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Connectivity of Elk Migration in Southwestern Alberta

by

Dale G. Paton

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ABSTRACT

The purpose of this study was to investigate the migration of a partially migratory population of 650 Rocky Mountain elk (*Cervus elaphus*) in the human dominated landscape of southwestern Alberta. I contribute previously unknown values for metrics known to be important for elk ecology and management, including: migration timing, distance, and duration . The Brownian bridge movement model was used to delineate a probabilistic estimate of elk migration corridors between seasonal ranges, to determine if elk use stopovers during migration and prioritize migration corridors. Elk used a number of stopovers during migration likely to maximize areas of rich forage due to spring green-up. Stopovers were found to be >500m from roads in areas of rugged terrain These stopover locations are critical components in altitudinal migration. Finally a predictive modeling process using graph theory methods (least cost and circuit theory) was undertaken to predict connectivity of the landscape for elk.

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ABBREVIATIONS

AIC..Akaike's Information Criterion
BBMM ....Brownian bridge movement model
BMV ....Brownian-motion variance
CAT.. connectivity analysis toolkit
CRW ....correlated random walks
FSH ....forage-selection hypothesis
GIS ....Geographic information system
GPS ....Global Positioning System
Hr .... hour
Km... kilometre
m .... metre
MCP ....Minimum Convex Polygon
NGO...non-government organization
RSF ....resource selection functions
RSH.. reproductive-strategy hypothesis
SSF..step selection function
SW...southwest
UD's.. utilization distributions
UTM..Universal Transverse Mercator coordinate system
VHF.. very high frequency

CHAPTER ONE: INTRODUCTION

Migration is an amazing phenomenon where wild animals travel from one seasonal range to another over long or short distances, then back to the original range (Berger 2004, Boyce 1991). Each seasonal movement is timed to follow the food and water resources necessary to maximize the basic requirements of survival in a historic pattern of moving across the land (Hedenstrom 2003, Holdo et al. 2009). Animal migration is a complex behaviour governed partly by genetics and population dynamics (Bolger et al. 2007). Critical characteristics of migration include navigation, timing of migration, site fidelity, social behaviour and morphological and physiological adaptations (Bolger et al. 2007). Migration has both costs and benefits for animals and defining these trade-offs are difficult (Bolger et al. 2007, Hebblewhite and Merrill 2009). There is a growing interest in why populations of migratory animals are declining globally (Wilcox 2007), with conservationists noting the importance of protecting migration corridors and dispersal of wildlife (Schaller 1988. Berger 2010).

Grazing by herbivores has a significant effect on ecosystems and a good understanding of migration is necessary to understand their functional role in ecosystems (Mysterud et al. 2012). Besides their economic and social value to humans, animal migrations cycle nutrients and facilitate additional ecological process. Migration promotes ecosystem resilience that enhances the ability of natural systems to recover from disturbances and stresses, including manifestations of climate change (Walther et al. 2002). The ecology of ungulates in the Rocky Mountains is strongly influenced by climate. Climate change affects summer precipitation, winter snow pack, and the timing of spring green-up, all of which control animal physiology, demography, diet, habitat selection and predator prey interactions. Migration is an important component of elk survival strategies. Similar to other herbivore species, elk migrate to higher elevations in the spring, due to retreating snow cover and greater food availability and return to winter range in the fall.

Maintaining elk populations provides ecological, social and economic benefits. Wildlife viewing and hunting generate millions of dollars to local economies. Elk can contribute to maintaining early successional habitat conditions which have declined over the past several decades due to influences such as fire suppression. Elk generate some concerns due to the potential for damage,

nuisance activity, and disease transmission. Agricultural damage is most common with elk foraging on and trampling crops, damage to fences and competition with livestock for forage (Hegel et al.2009). Other types of damage caused by elk include over-browsing of timber resources, vehicle collisions, nuisances and safety concerns due to habituation to humans.

Many causes for loss or decline of migration events arise from human influences that increase fragmentation, disturbance, deteriorate habitat quality and result in a loss of habitat connectivity (Berger 2004, Berger et al. 2006, Leu et al. 2008, Naylor et al. 2009, Sawyer et al. 2009).Although all the implications for disruption of migration are not well known, migration is important to the continuation of large, mobile ungulate populations (Bier and Noss 1998, Epps et al. 2005) and to predators that use elk as a food resource (Hebblewhite et al. 2006, Moorehouse 2010, Moorehouse and Boyce 2011, Nelson et al. 2012). Employing our growing knowledge of elk migration and movement patterns in management decisions is needed, even though it will be complicated because landscape management must also consider ecological, biophysical and social-economic processes important to other species besides elk (Bennet et al. 2011). Finally, conservation of migratory species requires identifying and mapping migratory routes (Thirgood et al. 2004, Sawyer et al. 2009, Strandberg et al. 2009) as well as understanding the role of individuals and environmental influences on migratory patterns (Alerstam 2006 and Bolger et al. 2008). My thesis provides new insights into the conservation of the migratory Castle-Carbondale elk herd by determining migration routes and associated metrics.

In southwestern Alberta the elk population is approximately 4,300 animals, separated into seven subpopulations, each having wintering and summering areas (Clark 1993, Jorgensen and Kansas 1992, Morgantini 1994). Five of the 7 herds are considered partially migratory based on their annual movements during the time period of my study (2007 – 2010). I chose to study the partially migratory Castle-Carbondale subpopulation because it had the highest sample size of collared elk. Secondly the home range of the herd is an area exposed to concentrated human activity from a wide variety of recreation and resource extraction activities (Muhly 2010, Northrup 2010). Finally, few elk migration studies have been conducted in areas with such a high influence of human activity from numerous sources. Quantitative data of elk migration are expected to be particularly important in this region due to this degree and types of human activity occurring on the landscape. Collared female elk were adults and juveniles, whereas only yearling

males were collared. Yearling males were collared to provide potential dispersal data and there were concerns within the study group that collaring of mature male elk could be detrimental to the elk during the rutting period when neck swelling occurs. It was possible the collar could become too tight on the neck resulting in negative consequences for the elk. The sampling regime intensity for elk in the Carbondale-Castle elk was comprised of 39 female elk and 14 male elk with their collars scheduled to collect GPS relocation fixes every 2 hours, 24 hours a day for a time period of 2 years, beginning in 2007 (Table 2-1). The age of elk varied from 1 year to 18 years.

If the dynamics of elk migration continue to be poorly understood, elk migratory behaviour could change, halt or become reduced in scope. It may result in more animals remaining on their winter range, creating new or increasing existing negative elk / human interactions and /or ecological damage such as overgrazing grasslands or crop damage (Hebblewhite et al. 2006, Ito et al. 2005). The population size could also be significantly reduced if migration were discontinued causing a shortage of food resources from too many elk on too small of a home range, resulting in over-use of some resources and changing ecological processes and loss of biodiversity through cascading effects (Ripple et al. 2001, Hebblewhite et al. 2006, Romme et al. 2011). High herbivore densities are also known to have negative impacts on plant communities, resulting in a reduction in biodiversity (Hebbblewhite et al. 2005). For these reasons, management agencies and resource extraction industries should be aware of the potential effects of human disturbance to migratory elk and take efforts to reduce disturbance.

PURPOSE AND OBJECTIVES

I studied the partially migratory Castle-Carbondale subpopulation comprised of approximately 650 elk (Clark 1993). I sought to delineate the migration route or routes used by Castle-Carbondale elk. The elk migrate up to 34 km straight line distance from their winter range, a montane / agricultural landscape to high elevation summer range on the Continental Divide in Alberta Canada. I hypothesized that:

- Elk would migrate along specific pathways each year without stopping over because the migration distance is relatively short, traversable by elk in a day or two.

- Fall migration would differ from the spring migration corridor.

From the potential results of my hypotheses testing I developed three objectives;

- If stopovers were used by elk, I would investigate their characteristics;
- Male and female seasonal migration stopovers would spatially differ, possibly from sexual segregation.
- If elk migrated on specific routes, I would use graph theory methods to assess the connectivity of the migration pathways of elk at local and regional scales.

Modeling and statistical analysis of elk global positioning systems (GPS) location point data were used to develop and support conservation planning for partially migratory elk herds in southwest Alberta. My program of study at the University of Calgary was interdisciplinary in nature providing an opportunity to combine resource management and research into my thesis. I have chosen to incorporate three disciplines: Biological Sciences, Geography and Resource Management into the design and implementation of my study.

THESIS STRUCTURE/CONTENTS

In Chapter Two I present a literature review of elk ecology, effects of human activity to wildlife, and applicable spatial ecology analysis techniques useful to this study. I identified methods to determine elk migratory phenotypes, spatial and geospatial ecology techniques to depict and understand migration route characteristics and investigate landscape connectivity for migration.

In Chapter Three I use the BBMM as an analytical framework (Sawyer et al. 2009) to identify: 1) a system of migration pathways and connected stopover sites for elk, and 2) prioritize population migration pathways based on their proportional degrees of use for 50 elk. My goal in Chapter Four was to use resource selection functions (RSF) to identify characteristics of stopovers by comparing used elk relocation points to randomly selected location points in the Castle-Carbondale elk home range. Chapter Five uses graph theory methods of least-cost path and/or current flow methods to investigate connectivity of elk migration routes for the Castle-Carbondale herd (local scale) as well as a regional scale analysis. In Chapter Six I use results of

all the thesis chapters to provide possible management strategies for conservation of migratory elk in southwest Alberta.

CHAPTER TWO: LITERATURE REVIEW

I present a literature review of elk ecology, effects of human activity to wildlife, and applicable options of spatial ecology analysis techniques useful to study elk migration. Methods are assessed to determine elk migratory phenotypes, spatial and geospatial ecology techniques to depict and understand migration route characteristics and investigate landscape connectivity for migration.

IMPORTANCE OF MIGRATIONS

Typically, migrating cervids in the temperate region select high elevation summer range and a low elevation winter range (Fryzell and Sinclair 1988, Sawyer et al. 2009). A downhill migration in fall to winter range is a response to weather conditions and a strategy to find wintering areas with shallow snow depth (Boyce 1991, White et al. 2010). Large herbivore migrations are universally considered vulnerable to human development (Berger 2004, Sawyer et al. 2009). The ability of animals to migrate is vital for the viability and maintenance of migrating populations. Halting or reducing migrations may result in a population decline of ungulates that can be amplified by additional disturbance events or increased predation pressure (Coulon et al. 2006, Hebblewhite et al. 2006, Harris et al. 2009, Voeten et al. 2009). When migratory ungulates are confined to one range, negative density-dependent effects may occur. This restriction to a single range can lead to reduced forage availability and quality (Christianson and Creel 2009). The highest quality forage is readily removed by dominant individuals or efficient foragers, leaving a more homogenous and less nutritious diet for other herd members (Mysterud et al. 2001, Nicholson et al. 2006). A lack of adequate nutrition will lead to reduced fertility and calf survival (Cook et al. 2004). Overgrazing by ungulates can negatively impact ecological processes, reducing grassland productivity, riparian area conditions, water quality and biodiversity (Frank and Goffman 1998, Stewart et al. 2009, Ripple et al. 2001, Romme et al. 2011).

Migration events are an ecological necessity for the existence of wide ranging populations and meta-populations, often essential to the genetics of these populations (Soule 1991, Coulon et al. 2006) and allow increased access to resources and habitat (Saher and Schmiegelow 2004). In some cases bottlenecks have developed in migration routes threatening future movement of species along the migration corridor (Williamson et al. 1988, Mahoney and Schaefer 2002, Ito et al. 2005, Berger et al. 2008). Maintaining connectivity between calving grounds, summer ranges and wintering grounds is expected to be important if not essential to migrating elk fitness and populations.

Much of the migration literature focuses on the event and process of migration; fewer efforts are dedicated to the ecological benefits of wide ranging grazers to ecosystems (Augustine and McNaughton 1998, Frank and Goffman 1998) or to the knowledge we could gain from studying functioning migration routes to advance corridor or linkage ecology (Chetkiewicz et al. 2006). Migratory ungulates serve an important stabilizing function on ecosystems by their grazing pressure on plants (Kie and Lehmkuhl 2001). Halting of migration can have destabilization effects on vegetative communities and species interaction (Kie and Lehmkuhl 2001) causing significant reductions in biodiversity (Manier and Hobbs 2007). Finally, effects of human-related disturbances on wildlife energetics, demography and habitat selection is particularly important among temperate ungulates whose survival depends on minimizing energy expenditures during winter (Hobbs 1989, Sawyer et al. 2006, Parker et al. 2009). Land and wildlife managers require information of migration timing, characteristics and corridor or travel routes used to incorporate into conservation of migrating animal populations and pathways. Once the migration corridors are known the reasons why elk use these areas can be explored and alternatives for management can be developed. Not only is this important for current elk management practices but for future management of numerous species, for maintaining connectivity of migration corridors and as a strategy to provide options for animals to adapt to changing climate (Soule et al. 2003, Minor and Urban 2008).

ROCKY MOUNTAIN ELK ECOLOGY AND LIFE HISTORY

Of the North American ungulates, elk are one of the most widely-distributed and frequently studied species. As a very common species they capture the curiosity of people due to their

tendency to be observed in impressively large herds, their regal stature as they alertly respond to human presence, and their apparent ability to adjust to human activity. These qualities are intertwined with their response to human disturbance, their selection of ecotone environments, topographic features such as slope, elevation, aspect and predation risk are also recognized to influence elk habitat selection patterns (Edge et al. 1987, Skovlin et al. 2004). Results of recent elk research are predominantly reporting elk avoidance responses to disturbance from human activity and resource development (Van dyke et al. 1997, Rowland et al. 2000, Frair et al. 2008, Hebblewhite and Merrill 2009, Naylor et al. 2009, Sawyer et al. 2009) potentially affecting their fitness and distribution. To a lesser degree, this response to human activity is true in areas of no hunting such as private lands and legislated protected areas (Rogala et al. 2011).

As an ecotone species, elk prefer a mosaic of forests and open grasslands providing security cover from predators and human disturbance, while corridors or secluded landscapes provide travel routes or security between seasonal habitats (Naylor et al. 2009). Travel corridors are essential for elk by providing security during travel or access to the best available habitats. In the case of elk migration, they may require a pathway with forage and stopover locations to and from seasonal ranges, similar to migrating deer (Sawyer et al. 2009). This study of Rocky Mountain elk in southwestern Alberta investigates the phenomenon of elk migration.

The elk population southwestern Alberta is comprised of three phenotypes defined by the animal's seasonal distribution on the landscape. These phenotypes are resident, migratory and disperser (Boyce 1991). Elk with seasonal home ranges overlapping entirely or predominantly are defined as resident elk. Migratory elk move from a winter range to a separate summer range and return to the same winter range, whereas dispersing elk will leave the winter range to another separate seasonal range, not returning to the original wintering area (Boyce 1991). Some elk populations are partially migratory, where one segment of a population undertakes seasonal migration and the other remains on a single range year round (Lundberg 1988, Hebblewhite et al. 2006). A majority of the elk population in southwestern Alberta is partially migratory.

To study elk migration and their movement patterns it is beneficial to have an understanding of what compels elk movement on the landscape over space and time (Willems and Hill 2009). This section of the literature review outlines relevant information regarding what is known about

how and why elk respond to landscape features, how they alter their movement in response to time of day, predator presence, landscape composition, and forage. Human uses of the landscape such as roads, agriculture, and residential development also affect elk distribution on the land, possibly reducing elk accessibility to forage and an increase in vigilance (Lung and Childress 2007) which in turn has the potential to reduce fitness (Rowland et al. 2000, Boyce et al. 2010, Stewart et al. 2010). In other cases human activities may improve elk habitat (Frair et al. 2008, Rumble and Gamo 2011). To present these concepts, I will describe applicable movement strategies used by elk to fulfill their life history requirements. The latter chapters provide a discussion of how these strategies relate to, or are expressed in, elk migration phenotypes and methods of analyses.

ELK BEHAVIOR AND FORAGING STRATEGIES

Understanding elk movement involves interpreting elk behaviour, or what motivates elk to move across the landscape. Patterns of elk activity are known to be circadian cycles between foraging and secure resting habitats with dawn and dusk shifts (Collins et al. 1978, Irwin and Peek 1983, Green and Bear 1990, Ager et al. 2003, Boyce et al. 2009). Evolutionary theory provides insights into a primary goal of elk which would be to optimize the use of available resources to ensure reproductive success (Geist 2002). Elk are ecological generalists that do not expend much energy contesting feeding sites with other animals, but respond by moving on to another area. Theory suggests an animal should remain in an area as long as the marginal rate of forage intake is greater than the average forage value of the landscape (Charnov 1976), and that foraging and movement strategies influence energy budgets and fitness (Moen et al. 1997). Efficient use of energy resources must be balanced with risks of predation (Kie 1999, Brown and Kotler 2004, Fortin et al. 2005), landscape structure (Crist et al. 1992, With et al. 1994), processes such as circadian rhythms (Bascompte and Villa 1997, Bergman et al. 2000, Morales and Ellner 2002) and behavioral states such as resting, foraging and relocating (Morales et al. 2004, Frair et al. 2005).

The distribution of migratory elk in the Rocky Mountains shifts seasonally to areas of available food supply (Merrill 1994). The winter diet is typically defined by snow conditions (Boyce 1991). Elk survive through the winter on grasses, particularly on wind-blown ridges, and move

to ranges where snow depths are lowest. If snow depths increase and grass is not accessible, elk will switch to eating tall shrubs or conifers (Singer 1995). During the spring, elk will begin grazing on plant species developing new growth such as grasses and in summer increase consumption of forbs or shrubs. Fall forage for elk includes dried grasses or re-growth of some grasses such as bunch grasses (Cook 2002, Smallidge et al. 2010). Opportunistically feeding on rich nutrients and biomass from forage is one of the reasons why elk travel, and this combination may be related to topographical relief and following an elevation gradient (Morgantini and Russel 1983, Hebblewhite and Merrill 2008, Hebblewhite and Merrill 2009, Webb et al. 2011).

Weather and topography also interact to affect elk behavioural foraging strategies. For example, landscape heterogeneity frequently originates from diverse topographic relief that affects the distribution of soils and microclimatic conditions associated with elevation, aspect, slope and drainage (Boyce 1991, Hedenstrom 2003). These factors influence local vegetation and affect patterns of elk habitat use due to food preference and availability. An additional important factor is elevation due to its relationship with temperature and precipitation, which is directly related to snow accumulation and plant phenology (Morgantini and Hudson 1989, Singh et al. 2010). Habitat use by elk may vary with elevation in different seasons. Elk use upper slopes in all seasons but in winter elk prefer upper south-facing slopes that are free of snow due to the effects of wind and solar radiation (D'Eon and Serrouya 2005). During summer elk use upper landscape locations related to cooling winds, visibility and cover type (Nelson and Burnell 1975).

ELK BEHAVIOUR AND REPRODUCTIVE SUCCESS

The goal of all animals is to maximize fitness. Mature male and female elk differ in their selection of habitat and choice of movement patterns due to different behavioural goals (Geist 1998). An important goal of the female is to guarantee security for her calf. Therefore, female elk may compromise access to the highest value food sources in a tradeoff to provide security for its calf in a foraging gain-predation risk trade-off (Geist 1998). Bulls, in contrast, seek out high quality food over security to provide the nutrients to reach large body and antler size important for successful breeding. Such differences in emphasis should result in spatial segregation of females and males (Geist 2002).

Reproductive success and timing is determined by the availability of nutrient rich food needed for gestation and lactation. In cold, high latitudes and altitudes, births must happen just before vegetative green up in early summer, thus providing the female with a high quality food source to produce rich milk for the calf (Cook et al. 2004). This in turn confines the timing of the rut to the latter part of September, as gestation takes 250 days with peak calving occurring in early June during a narrow window of abundant rich forage (Giest 2002). Calves born too early will suffer from poor milk yield and those born too late may not grow to a size where they are able to live through the winter (Geist 2002, Cook et al. 2004).

A breeding time period demands incredible energy expenditure by the bulls. This selects for bulls able to store large amounts of fat to support breeding and carry over after the rut, as the rut is a time period of reduced feeding and high energy expenditure. To be able to acquire the excess fat reserves for survival, elk appear to exhibit foraging strategies necessary to acquire an adequate supply in quality and quantity of food by being driven to high food consumption in the summer (Geist 2002).

MIGRATION OF ELK: INFLUENCES OF BEHAVIOUR, FORAGE AND WEATHER

Hypotheses for Migration

Patterns of migration have evolved in animals to take advantage of spatial and temporal variations in the environment. Selection should favour individuals that migrate if by migration their reproductive success is enhanced (Fryzell and Sinclair 1988). Reductions of predation risk and diet enhancement are two common hypotheses for migration (Fryzell and Sinclair 1988).

Theoretical models (Cohen 1967, Fryzell and Sinclair 1988) and the concept of evolutionarily stable strategies (Parker and Stuart 1976) are used to explain why individuals migrate. A common denominator of most models is reproductive success, and lifetime reproductive success is a function of both survivorship and birthrate. The adaptive significance of migration may be best understood by the forces of selection influencing these life-history parameters (Cohen 1967, Fryzell and Sinclair 1988). Quality and availability of forage affect survivorship and birthrate, and so does the risk of predation. Maximizing intake of nutrient rich forage and avoiding

predation are described as possible factors encouraging migration (Taylor and Taylor 1977, Albon and Langvatn 1992, Robinson et al. 2010).

Fall migrations for many populations of elk appear to be strongly influenced by snow depth, plant phenology, elevation, topography, and hunting pressure (Boyce 1991, Irwin 2002, Boyce et al. 2003, Smith 2007). The main driver causing migration to low elevation in fall is snow (Boyce 1991, Albon and Langvatn 1992, Hebblewhite et al. 2008). The mechanism of migration in spring is less clear. One important evolutionary influence for migration behavior may involve the length of time elk can have access to high quality nutrient rich food sources (Morgantini and Hudson 1989, Boyce 1991). High elevation vegetation on summer ranges is comprised of much higher nutritional value than food sources at lower elevations (Hebert 1973, Albon and Langvatn 1992) and elk distribution can be predicted on the basis of spring vegetation index values (Singh et al. 2010, Smallidge et al. 2010). This represents the forage maturation hypothesis which is commonly used to explain uphill migration in spring (Fryxell and Sinclair 1988) and was tested for elk and red deer (Hebblewhite et al. 2008, Albon and Langvatn 1992). However, theories describing the combination of presence of nutritious vegetation and altitudinal migration have yet to demonstrate increased fitness to migrating elk (see Mysterud et al. 2001).

Predation risk may also be an important function in migration (Hebblewhite and Merrill 2007). Migration could serve as a means to avoid areas with high predation risk (Edwards 1983, Festa-Bianchet 1988). The predation risk avoidance hypothesis could be applicable to migration with animals moving seasonally away from areas of high predation risk.

Another hypothesis, the avoidance of competition hypothesis which suggests that migration strategy could be controlled by genetics or a density-dependent selection which may result in a partial migration of a population. This could be conditional where genetics allows for adoption of a range of migratory behaviours (Fryzell and Sinclair 1988). Partially migratory populations of elk are found in North America and have been used to investigate if migration has fitness benefits for elk (Hebblewhite and Merrill 2009). A prediction of the avoidance competition hypothesis is that populations of partially migratory ungulates may have an increasing proportion of migrants at higher density (Mysterud et al. 2012).

Much of the discussion with population density is the lack of a good measure of variation in habitat quality which is necessary to assess a level of competition (Mysterud et al. 2012). Density dependence in a segment of migrants may be a good test of competition avoidance (Mysterud et al 2012). To access the effects of landscape structure on animal distribution one could investigate elements likely to reflect habitat quality, such as population density, home range size, and survival with variables such as vegetation structure and animal density using the ideal free distribution theory as a framework (Stewart and Komers 2012, Thompson and Gese 2012). According to the ideal free distribution, high quality habitat should be occupied to a certain threshold at which point completion or social structure forces animals into poorer quality areas (Thompson and Gese 2012).

For many species partial migration is common. It been noted in studies of elk and red deer (*Cervus elaphus*) (Woods 1991, Mysterud et al. 2011), moose (Alces alces) (Andersen 1991), mule deer (*Odoicoleus hemionas*) (Nicolson et al. 1997), and white-tailed deer (*Odocoleus virginianus*) (Forbes and Theberge 1995). Partial migration may be sustained by a demographic balancing of the two migratory methods (Lundberg 1988). Individual-based animal strategies may switch between migrant or resident states due to population density or with varying resource abundance (Lack 1968). Another strategy is to use a state-dependent migrant or resident strategy based on age or body condition (Adriaensen and Dhondt 1990, PetezpTris and Telleria 2002). The third possibility is a population level strategy where animals are migrant or resident and proportions are determined at the population level by density-dependent fitness (Lundberg 1988). Few studies have found a strong genetic basis for migration in ungulates (see McDevitt et al. 2009). When migration is based on the forage maturation hypothesis or predation risk, partial migration could be maintained where residents limit possible demographic costs of foregoing migration, even if a low frequency of residents is sustained in the population (Fryxell et al. 1988). Alternatively, the loss of migration could be expected when residents make risk-forage tradeoffs to reduce risk and achieve high forage on winter range year round (Hebblewhite and Merrill 2009). Understanding such dynamics would provide valuable insights into declines in migratory behaviour.

Elk Migration and Predators

Elk use a number of strategies to reduce the risk of predation and, in turn, increase survival (Winnie et al. 2006). In response to predation risk, animals increase vigilance (Lima and Dill 1990), reduce foraging time or movements (Sih and McCarthy 2002), change group size (Creel and Winnie 2005) and undertake habitat shifts to less risk areas or to refuges (Blumstein and Daniel 2002, Proffitt et al. 2010). One method to shift habitats to avoid predation is to migrate. Many North American large predators are unable to undertake long distance movements for prey during portions of the year because the predators must remain near their den sites to look after young until they are mobile (Fryzell and Sinclair 1988, Boyce 1991, Creel 2002).

Elk distribution is affected by the trade-offs between the risks of predation and the requirement to access the most nutritious food sources available (Robinson et al. 2010). In summer, forage is typically plentiful, resulting in elk having the option to move away from predators with low consequences to fitness. In contrast, predation threats on the winter ranges where forage is limited may force elk to be exposed to higher predation risk in favour of forage availability (Robinson et al. 2010). In other situations elk may stop migrating from winter ranges to summer range possibly because the winter range has greater security from predators due to the presence of humans (Hebblewhite 2006). In the case of hunting, elk and other animals adjust to predation risk by moving into areas of high security such as forest cover, rugged terrain, low road density areas, low traffic volumes, (Morgantini and Hudson 1985, Unsworth et al. 1998, Dill et al. 2003, Wright et al. 2006) or lands designated 'no hunting' (Vieira et al. 2003, Proffitt et al. 2010).

ELK MIGRATION, DISTURBANCE AND MANAGEMENT ISSUES

Migrating elk provide ecological benefits to the land when they move off winter range to the summer range allowing vegetation regrowth to occur. This cycle of grazing can work well in a winter range only used by wild ungulates, but frequently elk home ranges occupy land found in areas of multiple land-uses (Boyce 1991) where competition for resources can occur. Combined with the difficulties of elk competing for forage with cattle, elk can cause crop depredation problems, eating stored hay or grain crops in agricultural fields creating both direct and perceived conflicts (Hegel 2009). As well as direct competition, overgrazing by wild and domestic animals of a grassland ecosystem may reduce the viability of the grassland system,

reducing its productivity for both grassland dependent wildlife and the ranching industry (Frank and Goffman 1998, Kie and Lehmkuhl 2001). Mitigating or solving wildlife impacts to ranching activities is challenging. Wildlife damage management is complex because it involves biological, physical, economic and socio-cultural factors (Slate et al. 1992). Such diverse ranges of issues are why the increasing use of the land by people and the belief that people rights have priority over wildlife needs of habitat will continue to make management of wildlife complex (Cherney and Clark 2009).

Ecological Effects and Management of Roads

One of the most widespread modifications of the natural landscape has been from the construction and maintenance of roads (Forman 2003). Roads affect ecosystems in several ways, including: increased wildlife mortality, modification of animal behaviour, changing the physical environment, reduction of genetic interchange, spread of exotic plant species, and limiting dispersal of young (Beier 1995, Gerlach and Musolf 2000, Trombulak and Frissell 2000, Epps et al. 2005, Proctor et al. 2005). Roads with high human use have the potential to modify animal behaviour by causing animal avoidance of roads, resulting in a reduction in permeability of landscape (Gibeau et al. 2001, Dodd et al. 2007). Such changes in animal behaviour can result in future fragmentation or isolation of populations.

There are two main categories to describe the effects of roads on elk: indirect effects on habitat use and direct effects on individuals and populations. Roads are known to affect forested ecosystems, and they are the primary cause of wildlife habitat fragmentation (Forman 2003). Areas with high road density may not have patches of forest cover large enough to be effective habitat for elk, particularly in hunted populations (Rowland et al. 2004). Direct effects include: mortality from vehicles, elk avoiding areas near travelled roads, vulnerability to mortality from legal and illegal activity increases as road density increases. In areas of high road density, elk demonstrate evidence of higher levels of stress and increased movement rates (Lyon 1979, Rost and Bailey 1979, Morgantini and Hudson 1979, Wisdom et al. 1986, Frair et al. 2008). Management strategies that eliminate vehicle traffic on roads can reduce the indirect effects of roads (Witmer and deCalesta 1985) and could increase survival and reproduction due to reduced energy expenditure and less vulnerability to hunting (Cole et al. 1997, Shively et al. 2005),

provided the closure keeps out vehicles. Extensive shifts in elk distribution away from roads are a wide spread phenomenon, and at a landscape level have the potential to affect elk carrying capacity and elk distribution (Rost and Bailey 1979, Lyon 1983, Edge and Marcum 1991, Rowland et. al. 2000, Naylor et al. 2009).

Persistently high levels of disturbance from recreation and human developments on elk home ranges have the potential to impact ungulate reproductive performance (Yarmoloy and Geist 1988, Joslin and Youmans 1999, Phillips and Alldredge 2000, Wisdom 2007, Stankowich 2008) and alter migratory movement patterns. Elk will move from areas of high levels of disturbance to areas of low disturbance (Proffitt et al. 2010). In land management regimes of multi-use such as SW Alberta the movement of elk to areas of lower human disturbance might result in wildlife spending more time on private lands where there is low disturbance due to limited public access in comparison to public land ranges that often have much higher levels of human disturbance (Joslin and Youmans 1999, Northrup 2010). To find solutions to such issues, it will be necessary for management agencies to partner together in developing policies to take into account the needs of people, wildlife and land conservation (Brook 2007). Landscape management to reduce fragmentation and improve connectivity for wildlife movement is an essential concept to implement into the wildlife management solution (Carroll et al. 2011).

LANDSCAPE CONNECTIVITY

Connectivity of landscapes is considered to be important to the movement of genes, individuals, populations and species at a variety of time scales (Minor and Urban 2008). Over a short time period, connectivity may affect successful juvenile dispersal and limit the possibility of recolonization of unoccupied patches of habitat. At medium scales of time it may influence the ability of animals to migrate or persistence of metapopulations and at the longest time periods it could influence the ability of species to increase or modify their range due to climate change (Minor and Urban 2008).

Many North American habitats are becoming fragmented with increases of fragmentation expected to occur due to development and land use. Prugh et al. (2008) proposed fragmentation to be the greatest threat to most species in the temperate zone and Noss (1991) has stated it is the one greatest threat to biodiversity. Fragmentation can also restrict animal movements for

foraging, breeding, migration and dispersal making its effects a global issue for conservation of flora and fauna (Bennet 2003). As fragmentation of habitat continues, isolation of habitat patches increases and the need to restore landscape connectivity becomes greater (Noss 1987, Ogen 2012). Combining potential global changes due to climate change will confound the effects of fragmentation by reducing ecosystem and habitat resilience. This may further restrict a species ability to move to suitable habitats in response to climate change (Soule et al. 2003). Increased habitat fragmentation due to the impacts of climate change could result in socio-economic impacts for the costs of replacing lost ecosystem services such as water purification and retention or flood/erosion prevention (Kettunen and ten Brink 2006).

To understand and predict solutions for connectivity, analyses have been developed based on graph theory methods, euclidean distance and others (Calabrese and Fagan 2004). Graph theory is commonly used in connectivity theories and corridor delineation methods (Chetkiewicz et al. 2006, Urban et al. 2009). Graphs are a proven method to understand meta-populations and provide a means to undertake connectivity analyses of landscapes (Urban et al. 2009, Beier et al. 2010). Graph theory seems suitable for determining the connectivity of migratory habitat (O'Brien et al 2006). In addition the combination of graph theory and RSF models may provide a means of quantifying connectivity because it combines spatial topography with resource selection and is particularly useful in scenario testing by predicting the effects of adding or removing landscape elements (Chetkiewicz et al. 2006).

Scenario-testing is considered a tool for predicting effects of possible future developments and is a way to forecast what may occur considering long-term consequences of potential land use decisions. Identification of bottlenecks or sinks provides information of potential areas for restoration such as removal of active roads which may help to reduce or increase connectivity.

It has been suggested maintenance and restoration of connectivity between patches of high quality habitat is an important goal for conservation of animal populations (Rayfield et al. 2010). The increasing awareness of the negative effects of habitat fragmentation on ecological systems has improved efforts to reduce current fragmentation of natural systems as well as development of analytical tools required to predict and evaluate the effects of developments to a land base (Theobald et al. 2006).

Spatial Ecology and Modeling

A variety of statistical / modeling methodologies have been used to describe and study elk migratory behaviour (White and Garrot 1990, Felix et al. 2007). Defining migration is a complex task because migration characteristics vary between species, and individuals within the species. A number of definitions have been used in research projects with methods to determine elk migration phenotype. A common defining characteristic of migration is a shift in use of habitat, although this definition is complicated by different sex and age classes of ungulates potentially selecting habitats differently (Mysterud 1999, Bowyer and Kie 2006). A basic and frequently used definition of migration is presented by White and Garrot (1990). They define migration as a regular, round trip movement by individuals between two or more areas or seasonal ranges. A variety of methods may be used to define separation of seasonal ranges including minimum convex polygon (MCP) (White and Garrot 1990, Mysterud 1999), spatial distributions of median summer locations using complete linkage Euclidian distance (White et al. 2005), cluster analysis (White et al. 2007), and 95% kernel analysis (Felix et al. 2007). No minimum distance between seasonal ranges has been established as a standard in the definition of migration.

Seasonal Range Home Range Estimation

Migratory elk can be defined as one of three phenotypes defined by the animal's seasonal distribution on the landscape. These phenotypes are: resident, migratory and disperser (Boyce 1991). Elk with seasonal home ranges overlapping entirely or predominantly are defined as resident elk. Migratory elk move from a winter range to a separate summer range and return to the same winter range, whereas dispersing elk will leave the winter range to another separate seasonal range, not returning to the original wintering area (Boyce 1991). Some elk populations are partially migratory, where one segment of a population undertakes seasonal migration and the other remains on a single range year round (Lundberg 1988, Hebblewhite et al. 2006). I use seasonal home range analyses techniques to define each phenotype of elk.

Two frequently used methods of home range estimation are MCP and kernel density estimation. Kernel density estimates are the most commonly used method to assess and visualize animal

home ranges (Laver and Kelly 2008, Kie et al. 2010). With this method the most important issue is choosing an appropriate smoothing parameter (bandwidth). Bandwidth is critical in determining the outer contours of the home range estimate and it also affects estimation of the utilization distribution (Seaman and Powell 1996). A tested concession to reduce over-smoothing is to set the bandwidth at .70 (Bertrand et al. 1996) or .80 (Kie and Boroski 1996, Kie et al. 2002). Home range analysis is a fundamental methodological concept, with considerable discussion regarding how it is best measured (Kenward 2001, Kie et al. 2010, White and Garrot 1990). Accuracy of home range estimates is influenced by a number of artifacts of sampling, including the time between consecutive locations (Swihart and Slade 1985), the number of observations used to determine the analysis (Borger et al. 2006), and the technique used to collect data. A principal step in using home range analysis for radio telemetry studies is establishing an appropriate sampling protocol. Sample size and autocorrelation of data influence the estimation of home ranges. Two types of sample size need to be considered, the first is biological sample size; the researcher assumes that data are representative of the movements exhibited for the defined time period sampled. To ascertain the validity of the collected data, knowledge of the biology of the animal is required. Second, having an appropriate statistical sample size provides the best results from the home range estimate. Considerable discussion exists in the literature regarding the use of home range concept, its analyses and its usefulness to biological studies (White and Garrot 1990, Otis and White 1999). Autocorrelation of animal movements and the concept of time to independence has been a recent focus of scrutiny because of their influence on the results of statistical analyses (Powell 2000, Kenward 2001). However, subsequent evaluations have demonstrated removing autocorrelation can remove the biological signal of interest (De Solia et al. 1999, Otis and White 1999). In fact, recent studies illustrate we need to understand autocorrelation better, as a large amount of biological information is contained in the spatial and temporal autocorrelation structure of animal movements (Cushman et al. 2005, Kie et al. 2010). Animal behaviour is nearly always temporally autocorrelated; it is suspected autocorrelated location points will show more relevant behavioural information than independent data points would (Gurarie et al. 2009, Boyce et al. 2010). Others believe the structure of autocorrelation data should be understood for it may provide insights into interpreting the data (Cagnacci et al. 2010). For example, spatial data collected by GPS telemetry is often autocorrelated because of the structure of the topography, geology, soils,

hydrology and vegetation (Boyce et al. 2010). For this reason much of the spatial autocorrelation in animal use data can be attributed to the characteristic of highly autocorrelated landscapes.

Three methods are presented to explore the use of models attempting to include behavioural and movement processes of habitat selection: graph theory, step selection functions and Brownian bridge movement model. A fourth method, resource selection models reflect behavioural and movement processes and are popular resource use models.

Resource Selection Function

Resource selection functions (RSF) are models that estimate the probability of use of a resource and are able to achieve statistical rigor because the models are constructed using data (Boyce et al. 2002). Studies using RSF compare resource use of animals to the availability of those resources on the landscape (Manley et al. 2002). Models of RSF can be designed from presence / absence data, but in telemetry studies this may be challenging because lack of telemetry relocation data does not necessarily signify lack of use. Boyce et al. (2002) proposed the use of presence / available data instead of presence / absence data. A system of three different resource selection study designs for telemetry studies that incorporates used versus available data was suggested by Manley et al. (2002). Design I states available and used resource units are both defined for the complete population of animals being studied. For Design II, the available resource units are assumed to be the same for the whole animal population but the used units are set at the individual level. In Design III available and used resource units are identified for individual animals.

A resource unit is defined as a sampling unit of the landscape (e.g. pixel, or grid cell). It is comprised of predictor variables (covariates) which are habitat attributes that may be used to predict the relative probability of use for a resource unit (Manley et al 2002). Response variables can be stated as animal responses such as resource selection, home range use or survival, and predictor variables are usually environmental conditions such as elevation. The modeling process searches for the most parsimonious model from a collection of possible models. The most parsimonious model is described as model with sufficient parameters to avoid bias, but not too many that precision are lost (Burnham and Anderson 1992). Parsimony can be measured by

statistical indices such as Akaike's Information Criterion (AIC) and the model with the lowest AIC is deemed to be the most parsimonious model from a group of models. Models attempt to establish a solid basis for understanding a system; they are simplifications of real world systems and have clearly stated assumptions that can be used for testable hypotheses (Starfield 1997).

There are a number of sampling designs to estimate an RSF, for example, a random sample of resource units could be drawn and evaluated for the presence or absence of an animal (Boyce and McDonald 1999). Model coefficients can be estimated using logistic regression if occurrence is recorded as absence / presence (0,1), or a link function could be used for count data, such as Poisson regression or zero-inflated Poisson regression (Nielson et al. 2005). An alternative method is to use a sample of occupied resource units to contrast with a random sample of landscape locations using logistic discrimination function (Decesare and Pletscher 2006, Johnston et al. 2006). The predictive ability of the RSF can be assessed using the *k*-fold cross-validation methods outlined by Johnston et al. (2006).

The RSF can be used in a GIS to plot the relative probability of animal use across the study area at multiple scales (Boyce 2006, Bowyer and Kie 2006). This depiction of landscapes as a probabilistic function is an alternative to binary maps of habitat versus non-habitat. Such methods reflect a more complex understanding of the patterns of habitat use compared to a basic binary characterization of habitat. In addition, the models may be used to detect habitat associations of animals across scales (Boyce 2006). RSF models provide little insight about the movement of animals, but they do enable the researcher to depict habitats that are probably occupied by the study animal (Young and Shivik 2006). Using RSF's in GIS provides a map of areas of high probability of use and their proximity to one another, including areas of lower probability of use.

However, some habitats identified by modeling as potential habitat may not necessarily mean the habitats are productive and in the worst case scenario they may be a sink or obstacle to movement (Kristan 2003), particularly if good habitat become sinks (Ronce and Kirkpatrick 2001). Although it is possible, or even likely, habitats may at times represent low quality habitat that may still allow animals to move through them (Haddad and Tewksbury 2005).

RSF models are useful tools in attempting to understand habitats used and preferred by animals. Movement processes such as migration are determined in animals by a need for forage, to avoid predators, to utilize seasonal resources, to find mates, and to expand ranges (Kamler et al. 2007). Since movement is an obvious component of migration and dispersal it would be useful to include it in the modeling process. Until recently, incorporating movement and behaviour in models has been limited, partially due to the difficulty of quantifying them.

