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Movements, survival and habitat use by elk (Cervus elaphus) reintroduced to Northwestern Ontario

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Movements, survival and habitat use by elk (*Cervus elaphus*) reintroduced to northwestern Ontario

by

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Abstract

Once native to Ontario, eastern elk (*Cervus elaphus canadensis*) occupied much of the deciduous forest biome of eastern North America. However, increasing human settlement, as well as demands for meat and agricultural land resulted in their extirpation during the late 1800s and early 1900s. In 1995 the government of the province of Ontario announced an elk restoration initiative, and from 2000 to 2001 a total of 108 western elk (*Cervus elaphus manitobensis*) were translocated from Elk Island National Park (EINP), Alberta, to northwestern Ontario. Subsequent monitoring of the elk provided unique opportunities to measure their success in a boreal landscape, assess reintroduction methodologies, and to gain knowledge required for future management strategies. The specific objectives of this study were to examine the spatial behaviour, habitat relationships, and population characteristics of the recently reintroduced elk. As well, data relating to the transmission of two cervid parasites, *Fascioloides magna* and *Parelaphostrongylus tenuis*, on Ontario range were collected.

Two years after the initial reintroduction, 70% of the elk were still within 20 km of the release site. The remaining 30% (10 adult males and 12 adult females) permanently dispersed to the south, approximately 90 km from the release site. Mean maximum distance moved following release was farthest for elk translocated as adult males (68 $\pm$ 15 km), followed by adult females (37 $\pm$ 6 km), female calves (8 $\pm$ 1 km) and male calves (6 km $\pm$ 0.7 km).

Although no evidence of migration was observed, the elk ranged over a relatively large area (100% MCP: 5211 km^2). Mean individual home ranges were largest

for those translocated as adult females (56 $\pm$ 10 km^2), followed by female calves (40 $\pm$ 14 km^2), male calves (33 $\pm$ 9 km^2), and one adult male (16 km^2). No difference relating to sex, age or location (northern or southern portion of the study area) was observed.

Elk demonstrated non-random patterns of habitat use based on forest type, stand age, and elevation. In decreasing rank, forest stands used by elk established in the northern part of the study area, included red pine/white pine and mixed conifer, as well as cedar lowland, mixed hardwood, and poplar. Use of younger aged stands (< 25 years) and uplands were also important in the northern part of the study area. Elk in the southern portion of the study area selected mid-aged forest stands dominated by poplar.

Over the course of the 2-year study, the population of elk reintroduced to northwestern Ontario declined by 21%, limited, for the most part, by adult mortality (n=23). In order of decreasing importance, causes of adult mortality were translocation injury (26%), predation (17%), illegally shot animals (17%), road kill (9%), injury (4%), and drowning (4%). At the end of the study period elk translocated as adults had considerably lower survival (0.50 $\pm$ 0.09) than those translocated as calves (0.64 $\pm$ 0.18). Causes of adult mortality also differed by sex and location. It was estimated that 8 calves survived through the winter in each of 2001 and 2002, producing a calf:cow ratio of approximately 28:100. It was estimated that 85 elk were present on the landscape at the completion of this study, June 01, 2002.

To determine the efficacy of the treatment protocol for elk infected with *F. magna* in EINP, Alberta, fecal pellets were collected from elk both prior to treatment and following release in Ontario. Despite 2 treatments with the anthelminthic, triclabendazole, a small number of elk arrived in Ontario infected (5% -17%). In order to assess the relative risk of newly relocated elk becoming infected with either *F. magna* or *P. tenuis*, fecal pellets were collected from white-tailed deer resident near the elk release sites. Only white-tailed deer in the Fort Frances/Rainy River (38%) and Lake Huron/North (7%) shore had *F. magna* infection, while the prevalence of *P. tenuis* larvae was approximately 85% in all areas tested.

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Introduction

Once native to Ontario, eastern elk (*Cervus elaphus canadensis*) (O'Gara 2002) occupied the deciduous forest westward to approximately 95 degrees longitude, northward to about the 47th parallel, and southward to about the 34th parallel (O'Gara and Dundas 2002). However, as was the case across North America, increasing human settlement, as well as demands for meat and agricultural land resulted in the extirpation of these elk during the late 1800s and early 1900s (Ranta 1979; Ceballos and Ehrlich 2002). There have been several previous attempts to reintroduce elk to the province, the most recent being in the 1930s. However, due to concerns regarding the transmission of the parasite *Fascioloides magna*, most of these animals were destroyed (Kingscote 1950, 1951; Addison 1997). Two small remnant populations have survived in the Burwarsh/French River area of Ontario, and in 1996 they were estimated to number approximately 60 animals (Bellhouse and Broadfoot 1998).

In 1995, the Government of the province of Ontario announced a provincial elk restoration initiative, and from 1998 to 2001 a total of 443 western elk (*Cervus elaphus manitobensis*) (Polziehn et al. 1998; Polziehn et al. 2000; O'Gara 2002) were translocated from Elk Island National Park, Alberta, to several locations in Ontario, including Burwash/French River, Bancroft/North Hastings, Lake Huron/North Shore, and Lake of the Woods (Rosatte et al. 2002a, 2002b). This reintroduction effort provided unique opportunities to study the habits and survival of elk in parts of their historic range. Moreover, monitoring of the elk following release provided an assessment of reintroduction methodology, as well as insight relevant to future reintroduction efforts and management strategies.

Spatial behaviour

Knowledge of the spatial behaviour of a species is essential to understanding its ecology. Moreover, an understanding of the spatial behaviour of the elk reintroduced to northwestern Ontario (Lake of the Woods) is fundamental to assessing the overall success of the reintroduction effort, as well as determining key management strategies. Therefore, the first objective of this study was to investigate the spatial behaviour of the reintroduced elk, specifically examining their post-release dispersal and subsequent movements, as well as their annual and seasonal home ranges.

Stenseth and Lidicker (1992) define dispersal as a three part process, including emigration, transience, and immigration to a new range or social group. Three main hypotheses have been used to explain dispersal. These include inbreeding avoidance, resource competition, and mate competition (Gasaway 1980; Greenwood 1980; Dobson 1982; Bollinger et al. 1993). Costs of dispersal may include reduced survival and decreased reproductive success. However, studies have suggested that the costs of philopatry exceed the costs of dispersal (Wolff 1994). In general, females tend to establish ranges in or adjacent to their mother's group, while dispersal of male elk may be considerable (Boyce 1989). Male elk generally disperse during their second year, primarily during spring reproductive and fall breeding seasons (Clutton-Brock et al. 1982; de Vergie 1989). Dispersing yearling males in Colorado traveled an average of 79 km, with a maximum distance of 109 km (de Vergie 1989). Similarly, Petersburg et al. (2000) reported yearling male elk dispersing an average of 87 km, while Edge et al. (1986) reported dispersal of yearling male elk often exceeding 120 km.

Data on dispersal and movement of translocated wildlife immediately following release are limited. However, Rosatte et al. (2002a, 2002b) suggested that dispersal and post-release movements of translocated elk might be related more to the method in which animals were released, rather than to the aforementioned reasons. Two methods of release have been termed "hard" and "soft" (Bellhouse and Broadfoot 1998). A hard release simply involves releasing the animals as soon as they arrive and letting them explore the landscape. Although this is the simplest method, experience indicates that the animals tend to wander extensively following release, thereby enhancing the chances of mortality and reducing the chances of finding suitable mates the following autumn (Larkin et al. 2002). Soft release methods involve retaining animals in a holding facility for a period of at least 10 days, to several weeks or months (Rosatte et al. 2002a, 2002b). Some studies suggest that post-release movements and long distance dispersal may be minimized by a soft-release, presumably by enhancing social cohesiveness and release site fidelity (Morgantini and Hudson 1988; Rosatte et al. 2002a, 2002b).

Essential for understanding the spatial distribution of wildlife is the concept of home range. Home range is defined as the area traversed by an individual in its normal activities of food gathering, mating, and caring for young (Burt 1943). This definition, however, may also extend to include the area used by groups of animals (e.g. an elk herd). Sizes of home ranges of elk in western North America are extremely variable, often differing among populations. Edge et al. (1985) reported adult female elk in Montana occupying annual home ranges averaging 44 km^2. In another study in Montana, Edge et al. (1986) reported the annual range of two non-migratory cow-calf herds as 82 km^2 and 142 km^2. In central Ontario, individual annual home ranges of cow elk measured between 25 km^2 and 50 km^2 (Brown 1998). Edge et al. (1985) suggested that food availability, ambient temperature, biting insects, and availability of cover influenced home range size. Other studies have suggested that plant composition and forge density are important factors in determining the size of a home range, while social relationships and population density played a secondary role (Irwin 2002). Predation and human induced disturbances may also be influential (Irwin 2002).

Considerable differences in home range size relating to sex have also been reported in the literature, with male elk ranging over much larger areas than females (Geist 2002). For example, male elk in Pennsylvania had home ranges averaging 53 km^2, while females averaged only 7 km^2 (Cogan et al. 2001). Similarly, male elk in both Michigan and the Burwash region of Ontario apparently ranged over much larger areas than did females (Beyer 1987; Bellhouse and Broadfoot 1998). These differences may reflect different foraging and reproductive strategies. Beier (1987) hypothesized that male white-tailed deer (*Odocoileus vriginianus*) used areas of lower forage quality than females, thereby requiring larger home ranges to meet nutritional requirements. It may also be that lactating females need more water, requiring them to stay closer to water sources, or that males may be evicted by dominant females following insemination (Geist 2002).

On a yearly time scale, one of the most obvious patterns influencing the spatial distribution of elk is movements or migrations in response to seasonal changes (Skovlin 1982; Green and Bear 1990; Skovlin at al. 2002). Elk migrations, defined as regular round trips between two or more seasonal ranges (White and Garrott 1990), are usually classified as movement in relation to three broad seasonal habitat types: lowland winter range, mid-elevation transitional range, and upland summer range (Skovlin et al. 2002). Although migration is common among the Rocky Mountain subspecies (*Cervus elaphus nelsoni*) (Craighead et al. 1972; Morgantini and Hudson 1988; Boyce 1989), others including Roosevelt elk (*Cervus elaphus roosevelti*) and Tule elk (*Cervus elaphus nannodes*) do not show migratory behaviour. Similarly, eastern elk populations were apparently non-migratory (Murie 1951). The absence of migratory behaviour may result from a lack of physiographic zones or of a stimulus (e.g., severe weather) to make such movements necessary. Moran (1973) reported that Rocky Mountain elk released in Michigan demonstrated no sign of migration, probably the result of living in an area with little altitudinal change and relatively mild winters. Remnant herds of Rocky Mountain elk, originally introduced to central Ontario during the early 1930's, exhibit both migratory and non-migratory behaviour (Brown 1998). Elk in the Burwash region do not migrate, but use only a portion of their annual range during winter, while elk in the French River area migrate, traveling approximately 20 km between distinct summer and winter ranges (Brown 1998). Elk selected for translocation from Elk Island National Park to Ontario are from a non-migratory herd, as the Park is fenced. This may influence their behaviour once they are released on Ontario range (Bellhouse and Broadfoot 1998).

Habitat utilization

Habitat utilization by elk has been well documented (Skovlin et al. 2002). However, past research has been restricted to single scale analysis and has lacked the level of detail attainable by current advancements in GIS technology. Moreover, the northwestern Ontario release site is distinct in being a transition zone between the eastern deciduous and boreal forests, providing a variety of habitats from which the elk may select. Therefore, the second objective of this study was to investigate the scale-dependent habitat relationships of elk recently reintroduced to northwestern Ontario.

Habitat has four basic components, including food, cover, water, and space. Elk habitat selection, however, is a multidimensional concept, including the four basic components, as well as behaviour, topography, weather, and the interactions among these factors (Hobbs et al. 1981; Baker and Hobbs 1982; Skovlin 1982). Habitat selection is also largely a function of availability (Hobbs and Hanley 1990), as elk are considered habitat generalists (Skovlin et al. 2002).

Food selection and eating habits of elk are extremely variable, as they are found in many different vegetation types throughout North America (Skovlin et al. 2002). However, elk do exhibit certain preferences. Forage preference may vary among seasons and years, and appears to be strongly related to availability and phenology, which in turn is influenced by factors such as weather conditions (Nelson and Leege 1982; Unsworth et al. 1998). In general, elk prefer to graze, feeding in open areas including natural forest openings, clear-cut areas, and burned areas (Nelson and Leege 1982; Unsworth et al. 1998). Most studies indicate that elk prefer to consume grass rather than woody vegetation (Unsworth et al. 1998). Open grassy habitats seem most important during the spring and fall when cool season grasses are actively growing, with grass usually constituting more than 85% of the diet during the spring and fall months (Nelson and Leege 1982; Unsworth et al. 1998). Elk also show a strong preference for early successional communities, such as recent clear-cut areas, which provide high volumes of forage biomass (Parker 1990; Skovlin et al. 2002). During the summer months, when the growth of grasses slows, elk tend to feed on forbs, woody twigs, leaves, and when available, warm season grasses (Parker 1990; Unsworth et al. 1998). Some studies have reported that forbs constitute almost the entire summer diet (Skovlin 1982). Others have found that shrubs are more important, while in some cases high use of grass continues throughout the summer (Geist 1982).

Winter forage conditions are most critical for elk. During the winter, diet is influenced strongly by forage availability, as affected by snow conditions (Skovlin et al. 2002). In general, elk move to ranges where snow depths are minimal and feed on all available forage types, often digging through the snow to reach buried forbs and grasses (Jenkins and Starkey 1993; Unsworth et al. 1998). As winter progresses, elk are usually associated with areas that provide thermal cover and tend to consume woody browse (Parker 1990; Jenkins and Starkey 1993).

Although there is a lack of information regarding the habitat associations of eastern elk in Ontario, historical evidence suggests that they favoured open grassy habitats, including the prairie ecosystems of southwestern Ontario, grassy marshlands, and a variety of wetlands (i.e., bogs, fens, and swamps) (Bellhouse and Broadfoot 1998; Jost et al. 1999). Elk also appear to have been associated with Carolinian, deciduous, and mixed-wood forests, while avoiding the dense conifer forest stands, typical of the boreal forest (Bellhouse and Broadfoot 1998).

Elk translocated to both Michigan and Pennsylvania have demonstrated similar habitat and food selection to those living in western ecosystems (Buss 1967; Moran 1973; Devlin and Tzilkowski 1986). In general, elk translocated to the east foraged in open and early-seral habitat, especially young aspen and poplar (*Populus* spp.) and mixed conifer-hardwood forest types. Elk consumed grass and other cool season forage during the spring and autumn, and used areas that provided woody browse and thermal cover during the winter months. In Michigan, Moran (1973) observed a pronounced dietary shift from grass to woody browse after the first killing frost of autumn. Moreover, with the first snow cover, post-rut harem groups broke up and abandoned open areas for habitat offering woody forage and thermal cover (e.g., swamp conifer habitat, upland conifer habitat, and aspen/hardwood stands). In Pennsylvania, clear-cuts were most heavily used during the winter, suggesting selection for areas offering the most abundant forage (Devlin and Tzilkowski 1986).

Studies of forage selection in two elk herds introduced into the Burwash/French River regions of Ontario in the 1930's support the hypothesis that elk translocated to eastern North America will use habitats and forage classes similar to those used by native elk in western North America (Jost et al. 1999). Brown (1998) found that stands of aspen and poplar, white birch (*Betula papyrifera*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and open rock habitat were commonly selected by translocated elk. Also, Hamr and Fillion (1996) reported that elk made extensive use of wetlands during the spring and early summer, feeding on a variety of grasses (*Gramineae* spp.). Once digging became difficult due to snow cover or the depletion of ground sources of food, elk tended to feed on woody browse. Toward the end of the winter, elk moved into lowland conifer swamps, where they browsed on eastern white cedar (*Thuja occidentalis*) and less desirable species, such as balsam fir, pine (*Pinus* spp.) and spruce (*Picea* spp.). Furthermore, studies of elk food habits in central Ontario indicate that red maple *(Acer rubrum*), willow (*Salix* spp.), beaked hazel (*Corylus cornuta*), and various species of aspen and poplar are important winter foods (Jost et al. 1999). The rock tripe (*Umbilicaria mammulata*) is also an important winter food of the French River, Ontario herd. Finally, Ranta et al. (1982) found elk in central Ontario using a variety of habitat types during winter, with conifer habitats being particularly important.

Cover for security and thermal regulation is also an important factor influencing habitat selection by elk. Security or hiding cover, is a feature of habitat that provides elk with a means of escape from the threat of predators or harassment (Lyon and Christensen 1992). Usually some form of vegetation or topographic feature (Skovlin et al. 2002), security cover is of particular importance during hunting season and times of high human activity. For example, several studies have reported an increased use of cover by elk during autumn (Mclean 1972; Lonner 1976), and especially during the hunting season (Bohne 1974; Marcum 1975; Irwin and Peek 1979; Morgantini and Hudson 1979). Studies have also shown that activities, such as timber harvest, vehicular traffic, camping, fishing, or other recreational activities beyond a threshold distance of 0.8 km seldom alarm elk. However, activities within this distance resulted in evasive movements by elk to re-establish and maintain an adequate buffer zone between themselves and humans, with subsequent increased use of security cover (Ward 1973; Marcum 1975; Basile and Lonner 1979; Irwin and Peek 1979; Lyon 1979; Edge and Marcum 1985; Edge et al. 1987; Unsworth et al. 1998; Rowland et al. 2000). Hence, security cover appears to be a requirement for elk in the presence of human disturbance.

Thermal cover is a feature of habitat that aids elk in conserving energy and maintaining narrow tolerance limits of body temperature (Black et al. 1976). Inadequate thermal cover may prevent optimal elk use of summer range and significantly increases energy expenditures on winter range (Lyon and Ward 1982). As with security cover, thermal cover can be a timber stand with overstory for protection against winter cold or summer heat, or it can be a topographic feature, such as a small basin, which provides protection from chilling winds (Lyon and Ward 1982; Skovlin et al. 2002). In the Burwash region of Ontario, conifers dominated winter habitat selection by elk, presumably reflecting in large part the need for thermal regulation (Brown 1998).

In summer, upland forests provide shade from direct solar radiation (Skovlin et al. 2002). Relatively cool soil and microclimate conditions under shade help elk to conserve energy and dissipate heat. Older and more developed forest stands with "natural pruning" of lower branches permit wind movement. This provides elk with shade and cooling wind action, as well as good visibility (Lyon and Ward 1982; Millspaugh et al. 1998).

Although little has been done to quantify stand structure in terms of optimal winter thermal cover for elk, some generalizations can be made. In winter, evergreen conifer stands provide thermal cover superior to deciduous hardwoods (Skovlin et al. 2002). Moreover, closed or continuous canopies are superior to open or partially open canopies (Unsworth et al. 1998). Closely stocked stands with high stem densities are superior to those with relatively less stocking, and tall crowns probably have better insulating qualities than do short crowns. Despite differing thermal benefits, habitat selection by elk still seems to be based primarily on the availability of succulent vegetation and the absence of human disturbance (Marcum 1975; Franklin and Leib 1979; Peek et al. 1982; Edge and Marcum 1985; Marcum and Scott 1985; Unsworth et al. 1998). The use of thermal cover by elk seems to be important only during extreme summer or winter conditions, and at other times is probably preferred but not required (Peek et al. 1982; Cook et al. 1998).

Although secondary to the need for forage and cover, topographic features such as elevation and water (i.e., lakes, rivers, and wetlands) are also important to elk (Skovlin et al. 2002). In winter, elk use upper slopes that, because of wind, radiation, or shade pattern, are the first to become free of snow (Jeffery 1964; Jenkins 1984). Use of elevated landscapes in summer is apparent, and may be related to cooling wind patterns, visibility, or cover type. Valley drainage bottoms are also used during summer, most likely because they provide late-summer food and water (Pedersen et al. 1980; Jenkins 1984). Water is important to elk, as it is a physiological requirement for most metabolic processes. In many cases, water in the form of dew and succulent forage offsets the amount of surface water required by elk (Skovlin et al. 2002). However, Jeffery (1964) suggested that on summer range elk preferred areas within 0.5 km of water. Similarly, Bracken and Musser (1993) found that elk greatly preferred habitat within 0.2 km of water during spring, summer, and autumn.

Finally, the need for other specialized habitats, such as calving areas, rutting grounds and wallows has been demonstrated in the literature (Skovlin et al. 2002). However, they are poorly understood, difficult to predict, and apparently of lesser importance compared to those described above (Lyon and Ward 1982; Skovlin et al. 2002).

Population characteristics

Population characteristics are important response variables determining the success of any reintroduction effort. By monitoring key population characteristics such as survival, cause specific mortality, birth rates, and age and sex composition, researchers can readily assess the likelihood of long-term persistence, as well as determine effective management strategies. Therefore, the third objective of this study was to investigate the population characteristics of the elk recently reintroduced to northwestern Ontario.

Female elk are bred annually during the rutting period (September and October), usually producing a single calf in late May or early June (Raedeke et al. 2002). In general, females aged 3.5 to 7.5 are considered the most capable breeders, while males aged 7 to 12 are considered in their prime (Flook 1970). Although both male and female yearlings are capable of breeding, success varies greatly among populations and is thought to depend on individual growth and development, as well as the age and sex composition of the population (Raedeke et al. 2002).

The optimal adult male to female ratio for population growth is difficult to determine and few studies have reported any correlation between the lack of older males and declines in calf production. Bubenik (1985) suggested that 25 adult males per 100 adult females would maintain optimal calf production, although Noyes et al. (1996) observed significant population growth with 18 adult males per 100 adult females. Some studies have concluded that as few as 3 to 10 adult males per 100 adult females during the rut could result in population increases (Hines et. al 1985), while others have reported that below a threshold of approximately 10 adult males per 100 adult females, calf production can decline (Freddy 1987; Raedeke et al. 2002).

