eacker et al. 2017). Predation is often the dominant cause of

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mortality for juveniles (Singer et al. 1997, Ballard et al. 2001, Barber-Meyer et al. 2008, White et al. 2010, Quintana et al. 2016). Experimental manipulations of predator populations have been advocated to quantify the effects predators have on ungulate prey (Gasaway et al. 1992, Gaillard et al. 1998, Hayes et al. 2003, Griffin et al. 2011). Studies elsewhere have reduced predator populations in an attempt to improve ungulate survival with mixed conclusions (Ballard and Larsen 1987, Bartmann et al. 1992, Hayes et al. 2003, White et al. 2010, Hurley et al. 2011). However, low elk calf (*Cervus canadensis*) survival has also been attributed to poor forage conditions and low birth mass (Clutton-Brock et al. 1987, Singer et al. 1997, Smith et al. 2006). Forage, predation, and birth mass, however, can interact depending on weather conditions, ungulate density, and predator density, ultimately influencing population productivity. When faced with decreased recruitment resulting from low juvenile survival, wildlife managers need to understand underlying causes to develop management strategies that improve recruitment if that is a management objective. Studies that focus solely on top-down or bottom-up factors are restricted in their management utility; ideally the effects of nutrition and predation should be assessed simultaneously considering the independent and interactive role of predation and nutrition on ungulate population performance (Ballard et al. 2001, Monteith et al. 2014). If most juvenile mortality is compensatory, management actions that focus on decreasing proximate causes of juvenile mortality may ultimately fail. However, limiting factors may shift temporally within a population depending on environmental conditions, predator densities, hunting, or disease (Sæther 1997; Gaillard et al. 1998, 2000; Krebs 2009).

Nutritional condition of prime-age adult females reflects the ability of the habitat to support animals present at a given time (Parker et al. 2009, Cook et al. 2013), which can be a function of intraspecific competition for resources (Monteith et al. 2014) or the inadequacy of forage on the landscape to support animals in good condition (Cook et al. 2016). Ungulate populations under nutritional stress should initially experience decreased juvenile survival, increased age at primiparity, decreased pregnancy rates for prime-aged females and, lastly, decreased adult survival (Gaillard et al. 1998, 2000; Eberhardt 2002). Ingesta-free body fat (IFBF) is commonly used as an indicator of nutritional condition in ungulates (Torbit et al. 1985; Stephenson et al. 2002; Cook et al. 2004, 2007, 2013). Cook et al. (2013) determined that autumn IFBF is a result of summer range conditions and lactation status and is associated with probability of pregnancy and overwinter condition. Populations in good nutritional condition should experience high pregnancy and birth rates with adult females having relatively high levels of body fat. However, these populations may experience low juvenile or adult survival resulting from high predation rates. Quantifying top-down and bottom-up factors simultaneously can offer insight into the major factors limiting a given ungulate population (Monteith et al. 2014).

Our study was initiated in response to low autumn calf:female ratios (<25:100) observed during aerial surveys from

2002 to 2007 in an elk population in northern New Mexico, USA. We implemented spring black bear (*Ursus americanus*) harvest around calving areas during the last 2 years of our study. This was a short-term and targeted black bear management strategy aimed at improving calf survival. Our objective was to assess the influence of predation on calf survival, and ultimately hunting opportunity, by quantifying survival and cause-specific mortality of elk calves with and without increased spring harvest of black bears. We hypothesized that predation would be the dominant cause of calf mortality and that increased spring harvest of black bears would improve calf survival. If nutrition was the underlying factor behind low calf recruitment in our study area, however, manipulation of predator populations would do little to improve recruitment. Therefore, we also quantified indices of nutrition for lactating, prime-aged adult females. If nutrition was limiting this elk population, we predicted our nutritional condition indices, pregnancy, and autumn body fat of lactating prime-aged females, would be consistent with other nutritionally limited conspecifics across their range in western United States.

STUDY AREA

Our study area encompassed approximately 230 km² of elk summer range and approximately 1,000 km² of winter range in parts of Colfax and Taos counties on public and private land in northern New Mexico within the Sangre de Cristo Mountains from 2009–2012 (Fig. 1). Public lands included the Valle Vidal Unit of the Carson National Forest, and private lands included Vermejo Park Ranch (i.e., Vermejo; latitude and longitude of approximate study site center: 38.84°, -105.27°). Vermejo is a privately owned ranch managed for hunting, fishing, bison (*Bison bison*) production, and ecotourism. The Valle Vidal Unit permitted limited cattle grazing (864 female-calf pairs from 1



Figure 1. Location of elk calf survival study area in northern New Mexico, USA, 2009–2012.

Jun–15 Oct) and was managed for a variety of outdoor recreational opportunities.

Alpine tundra occurred in the highest elevations (3,600–3,900 m) on our study site and as elevation decreased the habitat transitioned into a subalpine zone dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), then into a montane zone characterized by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*). Below this montane zone the woodland zone was dominated by oak (*Quercus* spp.), mountain mahogany (*Cercocarpus* spp.), pinyon (*Pinus* spp.), and juniper (*Juniperus* spp.). Additionally, our study area had several large inter-mountain parks dominated by grasses and sedges. Dominant terrestrial fauna included elk, mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), black bear (*Ursus americanus*), coyote (*Canis latrans*), and mountain lion (*Puma concolor*).

Most elk calved in inter-mountain parks, which ranged from 2,800–3,100 m in elevation, but some calved in the alpine tundra habitat. All elk in our study functioned as a single herd and moved throughout our study area, across public and private lands. Elk density during our study was 2.5–4.5 elk/km², calf:female ratios were 24–31:100, and male:female ratios were 33–52:100 (New Mexico Department of Game and Fish [NMDGF], unpublished data). The elk population was managed for older age-class males and sustained some of the state's only once-in-a-lifetime public draw hunts for these mature males. Hunting male elk in the area was desirable for hunters on public and private lands. Annual elk harvest during our study was 600–900 males and 850–1,050 females. The estimated black bear density was 21.8 bears/100 km² (Gould et al. 2016). As part of another study, some black bears were global positioning system (GPS)-collared and moved throughout the study area and even into adjacent game management units and into Colorado, USA (Quintana 2016).

