University of Alberta

Conservation Corridors for Carnivores: Integrating Pattern and Process in the Canadian Rocky Mountains

by

Cheryl-Lesley Barbara Chetkiewicz

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Frontispiece

Humanity badly needs things that are big and fearsome and homicidally wild. Counterintuitive as it may seem, we need to preserve those few remaining beasts, places, and forces of nature capable of murdering us with sublime indifference. We need the tiger, *Panthera tigris*, and the saltwater crocodile *Crocodylus porosus*, and the grizzly bear, *Ursus arctos*, and the Komodo dragon, *Varanus komodoensis* ... to remind us that *Homo sapiens* isn't the unassailable zenith of all existence. We need these awesome entities because they give us perspective.

David Quammen, 1998, *Deep Thoughts from Wild Places*

I am a man who regrets the loss of his fur and his tail.

Loren Eiseley, 1987, *The Lost Notebooks of Loren Eiseley*

Too much time spent staring at a computer screen can dim our memories of the enthralling complexity of animals in the wild, increasing the risk that we are not only guided and inspired by theory, as we should be, but blinkered by it.

David W. Macdonald, 2001, *Carnivore Conservation*

Dedication

For the benefit of all living beings, but especially for large carnivores that patiently test our humanity and compassion in life after life.
We walked together for such a short time in this one.

ABSTRACT

Habitat loss, fragmentation, and urbanization threaten wide-ranging and area-sensitive large carnivores like grizzly bears (*Ursus arctos* L.) and cougars (*Puma concolor* L.). Within reserve networks, corridors are rarely designed to incorporate large carnivore resource selection and movement processes. I examine and model resource selection and movement based on data from Global Positioning System (GPS) radiocollared grizzly bears and cougars in Canmore and Crowsnest in the Canadian Rocky Mountains, Alberta, Canada. I examined three questions fundamental to corridor planning for large carnivores: 1) where are large carnivores more likely to occur?; 2) what landscape features promote their movements?; and, 3) how do these landscape features affect large carnivore movements?

Resource selection function (RSF) models suggested grizzly bears were more likely to occur in areas with high greenness values, a variable associated with bear forage. Cougars were more likely to occur in areas with low road density in Canmore during non-winter and in rugged terrain in Crowsnest Pass throughout the year. I developed least-cost paths based on the inverse of RSFs to identify potential corridors that might support movement of both species between patches of high RSF value.

Step selection function (SSF) models suggested movement of cougars occurred closer to paved roads and forest cover throughout the year and they avoided crossing paved roads in the non-winter season. During the berry season, movement of grizzly bears in Canmore and Crowsnest occurred closer to paved roads and shrubs. No large carnivore paths crossed slopes > 45 degrees. Patterns of selection and avoidance can be used to provide species- and landscape-specific guidelines for where movement might

occur (*sensu* functional connectivity). I combined SSF results with analyses of step length to show that grizzly bears and cougars moved faster near paved roads during the berry and winter seasons, respectively. Conversely, cougars in Canmore and grizzly bears in both landscapes moved more slowly near forest and shrubs during the winter and berry seasons, respectively.

Compared to conventional corridor designs based on perceived structural connectedness and habitat quality, my study illustrates how a diverse, empirically based modelling approach can be used to incorporate large carnivore behavioural processes more explicitly into corridor identification and design.

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Capturing and collaring grizzly bears and cougars in two landscapes is a team effort and Alberta Sustainable Resource Development (SRD) and Community Development staff in Canmore and Crowsnest were instrumental to my project. I am indebted to Jon Jorgenson, Steve Donelon, Cindy Hague, Ian Ross, Mike Jokinen, Melanie Percy, Scott Jevons, and Ron Wiebe for their efforts in Canmore. In Crowsnest, I had the pleasure of working with Dr. Carita Bergman, Jim Clark, Kirk Olchowy, John Clarke, Andrew Gustavson, Viola Robinson, John Elias, Perry Abramenko, and the fourlegged officers, Kuma and Mica. I am also grateful for digital data shared by Alberta SRD, particularly Scott Jevons and Lana Robinson.

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CHAPTER ONE

General Introduction

Habitat loss, fragmentation, and urbanization are major threats to large carnivores (Noss et al. 1996; Weaver et al. 1996; Sunquist & Sunquist 2001). For most large carnivores, moving through the matrix between fragments is problematic because they are more likely to come into conflict with humans (Woodroffe & Ginsberg 1998; Woodroffe 2000; Ginsberg 2001) or because they die trying to navigate around human developments such as roads (Noss et al. 1996). For large carnivores, these challenges are compounded by a long history of direct persecution and intolerance which continues to affect recovery and restoration of large carnivores throughout the world (Frank & Woodroffe 2001; Maehr et al. 2001). For wide-ranging and area-sensitive carnivores, conservation groups and management agencies design and create reserve networks, currently believed to offer the best solution for sustaining populations (Noss et al. 1996; Soulé & Terborgh 1999; Carroll et al. 2001). A number of conceptual frameworks used for designing reserve networks (Soulé & Terborgh 1999; Noss 2003; Beier et al. 2006, 2008) offer a systematic planning approach to identify conservation targets for focal species, such as large carnivores. In addition, these frameworks outline methodologies for identifying and prioritizing the basic elements of reserve networks to ensure persistence of target species.

