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RESEARCH ARTICLE

Movement and Spread of a Founding Population of Reintroduced Elk (*Cervus elaphus*) in Ontario, Canada

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Abstract

Monitoring the distribution and movements of a species following reintroduction can aid resource managers in assessing release-site fidelity, rates of spread, initial project success, and feasibility of (or need for) future releases. We used radio-telemetry to monitor an entire founding population of 70 elk (*Cervus elaphus*) during 16 months following their reintroduction to eastern Ontario, Canada. At the end of the study, elk were widely scattered over a 27,000 km^2 area. Dispersal distances ranged from 2 to 142 km; 50% of animals moved >40 km from the release site. Dispersal distances differed by time periods and age but not sex. Calves dispersed significantly shorter distances than adults and many mature elk were isolated during the rut. In contrast to a random distribution model, movements had a strongly southwestern directional bias, perhaps owing to prevailing winds from the same direction. Mortality during the study period was 27%; the primary causes of known mortalities were emaciation, collision with automobiles, and illegal shooting. During the first 1½ years, lack of release-site fidelity and high dispersal coupled with animal-human conflicts and mortalities likely contributed to an initial lag in population growth. Resource managers planning animal reintroductions should consider using methodologies that enhance site fidelity following release.

Key words: ***Cervus elaphus*, dispersal, elk, movements, population spread, reintroduction, restoration, translocation.**

Introduction

Translocation and reintroduction of animals are tools for conservation and wildlife management (Griffith et al. 1989) and may offer the only chance of survival for some free-ranging populations (Nielsen 1988; Ebenhard 1995). These tactics have been employed to reestablish species to former ranges, reinforce small and fragmented populations, relieve inbreeding, resolve human-animal conflict, as well as control populations of predators and prey (Jefferies et al. 1986; Kleiman 1989; Parker & Phillips 1991; Stussy et al. 1994; Wolf et al. 1996; Jones et al. 1997; Ruth et al. 1998; Saenz et al. 2002).

To enhance the success of reintroductions, the primary focus should be on maximizing initial population growth (Komers & Curman 2000). Determining the minimal number of individuals required for a population to maintain itself was a question first posed by Allee (1938). The issue has considerable impact on the initial stages of invasion and reintroductions: populations are small and the stochastic risk of extinction is high (Griffith et al. 1989; Caughley 1994). Predation, Allee effects, and dispersal capabilities are important considerations for reintroductions. Such factors can depress initial rates of population growth and spread (Lewis & Kareiva 1993; Stephens & Sutherland 1999).

Key to reintroduction success is the degree to which animals disperse from the release site—vital knowledge that can be approached from the context of diffusion (Robinette 1966; Bovet & Benhamou 1988). Population re-distribution through time results from the movement of all individuals constituting the population (Lima & Zollner 1996; Turchin 1998). A key dimension is the area occupied by the invading species (Higgins & Richardson 1996), which governs the extent to which density is reduced by dispersal (Lewis & Kareiva 1993). Indeed, dispersal may be more important than demographic parameters (such as birth rate) in determining regional population density (Fahrig & Merriam 1994).

Large mammals, such as elk (*Cervus elaphus*), have often been the subject of introduction and repatriation (Seddon

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et al. 2005; Clout & Russell 2008). In North America, elk have been transferred for re-stocking since the early 1900s (Lloyd 1927). In Ontario, Canada, elk were extirpated during the late 1800s and attempts were made to restore populations during the 1930s and 1940s. Most of those animals were culled by the 1950s, although a small, remnant herd managed to survive in the Burwash–French River area. From 1998 to 2001, additional restoration attempts for elk were initiated in four regions of the province (Rosatte et al. 2007). Because each individual can be tracked with radio-telemetry, these events represent uncommon opportunities to advance our knowledge of dispersal and population spread.

The objective of our study was to examine post-release movements and space use patterns of a reintroduced elk population in eastern Ontario. We quantified the survival, density, dispersal direction and distance of 70 individually tracked animals over the course of 16 months. Because we were able to monitor the fate and location of every animal in the population in its novel environment, our study provided a rare instance to quantify population spread and enhance our understanding of the role of dispersal in species restoration.

Methods

Our study focused on a founding population of 70 elk released in the Bancroft/North Hastings (BNH) region of eastern Ontario, Canada. Elk were released 9 January 2000 on Crown (public) Land near the hamlet of McArthur's Mills (45°04′N, 77°31′W), approximately 250 km NE of Toronto, Ontario. As a result of elk dispersion, the size of the study area was approximately 27,000 km^2.