Long-term (1980–2012) annual average precipitation was 63.5 ± 13 (SD) cm/year (35.5 ± 13.9 cm in the spring and summer, and 13.7 ± 10.7 cm in the winter (winter precipitation is presented as the snow water equivalent; Table S1, available online in Supporting Information). Long-term average daily minimum and maximum temperatures were -0.4°C ± 8.5 and 13.0 ± 10.0°C in the spring-summer and -10.6 ± 5.5°C and 1.7°C ± 5.0 in the winter (National Climate Data Center 2015; data averaged for 2 weather stations within our study area, Global Historical Climate Network stations: USS0005N16S at North Costilla, NM and USS0005N11S at Red River Pass, NM). During our study period (2009–2012), the average daily spring-summer minimum and maximum temperatures were -1.7°C and 10.5°C, and the average daily winter minimum and maximum temperatures were -9.1°C and 2.7°C; average annual precipitation was 54.7 cm.

METHODS

Weather Data

We calculated long-term (1980–2012) and study period (2009–2012) weather conditions by averaging data (annual

precipitation, spring and summer precipitation, winter precipitation, max. temp, min. temp) from 2 weather stations within our study area (National Climate Data Center 2015). We determined cumulative spring and summer precipitation (Mar–Aug) and calculated annual winter severity using methods similar to Jacques (2011), combining temperature and precipitation. We averaged water equivalent snow depth (WESD) and minimum winter temperature separately and developed a score that accumulated 1 point for each day that WESD exceeded the average during our study (8.1 cm) and 1 point for each day the minimum ambient temperature was below average (-10.2°C). Each day from 1 October through 31 March could accumulate between 0 and 4 points (2 points from each weather station). Our winter severity measure was specific to our study area and is not directly comparable to other winter severity measures.

Calf Capture and Handling

During May and June 2009–2012, we captured elk calves to determine cause-specific mortality and estimate survival rates. To minimize disturbance to elk, we used spotting scopes and binoculars to locate adult females with newly born calves in intermountain park calving areas (Pitman et al. 2014). We captured calves across the range of their herd, but our capture method was most successful in open landscapes (i.e., traditional calving areas). We captured calves by hand and equipped each with a very high-frequency (VHF) ear-tag radio-transmitter (model 3430, Advanced Telemetry Systems, Isanti, MN, USA or model V2E 154B, Sirtrack, New Zealand) with a 2-hour mortality switch (Pitman et al. 2014). We visually assessed calves for parasites and injuries and measured body mass, body length, chest girth, hind foot length, hind foot width, and dewclaw condition. We aged calves based on their behavior, appearance, dentition, navel healing, coat moisture, and dewclaw wear (Johnson 1951). After we processed calves, we released them at their capture site. We estimated birth mass by subtracting 0.85 kg for each day since birth (Johnson 1951, Thorne et al. 1976). We performed all animal captures in compliance with Texas Tech University's Animal Care and Use protocol (number 11006-03).

We monitored calves daily from capture (May and Jun) until August, after which we monitored them twice per month until 1 year of age. We located mortalities within 1–2 days of mortality detection to determine the cause of death by identifying site evidence and performing a field necropsy (Acorn and Dorrance 1998). We noted predator or scavenger sign within 100 m of the carcass, including tracks or scat and carcass consumption or scavenging patterns. During field necropsies, subcutaneous hemorrhaging and trauma indicated the cause of death. We characterized cause of death as predation, when predation-specific hemorrhaging was found and identified the predator if possible by dentition measurements, consumption patterns, and evidence surrounding the site (O'Gara 1978, Wade and Bowns 1980, Acorn and Dorrance 1998). If milk was not present in the stomach, we assumed starvation was the cause of death. We classified

mortalities as due to pneumonia when lesions on the lungs were present and there was no evidence of predation. We were only interested in non-anthropogenic causes of mortality and censored hunter-harvested elk from our survival analyses. However, we present the number harvested and their average age at death.

Black Bear Removal

We manipulated black bear populations by increasing harvest between 15 April and 21 June in 2011 and 2012 using a combination of hunting licenses and supplemental take by NMDGF personnel. All hunters were required to notify NMDGF if they harvested a black bear. We targeted spring black bear harvest and supplemental take by restricting hunters or NMDGF personnel to areas <5 km around known elk calving areas. Harvest of males or females without cubs occurred only on the Valle Vidal Unit. Vermejo Park Ranch did not implement a spring black bear season.

Summer Calf Survival

The first 4 weeks of life are generally when most mortalities occur for juvenile elk (Barber-Meyer et al. 2008, White et al. 2010), so we modeled summer survival (through 20 weeks) using a 3-stage approach (White et al. 2010, Monteith et al. 2014). We developed a set of biotic and environmental variables that we predicted would influence summer calf survival. Biotic factors included estimated birth mass, deviation from median birth date, total number of black bears harvested in spring, and total number of black bears harvested the previous fall. Environmental factors included current spring and summer precipitation and previous winter severity. We predicted that weather conditions during pregnancy and lactation may affect calf survival; specifically precipitation during the final trimester of pregnancy and lactation may be influenced by available forage on the landscape and previous winter severity may result in inadequate nutrition, possibly delaying birth dates (Cook 2002), which influence calf survival (Barber-Meyer et al. 2008). We modeled juvenile survival using extended Cox proportional hazards (Cox PH) models that allowed for time-dependent variables (Kleinbaum and Klein 2012) and compared model support using an information-theoretic approach (Burnham and Anderson 2002). We used a balanced model set for all stages of analysis; each variable we evaluated was included in the same number of models. For survival analyses we used the survival package in Program R (version 3.3.2; R Foundation for Statistical Computing, Vienna, Austria).

We modeled survival in 3 stages. In stage 1, we assessed base model structure; we did not include covariates but evaluated base model structures by developing a survival plot that varied by week. We visually inspected this survival plot to identify periods of relatively consistent survival (Barber-Meyer et al. 2008, Monteith et al. 2014). This resulted in several base model structures, which we compared using corrected Akaike's Information Criterion (AIC_c). In stage 2, we included population-level covariates that would influence all calves during that year including winter severity preceding calving, current spring and summer precipitation, current

spring black bear harvest, and previous fall black bear harvest. Lastly, in stage 3, we evaluated individual covariates (estimated birth mass and deviation from median birth date) in addition to the population-level covariates chosen from the previous stage of analysis. We moved models to subsequent stages that fit 3 criteria: they were within $\Delta AIC_c \leq 2$ of our top model in that stage, model-averaged parameter estimates included in the model had 90% confidence intervals that did not overlap 0, and variable importance weight was >0.50 (Arnold 2010, Monteith et al. 2014).

