SEX- AND AGE-SPECIFIC RESOURCE SELECTION AND HARVEST MORTALITY OF ELK: BALANCING DISEASE RISKS WITH CONSERVATION BENEFITS IN A FRAGMENTED AGRICULTURAL LANDSCAPE

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By

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ABSTRACT

Integrating the characteristics of landscape structure with species' attributes that determine animal movement and consequently disease risk is a complex, yet critical step for effective conservation and disease management. I examined movement behavior of elk (*Cervus canadensis manitobensis*) in response to factors such as habitat fragmentation and predation risk (i.e., human hunting) to better understand the landscape-level risk of disease spread in Manitoba. Objectives of this thesis were to: (i) identify sex- and age-specific habitat corridors for elk movement to assess the potential risk of disease spread between elk sub-populations; and (ii) evaluate sex- and age-specific elk distribution and hunter-kill sites during the hunting season to understand the impact of hunting on elk resource selection and to improve the effectiveness of current disease control programs.

Elk in the Riding Mountain region of southwestern Manitoba are endemic with bovine tuberculosis (*Mycobacterium bovis*; TB) and are threatened by the imminent emergence of chronic wasting disease (CWD). I used collared elk locations from a combined dataset of 413 non-migratory female and male elk that were captured in and around Riding Mountain National Park and Duck Mountain Provincial Park and Forest between 2002 and 2011. Elk were fitted with either a GPS satellite collar (24 F; 12 M) or very high frequency (VHF) radio-transmitter (191 F; 186 M). In addition, I used 796 locations of hunter-killed female and male elk collected between 2003-2012 from the agricultural-dominated lands that surround the two protected areas. These data were used to develop resource selection function (RSF) models, which are powerful analytical tools that characterize and predict the selection of resources by animals.

The RSF models integrated with graph theory revealed important sex-specific differences in resource selection during spring and summer (Mar-Aug) and identified potential habitat corridors between the two parks. The extent of connectivity across the fragmented agriculture-dominated landscape remained relatively constant across several spatial scales for both sexes and connectivity was greater for adult females compared with juvenile males. During the hunting season (Sept-Feb), sex- and age-specific differences in resource selection and hunter-kill sites were also evident. Adult males were rarely located outside of the parks, and were killed considerably less often than adult females and juvenile males, in close proximity to park boundaries. Adult females and juvenile males made some use of the agriculture-dominated landscape outside of the parks and were killed in a range of habitats located farther from the park boundaries.

My research demonstrates that habitat connectivity and hunting are more critical than previously appreciated in limiting the potential spread of TB and CWD infected elk across this highly fragmented landscape. However, the implications for long-term conservation of elk remain an important concern. The risk of TB and CWD spread among elk sub-populations is low; however, the socioeconomic and ecological implications of these diseases remain significant. My thesis results include detailed maps of functionally connected areas that facilitate elk movement, and thus pinpoint local areas of disease management concern. I also provide an example of a small-scale manipulation of hunter effort linked to disease prevalence, with mapped areas where hunting can be targeted at the highest risk individuals for disease transmission. Resource managers can use these maps as a complementary tool to evaluate both the short- and long-term implications of habitat fragmentation and hunting efforts to effectively balance elk conservation and mitigate disease risks.

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I would like to thank Patty and Bob Simpson for skillfully flying elk relocation flights, Bighorn Helicopters for safely doing elk captures, and the many Riding Mountain National Park staff who efficiently and safely assisted with monitoring collared animals. Special thanks to Richard Davis for sharing the hunter-killed data, Raea Gooding for assistance in the field, members of The Spatial Initiative (University of Saskatchewan), and the Wildlife Ecology and Community Engagement Lab for constant support and encouragement.

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Finally, I thank my partner Randy for his patience, constant motivation and loving support.

Dedication

For my grandfather, Dr. Louis-Charles Dugal, “Papa Lou” (1914-2011).

He was a courteous, humble and loving person, and a
dedicated research scientist.

He has been a great source of inspiration and motivation and
always believed in me.

I am truly grateful for his presence.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Land-use practices are fundamental to humans as they provide natural resources and ecosystem services such as food, shelter and fresh water (Foley et al. 2005). However, with an increase in the human population of seven-fold over the last century, the decline in native habitat and wildlife populations has been unprecedented (Pimm and Raven 2000; Shochat et al. 2006; Harte 2007). A major impact of the changing landscape has been habitat fragmentation, and it is at the interface between human and wildlife populations where this effect has been most drastic (Radeloff et al. 2005; Ditchkoff et al. 2006; Delahay et al. 2009). For example, anthropogenic practices such as agricultural intensification has fragmented ~40% of the land surface of the earth (Ramankutty and Foley 1999; Bruinsma 2003). Despite the large-scale environmental modification that has occurred, some wildlife continues to persist in fragmented landscapes. Indeed, many species are able to fulfill life-history requirements in a variety of habitat types and often benefit from agricultural-dominated lands (Nixon et al. 1991; Brook 2008; Brook and McLachlan 2009; Wrobel and Redford 2010).

Remnants of the natural environment occur as a mosaic of fragmented habitat areas. These areas range from smaller isolated habitat patches surrounded by intensive land use (collectively referred to as the matrix) to parks and protected areas (Janzen 1983; Wright 1996), established primarily for habitat and wildlife conservation purposes. Protected areas are an important component in conserving wild populations. However, developing an effectively connected reserve system while considering the conditions of the landscape matrix remains an important challenge (Fischer et al. 2005; Bennett et al. 2006). Few protected areas are large enough to sustain large animal populations (Miller and Harris 1977; Newmark 1985; Landry et al. 2001). As such, increased movement of many wide-ranging species exist beyond the park boundaries, creating significant socioeconomic and ecological impacts, as well as benefits (Conover 1998; Conover 2002; Wrobel and Redford 2010).

The maintenance or establishment of habitat corridors to connect isolated areas such as protected areas have become an important conservation tool in attempt to counter the effects of habitat loss and fragmentation (Bennett 1990; Hobbs 1992; Rosenberg et al. 1997; Dobson et al. 1999). Habitat corridors are intended to facilitate the movement of wildlife among otherwise-isolated habitat patches. However, little empirical evaluation has been attempted on this concept, and therefore the application of corridors remains highly controversial (Bennett 2003; Chetkiewicz et al. 2006). Furthermore, the effectiveness of habitat corridors remains ambiguous (Simberloff and Cox 1987; Dunning et al. 1992), as unanticipated consequences such as disease spread may occur (Simberloff and Cox 1987; Simberloff et al. 1992; Hess 1994; Bennett 2003).

In addition to the impacts of fragmentation, infectious diseases have also been recognized as one of the most significant threats to wild populations (Hess 1996; Gog et al. 2002; McCallum and Dobson 2002). Particularly in wild mammals, as they play an important role in the epidemiology of diseases that impact human health, agriculture and biodiversity (Delahay et al. 2009; Smith et al. 2009). As the landscape becomes increasingly fragmented, many species become largely constrained to protected areas, which can influence both the occurrence and transmission rate of disease among resident groups (Vander Wal et al. 2012). Yet the spread of disease occurs over multiple spatial scales (Cross et al. 2005), and many wide-ranging species frequently make use of the matrix, creating important challenges for disease management. Few studies have examined the underlying processes of disease spread such as host ecology (abundance and distribution), and how this may influence the emergence and re-emergence of disease (Plowright et al. 2008). As such, disease ecology within metapopulations remains poorly understood (Delahay et al. 2009).

Understanding the relationship between a host and the structure of a landscape is fundamental to effective conservation and disease management (Fahrig and Merriam 1994), and the recognition of animal behavior can indeed provide this link (Bélisle 2005). Organisms alter their movements according to multiple factors such as their response to the structure of the landscape, their perceptual range, and their response to predators. The role of natural predators certainly has a profound influence on animal behavior and has been well studied (Lima and Dill 1990; Ripple and Beschta 2004; Hebblewhite and Merrill 2009). However, in human-dominated landscapes, hunting is typically the major source of predation (Langvatn and Loison 1999; Hayes et al. 2002; Collins and Kays 2011), which can have similar or even stronger effects on animal behavior and the dynamics of populations (Ciuti et al. 2012).

1.2 Background and thesis objectives

The intermountain region between Riding Mountain National Park (RMNP) and Duck Mountain Provincial Park and Forest (DMPP&F), Manitoba, Canada, was once connected by continuous native vegetation, including extensive forest cover. However, human activities such as settlement, logging, road development and agricultural expansion over the last five decades have significantly fragmented the landscape, leaving small remnant patches of native forest (Fig.1.1).

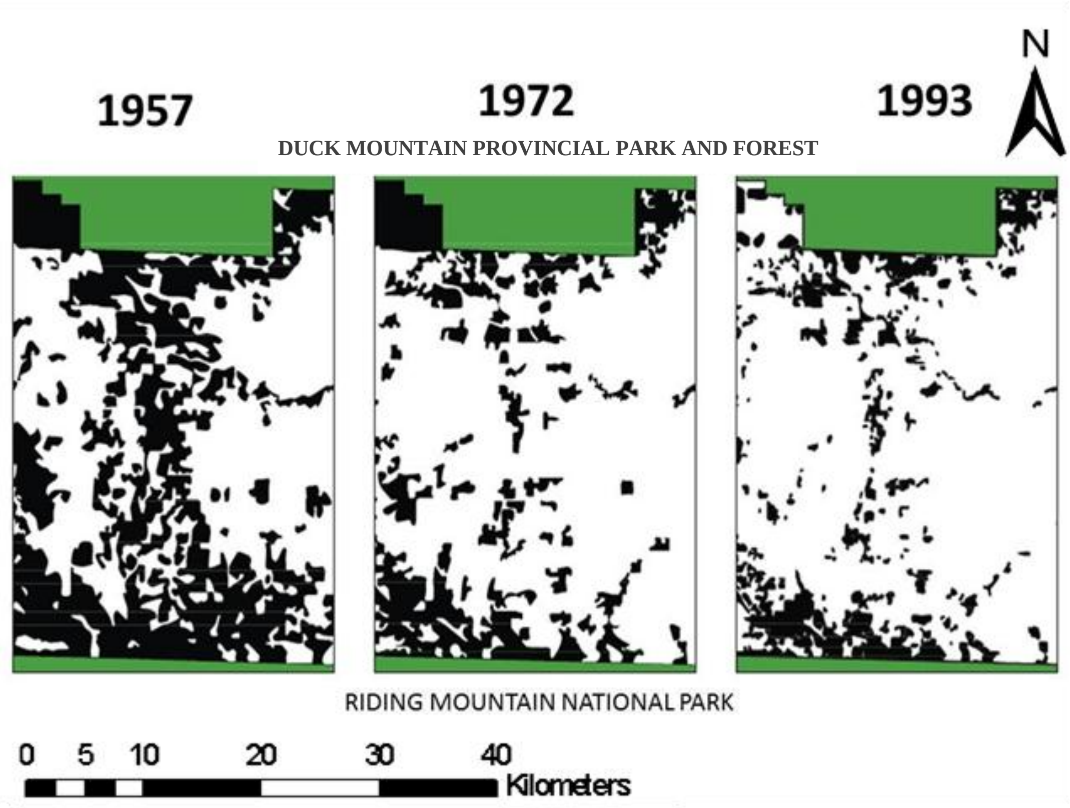

Figure 1.1. Extent of deciduous forest fragmentation between Riding Mountain National Park and Duck Mountain Provincial Park and Forest (1957-1993; Walker 2001).

Prior to European settlement, this region was used extensively by elk (*Cervus canadensis manitobensis*; Green 1933; Brook 2009). But as agricultural development began to intensify in the late 19th century along with unregulated hunting (deVos 1965), the regional population of elk was reduced from thousands to a small proportion of that number by the early 1900's (Brook 2009). Through the early part of the 20th century, concerns were expressed that elk could be extirpated from Manitoba if actions were not taken to conserve habitat and regulate hunting.

The establishment of RMNP in 1930 provided some protection for elk as hunting was prohibited within its boundaries, though RMNP was 26% smaller than the original Forest Reserve (Brook 2009). Between 1917 and 1933, the provincial government also prohibited hunting throughout Manitoba, which further helped increase elk numbers. In 1981, the provincial government created a special landowner-hunting season specifically for farmers and other landholders (Brook 2009), and by 2001, ungulate hunting was allowed by landowners on 67% of farms around RMNP (Brook 2008). The season length, number of available hunting permits and elk killed each year has varied greatly (Fig. 1.2). The Riding Mountain elk population has since fluctuated between 2000-6000 individuals (Parks Canada, unpublished data), likely in response to habitat alteration, natural predators and hunting.

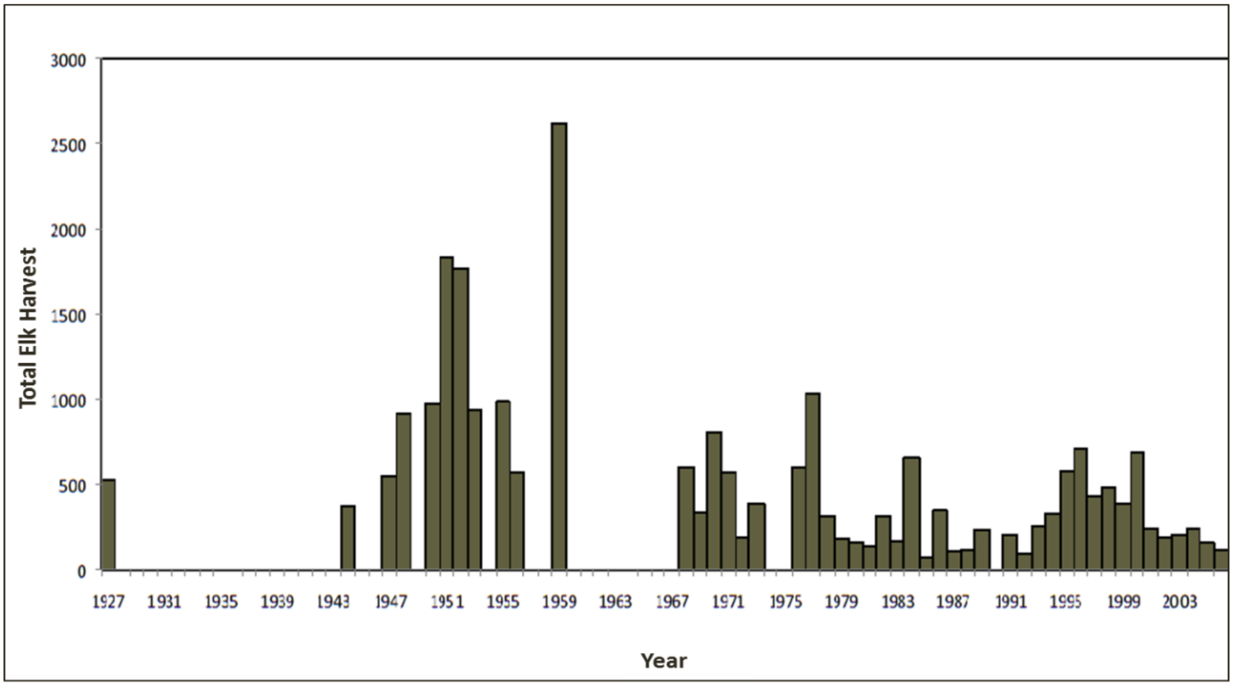

Figure 1.2. Elk kill estimates by licensed hunters around Riding Mountain National Park (1927-2006). No data are currently available for First Nations subsistence hunting (Brook 2009).

In addition to the impacts of fragmentation and hunting, the presence of endemic bovine tuberculosis (*Mycobacterium bovis*; TB) in the region has posed great challenges for the management of elk and their interactions with cattle farms (Brook and McLachlan 2009; Brook et al. 2012). Between 1991 and 2003, there were five outbreaks of TB affecting cattle herds in Manitoba (Nishi et al. 2006). After the second outbreak in 1997, it was suspected that wild elk could be the source of TB and, by 2001, elk were assumed to be the primary reservoir host (Lees 2004; Nishi et al. 2006). In total, 41 TB-infected elk have been identified since 1991 (Shury and Bergeson 2011). Moreover, the recent emergence of chronic wasting disease (CWD) in wild and farmed cervids in Saskatchewan and Alberta has caused considerable conservation and economic concern, as CWD is highly contagious and always fatal. Wild elk infected with CWD have been detected as close as 160 km from the Manitoba border, and with other Manitoba elk in such close proximity to these known cases, there is risk for disease spread between elk sub-populations.

The impacts of habitat fragmentation and disease on wildlife in the Riding Mountain region of Manitoba have caused considerable concern among wildlife managers, biologists and stakeholders. The purpose of my thesis was to improve our understanding of the complex interactions between elk movement, habitat fragmentation and the role of hunting to assess the landscape-level risk of endemic bovine TB and emerging CWD across an agricultural landscape. As such, this research aimed to understand the underlying processes that influence disease transmission risk between elk sub-populations, which will ultimately facilitate the development of more effective conservation and disease management solutions. My thesis objectives were to: (i) identify sex- and age-specific habitat corridors for elk movement to assess the potential risk of disease spread between elk sub-populations; and (ii) evaluate sex- and age-specific elk distribution and hunter-kill sites during the hunting season to understand the impact of hunting on elk resource selection and to improve the effectiveness of current disease control programs.

1.3 Hypothesis

Overall, I hypothesize that resource selection patterns of elk in the agricultural landscape are sex- and age-specific and that long-distance dispersal is limited due to landscape fragmentation and the widespread distribution of hunters around protected areas, and as such, the potential for disease spread between elk sub-populations is low. In Chapters 3 and 4, I expand on this overarching hypothesis by developing and evaluating several sets of competing hypotheses to predict the probability of elk use and disease risk on the landscape.

1.4 Thesis Structure

This document follows the format of a manuscript-style thesis. In this format, Chapter one provides a general introduction, Chapter two is a review of relevant literature, while both data-chapters (Chapters 3 and 4) are developed as stand-alone manuscripts. In Chapter 3, I introduce the concept of functional connectivity and use an integrated approach that combines sex-specific resource selection functions with graph theory to identify potential habitat corridors. The theme of sex-specific differences follows into Chapter 4 where I link predation risk-driven shifts in resource selection and hunter-kill sites for managing elk populations with disease. Finally, in Chapter 5, I summarize the key findings of this research and provide practical conservation and disease management recommendations intended for government agencies and other stakeholders.

All references in this thesis have been formatted according to the Journal of Wildlife Management Manuscript Guidelines.

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CHAPTER 2: LITERATURE REVIEW

2.1 Introduction: habitat loss and fragmentation

Dramatic changes to landscapes induced by anthropogenic activities, such as habitat loss and fragmentation are central challenges in wildlife conservation and disease management (Wilcove et al. 1998; Benton 2003; Smith et al. 2009). A habitat is organism-specific and can be defined as "the resources and conditions present in an area that produce occupancy, including survival and reproduction by a given organism" (*sensu* Hall et al. 1997). The loss of habitat is a process that results in a decrease in available habitat for a species, whereas habitat fragmentation includes both habitat loss and a change in the configuration of available habitat into spatially disjunct patches (Fig. 2.1).

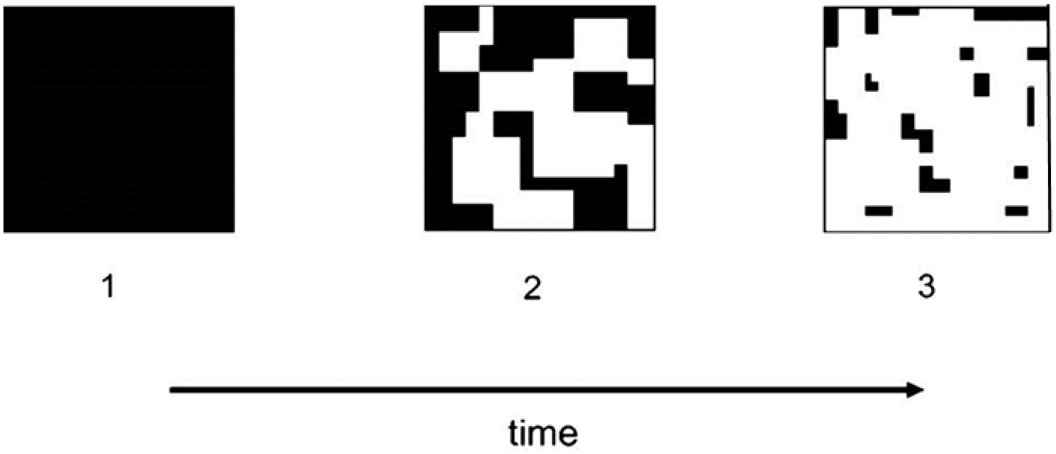

Figure 2.1. The process of habitat fragmentation where a "large expanse of habitat is transformed into a number of smaller patches of smaller total areas, isolated from each other by a matrix of habitats unlike the original" (adapted from Wilcove et al. 1986 and Fahrig 2003). Black areas represent habitat and white areas represent the matrix.

As native habitat becomes increasingly fragmented between parks and protected areas, there is a concomitant increase in other land cover types between habitat patches, collectively referred to as the matrix. The landscape matrix can be defined as the human-modified area of the landscape that represents a continuum of habitats for many species (Brady et al. 2011). The matrix has the potential to function as a barrier to movement for any species; however, it may also provide important habitat and resources within an animal's home range (Tubelis et al. 2007; Harper et al. 2008; Brook 2008).

The importance of the matrix is increasingly being acknowledged (Pita et al. 2007; Franklin and Lindenmayer 2009; Watling et al. 2011) for its influence on animal movement through the landscape and movement risk (Bender and Fahrig 2005; Brook 2008; Brady et al. 2011). Despite the fact that there is increasing recognition of the importance of landscapes as a whole, overlooking the matrix as potential viable habitat is still common in both research and conservation practice (Brady et al. 2011). Persistence of wildlife in human-modified landscapes depends on the entire landscape mosaic including habitat corridors (Bennett et al. 2006). Therefore, it is important that conservation strategies include landscape attributes from both parks and protected areas and the intervening matrix to understand the extent of habitat loss and fragmentation on species persistence (Cook et al. 2002; Vandermeer and Perfecto 2007).

The effects of fragmentation are commonly grouped under five categories that together define the spatial attributes of individual habitat patches in a fragmented landscape: (*i*) fragment area, (*2*) edge effects, (*3*) fragment shape, (*4*) fragment isolation, and (*5*) matrix structure (Ewers and Didham 2006). The implications of these effects on animals and ecological systems vary significantly as they "experience" the degree of fragmentation in a particular environment differently (Haila 2002; Ewers and Didham 2006). These implications are generally negative in terms of fitness (total reproductive output of an individual).

The negative effects of fragmentation are likely due to two main causes (Fahrig 2003). First, as the landscape becomes more fragmented into smaller, more isolated patches, the amount of available habitat for animals may become too small to sustain a local population. Furthermore, a species may experience higher mortality and reduced capacity to move through the matrix. As such, the persistence and overall size of the population may be reduced as individuals are confined to a large number of smaller patches. Secondly, habitat fragmentation may also create edge effects. Edge effects arise when a habitat contains more edge for a given amount of habitat.

These effects are the result of two adjacent ecosystems separated by an abrupt transition (edge) which can cause individuals to enter the matrix more frequently and expose animals to the negative impacts of the matrix (Murcia 1995). Consequently, predation rates may increase (e.g., Chalfoun et al. 2002) and the overall reproductive rate of a population may be reduced (Fahrig 2002). The matrix can therefore act as a population sink, which can be viewed as a region with inappropriate environmental conditions, preventing the establishment of species (Hoopes and Harrison 1998; Fahrig 2002; Gravel et al. 2010).

In contrast to the negative consequences of habitat fragmentation, it has long been recognized that there are also positive effects on some animal populations (Fahrig 2003). As first shown by Huffaker (1958), a fragmented landscape can support the existence of both predators and prey, as temporarily vacant patches can provide refuges for prey. Atkinson and Shorrocks (1981) showed enhanced coexistence between two competing species in fragmented patches, resulting from a trade-off between dispersal rate and competitive ability. In addition, fragmented patches may also provide a greater variety of habitat types (Law and Dickman 1998), particularly for species such as insects and amphibians that have various life stages with different habitat requirements. Indeed, many wide-ranging species make use of fragmented landscapes (Brook 2008; Brook 2010; Wrobel and Redford 2010) and often benefit from forage crops and reduced predator distribution and abundance (Nixon et al. 2007).

2.2 Habitat corridors: form, function and efficacy

The concept of habitat fragmentation emerged from the theory of island biogeography which described fragmented habitat patches as islands within a sea of inhospitable habitat (MacArthur and Wilson 1967). Attention has now largely shifted to metapopulation theory (Levins 1970) which also focuses on patchy habitats, extinction and colonization, but makes a stronger prediction regarding the importance of dispersal among fragmented patches. A metapopulation can be defined as a set of local populations distributed over a number of habitat patches that are connected by dispersal (Hanski 1991; Hanski and Gilpin 1997). Source-sink models have also been applied to fragmentation studies. These studies highlight the importance of individual movement from sources (e.g., protected areas) that can support the long-term persistence of populations, to landscapes such as the matrix (sink) that can increase the risk of mortality (Hoopes and Harrison 1998; Kanda et al. 2009). Through all these various spatial theories, they are unanimous in focusing on dispersal and habitat configuration. Collectively, these theories have led to the implementation of spatial strategies such as habitat corridors in promoting dispersal and to counter the effects of habitat loss and fragmentation (Rosenberg et al. 1997; Gilbert-Norton et al. 2010; Hodgson et al. 2011).

