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RESEARCH ARTICLE

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No long-term effect of black bear removal on elk calf recruitment in the southern Appalachians

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Abstract

In 2001 and 2002, 52 elk (*Cervus canadensis*; 21 males, 31 females), originally obtained from Elk Island National Park, Alberta, Canada, were transported and released into Cataloochee Valley in the northeastern portion of Great Smoky Mountains National Park (GRSM, Park), North Carolina, USA. The annual population growth rate (λ) was negative (0.996, 95% CI = 0.945–1.047) and predation by black bears (*Ursus americanus*) on elk calves was identified as an important determinant of population growth. From 2006 to 2008, 49 bears from the primary elk calving area (i.e., Cataloochee Valley) were trapped and translocated about 70 km to the southwestern portion of the Park just prior to elk calving. Per capita recruitment (i.e., the number of calves produced per adult female that survive to 1 year of age) increased from 0.306 prior to bear translocation (2001–2005) to 0.544 during years when bears were translocated (2006–2008) and λ increased to 1.118 (95% CI = 1.096–1.140). Our objective was to determine whether per capita calf recruitment rates after bear removal (2009–2019) at Cataloochee were similar to the higher rates estimated during bear removal (i.e., long-term response) or if they returned to rates before bear removal (i.e., short-term response), and how those rates compared with recruitment from portions of our study area where bears were not relocated. We documented 419 potential elk calving events and monitored 129 yearling and adult elk from 2001 to 2019. Known-fate models based on radio-telemetry and observational

data supported calf recruitment returning to pre-2006 levels at Cataloochee (short-term response); recruitment of Cataloochee elk before and after bear relocation was lower (0.184) than during bear relocation (0.492). Recruitment rates of elk outside the removal area during the bear relocation period (0.478) were similar to before and after rates (0.420). In the Cataloochee Valley, cause-specific annual calf mortality rates due to predation by bears were 0.319 before, 0.120 during, and 0.306 after bear relocation. In contrast, the cause-specific annual mortality rate of calves in areas where bears were not relocated was 0.033 after the bear relocation period, with no bear predation on calves before or during bear relocation. The mean annual population growth rate for all monitored elk was 1.062 (95% CI = 0.979–1.140) after bear relocation based on the recruitment and survival data. Even though the effects of bear removal were temporary, the relocations were effective in achieving a short-term increase in elk recruitment, which was important for the reintroduction program given that the elk population was small and vulnerable to extirpation.

KEYWORDS

black bear, *Cervus canadensis*, elk, Great Smoky Mountains National Park, population growth, recruitment, reintroduction, senescence, survival, *Ursus americanus*

The eastern subspecies of elk (*Cervus canadensis canadensis*) was once plentiful in the southern Appalachian Mountains of North Carolina and Tennessee, USA (Brickell 1737), but by the 1770s, elk numbers had begun to decline (Van Doren 1955). John James Audubon mentioned that a few eastern elk could still be found in the Allegheny Mountains of Virginia, USA, by 1851, but these elk were essentially gone from the remainder of their range (Gerhart 2005). That decline was most likely caused by overhunting for food, leather, and sport, and high rates of habitat loss from logging and farming (O'Gara and Dundas 2002).

National Park Service (NPS) policy is to restore native animal populations in parks when feasible, so a plan was developed that authorized the experimental release of elk into Great Smoky Mountains National Park (GRSM, Park) in North Carolina (Figure 1). In February 2001, 25 elk (13 males, 12 females) from Land Between the Lakes, Kentucky, USA, consisting of 4 calves, 5 yearlings, and 16 prime-aged adults (2–9 years of age), were chemically immobilized by darting with carfentanil–xylazine (Murrow 2007), transported to an on-site holding facility in Cataloochee Valley in GRSM, and released in April. The elk at Land Between the Lakes were of the Manitoban subspecies (*C. c. manitobensis*) that had originally been obtained from Elk Island National Park, Alberta, Canada. The following year, 27 elk (8 males, 19 females) consisting of 6 calves, 12 yearlings, and 9 prime-aged adults, were obtained directly from Elk Island National Park and were transported to the holding pen at GRSM in February 2002 and released in April.

Murrow et al. (2009) projected the finite annual growth rate (λ) based on survival and recruitment rates (i.e., the number of calves produced per adult female that survive to 1 year of age) from 2001 (i.e., 1 June 2001–31 May 2002) to 2005, which averaged 0.996 (95% CI = 0.945–1.047, 1.0 = stable growth) and the modeled population failed to attain a positive 25-year mean growth rate in 46% of the projections. Murrow et al. (2009) identified poor calf recruitment as an important determinant of the low projected population growth, with

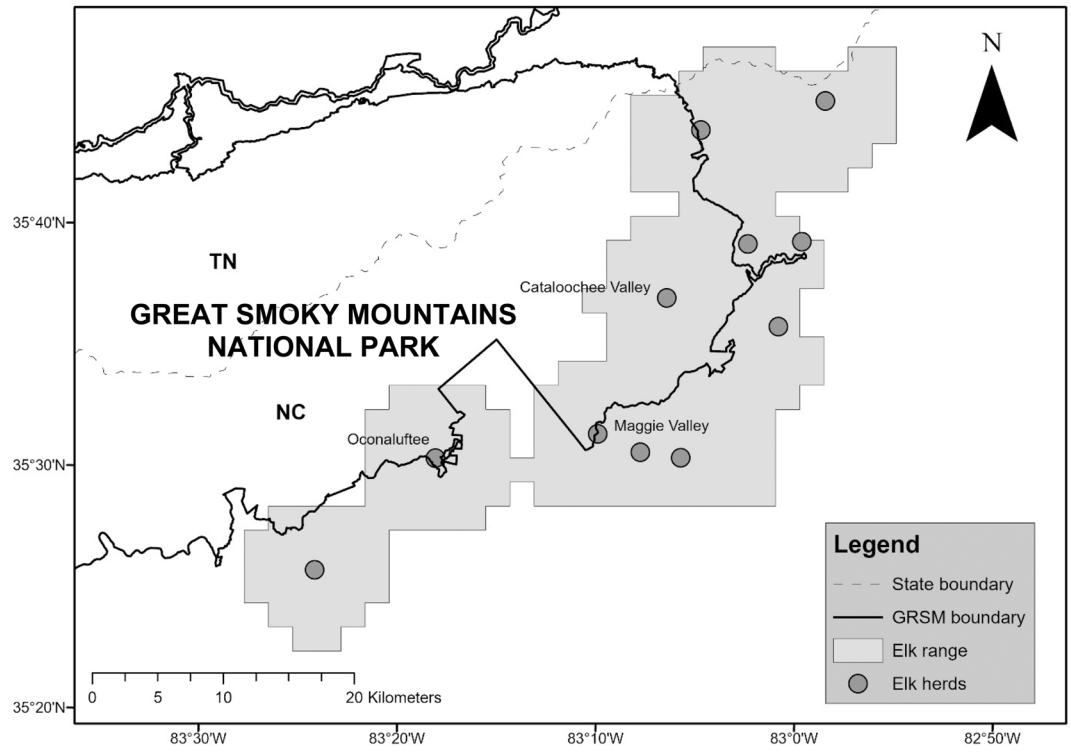

FIGURE 1 Presumed elk distribution (light gray) and known locations of elk populations in North Carolina (gray dots) in and around Great Smoky Mountains National Park (GRSM), North Carolina, USA, 2001–2020.

