

Population Distribution and Seasonal Resource Selection by Elk  
(*Cervus elaphus*) in Central Ontario

by

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## Abstract

Understanding population structure and resource selection are essential for wildlife management and conservation. I assessed the population structure and resource selection of elk (*Cervus elaphus*) in central Ontario. I used fuzzy and hierarchical cluster analyses to elucidate elk population structure based on spatial data collected from 41 radio-collared elk. I assessed impacts of habitat quality on space use using the minimum convex polygon (MCP) and fixed kernel methods. I evaluated resource selection by elk in winter, spring, summer, and fall, from December 2011 to August 2013, using resource selection functions (RSF's). I used a generalized linear mixed model (GLMM) to evaluate resource selection functions and used Akaike information criterion ( $AIC_c$ ) to select the best model of 20 candidate models constructed *a priori*. Models included parameters representing resources known to be important to elk: elevation, aspect, slope, distance to roads and water, and habitat. Both fuzzy and hard clustering indicated that elk in Central Ontario occur in a metapopulation that includes 5 subpopulations. The largest cluster consisted of a core group of 22 radio-collared elk located in Burwash with several satellite subpopulations spread along a 50km long north-south axis and a small subpopulation to the west located in Worthington. Survival rates among subpopulations were similar ranging from 0.71 to 0.83; however, anthropogenic causes of mortality were predominant only in the Burwash subpopulation. Space use and density of elk differed between core and satellite subpopulations. Resource selection by elk differed by time of day and season. In all seasons, elk selected open habitats at night and more forested areas during the day. Elk avoided areas close to roads in spring, but selected them in winter at night. Elk selected higher elevations in winter and for south facing slopes in spring and fall. Elk displayed strong crepuscular activity patterns in all seasons; however, movements were limited in winter. Understanding population structure is important in order to develop appropriate management plans. My results support the conclusion that population structure can be reliably assessed using spatial data. Resource selection is a dynamic process that changes with seasons, as well as animal activity across the diel period. Resource selection should include time of day in order to obtain a complete picture of resources important to a particular species and to support the conservation of habitats used for various animal activities.

## **Dedication**

I would like to dedicate this thesis to my two beautiful daughters with hopes that the natural world will captivate and inspire them half as much as it has with me.

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## General Introduction

Population ecology is the cornerstone of the management and conservation of any species. Populations may take various forms based on decision-making criteria used to define them, such as biological, political or research-based criteria (Mayr 1970). Biological populations have been traditionally defined as a group of interbreeding individuals in a given location (Mayr 1970). The physical boundaries of biological populations are often arbitrarily delineated, based on political decisions, and thus fail to incorporate meaningful ecological processes.

Understanding and describing populations are influenced by spatial and temporal scales (Thomas and Kunin 1999; Schaefer 2006). A population may seem continuous at a regional level, but may be composed of several spatially disjunct subpopulations at a local level (Morrison 2002).

Assessing population structure is a critical component of understanding population dynamics and implementing appropriate management and conservation decisions. Spatially-structured subpopulations may operate as metapopulations, interconnected through limited dispersal, and therefore require different management strategies than a single continuous population (Levins 1969; Hanski 1991; Wiens 1996)

Population processes are affected by the way individuals encounter and respond to the landscape. Understanding animal space use has been a central focus of ecology (Kernohan *et al.* 2001). The area an animal requires to secure adequate food, shelter and mating opportunity is defined as a home range (Burt 1943). Quantifying individual home range sizes reveals the area needed for animals to meet their daily and annual habitat requirements. Spatial behaviour of animals can reveal the factors influencing population processes such as site fidelity, interspecific competition, intraspecific competition and predation risk (Lagos *et al.* 1995; Williams *et al.*

2002; Larkin *et al.* 2004; Bjørneraas *et al.* 2012). Study duration and objectives are important considerations in assessing animal space use. Seasonal fluctuations in food availability and changes in animal behaviour can influence space use (Harris *et al.* 1990). Specified time periods are now commonly used to characterize animal space use such as seasonal, annual or multiannual home ranges (Kernohan *et al.* 2001). Home ranges ultimately provide important information on the minimum area of resources required to support functioning, self-sustaining populations.

Resources can be defined broadly as any abiotic or biotic elements directly used by an animal (Morrison 2002). Resources need to be quantified into measurable units and when resources are used disproportionately to availability, use is thought to be selective (Manly *et al.* 2002). Researchers have increasingly chosen a resource selection approach over strictly habitat selection, because it can account for variables that influence selection over static habitat types (McLoughlin *et al.* 2010). Resource selection has become a dominant tool for management and conservation, because it allows for the prioritization of resources for the focal species. Resources that are selected are assumed to positively influence fitness; however, quantification of this is difficult and rarely achieved (Boyce and McDonald 1999; Johnson *et al.* 2004). Resource selection occurs in a hierarchical fashion and is influenced by both spatial and temporal scales (Johnson 1980). Research has commonly ignored or failed to address temporal changes in resource selection by animals, resulting in incomplete pictures of wildlife and habitat relationships (Morrison *et al.* 1998). Sampling from a limited window in time can also overlook important resources associated with different animal behaviours (Palomares and Delibes 1992).

Elk (*Cervus elaphus*) were once common across most of North America (Ranta 1979). Unregulated hunting, land use conflicts and habitat loss resulted in their extirpation from the

eastern half of the continent (Ranta 1979). The last known elk in Ontario was shot in 1893 outside of North Bay (Seton 1927). Elk are a keystone species because they are important both ecologically and economically. During the early 1930s, several attempts to reintroduce elk into Ontario failed (Ranta 1979). During the late 1990s, 443 elk were reintroduced into Ontario over four years (Rosatte *et al.* 2007). Burwash, Ontario was one of four release sites in the province, where over 170 elk were released (Rosatte *et al.* 2007). A small remnant herd of elk persisted in Burwash and the French River from former reintroductions. The current provincial population estimate is 648-916 (MNR website). Spatial behaviour and forage selection of the remnant population was studied prior to restoration efforts (Brown 1998; Jost *et al.* 1999). Martin (2011) investigated acclimatization to the new habitat by the reintroduced elk and whether highway construction disturbed their spatial behaviour. A complete picture of elk resource selection has yet to emerge and important questions remained unanswered. What is the current elk distribution in central Ontario, 15 years post-restoration? How does resource selection by elk change with season and time of day? What are the seasonally-critical resources for elk? The objectives of this thesis are to better understand population structure and resource selection across different temporal scales through the seasons. The specific objectives for my thesis can be summarized as follows:

- Determine the spatial distribution of elk in central Ontario
- Assess the impact of habitat quality on elk spatial behaviour,
- Determine effects of temporal scale on resource selection
- Determine daily movements and activity patterns for elk.

## Literature Cited

- Bjørneraas, K., I. Herfindal, E. Solberg, B. Sæther, B. Moorter, and C. Rolandsen. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia* 168:231-243.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution* 14:268-272.
- Brown, G.S. 1998. Spatial Behaviour and habitat utilization of Wapiti (*Cervus elaphus*) in the French River and Burwash Regions of Ontario. MSc thesis School of graduate studies and research Laurentian University.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.
- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models, and observations. *Biological Journal of the Linnean Society* 42: 17-38.
- Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trehwella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data-a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20:97-123.
- Johnson D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61:65-71.
- Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* 41:238-251.
- Jost, M. A., J. Hamr, F. F. Mallory. 1999. Forage selection by elk in habitats common to the French River – Burwash region of Ontario. *Canadian Journal of Zoology* 77: 1429-1438.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. In: *Radio Tracking Animal Populations* Millspaugh, J. J. & Marzluff, editors San Diego Elsevier.
- Lagos, V. O., L. C. Contreras, P. L. Meserve, J. R. Gutiérrez, and F. M. Jaksic. 1995. Effects of Predation Risk on Space Use by Small Mammals: A Field Experiment with a Neotropical Rodent. *Oikos* 74:259-264.
- Larkin, J. L., J. J. Cox, M. W. Wichrowski, M. R. Dzialak, and D. S. Maehr. 2004. Influences on Release-Site Fidelity of Translocated Elk. *Restoration Ecology* 12:97-105.

- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237-240.
- Manly, B. F. J., L. L. McDonald, D. L. McDonald and W. P. Erickson. 2002. *Resource selection by animals* 2<sup>nd</sup> edn. Kluwer Academic Publishers, Dordrecht.
- Martin, M. 2011. Spatial behavior and habitat use by elk (*Cervus elaphus*) in response to highway construction and interprovincial relocation. MSc thesis School of graduate studies Laurentian University.
- Mayr, E. 1970. *Populations, species, and evolution: an abridgement of animal species and evolution*. Harvard University Press, Cambridge, Massachusetts, USA.
- McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology* 79:4-12.
- Morrison, M. L., B. G. Marcot and R. W. Mannan. 1998. *Wildlife-Habitat Relationships: Concepts and Applications*. 2<sup>nd</sup> ed. Madison, University of Wisconsin Press.
- Morrison, M. L. 2002. *Wildlife Restoration*. Island Press, Washington.
- Palomares, F., and M. Delibes. 1992. Data analysis and potential bias in radio-tracking studies of animal use. *Acta Oecologia*. 13:221-6.
- Ranta, B. 1979. Range and habitat relationships of wapiti (*Cervus canadensis*) in the Burwash-French River area of Ontario. M.Sc. Thesis, Carleton University, Ottawa.
- Rosatte, R., J. Hamr, J. Young, I. Filion, and H. Smith. 2007. The restoration of elk (*Cervus elaphus*) in Ontario, Canada: 1998–2005. *Restoration Ecology* 15:34-43.
- Schaefer, J. A. 2006. Towards maturation of the population concept. *Oikos* 112:236-240.
- Seton, E.T. 1927. *Lives of game animals*. Doubleday, Doran and Co. Inc, New York.
- Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68:647-657.
- Wiens, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics and management. Pages 53-84. *in* D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. Island Press, Covelo, California, USA.
- Williams, J. M., A. E. Pusey, J. V. Carlis, B. P. Farm, and J. Goodall. 2002. Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour* 63:347-360.

# Chapter 1: Metapopulation dynamics and space use by reintroduced elk (*Cervus elaphus*) in central Ontario

## Introduction

Accurate delineations of populations are paramount for understanding of population ecology and applications to, wildlife management and conservation. Populations, previously defined as an entity (Berryman 2002), are becoming increasingly viewed as a concept as they change with the parameters used to define them, such as spatial extent (Schaefer 2006). Populations are increasingly being defined by the spatial arrangement of individuals (Bethke *et al.* 1996; Mauritzen *et al.* 2002; Kamler *et al.* 2013). The most appropriate scale to evaluate spatial structure will vary depending on the objectives or questions being addressed (Thomas and Kunin 1999). Recent research has identified the subpopulation as an appropriate spatial scale to obtain information meaningful to biological processes, such as population dynamics (Schaefer *et al.* 2001; McLoughlin *et al.* 2002; Edwards *et al.* 2008).

Populations without any apparent spatial structure are deemed continuous or panmictic, where all individuals within the population freely mix and densities are uniform (Gilpin 1996). In the simplest terms, a metapopulation is a population of populations that is spatially structured (Hanski 1998). Originally coined by Levins (1969), metapopulation theory was modelled after the theory of island biogeography, characterized by different local extinction and recolonization rates of suitable habitat patches based patch size and distance to source populations (MacArthur and Wilson 1967). In classic metapopulation theory, each habitat has an equal probability of a dispersal event, the rate of colonization is proportional to the fraction of unoccupied habitats, and

each sub-population has the same extinction probability (Levins 1969; Levins 1974). Therefore, population persistence is a function of the rate of colonization being greater than the extinction probability. The Levins model assumes that there is no spatial correlation between the state of habitat patches, and that there are only two recognized states (vacant or at carrying capacity). However, Hanski (1991), and others (Harrison 1991; Simberloff 1995; Wiens 1996) state that relatively few natural systems conform to this model of metapopulation dynamics. More commonly, natural metapopulations consist of habitat patches of varying size and quality, indicating different extinction probabilities and thus more accurately reflect source-sink dynamics (Pulliam 1988; Hanski 1991). Hanski (1991) further illustrates this example by describing four classes of metapopulations: 1) patchy, effectively a single population; 2) classical, following Levins' model; 3) non-equilibrium, where patches operate as separate metapopulations; and 4) mainland-island, where a large population that is relatively immune to extinction is surrounded by smaller satellite subpopulations with higher extinction probabilities.

At its inception, metapopulation theory did not capture much of the attention of the scientific community. It was not until almost 20 years later that interest in metapopulations began to explode (Metz and Gyllenberg 2001). The explanation is simple; as habitat fragmentation increased globally at an alarming rate, many species occurred in habitat patches isolated from surrounding populations, thus forming metapopulations (Gutiérrez and Harrison 1996; Stith *et al.* 1996; Hunter 2002; Baguette and Schtickzelle 2003; Wiegand *et al.* 2005; Cushman 2006). Analysis of population structures has often been focused on populations in highly fragmented landscapes, or species that are highly endangered (Beier 1996; Tero *et al.* 2003). Many conservation initiatives, including restoration ecology, have used the framework of metapopulations, and often practitioners have no choice but to restore species in remaining local



habitat patches (Bleich *et al.* 1996). Few studies have assessed population structure in continuous landscapes, and even fewer have looked at the population structure of a species reintroduced. Wildlife restoration is becoming increasingly popular in conservation biology and post-release monitoring has largely focused on dispersal and survival (Kurzejeski *et al.* 1988; Warren *et al.* 1996; Carrie *et al.* 1999; Gross *et al.* 2000; Young 2002; Ryckman *et al.* 2010; Yott *et al.* 2011), while few studies have addressed the structure of restored populations. Here I assess the spatial structure of elk (*Cervus elaphus*) 15 years after re-introduction, in an unfragmented landscape. I hypothesized that elk spatial structure would be panmictic because the landscape is fairly homogenous, consisting of unfragmented forests. If there are no physical or ecological barriers, dispersal throughout the study area should be high. Previous research in the study area has described two distinct groups of elk, one in Burwash and one occupying the French River delta (Ranta 1979; Brown 1998), therefore at most I would expect to find two distinct spatially structured subgroups. I also hypothesized that space use will be inversely related to habitat quality with larger space use occurring in poorer quality habitats because of reduced food availability.

## **Materials and Methods**

### *Study Population*

Elk were reintroduced into Ontario in the early 1900s (Ranta 1979). Concerns over liver fluke (*Fascioloides magna*) transmission to cattle led to the removal of most elk populations in Ontario. A small remnant population of elk persisted in Burwash, and along the French River, 20-40 km south of Sudbury (Ranta 1979, Brown 1998; Jost 1999). In the late 1990's, elk were reintroduced into four different locations in Ontario over a four year period (Rosatte *et al.* 2007). Burwash received 172 elk between 1998 and 2001 (Rosatte *et al.* 2007). Elk were released over

15 years ago in Ontario and are now considered acclimatized to their environment in Ontario (Martin 2011).

### *Study Area*

The study took place in central Ontario, from Georgian Bay north to highway 17 near the City of Greater Sudbury (Figure 1). The study area is located in the Great Lakes St. Lawrence Eco-Region, dominated by forests interspersed with lakes, rivers and wetlands. The area is typical of post-glacial Precambrian Shield landscape, with numerous granite ridges and shallow soils. Climate is classified as continental, consisting of cold temperatures, warm summers and the absence of a dry season (Peel *et al.* 2007). Mean annual temperature from the Sudbury airport from 1981 to 2010 is 4.1°C (Environment Canada 2013). Snowfall occurs from November to March and snow depth measurement on site throughout winter of 2012-2013 frequently exceeded 60cm. Forested regions are a mix of deciduous *Populus spp.*, *Acer sp.*, *Quercus spp.*, *Betula spp.*, and coniferous *Pinus spp.*, *Picea spp.*, and *Abies balsamea* tree species. The study area consists mostly of intact wilderness with a major highway bordering the study area to the east and trans-Canada highway bisecting the area east-west on the northern fringe. A railway line runs north-south through the center of the study area.

### *Animal Capture/Monitoring*

At the onset of the present research, 24 adult females with functioning VHF collars were already present in the study area (Martin 2011). Elk were captured using net guns fired from helicopters. In February 2012, 13 elk (2 males and 11 females) were fitted with VHF radio-collars (LMRT, Lotek Wireless, Newmarket, ON), equipped with a mortality sensor. In addition, 6 adult females were fitted with GPS collars (Iridium, Lotek Wireless, Newmarket,

ON) programmed to record a location every hour. I attempted to distribute collars evenly among groups throughout the landscape, and to use the 6 GPS collars on elk in the core area. Elk groups were located using a combination of aerial surveys from helicopters and reports from the public. All radio collared elk were located weekly using standard radio telemetry techniques (White and Garrott 1990). Bearings were recorded from the highest possible local elevation point using the loudest signal method (Springer 1979). Bearings were recorded using a Silva compass with the declination adjusted to 10°W. Locations were estimated using mostly 3 bearings and occasionally 2, due logistic restraints, if the difference in angles was >30°. Triangulation was completed using 1:50,000 UTM, Zone 17 topographic maps. Elk were radio tracked during daylight hours from 2 hours after sunrise to 2 hours prior to sunset. Telemetry error was evaluated by placing dummy collars throughout the study area. Location error was 170m (SE ± 20.5m n=56). Mortality signals were investigated immediately upon change in pulse rate to determine cause of death. Cause of death was determined by the presence of predator sign (scat, tracks), external injuries and field necropsies were conducted when predation was not evident. Aerial surveys were flown twice a year in early winter and late winter using an EC 130 Ministry of Natural Resources (MNR) helicopter. GPS collar data were sub-sampled to retrieve 4 fixes per day separated by 6 hour intervals, thus retaining one fix per 24 hour period at 04:00, 10:00, 16:00 and 22:00 hours, respectively. Only fixes that had a positional dilution of precision of ≤ 5 and 3 dimensional vertical fix status were used in the analysis.

