Survival and cause-specific mortality of elk Cervus canadensis calves in a predator rich environment

Authors: DeVivo, Melia T., Cottrell, Walter O., DeBerti, Jon M., Duchamp, Joseph E., Heffernan, Lindsey M., et al.

Source: Wildlife Biology, 17(2) : 156-165

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/10-080

Wildl. Biol. 17: 156-165 (2011)
DOI: 10.2981/10-080

Original article

Survival and cause-specific mortality of elk *Cervus canadensis* calves in a predator rich environment

Melia T. DeVivo, Walter O. Cottrell, Jon M. DeBerti, Joseph E. Duchamp, Lindsey M. Heffernan, Jason D. Kougher & Jeffery L. Larkin

Quantification of basic demographic parameters such as survival rates and cause-specific mortality is important for effective species management. We conducted a 4-year study (during May 2005-June 2009) of elk *Cervus canadensis* calf survival and cause-specific mortality in Pennsylvania, USA. We captured and radio-collared 93 elk calves $\leq$ 7 days old and monitored them weekly to detect mortality and cause of death. Of the 93 radio-collared elk calves, 15 (16%) died during our study. Despite high black bear *Ursus americanus* and coyote *Canis latrans* densities, none of the mortalities were the result of predation. Causes of death included poaching (N = 3), legal harvest (N = 2), road kill (N = 2), pneumonia (N = 1) and rumen acidosis (N = 1). We were unable to determine the cause of mortality for six of the elk calves; however, predation was eliminated as a possible source of mortality in all unknown cases. Survival probabilities were similar between sexes and among years. Summer survival (birth-31 October) was 0.92 (SE = 0.03, N = 93) and winter survival (1 November - 1 April) was 0.90 (SE = 0.04, N = 79). Annual estimated elk calf survival was 0.82 (SE = 0.04, N = 93). Our findings suggest that Pennsylvania elk calves have a > 80% chance of survival to one-year of age, despite high densities of predators known to influence elk calf survival elsewhere. The high calf survival rates that we observed indicate the availability of high quality habitat leading to excellent physical condition of elk.

Key words: calf, Cervus canadensis, elk, predation, Pennsylvania, radio-collar, survival

Melia T. DeVivo, Joseph E. Duchamp, Lindsey M. Heffernan, Jason D. Kougher & Jeffery L. Larkin, Department of Biology, Indiana University of Pennsylvania, 975 Oakland Avenue, Indiana, Pennsylvania 15705, USA - e-mail addresses: mdevivo@uwyo.edu (Melia T. DeVivo); jduchamp@iup.edu (Joseph E. Duchamp); lindseyheffernan@gmail.com (Lindsey M. Heffernan); jason.d.kougher@usda.gov (Jason D. Kougher); larkin@iup.edu (Jeffery L. Larkin)
Walter O. Cottrell & Jon M. DeBerti, Pennsylvania Game Commission, Bureau of Wildlife Management, 2001 Elmerton Avenue, Harrisburg, Pennsylvania 17110, USA - e-mail addresses: wcottrell@state.pa.us (Walter O. Cottrell); jdeberti@state.pa.us (Jon M. DeBerti)

Corresponding author: Jeffery L. Larkin

Received 16 July 2010, accepted 24 January 2011

Associate Editor: Marco Festa-Bianchet

Quantification of basic demographic parameters such as survival rates and cause-specific mortality is important for effective species management (Caughley 1977, Raedeke et al. 2002). Knowledge of these parameters is particularly important for small, hunted populations to ensure the development of appropriate harvest plans. Despite free-ranging elk *Cervus canadensis* populations in seven eastern US states (Tennessee, Kentucky, Pennsylvania, Michigan, Wisconsin, North Carolina and Arkansas), limited published information exists regarding elk calf survival in eastern populations (Cogan 1999, Bender et al. 2002, Seward 2003, Murrow et al. 2009). Calves comprise a large proportion of most elk populations (Peek et al. 1967, Houston 1982) and variations in neonatal elk survival can strongly affect elk demographics (Taber et al. 1982, Raithel et al. 2007, Murrow et al. 2009). Poor calf recruitment was an important determinant of low population growth in a model for a reintroduced elk population in Great Smokey Mountain National Park (Murrow et al. 2009).

Moreover, fluctuations in calf survival explained 75% of the variation in population growth rates of elk in the Rocky Mountain region and northwestern United States (Raithel et al. 2007). Several factors can influence elk calf survival including maternal health and nutrition, birth weight, birth date, disease, predator densities and availability of neonatal cover (Raedeke et al. 2002). An understanding of elk calf survival in small, reintroduced populations such as those in the eastern United States is particularly valuable for determining factors that may limit recruitment and expansion into available habitat.

While nearly 100 years have passed since elk were reintroduced to portions of the eastern United States, there remains a need to elucidate those factors that most influence elk demographics in eastern populations. For example, although population estimates are conducted routinely, survival and fecundity estimates based on large sample sizes and rigorous analyses are lacking for the Pennsylvania elk population. Quantifying juvenile survival is an important step in gaining a better understanding of population dynamics of a reintroduced species (Dinsmore & Johnson 2005). Estimating age-specific vital rates and identifying factors that predispose various elk age classes to mortality will provide valuable information regarding projected population growth and subsequent colonization into available, but vacant, habitat in the eastern United States.