Scattered around the release site were abandoned and active farmlands (primarily for cattle), housing plots, and extensive tracts of secondary growth forests. White-tailed deer (*Odocoileus virginianus*) wintering areas were located throughout the study area (Bellhouse & Rosatte 2005) and the area was harvested for this game species as well as other species such as moose (*Alces alces*). Human density was minimal within a 15 km radius around the elk release site.

The 70 elk released in BNH were processed and radiocollared at Elk Island National Park, Alberta (Bork et al. 1997; Rosatte et al. 2002). The release group included 10 adult bulls, 4 yearling bulls, 33 adult cows, 3 yearling cows, 10 male calves, and 10 female calves (about 7 months of age). Elk were transported for approximately 48 hours in trailers and transferred into a holding pen in BNH, Ontario, 9 January 2000. The release was unintentionally "hard," that is no holding period. A few individuals escaped from the pen on the first day and the remaining animals were released on the same day. We conducted radio-tracking from 1 February 2000 to 31 May 2001 with most elk relocated either weekly or fortnightly. Missing elk were located using aerial telemetry. We recorded the approximate time and location of mortalities; where possible, the carcass was retrieved. Necropsies were performed at the Canadian Cooperative Wildlife Health Centre, University of Guelph, Guelph, Ontario. Emaciation was inferred from qualitative assessment of fat content of marrow in the femur and visceral fat reserves including kidneys and the abomasums (Caughley & Sinclair 1994, pp. 104–107).

We acquired point locations from sightings, aerial telemetry, and bi-angulation or triangulation of collared elk. Ground telemetry locations were determined by the intersection of two or more bearings (White & Garrott 1990, p. 49). Following Zimmerman and Powell (1995), dummy collar readings were used to estimate location error. To investigate temporal patterns of movement and space use, we partitioned the study into eight equal intervals: Period 1 (February and March 2000), Period 2 (April and May 2000), Period 3 (June and July 2000), Period 4 (August and September 2000), Period 5 (October and November 2000), Period 6 (December 2000 and January 2001), Period 7 (February and March 2001), and Period 8 (April and May 2001).

Total population range was the space denoted by all elk locations obtained during the entire study period (Schaefer et al. 2000). Using the Home Range Extension for Arcview, we estimated a 100% minimum convex polygon (MCP; Mohr 1947) for the entire elk population, for sex and age groups for each period, as well as for the entire study period. We selected the MCP because it provided an indication of the maximum size of the area of spread.

To quantify dispersal distance and all subsequent movements, we retained the individual as sample unit. Elk that died were eliminated from the sample pool during the next period following the mortality event. During each of the eight periods, we calculated straight-line distances and directions from the point of release to each animal location (White & Garrott 1990, pp. 114 and 126). Dispersal distance was denoted as the straight-line distance from the release site to the most distant animal location during each of the eight periods; dispersal direction was computed as the compass bearing for this same line. For each period, we computed the mean dispersal distance and direction for the population, as well as each sex-age group. We also calculated mean angular error, computed as angular deviation, and r, a measure of concentration (Zar 1999). We used Rayleigh's test of uniformity (Zar 1999, p. 617) to test elk distribution around the release point for each time period. Where appropriate, movement statistics are given as means (±SE). Where required, log transformations were used to correct for heteroscedasticity in movement data (Zar 1999, p. 279).

To test the effects of sex and age on dispersal estimates, we used a factorial ANOVA (Statistica, Statsoft Inc., Tulsa, OK, U.S.A.). Using repeated measures ANOVA, we compared dispersal distances among periods to examine temporal differences in movement rates and fidelity of elk alive at study completion. We examined fidelity by comparing relative changes in the number of individuals remaining at or returning to a particular location during the same period 1 year after release (White & Garrott 1990)—that is, the proportion of animals within various distances of the release site. We tested the furthest location of each elk alive during Periods 7 (February to March 2001) and 8 (April to May 2001) against the furthest location of the same individual 1 year earlier. If significant differences existed, we conducted post hoc comparisons using Tukey's HSD with an experiment-wise α of 0.05. p Values are two-tailed unless otherwise specified.

Results

Telemetry Monitoring

From 1 February 2000 to 31 May 2001, we compiled 1,941 elk locations for the herd. The number of recorded locations for each elk surviving until study completion ($n = 49$ animals) ranged from 16 to 56. Approximately 80% of all location estimates were obtained from ground radio-telemetry, 15% from aerial telemetry, and the remaining 5% from direct observations. The average error estimate (using two bearings) was 189 ± 41 m from dummy collar readings ($n = 10$).