Balanced sex ratios and age structures are important to the growth of a population. However, in reintroduced populations growth can be offset by high initial mortality and the wide spatial distribution of the sexes. According to Larkin et al. (2002) the population structure of elk reintroduced to Kentucky was initially heavily skewed towards yearlings, raising concerns regarding the breeding success and productivity of the herd. However, studies during the ensuing two years indicated that yearling males were capable breeders and calf production was good. Relatively high capture related and post-release mortality, and scattering of potential mates were subsequently thought to be responsible for an overall population decline. They concluded that more translocated elk or supplemental releases would be necessary to compensate for early mortalities and reduce the spatial segregation of males and females, thereby facilitating population growth.

As is the case in most wildlife populations, elk mortality during the first year of life is high, with considerable intra-uterine mortality, as well as high post-natal mortality being reported (Raedeke et al. 2002). Disease, severe winters, and predation by black bears (*Ursus americanus*), coyotes (*Canis latrans*), and wolves (*Canis lupus*) are important causes of mortality in sub-adult elk (calves and yearlings) (Raedeke et al. 2002). Among adult elk, causes of mortality, in decreasing order of importance, include hunting (both legal and illegal), predation, disease, malnutrition, exposure, harassment, and accidents (Unsworth et al. 1993; Ballard et al. 2000; Raedeke et al. 2002). In the Burwash/French River region of Ontario, drowning and collisions with trains were also important sources of mortality for elk (Bellhouse and Broadfoot 1998; Brown 1998).

Data on the growth rate of elk populations following a reintroduction are limited. However, Caughley (1970) suggested that populations of ungulates introduced to vacant habitat should closely conform to exponential growth models. Accordingly, McCorquodale et al. (1988) found the rate of increase for a colonizing elk population in central Washington to be as high as 30%. Likewise, the rates of increase for elk introduced to both Washington (Merrill 1987) and California (Gogan and Barrette 1987) were estimated at 34% and 29%, respectively. Although these data suggest that introduced elk populations have great growth potential in a variety of habitats, they likely represent the maximum for elk with high first year survival and favourable habitat conditions, and do not reflect the situation when conditions are less ideal (Raedeke et al. 2002). According to Moran (1973), elk reintroduced to Michigan grew at a rate of approximately 20% for the first 20 years, declining to 13% in later years.

Parasitological issues

A final issue, important to the health and vigor of any reintroduced population is the transmission of various diseases and parasites. Two parasites of potential importance in the transloaction of elk from Alberta to Ontario are the giant American liver fluke, *Fascioloides magna,* and the meningeal worm, *Parelaphostrongylus tenuis*. Therefore, the final objective of this study was to gather baseline data relating to the transmission of these two parasites on Ontario range.

Cervids of North America have co-evolved with the giant American liver fluke, *F. magna* (Greer 1982). It was first described by Bassi in 1875, who found it in an elk imported from North America to a zoological park near Turin, Italy (Erhardova-Kotrla

1971). Currently, *F. magna* is distributed in patches from coast to coast in the United States and throughout southern and central Canada (Pybus 2001).

Both elk and white-tailed deer are considered definitive hosts for this parasite, as the fluke matures and successfully completes its life cycle within them. Upon infection, flukes migrate for a time in the liver, apparently in search of another individual with which to pair (Pybus 2001). Although flukes are hermaphroditic, cross-fertilization is apparently preferred (Pybus 2001). Upon meeting, the two flukes become enclosed in a capsule. The capsules are continuous with bile ducts that allow eggs and metabolic wastes to drain out with the flow of bile into the intestine and be discharged with feces (Pybus 2001).

Once the eggs are released into water, a free-swimming ciliated larva (miracidium) hatches (Pybus 2001). Within 24 hours, the miracidium must locate and penetrate an aquatic snail, a required intermediate host (species of the family Lymnaeidae) (Lankester and Samuel 1998). Multiplication occurs, and several hundred individuals of another larval form (cercaria) are released from the snail. Cercariae then attach to aquatic plants, forming a protective cyst around themselves. These encysted metacercaria are the infective stage, and the life cycle is completed when an ungulate eats contaminated aquatic vegetation (Pybus 2001).

The liver fluke is virtually non-pathogenic in native cervids although fatal infections have been reported in individuals with high numbers of flukes (Pybus 2001). Mortality of infected white-tailed deer, black tailed deer (*Odocoileus hemionus columbianus*), elk, and red deer (*Cervus elaphus elaphus*), as well as experimentally infected fallow deer (*Dama dama*), elk, and mule deer (*Odocoileus hemionus hemionus*) has been reported (Pybus 2001). In moose (*Alces alces*), cattle (*Bos taurus*), bison (*Bison bison*), sheep (*Ovis aries*), and goats (*Capra hircus*), flukes wander extensively in the liver, creating bloody tunnels or tracts (Pybus 2001). In moose and bovids, extensive liver damage is compensated by an increase in organ size and the parasite does not reach sexual maturity (Lankester and Samuel 1998). In sheep and goats, the resultant tissue damage is usually fatal (Pybus 2001).

In the past, the primary concern with *F. magna* in Ontario was in relation to agriculture, as cattle and elk in the Burwash area of Ontario were heavily infected with the parasite during the 1940s and 1950s (Addison 1997). Finding a much higher prevalence of flukes in the introduced elk than in Ontario white-tailed deer, and the knowledge that elk translocated from Alberta were from a heavily infected herd, led to the conclusion that elk constituted a major reservoir of infection for Ontario livestock and wildlife. Subsequently, the elk reintroduced to Ontario in the 1930's were nearly eradicated (Addison 1997).

In Alberta, *F. magna* is known from elk in several areas; however, it is generally limited to the Rocky Mountain trench (Pybus 2001). The elk selected for translocation from EINP, Alberta are from a herd known to be infected with liver fluke (Thorne et al. 2002). However, prior to translocation, elk were treated with 10% triclabendazole, a proven treatment against liver flukes (Pybus et al. 1991).

Giant liver flukes are naturally occurring and often prevalent in the white-tailed deer herds of Ontario (Addison et al. 1988), and the presence of elk is not necessary to sustain high prevalences of the parasite. Studies since the 1950s have led to the conclusion that white-tailed deer are as efficient a host for this parasite in many parts of eastern North America, as are elk in the west (Addison et al. 1988). However, the presence of two co-existing capable hosts could result in an increase of fluke infestations in Ontario. Despite being of little importance in native cervids, the liver fluke has significant economic importance to the domestic cattle and sheep industries. Cattle losses are confined primarily to the contamination of the liver due to extensive fibrosis (Lankester and Samuel 1998). In domestic sheep, however, infection by as few as three flukes can be fatal. Therefore, to prevent these types of losses, liver fluke infestations in wild cervids of Ontario should be monitored and managed, particularly where white-tailed deer and elk share range with livestock.

Parelaphostrongylus tenuis is a parasite of white-tailed deer of the eastern deciduous forest biome and deciduous/coniferous ecotone of eastern and central North America (Lankester 2001). It is rare or absent in the coastal plains region of the southeastern United States and is absent in western North America. The precise limits, however, of its most westerly distribution are poorly known (Lankester 2001). It has been found in white-tailed deer in western Manitoba and in the United States east of a line projected south from western Minnesota, through central Oaklahoma, and into the extreme eastern portions of Texas. The central grasslands, being less hospitable for required intermediate gastropods, have been identified as a possible barrier that prevented the parasite's movement westward with white-tailed deer (Lankester 2001).

The life cycle of the meningeal worm is indirect, with terrestrial snails and slugs serving as intermediate hosts. A number of different species are suitable, although only a few are important as sources of infection in the wild (Lankester 2001). These include the slugs *Deroceras laeve* and *D. reticulatum*, and the small woodland snails *Discus* *cronkhitei, Zonitoides spp., Succinea spp.*, and *Cochlicopa spp*. (Platt 1989; Lankester and Peterson 1996; Lankester 2001). All of these species are fairly common and widely distributed throughout white-tailed deer range in eastern North America (Lankester 2001). Transmission to white-tailed deer occurs primarily in the autumn months when larvae acquired by gastropods during the spring and summer have reached the infective stage, and when young, susceptible deer feed low to the ground (Lankester 2001).

In white-tailed deer, infective third-stage larvae are released from the snail foot tissue after being accidentally ingested. The parasite then penetrates the wall of the abomasum and enters the abdominal cavity (Anderson and Strelive 1967). Migrating, possibly along nerves in the body wall toward the back, the larvae take approximately 10 days to reach the vertebral column. It is here that the parasites enter the tissue of the spinal cord and begin to develop in the dorsal horns of gray matter. The third-stage larva molts to the fourth, and the fourth molts again to the early fifth or sub-adult stage (Lankester 2001).

The infective larva grows from a length of approximately 0.10 cm to reach up to 7.6 cm as an adult (Lankester 2001). Forty days after infection, most of the maturing males and females leave the spinal cord and are found in the fluid-filled subdural space, between the cord and the covering dura membrane (Anderson 1963, 1965). They then migrate anteriorly into the cranium, becoming associated with large veins and venous blood sinuses in the dura. In particular, the worms are often located within the cavernous and intercavernous sinuses in the floor of the cranium surrounding the pituitary gland (Lankester 2001).

Female worms release eggs from the vulva near the posterior end of the body. The eggs are then swept away in the blood and travel to the right side of heart. From the heart the eggs are transported through the pulmonary artery to the lungs, where eggs in the one and two cell stage lodge in fine blood capillaries, becoming surrounded by fibrous tissue and forming tiny nodules (Lankester 2001). First-stage larvae develop within the entrapped egg, eventually emerging into the air spaces of the lung. Larvae are carried out of the lungs and up the trachea in a layer of mucous moved by cilia. In the oral cavity the larvae are swallowed and can be found in the feces approximately 90 to 137 days after infection (Rickard et al. 1994). Young, recently infected white-tailed deer pass more larvae than do older animals; however, most larvae are passed in the spring by deer of all ages (Slomke et al. 1995).

Once released, larvae occur only on the outside of the fecal pellet, in the covering layer of mucous (Lankester and Anderson 1968). They are readily removed by rain and melting snow, and are dispersed into the soil. They are resistant to deep freezing and limited periods of drying, and can most likely survive for several months (Shostak and Samuel 1984).

Naturally occurring disease caused by *P. tenuis* is rare in white-tailed deer (Eckroade et al. 1970; Prestwood 1970; Lankester 2001); however, this parasite can be devastating to other North American cervids and some exotic ungulates (Anderson 1971). The effects of *P. tenuis* on cervids other than the white-tailed deer have been described by Anderson et al. (1966), who determined that this parasite caused what is referred to as moose sickness. Anderson et al. (1966) and Anderson (1971, 1972) subsequently demonstrated the pathogenicity of this parasite for other native ungulates and determined experimentally that the meningeal worm is a significant pathogen in elk. Moreover, studies have concluded that this parasite has probably limited the success of past elk reintroductions into eastern North America (Anderson and Prestwood 1981; Raskevitz et al. 1991; Thorne et al. 2002). The meningeal worm, however, is probably not as pathogenic in elk as it is in moose and caribou (Anderson et al.1966), with the severity and outcome of infection being dose dependent (Samuel et al. 1992). A wide spectrum of impacts on elk at both the individual and population level has been reported for meningeal worm. For example Larkin et al. (2002), concluded that *P. tenuis* related mortality will limit the growth of reintroduced elk populations in Kentucky. On the other hand, populations of elk sympatric with infected white-tailed deer have persisted (Moran 1973; Woolfe et al. 1977), although individual elk have demonstrated clinical signs of meningeal worm infections (Moran 1973; Olsen and Woolfe 1978, 1979; Anderson and Prestwood 1981; Devlin and Drake 1989). Distinctive clinical signs include blindness, aimless wandering, staggering, tilting of the head, weakness or debilitation of the hindquarters, and circling movements (Lankester 2001).

Parelaphostrongylus tenuis does not occur naturally in Alberta, but, it is very common in white-tailed deer in Ontario (Lankester 2001). Therefore, the interest in *P. tenuis* arises from the potential negative impact of this parasite on the success of translocated animals onto Ontario range. Much of what is known about the relative susceptibility of the various cervids to *P. tenuis* comes from experimental infections, while measures of the impact on wild populations are scarce, particularly in the case of elk. Moreover, as was mentioned, this parasite is suspected of having played a role in the failure of several elk reintroduction efforts (Severinghaus and Darrow 1976; Anderson and Prestwood 1981; Samuel et al. 1992; Thorne et al. 2002; Larkin et al. 2002). It is, therefore, clear that predictions as to the success of elk translocated on to *P. tenuis* range are speculative at best, until better long term population data are available.

Objectives

In summary, the objectives of this study were to:

1. Investigate the spatial behaviour of elk reintroduced to northwestern Ontario, specifically examining their post-release dispersal and subsequent movements, as well as their annual and seasonal home ranges
2. Investigate the scale-dependant habitat relationships of elk recently reintroduced to northwestern Ontario
3. Investigate the population characteristics of the elk recently reintroduced to northwestern Ontario, specifically examining survival, cause-specific mortality, and recruitment
4. Gather baseline data relating to the transmission of *Fascioloides magna* and *Parelphostrongylus tenuis* on Ontario range

Study Area

The area inhabited by the recently re-introduced elk population encompasses approximately 10 000 km^2 in the Lake of the Woods region of northwestern Ontario, Canada (49°16'N, 93°42'W). It extends from the town of Sioux Narrows in the north to the Canada/USA border in the south, and from the town of Fort Frances in the east to the Ontario/Manitoba border in the west (Figure 1).

The study area is distinct in being a transition zone between the Great Lakes/St. Lawrence lowland and boreal forest regions (Rowe 1972). Consequently, the habitat varies markedly from north to south. The northern part of the study area is more typical of the boreal forest, underlain by the Canadian Shield and dominated by coniferous trees including black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*) (Rowe 1972). White birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) are also found in the region. The terrain varies from lowland peat bogs to exposed bedrock with many lakes and ponds. Elevation ranges from 100 m above sea level (a.s.l.) on the shores of the many lakes and rivers, to 490 m a.s.l. on adjacent hills and ridges. The mean elevation is 356 $\pm$ 10 m a.s.l (SE). The main ecological force in the region is natural disturbance, with the forest mosaic largely influenced by the size, intensity, and frequency of forest fires. More recently, however, clear-cut timber harvesting and forest fire suppression has influenced the tree species mix and forest age structure in this area.

The southern part of the study area is more typical of the Great Lakes/St.Lawrence lowland forest region (Rowe 1972). It lies between the boreal forest

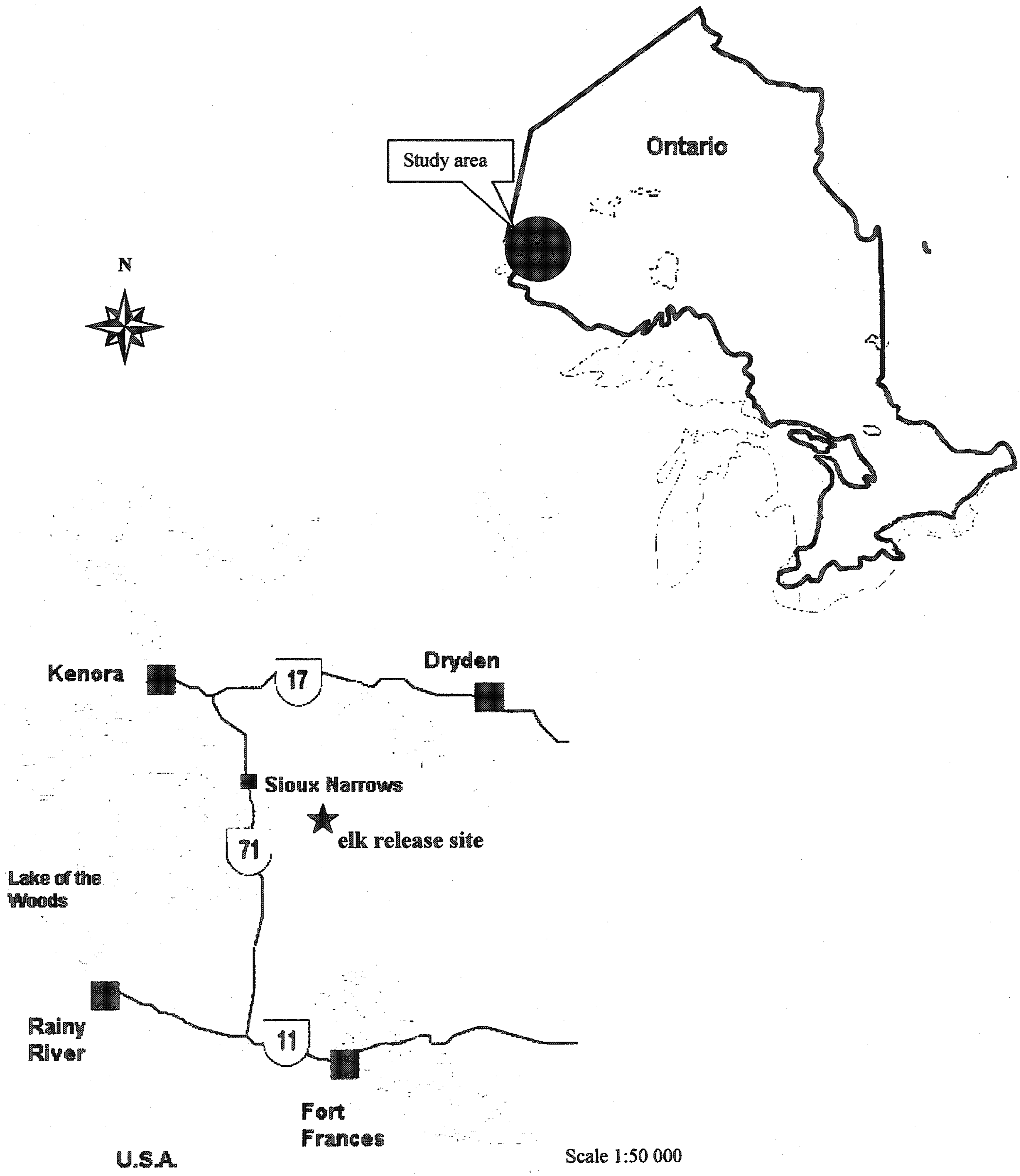


Figure 1: Map of the study area showing elk release site (49°16'N, 93°42'W)

and the eastern deciduous forest regions, and is therefore in itself transitional. It is characterized by a mixture of coniferous and deciduous trees, including white pine (*Pinus strobus*), red pine (*Pinus resinosa*), eastern hemlock (*Tsuga canadensis*), white cedar (*Thuja occidentalis*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and red maple (*Acer rubrum*). Species common in the boreal forest, such as black spruce, jack pine, trembling aspen and white birch may also be found. The terrain varies from exposed granite bedrock to gentle slopes with deep fertile soils. Elevation ranges from 40 m a.s.l. along the shores of lakes to 470 m a.s.l. on the many hills and ridges. The mean elevation is 348 $\pm$ 20 m a.s.l. The southern portion of the study area also has large areas converted for agricultural use, with many roads and towns.

The climate in the study area is described as cold temperate continental, with some local moderation by larger lakes and other topographic features (Brunskill and Schindler 1971). It varies from north to south, most notably, in terms of mean total snow depth, which on the last day of January, is considerably greater in the northern part of the study area (40 cm), than in the southern portion (28 cm) (Anonymous 2002). Moreover, spring “green-up” generally occurs one month earlier (mid to late April) in the southern portion.

The elk study area is home to a diverse fauna. Potential competitors include white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*). Potential predators include wolves (*Canis lupus*), coyotes (*Canis latrans*) and black bears (*Ursus americanus*). Although data comparing the relative abundance of various wildlife species in the northern and southern portions of the study area are not available, the density of white-tailed deer is higher in the south (Huchinson et al. 2003).

Materials and Methods

In January 2000, 60 elk were translocated from Elk Island National Park (EINP), Alberta to northwestern Ontario (Rosatte et al. 2002a, 2002b) (Table 1). Prior to translocation a comprehensive disease management plan was implemented according to Canadian Food Inspection Agency (CFIA) regulations. Elk were tested for diseases affecting native and domestic ungulates, including brucellosis and bovine and avian tuberculosis. Moreover, all animals were treated with 10% triclabendazole (Fascinex ™, Novartis Corp., New York, New York) (two doses, three days apart; 170 ml for adults and 100 ml for yearlings and calves) for control of liver flukes (*Fascioloides magna*) and Ivermectin (Ivomec ™, Merial Inc., USA)(10 mg/50 kg body weight) for control of various nematodes and ectoparasites. As part of a nutritional therapy program, elk translocated to Ontario during 2000 were given an oral treatment of a probiotic (Rum-Innoc-Gel ™, Bio-Ag Consultants and Distributors, Wellesley, Ontario), as well as Nutri-charge ™ electrolyte solution and pellets (STS Agriventures, Red Deer, Alberta). A vitamin E and selenium compound (Dystosel ™, Pfizer Animal Health Group, Pfizer Inc., Canada) was also provided to elk prior to transport to prevent capture myopathy. All elk were marked with uniquely numbered ear tags, while 30 were fitted with conventional VHF (very high frequency) radio-collars equipped with motion-sensitive mortality sensors (Model LMRT-4; 148-151 Mhz; Lotek Engineering Inc., Newmarket, Ontario).