We used model-averaging on coefficients across competing models in our model set to obtain parameter estimates to minimize the effects of uninformative parameters (Arnold 2010, Monteith et al. 2014). If the confidence intervals for parameter estimates did not overlap 0, we calculated hazard ratios by exponentiating the parameter estimate ($\exp[\beta]$) and inverting parameter estimates that were <0 ($1/\exp[\beta]$; Kleinbaum and Klein 2012). We calculated importance weights as the sum of weights across models that contained that variable and used them to rank variable importance (Burnham and Anderson 2002, Arnold 2010, Monteith et al. 2014). We report summer Kaplan–Meier survival estimates by year (Kleinbaum and Klein 2012). We also evaluated whether estimated birth mass differed by sex or year using analysis of variance and compared sex ratios by year using a chi-square test (Westfall and Henning 2013).

Annual Calf Survival

We were interested in whether targeted spring black bear harvest was effective at increasing annual calf survival. If other forms of mortality compensated for fewer calves dying of black bear predation in the summer and this ultimately resulted in the same annual survival rate, we might conclude that black bear predation was almost entirely compensatory and increased spring black bear harvest may not be a useful management tool. Additionally, because calf birth mass is often cited as influencing calf survival (Singer et al. 1997, Barber-Meyer et al. 2008), we assessed whether annual survival was related to birth mass. We developed Cox PH models and plotted graphical annual survival stratified by birth mass or spring black bear harvest levels (Kleinbaum and Klein 2012). Spring black bear harvest was categorized annually as light (1 bear harvested), moderate (11 bears harvested), and high (20 bears harvested). We stratified estimated birth mass into 3 categories using the 33% and 66% quantiles for estimated birth mass. We describe differences in hazard ratios for our calf survival by calf birth mass and spring black bear harvest level (Kleinbaum and Klein 2012).

Because we predicted black bear predation was an important source of mortality for calves in this study (Pitman 2013), we wanted to investigate this factor by evaluating whether there were mortality patterns of calves killed by black bears. We right-censored all calves that were not killed by black bears and analyzed this truncated dataset, by stratifying spring black bear harvest and estimated birth mass. This was a modified competing risks analysis whereby

we considered black bear predation to be the only event of interest (Kleinbaum and Klein 2012). We report hazard ratios to explain how calf birth mass and black bear harvest influenced hazard of mortality for elk calves. We also report annual Kaplan–Meier survival estimates by year (Kleinbaum and Klein 2012).

Nutritional Condition of Adult Females

We sampled hunter-harvested female elk during autumn and winters of 2009–2012 to assess nutritional condition by estimating IFBF. We required hunters to attempt to harvest the first legal elk they saw to minimize hunter selection bias. We estimated IFBF using the Kistner subset score or kidney fat (Cook et al. 2001). When possible, hunters brought whole carcasses to a field station for trained biologists, that had their results verified by others, to process. When this was not possible, guides and hunters returned only the kidneys, kidney fat, heart, and pericardium to the processing station. We used the Kistner subset score to estimate IFBF when feasible because it demonstrated superior performance compared to other methods evaluating body condition in dead animals (Cook et al. 2001). The Kistner subset score performed well across a range of IFBF and bias was small or nonexistent (Cook et al. 2001). Trained personnel scored the fat deposits on the kidneys, heart, and pericardium on a scale from 1–20. The Kistner subset score results from summing the scores of all fat deposits. We used the following model to estimate IFBF from the Kistner (KIST_{hpk}) subset score which consisted of scores of the heart, pericardium, and kidneys (Cook et al. 2001):

$$\text{IFBF} = -4.469 + 0.405 \times (\text{KIST}_{hpk})$$

We were unable to assign a Kistner subset score to some harvested elk because the kidneys, heart, pericardium, and associated fat were not properly removed from the carcass. If kidneys and kidney fat were appropriately removed, we used the kidney fat mass from these individuals to estimate IFBF (Cook et al. 2001). This method was not preferred because it demonstrated a smaller range of predictive ability. Specifically it was useful for animals between 6–13% body fat but lost predictive ability in animals above 16% body fat (Cook et al. 2001). We estimated body fat using kidney fat mass only in cases where the Kistner subset score was incomplete (20% of our observations of IFBF). We used the following

model to estimate IFBF from kidney fat (KF) mass (Cook et al. 2001):

$$\text{IFBF} = -13.05 + 4.573 \times (\ln[\text{KF mass}])$$

If we did not obtain complete samples for calculating IFBF using the Kistner subset score or kidney fat mass, we censored elk. We had some observations of IFBF <0%, which cannot occur so we standardized all values that estimated <1% IFBF to 1%. We assumed that because elk were alive, they had to have at least a small level of body fat; for example, pronghorn (*Antilocapra americana*) that died of starvation had body fat ranging from 1.1–2.9% (Depperschmidt et al. 1987). Additionally, we included these elk in our calculations because we did not want to bias our estimates high.

We aged elk using cementum annuli (I4; Matson’s Lab, Milltown, MT, USA) when possible and tooth wear when cementum aging was not possible (30% of age observations were determined using tooth wear). We classified elk as young (<2 yr), prime-aged (2–14 yr), and senescent (≥15 yr; Eberhardt et al. 2007, Cook et al. 2013). We recorded pregnancy and lactation status at our processing station if possible, and in the field if transport of the entire carcass was not feasible. We estimated herd-wide and age class-specific pregnancy rates, lactation rates, and IFBF. For these statistics, we used only the subset of elk with known ages (cementum annuli data available). We report annual and age class-specific pregnancy rates for animals harvested on or after 1 November. We report annual and age class-specific IFBF and lactation rates only for animals harvested in autumn (defined as 1 Nov–20 Dec; Cook et al. 2013).