### *Spatial Analysis*

Annual home range sizes were calculated for each individual that had a sufficient number of relocations. To determine sufficient relocations, each individual home range size was calculated using a minimum convex polygon (MCP) (Mohr 1947) and bootstrapped using 100

iterations. Individual home range size estimates that did not reach an asymptote were discarded. Asymptotes were typically obtained between 25 and 50 radio locations for VHF collared elk. Fixed kernel home range size estimates were calculated for each elk that had sufficient relocations. Fixed kernel estimates with the least squares cross validation (LSCV) method were used to calculate the utilization distribution for 0.95, 0.9, 0.8, 0.7, 0.6, 0.5, 0.4, 0.3, 0.2, 0.1 probabilities to assess space use throughout the utilization distribution. MCP was because it is the oldest and most widely used estimate and it allows for comparison to older studies. Kernel estimates were also used because they are more accurate estimates in many situations. Sample sizes varied among individuals; however, evidence suggests that differences in home range size estimates are explained more by variance among individuals than by different home range estimation methods, once a sufficient number of relocations are obtained (Borger *et al.* 2006). Home range size was compared between elk occurring in high density to elk occurring in low density using an unpaired t test. Elk association was assessed using Assoc1 software in order to meet the assumptions of animal independence (Weber *et al.* 2001). Of the elk that were closely associated (within 200m, 70% of the time), only one was randomly selected for analysis.

### *Cluster Analysis*

Fuzzy clustering (Odeh *et al.* 1992) was used to assess the spatial organization of elk in my study area. Individuals used for cluster analysis required at least 7 months of data. I calculated the median easting and northing in the Universal Transverse Mercator coordinate system for each animal to perform the cluster analysis similar to Bethke (1996) and Schaefer *et al.* (2001). The median was chosen as the most appropriate measure of central tendency, because it is unbiased to non-normal distributions and not sensitive to outliers (Bethke 1996; Zar 1999). Applying Fuzzy c means clustering to a data set requires selecting a weighting exponent ( $m$ ),

which determines the degree of fuzziness applied to the membership coefficients. At  $m=1$ , the algorithm equates to a hard clustering analysis where membership is exclusive. Previous work has shown that  $m$  performs optimally from 1.5 to 3 (Bedzek *et al* 1984). I chose  $m = 2$  to obtain relative fuzzy classification. Results were investigated by varying  $m$  from 1.5 to 3 and consistent results were obtained across the spectrum. In order to determine the appropriate number of clusters, the average silhouette width of 2 to 15 clusters was calculated. The average silhouette width is a validation for cluster analysis and measures tightness and separation of each cluster (Rousseeuw 1987). Average silhouette width is maximized when the appropriate number of clusters is selected (Rousseeuw 1987).

Hard clustering was used for comparative purposes. I used hierarchical clustering (Ward's method) with Euclidean distance. Hard clustering evaluates clusters based on all or nothing, where members either are, or are not part of a cluster, as there is no graded membership assigned. I determined the appropriate number of clusters by comparing the sum of squared error for a number of cluster solutions and identified an elbow in the plot (Everitt and Hothorn 2009). The elbow in the plot indicates that additional clusters do not have a strong impact in reducing the sum of squared error. Results were displayed using a dendrogram. Hard and fuzzy cluster analysis was performed using the Cluster package in R (Maechler *et al.* 2013).

Based on the results of the cluster analysis, individuals were assigned to the cluster where they had the highest membership coefficient. All relocations of elk belonging to a cluster were pooled. Space use for each cluster was evaluated with a fixed kernel method for 95% and 50% (core) probabilities to visualize spatial distribution of the cluster using the smoothing parameter plugin in Geospatial Modeling of the Environment (Beyer 2012). The plugin smoothing parameter was used instead of LSCV because several elk were pooled resulting in large numbers

of relocations near boundaries and LSCV often fails to converge (Gitzen *et al.* 2006). The degree of overlap was calculated for clusters that had overlapping boundaries at the 95% level. Overlap was calculated using the “utilization distribution overlap index” (UDOI), because it also considers the probability of use in the estimation (Fieberg and Kochanny 2005). Measures of UDOI were calculated in R using “adehabitatHR” (Calange 2006). Distances among core use areas (50% fixed kernel) were calculated for each cluster and finite survival rates were calculated for each identified cluster.

## **Results**

From December 2011 to August 2013, 3143 VHF relocations were obtained from 36 individual elk. Individual elk relocation numbers ranged from 4 to 136. Of the 6 GPS collars, 5 experienced failure prior to the projected retrieval date. GPS collar activity ranged from 7 to 18 months.

### *Cluster Analysis*

Fuzzy c means clustering and hard clustering provided consistent groupings for elk spatial data. Both fuzzy and hard clustering resulted in 5 clusters (Figures 1.2 and 1.3). Average silhouette width was highest (0.7) for 5 clusters (Figure 1.2), indicating a good resolution into well-defined clusters (Figure 1.4). Average maximum membership coefficient for each animal was 0.76 and ranged from .61 to 0.98 (Table 1.1). The largest cluster consisted of 22 elk located in Burwash with an average silhouette width of 0.76. French River represented a cluster consisting of 4 animals with an average membership coefficient of 0.71. Raft Lake, an area immediately south of the City of Greater Sudbury, was a cluster containing 6 individuals with an average membership coefficient of 0.82. Another cluster was defined in Worthington with 2 elk,

approx. 30km west of the City of Greater Sudbury. The cluster with the lowest average silhouette width was Sled Lake, containing 7 individuals with an average membership coefficient of 0.61. This group appeared to be the most sporadic with subgroups located within the cluster. Aerial surveys confirmed this, as the locations of the members of this cluster were the hardest to predict. This was reflected in the more fuzzy classification of this cluster. Raft Lake and Sled Lake were the two subpopulations with the closest linkage distance (Figure 1.5).

Dispersal events between subpopulations were not frequently observed. Only one elk dispersed from one subpopulation to another during the course of the study. Elk 151.781 spent two winters with the Burwash subpopulation, but dispersed to the Worthington subpopulation in August 2013. Each subpopulation occupied spatially distinct areas (Figure 1.6). Elk in the Burwash subpopulation had range overlap with the Sled Lake subpopulation only during winter. Elk from Burwash and Sled Lake subpopulations were occasionally observed together in winter; however, members of the Burwash subpopulation moved south each spring with no spatial overlap in any other season. Members of the Sled Lake subpopulation were never found in the field complex. Only the French River subpopulation contained elk whose individual home ranges did not overlap with other members of the same subpopulation.

From December 2011 to August 2013, 9 mortality events were investigated. Wolf (*Canus lycaon*) predation and train collision were the most common sources of mortality (Table 1.2). The Burwash sub-population contained the largest number of animals and had the highest incidence of mortality, accounting for 55% of the detected mortality events. The most common cause of death in Burwash was train collision, accounting for 60% of the mortality events, followed by wolf predation (20%), and gunshot (20%). There is no open season for elk in this study area and the gunshot mortality was a case of mistaken identity by a hunter. Raft Lake, Sled

Lake and French River each had one wolf predation event. One elk in Sled Lake died of unknown causes. The unknown cause of death occurred 2 months after capture, so post capture myopathy was ruled out. Throughout the duration of the study there were several confirmed elk sightings outside of the current known elk distribution range (Figure 1.1). In October 2012, a young bull elk washed up on the shore of Badgley Island, west of Killarney, approx. 50km from the closest subpopulation. In February 2013 a young bull elk was photographed on a farmer's field in New Liskeard, approx. 150km northeast of any known elk subpopulation. Also, in February 2013, two cow elk were seen by the regional MNR biologist in Gogama, approx. 150km north of any known elk subpopulation. Hunters regularly report elk sightings and breeding activity (bugling) around Agnew Lake, approximately 30km west of the Worthington subpopulation. In August 2012 a young bull was photographed from the north shore population, one of the other release sites in Ontario, and had travelled over 80km to the town of Webwood, approximately 40km west of the Worthington subpopulation.

### *Space Use and Density*

The Burwash subpopulation had the highest density of elk, as determined by aerial surveys, and occupied the smallest range area with the exception of Worthington. Members of the Worthington group were collared in February 2013 and I obtained only 7 months of spatial data for those animals. High apparent density resulted from the limited space used by the 2 collared elk and limited time of observation. One of the elk was re-collared from the original release in 1999, and likely restricted its space use due to old age. Thus data from the Worthington subpopulation should be viewed with caution. Population density ranged across subpopulations from 0.05 elk/km<sup>2</sup> at French River to 0.88 elk/km<sup>2</sup> at Burwash (Table 1.3).



Out of the 5 subpopulations identified by the cluster analysis, 3 had population ranges with some degree of mutual overlap (Figure 1.6). The Sled Lake subpopulation range overlapped with the Raft Lake subpopulation to the north, and with the Burwash subpopulation to the south. The UDOI overlap for the Sled Lake subpopulation was greater for Raft Lake (0.39) than for Burwash (0.14). There was no overlap between 50% core use areas among any subpopulations. Distances between core use areas among subpopulations ranged from 11.1 to 58.1km (Table 1.4).

In order to compare individual home range sizes, elk in low density subpopulations were pooled because of low sample sizes. This resulted in the comparison of individual home ranges from the highly dense core, Burwash subpopulation with individual elk home ranges from lower density surrounding satellite subpopulations. Worthington was excluded from this analysis because they had less than one year of data. In total, 39 elk had a sufficient number of radio telemetry locations for home range analyses. Of the 39 elk, 22 belonged to the core (Burwash subpopulation) and 17 were pooled from surrounding satellite groups. Of the 17 elk from satellite groups, 4 were from the French River subpopulation, 6 were from Raft Lake and 7 were from Sled Lake. Space use was consistently larger for satellite subpopulations compared to the core (Burwash subpopulation) for MCP ( $P < 0.01$ ), 95% fixed kernel ( $P < 0.01$ ), 50% core use areas ( $P < 0.01$ ), and throughout the utilization distribution (Figures 1.7 and 1.8).

Average MCP home range estimate for elk from the Burwash subpopulation was 47.1 km<sup>2</sup> (SE = 4.3). Average MCP home range estimate for members of satellite groups was 74.6 km<sup>2</sup> (SE = 8.4; Figure 1.6). Average space use using the 95% fixed kernel method for core and satellite groups was 47.9 km<sup>2</sup> (SE=6.3) and 86.4 km<sup>2</sup> (SE = 13.3), respectively. Mean core use area estimates (50% fixed kernel) were 11.3 km<sup>2</sup> (SE = 1.6) and 21.5 km<sup>2</sup> (SE = 3.6) for core and

satellite groups, respectively. Space use was consistently larger across the utilization distribution for satellite individuals, as compared to those from the core (Figure 1.8).

## **Discussion**

I found strong evidence for the existence of an elk metapopulation in the study area. Both hard and fuzzy clustering methods found optimal solutions at 5 clusters. Of the different metapopulations described by Harrison (1991), elk in the Sudbury area appear to resemble the mainland-island structure, with an obvious core surrounded by smaller satellite groups. Interestingly, subpopulations surrounding the core were smaller in regards to numbers and density, but utilized a larger area. Similarly, individual space use by elk in the satellite subpopulations was significantly larger than for the members of the core subpopulation. Decreased space use and higher density in the core subpopulation may indicate higher habitat quality. The core subpopulation had an atypical habitat feature of 7.5 km<sup>2</sup> of abandoned farm fields from a former federal prison that elk actively selected (Chapter 2). In the studied elk population, there were no physical barriers among subpopulations and spatial structure could be regulated by density-dependent habitat selection (Morris 1989). My study was limited to mostly female spatial behaviour. Only 2 young males (both under 2.5 years of age) were radio-collared. Although in some populations young males are more likely to disperse (Greenwood 1980), both males remained in their designated subpopulations. It is possible that the metapopulation structure would be somewhat different if adult males were included in the analysis. The mating system in elk is characterized by mature bulls competing for harems of cows. Despite bull dominance over other males, movement patterns of calf:cow groups during the rut is primarily

dictated by one or more adult females. Subpopulation formation in elk may be driven by female spatial behaviour, as seen in caribou (Schaefer *et al.* 2001).

True metapopulation structures, following the original definition of Levins (1969), are rarely observed in natural populations (Harrison 1991). Variations described by Harrison (1991) are more commonly observed. The Tule elk (*Cervus elaphus spp. nannodes*), similar to other elk across North America, was almost hunted to extinction. The current population of Tule elk went through an extreme bottleneck, and has since been translocated into numerous areas across California (McCullough *et al.* 1996; Williams *et al.* 2004). A metapopulation of Tule elk in California has been created by translocation; however, natural metapopulations have been identified in restoration areas, specifically the Owens Valley population (McCullough *et al.* 1996). Most identified metapopulations have resulted from landscapes becoming highly fragmented (Wiegand *et al.* 2005; Cushman 2006). In central Ontario elk and the Tule elk example, metapopulations were established after translocation, demonstrating the utility of the metapopulation model also in the study of habitats that are not highly fragmented.

Metapopulations are not static regardless of the model they resemble. Metapopulation persistence is influenced by demographic, genetic and environmental stochasticity (Shaffer 1981), predation, competition (Levins 1974), habitat (Harrison 1991), and anthropogenic disturbances (Ehrlich and Ehrlich 1981). A great utility of applying graded membership within and among subpopulations is the potential for identifying underlying mechanisms related to dispersal and metapopulation dynamics (Schaefer and Wilson 2002). In my study, the duration and sample size were insufficient to identify meaningful demographic trends in any subpopulation. Longer term studies, however, may be able to use fuzzy clustering to monitor temporal changes in metapopulations. I found a strong 5 cluster solution; however, one cluster

(Sled Lake) had a higher degree of fuzziness associated with its cluster. With lower individual membership coefficients and the lowest average silhouette width, could mean different extinction and dispersal probabilities for this subpopulation. Individuals with a reduced maximum membership coefficient could also be more likely to disperse. Alternatively, the overall heterozygosity may be greater in subpopulations that have lower membership coefficients from reduced philopatry and possibly increased gene flow. Incorporating fuzzy analysis into metapopulation models could reveal deterministic cause-and-effect relationships. Intense monitoring of populations could relate changes in fuzzy clustering analysis to changes in population density, habitat alterations, and other influential factors. Recently, fuzzy clustering analysis has been applied in numerous locations to identify population structures of caribou (Schaefer *et al.* 2001; Schaefer and Wilson 2002; Courtois *et al.* 2007; Shuter and Rogers 2012; Schaefer and Mahoney 2013) and white tailed deer (Klaver *et al.* 2008). Here, I applied fuzzy clustering to elk for the first time to reveal population structure. The ability of fuzzy clustering to incorporate ambiguity among natural populations should make it a powerful tool for unraveling the dynamics and spatial structure of populations (Schaefer and Wilson 2002).

The probability of extinction in each subpopulation may vary and the studied elk population structure may also reflect possible source – sink dynamics (Pulliam 1988). The relatively high density of elk in Burwash, along with the atypical habitat (the abandoned field complex), may represent higher habitat quality, and thus a source. The lower densities of elk and increased space use of surrounding satellite subpopulations may reflect lower habitat qualities with some, possibly, representing sinks. Sinks can only be identified with long-term trends in reproductive success and dispersal rates. Using population density as an indicator of habitat quality, however, can be misleading (Van Horne 1983). Animal densities can be a misleading

indicator of habitat quality when estimates are not taken during the limiting season (e.g. winter), when multi-annual variability in a populations is caused by small scale variation in food abundance, and finally, when dominant individuals exclude subordinates from high quality habitats (Van Horne 1983). My estimates were derived from early and late winter aerial surveys, circumventing the first concern. Since all elk subpopulations were in relatively close proximity to one another, small scale changes in food abundance due to abiotic factors were likely to equally affect all subpopulations. Lastly, territorial behaviour is largely limited to prime bulls during the breeding season (late summer to early fall). The other possibility, however, is that higher density exists in Burwash because this is the location of one of the release sites. This is unlikely, because 2 additional release sites were located near Halifax Lake, approximately 14 km west of Burwash and elk from these release sites either dispersed to Burwash or outlying areas, and opted not to winter in the release area. If the surrounding subpopulations were identified as sinks, this would impact elk management decisions. Sink habitats are known to have high abundances of predators (Lloyd *et al.* 2005). In my study area, predation by wolves occurred in all elk subpopulations, indicating that predators were present throughout the area. Density of wolves among subpopulations may differ and would be interesting to evaluate.

Metapopulations and source-sink dynamics can be influenced by density-dependent habitat selection (Morris 1989). In my study, elk subpopulations may have been structured on the basis of density dependent habitat selection and the ideal free distribution. The ideal free distribution theorizes that individuals should distribute themselves across the landscape at all times in order to maximize their fitness (Fretwell and Lucas 1970; Fretwell 1972). As the core population density increases, individual reproductive success would be expected to decrease (Morrison 1989; Coulson *et al.* 1997). Elk may occupy lower quality habitats in surrounding

subpopulations without incurring any loss in fitness if they follow the ideal free distribution model.

A major issue in evaluating the spatial structure of a population is that it is scale sensitive (Thomas and Kunin 1999). Populations can exist on multiple scales and vagueness among them is the cornerstone to a more inclusive population concept (Schaefer 2006). I studied population structure at the local scale and scaling up would likely produce different results. There were four separate elk release areas in Ontario (Rosatte *et al.* 2007), separated by 200 km or more. Evaluating the population structure at a regional level may reduce the metapopulation structure in the Burwash/French River region into a single panmictic population. Determining the population structure throughout the province could provide insights into the success and status of elk. If elk were to establish metapopulations at a larger scale, it would have a positive impact on restoration of elk in Ontario. One of the essential requirements in metapopulation dynamics is the genetic connectivity among subpopulations (Levins 1969). If elk subpopulations showed even low levels of connectivity at a larger scale, it would enhance their genetic diversity and reduce extinction probabilities.

## **Conclusions and Management Implications**

Elk spatial distribution in the Sudbury area reflects a metapopulation structure. Subpopulations are spatially structured and dispersal between even the farthest separated subpopulations was observed. Because of the spatial structure, management decisions implemented in one subpopulation cannot be assumed to impact neighbouring subpopulations. The observed metapopulation structure is most similar to the mainland/islands metapopulation model. In metapopulation management, this would translate into differing conservation

priorities. The Burwash subpopulation was identified as an obvious core (and potential source) and thus, is most important to manage for the continued persistence of the metapopulation. Human-induced mortality was the greatest cause of reduced survival in the Burwash subpopulation. Therefore I recommend that mitigation of human-caused mortality in the core area be a priority. Understanding the whole metapopulation dynamics could also have important management implications. It is thus recommended that survival rates within each subpopulation be evaluated in order to determine whether smaller satellite subpopulations are indeed sinks, reliant on immigration from the source, or if they are self-sustaining at lower densities following the ideal free distribution theory. The metapopulations in the study area would benefit from monitoring of juvenile elk survival in each subpopulation to determine cause-specific mortality and dispersal. A metapopulation was found based on spatial data of elk, it would also be interesting to see if the same population structure is found using genetic samples for each identified subpopulation.

