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Survival and cause-specific mortality of elk *Cervus canadensis* in Kentucky, USA

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Wildlife management relies heavily on high quality field data to analyze and predictively model animal population dynamics, evaluate population viability, and ultimately inform management decisions. During 2011–2015, we conducted a study to investigate survival and cause-specific mortality of male and female elk *Cervus canadensis* in a harvested population in southeastern Kentucky, USA, which was established via reintroduction a decade prior. Preliminary male elk survival data led state wildlife managers to modify hunting zone boundaries and establish several areas with limited hunter access mid-way (2013) through our study to attempt to improve male survival and prevent overharvest. Thus, we also investigated the effectiveness of limiting hunter access for improving male elk survival in one of these regulated areas. We captured and radio-monitored 237 (F91:M146) elk, of which 155 (65.4%) died by the conclusion of our study; harvest-related deaths were the leading causes of mortality for both sexes (85.2%; 132/155). Estimated mean annual female and male survival rates were 0.67 (95% CI = 0.53–0.81) and 0.57 (95% CI = 0.45–0.71), respectively. Results from Cox proportional hazards regression models indicated that females < 2 years-of-age ($HR_{\leq 2yoa} = 3.84$, $p = 0.004$) and males ≥ 5 years-of-age ($HR_{5yoa} = 1.83$, $p = 0.01$; $HR_{\geq 6yoa} = 2.26$, $p = 0.004$) had significantly higher hazards of dying compared to other sex-specific age classes. Support also existed for variation in female survival by herd. The establishment of areas that limited hunter access did not affect male elk survival, as estimates were similar pre and post-implementation. Given the probability of mortality from harvest was consistently much higher for both sexes relative to other causes, we suggest that reducing overall harvest permits likely would be the most effective management action for improving elk survival and reducing the potential of overharvest of this population.

Keywords: harvest, hunter access, survival

Ungulate population management is largely focused on maintaining populations that satisfy various, often competing stakeholder groups including both hunters and non-consumptive users. In North America, legal hunter harvest and predator control remain the primary management tools used to manipulate ungulate population dynamics (Stalling et al. 2002). Population-specific management strategies commonly focus on either preserving adequate security habitat for economically valuable trophy males in order to improve survival rates and optimize hunter opportunity (Lyon and Christensen 2002); or control the adult female cohort given that the survival and fecundity of adult females strongly dictates ungulate population growth (Gaillard et al. 1998, 2000). Ungulate avoidance of disturbance is well documented and most pronounced during the hunting season (Stankowich 2008, McCorquodale 2013, Proffitt et al. 2013, Thurfjell et al. 2017). Hunting season structure, length, and hunter density can result in behavioral shifts by ungulates (e.g. increased vigilance and movement patterns) that can decrease hunter success or cause disproportionate harvest of population cohorts, making it difficult to meet management objectives (Stalling et al. 2002, Proffitt et al. 2013).

North American elk *Cervus canadensis* were overexploited and eventually extirpated from their native range in the eastern USA by the late nineteenth century (Larkin et al. 2001). Reintroductions during the 1910s created a few isolated elk populations in Pennsylvania and Michigan (Larkin et al. 2001), but the species remained absent from the majority of its historical eastern range through most of the twentieth century. Between 1997 and 2002, a total of 1541 elk were reintroduced to the eastern portion of Kentucky, USA, to establish a resident population (Larkin et al. 2001, KDFWR [Kentucky Dept of Fish and Wildlife Resources] 2015). Population growth was apparently rapid, reaching a presumed abundance of 10 000 to 12 000 elk by the 2010s (KDFWR 2015). The first elk hunting season in Kentucky occurred during 2001, and hunting has subsequently remained the only applied management strategy since large carnivores are absent from the elk restoration area (KDFWR 2015); although, coyotes *Canis latrans* are present, and American black bears *Ursus americanus* have recently expanded range towards core elk population areas (Larkin et al. 2002a, Murphy et al. 2016). Approximately 700–1000 elk hunting permits have been available annually over the past decade.

Research on elk in Kentucky has focused on survival, movement patterns, and female elk pregnancy rates, all of which are important for population establishment and subsequent growth (Larkin et al. 2001, 2002a, b, 2003b). Only six males were part of initial research, and males have remained largely unstudied in this population. Following anecdotal reports from hunters and guides that the number of male elk had declined by the early 2010s, KDFWR implemented antler point restrictions and spike-only harvest permits to attempt to reduce harvest of male elk (KDFWR 2015). However, because the majority of lands in the Kentucky elk restoration area are privately owned, only 13.0% of the 16 802 km^2 area is publicly accessible (KDFWR 2015), there is an increased chance for hunters to overexploit elk on public lands. Consequently, state wildlife managers implemented a zone system in 2008 to attempt to spatially disperse hunters across the landscape and prevent hunters from clustering on particular lands. With continued concern over the number and availability of male elk to hunters, limited-entry areas (LEA) were established within zones in 2013. A LEA system is designed to limit the number of permits and/or hunters allowed within a specified area and has been shown to positively influence the number of male elk post implementation, particularly of mature age classes (Bender and Miller 1999). KDFWR aimed to minimize the likelihood of local overharvest by forming LEAs that encompassed areas with a high density of public land (KDFWR 2015).

