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Research Article

Pumas affect elk dynamics in absence of other large carnivores

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ABSTRACT We investigated survival, reproduction, and population growth (λ) for a declining elk (*Cervus canadensis nelsoni*) population in South Dakota, USA, 2011–2015. We obtained survival data from 125 calves and 34 yearlings. We determined survival and pregnancy rates for 42 adults (2–8 years old) and 39 old adults (≥8 years old). We combined population vital rates into a matrix model, which indicated a slightly growing population but with considerable uncertainty ($\bar{\lambda} = 1.03$, 95% CI = 0.93–1.13). Our elasticity analysis suggested asymptotic growth rates were most sensitive to proportional changes in old adult and adult female survival, followed by proportional changes in calf and yearling survival. Our life-stage simulation analysis further supported asymptotic growth rates being most sensitive to variation in survival, and most of the variation in λ we observed was a consequence of variation in annual calf survival ($R^2 = 0.58$). Annual calf survival was low (0.26, 95% CI = 0.05–0.52), and puma (*Puma concolor*) predation was the primary cause-specific mortality factor of calves (0.63, 95% CI = 0.51–0.76). Adult female survival was near its biological maximum (0.95, 95% CI = 0.87–0.99); therefore, managing for increased calf survival may be the most practical strategy for promoting elk population growth in this system. Managing this puma population at the lower end of the population objective and reducing white-tailed deer (*Odocoileous virginianus*) numbers (primary prey source) may allow for elk population growth in this system. © 2017 The Wildlife Society.

KEY WORDS Black Hills, calf survival, *Cervus canadensis nelsoni*, elasticities, fundamental niche, life-stage simulation analysis, predation, *puma concolor*..

Population growth rates (λ) of large, long-lived herbivores, such as elk (*Cervus canadensis*), are sensitive to small changes in prime-aged, adult female survival (Sauer and Boyce 1983); however, the magnitude of spatial or temporal variance in juvenile survival frequently influences observed population dynamics (Gaillard et al. 1998, Raithel et al. 2007). Managers grappling with stabilizing a declining ungulate population characterized by chronically low recruitment often focus on increasing adult female survival by restricting recreational harvest (Eberhardt et al. 2007), or increasing juvenile survival by reducing carnivore densities (White et al. 2010, Lewis et al. 2017) or increasing calving habitat security (Lehman et al. 2016). Balancing ungulate and carnivore management objectives is difficult (Proffitt et al. 2014) given diverse public attitudes (Schorr et al. 2014) and recolonizing, expanding carnivore populations (Smith et al. 2014). Managers must implement actions to meet population objectives, notwithstanding the inherent uncertainty involved in deriving inference across systems with differing predator-prey community compositions (Eacker et al. 2016).

In their comprehensive meta-analysis comprised of 45 elk populations across western North America, Brodie et al. (2013) demonstrated that variation in adult female survival is fundamentally influenced by harvest, an additive source of mortality that renders the influence of carnivores compensatory. Even with the effects of large carnivores in predator-rich communities, adult female elk survival was reduced <2%, and in the absence of human factors, was unrelated to puma (*Puma concolor*) presence (Brodie et al. 2013). Thus, reducing antlerless harvest quotas is an effective means to increase adult female survival in the face of expanding predator populations and increasing climatic variability (Brodie et al. 2013). However, protracted restrictions on elk harvest are unlikely to garner support from many stakeholder groups (Longmire 2014). Management to increase elk populations in systems with large predators will largely reflect female elk quotas and harvest vulnerability, which can be affected by road density and topographic complexity (McCorquodale et al. 2003, Stubblefield et al. 2006). In reality, adult female survival is relatively invariant

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spatially and temporally (mean within-study process variance across 12 studies, $\sigma^{-2} = 0.002$; Raithel et al. 2007), and approximates 0.85 ± 0.005, the mean across 42 harvested populations (Brodie et al. 2013).

In contrast, calf elk survival is highly variable temporally (e.g., within-study variance [Singer et al. 1997]) and spatially (e.g., across-study area variance [White et al. 2010]). Neonate elk survival (i.e., through 3 months) declined across 12 systems as the number of large carnivore species increased from 3 to 5 (Griffin et al. 2011). These systems from the northwestern United States all included, at a minimum, pumas, black bears (*Ursus americanus*), and coyotes (*Canis latrans*). Multi-predator systems are characterized by interspecific competition that can affect ungulate survival. Within multi-predator systems, Griffin et al. (2011) reported that puma predation on neonatal elk decreased with the addition of wolves (*Canis lupus*) and grizzly bears (*Ursus horribilis*). Puma prey switching from elk to mule deer (*Odocoileus hemionus*) was associated with increasing wolf abundance in the southern Yellowstone ecosystem (Elbroch et al. 2015*b*). Following the local extinction of jaguars (*Panthera onca*) on Barro Colorado Island, Panama, pumas shifted to larger prey (Moreno et al. 2006). Puma kill rates on ungulates increased by 48% during the active black bear season in western Colorado and northern California, presumably in response to kleptoparasitism by the dominant ursid (Elbroch et al. 2015*a*). Notably, across all of the North American multi-predator systems, ursids, alone or coupled with pumas, were consistently identified as the dominant predators of elk calves (Schlegel 1976, Singer et al. 1997, Raithel 2005, Barber-Meyer et al. 2008, White et al. 2010).