## Literature Cited

- Baguette, M., and N. Schtickzelle. 2003. Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *Journal of Applied Ecology* 40:404-412.
- Beier, P. 1996. Metapopulation models, tenacious tracking, and cougar conservation. Pages 293-324 in D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. Island Press, Covelo, California, USA.
- Berryman, A. A. 2002. Population: a central concept for ecology? *Oikos* 97:439-442.
- Bleich, V. C., J. D. Wehausen, R. R. Ramey, and J. L. Rechel. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353-373 in D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. Island Press, Covelo, California, USA.
- Bethke, R., M. Taylor, S. Amstrup, and F. Messier. 1996. Population delineation of polar bears using satellite collar data. *Ecological Applications* 6:311-317.
- Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.6.0.0). (software).
- Bezdek, J. C., R. Ehrlich, and W. Full. 1984. Fcm - the Fuzzy C-Means Clustering-Algorithm. *Computers & Geosciences* 10:191-203.
- Borger L., N. Franconi, G. D. Michele, A. Gantz, F. Meshci, A. Mancina, S. Lovari and T. Coulson 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*. 75:1393-1405.
- Brown, G.S. 1998. Spatial Behaviour and habitat utilization of wapiti (*Cervus elaphus*) in the French River and Burwash Regions of Ontario. MSc thesis School of graduate studies and research Laurentian University, Sudbury, Ontario.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516-519.
- Carrie, N. R., R. N. Conner, D. C. Rudolph, and D. K. Carrie. 1999. Reintroduction and Postrelease Movements of Red-Cockaded Woodpecker Groups in Eastern Texas. *The Journal of Wildlife Management* 63:824-832.
- Coulson, T., S. Albon, J. Pilkington, and T. Clutton-Brock. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. *Journal of Animal Ecology* 68:658-671.
- Courtois, R., J. P., Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience* 14:491-498.



- Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128:231-240.
- Edwards, M. A., J. A. Nagy, and A. E. Derocher. 2008. Using subpopulation structure for barren-ground grizzly bear management. *Ursus* (Knoxville) 19:91-104.
- Ehrlich, P. R., and A. H. Ehrlich. 1981. *Extinction: the causes and consequences of the disappearance of species*. New York, Random House.
- Environment Canada. 2013. Meteorological Service of Canada. , 2012. Atmospheric Environment Service, Environment Canada. [http://weather.gc.ca/canada\\_e.html](http://weather.gc.ca/canada_e.html)
- Everitt, B. S., and T. Hothorn. 2009. *A Handbook of Statistical Analyses Using R*. Chapman and Hall.
- Fieberg, J., and C. O. Kochanny. 2005. Quantifying Home-Range Overlap: The importance of the utilization distribution. *The Journal of Wildlife Management* 69:1346-1359.
- Fretwell, S. D. and H. L. Lucas. 1970. On terrestrial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-36.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University. Press, Princeton, NJ.
- Gilpin, M. 1996. Metapopulations and wildlife conservation: approaches to modelling spatial structure. Pages 11-28 in D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. Island Press, Covelo, California, USA.
- Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth Selection for Fixed-Kernel Analysis of Animal Utilization Distributions. *The Journal of Wildlife Management* 70:1334-1344.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140-1162.
- Gross, J. E., F. J. Singer, and M. E. Moses. 2000. Effects of disease, dispersal, and area on bighorn sheep restoration. *Restoration Ecology* 8:25-37.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41-49.
- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models, and observations. *Biological Journal of the Linnean Society* 42: 17-38.
- Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* 72:21-28.

- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3-16.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42:73-88.
- Hunter, M. D. 2002. Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology* 4:159-166.
- Jost, M.A., J. Hamr, F.F. Mallory. 1999. Forage selection by elk in habitats common to the French River – Burwash region of Ontario. *Canadian Journal of Zoology* 77: 1429-1438.
- Kamler, J. F., M. M. Gray, A. Oh, and D. W. Macdonald. 2013. Genetic structure, spatial organization, and dispersal in two populations of bat-eared foxes. *Ecology and Evolution* 3:2892-2902.
- Klaver, R. W., J. A. Jenks, C. S. Deperno and S. L. Griffin. 2008. Associating seasonal range characteristics with survival of female white-tailed deer. *The Journal of Wildlife Management* 72:343-353.
- Kurzejeski, E. W., and B. G. Root. 1988. Survival of reintroduced ruffed grouse in north Missouri. *The Journal of Wildlife Management* 52:248-252.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237-240.
- Levins, S., 1974. Dispersion and population interactions. *American Naturalist* 108: 207-228.
- Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecological Applications* 15: 1504-1514.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton: Princeton University Press.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K. 2013. *Cluster: Cluster Analysis Basics and Extensions*. R package version 1.14.4
- Martin, M. 2011. Spatial behavior and habitat use by elk (*Cervus elaphus*) in response to highway construction and interprovincial relocation. MSc thesis, School of Graduate Studies Laurentian University, Sudbury, Ontario.
- Mauritzen, M., A. E. Derocher, Å. Wiig, S. E. Belikov, A. N. Boltunov, E. Hansen, and G. W. Garner. 2002. Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. *Journal of Applied Ecology* 39:79-90.

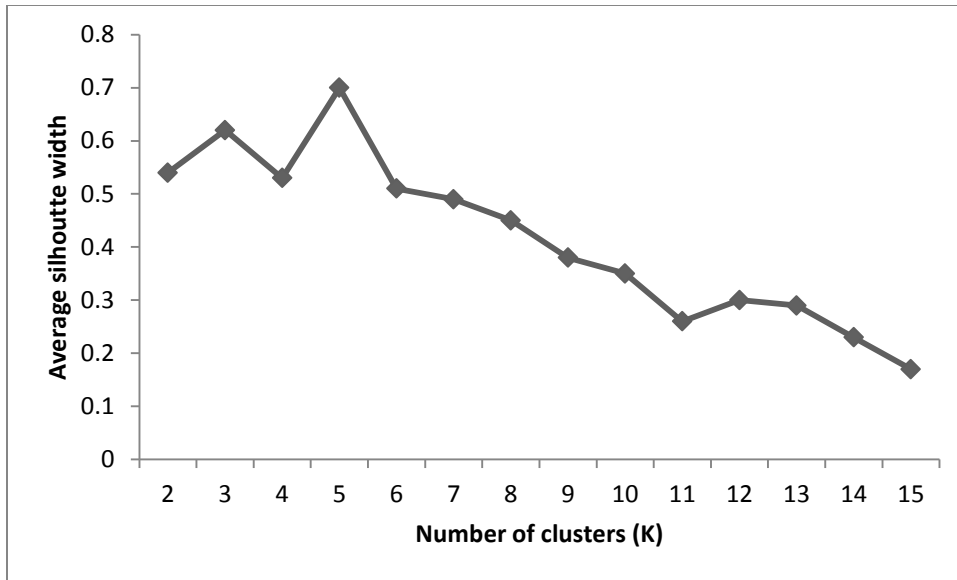
- McCullough, D. R., J. K. Fischer, and J. D. Ballou. 1996. From bottleneck to metapopulation: recovery of the tule elk in California. Pages 375-403 in D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. Island Press, Covelo, California, USA.
- McLoughlin, P. D., H. D. Cluff, R. J. Gau, R. Mulders, R. L. Case, and F. Messier. 2002. Population delineation of barren-ground grizzly bears in the central Canadian Arctic. *Wildlife Society Bulletin* 30:728-737.
- Metz, J. A. J., and M. Gyllenberg. 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268:499-508.
- Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37: 223-249.
- Morris, D. 1989. Density-dependent habitat selection: testing the theory with fitness data. *Evolutionary Ecology* 3:80-94.
- Odeh, I. O. A., D. J. Chittleborough, and A. B. McBratney. 1992. Soil pattern recognition with fuzzy-c-means: application to classification and soil-landform interrelationships. *Soil Science Society of America Journal* 56:505-516.
- Peel, M. C., B. L. Finlayson and T. A. McMahon. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11:1633-1644.
- Ranta, B. 1979. Range and habitat relationships of wapiti (*Cervus Canadensis*) in the Burwash-French River area of Ontario. M.Sc. Thesis, Carleton Univ., Ottawa.
- Richards, V. P., T. W. Greig, P. A. Fair, S. D. McCulloch, C. Politz, A. Natoli, C. A. Driscoll, A. R. Hoelzel, V. David, G. D. Bossart, and J. V. Lopez. 2013. Patterns of population structure for inshore bottlenose dolphins along the eastern United States. *Journal of Heredity* 104:765-778.
- Rousseeuw, P. J. 1987. Silhouettes - a Graphical Aid to the Interpretation and Validation of Cluster-Analysis. *Journal of Computational and Applied Mathematics* 20:53-65.
- Rosatte, R., J. Hamr, J. Young, I. Filion, and H. Smith. 2007. The Restoration of Elk (*Cervus elaphus*) in Ontario, Canada: 1998–2005. *Restoration Ecology* 15:34-43.
- Ryckman, M. J., R. C. Rosatte, T. McIntosh, J. Hamr, and D. Jenkins. 2010. Postrelease Dispersal of Reintroduced Elk (*Cervus elaphus*) in Ontario, Canada. *Restoration Ecology* 18:173-180.

- Schaefer, J. A., A. M. Veitch, F. H. Harrington, W. K. Brown, J. B. Theberge, and S. N. Luttich. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. *Oecologia* 126:507-514.
- Schaefer, J. A., and C. C. Wilson. 2002. The fuzzy structure of populations. *Canadian Journal of Zoology* 80:2235-2241.
- Schaefer, J. A. 2006. Towards maturation of the population concept. *Oikos* 112:236-240.
- Schaefer, J. A., and S. P. Mahoney. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. *Canadian Journal of Zoology* 91:767-774.
- Schaffer, M. L. 1981. Minimum population size for species conservation. *Bioscience* 31: 131-134.
- Shuter, J. L., and A. R. Rodgers. 2012. Delineating demographic units of woodland caribou (*Rangifer tarandus caribou*) in Ontario: cautions and insights. *Rangifer* 32: 159-182.
- Simberloff, D. 1995. Habitat fragmentation and population extinction of birds. *Ibis* 137: 105-111.
- Springer, J. T. 1979. Some sources and bias and sampling error in radio triangulation. *Journal of wildlife management* 54:169-174.
- Stith, B. M., J. W. Fitzpatrick, G. E. Woolfenden, and B. Pranty. 1996. Classification and conservation of metapopulations: a case study of the Florida scrub jay. Pages 187-215. *in* D. R. McCullough, editor. *Metapopulations and Wildlife Conservation*. Island Press, Covelo, California, USA.
- Tero, N., J. Aspi, P. Siikamäki, A. Jäkäläniemi, and J. Tuomi. 2003. Genetic structure and gene flow in a metapopulation of an endangered plant species, *Silene tatarica*. *Molecular Ecology* 12:2073-2085.
- Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68:647-657.
- Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zager. 1996. Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. *Conservation Biology* 10:547-553
- Weber, K. T., M. Burcham, and C. Les Marcum. 2001. Assessing independence of animal locations with association matrices. *Journal of Range Management* 54:21-24.
- Wiegand, T., E. Revilla and K. A. Moloney. 2005. Effects of habitat loss and fragmentation on population dynamics. *Conservation Biology* 19:108-121.

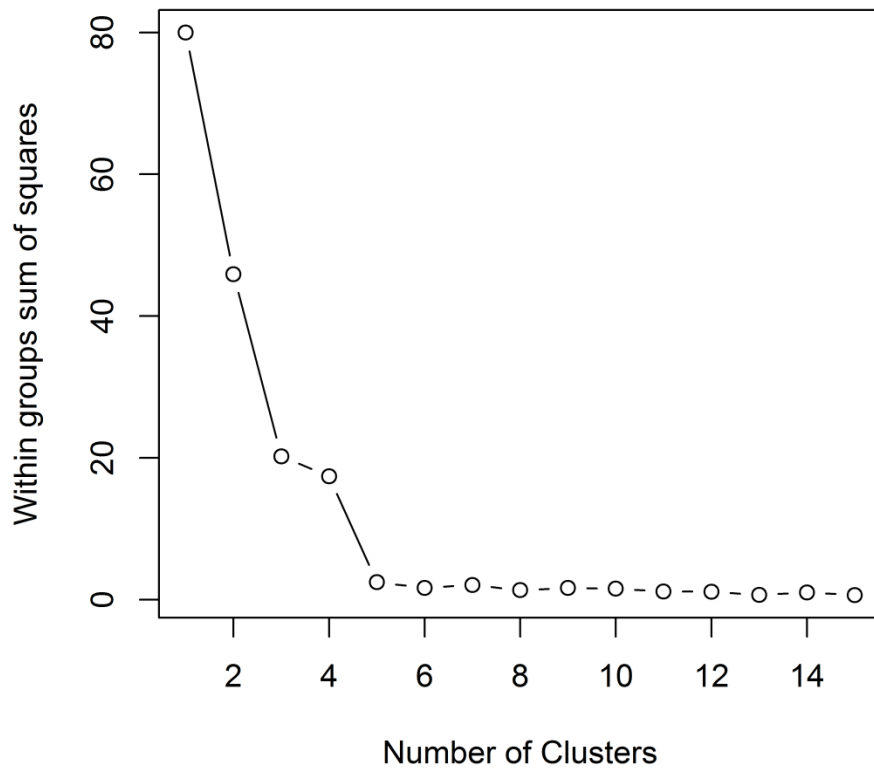
- Wiens, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics and management. Pages 53-84. *in* D. R. McCullough, editor. Metapopulations and Wildlife Conservation. Island Press, Covelo, California, USA.
- Williams, C. L., B. Lundrigan, and O. E. Rhodes Jr. 2004. Microsatellite DNA variation in Tule elk. *Journal of Wildlife Management* 68:109-119.
- Young, T. P. 2000. Restoration ecology and conservation biology. *Biological Conservation* 92:73-83.
- Yott, A., R. Rosatte, J. A. Schaefer, J. Hamr, and J. Fryxell. 2011. Movement and spread of a founding population of reintroduced elk (*Cervus elaphus*) in Ontario, Canada. *Restoration Ecology* 19:70-77.
- Zar, J. H. 1999. *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey, USA.



**Figure 1.1.** Elk range consisting of a minimum convex polygon around all elk radio locations and confirmed elk sightings.

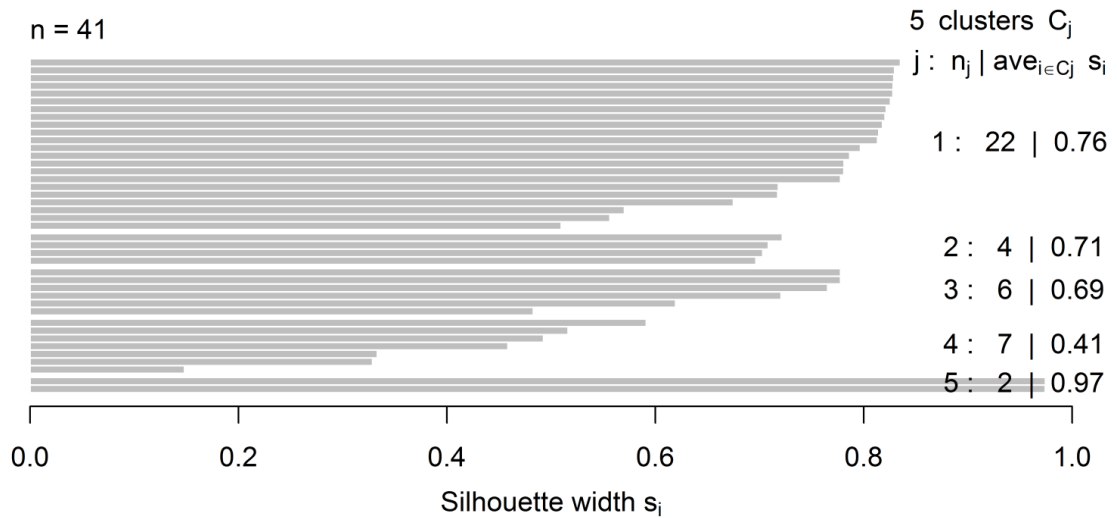


**Figure 1.2.** Average silhouette width for clusters 2 to 15 on spatial data for 41 elk in the Sudbury area. Appropriate number of clusters is defined when average silhouette width is maximized (K=5).

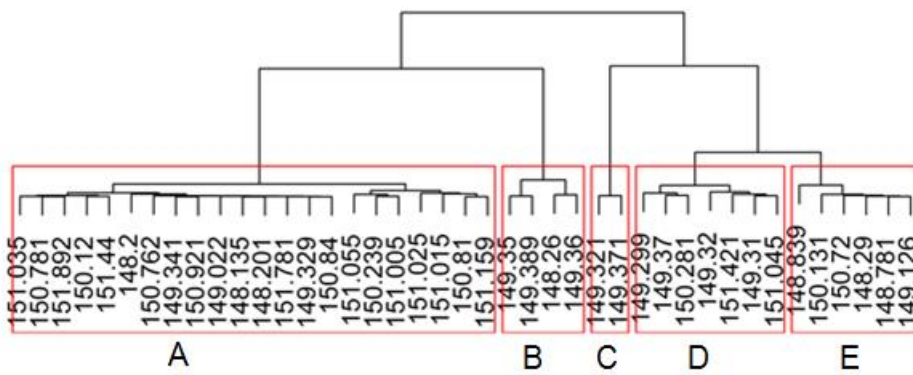


**Figure 1.3.** Within group sum of squares for clusters 2 to 15 using Ward's method. Appropriate number of clusters is indicated by a bend or elbow in plot ( $K=5$ ).