Graph Theory and Resource Selection Function

RSF's have been designed to predict areas where animals have a high likelihood of occurrence (Chetkiewicz et al. 2006). Areas of high RSF can be used to generate nodes or patches of habitat, and then the inverse of the RSF can be used to produce a cost surface as a substitute of movement using least-cost path analysis. The paths are validated using paths from out-of-sample GIS location data. The modeling process aligned well with the GPS data movement paths, validating the results (Chetkiewicz et al. 2006) . Graph theory is usually a depiction of habitat as nodes making it possible to identify the nodes using a variety of techniques.

Step Selection Functions

Another method of combining movement process and landscape pattern in modeling applies conditional logistic regression to quantify movement probabilities on landscapes using step selection functions (SSF). The analysis technique is similar to RSF's but instead of characterizing telemetry relocation data points in an RSF, it compares steps, defined as a segment between animal telemetry locations points on the land (Fortin et al. 2005). These segments or steps are compared with random steps from the same starting point to model the effects of landscape heterogeneity on movement and areas of high movement probability. Using this method, researchers determined elk movements were affected by roads, cover and wolf predation risk (Fortin et al. 2005). As well, high movement probability quantified by the SSF may be used to investigate distance and direction of movement in a defined landscape which would be valuable for linkage or corridor design (Chetkiewicz et al. 2006). Such analysis techniques and modeling methods would be useful for understanding animal migration as well.

Brownian Bridge Movement Model

Tracking a continuous path through space and time is the best method of quantifying movement, but most animals cannot be tracked this way (Turchin 1998). For most wildlife studies the only alternative is to use techniques such as GPS telemetry to collect locations at discrete intervals along the path. Until recently the most common method of depicting these movement pathways was to connect the location points with a line segment to depict the route (Berger and Berger 2006). Depicting animal movements using Brownian bridge movement model (BBMM) was first done by Bullard (1999) in presenting animal home ranges. Horne et al. (2007) further developed the model to use telemetry location points and associated error to develop a maximum likelihood means for empirically estimating a variance term related to the animal mobility. The BBMM is dependent on time-specific location data and the distribution of location error from telemetry which is assumed to be normally distributed (Horne et al. 2007). An empirical estimate of variance may be determined from location data used in the BBMM by assuming the path connecting any two location points is a Brownian bridge.

BBMM is a method to model animal location points in space and time. It is a continuous-time stochastic model of movement where the probability of being in an area during the time of observation is conditioned on starting or ending locations. A BBMM is very applicable to animal location data obtained by GPS or Very High Frequency (VHF) device with short time fix rates. The process provides an empirical estimate of the movement path of an animal using distinct location points collected at relatively short time intervals. The model also calculates utilization distribution connecting each pair of successive locations, which is an estimate of the relative time spent in an area during the time interval between those locations.

The BBMM is a good fit for describing space use of animals during migration or dispersal (Horne et al. 2007, Sawyer et al. 2009). It models the uncertainty in the movement path between telemetry location fixes along the migration path (Horne et al. 2007). Using location data collected at short time intervals, the model spatially depicts important attributes of migration routes such as stopover sites, movement corridors and the landscapes and habitats used for migration (Sawyer et al. 2009). The model has a larger focus on estimation rather than prediction like state-space models for analyzing and predicting animal movements (Morales et

al. 2004, Jonsen et al. 2005). BBMM is based on the properties of a conditional random walk between locations (Codling et al. 2008). Most animal movement is not truly random, so the use of a model based on stochastic movement is justified (Turchin 1998, Horne et al. 2007). When there is no other information available on how an animal moved from one point to another, the Brownian bridge can be used as an approximation of the actual movement path. As the time period between location pairs increases, the possibility of violating the assumption of random movement is more likely. Once this occurs, random movements between locations will become more and more unlikely and are more likely to reflect a biased random walk than a simple random walk (Horne et al. 2007).

This may lead one to ask; what is the maximum acceptable time interval between locations? The developers of the model stated there is no single answer that will apply to all situations (Horne et al. 2007), but some factors will be related to differing animals mobility. For a more mobile animal the utilization distribution will be less certain of the movement pathway than an animal which is less mobile. So until these relationships of movement are further understood the authors recommend users thoroughly evaluate if the assumption of a conditioned random walk with a constant movement rate represents their data (Horne et al. 2007). Taking these suggestions into consideration the model was developed using data with location fixes every seven hours so one could assume, as did Sawyer et al. (2007) that it would work with 2hr location intervals. Another model assumption is that the distribution of location error was normally distributed and used a single estimate of the variance. Individual variance can be used for each pair of points in the movement path. The calculations may be simplified by using a single estimate of the Brownian motion variance for all pairs of locations, as done by others (Sawyer et al. 2009, White et al. 2010). The probability distribution calculation of the animal movement path is dependent on the distance between location points in space and time, the error found with each location point, and the mobility of the animal (Horne et al. 2007). The one parameter a researcher can consider in the study design is the time interval between locations. A lower amount of time between successive points reduces the uncertainty of the actual path.

LANDSCAPE CONNECTIVITY ANALYSES

Graphs are built of nodes (points) and edges (lines connecting the points). Two nodes joined by an edge are considered connected. Habitat patches on a fragmented landscape are considered nodes, with edges between considered possible movement pathways. These basic characteristics of graph theory indicate why it has become an important tool in determining habitat connectivity for conservation planning (Urban and Keitt 2001, Beir et al. 2010, Chetkiewicz et al. 2006).

Patch connectivity is commonly calculated as a complex function of the cost to move between patches (Tischendorf and Fahrig 2001). These costs are usually considered to be a function of the distance between patches. A simple and often used measure is the Euclidean distance or the shortest distance from a patch to its nearest neighbor (Moilannen and Hanski 2001). Other studies use more complex methods where all surrounding patches within a dispersal distance contribute to its connectivity, in an isolation-by-distance manner (Hanski 1994). There is a rudimentary understanding that in a landscape mosaic the matrix in between habitat patches such as corridors, barriers, elements of fragmentation and land cover, to name a few, is an important factor in determining movement of animals among patches (Richetts 2001, Schadt et al. 2002). Habitat connectivity is a concept that forecasts the possibility of an animal to travel among high quality habitat patches considering both the spatial arrangement of the landscape and the animal's movement behaviour as it responds to the habitat spatial structure (Taylor et al. 1993, With et al. 1999, Brooks 2003, Fahrig 2007). Current studies on habitat connectivity have described the importance of the relationships between the spatial structure and quality of matrix between high quality habitat patches (Richetts 2001, O'Brien et al. 2006). The decision of what path the animal will take is ultimately dependent on the animal's behaviour and ability to move through lower quality matrix structure (D'Eon 2002, Belisle 2005). The concept of including aspects of the landscape matrix besides the presence of habitat needs a shift from a structural to a functional connectivity measure because the effect of different landscape elements on dispersal is species and behaviour specific.

To be effective, categorization of functional habitat connectivity needs to evaluate a landscape with consideration of an animal's perception of habitat connectivity (Wiens 1989). An animal's awareness of landscape spatial structure is expected to be primarily determined by aspects of

fitness including mortality and reproductive success. Physical effort (Stevens et al. 2004) and energy expenditure are two attributes that could affect fitness (Drielsma et al. 2007) experienced by individuals using a variety of land cover types (With et al. 1997, Driezen et al. 2007). Cost value represents the permeability of a grid cell for the movement of an individual species (Villalba et al. 1998) within the framework. Permeability stands for the fraction of individuals that would not be able or willing to cross the specific landscape attribute. It is not a measure of speed, it is a measure of the reluctance to use habitat for movement (Schadt et al. 2002). A method to quantitatively describe movement behaviour may be accomplished by applying specific animal cost values of habitat to the matrix to reflect the ecological quality of habitat at each cell to assess the cost to an animal moving through the matrix. Cost values are frequently a representation of a number of environmental variables applicable to animal use of habitat such as vegetation cover type, slope, water, elevation, roads and human developments.

Many studies assess cost values based on expert opinion (Clevenger et al. 2002, Johnson and Gillingham 2004, O'Brien et al. 2006). Some studies use methods such as compositional analysis where vegetation cells are rated based on species habitat preferences which is measured by the amount of time the species spends in each land cover type compared to its availability in the landscape (Kautz et al. 2006, O'Brien et al. 2006). Resource selection methods have also been used to quantify habitat preferences by investigating the relationship of environmental variables with occurrence data using regression models (Boyce and McDonald 1999, Manley et al. 2002). The inverse of these indices of land cover use ratings can be used as a value for land cover cost (Graham 2001, Chetkiewicz et al. 2006, Carroll 2010). Ideally, cost values should be based on field studies. Land cover classes and the setting of cost values in the friction layer is likely the most important step in the process of calculating effective distance; it is the link between the GIS data and the ecological - behavioural aspects of animal travel. The development of the least-cost modeling as an approach to incorporate detailed geographical information as well as behavioural aspects as a measure for connectivity is in development (Graham 2001, Schadt et al. 2002, Carroll et al. 2011).

Least-Cost Path

The least-cost modeling process originates from graph theory and is commonly used in applied land and species management projects and for research (Walter and Craighead 1997, Graham 2001, Schadt et al. 2002). It is relatively easy to use and the algorithm is available in many new GIS packages. In the least-cost model, every landscape unit (grid cell) is assigned a friction value related to its positive or hindering effects on the movement process being modeled. Typically, an input into GIS for a least-cost model uses grid maps. Much of the GIS data, such as linear infrastructure and habitat edges, are available in vector format that has to be converted to rasters and combined with grid based information before use in the model. Since the grid map is the only input, its quality has a large influence on the quality and reliability of the cost map output. A number of aspects need to be considered when producing the input map. For instance, relatively low resolution or large grid cells may be appropriate for general land cover since many vegetative parcels have larger dimensions. Yet resolution is critical for smaller or narrower elements on the landscape, such as roads and vegetative boundaries. In order to convert linear and smaller elements accurately the grid cell size of the map should be smaller than the width of the narrowest element in the landscape; otherwise smaller items may disappear from the grid and linear elements may become discontinuous. There are two potential consequences to this, one is corridors may become intersected by high resistant cells or important barriers may have holes where the cost path will be allowed to pass through because one cell or two cells touching by corners will allow the cost path to cross a barrier. Line elements either need to be portrayed at their actual width or they could be converted to polygons using GIS by buffering the linear attribute. The scale of the map should also fit for the species being studied. One means of selecting appropriate scale would be to use a size larger than the known dispersal distance of the animal (Walker and Craighead 1997). This becomes important for including the landscape surrounding the study area in the analysis (Carroll et al. 2011, Koen et al. 2010); particularly for elements and potential source patches for the species outside the study area which may affect the analysis results. One short fall of least-cost modeling procedures is that they always produce least-cost corridors by depicting the lands that provide lower resistance to animal movement, but these paths for animal movement and connectivity may still be poor (Jenness et al. 2010). Although least-cost path modeling methods are popular, it is widely recognized wildlife likely do not travel along a single path of least resistance and likely the amount of travel distance is much

larger (Theobald 2006). Current applications of least-cost methods are modeling multiple pathways, ranking their importance which provides multiple possibilities of connectivity for consideration in the planning exercise (Beier et al. 2008, Carroll et al. 2010).

Current Flow Analysis

Circuit theory is a recent method developed to understand patterns of gene flow and animal movement for development of a linkage. GIS is used to portray the landscape as a grid of squares with each grid called a raster and each square a pixel. Resistance values are assigned to each pixel as a function of pixel properties such as land cover, topography and human disturbance level. Resistance layers should be developed individually for each focal species because assigned attributes may not affect movement of every species the same way when more than one species is used in the analysis. This type of resistance raster is similar to the resistance raster used in least-cost modeling in that they are usually estimated using expert opinion and habitat use based on the literature. Resistance values in circuit theory are considered the reciprocal of movement probabilities and do not reflect energetic cost.

Typically, circuit theory models require application of a “current source” at one end of a core habitat block and a “ground” at the destination core habitat block, and are then modeled for “current flow” (McRae et al. 2008, Carroll et al. 2011) . This is assumed to be equivalent to the number of animals passing through each pixel as they disperse from one core habitat to the other. Movement channeled into a narrow area is represented as a pinch point so it is highlighted by the model Advantages of circuit theory are that it reflects the potential for the entire landscape of study to support animal movement as a graded map rather than a polygon that categorizes every pixel as either inside or outside the corridor. Pinch points represent weak points along the linkage, and it has the same data requirements as least-cost modeling. Even though circuit theory maps provide a wide range of movement possibilities about landscape connectivity, the map does not classify a distinct corridor (McRae et al. 2008). In fact, a polygon with areas of highest flow under current conditions may be a poor corridor because its potential to support animal movement will decrease in an unpredictable way when land outside the corridor is compromised by a conflicting land use. In contrast, a least-cost corridor does not change when land outside the corridor is impacted by development. Another possible drawback is that circuit

theory demarcation of flow may not highlight the best area to conserve a linkage. A linkage with a pinchpoint would have contracted flow, but a linkage without the constriction of a pinchpoint is an area of unconstrained flow and would be a better linkage to conserve. Both circuit theory and least-cost modeling do not consider the impact of mortality on successful movement (Tracey 2006). As it is now understood, circuit theory is a comprehensive method and one of the better analyses to depict landscape connectivity to identify the degree of threat to a linkage (McRae et al. 2008).

The literature regarding landscape connectivity suggests modeling based on the spatial arrangement of habitat and animal habitat preferences could be improved by using new methods to quantify animal movements based on behaviour, which would improve our understanding of movement events such as migration to ensure their conservation (Horne et al. 2007, Kenward 2001, Turchin 1991). Enhancing this understanding with movement behaviours will enable researchers to better predict habitat use particularly for dispersal and migration. By studying successful movement and migration pathways of species it may be possible to identify which variables are characteristic of existing movement corridors and apply those insights to predicting areas of connectivity for species where movement corridors are not known (Chetkiewicz and Boyce 2001). One possible method to accomplish this goal is to determine the spatial extent and characteristics of a movement corridor used by a flagship species such as elk during migration. This information combined with an understanding of the ecology of migrating elk could be used to develop local scale management strategies to conserve the species, its migration pathways, and, for a broader purpose, use the data to test the ability of an existing model to predict a known functioning migration route. An understanding of elk migration metrics will be useful for proper management of the human use on a landscape to benefit elk and their migration patterns.

Conservation biologists suspect the protection of isolated natural areas may not work for biodiversity conservation and linking areas into connected networks is needed to attain conservation goals, particularly if one considers climate change (Carroll 2010). Planning for connectivity involves blending process and pattern, and connectivity can be maintained by other methods besides corridors (Chetkiewicz et al. 2006). These are aspects which are relevant to maintaining elk migration.

Historical Management and Research of Castle-Carbondale Elk in SW Alberta

This section will summarize what has been recorded about the herd size, movements and distribution of the elk populations inhabiting the Castle-Carbondale region. Elk have been present in the Castle area for generations. Elk remains have been found in archeological sites in nearby Waterton National Park (WNP) dating back several thousand years (WLNP files 1992). Records of the North West Mounted Police from the 1870's noted large numbers of elk in the mountains and foothills west of Fort Macleod (Gibbard and Sheppard 1992). In the late 1800's a combination of disease, winters of cold temperatures and high snow loads, as well as over hunting had depleted the elk to near extirpation. Elk are reported to be have been killed by an unknown disease during 1879, possibly contracted from cattle (Gibbard and Sheppard 1992), which combined with excessive hunting resulted in the mortality of all the elk in SW Alberta and SE British Columbia (Gibbard and Sheppard 1992).

Castle-Carbondale Herd

In the Castle area, elk numbers were likely increasing during the 1920's and 30's because the area was managed as a Game Preserve. A fire in 1936 swept through the region, opening up large tracts of new habitat and the elk population quickly increased. By early 1950's elk were very common in the Castle with large numbers wintering in the O'Hagan, Carbondale Hill, Mount Backus, Beaver Mines Lake area, and along the Castle and Carbondale River, Screwdriver Creek, Byron Hill, Whistler Mountain and Maverick Hill. Land owners from that time period estimated there were about 3,000 elk in the Castle-Carbondale area in 1953 (Gibbard and Sheppard 1992). The areas status as a Game Preserve ended in 1954 and it was opened to hunting.

Elk studies in the early 1990's using VHF radio collars determined portions of this herd's summer range in the headwaters of the Carbondale and its tributaries, in the South and West Castle with a few animals staying near the winter range year round. This herd is known to intermingle with the Beauvais Herd (Morgantini 1992). Winter and summer seasonal home ranges for the Castle-Carbondale herd are located in Wildlife Management Units (WMU) 302 and 400.

Chapter Three: Using Brownian Bridge Movement Model to Depict Elk Linkage Zones in SW Alberta

Abstract

Anthropogenic disturbance leading to habitat loss and fragmentation may have adverse impacts on ungulate migration. Understanding the movement and dispersal patterns of elk (*Cervus elapus*) on public lands will facilitate management and benefit elk and other uses of land resources. I used a Brownian Bridge movement model (BBMM) to determine a probalistic estimate of an elk population migration route, distinguishing between stopovers and movement segments. My results of a partially migratory population traveling a modest migration distance demonstrated that the population used stopovers during the spring and fall. Although a number of seasonal stopovers were similar between spring and fall migrations, many differed. Migrations corridors were used repeatedly between years with some used by more individuals than others. A proportional use measure of use may be an appropriate method to prioritize migration corridors for conservation. My findings suggest management strategies could be beneficial for conservation of migration.

Introduction

Large herbivore migrations are globally considered threatened by human development. In order to conserve this phenomena researchers have begun to investigate the effects of habitat fragmentation, human disturbance, and the primary drivers of animal migrations (Berger et al. 2008, Harris et al. 2009, Hebblewhite et al. 2007, Mysterud et al.2001, Sawyer et al. 2009, Voeten et al. 2009). Migration events are considered to be an ecological necessity for the existence of populations and meta-populations, often essential to population genetics (Coulon et al. 2006, Soule 1991) and allowing for increased access to resources for migrating species (McCullough 1985, Schmiegelow 2007).

Elk (*Cervus elaphus*) migration, similar to numerous other species migration, is an adaptive behavioural strategy that evolved to avoid limitations on resource availability (Cook et al. 2004, Dingle 1985, Hebblewhite 2008) and to reduce potential predation risk (Fryzell and Sinclair

1988, Hebblewhite 2008). Seasonal movements by elk, from low elevation winter range to high elevation mountain ranges provide elk an opportunity to respond to climatic variation, following elevation gradients as they track optimal patches of nutrient rich vegetation for an extended time period, enhancing fitness and reproduction (Boyce 1991, Morgantini and Hudson 1989, Mysterud et al. 2001, Phillips and Alldredge 2000, Smallidge et al. 2010). In turn, elk contribute to ecosystems function by their grazing pressure on plants and influence on soil dynamics (Frank and Goffman 1998, Kie and Lehmkuhl 2001, Schoenecker et al. 2004). Elk foraging activity is part of a phenomena of top down trophic cascades, considered a prevailing explanation of riparian plant recovery as a result of decreased browsing by elk due to increased predation by a reintroduced wolf population in Yellowstone National Park (Ripple 2007, Ripple and Beschta 2004).

Beyond the ecological influences of elk distribution and densities to the land, an understanding of the growing effects of human disturbance is a prerequisite for management and distribution of elk populations (Lyon and Ward 1982, Millspaugh et al. 2001). Research has shown human activities requiring or creating roads caused avoidance responses by elk to the human use of roads (Cole et al. 1997, Frair et al. 2008, Lyon 1983, Rowland et al. 2000), including land uses and recreation (Cassier et al. 1992, Ferguson and Keith 1982, Morgantini and Hudson 1985, Naylor et al. 2009). There have been indirect habitat losses caused by avoidance of roads and trails by elk in both protected and non-protected public lands (Gagnon et al 2007, Naylor et al. 2009, Rogala et al. 2011). While studies of elk populations in areas of no elk hunting such as those on private land or of protected areas noted human activity indirectly created a spatial refuge (Hebblewhite et al. 2005). Others have determined elk can benefit from industrial activity such as timber management (Rumble and Gamo 2011) and road management (Cole et al. 1997, Forman et al. 2003, Frair et al. 2008). Road management by decommissioning roads or using gates to control access is beneficial to many species including elk (Frair et al. 2008, Northrup 2010). These documented effects of human activity indicate that an increase in human land use without planning for wildlife habitat use and movement requirements may have adverse or beneficial effects to migrating elk and landscape connectivity for wildlife.

Numerous types of human activity such as roads, resource extraction, residential development, and other forms of habitat alteration can reduce the landscape connectivity required for migration

and dispersal between meta-populations (Friar et al. 2008, Gagnon et al. 2007, Lyon 1979, Rowland et al. 2000). Understanding what degree of landscape connectivity is essential to the greatest diversity of species and at-risk animals is an evolving science. Understanding migration movements and dispersal patterns of elk on public lands and factors that affect these movements will facilitate elk management and help to develop management strategies to benefit elk and other species using land resources (Benkobi et al. 2005).

SW Alberta Case Study

In southwest Alberta, the home range of the Castle-Carbondale herd is located in an area administered under multiple jurisdictions in Alberta and British Columbia. Winter range is on Alberta public and private lands while summer range is public land located in both Alberta and British Columbia. Both elk seasonal ranges have experienced decades of use for cattle grazing, gas extraction, timber harvesting, off-highway vehicles and hunting. On public lands there is an increasing human disturbance footprint due to recreational activities and resource extraction. Such a multi-use management strategy results in an increase of infrastructure, human activity, road density and traffic on roads which have the potential to reduce landscape connectivity, crucial to many species including migratory elk (Dodd et al. 2007, Forman 2003, Lyon 1979, Rowland et al.2004, Trombulak and Frissell 2000). Road densities in the Castle-Carbondale are at levels known to affect elk movements (.55km/km^2) (Rowland et al.2004, Frair et al. 2008). In the Castle / Carbondale, predation risk is from a wide variety of carnivores such as grizzly bears, black bears, cougars, wolves, lynx, and coyotes. Human hunting appears to be the largest source of elk mortality.

Elk migration in SW Alberta is similar to many western ungulate populations in North America (Boyce 1991, Hebblewhite et al. 2008, Sawyer et al 2009, White et al. 2010) as elk migrate from low elevation winter ranges to high elevation mountain summer ranges (Morgantini 1995, Sheppard 1992). Rocky Mountain elk in southwest Alberta annually migrate to seasonal ranges, a round trip distance of 12 to 100 km, with one male elk from the Porcupine Hills herd migrating 300+km two consecutive years across provincial and international boundaries. Elk management in my study area has focused on population numbers, controlled by limited hunting permits for female elk and an open season using a selective harvest strategy for multi-branched male elk.

Winter range management involves restricted industrial activity during the winter months and defined stocking rates for cattle for summer grazing. Very little is known about elk summer range use or migration pathways. To effectively manage a partially migratory elk herd, managers require data to determine if preferred migration routes exist, what are the important route characteristics and whether they need to be conserved.

Understanding the migration and dispersion patterns and underlying factors affecting each should facilitate elk management. In my study area blocking or reducing connectivity of migratory movement routes could result in elk spending more time on wintering grounds located on private lands than on traditional ranges within provincial forest reserves (Joslin and Youmans 1999, Morgantini and Hudson 1985). Such displacement of elk has led to increased public perceptions of an overabundance of elk (Torstenson et al. 2002). A reduction in connectivity for migration can lead to changes in distribution (Hebblewhite et al. 2008, Rowland et al. 2000) increased elk use of a limited winter range and ultimately result in increased land owner difficulties from crop depredation. Additional consequences could be ecological losses and a reduction in habitat quality of critical winter habitat due to over grazing (Walter et al. 2010), effects to elk calving success (Phillips et al. 2000), potential reduction of elk fitness (Bender et al. 2008, Boyce et al. 2010, Stewart et al. 2010) and artificially decrease population size (Webb et al. 2011). Migration can enhance survival and recruitment by reducing predation risk (Fryzell and Sinclair 1988, White et al. 2010). In other circumstances elk may chose not to migrate due to increased potential of predation risk during migration and / or other land use or management changes which improve security from predators or increase availability of high quality forage on the winter range (Hebblewhite et al. 2006, Hebblewhite and Merrill 2007).

Based on my studies, Rocky Mountain elk in southwest Alberta annually migrate to seasonal ranges, a round trip distance of 20 to 100 km, with one male elk from the Porcupine Hills subpopulation (herd) (Clark 1993) migrating 300^{+}km two consecutive years, across provincial and international boundaries (Paton unpublished). The range of migration distances for the Castle-Carbondale subpopulation is 15 to 64 km. Increasing development and human activity may impact areas of elk migration because they utilize much of the land base where the increased human activity is most prevalent. Elk migration occurs on transitional range between winter and summer range.

The Castle-Carbondale subpopulation is one of seven subpopulations (herds) in SW Alberta representing a total population of approximately 4,300 elk. I used GPS collars to track relocations of 68 elk in the Castle-Carbondale herd of 650 animals from 2007 to 2010. A total of 21 elk were harvested by hunters or preyed upon by carnivores in their first season of collaring, resulting in 50 collars collecting adequate migration data for analysis. Individual elk were tracked for at least a two year period during a four year study acquiring relocation points every two hours. I use an investigative framework (Sawyer et al. 2009) applying the Brownian bridge movement model (Horne et al. 2007) to delineate and prioritize the population migration network. The BBMM analyses use migration GPS data to identify elk migration ecology such as movement corridors between habitat patches known as stopover areas which are expected to be important to elk for increasing body condition, resting, and calving (Horne et al. 2007, Sawyer et al. 2009, Sawyer and Kaufman 2011).

The Castle-Carbondale elk migrate up to 34km straight line distance from their winter range, a montane / agricultural landscape to high elevation summer range in the Crown of the Continent along the Continental Divide of Alberta, Canada. Migration attributes in this region are poorly understood. I hypothesize:

- Elk migrate along specific pathways each year without stopping over because the migration distance is relatively short, traversable by elk in a day or two.
- Fall migration pathways would differ from spring migration pathways;
- Male and female migration would spatially differ, possibly from sexual segregation.

STUDY AREA

The Castle-Carbondale study area encompasses approximately 1,000 km^2 in southwest Alberta. It represents a large component of an internationally recognized area known as the Castle Crown of the Continent (Figure 3-1). Alberta Environment and Sustainable Resource Development administer 100% of the public Forest Management Area. On the eastern boundary of the provincial forest reserve are private ranchlands intermixed with cropland. The study area includes portions of two municipal districts (M.D. Pincher Creek, Municipality of Crowsnest

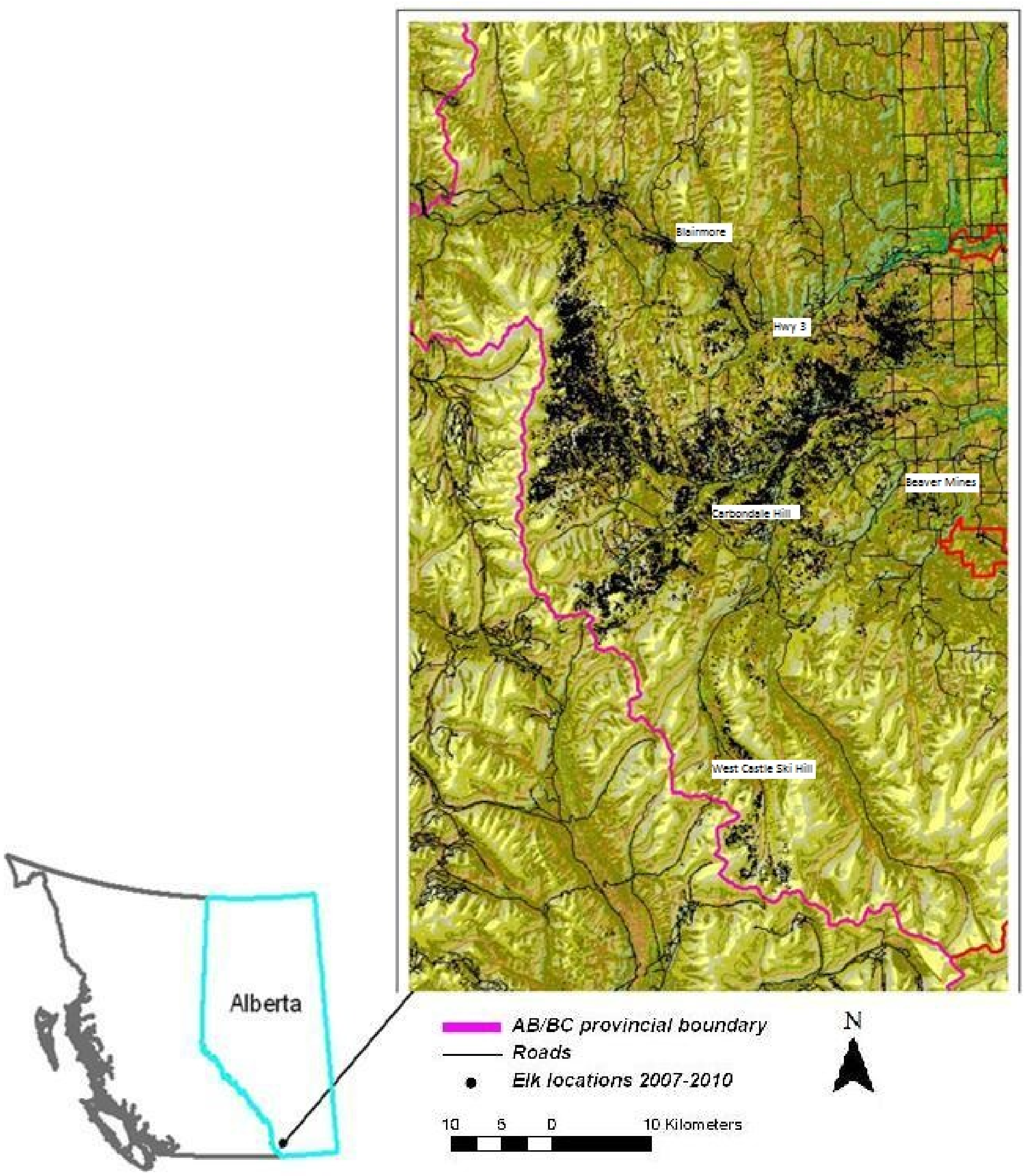
Pass). Livestock grazing occurs seasonally on public land and year-round on private land. Industrial activities in the area include forestry and natural gas extraction. Extensive human activity on the landscape is widely distributed, primarily from random camping, off-road vehicles, mountain biking, hiking, hunting, and fishing combined with winter activities of snowmobiling and skiing. The greatest human use in the study area occurs on public lands during the summer recreational season where limited enforceable restrictions apply and staff resources to enforce the existing regulations are few. The elk are hunted during September to November. Grizzly (*Ursus arctos*) and black bear (*Ursus americanus*), cougar (*Puma concolor*) and coyotes (*Canis latrans*) are potential predators in SW Aberta. Wolves (*Canis lupus*) are found in the study area with a small pack raising young during the duration of the study.

Migratory elk summer range is entirely on provincial land while winter range includes both private and provincial land. There are 2,273 km of roads in the study area with a density of 1.3km/km^2 on private land. The multi-use provincial land portion of the study area has a density of 0.55 km/ km^2 of roads.

Elevations range from 1250 to 2330 m. The four kilometre wide strip of private land on the eastern boundary represents transition range between grassland and montane, continuing westward along montane foothills, which quickly rise to subalpine and alpine environments of high elevation mountains along the Continental Divide between Alberta and British Columbia. Transitional range is the montane habitat found between the summer sub-alpine/alpine and montane winter ranges where migration routes occur. The area is composed of two natural regions and three natural subregions. The Rocky Mountain natural region is comprised of the Montane and Subalpine subregions and the Grassland natural region includes the Foothills Fescue subregion. Environmental characteristics of the Rocky Mountain natural region include cool summers (13.9 C), short growing season, high annual precipitation (798 mm) and the highest snow loads found in Alberta (Downing and Pettapiece 2006). The landscape is shaped by the prevailing Chinook winds, which create snow-free southwest facing slopes exposing winter grass and shrub forage for ungulates. Montane and Subalpine subregions consist of rugged terrain with elevations from 825 m to 2,300 m. Dominant vegetation is lodgepole pine (*Pinus contorta*) Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*) interspersed with grassland slopes, meadows, wetland complexes (Downing

and Pettapiece 2006) and clearcuts. The Foothills Fescue subregion typically is rolling hills (elevation 800 m to 1,525 m) dominated by mountain rough fescue (*Festuca campestris*), bluebunch fescue (*Festuca idahoensis*) and Parry's oatgrass (*Danthonia parryi*). Portions of the subregion in the eastern portion of the study area have been converted to cropland or tame pasture grass species.

Figure 3-1 Study Area for Castle-Carbondale Elk, 2007 – 2010 (location 694298 E 5483627 N)



MATERIALS AND METHODS

Capture, Collaring, and Data Collection

I used a helicopter and net-gun to capture 68 male and female elk aged 1 – 18 years on the winter ranges of southwestern Alberta from January to March during 2007-2010 (University of Alberta, Edmonton, Alberta, Canada. Animal Care Protocol number #536-1003 AR University of Alberta) (Fig.2-1). Elk were blindfolded and hobbled to allow collaring and sampling with low impact to the elk. Elk were fitted with Lotek 4400M GPS, 4400 GPS/Argos collars (Lotek, Newmark Ontario, Canada) and GEN4-GPS (Telonics, Mesa Arizona) equipped with mortality sensors that increased pulse rate if the collar remained motionless for >6 hours. GPS units were programmed to obtain location fixes every two hours (i.e. 12 per day). I located radio-collared elk from access roads at least once a month and some herds such as the Castle-Carbondale every week to confirm location and status. Collars from elk that died were refitted on new elk. The collars were outfitted with a remote drop off device programmed to disengage after 104 weeks. If the device failed, elk were recaptured annually by the helicopter using a net-gun method to retrieve the collars. Collar data were not used if elk were harvested during the hunting season in the first fall of collaring, if killed by predators, or collars failed before the first year of migrations were complete (one spring and fall migration defined a migratory elk), or if the elk was a resident or animals dispersed to another area.

Criteria to Determine Migratory Status of Elk

Elk populations such as the Castle-Carbondale herd are partially migratory, where one segment of a population undertakes seasonal migration while the other remains on a single range (Hebblewhite 2006, Lundberg 1988). Within a population of elk there may be a number of different phenotypes (Boyce 1991). In the partially migratory Carbondale-Castle herd there are migratory, resident and dispersal phenotypes. I assigned phenotypes as defined by Boyce (1991). Elk with seasonal home ranges overlapping entirely or predominantly were defined as resident elk. Migratory elk will move from a winter range to a separate summer range and return to the same winter range, whereas dispersing elk will leave the winter range to another separate seasonal range, not returning to the original winter range.

Table 3-1 Collared elk from the Carbondale-Castle herd 2007 – 2010

Elk ID	Capture date	Herd	Phenotype*	Sex	Age
E1	11-Jan-07	Carbondale	M	F	8
E2	11-Jan-07	Carbondale	M	F	6
E3	11-Jan-07	Carbondale	M	F	**UK
E4	11-Jan-07	Carbondale	M	F	1
E5	11-Jan-07	Carbondale	M	F	13
E6	11-Jan-07	Carbondale	M	M	1
E7	12-Jan-07	Carbondale	M	M	1
E8	12-Jan-07	Carbondale	M	M	1
E9	12-Jan-07	Carbondale	M	F	4
E10	12-Jan-07	Carbondale	M	M	1
E11	11-Jan-07	Carbondale	M	F	9
E12	11-Jan-07	Carbondale	M	F	UK
E13	11-Jan-07	Carbondale	M	M	1
E14	11-Jan-07	Carbondale	M	M	1
E15	11-Jan-07	Carbondale	D	M	1
E16	12-Jan-07	Carbondale	M	F	1
E17	12-Jan-07	Carbondale	M	F	15
E18	11-Jan-07	Carbondale	M	F	9
E49	13-Jan-07	Carbondale	R	F	5
E51	4-Feb-08	Carbondale	M	F	UK
E52	4-Feb-08	Carbondale	M	F	14
E53	4-Feb-08	Carbondale	M	F	4
E54	4-Feb-08	Carbondale	M	F	UK
E55	4-Feb-08	Carbondale	M	F	UK
E56	21-Feb-08	Carbondale	M	F	2
E57	13-Feb-08	Carbondale	M	F	4
E58	4-Feb-08	Carbondale	M	F	4
E59	4-Feb-08	Carbondale	M	F	7
E60	4-Feb-08	Carbondale	M	F	1
E61	21-Feb-08	Carbondale	M	F	4
E62	4-Feb-08	Carbondale	R	F	14
E63	4-Feb-08	Carbondale	M	M	1
E66	4-Feb-08	Carbondale	M	F	5
E67	21-Feb-08	Carbondale	M	F	2
E74	21-Feb-08	Carbondale	M	F	4
E75	21-Feb-08	Carbondale	M	F	4
E76	4-Apr-08	Carbondale	M	M	1
E77	21-Feb-08	Carbondale	M	F	16
E78	4-Feb-08	Carbondale	M	M	1
E79	21-Feb-08	Carbondale	M	F	14
E81	4-Apr-08	Carbondale	D	M	1

Elk ID	Capture date	Herd	Phenotype	Sex	Age
E82	4-Apr-08	Carbondale	M	M	1
E90	21-Feb-08	Carbondale	M	F	8
E95	26-Mar-09	Carbondale	M	M	1
E97	18-Mar-09	Carbondale	M	F	4
E98	20-Mar-09	Carbondale	M	F	5
E99	18-Mar-09	Carbondale	M	F	2
E100	20-Mar-09	Carbondale	M	F	1
E102	18-Mar-09	Carbondale	M	M	1
E103	26-Mar-09	Carbondale	M	F	14
E104	18-Mar-09	Carbondale	M	M	1
E106	20-Mar-09	Carbondale	M	M	1
E107	20-Mar-09	Carbondale	R	F	7
E110	20-Mar-09	Carbondale	M	F	7
E111	20-Mar-09	Carbondale	M	F	4
E115	10-Mar-10	Carbondale	M	F	16
E116	10-Mar-10	Carbondale	M	F	10
E117	10-Mar-10	Carbondale	M	F	15
E118	10-Mar-10	Carbondale	M	F	18
E119	10-Mar-10	Carbondale	M	M	1
E120	1-Apr-10	Carbondale	M	F	9
E121	10-Mar-10	Carbondale	M	F	4
E122	1-Apr-10	Carbondale	M	F	9
E123	10-Mar-10	Carbondale	M	F	3
E124	10-Mar-10	Carbondale	M	F	4
E126	10-Mar-10	Carbondale	M	F	UK
E127	10-Mar-10	Carbondale	M	F	3
E130	1-Apr-10	Carbondale	M	M	1

*Phenotype code *UK - Unknown
M – Migrant
R – Resident
D - Dispersal

I examined data from each individual to assess if they moved between separate seasonal ranges. Seasons were evaluated based on inflection points similar to Ferguson and Elkie (2006) using rates of movement and steady directional movement to the seasonal ranges. By plotting individual elk migration location points I determined the seasonal elk distribution patterns for 99% of the elk fit into the date segments identified for winter as January 1 - March 15, spring migration (April 1 – June 15) summer (June 16 - August 30), fall migration (September 1 - December 15). Selecting these dates to represent periods of elk seasonal use seemed logical since

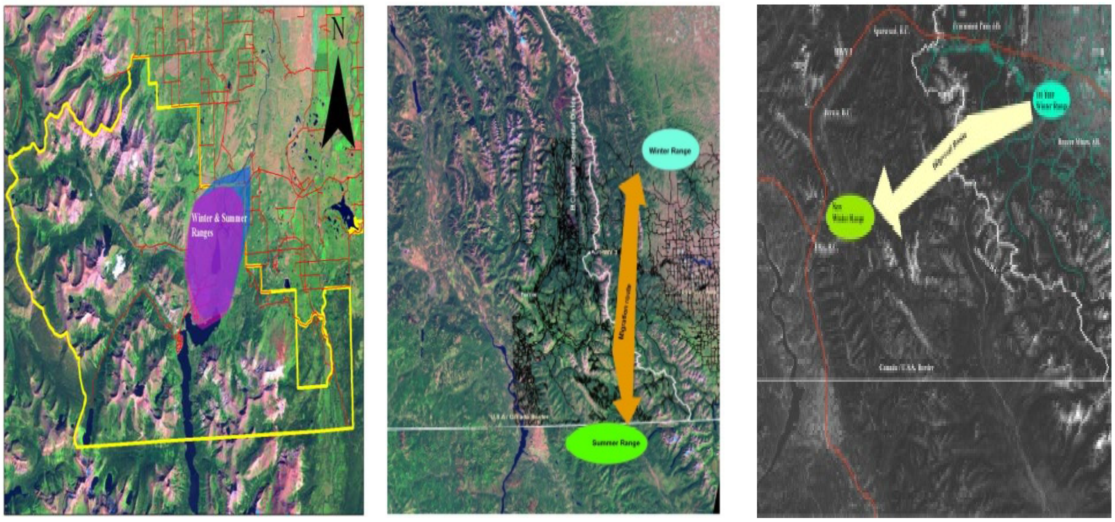
they represent the seasonal transitions of migration as determined by the data. Similar dates are used in other migration papers (Benkobi et al. 2005, Zhi-gao et al. 2008, and White et al. 2010). For the period of September 1 to December 30, numerous Castle-Carbondale elk moved between seasonal and transitional range many times during hunting season making it difficult to assess migration movements. In these cases elk would initially start migration going part way to the winter range or to the winter range but return back to the summer range, possibly from hunting disturbance. Later in the season the elk would eventually migrate back to the winter range. It was the final movement to the destination range that I used in my migration analyses. January 1 to March 15 is the core time period of winter range when elk were found within the 50% kernel from 2007 – 2010. Small numbers of collared elk began moving westward towards summer range soon after March 15 with most migrations starting in early May and completed by early June. Based on my data review, and observations of the elk herd these dates were considered representative of Castle-Carbondale elk migration and for relocation points needed for the Brownian bridge movement model to spatially depict elk migration.