Diamond (1975) and Wilson and Willis (1975) proposed that fragmented habitat patches linked by a habitat corridor would have greater conservation value compared with fragments that would otherwise be isolated. Habitat corridors traditionally have been considered narrow, continuous strips of habitat patches to facilitate movement of organisms and other ecological processes between areas of intact habitats (Rosenberg et al. 1997; Puth and Wilson 2001). Implicit in this definition are two assumptions: (*i*) corridors facilitate the movement of both biotic processes (e.g., animal movement, plant propagation, genetic exchange) and abiotic processes (e.g., water, energy, material), and (*ii*) corridors are process or species-specific (Jongman and Pungetti 2004). According to Jongman and Pungetti (2004), three types of corridors exist: (*i*) migration corridors that are used by migratory individuals between areas such as winter and summer habitat, (*ii*) dispersal corridors, used for one-way movements of individuals or populations from one area to another, and (*iii*) commuting corridors that link resources of a species' home range to support daily movements such as breeding, resting and foraging.

The simplistic pattern-based view of habitat corridors has received considerable attention from land managers and conservation biologists (Bennett 2003; Chetkiewicz et al. 2006). Linkages such as "wildlife corridors", "dispersal corridors", "greenways" and other forms of connecting features have been proposed and are widely being established or protected for conservation purposes (Jongman and Pungetti 2004). Habitat corridors can include artificial tunnels and underpasses that promote animal movement across barriers such as roads and highways. They may also act as major linkages of undisturbed natural forest or streamside riparian areas that link parks and protected areas (Bennett 2003). The inclusion of corridors in reserve design has demonstrated that increased movement among populations can be part of a successful strategy towards population persistence (Fahrig and Merriam 1994). The importance of such interchange has become a paradigm in conservation biology (Doak and Mills 1994; Cushman et al. 2010).

The widespread interest in habitat corridors as a conservation strategy has resonated with ecologists for two main reasons. First, the application of linkages as a practical application to directly counter the effects of habitat loss and fragmentation is intuitively appealing. Corridors are intended to reduce these effects by promoting individual movements among otherwise-isolated populations (Fahrig and Merriam 1994; Hodgson et al. 2011). Second, corridors can include a range of spatial scales and can be relevant to local conservation efforts and regional, national, and even international strategies (Bennett 2003). The acceptance of habitat corridors as a practicable concept for biodiversity conservation, however, has proceeded with little empirical evaluation (Chetkiewicz et al. 2006). Therefore, while conservationists are investing heavily in establishing and maintaining habitat corridors, how and if they really work remain unclear.

Thus, the concept of habitat corridors has also received considerable criticism, scepticism and debate (Simberloff and Cox 1987; Hess 1994; Hess and Fischer 2001), and the conservation benefits potentially gained from corridors have become a contentious issue. Some potential adverse consequences of corridors include increased (*i*) exposure to domestic animals and other wildlife species harbouring disease (Soulé and Simberloff 1986), (*ii*) edge-related natural predation risk (e.g., Weldon and Haddad 2005), and (*iii*) spread of catastrophes such as disease and other exotic species. The risk of disease spread in particular has received considerable attention (Simberloff and Cox 1987; Andreasen and Christiansen 1989; Hess 1994; Delahay et al. 2009). However, few studies have considered the spatial arrangement of habitat patches and connectivity of populations in facilitating disease spread (Hess 1996). According to Bennett (2003), the consequences of disease spread among corridors should not be dismissed and suggests that empirical studies and monitoring of existing habitat linkages are required to evaluate and mitigate these concerns.

There are two important limitations surrounding the effectiveness of habitat corridors (Chetkiewicz et al. 2006). The first limitation is that animal movement is assumed to increase within corridors and that animals do not venture into non-habitat (i.e., matrix) which is often not the case (Simberloff et al. 1992; Rosenberg et al. 1997; Baum et al. 2004). Although many researchers have asserted that corridors are important elements of conservation, few studies have actually demonstrated that corridors increase the speed and frequency of successful movements between habitat fragments or reserves. Furthermore, these studies generally fail to include individuals that may have moved through the matrix; therefore, it remains unknown what effect the corridors actually have on movement characteristics (Chetkiewicz et al. 2006). According to Fischer et al. (2004), organisms occupy a spectrum of habitats, and this artificial dichotomy created between habitat patches and the matrix can create fundamental difficulties for understanding the response of organisms to fragmentation. The second limitation is that there is often no assumption made about a particular species when connectivity is inevitably species-specific (Puth and Wilson 2001; Goodwin 2003). In fact, the effectiveness of corridors may even be sex- and age-specific, but only a few studies have addressed these differences, and have largely focused on smaller mammal species or birds (e.g., Davis-born and Wolff 2000; Coffman et al. 2001; Braunisch et al. 2010).

During the past 20 years, numerous studies have focused on habitat corridors, most of which aim to clarify their role in facilitating animal movements (Chetkiewicz et al. 2006). Most research acknowledges the purpose of corridors is to counter the effects of habitat loss and fragmentation, and there are indeed several conservation benefits of linking protected areas with corridors. Increased immigration is an example of a possible benefit which would ultimately enhance gene flow and increase genetic diversity (Beier and Noss 1998; Fahrig and Merriam 1994; Hodgson et al. 2011). This is related to the “rescue effect” concept by Brown and Kodric-Brown (1977) in which immigration reduces the extinction rate of a population and increases genetic diversity, overall fitness and persistence of an isolated population (Fig. 2.2).

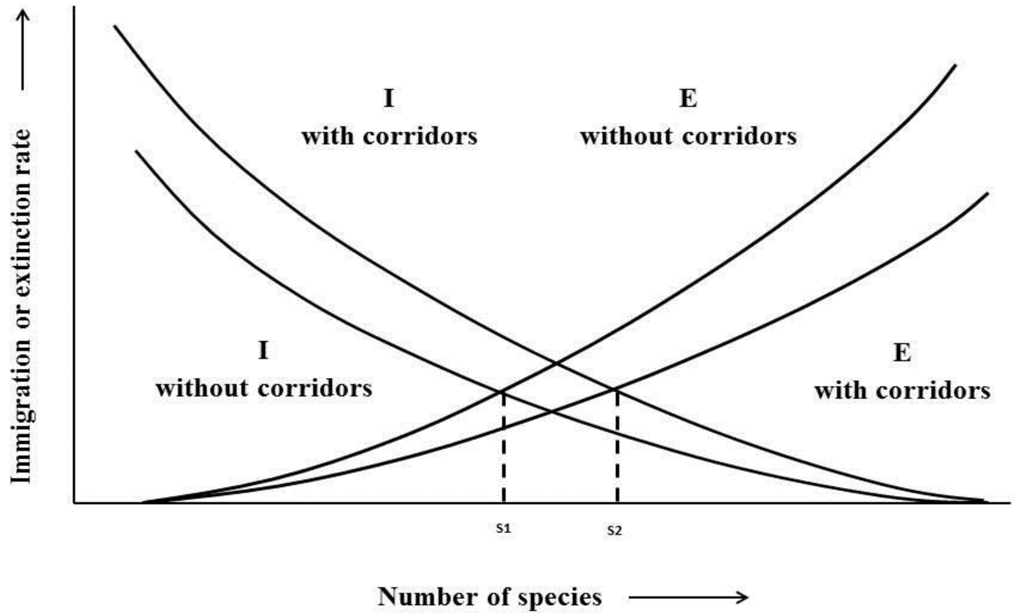

Figure 2.2. Theoretical effect of corridors on immigration rate (I), extinction rate (E), and resulting number of species in equilibrium island biogeographic model. Sl is the equilibrium number of species without corridors. S2 is the equilibrium number of species with corridors (Simberloff and Cox 1987).

Habitat corridors may also enable some species to avoid predation, accommodate range shifts due to climate change, and maintain ecological processes such as nutrient cycling (Bennett 2003; Hilty et al. 2006). However, many researchers argue that the corridor concept has been prematurely accepted and that many studies fail to consider or offer approaches to mitigate possible negative impacts (Simberloff et al. 1992).

2.3 Defining habitat connectivity

Our knowledge of the spatial and temporal scales of animal movements in human-dominated landscapes remains limited, which further exacerbates our understanding of the role that habitat corridors play in the conservation of species (Bélisle 2005; Kadoya 2009; Baldwin et al. 2010). Although some corridors may provide connectivity by facilitating animal movement among habitat patches, they do not determine connectivity entirely. The degree to which corridors contribute to connectivity depends not only on the structural nature of the corridors and the surrounding matrix, but the behavioral responses of organisms to the landscape and predators (Rosenberg et al. 1997; Beier and Noss 1998; Bélisle 2005).

The concept of connectivity was first introduced in landscape ecology by Merriam (1984) to describe the interaction between landscape structure and species' attributes in determining movement of organisms among habitat patches. Taylor et al. (1993) later defined functional connectivity as "the degree to which the landscape facilitates or impedes movement among resource patches". Functional connectivity can be defined on both structural and functional bases. The structural component (otherwise known as structural connectivity) is determined by the spatial arrangement of habitat patches, continuity of suitable habitat and distance between patches with no direct link to any behavioral attributes of organisms (e.g., With et al. 1997; Collinge 2000). The functional component refers to the organism's behavioral response to the structure of the landscape. It depends on how the organism actually perceives and responds to the landscape including the matrix (e.g., Gustafson and Gardner 1996; Tischendorf and Fahrig 2000*a*; Sweeney et al. 2007), where it may face higher rates of mortality and thus express different movement patterns (Wegner and Merriam 1990; Storch et al. 2005). The behavioral response is influenced by habitat requirements, degree of specialization, tolerance to altered habitats, response to predators, and ultimately, the animal's internal state and/or motivation (Bélisle 2005).

Structural connectivity has been widely used to predict the dispersal capacity of organisms across a fragmented landscape with no direct link to any behavioral attributes (Kindlmann and Burel 2008). Only recently has connectivity been used as a functional concept. The necessity to include behavioral responses of animals to the landscape has been described by Lima and Zollner (1996) and Haddad (1999), and discussed in depth by Bélisle (2005). Landscapes will have different degrees of connectivity for different species, and structurally connected habitat patches may not necessarily be functionally connected for all species of interest. Furthermore, functional connectivity may differ between ages and sex for many species (Davis-Born and Wolff 2000; Grimm and Railsback 2005; Bowne et al. 2006), and such variation in movement pathways can have important implications for conservation and management.

The term "connectivity" is often not well defined and it is clear that more precise definitions are needed to make better quantitative predictions. Functional connectivity is a key concept in landscape ecology; however, the actual study of this construct requires dealing with complex ecological systems that are often difficult to sample or experimentally manipulate (Bélisle 2005). The limited empirical knowledge about animal movement in fragmented landscapes has prevented an effective theoretical framework around the concept of functional connectivity. This is partially due to a misunderstanding that is centered around the multiple ways to measure the "functional" or behavioral component of connectivity (Tischendorf and Fahrig 2000*a*; Kindlmann and Burel 2008). Despite the lack of consensus surrounding this concept, the implications of connectivity for conservation are obvious, which has resulted in a proliferation of connectivity measures (Fahrig and Merriam 1994; Tischendorf and Fahrig 2000*a*,*b*).

2.4 Connectivity measures

Current animal movement modeling derives from two classic approaches described by Turchin (1998): *Lagrangian* and *Eulerian*. The Lagrangian approach involves the movement paths of individuals such as discrete steps and time segments. It characterizes the velocity, turning and directionality of the organism using a variety of measures such as computer simulations through heterogeneous landscapes. Most applications of Lagrangian approaches have involved small organisms such as insects (e.g., Schultz 1998). However, global positioning systems (GPS) and radio-telemetry are now widely used for larger animals such as ungulates to track movement over more broader and temporal scales (Chetkiewicz et al. 2006; reviewed by Millspaugh and Marzluff 2001). The Eulerian approach describes the expected pattern of space use by an individual or population; however, it does not provide the same level of detailed movement as Lagrangian approaches. This approach typically employs genetic techniques or stable isotopes which can provide estimates of dispersal or migration patterns (e.g., Proctor et al. 2004; Clark et al. 2006). Both these methods may also be integrated in which Eulerian models can be used to obtain general insights, whereas Lagrangian models can be used to test the validity of Eulerian results and to make predictions.

Early approaches to modeling landscape heterogeneity included general neutral models (e.g., Milne et al. 1989), percolation theory (e.g., Gardner et al. 1989), patch dynamic models (e.g., Levin 1976), and network models (e.g., Forman and Godron 1986). All of these models focus primarily on the presence of habitats or structural connectivity. Including all aspects of the landscape (including the matrix) requires a shift from a structural perspective to a more species-specific functional measure to account for the behavior of organisms. Least-cost modeling is a widely used approach for measuring functional connectivity that includes both landscape structure and behavioral aspects of the organism (Adriaensen et al. 2003). These models identify the shortest path which requires the least ‘cost’ for an animal to move between two patches (Beier et al. 2008) and have been applied to a number of species (Theobald 2006). The habitat patches are assigned a cost based on the sum of hypothetical energy expenditures, mortality risks, or other facilitating or hindering effects of landscape elements (Adriaensen et al. 2003). Individuals are then assumed to travel the path of least resistance or cost. Although all patches may be included in the analysis, the least-cost value represented in the model is only based on the cost to the nearest patch and other patches at higher effective distances are not included.

Little is published on the fundamentals and ecological assumptions underlying the use of least-cost analyses for modeling functional connectivity (Adriaensen et al. 2003; Beier et al. 2009). This method is often based on assumptions concerning animal movement that rely on expert opinion rather than empirical data (Beier et al. 2008). It also assumes that animals will choose the single optimum least-cost path or a single series of cells which resulted in the lowest cost value (Pinto and Keitt 2009). This creates important challenges as alternative paths with similar cost values that are important for connectivity are disregarded in the analysis.

An alternative to cost-distance modeling is to quantify connectivity using individual-based movement models (IBMMs). IBMMs adopt the Lagrangian approach developed as early as the 1960s, and were designed to incorporate observed or experimental data into simulation models (e.g., Revilla et al. 2004). The use of IBMMs such as correlated random walks (e.g., Barton et al. 2009) appears to be highly effective for quantifying movement processes. However, these models are mostly used for fine-scale analyses, as few studies have used IBMMs for predicting large-scale animal movements according to Turchin (1998), particularly for long-range movements by vertebrates (Koenig et al. 1996; except see: Boone and Hunter 1996 and Bergman et al. 2000).

Recently, a limited number of studies have used various simulation models combined with empirical data on larger, wide-ranging vertebrates (e.g., Forester et al. 2007; Fryxell et al. 2008). Some ecologists have even taken the concept of IBMMs further [Fortin et al. (2005), followed by Coulon et al. (2008)] and developed a statistical approach to these models, using probabilistic behavioral rules known as a step selection function. The challenge with these methods is collecting large amounts of empirical data, and they are generally used to predict movements at a finer scale rather than long range movements such as dispersal and migration (Fortin et al. 2005).

One method that offers particular promise for measuring functional connectivity is graph theory, which represents an intermediate approach for quantifying animal movement, in terms of data requirements and model complexity. Graph theory combines habitat data derived from a GIS with species-specific (or even potentially sex- or age-specific) movement data, and has been widely used to represent a landscape as a network of functionally interconnected habitat patches (Bunn et al. 2000; Urban and Keitt 2001; Pascual-Hortal and Saura 2008). This approach is particularly useful for dealing with complex ecological landscapes at broader scales, providing a reasonably detailed picture of potential connectivity for dispersing individuals. As a result, graph theory has been applied to numerous species on varying types of landscapes (Urban et al. 2009 for examples).

A graph can be characterized by two basic elements: the habitat patches or nodes and a set of connections or edges representing the potential for individuals to move between nodes. A path in a graph is a unique sequence of nodes, which may correspond to a habitat corridor. The nodes in the graph are typically binary depictions of habitat. However, they can also be identified probabilistically with a resource selection function (RSF; Manly et al. 2002) which could be considered an alternative data-based method to parameterize the model (Chetkiewicz et al. 2006). The inverse of the RSF (i.e., 1/RSF) can then be used to develop the cost or resistance surface. According to Zeller et al. (2012), quantifying resistance surfaces using an RSF can be a highly effective method for modeling connectivity and identifying habitat corridors. The links between nodes are typically obtained as Euclidean or least-cost distances, and potential connections between all pairwise combinations of habitat patches are established by considering the dispersal ability of the focal species at multiple scales (Pascual-Hortal and Saura 2006). By combining graph theory with RSF models, a more accurate representation of potential connectivity across the entire landscape (including the matrix) is achieved, offering considerable advantages over modeling approaches previously described.

2.5 Habitat selection and movement processes

Habitat selection is considered to be the behavioral process whereby an animal chooses which habitat or habitat components (i.e., resources) to use (Johnson 1980) disproportionately to the habitats that are available (Manly et al. 2002). Habitat selection is a decision-making process as individuals are confronted with choices in terms of habitat quality and the costs and benefits of acquiring and retaining space (Kennedy and Gray 1994). These choices occur within a spatial scale hierarchy (Table 2.1), and are affected by quantitative (i.e., spatial scale) and qualitative (i.e., types of spatial features) aspects of movement.

Table 2.1. Movement and habitat selection processes according to a spatial scale hierarchy (adapted from Johnson 1980 and Ims 1995; Chetkiewicz et al. 2006).

Spatial scale	Movement type	Habitat selection	Spatial structure
Resource patch	Searching (foraging) for resources	Selection of resources within a habitat patch (fourth order)	• Resource distribution • Food patch shape and size
Habitat patch	Searching for habitat patches; territory patrolling	Selection of habitat patches within a home range (third order)	• Food patch configuration • Shelter • Abiotic factors and topography
Matrix and habitat linkages (landscape)	Dispersal	Selection of a home range (second order)	• Patch parameters (e.g. size, shape) • Landscape parameters (connectivity, dispersal)
Region	Migration	Physical or geographical range	• Large-scale topography • Large-scale barriers

Movements at various scales are also affected by the internal state of the animal (e.g., motivation, nutritional condition) and influenced by sex and age-dependent factors (Ims 1995). All of these types of movements – foraging, patch searching, migration and dispersal can occur within habitat corridors (Bennett 2003; Gilbert-Norton et al. 2010), as well as for reproduction (Sieving et al. 2000; Brook 2010). For example, daily or regular movements such as foraging and patch searching typically occur when individuals either shelter or breed in one habitat and forage in another (Bennett 2003). Such movements are often exhibited by wide-ranging animals (Beier 1993). Migratory movements of wide-ranging animals may also be assisted by habitat corridors as some species typically follow well-defined routes that are characterized by connective habitats (Sawyer et al. 2009). However, many migratory animals generally travel through a range of habitat types and do not necessarily require habitat corridors (Bennett 2003). The use of habitat corridors for dispersal is considered to be most important (reviewed by Vos et al. 2002). Dispersal movements between populations have significant consequences for interpopulation gene flow (Slatkin 1987), population dynamics (Schwartz et al. 2002), the distribution and abundance of species (Clobert et al. 2001) and disease transmission (Long et al. 2005; Oyer et al. 2007). Dispersal may also facilitate range expansion (Swenson et al. 1998).

2.6 Causes and consequences of dispersal

Dispersal is a strategy to increase individual fitness in heterogeneous landscapes by changing the environment in which an individual lives, and has important implications for populations through genetic exchange (e.g., Coulon et al. 2004; Vander Wal et al. 2012). Dispersal is considered to be a permanent one-way movement of an individual from natal range or territory to adult range (Bullock et al. 2002), and may be voluntary or enforced, as well as environmentally determined or innate (Howard 1960). These permanent movements are hypothesized to be a mechanism to minimize inbreeding, reduce competition for resources or mates, or a combination of both (Proctor et al. 2004). Dispersal consists of three components: (*i*) leaving the natal site or social group (emigration), (*ii*) movement through unfamiliar ecological landscapes, and (*iii*) arrival into a new home range or social group (immigration; Wolff 1994). Dispersal can be influenced by a variety of factors including landscape structure and habitat quality (Long et al. 2005).

Dispersal movements are often highly variable among species, sex, age and location (e.g., Smith and Anderson 2001; Nixon et al. 2007). Experimental studies have also shown a positive density-dependant relationship, where an increase in population density can be an important driving force in dispersal for many taxa (e.g., insects: Otronen and Hanski 1983, vertebrates: Léna et al. 1998). Regardless of the main function for dispersal, significant costs are incurred by dispersing individuals, such as reduced survival and/or reproductive success while moving through unfamiliar territory (Wolff 1994). For most species, the costs and benefits of dispersal will vary according to how they interact with the environment, the scale of movement, and differences in life history characteristics, particularly between ages and sexes (Julliard 2000; Bowler and Benton 2005).

Many species exhibit age- and sex-specific differences in dispersal behavior where juvenile and sub-adult males are more likely to disperse among mammals (Cockburn 1992; Wolff 1993; Wolff 1994), and females are more likely to disperse among birds (Greenwood 1980). Differences in movement between sexes in mammals are expected because of sex-specific life strategies. Avoidance of both inbreeding and kin competition particularly among males has been implicated as most important in determining these strategies (Motro 1991). Dispersal in mammals may also be exhibited by females, although dispersal rates are generally lower as females tend to be philopatric. Philopatry among females can be defined as the tendency of an individual to return to or stay near their natal and breeding site or group, facilitating the evolution of altruistic traits among close relatives (Greenwood 1980). It is generally thought that females benefit from close association with female kin (Pusey 1980; Holekamp and Sherman 1989). In addition, females of some species such as elk (*Cervus canadensis*) tolerate female over male offspring from previous years (Clutton-Brock et al. 1982), which also tends to lead to dispersal in juvenile males. The consequence of female philopatry is that males must disperse to avoid inbreeding with their mothers or other female relatives. In summary:

female lactation → polygynous fathers → wandering strategy and/or intense male-male competition → short tenure of dominance (or in residence) → female philopatry → male inbreeding avoidance → male-biased dispersal (adapted from Wolff 1994).

It has been recognized that dispersal is of central importance to population biology and conservation (Long et al. 2005; Trakhtenbrot et al. 2005). However, limited empirical knowledge exists regarding dispersal behavior (particularly through habitat corridors) and the influence that habitat fragmentation has on dispersal, especially for vertebrates (Koenig et al. 1996). This is partly due to logistical difficulties in collecting data on movement paths of dispersing animals (Bennetts 2001). Furthermore little is known regarding the negative consequences of dispersal in potentially facilitating disease spread between populations or between species (Hansson 1992). Increased movement within corridors can increase disease spread between populations (Andreasen and Christiansen 1989), which ultimately puts species conservation at risk due to the direct disease impacts on animal health and unsustainable hunting. The ability to predict dispersal movements across a human-dominated landscape depends not only on the configuration of the landscape but also the risk of predation which has important implications for animal distribution and survival (Geist 2002; Mitchell and Lima 2002; Bowler and Benton 2005).

2.7 Role of natural predators and hunters

Animals must adopt behavioral strategies to trade off forage against the risk of predation and hunting mortality. As such, these trade-offs fundamentally drive the movement of many animals (Hebblewhite and Merrill 2009). Incorporating predation and hunter risk in modeling is therefore important and should be considered when examining and predicting animal movements in hunted populations (Ruckelshaus et al. 1997; Bowler and Benton 2005; Hebblewhite and Merrill 2009). Natural predation and hunting is often the major cause of differences in survival between dispersers and philopatric individuals (Gaines and McClenaghan 1980). The risk of mortality is also greater for dispersers due to greater activity rates and use of less familiar and lower-quality habitats (e.g., Yoder et al. 2004; Johnson et al. 2009). Such landscape-level risks not only affect the dynamics of animal populations through direct losses to predators or hunters, but may also indirectly affect the behavior and distribution of animals.

In order to reduce predation and/or hunter risk, prey respond either physiologically or behaviorally to decrease the probabilities of encounter, attack and capture (Lima and Dill 1990). Some behavioral responses include changes in resource selection (Darimont et al. 2009; Hebblewhite and Merrill 2009), increased vigilance (Liley and Creel 2008), reduced foraging time (Lima and Bednekoff 1999; Abramsky et al. 2002), grouping behavior (Creel and Winnie 2005; Gude et al. 2006; Proffitt et al. 2009) and reduced movement (Sih and McCarthy 2002). Population-level consequences associated with these responses may include reduction in survival, growth and reproduction (Lima 1998). However natural predation for example, can also have important long-term benefits for wildlife. Benefits may include stabilizing prey population dynamics (Halpern et al. 2005) and removing animals such as the weak and old, thereby reducing the incidence of the reproduction of genetically inferior individuals (Kramm 1975). Natural predators can even act as barrier to disease spread (i.e. the healthy herds hypothesis; Duffy et al. 2011).

When predation risk effects are considered in studies, behavioral responses are often analyzed between natural predators and their prey (e.g., Fortin et al. 2005; Hebblewhite and Merrill 2009; Fortin et al. 2009) and the effects of human predators (i.e. hunters) are often ignored, particularly in ungulate studies. In fact, the major source of predation upon ungulates such as elk (*Cervus canadensis*) and white-tailed deer (*Odocoileus virginianus*) in many parts of their current distribution comes from hunting rather than natural predators (Hayes et al. 2002; Collins and Kays 2011; Ciuti et al. 2012). For example, in southern Montana, Gude et al. (2006) and Proffitt et al. (2009) quantified the effects of wolf predation on elk behavior and distribution in the context of other influential variables such as hunting. They found that elk group size and distribution were more strongly influenced by hunting compared with wolves.