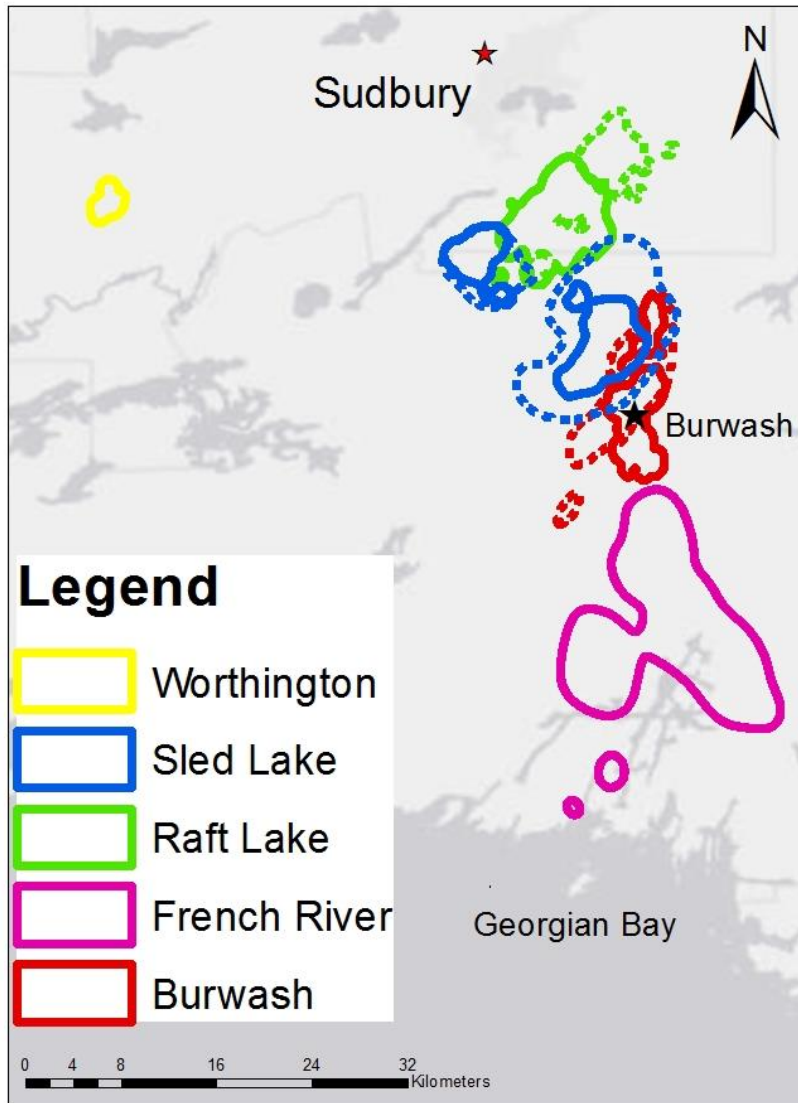




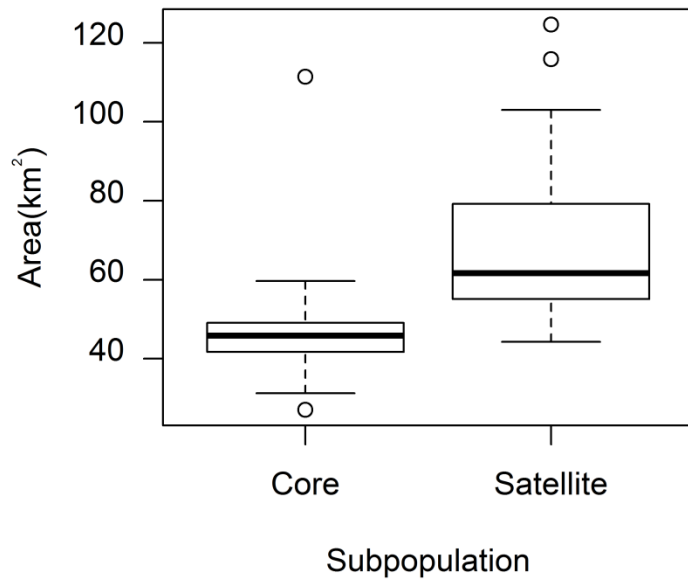
**Figure 1.4.** Silhouette plot for fuzzy membership coefficients of 41 elk in the Sudbury area. Plot is 5 clusters  $S_i$ = average silhouette width for each cluster 1:5. Cluster 1 = Burwash, cluster 2 = French River, cluster 3 = Raft Lake, cluster 4 = Sled Lake, cluster 5 = Worthington.



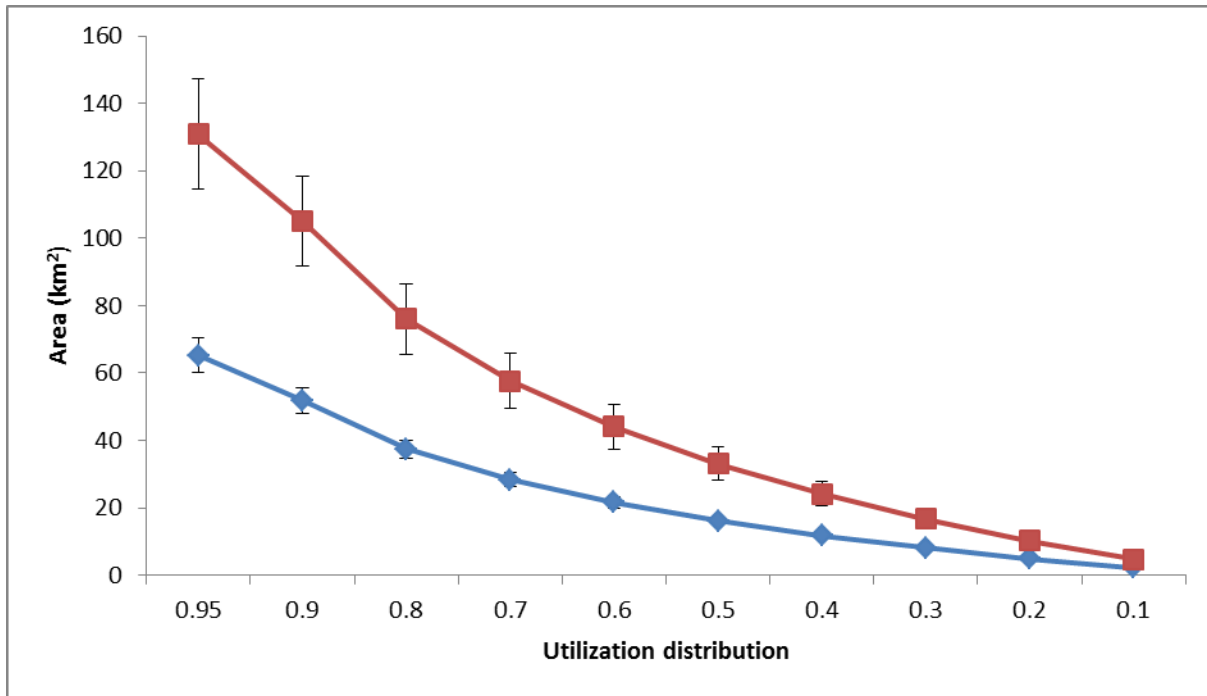
**Figure 1.5.** Cluster dendrogram of elk collar frequencies in the Sudbury area binned into a 5 cluster solution using hierarchical agglomerative clustering (Ward's method) based on Euclidean distance. A=Burwash, B= French River, C= Worthington, D= Sled Lake, E= Raft Lake.



**Figure 1.6.** Elk metapopulation structure in the Sudbury region. Solid lines represent pooled individuals that have a maximum fuzzy membership coefficient  $> 0.7$ . Dashed lines represent pooled individuals that have a maximum membership coefficient  $< 0.7$ . Subpopulation boundaries are delineated using 95% fixed kernel estimates and the Plugin smoothing parameter.



**Figure 1.7.** Boxplot showing home range size estimates (MCP) for elk belonging to core and satellite groups. Difference was significant with and without outliers ( $P < 0.05$ ). Error bars represent range of values and circles represent outliers.



**Figure 1.8.** Elk space use across the utilization distribution for core and satellite subgroups in the Sudbury area. Bars represent standard error of the mean. Diamonds represent the core subpopulation and squares represent the satellite groups.

**Table 1.1.** Average maximum fuzzy membership coefficients for 5 subpopulations of elk in the Sudbury area. SE = standard error of the mean, N= number of elk assigned to cluster.

Subpopulation	Mean (SE)	Min	Max	N
Burwash	77.6 (3.2)	47	92	22
French River	75.8 (3.0)	70	81	4
Raft Lake	82.3 (7.1)	48	94	6
Sled Lake	61.2 (4.5)	43	76	7
Worthington	98 (0)	98	98	2

**Table 1.2.** Cause-specific mortality events for 4 subpopulations of radio collared elk in the Sudbury region in 2012/2013.

Cause of Mortality	Number of Cases	Year	Subpopulation
Wolf predation	4	2012/2013	Burwash (1), French River (1), Sled Lake (1), Raft Lake (1)
Train collision	3	2013	Burwash (3)
Gunshot	1	2012	Burwash (1)
Unknown	1	2012	Sled Lake (1)
Total	9		Burwash (5), French River (1), Sled Lake (1), Raft Lake (1)

**Table 1.3.** Elk density and survival rate among the 5 subpopulations in the Sudbury area.

Subpopulation	Density elk/km <sup>2</sup>	SE	Survival rate
Worthington	0.51	0.21	N/A
Sled	0.22	0.05	0.71
Raft	0.17	0.03	0.83
French	0.05	0.01	0.75
Burwash	0.88	0.06	0.78

\*N/A – survival rate not available



**Table 1.4.** Distance (km) between core use areas (50% fixed kernel) of 5 subpopulations identified for elk in the Sudbury area.

	Burwash	French River	Sled Lake	Raft Lake
Burwash				
French River	17.8			
Sled Lake	11.1	28.4		
Raft Lake	18.3	39.2	11.6	
Worthington	47.2	58.1	36.9	39.5

## **Chapter 2: Seasonal space use and diel patterns of resource selection by elk (*Cervus elaphus*) in central Ontario**

### **Introduction**

Understanding animal space use and resource selection is fundamental to management decisions and land use practices in conservation and wildlife management. Resource selection is firmly rooted in the theory of natural selection and will favour animals that utilize resources that differentially increase their fitness relative to their conspecifics (Manly 1985). Understanding resources critical to a particular species is essential for increasing our knowledge of factors driving ecological processes. Typically, no one resource or habitat can satisfy all the needs of an animal, and therefore different resources may be used for different activities or during different seasons (Manly 2002; Boyce 2006; Moe *et al.* 2007; Godvik *et al.* 2009). A common trade-off in ecology exists when high quality forage exists in habitats that may have a higher risk of predation. Therefore animals must make a decision between secure resting locations with low food availability and high quality food patches in riskier environments (Myrsterud and Ims 1998). Resource selection is a dynamic process and is influenced by a variety of factors including predation (Creel *et al.* 2005), population density (van Beest *et al.* 2013a), food availability (Johnson and Sherry 2001), anthropogenic disturbances (Sawyer *et al.* 2006) and spatial and temporal scales (Beyer and Haufler 1994; Boyce *et al.* 2003).

Space use is a function of an animal's ability to meet all of its energetic and reproductive requirements and can be affected by seasonal distribution of resources (Luccarini *et al.* 2006). Space use by animals was first formally described by Burt (1947), who defined a home range as the area normally traversed by an individual while foraging, mating and rearing young. Useful

additions to the definition of home range include a defined probability of locating the animal, as well as a specified time period (i.e. multi-annual home range, annual home range and seasonal home range; Kernohan *et al.* 2001). Spatial behaviour of an animal is influenced by numerous factors including body mass, sex and age (Myserud *et al.* 2001), forage availability (Anderson *et al.* 2005) and predation (Gower *et al.* 2008).

Resource selection is now commonly evaluated using resource selection functions (RSFs) (Boyce and McDonald 1999; Boyce *et al.* 2002). A RSF is defined as any function that is proportional to the probability of a resource unit being used (Manly *et al.* 2002). In order to determine resource selection, used resources are compared to unused (used/unused design) or are compared to resources assumed to be available (use/available design) (Manly *et al.* 2002). When resources are used disproportionately to their availability, use is thought to be selective (Johnson 1980). A hierarchy in resource selection exists, starting with the geographic range of a species (1<sup>st</sup> order selection), selection of a home range within the geographic range (2<sup>nd</sup> order selection), selection of resources within the home range (3<sup>rd</sup> order selection) and finally the procurement of a food item at a feeding station (4<sup>th</sup> order selection) (Johnson 1980). There are 3 study designs that can assess resource selection in wildlife populations summarized by Thomas and Taylor (1990). Design 1 assesses selection at the population level where used resources are compared to those available across an entire study area. In Design 1, individuals are not identified and selection is assumed to be equal among all individuals within the population. Design 2 identifies individual resource use from marked individuals in the population, but availability is assumed to be the same for all individuals. Design 3 is similar to design 2, except that resource availability is measured separately for each individual.

Several researchers have focused on spatial scales in resource selection (Schaefer and Messier 1995; Rettie and Messier 2000; Boyce *et al.* 2003; McLoughlin *et al.* 2004; Beasley *et al.* 2006; Ciarniello *et al.* 2007a). However, few studies have addressed the effect of temporal scales on resource selection despite time being more influential on resource availability in many circumstances (Fahrig 1992). Selection can change when availability of resources increases or decreases, creating a functional response or variation based on trade-offs between activities such as foraging and resting (Myysterud and Ims 1998). Animals require different resources for such activities and considering these activities occur on a daily basis, determining resource selection across the diel period should reveal novel insights into animal resource requirements. Research has found changes in resource selection based on time of day in cervids (Bier and McCullough; Beyer and Haufler 1994; Godvik *et al.* 2009), bears (Moe *et al.* 2007) and carnivores (Onorato *et al.* 2011). Changes in resource selection are expected with changing availability of resources, requiring study duration to be as short as possible (Manly *et al.* 2002). Seasonal changes in availability of resources have resulted in RSFs separated by this temporal scale (Boyce 2006). Trade-offs associated with a finer temporal scale based on the time of day are important and often overlooked (Mayor *et al.* 2009).

Research assessing the effects of temporal changes on resource selection are lacking compared to studies assessing the effects of spatial scales. It has been well established that selection varies across spatial scales; however, less is known about the variation in selection within a single scale across the diel period. Currently, resource selection data are used to guide management and conservation decisions regarding land use practices and are based on sampling methods using only daytime sampling of animals. In this study I assessed the temporal effects of resource selection and space use during four seasons across the diel period in a large herbivore,

the North American elk (*Cervus elaphus*). I hypothesized that resource selection would differ throughout the diel period because of trade-offs associated with foraging and resting behaviours. Thus I predicted that high quality open foraging areas would be utilized primarily during nocturnal hours, while sheltered, forested areas would be selected during the day. I also tested the hypothesis that seasonal space use would be inversely related to food availability. I predicted that space use and daily movements would be larger in winter due to reduced food availability and smallest during summer when food availability is greater.

## **Methods**

### *Study population*

I studied a reintroduced population of elk in central Ontario. Elk were reintroduced from Elk Island National Park from 1998 to 2001. In my study area, 172 elk were reintroduced over a four year period (Rosatte *et al.* 2007). Now acclimatized to their environment, elk have changed from exploratory to home ranging behaviour (Martin 2011). The current population size estimate is 180-200 animals (Joe Hamr pers comm).

### *Study Area*

The study was conducted in Burwash, Ontario (46° 14' 34.894" N, 80° 51' 10.454" W) located 48km south of the City of Greater Sudbury. The study area is located in the Great Lakes St. Lawrence eco-region, a transitional mixed wood zone between the boreal forest to the north and the Carolinian forest to the south. The area consists mainly of conifer and hardwoods in a mixed heterogeneous forest. Common tree species include white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), largetooth aspen (*Populus grandidentata*), trembling aspen (*Populus*

*tremuloides*), white birch (*Betula papyrifera*), red oak (*Quercus rubra*) and red maple (*Acer rubrum*). Common understory species include blue bead lily (*Clintonia borealis*), lily of the valley (*Mianthemum canadense*), bush honey suckle (*Diervilla lonicera*), bunchberry (*Cornus canadensis*), starflower (*Trientalis borealis*), trout lily (*Erythronium americanum*) and false Solomon's seal (*Mianthemum racemosum*). The climate is continental, cold with warm summers and no dry season (Peel *et al.* 2007). Snow accumulates from November through March. In the winter of 2012, snow accumulation from the Sudbury airport measured 250.4cm (Environment Canada 2012). An early spring led to a fast melt and the area was snow free by March 16. The winter of 2013 had similar snow accumulation of 248.7cm (Environment Canada 2013); however, below average spring temperatures caused the onset of the snow-free period to be delayed until April 26. Snow depth frequently exceeds 60cm from onsite measurements. The area has numerous granite ridges with elevations ranging from 200m – 270m above sea level. The average elevation throughout the study area is 228m above sea level. The study area is bordered by a major 400 series highway to the east with newly installed wildlife fencing and wildlife over and underpasses. A CN railway runs from north to south through the study area. The study area is dominated by forests (63%), interspersed with numerous wetlands (5%). A unique feature of this area is the persistence of large open grassland habitats (12%, approx. 7.5km<sup>2</sup>), remnant from an industrial prison farm operational from 1914 to 1973. The eastern half of the property has been transferred to the Department of National Defence (DND) which currently uses the area for training. A very small amount of logging has occurred in the study area (3%). The study area supports healthy populations of both moose (*Alces alces*) and white tailed deer (*Odocoileus virginianus*). The predator assemblage is rich and diverse including black

bear (*Ursus americanus*), gray wolf (*Canis lupus*), eastern wolf (*Canis lycaon*), coyote (*Canis latrans*), lynx (*Lynx canadensis*) and bobcat (*Lynx rufus*).

### *Animal Capture/ Monitoring*

Elk were captured aerially by net guns fired from helicopters. Captured animals were fitted with a cattle ear tag to facilitate identification of individuals. Six females were fitted with GPS Iridium (Lotek wireless Newmarket, ON) collars, programmed to take a fix every hour for 2 years. Three adult female and two male (2.5 years old) were fitted with VHF radio collars (LMRT, Lotek wireless Newmarket, ON). Animal capture was approved by animal care protocol # 2012-01-01 at Laurentian University. In addition, 13 female elk with functioning VHF collars were already present in the study area (Popp *et al.* 2013). VHF collared individuals were radio-tracked weekly during the day and at night. Day was defined as the interval from at least one hour post sunrise to one hour prior to sunset. Night was defined as the period between one hour post sunset to one hour before sunrise. Elk were tracked using standard telemetry techniques (White and Garrott 1990). Locations were estimated through triangulation with a standard H or a Yagi 3 element antenna using a Lotek SRX 400 telemetry receiver or a bio tracker receiver (FW9Biotracker). Three bearings were used to accurately estimate an animal's position on most occasions; however, due to logistic constraints, only 2 bearings were used if the difference in angles was  $> 30^\circ$ . Locations were triangulated on a topographic map scale 1:25 000 UTM Zone 17T. Location estimates encompassed all field conditions during both day and night, as well as leaf-on and leaf-off periods throughout all seasons. Error was evaluated by placing dummy collars throughout the study area in locations frequented by elk. Location error was 170m (SE  $\pm$  20.5m n=56).