Kernel estimation of 95% was used to delineate seasonal winter and summer ranges. To determine seasonal ranges I used the Home Range Tools (Rodgers and Kie 2010) 95% fixed kernel with a band width of .8 (Kie et al. 2010). Animals were classified as migratory if the 95% fixed kernel summer and winter range isopleths did not overlap in extent (Figure 3-2). This method is repeatable and defensible given the biological question of seasonal ranges overlapping or not (Jacques et al. 2009, Kie et al. 2010). I chose to allow multiple polygons of the 50% isoline if the kernel created clustered polygons when calculating the core winter and summer seasonal ranges. I used the mean easting and northing based on the UTM coordinates of the location of each elk during winter and summer to measure the center of activity (Hayne 1949, Nicholson et al. 1997).

Initiation of migration was defined as the date the animal began a directed movement toward the summer range or winter range (Nicholson et al. 1997, White et al. 2010), depending on migration season, continuing on to the destination seasonal range. End of migration occurred when the migration pathway passed <1km from the median UTM location of the seasonal range the elk is migrating to (Evan et al. 2005, Grarrott and White 1987). Typically the elk would reach the centroid of a seasonal range within 24 hoursafter crossing the outer isoline of the seasonal range.

Figure 3-2 Methods used to determine separate resident elk, migrating elk and dispersing elk phenotypes using seasonal home range analyses (Boyce 1991)

Resident elk – seasonal ranges overlap	Migrating elk – separate ranges, 2 way movement.	Dispersing elk - separate ranges, no return to winter.



Elk Migration Data and Characteristics

From 2007 – 2010, 68 elk were collared; 19 in 2007, 24 in 2008, 12 in 2009, 13 in 2010. An attempt was made to capture elk from a variety of areas and groups distributed within the 153 km^2 winter range. Location collection of 325,396 GPS location points from 68 elk occurred from January 10, 2007 to December 30, 2010. I considered radio-collared elk as the experimental unit to allow for population-level inference (Erickson et al. 2001, Johnson et al. 2000, Otis and White 1999). Random sampling of animals was attempted (Otis and White 1999) by directing helicopter capture crews to collar individuals from different groups of elk located across the entire extent of a herd's foothill winter range.

To maximize sampling intensity I chose to collect two hour location fixes with the collar dropping off after two years. The collar was subsequently redeployed on a different elk. To control location error of data used for analyses, data were sorted to select all relocations with three-dimensional (3D) and two-dimensional (2D) values with a dilution of precision value <8 (Adrados et al. 2003, D'eon et al. 2005, Pepin et al. 2008, Rempel and Rodgers 1997).

Characteristics of migration such as timing, travel distance, duration of travel, step length and tortuosity of pathways provided data useful to interpretation of migration routes and behaviour of elk during migration. Distance of migration was calculated by two methods. First as displacement, the straight line distance between the first and last location points of the migration pathway. Second, as the total distance travelled during migration. Calculated by summing all the step lengths, which is the straight line distance between each two hour location point.

I selected step-length (i.e. distance between two hour relocations in metres) as a surrogate of elk mobility (Morales et al. 2004). Step length was computed using ARCMAP 9.2 (ESRI Inc., Redlands, CA) using Hawth's Tools extension (http:www.spatialecology.com/htools/).

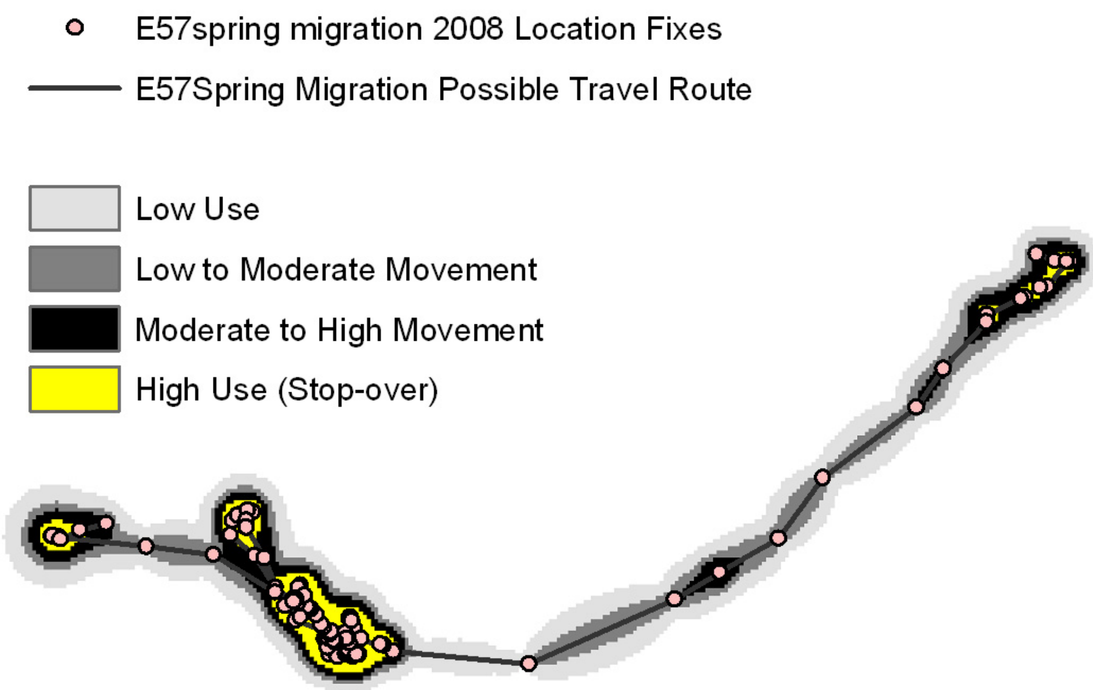
Using paired t-tests, I compared metrics between migration seasons, including timing of migration, days of migration, linearity of migration routes (defined as migratory displacement / actual migratory path, ranging from 0-1), number of stopovers and step lengths between seasons for the population and sexes. Migration location points used in the BBMM were consecutive location fixes between the start of migration to completion.

Modeling Elk Migration Routes

I input elk seasonal migration location data in a Brownian bridge movement model (BBMM) (Horne et al. 2007) to estimate individual elk utilization distribution (UD) for each seasonal migration. BBMM requires time specific location data, an error estimate for the location data, and grid-cell size for the UD output. My analysis with BBMM used two hour GPS relocation data from the migration time period, with an error estimate of 20m and a grid cell size of 100m. I had to use a 100m cell size because the BBMM script running in R statistical software was unable to complete the calculations for 140 seasonal migrations due to memory limitations. A sequence pathway of GPS location points were used from collar data collected between winter and summer home ranges during each spring and fall migration (Sawyer et al. 2009) to produce a BBMM graphic for each elk (Figure 3-3).

Figure 3-3 Example of an utilization distribution estimated for individual elk during the 2008 spring migration.

High-use areas represent stopover sites identified by numerous relocation and tortuous movements. Moderate use areas positioned between stopovers represent segments of migration movements where elk moved quickly in one direction. Low-use areas represent the areas of uncertainty for the probabilistic path.



The BBMM is a continuous time stochastic movement model, where the probability of being in an area is conditioned on the distance and elapsed time between successive locations; the location error and an estimate of the animal's mobility is referred to as "Brownian-motion variance" (BMV; Horne et al. 2007). Odd-numbered locations are considered independent observations from the Brownian bridges connecting the even-numbered locations, the BMV can be estimated by maximizing the likelihood of observing the odd locations (Horne et al. 2007).

Two assumptions associated with BBMM are: 1) location errors represent a bivariate normal distribution and 2) the movement between consecutive locations is random. The assumption of normally distributed errors is suitable for GPS telemetry, but the assumption of conditional random movement between consecutive locations may become less probable as time between

locations increases (Horne et al. 2007). Location data collected from elk were two hours apart, and migration data collected at seven hour intervals were successfully applied to BBMM analysis of caribou (Horne et al. 2007). Following the methods of previous studies (Horne et al. 2007, Sawyer et al. 2009), I consider the assumption of conditional random movement to be reasonable. Uncertainty of the actual pathway is integrated in the model using two ecological attributes of travel: the animal's mobility and a measurable location error (Horne et al. 2007, Sawyer et al. 2009). Calculations of BBMM were computed in R language for statistical computing (R Development Core Team 2009).

Migration routes modeled for the elk populations with BBMM are unique for they consider two metrics of migration behaviour: 1) time spent in an area and 2) rate of migration. Both metrics are used in this study to characterize high use areas where elk spent most of their time moving slowly, not moving or following a tortuous route, possibly foraging or resting, parturition in transition areas or during the spring waiting for snow depth to decrease allowing upward elevation movement to summer ranges. Moderate use areas are represented by areas where elk spend the least time and move quickly (Sawyer et al. 2009). From this I assume high use areas reflect stopover sites, likely used for foraging and resting habitat or security cover, while moderate use areas located between stopover sites represent migration movements (Sawyer et al 2009). Similar to other models (Forester et al. 2007, Frair et al. 2005, Johnson et al. 2002, Morales et al. 2004) the BBMM model output is based on the assumption that behavioural states such as migration movement and stopover events can be inferred from movement rates (Saher and Schmielgelow 2005). Validity of the assumption depends on the frequency of the movement data, behaviour types to be determined, and the potential such behaviours can be distinguished by movement rates (Boyce 2006, Nelson et al. 2004). One important difference between BBMM state-space process models is its focus on utilization as opposed to prediction (Horne et al. 2007), making it a good compliment to predictive models.

Estimating Population Level Migration Routes

I used the BBMM developed in the R language for statistical computing (R Development Core Team 2007) provided by Sawyer et al. (2009). After the UD (Utilization Distribution) of separate seasonal migration routes for each individual elk were calculated, I selected elk with >1

seasonal migration collected (n=50 elk), summed the cells values of all individual UDs and rescaled their cumulative pixel cell values to a sum of one, so the migration route of each elk was represented by one UD (Sawyer et al. 2009). I used the same rescaling process with the UDs of all elk to create an estimation of the multiple migration paths used by the Castle-Carbondale elk. Once the UDs were pooled, the BBMM (Brownian bridge movement model) output provided an estimate of the relative amount of use across the population level route (Sawyer et al. 2009).

Population level migration route UD values were put into 25% quartiles with the top 25% classified as high use and represented areas along the migration route where animals spent the most time. I assumed these areas were used for foraging or resting when elk moved slowly. Lower use areas represent movement corridors between stopover sites (Sawyer et al. 2009). Unlike other studies (Horne 2007, Sawyer et al. 2009, White et al. 2010), spring and fall migrations for many of the elk in my study did not follow the same route, so I pooled the two seasonal migration data sets together for the first BBMM analysis of the population. For comparison I separated fall and spring migrations for all elk then modeled these routes using the BBMM to visually evaluate if outputs differed. I collected data for fewer fall migrations due to harvest of elk, primarily of males.

To facilitate ranking of the conservation value of population migration routes, I assumed that route segments used by a higher proportion of the population had higher conservation value than portions used by a smaller segment of the population (Sawyer et al. 2009). I determined the proportion of sampled population that used each route segment by using a script in R (Neilson 2009) to calculate how many of the individual migration routes (99% UD) occurred within each 100 x 100m cell of the estimated population level route. Therefore cell values ranged from one to a potential maximum value equal to the total number of marked elk undertaking migration. Migration routes used by >10% of the sampled population were considered to have higher conservation priority than others. This 10% criterion was subjective decision intended to reflect routes used by more than one marked animal. Sawyer et al. (2009) suggested this to be an appropriate metric in the absence of a metric directly related to fitness.

I investigated whether the BBMM could be used to identify differences between male and female migration UD during spring or fall. Since my data consisted of both male and female elk, there

was the possibility the two sexes were using the landscape differently during migration, particularly during the hunting season when males are managed by an open season for males with three antlered branches or more and females are harvested by issuing a limited number of permits (n= 99 permits) (ASRD 2007-10). In some populations, male and female elk are known to display sexual segregation where males and females use habitats in their home ranges differently (Bleich et al. 1997, Gregory et al. 2009, Main et al. 2008, Ruckstuhl and Neuhaus 2002). I modeled migration UD's of male and female for both seasonal migrations to assess if there may be a visual difference in the BBMM migration UD's. The same evaluation method was used to compare spatial locations of stopovers from the BBMM, used by male and females for each seasonal migration. I used telemetry locations from all migratory elk to evaluate selection and fidelity to specific ranges.

RESULTS

I captured a total of 68 elk during 2007-2010. Eighteen animals were censored from the analyses due to mortality before one year of migration (n = 3), because they were residents (n =2), dispersed (n = 2), or censored due to no or insufficient data (n = 10). A total of 50 collars (38 female and 12 male elk) collected satisfactory data during migration to be used for Brownian Bridge Movement Model UD analysis. Collars collected a total of 325,396 telemetry relocation points from 2007 – 2010, of which 31,332 were GPS points during migration. Eighty-eight percent of the female elk were adults (two years or older) and 12% were yearlings (<2 years) during the first year of monitoring. Male elk were all approximately 1.5 years old when captured. The males only represented the age class of 3.5 years or less because I did not capture elk greater than 1.5 years old due to the high capture mortality risks with multi-branched elk during years of low snow depths.

During the four year study, two of the 21 collared elk died during migration as a result of predation by wolves. Mortalities during all seasons of the study occurred from a variety of sources including hunting and predators (Table 3-1). The total proportions of mortality sources of collared elk in this study were 28% of the collared animals, consisting of males (n=9) and females (n=10). The sample size of Castle-Carbondale elk we collared was reduced by 21% due to hunting over four years of study, compared to 7.5% from natural predators (Table 3-1). Wolf

predation of collared elk was low at 1 elk per year of study. There was one known active wolf den in the home range of Castle-Carbondale elk. GPS telemetry locations from elk rarely were found within 5km of the den site during the four years of study.

Table 3-1 Total number of elk mortalities (n = 21) and the mortality sources for the Castle-Carbondale herd, 2007-2010

Elk ID	Elk Sex	Elk Age	Cougar	Wolf	Hunter	Capture	Unknown
E2	F	6			1		
E6	M	2			1		
E7	M	2			1		
E10	M	1			1		
E11	F	10			1		
E12	F	n/a				1	
E13	M	2			1		
E17	F	15					1
E18	F	9			1		
E53	F	4	1				
E58	F	4			1		
E61	F	4			1		
E63	M	2		1			
E76	M	2			1		
E78	M	2			1		
E79	F	15		1			
E102	M	2		1			
E104	M	2			1		
E107	F	8			1		
E111	F	5			1		
E127	F	4		1			
Total			1	4	14	1	1

I used 138 migration events (73 spring and 65 fall) for analysis. Spring migration sample sizes were higher than fall migration because animal numbers were reduced by hunting and predation. Castle-Carbondale elk moved a mean round trip of 38 km (straight-line distance) to three core summer ranges. Thirty-three of the 50 migrating elk provided data for two - four summers returning to the same seasonal range each year, typically using the same migration route to summer ranges, but dispersing wider during fall migration. Pooled data from all years resulted in a mean duration for linear migration of 20 +/- 1 days in the spring and 21 +/- 2 days in the fall.

Castle-Carbondale elk spend approximately 11% of their yearly time in migration. Timing for migration varied for individuals and across years. Mean departure date of all spring migrations was May 2 (SD = +/-6.4 days, n= 73) and mean date of departure for all fall migrations was October 20 (SD = +/-17.4 days, n=65). A number of characteristics of migration movement and timing which may help understand elk migration characteristics and behaviour were summarized. (Table 3-2 and Table 3-3).

Table 3-2 Migration metrics for Castle-Carbondale elk from 2007 – 2010

Season					
Spring	**Migration metric**	**2007**	**2008**	**2009**	**2010**
	Number of elk	13	27	21	12
	Mean Departure date	24-Apr	6-May	6-May	2-May
	Minimum. Depart	3-Apr	13-Apr	28-Apr	19-Mar
	Maximum Depart	23-May	16-Jun	20-May	2-Jun
	Mean Arrival date	14-May	28-May	26-May	16-May
	Minimum Arrival date	23-Apr	29-Apr	12-May	2-Apr
	Maximum. Arrival	17-Jun	28-Jun	23-Jun	22-Jun
Fall	**Migration metric**	**2007**	**2008**	**2009**	**2010**
	Number of elk	11	27	15	12
	Mean Departure date	6-Nov	31-Oct	22-Oct	24-Oct
	Minimum Departure	30-Sep	15-Jan	26-Aug	23-Aug
	Maximum Departure	17-Jun	21-Jan	2-Dec	25-Nov
	Mean Arrival date	4-Dec	16-Nov	13-Nov	20-Nov
	Minimum Arrival	13-Oct	21-Jan	8-Sep	4-Sep
	Maximum Arrival	3-Feb	2-Feb	23-Dec	19-Dec

Table 3-3 Characteristics of elk migration for movements and stopovers from 2007 – 2010

Season	Migration characteristic	N	Mean	SE (+/-)	Minimum	Maximum
Spring	Migration days	73	20	1	2	65
	Migration displacement (km)		20	1	6	34
	Total migration path (km)		73	5	9	252
	Migration linearity		0.34	0.02	0.05	1
	Average step length (m)		370	140	170	830
	Number of stopovers		8	1	2	17
	Average distance between stopovers (km)		3.4	.30	.7	13.4
	Average distance between stopovers (km)		12	1.3	2.8	8.4
Fall	Migration days	65	21	2	1	68
	Migration displacement (km)		18	1	5	32
	Total migration path (km)		60	4	11	164
	Migration linearity		0.38	0.02	0.04	0.76
	Average step length		.31	.14	.14	.60
	Number of stopovers		7	2	1	17
	Average distance between stopovers (km)		3.7	.4	.4	21.3
	Average distance between stopovers (km)		12	2.5	3	16.4

I did not find significant differences between seasonal migrations for many of the migration characteristics tested with a paired t-test. There were common patterns in the data with the mean number of days of migration day consistent between spring and fall, yet between individuals the duration of migration were quite variable (Table 3-3). Such a pattern of individual variability was found in metrics such as total migration path, migration linearity, number of stopovers, and average distance between stopovers (Table 3-3). I found average step length (m) for all elk to be 66 m different between fall (308 +/- 13.8) m and spring (373 +/- 13.81) m (two sample t-test, $t = -3.68$, 63 d.f., $p < .05$). Spring mean step length of females was 58.7 m longer than their mean step length during fall migration (-3.47, 52 d,f., $p<5$). Male elk step lengths were also significantly different between fall and spring (-2.23, 10 d.f., $p<5$).

BBMM analysis provided a probabilistic measure of elk spring and fall population-level migration routes and key stopovers. Areas of animal relocation stopovers are assumed to

represent places of high elk use, while moderate-use segments are considered movement corridors to the next stopover or a seasonal range (Figure 3-4). Mean estimate of the Brownian motion variance for the elk population ranged was 3,533 m^2 (SE +/- 977m^2, n = 138 migrations). A low use designation represented areas of variance or uncertainty of the BBMM calculation and did not appear to be associated with stopovers or movement corridors (Sawyer et al. 2009).

Once I completed the population UD, migration data were separated to represent spring and fall elk migrations. I modeled a BBMM migration UD based on all individuals of each season, separate seasons for male (Appendix A).and female (Figure 3-5 and 3-6), and the degree of overlap between stopovers for each season and sex (Figure 3-7 and 3-8).

Maps of seasonal comparisons for female elk (Figures 3-5 and 3-6) illustrate potential differences in habitat use of female elk during spring and fall migrations. Stopovers in the migration route are represented by green coloration, movement areas in the migration are yellow shades and pink is an area of low probability of use during migration. The areas of high, medium-high and medium-low delineate most of the migration route with low use areas between the other levels of use representing possible direct travel areas. Gaps of low use coloration between medium use levels should be interpreted as quick movement areas where elk migrated quickly to the next segment of the migration corridor. The spring route (high use, medium use, and low use) is more direct and narrow compared to the fall migration which shifts away from the valley bottoms and roads (Figures 3-5 and 3-6). Stopovers during fall migration appear more fragmented and smaller in size than the spring migration. A comparison of spring and fall female BBMM migrations suggest there are three core areas of overlap of stopovers for both seasons of use, but with a shift away from the main river valley floors (Figure 3-7). Selection of stopover sites usually did not overlap between male and females (Figure 3-8).

My results indicate there are multiple pathways used by elk to access their summer ranges. I used a method outlined by Sawyer et al. (2009) where pathways used by >10% of the sampled population was considered to represent the highest conservation value (Figure 3-9).

Figure 3-4 BBMM of population migration routes of all male and female Castle-Carbondale elk from 2007-10

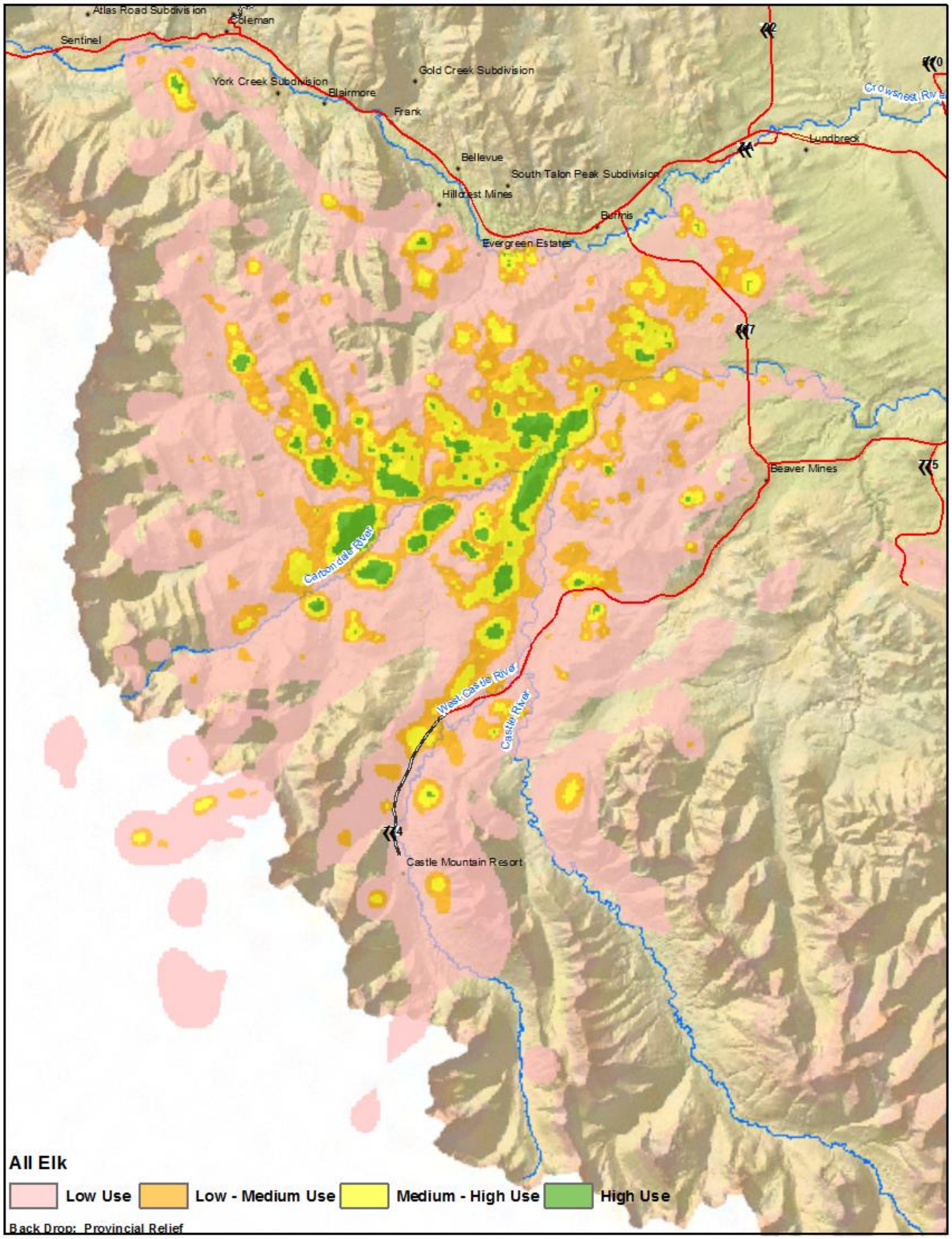


Figure 3-5 BBMM Carbondale-Castle female elk population of spring migration routes and stopovers, 2007-2010

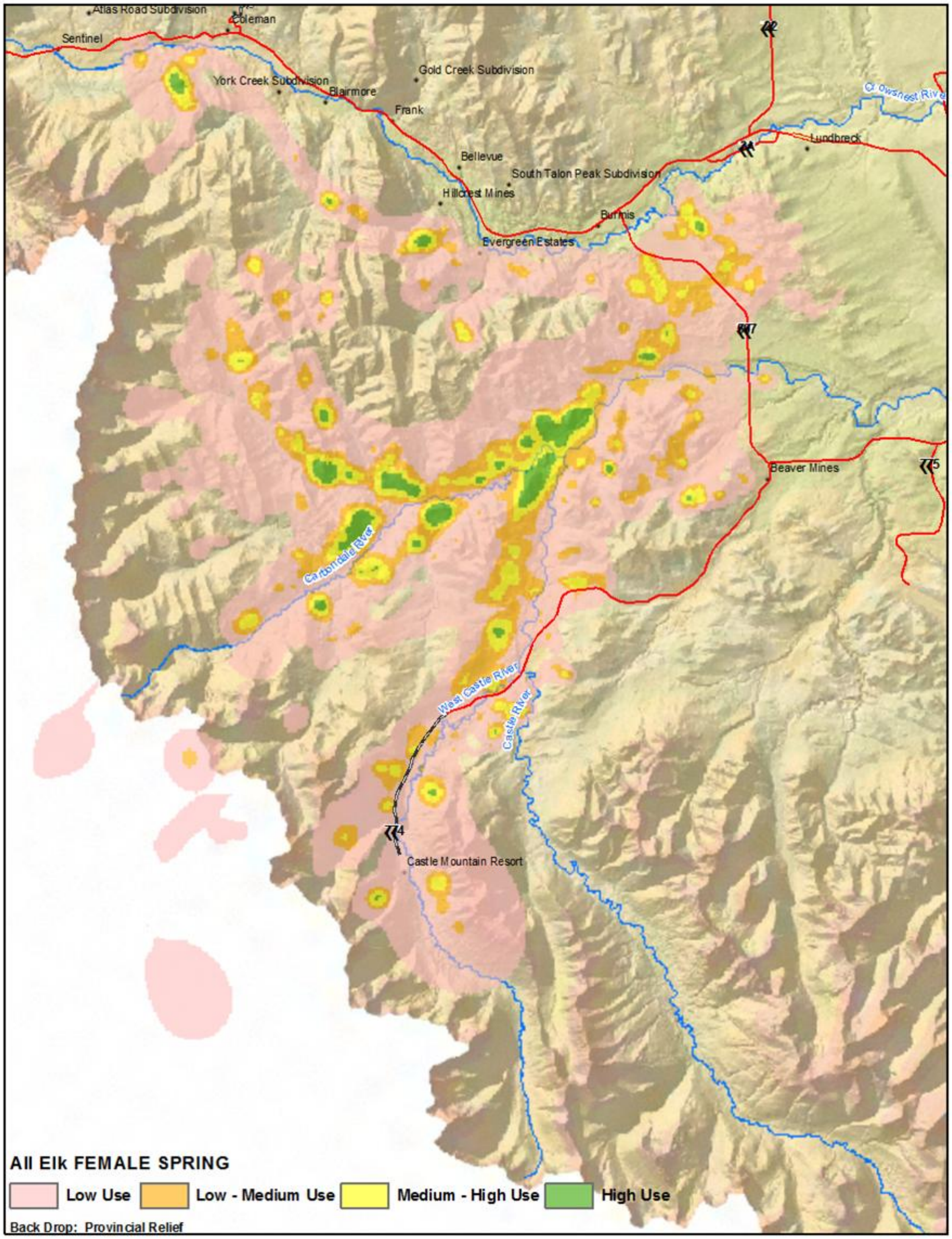


Figure 3-6 BBMM Carbondale-Castle female elk population of fall migration routes and stopovers, 2007-2010

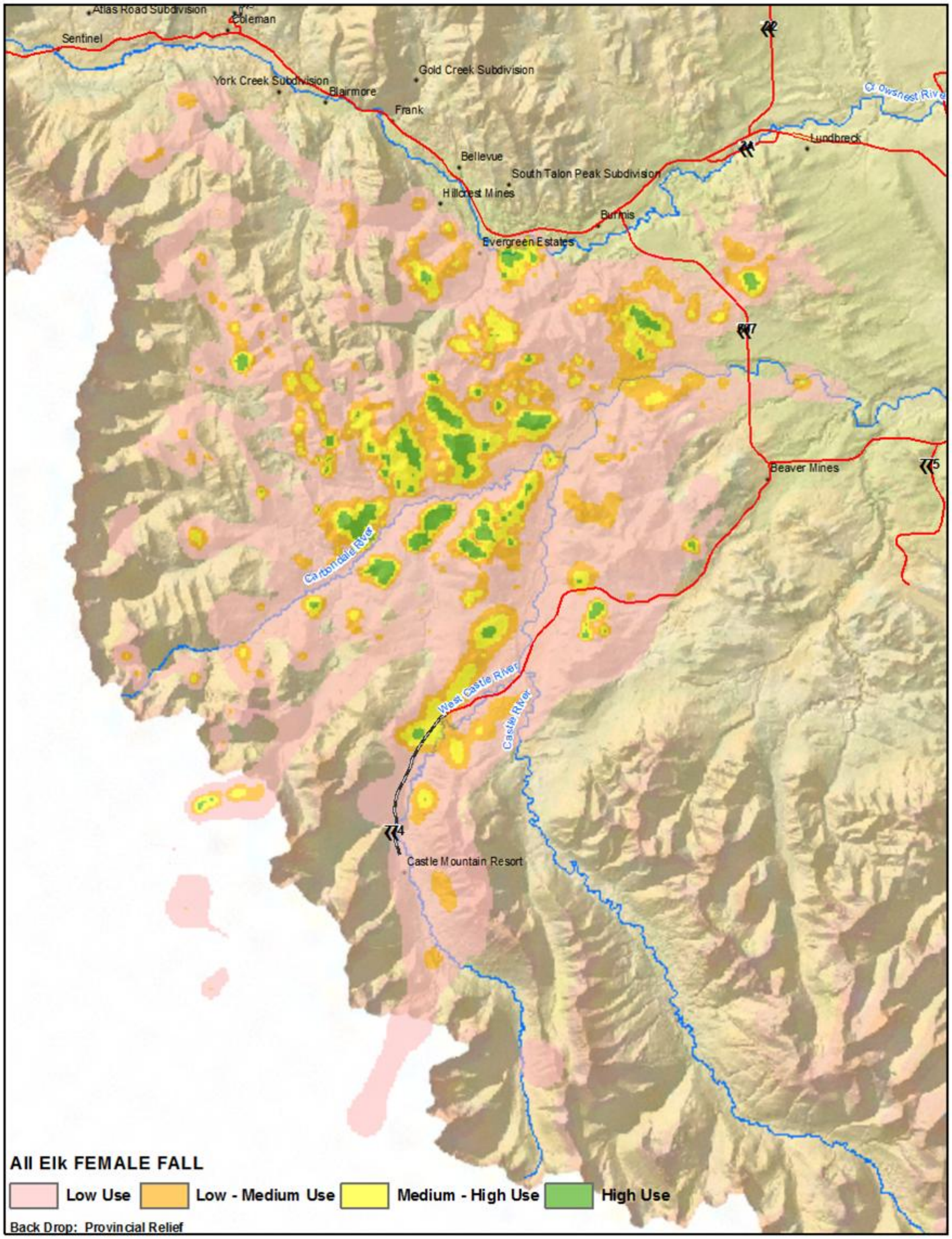


Figure 3-7 Comparison of BBMM Carbondale-Castle female elk population stopovers during spring and fall migration, 2007-2010

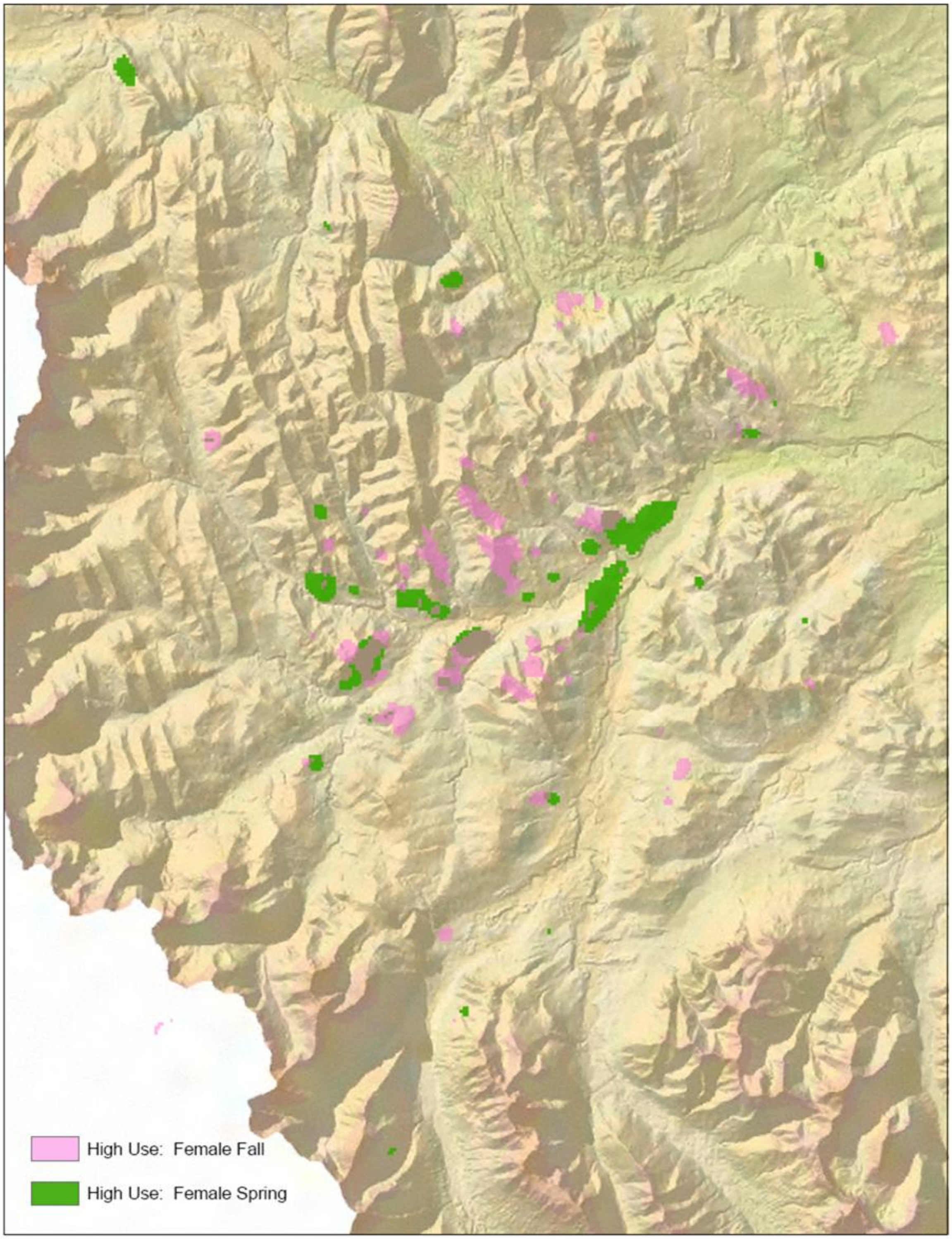


Figure 3-8 Comparison of BBMM Carbondale-Castle female/male elk population stopovers during spring migration, 2007-2010

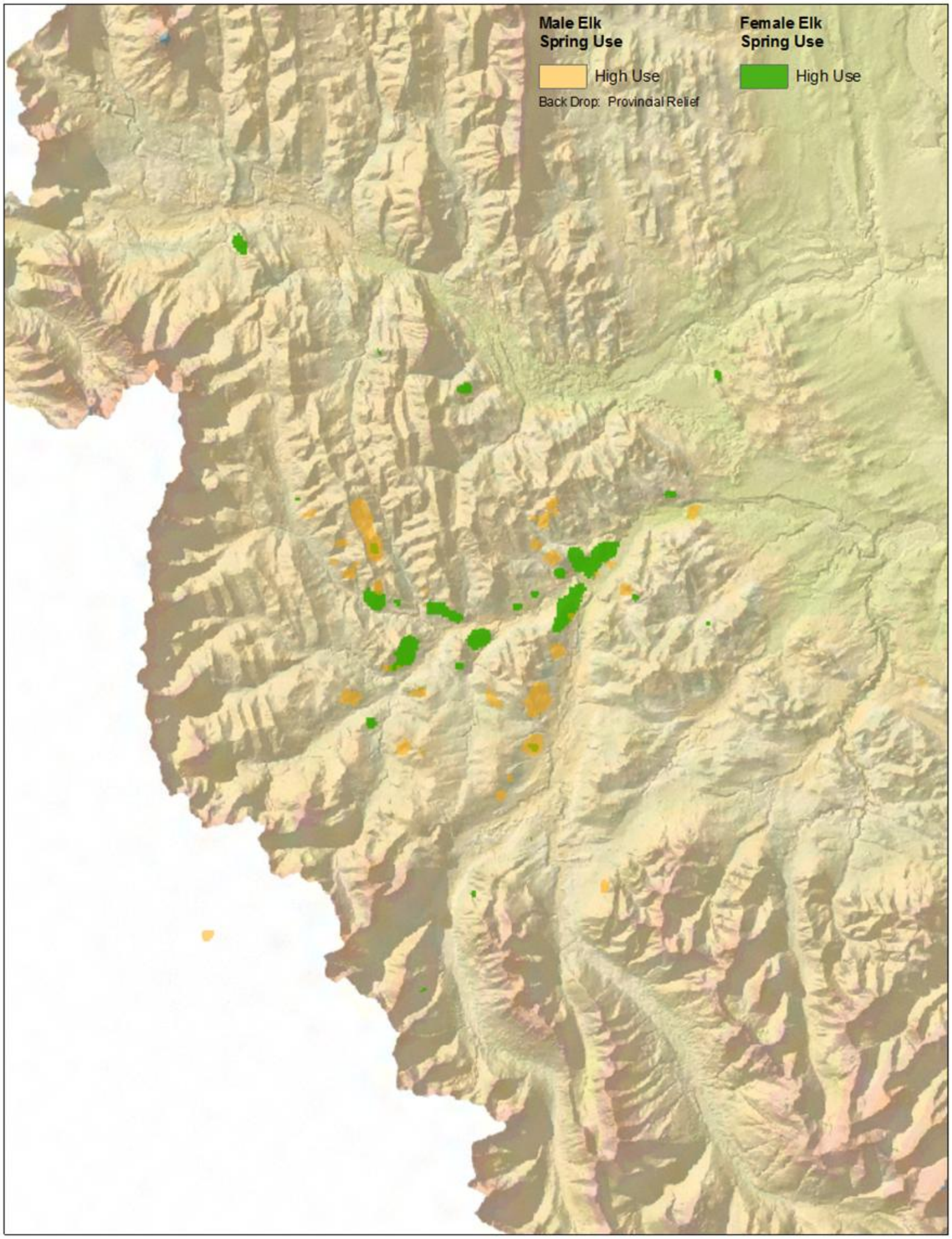
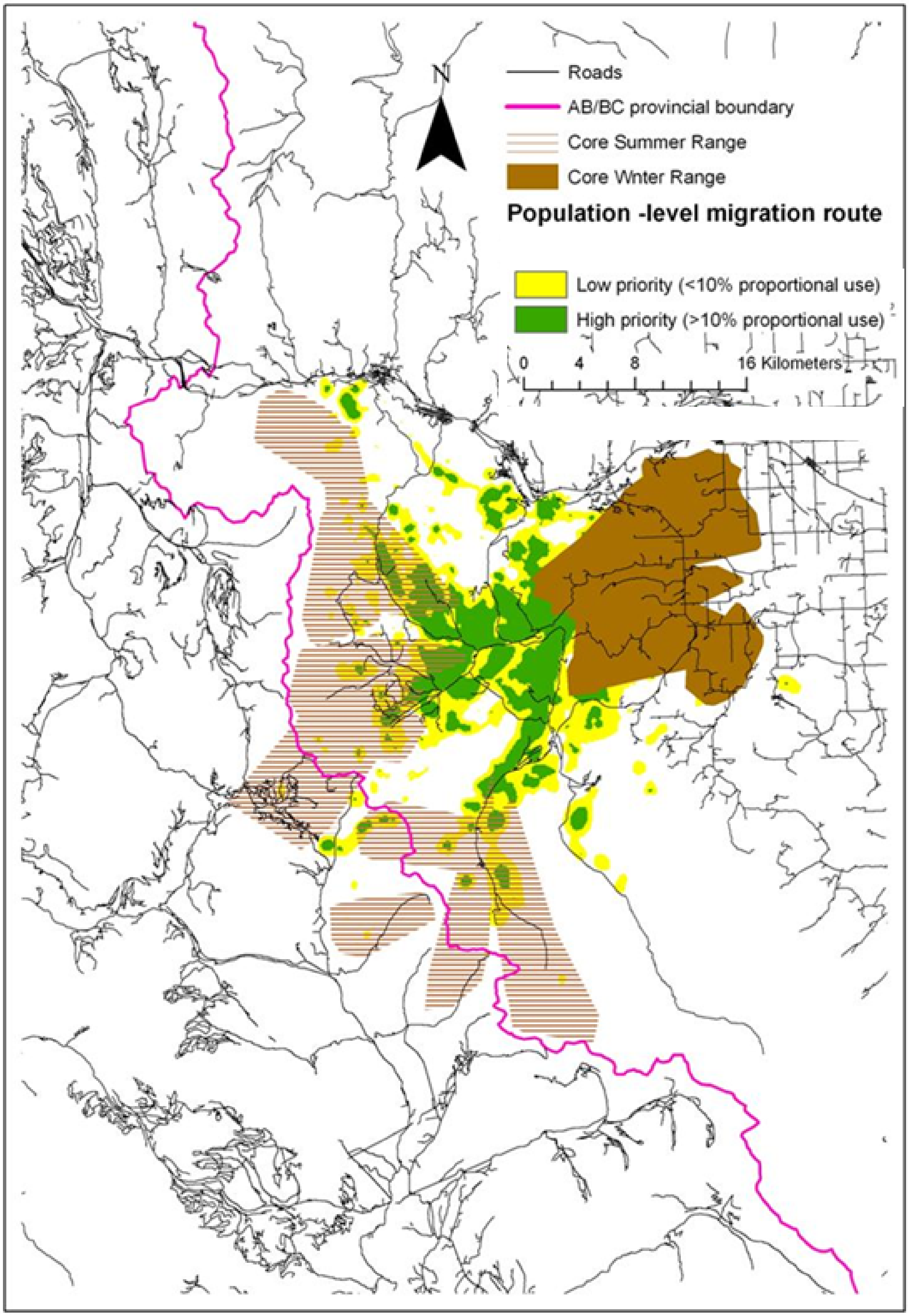


Figure 3-9 Castle-Carbondale elk migration is SW Alberta prioritization of migration pathways determined using proportional use of the collared population (>10%).