RESULTS

We captured and radio-tagged 245 calves (126 males, 119 females) from 2009–2012. Calves averaged 1.6 ± 1.37 (SD) days of age at capture (range = 0.25–6). Average estimated birth mass was 16.3 kg and did not differ by sex (males = 16.47 kg; females = 16.03 kg, $F_{1, 243} = 2.26$, $P = 0.134$). Birth mass differed by year ($F_{3, 243} = 7.41$, $P = 0.007$), and was lowest in 2010 (Table 1). Median birth date also differed by year ($F_{3, 76} = 16.18$; $P < 0.001$; Table 1), but sex ratio did not ($\chi^2 = 3.31$, $P = 0.340$; Table 1).

Table 1. Male (M) and female (F) elk calves captured in northern New Mexico, USA, 2009–2012 to estimate survival.

| | 2009 | 2010 | 2011 ^a | 2012 ^a |
|-------------------------------------|---------------|---------------|-------------------|-------------------|
| Number calves captured | 30 (19M, 11F) | 51 (22M, 29F) | 63 (34M, 29F) | 101 (51M, 50F) |
| Number calves censored ^b | 4 | 2 | 3 | 10 |
| Median birth date | 1 Jun | 6 Jun | 29 May | 7 Jun |
| Average birth mass in kg (SE) | 16.22 (0.32) | 15.19 (0.26) | 16.40 (0.29) | 16.71 (0.25) |
| Summer calf survival (SE) | 0.43 (0.09) | 0.35 (0.07) | 0.54 (0.06) | 0.48 (0.05) |
| Annual calf survival (SE) | 0.35 (0.09) | 0.33 (0.07) | 0.47 (0.06) | 0.44 (0.05) |
| Current spring bear harvest | 1 | 1 | 20 | 11 |
| Previous fall bear harvest | 20 | 29 | 21 | 57 |

^a 2011 and 2012 were when black bear population manipulation was occurring.

^b We censored calves because their fates could not be determined or because they were harvested by hunters ($n = 3$) and we were interested in evaluating non-anthropogenic causes of mortality.

Weather Data

Average long-term annual precipitation from 1980–2012 was 63.5 cm, with 35.5 cm occurring in spring and summer and 13.7 cm (water equivalent snow depth) in winter. Across our study years, precipitation was average to low, with the lowest annual precipitation (40.4 cm) observed in 2012, which was 34% below the long-term mean. Most of the deficits in annual precipitation observed were a result of low spring and summer precipitation (Table S1). Additionally, temperatures were generally warmer than the long-term average. The average maximum temperature from 1980–2012 was 9.6°C but ranged from 8.9°C to 11.9°C during our study, with 2011 being the only year lower than the long-term average. The average long-term minimum temperature from 1980–2012 was -3.5°C. Across years during our study, we observed a higher minimum temperature than the long-term average (-2.5°C to -1.0°C; Table S1).

Cause-Specific Mortality

Of 245 elk calves captured, 140 died before they were a year old. The primary proximate cause of mortality for elk calves during our study was black bear predation. Black bears preyed on calves that averaged 16 ± 19.2 (SE) days of age (range = 2–103 days, $n = 57$). The second most common cause of death was coyote predation; calves killed by coyotes were an average of 12 ± 16.7 days of age (range = 1–52 days, $n = 31$). Calves killed by mountain lions were an average of 134 ± 5.05 days of age at death (range = 5–365, $n = 20$). Other causes of mortality were unknown predator ($n = 11$, \bar{x} age at death = 56 days), unknown cause ($n = 13$, \bar{x} age at death = 130 days), pneumonia ($n = 2$, \bar{x} age at death = 8 days, range = 6–9), golden eagle (*Aquila chrysaetos*) predation ($n = 1$, age at death = 1 day), blunt force trauma ($n = 1$, age at death = 6 days), and drowning ($n = 1$, age at death = 6 days; Table 2). We right-censored 19 calves because their fates could not be determined ($n = 16$) or because they were legally harvested by hunters ($n = 3$). At 1 year of age, predation accounted for 88% of all uncensored mortalities (123 of 140 mortalities).

Black Bear Removal

Spring black bear harvest was low in 2009 and 2010, when 1 male black bear was harvested <5 km from calving areas in

spring, moderate in spring 2012 when 11 bears (9 males, 2 females) were harvested, and high in spring 2011 when 20 bears (18 males, 2 females) were harvested near calving areas. Autumn black bear harvest ranged from 20–57 and varied by year (2009 = 20, 2010 = 29, 2011 = 21, 2012 = 57). Black bear harvest did not occur uniformly throughout our study area. In particular, spring black bear harvest was focused exclusively on public land and near calving areas. However, radio- and GPS-tagged black bears (tagged as part of another study) and elk calves moved throughout our study area, across public and private land.

Summer Calf Survival

For the first stage of our analysis, we compared different time-dependent models (without covariates) to explain calf survival through 20 weeks of age. The base model structure with the most support indicated that survival was lowest during weeks 1–3, and increased during weeks 4–20 (Table 3). The closest competing model had a $\Delta AIC_c = 62.3$, so we moved only the highest ranked model to the second stage of our analysis.

For the second stage, we included black bear harvest (spring and autumn), previous winter severity, and current spring and summer precipitation (Table 3). We advanced model 2 (Table 3), which included an additive effect of spring black bear harvest, to the third stage of our analysis. Two other models in this stage were within $\Delta AIC_c \leq 2$ of our top model and included additive effects of spring black bear harvest, current spring and summer precipitation, and previous winter severity. The parameter estimates for spring and summer precipitation and previous winter severity, however, had 90% confidence intervals that overlapped 0 and the importance weights were <0.50.

In the final stage, we also evaluated estimated birth mass and deviation from median birth date in addition to the population-level covariate, spring black bear harvest. There were several competing models (Table 4), but importance weights indicated that estimated birth mass (importance weight = 0.98) and spring black bear harvest (importance weight = 0.68) were the most influential covariates (Table 4). Deviation from median birth date was also considered in this model set; however, the importance weight for this variable was only 0.25 (Table 4). The 90% confidence intervals for spring black bear harvest (estimate = -0.024; 90% CI = -0.044, -0.004) and estimated birth mass (estimate = -0.116; 90% CI = -0.179, -0.053; Table 4) did not overlap 0.