GPS collars were screened for accuracy using Positional Dilution of Precision (PDOP) error estimates and vertical fix status. Only those that acquired a 3 dimensional vertical fix were included in the analysis. In order to obtain precise location estimates, I retained fixes with a PDOP of  $\leq 5$ , reducing mean error to 9m (D'Eon *et al.* 2002). One issue often encountered in telemetry studies is the duration of time between subsequent fixes. Intervals too short in time may not allow successive locations to be treated as independent, a common assumption for most habitat selection analyses (Erickson *et al.* 2001). Intervals recorded too far apart yield a low number of samples for the study, making inferences about populations difficult. Current GPS technology allows for the collection of large amounts of data and in order to meet independence, some studies would need to discard over 90% of the data, which is unrealistic. Multiple locations obtained per day from GPS collars are frequently used in analyses (Sawyer *et al.* 2007; Proffitt *et al.* 2010; Meisingset *et al.* 2013). In order retain as much GPS information as possible; I used 4 fixes per day separated by 6 hour intervals. One fix was kept for hours 04:00, 10:00, 16:00 and 22:00 each day. This allowed for 2 fixes per day and 2 fixes per night periods each day. Both VHF and GPS locations were visually screened in Arc GIS to ensure each location was plausible. To identify closely-associated individuals, association coefficients were calculated for each elk in the study area using Assoc1 software based on a temporal association of 70% and a spatial association of 200m (Weber *et al.* 2001). If two or more individuals were found to be associated, one was randomly selected to be retained for analysis.

### *Seasonal Space Use*

Seasonal home ranges were delineated for each individual with at least 10 radio telemetry points during a given season (Courtois *et al.* 2007); however, most elk had >25 relocations per season. Seasons were delineated based on elk behaviour following Popp *et al.* (2013): winter (1



January-31 March), spring (1 April-30 June), summer (1 July-30 September) and fall (1 October-30 December). Individuals with seasonal home ranges for consecutive seasons (i.e. spring 2012 and spring 2013) were averaged. Differences in seasonal space use were assessed using the conventional minimum convex polygon (MCP) (Mohr 1947) and fixed kernel methods (Seaman and Powell 1996), using the Least Squares Cross Validation smoothing parameter to identify 95% and 50% (core) utilization distributions. MCP home range estimates were computed using Geospatial Modelling of the Environment (Beyer 2012). Kernel estimates were computed using R package *adehabitatHR* (Calenge 2006). Differences in space use between seasons were assessed using a linear mixed model with individual elk as a random effect in the R package *nlme* (Pinheiro *et al.* 2013).

### *Seasonal Movements*

Seasonal movements were calculated for the 6 elk outfitted with GPS iridium collars and organized in to 4 seasons as previously described. Daily movements were determined by calculating consecutive step lengths for all relocations and summed for a 24 hour period. Movements across the diel period were assessed for each season. Step lengths consisted of straight line distances between two consecutive fixes and were calculated for each elk for each hour over each 24 hour period. Movements across the diel period were categorized into previously described seasons in order to identify daily activity bouts. Only fixes with hourly intervals were used for step length calculations and time periods where data was censored were removed from analysis. Step lengths were averaged for each individual for each season for each 24 hour period and then averaged across individuals. Differences in daily movements between seasons were assessed using a linear mixed model and Tukey's post-hoc test to determine differences between the means

## Resource Selection

Habitat cover types were derived from the Ontario Ministry of Natural Resources (OMNR) Forest Resources Inventory (FRI) maps (2010). The original classification categorized 9 different polygon types; 1) brush and alder (areas containing “noncommercial” tree species or shrubs typically associated with poorly drained sites dominated by speckled alder (*Alnus incana* ssp. *rugosa*)), 2) developed agricultural land (lands which are cultivated for growing crops and abandoned agricultural lands), 3) grass and meadow (farm areas devoted to pasture for domesticated animals including abandoned grass and meadows), 4) open wetland (wet open areas containing mosses, grasses, sedges and small herbaceous plants), 5) rock (areas of barren or exposed rock supporting less than 25% scattered trees), 6) treed wetland (areas of dry or wet muskeg with widely spaced stunted trees), 7) unclassified areas (manmade non-forested areas, including utility corridors and gravel pits, mostly cleared of trees), 8) water (all water areas including lakes, ponds, reservoirs, streams and rivers) and 9) forest (forested areas capable of producing trees and supporting tree growth). Forest types were further broken down into 6 discrete forest types; lowland conifer (dominated by black spruce on poorly drained soils), conifer upland (mixed spruce, jack pine and fir stands on upland sites), Great Lakes St. Lawrence pines (white and red pine dominated stands), intolerant hardwoods (forest stands consisting primarily of trembling aspen, white birch, and balsam poplar (*Populus balsamifera*)), tolerant hardwoods (primarily maple) and upland mixed (mixed forest stands primarily spruce, jack pine, balsam fir and poplar). A small amount of logging has occurred in the area over the past 10 years. An updated GIS layer of logging activity in the area was obtained from the local forestry company (Vermillion Forest Management Ltd). A layer called CCUT was created for the logging activities in the last 10 years. Of the 9 originally classified polygon types, 4 were retained for

habitat analyses and 6 were added. Water, open wetland and treed wetland were removed because they had not been found to be important to elk or, because elk rarely used these habitats causing perfect or near perfect separation in the model. Developed agricultural land was combined with grassland habitats and forest was broken down into forest structure type. Conifer lowlands were removed because they rarely occurred in the study area. This resulted in 10 available habitat types; 1) brush and alder (BSH, 6%), 2) recently logged areas (CCUT 3%), 3) Great Lakes St. Lawrence Pines (GL\_PINE 7%), 4) conifer upland (coniferU 3%), 5) intolerant hardwoods (Intol\_H 38%), 6) tolerant hardwood (Tol\_H 5%), 7) upland mixed (UP\_M 13%), 8) grass and meadow (GRS 12%), 9) rock (RCK 4%) and 10) unclassified (UCL 3%).

Additional factors known to be important to elk (elevation, aspect, slope, distance to roads and distance to water), were also included in resource selection models. Elevation was obtained from a Digital Elevation Map (DEM) (OMNR 2006). Using Arc GIS v 10.0, DEM was transformed into a slope map in degrees and an aspect map ranging from 1 to 360°. Because of the issue of circular data (1 and 360 are extremes on the number scale but both represent a northern aspect), data were transformed using trigonometric functions as described by Zar (1999). The sine function was used to create a variable “eastness”, where numbers close to 1 represent eastern aspects and numbers close to -1 represented western aspects. The sine of angles 0° and 180° are 0 and angles < 180 are positive while angles > 180° are negative. Similarly, cosine of the angle was used to create a continuous variable for “northness”. The cosine of angles 90° and 270° = 0, and is positive for angles 0° < a < 90° and for 270° < a < 360°. The cosine is negative for angles between 90° and 270°. Values close to 1 represent northern aspects while values close to -1 represent southern aspects. Distance to roads and distance to water were calculated using the proximity tool in Arc GIS.

Seasonal resource selection was evaluated using resource selection functions (RSF; Manly *et al.* 2002). RSFs are attractive because they are capable of including both continuous and categorical variables. RSF models were calculated using logistic regression fitted with the logit function in the R package lme4 (Bates *et al.* 2013). A set of 20 candidate models was developed *a priori* based on resources known to be important to elk (Table 2.1; Brown 1998; Boyce *et al.* 2003; Anderson *et al.* 2005; Sawyer *et al.* 2007; Proffitt *et al.* 2010). Akaike information criteria (AIC<sub>c</sub>) for small sample sizes were used to rank models (Burnham and Anderson 2002). A generalized linear mixed model (GLMM) was used with individual elk included as a random effect in order to account for individual variation in sample size (equation 1) (Gilles *et al.* 2006). Therefore the RSF took the form:

$$g(x) = \ln \left[ \frac{\pi(x)}{1-\pi(x)} \right] = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \dots + \beta_n x_{nij} + \gamma_{0j} \quad \text{eqn (1)}$$

where  $x_n$  are covariates with fixed regression coefficients  $\beta_n$ ,  $\beta_0$  is the mean intercept, and  $\gamma_{0j}$  is the random intercept (random effect), equal to the difference between the mean intercept  $\beta_0$  for all groups and the intercept for group  $j$ .

RSF models were calculated for each season and separately for day and night resulting in 8 top models being selected out of 160 candidate models. Pearson correlation matrices were calculated for all continuous variables. Any variables that were moderately correlated (>0.5) were not included in the same model. All statistics were performed using R (R core team 2012). Resource availability was measured differently for VHF and GPS collared individuals. Because VHF fixes were separated by a longer time interval (up to one week), it was assumed that the entire home range was available between each subsequent fix. This was validated by the daily movement patterns of GPS collared elk. For each VHF relocation, 5 random locations were

generated within the 100% MCP, to assess availability. Availability and use were measured separately for each individual elk resulting in a Design 3, 3<sup>rd</sup> order selection study design (Johnson 1980). Thus, each individual elk had different resources available but it was the same for each season. Because the GPS collar fixes were separated by 6 hour intervals, the entire home range of the animal was not realistically available because an individual could not traverse its whole home range in 6 hours. To account for this, I used a similar approach to that of Arthur *et al.* (1996). Because movement rates change with time of day (Ager *et al.* 2003), a circular buffer equal to the 95 percentile of movements for GPS collared elk of that time interval was centered on the previous time interval to measure availability (i.e. for the 10:00 fix, availability was measured by placing a circular buffer around the 04:00 fix, equal to the 95<sup>th</sup> percentile of distance moved by GPS collared elk from 04:00 to 10:00). Within each buffer, 5 random points were generated. This design is not considered to be case control because availability was measured by how much the animal was capable of moving and not by how much the animal had actually moved.

## **Results**

From December 2011 to September 2013, 2183 VHF relocations were obtained for 18 individuals. Number of fixes per individual ranged from 4 to 154 with a mean of 114 (SE = 9.24). Of the 6 GPS collars deployed, 1 animal was not part of the Burwash subpopulation and was not used in the analysis of space use or resource selection. All of the 5 remaining GPS collars experienced collar malfunction; 2 collars were active for 168 and 198 days respectively, and the 2 longest lasting collars were functional for 527 and 533 days respectively. One GPS

collar retrieved from a dead elk was redeployed, replacing a failed collar but lasted only another 75 days. Mean fix success was high at 98.5%, and GPS screening for accurate fixes resulted in removal of 8% of the data. After the GPS data were sub-setted for 4 fixes per day separated by 6 hour intervals, the number of usable fixes per collar ranged from 521 to 1465 with a mean of 1009 (SE = 173.76).

Over the course of the study, 5 mortality events of collared animals were investigated. In the winter of 2013, 3 elk were killed by train collisions, 1 elk was accidentally shot by a deer hunter in November 2012, and 1 elk was killed by wolves in February 2012.

### *Seasonal Space Use*

Elk did not display typical migratory behaviour characterized by summer and winter ranges separated by long distances. Elk did display semi-migratory behaviour; during mid-winter they moved to the northern part of their range and utilized areas not visited during the summer. Elk movements appeared to be dependent on snow depth. When grazing was limited by deep snow, elk moved to parts of their home range characterized by higher elevations. The distance travelled was short (approx. 3km), but led to the use of distinct areas not used in the absence of snow. Space use differed among seasons for MCP ( $F_{3, 57} = 10.17$ ,  $P < .0001$ ) and 95% utilization distributions ( $F_{3, 57} = 3.99$ ,  $P < 0.01$ ) but no difference was found in the size of core use areas among seasons ( $F_{3, 57} = 1.87$ ,  $P = 0.11$ ). For MCP home range estimates, summer space use was significantly less than winter ( $P < 0.01$ ), spring ( $P < 0.001$ ) and fall ( $P < 0.001$ ) (Figure 2.1). Summer space use was only significantly smaller than spring ( $P < 0.01$ ), using the 95% fixed kernel estimates. For all 3 space use estimates, summer utilization distributions were the smallest, while spring were the largest. Winter space use in 2012 was significantly larger than in

the winter of 2013 ( $F_{1, 12} = 18.75$ ,  $P < 0.001$ ). There was no significant difference in space use between spring 2012 and spring 2013 ( $F_{1, 11} = 3.17925$ ,  $P = 0.1022$ ) or between summer 2012 and summer 2013 ( $F_{1, 14} = 0.30130$ ,  $P = 0.5917$ ).

### *Daily Movements*

Daily movements were greatest in spring ( $\bar{x} = 3412.64\text{m/day}$ ,  $SE = 308.71$ ), smallest during winter ( $\bar{x} = 1606.79\text{m/day}$ ,  $SE = 142.80$ ) and differed significantly among seasons ( $F_{3, 11} = 27.2697$ ,  $P < 0.0001$ ). Winter daily movements were significantly lower than those in summer ( $P < 0.0001$ ), spring ( $P < 0.0001$ ), and fall ( $P < 0.0001$ ). Elk daily movements remained relatively consistent across spring summer and fall seasons (Figure 2.2).

Elk displayed strong crepuscular movement patterns throughout the diel period in all seasons with peaks in movement associated with dawn and dusk (Figure 2.3). Elk displayed crepuscular activity in winter, but the magnitude of movements was smaller in comparison to spring, summer and fall. Spring movements peaked at 08:00 hours ( $\bar{x} = 279.20\text{m/h}$ ,  $SE = 37.33$ ) and again at 21:00 hours ( $\bar{x} = 337.83\text{m/h}$ ,  $SE = 40.41$ ). Hourly movements reached their lowest levels in mid-day at 12:00 ( $\bar{x} = 76.55\text{m/h}$ ,  $SE = 19.54$ ). During summer, elk movements peaked again at 08:00 hours ( $\bar{x} = 302.46\text{m/h}$ ,  $SE = 44.36$ ) and 21:00 hours ( $\bar{x} = 267.66\text{m/h}$ ,  $SE = 42.12$ ), and lowest movement rates were recorded at 13:00 hours ( $\bar{x} = 52.79\text{m/h}$ ,  $SE = 11.85$ ). Fall hourly movement rates peaked at 09:00 hours ( $\bar{x} = 286.28\text{m/h}$ ,  $SE = 36.70$ ) and at 19:00 hours ( $\bar{x} = 235.41\text{m/h}$ ,  $SE = 49.09$ ). Hourly movements reached their lowest rate during fall at 13:00 hours ( $\bar{x} = 47.76\text{m/h}$ ,  $SE = 12.59$ ). During winter, elk movements peaked at 09:00 hours ( $\bar{x} = 117.18\text{m/h}$ ,  $SE = 14.81$ ) and at 18:00 hours ( $\bar{x} = 100.01\text{m/h}$ ,  $SE = 13.58$ ). Lowest movement rates in winter across the diel period occurred at 05:00 hours ( $\bar{x} = 34.30\text{m/h}$ ,  $SE = 6.01$ ).

## *Resource Selection*

### *Spring*

The two top RSF models for spring during the day included distance to water, habitat and northness, distance to roads and habitat as important covariates. Day spring habitats selected by elk were recently logged areas and intolerant hardwood forests. Compared to the reference category, most habitat types were used less than available. Elk selected southern aspects, avoided water and avoided habitats close to roads. The top RSF models for spring during the night were models 1 and 15 accounting for 0.46 and 0.36 of the model weight, respectively (Table 2.2). The top model indicated strong selection for steep slopes with eastern and southern aspects during the night (Table 2.3). Similarly to daytime resource use, elk avoided areas close to roads and close to water at night. Most habitat types were found to be significant in the model, except for conifer upland and tolerant hardwoods. Grassland habitats were the most highly selected habitat type, followed by recently logged areas, unclassified lands and rock. Conifer upland had a positive  $\beta$  coefficient; however, it was not significantly selected. Brush and alder habitats were strongly avoided, as were most of the other forest types (Table 2.3)

### *Summer*

The top summer RSF model during the day carried 0.69 of the model weight (Table 2.4). During the day in summer, elk selected higher elevations on plateau's. The only habitat type significantly selected compared to the reference category was the recently logged areas. The top RSF model in summer during night included only distance to water and habitat (Table 2.5). Elk selected areas closer to water during the night and open habitats, such as grassland, unclassified and recently logged areas. Conifer upland habitats were used significantly more than available



during the night but significantly less than available during the day. Rock habitats were avoided during both day and night in the summer.

### *Fall*

There was no clear top RSF model for predicting elk resource selection in the fall during the day. Models 5 and 8 carried 0.57, and 0.42 of the model weight, respectively (Table 2.6). Model 5 included elevation and habitat as important predictors for elk distribution (Table 2.7). Model 8 included elevation, northness and habitat. In both models, elk selected higher elevations, conifer upland habitats and intolerant hardwood forest stands. In Model 8, elk selected for south-facing aspects. The top RSF model for night in the fall carried the majority of model weight 0.84 and included elevation and habitat (Table 2.6). Elk selected higher elevations, grassland, unclassified, recently logged areas, conifer upland and rock habitats (Table 2.7).

### *Winter*

Winter RSF top models for both day and night carried the majority of model weight 0.98 and 1 respectively (Table 2.8). During the day, the most important variables selected were elevation and habitat. Elk selected higher elevation and selected for the dominant forest type, intolerant hardwoods, during the day (Table 2.9). Winter RSF during the day was the only period in which all other habitat type coefficients were negative in relation to the reference category (Table 2.9). The top winter night RSF model carried all of the model weight and included elevation, slope, distance to roads, distance to water and habitat. Elk selected higher elevations, areas close to roads, steeper slopes and areas close to water (Table 2.9); selected habitats were grassland, unclassified and rock. Elk avoided roads during the day but selected areas close to roads with steeper slopes during the night. Conifer upland and tolerant hardwood forests were

utilized during the night but the selection coefficient was not significant. Rock habitats were selected during the night but not during the day.

## **Discussion**

### *a.) Resource Selection*

#### *(i) Habitat*

Elk resource selection patterns changed seasonally but differences in resource selection were more pronounced throughout the diel period (Figure 2.4). In all seasons, elk avoided open areas such as grasslands and unclassified habitats during the day, but these habitats were highly selected during the night. Elk selected the intolerant hardwood forest type most commonly throughout all seasons which is consistent with previous studies of elk in eastern North America (Jost 1999; Jenkins *et al.* 2007, Popp *et al.* 2013). Aspect, elevation, distance to roads, distance to water, slope and habitat were all influential predictors of elk resource selection; however, their importance varied with season. Previous habitat selection studies on elk in this region have not found selection of grasslands habitats (Brown 1998, Martin 2011, Popp *et al.* 2013). This was most likely due to the bias inherent in sampling only during the day. In the present study, elk utilized grassland primarily during the night, consistent with other studies of elk and red deer that found nocturnal foraging in open areas (Figure 2.5; Figure 2.6; Beyer and Haufler 1994; Adrados *et al.* 2008; Schaefer *et al.* 2008; Godvik *et al.* 2009). Godvik *et al.* (2009) found that red deer habitat selection in Norway was generally consistent across seasons, but changed throughout the diel period. Godvik *et al.* (2009) also found selection for pastures during the night and a shift to forested areas during the day. Not all studies however have found a primarily nocturnal use of grasslands. In Montana, elk were most commonly found in grassland flats during both the day and night periods (Proffit *et al.* 2010).