In February of 2001, an additional 48 elk were translocated from EINP, Alberta to northwestern Ontario (Table 1). Again, all animals were tested and treated for various diseases and parasites, as well as placed on a nutritional therapy program. All elk were

Table 1: Age and sex characteristics of elk reintroduced to northwestern Ontario during February/March 2000 and 2001

Year of release		Males YOY	Males YRL	Males AD	Males Total	Females YOY	Females YRL	Females AD	Females Total	Grand total
2000	Collared	4	1	4	9	6	1	14	21	30
	Non-collared	4	0	8	12	0	0	18	18	30
	Total	8	1	12	21	6	1	32	39	60
2001	Collared	8	3	7	18	5	5	15	25	43
	Non-collared	1	3	0	4	0	1	0	1	5
	Total	9	6	7	22	5	6	15	26	48
Total # of elk released		17	7	19	43	11	7	47	65	108

Note: YOY = calves 8-9 months; YRL = yearlings 20-21 months; AD = adults > 2.5 years marked with uniquely numbered ear tags, while 43 were fitted with conventional VHF radio-collars equipped with motion-sensitive mortality sensors. Further details of the capture, handling, and transportation techniques used during the reintroduction effort are available in Rosatte et al. (2002a, 2002b).

Upon arrival in northwestern Ontario, the elk were held in an enclosure adjacent to Cameron Lake (49°16'N, 93°42'W), allowing them to become familiar with their new surroundings and to recuperate from the lengthy trip. The length of the holding period varied from 11 days in 2000 to 17 days in 2001. Tracking of radio-collared elk began on the day following their release from the enclosure.

Animal locations

Radio-collared elk were located by radio-telemetry or direct observation during daylight hours once per week from May to the end of August, and once every two weeks between September and April. Both ground and aerial radio-telemetry techniques were used. Radio-telemetry locations were obtained by remote triangulation from roads using a roof mounted omni-directional antenna, a 4-element directional antenna, a portable receiver (Model TRX-2000S, Wildlife Materials Inc., Carbondale, Illinois and Model STR-1000, Lotek Engineering Inc., Newmarket, Ontario), a hand-held global positioning system (GPS) (Model Plus II, Garmin Inc., Olathe, Kansas), 1:50 000 topographic maps, and a compass. Bearings were plotted on 1:50 000 maps in the field to determine where subsequent readings should be taken and when a sufficiently precise location had been obtained (< 1 ha). A minimum of three bearings was used to determine the location of all elk. For each location, Universal Transverse Mercator (UTM) coordinates (North

American Datum 1983) were recorded to the nearest 50 m. The locations of directly observed animals were obtained by moving to the area where the animal was seen and noting the UTM coordinates with a hand-held GPS.

Elk were located from the air using both a helicopter (Bell 206B, A-Star 350) and fixed-wing aircraft (Dehaviland Turbo Beaver). The general location of the animal was determined, using a paired 3-element Yagi antenna attached to the aircraft and a portable receiver. Repeated low passes were then made to obtain a visual observation. Locations were recorded by marking the area where the animal was seen with a hand-held GPS, and by plotting the location on a 1:50 000 topographic map during the flight. UTM coordinates were recorded to the nearest 50 m.

The accuracy of both the ground and aerial radio-telemetry techniques used to locate the elk was determined by placing 35 radio-collars throughout the study area in locations where the elk were consistently found. Comparisons were then made between the actual locations of the radio-collars as determined by a hand-held GPS, and locations obtained using the same ground and aerial telemetry techniques described above.

Spatial behaviour

Movement of radio-collared elk was quantified, including both mean and maximum straight-line distances from the release site, as well as the direction of movement. Using ArcView GIS (Version 3.2, Environmental Systems Research Institute, Inc., Redlands, California) and Animal Movement Analyst ArcView Extension (Hooge and Eichenlaub 1997), those elk that survived and whose locations were known following the rutting period during the year in which they were released were included in the analysis. An elk was considered to have dispersed when a movement greater than 20 km was made in a single direction with no evidence of return (White and Garrott 1990). When no difference was found between release years, data were pooled and analysed for differences by sex and age using a one-way analysis of variance (ANOVA). In this test and all subsequent analyses, parametric tests were replaced with appropriate non-parametric tests when transformations did not achieve homogeneity of variance. All tests were completed using the Statistical Package for the Social Sciences (Version 10, SPSS Inc., Chicago, Illinois), and deemed significant at $\alpha<0.05$.

Home ranges were estimated for the population and for individual elk using the 100% minimum convex polygon method (MCP) (Mohr 1947). The adaptive kernel method (95% and 50% contour) was also used to calculate utilization distributions for individual elk (Worton 1989). Both estimations were calculated using Home Range Extension for ArcView (Rodgers and Carr 1998). Only individual elk with greater than 25 locations were included in the estimates.

The minimum convex polygon method has been widely used for estimating home range size and was used in this study for comparative purposes. The minimum convex polygon method involves connecting the peripheral points of a group of locations to create a convex polygon, the area of which can be calculated (Mohr 1947; White and Garrott 1990). Despite the widespread use of this method, there are several disadvantages. First, this method often requires more than 100 location points for the same animal to obtain reliable estimates of home range size (Bekoff and Mech 1984; Laundre and Keller 1984; Harris et al. 1990; Doncaster and MacDonald 1991). Sampling intensity of this magnitude may be difficult to achieve. Second, as the number of locations increases, the estimated size of the home range also increases. As a result, this method is influenced disproportionately by outlying points (Jennrich and Turner 1969). Third, an assumption of the minimum convex polygon method is that the locations are normally distributed within the home range. However, due to use of areas within an animal's home range, behavioural differences among animals in their movement patterns, and potential restrictions to animal movement within their home range (e.g., large water bodies), this assumption is rarely met (White and Garrot 1990). Consequently, home range size may be greatly overestimated and include areas that the animal never utilizes.

The adaptive kernel method of estimating utilization distributions is a non-parametric statistical method that estimates probability densities from a set of location points (Worton 1989). Although statisticians have used kernel density estimation since the 1950s, the kernel method has been applied to utilization distribution analysis of animal locations only for the past decade. In this type of analysis, the probability of finding an animal in any one place is described (Rodgers and Carr 1998). The method begins by centering a bivariate probability density function with unit volume over each recorded location point. A regular grid is then superimposed on the data and a density estimate is calculated at each grid intersection. A bivariate kernel density estimator is calculated over the entire grid using the density estimates at each grid intersection. The resulting kernel density estimator will thus have large values in areas with many location points and low values in areas with few location points. Utilization distribution estimates are derived by drawing contour lines based on the volume of the curve under the utilization distribution whose area can be calculated (Rodgers and Carr 1998).

The adaptive kernel method was selected for use in this study based on reasonable sample size requirements (30 to 50 locations points for the same animal), the ability to compute range boundaries that identify multiple centers of activity, computations incorporating the complete utilization distribution, nonparametric methodology, and the lack of sensitivity to outliers (Worton 1995; Seaman et al. 1999). Despite these many strengths, several weaknesses of the adaptive kernel method of analysis are evident; specifically, the lack of general variance expression, the assumption of independence, and the high sensitivity to smoothing parameters (Kernohan et al. 2001). It should be noted, however, that with the exception of smoothing parameter sensitivity, these weaknesses are not unique to kernel estimators.

Selecting an appropriate smoothing parameter or bandwidth is widely recognized as the most important part of deriving kernel density estimations (Silverman 1986; Worton 1995). The bandwidth controls the width of the individual kernels and therefore determines the amount of smoothing applied to the data. At small bandwidths, the individual kernels will be narrow and the kernel density estimate at a given point will be based on a small number of location points. This may not allow for variation among samples and may produce an extremely variable utilization distribution. At larger bandwidths, all local peaks and valleys are smoothed over a single surface, often obscuring the fine detail needed to identify centers of activity. Selection of an appropriate smoothing parameter depends on the original observations and should be determined through exploration of the data (Rodgers and Carr 1998). Following exploration of the data and considering the purposes of this study, least squares cross validation was considered to be the best choice.

Comparisons of 100% MCP and 95% adaptive kernel estimates were made between release years using an independent samples t-test. Comparisons were also made between the 50% contour of the adaptive kernel estimate, as it represents the core area of activity and is less affected by deviations from the assumptions of home range models (Hooge et al. 1999). When estimates did not differ between release years, data were pooled and analysed for differences relating to sex and age using an ANOVA. Differences relating to location (i.e., northern or southern portion of the study area) were also assessed, as were differences relating to season by examining the percent overlap of winter (November 1 – April 30) and summer (May 1 – October 31) ranges, as determined by snow cover.

Habitat utilization

Habitat data were assembled in a geographic information system (GIS) for the area encompassing all elk locations, totaling approximately 10 000 km^2. Data were compiled from various digital Terrestrial and Wetland Forest Resource Inventory Classification files for northwestern Ontario obtained from the Ontario Ministry of Natural Resources (1998). From these data sources, habitat variables associated with forest overstory and terrain attributes were derived.

Vegetation maps for northwestern Ontario are based on remotely sensed data. Although many of the error sources associated with aerial photogrammetry are not present in remotely sensed data, spatial inaccuracy and misclassification error remain a problem (McKelvey and Noon 2001). In order to determine both the spatial accuracy and the degree of correctness in the classification of habitat types, 271 random points in areas where the elk were commonly found were ground-truthed. A description of sampling and statistical protocol can be found in Vander Wal (2002). Data obtained for random points were compared to habitat data derived from digital Terrestrial and Wetland Ecosite Classification files obtained from the Ontario Ministry of Natural Resources (1998). At only 14% of the random points did site classification agree with that on the digitized base maps. This was deemed insufficiently accurate to assess elk habitat use. Subsequent, analysis was done instead using broad forest types (standard forest units) derived from forest resource inventory (FRI) species composition strings (Ontario Ministry of Natural Resources 1998) (Appendix 1). When compared to data gathered during ground truthing, 81% of the random points were classified correctly, thus providing a sufficiently valid database upon which to evaluate elk habitat use. In this study, the selection of habitat variables was based on the assumption that the ecology and habitat associations of elk are in large part influenced by habitat structure. The attributes measured included forest type, stand age, elevation, and distance to wetlands (Table 2).

Several assumptions are commonly made in habitat selection studies using radio-marked animals. First, it is assumed that radio-marked animals are a random sample of the population (Erickson et al. 2001). Radio-marking individuals throughout the study area and treating each as an independent experimental unit works to minimize errors associated with this assumption. Second, it is assumed that radiolocations are independent in time. This assumption is violated when radiolocation data are collected too frequently. To eliminate temporal dependencies, researchers must allow sufficient time between successive radiolocations. Tests of independence of successive locations of an animal have been derived (e.g., Schoener 1981; Swihart and Slade 1985) and can be

Table 2: Independent variables considered for analysis of habitat utilization by elk reintroduced to northwestern Ontario during February/March 2000 and 2001

Habitat variable	Description
Forest type	Standard Forest Unit (SFU)
1	Red pine/white pine forest
2	Cedar lowland
3	Black spruce lowland
4	Black spruce/deciduous forest
5	Jack pine dominant forest
6	Poplar dominant forest
7	White birch dominant forest
8	Other hardwood dominant forest
9	Black spruce/jack pine mixed forest
10	Balsam fir/conifer mixed forest
11	Hardwood mixed forest
Stand age	Stand age in years
1	1 – 25
2	25 – 50
3	51 – 76
4	77 – 101
5	102 – 127
6	128 – 152
7	153 – 178
8	179 – 203
9	204 – 229
Elevation	Elevation in metres
1	320m – 340
2	341m – 360
3	361m – 380
4	381m – 400
5	401m – 420
6	421m – 440
7	441m – 460
Distance to wetlands	Distance to nearest wetland in metres

Note: Continuous variables were used in multiple regression analysis, while categorical variables were used in compositional analysis applied to evaluate independence and determine the minimum length of time required between radiolocations. A third assumption is that one radio-marked animal's resource use is independent of all other radio-marked animals. A common violation of this assumption is when animals are territorial or gregarious, as in the case of elk. The effect of this dependency can be reduced by treating the animal as the experimental unit (i.e., not pooling radiolocations across animals) and by modeling the spatial autocorrelation and adjusting estimates and variances of selection. A fourth assumption is that resource availability does not change over the course of the study. This assumption can be met by incorporating significant changes in resource availability during the study period into the analysis. Finally, it is assumed that utilized resources are classified correctly. Telemetry error, uncertainties in the spatial delineation of habitat types, and habitat characteristics, such as small patch size and high edge ratio, may result in misclassification of true habitat use. Efforts to minimize this type of error include using random sampling within the error distribution around each location point to calculate the likelihood that the location could land in a different habitat type (Nams 1989; Samuel and Kenow 1992) and choosing the appropriate scale at which to effectively evaluate resource selection.

Scale is an important consideration in any resource selection study, and in most cases selection by a species is apparent at more than one scale (Porter and Church 1987). Johnson (1980) provides a framework for scaling resource selection. First-order selection includes studies at the largest scale over the entire geographic range of a species. Second-order selection includes selection of a home range from within the geographic range. Third-order selection includes selection of core (intensely used) areas within the home range, and fourth-order selection, includes the selection of particular resources. This framework explicitly incorporates large and small-scale resource features that may influence resource selection and is biologically based, thus reducing some arbitrariness in defining availability. Elk habitat relationships were analysed here at second and third-order selection scales according to Johnson's framework.

Several analytical techniques have been developed to evaluate habitat selection. These include the Neu et al. method (Neu et al. 1974; Byers et al. 1984), Johnson's method (Johnson 1980), Friedman's test (Friedman 1937; Conover 1999), compositional analysis (Aebischer et al. 1993), log linear modeling (Hastie and Pregibon 1992), discrete choice (Ben-Akiva and Lerman 1985; Cooper and Millspaugh 1999), discriminant function analysis (Dunn and Braun 1986), logistic regression (North and Reynolds 1996), and multiple regression (McCullagh and Nelder 1989). There is, however, no agreement as to which method of analysis is best in all cases (Alldredge and Ratti 1986,1992; Mclean et al. 1998), and the choice depends ultimately on the biological questions of interest, on how observations and individuals are weighted, and on the assumptions most likely to be satisfied (Alldredge and Ratti 1992).

For the purposes of this study both logistic regression and compositional analysis were used to assess habitat use by elk in northwestern Ontario. Logistic regression is useful in that it allows exploratory analysis of various characteristics of habitat that contribute to selection (Manly et al. 1993; Trexler and Travis 1993; Erickson et al. 2001). Furthermore, hypotheses are tested using specific characteristics of habitats rather than habitats as categories, and the relative importance of many variables is assessed simultaneously (Alldredge et al. 1998; Boyce and McDonald 1999). Despite these advantages, there are several drawbacks. First, logistic regression is not suited to highly correlated data. Therefore, variables that are highly correlated must be identified and eliminated by allowing only one of the variables in the analysis (Erickson et al. 2001).

Second, logistic regression requires the variance-covariance matrices to be equal. This is rarely achieved with ecological data. Finally, when data are pooled across animals, logistic regression relies on the assumption of independence of location points. A common violation of this assumption is when animals are gregarious and differential use of habitats by groups occurs. This assumption can be met by using the animal as the experimental unit. However, in this study the sample size (i.e., number of elk with sufficient re-locations) was too small to provide meaningful results. Multiple logistic regression was therefore used in this study only as an exploratory tool for the purpose of identifying the variables that contribute most to habitat selection. Further regression analysis was considered inadvisable since the data were not robust enough to meet all of the assumptions of the test and the small sample size precluded meaningful results.

Further analysis of habitat use was done using compositional analysis. This method is an extension of multivariate analysis of variance (MANOVA) that uses categorical covariates, requires multivariate normality, and uses the animal as the experimental unit (Aebischer et al. 1993). Instead of relying on individual points to define use, resource use is defined as the proportional use of resources within the estimated boundary (e.g., home range or utilization distribution) (Aebischer et al. 1993; Erickson et al. 2001). Using the animal as the experimental unit circumvents problems related to sampling level, the unit-sum constraint, and differential use by groups of individuals (Aebischer et al. 1993). Despite these advantages, there are several important assumptions that underlie this technique (Aitchison 1986). These include required spatial independence among radio-collared animals, compositions from different animals must be equally accurate, and multivariate normality. To account for unequal compositions, the log-ratios derived in the analysis can be weighted (Aebischer et al. 1993). Failure to meet the assumption of multivariate normality will influence significance values; however, randomization procedures can overcome this problem (Manly 1997).

Because a dichotomous dependent variable is required for logistic regression, information on habitat variables associated with known elk locations (used) and paired random points (non-used) were assembled in a database. Backward stepwise selection using the likelihood-ratio test was then used to describe the variable combinations that best differentiated landscapes used by elk from random landscapes (Hosmer and Lemeshow 1989). The improvement of fitted models over null models was evaluated according to the reduction in log-likelihood ratios, while the significance of variable coefficients was assessed using chi-squared tests of Wald statistics (Hosmer and Lemeshow 1989). Variables included in the best-fit models were also examined for multicollinearity using linear regression tolerance statistics, and non-linearity using the Box-Tidwell test (Menard 1995). Where collinearity occurred, Pearson correlation coefficients were inspected to identify offending variables and less significant (based on univariate tests) variables were excluded from further analysis.

Using compositional analysis, habitat selection was analysed at two spatial scales. At the coarse scale, selection was analysed according to Thomas and Taylor's (1990) design II where resource use is identified for each individual and resource availability is defined for the population. In this manner, the habitat characteristics included in an animal's utilization distribution (95% adaptive kernel) were compared to those of the area occupied by the population (100% MCP including all elk locations). Individual utilization distributions were estimated using the 95% adaptive kernel, as this method best represented the area used by an individual. Resource availability was defined using a 100% MCP around all elk locations, as this was sure to encompass all areas used by the population. At the fine scale, selection was analysed according to Thomas and Taylor's (1990) design III, where both resource use and resource availability are defined for each animal. In this manner, habitat characteristics of core utilization areas of individual elk (50% adaptive kernel) were compared to the entire utilization distribution (95% adaptive kernel) for the same animal.

Following methodology outlined by Aebischer et al. (1993), if habitat use was deemed non-random, habitats that were selected over others were identified by calculating the differences in log ratios for each pair of habitat categories, for each elk. The mean and standard error for these pairwise comparisons were then calculated across all elk, and habitat types were ranked by relative use using a paired t-test. The significance of t-tests was determined with the experiment wide error rate adjusted for the number of comparisons using Bonferoni criteria (Rice 1989). In a small number of instances, a habitat category was available, but not used by an individual elk. In these cases the zero value was replaced by 0.001, which is an order of magnitude less than the smallest recorded non-zero proportion. Habitat types that were absent from the home range estimations of all elk in a particular group, were considered not used and were eliminated from the analysis.

In order to test whether habitat selection was the same for elk released in northwestern Ontario during 2000 and 2001, each group was analysed separately. Moreover, those elk that dispersed to the southern portion of the study area, (Fort Frances/Rainy River) displaying different habitat associations, were also analysed separately.

Population characteristics

Annual age and sex-specific survival rates of elk were calculated using the apparent percent success estimator (APS) (Heisey and Fuller 1985). In this manner, survival estimates were calculated by determining the proportion of radio-collared elk surviving in each sex and age class during a given period. Following the recommendations of White and Garrot (1990), individuals whose radio-collar dropped off, or who were not located on a regular basis, were censored in the season in which contact was lost. Survival estimates were calculated separately for elk released in 2000 and 2001, as well as for each sex and age class. An overall estimate of survival was calculated by pooling data for all elk over the 2-year study period.

Although not commonly used, the use of APS estimator made comparisons between survival rates in northwestern Ontario and various other Ontario release sites possible. Moreover, the APS estimator is useful in that it assumes only that a random sample has been obtained (Winterstein et al. 2001). Also, only the initial number of radio-collared animals (number at risk) and the number that died during the study period (number of deaths) are required for the analysis. Despite its ease of use and relative simplicity there are several drawbacks to this method. First, survival rates calculated in this manner assume that the entire sample of animals was marked at the beginning of the study period and therefore each animal has the same date of entry into the study (Winterstein et al. 2001). This is not an issue if all radio-collared animals are released at the same time: however, in many radio-telemetry studies a staggered entry study design is used. Second, because the final survival rate is the weighted average of the survival rates of each mutually exclusive group (e.g., age class, sex) the results will be biased towards the group having the largest sample size. Finally, the use of APS precludes generating a survival curve unless it is assumed that survival is constant throughout the study.

The staggered-entry Kaplan-Meier survival procedure was also used in this study to estimate survival rates for the recently reintroduced elk population (Pollock et al. 1989). The Kaplan-Meier method of survival estimation was chosen because it has no underlying assumption of constant survival and provides unbiased estimates even when observations are censored. Moreover, because this method has been used extensively in the literature (Unsworth et al. 1993; Smith and Anderson 1998; Ballard et al. 2000; Petersburg et al. 2000; Raedeke et al. 2002), comparisons of survival estimates among studies are made with relative ease.

Kaplan-Meier survival estimates were calculated on a monthly basis, pooling data to determine seasonal, annual, and study period estimates. Survival was calculated on a monthly, rather than a weekly or daily basis for several reasons. First, although attempts were made to locate elk on a weekly or bi-weekly basis, not all elk were found regularly. Also, because elk are a long-lived species, detail gained from weekly estimates of survival rather than monthly estimates would not appreciably change the annual estimate. Log rank tests were used to test for differences in survival rates between release years (Pollock et al. 1989), as well as for differences between males and females translocated as adults and those translocated as calves, and elk establishing in the northern and southern portions of the study area.