Pumas were identified as the dominant cause of calf elk mortality in a multi-predator system in west-central Montana, USA (Eacker et al. 2016). Griffin et al. (2011) reported that only bear predation appeared to have an additive effect on calf elk mortality, but they believed the phenology of predation was dictating mortality patterns, as bear predation peaks over the first few weeks post-calving. Questions remain regarding whether pumas, if released from competition with black bears, grizzly bears, and wolves, are capable of heavily exploiting neonates during the first few weeks post-calving. Can the fundamental niche (Hutchinson 1959) realized by pumas include heavy neonate predation, a niche space occupied by grizzly (Barber-Meyer et al. 2008) or black bears (White et al. 2010) in other multi-predator systems?

Surveys indicated a large portion of elk (~60%) in our study area in the Black Hills, South Dakota, USA, may have been declining from 2003 to 2011. In Custer State Park (CSP) elk counts went from a high near 1,200 in 2003 down to under 200 in 2011, with evidence of chronically low recruitment (Lehman 2015, Lehman et al. 2016). Antlerless elk hunting was closed in CSP throughout our study, and elk management units adjacent to CSP were managed for conservative antlerless elk harvest (South Dakota Department of Game, Fish and Parks 2015). Public opinion surveys indicated that 93% of elk hunters and 62% of landowners would prefer to see the South Dakota elk population increase over the next 5 years (Longmire 2014). The Black Hills offered a unique opportunity to examine the fundamental niche of puma in the absence of other large carnivores (Moreno et al. 2006) because bears and wolves are absent. Our primary objectives were to estimate annual, age class-specific, female elk vital rates (survival and pregnancy rates); estimate the sensitivity of λ to incremental changes in vital rates using elasticities (de Kroon et al. 1986); examine how elasticity, coupled with observed temporal variation in vital rates in our system, affects variation in λ using life-stage simulation analysis (LSA; Wisdom et al. 2000); and estimate cause-specific mortality rates for adult and calf elk, 2 vital rates we expected to disproportionately affect elk population dynamics because of high elasticity or high temporal process variance, respectively. We predicted that adult female elk survival would have the highest elasticity of age classes and calf survival would explain most of the variation in growth rate.

STUDY AREA

The study area was located in Custer and Pennington counties in the southern part of the Black Hills physiographic region (Flint 1955). The study area consisted of interspersed public and private land, including CSP, which encompasses 286 km^2 (Fig. 1). Elevations ranged from 1,108 m to 2,208 m above mean sea level. Vegetation communities varied from northwest to southeast where forests dominated the landscape at higher elevations and grasslands dominated the southeastern portion of the study area. The climate was semiarid and varied southeast to northwest, with mean annual precipitation ranging 52–54 cm and mean annual temperature ranging 6–9°C across the study area (National Climatic Data Center 2015). The forested portion of the study area was dominated by ponderosa pine (*Pinus ponderosa*). Smaller patches of deciduous forest were characterized by aspen (*Populus tremuloides*), bur oak (*Quercus macrocarpa*), and paper birch (*Betula papyrifera*). Mountain pine beetle (*Dendroctonus ponderosae*) and wildfire disturbance created natural openings across the study area. Western snowberry (*Symphoricarpos occidentalis*) and common juniper (*Juniperus communis*) were common shrubs in the understory of pine forests (Hoffman and Alexander 1987). The eastern third of the study area was primarily a prairie ecosystem with native mixed-grass prairie, agriculture fields, and prairie woodlands comprised of green ash (*Fraxinus pennsylvanica*), cottonwood (*Populus deltoides*), and boxelder (*Acer negundo*; Larson and Johnson 1999).

Potential predators of elk included coyotes, puma (2011–2015 abundance 95% CI = 101–435), and bobcats (*Felis rufus*). The fence surrounding CSP was a 1.5–1.8-m-tall bison (*Bison bison*)-proof fence, but elk could move in and out of CSP and were part of a larger Black Hills population. Custer State Park is bordered on the south by Wind Cave National Park, on the west and north by Black Hills National Forest, and on the east and north by private lands.

