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Factors affecting reproduction and population growth in a restored elk *Cervus elaphus nelsoni* population

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In 1997, the Kentucky Department of Fish and Wildlife Resources began a restoration program intended to translocate 200 elk *Cervus elaphus nelsoni* per year over a nine-year period. Initially, the age structure of males in this restored elk population was heavily skewed toward the yearling age class. We examined the reproductive performance of this elk herd for two years. During 1998, the male:adult female ratio was 35:65 (corresponding to 54:100). In 1999, the male:adult female ratio was 45:62 (corresponding to 73:100). The proportion of yearling males declined from 89% in 1998 to 31% in 1999. We used radio telemetry to locate males and females during the rut and to document calf production. Calving rates during 1998 and 1999 were 53 and 92%, respectively. Post-release movements of adult cows (N = 22) to areas devoid of males averaged 21 km and ranged within 7-57 km. Temporary Allee effects may have been responsible for annual differences in calving rates. The calving season was 67 days when breeding was dominated by yearlings and 37 days when breeding was dominated by adults. A male age structure heavily skewed toward yearlings does not appear to limit population growth. Calving rates could be improved by reducing initial post-release wanderings of adult females. Distribution of potential mates may be more important to population growth rather than balanced sex ratios and age structures.

Key words: Allee effect, calving rate, Cervus elaphus nelsoni, elk, Kentucky, reproduction, restoration

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The re-establishment of elk *Cervus elaphus* populations is enhanced by immediate reproduction of translocated animals (Gogan & Barrett 1987). Transport mortality, release methodologies and initial survival of founders can lead to an unbalanced age and sex structure that is exacerbated by the reluctance of donor states to part with mature males (Potter 1982; L. Cornicelli, pers. comm.). Thus, many elk re-introductions use immature, reproductively inexperienced males that may not breed as effectively as adults (Lincoln 1971, Hines & Lemos

1979). If yearling males are not as successful as adults in impregnating females, calving rates may be insufficient to offset mortality. Additionally, delays in territory establishment, atypical social structure, out-of-season births, and breeding by inferior males (Clutton-Brock, Guinness & Albon 1982, FitzGibbon 1998) may result in lower than desired population growth during the initial years of establishment. Low reproduction accompanied by the high initial mortality expected in translocated herds may lead to restoration failure (Foose 1991). Andrewartha & Birch (1954: 335) noted that declining growth rate in a sparse population "may be carried so far that r becomes negative and the population proceeds to dwindle to extinction...but they (extinction events) are mostly missed because they are so difficult to see". Elk restoration in the eastern U.S. may provide the opportunity to better understand some of the factors affecting the success of reintroductions.

Rapid population growth might be expected when an ungulate population has a surplus of food resources (Riney 1964, Gogan & Barrett 1987). Calving rates of restored elk populations may serve as a measure of the nutritional plane and the degree of difficulty animals experience while acclimating to a new environment (Wisdom & Cook 2000). It is reasonable to expect high calving rates in Kentucky during the initial years of elk restoration resulting from mild winters and a surplus of resources resulting from the absence of conspecifics in the landscape for nearly 150 years.

On the other hand, other factors suggest that reproduction during the initial years of elk restoration may be considerably lower than that observed in western populations. First, a prolonged rut resulting from breeding dominated by subadult males may result in high calf mortality associated with late parturition (Clutton-Brock et al. 1982, Noyes, Johnson, Bryant, Findholt & Thomas 1996). An additional factor that may limit population growth of a newly established elk herd is low reproduction resulting from an individual's inability to find a suitable mate due to low population densities (Allee 1938). We examined reproduction in a restored elk herd when the male age structure was skewed heavily toward yearlings and again when the age structure was more evenly distributed between yearlings and adults.

Study area

The elk restoration zone covers a 14-county, 1.06 million ha area within the Cumberland Plateau physiographic region of southeastern Kentucky. Human population density in the restoration zone is low, with densities ranging from 30 to 60 people per km^2 (Watkins 1998). Black bear *Ursus Americanus* and coyote *Canis latrans* are the only potential elk predators in Kentucky. However, the black bear is rare in the study area and small- and medium-sized prey are sufficiently abundant so that coyote predation on elk calves will likely be minimal.

Elevations range within 244-488 m a.s.l. (Overstreet 1984). Of the restoration zone, 97% is dominated by mixed-mesophytic forest and rugged terrain (Braun 1950). However, coal mining and reclamation have converted 20% (50,000 ha) of the area used by elk during this study into flat-topped mesas and gently sloping grasslands.

Methods

During the winter of 1997/98, the Kentucky Department of Fish and Wildlife Resources (KDFWR) translocated 168 elk from Kansas and Utah (see Table 1). Details on capture and handling methods can be found in Maehr, Grimes & Larkin (1999). If determined to be disease-free, each elk was fitted with a Vhf radio-collar, loaded into a livestock trailer, transported nonstop to eastern Kentucky, and released upon arrival (hard release). There were no attempts to maintain pre-capture social groups.