Given the dated information on females and complete lack of information on males, we sought to 1) estimate survival and cause-specific mortality probabilities for both male and female elk, and 2) investigate if the implementation of the limited-entry area harvest strategy influenced elk survival. We hypothesized that hunter harvest would be the primary cause of mortality for both sexes in this population due to the relative lack of non-human predators within the area. Specifically, we hypothesized that the change to a limited-entry area system would increase male elk survival rates, as has been previously reported elsewhere. Finally, we hypothesized that survival rates for individual elk herds within the limited-entry area would vary based on the ownership type of lands that those herds primarily occupied.

Material and methods

Study area

Our study area was approximately 300 km^2 (1.8% of the elk restoration area) and was located in the Cumberland Plateau physiographic region of southeastern Kentucky, USA (Fig. 1). This area is characterized by rugged topography, including mountains and ridges of 300–1300 m in elevation, with deep drainages and narrow valleys. The climate is considered temperate humid continental (Hill 1976, Overstreet 1984), with an average annual temperature of 13°C, mean winter temperature of 4°C, and mean summer temperature of 22°C. Coal extraction in the form of mountain top removal surface mining was the dominant land use and has dramatically altered the topography and biota of the landscape, resulting in a mosaic of open grasslands, second and third growth forests, and active and repurposed inactive surface mines (Larkin et al. 2001, Pericack et al. 2018). On repurposed inactive mine sites, dense forest and steep mountains are replaced with man-made contoured valleys and mesas that were replanted with grasses and low-shrub vegetation following mining (Pericack et al. 2018). Both active and repurposed surface mines exist within our study area, including a ~9 km^2 tract of repurposed surface mine that was transitioned to a KDFWR Wildlife Management Area (PVB). Additional sites of interest included a public hunting area that was approximately 32 km^2, comprised of planted grasslands and forested areas with all-terrain vehicle and horse trails (ATV); and a 59 km^2 second growth forest that is a University of Kentucky-owned research forest where hunting was not permitted.

Capture and monitoring

We used corral trapping to capture female elk and juvenile (1.5 years of age [yoa]) males, whereas we used free-range darting to capture subadult and adult males and adult females. We captured elk after each annual elk hunting season ended; male elk captures occurred from 22 January to 31 July for each of three years (2011, 2012 and 2013). Female elk captures occurred from 1 February to 31 March for each of two years (2013 and 2014). We ceased female capture by 1 April each year to reduce the risk of injury to females and unborn calves. We chemically immobilized elk using Carfentanil citrate (Zoopharm, Windsor, Colorado, USA) at a dosage of 0.005–0.020 mg kg^{-1} of estimated body weight (Kreeger and Arnemo 2007), administered via a rifle-propelled dart or jabstick. We approached immobilized elk within five minutes of administering anesthetic and placed all elk in sternal recumbency to reduce the potential for bloat and aspiration. When possible, we did not chemically immobilize calves or yearling females that were captured in corral traps; instead, we used a working chute with a cattle head gate (Tarter Gate Cattlemaster Series 3, Dunnville, KY, USA) to secure the animal. We blindfolded all captured elk

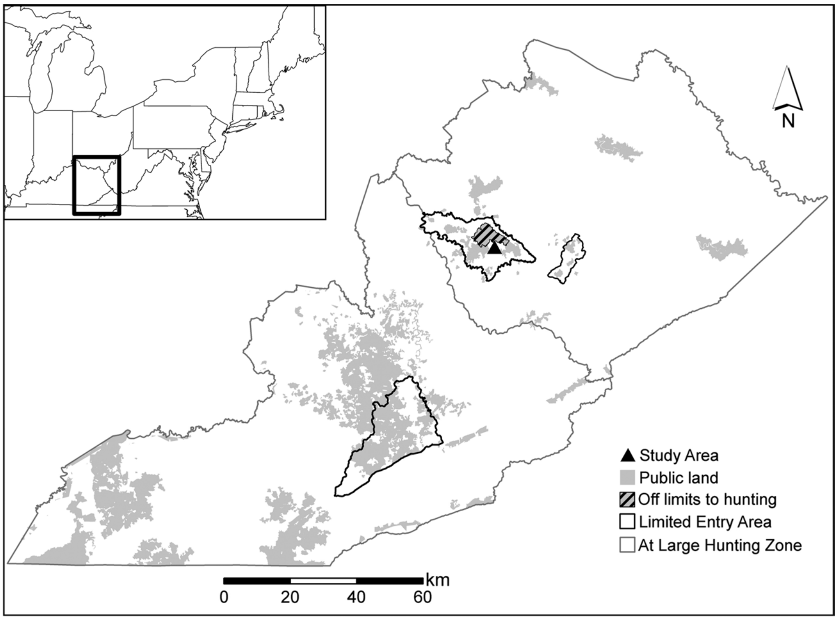

Figure 1. Map of the elk restoration area and elk hunting zones in southeastern Kentucky, USA. The elk restoration area is comprised of a 16 802 km^2 area that encompasses the southeastern portion of the state (inlay). Elk hunting zones within the restoration area changed during the course of our study. The area was divided into six hunting zones for the 2011 and 2012 seasons with limited publicly accessible lands. A limited-entry system was established in 2013 that include two 'at large' areas (outlined in gray) and three limited-entry areas (outlined in black). Our study area was completely encompassed within one of these limited-entry areas.

to reduce visual stressors and applied ophthalmic ointment to the eyes to reduce corneal damage. Respiration, pulse, rectal temperature and mucous membrane color were checked every five minutes during immobilization.