Patterns of elk mortality were examined by ground-tracking and assessing the carcass as soon as possible after receiving a mortality signal. Physical evidence, such as sign of other species (i.e., tracks, scat) and condition of the remains were used to determine the cause of death. In some cases, a veterinary pathologist (University of

Manitoba) performed necropsies to assess the cause of death. Mortalities were classified as either translocation injury (death within 1 month of release in Ontario due to injuries sustained during capture, bacterial infections developed during capture, capture myopathy, or injuries sustained during transport), predation, illegal shooting (accidental, malicious, or poaching), drowning, road kills (automobile and train), general injury, or cause unknown.

The number of calves born and surviving through the winter months was determined by helicopter surveys of radio-collared females conducted during February and March of each year of the study. Because not all elk in the study were radio-collared or visually observed during the survey, the total number of calves born each year and surviving through the winter months was proportionally estimated. Using both the survival estimates and the estimated number of calves born in northwestern Ontario, the size of the population (including the number of adult males and adult females) at the end of the study period (May 2002) was also estimated.

Fascioloides magna and *Parelaphostrongylus tenuis*

To determine the efficacy of the treatment protocol for elk infected with *F. magna* in EINP, fecal pellets were collected prior to treatment and upon arrival in northwestern Ontario. For comparison, samples were also obtained from recently translocated elk at two other sites (Bancroft and Lake Huron/North Shore) in Ontario. All pellets were collected during the first three months of 2001 and 2002, and were kept frozen at –20 °C until analysed. Fluke eggs were isolated from feces using a modified sedimentation/filtering technique (Flukefinder, Visual Difference, Moscow, Idaho) and eggs were identified using a dissecting microscope (25 X). The prevalence of infection and the mean intensity of eggs per gram of dried fecal material were calculated for each area.

To assess the relative risk of the newly relocated elk becoming infected with *F. magna* in Ontario, fecal pellets were collected from white-tailed deer resident near the release sites. These included Cameron Lake, Fort Frances/Rainy River, Bancroft, and Lake Huron/North Shore. All fecal pellets were collected during the first three months of 2000 and 2001, and examined using the Flukefinder.

The relative risk of the newly relocated elk becoming infected with *P. tenuis* in Ontario was assessed using the modified Baermann-beaker method (Forrester and Lankester 1997) on white-tailed deer fecal pellets collected during February and March 2001/2002 from Cameron Lake, Fort Frances/Rainy River, Bancroft, and Lake Huron/North Shore. Pellets from Lake Huron/North Shore were not collected until April 2002. Pellets were frozen at –20 °C for up to one month prior to examination. The prevalence and mean intensity of first-stage larvae per gram of dried feces was calculated for each area. Elk pellets were not tested for the presence of *P. tenuis* larvae, as infected elk seldom, if at all, pass more than a few larvae (Lankester 2001). Furthermore, many elk had not been present on the Ontario landscape long enough for patent infections to develop.

Comparisons of both prevalence of infection and mean intensity among areas sampled were made using the Statistical Package for the Social Sciences (SPSS Inc., Chicago, Illinois, USA). Prevalence data were first compared using a contingency test. Any differences were further analysed using the non-parametric multiple comparison test described by Dunn (1964). Similarly, mean intensity data were first compared using a

Kruskal-Wallis test, followed by a Tukey-type test for multiple comparisons of proportions (Zar 1999).

Results

From February 2000 to June 2002, 1563 locations were obtained for 73 radio-collared elk (Appendices 2 and 3). Seven hundred and sixty-four locations were obtained for elk released in 2000, while 799 were obtained for those released in 2001. Four elk in each of the 2000 and 2001 releases dropped their radio-collar during the study period (2000: 4 male calves; 2001: 1 adult male, 2 male calves, and 1 adult female). Radio-signals were lost from an additional 4 animals, 2 of whose radio-collars were thought to have been damaged during the translocation. Approximately 70% of the locations were obtained using ground and aerial radio-telemetry, while the remaining 30% were obtained by direct observation. Average location errors were 157 $\pm$ 11m ($\pm$SE) for ground radio-telemetry and 41 $\pm$ 4m for aerial radio-telemetry. Errors resulting from direct observation were assumed to be negligible.

Spatial behaviour

Fifty-nine of the original 73 radio-collared elk were repeatedly located enough times to provide reliable information on post-release dispersal and movement. Throughout the study, 70% of elk released in both 2000 and 2001 were consistently located within a 20 km radius of the release site (Figure 2). The remaining 30% (10 adult males and 12 adult females) permanently dispersed southward approximately 90 km from the release site, near the communities of Fort Frances and Rainy River. Dispersal generally occurred shortly after release (March to June), and no elk returned to the release area after having dispersed to the south (during the writing of this paper one adult female from the 2000 release and one adult male from the 2001 release returned to the

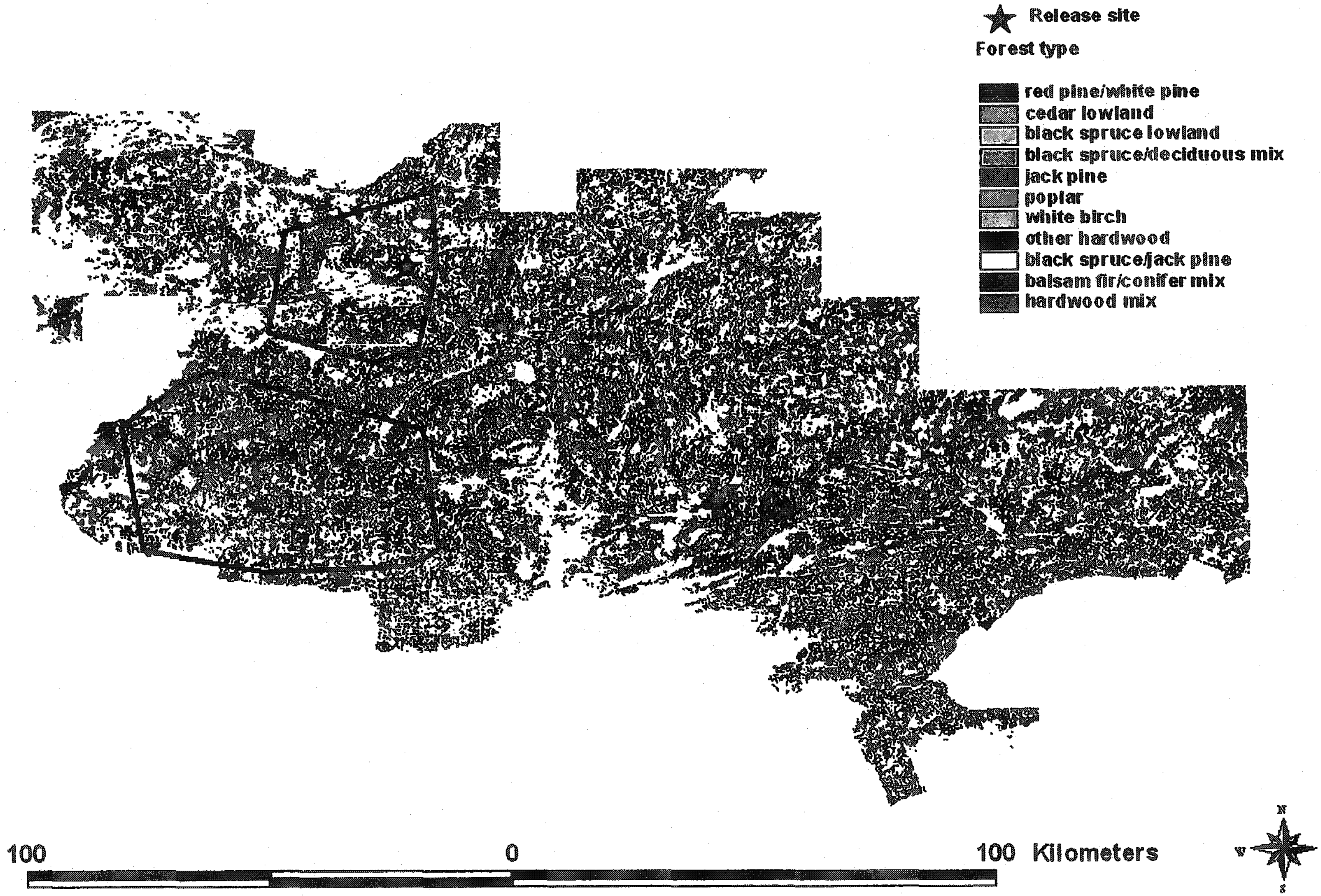


Figure 2: Figure illustrating northern and southern range of elk reintroduced to northwestern Ontario during February/March 2000 and 2001, as well as the heterogeneity of the landscape based on 11 forest types

northern portion of the study area after having established in the south for 2.5 years and 1.4 years, respectively). Moreover, all animals translocated to Ontario as calves and yearlings remained within 20 km of the release site, while all those that dispersed to the south were translocated as adults.

There was no difference in the mean maximum distance, mean distance, or mean direction moved between elk released in 2000 and 2001 (mean maximum distance: P=0.11; mean distance: P=0.12; mean direction moved: P=0.70). Data were therefore pooled across release years for further analysis. The mean maximum distance moved during the study period was farthest for elk reintroduced as adult males (68.0 $\pm$ 15.2 km), followed by adult females (37.2 $\pm$ 5.9 km), female calves (8.3 $\pm$ 1.3 km) and male calves (5.7 $\pm$ 0.7 km) (Table 3). Adult males moved significantly farther than both male and female calves (P<0.0001), whose dispersal did not differ from each other (P=0.11). The relationship between the adult females and other sex and age groups was statistically indeterminate. The mean distance moved during the study was farthest for elk released as adult males (34.0 $\pm$ 6.5 km), followed by adult females (23.2 $\pm$ 4.3 km), female calves (3.9 $\pm$ 0.7 km), and male calves (2.1 $\pm$ 0.3 km) (Table 3). Mean distance moved by adult males and females exceeded that of both male and female calves (P<0.001); however, no difference was found between the sexes of either age group (male and female calves: P=0.43; male and female adults: P=0.70). The mean direction moved by all elk during the study did not differ by age or sex (P=0.56), ranging from 164 $\pm$ 34.5 degrees for adult males, to 219 $\pm$ 28.3 degrees for female calves (Table 3). Hence, the direction of movement was predominately south-southwest for all elk.

Table 3: Mean maximum distance, mean distance and mean direction of movement from release site by radio-collared elk reintroduced to northwestern Ontario during February/March 2000 and 2001

	Age[1]	No. of elk	Mean max. distance moved (km)[2]	Standard error	Mean distance moved (km)	Standard error	Mean direction moved (°)	Standard error[3]
Male	AD	12	68.0	± 15.2	34.0	± 6.5	163.7	± 34.5
	YOY	11	5.7	± 0.7	2.1	± 0.3	215.4	± 32.5
Female	AD	25	37.2	± 5.9	23.2	± 4.3	212.3	± 21.6
	YOY	11	8.3	± 1.3	3.9	± 0.7	219.9	± 28.3

Note: AD = adults and yearlings (>1.5 years); YOY = calves 8-9 months

[1] Refers to the age of the animal at time of release

[2] Mean maximum distance moved from the release site between date of release and June 01, 2002

[3] Angular error calculated as (angular deviation/$\sqrt{n}$) (Zar 1999)

The population home range of elk released in 2000 was 2559 km^2 (100% MCP with all locations pooled), while that of those released in 2001 was 5211 km^2. There was, however, no difference in the size of mean individual home ranges (100% MCP and 95% adaptive kernel) between elk released in each of 2000 and 2001 (100% MCP: P=0.27; 95% adaptive kernel: P=0.37). Furthermore, no difference in mean individual home range size was found between elk located in the northern portion of the study area and those located in the south (100% MCP: P=0.54; 95% adaptive kernel: P=0.35). Data were therefore pooled for further analysis.

During the study, mean individual home ranges (100% MCP) were largest for elk translocated as adult females (55.7 ± 9.9 km^2), followed by female calves (39.7 ± 14.1 km^2), male calves (33.3 ± 9.1 km^2), and one adult male (16.0 km^2) (Table 4). There were, however, no significant differences relating to sex or age (P=0.23). Home ranges estimated by determining mean utilization distributions (95% adaptive kernel) were largest for elk translocated as female calves (37.0 ± 7.3 km^2), followed by adult females (30.2 ± 6.3 km^2), male calves (21.4 ± 5.2 km^2), and the one adult male (18.6 km^2) (Table 4). Again, however, there were no differences related to sex or age (P=0.33). Elk translocated as female calves had the largest mean core area (7.8 ± 1.6 km^2) (50% adaptive kernel), followed by adult females (4.6 ± 0.8 km^2), male calves (3.8 ± 1.1 km^2), and the one adult male (1.9 km^2), although differences relating to sex and age were not significant (P=0.08) (Table 4). Based on all estimations of home range (100% MCP, 95% adaptive kernel, and 50% adaptive kernel estimations), considerable overlap (89 ± 9.2%) existed between summer (May 01 – October 31) and winter (November 1 – April 30) ranges for 8 elk.

Table 4: Mean minimum convex polygon home range size (100 % MCP) and mean adaptive kernel utilization distribution estimates (95% and 50%) for radio-collared elk reintroduced to northwestern Ontario during February/March 2000 and 2001

	Age[1]	No. of elk	No. of locations (±SE)[2]	100% MCP (km^2)	Standard Error	95% adaptive kernel (km^2)	Standard error	50% adaptive kernel (km^2)	Standard error
Male	AD	1	34	16.0	-	18.6	-	1.9	-
	YOY	11	31 ± 1.1	33.3	± 9.1	21.4	± 5.2	3.8	± 1.1
Female	AD	25	31 ± 1.9	55.7	± 9.9	30.2	± 6.3	4.6	± 0.8
	YOY	11	36 ± 2.1	39.7	± 14.1	37.0	± 7.3	7.8	± 1.6

Note: AD=adults >1.5 years; YOY= calves 8-9 months
[1] Refers to age of the animal at time of release
[2] Mean numbers of locations collected from date of release to June 01, 2002

Habitat utilization

Best fit multiple regression models of habitat utilization for all elk located in the northern portion of the study area, and released in 2000 and 2001, were highly significant over null models (northern 2000: x^2=375.3, df=13, P<0.001; northern 2001: x^2=507.1, df=14, P<0.0001), achieving an overall correct classification of 71% and 74%, respectively. The habitat utilization model for elk that established in the southern portion of the study area was also significant (x^2=213.2, df=10, P<0.001), achieving an overall correct classification of 76%. In all models, forest type (P<0.0001), stand age (P<0.0001), and elevation (P<0.0001) were identified as significant predictors of elk habitat use. Distance to nearest wetland (northern 2000: P=0.70; northern 2001: P=0.42; southern 2000/2001: P=0.54) did not contribute in any model, and was therefore eliminated from further analysis.

Compositional analysis of habitat utilization examined at both coarse and fine scales (coarse scale: 95% adaptive kernel estimate vs. study area; fine scale: 50% adaptive kernel estimate vs. 95% adaptive kernel estimate), yielded similar results to the multiple logistic regression (Figures 3 through 5). Elk located in the northern portion of the study area, and released in both 2000 and 2001, demonstrated non-random patterns of use based on forest type (2000 coarse scale: x^2=191.58, df=11, P<0.0001; 2000 fine scale: x^2=36.84, df=9, P=0.02; 2001 coarse scale: x^2=186.34, df=11, P<0.0001; 2001 fine scale x^2=33.55, df=9, P=0.003), stand age (2000 coarse scale: x^2=65.95, df=7, P<0.0001; 2000 fine scale x^2=18.65, df=5, P=0.02; 2001 coarse scale: x^2=178.22, df=7, P<0.001; 2001 fine scale: x^2=29.73, df=5, P<0.001), and elevation (2000 coarse scale: x^2=159.59, df=6, P<0.0001; 2000 fine scale: x^2=37.43, df=5, P<0.0001; 2001 coarse scale: x^2=146.18, df=5, P<0.001; 2001 fine scale: x^2=37.91, df=5, P<0.001).

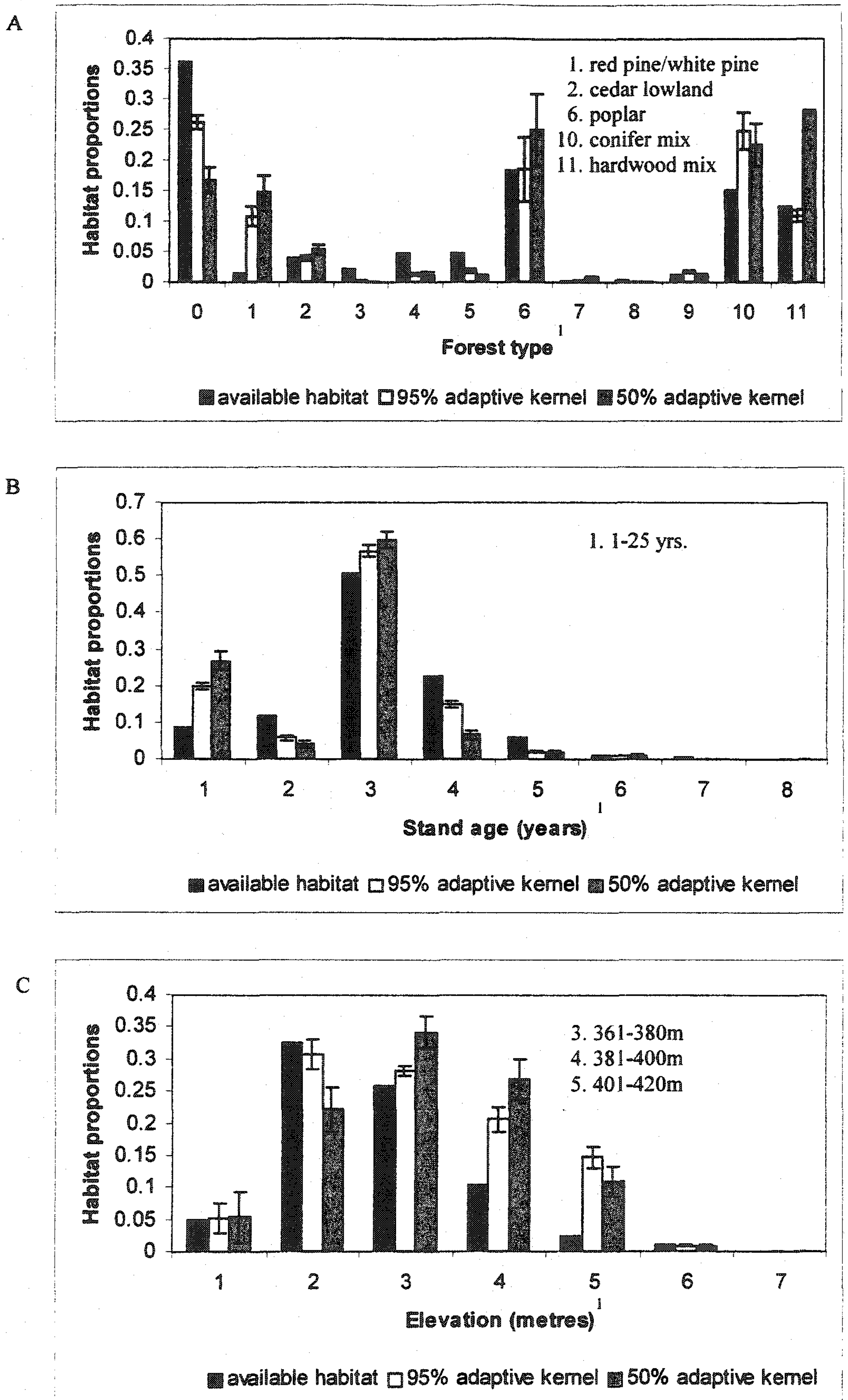
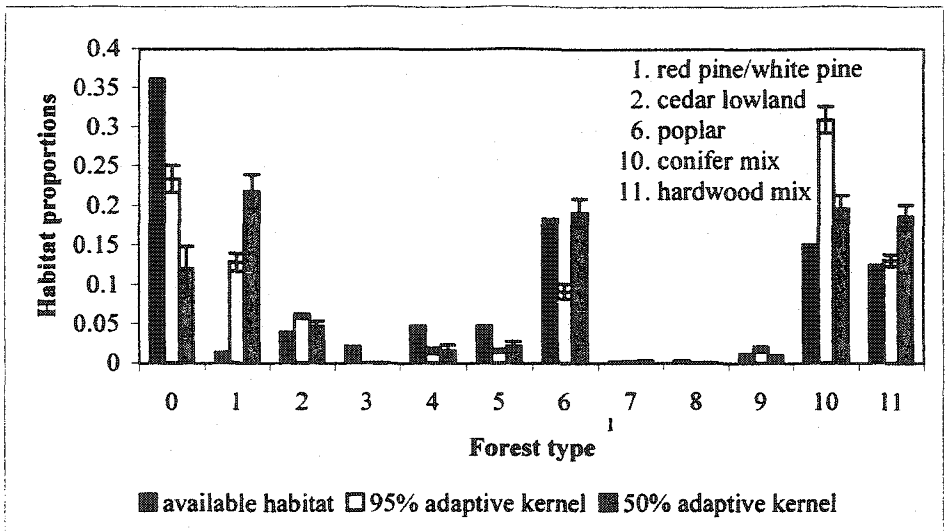


Figure 3: Proportional habitat use by elk located in the northern portion of the study area and released in northwestern Ontario in 2000, based on A) forest type, B) stand age, and C) elevation