A number elk used different migration routes between fall and spring (Figure 3-10), but the fall and spring routes did not differ entirely among years. Ninety-one (91%) of the 33 radio-collared elk studied for two or more winters portrayed fidelity to the same winter and summer range each year. A five year old female elk switched from the Castle-Carbondale winter range staying over in the Crowsnest Pass winter range for one winter and summer, then migrating back to its original winter range in the Lundbreck Hills the next season. These elk have been called "switchers" where an individual will migrate one year but not the next, possibly changing migration strategy based on current conditions (Boyce 1989, Woods 1991). Two elk dispersed to different winter ranges. Initiation dates of spring migration were variable between individual elk and between elk in different years. Mean date of the start of migration occurred near the initiation of calving time periods, April 23 in 2007, (SD = +/- 8.5 days, n = 8), May 6 in 2008 (SD = +/-5 days, n = 26), May 7 in 2009 (SD= +/-3.5 days, n =22), and May 3 in 2010 (SD=+/-23 days, n =10). As in other published research, the difference in initiation of spring migration may be related to precipitation and vegetation green-up (Morgantini and Hudson 1989, White et al. 2010).

Elk migration was distributed along 4 corridors travelling west or east to and from a 146km^2 winter range and a 540km^2 summer range spanning 53km north/south along the Continental Divide from Star Creek southward to the West Castle River valley (Fig. 3.9a). Geographically there were 4 primary areas of summer range, Star / York Creek, Lynx / Goat Creek, Lost / Carbondale Creek, and Syncline / West Castle. Elk could be found at elevations of 1200m in the winter to 1960m in the summer. In 2006 there were 638 elk on the winter range for a density of 4.4 elk/km^2.

Figure 3-9a BBMM Carbondale-Castle female elk population of spring migration routes and stopovers, 2007-2010.

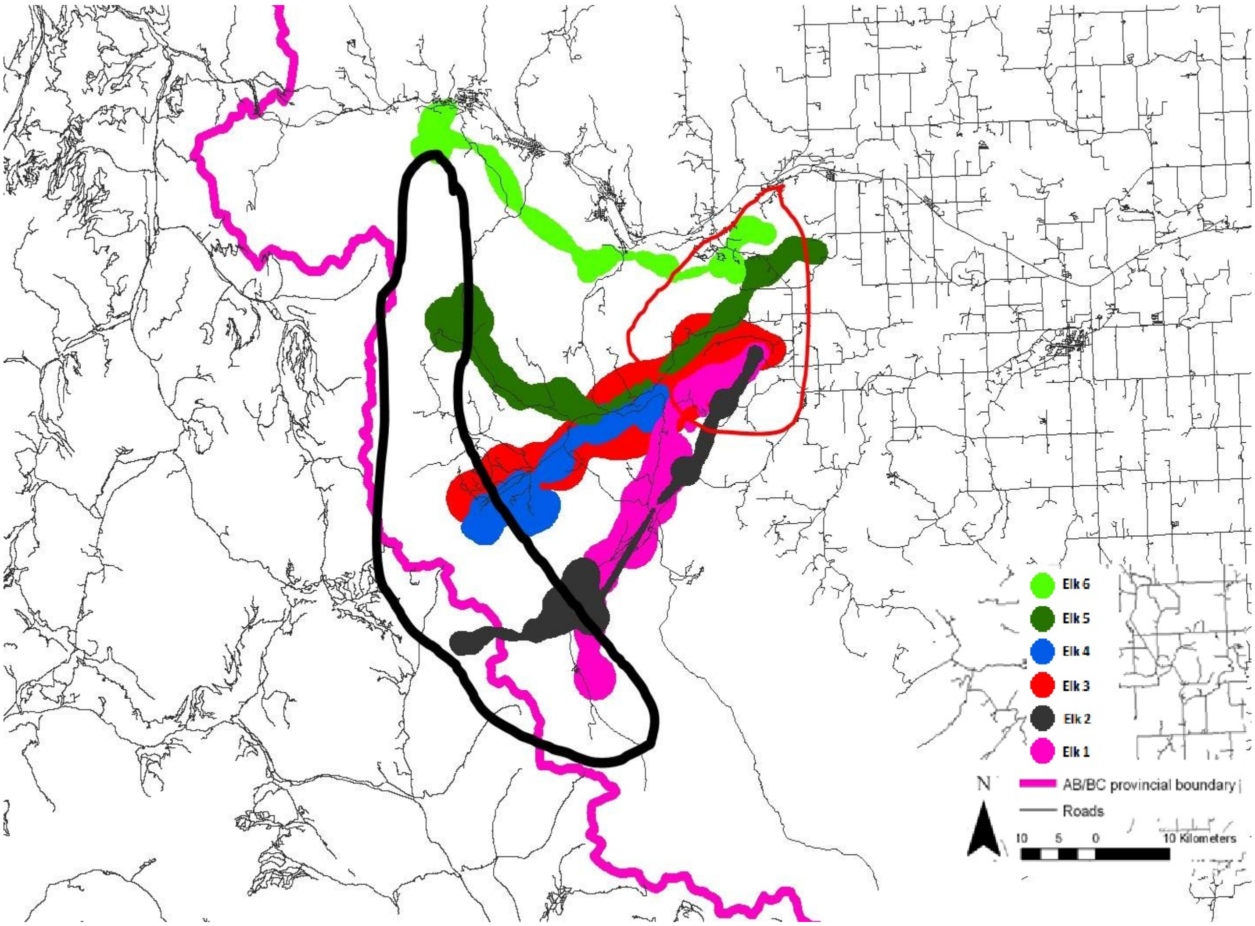
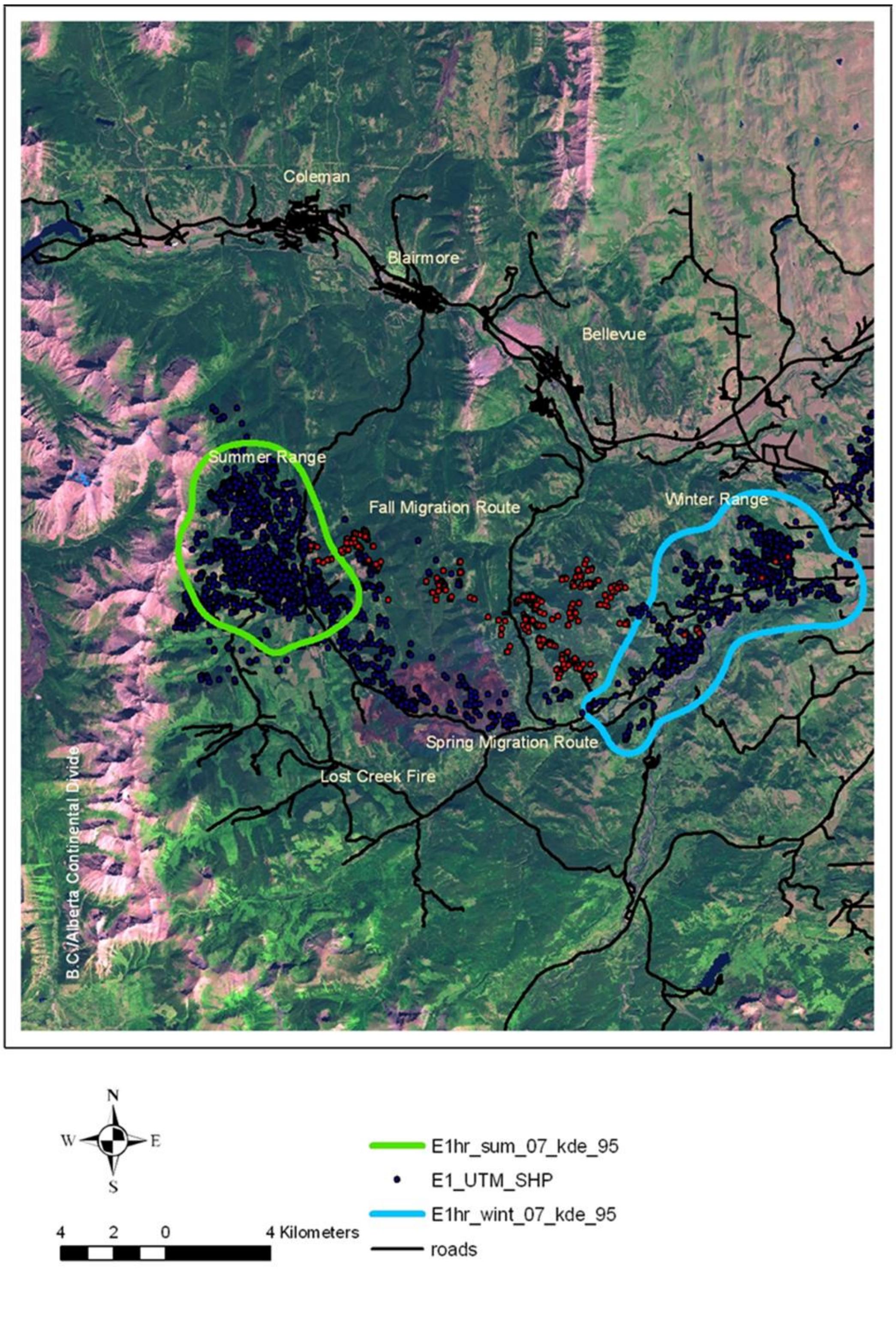


Figure 3-10 Castle-Carbondale elk using different spring and fall migration pathways



DISCUSSION

Elk mortality in study area

Elk in the human-dominated landscape of SW Alberta are exposed to a wide range of human activities and predators in a spatially complex landscape that may displace them from important habitat and expose them to increased mortality risks (Muhly et al. 2011, Webb et al. 2011). Capture related mortalities during the study were low with only one elk loss from the 68 elk captured. Another single animal died from unknown reasons not related to capture. The elk may have died of old age, for she was 15 years old. Where elk populations are hunted, hunting is one of the primary sources of elk mortality (McCorquodale et al. 2003, Unsworth et al. 1993) and often is much higher than carnivore predation (Allendorf and Hard 2009). The sample size of Castle-Carbondale elk collared was reduced by 21% due to hunting over four years of study, compared to 7.5% from natural predators (Table 3-1). Sample sizes for elk harvested by hunters and by predators were not high, but did reflect a pattern of hunters selecting primarily >2.5 year old males whereas the predators selected yearlings or females of lower reproductive capability such as the oldest age classes of females (Atwood et al. 2007, Wright et al. 2006). Alberta hunting regulations require male elk to have 3 points or more before they can be harvested, which in SW Alberta usually is an elk > 2 years old.

Elk are influenced spatially by the presence of predators (Gregory et al. 2009) and wolves occur within defined territories particularly during denning periods where their activities are close to the den while raising pups (Jedrzejewski et al. 2001, Fryzell and Sinclair 1988, Boyce 1991, Creel 2002). Elk migrating to the Castle drainage could encounter an active wolf den during migration. Rarely were elk GPS locations documented within five kilometers of the active den site. Wolf presence may have motivated the female elk in particular to move through the area in a quick and direct fashion to their summer ranges. Two elk died during migration as a result of wolf predation, although not near the wolf den. The wolf territory encompassed the entire elk home range and overlapped with cattle grazing areas (Moorehouse and Boyce 2011). The influx of summer livestock grazing and initiation of migration by elk may result in a replacement of cattle for elk as prey (Garrot et al. 2005, Moorehouse 2010). This is further complicated by wolf use of boneyards, areas used by ranchers to dispose of dead cattle during the year (Moorehouse

and Boyce 2011). This could reduce predation pressure on elk during summer and fall when cattle and elk are grazing on public land and private land.

One method for elk to avoid predation is to migrate; as suggested by the predation risk avoidance hypothesis (Mysterud et al. 2012). Predation may be an important driver for migration (Hebblewhite and Merrill 2007). Calves are more prone to predation and migration may be a means to avoid areas of high predation risk. It may also be best to live in solitude during calving season (Bergerud et al. 1984, Creel et al. 2005) to reduce the possibility of being detected by predators. There are grizzly bears, black bears, cougars, and coyotes that could prey upon elk neonates in SW Alberta. The extent of predation from most species is not known, except for the cougar which rarely preyed upon elk during 2 years of study (Banfield 2012). No collared elk during this study period died during winter, which can be a stressful and vulnerable time for elk.

Migration Metrics

Migration distance for the Castle-Carbondale elk was from 5- 34 km per seasonal migration (Table 3.3). The timing of spring migration did not vary annually. Most spring migrations starting the first week of May and ending the first week of June. Fall migration showed greater variability possibly due to hunting pressure and differences in occurrence of snowfall events. As in other published research, the difference in initiation of spring migration may be related to precipitation and vegetation green-up (Morgantini and Hudson 1989, White et al. 2010).

Movements of elk during the Castle-Carbondale herd migration were meandering with a slow rate of movement, (a defining characteristic of stopovers), interspersed with rapid migration movements between stopovers. Migration took from two to 65 days to travel a maximum linear distance of 34 km, indicating some elk spent a considerable portion of their migration time on the migration routes, while others moved quickly through. The mean of spring migrations was 20 days (SE +/-1.5, n=68) with those taking longer possibly calving on the transitions ranges and staying there until the young were more mobile. Longer time periods in stopovers and increased movements during mid-May to June were considered to be distinctive of female elk calving in Yellowstone National Park (Vore and Schmidt 2001). Fall migration had a mean duration of 21 days (SE +/-2, n= 61). Migration duration of Castle-Carbondale elk were variable possibly reflecting individual behavioural response to environmental and human disturbance conditions.

This contrasts from the quick few day migration events documented of bighorn sheep in B.C. (Dibbs 2007), the quick migration strategy of mule deer reported by Sawyer et al (2009) and the 7 day migration of an elk herd in Yellowstone (White et al. 2010). A second elk herd summering in Yellowstone National Park and wintered in an area open to hunting outside of the park averaged 43 days to complete fall migration. This delay to the winter range was likely to avoid hunting risk (White et al. 2010). These results are similar to Castle-Carbondale elk that display a flexible strategy to reduce hunting pressure by moving short distances in the fall to avoid hunters and moving slowly in the spring to take advantage or nutrient rich forage (Ciuti et al. 2012, Hebblewhite and Merrill 2009).

Ninety-five percent of the Castle-Carbondale herd migrates suggesting migration is beneficial to elk. Since they are a mountain elk population they can follow green-up of vegetation from lower winter range to high elevation summer ranges. The forage maturation hypothesis best explains upward migration due to plant phenology (Fryxell and Sinclair 1988, Hebblewhite et al. 2008, Mysterud et al. 2011). Early phenological plant stages are higher quality forage than mature plants. By following snowmelt and the elevational gradient of green-up, migrators are able to feed on higher quality plants for a longer duration than if they stayed at lower elevations typically found on winter ranges (Hebblewhite et al. 2008, Mysterud et al. 2012). Migrating Castle-Carbondale travel through montane habitats of topographical and plant diversity, which should extend the duration of new growing forage availability to elk. Southern aspects would be the first to green-up, with later access to north facing snow melt where low temperatures can prevail, result in delayed plant growth and enhanced digestibility (Hebblewhite et al. 2008, Mysterud et al. 2012). The slow rate of travel documented during elk spring migration could also be supported by the forage maturation hypothesis as elk move gradually to their summer range, taking advantage of the new growth of vegetation at varying elevations and aspects (Mysterud et al. 2012).

Population Migration

My study uses BBMM a utilization distribution model to spatially depict the extent of elk migration routes in a landscape of SW Alberta where increasing amounts of human activity are concentrated along roadways and trails throughout the landscape. I hypothesized due to the

modest distance between summer and winter ranges and the extent of human disturbance in the area (Muhly et al. 2011), the migrating portion of the Castle-Carbondale elk herd would travel quickly through transitional ranges and not stopover on route to the destination seasonal range. Using a population-level BBMM I identified a network of migratory corridors with stopovers connecting winter and summer ranges, thus failing to support my hypothesis.

Using the BBMM to model elk migration appears to be a useful method for identifying population-level pathways including stopover areas and areas of rapid migration movements to seasonal ranges (Figure 3-4). Migration routes were used consistently during each year of study as indicated by the repeated use of stopover sites and migration travel areas which are determined by the BBMM process (Fig 3-4). In fact, a number of Castle-Carbondale elk used the segments of migration route multiple times during their time on the transitional range, during either spring or fall migration seasons and occasionally in the summer. A migration study in Banff National Park, in an area with no hunting, also found some elk in the Bow Valley population moving back and forth between winter and summer ranges multiple times (Woods 1991). Males summering at high elevation ranges will move towards or to lower elevation winter ranges to increase their chances of finding females during the rutting period (Woods 1991). Response to environmental changes may be a partial explanation for the back and forth movements of some elk in my study. In the spring a few elk would start migration in mid-April but would return to the winter range after a deep late spring snowfall. In Africa, Serengeti wildebeest have been observed reversing direction and returned to previously vacated areas when temporary periods of drought interrupt the usual onset of the rainy season (Pennycuick 1975). These movement patterns illustrate the importance of migration corridors or segments of the route; not only for travel during migration to seasonal ranges, but also as an alternate route away from snow covered areas, calving sites and possibly escape from hunting pressure or predators.

To assess if migratory corridors differed between seasons I compared BBMM maps of spring and fall elk migration. There was a notable shift in many stopovers to areas not used during the spring, although two of the larger area stopovers were both used during the fall and spring by elk (Figure 3-7). Possibly a change in stopover use and return to a few of the spring stopovers may be related to a need for secure areas during the hunting season (Cole et al. 1997, Millspaugh, et al. 2000, Rumble et al. 2005).

Radio-collared adult female elk showed fidelity to travel routes and a return to the same summer and winter ranges in successive years. The Castle-Carbondale herd exhibited fidelity to the same topographical features used as core stopover areas during four years of study. Elk would stopover in the Carbondale-Lynx Creek foothills complex near the junction of three streams, Castle River, Carbondale River and Lynx Creek during spring and fall migration. From this topographic complex the elk on spring migration split into three different routes traveling to separate summer ranges in three different watersheds across a broad summer range along the Rocky Mountains (Figure 3-4My study supported the results of recent studies (White et al. 2007, Sawyer et al. 2009) suggesting temperate ungulates use a multiple-route migration strategy to migrate from a small winter range to a large summer range. Conservation of multiple routes is more complicated than one route because the increased possibility of developments and human activity will overlap the corridors. A population level analysis of elk migration (Fig. 3-9) depicts the priority migration areas for conservation of Castle-Carbondale elk migration. The high priority polygons delineate areas where elk migration would benefit from management guidelines to balance the conservation of movement areas between elk and human use. The current analysis (Fig. 3-9) considers both spring and fall migration to identify the high priority areas. This analysis illustrates the main migration moves along the lower Castle River to Carbondale Hill, Maverick Hill and Cherry Hill, separating into smaller corridors into the summer ranges.

This confirms a portion of Morgantini's results (unpublished data) during his telemetry elk study (1989- 92). He documented Castle-Carbondale elk separating into two subareas while on the summer ranges. A fourth route is used by a smaller proportion of the Castle-Carbondale herd to migrate from the northeastern segment of the winter range west to the Crowsnest River drainage. These migration movements and the ones migrating to the West Castle valley are similar to a traditional pattern of migration movement, where elk moved longer distances between stopover areas, as described by Sawyer et al. (2009). Individual migration pathways along the Carbondale River and to the Goat Creek drainage were different migrations, shorter in length but spending more time in a lower number of stopovers. These findings indicate a high percentage of Castle-Carbondale elk show fidelity to seasonal migration routes and seasonal ranges which may be advantageous to elk for it provides knowledge of seasonal resource availability (Wolf et al. 2009).

Spring and Fall Population Migration

My results, both at the individual and population scale, were different from other studies using BBMM (Sawyer et al, 2009, White et al. 2010). Instead of short stopovers of a few days followed by extended quick movements of travel towards the seasonal range destination, 32% of the elk in my study area displayed behaviour of staying an extended time period in stopovers within the migration route, gradually moving towards the summer range. The Castle-Carbondale herd exhibited high variability in its migration movements. Particularly in the spring, many of the individuals staying at stopovers for an extended time were utilizing the 17,765 ha area burned in the 2003 Lost Creek Fire. The segment of the Castle-Carbondale herd traveling along the Crowsnest drainage displayed a different movement strategy; one of shorter time periods spent in smaller stopover areas with longer segments of migration movement to the summer range. This herd does not travel through the Lost Creek burn site on route to summer range. A similar behaviour occurred in the fall during migration from summer range; individual elk would move part or all of the way to the winter range, then quickly and abruptly move back to the summer range. I hypothesize these actions could be a response to hunting activity which occurs from the first week of September until December 20 of each year or were movements to rutting areas (September – mid October). At other times elk would stay in one general location (stopover) for a few days, apparently secure from hunting pressure and other potential disturbances.

Castle-Carbondale elk displayed a number of movement patterns after splitting up into three sub-herds. In my study, elk moving through the Lost Creek fire burn of 2003 were more likely to stopover for a longer duration, possibly feeding on the new forbs and grasses found in the burn site. Elk traveling farther south into the Castle and south Carbondale areas moved more quickly and directly. Possibly there was less food available in the forested landscape and there was an active wolf den between the stopover hub and their summer range.

Migration Characteristics of Different Sexes

Separating male elk and female elk migrations from the population BBMM, I found the male elk appear to be using the transition range differently than the female elk (Figures 3-3 and 3-4). Male and female elk are known to spatially segregate themselves for time periods with the males possibly searching for the rich food supplies and willing to risk security for growing body mass

and antlers important for the rut (Geist 2002). Sexes may be segregated, but still use the same habitats and areas at different times of the year. There are examples of males and females using different habitats and areas outside the mating season resulting in seasonal movements between different areas (Ruckstuhl and Neuhaus 2005).

The various possible causes for sexual segregation continue to be debated. Females are expected to use more areas of security in an attempt to provide security for the calf at a cost of lower forage quality (Geist 2002). These responses could reflect sexual segregation with regard to resource utilization (Bleich et al. 1997, Main et al. 2008). Two possible ecological hypotheses are suggested for segregation in ungulates: forage-selection hypothesis (FSHs) and reproductive-strategy hypothesis (RSHs) (Gregory et al. 2009). FSHs predicts male and female use habitat differently in regards to food availability due to allometrically differences of body size no matter what the level of predation risk may be (Ruckstuhl and Neuhaus 2002). RSHs or predation-risk hypotheses suggests sexual segregation is a matter of different methods of survival tactics between males and females (Main 2008). However, the ecological significance of sex segregation between male and female elk may vary depending on scale. Sexual segregation may occur at the habitat spatial scale driven by reduction in predation risk (RSHs hypothesis), while differences in forage selection (FSH hypothesis) may explain segregation at the habitat-patch scale (Gregory et al. 2009).

From a management perspective, sexual segregation in the Castle-Carbondale herd poses a challenge. A multi-branched antler harvest criteria is in effect allowing for harvesting males of all age classes over two years of age. Female elk are managed using a draw system with limited tags being allotted each year. Male elk in the Castle-Carbondale are exposed to extensive hunting pressure starting early September until the last week of November. Hunting occurs in the public lands management area, an area occupied by elk during the summer, fall breeding season, a portion of the winter and during migration. If the sexes are spatially segregated over a large landscape there may be difficulties managing for both sexes. If males migrate through two management areas with two different hunting seasons, males may be overharvested because they are probably hunted in both the rutting areas (early season) and wintering range (late season) (Sibbald et al.2001). Elk management strategies could benefit by considering sexual segregation and migration during the hunting periods.

Yearling Male Elk Migration and Dispersal

Research suggests the mechanism of dispersal in animal populations has evolved to circumvent or lessen the probability of inbreeding depression and facilitates movements of individual animals from crowded ranges with concentrated competition (Martins et al. 2002). Vacant suitable habitat can be colonized or re-colonized by dispersing animals allowing for expansion of populations (Singer et al. 2000, Woodroffe 2003). Dispersal is commonly a characteristic of young animals and this was the case in my study. Male elk ≤2 years were the only elk to disperse in the Castle-Carbondale herd and other herds in SW Alberta.

Relocation data for male elk was entirely representative of elk <2 years old, a time period when their movements can be widespread and in some cases result in dispersal (Petersburg et al. 2000). A review of sex based dispersal (Greenwood 1980) suggested dispersal was female biased in most birds and male biased in a majority of the mammals. This may be related to different mating strategies where male birds defend territories (resources) and in mammals, males defend females. Males have the potential to increase individual reproduction by breeding with multiple females which according to the male – competition hypothesis, males should disperse as they reach sexual maturity because they are often unlikely to mate in their natal area (Dobson 1982). This suggests dispersal in polygamous ungulates such as elk would probably be male biased (Greenwood 1980, Martins et al. 2002). Female biased migration has been documented in one year old elk (Boyce 1989), although partial migration populations have had very little study. My study of female elk (1-18 yr.) and males less than 4 years appears to support the male-competition hypothesis.

I documented dispersals of yearling male elk to BC and Montana from the Castle - Carbondale herd (n = 2) and other herds (n = 2) in the population, suggesting yearling elk are the primary means of maintaining genetic diversity in this population. Dispersal of male elk from the Castle-Carbondale herd occurred on two occasions with both elk using the full extent of the population migration route to access their new home range. Switching occurred in one individual, a female which dispersed to the Crowsnest herd winter range, summered in the same area and the next winter travelled back to her original Castle – Carbondale winter range. Her movements, similar to the male dispersals occurred along migration pathways used by migrating Castle – Carbondale

elk while within the herd home range. This suggests that conserving migration corridors may also be valuable for elk dispersal and migration. Of the two elk dispersing, all survived on a new winter range. An additional 2 male yearling elk displayed exploratory movement behaviour where they stopped on summer range, then traveled 60+ km straight line distance westward over the Rocky Mountains moving through the Flathead Valley for about a month. One of the male elk went as far west as Fernie, BC before heading east, back to Alberta. In early July they both came back to a summer range used by other elk from the herd and ultimately migrated back to their natal winter range

Impact of Wildlife Land Use Management

Population utilization distribution of migration based on the BBMM illustrated that elk in this region have a strong fidelity to winter range, summer range and migration routes although for some elk the fall migration route differs from the spring (Fig.3-9a). In a number of cases a new route was selected during the fall hunting season (Figures 3-6 and 3-11). Hunting is an obvious disturbance to elk, yet many other human created disturbances have similar effects (Friar et al. 2008, Morgantini and Hudson 1985, Rumbleet al. 2005). Researchers have documented disturbance to elk creates a change in habitat use and diet (Edge and Marcum 1985), altered migration timing (Kuck et al. 1985), caused avoidance of roads (Rowland et al. 2004), avoidance of human activity (Wisdom et al. 2004), increased vigilance (Childress and Young 2003), created a negative physiological response (Millspaugh et al. 2001) and increased movements associated to human disturbance (Cole et al. 1997, Rumble et al. 2005) of elk. This evidence could be used by wildlife managers to justify conserving migration routes. The BBMM represents the present and possibly the last few decades of movement patterns of elk migration for the Castle-Carbondale herd as migration pathways are passed from mother to calves (Barber-Meyer et al. 2008). My results may be used as a baseline to quantitatively track any future changes in elk migration patterns (White et al. 2010) or changes in the number of elk migrating. In other areas, it has been suggested a reduction over years in the number of elk migrating may be linked to anthropogenic disturbance, habitat improvements and increased predation risk during migration or a combination of circumstances (Boyce 1991, Hebblewhite et al. 2006, Hebblewhite and Merrill 2011).

I have delineated elk migration routes and areas of importance to elk called stopovers that are expected to be important for increasing body condition and for some females, calving areas (Sawyer 2009). These results can be used to identify environments where potential development may occur with the least negative impact to elk migration. Important areas such as stopovers should be managed for conservation of migration routes. Resource managers looking to improve elk habitat may be able to use my results to identify management actions that could enhance elk habitat (restoration by selective logging or burning) on the transitional ranges. Future research investigating the connectivity of the migration routes would be an important component to conserving elk migration routes and other animals using the same areas for travel. Research on elk habitat requirements at a habitat and landscape scale during migration would provide perspective regarding the suitability of the land base between seasonal ranges to provide alternative options for migration pathways to change if the existing traditional route is blocked or severely compromised.

CONCLUSION

Migration Route Modeling

An essential aspect of maintaining and conserving migration corridors is to know where they are and why elk use the certain areas. Elk migration pathways were not spatially delineated for the Castle-Carbondale herd until this research was completed. Morgantini (1995) and others have described possible routes based on very high frequency (VHF) telemetry, anecdotal observations and historic records of Waterton Park wardens (Sheppard 1992). After four years of study tracking 38 female and 12 male elk with a total of 138 spring and fall migrations, we have a clearer understanding of the migration corridors used by the Castle-Carbondale herd.

Using the BBMM to calculate UD of migration I was able to model elk movements during migration events, with elk moving quickly between patches of habitat (stopovers) assumed to be important for foraging, resting and security. The distance of migration was modest with most elk moving through the transitional range within 20 days. Slow movement during spring is possibly due to the use of rich vegetation as forage in the migration corridors green-up. This would provide time for snow depths at higher elevation to recede and still provide elk with rich foods to

help replenish their body condition after the winter months. Some elk are known to stop for calving while migrating through the transitional range before getting to summer range.

Challenges of Elk Migration

Migrating elk (n=50) comprise 95% of the collared animals found in the Castle-Carbondale herd. They travel 10 – 34 km from the winter ranges to high elevation mountain summer ranges, passing through montane forest to subalpine and alpine meadows, with some stopping over in a six year old 17,765 ha burn. Direct and indirect human effects on the habitat resources in the study area can be high (Muhly 2010). Such impacts by humans need to be understood in areas such as SW Alberta (Arc Wildlife Services Ltd. 2004) where demand for natural resources and recreation is increasing (Naylor et al. 2009, Muhly 2010). To survive and produce young, ungulates must have options to select habitat with sufficient resources while reducing predation risk (Festa-Bianchet 1988, Houston et al. 1993). Humans influence wildlife distribution and fitness directly through activities such as recreation and disturbance from development (Fraire et al. 2008, Fryzell et al. 2010, Muhly 2010, Stankowich 2008) and by improving resources through agriculture or reducing predators (Muhly 2010). Migratory routes of adequate connectivity are required by the Castle-Carbondale elk to maintain migratory behaviour from winter to summer ranges. The continued existence of this partially migratory herd depends on being able to take advantage of high quality habitats on summer ranges.

Elk have the widest geographic distribution of any wild ungulate in the world (Clutton-Brock et al. 1982) and exhibit a diverse range of movement behaviours such as migration, residency, partial migration and dispersal (Adams 1982, Boyce 1991). Elk with home ranges in the mountains often undertake altitudinal migrations following vegetation changes over reasonably short distances. The species ability to adapt to the many environmental changes is one of the reasons they are widely distributed with increasing populations in many areas. A number of researchers have noted the elk's flexibility in movement patterns and how it allows them to adjust to a changing environment (Boyce 1991, Geist 1982, Morgantini 1988). Plasticity of elk can be high, although one main theme continues to be noted in studies over the last decade. It is displacement of elk from areas of human traffic, development and activity typically within 500 – 1000m. Such displacements have the potential to reduce the area of critical ranges available to

elk. This continuous loss of effective habitat may be the greatest challenge for maintaining elk migration and populations.

With 93% of elk from the Castle-Carbondale herd migrating, this research will be useful in managing the elk population. Knowing migration corridors of elk and important stopover areas will enhance wildlife managers' ability to maintain the movements of migratory elk. The BBMM results may be useful in managing the impacts of human activities temporally and spatially on the migration route.

The quantitative framework I used (Sawyer et al. 2009) models migration routes for both individuals and at a population scale. It delineates the Castle-Carbondale elk migration route providing options to plan developments be it roads or well sites in a way to conserve the core areas of migration. My results also support Sawyer et al. (2009) conclusions where movement and stopover areas may be distinguished based on different behavioural states; similar to others using non-linear curve fitting (Johnson et al. 2002), state-space models (Forester et al. 2007), Markov models (Franke et al. 2004), random walks (Morales et al. 2004) and first passage methods (Bailey and Thompson 2006). I found similar characterizations of movement routes as Sawyer (2010) did with mule deer, where elk displayed movement patterns of slow moving over an extended time period followed by quick movements through corridors to a new stopover. This differentiation between movements may be a useful management opportunity, since my modeling found that the elk population favoured some areas over others. These areas could be targeted for conservation as well as habitat enhancement opportunities.

Stopovers in the Sawyer study (2010) had higher forage quality compared to movement corridors connected to them, forage quality improved as elevation and distance from winter range increased. This would fit the strategy of migratory ungulates to follow the green-up of the most nutritious vegetation to maximize energy intake during the growing season (Albon and Langvatn 1992, Fryzell et al. 2004, Holdo et al. 2009). In my study many of the stopovers were located in a 2003 burn where forbs and grasses would green-up quickly, providing rich forage for elk (White et al. 1998). Two other migration routes not passing through the burn had fewer stopover sites of a smaller area than elk which passed through the burned area, possibly because elk using the burn were inclined to stay in areas of very rich nutritional forage for extended time periods.

The BBMM analyses highlighted an important stopover at the junction of Castle and Carbondale Rivers, located near the western boundaries of elk winter range. Elk are regularly observed here in the spring, feeding in the large meadows surrounded by aspen where some of the first green grass sprouts can be found (Paton 2005). From this topographic hub, the female elk select one of three routes traveling westward along three drainages to different summer ranges. This stopover within the winter range appears to be an important one for it is an area providing new spring forage as elk migrate through the winter range. The combination of winter range and a migration corridor / stopover in one area suggests it is very important for spring movement of elk to the summer ranges and should be considered critical elk habitat. In this chapter I used the BBMM to determine stopover sites and movement corridors along the migration route of the Castle-Carbondale elk herd. I visually reviewed and compared BBMM for differences between sexes, migration seasons and for all elk and both migration seasons at once. There appears to be differences in use between stopover by female elk during spring and fall migrations time periods. In Chapter Four, I develop a spring and fall resource selection function (RSF) for female elk migration pathways to understand their patterns of selection for a migration route and possible differences between spring and fall migration.

My study provides regional wildlife managers with quantitative data of migration corridors to manage potential future land use activities which may impact elk use of migration routes and eventually population dynamics and distribution. Migration events are important for they provide a means for greater numbers of elk to meet their life history requirements by increasing available range beyond wintering areas, enhancing their fitness and reducing negative grazing affects to winter ranges (Knight 1970, Rogala et al. 2011, Walter et al. 2010). Conservation of migration corridors has the potential to facilitate elk to continue to migrate thus reducing the likelihood of elk home ranges being limited to year round use of the migratory elk winter range. Increased elk use of habitat on the winter range will invariably increase depredation events causing increased complaints from private land owners. This may result in social pressure to reduce the numbers of an elk population managed by an arbitrary number rather than ecological considerations. From an ecological perspective large mammals such as elk are keystone species that affect ecosystem processes such as nutrient flows, nutrient cycling, and successional trajectories of plant communities (Kie et al. 2003). The potential losses of keystone species on

portions of the landscape are not well known indicating a cautionary approach of conserving migration is required.

Research Issues

My study design of maximizing sample units by removing and replacing collars on different elk after two years of tracking was useful in providing a larger sample size of elk and a broader understanding of elk migration. Location fixes of two hours and a location error of <20m provided a large number of accurate relocation fixes enabling modeling to portray elk migration UD. These temporal and spatial attributes of the study provide data of an appropriate scale useful for my research to characterize migration travel and stopover areas.

A common short-fall of migration studies is the length of time and variety of environmental conditions they represent due to changing conditions between years. A majority of migration studies are only one or two years and they usually do not reflect animal response to varying environmental conditions such as weather over time. With four years of study I was able to include a wider range of environmental conditions possibly providing a clearer picture of elk migration over time.

Collar reliability and the drop off mechanisms were at times a concern, particularly during the first year. I had a number of collars stop working, drop off prematurely or not drop off at all, reducing the final number of sample units. Fortunately my study collared numerous animals, providing a large sample size to use in analyses. Migration studies are further complicated by the trait of migrating animals tending to move very quickly through forested or rugged terrain between stopovers where it is difficult to acquire GPS relocations. Collection of two hour fixes worked well in this study with 93% of location fixes successful during migration. One limiting factor of a study of this magnitude is the cost of undertaking it. Collars and helicopters are expensive, so without the financial support of many organizations I would not have been able to succeed in achieving such a high level of data quality or volume.

Argos / GPS technology collars on male elk were an important component of the success of this study. Tracking yearling elk across mountainous terrain is no easy task. They can move large distances over a short time period and keeping track of some of the male locations would have

been impossible. Data fixes of the elk were sent from the collars to Argos satellites orbiting the earth, to a central data receiving facility in the USA where it was forwarded to the researcher's computer. Once a week the locations for male elk were updated, enabling us to efficiently track their travels remotely. This technology was not foolproof because collar failure resulted in a loss of potential data. Collaring yearling male elk from a hunted population of elk also reduced the amount of data I was able to collect of elk movements because a high percentage of males were harvested by hunters. Although, loss of these individuals did not provide insights into elk migrations; if they were shot in the first year, it did provide insights into human caused mortality and population demographics.

GPS technology has improved, enhancing my ability to study ungulates by providing increased frequency and accuracy of relocation points, but the methods to analyze movement data are limited. It is limited by the abilities of modeling to account for uncertainty in animal movements between known locations (Horne et al. 2007, Sawyer et al. 2009) and it is difficult to scale individual migration data to population level routes. Until recently, migration was investigated by connecting successive GPS location points of collared animals (Berger et al. 2006) which provided metrics such as timing, distances travelled and movement rates of migration. The draw back from such methods are that there is no defined area of route utilization based on error, thus we would not know if the route is 10m or 1km wide (Sawyer 2010). The BBMM used in my study was able to model the areas of route utilization.

Management Recommendations and Future Research

1. Conserve stopover sites; particularly those that may be used for calving.
2. Make all efforts to plan new development outside of migration route core areas.
3. Maintaining elk migration by conserving connectivity along the migration routes will help to circumvent possible conflicts between private land owners and elk populations on winter and migration ranges.
4. Implement land management plans which conserve areas of winter range and migration routes by putting private land into conservation easements or have critical habitat status on public land would be beneficial to elk and other species using the area.

5. Game management plans for elk should consider the potential of overharvesting of males that migrate through two wildlife management units during the rutting season and on to the winter range.

6. Reducing and managing roads and road densities particularly within core areas of winter and summer range, control new road developments within 300m to 1000m of migration corridors, depending on topography and forest cover. Gating roads can be one tool to achieve this goal.

7. Use prescribed burning or selective tree harvesting techniques to maintain stopovers vegetative conditions or create new stopover sites along migration routes with few stopover sties due to a closed canopy of trees.