Understanding the effects of hunting on populations has important management and conservation implications, which are especially important in human-dominated landscapes (Baldus et al. 2008; Organ et al. 2010; Webb et al. 2011; Ciuti et al. 2012). The ecological consequences of hunting animals vary across the landscape and studies have shown that hunting effects can be spatially uneven among populations due to the structural complexity of the landscape (e.g., Lyon and Burcham 1998). Hunting may also be uneven due to particular management decisions that often target hunter effort to specific sex- and age-classes. This can have important consequences for the dynamics of wildlife populations and individual behavior (Lindsey et al. 2007; Baldus et al. 2008; Organ et al. 2010).

Most management-oriented research has traditionally focused on the evolutionary consequences of selective hunting on the dynamics of wildlife, which can alter selective pressures and gene frequencies of populations and cause overexploitation (Ginsberg and Milner-Gulland 1994; Coltman et al. 2003; Langvatn and Loison 1999). For example, hunting of the largest male animals results in selection for smaller body size (Coltman et al. 2003) which can lead to a selective advantage for smaller individuals, and a sex ratio biased in favor of females

(Ginsberg and Milner-Gulland 1994; Laurian et al. 2000). However, relatively few studies have considered the indirect effects of hunting on animal movement and resource selection.

Many species will alter their use of habitats in response to hunting, trading a reduction in forage quality or quantity for increased security which in turn can reduce fitness. For example, elk in Alberta shifted away from nutritionally-favorable grassy meadows to forests during the hunting season resulting in a significant change in diet, and then reverted back to grazing in meadows in the absence of hunters (Morgantini and Hudson 1985). Swenson (1982) and Kufeld et al. (1988) also found that hunting caused mule deer (*O. hemionus*) to alter their movement into habitats with more adequate cover. Environmental factors such as roads can also influence animal movement and hunter success during the hunting season (e.g., Gratson and Whitman 2000; Hayes et al. 2002). However, few studies have considered the interacting effects of multiple factors (e.g., forest, road density, cropland and water cover) across a landscape during the hunting season (McCorquodale et al. 2003; Webb et al. 2011).

Behavioral responses may also differ among individuals depending on age and sex (McCorquodale 2003), and therefore individuals may experience dissimilar trade-offs that could result in different behaviors when disturbed (Main and Coblentz 1996; Mysterud et al. 2005). For example, Neumann et al. (2009) found that male moose (*Alces alces*) were more engaged in rutting activity during the hunting season compared with females. Individual males barely responded to other types of stimuli, which in turn can make them more vulnerable to human hunters. Risk-driven shifts in resource selection by female ungulates during the hunting season have been examined in several systems (Burcham et al. 1999; Conner et al. 2001; Vieira et al. 2003). However, the effect of hunting pressure on male resource selection and associated comparison with females remains largely unexplored.

In addition to understanding the spatial distribution of animals during the hunting season, knowing the distribution of hunter-kill sites across a landscape is equally important. Few studies have considered the risks of mortality in relation to landscape features between sexes during the hunting season, which can have important implications for conservation and management. McCorquodale et al. (2003) revealed differences in survival rates between sexes for elk during the hunting season. However, mortality risks across the landscape were not compared between sexes and instead were modeled for males only or combined for both sexes. As such, defining the spatial shifts in resource selection and the risks of mortality, especially during the hunting season remains a critical area of study in human-wildlife interactions. Particularly for a population with disease in regions where hunting is a major source of mortality for wildlife (Ericsson and Wallin 2001; Hayes et al. 2002; Collins and Kays 2011).

The influence of natural predation and human hunting are factors that may affect patterns of disease emergence and persistence in wild populations (Holt and Manojit 2007; Duffy et al. 2011) and should be considered when devising strategies for disease control (Wild et al. 2011). However, few studies have considered the implications of hunting for managing disease risk in wild populations. Although hunting has been applied in different ways during attempts to manage or eradicate wildlife diseases (e.g., Schmitt et al. 2002), it is often done in a coarse approach such as by culling overall populations, with no distinctions between sexes, ages, or specific locations. However such policies have been shown to be inefficient in many situations (Donnelly et al. 2003; Woodroffe et al. 2004, 2009). It is increasingly being recognized that disease is not distributed evenly in populations (e.g., Schmitt et al. 2002; Härkönen et al. 2007; Shury and Bergeson 2011). Therefore, management actions should be aimed at specific sex/age classes with the highest prevalence of disease and greatest potential for transmission. As such, understanding ways that hunting can be used to sustainably manage wildlife populations with disease remains largely unexplored.

2.8 Elk and disease in a fragmented landscape

Large mammals such as elk (*Cervus canadensis*) on the Canadian prairies are an important component in the functioning of ecosystem processes such as modifying plant communities (Kie et al. 2003), and as food for large predators such as wolves (Carbyn 1983; Ripple and Larsen 2000). Moreover, they are considered a keystone species and highly valued by hunters and eco-tourists. Prior to European settlement in the 1800s, elk were the most widespread cervid in North America (O’Gara and Dundas 2002). However, due to human activities such as agriculture, settlement, logging and uncontrolled hunting, the range of elk populations on the prairie-parklands contracted dramatically. Remnant herds of elk are found in Riding Mountain National Park (RMNP), Manitoba, Duck Mountain Provincial Park and Forest (DMPP&F), and west across Saskatchewan. Elk are closely associated with these protected areas. However, they often move across park boundaries and likely benefit from the surrounding agricultural land (e.g., agricultural crops; Brook 2008; Brook and McLachlan 2009; Chranowski 2009) and predator control by farmers (Stronen et al. 2007).

Elk are capable of long-distance dispersal in this region; however, the anthropogenically fragmented landscape that exists between the protected areas largely prevents these events from occurring. Nonetheless, there are indeed local and landscape-scale risks associated with elk movements such as disease spread across fragmented landscapes. Diseases are a result of the interactive process between a host, an agent and the environment (disease triangle; Wobeser 2006). However, few studies have examined the underlying processes of disease spread such as host ecology, and how this may influence the emergence and re-emergence of disease (Plowright et al. 2008). As such, the ecology of disease within metapopulations remains poorly understood (Delahay et al. 2009).

Bovine tuberculosis (TB), caused by the bacterium *Mycobacterium bovis*, is a zoonotic disease that has been extensively documented in both captive and free-ranging wildlife populations throughout North America. It is a chronic disease of cattle with important national and international trade implications. Eradication of the disease has often been impeded by the presence of TB in free-ranging wildlife (Wobeser 2009), including cervids (Brook and McLachlan 2009), badgers (Woodroffe et al. 2009) and possums (Ramsey and Efford 2010). Bovine TB is a contagious disease caused by infection in the lymph nodes that spreads to other organs such as the lungs and tonsils. Transmission of TB among livestock and wildlife can be airborne, as animals can infect one another directly by breathing, sneezing or coughing the bacteria (Garnett et al. 2002). Transmission may also be indirect through shared contaminated feeds, water, or pasture (Hutchings and Harris 1997; Phillips et al. 2003). The risks associated with TB between cattle and wildlife have largely been identified using conventional epidemiological models (e.g., Pillai et al. 2000; Smith 2001), but there is a growing recognition of the value of more interdisciplinary approaches (Brook and McLachlan 2009, Brook et al. 2012).

In Manitoba, there were five outbreaks of TB affecting cattle herds in Manitoba between 1991-2003 (Nishi et al. 2006). After the second outbreak in 1997, it was suspected that wild elk could be the source of TB, and it was not until 2001 that authorities assumed that elk were acting as TB reservoirs. Since 1991, TB-infected elk (n = 41), white-tailed deer (n = 11) and cattle (n = 14 herds) have been identified (Brook and McLachlan 2009; Shury and Bergeson 2011). Whole cattle herd depopulation is required by the Canadian Food Inspection Agency when individual cattle test positive for the disease. This is due to the difficulties in correctly identifying infected individuals using existing live animal tests and the slow progression of the disease. Currently, there is no effective treatment for individual infected cattle. In southwestern Manitoba, elk are assumed to be a primary reservoir host for TB in and around RMNP, and this poses great challenges for the management of elk and their interactions with cattle farms (Brook and McLachlan 2009; Brook et al. 2012).

In addition to TB, chronic wasting disease (CWD), an emerging prion disease in captive and wild cervids across the Canadian prairies, has become a significant issue in the past 15 years. It is a highly contagious neurodegenerative disease that is fatal to elk, white-tailed deer, mule deer and moose (*Alces alces*; Williams 2005; Saunders et al. 2012). The origins and evolutionary history of CWD are unclear, but uncontrolled epidemics have the potential to depress cervid populations (Gross and Miller 2001; Williams et al. 2002). This newly emerging neurological disease in Canada has infected 66 captive cervid populations resulting in depopulation (Belcher and Lokken 2008; Bollinger et al. 2004, Saskatchewan Ministry of Agriculture, unpublished data). Currently, there is no economical or efficacious treatment for individual infected cervids, and the disease has been fatal in all cases. Transmission of CWD prions may be intra- or inter-specific, and can occur by close contact through saliva and blood, or by environmental contamination through urine and feces (Williams et al. 2002). CWD prions can persist in the environment for at least for two years (Miller and Williams 2004) and likely longer.

Free-ranging cervids are endemic with CWD in pockets throughout Saskatchewan and eastern Alberta, and 15 US states. In Saskatchewan, CWD has been identified in 280 mule deer, 66 white-tailed deer, 4 elk and 66 cervid captive facilities (Canadian Cooperative Wildlife Health Centre, unpublished data, Bollinger et al. 2004, Saskatchewan Ministry of Agriculture, unpublished data). Low prevalence levels of CWD are common in wild elk populations. However, the disease has been reported as high as 11% in elk in Rocky Mountain National Park in Colorado (Sargeant et al. 2011), and as high as 100% in captive elk in Saskatchewan (Argue et al. 2007). The risks and implications of CWD transmission among and within cervid populations in Saskatchewan and Manitoba are of very high conservation and economic concern (Spraker et al. 1997). CWD-infected wild elk have been found as close as 160 km from the Manitoba/Saskatchewan border. A detailed understanding of areas that may facilitate elk and other species across the prairie-parkland ecosystem is therefore critical for effective monitoring and management of this rapidly emerging disease.

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CHAPTER 3: DYSFUNCTIONAL CONNECTIVITY FOR ELK (*CERVUS CANADENSIS MANITOBENSIS*) IN AN AGRICULTURE-DOMINATED LANDSCAPE: IMPLICATIONS FOR BALANCING DISEASE RISKS WITH CONSERVATION BENEFITS

3.1 Abstract

Understanding the link between animal distribution and landscape structure remains a central theme of ecological research. Connectivity of habitats is a major determinant of animal distribution, and the potential for habitat corridors as a conservation tool to facilitate wildlife movement through landscapes is widely recognized. Yet, corridors may have unanticipated negative consequences such as facilitating the spread of disease. I integrated inverse resource selection functions as cost movement surfaces with graph theory to objectively predict critical areas for long-distance dispersal movements by non-migratory elk (*Cervus canadensis manitobensis*) and consequently landscape-level disease risk. The landscape of southwestern Manitoba, Canada, has been fragmented by agriculture and settlement and is known to impede gene flow among elk sub-populations, as long-distance movements by elk are presumed to be rare between protected areas. I tested the hypothesis of low connectivity among protected areas using collared locations of 53 free-ranging elk (n = 40 adult females, n = 13 juvenile males). I confirmed that the overall functional connectivity is low for both sexes; however, greater connectivity exists for adult females compared with juvenile males (16% of habitat areas had a very high importance to overall connectivity for females compared with only 10% for males). Adult males rarely left protected areas, with < 1% of locations on the surrounding agriculture lands. This indicates the human-dominated agricultural matrix that separates protected areas acts a selective filter, i.e., is more permeable for adult females than juvenile and adult males. Given the existing sub-population structure of elk and the high degree to which the landscape impedes long-distance movement for all elk classes, the potential risk of bovine tuberculosis (*Mycobacterium bovis)* and chronic wasting disease spread is limited. However, extensive movements are known to occur, as three VHF-collared juvenile males and one VHF-collared adult female dispersed in southwestern Manitoba. Therefore, the socioeconomic and ecological implications associated with these diseases remain significant for elk. This research indicates that dysfunctional connectivity can help limit the spread of disease in wildlife, however the

implications for long-term conservation of connected populations across the prairie-parkland interface remain an important concern.

3.2 Introduction

Dramatic changes to natural landscapes, especially habitat loss and fragmentation associated with human activities, are central problems in wildlife conservation and disease management (Bennett 2003; Benton 2003). As remnants of the natural environment increasingly occur as fragmented patches embedded within a matrix of human-created habitat, the maintenance or establishment of linkages such as habitat corridors between natural areas have become an important conservation tool (Bennett 1990; Hobbs 1992; Dobson et al. 1997). Linkages that connect habitat patches are intended to facilitate wildlife movement such as dispersal among otherwise-isolated populations, thereby maintaining genetic integrity (Beier and Noss 1998; Fahrig and Merriam 1994; Hodgson et al. 2011). Other conservation benefits include retaining ecological processes such as nutrient cycling (Bennett 2003; Hilty et al. 2006) and accommodating range shifts due to climate change (Opdam and Wascher 2004). However, the effectiveness of habitat corridors remains ambiguous (Simberloff and Cox 1987; Dunning et al. 1992) as unanticipated consequences such as disease spread may occur (Simberloff and Cox 1987; Simberloff et al. 1992; Hess 1994; Bennett 2003). Such an effect puts species conservation at risk and could completely undermine the initial goal of habitat corridors to facilitate animal movements (Hess 1996). Nevertheless, few studies have considered the spatial arrangement of habitat patches and connectivity of populations in facilitating disease spread (Hess 1996; McCallum and Dobson 2002).

Disease is an important consideration in conservation efforts (e.g., Scott 1988; Cohn 1991; McCallum and Dobson 1995; Smith et al. 2006). As the landscape becomes fragmented into smaller, more isolated areas, many wildlife species remain within protected areas, which can increase both the occurrence and the transmission rate of the disease among resident groups (Vander Wal et al. 2012). However, the spread of disease occurs over multiple spatial scales (Cross et al. 2005), as many wide-ranging species such as white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*) frequently make use of the human-modified areas adjacent to protected areas, these areas being defined here as the matrix. Indeed, the risk of disease transmission is not only determined by individual movement, but the habitat connectivity that exists among sub-populations that may facilitate dispersal and consequently disease spread

(Cross et al. 2009; Cullingham et al. 2011; Vander Wal et al. 2012). It has been suggested that disease should not be considered a determining factor in habitat corridor management (McCallum and Dobson 2002). However, due to the presence of endemic and emerging diseases globally that have serious social and economic implications, the role of corridors in facilitating disease transmission should not be overlooked. As such, management is faced with having to balance the risk of disease spread with the conservation benefits of increased gene flow through connecting habitats.

Functional connectivity is referred to as “the degree to which the landscape facilitates or impedes movement among resource patches” (*sensu* Taylor et al. 1993), which is associated with the ease of movement such as dispersal (Bélisle 2005). This concept consists of a structural component, determined by the spatial arrangement of habitat patches (With et al. 1997; Tischendorf and Fahrig 2000). There is also a functional component, referring to the organism’s behavioral response to the structure of the landscape and, more specifically, how the organism perceives and responds to fragmented habitats (Bélisle 2005). There is now a general recognition that modeling functional connectivity should be based on a more detailed understanding of animal movement (With et al. 1997; Bélisle 2005; Goodwin 2003), and incorporating the matrix’s characteristics is increasingly being acknowledged (Pita et al. 2007; Franklin and Lindenmayer 2009).

The integration of resource selection functions (RSFs) with graph theory offers a powerful and effective approach to quantifying whole landscapes in terms of functional connectivity. The main advantage of employing RSFs is that they rely on species and landscape-specific empirical data, and can be used to characterize differences in selection between sexes which is important for species that exhibit ecological segregation [sexual differences in diet and habitat selection combined (Ruckstuhl and Clutton-Brock 2005)] and sexual segregation (Clutton-Brock et al. 1982; Bowyer 2004). Sex-based differences in connectivity are also particularly important with respect to disease, as the prevalence of diseases vary among sex and age classes, creating important challenges for managing disease spread among populations (Härkönen et al. 2007; Shury and Bergeson 2011; Saunders et al. 2012). RSFs can then be applied to a graph analysis which can be used to quantify multiple connective linkages that contribute to connectivity (Urban and Keitt 2001; Pinto and Keitt 2009; Urban et al. 2009). Graph theory bridges the gap between the structural aspects of the landscape and the behavioral responses of organisms such as dispersal characteristics, offering great potential for use within a metapopulation context (Bunn et al. 2000).

Here, I quantified functional connectivity for male and female non-migratory elk in a system where diseases with socioeconomic implications threaten resident ungulates in southwestern Manitoba, Canada. Specifically, I integrated resource selection with graph theory analyses to identify critical areas for elk movement and assess the landscape-level risk of disease spread between elk sub-populations through a matrix known to impede gene flow (Vander Wal et al. 2012). My objectives were to (*i*) identify key landscape covariates that influence sex-specific elk movement across an agriculture-dominated landscape, (*ii*) develop a predictive graph model for males and females separately to compare the inter-sexual differences in functional habitat connectivity, (*iii*) identify potential habitat corridors across the landscape, and (*iv*) infer the implications of a fragmented landscape for balancing objectives for elk conservation and disease risk.

3.3 Study area

The study area encompasses 4,500 km² of an agriculture-dominated landscape that extends from the northern border of Riding Mountain National Park (RMNP; 2,974 km^2; 50°51’50”N, 100°02’10”W) to the southern border of Duck Mountain Provincial Park and Forest (DMPP&F; 3,756 km^2; 51°39’58”N, 100°54’52”W). The area also extends west to the Manitoba-Saskatchewan border in southwestern Manitoba, Canada (Fig. 3.2). This area is characterized by an expansive transition zone between the southern Prairie ecozone and the northern Boreal Plain ecozone in southwestern Manitoba, Canada (Bailey 1968; Wiken 1986). Before the 1880s, the intermountain area was dominated by more extensive forest cover; however, human activities such as settlement, logging and agricultural expansion have significantly altered the landscape leaving <14% overall forest cover (Walker 2001). The remnant-fragmented patches of deciduous forest are composed of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*). The area also consists of rough fescue grasslands, wetlands and lakes. Fully 70% of the surrounding agricultural landscape is privately owned farmland (dominated by oilseed and cereal crop, pasture and hay production), 18% provincial crown land, 11% federal crown land and 1% Aboriginal reserve lands (Brook 2008). The landscape was divided into 0.65 km^2 quarter section units of land by the Dominion Land

Survey System (Richtik 1975) for agriculture and other purposes. The area also consists of an extensive network of unpaved gravel roads and is bisected by one major paved provincial highway. A regional elk metapopulation of ca. 2700 elk exists in the region (Parks Canada, unpublished data, Manitoba Conservation unpublished data). Gene flow between elk sub-populations is restricted (Vander Wal et al. 2012) and elk remain primarily within or near the remnant forest-dominated parks (Brook 2008; Brook and McLachlan 2009; Chranowski 2009).

In the Riding Mountain region, habitat fragmentation and disease have caused considerable concern for the conservation of several wide-ranging species. Wild elk and white-tailed deer are endemic with bovine tuberculosis (*Mycobacterium bovis*, TB [Brook and McLachlan 2009; Shury and Bergeson 2011; Vander Wal et al. 2012]), and this has led to frequent calls for elk population eradication (Brook et al. 2012). Chronic wasting disease (CWD) is also of high local concern (Brook and McLachlan 2006), as it is emerging across the Canadian prairies in mule deer (*O. hemionus*), white-tailed deer and elk. CWD has not yet been detected in Manitoba, but the study area is directly adjacent to the province of Saskatchewan, which has endemic CWD in wildlife (280 mule deer, 66 white-tailed deer, and 4 elk), and ranched cervids (66 farms; Canadian Cooperative Wildlife Health Centre, unpublished data). Establishment of endemic CWD in Alberta in 2005 resulted from infected wildlife from Saskatchewan moving across the border, so the potential for transmission of CWD into the study area is of critical concern. The area along the provincial border and between RMNP and DMPP&F in particular has the potential to become an unprecedented focus for endemic and emerging wildlife disease in the study area, with critical socioeconomic and ecological implications.

3.4 Methods

3.4.1 Study animals

A total of 413 free-ranging elk was captured in and around RMNP and DMPP&F during the winter months (December to March, 2002-2011) using a net-gun fired from a helicopter (Cattet et al. 2004). Animals were fitted with a Global Positioning System (GPS) satellite collar (24 F, 12 M) or a very high frequency (VHF) radio collar or ear transmitter (191 F, 186 M). Elk were classified as adult female (≥2.5-year-old) or juvenile male (<4-year-old; Flook 1970; Noyes et al. 1996). Adult males (≥4-year-old) were not included in the analysis due to a limited sample size as they largely remained in protected areas and made very little use of the agriculture-dominated lands. Juvenile female elk were not examined because calves largely follow adult females and have the same selection patterns (Weckerly 1999). Spatial errors associated with the GPS collars (mean = 15 ± 6 m) were determined by placing the collars at fixed locations for several weeks and were considered small enough to not bias the movement analyses (Johnson and Gillingham 2008). GPS locations were obtained daily (mean= 12 locations per day ~2 hour intervals) for up to 2 years (Brook and McLachlan 2009; Brook 2010). All GPS locations were screened for large positional outliers and positions collected within 24 h of capture were excluded (Bjørneraas et al. 2010).

VHF locations were collected using fixed-wing aircraft and ground triangulation (average 3 locations every 2 weeks ± 1.4) for up to 3.5 years (Brook 2008; Vander Wal et al. 2011). The analyses were limited to the spring and summer (March - August), as most animal movements and dispersals outside of the parks occurred during this period (Brook 2008; Chranowski 2009). In addition, I only used collared animals with a home range that extended out of a protected area, as I was only interested in the individuals that made use of the agricultural matrix frequently. These criteria reduced the final sample size to a total of 53 free-ranging elk (*n* = 40 adult females, *n* = 13 juvenile males).

This work was approved by the University of Saskatchewan (#20060067) and University of Manitoba Animal Research Ethics board (#F01-037), and adhered to the Canadian Council on Animal Care (2003) for humane animal use. Other permits included Manitoba Conservation Wildlife Scientific Permit No. WSP 02001, Riding Mountain National Park Research/Collecting Permit No. RMNP-000321, and Riding Mountain National Park Environmental Assessment Screening Report No. #RMNP 000321.

3.4.2 Characterization of landscape covariates

A set of *a priori* landscape covariates predicted to influence elk resource selection during the spring and summer (March - August) were derived from the literature (Appendix A, Table A.1.) and measured at the scale of the quarter section unit (*n* = 7375). Land ownership and land management decisions are largely made at the scale of the individual quarter section within the study area. Habitat types hypothesized to be selected by elk included grasslands and deciduous forest [local-level forest cover (within the quarter section) and landscape-level forest cover (within a 5 km buffer around quarter section)]. Other types included annual cropland (oilseed and cereal crops), perennial forage (hay and alfalfa), water cover (lakes and rivers) and distance to streams. GIS habitat layers were validated during telemetry relocations and ground surveys, which indicated an overall accuracy of 84% of vegetation assignment (Appendix B, Table B.1). The majority of map-misclassification was due to changes in agricultural cropland which was to be expected as cropping patterns change over relatively small scales, however overall patterns remain largely consistent.

Unpaved road density and paved highways were also assessed as covariates, using detailed provincial GIS layers (Manitoba Transportation and Government Services 2002), that were validated in the field and corrected (Brook 2008). All covariates were assessed using ArcGIS 10 (ESRI Inc.) with a 30 m spatial resolution map that was developed using Landsat 5 satellite imagery collected in 2003 (Geobase: http://www.geobase.ca). Topographic features (i.e. slope and elevation) were evaluated as potential covariates, however preliminary analysis showed these to be largely homogenous with little variation across the study area; therefore they were not included in the model development. All covariates were screened for correlations using a Spearman's rank correlation matrix for all possible pairs, and all had a $r_s < 0.5$. Multicollinearity was also tested using a combination of variance inflation factors (VIF) and variable cluster analysis (package Design, Harrell 2001). Cropland cover was removed from the full model for juvenile males as it had a VIF > 5.

3.4.3 RSF model development

Sex-specific RSF models (Manly 2002) were developed using binary logistic regression with presence and absence of animals as the dependent variable derived from GPS and VHF collared-animals. Use and availability were based on comparisons of the habitat characteristics of individual quarter sections, wherein the number of randomly generated available quarter sections equalled the number of used sections (1:1 ratio) throughout the study area. As such, the analysis corresponded to that of second-order selection (Johnson 1980).