Several studies have documented predation as a major source of elk calf mortality in the western United States (see Raedeke et al. 2002 for review). These studies suggest that predation on elk calves during the first few months of life may have a considerable impact on elk survival and recruitment (Raedeke et al. 2002). Bobcat *Lynx rufus*, black bear *Ursus americanus* and coyote *Canis latrans* are common predators throughout the eastern elk range, and the later two are known to contribute significantly to elk calf mortality (Raedeke et al. 2002, Barber-Meyer et al. 2008, Murrow et al. 2009). Predation by black bear and coyote was the primary cause of calf mortality in a small, recently reintroduced elk population in North Carolina (Murrow et al. 2009). Additionally, recruitment was low in an elk population reintroduced to Ontario in the late 1990s, in part, due to wolf *Canis lupus* predation (Rosatte et al. 2007). As such, it is reasonable to suggest that predation may play a considerable role in regulating calf survival and recruitment in other more established eastern elk populations.

Research that identifies causes of elk calf mortality will aid in determining the potential impact of predation on this cohort. Moreover, the quantification of elk calf predation rates will provide insight regarding how predators may influence the expansion of reintroduced elk populations into vacant habitat. The evaluation of calf survival and causes of mortality also serves as a metric of habitat quality (Bender et al. 2002). Well-nourished neonate elk experience a shorter duration of time, approximately the first four weeks post-birth, when predation and other non-hunting mortality risks are highest (Smith & Anderson 1996). In this paper, we present our findings from a 4-year study of elk calf survival and cause-specific mortality in Pennsylvania. Our objectives were to: 1) generate summer, winter and annual elk calf survival rates, 2) identify proximate causes of elk calf mortality and 3) examine the influence of birth weight and date on calf survival. We predicted that elk calf survival would be low and that predation would be a major cause of mortality due to high black bear and coyote densities in the region.

Methods and material

Study area

In the early 1900s, 177 elk were reintroduced to northern Pennsylvania (O'Gara & Dundas 2002). While population levels remained stagnant through the 1980s (100-200 elk), steady annual increases occurred during the 1990s (> 600 elk; DeBerti 2008). The observed increase in population size was attributed to habitat improvements intended to mitigate human/elk conflicts (DeBerti 2008). A limited-harvest hunting season was initiated in 2001 and from 2001 to 2009 465 elk licenses were issued with an 81% overall harvest success rate. In 2006, the Pennsylvania Elk Management Area (EMA) was expanded from 2,160 km^2 to 9,710 km^2 (DeBerti 2008). At the time of our study, the Pennsylvania elk population was estimated to number 700-800 individuals (DeBerti 2008).

We conducted our study within a 2,160-km^2 portion of the 9,710-km^2 EMA. The majority of the elk population remained within the study area throughout the course of our research even though the boundaries of the EMA were expanded in 2006. The EMA is located within the Allegheny Plateau

Physiographic Province and elevations range from 274 to 701 m a.s.l. (Cogan 1996, DeBerti 2006). The climate is humid continental with hot, humid summers averaging 21°C and cool to cold winters averaging 0°C (Pennsylvania State Climatologist 2006). Average annual precipitation from May 2005 to June 2009 was 82 cm (Pennsylvania State Climatologist). Average seasonal snowfall (October-April) from 2005 to 2009 was 117 cm (range: 38-156 cm), and snow often accumulated on the ground for seven months each year (Pennsylvania State Climatologist).

Public and private lands comprised approximately 74 and 26% of our study area, respectively (DeBerti 2006). The landscape in this region was dominated by forest (80%). Forest communities were consistent with those found in the transitional zone between mixed-oak forests to the south and northern hardwood forest to the north (Braun 1950). Continuous forests were interspersed with open habitats including reclaimed coal surface mines, utility rights-of-way, gas well sites, small farms, managed wildlife openings, riparian habitats, natural meadows and burned areas (wildfires; DeBerti 2006).

Human population density in our study area was on average < 20 people/km^2 (U.S. Census Bureau 2000). Black bear, coyote and bobcat were common throughout the study area. Black bear densities were estimated to be > 3 bears/5km^2 (Ternent 2006). While no density estimates are available for bobcat and coyote, annual harvest rates within our study area are consistently among the highest for the state (M. Lovallo, Pennsylvania Game Commission, pers. comm.).

Calf capture, handling and monitoring

We began searching for neonatal elk when radio-collared cows demonstrated parturient behaviour (Vore & Schmidt 2001), typically between mid-May and late-August 2005-2008. To locate newborn calves, we monitored radio-collared cow elk prior to parturition along with other cow elk that were observed opportunistically. Cows that isolated themselves from other elk and demonstrated high fidelity for a small area were suspected of having a newborn calf (Vore & Schmidt 2001). When this behaviour was observed, we visually monitored these cows for other signs indicative of calving such as reluctance to flee the area when approached by researchers and an enlarged udder (Vore & Schmidt 2001, Hudson & Haigh 2002). We captured calves that were ≤ 7 days old; therefore, only physical restraint was needed when handling animals. We followed animal welfare protocol as outlined by the Pennsylvania Game Commission Standard Operating Procedures, the American Society of Mammalogist (Gannon et al. 2007) and which were approved by the Institutional Animal Care and Use Committee at Indiana University of Pennsylvania (IACUC # 010607).