Mortality

Of the 70 reintroduced elk, 19 (27%) died by the end of the study. Prior to the start of this study, one cow died immediately following release from trauma due to broken ribs sustained during transport and was excluded from all subsequent analysis. One elk was euthanized soon after release due to broken bones sustained while traveling on ice, and another elk died from a leg injury. Six mortalities were of unknown cause, two elk were illegally shot, three were killed from vehicle collisions, and four elk died from emaciation. One elk is suspected to have died from predation. Although the carcass of this elk was never retrieved, the collar was torn and a black bear was spotted in the immediate vicinity of the collar. Approximately 68% (13/19) of elk mortalities occurred <20 km from the release site. Ninety percent of the mortalities resulting from emaciation or unknown causes also occurred within this radius. All mortalities >60 km from the release site were caused by human activities, including two vehicle collisions and the illegal shooting of a cow that dispersed >140 km. Only two mortality events occurred in Period 1. During Period 2, 40% of all documented deaths occurred, leaving only 85% of the elk population alive. Following Period 2, survival gradually declined until study completion.

Spatial Behavior

At the end of the study, the total range area for the elk population (all individuals for the entire study period) was 27,141 km^2 (Table 1) within which the population density was only 0.003 elk/km^2. Total range area was 19,052 km^{2}for females and 14,968 km^2 for males (Table 1). Dispersal distance and total range area were strongly correlated (Fig. 1). For the first half of this study, average dispersal distance and total range area increased in tandem but reached an asymptote by Period 4.

Table 1. Total range area (100% minimum convex polygons) for elk released in the Bancroft/North Hastings region of Ontario, Canada, February 2000 to May 2001.

Sex	*Age**	*n*	*Perimeter (km)*	*Total Range Area (km^2)*
Female	Calves	10	120	904
	Yearlings	3	303	6,297
	Adults	32	555	15,238
Male	Calves	10	150	921
	Yearlings	4	231	2,514
	Adults	10	530	14,968
Females		45	572	19,052
Males		24	530	14,968
Calves		20	155	1,194
Yearlings		7	370	8,581
Adults		42	656	27,141

* Age at time of release: adults (>2 years), yearlings (1.75 years) and calves (8–9 months).

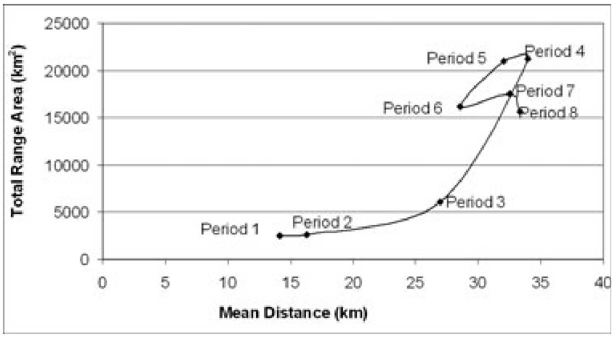

Figure 1. Mean dispersal distance and total range area (100% minimum convex polygons) for a founding population of elk following reintroduction in the Bancroft/North Hastings region, Ontario. Each period consists of 2 months, February 2000 to May 2001.

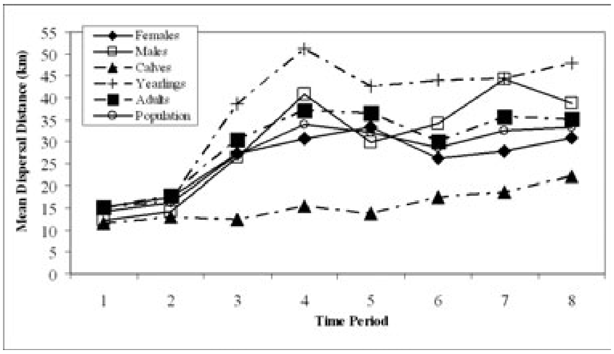

Figure 2. Mean dispersal distances by elk sex-age classes following reintroduction in the Bancroft/North Hastings region, Ontario. Each period consists of 2 months, February 2000 to May 2001.

Dispersal was immediate. Promptly after release (Period 1), movements were extensive but not until Period 3 did we detect differences among age-sex classes ($F_{[2,53]} = 8.52$, $p = 0.001$; Fig. 2). Post hoc comparisons indicated that calves dispersed substantially less than yearlings ($p = 0.040$) and adults ($p = 0.001$), and differences were also apparent between female calves and bulls ($p = 0.039$; Table 2). Overall, dispersal distances for elk alive at study completion were statistically different among periods ($F_{[4,180]} = 5.05$, $p = 0.007$) and age

Table 2. Dispersal distance, direction, and total range area through time for elk reintroduced in the Bancroft/North Hastings region of Ontario, Canada, February 2000 to May 2001.