A set of candidate *a priori* models were selected to predict the probability of elk use on the agricultural matrix and assessed the fit of all models using Akaike's information criterion (AIC) adjusted for sample size (ΔAIC_c) and model weights (w_i). All *a priori* models were compared and ranked according to their ability to explain probability of elk use. A multi-model inference approach was also used based on all possible combinations of covariates, including 2-way interactions (Burnham and Anderson 2002; Whittingham et al. 2005). All models were ranked based on a combination of covariates with the lowest ΔAIC_c for model inference performed in the R environment for statistical computing (R Version 2.11, www.rproject.org) with the Multi-Model Inference package (R package 0.13.3, http://CRAN.R-project.org/package=MuMIn). Results from all models with $\Delta AICc < 2.0$ were used to derive model-averaged coefficients, β_i, and standard errors to estimate relative probability of elk use (Burnham and Anderson 2002). The predictive performance of the RSF models were evaluated using *k*-fold cross-validation (Boyce et al. 2002), where k-partitions of the dataset are made following a test to training ratio of five subsets. Predictive capacity of partitioned models was evaluated against the withheld training data using Spearman's Rank correlations (r_s) between training and test data grouped within ten bins. All statistical analyses were performed in R (R Development Core Team 2012).

3.4.4 Graph theory modeling

Graph theory is often applied in landscape ecology studies as it provides a method for unifying and evaluating multiple aspects of connectivity at various scales (Urban and Keitt 2001; Calabrese and Fagan 2004; Minor and Urban 2007). Graph theory is highly efficient for representing the landscape pattern as a network of functionally interconnected patches and performing complex analyses that determine proximal and higher order landscape connectivity (Bunn et al. 2000; Urban and Keitt 2001; Pascual-Hortal and Saura 2008). A landscape graph G is characterized by two basic elements: the habitat patches or nodes $n(G)$ and a set of connections or edges $e(G)$, such that each edge e_{ij} equals the n_i to n_j link, representing the potential for individuals to move between nodes. A path in a graph is a unique sequence of nodes. The distance of a path from n_i to $n_j, n_k, \ldots, n_n$ is measured by the sum of the edges within the path between nodes. A path may correspond to a habitat corridor as it may symbolize the probability of an individual to directly disperse between two nodes through a given landscape. I used the CONEFOR Sensinode 2.2 (CS22; Saura and Torné 2009) program (www.conefor.org) to quantify functional habitat connectivity. This program allows for the spatial arrangement of the habitat (structural connectivity), dispersal distances, and the behavioral responses of individuals to the physical structure of the landscape to be taken into account (Tischendorf and Fahrig 2000; Theobald 2006).

3.4.5 Connectivity analysis

Quarter section centroids were considered as the individual nodes of the network as elk can use every quarter section in the study area. The inverse of the RSF (i.e., 1/RSF) values were then used as attributes for the edges to generate a cost or 'resistance' surface using the intervening landscape elements as a surrogate for resistance to movement. Therefore, edges with a higher 1/RSF value represented a higher movement cost (i.e., more resistance) than those with lower 1/RSF values. In this context, the estimation of resistance represents the willingness of an organism to move through a particular environment. A low resistance denotes ease of movement. A high resistance denotes restricted movement, or is used to represent an absolute barrier to movement. The use of resistance surfaces is increasingly being used in landscape ecology, particularly in metapopulation and corridor studies to represent habitat connectivity (Zeller et al. 2012). The probability of direct dispersal among nodes (p_{ij}) was modeled as a decreasing negative exponential function of the internode edge-to-edge Euclidean path (e.g., Bunn et al. 2000; Urban and Keitt 2001; Saura and Pascual-Hortal 2007):

$$p_{ij} = e^{-k \cdot d_{ij}} \tag{1}$$

where d_{ij} is the sum of the inverse RSF values of each edge linking two nodes i and j, and k is a constant set to make the function match to the probability-dispersal distance values. To characterize the degree of connectivity across the landscape, I applied a probabilistic model to determine the importance of each node to the graph's area-weighted flux (AWF):

$$AWF = \sum_{i=l}^{n} \sum_{j=1, i \neq j}^{n} p_{ij} \cdot a_i \cdot a_j \tag{2}$$

where n is the total number of nodes in the landscape, p_{ij} is the probability of direct dispersal between nodes i and j, and a_i and a_j are the attributes of the nodes i and j. AWF has been described by Bunn et al. (2000) and Urban and Keitt (2001) and is equivalent to a landscape-level version of the incidence function model measures (e.g., Moilanen and Nieminen 2002; Verheyen et al. 2004).

The AWF connection index computed through CS22 requires a probability distance threshold value that corresponds to the maximum dispersal distance an organism might travel. The largest distance between VHF locations (*n* = 12 M, *n* = 17 F) within a two-year period was calculated in GIS and clustered into three groups for females and males using a *k-means* cluster analysis. Therefore, functional connectivity was modeled using three landscape scales for males (*d* = 11 km, *d* = 13 km, *d*= 22 km) and three for females: (*d* = 11 km, *d* = 15 km, *d* = 25 km), representing examples of how differing dispersal thresholds could potentially influence estimates of connectivity across the landscape. See Fig. 3.1 for an overall schematic outline of this analysis.

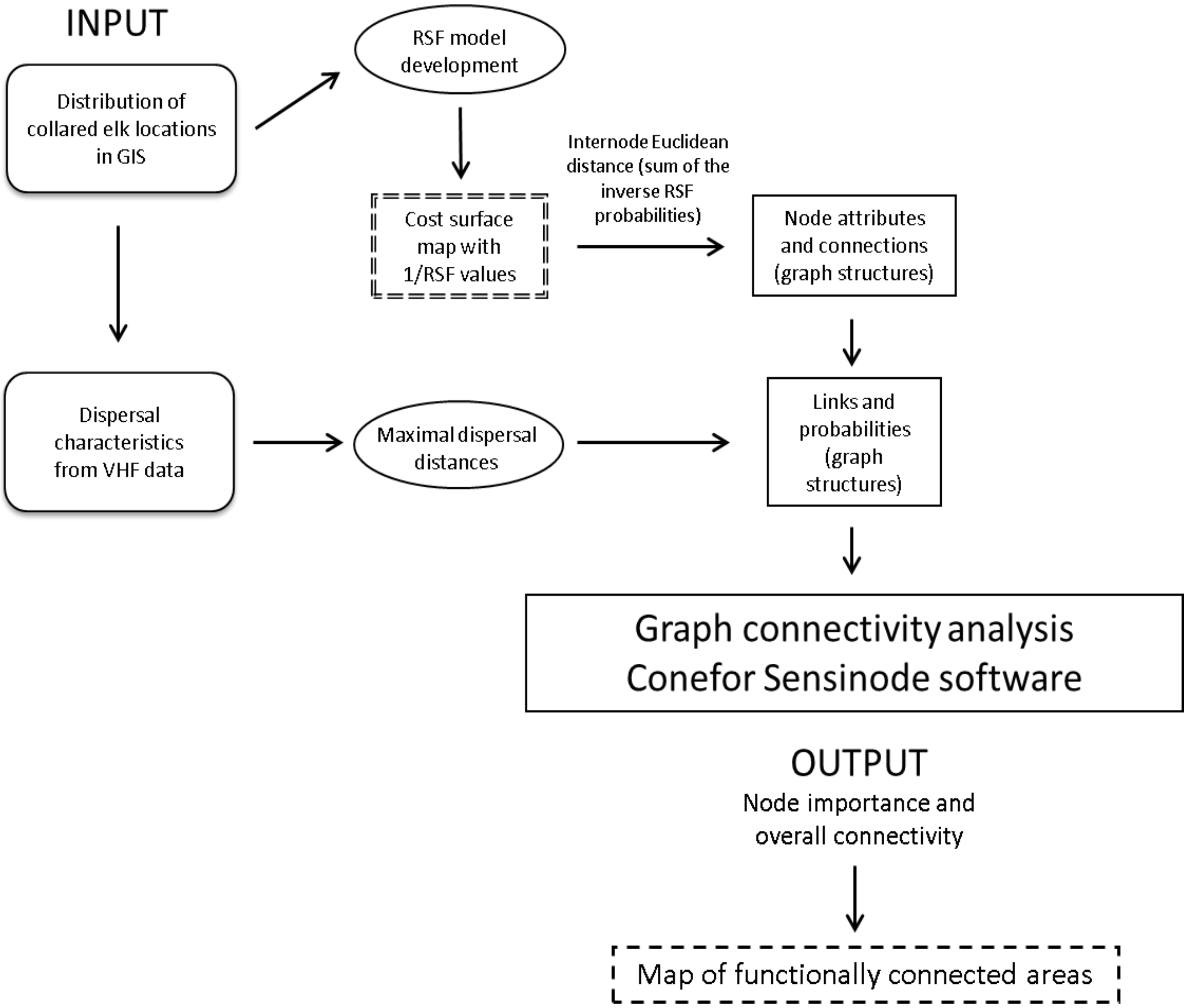

Figure 3.1. Methodological flow chart for connectivity analysis (adapted from Saura and Torné 2009).

3.5 Results

3.5.1 Elk dispersal and use of the agricultural matrix

During the spring and summer (Mar-Aug) from 2002-2011, 607-quarter sections were used by adult females, 106 by juvenile males, and 65 by adult males around RMNP and DMPP&F. All locations were compiled from a combination of GPS and VHF collared-animals. As such, adult females and juvenile males made frequent and regular use of the matrix, whereas adult males were rarely located outside of the protected areas. The majority of movements made by adult females and juvenile males into the matrix were short foray loops that extended out of the protected areas. However, three radio-collared juvenile males between 2004 -2009 dispersed 30 km from the northern border of RMNP to the southern border of DMPP&F, and one GPS collared adult female dispersed 30 km south of RMNP.

3.5.2 Resource selection functions

The elk RSF models revealed large differences in resource selection patterns between adult female and juvenile male elk. The analysis of candidate *a priori* models identified Model 1 ($AIC_w = 1.00$) to be the best model for predicting adult female resource selection, whereas Model 2 ($AIC_w = 0.50$) best predicted juvenile male resource selection (Table 3.1). Model-averaged results from all possible models revealed two models with a $\Delta\mathrm{AIC_c} < 2$ for adult females, and a total of 10 covariates retained in the top-ranked models. All covariates were found to be important (cumulative $w_i > 0.50$; Table 3.2). For juvenile males, 8 models with a $\Delta\mathrm{AIC_c} < 2$ were identified including 8 covariates retained in the top-ranked models. The most important covariates for juvenile male elk (cumulative $w_i > 0.50$) were grassland, and local- and landscape-level forest cover (Table 3.2). Overall, adult female elk avoided water and cropland cover, roads, wetlands and towns, and selected for forage, streams, grassland, and local- and landscape-level forest cover (Fig. 3.3). For juvenile males, water cover, streams and towns were avoided, whereas roads, wetlands, grassland, and local- and landscape-level forest cover were selected (Fig. 3.3). The predictive accuracy of the modeling results, assessed using hold-out data, was excellent for adult females ($r_s = 0.949$), but poorer for juvenile males ($\mathrm{r_s} = 0.579$).

3.5.3 Graph connectivity analysis

I simulated functional connectivity using three dispersal thresholds for juvenile males and three for adult females across the landscape (see Methods for details). The total contribution of individual nodes (n = 7375) to the connectivity network on the landscape was similar across all scales for both sexes. For juvenile males, the degree of connectivity remained relatively constant across all scales, with slightly higher valued nodes at d = 13km (Fig. 3.4A). At the maximal dispersal distance of 22 km (Fig. 3.4A; Fig. 3.5A), 53% of the nodes had a very low importance for connectivity (AWF < 0.02), and only 10% of nodes had high importance values (AWF ≥ 0.06). For adult females, connectivity across the landscape also remained relatively constant across all scales, but the landscape was slightly more connected at d = 25 km compared with the other two scales (d = 11 km, d = 15 km). At the maximal dispersal distance of 25 km (Fig. 3.4B; Fig. 3.5B), 64% of the nodes had a very low importance for connectivity (AWF < 0.02), whereas 16% of the nodes had high importance (AWF ≥ 0.06). Overall, there were 435 more nodes with higher importance (AWF ≥ 0.06) for adult females (d = 25 km) compared with juvenile males *(d* = 22 km). To test whether the overall connectivity of the landscape was indeed different between sexes, I estimated connectivity by regressing the AWF node values for juvenile males against adult females (Fig. 3.6; linear regression, n = 7375, R^2 = 0.449, P < 0.001). The regression revealed more nodes to have a higher connectivity value for adult females compared with juvenile males, indicating greater functional connectivity across the landscape for adult females compared with juvenile males.

3.6 Discussion

In this comparative study, dramatic differences were identified in how separate sex- and age-classes move through a fragmented agriculture-dominated landscape. An RSF-based graph theory analysis was used to quantify functional connectivity and the landscape was found to strongly influence female and male elk resource selection patterns in different ways. This study provides clear evidence of sex-based differences in connectivity and demonstrates that the overall connectivity of the fragmented landscape between RMNP and DMPP&F is greater for adult females compared with juvenile males. As such, I submit that each sex, particularly in an ungulate species that exhibits ecological (Bowyer 2004) and sexual segregation (Clutton-Brock et al. 1982; Ruckstuhl and Clutton-Brock 2005) should be considered separately when evaluating the role of habitat connectivity on movement patterns, to help focus conservation and disease management efforts more effectively. A small fraction (<1%) of collared adult male locations were found outside of protected areas; therefore, a quantitative analysis was not possible.

The persistence of many wildlife species in fragmented landscapes depends on the heterogeneity of the entire landscape including the composition and quality of the matrix separating large protected areas (Vandermeer and Perfecto 2007; Bennett et al. 2006; Brady et al. 2011). However, local and landscape-level factors that influence animal movement within the matrix are still poorly understood (Brady et al. 2011), and the risks associated with wildlife disease transmission remain largely unexplored. To devise effective conservation and management strategies for wildlife, multiple elements should be considered, such as the amount and configuration of habitat, matrix permeability, species' perceptions and dispersal behavior (Goodwin 2003; Bélisle 2005; Baguette and Van Dyck 2007). These factors must be integrated for a detailed understanding of disease ecology and the sex- and age-specific disease risk across a landscape. Indeed, this study demonstrates how graph theory can be used to incorporate a combination of such factors and that the matrix can be interpreted as anthropogenic filters for animal movement, and consequently, gene flow and pathogen transmission.

In the Riding Mountain region of Manitoba, agricultural expansion has fragmented the entire landscape outside of protected areas resulting in a mosaic of small, largely isolated patches of native deciduous forest and grassland (Walker 2001). Habitat fragmentation is widely recognized as one of the greatest threats to wildlife in Canada's national reserve networks (Parks Canada 2000; Coristine and Kerr 2011). However, some wildlife species such as wide-ranging ungulates can sometimes benefit from agricultural areas (Nixon et al. 2007; Brook 2008). White-tailed deer (*O. virginianus*) especially, are opportunistic foragers and highly adapted to agriculture-dominated landscapes (Côté et al. 2004). Results from the RSFs revealed selection for forest cover to be stronger for juvenile male elk and selection for grasslands to be stronger for adult females during spring and summer. The safety afforded to male elk in forests may be more important. Solitary males may perceive greater risk of predation from wolves (*Canis lupus*) or black bears (*Ursus americanus*) compared with more gregarious females that have increased predator detection and vigilance in open habitats (Delm 1990).

Using the RSF-informed graph theory analyses, I associated the nodes on the landscape with the highest importance to overall connectivity for both sexes (AWF ≥ 0.08) as potential habitat corridors. Although functional connectivity is greater for adult females, results indicate that females are largely constrained to the proximity of protected areas. Female elk use the matrix and fragmented corridors more so than juvenile and adult males, but there appears to be a threshold of movement for females, as the majority of their movements were within 15 km of the parks (i.e., mid-way between the parks). As such, the overall landscape (habitat corridor and surrounding matrix) clearly functions as an anthropogenic filter (differentially impedes movement) to long-distance movements for all sex- and age-classes of elk. The habitat corridors that exist seem to function as commuting not dispersal corridors (Jongman and Pungetti 2004), in that elk, especially females, only make daily movements into the corridors, rather than permanent one-way movements between protected areas. These movements are largely for breeding, resting and foraging for short periods of time, and dispersal events are rare.

Elk are considered highly mobile species (Kie et al. 2005), however the loss of habitat connectivity in the study area, especially over the last five decades (Walker 2001) has significantly influenced their capacity to disperse and interbreed between protected areas. Although juvenile male elk exhibit a greater biological propensity to disperse between protected areas compared with females (Cockburn 1992; Wolff 1994), dispersal events are rare in this area. Of the 413 elk marked with GPS and VHF radio-collars during the summer months, only three VHF-collared juvenile males dispersed 30 km from RMNP to DMPP&F between 2004 -2009. One VHF-collared adult female also dispersed 30 km south of RMNP during this time (Brook 2008; Vander Wal 2011). This reduced movement is likely a result of the combination of physiognomic features such as a dense network of roads, one paved highway with heavy traffic, and two highly fragmented habitat corridors. Intensive hunting pressure around the protected areas in the autumn and winter seasons further constrains elk to protected areas. Hunting is not evenly distributed across the surrounding matrix as the majority of animals are killed adjacent to the park borders. As such, the matrix may create a localized sink for elk, as mortality rates are much higher compared with inside the park. Intensely hunted areas that act as sinks for wildlife such as ungulates and carnivores around the peripheries of protected areas have been described by several authors (Woodroffe and Ginsberg 1998; Milner-Gulland et al. 2000; Robinson et al. 2008).

Although the current structural configuration of the landscape indicates some connectivity that may facilitate dispersal, the responses of individuals to the matrix suggest otherwise. The actual study of functional connectivity depends not only on structural connectivity but the perception and response of organisms to the landscape (Tischendorf and Fahrig 2000; Bélisle 2005). Most importantly, dispersal behavior is often considered the key process underlying this concept (Bélisle 2005; Baguette and Van Dyck 2007). As such, my findings, along with genetic dispersal estimates from elk in this area (Vander Wal et al. 2012) suggest that regional habitat connectivity on this landscape is dysfunctional for elk.

Genetic discontinuity is evident among elk sub-populations in the Riding Mountain region. Vander Wal et al. (2012) recently revealed three distinct genetic groups of elk, one in DMPP&F, and one in the east and west of RMNP. This indicates that if elk disperse between the sub-populations, the dispersers rarely successfully breed. In this region, elk are an endemic host of bovine tuberculosis (Lees 2004; Nishi et al. 2006), and most cases have been restricted to west RMNP (Nishi et al. 2006; Brook and McLachlan 2009; Shury and Bergeson 2011). However, given the degree to which the landscape impedes movement for both sexes and the frequency of dispersal rates between the parks, the potential risk of TB spread from RMNP to DMPP&F is limited (Vander Wal et al. 2012). However, only occasional long-distance movement is necessary to introduce a disease into a population. Indeed, three radio-collared juvenile male elk (including one TB-positive) dispersed from RMNP to DMPP&F; therefore, there remains a certain level of risk associated with these infrequent dispersal movements.

In addition to existing endemic disease concerns, my results have direct implications for emerging diseases in the region. The proximity of chronic wasting disease (CWD) infected elk in Saskatchewan and the looming concern for emergence into Manitoba elk populations presents a challenge. CWD is a fatal, highly infectious disease (*sensu* Williams 2005) that poses one of the greatest threats to the long-term persistence of viable and healthy cervid populations (Bollinger et al. 2004). Though CWD has been reported at lower prevalence levels relative to mule deer (*O. hemionus*) and white-tailed deer, prevalence is currently 10% in wild elk populations in Rocky Mountain National Park in Colorado and some areas in Wyoming (Saunders et al. 2012). Moreover, four wild elk in east-central SK have tested positive for the disease, only 160 km from the MB border (Bollinger and Zimmer 2012). These contemporary reports should therefore motivate increased interest about the implications of CWD spread for elk populations (Sargeant et al. 2011). Potential regional corridors that exist across the border may promote individual movement and consequently CWD, therefore representing a critical priority area for monitoring individual movement, particularly along the SK/MB border and between the protected areas. CWD has broad implications for the conservation and wildlife disease management (Spraker et al. 1997), and my findings exemplify that dysfunctional connectivity could to some degree lower the risk of disease emergence.

Conclusions

Integrating RSF models with graph theory analysis offers an effective framework in which functional landscape connectivity can be quantified from empirical information. This study indicates that the structural connectedness of a landscape plays an important role in determining sex- and age-based differences in movement responses. However, knowledge of individual dispersal patterns and confirmation from recent genetic estimates provides a stronger and more mechanistic understanding of connectivity, and ultimately the risk of disease spread. Moreover, the models highlight the need to make management decisions that reflect differences among sexes of a single species, as each sex and age class responded differently to landscape structure. These differences among classes are particularly important in disease management efforts as the diseases of concern are rarely evenly distributed in a population and prevalence is typically higher in older animals, especially males (Härkönen et al. 2007; Shury and Bergeson 2011; Saunders et al. 2012).

The disconnection of elk sub-populations between the protected areas suggests limited potential for long-distance spread of TB. However, the emergence of CWD poses a serious threat to elk in Manitoba, and if infected individuals move into Manitoba, results will be devastating to ungulate populations. Erring on the side of less connectedness is advisable for this system, particularly in areas that have been highlighted on the maps such as the fragmented corridors that exist between RMNP and DMPP&F, and along the SK/MB border. Facilitating long-distance movement of individuals by restoring existing habitat corridors is a conservation strategy that carries a high risk in the face of disease (Hess 1996). Conversely, promoting or restoring forested areas close to the park borders, away from habitat corridors and cattle would encourage daily movements outside of the parks, allowing animals to extend their home range.

Although dysfunctional connectivity may reduce the risk of disease spread, dispersal events are rare, and this has important long-term implications for the conservation of the Riding Mountain elk metapopulation. This region currently has large populations (each consistently

>1000 animals over the last 50 years), and strong population structures are more likely to maintain population viability and persistence (Gaggiotti 2003). However, it is reasonable to suspect possible loss of genetic diversity due to population isolation over time. Therefore genetic rescue by translocating individuals between the parks may be required, rather than promoting the increase of natural movement and consequently disease through habitat corridors.

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Table 3.1. Differences in Akaike information criterion ($\Delta AIC_c{}^a$), and AIC_c weights (w^b) for candidate RSF models during the spring and summer (Mar-Aug; 2002-2011) in southwestern Manitoba, Canada.

	Adult females		**Juvenile males**	
***A priori* models**	**$\Delta AIC_c{}^a$**	**$AIC_c w^b$**	**$\Delta AIC_c{}^a$**	**$AIC_c w^b$**
H_1 Forest + Forestbuff + Grassland + Road + Town + Crop + Water + Stream + Forage + Wetland	**0.00**	**1.00**	**--**	**--**
H_2 Forest + Forestbuff + Grassland	81.17	0.00	**0.00**	**0.50**
H_3 Forest + Forestbuff + Grassland +Water	77.99	0.00	**0.42**	**0.40**
H_4 Forest + Forestbuff + Forest*Forestbuff + Road + Town + Grassland	23.50	0.00	6.13	0.02
H_5 Forest + Forestbuff + Grassland + Road + Town + Stream + Water	23.80	0.00	5.79	0.03
H_6 Forest + Forestbuff + Grassland + Road + Town + Stream + Water + Forage	24.25	0.00	7.98	0.01
H_7 Forest + Forestbuff + Grassland + Road + Town + Stream + Water + Forage + Wetland	26.06	0.00	9.46	0.00
H_8 Forest + Forestbuff + Forest*Forestbuff	75.86	0.00	5.23	0.04
H_9 Forestbuff	87.69	0.00	11.83	0.00
H_{10} Forest	222.61	0.00	42.40	0.00

[a] AIC_c : Akaike's information criterion with small-sample bias adjustment (Burnham and Anderson, 2002).
[b] $AIC_c w$ represents the probability of that model being the best in the candidate model set.
Annual cropland was removed from the full model for juvenile males due to multicollinearity.

Table 3.2. Cumulative AICc[a] weights (w^b) for the covariates predicted to influence adult female and juvenile male elk resource selection in southwestern Manitoba (Mar-Aug; 2002-2011).

Covariate	Female elk	Male elk	Average Akaike cumulative weights, w_i	Δ Akaike cumulative weights, w_i
Forestbuff	**1.00**	**1.00**	**1.00**	0.00
Forest	**1.00**	**1.00**	**1.00**	1.00
Grassland	**1.00**	**1.00**	**1.00**	1.00
Water	**1.00**	0.36	**0.59**	0.54
Stream	**0.79**	0.27	**0.53**	0.52
Town	**1.00**	0.08	**0.54**	0.92
Road	**1.00**	0.08	**0.54**	0.92
Wetland	**0.61**	0.18	0.22	0.43
Forage	**0.81**	**--**	**--**	**--**
Crop	**1.00**	**--**	**--**	**--**

All covariates with $w > 0.50$ are bolded.

[a] AIC_c: Akaike's information criterion with small-sample bias adjustment (Burnham and Anderson, 2002).

[b] Cumulative AIC_c weight of a covariate which is the percent of weight attributable to models containing that particular covariate and is calculated by summing the AIC_c weights of every model containing that covariate.

[c]Covariates are described in Appendix A, Table A.1.

Annual cropland was removed from the full model for juvenile males due to multicollinearity.

Forage did not influence resource selection for juvenile males (cumulative Akaike weight = 0.00), therefore it was not included in model averaging.