We marked calves with a uniquely numbered ear-tag and fitted them with expandable break-away Vhf radio-collars that weighed approximately 450 grams (2005-2007 ATS, Minneapolis, Minnesota; 2008 Telonics, Mesa, Arizona) and were equipped with a 4-hour delay mortality sensor. We recorded weight, sex, age, capture location, date, time, radio-collar frequency and ear-tag number of each captured calf. Calves were aged based on hoof and navel characteristics as well as stature and stability as described by Johnson (1951). We estimated birth date by subtracting the estimated age at capture from the date of capture. We estimated male and female daily rate of gain by regressing capture weights on capture age (Smith et al. 1997). The slopes of regression lines represented daily rates of gain and estimated birth weights were compared between males and females. We considered birth weight < 11.4 kg as low and potentially detrimental to calf survival (Thorne et al. 1976). We handled each calf for approximately 10-15 minutes, after which they rejoined the cow once the researchers left the immediate area. We did not document any instances of calf abandonment after handling. We monitored radio-collared calves daily via ground-based radio-telemetry from the capture date to 31 July, and then weekly until transmitters expired or malfunctioned, calf death, the collar dropped off or the end of our study (2 June 2009). Mortality sites were investigated and carcasses retrieved within 24 hours of detecting a mortality signal. When mortality occurred we documented evidence from the field such as condition of the carcass and signs of other animals including tracks and/or scat. Carcasses were transported to the Pennsylvania State University's Animal Diagnostic Laboratory where a wildlife veterinarian conducted a complete necropsy to determine cause of death.

Estimating survival and statistical analysis

We used the Kaplan-Meier product-limit procedure modified for staggered entry (Kaplan & Meier 1958, Pollock et al. 1989) using Ecological Methodology

v. 6.1 software (Exeter Software, Setauket, New York) to estimate summer (birth - 31 October), winter (1 November - 1 April) and annual survival of elk calves. If the exact date of mortality was not known, we estimated the date of mortality as the midway-point between the date on which the calf was last observed to be alive and the date when the carcass was found. We censored calves that shed their radio-collars, had radio-collars that malfunctioned or for which radio contact was lost prior to one year of age. Censored calves were included in our analysis up until collar malfunction. We used the log-rank test to compare survival estimates between sexes and among years (Pollock et al. 1989). We assumed that all calf captures were independent events, all calves had an equal probability of survival and that handling and radio-collars did not affect survival or behaviour (Pollock et al. 1989).

Results

Capture and birth characteristics

We captured and radio-collared 93 neonate elk calves (N = 50 females, N = 43 males) over the 4-year study period (Table 1). All captured calves were ≤ 7 days old at the time of capture ($\bar{x} = 2.5 \pm 1.4$ days). Most (58%, N = 54) captured calves were born to radio-collared cows (see Table 1). Parturition of captured calves occurred from 28 May to 18 August, but 52% (N = 48) of all documented births occurred in the first week of June (see Table 1). Moreover, 80% (N = 74) of all documented elk births occurred within the first two weeks of June. Average birth weight of males ($\bar{x}$ = 16.6 kg, SE = 0.5, range: 9.2-21.2 kg, N = 39) was greater than that of females ($\bar{x}$ = 13.7 kg, SE = 0.3, range: 8.6-19.3 kg, N = 45; t = 5.03, $P < 0.0001$; see Table 1). Male calf rate of gain was 1.21 kg/day and female rate of gain was 1.55 kg/day. Of the 93 radio-collared calves, six (N = 4 females, N = 2 males) had estimated birth weights of < 11.4 kg (range: 8.6-10.8 kg). We were unable to weigh nine neonates due to equipment failure and animal stress. Annual, calf-to-cow ratios for radio-collared cows from 2005 to 2007 were 24:31, 22:31 and 30:46, respectively.

Survival

We censored 16 calves from survival estimates (N = 13 shed collars, N = 2 lost contact and N = 1 collar malfunction). We detected no difference ($\chi^2 < 3.84$, df = 1, $P > 0.05$) in survival probabilities between male and female calves or among years; therefore, we pooled data (Table 2).

Cause-specific mortality

Of the 93 radio-collared elk calves, 15 (16%) were known to have died within the first year of life. All mortality sites were investigated and carcasses retrieved within four days *post-mortem* (range: 0-4

Table 1. Capture and birth characteristics of elk calves captured during 2005-2008 in northcentral Pennsylvania, USA.

	Year				
	2005	2006	2007	2008	Total
Calf captures					
Total	22	15	28	28	93
Radio-collared cows	14	9	15	16	54
Uncollared cows	8	6	13	12	39
Calving period[a]					
Early (28-31 May)	1	0	5	1	7
Peak (1-7 June)	10	7	18	13	48
Late (8 June-18 August)	11	7	5	14	37
Sex					
Male	10	7	13	13	43
Female	12	8	15	15	50
Estimated mean birth weight (in kg)[b]					
Male, $\bar{x}$ (SE)	16.33 (0.57)	17.57 (2.27)	17.74 (0.60)	15.41 (0.78)	16.58 (0.45)
Female, $\bar{x}$ (SE)	14.05 (0.62)	13.07 (0.88)	14.30 (0.62)	13.14 (0.64)	13.71 (0.33)

[a] One calf from 2006 was not aged; therefore, parturition date was not determined.
[b] Calculated using methods described by Smith et al. (2006).