Monitoring of instrumented elk began immediately upon their release using both aerial and ground telemetry (Mech 1983). We located animals weekly and obtained less precise locations during mortality surveys that were conducted twice weekly. We used the minimum convex polygon method (Mohr 1947) to delineate use areas for groups of elk observed during the rut. We defined the rut period as 1 September to 15 November. When calculating calving rates, we assumed that all females observed in the presence of males during the rut participated in breeding.

We searched for calves from 15 May through 30 June in 1999 and 2000 (18 and 30 months post-release). This interval coincides with calving in established elk populations located at similar latitudes (Bear 1989). To ensure documentation of late parturition, we extended female monitoring through early August. We initiated searches for calves when females separated from the herd and restricted their movements (Johnson 1951, Arman 1974). When a female restricted her movements we searched for a calf approximately every other day. In addition to planned searches, we also saw calves while conducting telemetry flights and while ground-tracking in open habitats. Calf ages were estimated according to Johnson (1951). A Fisher's exact test was used to compare the proportion of females observed with calves in year one and year two (Zar 1999). We used P = 0.05 as the level of statistical significance.

We investigated all mortality signals and attempted to determine cause of death. When feasible, dead animals were brought to the University of Kentucky Livestock Disease Diagnostic Center (LDDC) where a complete necropsy was conducted and cause of death determined. If an animal could not be retrieved from the field, then the head, tissue samples (i.e. heart, lung, liver), and blood samples were collected and submitted to the LDDC.

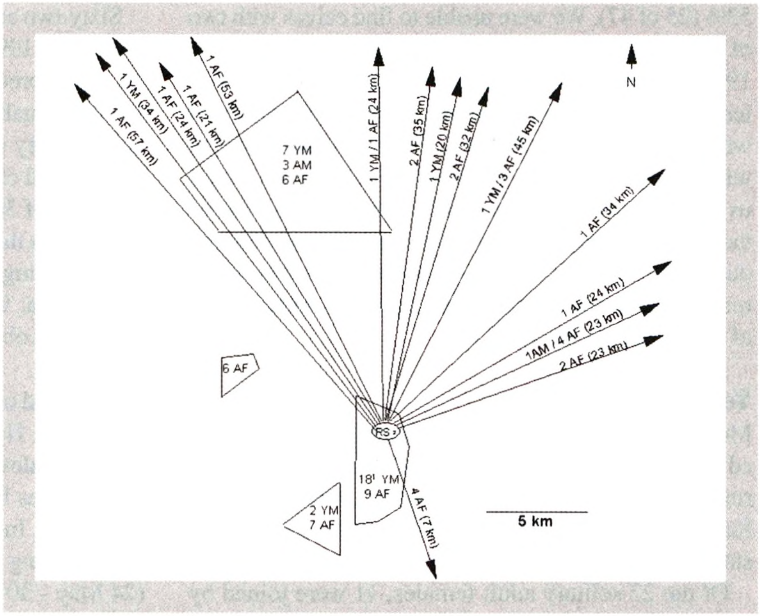

Figure 1. Dispersion pattern of elk during the rut in year one (1998) following release in Kentucky during the winter of 1997/98. Polygons represent composite home ranges (minimum convex polygon; Mohr (1947)) for groups of elk that remained together throughout the 1998 rut. Notes: [1] includes three yearling males with non-functioning transmitters that were observed, via ear tags, with this group throughout the 1998 rut; [2] RS = release site; AF = adult female, AM = adult male, and YM = yearling male.

Results

Year 1

Four shipments of elk (N = 9, 51, 54 and 54) were released from 17 December 1997 through 10 March 1998. Elk mortality prior to the 1998 rut was 33% (Table 1). This mortality, the low (N = 3) number of adult males released, and the advancement of animals into older age classes resulted in a 1998 male:adult female ratio of 35:65. Including yearling females, the male:female ratio was 45:100. Yearlings made up 89% of the males at the start of the rut in 1998 (see Table 1). Before 1 September, all adult males (N = 4) moved >10 km ($\bar{x}$ = 13 km) from the release site and established home ranges (Fig. 1). Of 31 yearling males, 17 remained within 5 km of the release site during 1998, seven settled in areas occupied by adult males, two moved >20 km from the release site and remained solitary throughout the rut, and two others moved 24 and 45 km northeast of the release site and had harems numbering one and three adult cows, respectively. Although transmitters failed on the three remaining yearling males, observations of ear-tags verified that they remained with a group of 15 yearling males within 5 km of the release site during the 1998 rut (see Fig.1).