We outfitted each captured elk with either a very high frequency (VHF) radio collar (model: LMRT-4; Lotek, Newmarket, ON) that was individually marked using a colored banding pattern, or a global positioning systems (GPS) collar (model: 8000 MGU; Lotek, Newmarket, ON); GPS collars were only deployed on males. We also applied numbered cattle ear tags to assist with visual individual identification. For all adult elk (> 2 yoa), we administered a local injection of 1 ml of lidocaine at a dosage of 20 mg kg^{-1} to the mental foramen prior to extracting one lower incisor (I4) for age determination via cementum annuli analysis (Fancy 1980). Yearling elk were aged by the presence of one pair of permanent incisors (Hudson and Haigh 2002). We collected 20 ml of blood from the jugular vein of each elk for blood parameter analysis. We recorded total elk body length, hind foot length, and chest girth for all captured elk, as well as the number of antler points, main beam lengths, length of inside spread, beam circumference, and sword point length for all male elk. Antler measurements were taken for male elk in velvet ($n = 39$) but were considered incomplete. Any signs of previous injuries or capture injuries were also noted. We used the antagonist Naltrexone hydrochloride at a dosage of 100 mg per 1 mg of Carfentanil citrate administered to recover immobilized elk, which we delivered via an intramuscular injection into the shoulder or hip. We then monitored elk until they became ambulatory and were out of immediate danger or self-injury (~ 4.5 min on average). All capture and immobilization procedures were approved by a Univ. of Kentucky Institutional Animal Care and Use Committee (protocol no. 2010-0726).

The Kentucky elk hunting season began in mid-September and continued for approximately 120 days annually during our study. The season was partitioned into five segments that included both separate and combined antler and antlerless archery, and two weeks of modern firearm for each class. Archery hunting closed during the four weeks (cumulative) of firearm hunting. We conducted mortality monitoring weekly or bi-weekly via ground or fixed wing air telemetry from mid-February to 31 July. We increased mortality monitoring to three times per week from 1 August to mid-February, encompassing one month prior to the hunting season through one month following the hunting season. We monitored males fitted with GPS collars twice per week via remote downloading of their activity and location data. We investigated all mortality signals within ≤ 12 h of detection. We either submitted dead elk either to the Lexington Diagnostic Disease Center (Univ. of Kentucky, Lexington, KY), or performed a field necropsy at the site of mortality. If viable, we accessed the brain via a lateral section through the skull, and both hemispheres were then formalin-fixed and submitted to the Southeastern Cooperative Wildlife Disease Study (Univ. of Georgia, Athens, GA) for meningeal worm *Parelaphostrongylus tenuis* confirmation testing (Bender et al. 2005).

Survival and cause-specific mortality

We used Cox proportional hazards regression, adjusted for staggered entry and right-censoring implemented in the R software package survival (Therneau and Grambsch 2000, Therneau 2015, <www.r-project.org>), to investigate the factors that may have influenced sex-specific elk survival. We evaluated the primary Cox regression assumption of proportional hazards for each variable in each fitted model by plotting the scaled Schoenfeld residuals against survival times and via a chi-square significance test implemented via the cox.zph function in the survival package (Therneau and Grambsch 2000, Therneau 2015). We computed variance inflation factors (VIF) to investigate multicollinearity between variables and we removed variables from the analysis if multicollinearity was detected (Tabachnick and Fidell 2001). We clustered elk in the analysis by individual identification number because some individuals were monitored for > 1 year and > 1 age class (i.e. correlated observations). We stratified all models by year to produce annual survival probabilities, thereby permitting evaluation of the influence of the limited-entry area on survival. We used Akaike's information criterion corrected for small sample size (AIC_c) for model selection and considered all models ≤ 4 ΔAIC_c competing (Burnham et al. 2011). We obtained sex-specific estimates by producing Kaplan–Meier survival curves from fitted Cox proportional hazards models. We estimated annual survival from the 6 February to 5 of February of the following year to encompass new capture efforts and the totality of the hunting season, including any potential wounding loss mortalities for a given year. To estimate cause-specific mortality probabilities that appropriately accounted for competing risks, we used nonparametric cumulative incidence functions implemented in the R package cmprsk (Heisey and Patterson 2006, Gray 2014).