Basic elements of reserve networks include corridors (sometimes called linkages), or portions of landscape that are expected to facilitate movement between two or more discrete landscape features (also called sites, sources, patches or core areas). Expert-opinion, empirical data, and modelling approaches have been used to identify where corridors may exist on the landscape (reviewed by Noss & Daly 2006). However, their effectiveness in providing connectivity has been debated (reviewed by Hilty et al. 2006). Connectivity is defined as the interaction between a particular species and the landscape and can be structural and functional (Taylor et al. 2006). Structural connectivity Structural connectivity focuses on habitat contiguity and the spatial arrangement of landscape elements whereas functional connectivity refers to an organisms' movement behaviour on the landscape. Corridors identified or designed based on patterns of perceived structural connectivity (to humans at least) may not facilitate movements (Hannon & Schmiegelow 2002; Bélisle & Desrochers 2002; Selonen & Hanski 2003; but see Haddad et al. 2003). Reviews of corridors acknowledge that integrating quantitative habitat selection and movement processes for focal species would be more likely to identify and support corridor designs that confer functional connectivity (Beier & Noss 1998; Vos, Baveco & Grashof-Bokdam, 2002; Chetkiewicz et al. 2006; Haddad & Tewksbury 2006). Moreover, a number of tools that integrate habitat selection and movement process may better support corridor identification and designs (Chetkiewicz et al. 2006). A multifaceted approach to corridor identification and design could make land-use decisions more reliable and defensible (Noss & Daly 2006; Beier et al. 2008). Since corridor planning for large carnivores tends to involve multiple land management jurisdictions and usually occurs within a complex socio-political climate (Ginsberg 2001; Mattson et al. 2006).

My goal in this dissertation is to develop and explore the utility of models that integrate resource selection and movement process with landscape heterogeneity for cougars (*Puma concolor* L.) and grizzly bears (*Ursus arctos* L.) in two landscapes in the Canadian Rocky Mountains, Alberta that present landscape-specific challenges to corridor design and implementation within the broader Yellowstone-to-Yukon transboundary conservation initiative (Gatewood 2003). Grizzly bears in Alberta have been recommended for threatened status since 2002 and recent population estimates suggest fewer than 500 animals (Stenhouse et al. 2003). In addition, genetic analyses of grizzly bears in Alberta suggest limited genetic connectivity of grizzly bear populations at the southern extent of their range in western Canada (Proctor et al. 2005). Habitat losses and high rates of human-caused mortality threaten the long-term persistence of grizzly bears in Alberta (Benn et al. 1998; McLellan et al. 1999; Nielsen et al. 2004a,b, 2006). Cougars have received much less research and management attention in Alberta (Fish and Wildlife Division 1992; Jalkotzy et al. 1999). I focused on two species to examine how habitat selection processes and movement might differ given their different ecological resilience profiles (Weaver et al. 1996).

Objectives

I address corridor conservation planning needs for cougars and grizzly bears in two landscapes in the Canadian Rocky Mountains of Alberta. Specifically, I examine how resource selection functions (RSF, Manly et al. 2002), least-cost paths (LCPs, Theobald 2006), step-selection functions (SSF, Fortin et al. 2005), and movement analyses based on step lengths (Turchin 1998) can inform both patch or site selection and corridor designs. I used Global Positioning (GPS) radiotelemetry data I collected for grizzly bears and cougars, in two landscapes in the Canadian Rocky Mountains, Alberta to build these models. I used the results to discuss the assumptions of different modelling approaches to corridor identification and design as well as their potential applications.

This dissertation is composed of six chapters, including this introductory chapter and a final chapter (Conclusions). Data-based chapters are organized into independent papers, one of which (Chapter 2) has been published. Chapter 2 follows the format for *Annual Reviews of Ecology, Evolution and Systematics*, Chapters 3 and 4 follow the format for the *Journal of Applied Ecology* and Chapter 5 follows the format for *Conservation Biology*.

Briefly, in Chapter 2, I and my co-authors review corridors in conservation. Specifically, we suggest that corridor planning would be improved if it incorporated processes of habitat selection and movement. We recommend a number of recent statistical and analytical tools including RSF, SSF, and other modelling approaches to improve corridor planning. In Chapter 3, I address how habitat selection of grizzly bears and cougars in two fragmented landscapes might inform corridor identification and design. Specifically, I develop and validate seasonal RSF models at the home range scale of availability to quantify habitat selection given landscape features, food resources, and roads. I combine seasonal RSF models with least-cost path analyses to locate potential corridors in both landscapes. In Chapter 4, I examine movement patterns of grizzly bears and cougars in two fragmented landscapes. Specifically, I quantify movement patterns with seasonal SSFs for both species and examine the response of selection to paved roads, landcover types, and terrain variables. I also develop models of step-length to examine how cougars and grizzly bears are moving in response to these same features. I combine the SSF models and step length analyses to highlight consistent movement types that might better inform corridor design and implementation. In Chapter 5, I examine how each modelling approach contributes to corridor planning. Specifically, I use the results from each approach to answer three fundamental questions for corridor design and implementation: 1) where are large carnivores more likely to occur?; 2) what landscape features support large carnivore movement?; and, 3) how are large carnivores moving? I use these results to highlight the application, limitations, and benefits that these approaches offer to corridor planning for large carnivores. Taken together, these chapters help address the need for a more robust and quantitative approach to corridor design for large carnivores. Quantifying the processes of habitat selection and movement provides a behaviourally-based link to current landscape conditions that can inform management and conservation of grizzly bears and cougars in Alberta and provide a framework for corridor-based research on large carnivores elsewhere.