Of the 65 adult females which were alive during the 1998 rut, two wore malfunctioning transmitters. Prior to the 1998 rut, 22 adult females moved to areas without males ($\bar{x}$ = 21 km; range: 7-57 km; see Fig. 1). Of the remaining 41 adult females, 11 (27%) died within nine months after the end of the rut, and 30 were observed with at least one male during the 1998 rut.

The overall adult female calving rate for 1999 was

Table 1. Number of juvenile, yearling and adult (≥2 years old) elk released in Kentucky during winter 1997/98 and the number remaining through August 2000.

	Males			Females			
Time period	Juvenile	Yearling	Adult	Juvenile	Yearling	Adult	Total
Winter 1997/98	41	4	3	20	27	73	168
1998 rut	17[a]	28(3)[b]	4	17[a]	13	63(2)[b]	142 (5)[b]
1999 rut	12[a]	14	25(6)[b]	13[a]	14	55(7)[b]	133 (13)[b]
August 2000	17[a]	12	30(8)[b]	0,25	12	48(6)[b]	137 (14)[b] (19)[c]

[a] Uncollared elk born in Kentucky
[b] Values in parentheses are the number of additional elk with failed transmitters known to be alive
[c] Number of elk for which fates are unknown

53% (25 of 47). We were unable to find calves with two of the 30 adult females observed with males during the 1998 rut because one transmitter failed and the other female died. Of the 28 remaining adult females observed with males during the 1998 rut, 25 (89%) were observed with a calf. Two collar failures and a death prevented us from confirming the presence of a calf with three of the 22 adult females that moved to areas devoid of males during the 1998 rut. No calves were observed with the remaining 19 adult females that occupied areas devoid of males during the 1998 rut.

Year 2

Mortality and the maturation of young animals resulted in a male:adult female ratio of 45:62 during the 1999 rut. Yearling males that were sired in Utah and born in Kentucky made up 31% (14 of 45) of the males at the start of the 1999 rut (see Table 1).

Of the 22 solitary adult females, 11 were joined by males prior to the 1999 rut (Fig. 2). In addition, four adult females returned to the release site, three died, one collar failed, and three remained solitary. Two of the females that remained solitary died prior to confirming their calving status in 2000.

Sixty-two adult females were present in the population during the 1999 rut, six died and six collars failed post-rut which prevented verification of calving. In addition, we were unable to verify reproduction in five females because they were in terrain that prevented observation. The overall calving rate for adult females in 2000 was 92% (35 of 38). One adult female was located 47 km away from the release site and was not observed with a male during the rut. When we excluded her from our calculation, 94% (35 of 37) of the remaining adult cows were observed with calves during the 2000 calving season.

We found no difference between annual calving rates (P = 0.64). However, when adult females in areas devoid of males were included in the analysis, the calving rate was lower in 1999 (53%) than in 2000 (92%; P < 0.001). In addition, the calving season was 30 days longer during 1999 (1 June - 6 August) than during 2000 (24 May - 30 June).

Population status

Capture-related mortality, post-release mortality, and movements away from potential mates caused the population to decline 13% (N = 146) by the start of the rut in 1999 (see Table 1). Only three females remained in areas devoid of males during the rut in 1999. However, mortality from meningeal worm *Parelaphostrongylus tenuis*, out-of-zone removals by KDFWR, automobile collisions, and other causes prevented population growth (see Table 1). By August 2000, we could account for 151 elk including 54 survivors from the initial release with functioning radio-collars, 14 survivors from the initial release with non-functioning radio-collars but known to be alive, 24 born during 1998 (all sired in Utah), 24 born during 1999 (sired in Kentucky), and 35 born in 2000 (see Table 1). We lost radio-contact with 19 animals (seven adult females and 12 adult males) from the initial release. If these 19 elk remained alive, the maximum population at the end of 2000 was 170, a three-year population growth of 1%. Alternatively, if all 19 were presumed to be dead, the population would have declined by 10%.