predation by American black bears (*Ursus americanus*) being the dominant calf mortality factor. Bear densities in GRSM were high (0.92 bears/km^2; Laufenberg 2010) and the translocated elk had no prior experience with bears.

In the eastern United States, black bear predation was not found to be an important mortality factor for elk calves in Michigan (Bender et al. 2002), Kentucky (Larkin et al. 2002), Tennessee (Kindall et al. 2011), or Pennsylvania (DeVivo et al. 2011). Predation by both black and grizzly bears (*Ursus arctos*) on western North American elk calves, however, has been well documented and bear predation is often additive rather than compensatory (Singer et al. 1997, Zager and Beecham 2006, Proffitt et al. 2014, Tatman et al. 2018, Berg et al. 2023). Because of the high incidence of bear predation on elk calves, NPS officials trapped and translocated 49 bears from the primary elk calving area in the Park (i.e., Cataloochee Valley) from 2006 to 2008. Bears were trapped just prior to elk calving and were translocated about 70 km from the calving area to the southwestern portion of GRSM, with the expectation that most would return (Sauer et al. 1969, Beeman and Pelton 1976, Rogers 1986, Stiver 1991), but not until elk calves were a few weeks old and less vulnerable to predators. Yarkovich et al. (2011) reported that, during years when bears were translocated from primary calving areas (2006–2008), annual calf recruitment correlated with the number of bears removed each year and the finite population growth rate increased to 1.118 (95% CI = 1.096–1.140). The bear relocation program was terminated in 2009 when the elk population transitioned from an experimental population classification to a resident Park species (NPS 2011).

As the experimental phase of the elk reintroduction ended and bear relocation was discontinued, park biologists anticipated that the elk had learned how to better cope with bear predation with greater maternal defensiveness and more effective use of hiding cover in the understory for newborn calves (Yarkovich et al. 2011). Zager and Beecham (2006) reported that although black and grizzly bear predation is an important proximate cause of neonatal mortality in ungulates, habitat quality and quantity are important ultimate factors. They suggested that

manipulating bear populations may be successful to boost elk recruitment in the short-term if predation is additive but that long-term success had not been demonstrated. Our objective was to evaluate whether calf recruitment rates after bear removal (2009–2019) at Cataloochee were similar to the higher rates estimated during bear removal (2006–2008; i.e., long-term response) or if they returned to rates before bear removal (2001–2005; i.e., short-term response), and how those rates compared with recruitment from portions of elk range where bears had not been relocated (i.e., non-Cataloochee elk). We predicted that Cataloochee calf recruitment would remain high after bear trapping ceased there but would be unrelated elsewhere in the region where bear trapping did not take place, and that recruitment would be stable for non-Cataloochee elk.

STUDY AREA

Our study took place from 1 June 2001 to 31 May 2020 in GRSM, which was 2,072 km^2 in size (35°26′ to 35°47′N latitude and 83°2′ to 84°0′W longitude) and located adjacent to large, forested tracts of land including Cherokee National Forest to the northeast in Tennessee and Nantahala and Pisgah national forests to the south and east in North Carolina. The Great Smoky Mountains are part of the Unaka Mountain Range in the Blue Ridge Province of the Southern Appalachian Highlands (Fenneman 1938). The terrain is predominantly steep-sloped and mountainous with elevations ranging from 230 m to 2,024 m. The climate was mesothermal perhumid (warm-temperate rain forest) and varied according to elevation, slope, and aspect (Thornthwaite 1948, Stephens 1969). Highest precipitation occurred in July and annual precipitation averaged 140 cm at lower elevations and 216 cm at higher elevations (Stephens 1969). Average annual temperatures ranged from −2°C in December and January to 31°C in July at lower elevations and from −8°C in February to 18°C in July at higher elevations (NPS 2023) with a temperature gradient of 4°C per 1,000-m change in elevation (Shanks 1954). On average, our study area received snowfall 7 days/year at lower elevations and 26 days/year at higher elevations (Shanks 1954). Common mammal species in the area included black bears, white-tailed deer (*Odocoileus virginianus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and eastern gray squirrels (*Sciurus carolinensis*).

Land within GRSM was 99% forested with closed oak (*Quercus* spp.), cove hardwood, hemlock (*Tsuga canadensis*), northern hardwood, open oak–pine (*Pinus* spp.), and spruce (*Picea rubens*)–fir (*Abies fraseri*) cover types (Shanks 1954). Forest cover and road densities were higher on public and private land adjacent to the Park where agricultural fields, pastures, and timber cutting resulted in a greater amount of forest openings. Most of the elk initially released in Cataloochee established home ranges in the immediate vicinity, but some elk dispersed to other grasslands in the Park (i.e., Oconaluftee, ~15 km away) and to areas outside the Park near the towns of Cherokee (~20 km away), Maggie Valley (~10 km away), and elsewhere in North Carolina (Figure 1). Many elk in those subpopulations were permanent residents, but male elk and even some females were known to meander between them. Elk–human conflicts occurred outside GRSM, which involved loss of crops, destroyed fences, and disturbance to cattle (Deerhake et al. 2016). Elk in this population were not hunted, but depredation permits were sometimes granted to landowners experiencing damage. Despite such conflicts, elk restoration in GRSM has long been supported by the public (Hastings 1986) and a survey by the North Carolina Wildlife Resources Commission reported that the majority of landowners in counties adjacent to GRSM were in favor of wild, free-ranging elk (Deerhake et al. 2016).