Birth mass had a strong influence on summer elk calf survival, calves that were born heavier had a higher probability of surviving through summer than those born lighter (hazard ratio = 1.124; 90% CI = 1.055–1.196). For every 1-kg increase in estimated birth mass, calves were 12.4% more likely to survive through the summer. We also found a positive influence of spring black bear harvest on summer calf survival (hazard ratio = 1.024; 90% CI = 1.004–1.045). For every additional bear harvested near calving areas, elk calves were 2.4% more likely to survive the summer. Estimated summer calf survival was lowest in 2009 (0.43, 95% CI = 0.40–0.46) and 2010 (0.35, 95% CI = 0.33–0.37) when the bear

Table 2. Causes of mortality for elk calves captured in northern New Mexico, USA, 2009–2012.

| Source of mortalities | 2009 | 2010 | 2011 | 2012 | Total |
|-----------------------|------|------|------|------|-------|
| Black bear | 7 | 16 | 10 | 24 | 57 |
| Coyote | 3 | 11 | 8 | 9 | 31 |
| Mountain lion | 3 | 2 | 7 | 8 | 20 |
| Golden eagle | 1 | 0 | 0 | 0 | 1 |
| Unknown predator | 1 | 4 | 5 | 4 | 14 |
| Total predation | 15 | 33 | 30 | 45 | 123 |
| Blunt force trauma | 0 | 0 | 0 | 1 | 1 |
| Drowning | 1 | 0 | 0 | 0 | 1 |
| Pneumonia | 0 | 1 | 0 | 1 | 2 |
| Unknown mortality | 2 | 0 | 3 | 8 | 13 |
| Censored ^a | 4 | 2 | 3 | 10 | 19 |
| Total mortality | 18 | 34 | 33 | 55 | 143 |

^a We right censored calves if their fate could not be determined (found only the radio-transmitter) or if they were legally harvested ($n = 3$) because we were only interested in non-anthropogenic causes of mortality.

Table 3. Cox proportional hazard models evaluated for summer (first 20 weeks of life) elk calf survival (S) in northern New Mexico, USA, 2009–2012. For each model, we provide the corrected Akaike's Information Criterion (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weight (w_i), likelihood, and number of parameters (K).

| Model | AIC_c | ΔAIC_c | w_i | Likelihood | K |
|--|---------|----------------|-------|------------|-----|
| Stage 1 ^a | | | | | |
| $S(1-3,4-20\text{ wk})$ | 1,491.3 | 0.0 | 1.00 | 1.00 | 3 |
| $S(1-2,3,4-20\text{ wk})$ | 1,553.6 | 62.3 | 0.00 | 0.00 | 4 |
| $S(1-2,3-4,5-20\text{ wk})$ | 1,559.4 | 68.0 | 0.00 | 0.00 | 4 |
| $S(1,2,3,4-20\text{ wk})$ | 1,584.3 | 93.0 | 0.00 | 0.00 | 5 |
| Stage 2 ^b | | | | | |
| $S(1-3,4-20\text{ wk} + \text{spring bear} + \text{winter severity})$ | 1,485.7 | 0.0 | 0.40 | 1.00 | 5 |
| $S(1-3,4-20\text{ wk} + \text{spring bear})$ | 1,487.0 | 1.3 | 0.21 | 0.52 | 4 |
| $S(1-3,4-20\text{ wk} + \text{spring bear} + \text{sp/su precip})$ | 1,497.3 | 1.6 | 0.18 | 0.45 | 5 |
| $S(1-3,4-20\text{ wk} + \text{spring bear} + \text{autumn bear})$ | 1,489.1 | 3.4 | 0.07 | 0.19 | 5 |
| $S(1-3,4-20\text{ wk} + \text{winter severity})$ | 1,490.1 | 4.4 | 0.04 | 0.11 | 4 |
| $S(1-3,4-20\text{ wk} + \text{sp/su precip} + \text{winter severity})$ | 1,491.1 | 5.5 | 0.03 | 0.07 | 5 |
| $S(1-3,4-20\text{ wk})$ | 1,491.3 | 5.7 | 0.02 | 0.06 | 3 |
| $S(1-3,4-20\text{ wk} + \text{winter severity} + \text{autumn bear})$ | 1,492.1 | 6.4 | 0.02 | 0.04 | 5 |
| $S(1-3,4-20\text{ wk} + \text{sp/su precip})$ | 1,493.2 | 7.5 | 0.01 | 0.02 | 4 |
| $S(1-3,4-20\text{ wk} + \text{autumn bear})$ | 1,493.3 | 7.6 | 0.01 | 0.02 | 4 |
| $S(1-3,4-20\text{ wk} + \text{autumn bear} + \text{sp/su precip})$ | 1,495.3 | 9.6 | 0.00 | 0.01 | 5 |
| Stage 3 ^c | | | | | |
| $S(1-3,4-20, \text{spring bear} + \text{mass})$ | 1,480.1 | 0.0 | 0.48 | 1.00 | 5 |
| $S(1-3,4-20, \text{mass})$ | 1,481.4 | 1.3 | 0.25 | 0.52 | 4 |
| $S(1-3,4-20, \text{birth date} + \text{mass} + \text{spring bear})$ | 1,482.1 | 2.0 | 0.17 | 0.36 | 6 |
| $S(1-3,4-20, \text{birth date} + \text{mass})$ | 1,485.0 | 3.9 | 0.07 | 0.14 | 5 |
| $S(1-3,4-20, \text{spring bear})$ | 1,487.0 | 6.9 | 0.02 | 0.03 | 4 |
| $S(1-3,4-20, \text{spring bear} + \text{birth date})$ | 1,488.9 | 8.8 | 0.01 | 0.01 | 5 |
| $S(1-3,4-20)$ | 1,491.3 | 11.3 | 0.00 | 0.00 | 3 |
| $S(1-3,4-20, \text{birth date})$ | 1,493.1 | 13.0 | 0.00 | 0.00 | 4 |

^a Survival patterns by week were evaluated in stage 1. For example, $S(1-3,4-20\text{ wk})$ restrained survival to be constant from weeks 1–3, which was assumed different from the constant survival rate estimated for weeks 4–20.