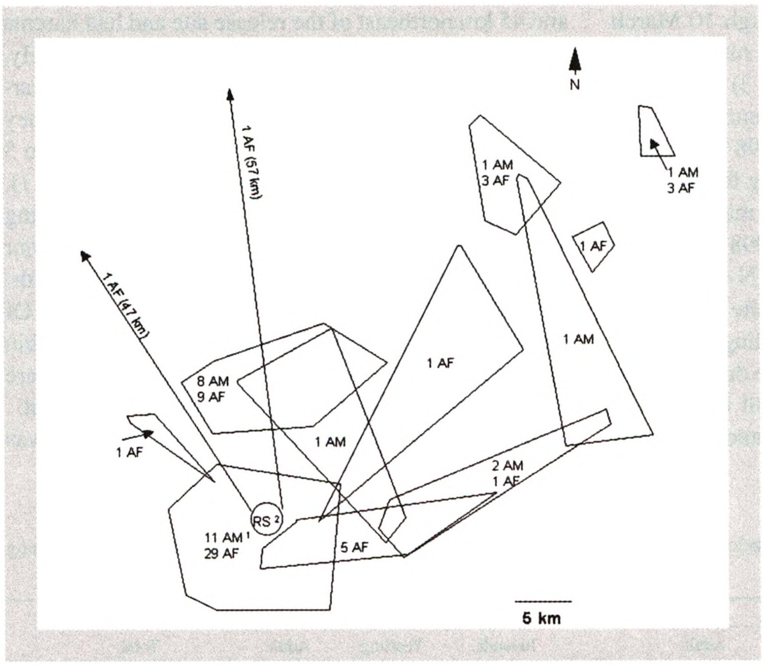

Figure 2. Dispersion pattern of elk during the rut in year two (1999) following release in Kentucky during the winter of 1997/98. Polygons represent composite home ranges (minimum convex polygon; (Mohr 1947)) for groups of elk that remained together throughout the 1999 rut. Notes: [1] includes three adult males with non-functioning transmitters that were observed, via ear tags, with this group throughout the 1999 rut; [2] RS = release site; AF = adult female, AM = adult male; includes one adult male with non-functioning transmitter that was observed, via ear tags, with this group throughout the 1999 rut.

Discussion

Typical adult male to female ratios in western elk herds range within 6-50:100 depending on whether harvest occurs or not (Mohler & Toweill 1982; L. Cornicelli, pers. comm.). Reproductive rates in such herds may not be affected until the ratio drops below six mature males:100 females (Hines, Lemos & Hartman 1985). The eastern Kentucky adult male to female ratio in 1998 was 5:100 (see Table 1). Furthermore, if yearling males are capable of breeding, then the male:adult female ratio of 45:100 during 1998 should have been sufficient to promote population growth. This did not occur, however, because extensive movements of 22 adult females and limited movements by most yearling males created a degree of sexual segregation that prevented breeding opportunities.

Allee (1938) suggested that there may be a critical density below which a population may experience an unrecoverable decline. Such low densities may prevent adults from finding suitable mates. Few empirical examples of the 'Allee effect' have been reported (Caro 1998). In eastern Kentucky elk, the Allee effect was apparent during 1998, but subsided in 1999 after potential breeding elk redistributed themselves and found mates.

If the goal of elk restoration is to establish a self-sustaining population over a large geographic area, such as eastern Kentucky, movements away from the release site are necessary. However, long initial movements can reduce mating opportunities and slow down population growth. Such long movements can result in temporary Allee effects, especially when the restoration zone is large (>1 million ha).

While temporary Allee effects may have limited population growth, our results support the assertion that breeding dominated by yearlings does not impact pregnancy rates of elk. Further, calving rates of eastern Kentucky elk that participated in breeding were comparable to elk in the northern Utah source herd (L. Cornicelli, pers. comm.) and other western elk populations (Taber, Raedeke & McCaughran 1982). The low first year population-wide reproductive output was a function of the unpredictable movements of elk in an unfamiliar landscape.

Simple breeding success by yearling males does not assure population growth in newly reintroduced herds, however. Breeding dominated by yearling males may retard population growth by delaying parturition to a suboptimal time of year (Clutton-Brock et al. 1982, Noyes et al. 1996). Past studies suggest that 6-25 adult males per 100 females may be necessary to ensure a short, synchronous calving season (Bubenik 1985, Hines at al. 1985, Noyes et al. 1996). The calving season in Kentucky decreased from 67 days in 1999 when yearling males dominated the breeding to 37 days in 2000 when two- and three-year old males dominated the breeding. Another possible explanation for the decreased rut length in 1999 may be improved body condition of females (Kohlmann 1999). In 1998, females may have been in poorer condition than in 1999 as a result of the translocation the previous winter. Nonetheless, few predators and a mild climate in eastern Kentucky may minimize the impact of late parturition on calf survivorship.

Conclusion

Yearling males were capable breeders in this newly established elk herd in Kentucky. Further, initial post-release movements can cause temporary Allee effects whereby many individuals fail to find mates. Spatial distribution of potential mates may be of greater importance to overall productivity in a newly established elk herd than are balanced sex ratios and age structures (Dobson & Poole 1998). Increased numbers of translocated animals may be necessary to achieve population densities that reduce initial Allee effects and facilitate population growth. Supplemental releases in a re-introduced moose *Alces alces* population facilitated reproduction and enhanced population viability (Schmitt & Aho 1988). If increasing the number of translocated animals is not possible, then managers should consider soft-release methods that enhance social cohesiveness and release site fidelity (Gogan & Barrett 1987, Stanley Price 1989). Such an approach would not only reduce the likelihood of restoration failure, but would enhance the prospects for quickly establishing viable herds.

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