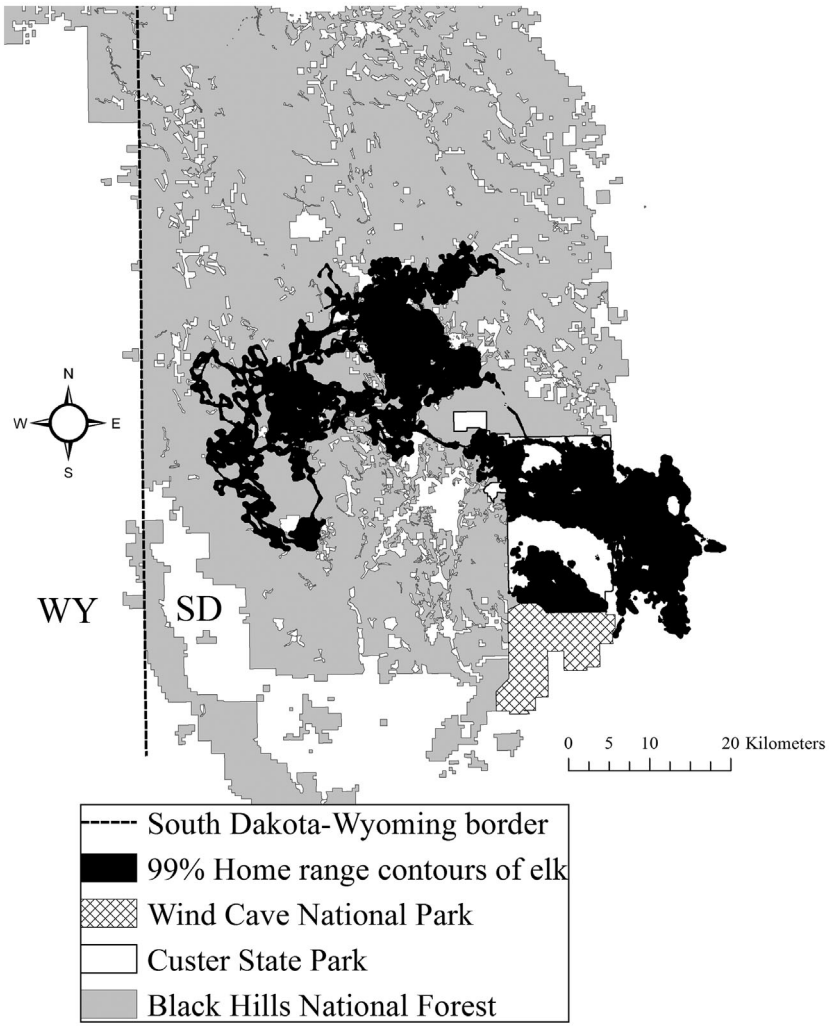

Figure 1. The Black Hills, South Dakota, USA study area where we studied elk demographics, 2011–2015. We provide the spatial distribution of elk using satellite home range locations with 99% Brownian bridge movement model contours.

METHODS

Capture and Radio-Telemetry

We captured female elk using darts fired from helicopters (QuickSilver, Peyton, CO, USA) during February 2011–2013. We sedated elk using butorphanol, azaperone, and medetomidine (Mich et al. 2008). We fitted captured elk with global positioning system (GPS)–very high frequency (VHF) telemetry collars (Telonics, Mesa, AZ, USA; Advanced Telemetry Systems, Isanti, MN, USA). We aged females as adults (>20 months) or subadults (≤20 months) using cementum annuli by extracting an upper canine tooth (Matson's Lab, Milltown, MT, USA; Hamlin et al. 2000). We assessed pregnancy in female elk using rectal palpation (Greer and Hawkins 1967, Vore and Schmidt 2001). We fitted females suspected of being pregnant with a vaginal implant transmitter (VIT; Advanced Telemetry Systems; Barbknecht et al. 2009). We drew blood from each collared female to verify pregnancy using protein-specific B radioimmunoassays (Noyes et al. 1997).

We located female elk daily from 1 April to 31 October. From 1 November to 31 March, we located elk 5 days/week. Starting 1 May, we closely monitored female elk movements and if we located females alone or they started to localize in one area, we located those elk twice daily and checked VIT signals in the morning and evening. Once the VIT signal indicated parturition, we attempted to locate the newborn. One investigator with telemetry gear attempted to locate and observe the dam. After the investigator visually located the dam, additional investigators began searching for the calf using a grid-like search to find the hiding calf. Once found, we fitted the calf with an expandable VHF radio-collar (Advanced Telemetry Systems). We recorded the sex and weighed the calf to the nearest 0.1 kg. All handling, marking, and monitoring procedures were approved by the South Dakota State University Research Committee (Animal Care and Use Committee Approval Number 11-012A).

Modeling Survival Probability and Estimating Reproductive Rates

We assumed survival of individual i during day t was a Bernoulli random variable:

$$y_{it} \sim \text{Bernoulli}\left(y_{i(t-1)}\phi_{it}\right),$$

where $y_{it} = 1$ if individual i survived day t, $y_{it} = 0$ if individual i died during day t, and where p_{it} represented daily survival probability (Royle and Dorazio 2008). We further assumed a logit-linear model for daily survival probability:

$$p_{it} = \text{logit}^{-1}(\beta_{0i} + (\beta_{1i}d_{it} + \beta_{2i}d_{it}^2)I(c_{it} = 1) + \beta_{3i}yr_{it} + \beta_{4i}a_{it} + \beta_{5i}oa_{it}),$$

which we model as a function of age (c_{it}, yr_{it}, a_{it}, and oa_{it} are dummy variables representing whether individual i was classified as a calf, yearling, adult, or old adult, respectively, at time t) and the number of days after a calf was born (denoted d_{it}). Model includes the intercept (β_{0i}) and slope coefficients (β_{1i}–β_{5i}). Note $I(c_{it} = 1)$ is an indicator function with values 1 if individual i is a calf at time t, and value 0 otherwise. We anchor capture days for all individuals at time $t = 0$. We began modeling survival probability at 1 day post-capture (i.e., at time $t = 1$).