METHODS

Elk calf recruitment

We monitored adult female elk (≥2 yr old) by visual observation and radio-telemetry using the same general methods as Murrow et al. (2009) and Yarkovich et al. (2011) from 2001 to 2020. All of the originally released

elk were equipped with either very high frequency (VHF) or global positioning system (GPS) radio-collars and we maintained a sample of elk for monitoring by replacing collars and collaring new individuals annually. We estimated the age for each adult animal based on tooth eruption and wear patterns (Quimby and Gaab 1957, Jensen 1999) and we grouped male and female elk into 5 age classes: calves (0 yr), yearlings (1 yr), prime-aged adults (2–9 yr), old-aged adults (10–14 yr), and senescent adults (≥15 yr; Raithel et al. 2007, Murrow et al. 2009, Yarkovich et al. 2011). Although elk were scattered throughout the eastern portion of the Park and on adjacent land, most elk monitored were concentrated around 2 grasslands in GRSM: Cataloochee Valley, where the original elk releases occurred, and Oconaluftee, where dispersing individual elk had established another subpopulation (Figure 1). We defined annual monitoring periods as beginning on 1 June when the peak of elk calving occurred and ending 31 May the following year (e.g., the 2001 monitoring period would begin 1 June 2001 and end 31 May 2002).

Adult female elk typically isolated themselves just prior to parturition, so if a female left the herd, we performed a calf search about 24 hours later. We located females with radio-telemetry and then performed systematic grid searches of areas within about 200 m of those locations. We searched the areas around the females twice daily during the early morning and late afternoon for up to 2 weeks until we successfully located and captured the calves. If we observed females giving birth, we waited several hours before handling the calves to allow for initial imprinting and post-natal care (Espmark 1971). We physically restrained and blindfolded calves to reduce stress (Vreeland et al. 2004) and we fitted them with expandable break-away VHF radio-collars equipped with mortality sensors (MOD-315; Telonics, Mesa, AZ, USA) and marked each calf with a 12-mm passive integrated transponder (PIT) tag (HPT12 FDX; Biomark, Boise, Idaho, USA). Calf handling typically took <5 minutes and we assumed any effects of our activities on calf survival were minimal.

We radio-located collared elk calves ≥1 times/day for up to 5 weeks (Vreeland et al. 2004) and ≥2 times/week thereafter to determine status (alive or dead) and general location. If we detected a mortality signal, we investigated the area to determine mortality cause. Evidence of predation included claw marks, canine punctures, broken vertebrae, or internal hemorrhaging on the calf carcass and predator sign left at the kill site (Wade and Bowns 1993, Mattson 1997, Halbritter et al. 2008). We identified black bear predation by broken vertebrae and puncture wounds found on or near the dorsal inferior portion of the neck and withers, whereas predation from canids typically displays as lacerations and tearing to the ventral superior portions of the neck. We examined hemorrhaging patterns surrounding these wounds to determine predation (pre-mortem hemorrhaging) versus scavenging (post-mortem seepage). Other evidence of species involved included tracks, hair, or the direct presence of the predator at the kill site. We determined survival of a few uncollared calves with known females by periodic visual observations throughout the year and we added those data to the known-fate dataset only if the females or female-calf pairings were regularly observed. In cases when a female exhibited physical signs of parturition (e.g., bloody vaginal discharge, reduced size of abdomen, visibly engorged teats, defensive posturing), but we never observed a calf, we classified the female as having given birth and attributed the loss to unknown causes. Elk whose movements were centered on Cataloochee Valley (i.e., permanent residents of Cataloochee Valley), where bears were removed, were classified as Cataloochee elk and all others were classified as non-Cataloochee elk, where no bear removals took place.

Survival rates of elk calves that we captured and radio-collared are potentially maximum rates, as they were applicable only to calves that were born viable and survived long enough to be observed. Although this potential bias can be overcome if it is known whether females are pregnant before calf capturing begins (Bender et al. 2002), we did not perform pregnancy tests on free-ranging elk. Therefore, instead of estimating calf survival, we estimated calf recruitment (i.e., the number of calves produced per adult female that survive to 1 year of age), which does not require the estimation of pregnancy rates. To code the data, we classified adult females (consisting of collared and some visible uncollared females) that did not produce calves as having calf mortalities at the time the calves would have been born (estimated as 1 June) and females that produced calves that died before May 31 the following year as having calf mortalities at the time of each calf's death. Thus, each known female had a capture history depicting

whether she produced a calf and whether that calf survived to 1 year of age. We summarized all telemetry data monthly to create the capture histories. We used known-fate analysis based on the Kaplan-Meier estimator in Program MARK to model calf recruitment from the monthly observations of individual females and calves in the population over intervals of 1 year (White and Burnham 1999). This methodology is similar to the use of adult female:calf ratios to estimate recruitment (Bender et al. 2002) except that individuals were followed over time so that we could incorporate the dates when calves died into the known-fate model. This approach has the added benefit of being able to directly compare recruitment rates by age class and year and to evaluate other covariates in an information-theoretic context for hypothesis testing.

We used Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 1998) to test the hypothesis that calf recruitment remained high after cessation of bear trapping (long-term response; before [2001–2005] recruitment rates would be lower than during [2006–2008] or after [2009–2019] bear relocation), or that calf recruitment returned to levels before bear trapping began (short-term response; before and after recruitment rates would be lower than during bear relocation). We evaluated an interaction between bear-removal years and location to test the hypothesis that the treatment effect differed where bears were (Cataloochee) and were not relocated (non-Cataloochee). We also fit an annual model and evaluated age of the mother as a covariate and fit models with constant and unequal monthly recruitment rates. We viewed models with $\Delta AIC_c < 2$ as competing (Burnham and Anderson 1998) and 95% confidence intervals of covariates (i.e., β-values) that did not include zero as significant effects. We estimated 95% confidence intervals of summary parameters using the delta method via the emdbook package in Program R version 4.2.1 (Bolker 2020, R Core Team 2022). We estimated calf recruitment from 2001 to 2019, though we used only recruitment data since bear relocation was terminated (2009–2019) to estimate population growth.

Yearling and adult elk survival

To estimate survival for elk ≥1 year of age, we fit those animals with VHF or GPS radio-collars equipped with mortality sensors, and we radio-located elk ≥2 times per week to determine activity status. We equipped radio-collars for adult male elk with elastic material to allow for swelling of the neck during rut. In the event of a malfunctioning or dropped collar or a low battery, we chemically immobilized the animal and replaced the collar if possible. We removed carcasses of dead elk and transported them to the University of Tennessee College of Veterinary Medicine for necropsy when feasible. We summarized survival data for yearling and adult elk monthly and we used known-fate analysis in Program MARK to estimate annual survival for each sex and age class. We modeled elk survival as differing by month, year, sex, location (Cataloochee vs. non-Cataloochee), and age class. Again, we estimated survival for elk ≥1 year of age from 2001 to 2019, though we used only the data from 2009 to 2019 to estimate population growth.