[1] A full description of habitat variables is presented in Table 2

A



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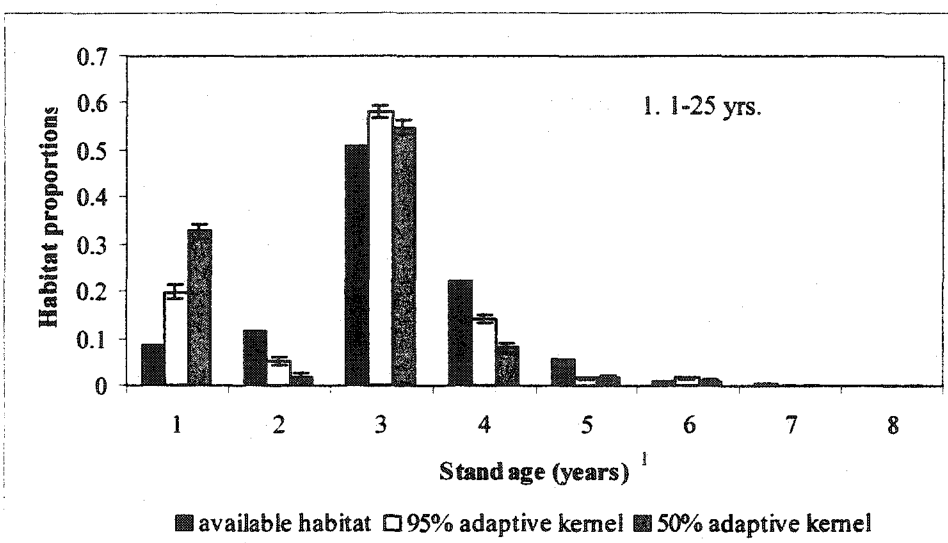

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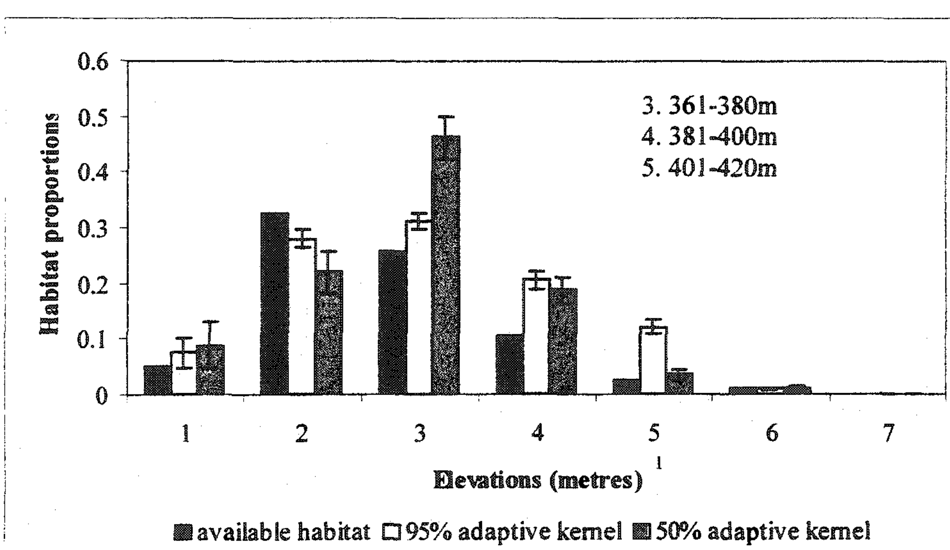

Figure 4: Proportional habitat use by elk located in the northern portion of the study area and released in northwestern Ontario in 2001, based on A) forest type, B) stand age, and C) elevation

[1] A full description of habitat variables is presented in Table 2

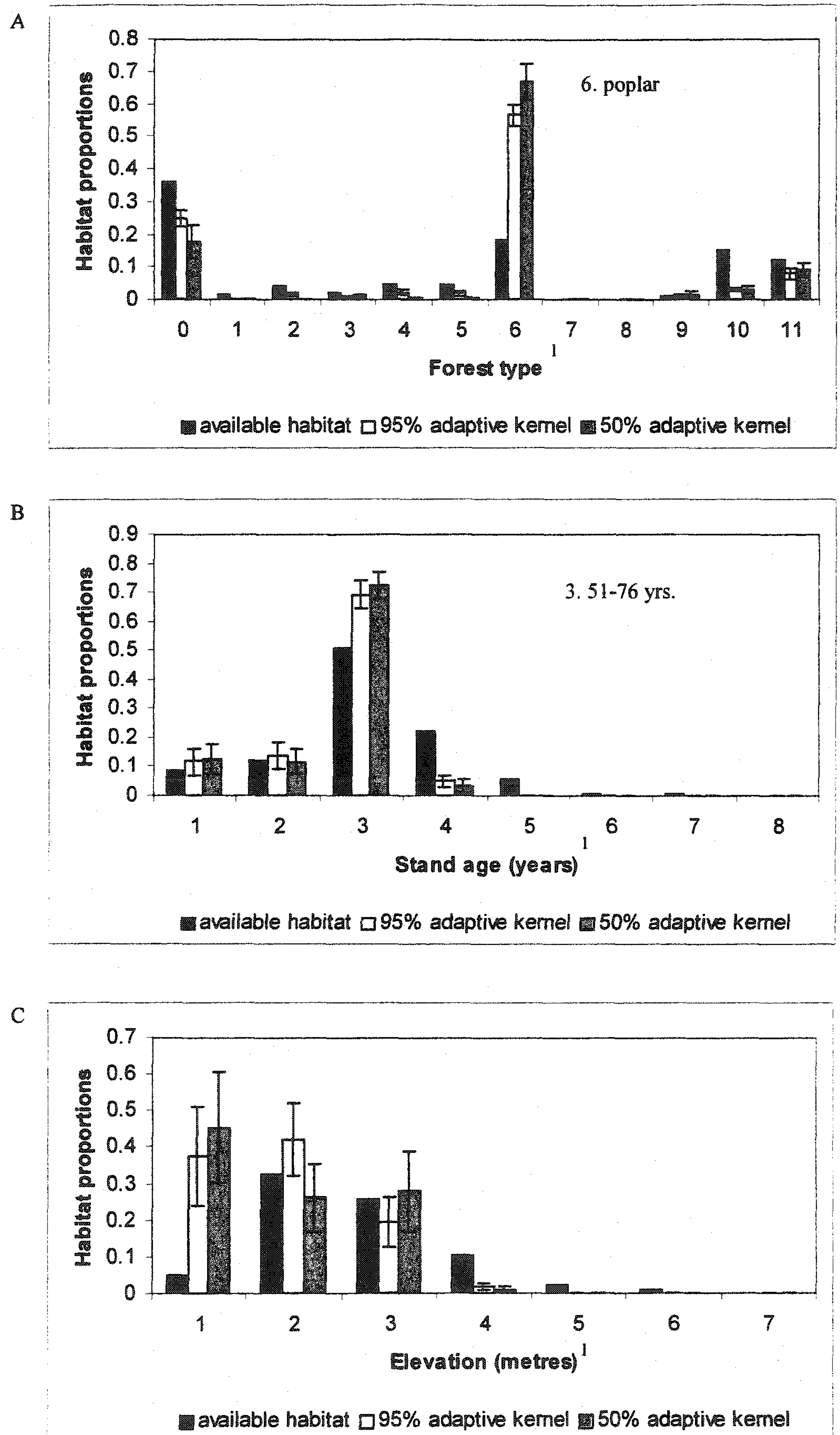

Figure 5: Proportional habitat use by elk located in the southern portion of the study area and released in northwestern Ontario in 2000 and 2001, based on A) forest type, B) stand age, and C) elevation

[1] A full description of habitat variables is presented in Table 2

At the coarse scale, utilization distributions of elk located in the north and released in 2000 were dominated by red pine/white pine, followed in decreasing rank by balsam fir/conifer mix, black spruce/jack pine mix, cedar lowland, hardwood mix, white birch, water (lakes, rivers, ice), poplar, black spruce/deciduous mix, jack pine, black spruce lowland, and other hardwoods (Table 5). Paired t-tests performed within habitat rankings indicated that habitat types dominated by red pine/white pine were used more than all other habitat types, while black spruce lowland and other hardwoods were used less than all other habitat types. Utilization distributions of elk released in 2001 were also dominated by red pine/white pine, followed in decreasing rank, by cedar lowland, balsam fir/conifer mix, poplar, hardwood mix, water, black spruce/jack pine mix, jack pine, white birch, black spruce/deciduous mix, black spruce lowland, and other hardwoods (Table 5). Again, paired t-tests indicated that red pine/white pine was used more than any other habitat type, while habitats dominated by other hardwoods were used less than all other habitat types.

At the fine scale, utilization distributions of elk located in the north and released in 2000 were dominated by poplar, followed by cedar lowland, hardwood mix, white birch, red pine/white pine, balsam fir/conifer mix, water, black spruce/deciduous mix, jack pine, and black spruce/jack pine mix (Table 6). Paired t-tests performed within the habitat rankings indicated that the top five ranks (poplar, cedar lowland, hardwood mix, white birch, and red pine/white pine) were not significantly different, while habitat types dominated by black spruce lowlands and other hardwoods were not used by elk. Similarly, utilization distributions of elk released in 2001 were dominated by poplar, followed by red pine/white pine, hardwood mix, white birch, balsam fir/conifer mix,

Table 5: Coarse scale habitat ranks for elk reintroduced to northwestern Ontario during February/March 2000 and 2001

Habitat variable	Numerical designation of habitat types in decreasing rank order[1]											
Forest type												
North 2000	1	10	9	2	11	7	0	6	4	5	3	8
North 2001	1	2	10	6	11	0	9	5	7	4	3	8
South 2000/2001	6	0	11	10	4	2	3	5	9	7	8	1
Stand age												
North 2000	1	2	3	4	5	6	8	7				
North 2001	1	3	4	2	6	5	8	7				
South 2000/2001	3	1	2	4	5	6	7	8				
Elevation												
North 2000	5	4	3	2	6	1	7					
North 2001	5	4	3	2	6	7	1					

Note: Solid horizontal lines span rankings that are not significantly different from each other as determined by pairwise t-tests
Note: Habitat types that were absent from the home range of all elk in a particular group were considered not used, and were eliminated from the analysis

[1]Forest type (standard forest units)

0	Water (lakes, rivers, ice)
1	Red pine/white pine
2	Cedar lowland
3	Black spruce lowland
4	Black spruce/deciduous
5	Jack pine
6	Poplar
7	White birch
8	Other hardwoods
9	Black spruce/jack pine mix
10	Balsam fir/conifer mix
11	Hardwood mix

Stand age (years)

1	1 – 25
2	25 – 50
3	51 – 76
4	77 – 101
5	102 – 127
6	128 – 152
7	153 – 178
8	179 – 203
9	204 – 229

Elevation (metres)

1	320 – 340
2	341 – 360
3	361 – 380
4	381 – 400
5	401 – 420
6	421 – 440
7	441 – 460

Table 6: Fine scale habitat ranks for elk reintroduced to northwestern Ontario during February/March 2000 and 2001

Habitat variable	Numerical designation of habitat types in decreasing rank order[1]									
Forest type										
North 2000	6	2	11	7	1	10	0	4	5	9
North 2001	6	1	11	7	10	2	0	5	4	9
Stand age										
North 2000	1	3	5	4	2	6				
North 2001	1	3	4	5	6	2				
Elevation										
North 2000	3	4	2	5	6	1				
North 2001	3	4	2	6	1	5				

Note: Solid horizontal lines span rankings that are not significantly different from each other as determined by pairwise t-tests
Note: Habitat types that were absent from the home range of all elk in a particular group were considered not used and were eliminated from the analysis

[1]Forest type (standard forest units)

0	water (lakes, rivers, ice)
1	red pine/white pine
2	cedar lowland
3	black spruce lowland
4	black spruce/deciduous
5	jack pine
6	poplar
7	white birch
8	other hardwoods
9	black spruce/jack pine mix
10	Balsam fir/conifer mix
11	Hardwood mix

Stand age (years)

1	1 – 25
2	25 – 50
3	51 – 76
4	77 – 101
5	102 – 127
6	128 – 152
7	153 – 178
8	179 – 203
9	204 – 229

Elevation (metres)

1	320 – 340
2	341 – 360
3	361 – 380
4	381 – 400
5	401 – 420
6	421 – 440
7	441 – 460

cedar lowland, water, jack pine, black spruce/deciduous mix, and black spruce/jack pine mix (Table 6). Paired t-tests found no significant difference between the top 4 rankings (poplar, red pine/white pine, hardwood mix, and white birch), and, again, elk did not use habitats dominated by black spruce lowlands or other hardwoods.

At both the coarse and fine scales, elk located in the north and released in 2000 and 2001 used habitats ranging in age from 1-25 years, with use declining for older stands (Tables 5 and 6). Exceptions were stands aged 26-50 years old, which at the fine scale were used less than would be expected by chance. Furthermore, at both the coarse and fine scales, habitats that ranged in elevation from 340m-400m a.s.l. were used by elk at a greater rate than would be expected by chance, while use declined for lower and higher areas (Tables 5 and 6). Exceptions were habitats that ranged in elevation from 400m to 420m, which at the coarse scale were used more than any other habitat type.

Habitat use by elk that established in the southern portion of the study area examined at the coarse scale demonstrated non-random patterns based on forest type (x^2=130.58, df=11, P=0.002) and stand age (x^2=59.24, df=7, P<0.0001); however, habitat use based on elevation was random (x^2=12.14, df=7, P=0.08). At the fine scale, patterns of habitat use based on all variables were random (forest type x^2=26.44, df=10, P=0.50; stand age x^2=11.62, df=4, P=0.07; elevation x^2=3.80, df=3, P=0.42). Elk in the south used habitats dominated by poplar, followed by water, hardwood mix, balsam fir/conifer mix, black spruce/deciduous mix, cedar lowland, jack pine, black spruce/jack pine mix, white birch, other hardwoods, and red pine/white pine (Table 5). Paired t-tests performed within the rankings indicated that habitats dominated by poplar were used significantly more than all other types, while habitats dominated by red pine/white pine were used less than all other types. Stands aged 1-76 years were most frequently used (Table 5). Forest stands over 77 years old were used less than would be expected by chance.

Population characteristics

At the end of the study period, June 01, 2002, the APS survival rate for all radio-collared elk released in northwestern Ontario was 0.62. The overall survival rate for elk released in 2000 was lower (0.58) than for those released in 2001 (0.65). However, patterns of survival for elk released in 2000 and 2001 were similar, with the exception of the first 3 to 4 months on the landscape, where elk released in 2001 experienced higher rates of translocation related mortality than those released in 2000 (Tables 7 and 8; Figure 6).

Elk released in 2000 suffered no mortality during their first four months on the landscape (February 2000 to May 2000) (Table 7 and Figure 6). However, during the following year, the overall survival rate dropped to 0.77, with survival ranging from 0.20 for adult males to 0.85 for adult females. Male and female yearling elk experienced no mortality from June 2000 to June 2001. From June 2001 to June 2002, the average survival rate for all elk was higher than the previous year at 0.83, with adult males experiencing no mortality and adult female survival rates averaging 0.82.

The survival rate during the first three months following release in 2001 (March 2001 to May 2001) was 0.83, with adult males averaging 0.83 and adult females averaging 0.57 (Table 8 and Figure 6). Calves and yearlings experienced no mortality during their first three months on the landscape. From June 2001 to June 2002, the overall survival rate dropped slightly to 0.80, with adult females having the lowest rate at

Table 7: Age and sex-specific survival rates for radio-collared elk reintroduced to northwestern Ontario during February 2000, estimated using apparent percent success (APS) methodology

		Males				Females				Grand
Time period		YOY	YRL	AD	Total	YOY	YRL	AD	Total	total
Feb 01, 2000	No. of elk	4	1	4	9	6	1	13	20	29
To	No. of deaths	0	0	0	0	0	0	0	0	0
May 31, 2000	Survival Rate	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
June 01, 2000[1]	No. of elk	0	3	5	8	0	6	13	19	27
To	No. of deaths	0	0	4	4	0	0	2	2	6
May 31, 2001	Survival rate		1.00	0.20	0.56		1.00	0.85	0.89	0.78
June 01, 2001	No. of elk	0	0	1	1	0	0	17	17	18
To	No. of deaths	0	0	0	0	0	0	4	4	4
May 31, 2002	Survival Rate			1.00	1.00			0.76	0.76	0.78
						Overall survival for radio-collared elk				0.58

Note: YOY = calves 8-9 months; YRL = yearlings; AD = adults
Note: Six elk were censored in this analysis due to dropped radio-collars and loss of radio signal
[1] June 01 is the median birth date for elk and was considered the date on which elk moved into the next older age class

Table 8: Age and sex-specific survival rates for radio-collared elk reintroduced to northwestern Ontario during March 2001, estimated using apparent percent success (APS) methodology

		Males				Females				Grand
Time period		YOY	YRL	AD	Total	YOY	YRL	AD	Total	total
March 01, 2001	No. of elk	8	3	6	17	5	5	14	24	41
To	No. of deaths	0	0	1	1	0	0	6	6	7
May 31, 2001	Survival rate	1.00	1.00	0.83	0.94	1.00	1.00	0.57	0.75	0.83
June 01, 2001[1]	No. of elk	0	6	8	14	0	5	11	16	30
To	No. of deaths	0	1	2	3	0	0	3	3	6
May 31, 2002	Survival rate	-	0.83	0.75	0.79	-	1.00	0.73	0.79	0.80
						Overall survival for radio-collared elk				0.65

Note: YOY = calves 8-9 months; YRL = yearlings; AD = adults
Note: Six elk were censored in this analysis due to dropped radio-collars and loss of radio contact
[1] June 01 is the median birth date for elk and was considered the date on which elk moved into the next older age class

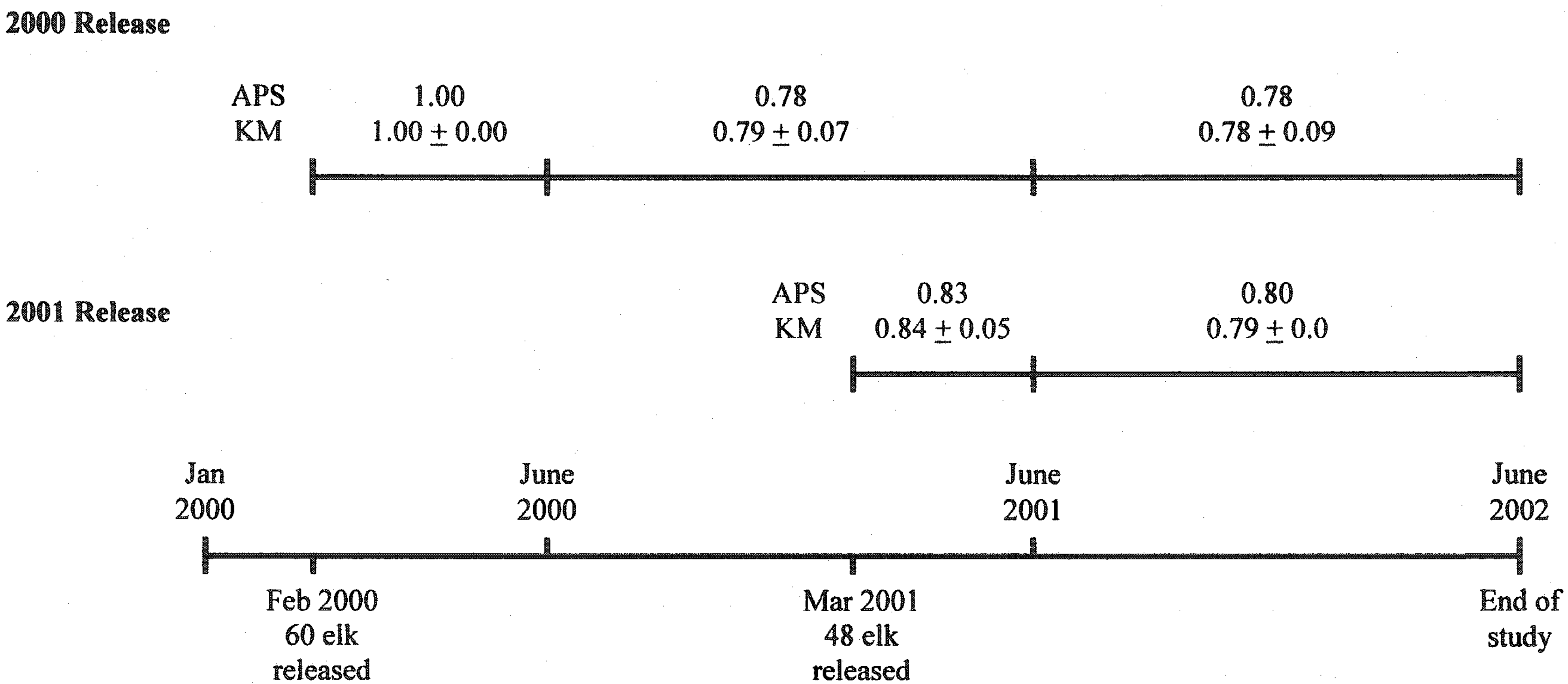

Figure 6: Time line showing apparent percent success (APS) and Kaplan-Meier (KM) estimated survival rates for elk reintroduced to northwestern Ontario during February/March 2000 and 2001

Note: Survival rates include mortality attributed to translocation injury

0.73, followed by adult males at 0.75 and yearling males at 0.83. Again, yearling females experienced no mortality during this period.