Risk of predation by wolves has been demonstrated to alter habitat selection and group size in elk (Creel *et al.* 2005; Gower 2008; but see White *et al.* 2008). Human hunting pressure can also influence elk habitat selection, causing individuals to shift from foraging in preferred meadows into more forested areas that provide cover (Morgantini and Hudson 1985). It has been observed that wolves hunt primarily during the night and early morning (Becker *et al.* 2008; Gower *et al.* 2008). The primary response of elk to wolf attacks is to flee (Becker *et al.* 2008; McNunlty *et al.* 2007; White *et al.* 2008). Inhabiting open areas during higher predation risk times would allow the flight response to be most effective as obstructions in forested habitats may hinder elk movement more so than wolf movements. Mao *et al.* (2005) found that elk selected grasslands and open areas less in the summer after wolves were reintroduced into Yellowstone National Park; however, selection of open areas increased in the winter. Wolf predation on elk is largely limited to winter snow cover periods (Mao *et al.* 2005). During the period of highest predation risk for elk (winter), Mao (2005) found that they increased their use of open areas, suggesting that gregarious behaviour in open areas is an effective anti-predator strategy. Elk in our study area selected grassland habitats throughout the year, but less in winter compared to other seasons. Interestingly, Kittle *et al.* (2008) found that elk did not avoid areas where wolf activity was present within the scale of the home range. In my study area, there is no open hunting season for elk. The primary factors influencing resource selection by elk would thus be limited to predation risk, anthropogenic disturbance, thermal cover, and food availability.

*(ii) Aspect*

Aspect was included in the top RSF models for spring and fall. South facing slopes were selected in both seasons during day and night periods. During the spring, south facing slopes are

the first to become snow free allowing for earlier plant development, offering high nutritional forage to elk. This is consistent with other studies that have found the selection for south facing aspects in spring (Coe *et al.* 2011). Utilizing southern slopes in spring would enable elk to quickly replenish body reserves depleted during winter. During the late fall, temperatures begin to cool and snow can begin to accumulate. Selection of south facing slopes during the cooling off period may provide thermal advantages to elk and assist in thermoregulation. Interestingly, aspect was not part of the top models in winter for day or night periods. Several studies have found that elk select south facing slopes during winter (Unsworth *et al.* 1998; Sawyer *et al.* 2007; Coe *et al.* 2011) but see Baasch *et al.* (2010) for conflicting results. In my study, elk were frequently found using south facing slopes in winter, but the parameter was never included in top models. This may be because of the topography in the area in that on ridge tops, aspect may become irrelevant. Others have found that elk select northern aspects during summer because of cooler temperatures, denser cover and high quality forage (Millspaugh *et al.* 1998; Skolvin *et al.* 2002); however, this pattern was not observed in my study.

### *(iii) Elevation*

Similar to other studies (Skolvin *et al.* 2002). I found elevation to be an important predictor of elk distribution across the landscape. Elk selected higher elevations in summer, fall, and winter but preferred lower elevations in spring. Elevation was the only significant predictor variable besides habitat during the day in winter. Selection of higher elevation in winter was similar to previous findings in my study area (Kittle *et al.* 2008). Kittle *et al.* (2008) found elevation to be more important than predation risk. Elk in my study area selected higher elevations because of the limited topography, where ridge tops frequently have shallower wind swept snow, and may provide a vantage point to scan for predators. This is in contrast to elk in

western North America which select lower elevations in winter as higher mountainous areas are subject to extreme snow accumulation (Sweeny and Sweeny 1984; Boyce *et al.* 2003).

(iv) *Distance to roads*

The influence of roads on space use by elk has been of great interest and is well studied (Perry and Overly 1977; Lyon 1979; Witmer and DeCalesta 1985). Current research shows that elk generally tend to avoid roads (Rost and Bailey 1979; Lyon 1983; Rowland *et al.* 2000; Stewart *et al.* 2010; Montgomery *et al.* 2013). Unsworth *et al.* (1998) found that selection for forested habitats by elk increased when roads were present within their home range. In eastern North America, reintroduced elk in Wisconsin avoided roads at larger scales, but selected areas closer to roads within the home range (Anderson *et al.* 2005). Similarly, I found that during most seasons elk were negatively associated with roads; however, distance to roads was only included in top models for spring day/night and winter night periods. During spring, elk avoided roads in both day and night periods. It has been shown that human disturbances can decrease elk calf survival (Phillips and Aldredge 2002). Elk may select areas away from roads in order to minimize disturbance during the neonate period when calves are most vulnerable. Avoidance of roads by elk is also related to traffic volumes as secondary roads with lower traffic volumes can be utilized by elk as travel corridors and foraging opportunities (Baasch *et al.* 2010). In my study, elk selected areas close to roads in winter at night. Elk selection of areas close to roads during winter has been reported by (Sawyer *et al.* 2007); however, the authors suggested that this may have been due to decreased human activity and traffic volumes during the winter. They further suggested that if winter traffic volumes increased to summer levels, they would expect elk to exhibit a similar avoidance of roads. In our study area, there should be no seasonal difference in traffic volume for the majority of the roads as they are open and maintained year

round and their range is bordered by a major 400 series highway. Elk tracks and craters (specific foraging events from digging through snow), are frequently observed along roadsides and elk may be attracted to these zones during winter for foraging opportunities when food availability is at its lowest. Roadsides are frequently seeded with a highly nutritious pasture seed mix and may enhance forage biomass in these areas. Another possibility is that elk may be exhibiting predator avoidance behaviour at a larger scale, as wolves are known to avoid areas of human activity (Whittington *et al.* 2005). Regardless, use of resources close to roads by elk during winter at night may create a higher risk of vehicle collision as road conditions are poorer, and visibility is limited. Meisingset *et al.* (2013) also found that elk were more likely to cross the road or use areas in closer proximity to roads during the night in winter and autumn.

*b.) Seasonal Space Use*

My hypothesis that high summer food availability significantly reduces space use by elk was supported. Winter space use was expected to be greatest because food availability is lowest; however, it was not significantly different from spring or fall space use. Spring ranges were the largest for all space use estimates. Smallest ranges would be expected in the spring due to mobility restrictions associated with calving and calf rearing. Space use by elk increased during this period, possibly because they seek out high quality forage patches to recoup energy lost during winter. Alternatively, elk may display larger space use due to calving as they seek out isolated areas associated with cover in the proximity of quality feeding patches. I did not find any difference in space use between years for spring and summer; however, space use differed significantly between the winters of 2012 and 2013. In 2012, the Sudbury area experienced a relatively mild winter with an early thaw and unseasonably warm temperatures during the month of March. In contrast, the winter of 2013 was relatively severe with below average temperatures

and the snowpack persisting well into April. This difference in space use between years likely reflects the severity of the winter and demonstrates how severe winters can negatively impact space use by elk. Anderson *et al.* (2005) found that elk home ranges were smaller when food availability was greater. Studying 3 distinct elk populations in Alberta, Yellowstone, and Wisconsin, they concluded that elk home range size was inversely related to forage biomass. Furthermore they found that home ranges were larger in winter compared to summer, compensating for lack of food availability due to snow, and food quality from plant senescence. Despite the negative relationship between food availability and animal space use, many studies involving large-bodied herbivores in temperate regions have found restricted or reduced activity and space use during winter in relation to snow depth (Myrsterud *et al.* 2001; Dussault *et al.* 2004; Luccarini *et al.* 2006; Rivrud *et al.* 2010; van Beest 2011). Elk are large herbivores and larger animals are capable of storing higher levels of fat reserves suggesting that they may be able to reduce space use during winter and live off reserves (Myrsterud *et al.* 2001). As winter typically results in poorer quality and reduced abundance of food, many ungulates lose mass during the winter. Jerina (2012) found that unfed red deer in Slovenia had home ranges 3 times larger than those exposed to long term supplementary feeding, suggesting that space use can be ultimately related to food availability.

### *c.) Daily movements*

Elk in my study area displayed consistent daily movement rates across seasons except for winter when daily movements were significantly lower than in all other seasons. I found that elk displayed a strong crepuscular activity pattern with greater movement occurring around dusk and

dawn, a common pattern frequently observed in elk elsewhere and in other cervids (Beier and MucCullough 1990; Green and Bear 1990; Ager *et al.* 2003; Kie *et al.* 2005; Webb *et al.* 2010; Webb *et al.* 2011). Average daily movements during snow-free periods were similar to those reported for elk in other regions (Brook 2010; Webb *et al.* 2011)). Wichrowski *et al.* (2005) found that elk reintroduced into Kentucky had significantly different movement rates among seasons, but found no differences between sexes; they reported highest daily movement rates during winter. The difference in movement rates during winter between Kentucky and Ontario is likely influenced by snow cover presence in our study area. Elk in Manitoba, where climate is similar to that in Ontario, showed lowest movement rates during winter (van Beest *et al.* 2013b), as did moose in Quebec (Leblond *et al.* 2010). Interestingly, I found movements were smallest during winter, but seasonal space use was smallest in summer. The apparent lack of relationship between daily movements and space use may be related to forage availability and quality. During the summer, forage is locally abundant allowing elk to utilize a smaller area while obtaining sufficient food. Winter mobility is likely restricted by snow conditions; however, forage selection may also play an important role in determining space use by elk. Elk, characterized as intermediate feeders, typically switch from a graminoid-dominated diet, to a browsing diet once snow conditions prevent access to ground level vegetation (Christianson and Creel 2007). Browse forage is more patchily distributed and although elk have lower daily movements during the winter, their overall space use may be larger in order to maintain minimum energy intake levels.

Resource selection has become a dominant tool used by managers and biologists to identify important habitats across various wildlife taxa. While some researchers admit that RSFs may be affected by time of day (Boyce *et al.* 2003, Ciarniello *et al.* 2007b), relatively few have



addressed these concerns in subsequent research. Researchers have identified changing resource selection patterns in wildlife from day to night periods (Mysterud *et al.* 1999; Schwartz and Arthur, 1999; Onorato *et al.* 2010); however, the majority of resource selection studies do not consider time of day. I found that there was a greater difference in resource selection across the diel period than among seasons. Boyce *et al.* (2003) pointed out that changes in seasonal variation in food abundance and distribution should provide sufficient grounds for seasonal RSF models. RSFs should continue to be evaluated by season; however, the inclusion of time of day in RSF models would substantially increase valuable knowledge about resource selection across the diel period. For species known to be active during nocturnal hours this is paramount in order to obtain a complete picture of resource selection. Moe *et al.* (2007) studying brown bears found that habitat selection changed between day and night and including all samples into a model across the entire 24 hour period showed no selection. In the present study, such a pooling of data would have resulted in grassland habitats not being selected by elk even though they were significantly selected during all seasons. In order to understand the habitat requirements of any species, all activity states must be addressed by resource selection modelling, including foraging and resting.

## **Conclusions and Management Recommendations**

Elk displayed a trade-off in resource selection between different activity states. During the night, elk used highly productive foraging habitats such as grasslands and recently logged areas. During the day, elk selected cover in forested habitats. Elk resource selection changed among seasons and no one model could adequately describe elk resource selection for multiple

seasons, as well as both day and night periods. Seasonal space use was smallest during summer and daily movements were restricted during winter. The atypical Burwash abandoned field complex provides a unique habitat that elk actively select. Natural colonization of tree and shrub species will degrade this habitat over time. It is recommended that this grassland habitat be maintained through prescribed burning or thinning of colonizing tree species to allow favoured elk habitat to persist. Elk selected for areas close to roads in winter at night. This could potentially increase the risk of vehicle collisions in this area. Although highway mitigation such as fencing is present in the study area, it is generally absent from the winter range except for a small 200m stretch of fence. It is therefore recommended to increase mitigation such as fencing in this area.

## Literature Cited

- Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer. *Journal of Mammalogy* 84:1076-1088.
- Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao, and M. S. Boyce. 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology* 20:257-271.
- Anderson, P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management* 69:298-310.
- Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* 77:215-227.
- Baasch, D., J. Fischer, S. Hygnstrom, K. VerCauteren, A. Tyre, J. Millspaugh, J. Merchant, and J. Volesky. 2010. Resource selection by elk in an agro-forested landscape of northwestern Nebraska. *Environmental Management* 46:725-737.
- Bates, D., M. Maechler and B. Bolker. 2013. Lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.
- Beasley, J. C., T. L. Devault, M. I. Retamosa, and O. E. Rhodes Jr. 2006. A hierarchical analysis of habitat selection by raccoons in northern Indiana. *Journal of Wildlife Management* 71:1125-1133.
- Becker, M. S., R. A. Garrott, P. J. White, C. N. Gower, E. J. Bergman and R. Jaffe. 2008. Wolf prey selection in an elk-bison system: Choice or circumstance? In R. H. Garrot, P. J. White, and F. G. R. Watson, editors. *The Ecology of large mammals in central Yellowstone: Sixteen years of integrated field studies*. San Diego: Elsevier 305-338.
- Beyer, E., Jr., and J. B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. *The Journal of Wildlife Management* 58:178-180.
- Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.6.0.0). (software). URL: <http://www.spatial ecology.com/gme>.
- Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:5-51.
- Boyce, M. S. 2006. Scale for resource selection functions. *Diversity and Distributions* 12:269-276.

- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution* 14:268-272.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281-300.
- Boyce, M. S., M. G. Turner, J. Fryxell and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421-431.
- Brook, R. K. 2010. Habitat selection by parturient elk (*Cervus elaphus*) in agricultural and forested landscapes. *Canadian Journal of Zoology* 88:968-976.
- Brown, G.S. 1998. Spatial behaviour and habitat utilization of wapiti (*Cervus elaphus*) in the French River and Burwash Regions of Ontario. MSc thesis School of Graduate Studies and Research Laurentian University.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516-519.
- Christianson, D. A., and S. Creel. 2007. A review of environmental factors affecting elk winter diets. *Journal of Wildlife Management* 71:164-176.
- Ciarniello, L. M., M. S. Boyce, D. R. Seip, and D. C. Heard. 2007a. Grizzly bear habitat selection is scale dependent. *Ecological Applications* 17:1424-1440.
- Ciarniello, L. M., M. S. Boyce, D. C. Heard, and D. R. Seip. 2007b. Components of grizzly bear habitat selection: density, habitats, roads, and mortality risk. *The Journal of Wildlife Management* 71:1446-1457.
- Coe, P. K., B. K. Johnson, M. J. Wisdom, J. G. Cook, M. Vavra, and R. M. Nielson. 2011. Validation of elk resource selection models with spatially independent data. *Journal of Wildlife Management* 75:159-170.
- Courtois, R., J. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Ecoscience* 14:491-498.
- Creel, S., J. J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387-3397.

- D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430-439.
- Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* 11:321–328.
- Environment Canada. 2012. Meteorological Service of Canada. , 2012. Atmospheric Environment Service, Environment Canada. [http://weather.gc.ca/canada\\_e.html](http://weather.gc.ca/canada_e.html)
- Environment Canada. 2013. Meteorological Service of Canada. , 2012. Atmospheric Environment Service, Environment Canada. [http://weather.gc.ca/canada\\_e.html](http://weather.gc.ca/canada_e.html)
- Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. In. J. J. Millspaugh, and J. M. Marzluff, editors. *Radio Tracking and Animal Populations*. San Diego, Elsevier 211-245.
- Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699-710.
- Gower, C. N., R. A. Garrot, P. J. White, F. G. R. Watson, S. S. Cornish, and M. S. Becker. 2008. Spatial response of elk to wolf predation risk: using landscape to balance multiple demands. In. R. H. Garrot, P. J. White, and F. G. R. Watson, editors. *The Ecology of large mammals in central Yellowstone: Sixteen Years of Integrated Field Studies*. San Diego: Elsevier 373-399.
- Green, R. A., and G. D. Bear. 1990. Seasonal cycles and daily activity patterns of rocky mountain elk. *Journal of Wildlife Management* 54:272-279.
- Jenkins, D. A., J. A Schaefer, R. Rosatte, T. Bellhouse, J. Hamr, and F. F. Mallory. 2007. Winter resource selection of reintroduced elk and sympatric white-tailed deer at multiple spatial scales. *Journal of Mammalogy* 88:614-624.
- Jerina, K. 2012. Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. *Journal of Mammalogy* 93:1139-1148.
- Johnson D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Johnson, M. D., and T. W. Sherry. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology* 70:546-560.
- Jost, M. A., J. Hamr and F. F. Mallory. 1999. Forage selection by elk in habitats common to the French River – Burwash region of Ontario. *Canadian Journal of Zoology* 77: 1429-1438.

- Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41:300-314.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. In: *Radio Tracking Animal Populations* Millspaugh, J. J. & Marzluff, editors San Diego Elsevier 321-347.
- Kie, J. G., A. A. Ager, and R. T. Bowyer. 2005. Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. *Landscape Ecology* 20:289-300.
- Kittle, A., J. Fryxell, G. Desy, and J. Hamr. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia* 157:163-175.
- Leblond, M., C. Dussault, and J. P. Ouellet. 2010. What drives fine-scale movements of large herbivores? A case study using moose. *Ecography* 33:1102-1112.
- Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. *Journal of Forestry* 77:658-660.
- Luccarini, S., L. Mauri, S. Ciuti, P. Lamberti and M. Apollonio. 2006. Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. *Ethology Ecology & Evolution* 18:127-14.
- Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. *Journal of Forestry* 81:592-595
- Manly, B. F. J. 1985. *The Statistics of Natural Selection*. Chapman & Hall, London.
- Manly, B. F. J., L. L. McDonald, D. L. McDonald and W. P. Erickson. 2002. *Resource selection by animals* 2<sup>nd</sup> edn. Kluwer Academic Publishers, Dordrecht.
- Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69:1691-1707.
- Martin, M. 2011. Spatial behavior and habitat use by elk (*Cervus elaphus*) in response to highway construction and interprovincial relocation. MSc thesis, School of Graduate Studies Laurentian University.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, S. P. Mahoney. 2009. Habitat selection at multiple scales. *Ecoscience* 16:238-247.
- McLoughlin, P. D., L. R. Walton, H. D. Cluff, P. C., Paquet, and M. A. Ramsay. 2004. Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy* 85:576-580.