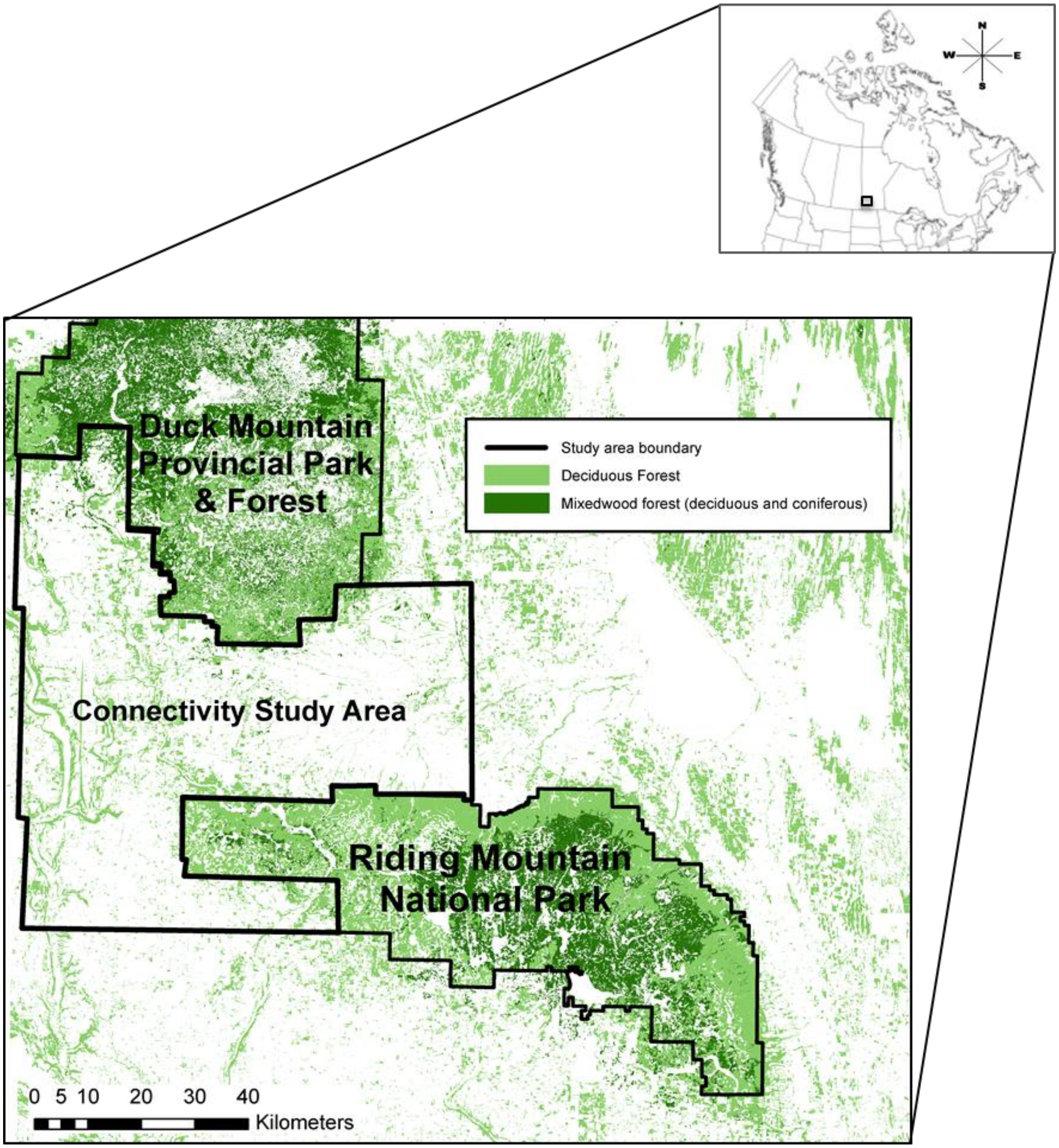


Figure 3.2. Connectivity study area located in the intermountain region that extends from Riding Mountain National Park (RMNP) to Duck Mountain Provincial Park & Forest (DMPP& F), and west to the SK/MB border, in southwestern Manitoba, Canada. Forest covariates were assessed using a 30 m spatial resolution map that was developed using Landsat 5 satellite imagery collected in 2003 and validated in 2011.

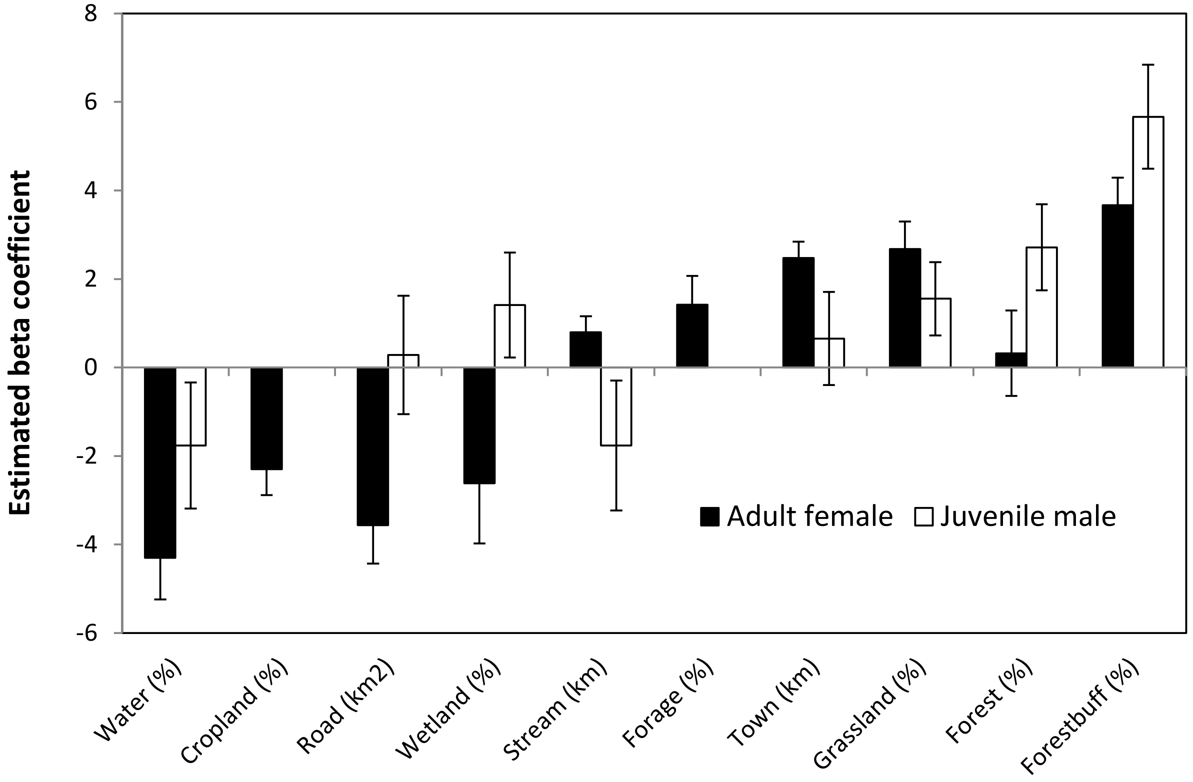
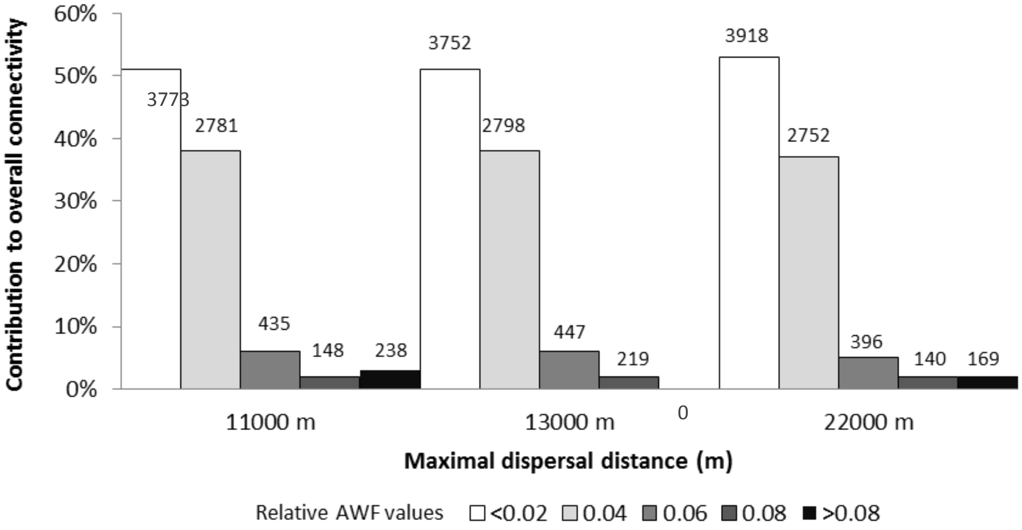


Figure 3.3. Model averaged coefficients (±S.E.) for environmental covariates from logistic regression resource selection function models for adult female and juvenile male elk during the spring and summer (Mar-Aug; 2002-2011) in southwestern Manitoba, Canada.

A) Juvenile Males



B) Adult Females

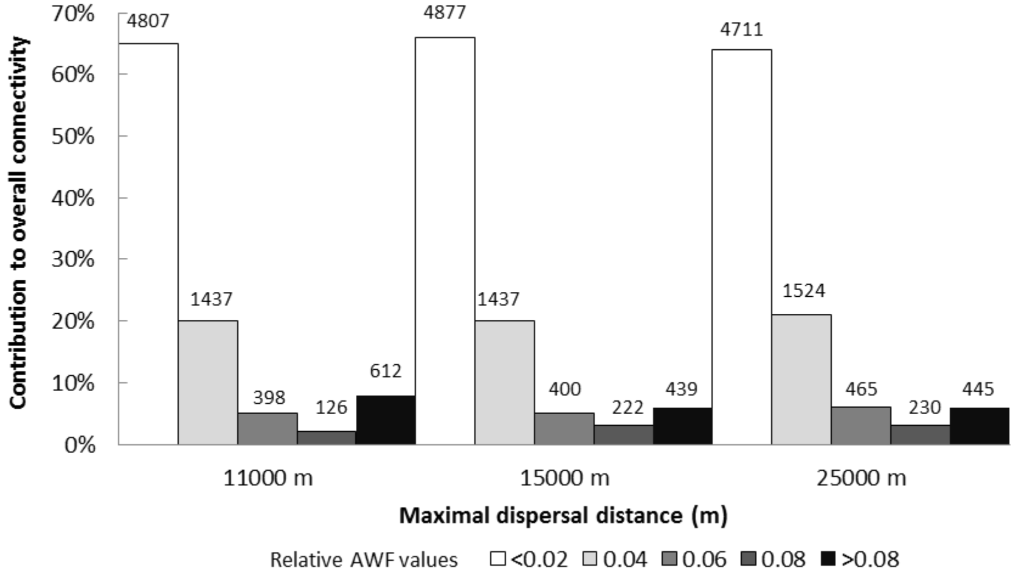


Figure 3.4. Total number of nodes with corresponding AWF importance values and relative contribution to overall connectivity as a function of maximal dispersal distance for A) juvenile males and B) adult females.

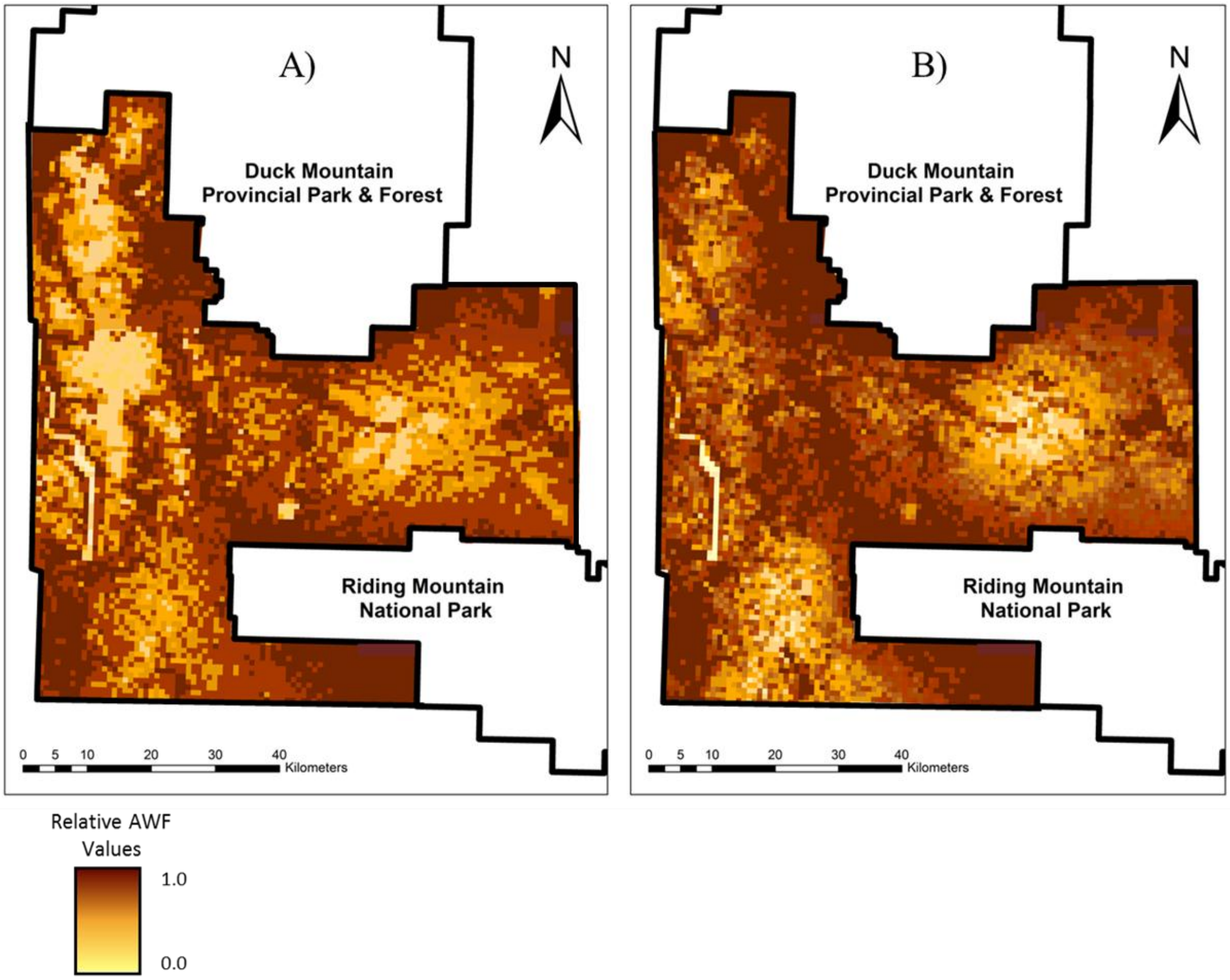


Figure 3.5. Importance of each node in terms of its individual contribution to the overall connectivity as measured by AWF, the graph's area-weighted flux [Eq. (2)] for A) juvenile male elk and B) adult female elk (March - August; 2002-2011), using maximal distance thresholds of 22 km for juvenile males and 25 km for adult females. The resultant AWF values were rescaled to a range between 0-1 and shown in 10 importance classes, each representing the same number of nodes. Darker nodes indicate a higher importance to overall connectivity and lighter areas represent lower importance to overall connectivity.

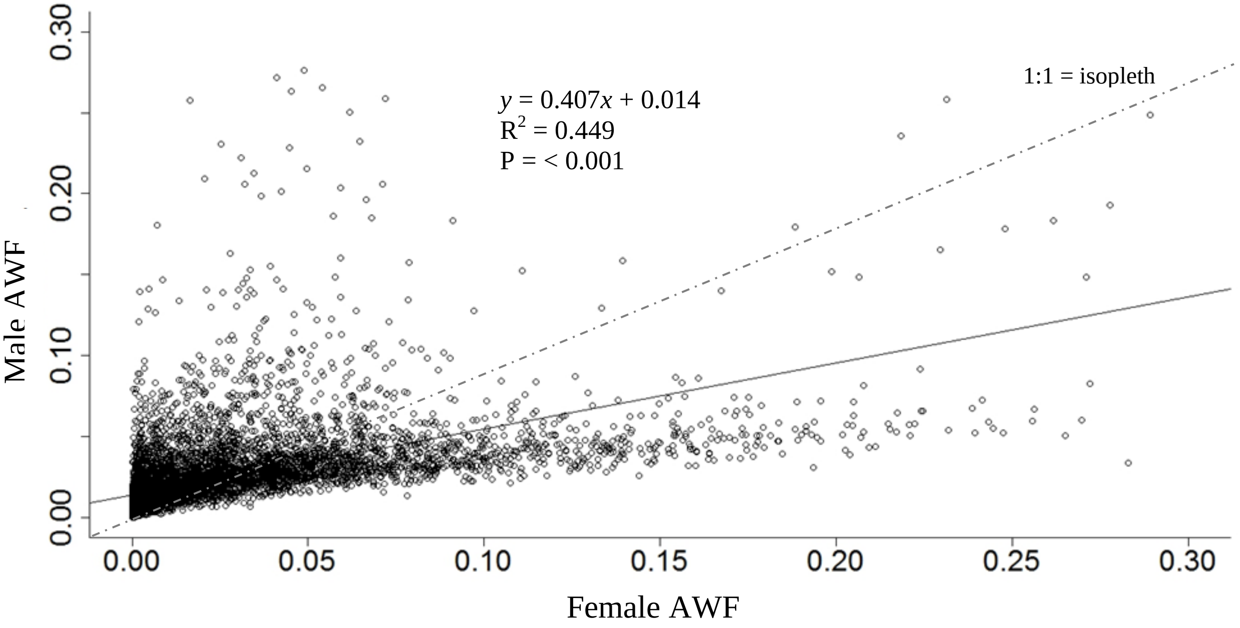


Figure 3.6. Linear regression model comparing each node on the landscape (n = 7375) with the relative AWF values for adult female and juvenile male elk, using maximal distance thresholds of 22 km for juvenile males and 25 km for adult females. A higher AWF value for a node indicates a greater importance to the overall connectivity of the landscape. The position of the regression line relative to the isopleth line indicates that more nodes on the landscape have a higher AWF value (greater connectivity) for females compared with males.

CHAPTER 4: TARGETING HUNTING EFFORT BASED ON HOST DEMOGRAPHY AND RESOURCE SELECTION TO MANAGE ENDEMIC AND EMERGING DISEASES

4.1 Abstract

Endemic and emerging diseases are rarely uniform in their spatial distribution or in the prevalence at which they occur in different sexes and ages of wildlife. Spatial models that link risk-driven shifts in resource selection and mortality of animals during the hunting season may effectively quantify and predict host occurrence patterns and subsequently assist in disease management targeted at highest risk individuals. I used resource selection functions (RSFs) and selection ratios (SRs) to quantify sex- and age-specific resource selection patterns of collared (*n* = 67) and hunter-killed (*n* = 796) non-migratory elk (*Cervus canadensis manitobensis*) during the hunting season between 2002 to 2012, in southwestern Manitoba, Canada. Dramatic differences in resource selection patterns between sexes and ages were evident. Distance to protected area was the most important covariate influencing resource selection for both sexes. Collared adult males [which are most likely to be infected with bovine tuberculosis (*Mycobacterium bovis*) and chronic wasting disease] were rarely outside of protected areas and selected for areas close to the park. Adult females and juvenile males made some use of the agriculture-dominated landscape and selected areas further from the park boundaries. The RSFs for adult females and juvenile males showed marked differences in resource selection patterns during the hunting season at a fine-scale (i.e., 65 ha patch). Adult female selection was negatively associated with landscape-level forest cover, roads, towns, highways, water and crop cover, and positively associated with local-level forest cover. Juvenile male selection was negatively associated with landscape-level forest cover, roads, towns and water cover, and positively associated with local-level forest cover. Local-level forest cover, roads and water cover was more important to males compared with females. Hunter-kill sites for both sexes was negatively associated with increasing distance to parks, towns, and increasing road density, and positively associated with local- and landscape-level forest cover and distance to streams. Here, I show that in a system where hunting is a major source of mortality, the combination of host distribution and hunter-kill locations is a promising approach to understand, predict, and map areas where hunter-kills can be focused on animals of greatest concern with respect to disease. I

present a straightforward approach to mapping specific areas where the probability of an elk kill is less than the probability of elk use, based on the analysis of collared and hunter-killed animals. These areas can be targeted at the highest risk individuals in order to effectively manage bovine tuberculosis and other transmissible diseases in a highly fragmented landscape.

4.2 Introduction

Hunting has become an integral part of conservation biology as it influences movements, resource selection and population dynamics of wildlife (Lindsey et al. 2007; Baldus et al. 2008; Organ et al. 2010). Most management-oriented research has traditionally focused on the evolutionary consequences of selective hunting on the dynamics of wildlife, which can alter selective pressures and gene frequencies of populations and cause overexploitation (Ginsberg and Milner-Gulland 1994; Langvatn and Loison 1999; Coltman et al. 2003). However, relatively few studies have considered the direct and indirect implications of hunting for managing disease risk in wild populations (Grear et al. 2006; Wild et al. 2011), especially at fine spatial scales. Hunting may affect patterns of disease emergence and persistence in wild populations and should be considered more often when devising strategies for disease control (Holt and Manojit 2007; Wild et al. 2011). As such, targeting the specific distribution of hunter effort remains an important but neglected opportunity in controlling transmissible disease in wildlife.

Hunting has been used to manage or eradicate wildlife diseases in the past (e.g., Schmitt et al. 2002), however it has typically been employed at coarse spatial scales. Hunter effort is then adjusted broadly through a licensing or quota system to reduce the overall host population size (e.g., Dobson and Meagher 1996). Importantly, hunting has also often been the primary source of animals for disease monitoring. However, it clear that disease is rarely distributed evenly in populations (Miller and Conner 2005; Härkönen et al. 2007; Shury and Bergeson 2011) and management actions should be aimed at the specific sex and age classes with the greatest potential for intra- and inter-specific transmission. Furthermore, management is challenged by the different approaches that may be required in areas where wildlife are threatened by both endemic and emerging diseases. Hunter effort could be allocated to endemic diseases within a core spatial area, however hunter effort may need to be more dispersed to monitor and prevent the ingression of diseases that are emerging.

The ecological consequences of hunter effort vary across the landscape with predation risk and habitat structure and can generate a ‘landscape of fear’ (Hernández and Laundré 2005;

Laundré et al. 2010; Ciuti et al. 2012). When foraging during the hunting season, prey will often shift their distribution away from riskier areas to minimize the probability of predation by hunters [e.g., mule deer, *Odocoileus hemionus* (Swenson 1982) and elk, *Cervus canadensis* (Morgantini and Hudson 1985)]. Consequently, such landscape-level risks can modify resource selection patterns (Kufeld et al. 1988; Burcham et al. 1999) and influence disease spread. Landscape structure can also have a modulating effect on the occurrence of potential disease risk “hot-spots”. Therefore understanding the relationship between a host and the configuration of the landscape is critical for understanding and managing the risk of disease between and within sub-populations.

In addition to understanding the spatial distribution of animals during the hunting season, knowing the distribution of hunter-kill sites across a landscape is equally important. This is particularly true in regions where hunting is a major source of mortality (Unsworth et al. 1993; Hayes et al. 2002; Collins and Kays 2011). Considerable research on ungulates has focused on direct and indirect predation and risk effects of natural predators on prey (Lima and Dill 1990; Kie 1999; Creel and Christianson 2008), though hunting can have similar or even stronger effects on animal behavior (Ciuti et al. 2012). For example, Gude et al. (2006) and Proffitt et al. (2009) found that hunting constituted a greater effect on elk behavior, such as grouping and distribution than did naturally occurring predators such as wolves. Moreover, hunters do not exert the same selective pressure as natural predators (Festa-Bianchet 2003) representing a fundamental shift in historical predator-prey dynamics.

Models that link risk-driven shifts in resource selection and mortality between sexes during the hunting season may also be useful for focusing disease control efforts, particularly in species that exhibit ecological segregation (sexual differences in diet and habitat selection combined [(Bowyer 2004) and sexual segregation (Clutton-Brock et al. 1982; Ruckstuhl and Clutton-Brock 2005)]. Resource selection patterns and mortality of female ungulates subject to hunting pressure has been examined in detail in several systems (Burcham et al. 1999; Conner et al. 2001; Vieira et al. 2003); however, the effect of hunting pressure on males and associated comparison with females remains largely unexplored. The risk of hunting is likely perceived differently between sexes, as explained above (McCorquodale et al. 2003; Schauber and Woolf 2003; Bowyer 2004; Ciuti et al. 2012), and this could evoke different behaviors with subsequent implications for disease spread. For example, Neumann et al. (2009) found that male moose

(*Alces alces*) were insensitive to stimuli not related to mating, in contrast to females, which consequently increases male vulnerability to hunters. Furthermore, the risk of mortality in relation to landscape features may differ between sexes (Bowyer 2004). However, few studies have directly tested the interacting effects of multiple environmental factors that influence the likelihood of animals being killed during the hunting season (but see McCorquodale et al. 2003 and Webb et al. 2011).