Table 2. Elk calf summer (birth-31 October), winter (1 November-1 April) and annual survival estimates in northcentral Pennsylvania for calves captured during 2005-2008. Survival estimates between sexes and among years were similar ($P > 0.05$); therefore, we pooled data.

						Survival		95% C.I.	
Year	Period	Sex	N collared	N mortalities	N censored	Rate	SE	Lower	Upper
2005	Annual	Both	22	3	2	0.85	0.08	0.70	1.00
2006	Annual	Both	15	1	2	0.93	0.07	0.79	1.00
2007	Annual	Both	28	5	12	0.79	0.08	0.62	0.95
2008	Annual	Both	28	6	0	0.79	0.08	0.63	0.94
2005-2008	Annual	Male	43	3	8	0.92	0.04	0.84	1.00
2005-2008	Annual	Female	50	10	9	0.78	0.06	0.67	0.90
2005-2008	Summer	Both	93	7	7	0.92	0.03	0.86	0.98
2005-2008	Winter	Both	79	8	4	0.90	0.03	0.83	0.96
2005-2008	Annual	Both	93	15	16	0.82	0.04	0.74	0.90

days). Age at time of death ranged from 11 to 249 days and averaged 123 days. Documented causes of calf mortality included poaching (N = 3), legal harvest (N=2), road kill (N=2), pneumonia (N=1) and rumen acidosis (N = 1; Table 3). The cause of mortality for six elk calves was undetermined. However, the excellent condition of these six carcasses combined with no evidence of external trauma (i.e. bite or claw wounds) eliminated predation as a possible cause of mortality. One low-birth weight calf was legally harvested and one died of an unknown cause when it was 11 days old. The remaining four low-birth weight calves survived beyond the duration of our study. Mortality of calves born after the peak calving period (five of 32 known fates) was similar to that of calves born during the peak calving period (10 of 50 known fates). Causes of mortalities of calves that were born after the peak calving period were legal harvest (N= 1), road kill (N = 1), rumen acidosis (N = 1) and unknown (N=2).

Discussion

Our estimate of annual calf survival (0.82) was similar to those previously reported for calves in eastern elk populations in Pennsylvania, Michigan and Kentucky (see Table 3; Cogan 1999, Bender et al. 2002, Seward 2003). Our annual survival estimate was much higher than that for calves in a reintroduced elk population in Great Smokey

Table 3. Comparison of calf survival rates among elk populations throughout North America.

Area	Summer	Winter	Annual	Source
Eastern populations				
Kentucky			0.77	Seward 2003
Michigan	0.90	0.97	0.87	Bender et al. 2002
Pennsylvania	0.92	0.90	0.82	Our study
Pennsylvania			0.71	Cogan 1999
North Carolina			0.59	Murrow et al. 2009
Western populations				
California	0.85			Howell et al. 2002
Northcentral Idaho	0.18-1.00			White et al. 2010
Northcentral Idaho	0.00-0.84		0.06-0.83	Zager et al. 2005
Northcentral Idaho	0.32			Schlegel 1976
Montana		0.82-0.86		Knight 1970
Northern Yellowstone	0.65	0.72	0.43	Singer et al. 1997
Northern Yellowstone	0.29	0.90	0.22	Barber-Meyer et al. 2008
Northwestern Wyoming	0.84	0.84	0.58	Smith & Anderson 1998
Northwestern Wyoming		0.26-0.69		Sauer & Boyce 1983
Southeastern Washington			0.47	Myers 1999

Mountain National Park, which averaged 0.59 (Murrow et al. 2009). Additionally, our summer, winter and annual calf survival estimates in Pennsylvania exceeded those reported for most western elk populations (see Table 3). Contrary to our prediction, predation was not a documented source of calf mortality. This finding is similar to that from a previous study in Pennsylvania, whereby only one of 30 (3%) radio-collared elk neonates was preyed upon by a black bear during 1993-1996 (Cogan 1999). The low predation and subsequent high elk calf survival observed in our study could indicate excellent physical condition of cows and mild winter climates (Clutton-Brock et al. 1987, Singer et al. 1997). Cow elk in excellent condition should produce healthy calves that develop quickly and reduce their vulnerability to predation and other causes of mortality (Thorne et al. 1976, Bender et al. 2002). A concurrent study that examined elk diet in our study area reported seasonal levels of faecal crude protein for adult cow and calf that were higher than required minimal levels (Heffernan 2009). Moreover, faecal crude protein levels for adult cows were highest during spring and summer (Heffernan 2009), the seasons when reproductive demands are greatest (Cook 2002). These findings indicate that cows and calves were acquiring a high quality diet (Heffernan 2009), potentially diminishing the effects of low birth weight, reduced daily growth rates and/or later parturition dates on calf survival (Cook et al. 2004).