APPENDIX A - ELK MIGRATION

Figure A-9 BBMM population utilization distributions for combined fall male and female elk, 2007-2010

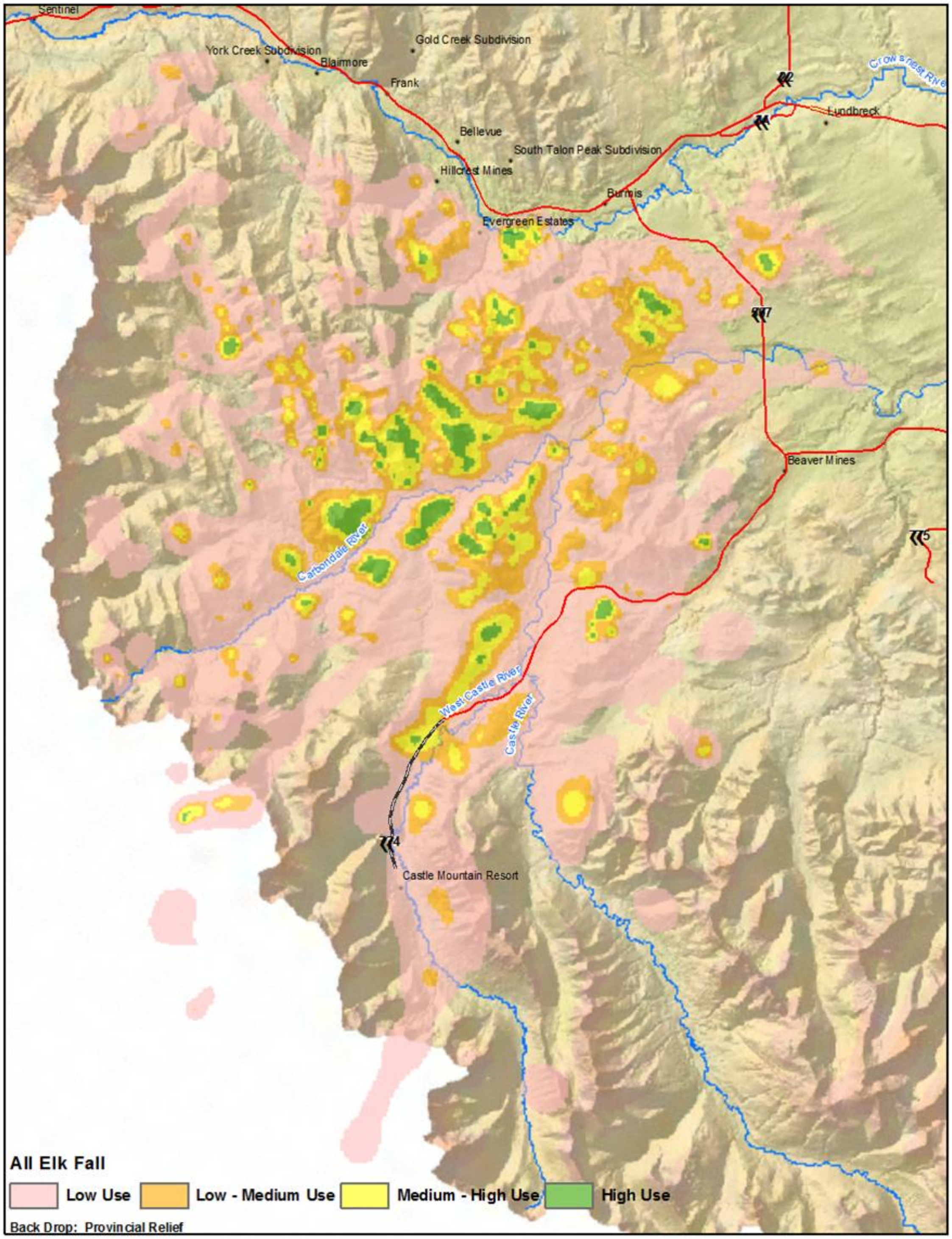


Figure A-10 Spring utilization distribution of all elk migrations from 2007-2010

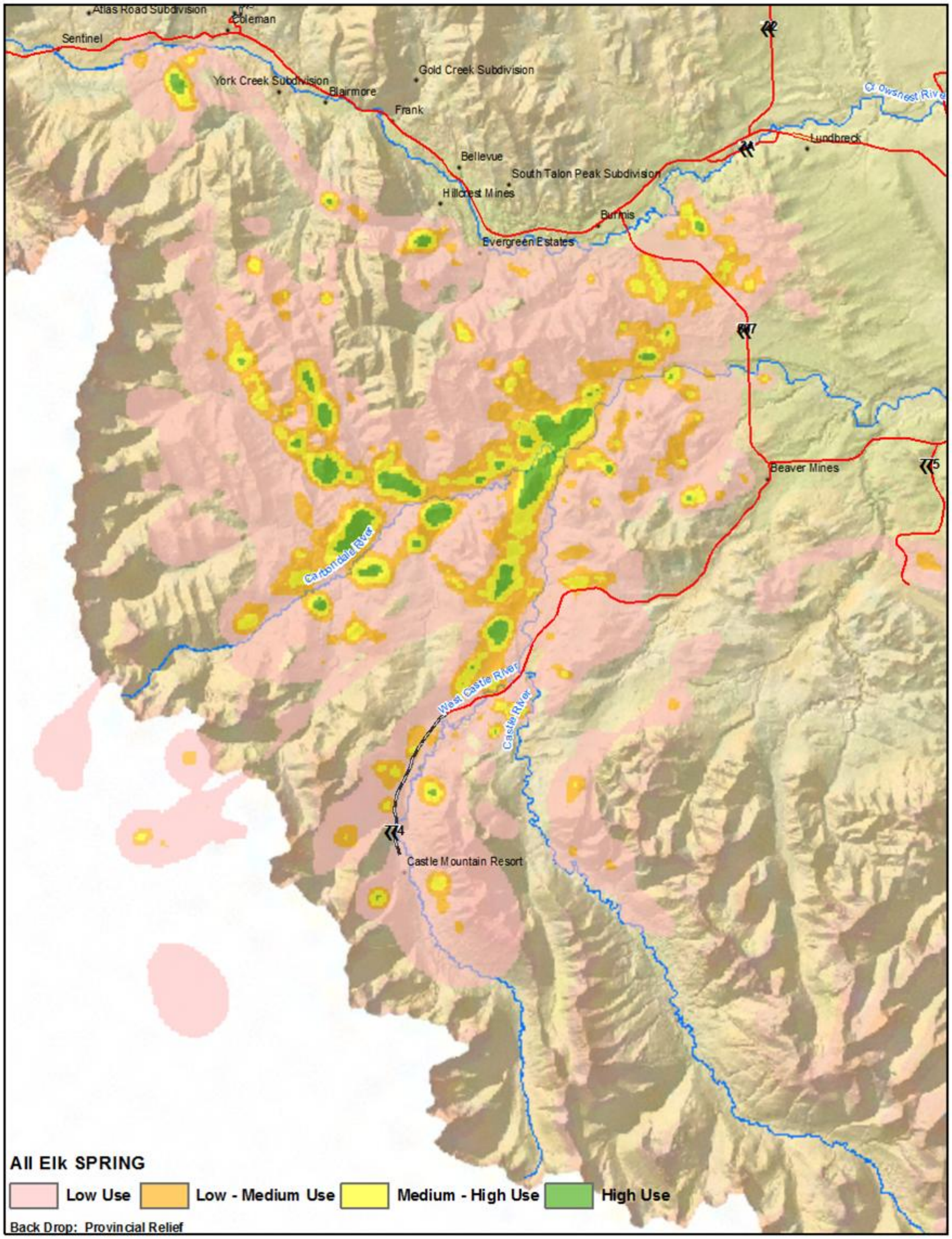


Figure A-11 Fall population utilization distribution of all male elk migrations from 2007-2010

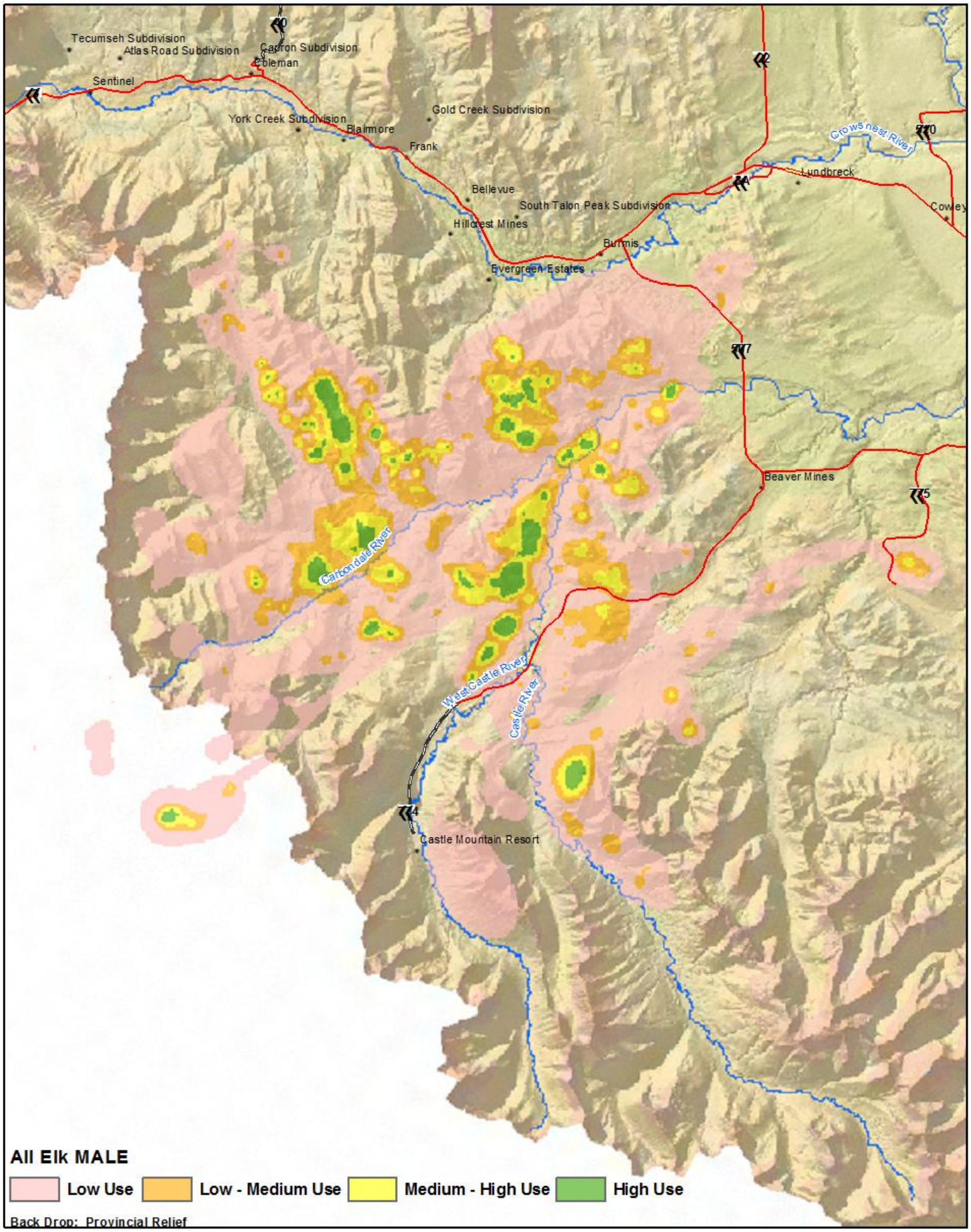


Figure A-12 Spring utilization distribution of male elk migrations from 2007-2010

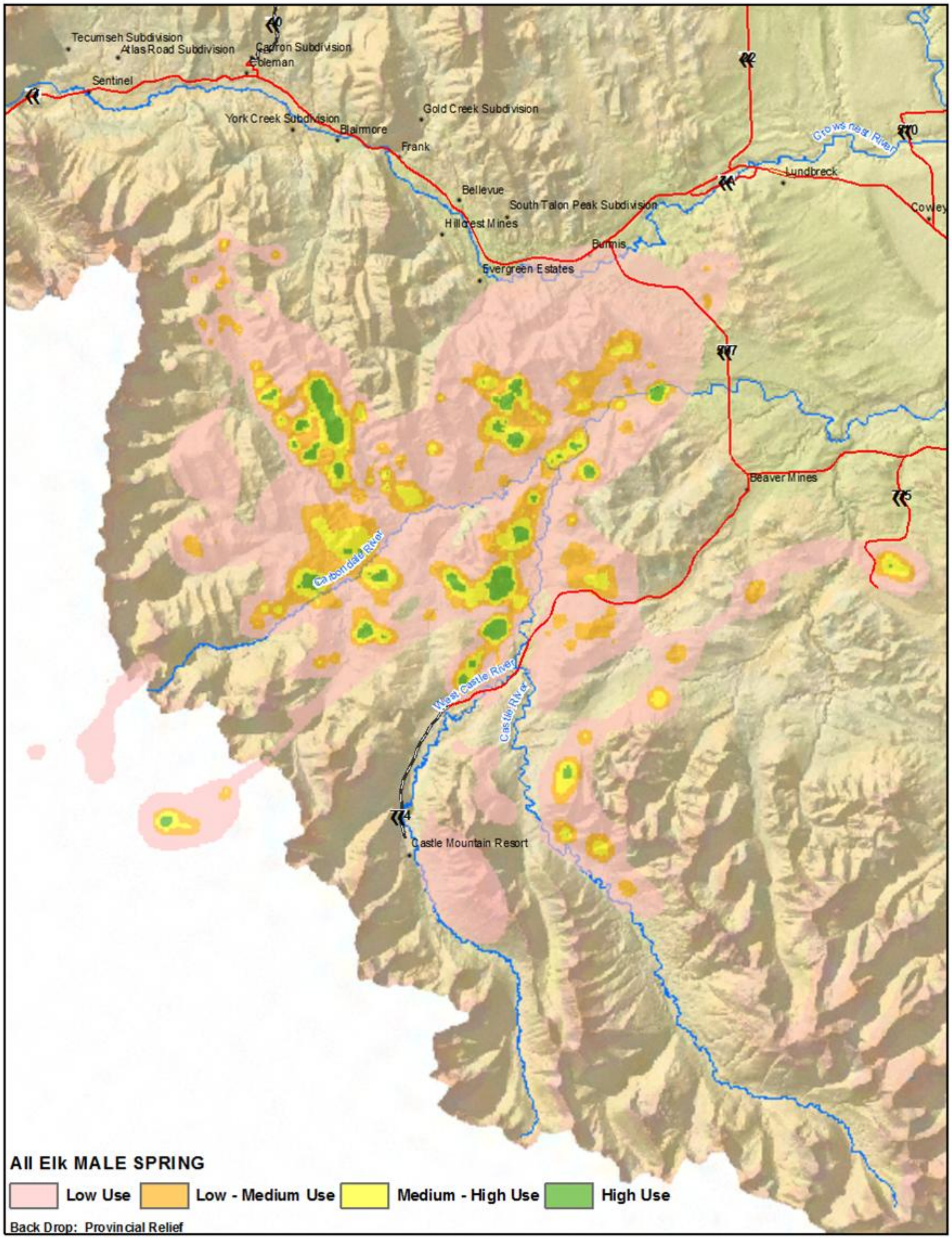
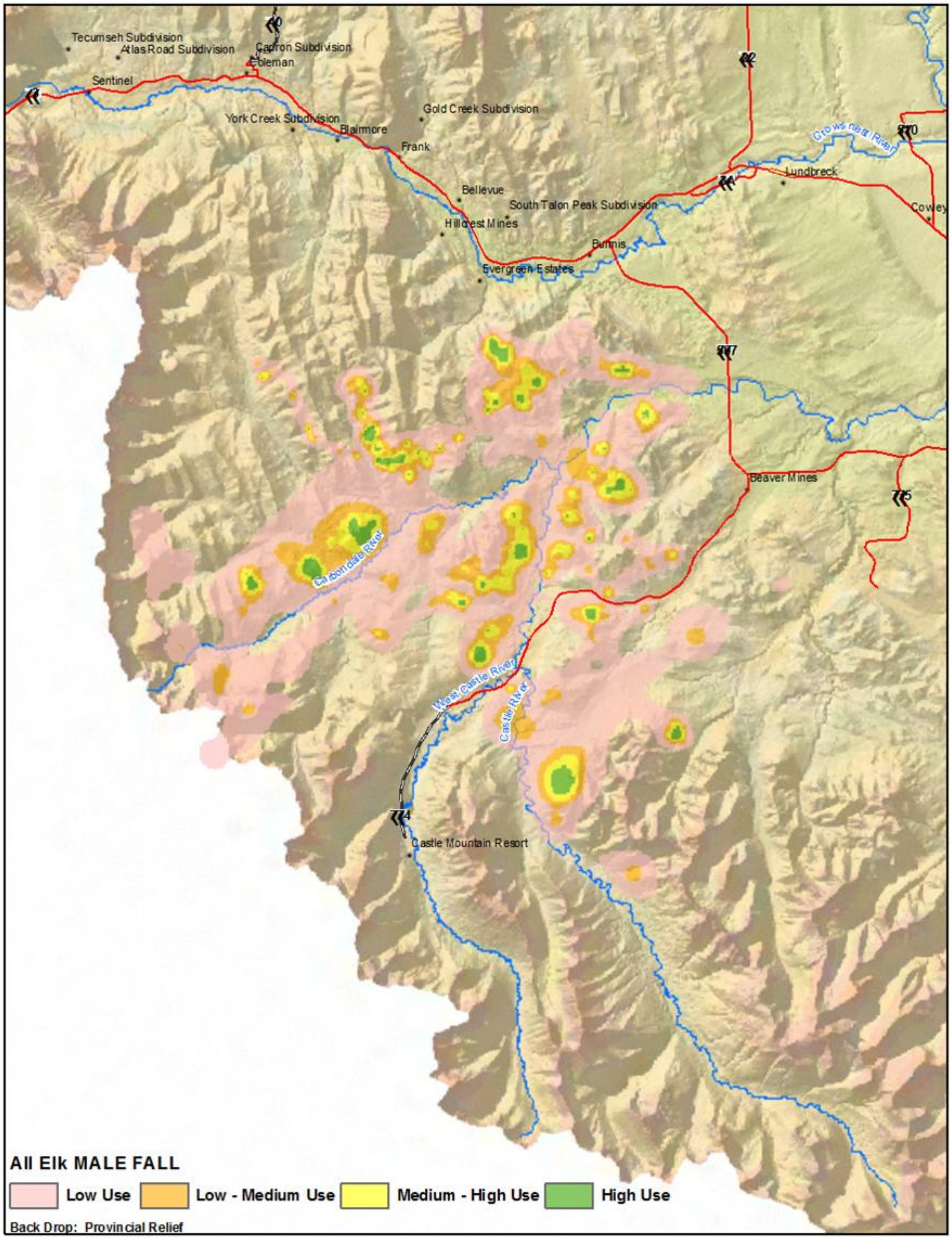


Figure A-13 Fall utilization distribution of male elk migrations from 2007-2010



CHAPTER FOUR: ELK STOP-OVER AREAS

ABSTRACT

Stopover ecology, well known in avian ecology, has recently been shown to be a strategy of ungulate migrants in temperate regions. I used fine-scale global positioning systems (GPS) migration data and logistic regression to quantify stopover characteristics for seasonal migrations of elk in the Rocky Mountains of Alberta. Elk completed migrations up to 34km in 2 to 65 days. Using logistic regression to compare elk GPS locations with random points within the elk herd home range I found elk avoided roads by a mean of 525 m, used areas of lower canopy, lower slopes, and higher terrain ruggedness. Avoidance of roads appeared to be more important to elk than avoiding known wolf habitat. I hypothesize stopovers have an strategic role in this migration providing access to rich nutritional forage in the spring and increased security for elk during the fall migrations which coincides with hunting season.

INTRODUCTION

Migration is an event undertaken by a wide range of species to access areas of additional nutrient rich forage and meet energetic requirements on their way to traditional breeding or summering ranges. For some species such as ungulates in heterogeneous mountain landscapes, migration enables them to maximize the availability of high quality habitats required to complete their annual life cycles (Morgantini and Hudson 1989, Boyce 1991, Mysterud et al. 2011).

The primary limiting factor in many migrating animals is the energetic requirements needed to finish migration, particularly bird species. To complete migrations, especially long distance, animals may use a strategy of pausing to feed in habitat patches called stopovers. These are found along the migration pathway and provide rich food sources and a place to rest and replenish energy reserves (Mara et al. 2005). Avian migration and stopover strategies have been studied for decades (Alerstam et al. 2003). Maximizing fitness is a priority of all species therefore the strategy of birds using stopovers may help researchers understand the strategies of ungulates stopover use. However, our knowledge of migrating ungulate stopovers is very limited. Only recently, has research investigated if stopovers also used by ungulates (Hedenstrom 2008, Sawyer and Kaufman 2011). Understanding the metrics of stopover

locations and habitat characteristics may add to our understanding of life histories, population dynamics (Salewski and Schaub 2007), and the development of conservation plans (Shimzaki et al. 2004) of migratory ungulates.

Avian migration strategy can be based on quick movements with stopovers to refuel along the journey because their relatively small body size reduces their ability to carry large fuel loads (Akesson and Hedenstrom 2007). Some avian individuals fly non-stop during their migrations while others pause at stopover sites (Chevallier et al. 2010). An optimal stopover site should provide access to food, water and security cover so species can restore energy expended during the preceding migration activity and replenish energy reserves for the remaining trip (Hutto 1998, Morris et al. 1996). Many ungulates migrations are different than most bird migrations. Temperate ungulates could complete a typical migration (20 -150km) quickly since they are able to travel 20 – 50 km in a day. However, such a strategy may not provide fitness benefits (Sawyer and Kauffman 2011). In ungulates, maximizing nutrition and improving body condition to enhance fitness is known to be a high priority (Cook et al. 2004, Parker et al. 2009, Sawyer and Kaufman 2011). Rather than migrating quickly, ungulates appear to use the strategy of slow migration movements while maximizing foraging of high quality foods (Hebblewhite et al. 2008, Sawyer et al. 2009, Sawyer and Kaufman 2011). Maximum energy inputs occur when plants are less mature and highly digestible (Hebblewhite et al. 2008). After elk survive winter they must consume nutrient rich vegetation to maximize fitness while reducing predation risk from both human and native predators. Completing migration as a quickly as possible as observed in birds does not seem to have any obvious fitness benefits for ungulates. Understanding stopovers characteristics during elk migration could assist in the development of new conservation strategies for migrating ungulates (Sawyer et al. 2009).

OBJECTIVES

I used fine scale elk movement data from GPS collars to determine stopover areas in Chapter Three. Why elk stop and use these areas is not well known. The objectives for my study were developed to determine characteristics of the stopovers used by elk during migration. The predictions of my study were elk would: 1) use stopovers removed from roads; 2) canopy closure would be greater than 50% and less than 80% to provide forage and security cover; 3) elevation

would be near valley bottoms, particularly in the spring when elk hunting does not occur and few people are in the area; 4) terrain ruggedness would be modest to make travel easy thus limiting energy expenditure; and 5) elk would reduce use of areas used by wolves.

STUDY AREA

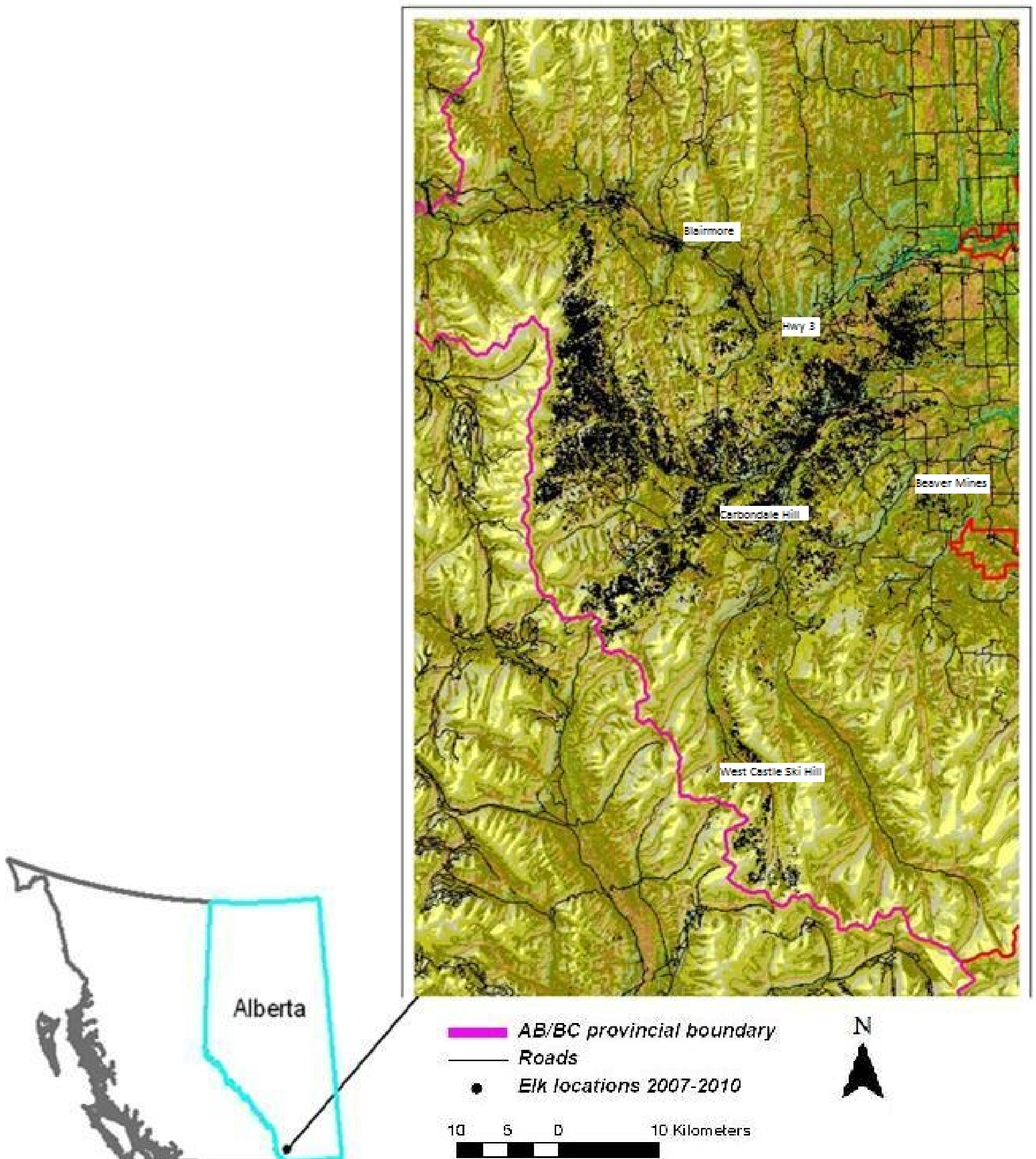
The Castle-Carbondale study area encompasses approximately 1000 km^2 in southwest Alberta. It represents a large component of an internationally recognized area known as the Castle Crown of the Continent (Figure 4-1). Alberta Sustainable Resource Development administers 100% of the public forest reserve. On the eastern boundary of the provincial forest reserve are private ranchlands intermixed with cropland. The study area includes portions of two municipal districts (M.D. Pincher Creek, Municipality of Crowsnest Pass). Livestock grazing occurs seasonally on public land and year-round on private land. Industrial activities in the area include forestry and natural gas extraction. Human activity on the landscape is widely distributed, comprised of random camping, off-road vehicles, mountain biking, hiking, hunting, and fishing combined with winter activities of snowmobiling and skiing.

Elevations range from 1250 to 2330 meters. The four kilometre wide strip of private land on the eastern boundary represents a transition zone between grassland and montane, continuing westward along montane foothills, which quickly rise to subalpine and alpine environments of high elevation mountains along the Continental Divide between Alberta and British Columbia, Canada. The area is composed of two natural regions and three natural subregions. The Rocky Mountain natural region is comprised of the Montane and Subalpine subregions and the Grassland natural region includes the Foothills Fescue subregion.

Environmental characteristics of the Rocky Mountain natural region include cool summers (13.9 Celsius), short growing season, high annual precipitation (798 mm) and the highest snow loads found in Alberta (Downing and Pettapiece 2006). The landscape is shaped by the prevailing Chinook winds which create snow-free southwest facing slopes exposing winter grass and shrub forage for ungulates. Montane and Subalpine subregions consist of rugged terrain with elevations from 825m to 2,300m. Dominant vegetation is lodgepole pine (*Pinus contorta*) Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*) interspersed with grassland slopes, meadows, wetland complexes (Downing and

Pettapiece 2006) and clearcuts. The Foothills Fescue subregion typically is rolling hills (elevation 800 m to 1,525 m) dominated by mountain rough fescue (*Festuca campestris*), bluebunch fescue (*Festuca idahoensis*) and Parry's oatgrass (*Danthonia parryi*). Portions of the subregion in the eastern part of the study area have been converted to cropland or tame pasture grass species.

Figure 4-1 Study area for Castle-Carbondale elk, 2007 – 2010. (location 694298 E 5483627 N)



MATERIALS AND METHODS

Capture, Collaring, and Data Collection

My project used a helicopter and net-gun to capture 39 female elk and 14 male elk on the winter ranges of southwestern Alberta from January to March during 2007-2010 (University of Alberta [Edmonton, Alberta, Canada] Animal Care Protocol number 353112). Elk were blindfolded and hobbled to allow collaring and sampling with low impact to the elk. Elk were fitted with Lotek 4400M GPS, 4400 GPS / Argos collars (Lotek,Newmark Ontario, Canada) and GEN4-GPS (Telonics, Mesa Arizona) equipped with mortality sensors that increased pulse rate if the collar remained motionless for >6 hours. GPS units were programmed to obtain location fixes every two hours (i.e. 12 per day). We located radio-collared elk from access roads at least once a month and some herds such as the Castle-Carbondale every week to confirm location and status of the elk. Collars from elk that died were refitted on new elk. The collars were outfitted with a remote drop off device programmed to disengage after 104 weeks. When the device failed elk were recaptured by the helicopter with net-gun method to retrieve the collars.

Identifying Migratory Elk

Elk populations such as the Castle-Carbondale herd are partially migratory, where one segment of a population undertakes seasonal migration while the other remains on a single range (Hebblewhite 2006, Lundberg 1988). Within a population of elk there may be a number of different phenotypes (Boyce 1991). In the partially migratory Carbondale-Castle herd there are migratory, resident and dispersal phenotypes. I assigned phenotypes as defined by Boyce (1991). Elk with seasonal home ranges overlapping entirely or predominantly are defined as resident elk. Migratory elk will move from a winter range to a separate summer range and return to the same winter range, whereas dispersing elk will leave the winter range to another separate seasonal range, not returning to the original winter range. Random sampling of animals was attempted (Otis and White 1999) by directing helicopter capture crews to collar individuals from different groups of elk located across the entire extent of a herd's winter range. To maximize sampling intensity we chose to collect two hour location fixes with the collar dropping off after two years, the collar was later redeployed on a different elk. To control location error of data used for analyses, data were sorted to select all relocations with three-dimensional (3D) and two-

dimensional (2D) values with a dilution of precision value <8 (Adrados et al. 2003, D'eon et al. 2005, Pepin et al. 2008, Rempel and Rodgers 1997).

From 2007 – 2010, 68 elk were collared; 19 elk in 2007, 24 elk in 2008, 12 elk in 2009, 13 elk in 2010. Data were imported into ArcGIS 9.2 (Environmental Systems Research Institute, Inc. Redlands, California, USA). To reflect seasonality of stopover use I separated elk migration data into two migration events: spring migration and fall migration. Migration data of 31,226 GPS relocation points were collected from 50 migrating elk during the four years of study. Stopover relocation points were 99% of the migration data.

Variable Selection

In chapter three I determined elk used stopovers during migration. A number of GIS data bases were available to represent the availability of forage for ungulates during migration. To assess characteristics of stopovers I identified 9 potential variables from the literature. They were elevation, terrain ruggedness, canopy cover, aspect, open area, distance to roads, road density, NDVI (forage quality) and predation habitat. A wolf resource selection function was available for the area (Muhly et al. 20010) to represent wolf habitat. NDVI was not readily available to represent forage quality which is expected to be important to elk migration in mountainous areas. I used open meadows, canopy cover and elevation as alternatives to NDVI. Some of the best areas of forge supply are found in open meadows. Open meadows and security cover such as trees can be characterized by canopy measurements. Aspects comprised of southerly slopes will green-up sooner in the spring and altitude will represent the elevation gradient. These are all attributes of the process of vegetation green-up. Predation risk is an important consideration for ungulates as they migrate (Pomeroy et al. 2006, Sawyer 2009). Reduced predation risk is expected to be part of the benefits of migration, although the risk of predation may affect stopover selection by animals (Pomeroy et al. 2006, Sawyer 2009). To reduce the risk of predation ungulates will use habitats of rugged terrain, higher altitude, increased distance from roads and areas of lower road densities. Elk distance from roads and road densities have been used to represent human disturbance to elk (Rowland et al. 2000, Frair et al. 2008, Webb et al. 2011) and an RSF for wolves will represent a important predator for elk in the area (Muhly et al. 2010). I propose these metrics may be able to represent characteristics of elk stopovers. I created

resource selection function (RSF) models for both seasonal migrations to evaluate habitat selection variables for female elk during different spatial and temporal scales. I compared characteristics of stopovers with random points found within the home range of the Castle-Carbondale elk herd. RSFs were binomial models with dependent variable 0 (associated habitat features of random points) or 1 (with associated habitat points used by elk). Random points were selected from within the minimum convex polygon of the elk population home range. For all analyses 2:1 ratio of random points were used for comparison to elk habitat points. I evaluated habitat selection for only female elk using logistic selection functions (R Development Core Team. 2009) to estimate resource selection functions (RSFs: Johnson et al. 2006, Manley et al. 2002). Used and random available locations were related to eight variables: wolf RSF (wolfrsf), canopy cover (canopycover), south aspect represented as cosine aspect (cosaspect), log transformed altitude (L.altitude), log transformed ruggedness (L.ruggedness), log transformed density roads within three kilometers (L.densroad3k), log transformed distance to road (L.distroad) and openarea. Correlation among variables was assessed using Pearson's Correlation ($r > 0.7$ was considered highly correlated) and any variable higher was removed because of high correlation with other variables. The variable percent canopy and open area had a high correlation with each other. I chose to use both variables but not in the same model. Nine a priori models (Table 4-1) were considered for both spring and fall migration events and Akaike's Information Criteria (AIC) was used for model selection (Burnham and Anderson 2002).

Table 4-1 Variables used in the spring and fall elk migration models with predicted effects of variables

	Description	Source	Data resolution	Predicted effect
wolfrsf	Wolf resource selection function	Muhly et al. 2010 Oikos	30 m	-
canopycover	% canopy cover	SRD	30 m	-
cosaspect	Aspect	SRD	30 m	+
L.altitude	Log transformed altitude	GIS data SRD	30 m	-
L.ruggedness	Log transformed terrain ruggedness	GIS derived Riley et al. 1999	30 m	-
L.densroad3k	Log transformed road density within 3km (km^2 per km)	Road data SRD	30 m	+
L.distroad	Log transformed distance to nearest road	Road data SRD	30 m	+
openarea	Open areas	SRD Collinear with Canopy cover – used in different models	30 m	-

*Alberta Sustainable Resources and Development (SRD)

Display of the RSF models occurred in GIS using the following relationship:

$$RSF(x) = \exp(\beta 1x1 + \beta 2x2 + \ldots + \beta nxn)$$

Where (x) value of landscape variables, β is the selection coefficients of that variable (Manley et al. 2002). Models were calculated in R statistical software package. AIC was used to confirm the best model for both spring and fall migration.

RESULTS

I collected data from 50 migrating elk comprised of 12 males and 38 females from 2007 to 2010. Only the GPS data points collected during migration of the 38 female elk were used for stopover characteristics analysis. The wide differences in Δ AICc and w_i between the different models confirm the strength of the best model (Table 4-2). AIC selected the same model as the most parsimonious model for spring and fall migration (Table 4-2, 4-3).

The spring model consisted of the best model being rated much higher than the second model based on the difference in the Δ AICc and w_i values (Table 4-2). Fall migrations best model contained the same variables as the spring with the difference between the best and second model less distinct (Table 4-3). This suggests for both models the location points in stopovers were significantly different from random points in the study area.

Table 4-2 Spring Migration AIC Candidate RSF Model Rankings

	AIC	Δ AICc	w_i
wolfrsf+ canopycover+cosaspect + L.altitude+L.ruggedness+ L.densroad3k +L.distroad	**53978.82**	**0.0**	**1.0000**
wolfrsf+ openarea+cosaspect +L.altitude+ L.ruggedness+ L.distroad +L.densroad3k	54073.63	94.8	0
canopycover+cosaspect +L.altitude+ L.ruggedness+ L.distroad+ L.densroad3k	54575.57	596.8	0
openarea+cosaspect +L.altitude+ L.ruggedness+ L.distroad+ L.densroad3k	54682.17	703.3	0
wolfrsf+ canopycover+cosaspect +L.altitude+ L.ruggedness	54726.11	747.3	0
wolfrsf+ openarea+cosaspect +L.altitude+ L.ruggedness	54819.45	840.6	0
canopycover+cosaspect +L.altitude+ L.ruggedness	55298.5	1319.7	0
openarea+cosaspect +L.altitude+ L.ruggedness	55405.55	1426.7	0
Null model	61452.08	7473.3	0

Table 4-3 Fall migration AIC candidate RSF model rankings

	AIC	Δ AICc	w_i
wolfrsf+ canopycover+cosaspect + L.altitude+L.ruggedness+ L.densroad3k +L.distroad	**55764.73**	**0.0**	**0.9941**
wolfrsf+ openarea+cosaspect +L.altitude+ L.ruggedness+ L.distroad +L.densroad3k	55774.99	10.3	0.0059
canopycover+cosaspect +L.altitude+ L.ruggedness+ L.distroad+ L.densroad3k	56155.12	390.4	0
openarea+cosaspect +L.altitude+ L.ruggedness+ L.distroad+ L.densroad3k	56167.32	402.6	0
wolfrsf+ canopycover+cosaspect +L.altitude+ L.ruggedness	58685.44	2920.7	0
wolfrsf+ openarea+cosaspect +L.altitude+ L.ruggedness	58693.35	2928.6	0
canopycover+cosaspect +L.altitude+ L.ruggedness	59060.6	3295.9	0
openarea+cosaspect +L.altitude+ L.ruggedness	59073.37	3308.6	0
Null model	61368.69	5604.0	0

In both spring and fall models, stopover sites had the following attributes;

- lower canopy cover,
- southern facing slopes,
- higher probability to encounter a wolf,
- lower altitude,
- high road density,
- large distance from road.

Four variables found in both seasonal migration models had a positive effect on the model. The variables were wolfrsf, ruggedness, density of roads within three kilometers and distance (Table 4-3, Table 4-4). These results suggest that elk selected areas where wolves could be present; terrain is rugged, with road densities within three kilometers less than one kilometer per km^2 and distances from roads greater than 486m. For per cent canopy cover, aspect and elevation, there was a negative relationship with elk stopovers (Table 4-3). My model suggests elk stopovers were in areas of lower canopy cover, lower elevation, and more southerly aspects of the landscape (Table 4-3).

Table 4-3 Best Spring Female Elk Migration Model

	Estimate	*Std. Error +/-*
(Intercept)	50.6300	0.9289
wolfrsf	0.0303	0.0012
canopycover	-0.0077	0.0004
cosaspect	-0.0964	0.0152
L.altitude	-18.6800	0.2982
L.ruggedness	1.7760	0.0472
L.densroad3k	1.4260	0.1016
L.distroad	0.4859	0.0201

Table 4-4 Best Fall Female Elk Migration Model

	Estimate	*Std. Error +/-*
(Intercept)	21.8600	0.8792
wolfrsf	0.0255	0.0013
canopycover	-0.0025	0.0003
cosaspect	-0.0750	0.0149
L.altitude	-10.0900	0.2752
L.ruggedness	1.3400	0.0483
L.densroad3k	3.5830	0.1067
L.distroad	1.1290	0.0275

Migration metrics for elk stopovers were slightly different in spring compared to fall use (Tables 4-5, 4-6). Elk preferred lower elevations, lower canopy cover, southerly aspects, road densities of 1km per km^2, in rugged terrain and were found on average 525m from a road during spring migration (Table 4-5). In the fall elk selected higher elevations for travel, a southeast aspect,

areas of higher canopy cover, .98km per km^2, and a mean distance of 678m from a road (Table 4-5).

Table 4-5. Spring stopovers characteristics of the Castle – Carbondale migratory elk, 2007 - 2010

Variable	*mean*	*sd* +/-	*Range*
Altitude (m)	1488.37	129.40	1198 - 2169
Aspect (°)	162.57	80.86	-1 – 359.34
Canopycover (%)	27.94	30.80	0 - 83
densroad3k (km/km2)	1.00	0.47	0 – 2.68
Distroad (m)	525.87	407.07	0 - 3600
ruggedness	18.98	10.00	0 – 64.24

Table 4-6 Fall stopover characteristics of the Castle – Carbondale migratory elk, 2007 -2010

Variable	*mean*	*sd* +/-	*Range*
Altitude (m)	1547.04	142.24	1200 - 2192
Aspect (°)	152.80	93.80	-1 – 359
Canopycover (%)	32.93	31.83	0 - 83
densroad3k (km/km²)	0.98	0.419	0- 2.7
Distroad (m)	677.57	447.90	0 - 3356
ruggedness	20.11	9.152	0 – 61.20

DISCUSSION

Individual elk exhibited a variety of selection differences between the mean of their group for each migration season (Table 4-5, Table 4-6). Fall migration primarily differed from spring variables by an increase in distances to roads, canopy cover, terrain ruggedness and elevation. Elk models in my analysis had positive coefficients for elevation, wolf RSF, road density and distance form roads indicating a preference or tolerance for these variables during use of stopovers. Elk used stopovers while avoiding human disturbance were apparent by the response of elk willing to be at risk in wolf habitat rather than the negative effect of disturbance by humans which are associated with roads, hunting activity and road densities (Table 4-5 and Table 4-6). Predation effects from wolves were limited to the one wolf pack in the area during the years of study so it may be perceived by elk the risk was low or infrequent. Coefficients from the elk logistic regression in spring and fall indicated most elk selected for areas with low to mid elevation, low per cent canopy cover, lower road densities and hundreds of meters away from roads.