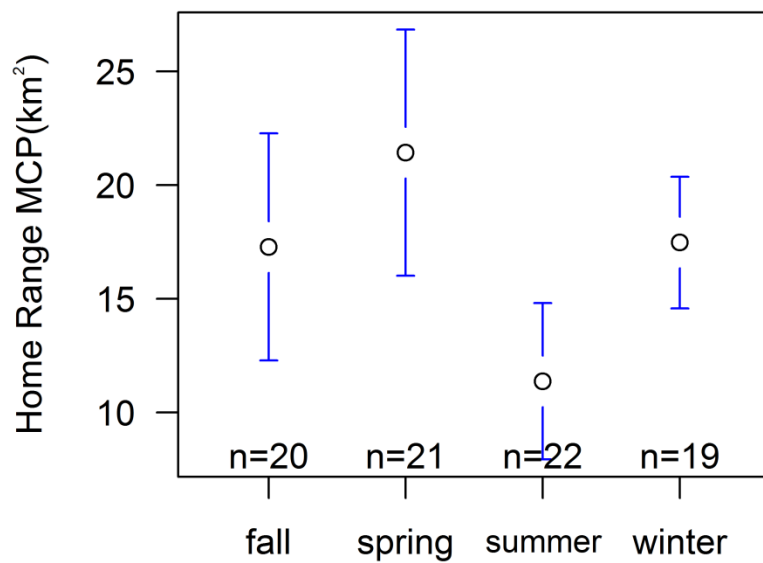
- Meisingset, E. I., L. F., Loe, Ø. Brekkum, B. Van Moorter, A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. *Journal of Wildlife Management* 77:181-191.
- Millsbaugh, J. J., K. J. Raedeke, G. C. Brundige, C. C. Willmott. 1998. Summer bed sites of elk (*Cervus elaphus*) in the Black Hills South Dakota: conditions for thermal cover management. *American Midland Naturalist* 139:133-140.
- Moe, T. F., J. Kindberg, I. Jansson, and J. E. Swenson. 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology* 85:518-525.
- Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37: 223-249.
- Montgomery, R. A., G. J. Roloff, and J. J. Millsbaugh. 2013. Variation in elk response to roads by season, sex, and road type. *Journal of Wildlife Management* 77:313-325.
- Morgantini, L. E., and R. J. Hudson. 1985. Changes in diets of wapiti during a hunting season. *Journal of Range Management* 38:77-79.
- Mysterud, A., and R. A. Ims. 1998. Functional response in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435-1441.
- Mysterud, A., F. J. Pérez-Barberia, and I. J. Gordon. 2001. The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia* 127:30-39.
- Onorato, D. P., M. Criffield, M. Lotz, M. Cunningham, R. McBride, E. H. Leone, O. L. Bass, and E. C. Hellgren. 2011. Habitat selection by critically endangered Florida panthers across the diel period: implications for land management and conservation. *Animal Conservation* 14:196-205.
- Pinheiro J., D. Bates, S. DebRoy, D. Sarkar and the R Development Core Team (2013). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-108.
- Peel, M. C., B. L. Finlayson and T. A. McMahon. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11:1633-1644.
- Perry, C., and R. Overly. 1977. Impact of roads on big game distribution in portions of the Blue Mountains of Washington, 1972-1973. Washington Game Department Report, Olympia, WA. 38pp.
- Phillips, G. E., and A. W. Aldredge. 2002. Reproductive success of elk following disturbance by humans during calving season. *Journal of Wildlife Management* 64:521-530.

- Popp, J. N., D. N. C. McGeachy, and J. Hamr. 2013. Elk (*Cervus elaphus*) Seasonal habitat selection in a heterogeneous forest structure. *International Journal of Forestry Research* 2013:1-7.
- Proffitt, K. M., J. L. Grigg, R. A. Garrott, K. L. Hamlin, J. Cunningham, J. A. Gude, and C. Jourdonnais. 2010. Changes in elk resource selection and distributions associated with a late-season elk hunt. *Journal of Wildlife Management* 74:210-218.
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
- Rettie, W. J, and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466-478.
- Rivrud, I. M., L. E. Loe, and A. Mysterud. 2010. How does local weather predict red deer home range size at different temporal scales? *Journal of Animal Ecology* 79:1280-1295.
- Rosatte, R., J. Hamr, J. Young, I. Filion, and H. Smith. 2007. The restoration of elk (*Cervus elaphus*) in Ontario, Canada: 1998–2005. *Restoration Ecology* 15:34-43.
- Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* 43:634-641.
- Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64:672-684.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDondald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396-403.
- Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. *Journal of Wildlife Management* 71:868-874.
- Schaefer, J. A., and F. Messier. 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18:333-344.
- Schaefer, J. A., N. Morellet, D. Pépin and H. Verheryden. 2008. The spatial scale of habitat selection by red deer. *Canadian Journal of Zoology* 86:137-1345.
- Schwartz, C. C. and S. M. Arthur. 1999. Radiotracking large wilderness mammals: Integration of GPS and ARGOS technology. *Ursus* 11:261-274.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075-2085.

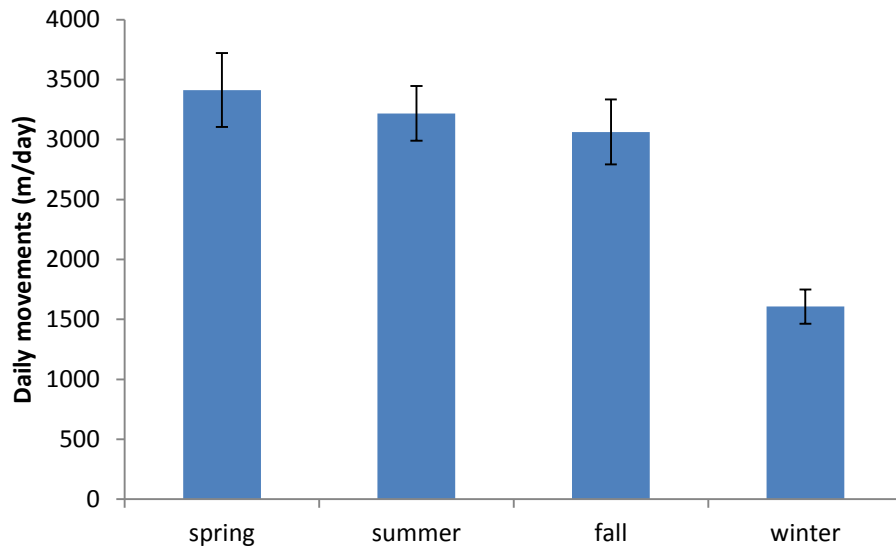


- Skolvin J.M., P. Zager, and B.K. Johnson 2002. Elk habitat selection and evaluation. Pp 531-556 in D.E. Toweill and J. W. Thomas, editors. *North American Elk: Ecology and Management*. Smithsonian Institution Press, Washington, D.C., USA.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, and M. A. Hurley. 2010. Spatial distributions of mule deer and North American elk: resource partitioning in a sage-steppe environment. *American Midland Naturalist* 163:400-412.
- Sweeney, J. M., and J. R. Sweeney. 1984. Snow depths influencing the winter movements of elk. *Journal of Mammalogy* 65:524-526.
- Thomas, D.L., and Taylor, E.J. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322-330.
- Unsworth, J. W., L. Kuck, E. O. Garton, and B. R. Butterfield. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. *Journal of Wildlife Management* 62:1255-1263.
- van Beest, F. M., Rivrud, I.M., Loe, L.E., Milner, J.M. and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology* 80:771-785.
- van Beest, F. M., A. Uzal, E. Vander Wal, M. P. Laforge, A. L. Contasti, D. Colville, and P. D. McLoughlin. 2013a. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *Journal of Animal Ecology* published online.
- van Beest, F. M., E. Vander Wal, A. V. Stronen, and R. K. Brook. 2013b. Factors driving variation in movement rate and seasonality of sympatric ungulates. *Journal of Mammalogy* 94:691-701.
- Vankat, J. L. 1979. *The natural vegetation of North America: an introduction*. John Wiley and Sons, Toronto.
- Webb, S. L., K. L. Gee, B. K. Strickland, S. Demarais, and R. W. Deyoung. 2010. Measuring fine-scale white tailed deer movements and environmental influences using GPS collars. *International Journal of Ecology*. Article ID 459610, 12 pages.
- Webb, S. L., M. R. Dzialak, S. M. Harju, L. D. Hayden-Wing, J. B. Winstead. 2011. Effects of human activity on space use and movement patterns of female elk. *Wildlife Society Bulletin* 35:261-269.
- Weber, K. T., M. Burcham, and C. Les Marcum. 2001. Assessing independence of animal locations with association matrices. *Journal of Range Management* 54:21-24.
- White, G. C., and R. A. Garrott. 1990. *Analysis of wildlife radio-tracking data*. Academic Press Inc., San Diego.

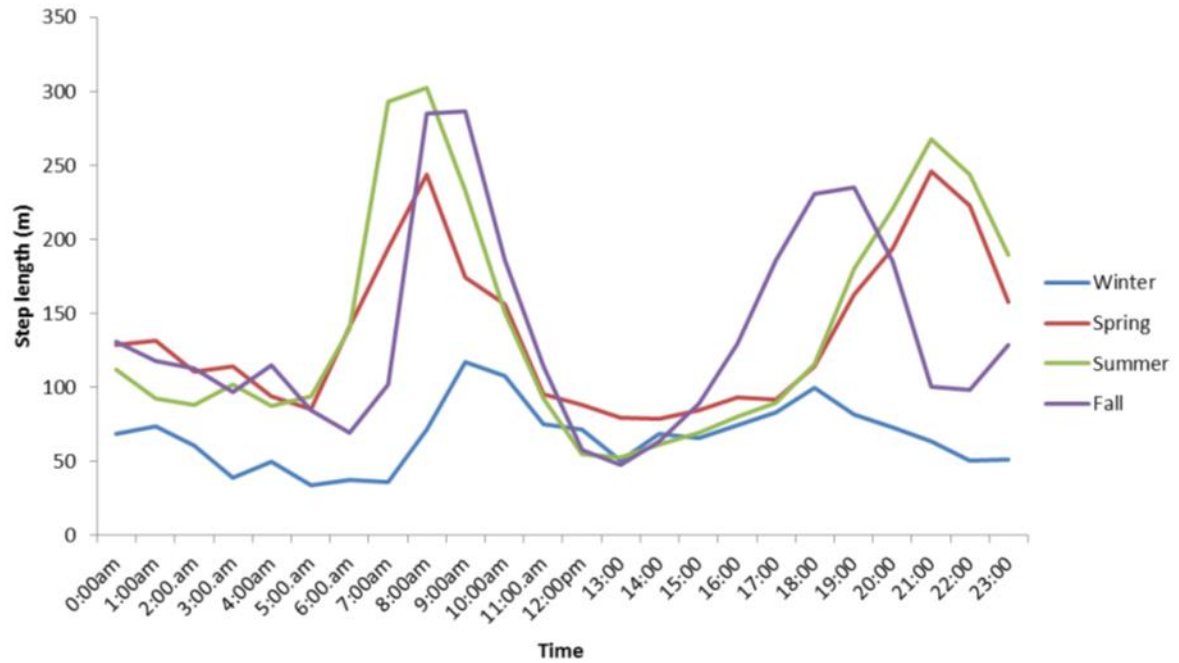
- White, P. J., R. A. Garrott, S. Cherry, F. G. R. Watson, C. N. Gower, M. S. Becker and E. Meredith. 2008. In R. H. Garrott, P. J. White, and F. G. R. Watson, editors. *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies*. San Diego: Elsevier.451-477.
- Whittington, J., C. C. St Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15:543-553.
- Wichrowski, M. W., D. S. Maehr, J. L. Larkin, J. J. Cox, and M. P. O. Olsson. 2005. Activity and movements of reintroduced elk in southeastern Kentucky. *Southeastern Naturalist* 4:365-374.
- Witmer, G. W., and D. S. deCalesta. 1985. Effects of forest roads on habitat use by Roosevelt elk. *Northwest Science* 59:122-125
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey, USA.



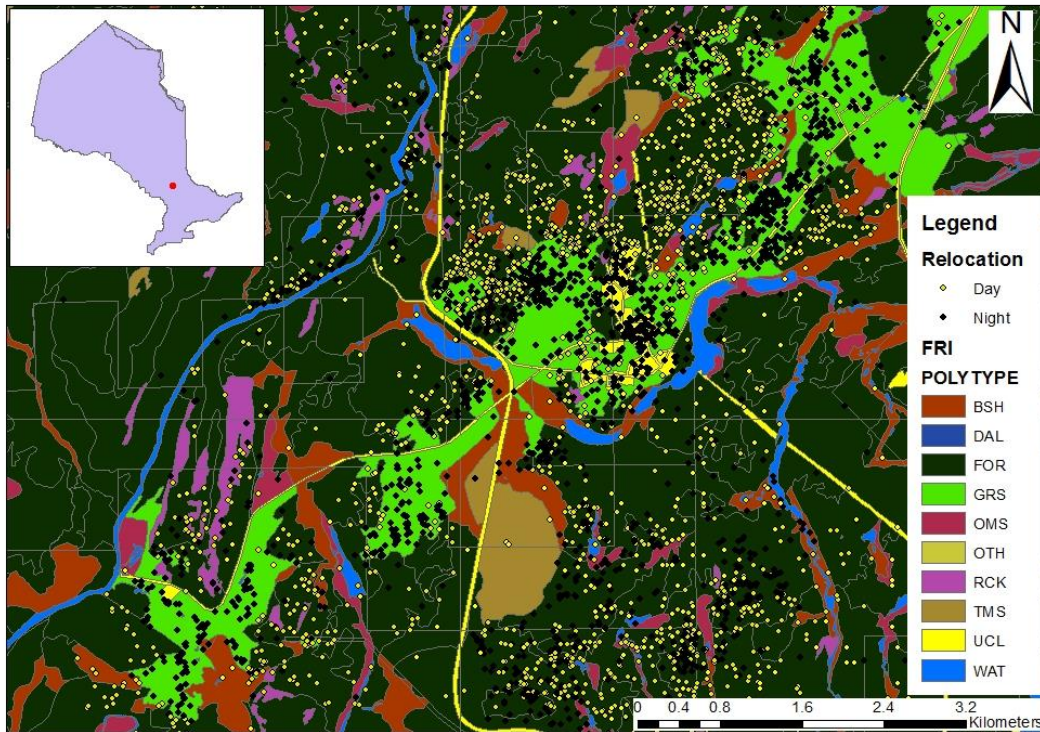
**Figure 2.1.** Elk seasonal home range using minimum convex polygon method (MCP km<sup>2</sup>). n = number of elk with radio collars tracked in each season. Error bars represent standard error of the mean.



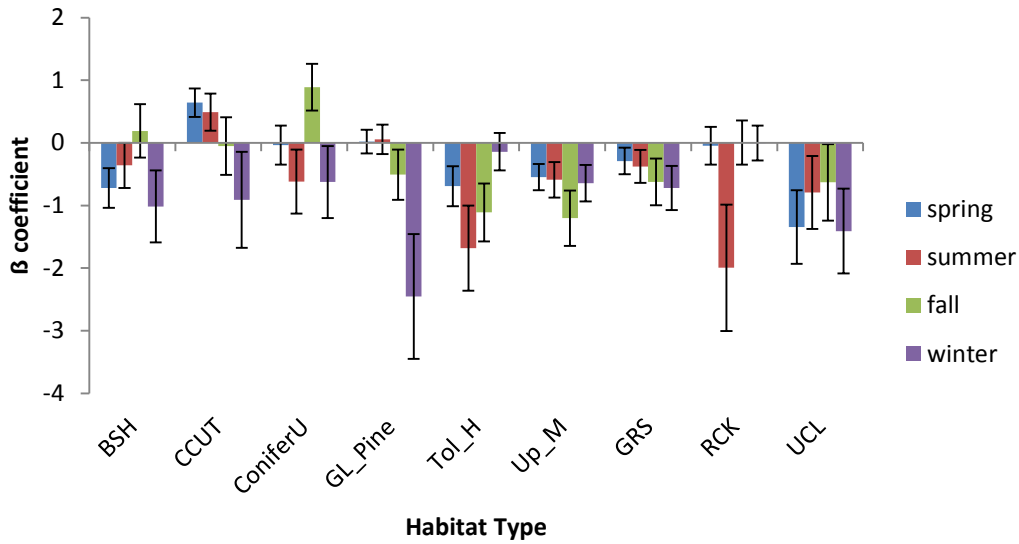
**Figure 2.2.** Mean daily movements of elk in spring (N=6), summer (N=6), fall (N=5) and winter (N=4). Error bars represent standard error of the mean.



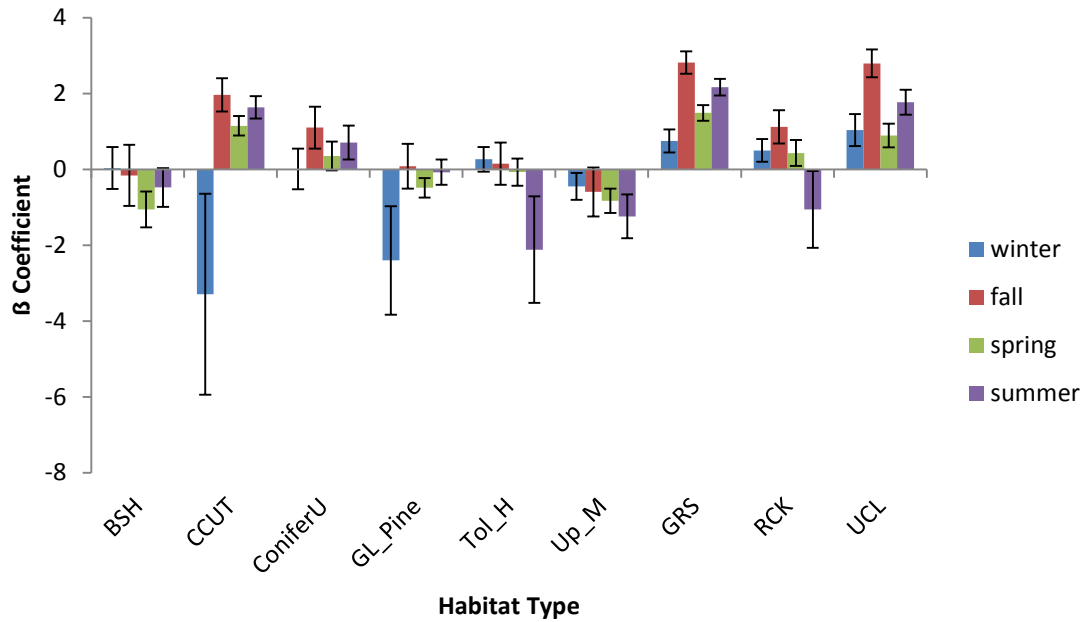
**Figure 2.3.** Elk activity patterns and mean hourly step length throughout the diel period in winter (N=4), spring (N=6), summer (N=6) and fall (N=5).