Elk calf survival is also a function of the availability of habitat that provides security from human-related disturbances and predators (Phillips & Alldredge 2000). Cow elk in Colorado that were subjected to simulated human disturbance during the calving season showed a decrease in calf-to-cow ratios due to increased calf mortalities (Phillips & Alldredge 2000). The majority (62%, N = 8) of calf mortalities observed in our study were human-related. Human-caused calf mortalities included poaching (N = 3), hunter harvest (N = 2), road kill (N = 2) and rumen acidosis caused by artificial feeding (N = 1). Human encroachment into elk habitat increases the need for elk management strategies that account for human-related disturbances (Lyon & Christensen 2002). Although more than half of the calf mortalities observed in our study were human-related, no single source of known mortality appeared to greatly influence elk calf survival. The six unknown causes of calf mortalities could have been related to a single source but, unfortunately, we were unable to examine the implications of these deaths.

Average male (16.6 ± 0.5 kg) and female (13.7 ± 0.3 kg) birth weights in our study were comparable to male and female birth weights for Kentucky (16.4 ± 0.6 kg and 15.2 ± 0.5 kg; Seward 2003) and Wyoming (16.6 ± 0.29 kg and 15.2 ± 0.31 kg; Smith et al. 2006). Several studies have suggested that birth weight is a good predictor of elk calf survival (Thorne et al. 1976, Clutton-Brock et al. 1987, Smith et al. 1997, Singer et al. 1997, Smith et al. 2006). Thorne et al. (1976) found that elk calves in western Wyoming with birth weights of < 11.4 kg had < 50% chance of survival. Smith & Anderson (1998) found no correlation between calf birth weight and survival in the Jackson elk herd. However, a later study conducted within the Jackson elk herd demonstrated a significant increase in mortality of low birth weight calves (Smith et al. 2006). Smith et al. (2006) suggested that the effect of birth weight on calf mortality may be explained by increased predation by bears and coyotes due to poor spring food resources for both predators and prey. Low birth weight did not appear to negatively impact elk calf survival in our study, considering that only one of six light-born calves died of natural causes. The concurrent study on seasonal diet of Pennsylvania elk demonstrated the availability of high quality forage for elk (Heffernan 2009). Proper nutritional condition of cow elk during gestation likely influenced the production and maintenance of healthy calves (Thorne et al. 1976, Cook et al. 2004). As such, our results provide support for the Smith et al. (2006) hypothesis that availability of high quality forage may mitigate the negative effects of low birth weight by limiting predation of alternative prey such as elk calves by black bears and coyotes.

Date of birth also has been known to influence calf survival in some elk populations (Singer et al. 1997, Smith & Anderson 1998). Survival of elk calves during winter was negatively correlated with late parturition date in northern Yellowstone and Grand Teton National Parks (Singer et al. 1997, Smith & Anderson 1998). Based on our findings, it appears that late parturition did not predispose elk calves to mortality. The relatively mild winters, more predictable spring weather and availability of high quality forage in Pennsylvania compared to western states likely contributed to mitigating the effects of low birth weight and late parturition on elk calf survival.

Our most unexpected finding was that predation was not documented as a cause of elk calf mortality, and calf survival was high despite ecologically meaningful populations of black bear, bobcat and coyote. Predation is the most commonly documented cause of neonatal elk mortality in North America (Schlegel 1976, Singer et al. 1997). Black bears and coyotes accounted for 24% (N = 20) and 11% (N = 9), respectively, of all elk calf predation deaths (N = 98) within the first 30 days after birth in Yellowstone National Park (Barber-Meyer et al. 2008). Predation by black bears and coyote was the dominant elk calf mortality factor in North Carolina, accounting for 92% (N = 12) of all documented mortalities (Murrow et al. 2009). While only a few instances of coyote predation on neonate elk were reported in Kentucky, researchers cautioned that coyote predation may contribute to slow growth of that reintroduced population (Seward 2003). Cox (2003) suggested that as reintroduced elk populations in the eastern United States grow, there was a need to investigate relations among coyote, elk and white-tailed deer *Odocoileus virginianus*.

The significance of predation is not consistent among all eastern elk populations. Annual elk calf survival in Michigan was 0.87 despite the presence of black bear and coyote (Bender et al. 2002); and annual elk calf survival in a reintroduced Wisconsin population was 0.86 in an area occupied by black bear and gray wolf (Lizotte 1998). Only one case of black bear predation on an elk calf was reported previously in Pennsylvania (Cogan 1999), and we did not document a single predation event over our 4-year study. Interestingly, black bear and coyote predation accounted for nearly 70% of white-tailed deer fawn mortalities in a recent study conducted within the Pennsylvania elk range (Vreeland et al. 2004).

One explanation for the lack of elk calf predation by black bears and coyote is that elk are novel prey compared to Pennsylvania's abundant white-tailed deer. Early age of first reproduction (< 1 year) and twining is common in Pennsylvania white-tailed deer (Rosenberry et al. 2009). As such, local predators may not have learned or had the need to exploit elk as a primary food source (Smith et al. 2000). Reintroduced wolves in Yellowstone National Park killed fewer bison *Bison bison*, a novel prey species, than elk which were a more abundant, familiar prey and easier to kill (Smith et al. 2000). Similarly, white-tailed deer fawns in our study area may be easier to capture due to differences in size, densities and maternal defensive behaviour when compared to elk (de Vos et al. 1967, Waldrip & Shaw 1979, Cogan 1999). Species-specific antipredatory behaviour is an important factor that determines deer vulnerability to coyote predation (Lingle & Pellis 2002). White-tailed deer typically flee from predators (Lingle 2001). Conversely, cow elk can deter medium-sized predators such as coyotes (Altmann 1952, Gese 1999) and can lure larger predators away from their calves (Altmann 1963). Thus, fawn abundance may dilute the number of elk calves that predators kill due to prey satiation.