We fit three a priori Cox proportional hazards models for each sex that included additive combinations of age class and herd location as predictor variables. We grouped males and females by age class differently to reflect the differing reproductive values (Noyes et al. 1996, Wright et al. 2006). Females were grouped as yearlings (< 2 yoa, n = 22), adult (2–8 yoa, n = 62), and old adult (≥ 9 yoa, n = 9), whereas males were grouped as juveniles (2 yoa, n = 31), subadults (3 yoa, n = 34), young adult (4 yoa, n = 39), adults (5 yoa, n = 28), and old adult (≥ 6 yoa, n = 19). Herd location represented the general area where each elk was captured, which differed by landownership type. We calculated antler scores for males, which was a compilation score of antler characteristics that included main beam length, antler beam circumference, total points, and brow length for each side and antler spread, but excluded these scores from our analyses given measurements were incomplete for several males. Recaptures only occurred to recover GPS collars in the event of a collar failure or if a collar prematurely dropped from an elk. Therefore, we could not obtain updated antler measurements for males that were monitored >1 year unless a mortality occurred.

Results

We captured 244 elk (151 male and 93 female) during 2011–2014; collars on two females and six males dropped off prematurely prior to the end of the study or death occurring, which we right-censored. Two females and one male died from capture myopathy and were omitted from the analyses. We euthanized one female and five males because of deteriorating body condition and increased behavioral abnormalities, but we retained these elk in the analyses. We removed four additional males from our data set because of incomplete records. Thus, monitoring data from a total of 91 females and 146 males (n = 237 total elk) were used in our analyses.

Among the remaining 237 elk, a total of 155 (65.4%) elk died during our study period. Hunter harvest was the primary cause of mortality, with 85.2% (132/155) of mortalities being from hunter harvest or wounding loss (i.e. shot by a hunter but not recovered; Table 1). Of those harvest-related mortalities, 56.1% were from firearm, 33.3% were from archery (including crossbow), and 10.6% were from wounding loss (archery = 7.6%; firearm = 3.0%). Wounding loss from archery was not documented in female elk nor was wounding loss from firearms documented in male elk. Nine males succumbed to death from diseases compared to just three females (total disease frequency = 5.1%). Diseases documented included lungworm *Dictyocaulus viviparous* (n = 1 F), meningeal worm *P. tenuis* (n = 1 F and 9 M), and sulfur toxicity (n = 1 F). Other non-harvest causes of mortality were only documented in male elk, with 11 males (4.6%) succumbing to causes such as poaching (n = 1), vehicle collisions (n = 4), fence entanglement (n = 2), euthanasia after becoming trapped in a mine slurry pond (n = 1), and unknown causes (n = 3).

Survival

For male and female elk, ranges of VIF for the predictor variables were 1.03–1.44 and 2.12–5.51, respectively; therefore, we considered multicollinearity low and retained variables in our analyses. Because some support existed for male location violating the proportional hazards assumption (p = 0.06), although statistically insignificant at the 95% confidence level, we included an interaction between time and herd location in all models that included herd location. Only one model was supported for males (≤ 4 ΔAIC_c), which suggested that survival was influenced by age class only (Table 2). Males 5 and ≥ 6 years-of-age had 1.83 (95% CI = 1.13–2.98) and 2.26 (95% CI = 1.30–3.95) higher hazard ratios, respectively. Estimates of male elk survival was 0.70 (95% CI = 0.58–0.86), 0.43 (95% CI = 0.34–0.55), and 0.57 (95% CI = 0.47–0.69) for 2011, 2012 and 2013, respectively (Table 3). Three models were supported for females (≤ 4 ΔAIC_c); the top two models both included age class and only differed by the inclusion or exclusion of herd location, whereas the third model excluded age class but included herd location (Table 2). Given the support for those predictor variables, we only present results from the most parsimonious top model that included both age class and herd location. Yearling females had a 3.84 (95% CI = 1.52–9.70) higher hazard ratio, and females in the PVB and

Table 1. Causes of elk mortality in southeastern Kentucky, USA. A total of 237 elk (F = 91; M = 146) were radio-monitored from 2011 to 2015, of which 155 (65.4%) died.

	Overall	Male	Female
Legal harvest	49.8% (118)	47.9% (70)	52.7% (48)
Wounding loss	5.9% (14)	6.8% (10)	4.4% (4)
Disease	5.1% (12)	6.2% (9)	3.3% (3)
Other	4.6% (11)	7.5% (11)	0.0% (0)
Censored	3.4% (8)	4.1% (6)	2.2% (2)

Table 2. Model selection of stratified Cox proportional hazards models explaining survival of male and female elk in southeastern Kentucky, USA (2011–2015). We stratified by year to produce annual estimates of survival for comparisons and to evaluate the efficacy of a limited-entry area that was established in 2013. We considered the influence of age class and herd location (Herd) on survival of both sexes. We also included an interaction (:) between herd location and time on male survival to overcome violation of the proportional hazards assumption for Herd. We clustered our data by elk identification number (ID) because some individuals were monitored over multiple years and through >1 age class (i.e. correlated observations).