Period	*Date*	*Age–Sex Class*[a]	*n*	*Maximum Distance (km)*	*Mean Distance (km)*	*SE*	*Mean Direction (°)*	*SE*[b]	*r Value*[c]	*Total Range Area*[d] *(km^2)*
1	February to March 2000	Female calves	10	31.1	10.2	3.9	212	49.3	0.63	101
		Female yearlings	3	66.6	26.0	20.3	267	43.6	0.71	362
		Female adults	32	68.5	15.7	2.6	260	61.5	0.42	2,150
		Male calves	10	37.7	12.8	5.3	213	48.6	0.64	75
		Male yearlings	4	9.1	7.2	0.9	142	30.2	0.86	25
		Male adults	10	49.0	13.7	4.7	221	36.3	0.80	800
		Population	69	68.5	14.1	6.3	229	58.1	0.49	2,480
2	April to May 2000	Female calves	10	36.0	12.0	4.4	205	20.0	0.94	113
		Female yearlings	3	62.6	24.3	19.2	282	32.1	0.84	590
		Female adults	32	62.4	18.5	2.4	273	49.5	0.63	2,111
		Male calves	10	39.9	14.1	5.0	204	43.6	0.71	199
		Male yearlings	3	15.2	8.8	3.6	213	70.2	0.25	67
		Male adults	9	49.2	15.9	4.8	253	33.3	0.83	240
		Population	67	62.6	16.3	6.6	246	51.1	0.60	2,597
3	June to July 2000	Female calves	6	23.9	9.2	3.1	240	49.4	0.63	128
		Female yearlings	3	84.6	47.6	21.7	276	38.3	0.78	1,833
		Female adults	30	83.6	28.8	3.9	268	51.0	0.60	5,986
		Male calves	8	27.3	14.7	4.5	193	31.3	0.85	540
		Male yearlings	3	62.1	29.6	17.4	209	17.4	0.95	376
		Male adults	9	66.7	35.8	7.3	226	45.3	0.69	2,920
		Population	59	84.6	27.0	9.6	243	52.0	0.59	6,141
4	August to September 2000	Female calves	5	24.5	10.8	3.6	234	60.8	0.44	139
		Female yearlings	3	88.8	60.7	25.8	271	48.4	0.64	3,714
		Female adults	29	129.5	30.9	5.1	275	56.0	0.52	7,068
		Male calves	7	33.7	18.8	5.8	186	31.4	0.85	361
		Male yearlings	3	92.9	41.7	26.0	176	15.2	0.96	692
		Male adults	8	115.5	59.5	15.6	191	48.6	0.64	9,497
		Population	55	129.5	33.9	13.6	236	60.4	0.44	21,176
5	October to November 2000	Female calves	5	24.3	11.7	4.3	218	30.1	0.86	241
		Female yearlings	3	98.3	60.9	29.8	234	20.8	0.93	2,373
		Female adults	29	142.3	34.0	5.7	290	62.0	0.42	11,602
		Male calves	7	27.3	15.4	4.4	174	37.5	0.79	173
		Male yearlings	2	24.3	15.0	9.3	188	5.1	1.00	76
		Male adults	7	105.5	52.1	15.4	225	55.6	0.53	6,850
		Population	53	142.3	32.6	11.5	239	62.4	0.41	21,051
6	December 2000 to January 2001	Female calves	5	24.0	9.6	4.1	199	14.1	0.97	66
		Female yearlings	3	94.5	60.8	28.2	212	18.9	0.95	2,123
		Female adults	28	92.2	25.4	4.3	258	62.0	0.41	7,545
		Male calves	7	47.8	23.3	8.7	200	43.1	0.72	249
		Male yearlings	2	24.0	19.1	4.9	198	1.0	1.00	62
		Male adults	6	137.9	51.9	18.8	183	60.5	0.44	5,188
		Population	51	137.9	28.5	11.5	222	57.6	0.49	16,181
7	February to March 2001	Female calves	5	38.1	12.6	6.5	208	38.9	0.77	150
		Female yearlings	3	92.5	59.6	27.9	210	21.2	0.93	2,062
		Female adults	28	93.1	27.0	4.7	260	64.3	0.37	10,223
		Male calves	7	48.1	23.0	8.9	201	51.5	0.59	141
		Male yearlings	2	38.1	21.6	16.5	184	10.5	0.98	45
		Male adults	6	137.8	76.4	15.9	160	50.9	0.61	6,105
		Population	51	137.8	32.6	13.4	219	61.3	0.43	17,544
8	April to May 2001	Female calves	5	45.6	20.1	8.5	185	63.0	0.39	439
		Female yearlings	3	96.3	62.7	29.6	216	16.0	0.96	3,586
		Female adults	26	92.6	29.3	4.7	274	64.0	0.38	7,560
		Male calves	7	50.0	23.7	9.4	200	53.0	0.57	275
		Male yearlings	2	45.6	25.9	19.7	191	18.0	0.95	63
		Male adults	6	135.2	60.8	15.9	168	61.0	0.44	6,143
		Population	49	135.2	33.3	14.6	227	65.0	0.35	15,649

[a] Age at time of release: adults (>2 years), yearlings (1.75 years) and calves (8–9 months).