Elk in the Castle-Carbondale herd displayed increased mean values for elevation, per cent canopy cover, terrain ruggedness and distance from roads in the fall compared to spring migration. A number of effects increased during fall migration, possibly due to higher use of roads by recreationalists and hunters (Proffitt et al. 2009, Webb et al. 2011), further suggesting the variables were strong in detecting elk resource selection. Similar results have been noted in other studies where human activities such as recreation, hunting, timber harvest, roads and oil and gas development occurred (Frair 2005, Naylor et al. 2009, Proffitt et al. 210, Webb et al. 2011). Elk occupying landscapes with human disturbance are known to adjust their movement strategies away from human disturbance sources such as roads, hunting, and recreational activities (Naylor et al. 2009, Proffitt et al. 2010).

Roads

Areas with high road density may not have patches of forest cover large enough to provide effective habitat for elk, particularly in hunted populations (Rowland et al. 2004). Extensive

shifts in elk distribution away from roads are a widespread phenomenon, and, at a landscape level, have the potential to affect elk carrying capacity and elk distribution away from high value habitats near roads or human disturbance (Rost and Bailey 1979, Lyon 1983, Edge and Marcum 1991, Rowland et. al. 2000).

In the current study the mean distance elk avoid roads during the spring was 526m (SD +/- 407.07) and in the fall it was 677m (SD +/-.447.09). Based on the SD of avoidance of elk to roads it appears a large degree of variability of individual elk occurs in response to roads with distance from road values ranging from 0 m – 3600m.This suggests there is a wide range of tolerance by individual elk for roads. This avoidance of roads is may be representative of the wide range of responses depending on sex, age, or seasons (Vistnes et al. 2004). Females with young are usually the most sensitive (Appollonio et al. 2005, Ciuti et al.2004). Road avoidance may lead to an increase in ungulate density in areas away from potential disturbance sources, resulting in increased competition or greater risk from predation (Gill and Sutherland 2000, Vistnes and Nellemann 2007). For avoidance behaviour to occur there needs to be alternative habitat available, although it may not be the same quality of habitat the animal was displaced from. This will result in animals displaced to lower quality habitat (Gill et al. 2001).

In my study, stopover locations during both elk seasonal migrations exhibited selection for areas of low road density (Table 4-4, 4-5). Their distribution indicates avoidance of areas less than 526 m from roads (mean distance) during spring migration and 668 m during fall migration. Using an RSF model and GPS telemetry data from elk in West Central Alberta, researchers (Frair et al. 2008) found the effects from roads saturated the landscape. There were no refuges greater than one kilometre from a road when the road density is approximately 1.6 km km^2. The elk population in my study selected areas with road densities of approximately 1km per km^2 within a distance of three kilometers from their relocation point.

Research has shown anthropogenic activities can create conditions that increase productivity of forage resources for elk, such as some timber harvest methods, agriculture or prescribed burns (Fraire et al. 2008, Rumble and Gamo 2011). Yet these same human influences can have a negative impact on elk by reducing and degrading habitat through road development, reduction of security cover, and increasing the subsequent vehicular traffic on roads (Friare et al. 2008,

Rowland et al. 2000). Such changes influence elk behaviour and fitness by requiring increased vigilance (Lung and Childress 2007), and elk avoidance of suitable habitats near major roads or in areas of high road density (Boyce et al. 2010, Fraire et al. 2008). In turn, increasing road networks provide humans easy access to elk habitat, which can lead to increased elk mortality due to animal harvest or vehicle collision and a reduction in suitable habitat due to avoidance from an expanding human disturbance footprint (Benitez-Lopez et al. 2010, Webb et al. 2011). Castle-Carbondale elk are exposed to all these human created pressures to varying degrees on both their seasonal ranges and migration corridors (Moorehouse 2010, Muhly 2010, Northrup 2010).

My study suggests elk responses to wolf predation risk (RSF model of SW Alberta wolves, Muhly et al. 2011) are less than responses to human predation risk represented by roads and road densities. Proffitt et al. (2009) indicated during their study where hunters occurred, elk responses to wolves were less than responses to human predation risk.

Percent Cover of Canopy

Migrating female elk selected stopovers with low forest canopy cover (mean = 28% spring and 33% fall) when compared to random locations in their home range. Lower canopy cover is typically related to greater forage availability in forests with a more open over-story. During spring migration low canopy cover forests or meadows would green-up sooner as elk migrate to higher elevation summer ranges (Hebblewhite et al. 2008).

Thirty-two percent of the elk migrated through the footprint of the 2003 Lost Creek fire where a rich supply of forbs and grasses would be available in spring in an area of low canopy cover. Research in Yellowstone National Park after the large fires of 1988 reported that grass biomass increased quickly in a few years (Romme et al. 2011) and patterns of elk habitat use followed forage recovery patterns. Elk used burned forests randomly during the first three years post fire then selected burned forests 12-14 years post fire (Boyce et al. 2003, Mao et al. 2005) and are predicted to see these positive effects for up to 30 years (Singer et al. 1989). Detailed elk migration movements are not known before the Lost Creek fire occurred, but present use and research suggests migrating elk are and will be able to utilize the post fire vegetation for many years to come.

Female elk selecting for lower canopy cover at stopovers may also be displaying this behaviour in an attempt to find the balance between quality food sources and predation risk to balance food and danger for both the female and her calf (Kotler eta al. 2004, Pomeroy et al. 2006). Lower canopy cover would provide more light for plant growth of forbs and grasses as well as providing greater visibility to detect predators such as wolves or humans (Laundre et al 2001). Alternately, risk of predation by wolves may increase selection for forested habitats where detection of prey by predators is lower (Creel et al. 2005). In SW Alberta elk responses to wolf predation risk (RSF model of SW Alberta wolves) seem to be less than human predation risk represented by roads and road densities. Proffitt et al. (2009) indicated in their study where hunters occurred, elk responses to wolves were less than responses to human predation risk.

Terrain Ruggedness

Terrain affects the grazing and traveling behaviour of ungulate species such as elk (Anderson et al. 2005, Forester et al. 2007). Elk react to wolf presence by increased use of steep slopes and rugged terrain combined with increased pathway sinousity (Laporte et al. 2010). The use of rugged terrain and steep slope by elk as refuge from predation has been documented in elk studies (Frair et al. 2005). Such a response is common in ungulates and is an effective anti-predator response (Bleich 1999, Hamel and Côté 2007). In a hunted elk population such as the Castle-Carbondale herd, elk may respond to humans in similar ways as they do canine predation risk (Proffitt et al. 2010). Therefore, the risk-disturbance hypothesis may also explain avoidance by animals of nonlethal human activity, which suggest animals would display the same behaviour used by prey when encountering human predators (Berger et al. 1993, Frid and Dill 2002). It is probable that the results of the logistic regression (elk selecting for rugged terrain) is a response to both human disturbance represented by roads and the potential to encounter a wolf. The disturbance is greater during the fall probably due to the influence of hunting activity (Proffitt et al. 2010).

Using rugged terrain is an effective method to reduce predation risk by elk. Although my model does not examine the interaction between these variables, the overall separate effects of roads of wolves are less predation risk than roads.

Aspect

Studies have noted elk prefer specific aspects depending on the season. Skovlin et al. (2002) found elk in winter preferred upper south facing slopes because of wind and solar radiation where slopes become bare of snow. Results from western Oregon (Moeller 2010, Witmer and deCalesta 1985) found migratory elk spent a greater percentage of their time on southern aspects during all four seasons of the year. During the four years of my study, the elk population typically used stopovers with southern aspects of 153 and 163 degrees during spring and fall migration. There were individuals that used northerly and northeast facing slopes but they were not common. Particularly during the spring, south and southwest slopes would green up the quickest providing nutrient rich forage for migrating elk to replenish their bodies after winter.

Wolf

My model suggests elk are willing to risk contact to potential wolf predation rather than risk exposure to human activity associated with roads. This aversion to human activity which was represented by roads and road densities increased in the fall during hunting season (677m versus 525m). Such a behavioural response may suggest that elk are able to discern temporal variation in predation (Gude et al. 2006, Proffitt et al. 2010). In Yellowstone National Park, elk respond to wolf predation risk by moving to another area within one or less days after exposure (Creel et al. 2005). Elk may also respond to wolf predation risk by choosing forested areas where risk of detection by predators is lower (Creel et al. 2005) or at other times elk groups have selected grassland flats for their ease of detecting wolves or movement and maneuverability for escape (Proffitt et al 2010). When exposed to predation risk from humans the behavioural response was greater than if the risk was from wolves (Proffitt et al. 2009). Elk respond to changes in predation risk over time periods of a week or months but they did not respond during diurnal time scales (Proffitt et al. 2010).

CONCLUSION

My analysis of the Castle-Carbondale elk herd use of stopovers during migration indicates stopovers are preferentially selected based on eight of nine habitat metrics when compared to random sites within the MCP home range of the elk population. Elk use the same stopovers

during each season of migration denoting the areas importance for elk. A study of mule deer (Sawyer and Kaufmann 2011) also identified annual use of stopovers and they found higher forage quality was available at stopovers compared to movement corridors. Forage values in stopovers also increased along the elevational gradient as distance from winter range increased (Sawyer and Kaufmann 2011). My study found elk used stopovers repeatedly during spring migrations but stopover use shifted away from spring sites during fall migration and hunting season (Table 4-4, 4-5).

Conservation of stopover sites for migratory birds has become a worldwide initiative reflecting the significance of the areas to avifauna (Hutto 1998a). Birds will stop at these sites year after year during migration. In the case of ungulate use, stopovers are less known but this study indicates elk have a preference for sites along the migration route where they stopover regularly. Another study of migrating mule deer showed fidelity to stopovers during different seasons and years, suggesting the sites may be important for conservation of migratory ungulates (Sawyer and Kaufman 2011). They suggested, the importance of individual stopovers along the migration route will be difficult to quantify (Sawyer and Kaufmann 2011). In the Castle – Carbondale migration network there are stopovers which overlap with winter range and a number are nodes or hubs of connection for multiple migration routes. While all stopovers may have important forage resources, security features or combinations of both. Stopovers used during multiple seasons time such as winter and spring migration or spring and fall migration may require a higher priority of conservation. Additional study could develop models using vegetation indices such as NDVI associated to each elk GPS point during migration. Allowing for two way interactions in the model between the wolf RSF and roads could provide additional insights to my current results.

CHAPTER FIVE: CONNECTIVITY OF ELK MIGRATION PATHWAYS IN SW ALBERTA

ABSTRACT

Increased recreation activity, industrial development and predator populations have the potential to influence ungulate movements such as seasonal migrations. Conservation efforts often focus on the habitat, viability requirements and connectivity for umbrella or keystone species such as elk. In this study I use two connectivity modeling methods designed to assess connectivity, least cost path and circuit theory. I obtained an existing resource selection model (RSF) of elk use in SW Alberta then used the inverse of these data to develop a cost surface for use in the model (Connectivity Analyses Toolkit). Preliminary results suggest the model confers with expert knowledge based on regional and local scale assessments. Further quantitative assessment is required to fully validate the model using migration and dispersal data not used in the model development.

INTRODUCTION

Loss of habitat and fragmentation are detrimental to biodiversity from global to local spatial scales (Crooks and Sanjayan 2006, Noss and Daly 2006, Laita et al. 2011). Fragmentation has always been part of the ecological variation of habitat and does not necessarily threaten many species (Baggio et al. 2011). What is of concern is the accelerated nature of fragmentation due to human population growth, infrastructure development and urban sprawl increasing the rate and scale of fragmentation that threatens species persistence (Baggio et al. 2011). Habitat loss from human sources reduces the total amount of habitat by breaking up core areas necessary for many species (Kindlmann and Burel 2008). This creates habitat fragmentation which confounds and increases the effect of direct habitat loss (Andren 1994). The ecological effects of both are intertwined and may be understood or measured using the concept of connectivity (Gilbert-Norton et al. 2010, Laita et al. 2011). The concept of connectivity refers to the connections between species and the habitats they utilize (Schumaker 1996). A particular landscape will provide different degrees of connectivity, depending on behaviour, habitat preferences and dispersal abilities of a particular species (Calabrese and Fagan 2004). Although species vary a

great deal in their response to fragmentation it is invariably detrimental to natural ecosystems (Johnson et al. 2005, Johnson and Klemens 2005).

Landscape permeability, also known in landscape ecology as connectivity, assesses the degree to which organisms are able to traverse a landscape (Taylor et al. 1993, Tischendorf and Fahrig 2000). Connectivity is comprised of both structural and functional connectivity, where structural connectivity relates to linkage of habitat patches by their adjacency (Keitt et al. 1997). Functional connectivity relates to linkage of habitat patches by processes that reflect dispersal and movement behaviour of species (Brooks 2003, Goodwin and Fahrig 2002). The foundation of the functional connectivity concept is that the connectivity experienced by an animal is based on the behavioural responses of the animal to physical landscape structure (Kindlmann and Burel 2008).

A reduction or obstruction of animal movements can have significant consequences for conservation of biodiversity (Taylor et al. 1993, Minor and Urban 2008). Maintaining habitats for animal travel areas enables juvenile dispersal, recolonization of unused habitats, seasonal migration and metapopulation dynamics (Gilpin and Soule 1986). With climate change added to the list of habitat influences managers need to consider long term management strategies for maintaining movements of animals. Animals will need suitable habitat for range shifts to conserve movement opportunities and genetic diversity (Minor and Urban 2008, Schemske et al. 1994).

The loss of connectivity throughout landscapes worldwide has led researchers to investigate the effects of habitat fragmentation and human disturbance to animal migrations (Berger et al. 2008, Harris et al. 2009, Hebblewhite et al. 2008, Mysterud et al.2001, Sawyer et al. 2009, Voeten et al. 2009). Completing these migration movements are believed to be essential to migratory elk populations and meta-populations (Coulon et al. 2006, Schmiegelow 2007). Elk migration is an adaptive behavioural strategy that evolved to avoid constraints on resource availability in temperate regions (Cook et al. 2004, Hebblewhite 2008). Movement to seasonal mountain ranges allows elk to access optimal patches of nutrient rich vegetation for an extended time period, enhancing fitness and reproduction (Mysterud et al. 2001, Phillips and Alldredge 2000, Smallidge et al. 2010). In turn, elk contribute to ecosystems function and biodiversity by their

grazing pressure on plants and influence on soil dynamics (Frank and Goffman 1998, Kie and Lehmkuhl 2001). Migrating elk are part of a functioning ecosystem and maintaining the connectivity of their migration pathways to ensure the migration strategy is not discontinued is valuable. Connectivity for ungulates is not only important to migration but to ungulate dispersal. Fragmentation can affect ungulate meta-population dynamics such as gene flow between subpopulations (Coulon et al. 2004), therefore conserving dispersal routes for ungulate is essential.

My objective for this chapter is to complete a local and regional connectivity analysis for elk to identify areas where conservation efforts could be implemented for elk migration and dispersal. Such knowledge will add to the existing corridor research completed for carnivores (Apps 1997, Kansas 2002, Chetkiewicz and Boyce 2009).

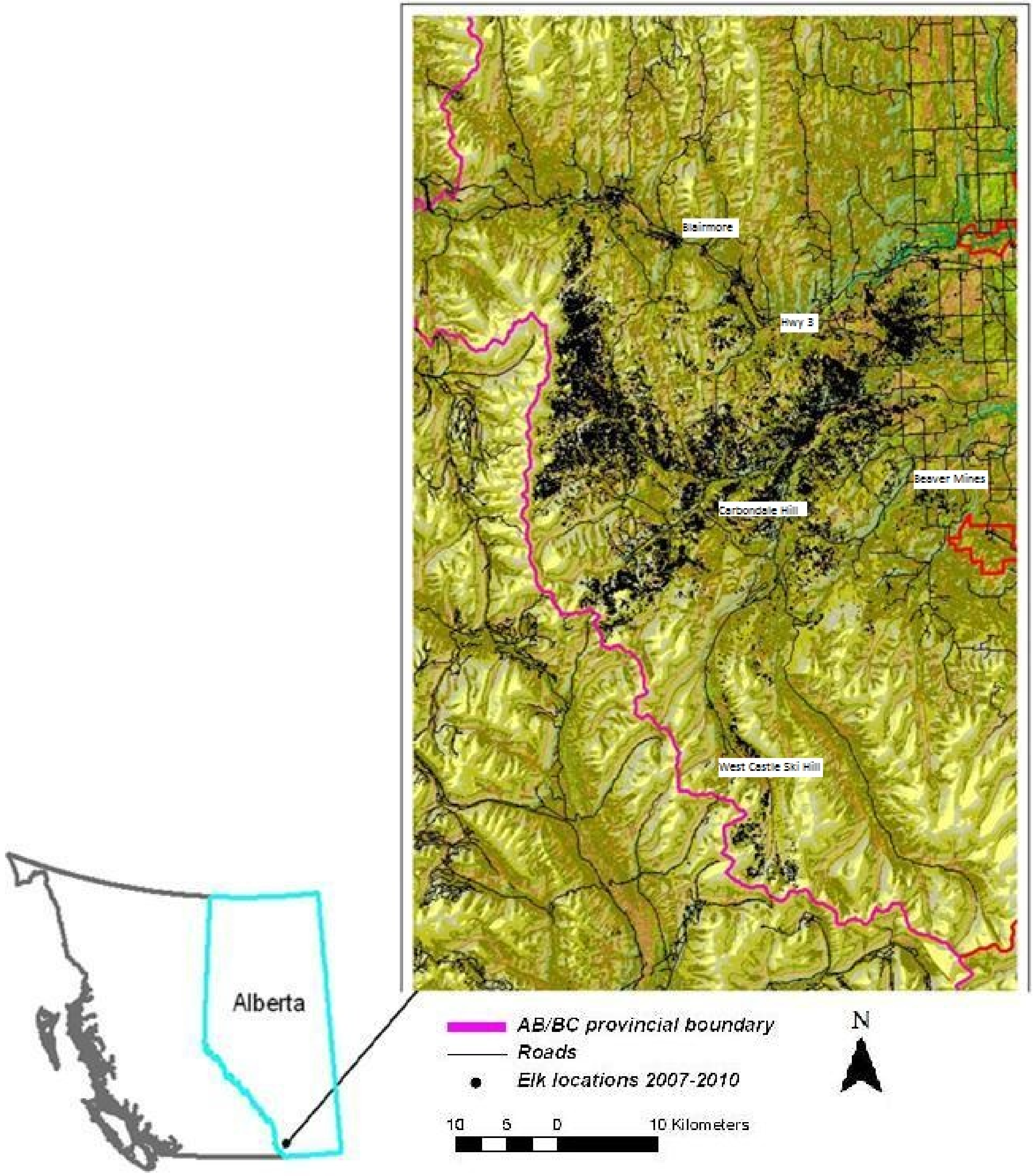
STUDY AREA

The Castle-Carbondale study area encompasses approximately 1004 km^2 in southwest Alberta. It represents a large component of an internationally recognized area known as the Castle Crown of the Continent (Figure 5-1). Alberta Sustainable Resources administers 100% of the public forest reserve. On the eastern boundary of the provincial forest reserve are private ranchlands intermixed with cropland. The study area includes portions of two municipal districts (M.D. Pincher Creek, Municipality of Crowsnest Pass). Livestock grazing occurs seasonally on public land and year-round on private land. Industrial activities in the area include forestry and natural gas extraction. Human activity on the landscape is widely distributed, comprised of random camping, off-road vehicles, mountain biking, hiking, hunting, and fishing combined with winter activities of snowmobiling and skiing.

Elevations range from 1250 to 2330 meters. The four kilometre wide strip of private land on the eastern boundary represents a transition zone between grassland and montane, continuing westward along montane foothills, which quickly rise to subalpine and alpine environments of high elevation mountains along the Continental Divide between Alberta and British Columbia, Canada. The area is composed of two natural regions and three natural subregions. The Rocky Mountain natural region is comprised of the Montane and Subalpine subregions and the Grassland natural region includes the Foothills Fescue subregion. Environmental characteristics

of the Rocky Mountain natural region include cool summers (13.9 Celsius), short growing season, high annual precipitation (798 mm) and the highest snow loads found in Alberta (Downing and Pettapiece 2006). The landscape is shaped by the prevailing Chinook winds which create snow-free southwest facing slopes exposing winter grass and shrub forage for ungulates. Montane and Subalpine subregions consist of rugged terrain with elevations from 825m to 2,300m. Dominant vegetation is lodgepole pine (*Pinus contorta*) Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*) interspersed with grassland slopes, meadows, wetland complexes (Downing and Pettapiece 2006) and clearcuts. The Foothills Fescue subregion typically is rolling hills (elevation 800 m to 1,525 m) dominated by mountain rough fescue (*Festuca campestris*), bluebunch fescue (*Festuca idahoensis*) and Parry's oatgrass (*Danthonia parryi*). Portions of the subregion in the eastern portion of the study area have been converted to cropland or tame pasture grass species.

Figure 5-1 Study area for Castle-Carbondale elk, 2007 – 2010 (location 694298 E 5483627 N)



MATERIALS AND METHODS

Capture, Collaring, and Data Collection

A helicopter and net-gun were used to capture 38 female and 14 male migratory elk on the winter ranges of southwestern Alberta from January to March during 2007-2010 (University of Alberta [Edmonton, Alberta, Canada] Animal Care Protocol number 353112). Elk were blindfolded and hobbled to allow collaring and sampling with low impact to the elk. Elk were fitted with Lotek 4400M GPS, 4400 GPS/Argos collars (Lotek,Newmark Ontario, Canada) and Telonics GPS (Telonics, Mesa Arizona) equipped with mortality sensors that increased pulse rate if the collar remained motionless for >6 hours. GPS units were programmed to obtain location fixes every two hours (i.e. 12 per day). I located radio-collared elk from access roads at least once a month and some subpopulations such as the Castle-Carbondale every week to confirm location and status of the elk. Collars from elk that died were refitted on new elk. The collars were outfitted with a remote drop off device programmed to disengage after 104 weeks. When the device failed elk were recaptured by the helicopter with net-gun method to retrieve the collars.

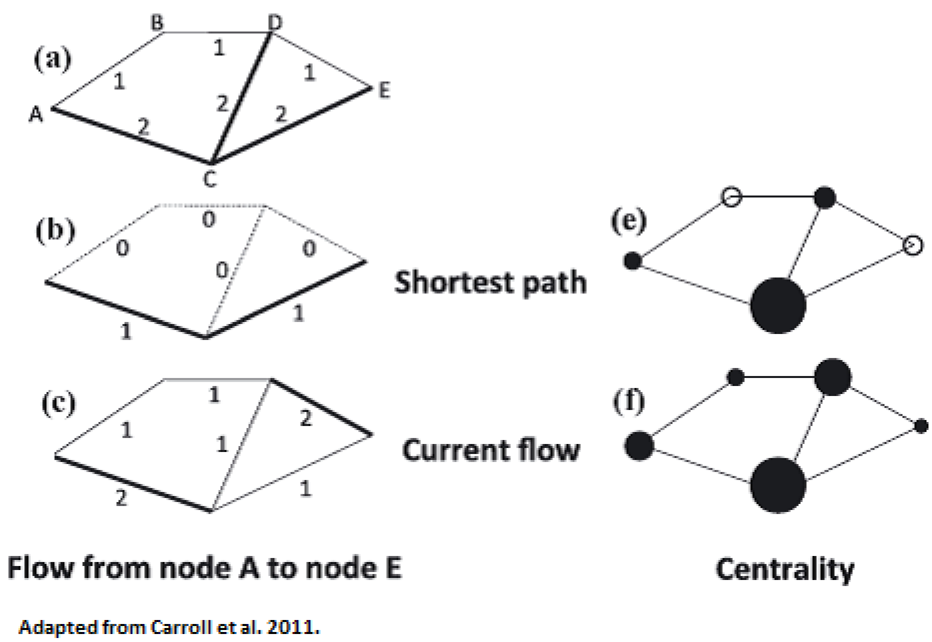
Network Models

A network modeling framework is well suited to assess connectivity of landscape heterogeneity (Brooks 2006, Carroll 2012, Fall et al. 2007, Urban and Keitt 2001, Urban et al. 2009). A network is represented by a set of nodes that are connected by edges that connect pairs of nodes (Brande and Fleischer 2005) (Figure 5-2). When planned for conservation purposes, nodes represent habitat patches, core areas or reserves and edges reflect the possibility for dispersal (Minor and Urban 2008). Weights are assigned to nodes and edges to provide information regarding their degree of connectivity, based on the size of nodes or the distance of edges in a landscape. Including the spatial properties of nodes and edges is common in landscape applications. Nodes can be defined as two dimensional patches with fixed locations and edges can be defined as geo-referenced links between nodes connecting core nodes moving along

routes of shortest or best connectivity based on suitability of the intervening matrix determined by least-cost routes or circuit theory (Figure 5-2) (Carroll et al. 2011, Fall et al. 2007).

I conducted a method of regional and local analysis using current theory and shortest path analysis to assess landscape connectivity for migrating and dispersing elk. The source area for the local analysis was elk winter range and the targets were a long and narrow a north-south orientated summer range on the eastern aspect of the Rocky Mountains. The approximately 5000 km^2 regional connectivity analysis included seven elk subpopulations located in SW Alberta. The analyses predicted the best connected pathways for migration and dispersal of elk subpopulations at two different scales.

Figure 5-2 Network Modeling Framework



Data Analysis

I used the software package Connectivity Analyses Toolkit (CAT) for analysis. For an elk habitat file I used a previously developed resource selection function (RSF) representing all elk in the regional study area (Muhly et al. 2008). I used the inverse of the elk all season regional RSF model to generate a cost surface for shortest path analyses. An assumption was made that higher RSF values represented lower costs to movement than low RSF values (Chetkiewicz and Boyce

2009). I transformed the elk RSF created for the regional study area into an .ascii file necessary for connectivity analysis. There are three procedures to prepare the data for analyses and presentation. The first is creation of hexmaps, second a graph file, and third a connectivity shapefile which can be displayed in ArcMap GIS. Three types of linkage mapping methods are possible, the shortest (least-cost path), current flow and network flow (Carroll et al. 2011). The three techniques consider first the single shortest path, second the probalistic flow of all possible paths, and lastly the optimal flow which will evaluate all possible paths but not use them all. For my investigations the least-cost and current flow centrality metrics were used to evaluate connections between all pairs of nodes on a landscape, both have similarities, but are very complimentary when used together. The third method, network flow, was not used in this study because of computational challenges of computer memory requirements and analysis times of numerous days (Carroll et al. 2011). Different methods allow for different assumptions about animal movement. Shortest path identifies and ranks the one or several shortest paths that connect each pair of nodes on a graph and totals the quantity of shortest paths the node is included in (Borgatti and Everett 2006). A loss of the node that is found within a large number of the shortest paths will disproportionately lengthen distance and time travelled between nodes (Brandes 2001). An inherent characteristic of shortest path is the individual dispersing is assumed to have a landscape perspective of the optimum pathways available to it (Freeman 1977). Results from the shortest path analysis illustrate the minimum number of linkages within the region whose loss would greatly reduce regional connectivity.

Current flow determines the centrality or importance of a node by how often, summed over all node pairs the node is traversed by a random walk between two other nodes (Newman 2005). This basically tabulates all paths between nodes, not only the shortest (McRae et al. 2008).

Current flow compliments the shortest path method by detecting areas of redundancy within a possible linkage which could provide alternatives to the shortest paths. Areas of redundancy provides insights to the potential resilience of the linkage and how it may be able to shift to redundant areas to allow for changing environmental and land use patterns (Carroll et al. 2011). Areas of narrow high current flow may identify pinch points, places where connectivity values may be constrained in narrow linkages. Such narrow linkages could be further evaluated using as

shortest path subset, to investigate how the pinch point may be improved to increase or maintain its connectivity.

I used shortest path and current flow metrics in the program CAT to assess connectivity for seven Rocky Mountain elk subpopulations across a regional landscape in SW Alberta. The Connectivity Analysis Toolkit for the regional assessment used a new connectivity analysis method where source and target patches are not designated (Carroll et al. 2011). I compare my regional results with efforts from a multispecies linkage assessment across Highway 3 and local knowledge of elk movement corridors in the area. A second analysis (local scale) used the two complimentary connectivity metrics but designated a source (winter range) and target (summer range) to assess connectivity of elk migration pathways. The local scale analysis extent was the Castle-Carbondale elk subpopulation home range. The results of the local analysis were compared with BBMM migration map outputs from Chapter 3.

RESULTS

Results from the regional analysis provide an assessment of the best shortest paths across my regional and local study areas. The process ranks the shortest paths throughout the study extent (Figure 5-3). GPS relocation data from collard elk found very few animals migrated north and south (n=1), whereas a larger number of elk were noted to move north and south while undertaking dispersal (n = 4). East and west movements are representative of migration or dispersal. The regional shortest path assessment of connectivity predicts the minimal number of quality movement areas across the landscape for elk. The analysis suggests there are numerous quality movement pathways in the region which are predicted to provide connectivity for elk to move east to west and north to south. These movement pathways would represent potential dispersal corridors for elk between the seven subpopulations of elk found in SW Alberta, British Columbia and populations of the northern United States.

In addition to the significance of maintaining regional connectivity it is important to conserve local scale connectivity necessary for migration of elk in SW Alberta. Local scale shortest path connectivity modeling predicts two areas of higher quality connectivity pathways for Castle-Carbondale elk migration from their eastern winter range to the mountainous summer range found along the continental divide in Alberta and British Columbia (Figure 5-4). The two

pathways of highest connectivity correspond with population migration UD's using the BBMM in Chapter Three. The BBMM represents the UD of elk migration GPS locations from 38 female and 12 male elk. In addition to the two highest quality pathways the shortest path analysis indicates there are a number of other connected pathways as possible alternatives for elk migration.

I conducted a second connectivity analysis using circuit theory methods (Figure 5-5). The output from this method indicates there is a pinch point or narrowing in connectivity of the potential migration pathway (yellow area). Adjacent to the pinch point of high connectivity there are additional well connected areas suggesting that adjacent areas may be suitable for elk to shift their migration pathway (dark blue area). Shortest path and current theory methods of connectivity analysis provide complementary perspectives (Carroll et al 2011). The shortest path denotes the shortest quality path for movement while the current theory method considers all possible paths. Overlaying the current flow path output with the shortest path map provides additional information to understand possible options for elk migration, particularly in areas of narrow connectivity (Carroll et al. 2011). When interpreting the current flow map (Figure 5-5), wider linkages such as the yellow does not mean that more area is needed to conserve connectivity, it just means there are numerous options for movement that have good connectivity (McRae et al 2008). For both analyses I assume that preferred high-quality habitat makes a better corridor than less-preferred habitat.

DISCUSSION

The graph-theoretic approach provides a measure of habitat connectivity similar to metapopulation theory which states that the importance of each habitat patch in maintaining overall connectivity of the graph can be attributed to its topographical position and patch characteristics (Urban et al 2009). The CAT provides tools for linkage mapping which focuses on the relative importance of sites for maintaining connectivity across a landscape (Caroll et al. 2011).

With natural habitats being lost or changed throughout the world, conservation efforts are being implemented to conserve plant and animal species. In Alberta as in a few other areas along the Continental Divide, researchers have investigated the ability of rarer animals such as carnivores

to move north and south along a continental travel corridor (Apps 1997, Weaver 2001, Chetkiewicz and Boyce 2002, Carroll et al. 2001). These areas have been promoted by international groups such as the Wildlife Conservation Society and Yellowstone to Yukon Conservation Initiative (Yellowstone 2 Yukon 2004) to conserve North American animal populations using indicator or umbrella carnivore species such as the grizzly bear (Carroll et al. 2001, Ray et al. 2005). Additional projects with similar connectivity and biodiversity objectives use multispecies assessments comprised of a suite of animal groups (amphibians, birds, ungulates and carnivores) (Penrod et al. 2001, Southern Rockies Ecosystem Project 2005, Washington Habitat Connectivity Work Group (WHCWG) 2010, Home et al. 2012). Multispecies connectivity research includes ungulates and other species guilds as part of assessment of the connectivity for continental animal movement. The outcomes provide a rounded ecological assessment of landscape connectivity. The results of my connectivity analysis could compliment the knowledge learned from carnivore connectivity assessments to provide additional understanding of wildlife movement along the Continental Divide.

In this study, I investigated the importance and modeled the existing connectivity of a portion of the continental movement route using the ungulate species, elk. I have implemented a graph theory method represented by two types of analysis: 1) shortest path (least-cost) and 2) current flow methods based on circuit theory, to assess and identify potential movement areas of elk in SW Alberta. The regional area of analysis provides insights to possible dispersal, migration or exploratory routes for elk to British Columbia and across the International Boundary into the United States. The regional study area also provides insights of potential movement linkage zones for elk across Highway 3 in Alberta and B.C. Studies have noted Highway 3 as a fracture zone for the movement of wildlife north and south along the Continental Divide (Apps 1997, Chetkiewicz 2001, Clevenger et al. 2010). The shortest path results for elk support a number of the linkage zones determined by expert opinion to conserve for multispecies movement across Highway 3 (Figure 5-3). The least-cost analysis using RSF data from my elk study predicted highway crossing areas in the Crowsnest West Linkage Zone as well as in the Crowsnest East Linkage Zone. The highest rated corridor using expert opinion methods was the Rock Creek Linkage where conservation efforts are in progress (Clevenger et al. 2010). The Crowsnest West Linkage Zone is located in the Municipality of the Crowsnest Pass where land use consists of land conservation efforts by the Nature Conservancy of Canada and human development

activities such as country residential acreages and industrial development. These activities in the Crowsnest Pass areas are located within the core winter range of the Crowsnest Pass elk subpopulation. Local knowledge and a program called Road Watch have documented elk crossing Highway 3 which bisects the winter range (Lee et al. 2006).

The least-cost analysis modeled multiple possible routes within the regional study area suggesting habitat connectivity for elk is likely still reasonable. This is not a surprise since elk are considered adaptable, habitat generalist species frequently occupying ecotones (Geist 2002). Although research in the U.S. over the last few decades suggests increasing displacement of elk from traditional and in some cases high quality habitats due to human activities (Rowland et al. 2005). High traffic volume roads such as Highway 3 represent a threat to connectivity for wildlife movement north or south. As traffic volumes increase in the near term and if in the long term Highway 3 is twinned the permeability of these movement areas will be reduced (Clevenger et al. 2010). Elk movement across secondary Highway 507 is frequent as elk cross between Lundbreck Hills and Byron Mountain. Two additional secondary crossings occur on Highway 507. The first is by the Castle River Bridge and the second is near the Screwdriver Creek highway crossing.

The Livingstone Range and a majority of the Lundbreck Hills are comprised of controlled human access to private land, low traffic volume roads, interspersed with small parcels of public lands. Based on my analysis these areas appear to represent areas of higher quality connectivity for elk than areas found in eastern sections of public land along the Continental Divide. Possibly this is due to higher road density, traffic volumes or higher human activity on public lands which can be significant human disturbance sources (Webb et al. 2011).

Castle-Carbondale Elk Migration Pathway Connectivity

A local scale analysis of the Carbondale elk subpopulation was conducted using a source habitat patch defined by the eastern extent of the winter range with a target patched defined by the westward edge of the elk subpopulations summer range. I used the least-cost path analysis and circuit theory methods to determine the areas of least resistance for migration of elk and possible pinch points. Based on a visual assessment of overlaying the least-cost path and circuit migration pathways, I was able to identify potential areas on the migration pathway where

connectivity has been reduced (Figure 5-6). The most connected pathways are depicted in red with alternate routes shown in orange and pink. The best modeled routes for connectivity closely mirror two of the migration routes from the BBMM analysis of the Castle-Carbondale population (Chapter Three). Based on results of this model the current migration pathways have segments that are well connected. The shortest path route also identified the mountain passes crossing the Continental Divide from Alberta to BC as quality routes for elk to use. In fact they are the only routes available to elk to move across the Continental Divide and are used by migrating elk. During my study, two dispersing elk traveled through mountain passes to a new winter range in British Columbia and Montana.

Figure 5-3. Graph analysis of habitat connectivity for an elk population of SW Alberta using two linkage mapping methods based on shortest path

Red is the best path, followed by yellow and then pink. The local area analysis boundaries are represented by the rectangle outline.

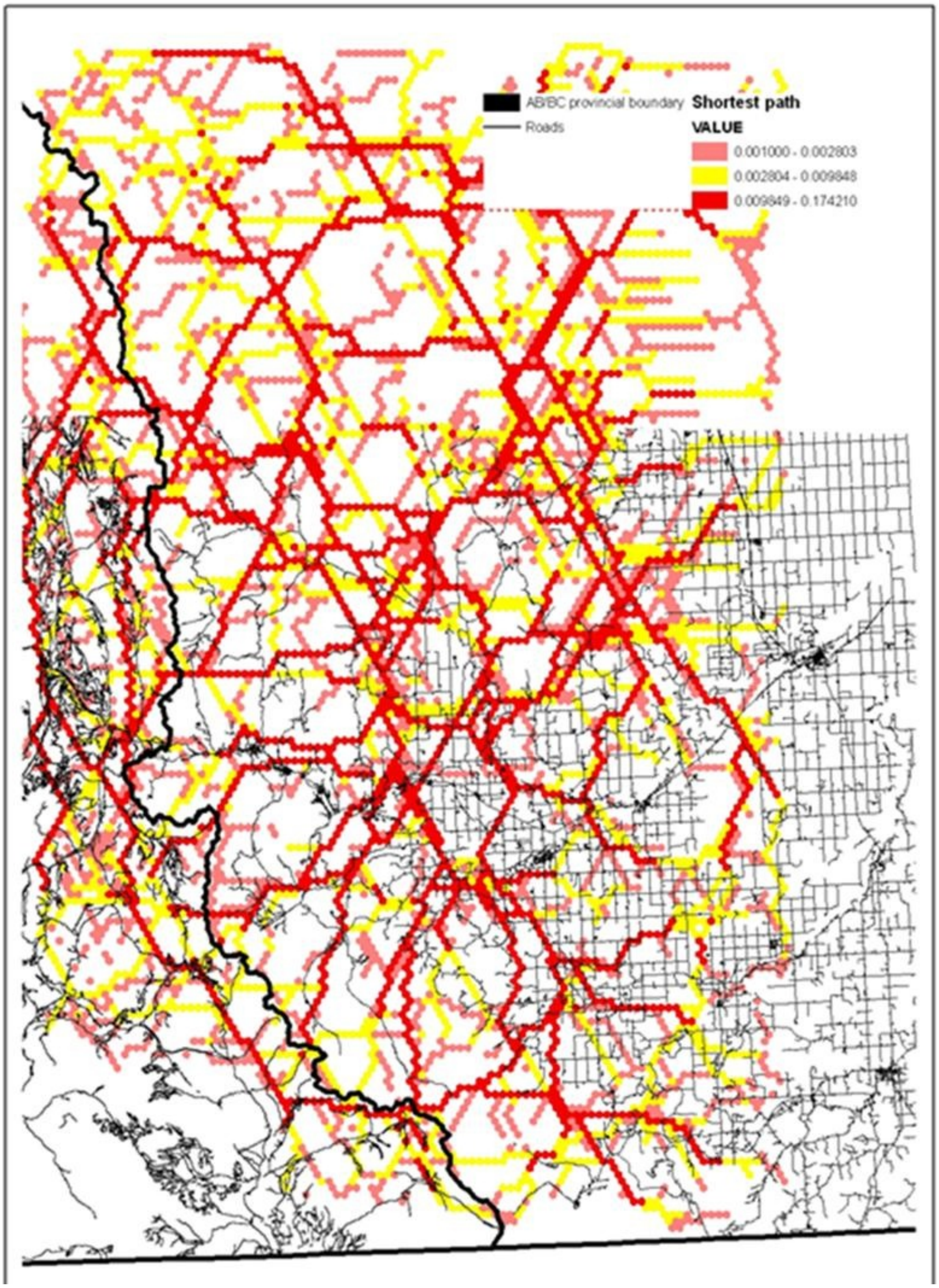


Figure 5-4 A local scale graph analysis of habitat connectivity for the Castle-Carbondale herd from the Alberta population of elk using the shortest path technique.

Red is the best path, followed by yellow and then pink. Gas well sites are named WAT-#.