Model	K	AIC_c	ΔAIC_c	logLik
Males				
Age Class + Strata(Year) + Cluster(ID)	4	795.44	0.00	–393.51
Age Class + Herd + Herd:Time + Strata(Year) + Cluster(ID)	13	804.82	9.38	–387.30
Herd + Herd:Time + Strata(Year) + Cluster(ID)	9	814.00	18.56	–397.02
Females				
Age Class + Herd + Strata(Year) + Cluster(ID)	6	416.43	0.00	–201.34
Age Class + Strata(Year) + Cluster(ID)	2	418.01	1.58	–206.89
Herd + Strata(Year) + Cluster(ID)	4	420.25	3.82	–205.71

SJ7 herds had 0.39 (95% CI = 0.16–0.97) and 0.27 (95% CI = 0.09–0.83) lower hazard ratios, respectively. Estimates of female elk survival was 0.65 (95% CI = 0.50–0.83), 0.69 (95% CI = 0.59–0.84), and 0.67 (95% CI = 0.54–0.84) for 2013, 2014, and 2015, respectively (Table 3).

The probability of mortality from harvest was higher over the entire study period for both male and female elk than from all other documented causes of mortality; annual probabilities of mortality from other causes were generally nominal (Table 4). There was no statistically significant difference in mortality from legal harvest between sexes or age classes (Table 4, Fig. 2a–b). Point estimates for mortality from harvest varied among female herd locations, but 95% confidence intervals overlapped among estimates for all herd locations (Table 4, Fig. 2c).

Discussion

Adult ungulate survival rates are high and fairly stable in non-hunted populations (Festa-Bianchet 2007). For instance, reported survival rates of red deer *Cervus elaphus* and elk in non-hunted populations range from 0.9 to 1.0 for both males and females (Larkin et al. 2003b, Catchpole et al. 2004, Brodie et al. 2013). Survival of juvenile age classes (≤ 2 yoa) is highly variable and disproportionately influenced by population density, resource quality, and non-human predation compared to adult survival (Gaillard et al. 1998, 2000, Festa-Bianchet 2007). Nevertheless, legal hunter harvest is the primary cause of ungulate mortality globally, and is a common tool used by managers to manipulate population demographics. To effectively manage populations to meet multiple objectives, an understanding of how different hunting strategies, particularly in relationship to land ownership types, influence survival is necessary.

Frequencies of harvest-related mortality in other states in the eastern USA ranged from 10.0% in Pennsylvania (Banfield and Rosenberry 2015) to 58.0% in Michigan (Bender et al. 2005). This variation is largely due to state-specific harvest regulations, given the extirpation of most native large carnivores from the majority of the eastern USA (e.g. mountain lions *Puma concolor*, gray wolves *Canis lupus* and red wolves *Canis rufus*). Survival rates of male elk in

Table 3. (A) Annual survival probabilities and associated 95% confidence intervals for male and female elk in southeastern Kentucky, USA, from the top stratified sex-specific Cox proportional hazards models. (B) Hazard ratios of variables related to time to death from the top male and female elk stratified Cox proportional hazards models. One level of each variable was used as a reference and was thus part of the intercept.

(A)	2011	2012	2013	2014	2015	$\bar{x}$
Males	0.70 (0.58–0.86)	0.43 (0.34–0.55)	0.57 (0.47–0.69)	–	–	0.57 (0.45–0.71)
Females	–	–	0.65 (0.50–0.83)	0.69 (0.59–0.81)	0.67 (0.54–0.84)	0.67 (0.53–0.81)

(B) Variable	β	HR (95% CI)	Z	p > |z|
Males				
Age class				
2	–0.78	0.46 (0.18–1.17)	–1.62	0.10
3	–0.26	0.77 (0.40–1.47)	–0.79	0.43
5	0.61	1.83 (1.13–2.98)	2.44	0.01
≥ 6	0.82	2.26 (1.30–3.95)	2.89	0.004
Females				
Age class				
1	1.34	3.84 (1.52–9.70)	2.84	0.004
3	0.41	1.50 (0.59–3.82)	0.85	0.39
Herd				
PVB	–0.93	0.39 (0.16–0.97)	–2.02	0.04
SF	–0.59	0.55 (0.24–1.27)	–1.40	0.16
SJ7	–1.32	0.27 (0.09–0.83)	–2.28	0.02
SC	0.52	1.69 (0.81–3.53)	1.39	0.16

Table 4. Estimated cause-specific mortality probabilities and 95% confidence intervals for males and females by year (A), for males by age class (B), for females by age class (C) and for females by herd (D) in southeastern Kentucky, USA (2011–2015) from nonparametric cumulative incidence functions, based on results from the top sex-specific stratified Cox proportional hazards models.