Kaplan-Meier estimations of survival were similar to those derived using APS. Overall survival during the study period was 0.57 $\pm$ 0.08, with survival averaging 0.63 $\pm$ 0.09 for elk released in 2000 and 0.66 $\pm$ 0.08 for those released in 2001 (Table 9). Annual survival functions varied slightly (Table 6); however, no significant difference was detected (x^2=1.37, df=2, P=0.10). Furthermore, overall survival functions did not differ between release years (x^2=1.52, df=1, P=0.22), or between elk establishing in the northern (0.55 $\pm$ 0.09) and southern (0.64 $\pm$ 0.10) portions of the study area (x^2=0.02, df=1, P=0.88). Data were therefore pooled across release years and north and south locations for further analysis.

There was no difference in survival relating to season (winter: 0.93 $\pm$ 0.08; November 01 – April 30; summer: 0.87 $\pm$ 0.08; May 01 – Oct 30) (x^2=0.92, df=1, P=0.68). Moreover, survival did not differ between male (0.68 $\pm$ 0.09) and female elk (0.56 $\pm$ 0.09) (x^2=0.07, df=1, P=0.79). Survival did, however, differ with regard to age, as survival for elk released in northwestern Ontario as calves (male and female) (0.64 $\pm$ 0.18) greatly exceeded that of adults (male and female) (0.50 $\pm$ 0.09) (x^2=5.82, df=1, P=0.016) (Table 9).

Due to considerable mortality caused by injuries suffered during translocation in 2001, the overall survival rate, as well as the survival rate for elk released in 2001 was low. Excluding mortalities attributed to translocation injuries, the overall survival rate for elk released in northwestern Ontario based on Kaplan-Meier methods of estimation was 0.64 $\pm$ 0.09, while the survival rate for elk released in 2001 was 0.77 $\pm$ 0.07.

Table 9: Age specific survival rates for elk reintroduced to northwestern Ontario during February/March 2000 and 2001, estimated using Kaplan-Meier methodology

	Adults[1]				YOY[2]				All Elk			
Release year/time period	No. of elk	No. of deaths	Survival rate	SE	No. of elk	No. of deaths	Survival rate	SE	No. of elk	No. of deaths	Survival rate	SE
2000												
Feb 01, 2000 to May 31, 2000	19	0	1.00	$\pm$ 0.00	10	0	1.00	$\pm$ 0.00	29	0	1.00	$\pm$ 0.00
June 01, 2000 to May 31, 2001	18	6	0.68	$\pm$ 0.10	9	0	1.00	$\pm$ 0.00	27	6	0.79	$\pm$ 0.07
June 01, 2001 to May 31, 2002	12	2	0.83	$\pm$ 0.10	6	2	0.67	$\pm$ 0.16	18	4	0.78	$\pm$ 0.09
2001												
Mar 10, 2001 to May 31, 2001	29	7	0.76	$\pm$ 0.07	13	0	1.00	$\pm$ 0.00	42	7	0.84	$\pm$ 0.05
June 01, 2001 to May 31, 2002	19	5	0.74	$\pm$ 0.10	11	1	0.90	$\pm$ 0.09	30	6	0.79	$\pm$ 0.08
Study Period	44	20	0.50	$\pm$ 0.08	17	3	0.64	$\pm$ 0.18	61	23	0.57	$\pm$ 0.08

Note: Survival rates did not differ among years (x^2=1.57, df=1, P=0.942)
Note: Twelve elk were censored in this analysis due to dropped radio-collars and loss of radio signal
[1] Adults = elk released as adults or yearlings
[2] YOY = elk released as calves (8-9 months)

Although the exclusion of mortalities attributed to translocation injuries increased the overall rate of survival, as well as the rate of survival for elk released in 2001, no differences relating to release year (x^2=0.01, df=1, P=0.928), geographic location (i.e. north/south) (x^2=0.03, df=1, P=0.398), or sex (x^2=0.60, df=1, P=0.438) were found. Differences relating to age (x^2=3.65, df=1, P=0.018), however, were still apparent.

During the study period there were 23 recorded mortalities of radio-collared elk (9 adult males and 14 adult females) (Table 10). In order of decreasing importance, the causes of mortality were translocation injury (26%), predation (17%), illegal shooting (17%), road kill (9%), injury (4%), and drowning (4%). A further 22% of the mortalities were attributed to unknown causes. All mortalities attributed to translocation injuries occurred in 2001. All mortalities attributed to predation were thought to be caused by wolves. All elk illegally shot were adult males. Moreover, all mortalities attributed to illegal shooting and road kills occurred in the southern portion of the study area (Fort Frances/Rainy River; 2 elk were also shot in Williams, Minnesota and 1 elk was hit by a train in Ely, Minnesota), while all mortalities attributed to predation and translocation injury occurred in the northern part of the study area (Cameron Lake).

A rough estimate of the number of male elk surviving to the end of the study period (excluding recruitment) was possible. During 2000, 21 male elk were released (8 calves, 1 yearling, 12 adults) in northwestern Ontario, nine of which were radio-collared (4 calves, 1 yearling, and 4 adults). All radio-collared male calves dropped their collars. Four of the 5 remaining radio-collared elk (1 yearling and 4 adult males) died, resulting in a mortality rate of 80%. Applying the mortality rate for radio-collared male elk to the

Table 10: Causes of mortality among radio-collared elk reintroduced to northwestern Ontario during February/March 2000 and 2001

Time Period	Cohort	Translocation injury	Predation	Injury	Shot	Drown	Road Kill[1]	Unknown	Total
Feb 2000 to Feb 2001	1st release	0	0	0	2 (0.40)	0	1 (0.20)	2 (0.40)	5
Feb 2001 to Feb 2002	1st release	0	0	0	1 (0.33)	0	0	2 (0.67)	3
	2nd release	6 (0.60)	1 (0.10)	1 (0.10)	1 (0.10)	0	1 (0.10)	0	10
	Total	6 (0.46)	1 (0.08)	1 (0.09)	2 (0.15)	0	1 (0.08)	2 (0.15)	13
Feb 2002 To June 2002	1st release	0	1 (1.00)	0	0	0	0	0	1
	2nd release	0	2 (0.50)	0	0	1(0.25)	0	1 (0.25)	4
	Total	0	3 (0.60)	0	0	1 (0.20)	0	1 (0.20)	5
	Total	6 (0.26)	4 (0.17)	1 (0.04)	4 (0.17)	1 (0.04)	2 (0.09)	5 (0.22)	23

Note: numbers in parentheses show the associated cause specific mortality rate
[1] Includes 1 elk killed by train

known number of non-collared male elk, an estimated 10 male elk from the 2000 release survived to the end of the study period (Table 11).

In 2001 an additional 22 male elk were released in northwestern Ontario (9 calves, 6 yearlings, and 7 adults), 18 of which were radio-collared (8 calves, 3 yearlings, and 7 adults). During the study period, 4 dropped their radio-collars and 4 radio-collared elk died for an overall mortality rate of 29%. Applying the mortality rate for radio-collared male elk to the known number of non-collared male elk, an estimated 16 male elk from the 2001 release survived to the end of the study period (Table 11). Overall, 26 reintroduced male elk (> 2 years old) were estimated to have survived to the end of the study period. Similarly, 43 reintroduced female elk (> 2 years old) were estimated to be alive on June 01, 2002, for a total of 69 elk and an adult female to male ratio of approximately 2:1 (Table 11).

Using the data collected during aerial surveys of adult females (>2 years) it was estimated that eight calves were born and survived through the winter months in each of 2001 and 2002 (Table 12). The calf:cow ratio was therefore 30% in 2001, and 27% in 2002. By adding the estimated number of calves born in northwestern Ontario to the estimated number of reintroduced animals alive, 85 elk were present on the landscape at the completion of this study, June 01, 2002 (Table 11 and Figure 7).

Fascioloides magna and *Parelaphostrongylus tenuis*

The prevalence of first-stage *P. tenuis* larvae in white-tailed deer pellets collected near elk release sites ranged from 69% in Sioux Narrows to 87% in Lake Huron/North Shore (Table 13). There were, however, no differences in prevalence among the areas

Table 11: Estimated elk population in northwestern Ontario at end of study period, June 01, 2002

Release year	Sex	Age[1]	No. of elk released	No. of elk collared [2]	% mortality in collared elk	No. of collared elk alive	Est. no. of non-collared elk alive	Est. total no. of elk alive
2000	Male	AD	12	4	75	1	2	3
		YRL	1	1	100	0	0	0
		YOY	8	0	17 [3]	0	7	7
		Total	21	5	80	1	9	10
	Female	AD	32	12	25	9	15	24
		YRL	1	1	100	0	0	0
		YOY	6	6	33	4	0	4
		Total	39	19	32	13	15	28
2001	Male	AD	7	6	33	4	1	5
		YRL	6	3	33	2	2	4
		YOY	9	6	17	5	2	7
		Total	22	15	27	11	5	16
	Female	AD	15	12	58	5	1	6
		YRL	6	5	40	3	1	4
		YOY	5	5	0	5	0	5
		Total	26	22	41	13	2	15
							Estimated no. of original elk alive	69
							Estimated no. of calves born[4]	16
							Estimated total elk population	85

Note: AD = adults; YRL = yearlings; YOY= calves 8-9 months

[1] Refers to age of elk at time of release

[2] # of collared elk does not include animals whose radio-signals were lost during the study period or those that dropped their radio-collar

[3] Due to dropped collars no information relating to mortality was available for male calves released in 2000. The mortality rate for male calves released in 2001 was therefore applied

[4] Estimated # of calves for elk released in 2000 includes two years (8 calves born in 2000 and 8 calves born in 2001)

Table 12: Estimated number of calves surviving through the winter with adult female elk (>2 years old) reintroduced to northwestern Ontario during February/March 2000 and 2001

Date of survey	Cohort	No. of collared adult females observed	No. of calves with collared adult females[1]	Calf/Cow ratio (%)	No. of adult females in population	Est. total no. of calves
Feb. 2001		10	3	30%	27	8
Mar. 2002	2000 release	9	2	22%	23	5
	2001 release	6	2	33%	8	3
	Total	15	4	27%	31	8
			Overall number of calves born and surviving through the winter			16

[1] Based on aerial surveys of radio-collared adult females during February and March of 2001and 2002

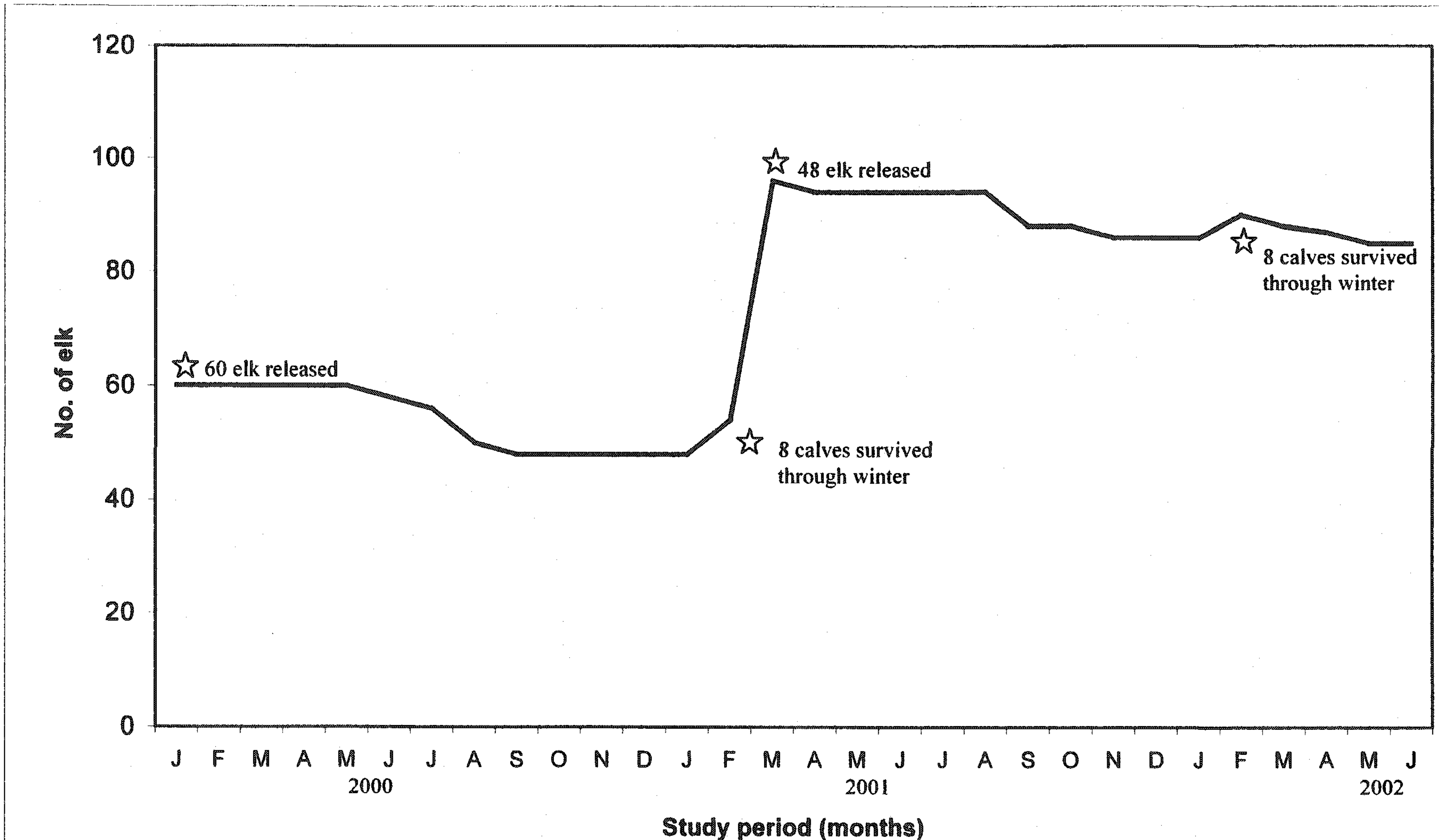

Figure 7: Estimated elk population from the initial release on February 01, 2000 to the end of the study period, June 01, 2002

Table 13: Prevalence and intensity of *Parelaphostrongylus tenuis* larvae in white-tailed deer pellets collected at Ontario elk reintroduction sites

Fecal pellet collection period	Location	Prevalence		Intensity of larvae in feces[1]	
		No. infected/ no. collected	%	Mean	Standard error
Feb/Mar 2001	Sioux Narrows	33/48	69	73.5	± 19.5
Feb/Mar 2002	Cameron Lake/Sioux Narrows	22/26	85	168.1	± 57.3
Feb/Mar 2002	Fort Frances/Rainy River	18/21	86	44.8	± 19.0
Jan/Feb 2002	Bancroft	18/22	82	76.7	± 21.7
Mar/Apr 2002	Lake Huron/North Shore	13/15	87	161.9	± 40.4

[1] Intensity values expressed as larvae/gram of dried feces

sampled (x^2=0.92). The mean intensity of first-stage *P. tenuis* larvae differed among sites (P=0.04), with Cameron Lake/Sioux Narrows and Lake Huron/North Shore having significantly higher mean intensities and than Fort Frances/Rainy River, Sioux Narrows, and Bancroft (Table 13).

Fascioloides magna eggs were found only in white-tailed deer pellets collected in Fort Frances/Rainy River (39%) and Lake Huron/North Shore (6.7%) (Table 14). The mean intensity was 109.45 ±15.20 eggs per gram of dried feces in Fort Frances/Rainy River and 18.75 ± 0.0 eggs per gram in Lake Huron/North Shore.

The prevalence and mean intensity of *F. magna* eggs in elk pellets collected from the source population at EINP, Alberta, prior to treatment with 10% triclabendazole was 42% and 78 ±18.6, eggs per gram respectively (Table 15). No *F. magna* eggs were found in the feces of elk at Fort Frances/Rainy River or Lake Huron/North Shore, but 7% of elk released at Cameron Lake and 17% at Bancroft were passing *F. magna* eggs. Mean intensities of eggs in pellets were similar for elk released at Cameron Lake during 2001 and Bancroft (52 ±1.6 and 51 ± 3.6 eggs per gram, respectively).

Table 14: Prevalence and intensity of *Fascioloides magna* eggs in white-tailed deer pellets collected at Ontario elk reintroduction sites

Fecal pellet collection period	Location	Prevalence: No. infected/ no. collected	Prevalence: %	Intensity of eggs in feces[1]: Mean	Intensity of eggs in feces[1]: Standard error
Feb/Mar 2001	Sioux Narrows	0/48	0	0	± 0
Feb/Mar 2002	Cameron Lake/Sioux Narrows	0/26	0	0	± 0
Feb/Mar 2002	Fort Frances/Rainy River	8/21	38	109.5	± 15.2
Jan/Feb 2002	Bancroft	0/22	0	0	± 0
Mar/Apr 2002	Lake Huron/North Shore	1/15	7	18.8	± 0

[1] Intensity values expressed as eggs/gram of dried feces

Table 15: Prevalence and intensity of *Fascioloides magna* eggs in elk pellets from the source population at Elk Island National Park, Alberta and in elk after translocation to Ontario

Fecal pellet collection period	Location	Prevalence: No. infected/ no. collected	Prevalence: %	Intensity of eggs in feces[5]: Mean	Intensity of eggs in feces[5]: Standard error
Jan/Feb 2001	Elk Island National Park[1]	5/12	42	78.2	± 18.7
Feb/Mar 2001	Cameron Lake[2]	4/57	7	4.0	± 0.2
Feb/Mar 2001	Cameron Lake 2001 Release[3]	2/44	5	51.6	± 1.7
Feb/Mar 2002	Cameron Lake[4]	3/29	10	9.3	± 0.7
Feb/Mar 2002	Fort Frances/Rainy River[4]	0/13	0	0	± 0
Jan/Feb 2002	Bancroft[4]	4/23	17	51.4	± 3.6
Feb/Mar 2002	Lake Huron/North Shore	0/30	0	0	± 0

[1] Prior to treatment with 10% triclabendazole
[2] Fecal pellets collected were from elk that had been in Ontario 1year
[3] Fecal pellets collected were from elk in holding pen
[4] Fecal pellets collected were from elk that had been in Ontario for 1-2 years
[5] Intensity values expressed as eggs/gram of dried feces

Discussion

The reintroduction of wildlife provides unique opportunities to study both the biology and ecology of a species in its historical range, as well as evaluate the success of the reintroduction methodology and provide a basis for future management strategies. Important practical questions asked following reintroduction programs are 1) where are the animals in relation to a carefully chosen release site 2) how are they doing demographically 3) and what factors are responsible for these patterns? This study tried to examine these issues.

Spatial Behaviour

Two years after the initial reintroduction, 70% of elk translocated to northwestern Ontario were still within 20 km of the release site. This included all animals translocated as calves and yearlings. The remaining 30% (all adults) dispersed approximately 90 km to the south shortly after being released. Movements following release were, therefore, farthest for animals translocated as adults, followed by those translocated as sub-adults (calves and yearlings).

Similar patterns of post release dispersal and movement have been reported for at least 4 introduced elk populations. In Kentucky, the majority of elk could be found within 20 km of the release site two years after the initial release, while 22 adult elk moved distances ranging from 21 km to 57 km (Larkin et al. 2002). Likewise, 2 years after release, 76% of elk reintroduced (ages not specified) to Tennessee could be found within a 10 km radius of the release site, while the remaining 24% moved distances ranging from 20 km to 70 km (Muller 2002). In Pennsylvania, two adult males and one adult female dispersed shortly after release, never to return to the release area; maximum distances moved were 69 km for adult males and 29 km for the adult females (Cogan et al. 2001). Patterns of post release dispersal for adult females reintroduced to other areas of Ontario varied; however, long distance dispersal (> 50 km) of adult females upon release was reported in the Burwash/French River, Bancroft/North Hastings, and Lake Huron/North Shore regions (Rosatte et al. 2002a, 2002b).

Several studies of white-tailed deer have also reported considerable post-release dispersal. Jones et al. (1997) reported that translocated white-tailed deer did not remain together following release, dispersing an average of 24 km. Moreover, Hawkins and Montgomery (1969), and Cromwell et al. (1999) found that upon release most translocated white-tailed deer dispersed over considerable distances, producing comparatively large home range estimates.

Published literature documenting the dispersal of elk in established populations is extensive, with dispersal being described as a three-part process including emigration, transience, and immigration to a new range or social group (Stenseth and Lidicker 1992). Relatively sudden, long distance movements from traditional range to new areas have been documented for all age and sex classes (Craighead et al. 1972; Rickard et al. 1977); however, most studies report male-biased dispersal (Clutton-Brock et al. 1982; Edge et al. 1986; de Vergie 1989). For example, in Mount Rainer National Park, though overall dispersal was low, young males accounted for 72% of all dispersals (Bradley 1982). In general, male elk disperse in their second year, primarily during the spring reproductive and fall breeding seasons (Clutton-Brock et al. 1982). Three main hypotheses attempt to explain the dispersal of sub-adult male elk in established populations. These include resource competition, mate competition and inbreeding avoidance (Wolff 1994). Indeed, these factors may play a role in the dispersal of elk in northwestern Ontario; however, they may be of lesser importance during the initial stages of a reintroduction.

There are several convincing hypotheses that can explain the observed pattern of elk dispersal following release in northwestern Ontario. First, the fidelity of 70% of the elk to the release site may reflect the success of a well placed release site, the adaptive nature of the species or the age structure of the population. Prior to the reintroduction, the northwestern Ontario release site was selected based on a number of factors considered important to elk (Hutchinson et al. 2003). The fidelity to the release site may therefore reflect the successful placement of the release site, where the elk are able to satisfy their habitat needs. Furthermore, elk are a highly opportunistic species and are often considered habitat generalists (Skovlin et al. 2002). This is manifested in their catholic food habitats and wide geographic range (Kufeld et al. 1973; Skovlin et al. 2002). Therefore, simple opportunity may have influenced the observed fidelity to the release site, as elk were able to satisfy their habitat needs without dispersing across the landscape. Finally, the relatively short distances (<20 km) moved by sub-adults suggests that younger animals may have stronger fidelity to a release site and may be less likely to make long distance exploratory movements.