Cause-specific mortality

We used the monthly survival data for calves, yearlings, and adult elk from 2001 to 2019 to estimate annual cause-specific mortality rates as cumulative incidence functions (Heisey and Patterson 2006) using the R package wild1 (Sargeant 2011). As described above, we compared cause-specific mortality rates before, during, and after bear removal to determine if the response was short- or long-term. We tested for different responses by Cataloochee versus non-Cataloochee elk with an interaction effect. Finally, we estimated cause-specific mortality rates due to meningeal worm (*Parelaphostrongylus tenuis*). This parasite inhabits the central nervous system of its primary host, white-tailed deer, which rarely experiences adverse effects (Anderson 1972, Maze and Johnstone 1986). This is the most common disease in restored elk populations in the eastern United States (Eveland et al. 1979,

Raskevitz et al. 1991, Larkin et al. 2003*a*, Chitwood et al. 2018) and may have contributed to the failure of several elk reintroduction attempts in the past (Carpenter et al. 1973, Severinghaus and Darrow 1976).

We estimated cause-specific mortality rates of yearling and adult elk by location, age class, and early (2001–2009) versus late (2010–2019) periods to see if meningeal worm disease prevalence changed over time. We tested for differences in annual cause-specific mortality rates for the scenarios described above based on non-overlapping 95% confidence intervals or chi-square tests with Program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989).

Population growth

We estimated population growth and variance using an individual-based model (Program RISKMAN, version 1.5.413; Ontario Ministry of Natural Resources, Toronto, Ontario, Canada; Taylor et al. 2002, 2003, 2005). Program RISKMAN tracks the fates of individuals in the population depending on whether they live, die, or reproduce based on probability distributions, with the number and age of the animals left at the end of an annual cycle being summed over 1 year or a period of years. This routine required estimates of starting population size, maximum age, maximum reproductive age, standing age distribution, calf survival, age-specific male and female survival, calf sex ratio, and age-specific calf production rates. Larkin et al. (2003*b*) reported that 50% of yearling elk on a high-nutritional diet in Kentucky produced calves. We documented no reproduction by yearlings so we set the minimum age of reproduction at 2, which is higher than in Kentucky but lower than most western elk herds (Bubenik 1982, Hudson et al. 1991). We set the maximum age of reproduction at 20 because we estimated recruitment for females up to 20 years of age and we set the maximum age at 24 because several females in the population were known to be >20 years old. To use calf recruitment rates in the projections instead of calf survival, we set survival of calves at 1.0 (SE = 0) and input our calf recruitment rate estimates for calf production rates for each adult age class. Program RISKMAN provides a stochastic option that uses the variance of input parameters and Monte Carlo techniques to generate a distribution of results, and that distribution is used to estimate the variance of summary parameters (e.g., number at time *i* and the annual growth rate [λ]). We used the sampling standard errors for each parameter rather than annual process standard errors because we did not project future growth. We had no data on effects of elk density on vital rates and assumed that population processes would be little affected at the low elk densities we encountered in our study area. Wisdom et al (2000) demonstrated the importance of including covariation of vital rates in simulation studies of population growth so we allowed vital rates to covary by year.

We began the simulations with the standing age distribution of 93 elk in GRSM on 31 May 2009 (end of the 2008 annual cycle) based on data from Yarkovich (2009). The data for input parameters came from our model estimates from the period after bear removal (2009–2019). We applied the age-specific vital rates based on our top models (Table 1) in a stochastic fashion to the standing age distribution in Program RISKMAN at the beginning of the year, and estimated the number of elk at the end of 1 year based on those projections. We imported the age and sex distributions at the end of that year as starting conditions for the next year's run and repeated this process for each year from 2009 to 2019. We estimated the standard deviation of output parameters based on 5,000 stochastic trials.

RESULTS

Elk calf recruitment

From June 2001 to May 2020, we documented 419 potential calving events (173 Cataloochee and 246 non-Cataloochee events) including adult females that could have but did not produce calves. We radio-collared or

TABLE 1 Program RISKMAN input values used for elk population projections, Great Smoky Mountains National Park, North Carolina, USA, 2009–2019.

RISKMAN inputs	Value	SE
Stochastic trials	5,000	
Initial population	93	0
Maximum age (years)	24	0
Maximum litter size	1	0
Minimum age of reproduction	2	0
Maximum age of reproduction	20	0
Calf sex ratio	0.478	0.002
Recruitment (age 2–9)	0.340	0.031
Recruitment (age 10–14)	0.486	0.062
Recruitment (age 15–20)	0.114	0.046
Male survival (yearlings)	0.667	0.105
Male survival (age 2–9)	0.900	0.030
Male survival (age 10–14)	0.754	0.057
Male survival (age 15–20)	0.742	0.080
Female survival (yearlings)	0.817	0.059
Female survival (age 2–9)	0.949	0.014
Female survival (age 10–14)	0.869	0.031
Female survival (age 15–20)	0.862	0.041

observed 222 of the calves produced (98 males, 107 females, 17 sex unknown; proportion male = 0.478, SE = 0.002). We documented 58 (25 males, 24 females, 9 sex unknown) calf mortalities from 2001 to 2019, 41 of which had determinable causes; undeterminable causes were usually the result of physical degradation because of delayed investigation. Of the 41 mortalities with known causes, 22 (53.7%) were due to bear predation (Table 2).

The short-term bear response model with recruitment rates differing by month and differing during bear removal years compared with the other 2 periods (differed monthly + during bear relocation × location + mother age) was supported more than the long-term model (differed monthly + before bear relocation × location + mother age) with recruitment rates during and after bear removal differing from rates before removal ($\Delta AIC_c = 10.520$), thus rejecting our hypothesis of long-term effects on calf recruitment after bear relocation (Table 3). A time-invariant model (differed monthly + year constant + location + mother age) was not supported ($\Delta AIC_c = 10.029$). Annual recruitment rates were higher for all mother age classes combined during bear relocation at Cataloochee (0.492, 95% CI = 0.380–0.604) than periods before or after (0.184, 95% CI = 0.133–0.235), but rates were similar for non-Cataloochee elk during bear relocation (0.478, 95% CI = 0.356–0.601) when compared with before or after (0.420, 95% CI = 0.356–0.484).