Here, I quantified resource selection functions and selection ratios for juvenile male, adult male, and adult female non-migratory elk during the hunting season. In this system, hunting is the major source of mortality, and transmissible diseases with severe socioeconomic and ecological implications threaten resident ungulates, especially bovine tuberculosis (*Mycobacterium bovis;* TB) and chronic wasting disease (CWD). My objectives were to (*i*) quantify intra-specific differences in elk resource selection during the hunting season, (*ii*) evaluate and predict hunter mortality in relation to multiple landscape features, and (*iii*) develop maps that identify hotspots of disease risk at fine spatial scales to optimize hunter distribution and effort to improve disease monitoring and control programs. I hypothesized that distance to protected area would be the most important covariate influencing elk distribution for both sexes, as elk remain in close proximity to refuges such as parks where hunting is not allowed (Conner et al. 2001; Brook and McLachlan 2009; Prediction 1). Based on anticipated sexual differences in distribution and behavior during the hunting season (Bowyer 1981; Unsworth et al. 1998; McCorquodale et al. 2003), resource selection functions were expected to be sex-specific (Prediction 2). Finally, hunter-kill sites are expected to be linked to the juxtaposition of multiple habitat covariates including distance to protected area, forest cover, road density, and open habitats such as agricultural cropland and wetlands (Prediction 3).

4.3 Study Area

4.3.1Description of study area

The Greater Riding Mountain Ecosystem (GRME) is in a transition zone between the Prairies and the northern Boreal Plains ecozones in southwestern Manitoba, Canada (Bailey 1968; Wiken 1986). It includes the Riding Mountain Biosphere Reserve, an area designated as a zone of cooperation by the United Nations Educational, Scientific and Cultural Organization in 1986 (Edge and McAllister 2009). At its core are two protected areas: Riding Mountain National Park

(RMNP; 2,974 km^2; 50°51’50”N, 100°02’10”W) and Duck Mountain Provincial Park and Forest (DMPP&F; 3,756 km^2; 51°39’58”N, 100°54’52”W).

The study area (Fig. 4.1) focuses solely on the agriculture-dominated landscape that surrounds the protected areas. This area was historically native grassland, once dominated by more extensive deciduous forest cover; however, agricultural expansion has largely replaced grasslands and fragmented remaining forested areas over the last five decades (Walker 2001). At the time of the study, the surrounding agricultural landscape consisted of a mosaic of privately-owned farmland (pasture and grain land; 70%), provincial crown land (18%), federal crown land (11%) and First Nation Reserves (1%; Brook 2008). The study area boundary (based on a 20 km buffer around the two large protected areas) encompasses a regional population of ca. 2700 elk, (Parks Canada and Manitoba Conservation, unpublished data). Elk remain largely within or near the forest-dominated protected areas but make extensive use of the adjacent farmland (Brook 2008; Chranowski 2009; Brook et al 2012).

4.3.2 Endemic and emerging disease

The GRME also includes the Riding Mountain Eradication Area (RMEA) which was created around RMNP in 2003 by the Canadian Food Inspection Agency in response to the increase in bovine tuberculosis [*Mycobacterium bovis*, TB, (Brook and McLachlan 2009; Vander Wal et al. 2012, Brook et al. 2012)] infected positive cattle herds from 1991 – 2002 (Fig. 4.1). In an attempt to eradicate the disease from livestock, intensive testing and controls on cattle movement were implemented in this area. Elk and white-tailed deer (*Odocoileus virginianus*) are both free-ranging hosts for TB. Bovine TB has not yet been detected in moose (*Alces alces*; Parks Canada unpublished data). Elk in RMNP have a prevalence of 2.6% in individuals >8 years old and 0.2% in elk <1 year old. The overall prevalence by sex is 1.2% in males and 0.7% in females (Shury and Bergeson 2011).

Chronic wasting disease (CWD) has not been detected in ungulates in the study area or anywhere else in Manitoba. However, CWD has emerged across the Canadian prairies over the last decade as an important disease of concern in mule deer, white-tailed deer and elk (Saunders et al. 2012). The study area is directly adjacent to the province of Saskatchewan, which has endemic CWD in wildlife (280 mule deer, 66 white-tailed deer, and 4 elk) and 66 cervid captive facilities (Canadian Cooperative Wildlife Health Centre and Saskatchewan Ministry of Agriculture, unpublished data). Establishment of endemic CWD in Alberta in 2005 resulted from infected wildlife from Saskatchewan moving across the border (Habib et al. 2011), so the potential for transmission of CWD into the study area is of critical concern. The risk of CWD moving into Manitoba and becoming endemic in the elk population therefore remains high given that there have been no significant proactive management efforts to limit the spread of the disease between elk sub-populations in SK and MB.

4.3.3 Hunting and natural predators

Although licensed hunting of elk has been ongoing since the early 1900's, and subsistence hunting by Aboriginal people has been occurring for many hundreds and thousands of years, the impacts of hunters on wildlife remain largely unexplored. With only one recent small-scale exception, licensed hunting has never been permitted within the boundaries of the federal RMNP since its establishment in 1930. Licensed hunting is permitted within DMPP&F and on the agriculture matrix (defined here as the human-dominated area that surrounds both of these protected areas) during autumn and winter. Aboriginal elk hunting is legally permitted through treaty rights in the entire region except inside RMNP at any time of the year, though the numbers killed are not known. In contrast to hunting, the influence of natural predators on wildlife in the area has been well studied. A stable grey wolf (*Canis lupus*) population of approximately 70-75 individuals (Stronen et al. 2011) are the primary predators of elk (Carbyn 1983; Paquet 1992; Sallows 2007), while black bears (*Ursus americanus*) are important predators of elk calves (Paquet 1991). Predators on the agricultural matrix are relatively uncommon as they are frequently shot throughout the year (Stronen et al. 2007).

4.4 Methods

4.4.1 Study animals

Between 2002 and 2011, a total of 413 free-ranging elk were captured in and around RMNP and DMPP&F during the winter months (December to March) using a net-gun fired from a helicopter (Cattet et al. 2004) and fitted with a Global Positioning System (GPS) satellite collar (24 F, 12 M), or a very high frequency (VHF) radio collar or ear transmitter (191 F, 186 M). Locations of each GPS collared-animal were obtained daily (mean= 12 locations per day) for up to 2 years (Brook and McLachlan 2009). All GPS locations were screened for large positional outliers and positions collected within 24 h of capture were excluded, which is typically done when assessing fine-scale animal movements (Bjørneraas et al. 2010). Locations of each VHF collared animal were collected using fixed-wing aircraft and ground triangulation (average 3 locations every 2 weeks ± 1.4) for up to 3.5 years (Brook 2008; Vander Wal et al. 2011). I was interested in comparing hunter-killed elk locations with collared elk locations during the hunting season only. Therefore, only collared elk locations from September to February during daylight hours were used (average 8h00-18h00), as hunting is only permitted a half-hour before sunrise until a half-hour after sunset. I also only selected animals with a home range that extended out of RMNP in order to compare collared and hunter-killed locations on the agricultural matrix where hunting is allowed. As a result, these criteria reduced the final sample size to 16 GPS collared-animals, and 51 VHF collared. Elk were classified as adult female (≥2.5-year-old), adult male (≥4-year-old), and juvenile male (<4-year-old; Flook 1970; Noyes et al. 1996). Juvenile female elk were not included in the analysis as they largely follow adult females and have the same selection patterns (Weckerly 1999).

4.4.2 Hunter-killed elk data

It is mandatory for all licensed hunters in the majority of the study area to submit biological samples (complete head, upper neck and lungs, and reproductive tract for females) of killed elk to Manitoba Conservation, the provincial wildlife management agency. Manitoba Conservation, in cooperation with Parks Canada and experienced lab staff tested these samples for the presence of TB primarily and CWD. For each sample, recorded data for each animal included sex, age (estimated by tooth wear and antler growth and verified with tooth cementum analysis; Keiss 1969), date, and location of the kill. Each location was subsequently associated with the centroid of the quarter section in which it occurred. Quarter sections are 0.65 km^2 units of land for agriculture and other purposes as defined by the Dominion Land Survey System (Richtik 1975). Land ownership, land management, and hunter access decisions are largely made at the scale of the individual quarter section within the study area, so the quarter section is the appropriate scale for this analysis. Hunter-killed elk were also classified as adult female (≥2.5-year-old), adult male (≥4-year-old), and juvenile male (<4-year-old; Flook 1970; Noyes et al. 1996). Kill sites were collected from September to February (n = 455 adult F; 135 adult M; 311 juvenile M; Manitoba Conservation and Parks Canada, 2003-2012, unpublished data).

4.4.3 Environmental covariates

A set of *a priori* environmental covariates was derived from the literature predicted to influence elk resource selection and hunter-kill sites during the hunting season (Appendix A, Table A.2). Habitat types included local-level forest cover within the quarter section and landscape-level forest cover within a 5 km buffer around the quarter section, grassland cover, annual cropland (oilseed and cereal), and perennial forage (hay and alfalfa). Water cover (lakes and rivers), distance to streams, and distance to protected area (DMPP&F and RMNP) were also included. Environmental covariates were measured at the scale of the quarter section (*n* = 20,970) with ArcGIS 10 (ESRI Inc.) and an existing 30 m spatial resolution vegetation map that was developed using Landsat-5 satellite imagery collected in 2003 (Geobase; http://www.geobase.ca). The vegetation map was field-validated during ground surveys in 2011, and an overall accuracy of 84% of vegetation was achieved, with the majority of map-misclassification due to changes in cropland. This was expected as cropping patterns change over relatively small scales, however overall patterns remain largely consistent.

Unpaved gravel road density and paved highways was also assessed using detailed provincial GIS layers (Manitoba Transportation and Government Services 2002) that were field-validated and corrected (Brook 2008). Topographic features (i.e., slope and elevation) were evaluated as potential covariates as they have been identified as important to elk for detecting hunters (Unsworth et al. 1993; Conner et al. 2001). However, preliminary analysis showed these to be largely homogenous with little variation across the study area, so they were not included in the models. All covariates were screened for intercorrelations and collinearity using Spearman's rank correlation and Variance Inflation Factors (package Design, Harrell 2001; R Development Core Team 2010). If two covariates were correlated ($r_s \leq 0.5$ or VIF > 5), the less significant of the two covariates was removed. Multicollinearity was detected between the covariates distance to town and distance to highway for collared juvenile males ($r^2 = 0.6$), therefore distance to highway was removed. For hunter-killed juvenile males, cropland cover had a VIF > 5, therefore it was also removed from model development.

4.4.4 Model development and selection

Sex- and age-specific elk resource selection functions (RSFs) and resource selection ratios (SRs; Manly et al. 2002) were developed for collared and hunter-killed elk separately. The presence or absence of locations was considered the dependant variable. Individual sets of SRs were calculated for adult female, adult male, and juvenile male elk for the period of the elk-hunting season. Adult males were not included in the RSF development due to a limited sample size of locations that were outside of protected areas. Resource use and availability were based on individual quarter sections as sample units, therefore the number of randomly generated available quarter sections equalled the number of used sections (1:1 ratio) throughout the entire study area. As such, the analysis corresponded to that of second-order selection (Johnson 1980).

For the development of sex-specific RSFs, I first developed a set of candidate *a priori* models to predict the probability of elk use or kill, using an information-theoretic approach to assess the fit of all models (Burnham and Anderson 2002). Akaike's information criterion adjusted for sample size (ΔAIC_c) and model weights (w_i) were then used to assess the fit of all models. I compared and ranked all *a priori* models according to their ability to explain both the probability of elk use and kill. A multi-model inference approach was also used based on all possible combinations of independent covariates, including 2-way interactions (Burnham and Anderson 2002; Whittingham et al. 2005). All models were ranked based on a combination of covariates with the lowest ΔAIC_c for model inference performed in the R environment for statistical computing (R Version 2.11, www.rproject.org) with the Multi-Model Inference package (R package 0.13.3, http://CRAN.R-project.org/package=MuMIn). All models with $\Delta AICc < 2.0$ (Burnham and Anderson 2002) were retained and resultant β coefficients and standard errors were used to derive the relative probability of elk use (elk collared data) or kill (hunter-killed elk locations) to produce RSFs maps. All predicted RSF scores were rescaled to a range of 0-1 for comparability and extrapolated across the entire study area.

Disease risk management maps were generated by identifying specific areas (quarter sections) of disease management concern where hunter effort is less than use by collared elk. This was determined by calculating the difference in RSF scores between collared and killed elk for both sexes. The performance of the RSFs was evaluated using the *k*-fold cross-validation procedure (Boyce et al. 2002) on the best model for both sexes by partitioning the data into five subsets. Cross-validated Spearman rank correlations (r_s) were calculated between training and test data grouped within ten bins. All statistical analyses were performed in R (R Development Core Team 2012).

Selection ratios (SRs) were also calculated for covariates from the best model of both sexes using the ratio of the proportion used to the proportion available:

$$w_i = \frac{o_i}{\pi_i}$$

where O_i refers to the proportion of the *i*th covariate used at the collared or killed sites, and π_i represents the proportion available of that same covariate as determined by randomly generated locations throughout the study area. The selection threshold is 1. If use of any given habitat is greater than its availability (i.e., selection is occurring), then SR >1. If SR < 1, the habitat category is used less than available (i.e., avoided). If SR = 1, the habitat category is used as a function of its availability and is neither selected nor avoided.

4.5 Results

Marked differences in resource selection and distribution of hunter-killed animals among adult female, juvenile male and adult male elk were found. Collared adult male elk were rarely located outside of the protected areas and were killed in low numbers relative to their overall numbers along the boundary of RMNP. Adult females and juvenile males made considerable use of the agriculture-dominated landscape outside of the protected areas where hunting occurs, and were killed in a range of habitats. For collared animals of both sexes, distance to protected area (RMNP and DMPP&F) was found to be the most important covariate [Table 4.1 and 4.2A (average AIC_w = 1.00)] influencing resource selection as predicted (Prediction 1). Similarly, hunter-kill sites for both sexes was also primarily driven by distance to protected area [Table 4.1 and 4.2B (average AIC_w = 1.00)]. The RSFs revealed the probability of collared juvenile male occurrence to be closer to protected areas (β_park = -27.257) compared with collared adult females (β_park = -15.284, Fig. 4.2A). Killed elk were also found closer to protected areas (male β_park = -0.619, female β_park = -1.860, Fig. 4.2B).

Moreover, important differences in resource selection patterns between sexes were identified (Prediction 2). For example, the analysis of candidate *a priori* models (Table 4.1) identified Model 1 (AIC_w = 0.99) to be the best model for adult females compared with Model 2 (AIC_w = 0.56) for juvenile males. The most notable difference between these models was local-level forest within the quarter section, which was only present in the juvenile male model. Model-averaged results showed the most important covariates for predicting adult female occurrence were: distance to protected area, highways and towns, landscape-level forest cover, and crop cover (cumulative Akaike weight > 0.50; Table 4.2A). For juvenile males, the most important covariates were: distance to protected area and towns, local- and landscape-level forest cover, roads, and cover types of crop and water (cumulative Akaike weight > 0.50). Therefore during the hunting season, local-level forest, roads, and water cover were more important to juvenile males compared with adult females. Females avoided landscape-level forest, roads, towns, highways, water and crop cover, and selected local-level forest (Fig. 4.2A), whereas juvenile males showed strong aversion to landscape-level forest, roads, towns and water cover, and selected crop and local-level forest cover. Sexual differences, as determined from these resource selection coefficients were apparent (Fig. 4.3). The predictive accuracy using withheld model-testing data was ($r_s = 0.715$) for collared adult females and ($\mathrm{r_s} = 0.720$) for collared juvenile males, indicating reasonably strong predictive accuracy.

The analysis using selection ratios (SRs, Fig. 4.4) further corroborates these findings, indicating that female and male elk use the landscape differently during the hunting season. Collared adult males had the highest SR for areas close to the parks (SR = 6.01, < 2km) compared with juvenile males (SR = 5.29) and adult females (SR = 4.96). Collared adult males also had the highest SR for areas with the lowest density of roads (SR = 2.87, < 0.002 km^2) and for areas farthest from highways (SR = 15.44, > 8 km).

Kill sites for both sexes were a function of multiple habitat covariates (Prediction 3). The candidate *a priori* models (Table 4.1) identified Model 4 ($AIC_w = 0.72$) to be the best model for predicting adult female kill sites, and Model 3 ($AIC_w = 0.69$) for juvenile male kills. The most notable difference between adult females and juvenile males was local-level forest and grassland cover which was only present in the female model. Model-averaged results showed multiple covariates to be important for predicting kill sites for both sexes ($AIC_w > 0.5$, Table 4.2B). Adult females and juvenile males were killed closer to parks and streams, and in sections with local- and landscape-level forest cover. Both groups were also killed away from roads, wetlands, grassland and water cover, highways and towns (Fig. 4.2B). The predictive accuracy using withheld model-testing data was ($r_s = 0.868$) for adult females and ($\mathrm{r_s} = 0.824$) for juvenile males.

The probability of a kill for both sexes is represented as RSFs in Fig. 4.3. SR's for hunter-killed elk showed adult males to be killed in very different habitats compared with adult females and juvenile males (Fig. 4.5). For example, adult males were killed much closer to parks (SR = 5.75, < 2 km) compared with adult females (SR = 2.19) and juvenile males (SR = 3.02). Adult males were also killed in areas with less roads (SR = 2.21, < 0.002 km^2), furthest from towns (SR = 8.23, > 20 km), and in heavily forested areas (SR = 3.7, > 80% forest cover).

The predictive maps highlight disease risk management areas of concern for juvenile male and adult female elk (Fig. 4.6). These areas show quarter sections where the probability of a kill is less than the probability of elk use based on the analysis of collared and hunter-killed animals. The distribution of areas for disease risk concern is more heterogeneous for juvenile males compared with adult females, with the most important areas being close to the park borders, such as the northern border of RMNP, and along with the southeastern and northwestern borders of DMPP&F. Disease management areas for adult females is more uniform, with the most important areas focused mainly in the northwestern corner of RMNP, and areas along the western border of DMPP&F.

4.6 Discussion

Few applications of hunting to disease management attempt to target hunter effort at fine spatial scales or individual cohorts of a species. However, my results clearly reveal sex and age dissimilarities in resource selection and kill sites during the hunting season that should be reflected separately for managing disease. The prevalence of TB varies dramatically within the Riding Mountain elk population in the study area, which is consistent with other studies of TB that show important variation among cohorts (McCarty and Miller 1998; Schmitt et al. 2002, Shury and Bergeson 2011). Management of wildlife diseases has typically been characterized by reactive, unsustainable interventions that have often ignored the fundamental importance of how host ecology and behavior may influence disease in complex landscapes (Woodroffe 1999; Delahay et al. 2009). Here, I present a straightforward approach to mapping specific areas where hunting can be targeted in areas with the highest risk individuals using data that are typically collected in disease management programs. This strategy creates important opportunities for a more proactive approach to disease control, where management programs are based on contemporary analytical tools such as GIS that enhance our ability to evaluate the relationship between host ecology and disease risk. Thus, effort can be optimized to improve disease monitoring, target removal of individual animals considered at highest risk, and identify areas where existing hunting effort is inadequate.

In this study, collared adult females selected areas much further from the parks compared with collared adult and juvenile males. It is possible that females in more open areas perceive less predation risk when foraging in large groups compared with more solitary males due to dilution effects (Hebblewhite and Pletscher 2002). My results also indicate that the majority of killed males (predominately adult males) were much closer to the RMNP boundary than females. This indicates that hunter success is largely predicated on the distribution of individual animals (Lyon and Burcham 1998), forcing males to remain in or close to the park. These results corroborate with other studies that hunting creates a landscape of fear, causing individuals to remain in or close to refuge areas for protection [mule deer: Swenson 1982; white-tailed deer: Vercauteren and Hygnstrom 1998; elk: Morgantini and Hudson 1985; Burcham et al. 1999; wild boar (*Sus scrofa*): Clayton et al. 1997]. It is also possible that during the rut, which coincides with part of the hunting season, males near the park boundaries allocate more time to mating-related behavior rather than foraging or vigilance (Bowyer 1981; Clutton-Brock et al. 1982; Wolff and Horn 2003). This type of muted antipredator response may render individuals more vulnerable to hunters (Neumann et al. 2009), particularly with younger males (<4y), which may be a result of inexperience compared with mature adult males (Wolf et al. 2009).

Other environmental factors had a modulating effect on elk resource selection and hunter-kill sites during the hunting season. Both sexes selected local- and landscape-level forest cover, presumably for protection from predators (Swenson 1982; Unsworth et al. 1998; Hayes et al. 2002); however, selection was stronger for males, particularly adult males. It is reasonable to suspect that security on the agriculture-dominated lands would be more important for solitary males compared with females in groups (Hillis et al. 1991), as they would perceive greater hunter risk. Moreover, my results showed that local- and landscape-level forest cover were important predictors of a kill for both sexes.

The availability of agricultural crops was also an important factor influencing elk habitat selection in this study. Adult females strongly avoided these areas during the hunting season. Likely because during this time these areas lacked sufficient hiding cover, had lower forage value having already been harvested, and perceived greater risk from hunters in open areas (Morgantini and Hudson 1985; Skovlin et al. 2002). Previous studies have found ungulates to move onto private land as an alternative form of security to minimize encounters with hunters (Burcham et al. 1999; Conner et al. 2001; Vieira et al. 2003), as hunting was not allowed on these lands. In contrast, hunting is permitted on 70% of privately-owned land with permission of the landowner in the study area (Brook 2008), however I did not find cropland to be an important predictor of a kill.

Elk also avoided areas with heavy road traffic during the hunting season, suggesting that elk associate roads with increased hunter risk and disturbance (Unsworth et al. 1997 & 1998; Rowland et al. 2000). Collared males (both age classes) showed stronger aversion to roads compared with collared adult females, which concurs with findings from McCorquodale et al. (2003). High road density has been shown to reduce local hunter success of elk over time, either due to increased hunting pressure causing animals to avoid these areas (Gratson and Whitman 2000), or increased access by hunters (Brinkman et al. 2007). My results suggest that both sexes were killed in areas with relatively low road density in this region, suggesting hunters will expend more effort and are successful in habitat types with few or no roads (Lebel et al. 2012).

An important failure of most disease management programs, as with this particular study area, is that initiatives to control TB have not been conducted as experiments, so the overall results of these efforts remain unknown. However, this study provides an example of a small-scale manipulation of hunter effort that is tied directly to elk distribution and kills, which could ultimately be linked to TB and CWD prevalence. In addition, the disease management maps provide a complementary tool that allows managers to precisely evaluate the implications of hunting for disease control and creates an opportunity to apply incentives and regulations to target hunting effort.

Sex and age classes, particularly for ungulates, should be considered separately to focus hunting effort more effectively in these areas. Specifically, efforts should be targeted to adult male elk which have the highest prevalence of TB in the area (Shury and Bergeson 2011). Adult males rarely leave RMNP and use very specific habitats directly adjacent to the RMNP boundary. As such, targeting this highest risk cohort requires hunter effort to be concentrated in areas within < 2 km from the RMNP border, with very low road density (< 0.002 km^2), and with at least 80% forest cover.

The resource selection ratios and the disease management map for adult females indicate that hunters should target individuals in quarter sections that are further from the park boundary (within 10 km), since females move further from the park compared with males and are not hunted as effectively. Hunters should also focus in sections with very low road density (<0.002 km^2) and with at least 40% forest cover. Areas with significant forest cover at a distance within

5km of the quarter section should also be targeted as this covariate was highly important to collared adult females during the hunting season. As for juvenile males, collared individuals were also found close to the RMNP boundary, however those killed were found further from the parks, therefore efforts should be made closer to protected areas (< 2km). Increased efforts in sections with very low road density (<0.002 km^2) and with at least 80% forest cover would also be effective.

The landscape-scale risk of pathogen transmission in southwestern Manitoba and across the MB/SK border is complex, as multi-host (i.e., elk, white-tailed deer) disease systems are present across the landscape. In southwestern Manitoba, elk are likely the primary reservoir hosts of TB (Lees 2004; Nishi et al. 2006; Shury and Bergeson 2011) where most cases have been restricted to western RMNP (Brook and McLachlan 2009; Shury and Bergeson 2011). Elk sub-populations are clustered into three distinct genetic groups (DMPP&F, east and west RMNP; Vander Wal et al. 2012), indicating their movements are largely restricted to the parks. This reduced movement is likely a result of intensive and widespread hunting pressure around the parks, which my results corroborate, combined with the highly fragmented agricultural matrix acting as an anthropogenic filter. As a result, the probability of long-distance disease spread between the parks is low for elk. Increased hunting pressure along the borders of protected areas should continue to generate a landscape of fear for elk and remove bold animals venturing far out from protected areas. This pressure would ultimately restrict animals and disease to RMNP and reducing the risk of wildlife-livestock interactions. Efforts should also be made to improve hunters' efficiency (Lebel et al. 2012), and ensure that hunter effort better matches with animal distribution to avoid creating areas with little or no hunting pressure where animals can cluster and survive (Burcham et al. 1999; Conner et al. 2001; Vieira et al. 2003).

In contrast to TB, the concern for CWD emergence in Manitoba presents a different challenge, as potential regional corridors that exist across the border may promote elk movement and consequently disease spread. The disease management maps show one of the most important areas for targeting both sexes is along the northwestern border of DMPP&F near Saskatchewan, suggesting this area should be a primary focus for monitoring and preventing emerging CWD. Increased hunter effort in this area, especially towards adult male elk which are known to have higher prevalence of CWD in other areas (Miller et al. 2000; Miller and Conner 2005), could help limit elk movements from extending across the border and consequently disease.

The aim of sustainable wildlife management is to design a hunting policy that simultaneously optimizes population sex and age structure, elk density and hunter-kill levels in the face of increasing pressures such as changing habitat conditions and disease threat. However, few management plans adequately account for the threat of disease in an area such as Manitoba where endemic TB and emerging CWD simultaneously threaten resident ungulates. Replication of these methods in other areas would extend the body of knowledge on disease risk and management in metapopulations. It would also provide the basis for improved disease testing and more effective targeting to manage individual cohorts at greatest risk of disease transmission in a population.