[b] Angular error calculated as: angular deviation $\sqrt{n}$ (Zar 1999).

[c] *r* Value, a measure of concentration, varies from 0 (maximum dispersion) to 1 (all data concentrated in the same direction; Zar 1999).

[d] Total range area is based on minimum convex polygons.

classes ($F_{[4,180]} = 2.75$, $p = 0.030$). At no time, however, was distance statistically dependent on sex. The salient difference stemmed from calves that dispersed significantly less than adults of both sexes (Table 2).

The distribution of elk around the release site was never representative of a random distribution model (Rayleigh's z ranged from $z_{67} = 24.27$, $p < 0.001$, Period 2, to $z_{49} = 6.15$, $p < 0.002$, Period 8). Indeed, a southwesterly bias was evident during Period 1 ($229° \pm 58°$) and persisted throughout the study (Table 2).

A year after reintroduction, elk showed little fidelity to the release site. Elk during Period 7 were significantly farther from the point of release than 1 year earlier ($p < 0.001$). Similarly, during Period 8, the surviving elk ($n = 49$) were statistically more distant than these same individuals were during Period 1 ($p < 0.001$) and Period 2 ($p = 0.037$). Average dispersal for the herd 1½ years following reintroduction was 33.3 ± 14.6 km (Table 2; Fig. 1).

Discussion

The willingness of animals to remain where released is an important determinant of reintroduction success (Rogers 1988). This factor is critical to the viability of a translocated population (Hamilton 1962), as the initial distribution and density of individuals are vital in determining whether a population can establish itself (Etienne et al. 2002). In our study, BNH elk displayed little fidelity to the release site, exhibiting high mobility and movement across an immense (27,000 km^2) region. One and a half years following release, only 16% of the elk were located within 10 km of the release pen, 27% within 20 km, whereas 37% were >40 km away. The release site was chosen as it contained high quality habitat for elk. If elk disperse to areas with less desirable habitat, survival may not be as high, especially during severe winters in Ontario. Our results are in stark contrast to other reintroductions of the species: 75% of collared elk <10 km 1½ years after release in northwestern Ontario (McIntosh, 2003); more than half of elk <5 km after 6 months in the Burwash–French River area, Ontario (Rosatte et al. 2002); 53, 55, and 82% of elk <10 km 1 year following reintroductions in Kentucky (Larkin et al. 2004); and 76% <10 km after 2 years in Tennessee (Muller 2002). Indeed, not until 2–3 years following reintroduction did BNH elk shift from a dispersive to a home-range phase (Fryxell et al. 2008).

As elk are gregarious in nature, one may question the impact of group dynamics on movements in this study. For instance, when released, did elk travel as a group and because we used the individual as the sampling unit possibly bias the results? Although we acknowledge that elk are social animals, we felt our approach was preferable to treating radiolocations as independent (where serial correlation is a problem) or attempting to adjust the number of degrees of freedom (based on fluid associations of our study elk). Also, the social hierarchical behavior typically displayed in established elk herds cannot be readily compared with the social behavior of a founding elk population immediately following a hard release. During the first 1.5 years following reintroduction, social groups were fluid and evolving; they were not always functional or defined. Such behavior has direct implications for population establishment. Grouping behavior of elk, particularly females, may increase the potential for successful mate-location during the rut (as presence of sign and scent accumulates). When the BNH elk were studied over a longer period of time (4 years), elk that remained solitary experienced lower survival and elk had a higher mortality rate the further they moved from the release location (Haydon et al. 2008).

Translocation and dispersal are clearly linked. Models of dispersal distances, animal movement, and population spread (Hengeveld 1989; Van den Bosch et al. 1992; Veit & Lewis 1996), therefore, might be valuable but empirical tests of these models are limited (e.g. Bergman et al. 2000). Often only a few individuals move exceptionally farther than the remainder of that population (Taylor 1978). Consequently, the distribution of dispersal distances is typically negatively skewed with a long tail—a pattern observed for many reintroduced and established animal populations (Dunham 2000; Larter et al. 2000; Byrom 2002; Forsman et al. 2002). In our study, however, dispersal distances did not fit a negative skew distribution model: 60% of surviving elk dispersed >30 km, 33% in excess of 50 km. Moreover, movement rates for the BNH elk herd were not constant with time (Fig. 2). Such movements are not well represented by a random diffusion model (Skellam 1951). We believe that the hard release methodology likely contributed to the dispersion of elk following release in our study.