^b Covariates evaluated in stage 2 were black bear harvest (spring bear, autumn bear), previous winter severity (winter severity), and current spring and summer precipitation (sp/su precip).

^c Covariates evaluated in stage 3 included spring black bear harvest (spring bear), deviation from median birth date (birth date), and estimated calf birth mass (mass).

population was not manipulated and precipitation was near the long-term mean, but summer calf survival was higher during bear population manipulation and during dry years of 2011 (0.54, 95% CI = 0.53–0.55) and 2012 (0.48, 95% CI = 0.47–0.49; Tables 1 and S1).

By 3 weeks of age, 67% of all mortalities (94 of 140) and 84% (48 of 57) of black bear predation events had occurred. By 31 August, 81% of all mortalities (113 of 140) and 98% of bear mortalities (56 of 57) had occurred.

Annual Calf Survival

Our spring black bear harvest variable had 3 logical strata: low (1 bear), moderate (11 bears), and high (20 bears). The strata we used to compare the effect of estimated birth mass

were light ($\leq 15.1\text{ kg}$; $n = 81$), average (15.2–16.9 kg; $n = 80$), and heavy ($\geq 17.0\text{ kg}$; $n = 84$).

Birth mass did not appear to influence annual calf survival ($P = 0.124$; Table S2 and Fig. S1, available online in Supporting Information). There was evidence that when black bear harvest was low, calves were 1.5 (95% CI = 0.97–2.32) times more likely to die than if black bear harvest was high ($P = 0.068$); however, there was no detectable difference in hazard ratios between moderate and high spring black bear harvest levels ($P = 0.716$; Fig. 2). The range of point estimates for summer survival during low spring black bear harvest were 0.35–0.43 and 0.48–0.54 during moderate to high spring black bear harvest (Table 1). This difference

Table 4. Model-averaged parameter estimates with 90% confidence intervals and importance weights from models explaining summer elk calf survival in northern New Mexico, USA, 2009–2012.

| Parameter | Estimate | 90% CI | Importance weight |
|-----------------------------|----------|-----------------|-------------------|
| Stage 2 | | | |
| Current spring bear harvest | –0.0653 | –0.1306, 0.0000 | 0.87 |
| Previous winter severity | –0.0256 | –0.0909, 0.0397 | 0.49 |
| Spring/summer precipitation | –0.0001 | –0.0002, 0.0001 | 0.22 |
| Stage 3 | | | |
| Mass ^a | –0.116 | –0.179, –0.053 | 0.98 |
| Current spring bear harvest | –0.024 | –0.044, –0.004 | 0.68 |
| Birth date ^b | 0.004 | –0.025, 0.033 | 0.25 |

^a Estimated birth mass.

^b Deviation from median birth date.

Table 5. Ingesta-free body fat (IFBF), lactation rates, and pregnancy rates for female elk harvested from autumn and winter in northern New Mexico, USA, 2009–2012. Age class was categorical: young (1.5 yr), prime (2–14 yr), and old (>14 yr). We calculated pregnancy rates for animals harvested on or after 1 November of each year. We calculated IFBF for elk harvested from 1 November–20 December and lactation rate for animals harvested in autumn (1 Oct–20 Dec).

| Age class | Lactation rate | SE | Pregnancy rate | SE | Autumn IFBF (%) | | | | | |
|------------|----------------|------|----------------|------|-----------------|------|---------------|------|-------------------|------|
| | | | | | Lactating | SE | Non-lactating | SE | Lactating and non | SE |
| Young | 0.00 | NA | 0.14 | 0.04 | 0.00 | NA | 8.46 | 0.50 | 8.46 | 0.50 |
| Prime-aged | 0.35 | 0.02 | 0.88 | 0.01 | 10.23 | 0.34 | 12.83 | 0.20 | 11.94 | 0.19 |
| Senescent | 0.22 | 0.06 | 0.47 | 0.05 | 5.63 | 1.17 | 8.53 | 0.83 | 7.90 | 0.71 |
| Herd wide | 0.27 | 0.02 | 0.82 | 0.01 | 9.98 | 0.34 | 12.07 | 0.21 | 11.41 | 0.19 |

held relatively steady through the end of the first year of life, when annual survival ranged from 0.33 to 0.35 during light spring black bear harvest and from 0.44 to 0.47 during moderate to high bear harvest (Table 1).

When considering only calves killed by black bears, lighter calves were 2.82 (1.44–5.54) times more likely to die of black bear predation than heavy calves ($P=0.003$). Light calves also had a lower survival rate than average-weight calves ($P=0.040$). The risk of black bear predation was 2.11 (1.00–4.44) times higher when black bear harvest was low compared to when harvest was high ($P=0.049$), but there

was no evidence suggesting a difference in survival between high and moderate black bear harvest ($P=0.260$; Fig. 2 and Table S2).

Nutritional Condition of Adult Females

Females ($n=1,808$) were harvested in autumn and winter 2009–2012 (Table S3, available online in Supporting Information). All elk were harvested within approximately 50 km of the study site center. We estimated IFBF of 1,130 elk using the Kistner subset score and 284 using kidney fat mass (Cook et al. 2001); the remaining individuals ($n=394$) did not have enough data to estimate IFBF. Across years, animals averaged 7.4 ± 4.1 years of age (range = 0.5–25) at harvest.

Across years and age classes, $82 \pm 1\%$ ($n=1,335$) of all harvested females were pregnant. Pregnancy rate was greatest for prime-aged females ($88 \pm 1\%$, $n=871$; Table 5). Across years (2009–2012) and age classes, $33 \pm 2\%$ of prime-aged and senescent females harvested in late autumn were lactating (Table 5). Prime-aged females that were lactating had lower autumn body fat ($10.23 \pm 0.40\%$) than non-lactating females ($13.09 \pm 0.20\%$; $F_{1, 225} = 26.52$; $P < 0.001$). Across years, average autumn IFBF of prime-aged lactating females ranged from a low of 11.50% (95% CI = 10.65–12.34%) in 2011 to a high of 13.55% (95% CI = 12.82–14.27%) in 2010 (Table 6).