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Table 4.1. Differences in Akaike information criterion (Δ AICc[a]), and AICc weights (*w*[b]) for adult female and juvenile male candidate RSF models during the hunting season (Sept-Feb; 2002-2012) in southwestern Manitoba, Canada.

	Collared Females		**Collared Males**		**Killed Females**		**Killed Males**	
Hypothesized Models	**ΔAICc[a]**	**$AIC_c w$[b]**	**ΔAICc[a]**	**$AIC_c w$[b]**	**ΔAICc[a]**	**$AIC_c w$[b]**	**ΔAICc[a]**	**$AIC_c w$[b]**
H_1 Park + Forestbuff + Highway + Town + Crop +Water	**0.00**	0.99	**--**	**--**	28.88	<0.001	18.18	<0.001
H_2 Park + Forest + Forestbuff + Crop + Town +Water	30.10	<0.001	**0.00**	0.56	22.18	<0.001	20.13	<0.001
H_3 Park + Road + Stream + Forestbuff + Town +Water	29.37	<0.001	4.81	0.05	3.95	0.10	**0.00**	0.69
H_4 Park + Forest + Forestbuff + Road + Stream +Town + Water + Grassland	31.92	<0.001	0.91	0.36	**0.00**	0.72	2.59	0.19
H_5 Park + Forest + Forestbuff + Road + Highway + Town + Crop + Water + Stream + Forage + Grassland + Wetland	8.94	0.01	6.41	0.02	5.16	0.05	7.27	0.02
H_6 Park + Forest + Park * Forest +Road +Stream +Town + Water	32.05	<0.001	23.35	0.00	3.41	0.13	3.55	0.12
H_7 Park + Forest +Forestbuff	61.73	<0.001	8.07	0.01	37.90	<0.001	29.62	<0.001
H_8 Park + Forest + Park * Forest	61.80	<0.001	22.22	0.00	43.86	<0.001	39.25	<0.001
H_9 Park	62.01	<0.001	24.88	0.00	52.98	<0.001	44.96	<0.001
H_{10} Forest	196.67	<0.001	75.39	0.00	89.29	<0.001	68.46	<0.001

[a] AIC_c : Akaike's information criterion with small-sample bias adjustment (Burnham and Anderson, 2002).

[b] $AIC_c w$ represents the probability of that model being the best in the candidate model set.

Table 4.2. Cumulative AIC$_c$^{a} weights (w^b) for the covariates hypothesized to influence A) collared adult female and juvenile male elk, and B) hunter-killed adult female and juvenile male elk during the hunting season (Sept-Feb; 2002-2012).

A)

Covariate	Female elk	Male elk	Average Akaike cumulative weights, w_i	Δ Akaike cumulative weights,w_i
Park	**1.00**	**1.00**	**1.00**	0.00
Forestbuff	**1.00**	**1.00**	**1.00**	0.00
Highway	**1.00**	**--**	**--**	**--**
Town	**1.00**	**1.00**	**1.00**	0.00
Crop	**1.00**	**0.68**	**0.64**	0.73
Forest	0.36	**1.00**	**0.68**	0.64
Road	0.48	**0.64**	**0.56**	0.16
Water	0.50	**0.67**	**0.59**	0.17

B)

Covariate	Female elk	Male elk	Average Akaike cumulative weights, w_i	Δ Akaike cumulative weights
Park	**1.00**	**0.96**	**0.98**	0.02
Road	**1.00**	**1.00**	**1.00**	0.00
Water	**1.00**	**1.00**	**1.00**	0.00
Stream	**1.00**	**1.00**	**1.00**	0.00
Town	**1.00**	**1.00**	**1.00**	0.00
Forestbuff	**0.75**	**0.73**	**0.74**	0.02
Grassland	**1.00**	0.18	**0.59**	0.82
Forest	**0.68**	0.35	**0.52**	0.33
Highway	0.32	**0.60**	0.46	0.28
Wetland	0.45	0.40	0.43	0.05

All covariates with $w > 0.5$ are bolded.

[a] AIC$_c$: Akaike's information criterion with small-sample bias adjustment (Burnham and Anderson, 2002).

[b] Cumulative AIC$_c$ weight of a covariate, which is the percent of weight attributable to models containing that particular covariate and is calculated by summing the AIC$_c$ weights of every model containing that covariate.

[c]Covariates are described in Appendix A, Table A.2.

Highway was removed from the full model for collared juvenile males due to multicollinearity.

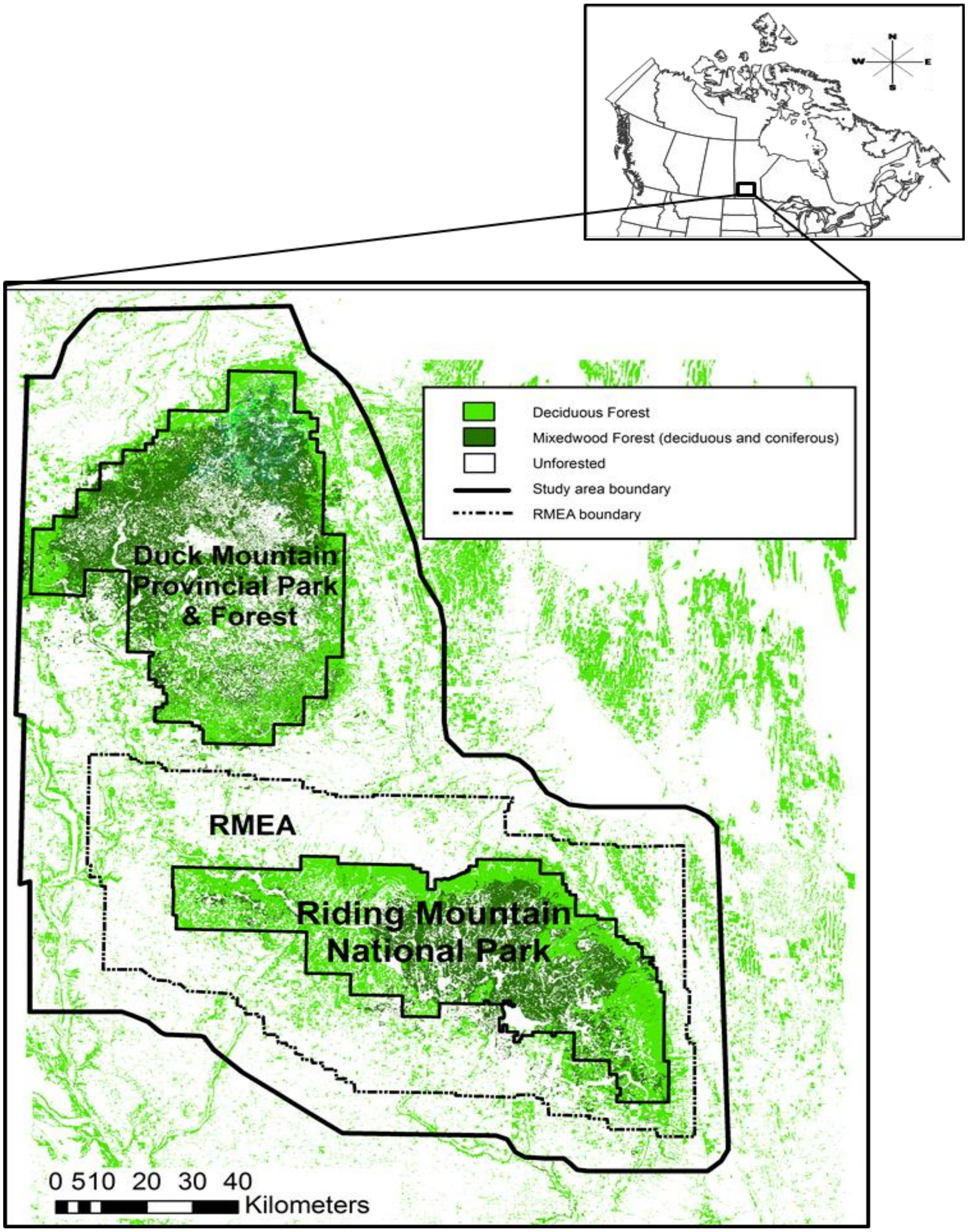

Figure 4.1. Map of study area located on the agriculture-dominated lands surrounding Riding Mountain National Park and Duck Mountain Provincial Park and Forest in southwestern Manitoba, Canada. The Riding Mountain Eradication Area (RMEA) boundary is represented by the hashed line. Forest covariates were assessed using a 30 m spatial resolution map that was developed using Landsat 5 satellite imagery collected in 2003 and validated in 2011.

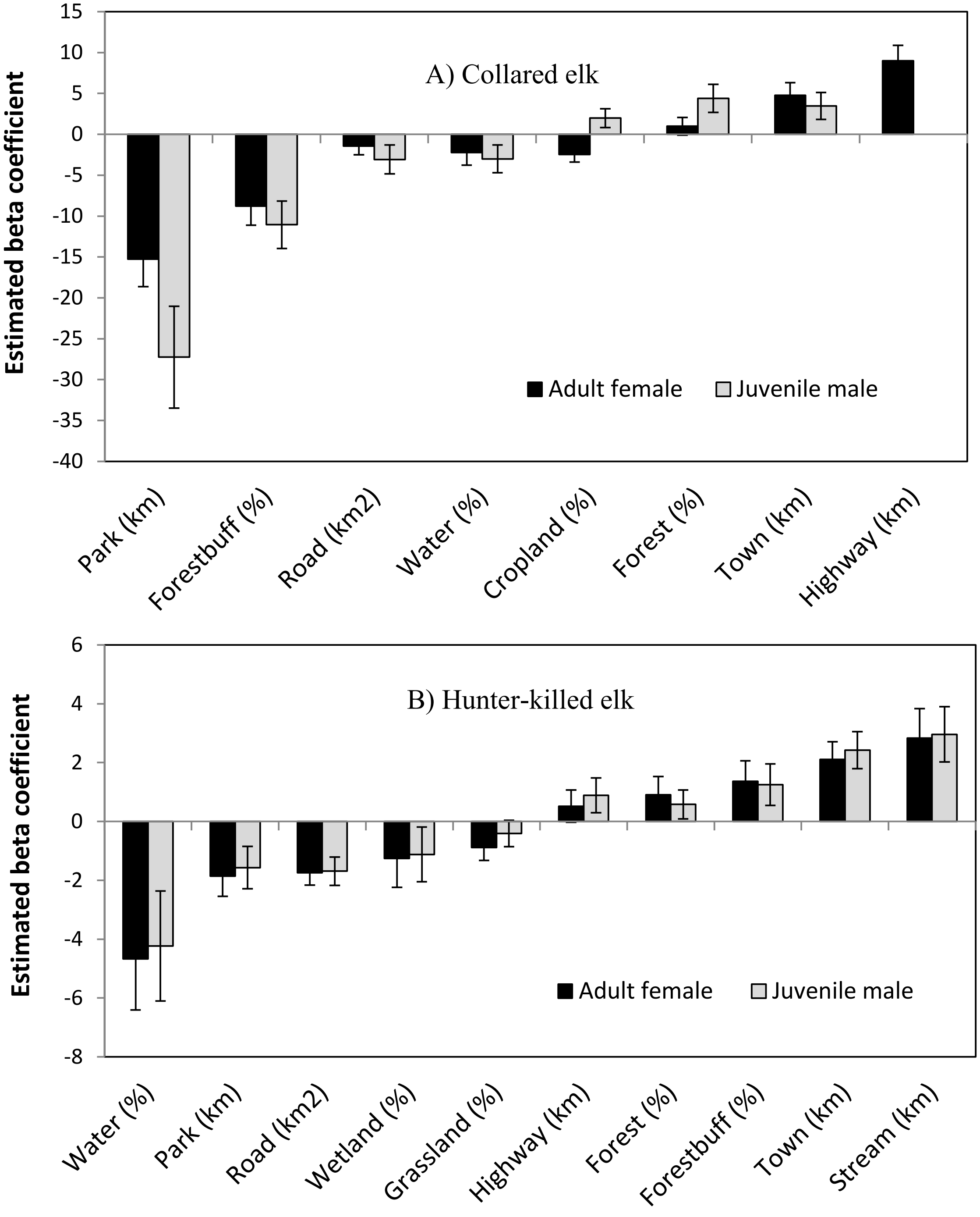

Figure 4.2. Model averaged coefficients (± S.E.) for covariates from logistic regression resource selection function models for A) collared elk and B) hunter-killed elk during the hunting season (Sept-Feb; 2002-2012) in southwestern Manitoba, Canada. Estimates were derived from an average of all possible models with a change in Akaike value less than 2 (ΔAIC, 2.0).

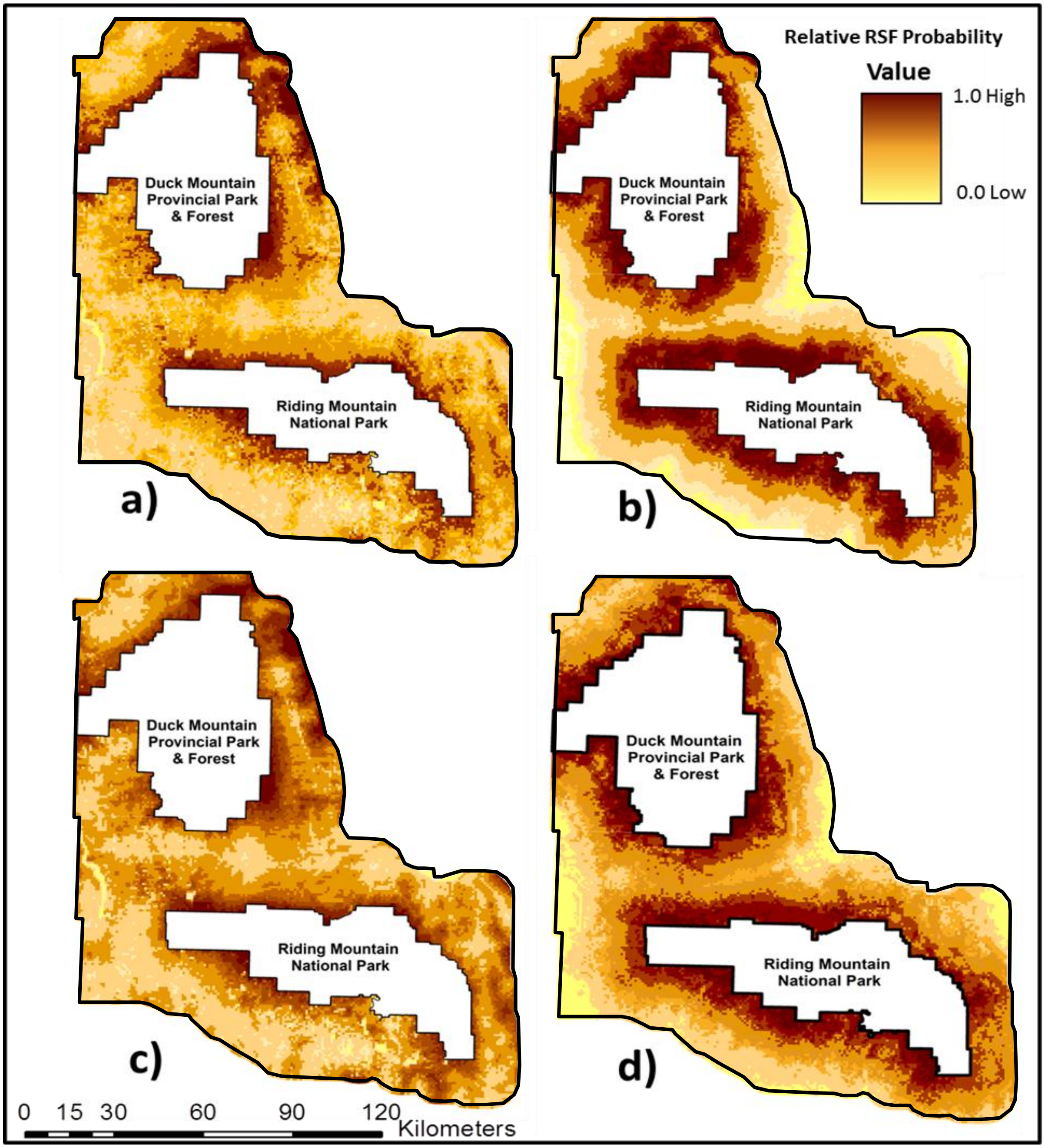

Figure 4.3. Interpolated map surfaces representing a resource selection function model for a) collared adult females, b) collared juvenile males, c) hunter-killed adult females, and d) hunter-killed juvenile males in southwestern Manitoba (Sept-Feb; 2002-2012). Darker shaded areas represent a high probability of elk occurrence/kill whereas lighter shaded areas represent a low probability of elk occurrence/kill.

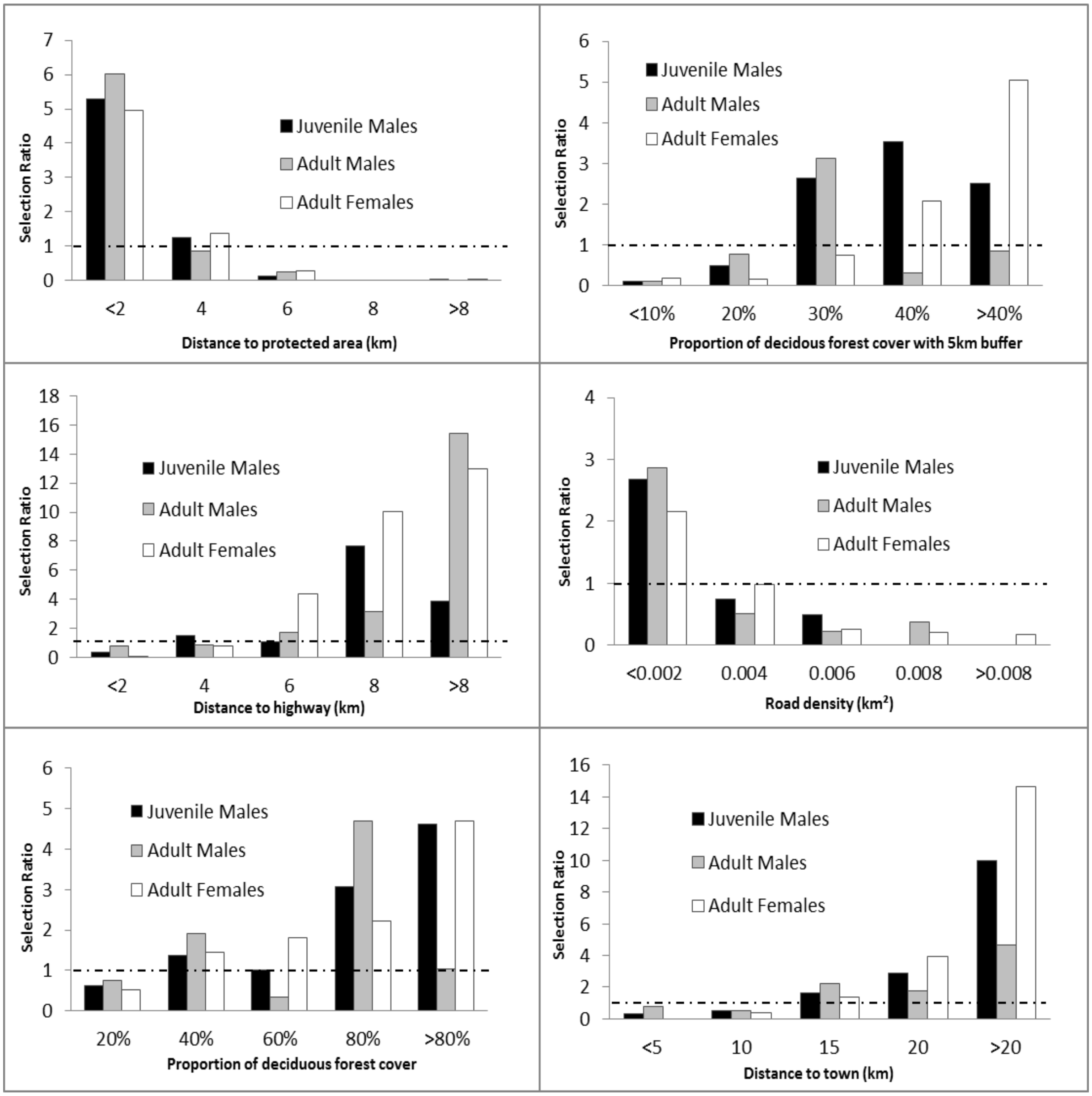

Figure 4.4. Selection ratios for the six covariates identified as most important to **collared** elk from the RSF models during the hunting season (Sept-Feb; 2002-2011) in southwestern Manitoba. Values > 1 indicate use is greater than availability and the animal is selecting for that covariate, whereas values < 1 indicate use is less than availability and the animal is avoiding that covariate.

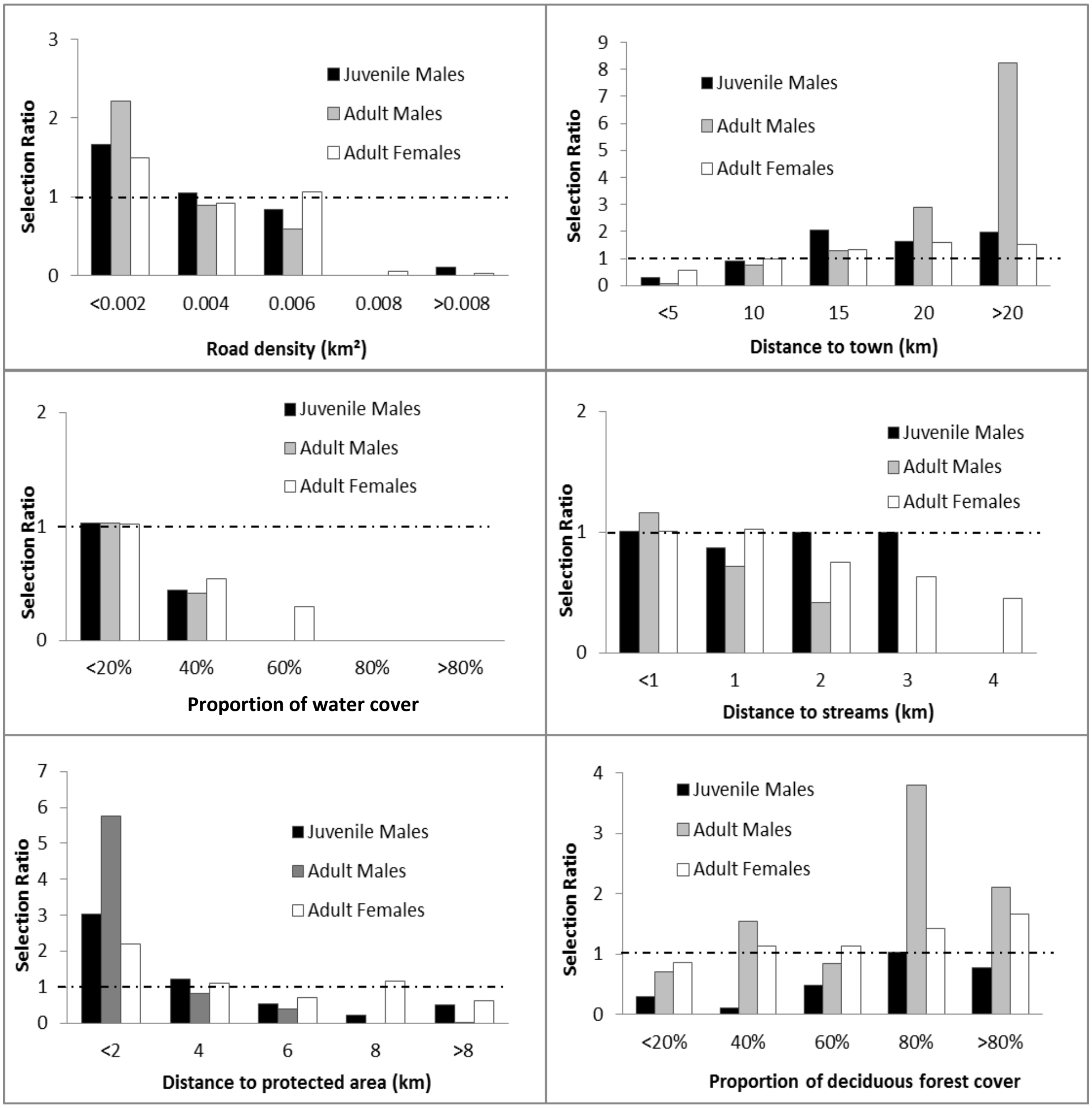

Figure 4.5. Selection ratios for the six covariates identified as most important for **hunter-killed** elk from the RSF models during the hunting season (Sept-Feb; 2003-2012) in southwestern Manitoba. Values > 1 indicate use is greater than availability and the animal is selecting for that covariate, whereas values < 1 indicate use is less than availability and the animal is avoiding that covariate.