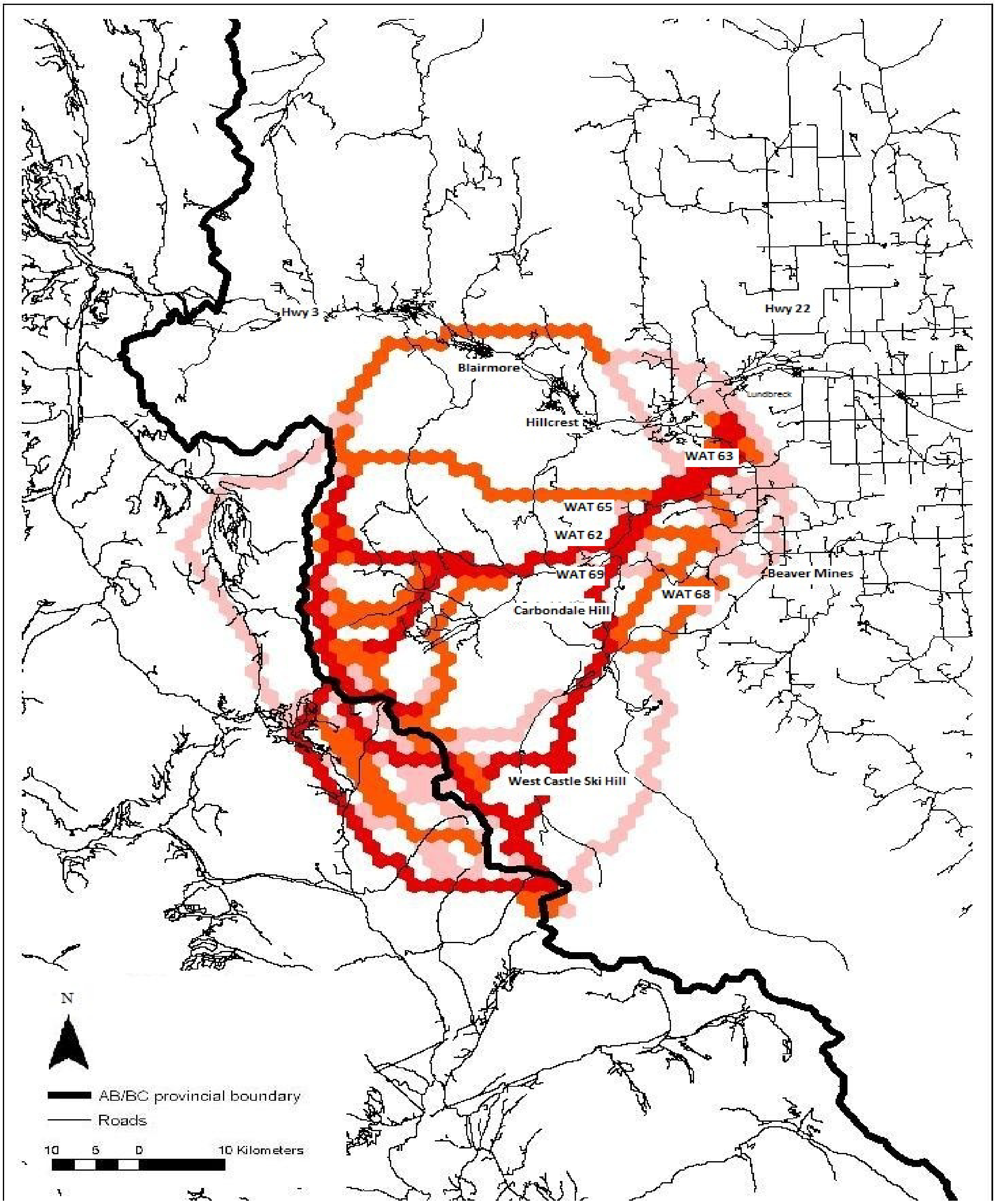


Figure 5-5 A local scale graph analysis of habitat connectivity for the Castle-Carbondale herd from the Alberta population of elk using the current flow technique.

Green areas are winter and summer ranges, yellow represents the best connected areas, next dark blue fading to lighter blue representing lower connectivity. Gas well sites are named WAT-#.

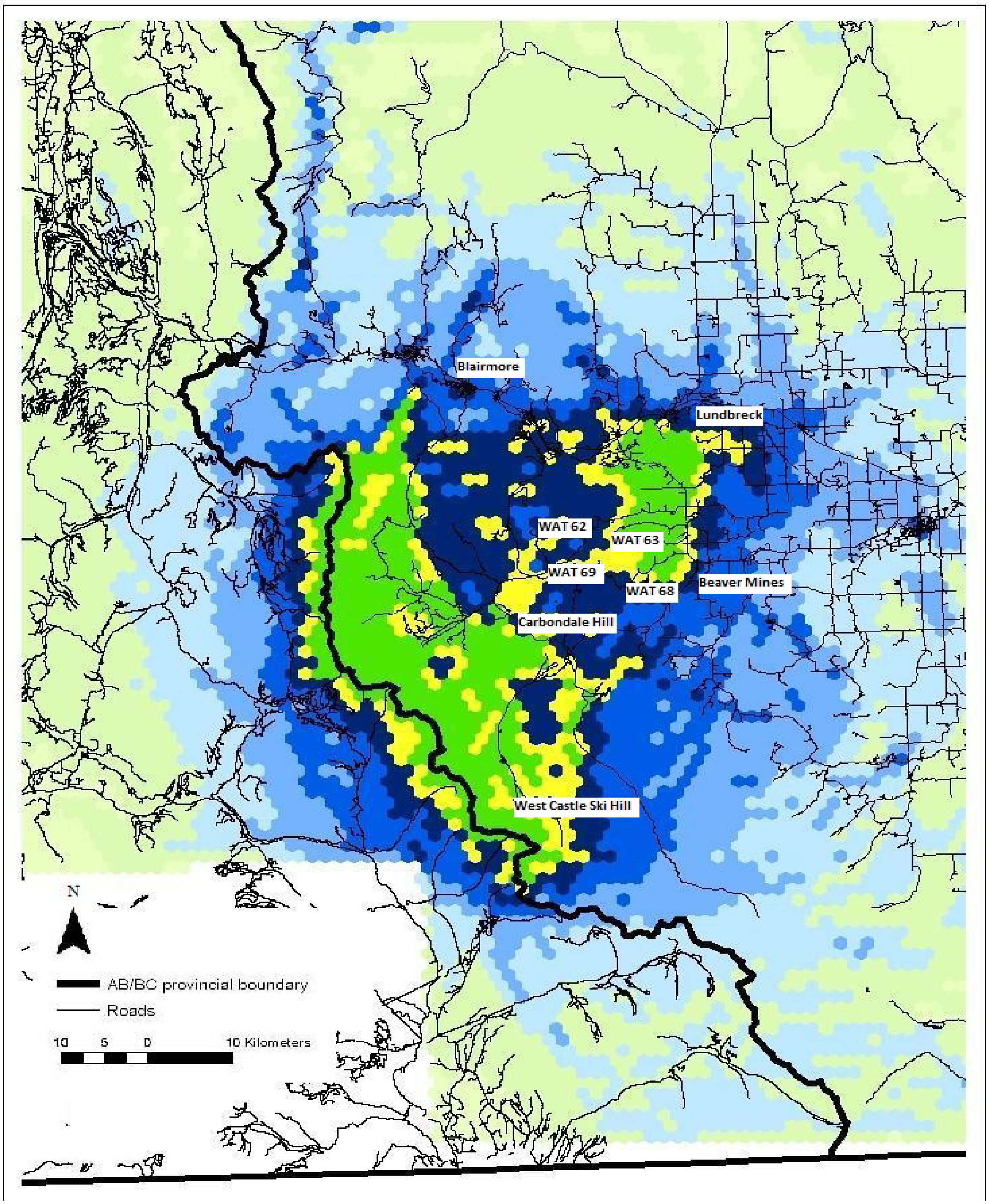
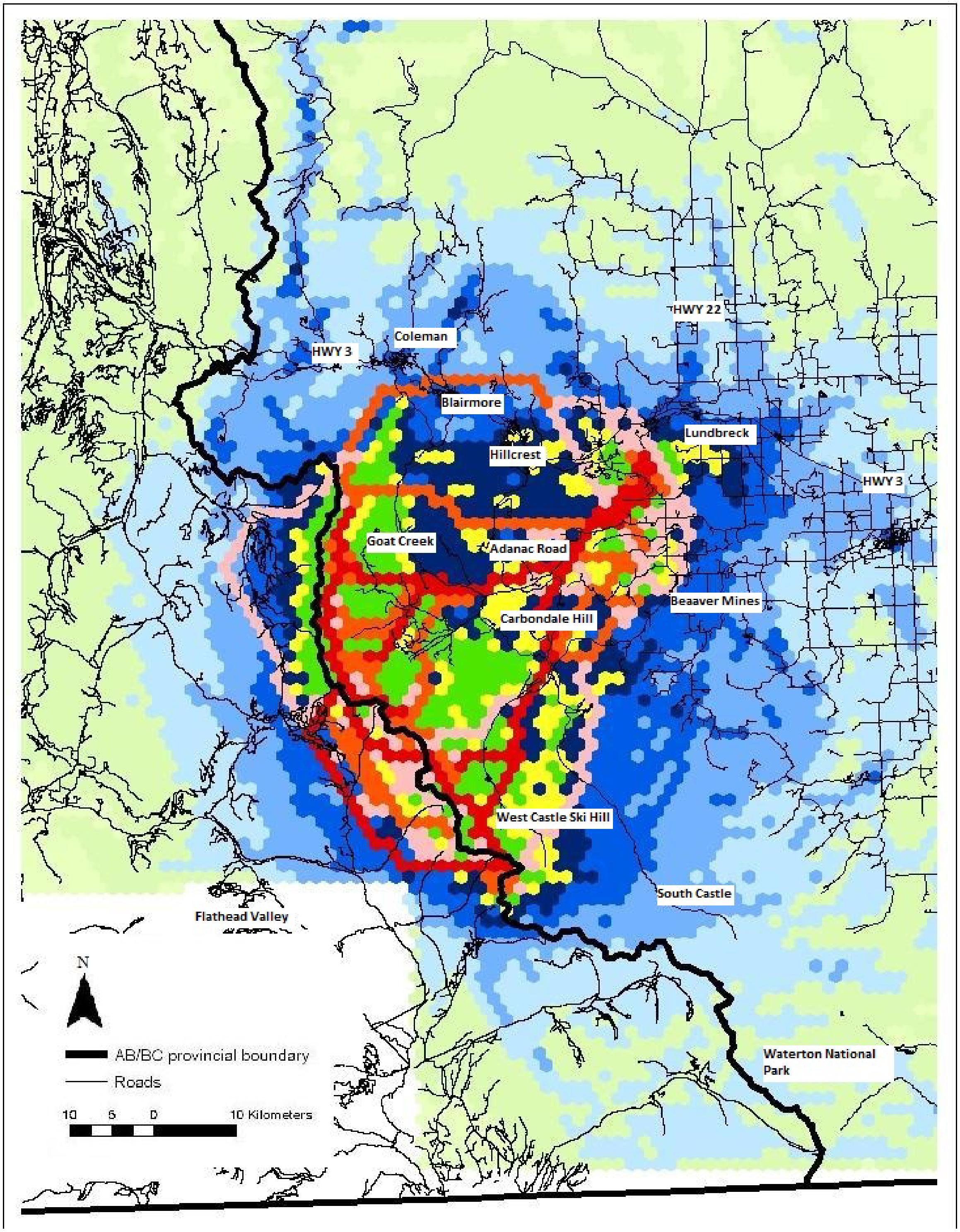


Figure 5-6 A local scale graph analysis of habitat connectivity for the Castle-Carbondale herd from the Alberta population of elk using the shortest path and current flow techniques



CONCLUSION

Using the shortest path and current flow methods the model predicted segments of known migration routes for elk in a local analysis of the Castle-Carbondale study area. At a regional scale the modeling results closely coincided with Highway 3 wildlife crossing areas determined by expert opinion (Clevenger et al. 2010). One of the possible reasons for our positive results was the availability of a fine scale RSF model built from recent elk GPS telemetry data in the same study area. Although beyond the scope of this project, my connectivity analysis needs to be validated to assess the models ability to predict known GPS dispersal routes for individual animals (Sawyer et al. 2011). Results from my project indicate the ability of the CAT to model potential movement zones appears to be effective. Further quantitative assessment is required to validate the model's ability to predict elk migration and dispersal corridors.

My study demonstrates the potential for the applied value of graph-based analysis to estimate connectivity which may compliment other ecological data for landscape connectivity. One of the challenges of modeling is to interpret model outputs appropriately given their limitations and assumptions (Nichols 2001, Sawyer et al. 2011), realizing the best model predictions are imperfect representations of the real world (Conroy 1993). My intent for the connectivity modeling had two purposes. One was to provide additional information for managers to consider in the balance of wildlife conservation and resource development and secondly to increase awareness of wildlife connectivity requirements in SW Alberta.

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Chapter six: key Results, Management Recommendations, and Future Research

Introduction

Maintaining migrating elk populations in SW Alberta will require specific efforts to retain critical habitats and landscape characteristics required by elk to continue their seasonal movements from winter to high elevation summer ranges. These efforts will benefit elk and will also help humans to utilize the same landscape and reduce detrimental effects. If elk were to stop migrating, their contribution to the ecosystem would be lost due to reduced grazing on summer and transitional ranges. Large keystone mammal species such as elk have been shown to affect ecosystem processes such as nutrient flows, nutrient cycling and successional trajectories of plant communities (Kie et al. 2003). A reduction in the area of elk distribution and subsequent population size would be a loss of biomass for predators from winter and spring mortalities, and direct predation of calves and adult elk through the seasons. The change in elk distribution would impact vegetation dynamics by overgrazing on the winter range and undergrazing on other ranges, resulting in a negative impact on plant productivity and biodiversity. Predator species using elk biomass as a source of food may in turn change their distribution to overlap with the changed elk distribution (Nelson et al. 2012). Finally, a permanent shift of elk and predators to elk winter range would likely result in increased negative human / wildlife interactions.

In Chapter Three, I documented the migration pathways of the Castle-Carbondale elk subpopulation using the BBMM. Individual and population pathways were modeled using elk GPS relocation points collected during migration. The Brownian bridge model framework was used to prioritize the areas of most importance to the Castle-Carbondale elk subpopulation. Chapter Four defined the characteristics of elk migration stopover sites as areas with rugged terrain, low canopy cover, at mid elevations located greater than .5km from roads. For Chapter Five, I used a resource selection function model of elk habitat use constructed from data in the study are to assess connectivity of the migration routes and potential dispersal paths using shortest path and circuit theory at both local and regional scales.

RESEARCH FINDINGS

Migration Pathways

With greater than 90% of elk from the Castle-Carbondale subpopulation migrating, this research will be very applicable to managing the elk herd. Knowing migration corridors and important stopover areas will enhance wildlife managers' ability to maintain migration movements of migratory elk and to manage the impacts of human activities. GPS technology has improved, enhancing my ability to study ungulates by providing increased frequency and accuracy of relocation points, but the methods to analyze movement data are limited. It is limited by the abilities of modeling to account for uncertainty in animal movements between known locations (Horne et al. 2007, Sawyer et al. 2009) and by the difficulty to scale individual migration data to population level routes. Until recently, migration was investigated by connecting successive GPS location points of collared animals (Berger et al. 2006) which provided metrics such as timing, distances traveled and movement rates of migration. The draw back from such methods are that there is no defined area of route utilization based on error, thus we would not know if the route is 10m or 1km wide (Sawyer 2010).

The quantitative framework I used, modeled migration routes for both individual and population levels. I also calculated the Brownian bridge variance which is used to depict a migration route with a variance estimate of relative use along the migration route. It provided an estimate of probability of a elk migration UD that can be used to assess development options be it roads or well sites away from the core areas of migration. My results also support results from other studies (Sawyer 2010) where movement and stopover areas may be distinguished based on different behavioural states. This is also consistent with other research that used non-linear curve fitting (Johnson et al. 2002), state-space models (Forester et al. 2007), Markov models (Franke et al. 2004), random walks (Morales et al. 2004) and first passage methods (Bailey and Thompson 2006). Elk use of stopovers was followed by quick movements through travel routes to a new stopover. This differentiation between movements may be a useful management

opportunity, for my modeling found the elk population favoured some areas over others. These areas could be targeted for conservation as well as habitat enhancement opportunities.

The BBMM analyses highlighted an important stopover at the junction of Castle and Carbondale Rivers, located near the western boundaries of elk winter range. Elk are regularly observed here in the spring, feeding in the large meadows surrounded by aspen where some of the first grass green-up frequently occurs (Paton 2005). From this topographic hub, the elk select one of three routes traveling westward along three drainages to different summer ranges. This stopover within the winter range appears to be an important one for it is an area providing new spring forage as elk migrate through the winter range. The combination of winter range and a migration corridor/stopover in one area suggests it is very important for spring movement of elk to the summer ranges and should be considered critical migratory habitat. The site is also located within 1.5km of a well site and crosses a gated access road used by gas field workers. This example illustrates how elk and human activity can be compatible within limits using appropriate mitigation strategies.

Stopover Ecology

In Chapter Four, I develop a spring and fall resource selection function (RSF) for female elk migration to understand their patterns of selection for stopovers and possible differences between seasons. There were differences in use between stopovers by female elk during spring and fall migrations. A comparison of habitat characteristics of stopover sites with random locations within the Castle-Carbondale elk home range found stopover sites were in areas of rugged terrain, with low canopy cover, mid elevations, and at least 500m away from roads.

Stopovers in the Sawyer study (2010) had higher forage quality compared to movement corridors connected to them, forage quality improved as elevation and distance from winter range increased. This would fit the strategy of migratory ungulates to follow the green-up of the most nutritious vegetation to maximize energy intake during the growing season (Albon and Langvatn 1992, Fryzell et al. 2004, Holdo et al. 2009). In my study the largest concentration of stopover areas were located in a 2003 Lost Creek fire footprint where forbs and grasses would green-up quickly, providing rich forage for elk. Two other migration routes not passing through the burn

had fewer stopover sites of a smaller area than the Lost Creek fire, possibly because elk using the burn were inclined to stay in areas of very rich nutritional forage for extended time periods.

There appears to be differences in use between stopovers by female elk during spring and fall migrations. A comparison of habitat characteristics of stopover sites with random locations within the Castle-Carbondale elk home range found stopover sites were in areas of rugged terrain, with low canopy cover, mid elevations, and at least 500m away from roads.

LANDSCAPE CONNECTIVITY FOR SW ALBERTA ELK

Landscape Connectivity for the Castle-Carbondale Elk Subpopulation

My study provides additional data regarding the effects of environmental and anthropogenic effects on elk movement ecology. I delineate the migration pathways for elk for the Castle-Carbondale subpopulation and assess connectivity of the landscape for elk movement at a regional and local scale. My results will provide insights to help manage and possibly mitigate for human influence on elk movement patterns, providing information to develop a strategy for conservation and management. Here I summarize possible management opportunities based on my study results.

MANAGEMENT RECOMMENDATIONS

1. Conserve stopover sites; particularly those that may be also used for calving, wintering areas or by multiple migration routes. Stopovers are important areas for animals to rest, forage and build-up body reserves critical for nursing and winter survival. This may influence productivity. A long term reduction of female elk productivity will affect population size.
2. When possible, plan new development outside of migration route core areas. A loss of migration habitat could lead to eventual loss or reduction of migratory behaviour in elk. Such a loss has the potential to increase human-elk land use issues. There may be a reduction in ecological processes due to elk grazing and a possible change in distribution of carnivores that utilize ungulates as food. The distribution change could be a shift in wildlife from seasonal use of summer ranges in the mountain regions to wintering areas. Increased wildlife use in areas of human settlement creates the likelihood of increased wildlife management issues.

3. Implement land management plans to conserve areas of winter range and migration routes by putting private land into conservation easements or to have critical habitat status on public land would be beneficial to elk and other species using the area.
4. Game management plans for elk should consider the impacts of harvesting males that migrate through two wildlife management units during the rutting season and on to the winter range.
5. Reduce and control human activity on roads within migration routes particularly new road developments using a 300 - 1000m buffer from the migration route. The buffer size will depend upon site conditions such as topography and forest cover. In dense forest a 300m buffer is adequate, but in open meadows or clearcuts elk can be disturbed by certain types of disturbance 1 km away. Likewise terrain, measured by viewscapes could have large effects. Since the intensity of road use is typically more critical than road densities, in most cases the use of a gated road could be acceptable. New roads closer than 500m from stopover sites may be acceptable if access within appropriate distance (point 5) is controlled using gates and the roads are decommissioned after they are no longer being used by industry.
6. Continuing to remove roads by gating or re-sloping road bed to reduce traffic volumes in wildlife movement corridors would be another positive step to maintaining and increasing connectivity for animals.
7. Conserve migrating elk highway crossing areas by building structures for them to move under the highway or reduce speeds limits with signage on low traffic volume paved roads.

FUTURE RESEARCH

Recommendation: Develop studies to understand the link between elk productivity parameters and level of disturbance which are important to understanding the costs of human development in elk habitat.

Recommendation: Additional work is required on identifying development thresholds (e.g. traffic volumes) at which elk use of migration pathways could be significantly reduced.

Recommendation: Incorporating variables such as NDVI and volumes of road traffic into the stopover model would enhance the existing model.

Recommendation: An important concept of maintaining linkage zones is to provide movement corridors for multiple species. Future work could expand upon the elk connectivity map products with additional species to build upon the expert based predictions currently available for Highway 3 crossing areas and future road improvement projects which may occur on Highways 22, and 507.

Recommendation: Compare predictions of least-cost and current flow models with empirical data on dispersal.

Recommendation: Further analysis is required to understand the important role of dispersal in SW Alberta elk populations.

My study may be the first verified account of dispersal and migration movements of young bull elk to subpopulations of elk in Alberta, British Columbia and Montana. The sample size for these movements was not large enough to allow for comprehensive analysis of why these movements occurred or preferences of habitat during dispersal. Future examination of existing data sets or additional field sampling of 2.5 year old bulls would help to understand the movement of these individuals, which are important for the metapopulation dynamics of a population.

Recommendation: Elk migration routes represent functioning corridors for movement between seasonal ranges. During this study dispersing elk also used portions of the migration route to disperse to other metapopulations. Further investigating the qualities and characteristics of a migration route may provide insights into corridor conservation strategies and understanding.

Recommendation: Future connectivity analysis for elk would benefit from the use of a RSF built with location points representing only migration time periods. This may best represent the spatial and temporal movement periods of migrating and dispersing elk.

Recommendation: Fine scaled analysis of stopovers sites regarding habitat features such as vegetation association are important in public lands used as rangeland for cattle.

Recommendation: Repeating the delineation of migration routes using BBMM for additional migratory herds such as Crowsnest, Oldman and Livingstone.

LITERATURE CITED

Adams, A.W. 1982. Migration. Pages 301-321 In Elk of North America: ecology and management. (Eds.) J.W. Thomas and D.E. Toweill, Stakpole Books Harrisburg Penn.

Adrados C., G. H. Verheyden, B. Cargnelutti, D. Pepin, G. Janeau. 2003. GPS approach to study fine-scale site use by wild red deer during active and inactive behaviors. Wildlife Society Bulletin 31:544-552.

Adrianensen, F. and A.A. Dhondt .1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. – J. Anim. Ecol. 59: 1077–1090.

Adrieansen, F., J.P. Chardon, G.DeBlust, E. Swinnene, S. Villalba, H. Bulinck, E. Matthysen. 2003. The application of least-cost modeling as a functional landscape model. Landscape and Urban Planning 64:233-247.

Ager, A.A., B.K. Johnson, J.W. Kern, ands J.G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. 2003. Journal of Mammalogy 83:1076-1088.

Åkesson, S and A. Hedenström. 2007. How migrants get there: Migratory performance and orientation. BioScience 57:123–133

Albon, S.D. and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502-513.

Alerstam, T., Hendenstrom, A., and Akesson, S. 2003. Long-distance migration: evolution and determinants. Oikos 103:247-260.

Alerstam, T. 2006 Conflicting evidence about long-distance animal navigation. Science 313, 791–794.

Allendorf, F.W. and Hard, J.J. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. PNAS 106:9987-9994.

Andersen, R. 1991. Habitat deterioration and the migratory behavior of moose in Norway. – J. Appl. Ecol. 28: 102–108.

Anderson, DP, Forester JD, Turner MG, Frair JL, Merrill EH. 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landscape Ecology 20: 257–271

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

Apollonio M., S. Ciuti, and S. Luccarini. 2005. Long-term influence of human presence on spatial sexual segregation in fallow deer (*Dama dama*) Journal of Mammalogy 86: 937-946

Apps, C. 1997. Identification of grizzly bear linkage zones along the Highway 3 corridor of southeast British Columbia and SW Alberta. Aspen Wildlife Research, Calgary, Alberta, Canada. 45pp.

Apps, C.D., J. L. Weaver, P. C. Paquet, B. Bateman, B. N. McLellan. 2007. Carnivores in the southern Canadian Rockies: core areas and connectivity across the Crowsnest Highway. WCS. Canada Conservation Report No. 3,

Arc Wildlife Services Ltd. 2004. Selected Ecological Resources of Alberta's Castle Carbondale: A synthesis of current knowledge. Compiled by Arc Wildlife Services Ltd., Calgary. Prepared for CPAWS Calgary and Shell Canada. 215pp.ASRD 2007-10

Atwood, T.C., E.M. Gese, K.E.Kunkel. 2007. Comparative patterns of predation by cougars and re-colonizing wolves in Montana's Madison range. Journal of Wildlife Management 71:1098-1106.

Augustine, D.J. and S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62: 1165-1183.

Baggio, J.A., K. Salau, M.A. Janssen, M.L. Schoon, O. Bodin. 2011. Landscape connectivity and predator-prey population dynamics. Landscape Ecology 26:33-45.

Bailey, H., and P. Thompson. 2006. Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. Journal of Applied Ecology 75:456–465.

Barber-Meyer, S.M., L.D. Mech and P.J. White. 2008. Elk calf arrival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 160:1-30.

Bascompte. J. and Vilà, C. 1997. Fractals and search paths in mammals. Landscape Ecology 12: 213-221Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228-237.

Beier, P., Majka, D.R. and Spencer, W.D. 2008. Forks in the roads: choices in procedures for designing wild land linkages. Conservation Biology, 22: 836-851.

Belisle, M., 2005. Measuring landscape connectivity: the challenge of behavioral land-scape ecology. Ecology 86:1988-1995.

Bender, L.C., Cook. J.G., Cook. R.C., Hall. P.B. 2008. Relations between nutritional condition and survival of North American elk (*Cervus elaphus*). Wildlife Biology 14:70-80.

Benitez-Lopez A., R. Alkemade, P.A. Verweij. 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. Biological Conservation 143:1307-1316.

Benkobi, L., M.A. Rumble, C.H. Stubblefield, R.S. Gamo, J.J. Millspraugh 2005. Seasonal migration and home ranges of female elk in the Black Hills of South Dakota and Wyoming. The Prairie Naturalist 37:151-166.

Bennett, D.A. and W. Tang. 2006. Modeling adaptive, spatially aware, and mobile agents: elk migration in Yellowstone. 20:1039-1066.Bennet, et al. 2011 if you meant 2001 it would be: Bennett, K.D., J.R. Biggs, and P.R. Fresquez. 2001. Determination of location error associated with global positioning system radio collars in relation to vegetation and topography. West North American Naturalist Pp 19.

Berger et al. 1993 if you meant 1983 it would be: Berger, J., Daneke, D., Johnson, J. & Berwick, S. H. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. – Biological Conservation 25: 193-208.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320-331.

Berger J, Cain SL, Berger KM. 2006. Connecting the dots: An invariant migration corridor links the Holocene to the present. Biology Letters 10: 1–4.

Berger, J. 2007. Fear, human shield, and the redistributionof prey and predators in protected areas. Biology Letters 3:620 – 623.

Berger J., K.M. Berger, S. Bergen, B. Bayarbaatar, A.Fine, B. Lkhagvasuren, J. K. Young, P. Zahler. 2008. Migration bottlenecks, climate and the conservation of Pleistocene relicts in Central Asia. The Open Conservation Biology Journal 2:9-10.

Berger, J., S. Zack, K. Ellison, and E. Cheng. 2010. Migrants across air, land and water: Framing science to achieve conservation for National Park Lands. Wildlife Conservation Society Report, March 2010. Bozeman, MT. U.S.A.

Bergerud, A.T., H.E. Butler, and D.R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62:1566-1575. B421-431.

Bergman, C.M., J.A. Schaefer and S.N. Lutich. 2000. Caribou movement as ad correlated random walk. Oecologia 123:364-374.

Bertrand et al. 1996 Bertrand, M. R., DeNicola, A. J., Beissinger, S. R. &Swihart, R. K. 1996 Effects of parturition on home ranges and social affiliations of female white-tailed deer. Journal Wildlife Managment. 60, 899–909.

Breier, P., W. Spencer, R.F. Baldwin, and B.H. McRae. 2010. Toward best practices for developing regional connectivity maps. Conservation Biology 25:879-892.

Beier, P., and Noss, R.F.1998. Do Habitat Corridors Provide Connectivity? Conservation Biology 12: 1241-1252.

Bleich, V.C., Bowyer, R.T., Wehausen, J.D..1997. Sexual Segregation in Mountain Sheep: Resources or Predation? Wildlife Monographs. 134:3-50.

Blumstein, D. T. and , J. C. Daniel. 2002. Isolation from mammalian predators differentially affects two congeners. Behav. Ecol. 13, 657—663.

Bolger, D.T., W.D. Newmark, T.A. Morrison and D.F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63-77.

Bleich, V.C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. Journal of Mammalogy 80: 283–289.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2007. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 10:1-15.

Borgatti, S. P., A. Mehra, D. J. Brass, and G. Labianca, 2009. Network analysis in the social sciences. Science 323:892-895.

Borger, L., N. Franconi, G.Michele, A. Gantz, F. Meschi, A. Manica, 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.

Bowyer, R.T. and J.G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity of Distributions 12:244-257.

Boyce, M. S. 1989. The Jackson Elk Herd: intensive wildlife management in North America. Cambridge University Press, Cambridge, UK.Boyce, M.S. 1991. Migratory behaviour and management of elk (*Cervus elaphus*) Applied Animal Behaviour Science 29:239-250.

Boyce M.S. 1991, Migratory behaviour and management of elk (*Cervus elaphus*).Applied Animal Behavior Science. 29:239-250.

Boyce, M.S. and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends Ecological Evolution. 14:268-72.

Boyce, M.S., P.R. Venier, S.E. Nielsen, F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281-300.

Boyce, M.S., J.S. Mao, E.H. Merrill, D. Fortin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421-431.

Boyce, M.S. 2006. Scale of resource selection functions. Diversity Distribution 12:269-276.

Boyce, M.S., Pitt, J.A. Northrup, J.M., Morehouse, A.T., Knopff, K.H., Cristescu, B., Stenhouse, G.B., 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. Philosophical Transactions of the Royal Society B 365, 2213–2219.

Boyce, M.S., J.Pitt, J.M. Northrup, A.T. Morehouse, K.H. Knoptt, B. Cristescu, and G.B. Stenhouse. 2010. Philosophical Transactions of The Royal Society B 365:2213-2219.

Brandes, U. and D. Fleischer. 2005. Centrality Measures Based on Current Flow. Proceedings of the 22nd Symposium Theoretical Aspects of Computer Science 533-544.

Brandes, U. and T. Erlebach, 2005. Network analysis: methodological foundations. Springer, Berlin Heidelberg. Germany.

Brooks, C. P., 2006. Quantifying population substructure: extending the graph-theoretic approach. Ecology 87:864{872.

Brooks, C. P., 2003. A scalar analysis of landscape connectivity. Oikos 102:433-439.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. Ecolological Letters 7:999–1014.

Bullard, F. 1999. Estimating the home range of an animal: a Brownian bridge approach. Thesis. University of North Carolina, Chapel Hill, North Carolina, USA.

Burcham, M., W. D. Edge, and C. L. Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin 27:833–839.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verla, Inc. New York, New York, USA.

Cagnacci, F., Boitani,L., Powell, R.A., and Boyce, M.S. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of The Royal Society B 365:2157-2162.

Calabrese, J.M. and W.F. Fagan. 2004. A comparison-shoppers guide to connectivity metrics. Frontiers Ecological Environment 10:529-536.

Carroll, C., R.F. Noss, and P.C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications.

Carroll, C. 2010. Connectivity analysis toolkit user manual. Version 1.0. Klamath Center for Conservation Research, Orleans, California. Available from www.connectivitytools.org (accessed January 2011).

Carroll, C., B.H. McRae, and A.Brookes. 2011. Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. Conservation Biology 26:78-87.

Cassier, E.F., D.J. Freddy, and E.D. Ables. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. Wildlife Society Bulletin 20:375-381.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology 9:122-136.

Chernetsov, N. 2006. Mini-review. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology

Cherney, D.N. and S.G. Clark. 2009. The American west's large mammal migration: clarifying and securing the common interest. Policy Science 10:125-132.

Chetkiewicz, C.L.B. and M.S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46:1036–1047.

Chetkiewicz, C.B., C.C. St. Clair and M.S. Boyce. 2006. Corridors for Conservation: Integrating Pattern and Process. Annual Review of Ecology, Evolution and Systematics 37:317-314.

Chetkiewicz, C.L. and Boyce, M.S. 2002. Carnivores and Corridors in the Crowsnest Pass. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Report No. 50. Edmonton, AB. 52 pp

Chevallier, D., Y. Le Maho, P. Brossault, f. baillon, S. Massemin. 2010. The use of stopover sites by Black Storks (*Ciconia nigra*) migrating between West Europe and West Africa as revealed by satellite telemetry. Journal of Ornithology

Childress, M.J. and M.A.Lung. Predation risk, gender and the group size effect: does elk vigilance depend on the behaviour of conspecifics? Animal Behaviour 66:389-398.

Christianson, D., and S. Creel. 2009. Effects of grass and browse consumption on the winter mass dynamics of elk. Oecologia 158:603–613.

Ciuti, S., Davini, S., Luccarini, S. & Apollonio, M. 2004. Could the predation risk hypothesis explain large-scale spatial sexual segregation in fallow deer (*Dama dama*) – Behavioural Ecology and Sociobiology 56: 552-564.

Ciuti S, Muhly T.B., Paton D.G., McDevitt A.D., Musiani M., Boyce M.S. 2012. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society, B 279:4407-4416.

Clark, J. 1993. Rocky Mountain elk winter range surveys for WMU 402. Unpublished Fish and Wildlife report. 12pp.

Clevenger. A.P., J. Wierzchowski, B.Chruszcz, K. Gunson. 2002. GIS-generated, expert –based models for identifying wildlife habitat linkages and planning mitigation passages. Conservation Biology 16:503-14.

Clevenger, A., C. Apps, T. Lee, M. Quinn, D. Paton, D. Poulton, A. Ament. 2010. Highway 3: Transportation Mitigation for Wildlife and Connectivity. Final Report. 136pp.

Clutton-Brock T.H., F.E. Guinness, S.D. Albon .1982. Red deer: behavior and ecology of two sexes. University of Chicago Press.

ChicagoCodling, E.A., M.J. Plank, S. Benhamou. 2008. Random walk models in biology. Journal of the Royal Society Interface. 5:813-834.

Cohen, D. 1967. Optimization of seasonal migration behavior. The American Naturalist 101:5-17.

Cole, E.K., M.D. Pope, R.G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115-1126.

Collins, W.B., Urness, P.J., Austin, D.D. Elk diets and activities on different lodgepole Pine habitat segments. 1978. The Journal of Wildlife Management. 42:799-810.

Conroy, M.J. 1993. The Use of Models in Natural Resource Management: Prediction, Not Prescription. Transactions of the 58th North American Wildlife and Natural Resources Conference: 509-519.

Cook, J.G. 2002. Nutrition and food. Chapter 15: Pg. 531-555, in North American Elk: Ecology and Management.Toweill, D.E. and J.W. Thomas. (Eds.). Wildlife Management Institute Book, Smithsonian Institution Press, Washington. 962pp.

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

Coulon, A.G., J.F. Cosson, J.M.A. Angibault, S. Aulangnier, B.Cargnelutti, M. Galan, A. Hewison. 2006. Genetic structure is influenced by landscape feature: Empirical evidence from a roe deer population. Molecular Ecology 15:1669-1679.

Creel, S. and J.A. 2002. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour 69:1181-1189.

Creel S, Winnie JAJ (2005) Responses of elk herd size to fine scale spatial and temporal variation in the risk of predation by wolves. Animal Behavior 69: 1181–1189

Creel, S., J. Winnie, Jr., B. Maxwell, K.Hamlin, M. Creel. 2005. Elk alter habitat selections as an antipredator response to wolves. Ecology 86:3387-3397.

Crist, T.O., S. Guerting, J.A. Wiens and B .T. Milne. 1992. Animal movements in heterogeneous landscapes: an experiment with Eleodes beetles n shortgrass prairie. Functional Ecology 6:536-544.

Crooks, K. R. and M Sanjayan. 2006. Connectivity Conservation. Cambridge University Press, Cambridge, NY. 712pp.

Cushman, S.A., Chase M., and C. Griffin. 2005. Elephants in space and time. Oikos 109:331-341.

D'eon R.G. 2003. Effects of a stationary GPS fix-rate bias on habitat-selection analyses. Journal of Wildlife Management 67:858-863.

D'eon R.G. and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736-744.

De Solla, S.R., R. Bonduarinsky, and R.J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68:221-234.DeCesare, N.J. and D. H. Pletscher. 2006. Movement, connectivity, and resource selection of Rocky Mountain bighorn sheep. Journal of Mammalogy 87:531-538.

D′eon et al. 2005 could it maybe be: D'eon R.G. and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736-744.

Dibb, A.D. 2007. Spatial analysis of bighorn sheep movement in the Radiom Hot springs area, British Columbia: Modelling and management. M.Sc. Thesis, University of Calgary, Calgary, Alberta, Canada.

Dill, L.M., M.R. Heithaus and C.J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84: 151-1157.

Dingle, H. 2006. Animal migration: is there a common migratory syndrome? Journal of Ornithology 147: 212–220.

Dobson, F.S. 1982. Competion for mates and predominant juvenile male dispersal in Greenwood, 1980 in Woods 1991.

Dodd, N.L., J.W. Gagnon, S. Boe, R.E. Schweinsburg. 2007. Assessment of elk highway permeability by using global positioning telemetry. Journal of Wildlife Management 71:1107-1117.2007.

Downing, D.J. and W.W. Pettapiece. 2006. Natural regions and sub-regions of Alberta.Government of Alberta. Available from: http;//tpr.alberta.ca/parks/heritagenfocentre/default.apx.(Accessed Feb 10, 2011).

Drielsma, M., S. Ferrier, and G. Manion, 2007. A raster-based technique for analysing habitat conguration: The cost-benet approach. Ecological Modelling 202:324-332.

Driezen, K., F. Adriaensen, C. Rondinini, C. P. Doncaster, and E. Matthysen, 2007. Evaluating least-cost model predictions with empirical dispersal data: A case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). Ecological Modelling 209:314-322.

Edge, W.D., C.L. Marcum and L.L. Olsen. 1985. Effects of logging activities on home-range fidelity of elk. The Journal of Wildlife Management, 49:741-744.

Edge, W.D., C.L. Marcum and L.L. Olsen. 1985. Effects of logging activities on home-range fidelity of elk. The Journal of Wildlife Management, 49:741-744.

Edge, W. D., C. L. Marcum, and S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. Journal of Wildlife Management 51:844-851.

Epps, C.W., P.J.Palsholl, J.D.Wehausen, G.K. Roderick, R.R. Ramey II, and D. McCullough. 2005. Highways block gene flow and cause rapid decline in genetic diversity of desert sheep. Ecology Letters 8:1029-1038.

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. Pages 209–242 in Millspaugh, J. J. and J. M. Marzluff, editors. Radio tracking and animal populations, Academic Press, San Diego, California, USA.

ESRI. 2005. ArcGIS Version 9.1. Environmental Systems Research Institute, Inc., Redlands, CA.

Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003-1015.

Fall, A., M.-J. Fortin, M. Manseau, and D. O'Brien, 2007. Spatial graphs: principles and applications for habitat connectivity. Ecosystems 10:448-461.

Felix et al. 2007 any chance you mean: Felix, A.B., D.P. Walsh, B.D. Hughey, H. Campa III, and S.R. Winterstein. 2006. Applying landscape-scale habitat–potential models to understand deer spatial structure and movement patterns. The Journal of Wildlife Management 71:804-810.

Ferguson, S. H., P. C. Elkie. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus*). Journal of the Zoological Society of London, 262:125-134.

Ferguson, M.A.D. & Keith, L.B. 1982. Influence of nordic skiing on distribution of moose and elk in Elk Island National Park, Alberta. - Canadian Field and Nature 96: 69-78.

Fischer, J. and D. B. Lindenmayer, 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265-280.

Forbes, G. J. and J. B Theberge. 1995. Influences of a migratory deer herd on wolf movements and mortality in and near Algonquin Park, Ontario. – In: Carbyn, L. N. et al. (eds), Ecology and conservation of wolves in a changing world. Can. Circumpolar Inst., pp. 303–313

Forester JD, Ives AR, Turner MG, Anderson DP, Fortin D. 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs 77:285–299

Forman, R.T.T., Sperling, D., Bissonette, J., Clevenger, A., Cutshall, C., Dale, V., Fahrig, L., France, R., Goldman, C., Heanue, K., Jones, J., Swanson, F., Turrentine, T., and A.Winter 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC,

Fortin, D., H. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne and J.S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320-1330.

Frair, J.L.2005. Survival and movement behaviour of resident and translocated wapiti (*Cervus elaphus*): implications for their management in west-central Alberta, Canada. University of Alberta. Edmonton, Alberta, Canada.

Frair, J.L., E.H. Merrill, H.L. Beyer, J.M. Morales, D.R. Visscher and D. Frtin. 2005. Scales of movement by elk (*Cervus elaphus*) in response to hererogeneity in forage resources and predation risk. Landscape Ecology 20:273-287.

Frair, J.L., E.H. Merrill, D.R. Visscher, D. Fortin, H.L. Beyer, J.M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20:271-287.

Frair, J.L., Merrill, E.H., Beyer, H.L. & Morales, J.M. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology 45:1504–1513.

Frank, D.A. and P.M. Goffman 1998. Ungulate vs. landscape control of soil C and N process in grasslands of Yellowstone National Park. Ecology 79:2229-2241.

Franke, A., T. Caelli, and R. J. Hudson. 2004. Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models. Ecological Modeling 173:259–270.

Frid, A. & Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. – Conservation Ecology 6 (1): 11. http://www.consecol.org/vol6/iss1/art11.

Fryxell, J. M. et al. 1988. Why are migratory ungulates so abundant? – American Naturalist 131: 781–798.

Fryxzell, J.M. and A.R.E. Sinclair. 1988. Causes and consequences of migration by large herbivores. TREE 3:237-241.