The apparent disparity between elk calf and deer fawn predation rates in Pennsylvania may also reflect previously observed differences between deer and elk neonate resting sites. White-tailed deer fawn rest sites in Oklahoma were located in more open habitats and were less concealed compared to sympatric elk calf rest sites (Waldrip & Shaw 1979). White-tailed deer fawn rest sites have not been examined in our study area; however, we did observe fawns in areas where elk calves were found. Although deer and elk neonates occupied similar areas, further investigation of micro-habitat characteristics at rest sites is necessary to reveal any similarities or differences between these two species.

Management implication

When attempting to expand the range of a reintroduced population, it is critical to identify factors that may limit population growth. This is particularly true for a small population of elk where stochastic events could have significant impacts on population viability (Mills et al. 2005). Results from our study indicate that calf survival is not likely limiting elk population growth and expansion. While it is possible that we missed some predation events that occurred prior to radio-collaring, predation of neonate elk in Pennsylvania is likely rare and the result of chance encounters rather than predators actively seeking out this prey species. Nonetheless, calf survival is only one demographic parameter needed to predict population viability (Dinsmore & Johnson 2005). While survival and reproductive rates have also been quantified for adult elk in Pennsylvania (J. Deberti, unpubl. data), limited information exists regarding the yearling cohort. As such, we recommend that future research focus on quantifying yearling survival to better model overall population growth.

Although our study shows a high probability of survival for elk calves, this value may decrease as elk move into the recently expanded portions of the EMA in Pennsylvania. Prior to the expansion of the EMA, cow and neonate elk selected areas characterized as ecotonal between deciduous forest and herbaceous openings (DeVivo 2009). As elk move into the more heavily forested regions of the expanded EMA where ecotonal habitat preferred by cows and neonates is limited, elk calf survival and recruitment should be reevaluated and potential management of forest openings in the expanded EMA should be reassessed. Changes in elk calf survival may also occur during this expansion because more heavily forested areas of the EMA have increased black bear densities (Ternent 2006). Pennsylvania offered a unique situation in which even the added effects of low birth weight and later birth date did not predispose elk calves to predation. An increase in predation could offer insight into factors that predispose neonate elk to black bear and coyote. Predator management alone in the face of reduced calf survival may not address the actual proximate causes of mortality (White et al. 2010). Continued periodic evaluation of elk calf survival and causes of mortality should be a priority for any managed population. As management activities are implemented, periodic estimation of elk calf survival and causes of mortality is a critical tool for evaluating potential elk population growth and expansion in eastern North America.

Acknowledgements - funding for our research was provided by the Rocky Mountain Elk Foundation and the Pennsylvania Game Commission. Graduate student stipends were provided by Indiana University of Pennsylvania and IUP Research Institute. We thank the Department of Conservation and Natural Resources for their assistance during our study, and Pennsylvania State University, Animal Diagnostic Laboratory for conducting necropsies. We appreciate all those who contributed to data collection and the success of this project, especially W. Dixon, D. Dusza, M. Gritzer, J. McBride, D. McDowell, C. Mulvihill, T. Murphy, T. Ross, C. Shannon, A. Olson and K. Upperman. We thank the two anonymous reviewers for providing useful comments on this manuscript.

References

Altmann, M. 1952: Social behavior of elk, *Cervus canadensis nelsoni*, in the Jackson Hole area of Wyoming. - Behavior 4: 116-143.

Altmann, M. 1963: Naturalistic studies of maternal care in moose and elk. - In: Rheingold, H.L.(Ed.); Maternal behavior in mammals. John Wiley and Sons, New York, New York, USA, pp. 233-253.

Barber-Meyer, S.M., Mech, L.D. & White, P.J. 2008: Elk calf survival and mortality following wolf restoration to Yellowstone National Park. - Wildlife Monographs 169: 1-29.

Bender, L.C., Carlson, E., Schmitt, S.M. & Haufler, J.B. 2002: Production and survival of elk (*Cervus elaphus*) calves in Michigan. - American Midland Naturalist 148: 163-177.

Braun, E.L. 1950: Deciduous forests of eastern North America. - Hafner, New York, New York, USA, 596 pp.

Caughley, G. 1977: Analysis of vertebrate populations. - John Wiley & Sons, New York, New York, USA, 234 pp.

Clutton-Brock, T.H., Major, M., Albon, S.D. & Guinness, F.E. 1987: Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. - Journal of Animal Ecology 56: 53-67.

Cogan, R.D. 1996: Management plan for elk in Pennsylvania. - Bureau of Wildlife Management, Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA, 35 pp.

Cogan, R.D. 1999: Elk population survey. Annual Report. - Bureau of Wildlife Management, Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA, 6 pp.