We accounted for repeated observations on individuals, and simultaneously partitioned process and sampling variance (Laufenberg et al. 2016), by fitting a random coefficients model. We assumed each coefficient β_{ji} was a Gaussian random variable:

$$\beta_{ji} \sim \text{Gaussian}\left(\mu_j, \sigma_j^2\right),$$

where μ_j and σ_j^2 represented the population-level mean and variance, respectively, of the model coefficients.

We fit this model using Bayesian methods. We assumed a flat prior distribution for μ_0 (the mean of the population-level intercept coefficient) and assumed logistic (0, 1) prior distributions for all other population-level means (μ_1–μ_5). We selected this prior distribution because it translated to a uniform distribution in the inverse logit scale (i.e., if $\nu \sim$ logistic [0, 1], $\text{logit}^{-1}[\nu] \sim$ uniform [0, 1]). We selected inverse gamma (1, 1) prior distributions for variance parameters σ_j^2, which provided little prior information. We fit our model with OpenBUGS version 3.2.3 revision 1012 (Lunn et al. 2000) via the R2OpenBUGS version 3.2-3.2 interface (Sturtz et al. 2005) in program R version 3.4.0 (R Core Team 2017). We ran 3 chains for each model using trace plots to determine an adequate burn-in period and subsequently ran models until we achieved reasonable convergence ($\hat{R} \leq 1.1$; Gelman et al. 2014).

We classified adult and old adult females as pregnant or not pregnant each spring, and obtained raw yearling pregnancy rates from Sargeant et al. (2011), a study conducted in nearby Wind Cave National Park. We estimated pregnancy rates as a function of age class (yearling, adult, and old adult) with a Bayesian logistic regression model. We estimated sex ratios of calves at birth with a Bayesian beta-binomial model (Bolker 2008). We assumed flat prior distributions for all parameters in both models, and performed computations in OpenBUGS as described above.

Estimating Asymptotic Population Growth Rates

We combined estimates of survival probabilities and reproductive rates into a female-based post-breeding projection matrix (Caswell 2001):

$$\mathbf{A} = \begin{bmatrix} 0 & S_Y F_Y \pi & S_A F_A \pi & S_O F_O \pi \\ S_C & 0 & 0 & 0 \\ 0 & S_Y & P_A & 0 \\ 0 & 0 & G_A & S_O \end{bmatrix},$$

where S_C, S_Y, S_A, and S_O represent annual survival probabilities of calves, yearlings, adult, and old adults, respectively; F_Y, F_A, and F_O represent the probabilities a female of the respective age class is impregnated; π is the probability of birthing a female (we assumed pregnant females always give birth to 1 calf; Raedeke et al. 2002); and P_A and G_A are the probabilities of an adult remaining within the adult stage class, and an adult transitioning to the old adult stage class, respectively. We estimated P_A and G_A as functions of S_A following Crouse et al. (1987:equations 1 and 2, respectively). We estimated asymptotic population growth rates, denoted λ, by obtaining the dominant eigenvalue of $\mathbf{A}$. We estimated the elasticity of λ, denoted $\mathbf{E}$, to proportional changes in each matrix element following Caswell (2001: equation 9.73).

We accounted for uncertainty in λ and $\mathbf{E}$ by obtaining random realizations of survival probabilities and reproductive rates. We obtained 3,000 posterior draws of estimated survival probabilities and reproductive rates from the models described above. For each random draw, we constructed a unique projection matrix $\mathbf{A}$, from which we calculated λ and $\mathbf{E}$. Finally, we used LSA (Wisdom et al. 2000) to correlate changes in λ with associated changes in corresponding survival probability, pregnancy rate, and sex ratio.

Cause-Specific Mortality

We determined cause-specific mortality of elk using several diagnostics. When we located a mortality, we photographed and necropsied the carcass immediately. We scrutinized mortality sites for predator sign. We classified cause of mortality as: 1) predation when evidence at the mortality site indicated that the elk had been alive when attacked (e.g., hemorrhaging); 2) hunter harvest; 3) dystocia (Lehman et al. 2012); 4) vehicle collision; 5) sepsis infection; 6) abnormal calf from birth defects; 7) malnutrition; and 8) unknown if mortality cause could not be determined.

We further assigned predation-caused mortalities to species of predator based on characteristics of predator kills (O'Gara 1978). We investigated the area for cache sign, drag marks, scat, and we searched shrubs, downed woody debris, and other vegetation at the site for hairs of predators. We necropsied elk remains, looking for signs of hemorrhaging and bite marks, and we measured bite marks to the nearest mm. We sent saliva, predator hairs, and scat to a lab for mitochondrial DNA analysis to determine species presence at the predation site (Onorato et al. 2006). We placed infrared cameras at predation sites to photograph and identify predator species returning to the carcass immediately following the predation. We classified the mortality as unknown predation if we observed hemorrhaging but could not identify any additional predator characteristics.