The dispersal of 22 adult male and female elk shortly after release may reflect initial exploratory movements and habitat preferences, as well as the social nature of elk. Initial adult-biased, exploratory movements have been documented in several reintroduced elk populations, including Kentucky (Larkin et al. 2002), Tennessee (Muller 2002), Pennsylvania (Cogan et al. 2001), and other sites in Ontario (Rosatte et al. 2002a, 2002b). Therefore, the dispersal of adult elk to the south may reflect the movements of the animals as they explore their new surroundings. Furthermore, the southern portion of the study area is largely agricultural, providing large openings and easily obtained forage. Many studies of the habitat associations of elk in western populations indicate that they prefer to graze, feeding in open areas, including agricultural lands (Lyon and Christensen 2002; Skovlin et al. 2002). As well, studies of elk introduced to Michigan, Pennsylvania, and Virginia have reported high use of agricultural areas, often resulting in significant management challenges (Moran 1973; Devlin and Tzilkowski 1986; Van Deelen et al. 1997; Cogan et al. 2001). In addition to the availability of agricultural openings, the southern portion of the study area receives significantly less snow than does the northern portion, with spring green-up occurring one month earlier (Anonymous 2002). The dispersal and subsequent establishment of elk in the south may therefore be related to habitat, in particular forage availability, as affected by snow conditions. Finally, there are approximately six elk farms scattered throughout the southern portion of the study area, and during the rutting period of both 2000 and 2001 male and female elk were found in the vicinity of these farms. Morgantini and Hudson (1988) concluded that the dispersal of introduced elk may be influenced by associations with remnant groups of indigenous elk. Presumably, these elk farms could function in the same manner, drawing elk south in search of social relationships and suitable mates.

Dispersion following a reintroduction may also be related to the length of the holding period prior to release (i.e., soft release vs. hard release) (Rosatte et al. 2002a, 2002b). It has been suggested that animals held longer in an enclosure prior to reintroduction on a new landscape become more familiar with their surroundings and develop social bonds, thereby enhancing release site fidelity. Elk translocated to northwestern Ontario in 2000 were held in an enclosure 11 days prior to release, while those released in 2001 were held 17 days. There were, however, no differences relating to the number of elk dispersing, the mean distance moved, or the maximum distance moved between the two release years. Although the two holding periods did not differ greatly, the results of this study do not support the hypothesis that the length of holding time influences dispersal.

According to Baker (1982), initial exploratory movements or dispersion by introduced animals away from the release site may be followed by a seasonal return to those areas or migration. However, despite considerable post-release dispersal, elk reintroduced to northwestern Ontario demonstrated no evidence of migration. Similar results have been reported for elk throughout eastern North America (Irwin 2002). For example, eastern elk populations were apparently non-migratory (Murie 1951). Likewise, Moran (1973) reported that western elk released in Michigan demonstrated no signs of migration, and western elk introduced to the Cedar River area in Washington were non-migratory, remaining in the lowlands year round (Taber 1976). Remnant elk herds in the Burwash region of Ontario also do not migrate, using a portion of their annual range during winter months (Brown 1998).

One can generalize that elk migrate annually in response to severe winter weather, such as cold temperatures and deep snow, or to changes in the availability and quality of forage (Irwin 2002). Similarly, spring migrations are apparently triggered by receding snow and the onset of spring green-up, which proceeds most rapidly in elevated areas with advancing day length (Dalke et al. 1965). The absence of migratory behaviour in northwestern Ontario, and indeed most of eastern North America, may therefore be related to living in an area with little altitudinal change and relatively mild winters. Moreover, the absence of seasonal changes in food availability and predation may also be influential (Fryxell et al. 1988).

Despite the absence of migration and considerable release site fidelity among younger animals, elk released in northwestern Ontario in both 2000 and 2001 ultimately ranged over a relatively large area (5211 km^2). Witmer and Cogan (1989) considered the size of available elk range a key component to the success of an introduction and recommended a minimum range of 503 km^2. Similarly, Schonewald-Cox (1986) estimated that a population of 1500 to 2000 elk (the number needed to prevent loss of genetic diversity) would require at least 1036 km^2 of habitat to be successful. Occupied elk ranges in eastern North America vary in size from 31 km^2 in Oklahoma to 6540 km^2 in Kentucky (Missouri Department of Conservation 2000). Witmer (1990) credited the success of Michigan's elk reintroduction to the fact that Michigan had greater than 1554 km^2 of elk range. Likewise, the ultimate failure of the Missouri herd was related to the use of an enclosure that was only 6 km^2 (Witmer 1990). Moreover, some have suggested that herd size in both Pennsylvania and central Ontario (Burwash) may be restricted by the fact that there is limited range available (518 km^2 and 640 km^2, respectively) (Ranta 1979; Witmer 1990). Such constraints should not limit the success of elk reintroduced to northwestern Ontario.

Elk released in 2001 ranged over an area twice the size of those released in 2000. One possible explanation for this difference is the displacement of elk introduced in 2001 by those already on the landscape. Moreover, sizes of home ranges can vary greatly as reintroduced animals explore the new landscape (Knight 1970; Craighead et al. 1972). The most likely explanation, however, is differences in sampling effort. Although total numbers of locations obtained were similar for elk released in each of 2000 (n=764) and 2001 (n=799), sampling over time differed. Sampling effort was greater during the initial post-release exploratory period for elk released in 2001, possibly overestimating their true range.

Mean individual home ranges of female elk (100% MCP: 55.7 $\pm$ 46.1 km^2) reintroduced to northwestern Ontario were similar in size to those reported in the literature for established elk in the west. For example, the mean annual home range (100% MCP) of 31 female elk in Montana during two consecutive years was 45 km^2 (range 16 km^2 to 100 km^2) (Edge et al. 1985). Similarly, in the Burwash/French River region of Ontario individual annual home ranges (100% MCP) of female elk measured between 25 km^2 and 50 km^2 (Brown 1998), and in Michigan they measured between 17 km^2 and 41 km^2 (Beyer 1987). The home ranges of individual females in northwestern Ontario were, however, larger than has been reported for elk introduced to Pennsylvania (11 km^2) (Cogan 1987). This may reflect the large amount of range available to elk in northwestern Ontario or other differences in other resource components.

The home range of one male elk (100% MCP: 16 km^2) reintroduced to northwestern Ontario was considerably smaller than has been reported in the literature for both males and females. This difference is undoubtedly a reflection of sample size, as only one male was radio-collared long enough to provide a reliable estimate of home range. Differences in home range size between sexes have been reported widely in the literature, and likely exist in northwestern Ontario. Male elk are almost always found to occupy larger areas than females (Geist 2002). For example, in Pennsylvania, adult male and female home ranges averaged 33 km^2 and 11 km^2, respectively (Cogan 1987). In Michigan, male elk home ranges averaged 34 km^2 and 59 km^2 during the rut and non-rut periods, respectively, while that of cow elk averaged 17 km^2 and 41 km^2, respectively (Beyer 1987). Sex related differences in the size of home ranges may result from differing foraging and reproductive strategies (Geist 2002). Beier and McCullough (1990) hypothesized that male white-tailed deer used areas of lower forage quality than females and therefore required larger home ranges to meet nutritional needs. Conversely, Geist (1982) suggests that bull elk select summer ranges that provide high quality forage to build fat reserves needed for the large energy expenditures during the rut and winter.

The mean individual home ranges of elk translocated to northwestern Ontario as calves (who subsequently became yearlings shortly after release), were the most variable, with females calves having the largest home range (95% and 50% adaptive kernel) when compared to all other sexes and ages. Similar results have been reported for other ungulates. Houston (1968) observed home ranges of yearling moose that were much larger than those of adults. Likewise, Addison et al. (1980) reported that yearling moose exhibited wandering lifestyles, showing no signs of establishing a home range until their second year. The large home ranges exhibited by young animals, are generally attributed to dispersal and the establishment of a new home range (Hundertmark 1998).

Habitat Utilization

Resource selection studies need to be interpreted in terms of what resources were considered available. A common approach, and that taken in this study, is to evaluate robustness of the results by modelling selection at different spatial scales (Erickson et al. 2001). Models and relationships that do not change when the scale is varied should be considered most reliable. In this study habitat relationships were examined at the second (home range selection within the study area) and third (within home range selection) order scales according to Johnson's (1980) framework. Habitat utilization patterns that did not change when availability was altered were considered most reflective of elk habitat use in northwestern Ontario.

Although elk are flexible in the habitats they use (Skovlin et al. 2002), general patterns were apparent in this study. Forest stands used (both summer and winter) by elk that established in the northern part of the study area (both 2000 and 2001 release) included pine (red pine and white pine) and mixed conifer stands, as well as cedar lowland, mixed hardwoods, and poplar. Use of younger aged stands (< 25 years) and uplands were also important in the northern part of the study area. Elk in the southern portion of the study selected mid-aged stands dominated by poplar.

Similar patterns of habitat use based on forest type have been described for elk across North America (Skovlin 1982; Skovlin et al. 2002). The use of conifers, including red pine, white pine, cedar, and balsam fir, has been well documented in the literature, and is thought to provide elk with thermorgulaory advantages (Beall 1976; Skovlin 1982; Skovlin et al. 2002), security, and winter browse (Morgantini and Hudson 1979). Peek et al. (1982) documented the use of conifer dominated stands by elk during periods of severe weather, likely reflecting the need for thermal cover. Similarly, Moran (1973) found that conifer stands were of great importance to elk in Michigan during harsh winters. According to Jost et al. (1999), eastern white cedar was used extensively by remnant elk herds in the Burwash/French River region of Ontario during the late summer and early spring. Moreover, Ranta et al. (1982) concluded that eastern white cedar was one of the most heavily browsed items in the Burwash/French River region during the late winter and early spring.

Indeed, use of conifer dominated stands by elk in the northern portion of the study area likely reflects the requirement for cover and winter browse. However, it is important to note that a portion of the study area that was classified as red pine/white pine was harvested during the past 5 to15 years, creating openings with early successional communities and ecotones, where different types of vegetation are juxtaposed. Elk are often associated with such early successional communities, as they provide large volumes of forage biomass in the form of grasses and regenerating stems (Skovlin et al. 2002). For example, Lonner (1977) found a close relationship between the density of regenerating trees and elk use across several forest habitats. Likewise, elk are often found in ecotone communities, which provide a higher diversity and greater quantity of forage plants than do either of the adjacent communities individually (Skovlin et al. 2002). Winn (1976) demonstrated that the frequency of plant species and herbage biomass in an ecotone was two times greater than found 50m into a meadow. Accordingly, small clear-cuts in the Blue Mountain region of Oregon were highly attractive to elk, receiving more use than did partially cut or adjacent uncut stands (Skovlin et al. 1989). Moreover, Leckenby (1984) found that at least 80% of elk use in summer forage areas occurred within 2.7 km of ecotone communities, with elk use decreasing with increased distance from the interface of forest and non-forest communities.

Elk in both the northern and southern portion of the study area used habitats dominated by poplar, while only those in the north used habitats dominated by mixed hardwoods. These forest stands are important to elk, as they provide a wide variety of desirable forage, including young poplar and white birch, as well as mountain maple (*Acer spicatum*) and red maple (*Acer ruberum*) (Jost et al. 1999; Skovlin et al. 2002). Beyer (1987) reported that use of poplar and mixed hardwood stands by elk introduced to Michigan was high during all seasons. Similarly, poplar was an important component of elk winter diets in Pennsylvania (Devlin and Tzilkolwski 1986). In a study of forage preference, Jost et al. (1999) found that mixed hardwood habitats in the Burwash/French River region of Ontario contained the largest number of browse species consumed by elk, and appeared to represent the most important elk habitat in this region. They also determined that poplar was important as winter forage. Likewise, Gates and Hudson (1981) found that although elk prefer to graze, in the boreal mixed wood forests of Alberta they rely heavily on browse during the winter, often selecting poplar and mixed hardwood stands.

Habitats dominated by black spruce lowland, black spruce deciduous forest, and jack pine were used less than might be expected by chance in both the northern and southern portion of the study area. These results are not surprising based on the fact that historic evidence suggests that the eastern elk avoided dense conifer stands typical of the boreal forest (Murie 1951). Moreover, black spruce and jack pine stands do not support a dense understory, as the ground cover typically consists of bedrock, needle litter, lichen and feathermoss (Racey et al. 1996). These stands would, therefore, provide very little in the way of forage for elk. Forest stands dominated by other hardwoods, including maple, oak, and elm, were also used less than might be expected by chance in both the north and south. This may reflect the fact that these habitats are found very infrequently within the study area.

Water in the form of lakes, rivers, and ice, was also used less than might be expected by chance in both the northern and southern portions of the study area. As well, the distance to nearest wetland did not contribute to habitat selection. Similar results have been reported for elk in the Burwash region of Ontario, where avoidance of water bodies, including wetlands, was demonstrated across all seasons (Brown 1998). These results may reflect the fact that there is an abundance of succulent forage in the area, thereby offsetting the need for surface water (Skovlin et al. 2002). For example, water in the form of dew, in succulent forage, and that produced by metabolic processes can significantly reduce the amount of surface water required by elk (Skovlin et al. 2002). More likely, however, elk were located within 0.2 km to 0.8 km of surface water in the summer (Jeffery 1964; Bracken and Musser 1993) and used frozen lakes and rivers as travel corridors in the winter (Brown 1998), an occurrence that may not have been detected here.

Traditionally, mature forests are considered poor foraging areas for elk in comparison to early stages of forest regeneration following fire and timber harvest (Harper 1985; Skovlin et al. 2002). Elk in the northern portion of the study area used habitats dominated by forest stands 1-25 years of age, and were often seen foraging in recent clear cuts. Studies of elk introduced to Michigan reported similar results, as elk were often found foraging in early successional habitat, especially young poplar and mixed conifer/hardwood types (Moran 1973). Similarly, the use of early successional forests has been documented in the west, likely reflecting the greater availability of grasses and herbaceous forage in more open forest stands, as well as the creation of important ecotone communities (Jenkins and Starkey 1993; Unsworth et al. 1998).

Elk that established in the southern portion of the study area met their habitat requirements by utilizing mid-aged forest stands. This contrasted with the younger aged stands used in the north, possibly reflecting a greater need for security cover. The southern portion of the study is largely agricultural, with many roads and small towns. In order to avoid disturbances associated with increased human presence, elk may have sought out small closed-canopy patches of mid-aged poplar. Unsworth et al. (1998) found that elk in areas with abundant roads demonstrated a pronounced preference for closed-canopy timber habitats, presumably in response to increased disturbance. Furthermore, it is important to note that elk may have foraged in adjacent open and younger aged habitats during the early morning and night. This behaviour would have been recorded infrequently, as most radio-locations were determined during daylight hours.

The use of topographic features, including elevation, slope, and aspect, has been well documented for elk in western North America, and, indeed, the importance of site elevation (both upper and lower) is emphasized in almost every study of habitat use (Skovlin et al. 2002). Although the topography in northwestern Ontario is not as dramatic as might be found in the west, elk in the northern portion of the study area used upland and ridge habitats at a greater rate than would be expected by chance. Uplands were also important for remnant elk herds in the Burwash region of Ontario (Ranta 1979; Jost 1997; Brown 1998). These studies concluded that ridge habitats were important to elk provided selected food items were available, such as common hairgrass (*Deschampsia flexuous*) and acorns, particularly in late summer and early autumn. Ridge habitats were also used in early summer to obtain selected browse items, including balsam poplar and largetooth aspen.

Upland sites may also be important because of their microclimate. Elk use of upland sites in the summer may be related to cooling wind patterns (Skovlin et al. 2002). Julander and Jeffery (1964) observed that elk preferred ridge tops during summer, while Dalke et al. (1965) found that elk selected ridges during the spring and summer in central Idaho. Similarly, elk in the Burwash region were seen bedding on ridge tops during sunny winter days, likely maximizing the amount of energy absorbed from the sun (Brown 1998). Predator and pest avoidance may also make upland and ridge habitats desirable to elk (Skovlin et al. 2002). In this study, upland habitats were seemingly not important to elk established in the south. This may reflect the mild winters as compared to those in the north, as well as lower predation.

Finally, although data analysis did not reflect seasonal changes in habitat use by elk, observations made while on the ground and during aerial surveys did suggest seasonal shifts. For example, during the winter and summer months elk were commonly located in upland areas dominated by conifer stands. This may reflect their need for thermal cover and valuable browse in winter and for shade, as well as forage, during summer (Skovlin et al. 2002). In the autumn of both 2000 and 2001, large groups of elk were seen in openings produced by recent clear cutting. This may reflect the kind of habitat needed by adult males to maintain their harems, a task that is more easily accomplished in open areas (Geist 2002).

Population Characteristics

Over the course of this 2-year study, the population of elk reintroduced to northwestern Ontario (including calf recuitment) declined at a rate of 21% (23/108) if early mortalities attributed to translocation injury were included, and at 15% if excluded. Caughley (1970) suggested that in the initial stages, increases in numbers of ungulates introduced to vacant habitat should closely conform to exponential growth rates. Studies of both colonizing and introduced elk populations have reported the annual rate of increase to be as high as 34% (Merrill 1987; Gogan and Barrette 1987; McCorqudale et al. 1988; Eberhardt et al. 1996). There is therefore no doubt that new elk populations can achieve rapid population expansion, however, these rates likely represent the maximum and do not reflect the situation when conditions are less than ideal. In northwestern Ontario, high adult mortality was the most important limitation to the growth of the population.

Throughout the study period, elk released in northwestern Ontario had an overall survival rate of approximately 0.57 (APS and Kaplan-Meier). This rate was similar to that of elk released in the Burwash/French River area (0.55), but lower than those reintroduced to Bancroft (0.69) and the Lake Huron/North Shore region (0.84) (Rosatte et al. 2002a, 2002b). The survival rate for elk in northwestern Ontario was also lower than has been reported for many unhunted populations in North America (White 1985; Unsworth et al. 1993; Eberhardt et al. 1996). For example, survival rates for unhunted segments of Idaho's, Washington's, and New Mexico's elk populations were 0.89, 0.98, and 0.91, respectively (White 1985, Unsworth et al. 1993, Eberhardt et al. 1996).

The comparatively low survival rate for elk reintroduced to northwestern Ontario can in part be explained by post-translocation mortality, seen in the first 3 months following release. A total of 6 elk (1 adult male and 5 adult females) died or were euthanised due to injuries suffered during capture and translocation. Similar post-translocation mortality has been reported for other cervids (Franzmann 1998; Thorne et al. 2002). For example, Beringer et al. (1996) reported probable capture related death rates ranging from 6% to 16% for white-tailed deer. Likewise, Larkin et. al (2002) reported that capture related injuries were the primary cause of death for elk introduced to Kentucky.

In most studies post-translocation mortality is related to capture method and handling protocol (Beringer et al. 1996). However, it is unclear why post-translocation mortality occurred only following the 2001 release. Capture and handing of elk was the same in both 2000 and 2001, with the exception of an oral probiotic, which was given to elk prior to translocation in 2000.

The comparatively low rate of survival in northwestern Ontario also reflects high adult mortality attributed to wolves and illegal shooting (accidental, malicious, and poaching). Predation by wolves was important during the winter in northwestern Ontario. Likewise, Rosatte et al. (2002a, 2002b) also reported high winter predation rates in elk reintroduced to the Burwash/French River region of Ontario. In Riding Mountain National Park, Manitoba, elk were the major prey species of wolves during the winter months, outranking moose by a ratio of 15:1 (Carbyn 1983). These studies also found that relatively small wolf packs (3 animals) were effective in killing adult elk, even when snow depth was low. In Minnesota, most white-tailed deer mortalities occurred from

January to April, when wolf predation was greatest on all sex and age cohorts (Nelson and Mech 1986).

Seventeen percent of all moralities and 80% of adult male elk mortality in northwestern Ontario could been attributed to illegal shooting (accidental, malicious, and poaching). This was not unexpected, as illegal shooting has been documented as the major source of male mortality in many unhunted elk populations. Moran (1973) reported that illegal shooting of elk during the regular white-tailed deer season accounted for the greatest annual known loss of elk in Michigan. Moreover, during the 1960s and 1970s, illegal shooting was thought to have equaled or exceeded annual calf production, thereby resulting in a population decline in Michigan (Moran 1973; Bellhouse and Broadfoot 1998). The growth of the elk population in Pennsylvania has also been limited by poaching (Parker 1990). As well, illegal shooting is a significant mortality factor for elk reintroduced to the Bancroft and Lake Huron/North Shore regions of Ontario (Rosatte et al. 2001, 2002).

Higher rates of predation and deaths due to illegal shooting may occur in a reintroduced population because translocated animals are unfamiliar with the area and may be less knowledgeable about escape terrain and hiding cover (Nicholson et al. 1997). For example, O'Bryan and McCullough (1985) observed a higher rate of mortality in black-tailed deer that were recently translocated compared with resident deer. Also, elk in EINP (the source population) are not hunted or subject to predation (Rosatte et al. 2002b). It is, therefore, reasonable to expect that survival of elk in northwestern Ontario will increase in future years, as post-translocation mortality is no longer a factor, sportsmen become better informed regarding the presence of elk, and the elk get to know their new landscape and can escape from predators and hunters with greater success.