Recruitment rates for all maternal age classes and locations combined from 2001 to 2019 averaged 0.340 calves of either sex per adult female (95% CI = 0.326–0.355). Prime-aged mothers (2–9 yr) had an average annual recruitment rate from 2001 to 2019 of 0.370 calves/adult female (95% CI = 0.352–0.389), old-aged mothers (10–14 yr) averaged 0.516 calves/adult female (95% CI = 0.486–0.545), and senescent mothers (≥15 yr) averaged 0.135 calves/adult female (95% CI = 0.109–0.160). Overall recruitment was lower for Cataloochee (0.233, 95%

TABLE 2 Mortality causes and frequencies and pooled annual cumulative incidence function cause-specific mortality rates for calves and non-calf elk, Great Smoky Mountains National Park, North Carolina, USA, 2001 to 2019.

	Calves					Yearlings and adults				
Mortality cause	Number	Percent	Mortality rate	LCL[a]	UCL[b]	Number	Percent	Mortality rate	LCL	UCL
Bear predation	22	37.9	0.101	0.044	0.158	1	1.2	0.001	0.000	0.007
Unknown	17	29.3	0.078	0.023	0.133	40	46.5	0.048	0.026	0.070
Vehicle	7	12.1	0.032	0.000	0.091	10	11.6	0.012	0.000	0.028
Unknown predation	6	10.3	0.028	0.000	0.085	0	0.0	0.000	0.000	0.000
Meningeal worm	3	5.2	0.014	0.000	0.030	10	11.6	0.012	0.000	0.030
Other disease	2	3.4	0.009	0.000	0.064	5	5.8	0.006	0.000	0.020
Stress	1	1.7	0.005	0.000	0.060	3	3.5	0.004	0.000	0.012
Poaching	0	0.0	0.000	0.000	0.000	6	7.0	0.007	0.000	0.023
Accident	0	0.0	0.000	0.000	0.000	6	7.0	0.007	0.000	0.023
Human conflict	0	0.0	0.000	0.000	0.000	5	5.8	0.006	0.000	0.016
Total	58					86				

[a]95% lower confidence limit.

[b]95% upper confidence limit.

CI = 0.218–0.247) compared with non-Cataloochee elk (0.429, 95% CI = 0.412–0.467). There was a positive interaction effect between location and bear removal (β = 1.152, 95% CI = 0.703–1.601) indicating that the response differed between the 2 locations in the Park. At Cataloochee, recruitment rates for prime-aged mothers were 0.192 (95% CI = 0.129–0.276) before and after bear relocation and 0.543 (95% CI = 0.364–0.712) during bear relocation, for old-aged mothers were 0.313 (95% CI = 0.202–0.449) before and after bear relocation and 0.681 (95% CI = 0.479–0.833) during bear relocation, and for senescent mothers were 0.047 (95% CI = 0.015–0.135) before and after bear relocation and 0.250 (95% CI = 0.096–0.512) during bear relocation. For non-Cataloochee elk, recruitment rates for prime-aged mothers were 0.462 (95% CI = 0.389–0.536) before and after bear relocation and 0.529 (95% CI = 0.318–0.739) during bear relocation, for old-aged mothers were 0.608 (95% CI = 0.485–0.732) before and after bear relocation and 0.668 (95% CI = 0.466–0.871) during bear relocation, and for senescent mothers were 0.189 (95% CI = 0.061–0.316) before and after bear relocation and 0.228 (95% CI = 0.014–0.462) during bear relocation. Recruitment rates before and after bear-removal years at Cataloochee were lower than non-Cataloochee areas, particularly for prime-aged and old-aged mothers (Figure 2). Recruitment rates for all areas combined from 2009 to 2019 were 0.340 (95% CI = 0.279–0.401), 0.486 (95% CI = 0.364–0.608), and 0.114 (95% CI = 0.024–0.204) for prime-aged, old-aged, and senescent females, respectively, which we used for growth rate estimation (Table 1).

Yearling and adult elk survival

From June 2001 to May 2020, we monitored 129 yearling and adult elk (48 males, 81 females) and documented 86 (38 males, 48 females) mortalities; of those, cause of mortality could be determined for 46 (53.5%, Table 2). Of the 46 mortalities whose cause was known, 10 (21.7%) were due to meningeal worm and 10 (21.7%) were caused by vehicle collision.

TABLE 3 Information-theoretic results for models to estimate recruitment of elk calves at Great Smoky Mountains National Park, North Carolina, USA, 2001–2019.

Model	AIC_c[a]	ΔAIC_c[b]	AIC_c weight	Model likelihood	K[c]	Deviance
differed monthly[d] + during bear relocation[e] × location[f] + mother age[g]	659.545	0.000	0.718	1.000	12	635.402
differed monthly + during bear relocation + location + mother age	661.681	2.136	0.247	0.344	11	639.560
differed monthly + year × location + mother age	666.168	6.623	0.026	0.037	30	605.304
differed monthly + year constant + location + mother age	669.575	10.029	0.005	0.007	10	649.474
differed monthly + before bear relocation[h] × location + mother age	670.065	10.520	0.004	0.005	12	645.921
differed monthly + during bear relocation + location	676.169	16.624	0.000	0.000	9	658.086
differed monthly + year + mother age	690.428	30.883	0.000	0.000	27	635.727
differed monthly + year	704.682	45.137	0.000	0.000	25	654.080

[a]Akaike's Information Criterion corrected for small sample sizes.

[b]Difference in AIC_c score compared with top model.

[c]Number of parameters.

[d]Recruitment varied across months.

[e]During bear relocation differing from before or after (i.e., returned to lower recruitment).

[f]Cataloochee versus non-Cataloochee.

[g]2–9 (prime-aged), 10–14 (old-aged), ≥15 (senescent).

[h]Before bear relocation differing from during or after (i.e., recruitment remained high).

The top known-fate model consisted of survival being constant across months and independently varying by sex and age class (age class + sex; Table 4). A similar model with location as a covariate was not supported (ΔAIC_c = 1.999; β = 0.013, 95% CI = −0.420–0.446). Estimates of annual survival from 2001 to 2019 for male elk ≥1 year of age averaged 0.785 (95% CI = 0.730–0.841) and females averaged 0.884 (95% CI = 0.854–0.915). Male survival varied by age class, averaging 0.734 (95% CI = 0.613–0.855) for yearlings, 0.896 (95% CI = 0.858–0.933) for prime adults, 0.767 (95% CI = 0.671–0.864) for old adults, and 0.746 (95% CI = 0.592–0.900) for senescent adults. For females, annual survival from 2001 to 2019 averaged 0.855 (95% CI = 0.785–0.925) for yearlings, 0.946 (95% CI = 0.926–0.966) for prime adults, 0.874 (95% CI = 0.822–0.927) for old adults, and 0.862 (95% CI = 0.781–0.942) for senescent individuals. Survival estimates from 2009 to 2019 used for population projection were similar to the 2001 to 2019 rates (Table 1).