The tail of the dispersal distribution is often most difficult to quantify. Such observations are rare and anecdotal. Although the greatest dispersal distance during our study was 142 km, 3 years following reintroduction into BNH the carcass of an elk that had dispersed >350 km from the release site was found in Quebec (Rosatte, unpublished data). Dispersal events of >600 km have been recorded for reintroduced elk in Alberta (Chisholm, unpublished data). Again, these "outlier" animals would not contribute to population growth of the BNH herds.

Uniformity of spread is also anticipated if movement from a point source is unrestricted and non-directional (Skellam 1951) and is typically assumed in models of animal movement (Cain 1985), invasive spread (Kot et al. 1996) and metapopulations (Hanski & Gilpin 1997). Such was not the case for BNH elk (Table 2). We surmise that this southwest directional bias may reflect prevailing winds, a known influence on the cervid flight response. In reindeer (*Rangifer tarandus*), for instance, escape direction is most commonly upwind (Reimers et al. 2006). Indeed, in the nearby city of Peterborough (44°14′N, 78°22′W), prevailing winds are southwesterly 5 months of the year (westerly otherwise) and gusts are most frequently from the southwest (Environment Canada 2008). Because dispersing, solitary elk tend to move more than grouped animals (Haydon et al. 2008), this may have heightened the directional bias. However, other factors such as habitat and geographical features cannot be overlooked as playing some role in the directional movement of elk in our study.

For many taxa, movement and population density are age dependent (Greenwood 1980; Hastings 1992). Indeed, in our study, age was a strong determinant of dispersal distance. Dispersal distances for adults and yearlings were more than double that for calves, similar to other elk restorations (e.g. Larkin et al. 2002, 2004; Ryckman et al. 2009). One may question why calves did not remain with dispersing adults. It important to note that at the time of release, calves were about 7 months of age and they were nearly 2 years old by the end of the study. As the study progressed, the calves became independent of the cows. Furthermore, the elk were released during the winter. The mobility of calves in comparison with adults may have been initially hindered due to the harsh winter and snow depth. During this study, most adult elk that initially dispersed away from the release site never returned to the area of release. Also, due to the methods in which elk were captured at Elk Island National Park, it is unknown whether calves were released with their maternal parent; there would be no mother:offspring bond.

There is intricate interplay between dispersal and population density. Although dispersal is linked to total range area, as demonstrated in this and other studies (e.g. Dunham 2000), density can also affect dispersal. Animals may undergo saturation dispersal when densities approach carrying capacity (South 1999). With elk density far below 1 animal/km^2, the carrying capacity of BNH likely had little impact on dispersal. Under the abundant-centre hypothesis (i.e. that organism abundance declines from range center to periphery; Sagarin & Gaines 2002), such low densities might be expected at the edge of a species' range. BNH is near the northern margin of historical distribution for *Cervus elaphus* (Banfield 1974).

There are many influences on the outcomes of translocations, including source stock, number of individuals released, release procedures, and site selection (Nielsen 1988; Green 1997; Kolar & Lodge 2001). In particular, hard releases—immediate liberation into the new environment—may result in higher dispersal and mortality rates (Bright & Morris 1994; Carbyn et al. 1994). Our study elk experienced an unintended hard release that may have contributed to the initial high dispersal rates. Soft-release, the temporary provision of food or shelter, is recommended for species with long-distance dispersal tendencies (Stephens & Sutherland 1999). The social cohesion and site tenacity of Tule elk reintroduced in California, for example, was attributed largely to holding animals in small pens for 3–6 months prior to release (Gogan & Barrett 1988). Ryckman et al. (2009) also noted in Ontario that extended conditioning periods for elk prior to release promoted philopatry. Planned and well-documented reintroductions (i.e. Stanley Price 1989) remain rare. Nevertheless, only with careful documentation and comparison of these events will we arrive at greater understanding of such effects.

Implications for Practice

- Monitoring the distribution and movements of elk following reintroduction can aid resource managers in assessing release-site fidelity, rates of spread, initial project success, and feasibility of future releases.
- Managers planning to restore elk should consider holding elk for a period of time prior to release to increase release-site fidelity and maximize population growth.
- The primary causes of known mortalities in our study were emaciation, collision with automobiles, and illegal shooting. Managers planning restorations should consider actions to minimize these mortality factors to increase the likelihood of restoration success.

Acknowledgments

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LITERATURE CITED

Allee, W. 1938. The social life of animals. W. Norton, New York.

Banfield, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Toronto.

Bellhouse, T., and R. Rosatte. 2005. Assessment of the potential for negative interaction between reintroduced elk (*Cervus elaphus*) and resident white-tailed deer (*Odocoileus virginianus*) in their wintering areas of Ontario, Canada. Mammalia **69:**35–56.