	Males			Females		
(A) Cause	2011	2012	2013	2013	2014	2015
Legal harvest	0.18 (0.08–0.30)	0.44 (0.33–0.54)	0.29 (0.19–0.39)	0.39 (0.24–0.54)	0.28 (0.18–0.38)	0.25 (0.14-0.38)
Disease	0.08 (0.03–0.18)	0.02 (0.01–0.07)	0.04 (0.01–0.99)	0.02 (0.01–0.11)	0.03 (0.01–0.09)	0.00 (0.00-0.00)
Wounding loss	0.00 (0.00–0.00)	0.04 (0.02–0.10)	0.07 (0.03–0.15)	0.02 (0.01–0.11)	0.03 (0.01–0.09)	0.02 (0.01–0.09)
Other	0.00 (0.00–0.00)	0.07 (0.03–0.14)	0.07 (0.02–0.14)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)
	Age class					
(B) Cause	2	3	4	5	6	
Legal harvest	0.22 (0.08–0.41)	0.17 (0.08–0.30)	0.32 (0.21–0.43)	0.47 (0.33–0.61)	0.40 (0.24–0.56)	
Disease	0.00 (0.00–0.00)	0.04 (0.01–0.13)	0.00 (0.00–0.00)	0.08 (0.02–0.18)	0.09 (0.02–0.21)	
Wounding loss	0.00 (0.00–0.00)	0.04 (0.01–0.13)	0.06 (0.02–0.14)	0.02 (0.01–0.10)	0.09 (0.02–0.21)	
Other	0.00 (0.00–0.00)	0.04 (0.01–0.13)	0.05 (0.01–0.12)	0.06 (0.02–0.16)	0.09 (0.02–0.21)	
	Age class					
(C) Cause	1	2	3			
Legal harvest	0.45 (0.24–0.65)	0.27 (0.19–0.35)	0.31 (0.10–0.56)			
Disease	0.00 (0.00–0.00)	0.02 (0.01–0.06)	0.00 (0.00–0.00)			
Wounding loss	0.05 (0.01–0.20)	0.02 (0.01–0.05)	0.08 (0.01–0.30)			
Other	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)			
	Herd					
(D) Cause	ATV	PVB	SF	SJ7	SC	
Legal harvest	0.35 (0.22–0.47)	0.22 (0.10–0.39)	0.33 (0.19–0.48)	0.21 (0.10–0.35)	0.60 (0.07–0.90)	
Disease	0.04 (0.01–0.12)	0.03 (0.01–0.14)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	
Wounding loss	0.06 (0.01–0.14)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.03 (0.01–0.13)	0.00 (0.00–0.00)	
Other	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	0.00 (0.00–0.00)	

Kentucky are comparable to other hunted populations in North America but were generally towards the lower bound of the reported range. For example, annual survival rates of male elk range from 0.60 to 0.67 in Idaho, Alberta and Michigan (Moran and Ozagoa 1973, Unsworth et al. 1993, Hegel et al. 2014), to greater than 0.80 in Washington (McCorquodale et al. 2011).

We found that survival probability of males was substantially influenced by age class, with older age class males (≥ 5 yoa) having 2 to 2.5 times higher hazards of dying compared to younger age classes (Table 3b). Although reports of survival probabilities by individual age class from other studies are limited, McCorquodale et al. (2011) reported no difference in survival between subadult (2–3 yoa) and adult (≥ 4 yoa) male elk in Washington, USA; whereas Bierderbeck et al. (2001) reported a cumulative mortality rate of > 90.0% for males by the age of 4 in Oregon, USA. These differences likely stem from differences in harvest regulations between those two states; harvests in Washington were spike-only harvest after several years of illegal killings (McCorquodale et al. 2011), whereas minimum point restrictions and any-male harvests were in effect in Oregon (Bierderbeck et al. 2001). Although we did not include antler scores in our analysis, results from a survey of elk hunters in Kentucky suggested no intentional harvesting of males based on antler size (KDFWR 2014). When presented with male elk (≥ 2 yoa) of varying antler and body size, an average of 79.7% (551/691) of surveyed hunters indicated a willingness to harvest any of the males presented (KDFWR 2014), suggesting that hunters in Kentucky do not selectively discriminate among males based on traditional trophy characteristics. We note that this finding may contradict the general trend among ungulate hunters and it is axiomatic that surveyed opinion does not necessarily correlate with practice.

Similar to males, harvest was also the leading cause of female elk mortality in Kentucky (94.5% of deaths). The estimated average annual female survival rate of 0.67 (CI = 0.53 – 0.81) in this population is comparable to rates reported from other populations in North America, although it is also near the lower bound of reported ranges. Brodie et al. (2013) investigated 45 elk populations in the western USA and reported a mean female survival rate of 0.84, whereas Webb et al. (2011) reported a female survival rate of 0.80. Manipulation of adult female survival is the primary management tool used to influence elk population dynamics, but a consistent trend of female survival as low as our estimate could negatively impact long-term population productivity and stability (Gaillard et al. 1998, 2000, Stalling et al. 2002). We also found that younger female elk had a nearly four-fold higher risk of mortality compared to adults (e.g. ≥ 2 yoa; Table 3b). Recent research suggested that with increasing age, female elk may learn to avoid hunters and have a strong negative behavioral response to archery harvest techniques given the necessary proximity of archery hunters to individuals (Thurfjell et al. 2017). Although we did not have individual elk movement data in response to hunters, this learned behavior could explain the low survival rate of younger females.