Cause-specific mortality

From June 2001 to May 2020, we monitored 58 calves and recorded 22 mortalities due to bear predation and 6 from predator species that could not be confirmed. Cause-specific calf mortality rates due to bear predation were 0.101 (95% CI = 0.044–0.158), followed by unknown (0.078, 95% CI = 0.023–0.133; Table 2). We recorded 19 calf mortalities due to bear predation on elk calves at Cataloochee and annual cause-specific mortality rates were 0.319 (95% CI = 0.075–0.563) before, 0.120 (95% CI = 0.000–0.296) during, and 0.306 (95% CI = 0.145–0.467) after bear

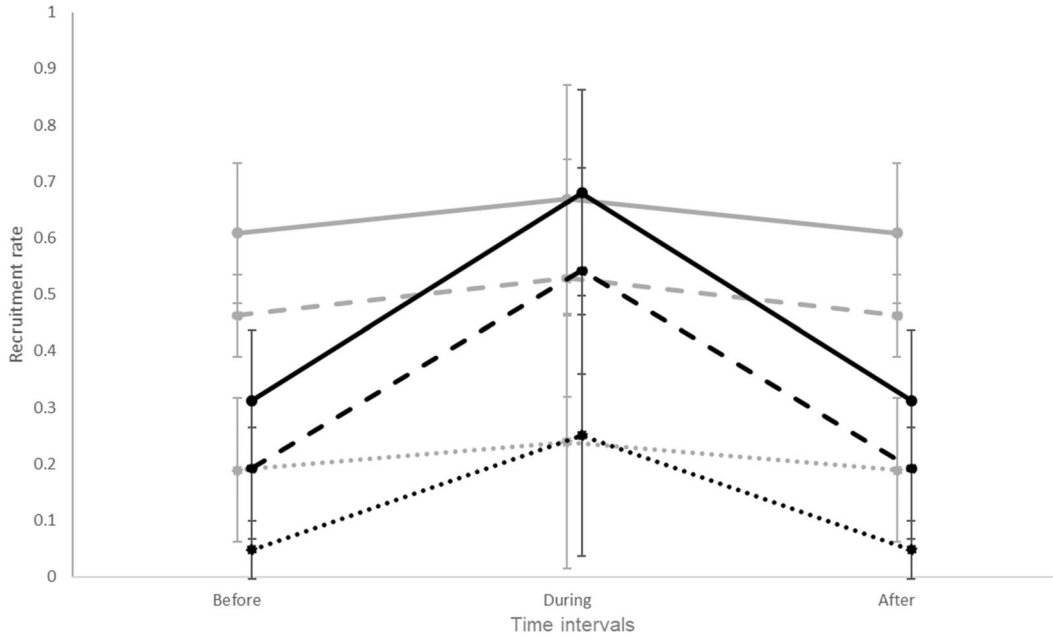

FIGURE 2 Annual calf recruitment rates before, during, and after bear removal at Cataloochee (black lines) compared with elk outside of Cataloochee (gray lines) in Great Smoky Mountains National Park, North Carolina, USA, 2001–2019. Error bars represent 95% confidence intervals. Prime-aged females (2–9 yr) are depicted by dashed lines, old-aged females (10–14 yr) by solid lines, and senescent females (≥15 yr) by dotted lines.

TABLE 4 Information-theoretic results for models to estimate survival of yearling and adult elk at Great Smoky Mountains National Park, North Carolina, USA, 2001–2019.

Model	AIC_c[a]	ΔAIC_c[b]	AIC_c weight	Model likelihood	K[c]	Deviance
age class + sex	972.815	0.000	0.586	1.000	5	962.809
age class + sex + location[d]	974.814	1.999	0.216	0.368	6	962.805
differed monthly[e] + age class × location + sex	977.515	4.700	0.056	0.095	16	945.458
age class × location + sex	978.721	5.907	0.031	0.052	9	960.703
year	996.733	23.918	0.000	0.000	12	972.700

[a]Akaike's Information Criterion corrected for small sample sizes.

[b]Difference in AIC_c score compared with top model.

[c]Number of parameters.

[d]Cataloochee and non-Cataloochee.

[e]Survival rates varied across months.

relocation. Cause-specific mortality rates due to bear predation on calves did not differ before versus during and after bear removal (long-term effect; $\chi^2 = 0.582$, $P = 0.445$) as predicted but there was marginal evidence bear predation was lower during versus before and after bear relocation (short-term effect; $\chi^2 = 2.706$, $P = 0.100$). In non-Cataloochee areas, we recorded only 4 mortalities due to predation (3 by bears and 1 from dog or coyote) and the annual cause-specific mortality rate due to bear predation was 0.033 (95% CI = 0.000–0.101) after bear

relocation. We recorded no mortalities due to bear predation before or during bear relocation at non-Cataloochee areas.

We monitored survival of 86 yearling and adult elk from June 2001 to May 2020 and recorded 10 mortalities due to meningeal worm resulting in a cause-specific mortality rate for the pooled dataset (2001 to 2019) of 0.012 (95% CI = 0.000–0.030; Table 2). Mortality due to meningeal worm did not differ between early and late periods ($\chi^2 = 1.701$, $P = 0.192$), by location (i.e., Cataloochee vs. non-Cataloochee; $\chi^2 = 2.030$, $P = 0.154$), or by age class ($\chi^2 = 1.300$, $P = 0.254$). The annual mortality rate due to vehicle kills was 0.012 (95% CI = 0.000–0.028).

Population growth

Based on survival and recruitment rate estimates from the top models (Table 1), growth simulations from 2009 to 2019 resulted in a mean population growth rate (λ) of 1.062 (95% CI = 0.979–1.140) and an increase from 93 elk in GRSM in 2009 to 179 elk (95% CI = 110–248, 70 males, 109 females) on 31 May 2020 (Figure 3). Most of the population consisted of females because of the difference in survival rates between the 2 sexes and a calf sex ratio slightly favoring females.