We collected organs, blood, and tissue for disease analysis at a diagnostic lab. We tested all elk that had viable brain tissue remaining for chronic wasting disease (CWD). We tested all elk that had viable blood and spleen organs for epizootic hemorrhagic disease (EHD). We classified animals that tested positive for bacteria species in lymph nodes as dying from sepsis infection (Williams and Barker 2001). We classified elk that lacked subcutaneous, mesenteric, and kidney fat and had femur marrow that appeared translucent but gelatinous and tested negative for infection or disease as dying from malnutrition (Sargeant et al. 2011).

We estimated cause-specific mortality rates using cumulative incidence functions (CIF; Heisey and Patterson 2006). We used the wild1 package of Program R (Sargeant 2014) to estimate CIFs, which allowed the estimation of cause-specific mortality in the presence of competing mortality factors (Heisey and Patterson 2006). Competing factors occur when an animal is exposed to >1 potential cause of mortality, and the incidence of one event prevents others from occurring.

RESULTS

We obtained survival data from 184 individual elk; we initially captured 125 as calves ($n = 94$ with the aid of VITs, $n = 31$ without VITs) during ≥1 time step. As calves aged, 32 transitioned to yearlings for monitoring during the study. We monitored 34 yearlings during ≥1 time step and 6 transitioned to adults during the study. We monitored 42 adults during ≥1 time step and 18 transitioned to old adults during the study. We monitored 39 old adults during ≥1 time step. We monitored some individuals over multiple years, while they transitioned to older age classes, which is why the number of elk in each stage totals ≥184 elk.

Annual survival probability varied substantially among age classes and were 0.26 (95% CI = 0.05–0.52), 0.81 (95% CI = 0.43–0.99), 0.95 (95% CI = 0.87–0.99), and 0.94 (95% CI = 0.83–0.99) for calves, yearlings, adult females, and old adult females, respectively. Similarly, pregnancy rates varied substantially among age classes and were 0.10 (95% CI = 0.01–0.24), 0.93 (95% CI = 0.86–0.97), and 0.85 (95% CI = 0.74, 0.93) for yearlings, adults, and old adults, respectively. The estimated probability a calf was female was 0.53 (95% CI = 0.34–0.72).

Combining survival and reproductive rate estimates into a matrix projection model indicated a slightly growing population, although with considerable uncertainty ($\bar{\lambda} = 1.03$, 95% CI = 0.93–1.13; Fig. 2). The elasticity analysis determined asymptotic growth rates were most sensitive to proportional changes in old adult and adult female survival probabilities, followed by proportional changes in calf and yearling survival probabilities (Table 1). Asymptotic growth rates were least sensitive to proportional changes in reproductive rates. Elasticity analysis demonstrates how sensitive asymptotic growth rates are to proportional changes in vital rates, although some vital rates are more variable within and among years than others. Our LSA analysis corroborated asymptotic growth rates were most sensitive to variation in survival probabilities, but because of the substantial temporal variation in estimated calf survival relative to other vital rates, most of the variation in λ we observed was a consequence of variation in calf survival ($R^2 = 0.58$; Fig. 3), followed by old adult, yearling, and adult female survival ($R^2 = 0.16$, 0.15, and 0.08, respectively), and sex ratio ($R^2 = 0.07$). Variation in pregnancy rates had no detectable impact on variation in λ.

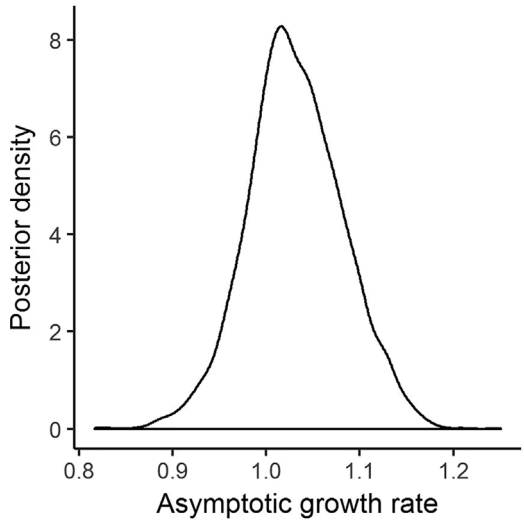

Figure 2. Posterior density of estimated asymptotic growth rate of elk in our study between 2011 and 2015 in the Black Hills, South Dakota, USA. Values <1 indicate declining abundance, whereas values >1 indicate increasing abundance.

Most mortality risk for adult female elk was related to hunting followed by puma predation (Table 2). We documented 1 puma predation for a yearling. Cause-specific mortality risk for calves was overwhelmingly associated with predation by puma (59 of 73 documented mortalities), followed by predation from coyotes (7 of 73 documented mortalities). Non-predation deaths only accounted for 7% of calf mortality (Table 2). Lab results indicated no elk died from CWD or EHD. We did not include some predation mortalities ($n = 6$ puma, $n = 1$ coyote) that we detected using VITs at parturition sites before we were able to mark calves for our mortality and survival analysis.

DISCUSSION

Adult female elk survival in our study (0.95 ± 0.03) was higher than the mean (0.85 ± 0.005) reported across 42 harvested elk populations (Brodie et al. 2013); in the absence of a total regional moratorium on antlerless harvest, this vital rate is likely at, or near, its upper limit (Raithel et al. 2007).