Other causes of mortality such as vehicle collisions and disease were commonly reported in eastern USA elk populations but were infrequently reported in western

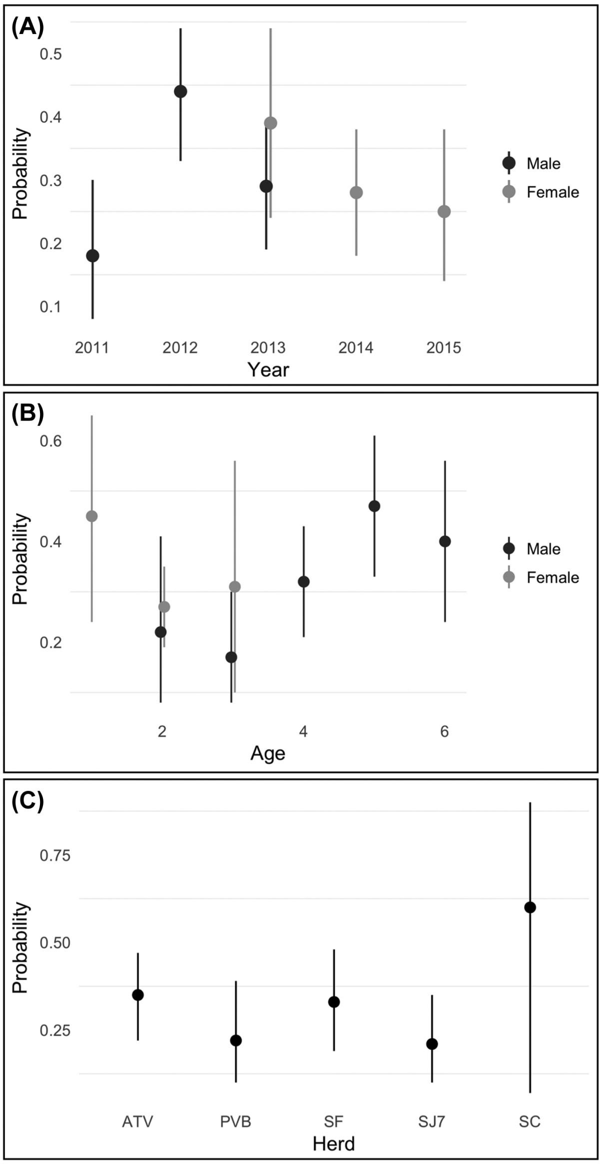

Figure 2. Estimated probabilities of mortality from legal harvest for male and female elk across years (A), by age class for each sex (B), and individual female herds (C) in southeastern Kentucky, USA. Legal harvest was the most probable cause of mortality for both sexes, and probabilities of mortality from harvest did not vary between the sexes (B) or among individual female herds (C).

USA elk populations (Keller et al. 2015). The probabilities of either sex dying from other causes were also low in Kentucky elk, including deaths from *Parelaphostrongylus tenuis*. Infection of *P. tenuis* was originally thought to be a serious concern for elk restoration efforts in the eastern USA (Larkin et al. 2001, 2003a), but it resulted in only 12 mortalities among our sample of Kentucky elk (5.1%; Table 1). In contrast, a total of 24.0% of mortalities in the recently reintroduced elk population in Missouri, USA resulted from *P. tenuis* infection (Chitwood et al. 2018). This was more similar to what was reported in the Kentucky founder group, with 24.8% (36/145) of all mortalities being suspected from *P. tenuis* infection; although, only 5.5% (8/145) were confirmed (Larkin et al. 2003a). Density of white-tailed deer *Odocoileaus virginianus*, a common host of *P. tenuis*, is considered an important factor in the prevalence of this parasite (Slomke et al. 1995). The presumed average density of deer in southeastern Kentucky is approximately 3.6 deer km^{-2} (KDFWR unpubl.), whereas elk released into Missouri appear to inhabit an area with possibly greater deer density (Chitwood et al. 2018). Thus, *P. tenuis* may not be a concern in established elk populations, but it could still impede reintroduction efforts, particularly in areas with moderate to high white-tailed deer densities.

During the first two years of our study, the elk restoration area was divided into six elk hunting zones. A total of 115 permits were available for males within the 2670 km^2 zone that encompassed our study area. Point estimates of male survival during those first two years were 0.70 (95% CI = 0.58–0.80) and 0.43 (95% CI = 0.34–0.55), respectively, supporting a significant decline. Our study area included some of the few publicly accessible lands within the hunting zone, which KDFWR preemptively concluded caused hunters to congregate in the area and reduce male survival in 2012. Subsequently, KDFWR restructured hunting zones in 2013 into two 'at large' areas and three LEAs to attempt to reverse this trend (Fig. 1). Our study area was entirely encompassed within one LEA, for which male harvest permits were also reduced by 55%. Although the point estimate of male survival in 2013 increased by ~ 32%, the 95% confidence interval for 2013 overlapped with both the 2011 and 2012 male survival confidence intervals, indicating the LEA was ineffective. We acknowledge that this could have been the result of other factors that we could not account for, such as sampling error or stochastic variation. In addition, male elk vulnerability to harvest is greater when the hunting season coincides with the rut (Hayes et al. 2002), as is the case in Kentucky. Nearly all harvest of male elk occurred within a 21 to 30-day period overlapping the peak of the rutting season. Therefore, continued monitoring of male survival and mortality is necessary to fully investigate the potential long-term efficacy of LEAs in Kentucky.