DISCUSSION

Though confidence intervals for elk calf recruitment were wide, we were able to demonstrate a short-term effect of bear removal on calf recruitment in the Cataloochee area, whereas we did not identify a change in recruitment in the other areas of the Park (Figure 2). However, there was only marginal evidence that cause-specific mortality

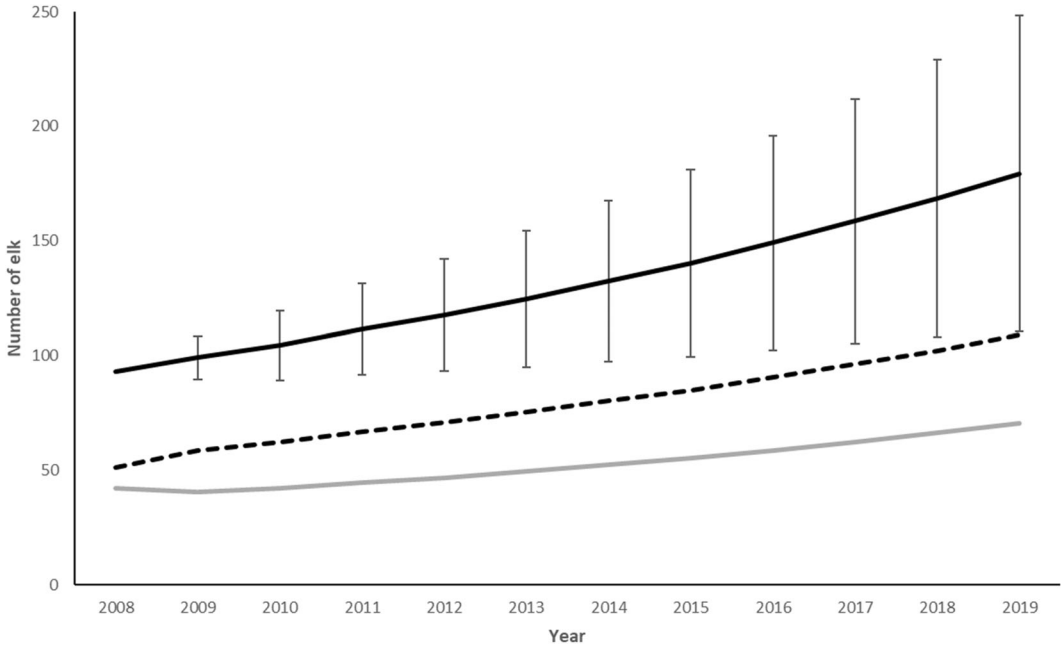

FIGURE 3 Number of elk in Great Smoky Mountains National Park, North Carolina, USA, based on growth projections from vital rates of radio-monitored animals, 2008–2019. The total elk population is the solid black line, females are the dashed line, and males are the gray line. Error bars represent 95% confidence intervals and years begin on 1 June and end 31 May the following year.

rates due to bear predation were lower during bear removal ($P = 0.10$). An important assumption of the cumulative incidence function method is that time of death is estimated with negligible error (Heisey and Patterson 2006) and our monthly intervals may have been too long to produce precise cause-specific estimates. The proportion of known calf mortalities attributed to bear predation (0.379) was high and similar to rates from some western elk studies (Washington, 0.150, Myers et al. 1998; Wyoming, 0.500, Smith and Anderson 1996; Idaho, 0.364–0.660, Schlegel 1976, Zager and White 2003). Bears are opportunist rather than obligate carnivores (Herrero 1978), so it is perhaps not surprising that predation rates vary. Elk recruitment has been reported to negatively correlated with bear density (White et al. 2010, Lukacs et al. 2018) and Humm and Clark (2021) reported that bear densities were higher at Cataloochee Valley compared with Oconaluftee and areas outside the Park. Both Yarkovich et al. (2011) and Murrow et al. (2009) reported that elk reintroduced in 2001 and 2002 were naïve to bears as predators but in later years witnessed female elk defending neonates against bears within Cataloochee. Similar elk behavior has been documented for elk in Yellowstone National Park following reintroduction of wolves (*Canis lupus*; Laundré et al. 2001, Wolff and Van Horn 2003, Creel et al. 2005, Fortin et al. 2005, Halofsky and Ripple 2008). Our results, however, suggest that any behavioral adaptations by elk to predators were insufficient to increase calf recruitment following the cessation of bear trapping and any effects of bear removal on elk recruitment were short-lived. The enhancement and reestablishment of early successional stage cover types through prescribed fire and mechanical vegetation manipulation could help enhance elk foraging habitat in the Park and may help reduce calf predation as a result of greater shrub cover (Singer et al. 1997).

Schlegel (1976) reported that elk survival and recruitment increased following the removal of 75 black bears from their central Idaho study area but returned to previous levels after 2 years. Yarkovich et al. (2011) reported that many bears (16 of 30) did not return to Cataloochee after relocation. It may have taken time for the bear population to fully recover from the relocation losses, and our calf recruitment rates may have exhibited a lag effect following the cessation of bear removal. Indeed, a *post hoc* model with 2 years added to the bear relocation period performed better than the otherwise equivalent original model (differed monthly + during bear relocation × location + mother age], $\Delta AIC_c = 11.428$). Zager and Beecham (2006) reviewed the literature on bear predation on ungulate neonates and concluded that bear predation can be additive when ungulate densities are low and that, although predator reduction may be a short-term solution to low ungulate recruitment rates, longer-term success had not been demonstrated. Proffitt et al. (2020) reported that a reduction in mountain lion (*Puma concolor*) populations corresponded with a short-term increase in elk recruitment and population growth that lessened over time as the predator reduction treatment was reduced. Finally, Sinclair et al. (2003) reported that the removal of predators was associated with an increase in ungulates in the Serengeti ecosystem in Africa but that ungulate populations returned to previous levels after predators were restored. Our results support the conclusions of these studies.

Age of the mother was an important determinant of recruitment rates (Paterson et al. 2022) but, unlike some other studies (Raithel et al. 2007, Bender and Piasecke 2019), we observed higher calf recruitment in old-aged elk (0.516, 95% CI = 0.486–0.545) than in prime-aged elk (0.370, 95% CI = 0.352–0.355). A possible reason for this is that older females may have had more experience with bears and knew how to better avoid depredations on calves. Senescence in elk has been documented as early as age 8 (Moran 1973) and 9–12 years of age in red deer (*Cervus elaphus*). Senescence in female elk can affect pregnancy rates, calf survival, and population growth (Bender and Hoenes 2017, Bender and Piasecke 2019, Hoy et al. 2020, Paterson et al. 2022). Bender and Hoenes (2017) noted that the effects of senescence on population productivity in ungulates is difficult to reduce because low recruitment rates tend to skew the age distribution toward older age classes further, thus propagating the effect over time. Some of the older-aged females in our study have been radio-monitored for many years and the proportion of senescent females in the population at Cataloochee increased over time and was higher than for the non-Cataloochee elk in the study area (Figure 4). Given that senescent females had much lower recruitment rates (0.135) than prime (0.370) or old-aged females (0.516), we suggest that the low calf recruitment in Cataloochee was at least partly due to lower pregnancy rates related to senescence. Regardless, the effect of bear