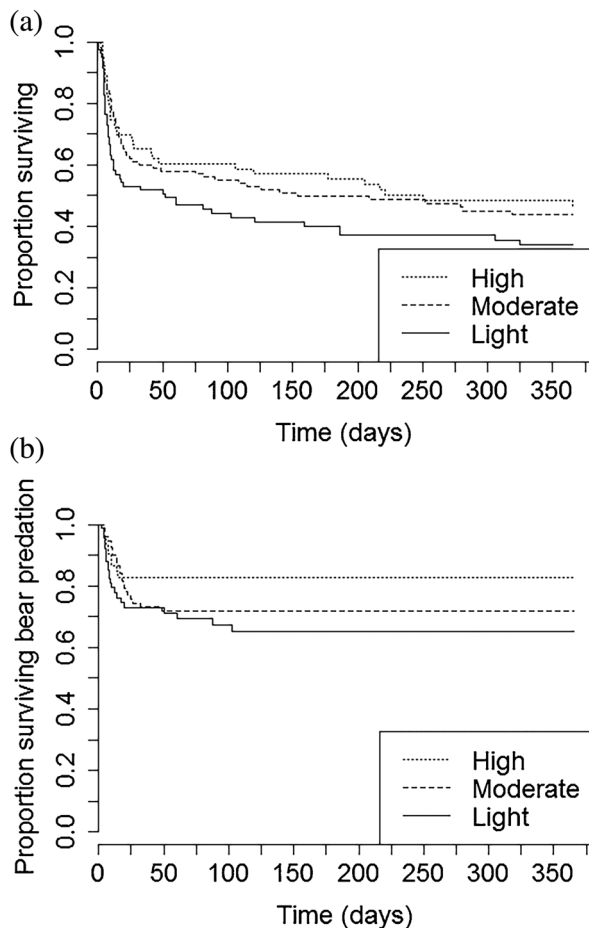


Figure 2. Kaplan–Meier survival curves for annual elk calf survival in northern New Mexico, USA, 2009–2012. Survival is subset by spring black bear harvest level (high [20 bears harvested], moderate [11 bears harvested], and minimal [1 bear harvested]). We evaluated the full set of data with all mortalities included (a), and only calves dying of black bear predation (b).

DISCUSSION

Our results confirm that black bear predation can be a major cause of mortality for elk calves during their first summer and that targeted spring black bear harvest near calving areas can improve calf survival. Calf survival was higher during summer, and remained higher through the first year when targeted spring black bear harvest was moderate to high. Adult female elk were able to acquire adequate body fat and were in relatively good body condition during late autumn, consistent with elk that have adequate nutritional resources. Low calf recruitment despite relatively high pregnancy rates and prime-aged lactating adult female body fat in the study area indicated that predation may have limited population performance.

During our study the primary proximate cause of elk calf mortality was predation, with black bears being the dominant predator of calves during their first summer, before and during experimental manipulation of the black bear population. When the level of spring black bear harvest was low, summer

Table 6. Median harvest date and autumn ingesta-free body fat (IFBF) of prime-aged antlerless elk harvested in northern New Mexico, USA, 2009–2012.

| Hunt year | Prime-aged IFBF, autumn ^a (%) | 95% CI | Prime-aged lactating IFBF, autumn (%) | 95% CI | Median harvest date (range) |
|-----------|--|-------------|---------------------------------------|-------------|-----------------------------|
| 2009 | 11.85 | 11.10–12.60 | 11.56 | 10.75–12.37 | 10 Jan (28 Nov–31 Mar) |
| 2010 | 13.55 | 12.82–14.27 | 12.78 | 11.94–13.62 | 8 Jan (11 Oct–28 Mar) |
| 2011 | 11.50 | 10.65–12.34 | 10.14 | 9.38–10.90 | 24 Dec (3 Oct–30 Jan) |
| 2012 | 12.24 | 11.41–13.06 | 10.59 | 9.66–11.52 | 28 Dec (20 Oct–31 Jan) |

^a We calculated autumn body fat for sport harvested elk from 1 November–20 December of each year.

calf survival ranged from 0.35 to 0.43 and on the low end of the range reported in 12 studies (\bar{x} = 0.61, range = 0.31–0.84; Griffin et al. 2011). This lower survival rate was maintained throughout the first year (survival rate of 0.33–0.35) compared to the range reported in other studies (0.22–0.58). However, spring black bear harvest increased summer (0.48–0.54) and annual (0.44–0.47) calf survival rates. This suggests that black bear predation was at least partially additive because no other mortality factor compensated for decreased black bear predation. Ursid predation has been reported as a primary cause of juvenile ungulate mortality (Raithel 2005, Smith et al. 2006, Barber-Meyer et al. 2008, White et al. 2010, Griffin et al. 2011). In their review of 12 elk calf survival studies, Griffin et al. (2011) similarly reported that ursid predation was consistently additive. If compensatory mortality was occurring during our study, we would expect that another form of mortality would make up for the decreased ursid predation, which we did not observe.

Black bear predation on elk calves was not exclusively additive during our study. We observed some mass-dependent black bear predation on elk calves, suggesting ursid predation may not have been entirely additive. Although other studies reported that estimated birth mass influences survival probability of calves (Singer et al. 1997, Smith et al. 2006, White et al. 2010), our data expands on this observation and suggests mass-dependent predation may be partly influenced by a single mortality factor or lighter calves may be more vulnerable to mortality longer. Barber-Meyer et al. (2008) hypothesized that compensatory ursid predation could occur depending on behavior of calves once detected by a bear, which could be partially determined by their condition. In moose (*Alces alces*), Keech et al. (2000) reported that females with high body fat typically gave birth to heavier calves. Additionally, female ungulates in poor condition may need to forage more frequently or at farther distances, which could render juveniles more vulnerable. Females in good condition, however, may be able to devote more time to protection of their young by remaining close to them. The extent to which adult female elk challenge black bears when their calf is threatened is unknown. Regardless of the mechanism, the size-dependent black bear mortality we observed suggests that black bear predation may have been partly compensatory, whereas our observation that calf survival increased during moderate to high spring black bear harvest suggests black bear predation may have been partly additive. These observations are consistent with Monteith et al. (2014), who caution against attempts to conclude that mortality is exclusively additive or compensatory but rather recommend viewing mortality factors on a continuum.