**Figure 2.4.** Map of study area with different habitat types (see methods for full description) and elk relocations from GPS and VHF collared animals during day and night periods for spring, summer and fall 2012 and 2013.



**Figure 2.5.** RSF estimates for habitat types for spring, summer, fall and winter during daytime. Significant if error bars (95% confidence intervals) do not overlap with 0. Intolerant Hardwood Forests is the reference category. BSH = Brush and Alder, CCUT= Recently Logged Areas, ConiferU= Conifer Upland, GL\_Pine= Great Lakes St. Lawrence Pine, Tol\_H = Tolerant hardwood forest, Up\_M = Upland Mixed, GRS = Grassland, RCK = Rock, UCL = Unclassified Habitats



**Figure 2.6.** RSF estimates for habitat types for spring, summer, fall and winter during nighttime periods. Significant if error bars (95% confidence intervals) do not overlap with 0. Intolerant Hardwood Forests is the Reference Category. BSH = Brush and Alder, CCUT= recently logged areas, ConiferU= Conifer upland, GL\_Pine= Great Lakes St. Lawrence Pine, Tol\_H = Tolerant hardwood Forest, Up\_M = Upland Mixed, GRS = Grassland, RCK = Rock, UCL = Unclassified Habitats



**Table 2.1.** Covariates included in 20 *a priori* RSF models and number of parameters (fixed effects only).

Model	Covariates	K
1	Elevation+Slope+Northness+Eastness+NearW+NearR+Habitat	16
2	NearW + NearR + Habitat	13
3	NearW + Habitat	12
4	NearR + Habitat	12
5	Elevation + Habitat	12
6	Northness + Eastness + Habitat	13
7	NearR +Northness+Habitat	13
8	Elevation + Northness + Habitat	13
9	Northness + Elevation+ NearR + Habitat	14
10	Northness + Elevation + NearR + NearW + Eastness + Habitat	16
11	Northness + Elevation + NearR	4
12	NearW + Eastness+ Northness + Elevation + NearR	6
13	NearW + NearR	3
14	Slope + Habitat	12
15	Slope + Elevation + Northness + NearR + Habitat	15
16	Eastness + Elevation + NearR + Habitat	15
17	Elevation + NearR + Northness + NearW + Habitat	15
18	Elevation + Slope + Habitat	13
19	Slope+Elevation + NearW + NearR+ Habitat	15
20	Elevation + Slope + Eastness + NearW + Habitat	15

\*The variable habitat is categorical and consists of 10 habitat types

NearW represents distance to water

NearR represents distance to roads

**Table 2.2.** Top 5 models characterizing elk resource selection in central Ontario in spring for day and night time periods. K represents the number of fixed effects included in model,  $w_i$ = model weight. Model covariates described in Table 2.1.

Season	Model #	K	AICc	$\Delta$ AICc	$w_i$
Spring Day	3	11	8538.40	0.00	0.49
	7	12	8538.67	0.27	0.43
	8	12	8543.67	5.27	0.04
	6	12	8544.67	6.27	0.02
	2	12	8545.67	7.27	0.01
Spring Night	1	14	6370.00	0.00	0.46
	15	13	6370.50	0.50	0.36
	9	14	6372.00	2.00	0.17
	17	12	6378.67	8.60	0.01
	8	15	6383.00	13.00	0.00

**Table 2.3.** Top spring RSF models for day and night periods with lower and upper bound 95% confidence intervals.

	Spring Day			Spring Night		
	$\beta$	lower	upper	$\beta$	lower	upper
(Intercept)	<b>-2.614</b>	<b>-4.889</b>	<b>-2.485</b>	<b>-2.336</b>	<b>-3.735</b>	<b>-0.937</b>
Slope	-	-	-	<b>0.037</b>	<b>0.016</b>	<b>0.057</b>
Elevation	-	-	-	-0.005	-0.011	0.000
NearR	<b>-0.009</b>	<b>-0.016</b>	<b>-0.002</b>	<b>-0.002</b>	<b>-0.003</b>	<b>-0.001</b>
Eastness	-	-	-	<b>0.148</b>	<b>0.056</b>	<b>0.240</b>
Northness	<b>-0.179</b>	<b>-0.264</b>	<b>-0.094</b>	<b>-0.269</b>	<b>-0.368</b>	<b>-0.170</b>
NearW	-	-	-	-0.001	-0.001	0.000
BSH	<b>-0.769</b>	<b>-1.087</b>	<b>-0.451</b>	<b>-1.058</b>	<b>-1.530</b>	<b>-0.585</b>
CCUT	<b>0.589</b>	<b>0.361</b>	<b>0.817</b>	<b>1.145</b>	<b>0.888</b>	<b>1.403</b>
ConiferU	-0.154	-0.466	0.159	0.352	-0.024	0.728
GL_Pine	0.003	-0.191	0.185	<b>-0.486</b>	<b>-0.742</b>	<b>-0.229</b>
Tol_H	<b>-0.669</b>	<b>-0.988</b>	<b>-0.350</b>	-0.073	-0.430	0.285
Up_M	<b>-0.568</b>	<b>-0.779</b>	<b>-0.356</b>	<b>-0.831</b>	<b>-1.150</b>	<b>-0.511</b>
GRS	<b>-0.415</b>	<b>-0.629</b>	<b>-0.202</b>	<b>1.487</b>	<b>1.282</b>	<b>1.692</b>
RCK	0.015	-0.286	0.316	<b>0.430</b>	<b>0.091</b>	<b>0.770</b>
UCL	<b>-1.410</b>	<b>-1.999</b>	<b>-0.822</b>	<b>0.892</b>	<b>0.583</b>	<b>1.201</b>

\*Significance is determined by 95% confidence intervals that do not include 0 highlighted in bold.

† For Habitat covariates, Intolerant Hardwood Forest was used as the reference category.

BSH = Brush and Alder, CCUT= Recently Logged Areas, ConiferU= Conifer Upland,

GL\_Pine= Great Lakes St. Lawrence Pine, Tol\_H = Tolerant hardwood forest,

Up\_M = Upland Mixed, GRS = Grassland, RCK = Rock, UCL = Unclassified Habitats

**Table 2.4.** Top 5 models characterizing elk resource selection in central Ontario in summer for day and night time periods. K represents the number of fixed effects included in model,  $w_i$ = model weight. Model covariates described in Table 2.1.

Season	Model #	k	AICc	$\Delta$ AICc	$w_i$
Summer Day	18	12	5137.00	0.00	0.69
	5	11	5139.33	2.33	0.21
	3	11	5142.33	5.33	0.05
	14	11	5142.33	5.33	0.05
	8	12	5149.00	12.00	0.00
Summer Night	3	11	4891.33	0.00	0.95
	5	11	4898.33	7.00	0.03
	2	12	4901.00	9.67	0.01
	18	12	4901.00	9.67	0.01
	14	11	4903.33	12.00	0.00

**Table 2.5.** Top summer RSF models for day and night periods with lower and upper bound 95% confidence intervals.

	Summer Day			Summer Night		
	$\beta$	lower	upper	$\beta$	lower	upper
(Intercept)	<b>-6.801</b>	<b>-8.625</b>	<b>-4.978</b>	<b>-6.778</b>	<b>-8.792</b>	<b>-4.764</b>
NearW	-	-	-	0.001	0.000	0.001
Elevation	<b>0.015</b>	<b>0.008</b>	<b>0.023</b>	-	-	-
Slope	<b>-0.051</b>	<b>-0.081</b>	<b>-0.022</b>	-	-	-
BSH	-0.360	-0.722	0.003	-0.381	-0.905	0.143
CCUT	<b>0.489</b>	<b>0.190</b>	<b>0.788</b>	<b>1.647</b>	<b>1.348</b>	<b>1.947</b>
ConiferU	<b>-0.620</b>	<b>-1.133</b>	<b>-0.107</b>	<b>0.807</b>	<b>0.346</b>	<b>1.267</b>
GL_Pine	0.054	-0.184	0.292	-0.028	-0.359	0.304
Tol_H	<b>-1.682</b>	<b>-2.366</b>	<b>-0.998</b>	<b>-2.123</b>	<b>-3.530</b>	<b>-0.716</b>
Up_M	<b>-0.590</b>	<b>-0.873</b>	<b>-0.307</b>	<b>-1.154</b>	<b>-1.735</b>	<b>-0.573</b>
GRS	<b>-0.376</b>	<b>-0.650</b>	<b>-0.102</b>	<b>2.216</b>	<b>1.971</b>	<b>2.462</b>
RCK	<b>-1.995</b>	<b>-3.009</b>	<b>-0.982</b>	<b>-1.098</b>	<b>-2.115</b>	<b>-0.081</b>
UCL	<b>-0.793</b>	<b>-1.381</b>	<b>-0.206</b>	<b>1.798</b>	<b>1.463</b>	<b>2.133</b>

\*Significance is determined by 95% confidence intervals that do not include 0 highlighted in bold.

† For Habitat covariates Intolerant Hardwood Forest was used as the reference category.

BSH = Brush and Alder, CCUT= Recently Logged Areas, ConiferU= Conifer Upland,

GL\_Pine= Great Lakes St. Lawrence Pine, Tol\_H = Tolerant hardwood forest,

Up\_M = Upland Mixed, GRS = Grassland, RCK = Rock, UCL = Unclassified Habitats

**Table 2.6.** Top 5 models characterizing elk resource selection in central Ontario in fall for day and night time periods. K represents the number of fixed effects included in model,  $w_i$ = model weight. Model covariates described in Table 2.1.

Season	Model #	K	AICc	$\Delta$ AICc	$w_i$
Fall Day	5	11	3939.00	0.00	0.57
	8	12	3939.57	0.57	0.43
	18	12	3951.57	12.57	0.00
	9	13	3954.67	15.67	0.00
	15	14	3980.00	41.00	0.00
Fall Night	8	12	3620.57	0.00	0.85
	5	11	3624.00	3.43	0.15
	18	12	3637.57	17.00	0.00
	9	13	3637.67	17.10	0.00
	17	14	3663.00	42.43	0.00

**Table 2.7.** Top fall RSF models for day and night periods with lower and upper bound 95% confidence intervals.

	Fall Day			Fall Night		
	$\beta$	lower	upper	$\beta$	lower	upper
(Intercept)	<b>-14.547</b>	<b>-16.495</b>	<b>-12.599</b>	<b>-12.022</b>	<b>-14.198</b>	<b>-9.847</b>
Northness	-	-	-	<b>-0.288</b>	<b>-0.424</b>	<b>-0.151</b>
Elevation	<b>0.048</b>	<b>0.040</b>	<b>0.056</b>	<b>0.032</b>	<b>0.023</b>	<b>0.041</b>
BSH	0.190	-0.238	0.618	-0.161	-0.966	0.644
CCUT	-0.053	-0.517	0.411	<b>1.961</b>	<b>1.523</b>	<b>2.400</b>
ConiferU	<b>0.887</b>	<b>0.511</b>	<b>1.264</b>	<b>1.101</b>	<b>0.547</b>	<b>1.654</b>
GL_Pine	<b>-0.508</b>	<b>-0.909</b>	<b>-0.107</b>	0.083	-0.509	0.675
Tol_H	<b>-1.111</b>	<b>-1.575</b>	<b>-0.648</b>	0.149	-0.411	0.710
Up_M	<b>-1.203</b>	<b>-1.646</b>	<b>-0.760</b>	-0.597	-1.243	0.049
GRS	<b>-0.624</b>	<b>-1.003</b>	<b>-0.245</b>	<b>2.816</b>	<b>2.520</b>	<b>3.113</b>
RCK	0.004	-0.351	0.359	<b>1.116</b>	<b>0.677</b>	<b>1.556</b>
UCL	<b>-0.631</b>	<b>-1.253</b>	<b>-0.010</b>	<b>2.793</b>	<b>2.427</b>	<b>3.158</b>

\*Significance is determined by 95% confidence intervals that do not include 0 highlighted in bold.

† For Habitat covariates Intolerant Hardwood forest was used as the reference category.

BSH = Brush and Alder, CCUT= Recently Logged Areas, ConiferU= Conifer Upland,

GL\_Pine= Great Lakes St. Lawrence Pine, Tol\_H = Tolerant hardwood forest,

Up\_M = Upland Mixed, GRS = Grassland, RCK = Rock, UCL = Unclassified Habitats

**Table 2.8.** Top 5 models characterizing elk resource selection in central Ontario in winter for day and night time periods. K represents the number of fixed effects included in model,  $w_i$ = model weight. Model covariates described in Table 2.1.

	model #	K	AICc	$\Delta$ AICc	$w_i$
Winter Day	5	11	4919.00	0.00	0.99
	18	12	4927.57	8.57	0.01
	8	12	4932.57	13.57	0.00
	9	13	4943.67	24.67	0.00
	4	11	4953.00	34.00	0.00
Winter Night	19	14	4000.00	0.00	1.00
	3	11	4040.00	40.00	0.00
	2	12	4047.57	47.57	0.00
	17	14	4073.00	73.00	0.00
	12	5	4089.29	89.29	0.00



**Table 2.9.** Top winter RSF models for day and night periods with lower and upper bound 95% confidence intervals.

	Winter A			Winter Night		
	$\beta$	lower	upper	$\beta$	lower	upper
(Intercept)	-7.252	-8.774	-5.729	<b>-9.792</b>	<b>-11.606</b>	<b>-7.978</b>
Elevation	<b>0.020</b>	<b>0.014</b>	<b>0.026</b>	<b>0.020</b>	<b>0.013</b>	<b>0.028</b>
NearR	-	-	-	<b>0.004</b>	<b>0.003</b>	<b>0.005</b>
slope	-	-	-	<b>0.107</b>	<b>0.084</b>	<b>0.130</b>
BSH	<b>-1.016</b>	<b>-1.592</b>	<b>-0.440</b>	0.035	-0.517	0.586
CCUT	<b>-0.910</b>	<b>-1.679</b>	<b>-0.140</b>	<b>-3.295</b>	<b>-5.944</b>	<b>-0.646</b>
ConiferU	<b>-0.626</b>	<b>-1.203</b>	<b>-0.049</b>	0.010	-0.526	0.545
GL_Pine	<b>-2.452</b>	<b>-3.448</b>	<b>-1.456</b>	<b>-2.401</b>	<b>-3.829</b>	<b>-0.972</b>
Tol_H	-0.143	-0.440	0.154	0.266	-0.060	0.592
Up_M	<b>-0.646</b>	<b>-0.939</b>	<b>-0.354</b>	<b>-0.447</b>	<b>-0.800</b>	<b>-0.094</b>
GRS	<b>-0.721</b>	<b>-1.079</b>	<b>-0.362</b>	<b>0.752</b>	<b>0.448</b>	<b>1.056</b>
RCK	-0.003	-0.283	0.277	<b>0.499</b>	<b>0.198</b>	<b>0.800</b>
UCL	<b>-1.408</b>	<b>-2.090</b>	<b>-0.727</b>	<b>1.037</b>	<b>0.616</b>	<b>1.457</b>

\*Significance is determined by 95% confidence intervals that do not include 0 highlighted in bold.

† For Habitat covariates Intolerant Hardwood forest was used as the reference category.

BSH = Brush and Alder, CCUT= Recently Logged Areas, ConiferU= Conifer Upland,

GL\_Pine= Great Lakes St. Lawrence Pine, Tol\_H = Tolerant hardwood forest,

Up\_M = Upland Mixed, GRS = Grassland, RCK = Rock, UCL = Unclassified Habitats

## General Conclusions

Elk in the Sudbury area appear to have distributed themselves across the landscape in a metapopulation structure, most closely resembling a mainland/island pattern, with a core population in the Burwash area surrounded by satellite subpopulations. Dispersal to the most distant subpopulation from the core was observed. Elk were also confirmed in numerous areas outside of the current elk population range, indicating that dispersal is taking place at a larger scale, or additional subpopulations exist that have remained undetected. Space used by elk was significantly smaller for individuals residing the core subpopulation compared to the surrounding satellite groups. Increased space use and lower population densities may be an indication of lower habitat quality in satellite subpopulations compared to the core subpopulation in Burwash. Adult survival rates were moderately high in all subpopulations. Railway collision was the leading cause of elk death in the Burwash subpopulation. Mitigating railway mortality would greatly increase adult survival rates. Monitoring survival and recruitment rates among the 5 subpopulations identified in the metapopulation would reveal novel insights into population dynamics and possibly identify if surrounding satellite subpopulations are sinks, or likely to remain viable on their own. In the present study, an elk metapopulation was observed based strictly on spatial data, but it would be interesting and informative for management to investigate whether this metapopulation structure is also observed at the genetic level.

Observations of resource selection by elk in the Burwash subpopulation were effected by variations in temporal scale. Elk resource selection changed with seasons, but differences were more pronounced from day to night. Elk selected grassland habitats during the night and intolerant hardwood forests during the day in all seasons. In order to obtain a clear picture of resource selection by any animal that is active both day and night, 24 hour sampling subdivided

by time of day should be considered in the analysis. None of the tested RSF models accurately characterized resource selection for elk across seasons or the diel period, indicating that resource selection is a dynamic process, changing with food availability and activity of the animal.

#### Summary and Recommendations:

- Elk in the Sudbury area have established a metapopulation structure with a core subpopulation in Burwash, surrounded by satellite subpopulations resembling a mainland-island structure.
- Satellite subpopulations have lower elk densities and greater individual space use, indicating possibly lower habitat quality.
- Resource selection changed more drastically from day to night than among seasons, indicating that management activities need to consider behaviour across the diel cycle.
- Elk actively selected the grassland habitat in Burwash and its conservation should be a management priority.
- Human caused mortality in the core population was the largest factor reducing elk survival in Burwash. Mitigating train elk collisions would improve elk survival in Burwash