Cook, J.G. 2002: Nutrition and food. - In: Toweill, D.E. & Thomas, J.W.(Eds.); Elk of North America: ecology and management. Wildlife Management Institute, Washington, D.C., USA, pp. 259-349.

Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D. & Irwin, L.L. 2004: Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. - Wildlife Monographs 155: 1-61.

Cox, J.J. 2003: Community dynamics among reintroduced elk, white-tailed deer, and coyote in southeastern Kentucky. - Ph.D. thesis, University of Kentucky, Lexington, Kentucky, USA, 292 pp.

DeBerti, J.M. 2006: Management plan for elk in Pennsylvania 2006-2016. - Bureau of Wildlife Management, Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA, 41 pp.

DeBerti, J.M. 2008: Project annual job report: Elk population survey/Elk harvest management. - Bureau of Wildlife Management, Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA, 9 pp.

DeVivo, M.D. 2009: Elk calf survival, movements, and neonatal habitat use in northcentral Pennsylvania. - M.Sc. thesis, Indiana University of Pennsylvania, Indiana, Pennsylvania, USA, 86 pp.

de Vos, A., Brokx, P. & Geist, V. 1967: A review of social behavior of the North American cervids during the reproductive period. - American Midland Naturalist 77: 390-417.

Dinsmore, S.J. & Johnson, D.H. 2005: Population anaylsis in wildlife biology. - In: Braun, C.E.(Ed.); Techniques for Wildlife Investigations and Management. Port City Press, Baltimore, Maryland, USA, pp. 154-184.

Exeter Software 2009: Ecological Methodology v 6.1. - Setauket, New York, New York, USA. Available at: http://www.exetersoftware.com (Last accessed on 20 October 2009).

Gannon, W.L. & Sikes, R.S. & the Animal Care and Use Committee of the American Society of Mammalogists. 2007: Guidelines of the American Society Mammalogists for the use of wild mammals in research. - Journal of Mammalogy 88: 809-823.

Gese, E.M. 1999: Threat of predation: do ungulates behave aggressively towards different members of a coyote pack. - Canadian Journal of Zoology 77: 499-503.

Heffernan, L.M. 2009: Food habitats of elk (*Cervus elaphus nelsoni*) in northcentral Pennsylvania. - M.Sc. thesis, Indiana University of Pennsylvania, Indiana, Pennsylvania, USA, 140 pp.

Houston, D.B. 1982: The northern Yellowstone elk: ecology and management. - Macmillan Publishing Company, New York, New York, USA, 474 pp.

Howell, J.A., Brooks, G.C., Semenoff-Irving, M. & Greene, C. 2002: Population dynamics of Tule elk at Point Reyes National Seashore, California. - Journal of Wildlife Management 66: 478-490.

Hudson, R.J. & Haigh, J.C. 2002: Physical and physiological adaptations. - In: Toweill, D.E. & Thomas, J.W. (Eds.); Elk of North America: ecology and management. - Wildlife Management Institute, Washington, D.C., USA, pp. 199-258.

Johnson, D.E. 1951: Biology of the elk calf *Cervus canadensis nelson*. - Journal of Wildlife Management 15: 396-410.

Kaplan, E.L. & Meier, P. 1958: Nonparametric estimation from incomplete observations. - Journal of the American Statistical Association 53: 457-481.

Knight, R.R. 1970: The Sun River elk herd. - Wildlife Monographs 23: 1-66.

Lingle, S. 2001: Anti-predator strategies and grouping pattern in white-tailed deer and mule deer. - Ethology 107: 295-314.

Lingle, S. & Pellis, S.M. 2002: Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. - Oecologia 131: 154-164.

Lizotte, T.E. 1998: Productivity, survivorship, and winter-feeding ecology of an experimentally reintroduced elk herd in northern Wisconsin. - M.Sc. thesis, University of Wisconsin, Stevens Point, Wisconsin, USA, 86 pp.

Lyon, L.J. & Christensen, A.G. 2002: Elk and land management. - In: Toweill, D.E. & Thomas, J.W.(Eds.); Elk of North America: ecology and management. - Wildlife Management Institute, Washington, D.C., USA, pp. 557-582.

Mills, L.S., Scott, J.M., Strickler, K.M. & Temple, S.A. 2005: Ecology and management of small populations. - In: Braun, C.E.(Ed.); Techniques for Wildlife Investigations and Management. Port City Press, Baltimore, Maryland, USA, pp. 691-713.

Murrow, J.L., Clark, J.D. & Delozier, E.K. 2009: Demographics of an experimentally released population of elk in Great Smoky Mountains National Park. - Journal of Wildlife Management 73: 1261-1268.

Myers, W.D. 1999: An assessment of elk population trends and habitat use with special reference to agricultural damage zones in the northern Blue Mountains of Washington. - Final Report, Washington Department of Fish and Wildlife, Olympia, Washington, USA, 172 pp.

O'Gara, B.W. & Dundas, R.G. 2002: Distribution: past and present. - In: Toweill, D.E. & Thomas, J.W.(Ed.); Elk of North America: ecology and management. - Wildlife Management Institute, Washington, D.C., USA, pp. 67-120.

Peek, J.M., Lovaas, A.L. & Rouse, R.A. 1967: Populations changes within the Gallatin elk herd, 1932-1967. - Journal of Wildlife Management 31: 304-315.