For the duration of female elk monitoring, the spatial extents of the LEAs did not change. The SF7, SF, PVB and ATV female herds resided within the LEA (Fig. 3), and variation in survival existed among these herds, with members of the PVB and SF7 herds having lower hazards of dying (Table 3b). Both the SF and SF7 herds primarily resided on privately owned lands, whereas the PVB and ATV herds mostly resided on public lands that differed in hunter accessibility (Slabach unpubl.). PVB is a Wildlife Management Area that was closed to firearm hunting for elk, but it is bordered by land that was open to public hunting as part of a lease agreement. In contrast, the ATV site is a recreational area comprised of a matrix of public and private lands. At the time of our study, large portions of the ATV site were open to public hunting via both modern firearm and archery methods. Female mortality from firearms disproportionately affected the ATV herd, with 46.0% (19/41) of all firearm mortalities occurring within this herd compared to 12.2% (5/41) in the PVB and SF7 herds. These frequencies were also significantly different ($\chi^2 = 12.84$, df = 2, p = 0.002). The proportion of archery mortalities was approximately equal among sites.

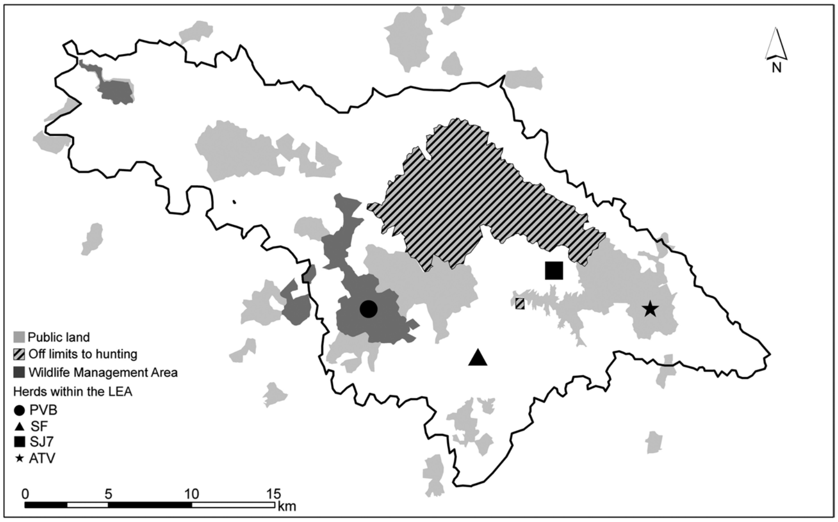

Figure 3. Hunter access differences among sites resulted in varied hazards of death among female herds. The SF and SF7 herds mostly resided on private lands, whereas the PVB and ATV herds resided on mixed ownership sites. The PVB site is a Wildlife Management Area closed to firearm hunting for elk. Comparatively fewer lands that could possibly serve as refugia from harvest were available for the ATV herd; thus, easier hunter access within the ATV site may have increased vulnerability of the ATV herd to harvest.

A total of 237 female elk permits were available during 2012 for the hunting zone that included our study area, resulting in a hunter density of 0.08 hunters per km^2 for female harvest. With the formation of the LEA in 2013, permits were reduced by 12.6%; however, the LEA encompassed 88.0% less land area than did the boundary of the original hunting zone (2670 km^2 in 2012 versus 312 km^2 in 2013). Therefore, hunter density for female harvest actually increased by 647.5%, given permits were nominally reduced with the formation of the LEA. Presumably, hunter density and pressure remained high for the 2013 and 2014 seasons. Thus, our results suggest that a limited-entry strategy that does not directly reduce hunter density via a reduction in permits may allow hunters to continue congregating on more easily accessible public lands.

Management implications

A majority of our study area was accessible by motorized vehicles. Both female and male elk select for habitats with lower human and road densities (Raedeke et al. 2002, Proffitt et al. 2013, Ranglack et al. 2017). In a mixed ownership landscape, this behavioral choice is especially important given the potential reduction of resident elk numbers via local overharvest or elk movement into refugia, reducing the number of elk available to hunters (Proffitt et al. 2013). In theory, a limited-entry strategy could reduce hunting pressure on older age class males and offset the high mortality rates that we observed in these age classes (Bender and Miller 1999). Because of hunter accessibility and limited availability of public lands, decreasing hunter density via further reductions in allotted annual permits would likely be a more successful management strategy for improving elk survival in Kentucky. Although a limited-entry strategy theoretically provides managers with improved control of hunting pressure and harvest within a given area, we suggest that this strategy should be informed by land ownership type, elk density and sex-specific elk behavioral differences.

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