Throughout the study period, elk translocated as adults had considerably lower survival than calves. This differs from survival patterns in both western and other reintroduced populations in Ontario, where survival rates for adults generally exceed those of sub-adults (calves and yearlings) (Raedeke et al. 2002; Rosatte et al. 2002a, 2002b). Patterns of survival in northwestern Ontario may have been influenced by several factors. First, all elk translocated as both calves and yearlings remained close to the release site, never venturing more than 20 km in any direction. Increased fidelity to the release site may have limited encounters with both humans (e.g., hunters) and predators, thereby increasing the chance of survival. Second, once released, radio-telemetry indicated that calves and yearlings tended to remain in relatively large groups, thereby employing the selfish herd strategy of predator avoidance (Geist 2002). Adult elk tended to remain alone or in small groups. Finally, all elk that died as a result of translocation injury were older animals, suggesting that younger animals were better able to cope with the physical and physiological stress of translocation.

Patterns of mortality differed between adult males and females, as well as between those animals located in the northern portion of the study area and those located in the south. The principal cause of mortality for adult females in northwestern Ontario varied between years. During 2000, most mortalities were attributed to unknown or natural causes (i.e., old age), while during 2001, most adult female mortalities were attributed to post-translocation mortality and predation. The principal cause of mortality for adult males was illegal shooting. Although this is uncommon in an unhunted population, as was mentioned previously male elk reintroduced to both Michigan and other sites in Ontario experienced high rates of mortality attributed to illegal shooting (Moran 1973; Rosatte et al. 2002a, 2002b).

Patterns of elk mortality in the northern and southern portions of the study area reflect characteristics of these habitats. All mortalities occurring in the northern portion of the study area, where human disturbance was minimal, could be attributed to predation, post-translocation deaths, and drowning, while all mortalities in the southern portion of the study area, where human disturbance was considerable, were attributed to illegal shooting, collision with cars or trains, and accidental injury (i.e., injury during the rut).

Using data collected during aerial surveys of radio-collared adult females (>2 years), an estimated 8 calves survived through the winter months in each of 2000 and 2001, producing a calf:cow ratio of approximately 28:100. This is similar to values reported for comparable western herds. For example, the calf:cow ratio for the Sun River elk herd in Montana was 25:100 in 1964 and 23:100 in 1965 (Knight 1970). Likewise, Schwartz and Mitchell (1945) reported calf:cow ratios in February and March ranging from 21:100 to 26:100. The calf:cow ratio of elk reintroduced to the Burwash/French River and Lake Huron/North Shore regions of Ontario were also similar, ranging from 14:100 to 32:100 (Rosatte et al. 2002a, 2002b).

The calf:cow ratio in northwestern Ontario was, however, lower than that of elk reintroduced to the Bancroft region of the province. (40:100 in March 2001 to 38:100 in March 2002) (Rosatte et al. 2002a). This may reflect lower predation rates on calves. Although no predator-specific data describing the causes of mortality for calves in northwestern Ontario is available, significant predation on neonatal calves by black bears, wolves, and coyotes has been reported for many elk populations. Singer et al. (1997) reported that predation was the greatest source of calf mortality (44%) for elk in Yellowstone National Park, with most mortality occurring when calves were 3 to 10 days old. Schlegel (1976) found that 38 of 53 marked calves in Idaho were killed by black bears. Wolves killed more elk calves than hunters in the area of Glacier National Park, Montana (Boyd et al. 1994). As well, wolf-killed elk calves were observed during the winters of 1999, 2000, and 2001 in the Nippising/French River region of Ontario (Rosatte et al. 2002a, 2002b). Moreover, according to McCullough (1969), coyote predation accounted for roughly 30% of neonatal mortalities observed in Tule elk calves. Also, during three consecutive summers, coyotes killed 11 calves in Yellowstone National Park (Singer et al. 1997).

Fascioloides magna* and *Parelaphostrongylus tenuis

It is well established that *Fascioloides magna* can be translocated along with infected cervids, particularly elk (Kingscote 1950; Pybus 2001). Data collected from elk translocated to Ontario indicate that, despite two treatments with 10% triclabendazole, a small number of elk arrived in Ontario infected with the parasite. One dose of 10% triclabendazole (30 to 100 mg/kg body weight) was proven 98% effective against adult flukes, but 10% of immature flukes survived (Pybus et al. 1991). A more stringent protocol, requiring a second treatment of 10% triclabendazole (three days after the first) was implemented for elk captured in EINP (Rosatte et al. 2002a, 2002b). Yet, results reported here indicate that efficacy was still less than 100%.

Fascioloides magna already occurs in white-tailed deer throughout much of Ontario (Kingscote 1950; Pybus 2001); however, its distribution is discontinuous and there are many areas where it is not regularly found (Addison et al. 1988; Pybus 2001). Following examination of fecal pellets collected from white-tailed deer resident in elk release areas, only those in the Fort Frances/Rainy River and Lake Huron/North Shore regions of Ontario were found infected.

The distribution of *F. magna* in Ontario presumably reflects local conditions of wetland habitats and snail availability, ungulate use and movements, as well as seasonal variations in moisture and temperature (Pybus 2001). One might, therefore, reasonably conclude that areas where the parasite is absent in resident white-tailed deer will also be unsuitable for transmission among reintroduced elk. However, factors that may exclude the parasite can change and it has been reported to come and go over time. For example, *F. magna* was found for the first time in elk and moose of EINP in 1987. This followed five decades of extensive population reduction, where veterinary inspectors did not record *F. magna* in the livers of hundreds of deer, moose, elk, or bison (Thorne et al. 2002). Moreover, EINP is completely fenced and there have been no recent translocations of ungulates to the park that can explain its appearance (Thorne et al. 2002). Likewise, at the Canadian Forces Base, Camp Wainwright in east-central Alberta, liver flukes were once abundant, but are now gone (Thorne et al. 2002).

The prevalence of *F. magna* in white-tailed deer in both the Fort Frances/Rainy River (38%) and Lake Huron/North Shore (7%) region of Ontario was lower than has been reported, for example, in the Peterborough Game Reserve (68%) (Addison et al. 1988). However, white-tailed deer across the Province show an overall prevalence of only 12% (Addison 1997). The prevalence of *F. magna* tends to be higher in river/swamp habitats than dry uplands (Trainer 1969; Mulvey et al. 1991). In particular, shallow, slightly alkaline, warm water lowlands with minimal canopy cover are inclined to have a greater abundance of infected snail intermediate hosts. Such areas are also attractive to various cervids. The prevalence of *F. magna* also increases in areas where infected cervids congregate or spend prolonged periods (Pybus 2001). For example, a prevalence of 86% was recorded for elk in the Bow Valley of Alberta, where large numbers of elk occur year- round (Pybus 1990). Similarly, up to 80% of snails were infected in an area used for supplemental feeding of red deer in Czechoslovakia (Erhardova-Kotrla 1971). Finally, seasonal conditions of moisture and temperature affect the abundance and activity of intermediate hosts, as well as embryonation and subsequent development of the parasite (Pybus 2001). Prolonged snow cover in the spring has been reported to delay the emergence of snails, as well as extend the development time of miracidia within eggs (Pybus 2001). The high density of white-tailed deer in the Fort Frances/Rainy River and Lake Huron/North Shore regions of Ontario, and seemingly suitable climate for *F. magna* transmission, will no doubt ensure the future infection of elk translocated to these regions of the Province.

Parelaphostrongylus tenuis does not occur naturally in western North America. However, it is common in white-tailed deer in Ontario (Whitlaw and Lankester 1994; Slomke et al. 1995), and prevalence was comparatively high in all areas that have received translocated elk. The relative importance of *P. tenuis* as a mortality factor in elk reintroduced to eastern North America is unclear. Meningeal worm can cause debilitating neurologic disease and death in free ranging elk, and probably limited the success of past reintroduction to eastern North America (Lankester 2001). Elk introduced to the Adirondacks apparently failed as a result of the parasite (Severinghaus and Darrow 1976). Likewise, elk introduced to Pennsylvania (Woolf et al. 1977; Eveland et al. 1979), Minnesota (Bryant and Maser 1982), Arkansas (Thorne et al. 2002), and Kentucky (Larkin et al. 2003) have evidently struggled. However, despite sporadic cases of parelaphostrongylosis, a few native populations and some introduced herds have persisted on range with infected white-tailed deer. Elk reintroduced to both Michigan (Moran 1973) and Oklahoma (Raskevitz et al. 1991) have achieved significant population growth, possibly because of habitat selection and foraging behaviour that separated the elk from infected white-tailed deer .

The severity and outcome of infection in elk may also be dose dependent. Studies of both white-tailed-deer and moose suggest that a protective immunity can result from initial exposure to a small, non-fatal dose of the larvae (Lankester 2002). Similarly, elk experimentally infected with low number of infective larvae (< 15) apparently survived (Samuel et al. 1992). Therefore, mortality of elk is probably related the number of infected larvae ingested at first infection, and subsequent, the specific damage caused by worms within the central nervous system (Lankester 2002). It has yet to be determined whether a degree of acquired immunity will, in time, reduce observed herd mortality following a reintroduction (Lankester 2002).

The importance of *P. tenuis* as a mortality factor in elk reintroduced to Ontario will depend mostly on the densities of infected white-tailed deer, the number and rate at which larvae in snails are ingested, and the extent of habitat overlap between the two cervids. Consequently, long term monitoring of white-tailed deer densities, intensity of

P. tenuis, growth of the introduced elk population, and serological evidence of contact with the parasite will help determine the likelihood of success (Lankester 2001).

Summary

All elk translocated to northwestern Ontario as calves and yearlings stayed within 20 km of the release site. This age cohort also experienced higher survival rates than those translocated as adults. Although limited breeding by sub-adults may delay the growth of the population, this may be out-weighed by their increased survival. Any future reintroductions should, therefore, be comprised of good proportions of calves and yearlings.

Over the period of two years, the elk population reintroduced to northwestern Ontario declined from 108 to an estimated 85 animals. A high proportion of adult mortality resulted from translocation injuries, wolf predation, and illegal shooting. If future mortality and recruitment rates remain unchanged, the elk population in northwestern Ontario will likely face a slow decline. On the other hand, in the absence of translocation injury, and if wolf predation deceases as the elk become more familiar with the landscape and accidental shooting declines with greater hunter awareness, the population may in fact show a modest increase over the next few years.

The reintroduced elk presently form two distinct groups: one in the northern part of the study area around Cameron Lake, and the other approximately 90 km to the south in the vicinity of Fort Frances/Rainy River. Forest stands used by elk in the north included pine and mixed conifer stands, as well as cedar lowland, mixed hardwoods, and poplar. Use of younger aged stands and uplands were also important to elk in the northern portion of the study area. Elk that established in the south selected mid-aged poplar stands dominated by poplar. Although the specific causes of mortality differed in the north and south, overall survival and recruitment rates were similar for animals in both locations.

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Appendix 1: Structured Query Language used to calculate standard forest units

Water = SFU 0

PRMWX/PWDOM/PRDOM = SFU 1
[Pw]+[Pr] >= 4
([Pw] >= 4) and ([SFU] <> 1)
([Pr] >= 7) and ([SFU] <> 1)

OCLOW = SFU 2
[Ce]+[La] >= 5 Or [WG] = 17 Or [WG] = 18 And [Pr]+[Pw]+[Pj]+[Sw]+[Bw] < 1

SBLOW = SFU 3
(([Sb]+[Ce]+[L]>=10) and ([Sc]="3") or ([Sc]="4")) or (([Sb]+[Ce]+[L] = 10) and ([Ce]+[L]>=1) and ([Sc]="1") or ([Sc]="2")) and ([SFU] <> 2)

SBDEE/SBSHA = SFU 4
([Sb] >= 7) and ([Po]+[Bw] <= 2) and ([Stk] >= 0.6)
([Sb] >= 7) and ([Po]+[Bw] <= 2) and ([SFU] <> 4) and ([Sc] <> "3") and ([Sc] <> "4")

PJDEE/PJSHA = SFU 5
([Pj] >= 7) and ([Po]+[Bw] <= 2) and ([Stk] >= 0.6)
([Pj] >= 7) and ([Po]+[Bw] <= 2) and ([SFU] <> 6)

PODEE/POSHA = SFU 6
([Po] >= 7) and ([Stk] >= 0.5)
([Po] >= 7) and ([SFU] <> 8)

BWDOM = SFU 7
([Bw] >= 6) and ([Bw]+[Po] >= 7)

OTHHD = SFU 8
([Mh]+[Ms]+[Or]+[Ow]+[Bd]+[E] >= 3)

SBMX1/PJMX1 = SFU 9
([Pr]+[Sb]+[Pj]+[Sw]+[B] >= 7) and ([B] <= 1) and ([Po] +[Bw] <= 2) and ([Sb]+[Sw] > [Pj]) and ([SFU] <> 4) and ([SFU] <> 5) and ([Sc] <> "4") and ([Sc] <> "3")
([Pr]+[Sb]+[Pj]+[Sw]+[B] >= 7) and ([B] <= 1) and ([Po] +[Bw] <= 2) and ([Pj] >= ([Sb]+[Sw])) and ([SFU] <> 6) and ([SFU] <> 7) and ([SFU] <> 1)

BFDOM/ CONMX = SFU 10
([B] >= 4) and ([B]+[Sw]+[Sb]+[Pj] >= 5)
([Pw]+[Pr]+[Sb]+[Sw]+[B]+[Pj]+[Ce]+[L] >= 5) and ([SFU] < 4) and ([SFU] <> 2) and ([SFU] <> 1) and ([Sc] <> "4") and ([Sc] <> "3")

HRDOM/ HRDMW = SFU 11
([Po]+[Bw]+[Mh]+[Ab]+[Ms]+[Or]+[Ow]+[E] >= 7) and ([SFU] < 4)
([Po]+[Bw]+[Mh]+[Ab]+[Ms]+[Or]+[Ow]+[E] >= 5) and ([SFU] < 4)

This SQL was added to the end to convert some lowland Sb that was put into other SFU's back to SBLOW
(([Sb] > 7) and ([Sc] = "3")) or (([Sb] > 7) and ([Sc] = "4"))

Appendix 2: Number of re-locations for radio-collared elk reintroduced to northwestern Ontario in February 2000

Sex	Ear Tag	Collar Frequency	Age[1]	2000 Winter	2000 Summer	2000 Total	2001 Winter	2001 Summer	2001 Total	2002 Winter	2002 Summer	2002 Total	Total Winter	Total summer	2002 Grand total	St
Males	69	149.578	AD	0	1	1	0	0	0	0	0	0	0	1	1	M
	70	149.551	AD	3	2	5	4	0	4	4	0	4	11	2	13	
	71	149.500	AD	1	1	1	0	0	0	0	0	0	1	1	2	M
	73	149.476	AD	0	3	3	0	0	0	0	0	0	0	3	3	M
	76	149.526	YRL	0	3	3	0	0	0	0	0	0	0	3	3	M
	112	150.750	YOY	6	2	8	7	6	23	0	0	0	13	18	31	D
	113	150.561	YOY	5	4	9	9	18	27	2	0	2	16	22	38	D
	114	150.840	YOY	4	2	6	6	1	7	0	0	0	10	3	13	D
	115	149.180	YOY	4	2	6	9	15	24	1	0	1	14	17	31	D
Females	78	149.426	AD	1	2	3	2	9	11	10	0	10	13	11	24	
	79	149.951	AD	4	3	7	2	1	3	0	0	0	6	4	10	M
	80	149.925	AD	3	1	4	4	16	20	0	0	0	7	17	24	M
	81	149.376	AD	0	0	0	0	0	0	0	0	0	0	0	0	M
	82	150.001	AD	3	1	4	5	16	21	8	1	9	16	18	34	
	83	149.400	AD	0	3	3	0	0	0	0	0	0	0	3	3	M
	84	149.451	AD	0	0	0	4	12	16	10	1	11	14	13	27	
	85	149.801	AD	3	0	3	10	18	28	4	0	4	17	18	35	
	86	150.026	AD	2	1	3	0	0	0	0	0	0	2	1	3	M
	87	149.726	AD	1	1	2	4	15	19	8	1	9	13	17	31	
	89	149.751	AD	6	2	8	10	19	29	9	0	9	25	21	46	
	90	149.876	AD	4	3	7	10	20	30	7	2	9	21	25	46	
	91	149.901	AD	6	3	9	11	20	21	7	1	8	24	24	48	
	92	149.851	AD	1	0	1	7	11	18	9	0	9	17	11	28	
	76	149.976	YRL	3	2	5	4	9	13	0	0	0	7	11	18	M
	88	149.651	YOY	6	3	9	11	21	32	7	1	8	24	25	49	M
	111	149.776	YOY	5	3	8	11	18	29	8	0	8	24	21	45	
	118	149.626	YOY	4	2	6	10	18	28	0	0	0	14	20	34	M
	119	149.676	YOY	5	3	8	11	19	30	5	1	6	21	23	44	
	120	149.702	YOY	4	4	8	8	19	27	5	1	6	17	24	41	
	122	149.825	YOY	4	2	6	7	19	26	7	1	8	18	22	40	
										Total # of locations			365	399	764	

Note: AD = adults; YRL = yearlings 20-21 months; YOY = calves 8-9 months
Note: Grand total is from Feb 2000 (date of release) to June 01, 2002
Note: Winter period is from November 01 to April 30; summer period is from May 01 to October 31
Note: Mort = confirmed dead; Drop = dropped radio-collar; Miss = unable to receive radio signal
[1] Refers to the age of the animal at time of release
[2] Status of collar at last recorded re-location

Appendix 3: Number of re-locations for radio-collared elk reintroduced to northwestern Ontario in March 2001

Sex	Ear Tag #	Collar frequency	Age[1]	2001 Winter	2001 Summer	2001 Total	2002 Winter	2002 Summer	2002 Total	Total Winter	Total summer	Grand Total	Status[2]
Males	419	150.701	AD	5	6	11	5	0	5	10	6	16	
	425	149.975	AD	4	6	7	9	0	9	13	6	19	
	426	148.560	AD	4	2	6	8	0	8	12	2	14	
	428	150.451	AD	1	7	8	0	0	0	1	7	8	Drop
	434	150.277	AD	2	0	2	0	0	0	2	0	2	Mort
	436	150.151	AD	5	9	14	5	0	5	10	9	19	
	437	149.300	AD	1	4	5	0	0	0	1	4	5	Mort
	412	149.312	YRL	2	7	9	2	0	2	4	7	11	
	431	150.180	YRL	3	5	8	0	0	0	3	5	8	Mort
	441	151.700	YRL	7	21	28	6	0	6	14	21	34	
	400	150.351	YOY	7	7	14	5	0	5	12	7	19	
	402	150.771	YOY	5	19	24	3	0	3	8	19	27	
	405	150.727	YOY	7	18	25	5	0	5	12	18	30	
	406	148.851	YOY	7	20	27	6	0	6	13	20	33	
	407	149.476	YOY	7	22	29	1	0	1	8	22	30	Drop
	408	150.402	YOY	4	20	24	3	1	4	7	21	28	Mort
	409	148.400	YOY	7	18	25	8	2	10	15	20	35	
	440	151.561	YOY	3	3	6	0	0	0	3	3	6	Drop
Females	394	151.462	AD	4	6	10	8	0	8	12	6	18	
	411	148.276	AD	7	19	26	6	0	6	13	19	32	
	413	148.302	AD	3	0	3	0	0	0	3	0	3	Mort
	415	148.027	AD	1	20	21	0	0	0	1	20	21	Drop
	417	148.152	AD	7	17	24	4	0	4	11	17	28	Mort
	418	148.352	AD	0	0	0	0	0	0	0	0	0	Mort
	422	148.252	AD	0	3	0	0	0	0	0	3	3	Miss
	424	151.855	AD	3	0	3	0	0	0	3	0	3	Mort
	433	150.301	AD	1	0	1	0	0	0	1	0	1	Mort
	435	148.636	AD	1	3	4	1	0	1	2	3	5	
	442	151.671	AD	1	0	1	0	0	0	1	0	1	Mort
	443	150.931	AD	1	4	5	1	0	1	2	4	6	
	444	150.427	AD	3	1	4	0	0	0	3	1	4	Miss
	447	150.176	AD	6	9	15	9	1	10	15	10	25	
	448	148.412	AD	2	2	4	0	0	0	2	2	4	Mort
	416	148.236	YRL	7	19	26	4	0	4	11	19	30	Mort
	420	148.201	YRL	8	17	25	4	2	6	12	19	31	
	421	148.177	YRL	3	3	6	0	0	0	3	3	6	Mort

Females	427	150.227	YRL	7	17	24	8	2	10	15	19	34
	316	149.222	YRL	7	20	27	8	0	8	15	20	35
	398	151.725	YOY	7	20	27	7	0	7	14	20	34
	401	148.101	YOY	6	17	23	5	1	6	11	18	29
	403	148.325	YOY	7	20	27	7	1	8	14	21	35
	404	150.502	YOY	7	17	24	5	2`	7	12	19	31
	410	150.476	YOY	4	17	21	5	1	6	9	18	27
								Total # of Locations		333	457	790

Note: AD = adults; YRL = yearlings 20-21 months; YOY = calves 8-9 months
Note: Grand total is from March 01 2001 (date of release) to June 01, 2002
Note: Winter period is from November 01 to April 30 and summer period is from May 01 to October 31
Note: Mort = confirmed dead; Drop = dropped radio-collar; Miss = unable to receive radio signal
[1] Refers to the age of the animal at time of release
[2] Status of collar at last recorded re-location