Pennsylvania State Climatologist 2006: Climate of Pennsylvania. - Available at: http://climate.met.psu.edu (Last accessed on 19 October 2009).

Phillips, G.E. & Alldredge, A.W. 2000: Reproductive success of elk following disturbance by humans during calving season. - Journal of Wildlife Management 64: 521-530.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. - Journal of Wildlife Management 53: 7-15.

Raedeke, K.J., Millspaugh, J.J. & Clark, P.E. 2002: Population characteristics. - In: Toweill, D.E. & Thomas, J.W.(Eds.); Elk of North America: ecology and management. - Wildlife Management Institute, Washington, D.C., USA, pp. 449-492.

Raithel, J.D., Kauffman, M.J. & Pletscher, D.H. 2007: Impact of spatial and temporal variation in calf survival on the growth of elk populations. - Journal of Wildlife Management 71: 795-803.

Rosatte, R., Hamr, J., Young, J., Filion, I. & Smith, H. 2007: The Restoration of Elk (*Cervus elaphus*) in Ontario, Canada: 1998-2005. - Restoration Ecology 15: 34-43.

Rosenberry, C.S., Fleegle, J.T. & Wallingford, B.D. 2009: Management and biology of white-tailed deer in Pennsylvania 2009-2018. - Bureau of Wildlife Management, Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA, 121 pp.

Sauer, J.R. & Boyce, M.S. 1983: Density dependence and survival of elk in northwestern Wyoming. - Journal of Wildlife Management 47: 31-37.

Schlegel, M. 1976: Factors affecting calf elk survival in northcentral Idaho, a progress report. - Proceedings of the Western Association of State Game Fish Commission 56: 342-355.

Seward, N.W. 2003: Elk calf survival, mortality, and neonatal habitat use in eastern Kentucky. - M.Sc. thesis, University of Kentucky, Lexington, Kentucky, USA, 68 pp.

Singer, F.J., Harting, A., Symonds, K.K. & Coughenour, M.B. 1997: Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. - Journal of Wildlife Management 61: 12-25.

Smith, B.L. & Anderson, S.H. 1996: Patterns of neonatal mortality of elk in northwest Wyoming. - Canadian Journal of Zoology 74: 1229-1237.

Smith, B.L., Anderson, S.H. & Robbins, R.L. 1997: Early development of supplementally fed, free-ranging elk. - Journal of Wildlife Management 61: 26-38.

Smith, B.L. & Anderson, S.H. 1998: Juvenile survival and population regulation of the Jackson elk herd. - Journal of Wildlife Management 62: 1036-1045.

Smith, B.L., Williams, E.S., McFarland, K.C., McDonald, T.L., Wang, G. & Moore, T.D. 2006: Neonatal mortality of elk in Wyoming: Environmental, population, and predator effects. - U.S. Department of Interior, U.S. Fish and Wildlife Service, Biological Technical Publication, BTP-R6007-2006, Washington D.C., USA, 32 pp.

Smith, D.W., Mech, L.D., Meagher, M., Clark, W.E., Jaffe, R., Phillips, M.K. & Mack, J.A. 2000: Wolf-bison interactions in Yellowstone National Park. - Journal of Mammology 81: 1128-1135.

Taber, R.D., Raedeke, K.J. & McCaughran, D.A. 1982: Population characteristics. - In: Toweill, D.E. & Thomas, J.W. (Eds.); Elk of North America: ecology and management. - Wildlife Management Institute, Washington, D.C., USA, pp. 279-298.

Ternent, M.A. 2006: Management and biology of black bears in Pennsylvania 2006-2015. - Bureau of Wildlife Management, Pennsylvania Game Commission, Harrisburg, Pennsylvania, USA, 73 pp.

Thorne, E.T., Dean, R.E. & Hepworth, W.G. 1976: Nutrition during gestation in relation to successful reproduction in elk. - Journal of Wildlife Management 40: 330-335.

United States Census Bureau 2000: Census. - Available at: http://census.gov/ (Last accessed on 20 June 2009).

Vore, J.M. & Schmidt, E.M. 2001: Movements of female elk during calving season in northwest Montana. - Wildlife Society Bulletin 29: 720-725.

Vreeland, J.K., Diefenbach, D.R. & Wallingford, B.D. 2004: Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns. - Wildlife Society Bulletin 32: 542-553.

Waldrip, G.P. & Shaw, J.H. 1979: Movements and habitat use by cow and calf elk at the Wichita Mountains National Wildlife Refuge. - In: Boyce, M.S. & Hayden-Wing, L.D. (Eds.); North American Elk: behavior, ecology and management. The University of Wyoming, Laramie, Wyoming, USA, pp. 177-184.

White, C.G., Zager, P. & Gratson, M.W. 2010: Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. - Journal of Wildlife Management 74: 355-369.

Zager, P., White, C. & Pauley, G. 2005: Elk ecology. Study IV. Factors influencing elk calf recruitment. Job #s 1-3. Pregnancy rates and condition of cow elk. Calf mortality causes and rates. Predation effects on elk calf recruitment. Federal Aid in Wildlife Restoration, Job Progress Report, W-160-R-32, Subproject 31. - Idaho Department of Fish and Game, Boise, Idaho, USA, 32 pp.