Bergman, C. M., J. A. Schaefer, and S. N. Luttich. 2000. Caribou movement as a correlated random walk. Oecologia **123:**364–374.

Bork, E. W., R. J. Hudson, and A. W. Bailey. 1997. Upland plant community classification in Elk Island National Park, Alberta, Canada, using disturbance history and physical site factors. Plant Ecology **130:**171–190.

Bovet, P., and S. Benhamou. 1988. Spatial analysis of animals' movements using a correlated random walk model. Journal of Theoretical Biology **131:**419–433.

Bright, P. W., and P. A. Morris. 1994. Animal translocation for conservation: performance of dormice in relation to release methods, origin, and season. Journal of Applied Ecology **31:**699–708.

Byrom, A. E. 2002. Dispersal and survival of juvenile feral ferrets *Mustela furo* in New Zealand. Journal of Applied Ecology **39:**67–78.

Cain, M. L. 1985. Random search by herbivorous insects: a simulation model. Ecology **66:**876–888.

Carbyn, L. N., H. J. Armbruster, and C. Mamo. 1994. The swift fox reintroduction program in Canada from 1983 to 1992. Pages 247–271 in M. L. Bowles and C. J. Whelan, editors. Restoration of endangered species: conceptual issues, planning, and implementation. Cambridge University Press, Illinois.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63:**215–244.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife ecology and management. Blackwell Science, Cambridge, Massachusetts.

Clout, M. N., and J. C. Russell. 2008. The invasion ecology of mammals: a global perspective. Wildlife Research **35:**180–184.

Dunham, K. 2000. Dispersal pattern of mountain gazelles Gazella gazelle released in central Arabia. Journal of Arid Environments **44:**247–258.

Ebenhard, T. 1995. Conservation breeding as a tool for saving animal species from extinction. Trends in Ecology and Evolution **10:**438–443.

Environment Canada. 2008. Canadian Climate Normals 1971–2000 (available from www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html).

Etienne, R., B. Wertheim, L. Hemerik, P. Schneider, and J. Powell. 2002. The interaction between dispersal, the Allee effect and scramble competition affects population dynamics. Ecological Modeling **148:**153–168.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8:**50–59.

Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl, S. G. Sovern, M. Taylor, et al. 2002. Natal and breeding dispersal of northern spotted owls. Wildlife Monographs No. 149.

Fryxell, J., M. Hazell, L. Börger, B. Dalziel, D. Haydon, J. Morales, T. McIntosh, and R. Rosatte. 2008. Multiple movement modes by large herbivores at multiple spatio-temporal scales. Proceedings of the National Academy of Sciences of the United States of America **105**:19114–19119.

Gogan, P., and R. Barrett. 1988. Lessons in management from translocations of Tule elk. Pages 275–285 in L. Nielsen and R. Brown, editors. Translocation of wild animals. Humane Society, Wisconsin.

Green, R. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology **66:**25–35.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior **28:**1140–1162.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science **245:**477–480.

Hamilton, R. 1962. Factors affecting dispersal of deer released in Indiana. Journal of Wildlife Management **26:**79–85.

Hanski, I. A., and M. E. Gilpin, editors. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California.

Hastings, A. 1992. Age dependent dispersal is not a simple process: density dependence, stability and chaos. Theoretical Population Biology **41:**388–400.

Haydon, D. T., J. M. Morales, A. Yott, D. A. Jenkins, R. Rosatte, and J. M. Fryxell. 2008. Socially-informed random walks: incorporating group dynamics into models of population spread and growth. Proceedings of the Royal Society B **275:**1101–1109.

Hengeveld, R. 1989. Dynamics of biological invasions. Chapman & Hall, London.

Higgins, S. I., and D. M. Richardson. 1996. A review of models of alien plant spread. Ecological Modeling **87:**249–265.

Jefferies, D. J., P. Wayre, R. M. Jessop, and A. J. Mitchell-Jones. 1986. Reinforcing the native otter *Lutra lutra* populations in East Anglia: an analysis of the behaviour and range development of the first release group. Mammal Review **16:**65–79.

Jones, M. L., N. E. Mathews, and W. F. Porter. 1997. Influence of social organization on dispersal and survival of translocated female white-tailed deer. Wildlife Society Bulletin **25:**272–278.

Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. Bioscience **39:**152–161.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution **16:**199–204.

Komers, P. E., and G. P. Curman. 2000. The effect of demographic characteristics on the success of ungulate reintroductions. Biological Conservation **93:**187–193.

Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology **77:**2027–2042.

Larkin, J. L., J. J. Cox, M. W. Wichrowski, M. R. Dzialak, and D. S. Maehr. 2004. Influences on release-site fidelity of translocated elk. Restoration Ecology **12:**97–105.