Table 1. Elasticity of asymptotic growth rates to proportional changes in vital rates of elk in the Black Hills, South Dakota, USA, 2011–2015.

Vital rate		95% CI
Old adult female survival probability	0.48	0.18–0.87
Adult female survival probability	0.30	0.09–0.48
Calf survival probability	0.07	0.01–0.13
Yearling survival probability	0.07	0.01–0.13
Old adult fecundity	0.04	0.01–0.05
Adult fecundity	0.03	0.002–0.08
Yearling fecundity	0.001	0.000–0.004

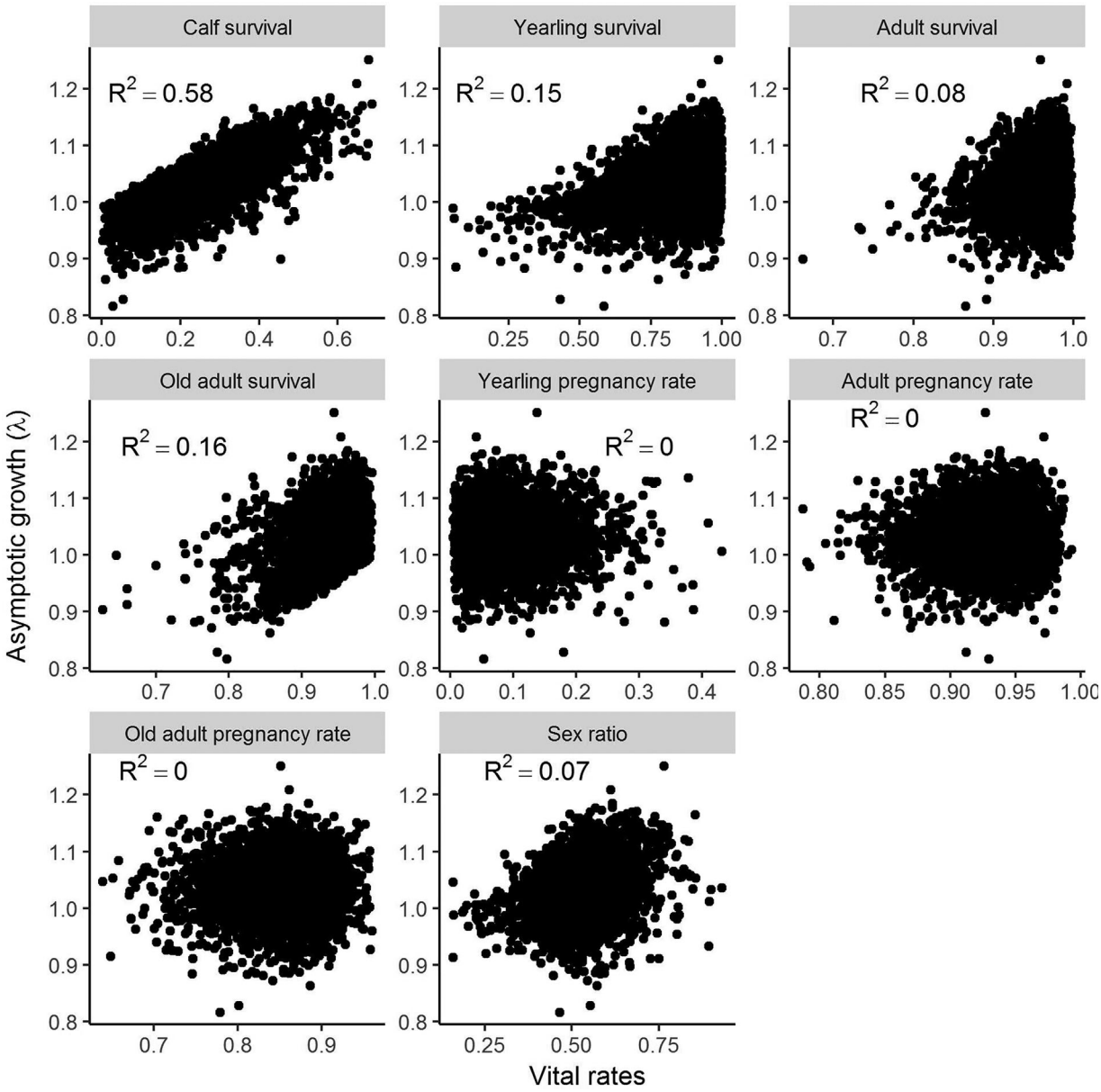

Figure 3. Realizations of estimated asymptotic population growth rates (λ) of elk as a function of survival and reproductive rates of calves (0–1 years old), yearlings (1–2 years old), adult females (2–8 years old), and old adult females (≥8 years old) between 2011 and 2015 in the Black Hills, South Dakota, USA. Scatterplots are based on 3,000 random realizations of estimated vital rates.