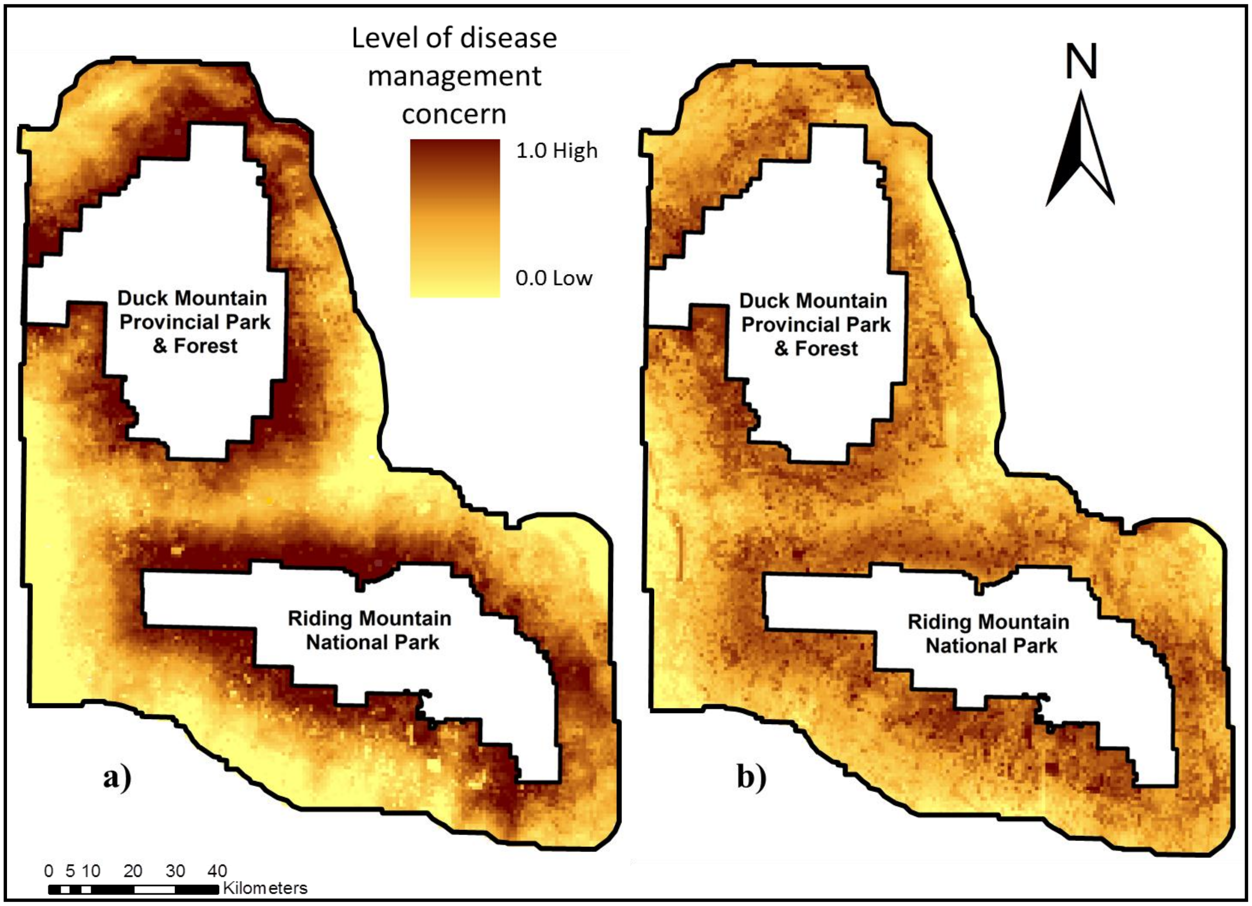

Figure 4.6. Predictive maps highlighting disease risk management areas for a) juvenile male and b) adult female elk, which largely reflect areas where they are known to strongly select but are not hunted effectively in southwestern Manitoba, Canada. Varying levels of disease management concern were obtained by calculating the difference in RSF scores between elk occurrence (Fig. 4.3A and B) and hunter-killed sites (Fig. 4.3C and D). Darker shaded sections represent areas where managers should target hunter efforts more effectively.

CHAPTER 5: GENERAL DISCUSSION

5.1 Synthesis and review

The purpose of my thesis was to understand the complex interactions between elk movement, habitat fragmentation and the role of hunting to assess the landscape-level risk of endemic bovine TB and emerging CWD across an agricultural landscape. As such, this research provides valuable insights into the underlying processes that influence disease risk between elk sub-populations, which will ultimately facilitate the development of more effective conservation, and disease management solutions. Objectives of this thesis were to: (i) identify sex- and age-specific habitat corridors for elk movement to assess the potential risk of disease spread between elk sub-populations; and (ii) evaluate sex- and age-specific elk distribution and hunter-kill sites during the hunting season to understand the impact of hunting on elk resource selection and to improve the effectiveness of current disease control programs. This chapter synthesizes the key findings of this research and provides conservation and disease management recommendations intended for government agencies and other stakeholders.

5.2 Thesis objective #1: identify sex- and age-specific habitat corridors for elk movement to assess the potential risk of disease spread between elk sub-populations.

Understanding the link between animal distribution and landscape structure remains a central theme of ecological research. Habitat corridors are intended to facilitate wildlife movement such as dispersal among otherwise-isolated populations, thereby maintaining genetic integrity (Fahrig and Merriam 1994; Beier and Noss 1998; Hodgson et al. 2011). However, unanticipated consequences such as disease spread may occur (Simberloff and Cox 1987; Simberloff et al. 1992; Hess 1994; Bennett 2003). I quantified functional connectivity for elk across a highly fragmented landscape to identify potential habitat corridors and predict the risk of long-distance disease spread between protected areas. Habitat structure was integrated with movement behavior to produce landscape-scale maps of functionally connected areas for elk, and I found clear evidence for sex-and age-based differences in functional connectivity.

Adult females and juvenile males made frequent and regular use of the landscape surrounding the parks during spring and summer, but adult males rarely strayed beyond the park boundaries. Most movements made by adult females and juvenile males were short foray loops that extended out of the protected areas. However, three VHF-collared juvenile males dispersed from RMNP to DMPP&F and one VHF-collared adult female dispersed south approximately 33 km.

Although the overall connectivity of the landscape is greater for adult females compared with juvenile males, females are largely constrained to the proximity of RMNP and DMPP&F (i.e., 99% of all locations are within 10km). Two highly fragmented habitat corridors exist between the protected areas, but they appear to only support short, daily forays for all elk classes and dispersal movements are rare. As such, the overall landscape composition (habitat corridors and surrounding matrix) creates an anthropogenic filter to long-distance movements for all sex- and age-classes of elk. These findings along with recent genetic dispersal analyses of the elk metapopulation in this area suggest that regional habitat connectivity on this landscape is dysfunctional for elk.

Functional connectivity is a multi-scale concept. It depends not only on the structural configuration of the landscape but species' movement abilities and their response to the landscape (Tischendorf and Fahrig 2000; Bélisle 2005; Luque et al. 2012), and dispersal behavior is often considered the key process underlying this concept (Bélisle 2005; Baguette and Van Dyck 2007). Functional connectivity quantification also necessitates the consideration of genetic estimates. I have developed an effective framework that considers all of these factors, which has ultimately provided a strong basis for assessing the risk of disease spread across a fragmented landscape.

Habitat fragmentation and disease have caused considerable concern among biologists, wildlife managers, and landowners throughout the study area (Brook and McLachlan 2006). As such, management is faced with having to balance the risk of disease spread between protected areas with the conservation benefits of increased gene flow through connective habitats. The establishment or maintenance of habitat corridors to counter the effects of habitat loss and fragmentation is an important conservation tool for maintaining genetic integrity (Simberloff and Cox 1987; Fahrig and Merriam 1994; Beier and Noss 1998). However, managers must consider the heavy risks that are imposed when individual movement and consequently disease are enhanced (Hess 1996). Given the degree to which the landscape impedes movement for all sex- and age-classes of elk, the risk of TB from RMNP to DMPP&F is limited. However, extensive movements are known to occur, as three VHF-collared juvenile males dispersed between the parks, and one VHF-collared adult female dispersed south of RMNP. Therefore, the implications associated with these infrequent long-distance movements indicate that the potential for disease spread exists. The potential risks are underscored by the fact that one of the juvenile male elk that dispersed from RMNP to DMPP&F was subsequently tested positive for bovine TB.

The risk of CWD emergence is of critical concern, as it is spreading widely and quickly across the Canadian prairies in mule deer, white-tailed deer and elk. CWD has not yet been detected in Manitoba, however the study area is directly adjacent to Saskatchewan, which has endemic CWD in wildlife and ranched elk (Canadian Cooperative Wildlife Health Centre, unpublished data). The establishment of endemic CWD in Alberta in 2005 resulted from infected wildlife from Saskatchewan moving across the border. So the potential for transmission of CWD moving into Manitoba seems very likely in the next decade, especially given that there are no substantive efforts to contain the disease spread. Areas along the provincial border and the corridors between RMNP and DMPP&F have the potential to become an unprecedented focus for CWD. Although the connectivity of the landscape and the potential for long-distance movement by elk and consequently disease across the provincial border is low, the broad socioeconomic implications of these diseases remain highly significant.

The management of CWD in wild cervids remains a challenge (Williams et al. 2002), as the majority of strategies for limiting the spread of this disease have proven to be insufficient. In the Wyoming-Colorado-Nebraska area where CWD is endemic, several bans have been placed on artificial feeding of cervids to limit disease transmission (Williams et al. 2002). However, artificial feeding and baiting of wildlife continues to occur on public and private land throughout much of Canada, which has caused great concern regarding the transmission of infectious diseases. In Saskatchewan, baiting of wildlife for hunting purposes is permitted in five of Saskatchewan’s 34 provincial parks and on public and private land. In Manitoba, artificial feeding and attracting cervids is illegal in the disease Surveillance Zones, and baiting for the purpose of hunting is illegal throughout the entire province for big game animals, excluding black bears and wolves. However, existing bans are limited by a need for more intensive monitoring and enforcement. The artificial baiting and feeding that continues to occur are exacerbating the risk of disease transmission on a local level for CWD (Spraker et al. 1997) as well as TB (O’Brien et al. 2002; Miller et al. 2003). Clearly stronger efforts are required to prevent these activities from occurring and the subsequent spread of disease between elk sub-populations in Saskatchewan and Manitoba.

Selective culling of mule and white-tailed deer has been practiced throughout endemic areas such as Colorado and Wyoming, however this approach has been largely ineffective for reducing disease prevalence in affected populations (Williams et al. 2002; Conner et al. 2007). Selective culling near CWD cases outside the core endemic areas such as in Saskatchewan, South Dakota and Colorado has also been done to provide data on the extent of disease spread. However, this top-down approach may have serious implications for social animals, and may actually exacerbate the risk of disease spread (Nishi et al. 2005; Donnelly et al. 2006; Woodroffe et al. 2009). Models of CWD epidemic dynamics suggest early intervention such as generalized population reduction as the most promising approach to preventing CWD from spreading to new areas (Gross and Miller 2001). Several CWD positive wild elk have been identified as close as 160 km from the provincial border; therefore, reducing populations of elk near the border could potentially lower the risk of CWD from emerging into Manitoba. Hunter efforts could also be targeted in specific areas where elk are known to occur and at the highest risk individuals to increase disease surveillance and the limit movement between provinces. This would create an important opportunity for managers to take a more proactive approach to disease management in MB (Chapter 4).

Selective predation by natural predators such as wolves may also affect patterns of prevalence and disease emergence, and may help to eliminate pathogens or prevent the establishment of disease in new geographic areas (Heesterbeek and Roberts 1995; Gross and Miller 2001; Packer et al. 2003). It has been shown that natural predators have a greater selectivity for diseased prey (e.g., Murray et al. 1997; Voříšek et al. 1998), as poorer body condition of prey slows avoidance behavior and decreases awareness. Other cues or factors may also be used by predators to select compromised prey (reviewed by Wild et al. 2011). Based on the behavioral changes that occur early on in the course of CWD infection, it is possible that wolves may have great potential for selecting infected prey, and prevent agent shedding in the environment early on. Wild et al. (2011) simulated the potential impacts of predation on the dynamics of deer populations and found that predation could markedly decrease CWD prevalence in an infected population, and prevent the emergence of disease into new locations. Although natural predation may be a useful tool for managing CWD, the current range of wolves on the Canadian prairies and parklands does not overlap with the distribution of CWD. Wolf restoration, particularly in DMPP&F and near the provincial border would provide an opportunity to evaluate the effects that selective predation may have on the possible emergence of CWD in Manitoba.

The most important message of this work is that the role of dysfunctional connectivity across the prairie-parkland interface in limiting the spread of disease in wildlife is likely more critical than previously appreciated. Facilitating long-distance movement of individuals between protected areas by restoring existing habitat corridors is a conservation strategy that carries a high risk in the face of disease (Hess 1996). Only some movement among sub-populations is required to sustain a metapopulation. According to Gilpin (1987), only one migrant per generation is needed to maintain within-population diversity, yet transmission of disease to a new area previously uninfected requires only a single infected animal to disperse. However, there may be important implications for the long-term conservation of the Riding Mountain elk metapopulation. Resource managers may consider the possibility of genetic rescue in this system and translocate selected individuals between protected areas rather than restoring habitat corridors (Simberloff and Cox 1987). However, the challenge is compounded by poor TB tests for wildlife, and confirmed diagnosis of CWD is based on brain examination only (Williams and Young 1993). Animals are currently moving without any controls or disease testing, so facilitated movements would at least provide some measure of disease testing, despite the limits of existing tests.

Elk in the study area make frequent use of the surrounding matrix throughout the year, and the extent of forest cover remains one of the most important variables that influence elk movement outside the parks. Forested areas clearly support daily movements for elk such as resting, foraging (most notably for high quality food resources such as pasture, hay, and grain) and even calving (Brook 2008; Brook 2010). Therefore, conservation efforts to restore or preserve forested patches in areas other than in the fragmented corridors and away from cattle may promote further short-range foray movements, allowing animals to extend their annual home range. Hunting is also very important on the surrounding lands for locals, particularly landowners, as hunting is prohibited within RMNP. Therefore, the maintenance or increase of forested patches would encourage elk to move across the park boundary, providing additional hunting opportunities. Moreover, elk are highly valued by locals. More than half of all farmers in the Riding Mountain region (56%) enjoy seeing elk on their land, and indicate one of the greatest benefits of living near the parks is seeing wildlife (Brook and McLachlan 2006; Brook 2008).

5.3 Thesis objective #2*:* evaluate sex- and age-specific elk distribution and hunter-kill sites during the hunting season to understand the impact of hunting on elk resource selection and to improve the effectiveness of current disease control programs.

Understanding the underlying processes of disease risk such as host ecology is fundamental to effective disease management of wild populations (Fahrig and Merriam 1994; McCallum and Dobson 1995). The influence of hunting pressure on animal distribution and resource selection may affect patterns of disease transmission and persistence, and understanding ways that hunting can be applied to specific areas with high risk individuals remains a neglected but critical area of study in human-wildlife interactions. Here I have explored how hunting can be applied to elk threatened by endemic and emerging disease in a highly fragmented landscape in efforts to reduce the risk of long-distance disease spread. The predictive RSF maps provide a direct link between sex- and age-specific host distribution and hunter-kill sites during the hunting season, highlighting the critical need to make management decisions that reflect differences among sexes and ages of a single species.

Marked differences in resource selection and distribution of killed animals were found among adult male, juvenile male, and adult female elk, which highlights the importance of considering these classes separately in order to focus hunting efforts more effectively. Collared adult males in particular were rarely located on the agriculture-dominated land outside of RMNP during the hunting season. Moreover, the majority of hunter-killed locations were found right along the park border (i.e., <1 km from the boundary) in heavily forested areas. Juvenile males and adult females made some use of the surrounding lands, however adult females were found further from the park boundary compared with juvenile males. The few killed adult males around RMNP could in part be explained by the current sex and age ratio of the population, as there are many more adult females and juvenile males compared with adult males.

In addition to distance to protected area, which was the most important predictor of elk occurrence during the hunting season, selection for forest was also important for elk, presumably to benefit from close protective cover. Forest cover was also more important to adult and juvenile males. It is reasonable to suspect that security outside of the park would be more important for solitary males compared with females in groups (Hillis et al. 1991), as they would perceive greater hunter risk . Kill sites for both adult females and juvenile males occurred further out from the park compared with adult males. Kill sites were similar among all classes and were a function of multiple environmental factors. The majority of locations were found in areas with dense forest, few roads, further from large bodies of water and close to streams.

The mapped probabilities of elk occurrence from the collar and hunter-killed data, and the resulting disease risk management maps provide a straightforward approach for hunters to target the highest risk individuals that are more likely to be infected with disease. As such, this strategy creates an important opportunity for managers to take a more proactive and locally targeted approach to disease management. An important limitation in this study area so far is that management actions have not been conducted as experiments. Several disease management actions for TB have been implemented simultaneously, including barrier fencing, habitat modification inside RMNP, and regulations regarding baiting and feeding of elk. However, TB continues to exist in the Riding Mountain elk populations. Therefore I have provided an example of a small-scale experimental manipulation of hunter effort that can be tied directly to elk distribution, hunter-kill and ultimately disease prevalence.

In the Riding Mountain region, elk are free-ranging hosts of TB, and prevalence rates vary dramatically among sex and age classes. Elk in RMNP have a prevalence of 2.6% in individuals >8 years old and 0.2% in elk <1 year old. The overall prevalence by sex is 1.2% in males and 0.7% in females (Shury and Bergeson 2011). As such, management actions should be aimed at specific sex/age classes with the highest prevalence of disease, specifically adult males which have the highest prevalence in this area (Shury and Bergeson 2011). However, the greatest disease management challenge in this area is that adult males rarely leave the park. Therefore, managers may consider targeting hunter effort in the park in order to reduce the number of adult males, and prevent infected individuals from venturing out of the park.

The disease management maps for elk also create an opportunity to apply incentives and regulations to target hunting effort at very fine scales (i.e., quarter section). In order for hunting to be an effective tool for disease management, hunter effort could be targeted at finer scales than individual Game Hunting Areas in Manitoba. Furthermore, efforts could be targeted in areas with a lower probability of hunter-kill success. The success of hunters is predicated on prey detection and accessibility (Lebel et al. 2012), and hunters tend to focus efforts only in the very best habitats such as in areas that are characterized by low vegetation cover and high visibility (Millspaugh et al. 2000; Brinkman et al. 2009). Further incentives may be required to redirect hunters to these areas in order to target high-risk individuals.

Elk movements are largely restricted to within the parks, and this is likely due to the combined effects of intense hunting pressure right along the park borders and a highly fragmented landscape that is known to impede gene flow. As such, the potential for TB to be spread between elk sub-populations is limited. The agriculture-dominated landscape during the hunting season clearly generates a "landscape of fear" for elk, where animals constantly adjust their behavior in response to changing levels of risk (Hernández and Laundré 2005; Laundré et al. 2010; Ciuti et al. 2012). As such, animals tend to shift their distribution and remain either within or close to the park for security. These risk-driven shifts are not only important for preventing long-distance movements and disease between the parks, but also for reducing cattle-elk interactions at a local level, which has important socioeconomic implications. Transmission of TB between elk and livestock may occur on pastures (Brook and McLachlan 2009) and cattle winter feeding areas (Brook et al. 2012), and if any cattle herd tests positive for TB they are destroyed (Koller-Jones et al. 2006).

The concern for emerging disease such as CWD creates an important challenge in this area. CWD has not yet been detected in Manitoba, however several wild elk have tested positive for the disease only <160 km from the provincial border. The risk of CWD emergence into Manitoba is low, as the connectivity across the landscape does not support frequent long-distance movements (Chapter 3). However, the implications of CWD remain highly significant as it takes only one CWD-infected disperser to create a critical disease hazard in Manitoba. The highest risk areas for targeting elk [especially adult males that are more likely to be infected with CWD in other areas (Miller et al. 2000; Miller and Conner 2005)] are along the provincial border and the identified fragmented corridors that connect the protected areas (Chapter 3). These areas should be a priority for disease management, not only for reducing the risk of long-distance disease spread, but for optimizing disease surveillance. Increased hunter effort targeted at the highest risk individuals for TB specifically should be redirected to the northwestern corner of RMNP, which is the core area for TB-infected individuals. However the distribution of CWD in wild populations near the provincial border is relatively unknown, therefore hunter effort may need to be more dispersed along the border and western areas of DDPP&F to limit the spread of disease into Manitoba.

5.4 Conclusion

The management of endemic and emerging disease in the Riding Mountain region is clearly a formidable task, particularly because multi-host wildlife such as elk and white-tailed deer are present across the landscape and interact in complex ways. Here I present an approach to understanding the underlying processes of disease spread (host distribution and response to hunting) for elk and how this may influence the risk of disease spread between protected areas. My research indicates that dysfunctional connectivity and hunting can help limit the spread of TB and CWD across the highly fragmented landscape. However, the implications for long-term conservation of elk remain an important concern. In order to devise effective conservation and disease management strategies for wildlife, multiple factors must be considered, such as the presence of habitat corridors, matrix permeability, dispersal characteristics, gene flow, and the influence of predation at multiple scales.

My thesis has provided an effective framework in which all of these factors described above may be considered, providing a strong basis for assessing the risk of disease spread across the landscape. The risk of TB and CWD spread between elk sub-populations is currently low, however the socioeconomic and ecological implications of these diseases remain significant for multiple species including human hunters. I have provided detailed maps of functionally connected areas that may facilitate elk movement, and thus pinpoint local areas of disease management concern. I also provide an example of a small-scale manipulation of hunter effort linked to disease prevalence, with mapped areas where hunting can be targeted at the highest risk individuals for disease transmission. Resource managers can use these maps as a complementary tool to evaluate both the short- and long-term implications of habitat fragmentation and hunting efforts to effectively balance elk conservation and mitigate disease risks.

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APPENDIX A: ENVIRONMENTAL COVARIATES

Table A.1. *A priori* selection of environmental covariates for elk (*Cervus canadensis manitobensis*) used in Chapter 3 to derive resource selection function models at the scale of the quarter section (n = 7375) during the spring and summer (Mar-Aug) in southwestern Manitoba, Canada.

Covariate	Mean ± S.E.	Description of covariate
Forest	0.15 ± 0.002	Proportion of deciduous forest cover within the quarter section
Forest buffer	0.17 ± 0.001	Proportion of deciduous forest cover within a 5 km buffer around quarter section
Road	0.004 ± <0.001	Density of roads (km^2)
Town	9.12 ± 0.062	Minimum distance to town (km)
Highway	2.49 ± 0.021	Minimum distance to highway (km)
Cropland	0.49 ± 0.004	Proportion of annual cereal/oilseed
Stream	0.80 ± 0.014	Distance to stream (km)
Water	0.02 ± 0.001	Proportion of water cover including lakes and rivers
Perennial forage	0.04 ± 0.001	Proportion of perennial forage crops
Wetland	0.01 ± <0.001	Proportion of marsh and fen
Grassland	0.25 ± 0.003	Proportion of grassland

Table A.2. *A priori* selection of environmental covariates for elk (*Cervus canadensis manitobensis*) used in Chapter 4 to derive resource selection function models at the scale of the quarter section (*n* = 20,970) during the hunting season (Sep-Feb) in southwestern Manitoba, Canada.

Covariate	Mean ± S.E.	Description of covariate
Park	1.67 ± 0.01	Minimum distance to protected area or refuge (RMNP and DMPP&F; km)
Forest buffer	0.20 ± 0.01	Proportion of deciduous forest cover within a 5 km buffer around quarter section
Town	9.08 ± 0.12	Minimum distance to town (km)
Highway	2.32 ± 0.03	Minimum distance to highway (km)
Forest	0.18 ± <0.001	Proportion of deciduous forest cover within the quarter section
Road	0.01 ± <0.001	Density of roads (km^2)
Cropland	0.44 ± 0.01	Proportion of annual cereal/oilseed
Stream	0.79 ± 0.01	Minimum distance to stream (km)
Water	0.03 ± <0.001	Proportion of water cover including lakes and rivers
Forage	0.04 ± <0.001	Proportion of perennial forage crops
Wetland	0.02 ± <0.001	Proportion of marsh and fen
Grassland	0.25 ± <0.001	Proportion of grassland

APPENDIX B: FIELD VALIDATION OF LAND COVER/VEGETATION DATA

An independent accuracy assessment using ground-reference data is an integral component of any land cover monitoring effort. The four primary land cover classes: deciduous forest, grassland, perennial forage and wetland comprise the large majority of the connectivity study area (see Chapter 3). These classes were validated in the project study area (June 2011), which extends from the northern border of RMNP to the southern border of DMPP&F, and west to the Saskatchewan/Manitoba border. The accuracy assessment was determined by terrestrial surveys using the Trimble Juno SC series to generate 400 random points distributed throughout the study area (100 points/land cover class). Information was collected at each random point such as the GPS location and habitat type. An error matrix was then calculated to compare reference sites to information on the digital map (Table B.1). An overall accuracy level of 84% was identified for all four land cover classes.

Table B.1. Error matrix classification of deciduous forest, grassland, forage cropland and wetland habitat areas (*n* = 400; June 2011) in the Riding Mountain region, southwestern Manitoba, Canada.

		Reference Data (User)				
	Landscape variables	Deciduous forest	Grassland	Forage cropland	Wetland	User’s accuracy %
Classified Data (Producer)	Deciduous forest	100	1	1	1	97
	Grassland	0	82	5	0	94
	Forage cropland	0	2	62	1	95
	Wetland	0	0	0	98	100
	Agricultural cropland	--	15	32	--	--
	Producer’s accuracy %	100	82	62	98	