In addition to the size-dependent black bear mortality we observed during our study, we found that high to moderate spring black bear harvest targeted near calving areas improved summer and annual calf survival over baseline low spring bear harvest. However, the cumulative effect of spring black bear harvest may have influenced this observation. Our highest spring black bear harvest occurred in 2011 with 20 black bears being harvested. The following year (2012), we had moderate spring harvest (11 black bears) but this was also the final year of our study. Perhaps the 20 black bears harvested in the spring of 2011 helped improve survival in 2012. We caution that we had no data to test this carryover effect, but we cannot rule out the possibility.

We think that our timing of moderate to high spring black bear harvest had a more direct effect on calf survival because it preceded or overlapped calving. White et al. (2010) also experimentally manipulated black bear and cougar populations in Idaho, USA, and reported that increased bear harvest, particularly in spring, improved calf survival. In addition, Rayl et al. (2015) suggest predator reductions during the caribou (*Rangifer tarandus*) calving season may be most effective at improving calf survival. Considering the estimated black bear density during our study was 21.8 bears/100 km² (Gould et al. 2016), the spring black bear harvest of 20 bears in 2011 and 11 bears in 2012 over our 230-km² study area was substantial.

Black bears were not the only predators of elk calves during our study. Coyotes and mountain lions also killed elk calves, accounting for 39% of known mortalities. Most predation mortalities occurred in the first several weeks of life, similar to previous studies (Raithel 2005, Barber-Meyer et al. 2008, White et al. 2010, Griffin et al. 2011). Coyotes killed calves during their first several weeks of life but not thereafter. Conversely, mountain lions did not specialize on newly born calves but instead killed older individuals as reported for other ungulates (Barber-Meyer et al. 2008, White et al. 2010, Monteith et al. 2014, Quintana et al. 2016). Mountain lions were responsible for all identifiable (6 of 8) overwinter mortality observations; however, we may have underestimated mountain lion predation because our sample size of marked calves was smaller by late summer. Many juvenile ungulate mortality studies struggle with small sample sizes going into winter. Eacker et al. (2016) supplemented their sample at the onset of winter size by capturing 6-month-old calves. Future studies could consider this because it may result in improved estimates of overwinter survival and causes of mortality.

In addition to investigating predation-caused mortalities, we also looked into the role that precipitation may have

played in calf survival. The National Weather Service (2011, 2012) reported that our study area was experiencing extreme or exceptional drought throughout 2011 and 2012. They classify these stages of drought as experiencing widespread water shortages, crop-pasture losses, and highly elevated fire risk (National Weather Service 2011, 2012). Given these consequences of drought during our study, we might expect calf survival to be poorer during drought years because drier conditions typically reduce forage availability (Sala et al. 1988) for parturient females, resulting in lower calf birth weight. However, we found that both summer and annual calf survival was higher during extreme to exceptional drought years (2011–2012) when spring black bear harvest was moderate or high. We caution that we did not explicitly test this interaction and we had only 4 years of data. We observed lower than average spring and summer precipitation in 2011 and 2012, yet autumn prime-aged lactating female body fat estimates were >10%. The spring and summer months likely affect the available forage that a parturient female needs to give birth to a healthy calf and sustain it during lactation. Our observations that calf survival was higher during drought years, spring and summer precipitation was insignificant in explaining calf survival, and prime-aged lactating females were still able to accrue adequate autumn body fat is in direct contrast to what would be expected if most individuals in the population were severely nutritionally limited. The moderate to high spring black bear harvest during these drought years suggests that calf survival may have been even higher if we had manipulated spring black bear harvest during non-drought years. Furthermore, we would expect black bear predation on calves to be higher during drought years because other black bear resources (forage, mast) are more limited and calf hiding cover may be reduced. It is also possible that drought conditions could result in black bears using the landscape differently during the calving period, perhaps moving out of calving areas or foraging differently.

Despite being under the added stress of drought during part of our study, our observations of IFBF were consistent with elk herds experiencing adequate nutrition that did not limit pregnancy and survival rates, suggesting the habitat was at least adequate for the density of elk present. IFBF of prime-aged lactating elk in autumn in other regions has been observed to range from 5.5% to 12.4% (Cook et al. 2013). Our IFBF estimate of prime-aged lactating elk (10.23%) was on the higher end of observations by Cook et al. (2013) and higher than the range reported specific to the Rocky Mountains (5.9–9.6%; Cook et al. 2013), even during exceptional or extreme drought years (2011–2012). Additionally, our high pregnancy rate is consistent with elk herds experiencing adequate nutritional resources (Cook et al. 2013).

Although we were unable to couple body condition measurements of specific adult females with the fates of their calves, it is plausible maternal condition influenced calf survival based on higher birth mass elk calves having a higher probability of survival. Despite not having these data, our sample sizes were adequate to assess nutritional condition of the population.

Another shortcoming of our study is that our summer and annual survival estimates are probably conservative. We expect that calf survival was likely lower than we were able to detect because we captured calves using visual observations instead of vaginal implant transmitters (Gilbert et al. 2014, Chitwood et al. 2016). We were able to catch calves ranging from 0.25–6 days of age and observed that 16% of mortalities had occurred by day 6. Because we did not capture all calves directly following birth, we likely missed a proportion of calves that were born but died prior to detection and capture. This was probably minimized because calves averaged 1.6 days of age at capture, but it is possible that some proportion of these missed calves may have died because of starvation, predation, or other factors.

MANAGEMENT IMPLICATIONS

Our results demonstrated that elk calf survival may be increased by a spring black bear harvest strategy that is targeted near calving grounds. Sustaining higher spring black bear harvest for multiple years with hunter effort alone may be logistically difficult and possibly undesirable to stakeholders. In New Mexico, bear hunters can only legally harvest 1 bear per license year and some spring hunters chose not to harvest so they would have an opportunity to hunt again in autumn. In this area, agency effort toward targeted spring bear harvest near calving areas would likely need to be included in harvest plans. A combination of an evaluation of the nutritional condition of adult female elk and an assessment of cause-specific calf survival can be used to assess the limiting nature of predation and nutrition in some settings and, depending on management goals, could be used to focus management strategies that may have a higher probability of success. Additionally, obtaining data on herd-wide condition and vital rates from hunter harvested female elk may be advantageous in situations where funding is limited.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.