However, calf elk survival in our study (0.26 ± 0.12) was lower than the mean (0.35 ± 0.03) reported across 13 elk populations (Raithel 2005) and was well below the upper range from other systems (e.g., 0.72 [Smith and Anderson 1996], 0.62 [Singer et al. 1997], 0.73 [Raithel 2005], 0.78 [White et al. 2010]). In the 4 systems with high calf survival mentioned above, black bears were the primary predator of elk calves in 3 of 4 studies. Black bear predation in several studies ended by 28 days after birth (Singer et al. 1997, Raithel 2005, Rearden 2005, Barber-Meyer et al. 2008, White et al. 2010); perhaps calves suffered little predation after the early neonatal period, resulting in higher annual survival.

We estimated that calf elk survival explained over 3 times more of the variation in λ than variation in adult female survival. Our results support a growing body of evidence that targeting neonatal ungulate survival, despite its low elasticity, can strongly influence λ (Gaillard et al. 1998, Raithel et al. 2007, Barber-Meyer et al. 2008, Boertje et al. 2010, White et al. 2010). In the absence of ursids and wolves, puma predation was the dominant source of mortality on calf elk and limited elk population growth. Non-puma predation was 10 times less prevalent than puma predation. Puma predation rates of 0.12–0.14 on calf elk was the dominant source of mortality in a multi-predator system in west-central Montana (Eacker et al. 2016); in comparison, our estimate of puma predation on calf elk exceeded 0.60. Although we lacked the statistical power of the Griffin et al. (2011) meta-analysis to formally assess whether puma predation constituted an additive source of

Table 2. Estimates of annual mortality rates with 95% confidence intervals and number of deaths observed (*n*) for elk monitored in the Black Hills, South Dakota, USA, 2011–2015.

Age class			
Mortality factor	***n***	**Mortality rate[a]**	**CI**
Adult (≥2 years of age)			
Puma	5	0.04	0.01–0.08
Hunter harvest	8	0.07	0.02–0.12
Dystocia	1	0.01	0.00–0.03
Vehicle collision	2	0.02	0.00–0.04
Infection septicemia	1	0.01	0.00–0.03
Unknown	1	0.01	0.00–0.03
Total	18	0.16	0.09–0.22
Yearling			
Puma	1	0.08	0.00–0.22
Total	1	0.08	0.00–0.22
Calf			
Puma	59	0.63	0.51–0.76
Coyote	7	0.06	0.00–0.13
Bobcat	1	0.02	0.00–0.06
Unknown predation	1	0.01	0.00–0.02
Total predation	68	0.72	0.61–0.81
Malnutrition	2	0.01	0.00–0.03
Unknown	1	0.01	0.00–0.02
Other[b]	2	0.05	0.00–0.20
Total	73	0.79	0.70–0.88

[a] We estimated cause-specific mortality using cumulative incidence functions (Heisey and Patterson 2006).

[b] For the other category, 1 calf was born with a defect and abnormally developed in 2012. In 2013, 1 calf fell into a rock crevice and died.

mortality, given the magnitude and phenology of puma predation in our case study, we posit that pumas can affect additive mortality as the only apex predator in the system, similar to that of bears in other multi-predator systems (Griffin et al. 2011). The phenology of puma predation on calves in our system mirrored that of ursid predation in multi-predator systems (Singer et al. 1997, Raithel 2005, Rearden 2005, Barber-Meyer et al. 2008, White et al. 2010), as calves were primarily killed by puma as neonates (mean age at time of death = 49 days old; Lehman et al. 2017). However, unlike bear predation ending after the first 28 days of life (Singer et al. 1997, Raithel 2005, Rearden 2005, Barber-Meyer et al. 2008, White et al. 2010), we documented continued predation of elk calves throughout the first year. Most calves were killed in their first 60 days (71%), but 29% were killed later in the year (Lehman 2015). Calf elk were mostly killed by puma within the core of their home range in high elk use areas (Lehman 2015, Lehman et al. 2017). Without competition from other large predators, our evidence suggested that the fundamental niche (Hutchinson 1959) of the puma included heavy predation on neonatal elk, similar to grizzly and black bears in systems with a richer predator community (Barber-Meyer et al. 2008, White et al. 2010).

In North America after decades of protection and apex predator management programs, puma have successfully recovered from near extirpation in the early 1900s, leading to reestablishment in many areas (Berger and Wehausen 1991, Boyce and Byrne 2009). Since its listing as a South Dakota state-threatened species in 1978, pumas have increased (South Dakota Department of Game, Fish, and Parks 2010). In 1997, South Dakota Department of Game, Fish, and Parks estimated 40–50 puma resided in the Black Hills, and during our study, estimates of puma abundance for adults and sub-adults was 101–435 (K. A. Robling, South Dakota Department of Game, Fish, and Parks, unpublished data). A 2- to 10-fold increase in the puma population over a 20-year period in the Black Hills was a substantial change in the predator community; elk were previously only exposed to coyotes as the primary predator with low densities of puma through the 1990s (South Dakota Department of Game, Fish, and Parks 2010). Remarkably, no radio-marked elk were killed by puma from 1993 to 1997 during an extensive elk research project from our study area (Millspaugh 1999). Perhaps a dramatic shift in the predator community after a long absence of specific predators may lead to prey becoming naïve to those predators (Jamieson and Ludwig 2012, Jachowski et al. 2016). Elk survival was higher in areas with continued exposure to either human or wolf predation when compared to elk populations naïve to such predators (Frair et al. 2007). We hypothesize that elk maintained cues and habitat selection to avoid predation by coyotes, but this elk population has not had time to develop similar strategies since the rapid recovery of puma in the Black Hills (Lima and Bednekoff 1999, Kuijper et al. 2014).