Fryxell, J.M., Wilmshurst, J.F. & Sinclair, A.R.E. 2004. Predictive models of movement by Serengeti grazers. Ecology, 85, 2429–2435.

Fryxell, J.M., Packer, C., McCann, K., Solberg, E.J. and Saether B.-E. 2010. Resource management cycles and the sustainability of harvested wildlife populations. Science 328:903-905.

Garrott, R. A., J. A. Gude, E. J. Bergman, C. Gower, P. J. White, and K. L. Hamlin. 2005.

Generalizing wolf effects across the Greater Yellowstone Area: a cautionary note.

Wildlife Society Bulletin 33:1245-1255.

Geist, V. 1982. Adaptive behavioral strategies. Pages 219-277 in J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.Geist, V. 1998. Deer of the World. Their evolution, behaviour and ecology. Stackpole Books, Mechanicburg, Pennsylvania. 448pp.

Geist, V. 2002. Adaptive behavioral strategies. Pages 389-432 in Dale E. Toweill and Jack Ward Thomas, (Eds.) North American elk: Ecology and Management. Smithsonian Institute Press, Washington, D.C. 962pp.

Gerlach, G. and K.Musolf. 2000. Fragmentation of a genetic landscape as a cause for genetic subdivision in bank voles. Conservation Biology 14:1066-1074.

Gibbard, M.J. and D.H. Sheppard. 1992. Castle Wilderness Environmental Inventory. Unpublished report for Castle Crown Wilderness Coalition. Special Publication No. 1. 168pp.

Gibeau,M., A.P. Clevenger, S. Herrero, and J. Wierzchowski. 2001. Effects of highways on grizzly bear movement in the Bow River Watershed, Alberta, Canada. Pages 458-472 in G. Evnik and K.P. McDermott, editors. 2001 Proceedings of the International Conference on Ecology, North Carolina State University, Raleigh, USA.

Gilbert-Norton, L., R. Wilson, J. R. Stevens and K. H. Beard. 2010. A meta-analytic review of corridor effectiveness. Conservation Biology 24:660-668.

Gill, J.A., Sutherland, W.J., 2000. The role of behavioural decision-making in predicting the consequences of human disturbance. In: Gosling, L.M. & Sutherland, W.J. (Eds.), Behaviour and Conservation. Cambridge University Press, Cambridge.Gill.

Gilpin, M. E. and M. E. Soule, 1986. Minimum viable populations: processes of species extinction. In M. Soule, editor, Conservation biology: the science of scarcity and diversity, pages 19-34. Sinauer Associates Inc., Sunderland, Massachusetts.

Goodwin, B. J. and L. Fahrig, 2002. How does landscape structure influence landscape connectivity? Oikos 99:552-570.

Graham, C. H., 2001. Factors influencing movement patterns of Keel-billed Toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology 15:1789-1798.

Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51:634-643.

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.

Gerlach, G. and K.Musolf. 2000. Fragmentation of a genetic landscape as a cause for genetic subdivision in bank voles. Conservation Biology 14:1066-1074.

Greenwood, P. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour. 28:1140-1162.

Gregory, A.J., M.A. Lung, T.M. Gering, and B.J. Swanson.. 2009. The importance of sex and spatial scale when evaluating sexual segregation by elk in Yellowstone. Journal of Mammalogy 90:971-979.

Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. Ecological Applications 16:285–298.

Gurarie, E., Andrews, R.D., and Larie, K.L. 2009. A novel method for identifying behavioural changes in animal movement data. Ecological Letters 12, 395-408.

Haddad, N.W. and J.J. Tewksbury. 2005. Low-quality habitat corridors as movement conduits for two butterfly species. Ecological Applications 12:250-57.

Hamel S, Côté SD .2007. Habitat use patterns in relation to escape terrain: are alpine ungulate females trading off better foraging sites for safety? Canadian Journal of Zoology 85: 933–943.

Hanski, I., 1998. Metapopulation dynamics. Nature 396:4149-4154.

Harris, G., S. Thirgood, J.G.C. Hopcraft, J.P.G.M. Cromost, J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7:55 - 76.

Hayne, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1-18.

Hebblewhite, M., C. A. White, C. Nietvelt, J. M. McKenzie, T. E. Hurd, J.M. Fryxell, S. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 76:2135–2144.

Hebblewhite, M., E.H. Merrill, L.E. Morgantini, C.A. White, J.R. Allan, E. Bruns, L. Thurston, T.E. Hurd. 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin 34:1280-1294.

Hebblewhite, M., E.H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377–387.

Hebblewhite, M., Merrill, E.H. 2008. Modeling wildlife-human relationships for social species with mixed-effects resource selection functions. Journal of Applied Ecology 45:834-844.

Hebblewhite, M., E. Merrill and G. McDermid 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141-166.

Hebblewhite, M., Merrill, E.H. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445-3454.

Hebert, D.M. 1973. Altitudinal migration as a factor in the nutrition of Bighorn sheep. Ph.D. dissertation, University of British Columbia, Vancouver. 186pp.

Hedenstrom, A. 2003. Optimal migration strategies in animals that run: a range equation and its consequences. Animal Behaviour 66:631-636.

Hedenstrom, A. 2003. Optimal migration strategies in animals that run: a range equation and its consequences. Animal Behaviour 66:631-636.

Hegel, T.M., Gates, C.C. and Eslinger, D. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90:222-235.

Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101:1–39.

Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. American Naturalist 173:43–445.

Home, R., C. Keller, P. Nagel, N. Bauer, and M. Hunziker. 2009. Selection criteria for flagship species by conservation organizations. Environmental Conservation 3:1-10.

Horne, J.S., E.O. Garton, S.M. Krone, and J.S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354-2363.

Houston, A.I., McNamara, J.M., and Hutchinson, J.M.C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions: Biological Sciences 341:375-397.

Hutto RL. 1998a. Using landbirds as an indicator species group. In: Marzluff JM, Sallabanks R (Eds.) Avian conservation: research and management. Island Press, Washington, pp 75–91.

Hutto, R. L., 1998. On the importance of stopover sites to migrating birds. *The Auk*, 115: 823–825.

Irwin, L.L. 2002. Chapter 10 Migration: Pg. 493-514, in North American Elk: Ecology and Management.Toweill, D.E. and J.W. Thomas. (Eds.). Wildlife Management Institute Book, Smithsonian Institution Press, Washington. 962pp.

Irwin, L.L. and J.M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management 47:664-672.

Ito, T., Miura, N., Lhagvasuren, B., Enkhbileg, D.,Takatsuki, S., Tsunekawa, A., and Jiang, Z. 2005. Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. Conservation Biology 19: 945–48.

Jacques, C. N., Jenks, J. A. & Klaver, R. W. 2009 Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. Journal of Mammalogy 90:433–441.

Jedrzejewski, W., J.K. Schmidt, J. Theuerkauf, B. Jedrzejewska, and H. Okarma. 2001. Daily movement and territory use by radiocollared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Canadian Journal of Zoology 79:1993–2004.

Jenness, J., D.Majka, P.Beier. 2010. Corridor Designer Evaluation Tools. 93pp.

Johnson, E.A. and Klemens, M.W. 2005. Nature in Fragments: The Legacy of Sprawl.Columbia University Press, New York.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64:685–697.

Johnson, C.J., K.L. Parker, D.C. Heard, M,P. Gillingham. 2002. Movement patterns of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225-35.

Johnson, C. J. and M. P. Gillingham, 2004. Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. Journal of Applied Ecology 41:1032-1041.

Johnson, C.J., M.S. Boyce, R.L. Case, H.D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs 160:36pp.

Johnston, C.J., S.E. Nielsen, E.H. Merrill, T.L. McDonald, M.S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347-57.

Jonsen, I.D, J.M. Fleming, and R.A. Myers. 2005. Robust state-space modeling of animal movement data. Ecology 86:2874-2880.

Jorgensen, J. and J. Kansas. 1992. Elk summer surveys for the eastern slopes south of Highway 3. Unpublished report Alberta Fish and Wildlife 10pp.

Joslin, G., and H. Youmans, coordinators. 1999. Effects of recreation on Rocky Mountain wildlife: A Review for Montana. Committee on Effects of Recreation on Wildlife, Montana Chapter of the Wildlife Society. 307 pp. The Wildlife Society, Helena, Montana, USA.

Kamler, J.F., B. Jedrzejewska, and W. Jedrzejewski. Activity patterns of red deer in Bialowieza National Park, Poland. 2007. Journal of Mammalogy 88:508-514.

Kansas, J.L. 2002. Large carnivore status and movement in the Castle – Carbondale region. Unpublished report Urusus Ecosystem Management Ltd. for Shell Canada Ltd. 47pp.

Kautz, R., R. Kawula, T. Hoctor, J. Comiskey, D. Jansen, D. Jennings, J. Kasbohm, F. Mazzotti, R. McBride, L. Richardson, and K. Root, 2006. How much is enough? Landscape-scale conservation for the Florida panther. Biological Conservation 130:118-133.

Keitt, T., D. Urban, and B. T. Milne, 1997. Detecting critical scales in fragmented landscapes. Ecology and Society 1:4.

Kenward, R.E. 2001. Historical and practical perspectives. Pages 3-12 in J.J. Millspaugh and J.M. Marzluff, editors. Radio tracking and animal populations. Academic Press. San Diego, California. USA.

Kettunen, M and ten brink, P. 2006. Value of Biodiversity - Documenting examples where biodiversity loss has led to the loss of ecosystem services. Final report for the European Commission. Institute for the European Environmental Policy (IEEP), Brussels, Belgium.

Kie,J.G. 1999. Optimal foraging and risk of predation: effects on behaviour and social structure in ungulates. Journal of Mammalogy 80:1114-1129.

Kie, J. G., AND Boroski. B. B. 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. Journal of Range Management 49:482-488.

Kie, J.G., J.F. Lehmkuhl. 2001. Herbivory by wild and domestic ungulates in the Intermountain West. Northwest Science 75:55-61.

Kie, J. G., R. T. Bowyer, B. B. Boroski, M. C. Nicholson, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530–544.

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.

Kie,J.G., J. Matthiopoulos, J. Fieberg, R.A. Powell, F. Cagnacci, M.S. Mitchell, J. Gaillard, and P.R. Moorcoroft. 2010. The home-range concept: are traditional estimators still relevant

with modern telemetry technology? Philosophical Transactions of The Royal Society B 365 2221-2231.

Kindlmann, P. and F. Burel. 2008. Connectivity measures: a review. Landscape Ecology 23:879–890.

Knight, R.R. 1970. The Sun River elk herd. Wildlife Monograph No. 23. The Wildlife Society, Washington, D.C. 66pp.

Kochert, M.N., M. R. Fuller, L.S. Schueck, L.Bond, M. J. Bechard, B. Woodbridge, G.L. Holroyd, M. S. Martell and U.Banasch. 2011. Migration Patterns, Use of Stopover Areas, and Austral Summer Movements of Swainson's Hawks (Patrones de Migración, Uso de Áreas de Parada y Movimientos durante el Verano Austral en *Buteo swainsoni*). The Condor 113:89-106.

Koen, E.L., C.J. Garroway, P.J. Wilson, J. Bowman. 2010. The effect of map boundary on estimates of landscape resistance to animal movement. PLoS ONE 5:1-8.

Kotler BP, Brown JS, Bouskila A. 2004. Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. Ecology 85:917–22.

Kristan, W.B.I. 2003. The role of habitat selection behaviour in population dynamics: Source-sing systems dynamics and ecological traps. Oikos 103:457-68.

Kuck, L., G.L. Hompland, and E.H.Merrill. 1985. Elk calf response to simulated mine Disturbance in southeast Idaho. Journal of Wildlife Management 49:751 -757.

Lack, D. 1968. Bird migration and natural selection. – Oikos 19: 1–9.

Laita et al. 2011 Laita, A., J.S. Kotiaho, and M. Monkkonen. 2011. Graph-theoretic connectivity measures: what do they tell us about connectivity? Landscape Ecology 26:951-967.

Laundre J.W., Hernandez L., Altendorf K.B. 2001. Wolves, elk, and bison: reestablishing the ‘‘landscape of fear’’ in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1402–9.

Laporte I, Muhly T.B, Pitt J.A, M. Alexander, Musiani M .2010. Effects of Wolves on Elk and Cattle Behaviors: Implications for Livestock Production and Wolf Conservation. PLoS ONE 5:345-352.

Laver, P.N. and M.J. Kelly. 2008. A critical review of home range studies. Journal of Wildlife Management 72:290-298.

Lee, T, M.S. Quinn, and D. Duke. 2006. Citizen, Science, Highways, and Wildlife: Using a web-based GIS to engage citizens in collecting wildlife information. Ecology and Society 11:11. [online] URL: http://www.ecologyandsociety.org/vol11/iss1/art11/

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large scale analysis of anthropogenic impacts. Ecological Applications 18:1119–1139.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling.2007. Effects of habitat on GPS collar performance using data screening to reduce location error. Journal of Applied Ecology 44:663–671.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zooloogy 68:619–40.

Lundberg, P. 1988. The evolution of partial migration in birds. Trends Ecological Evolution 3:172-175.

Lung, M.A. and M.J. Childress. 2007. The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. Behavioral Ecology 18:12–20.

Lyon, L.J. 1979. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry 77:658-660.

Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. Journal of Forestry 81:592-595.

Lyon, L.J. and A.L. Ward. 1982. Elk and Land Management. Pages 443-478. In Elk of North America: ecology and management. (Eds.) J.W. Thomas and D.E.Toweill, Stackpole Books Harrisburg Penn.

Mahoney, S.P. and Schaefer, J.A. (2002) Long-term changes in demography and migration of Newfoundland caribou. Journal of Mammalogy 83:957–63.

Main, M. B. 2008. Reconciling competing ecological explanations for sexual segregation. Ecology 89:693–704.

Mainer, D.J., and T.N. Hobbs. 2007. Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function. Oecologia 152:739-750.

Manley, B.F.J., L.L. McDonald, D.L. Thomas, T.L. MacDonald, W.P. Erickson. 2002. Resource selection by animals, 2nd edition, Kluwer Academic Publishers, Dordrecht, Netherlands.221pp.

Mao, J.S., M.S. Boyce, D.W.Smith, F.J.Singer, D.J. Vales, J.M. Vore, E.H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691-1701.

Martins, A.G., N.T. Netto, S. Aulangnier, A. Borges, M. Dubois, L. Vicente, J.F. Gerard, and M.L. Maublanc. 2002. Population subdivision among mouflon sheep (*Orvis gemelini*) ewes and ranging behavior of rams during the rut. Journal of Zoology 258: 27-37.

McCorquodale, S. M. 1991. Energetic considerations and habitat quality for elk in arid grasslands and coniferous forests. Journal of Wildlife. Management 55:237–242.

McCoy, J.E., D.G. Hewitt, and F.C. Bryant. 2005. Dispersal of yearling male white-tailed deer and implications for management. Journal of Wildlife Management 69:366-376.

McDevitt, A. D. et al. 2009. Survival in the Rockies of an endangered hybrid swarm from diverged caribou lineages. – Mol. Ecol. 18: 665–679.

McRae, B.H., B.G. Dickson, T. Keitt, and V.B, Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712-2724.

Merrill, E.H.1994. Thermal constraints on use of cover types and activity time of elk. Applied Animal Behaviour Science 29:251-267.

Millspaugh, J.J, and J.M. Marzluff. 2001. Radio Tracking and Animal Populations, Academic Press, San Diego, U.S.A. 474pp.

Minor, E. S. and D. L. Urban, 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. Conservation Biology 22:297-307.

Moeller, B.J. 2010. Migratory and non-migratory movements and habitat use by female elk in the Cascade Range of Washington. M.Sc. Thesis, the Evergreen State College, Washington USA.

Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. Journal of Wildlife Management 60:659-668.

Moilannen, A. and I. Hanski. I. 2001. On the use of connectivity measures in spatial ecology. Oikos 95: 147-151.

Mara, P.P., C.M. Francis, R.S. Mulvihill, F.R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307-315.

Moorehouse 2010, Prey composition, habitat selection and movement of wolves in southwest Alberta. M.Sc. Thesis, University of Alberta, Edmonton, Alberta, Canada.

Moorehouse, A. T. and M. S. Boyce. 2011. From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. Frontiers in Ecology and Environment

Morales, J.M. and S.P. Ellner. 2002. Scaling up movement in heterogeneous landscapes: the importance of behavior. Ecology 83:2240-2247.

Morales, J.M., D.T. Haydon, J.L. Friar, K.E. Holsinger and J.M. Fryxzell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85: 2436-2445.

Morgantini, L.E. 1988. Behavioral adaptive strategies of wapiti (*Cervus elaphus*) in the Rocky Mountains. PhD Thesis, University of Alberta, Alberta. 193 pp.

Morgantini, L.E., Hudson, R.J., 1988. Migratory patterns of the wapiti, (*Cervus elaphus*), in Banff National Park, Alberta. Canadian Field-Naturalist 102, 12–19.

Morgantini, L.E., 1994. Regional Elk Study Strategy Planning Meeting, Blairmore, Alberta. 21pp.

Morgantini, L. E. 1995. The Ya Ha Tinda: an ecological interview. Technical Report. Calgary, AB: Parks Canada, Alberta Region. 105 pp.

Morgantini, L.E. and R.J. Hudson. 1979. Human disturbance and habitat selection in elk. P. 132-139, in North American elk ecology: ecology, behavior and management. Ed. M.S. Boyce, and L.D. Hayden-Wing. Laramie University, Wyoming.

Morgantini, L.E. and R.J. Hudson. 1985. Changes in diets of wapiti during hunting season. Journal of Range Management. 38:77-79.

Morgantini, L.E. and R.J. Hudson. 1989. Nutritional significance of wapiti (*Cervus elaphus*) migrations to alpine ranges in western Alberta, Canada. Artic and Alpine Research 21:288-295.

Morgantini, L.E. and W.B. Russel. 1983. An assessment of three selected winter ranges in the Rocky Mountains Region. Prepared for the Alberta Fish and Wildlife Division by Wildland Consultants Ltd. Edmonton, Alberta. 260pp

Morris SR, Holmes DW, Richmond ME.,(1996). A ten-year of stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. Condor 98:395–409

Muhly, T.B. 2010. Direct, indirect and predator-mediated effects of humans on a terrestrial food web: implications for conservation. Thesis to the University of Calgary for the degree of Doctor of Philosopy. Falculty of Enviromental Design. Calgary, Alberta. 172pp.

Muhly, T.B., M. Alexander, M.S. Boyce, R. Creasey, M. Hebblewhite, D. Paton, J.A. Pitt, and M. Musiani. 2010. Differential risk effects of wolves on wild versus domestic prey have consequences for conservation. Oikos 119: 1243-1254.

Muly, T.B, C. Semeniuk, A. Massolo, L. Hickman, M. Musiani. 2011. Human activity helps prey win the predator prey space race. PLoS ONE 6:e17050.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology 247:479-486.

Mysterud, A, R.Langvatn, N.G. Yoccoz, and N.C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of variable topography. Journal of Animal Ecology 70:915-923.

Mysterud, A. et al. 2011 Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? – Oikos 000: 000–000.

Naylor, L.M., M.J. Wisdom, R.G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management 73:328-338.

Nelson, J.R. and D.G. Burnell.1975. Elk-cattle competition in central Washington.in Range multiple use management. University of Idaho, Moscow. 172pp.

Nelson, M.E., L.D. Mech, and P.F. Frame. 2004. Tracking of white-tailed deer migration by global positioning system. Journal of Mammalogy 85:505-510.

Nelson, A.A., M.J. Kauffman, A.K. Middleton, M.D. Jimenez, D.E. McWhirter, J. Barber and K. Gerow. 2012. Elk migration patterns and human activity influence wolf habitat use in the Greater Yellowstone Ecosystem. Ecological Applications 21:1-41.

Newman, M. E. J. 2005. A measure of betweenness centrality based on random walks. Social Networks 27: 39-54.

Nichols, J.D. 2001. Using Models in the Conduct of Science and Management of Natural Resources. Chapter 2 in T.M Shenk and A.B Franklin (Eds.). Modeling in Natural Resource Management: Development, Interpretation, and Application. Island Press, Washington, D.C.

Nicholson, M.C., Bowyer, R.T., Kie, J.G., 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78, 483–504.

Nicholson, M.C., R.T. Bowyer and J.G. Kie 2006. Forage selection by mule deer: does niche breadth increase with population density. Journal of Zoology 269:39-49.

Nielson, S.E., C.J. Johnson, D.C. Heard, M.S. Boyce. 2005. Can models of presence-absence be used to scale abundance? Two case studies considering extremes in history. Ecography 28:197-208.

Northrup J. 2010. Grizzly bears, roads, and human–bear conflicts in southwestern Alberta . MSc thesis. Edmonton, Canada: University of Alberta.

Noss, R.F. 1987. Corridors in real landscape: A reply to Simberlof and Cox. Conservation Biology, 1(2): 159-164.Noss, R. F., and K. M. Daly. 2006. Incorporating connectivity into broad scale conservation planning. Pages 587–619 in K. R. Crooks and M. A. Sanjayan, (Eds). Connectivity conservation, Cambridge University Press, Cambridge, United Kingdom.

Norris, K. and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97: 265-268.

O'Brien, D., M. Manseau, A. Fall, and M.-J. Fortin, 2006. Testing the importance of spatial configuration of winter habitat for woodland caribou: An application of graph theory. Biological Conservation 130:70-83.

Ogden, L.E. 2012. Road ecology: reconnecting a fragmented landscape BioScience 62:100-101.

Otis, D. L. and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039–1044.

Parker, G.A. and R.A. Stuart. 1976. Animal behavior as a strategy optimize: evolution of resource assessment strategies and optimal emigration thresholds. The American Naturalist 110:1055-1076.

Parker, K.L., P.S. Barboza, and M.P. Gillingham. 2009. Nutrition integrates environmental response of ungulates. Functional Ecology 23:57-69.

Paton, D.G. 2005. Wildlife monitoring of elk in the Castle-Carbondale. Unpublished report. Anatum Ecological Consulting Ltd. for Shell Canada. 55pp.

Pennycuick, L. 1975. Movements of the migratory wildebeest population in the Serengeti areas between 1960 and 1973. East African Wildlife Journal, 13, 65–87.

Penrod, K. L., R. Hunter, and M. Merrifield. 2001. Missing Linkages: restoring connectivity to the California landscape. California Wilderness Coalition, The Nature Conservancy, US Geological Survey, Center for Reproduction of Endangered Species, and California State Parks.

Pepin, D. , C. Adrados, G. Janeau, J. Joachim, C. Mann. 2008. Individual variation in migratory and exploratory movements and habitat use by adult roe deer (*Cervus elaphus* L.) in a mountainous temperate forest. Ecological Resources 23:1005-1013.

Petersburg, M.L., A.W. Aldredge, and W.J. de Vergie. 2000. Emigration and survival of 2-year-old male elk in northwestern Colorado. Wildlife Society Bulletin 28:708-716.

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

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

Pomeroy, A. C., R. W. Butler, and R. C. Ydenberg. 2006. Experimental evidence that migrants adjust usage at stopover site to trade off food and danger. Behavioral Ecology 17:1041–1045.

Powell, R.A.. 2000. Animal home ranges and territories and home range estimators. Research Techniques in Animal Ecology Controversies and Consequences. (Eds). L. Boitani and T.K. Fuller, pp 65-110. Columbia University Press. New York.

Proctor, M.F., B.N. McLellan, C. Strobeck, and R.M.R. Barclay. 2005. Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. Philosophical Transactions of The Royal Society B 272, 2409-2416.

Proffitt, K., J. Grigg, R. A. Garrott, and K. L. Hamlin. 2009. Elk behavioral responses to predation risk: contrasting effects of wolves and human hunters. Journal of Wildlife Management 73:345–356.

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.

Prugh, L.R., K. E. Hodges, A.R.E. Sinclair and J.S. Brahares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceeding of the National Academy of Sciences of the United States of America. PNAS 2009 106 349-350.

R Development Core Team. 2009. R: a language environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, J., K. Redford, R. Steneck and J. Berger. 2005. Large Carnivores and the Conservation of Biodiversity. Island Press.

Rayfield ,B.,M. Fortin and A.Fall. 2010. The sensitivity of least-cost graphs to relative cost surface values. Landscape Ecology 25:519-532.

Rempel, R.S. and A.R. Rogers. 1997. Effects of differential correction on accuracy of a GPS animal location system. Journal of Wildlife Management 61:525-530.

Ricketts, T. H., 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158:87-99.

Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation 138, 514–519.

Ripple, W.J. and R.L. Beschata. 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana. U.S.A. Forest Ecology and Management 200:161-181.

Ripple, W.J., E.J. Larsen, R.A. Renkin, and D.W. Smith. 2001, Trophic cascades among wolves, elk, and aspen on Yellowstone National Parks northern range. Biological Conservation 102:227-234.

Robinson, G. G., M. Hebblewhite, and E. H. Merrill.2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? Oecologia 163:265-275.

Rodgers, A.R. and J.G. Kie. 2010. HRT: home range tools for ArcGis. Version 1.1 June 2007. Users manual. 24pp.

Rogala, J.K., M. Hebblewhite, J. Whittington, C.A. White, J. Coleshill, and M. Musiani. 2011. Human activity deferentially redistributes large mammals in the Canadian Rockies National Parks. Ecology and Society 16:16.

Romme, W.H., M.S. Boyce, R. Griesswell, E.H. Merrill, G. W. Minshall, C. Whitlock, and M. G. Turner. 2011. Yellowstone fires: lessons about disturbance and ecosystems. Ecosystems. Published on-line Springer Sciences and Business Media. 14pp.

Ronce, O. & Kirkpatrick, M.2001. When sources become sinks: migrational meltdown in heterogeneous habitats. Evolution 55: 1520–1531.

Rost, G.R. and J.U.A. Baily. 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management: 43:634-641.

Rowland, 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.

Rowland et al. 2004 Rowland, M. M., 1. W. Wisdom, B. K. Johnson, and M. A. Penninger. 2004. Effects of roads on elk: implications for management in forested ecosystems. Transactions of the North American Wildlife and Natural Resource Conference 69:79-86.

Rowland, M.M,, M.J.Wisdom, B.K. Johnson, and M.A. Penninger. 2005. Effects of Roads on Elk: Implications for Management in Forested Ecosystems. Pages 42-52 in Wisdom, M.J. technical editor, The Starkey Project: a synthesis of long-term studies of elk and mule deer. 211p.

Ruckstuhl, K.E. and P. Neuhaus. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. Biological Reviews 77:77–96.

Ruckstuhl, K.E. and P. Neuhaus. 2005. Activity Asynchrony and Social Segregation. Chapter 10 in Ruckstuhl, K.E. and P. Neuhaus (Eds.). Sexual Segregation in Vertebrates: Ecology of Two Sexes. Cambridge University Press, Cambridge, UK.

Rumble M.A., R.S. Gamo. 2011. Habitat use by elk (*Cervus elaphus*) within structural stage of a managed forest of the northcentral United States. Forest Ecology and Management 261:958-964

Rumble, M. L. Benkobi, and R.S. Gamo. 2005. Elk responses to humans in a densely roaded area. Intermountain Journal of Sciences 11:10-24.

Saher, D.J. and F.K.A. Schmiegelow. 2005. Movement pathways and habitat selection by woodland caribou during spring migration. Rangifer 16:143-154.

Salewski V, Schaub M. 2007. Stopover duration of palearctic passerine migrants in the western sahara - independent of fat stores? Ibis 149:223–236.

Saher, D. J., and F. K. A. Schmiegelow. 2004. Movement pathways and habitat selection by woodland caribou during spring migration. Rangifer 16:143–154.

Sawyer, H., R. Nielson, F. Lindzey, and L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

Sawyer, Hall, Matthew J. Kauffman, Ryan M. Nielson, and Jon S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Sawyer, H. and M.J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1365-2656.

Schadt, S., F. Knauer, P. Kaczensky, E. Revilla, T. Wiegand, and L. Trepl, 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. Ecological Applications 12:1469-1483.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G. Bishop, 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584-606.

Schoenecker, K.A., F.J. Singer, L.C. Zeigenfuss, D.Binkley and R.S.C. Menezes. 2004. Effects of elk herbivory on vegetation and nitrogen processes. Journal of Wildlife Management 68:837-849.

Schultz R.D. and J.A. Bailey. 1978. Responses of national park elk to human activity. Journal of Wildlife Management 42:91-100

Schumaker NH. 1996. Using landscape indices to predict habitat connectivity. Ecology 77: 1210–25.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.

Shimzaki et al. 2004 Shimazaki, H., M. Tamura, Y. Darman, V. Andronov, M. Parilov, M. Nagendran, and H. Higuchi. 2004. Network analysis of potential migration routes applied to identification of important stopover sites for Oriental White Storks (*Ciconia boyciana*). Ecological Resources 19:683–698.

Shively, K.J., W.A. Alldredge, G.E. Phillips. 2005. Elk reproductive response to removal of calving season disturbance by humans. Journal of Wildlife Management 69:1073-1080.

Sibbald AM, Hooper RJ, Gordon IJ, Cumming S. 2001 Using GPS to study the effect of human disturbance on the behaviour of red deer stags on a highland estate in Scotland. In: Sibbald AM, Gordon I J (Eds) Proceedings of the conference on tracking animals with GPS. Macaulay Institute, Aberdeen, UK, pp 39-44.

Sih, A., G. Englund, and D. Wooster, 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution 13:350-355.

Singer, F.J., Norland, J.E., 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Canadian Journal of Zoology 72, 1383–1394.

Singer, F.J.1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. Northwest Science 69:191-195.

Singer, F.J., M.E. Moses, S. Bellew and W. Sloan. 2000. Correlates to colonization of new patches by translocated populations of bighorn sheep. Restoration Ecology 8:66-74.

Singh, N.J., I.A. Grachev, A.B. Bekenov and E.J. Milner-Gulland. 2010. Tracking greenery across a latitudinal gradient in centeral Asia – migration of the saiga antelope. Diversity and Distributions 16:663-675.

Skovlin, J. M. 1982. Habitat requirements and evaluations. In: Thomas, J. W.; Toweill, D. E., (Eds.). Elk of North America: ecology and management. Harrisburg, PA: Stackpole Books:369–412.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2004. Elk habitat selection and evaluation. Pages 531-555 in Toweill, D. E., and J. W. Thomas, (Eds.). North American Elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

Slate, D. Owens R., G. Connolly and G. Simmons. 1992. Decision making for wildlife damage management. Transactions of the North American Wildlife and Natural Resources Conference 57:51-62.

Smallidge, S.T., T.T. Backer, D. VanLeeuwen, W.R. Gould, and B.C. Thompson. 2010. Elk distributions relative to spring normalized difference vegetation index values. International Journal of Ecology 20:1-10.

Smith, B. 2007. Migratory behavior of hunted elk. Northwest Science, 81:251-264. 69:1073-1080.

Soule, M. E., J. A. Estes, J. Berger, and C. Martinez Del Rio, 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238-1250.

Southern Rockies Ecosystem Project. 2005. Linking Colorado's landscapes: a statewide assessment of wildlife linkages, phase I report. Available at http://nativeecosystems.org/campaigns/linkingcolorados- landscapes (accessed May 2011).

Soule, M. E., J. A. Estes, J. Berger, and C. Martinez Del Rio, 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238-1250.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141:2159-2173.

Starfield, A.M. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61:261-270.

St. Clair and A. Forrest. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, *Cervus elaphus*. Behaviour 146:393-413.

Stevens, V. M., E. Polus, R. A. Wesselingh, N. Schtickzelle, and M. Baguette, 2004. Quantifying functional connectivity: experimental evidence for patch-specfic resistance in the Natterjack toad (*Bufo calamita*). Landscape Ecology 19:829-842.

Stewart, A. and P.E. Komers. 2012. Testing the ideal free distribution hypothesis: moose response to changes in habitat amount. International Scholarly Research Network. ISRN Ecology Volume 12, Article ID 945209.dci:10 5402/20012/945209.

Stewart, K.M., R.T. Bowyer, J.G. Kie, R.W. Ruess. 2009. Population density of North American elk: effects on plant diversity. Oecologia 161:303-312.

Stewart, K.M., R.T. Bowyer,J.G.Kie, M.A. Hurley. 2010. Spatial distributions of mule deer and North American elk: resource partitioning in a sage-steppe environment. American Naturalist 163:400-412.

Strandberg, R., Klaassen, R. H. G.,Hake, M., Olofsson, P. and Alerstam, T. 2009 Converging migration routes of Eurasian hobbies (*Falco subbuteo*) crossing the African equatorial rain forest. Proceeding Royal Society B 276: 727–733

Swihart, R.K. and N.A. Slade. 1985. Influences in sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

Rumble, M. L. Benkobi, and R.S. Gamo. 2005. Elk responses to humans in a densely roaded area. Intermountain Journal of Sciences 11:10-24.

Taylor, L.R. and R.A.J. Taylor. 1977. Aggregation, migration and population mechanics. Nature 265:415-421.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam, 1993. Connectivity is a vital element of landscape structure. Oikos 68:571-573.

Theobald, D. M., 2006. Exploring the functional connectivity of landscapes using land-scape networks. In K. Crooks and M. Sanjayan, editors, Connectivity conservation, pages 416-443. Cambridge University Press, Cambridge.

Theobald, D. M., 2006. Exploring the functional connectivity of landscapes using landscape networks. In K. Crooks and M. Sanjayan, editors, Connectivity conservation pages 416-443. Cambridge University Press, Cambridge.

Thirgood, S. et al. 2004 Can parks protect migratory ungulates? The case of the serengeti wildebeest. Animal Conservation 7, 113–120.

Tischendorf, L. and L. Fahrig, 2000. How should we measure landscape connectivity? Landscape Ecology 15:633-641.

Tischendorf, L., 2001. Can landscape indices predict ecological processes consistently? Landscape Ecology 16:235-254.

Torstenson, W. L., M. W. Tess, and J. E. Knight. 2002. Elk management strategies and profitability of beef cattle ranches. Journal of Range Management 55:117–126.

Thompson, C.M. and E.M. Gese. 2012. Swift foxes and ideal free distribution: relative influences of vegetation and rodent prey base on swift fox survival, density and home range size. International Scholarly Research Network. ISRN Zoology Volume 2012, Article ID 197356.dci:10 5402/2012/197356.

Thompson, M.J. and R.E. Henderson. 1998. Elk habituate as a credibility challenge for professional. Wildlife Society Bulletin 26:477-483.

Tracey, J.A. 2006. Individual-based modeling as a tool for conserving connectivity. Pages 343-368. (Chapter 14) in KR Crooks and M.A. Sanjayan. Conectivity Conservation. Cambridge University Press.

Trombulak, S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial aquatic communities. Conservation Biology 14:18-30.

Turchin, P. 1991. Translating foraging movements in herterogeneous environments into the spatial distribution of foragers. Ecology 72: 1253-1266.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer Associates, Sunderland, Massachusetts, USA.

Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205-1218.

Urban, D. L., E. S. Minor, E. A. Treml, and R. S. Schick, 2009. Graph models of habitat mosaics. Ecology Letters 12:260-273.

Van Dyke, W.A. and W.C. Kein. 1996. Response of elk to installation of oil wells. Journal of Mammalogy 77:1028-1041.

Van Dyke, F.G. and W.C. Klein. 1997. Response of elk to installation of oil wells. Journal of Mammalogy 77:1028-1041.

Vieira, M.E., M.M. Conner, G.C. White and D.J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. Journal of Wildlife Management 67:717-728.

Villalba et al. 1998 Villalba S., Gulinck H., Verbeylen G. and Matthysen E. 1998. Relationship between patch connectivity and the occurrence of the European red squirrel, (*Sciurus vulgaris*), in forest fragments within heterogeneous landscapes. In: Dower J.W. and Bunce R.G.H. (eds). Key Concepts in Landscape Ecology. IALE, Preston, UK, pp. 205–220.

Vistnes, I., Nellemann, C., Jordhøy, P. & Strand, O. 2004. Effects of infrastructure on migration and range use of wild reindeer. Journal of Wildlife Management 68: 101-108.

Vistnes, I., and Nellemann, C. 2007. Impacts of human activity on reindeer and caribou: The matter of spatial and temporal scales. The 14th Nordic Conference on Reindeer and Reindeer Husbandry Research Vantaa, Finland, 20th – 22nd March 2006, Rangifer Report No. 12(2007):47-56.

Voeten, M.M., C.A.D.M. van de Vijver, H. Olff and F. van Langevelde. 2009. Possible causes of decreasing migratory ungulate populations in an East African savanna after restrictions in their seasonal movements African Journal of Ecology 48:169-179.

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

Walker, R., and L. Craighead. 1997. Analyzing wildlife movement corridors in Montana using GIS. 1997. In Proceedings of the 1997 International ESRI Users conference. Environmental Sciences Research Institute, Redlands, California. Available from http://gis.esri.com/ library userconf/proc97/proc97/to150/pap116/p116.htm (accessed January 2010).

Walter, D.W., M.J. Lavelle, J.W. Fischer, T.L. Johnson, S.E. Hygnstrom, and K.C. VerCauteren. 2010. Wildlife Research 37:630-646.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, O. Hoegh-Guldberg and F. Bairlein, 2002. Ecological responses to recent climate change. Nature 416: 389–395.

Walton 2001 could it be: Walton, L. R., H. D. Cluff, P. C. Paquet, and M. A. Ramsay. 2001. Movement patterns of barren ground wolves in the central Canadian arctic. Journal of Mammalogy 82:867.

Washington Habitat Connectivity Work Group (WHCWG). 2010. Connected landscapes project. WHCWG. Available from http://waconnected.org/ (accessed November 2011).

Weaver, J.L. 2001. The Transboundary Flathead: A critical landscape for carnivores in the Rocky Mountains. Western Conservation Working Papers 18:1-62.

Webb S.L., M.R.Dzialak, J.J. Wondzell, S. M. Harju, L.D. Hayden-Wing, and J.B.Winstead. 2011. Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. Population Ecology 44: 1-11.

White, G.C. and R.A. Garrott. 1990. Analysis of wildlife radiotracking data. Academic Press, Inc. Toronto, Canada. 383pp.

White, G. C., and R. A. Garrott. 1990. Yellowstone's ungulates after wolves expectations, realizations, and predictions. Biological Conservation 125:141–152.

White, P.J., T.L. Davis, K.K. Barnowe-Meyer, R.L. Crabtree, and R.A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. Biological Conservation 135:502-510.

White, P.J.. K.M. Proffitt, D.L. Mech, S.B. Evans, J.A. Cunningham and K.L. Hamlin. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. Journal of Mammalogy 94:827 -837.

White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin 26:449–462.

Wilcove, D. 2007. No way home: the decline of the world's great migrations. Covello: Island Press. USA

Wiens, J. A., 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Willems, E.P. and R.A. Hill. 2009. Predator-specific landscapes of fear and resource distribution: effects of spatial range use. Ecology 90:546-555.

Williamson, D., Williamson, J., and Ngwamotsoko, K.T. 1988. Wildebeest migration in the Kalahari. African Journal of Ecology, 26, 269–80.

Winnie, J., D. Christianson, S.Creel and B.Maxwell. 2006. Elk decision-making rules are simplified in the presence of wolves. Behavioral Ecology and Sociobiology 61:277-289.

Wisdom, M. J., H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2004. Effects of off-road recreation on mule deer and elk. Transactions of the North American Wildlife and Natural Resources Conference 69: 85-96.

Wisdom, M.J. 2007. Shift in spatial distribution of elk away from trails used by all-terrain vehicles. Report 1, May 2007, USDA Forest Service, Pacific Northwest Research Station, La Grande Oregon.

With, K. A., 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25-36.

With, K. A., R. H. Gardner, and M. G. Turner, 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78:151-169.

With, K. A., S. J. Cadaret, and C. Davis, 1999. Movement responses to patch structure in experimental fractal landscapes. Ecology 80:1340-1353.

Witmer, G.W. and D.S. deCalesta. 1985. Effect of forest roads on habitat use by Roosevelt elk. Northwest Science 59:122-125.

Wolf, M., Frair, J., Merrill, E. and Turchin, P. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection *in* wapiti (*Cervus elaphus*). Ecography 32:401-410.

Woodroffe, R. 2003. Dispersal and Conservation: A behavioral Perspective on Metapopulation Persistence. Chapter 3 in Festa-Bianchet, M. and M. Apollonio (Eds.). Animal Behavior and Wildlife Conservation. Island Press, Washington, D.C.

Woods, J.G. 1991. Ecology of a partially migratory elk population. Ph.D dissertation. University of British Columbia, Vancouver. 149pp.

Wright, G.J., R.O. Peterson, D.W. Smith, and T.O. Lemkey. 2006. Selection of Northern Yellowstone elk by gray wolves and hunters. Journal of Wildlife Management 70:1070-1078.

Yarmoloy, C.M.B. and V. Geist. 1988. Behavioral responses and reproduction of mule deer does following experimental harassment with an all-terrain vehicle. Canadian Field Naturalist 102:425-429.

Yellowstone to Yukon Conservation Initiative (Y2Y). 2004. Yellowstone to Yukon: a blueprint for wildlife conservation. Y2Y, Canmore, Alberta. Available from http://www.y2y.net (accessed May 2011).

Young, J.K. and J.A. Shivik. 2006. What carnivore biologists can learn from bugs, birds, and beavers: a review of spatial theories. Canadian Journal of Zoology 84:1703-1711.

Zhi-gao, Zeng, A.K. Skidmore, Y. Song, T. Wang, H. Gong. 2008 Seasonal altitudinal movements of golden takin in the Qinling mountains of China. Journal of Wildlife Management 72:611-617.