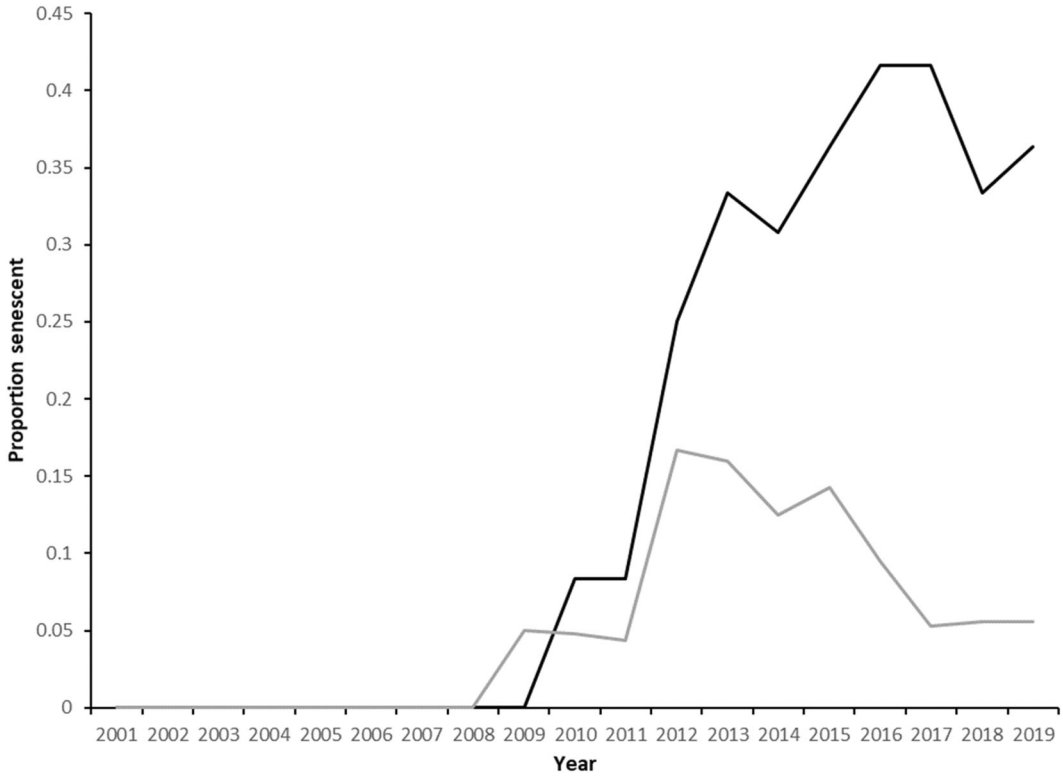

FIGURE 4 Proportion of the combined yearling and adult female elk populations composed of senescent animals (≥15 years of age) at Cataloochee (black line), and elsewhere (non-Cataloochee elk) in Great Smoky Mountains National Park (gray line), North Carolina, USA, 2001–2019.

removal on calf recruitment was evident in non-senescent age classes of female elk at Cataloochee but not elsewhere (Figure 2).

The proportion of known adult (≥2 yr) elk mortalities attributed to meningeal worm in our study was 0.217, which is lower than reported for Kentucky (0.453; Popp et al. 2014) but higher than Tennessee (0.139 [adjusted to known mortalities only]; Kindall et al. 2011), and Arkansas (0.118; Popp et al. 2014). Ten deaths over our entire study period were linked to meningeal worm, but we only recorded 1 case after 2010. Although there was no age class effect ($\chi^2 = 1.300$, $P = 0.254$), we recorded no deaths associated with meningeal worm in elk >10 years old, with most deaths being in elk <4 years old. Larkin et al. (2003*a*) reported similar results whereby most meningeal worm deaths in Kentucky occurred in elk <3 years of age. In contrast, Chitwood et al. (2018) reported that older translocated elk were associated with meningeal worm deaths in Missouri, USA. Infected elk are prone to secondary infections or developing abnormal behaviors that may lead to increased risk of predation, vehicle collisions, or removal by wildlife officials. These mortalities may not be reported as being linked to meningeal worm so our estimate likely was biased low (Keller et al. 2015). Although meningeal worm was among the predominant adult elk mortality factors in our study area, Popp et al. (2014) concluded that the negative effect of meningeal worms on elk reintroduction success in the eastern United States appears lower than initially suspected. Prescribed fire may help reduce the presence of the gastropod intermediate host for meningeal worm (Alexy 2004). Vehicle kills were also an important mortality factor and most were at Oconaluftee where a busy highway was adjacent to a large meadow commonly used by elk.

We could not estimate population growth rates by location because the standing age distribution of elk in outlying areas was not known. However, population growth was likely higher for non-Cataloochee elk based on our

higher estimated recruitment rate and equivocal survival rates compared with Cataloochee elk. Most predation events occurred in and adjacent to the grasslands at Cataloochee and Yarkovich et al. (2011) and Murrow et al. (2009) observed individual female elk that had previously lost calves to bears within Cataloochee moving to areas outside GRSM to successfully give birth. Burcham et al. (1999) report elk moving from public to private land to avoid pressure from hunters or predators and bear predation events in our study were much less common along the periphery (i.e., Oconaluftee) and outside the Park. Furthermore, the amount of grassland in GRSM was limited (0.51%; Homer et al. 2015) and agricultural areas in surrounding private land have been colonized by dispersing elk that were not radio-collared as part of our study. Thus, our estimated population growth rates at Cataloochee are likely lower than in areas outside the Park boundary.

MANAGEMENT IMPLICATIONS

Even though there were no long-term effects of bear relocation on elk calf recruitment, bear translocation may have been an effective management strategy during the early phases of elk population reestablishment, as bear relocation and associated increases in recruitment rates occurred during a time when the fledgling elk population was vulnerable to extirpation. Management reductions of black bears may produce short-term increases in calf recruitment, but these effects may return to pre-management levels within 1 to 3 years. Moreover, the removal of more bears from Cataloochee may not produce the desired effect given the number of senescent female elk there. Options for managing the senescent elk in the Cataloochee herd are limited, as elk in the Park are protected from hunting. The growth potential for this elk population may be greatest on public and private lands adjacent to GRSM where fields and other openings are in greater supply and where bear population densities are lower.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

We conducted all capture and handling in accordance with the University of Tennessee Office of Laboratory Animal Care (number 1706).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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