In multi-predator systems, as the number of predator species increased, neonate survival generally declined, particularly in communities with 5 versus 3–4 predators (Griffin et al. 2011). Our system had only 1 large carnivore, yet calf survival in the Black Hills was consistently lower than reported in several 5-predator systems (Griffin et al. 2011). It has been hypothesized that an increasing, inversely density-dependent predation rate could occur, given a declining prey population and a stable puma population (Rominger et al. 2004, DeCesare et al. 2010). These effects may manifest given the propensity of puma to readily prey on alternate prey, ultimately subsidizing the puma population (Rominger et al. 2004, DeCesare et al. 2010). We hypothesize that in our area, elk abundance has not recovered because the puma population was sustained by white-tailed deer as primary prey, keeping calf elk recruitment suppressed. White-tailed deer (*Odocoileous virginianus*) are abundant in our study area; they have increased from roughly 38,000 to 51,000 during 2013–2016 based on population modeling in the Black Hills (South Dakota Department of Game, Fish, and Parks 2017). A study of puma diets in the Black Hills indicated deer (*Odocoileus spp.*) comprised the majority of puma diets (83%), and white-tailed deer were the dominant species (63%; Smith 2014). Similar patterns of elevated puma predation on less abundant woodland caribou (*Rangifer tarandus caribou*) and mule deer (*Odocoileus heminous*) were observed in areas with abundant white-tailed deer (Kinley and Apps 2001, Robinson et al. 2002).

We hypothesize elk calf survival in our area has been poor since the mid-2000s. The emergence of a recently expanding puma population preying on elk calves during the early neonatal period is a risk that elk had not been exposed to in several decades. Even if elk adapt to this risk via habitat selection (Fogarty and Lehman 2016, Lehman et al. 2016), elk may not rebound because of high

density white-tailed deer acting as a prey base that subsidizes puma at a higher population density, in turn suppressing calf survival. Predator removal is controversial and may only have short-term benefits for ungulate recovery (Hurley et al. 2011). Long-term solutions may include reductions or removal of primary prey, which may benefit a declining species by reducing predator limitation from puma, such as what occurred on the Patagonian steppe where the native guanaco (*Lama guanicoe*) increased when alternate prey (i.e., domestic sheep) were reduced or removed in some areas (Novaro and Walker 2005).

We recognize that our vital rate modeling analysis (stable population with a lot of uncertainty) did not match our aerial survey results from CSP leading up to the initiation of our study. We suspect this may have been the case for several reasons. First, there was considerable uncertainty regarding asymptotic growth rates and the population may indeed still be declining. Additionally, our aerial surveys did not account for imperfect detection, and was conducted only within CSP, although elk routinely moved into and out of the park. Although such a strong decline in aerial counts is almost certainly related to an actual change in underlying abundance, it is possible aerial surveys alone may exaggerate the apparent rate of decline. Finally, by the time we initiated the study (2011), population growth rates may have indeed stabilized following a decade of decline.

Our use of vaginal implant transmitters to target dam-specific neonates allowed us to reduce negative bias in our mortality estimates, because newborns dying from predation or other factors immediately postpartum were more likely detected in our study (Ozoga and Clute 1988, Adams et al. 1995, Pojar and Bowden 2004). A substantial portion of calf elk predation mortality occurred within 5 days of parturition (26%), or during the hiding phase (Geist 1982, Lehman 2015), and without VITs our negative bias potentially would have been much greater. However, the use of VITs did not prevent the loss of some calf survival data; we did not include some dead calves that we found predated ($n = 6$ puma, $n = 1$ coyote) before we could radio-mark them at parturition sites. Even scanning for VIT signals twice a day (morning and evening), we were still unable to mark a small percentage ($\sim$7%) of calves prior to their mortality. Our work highlights the importance of incorporating VITs into future studies estimating neonate ungulate cause-specific mortality.

MANAGEMENT IMPLICATIONS

Because adult female elk survival was near its biological maximum in our system, managing for increased calf survival may be the most practical strategy to increase the elk population. There is an inherent trade-off between elk and puma numbers in this system because this system has only 1 large carnivore. Recovery of this elk population might be supported by 2 logical management actions. First, implementing methods such as hound hunting in elk management units experiencing poor elk calf survival, such as CSP, should enhance harvest of puma in those areas and increase elk survival. Reducing the puma population to support elk population objectives must also consider effects on puma populations in the Black Hills (South Dakota Department of Game, Fish, and Parks 2010). We hypothesize that managing pumas at the lower end of their population objective may promote positive growth of the elk population in the short-term. However, long-term management needs to consider the white-tailed deer population acting as the primary food source for puma in this system. Reducing the white-tailed deer population through hunter harvest of antlerless deer may stabilize the puma population at a lower population density.

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