Larkin, J. L., D. S. Maehr, J. J. Cox, J. M. W. Wichrowski, and R. D. Crank. 2002. Factors affecting reproduction and population growth in a restored elk *Cervus elaphus nelsoni* population. Wildlife Biology **8:**49–54.

Larter, N. C., A. R. E. Sinclair, T. Ellsworth, J. Nishi, and C. C. Gates. 2000. Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. Animal Conservation **4:**299–309.

Lewis, M. A., and P. M. Kareiva. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology **43:**141–158.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution **11:**131–135.

Lloyd, H. 1927. Transfer of elk for restocking. Canadian Field Naturalist **41:**126–127.

McIntosh, T. 2003. Spatial behaviour and habitat selection of elk (*Cervus elaphus*). Unpublished M.Sc. thesis, Lakehead University, Thunder Bay, Ontario.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist **37:**223–249.

Muller, L. 2002. Tennessee elk restoration project: summary of 2001/02 activities. Department of Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, Tennessee.

Nielsen, L. 1988. Definitions, considerations, and guidelines for translocation of wild animals. Pages 12–49. in L. Nielsen and R. Brown, editors. Translocations of wild animals. Wisconsin Humane Society, Milwaukee, Wisconsin/Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.

Parker, W. T., and M. K. Phillips. 1991. Application of the experimental population designation to recovery of endangered red wolves. Wildlife Society Bulletin **19:**73–79.

Reimers, E., F. L. Miller, S. Eftestol, J. E. Colman, and B. Dahle. 2006. Flight by feral reindeer Rangifer tarandus tarandus in response to a directly approaching human on foot or on skis. Wildlife Biology **12:**403–413.

Robinette, W. L. 1966. Mule deer home range and dispersal in Utah. Journal of Wildlife Management **30:**335–349.

Rogers, L. 1988. Homing tendencies of large mammals: a review. Pages 76–86 in L. Nielsen and R. Brown, editors. Translocation of wild animals. Wisconsin Humane Society Milwaukee, Wisconsin/Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.

Rosatte, R., J. Hamr, B. Ranta, J. Young, and N. Cool. 2002. Elk Restoration in Ontario, Canada. Infectious Disease Management Strategy, 1998–2001. Annals of the New York Academy of Sciences **969:**358–363.

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

Ruth, T. K., K. A. Logan, L. L. Sweanor, M. C. Hornocker, and L. J. Temple. 1998. Evaluating cougar translocation in New Mexico. Journal of Wildlife Management **62:**1264–1275.

Ryckman, M., R. Rosatte, T. McIntosh, J. Hamr, and D. Jenkins. 2009. Post-release dispersal of reintroduced elk (*Cervus elaphus*) in Ontario, Canada. Restoration Ecology **17** (Published Online). doi: 10.1111/j.1526-100x.2009.00523.x.

Saenz, D., K. A. Baum, R. N. Conner, D. C. Rudolph, and R. Costa. 2002. Large-scale translocation strategies for reintroducing red-cockaded woodpeckers. Journal of Wildlife Management **66:**212–221.

Sagarin, R. D., and S. D. Gaines. 2002. The 'abundant centre' distribution: to what extent is it a biogeographic rule? Ecology Letters **5:**137–147.

Schaefer, J. A., C. M. Bergman, and S. N. Luttich. 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology **15:**731–739.

Seddon, P. J., P. S. Soorae, and F. Launay. 2005. Taxonomic bias in reintroduction projects. Animal Conservation **8:**51–58.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika **38:**196–218.

South, A. 1999. Dispersal in spatially explicit population models. Conservation Biology **13:**1039–1046.

Stanley Price, M. R. 1989. Animal reintroductions: the Arabian Oryx in Oman. Cambridge University Press, Cambridge.

Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution **14:**401–405.

Stussy, R. J., W. D. Edge, and T. A. O'Neil. 1994. Survival of resident and translocated female elk in the Cascade Mountains of Oregon. Wildlife Society Bulletin **22:**242–247.

Taylor, R. A. J. 1978. The relationship between density and distance of dispersing insects. Ecological Entomology **3:**63–70.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland.

Van den Bosch, F., R. Hengeveld, and J. A. J. Metz. 1992. Analyzing the velocity of animal range expansion. Journal of Biogeography **19:**135–150.

Veit, R. R., and M. A. Lewis. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. American Naturalist **148:**255–274.

White G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academy Press Inc., San Diego, California.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology **10:**1142–1154.

Zar, J. 1999. Biostatistical analysis. Prentice Hall, New Jersey.

Zimmerman, J. W., and R. A. Powell. 1995. Radio-telemetry error: location error method compared with error polygons and confidence ellipses. Canadian Journal of Zoology **73:**1123–1133.