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CHAPTER TWO

Corridors for conservation: integrating pattern and process[1]

1. Introduction

Corridors are cornerstones of modern conservation. Corridors traditionally have been viewed as linear strips of habitat to facilitate movement of organisms through landscapes (Puth & Wilson 2001). Corridors, often in association with the charismatic megafauna whose populations they are designed to conserve, are a fundamental component of wildland conservation, particularly in North America, where many regional and several continental-scale corridor initiatives are underway (Nelson et al. 2003). International corridors foster new levels of transboundary conservation, elevating corridors from an ecological to political and socioeconomic tool (Zimmerer et al. 2004). Despite the wide-spread application of corridors, much current practice causes them to fall far short of their conservation promise. On-the-ground applications of corridors usually are based on simplistic depictions of habitats that are assumed to provide the associated ecological processes. Typically, corridor applications proceed with little species-specific information and limited evaluation, and they are rarely published or reviewed in scientific journals (Vos et al. 2002, but see Beier et al. 2006). In some cases, corridors, selected for their political appeal, are being plunked down willy-nilly on landscapes that already have been carved up for other purposes. This makes the provision of practical corridor

[1] *A version of this chapter has been published. Chetkiewicz, C-L B., St. Clair, C.C., and Boyce, M.S. 2006. Annual Review of Ecology, Evolution, and Systematics. 37: 317-42. Reprinted with permission from Annual Review of Ecology, Evolution, and Systematics.*

guidelines for managers as big a challenge today as it was over a decade ago (Hobbs 1992).

A grizzly bear (*Ursus arctos*) tagged as "99" and his victim provides a compelling study in the failings of this approach. This young male bear wandered into the fringes of the burgeoning town of Canmore, Alberta in late May, 2005. After showing indifference to human encounters, it was captured on a local golf course and relocated by government conservation officers. A week later, "99" was detected in a designated wildlife corridor above the town of Canmore, one that was a scant 1000 m wide, perforated with human-use trails, and sandwiched between a recently built golf course and steep slopes above the townsite. By the day's end, both the bear and a young woman were dead, and the world tuned in to Alberta's first grizzly caused human fatality in seven years. Critics were quick to blame the wildlife policy that relocated the bear. But the bigger failing occurred years previously with the designation of the corridor. Corridors based on scant biological data supported Canmore's rapid development during the 1990s obliterating much of the wildlife habitat in this montane valley. Too little fertile and connected habitat remains in the valley that contains Canmore to support grizzly bear movement to adjacent protected areas in the Canadian Rocky Mountains (Herrero 2005). Indeed, examining movements of three other grizzly bears in this area suggests that the designated corridors actually are avoided and the oft-assumed distinction between corridor and matrix is not apparent (Figure 1a). Despite various planning guidelines supporting corridor designations (BCEAG 1999), the corridor designs in Canmore require important modifications, at least for grizzly bears. We suggest that more sophisticated approaches to corridor designs not only are possible but essential if corridors are to realize their potential for conserving biodiversity.

Although they have limitations (Simberloff & Cox 1987, Hobbs 1992, Simberloff et al. 1992, Collinge 2000), corridors have been promoted widely as a conservation strategy. Since their introduction as a tool for game management in the 1940s (reviewed by Harris & Scheck 1991), over 700 scientific papers concerning corridors have been published. Most acknowledge that the purpose of corridors is to counter the effects of habitat loss and fragmentation, which are the most important causes of biodiversity loss worldwide (Sih et al. 2000, Dirzo & Raven 2003). Corridors are expected to slow these effects by increasing the movement of individuals among otherwise-isolated populations (e.g., Gilbert et al. 1998, Gonzalez et al. 1998), thereby rescuing populations from stochastic local extinctions (e.g., Brown & Kodric-Brown 1977, Reed 2004), maintaining genetic diversity (e.g., Mech & Hallett 2001, Hale et al. 2001), and retaining ecological processes (Bennett 1999, Soulé & Terborgh 1999, Levey et al. 2005, Haddad & Tewskbury 2006). Additionally, corridors might serve to provide routes and habitats for movement of organisms responding to climate change (Channell & Lomolino 2000). Other approaches to conserving biodiversity might be more effective than corridors (Schultz 1998, Hannon & Schmiegelow 2002), or offer better return on the investment of limited conservation dollars (Simberloff & Cox 1987, Hobbs 1992, Simberloff et al. 1992). We do not address these issues here. Rather, we assume that corridors will continue to occupy the conservation toolbox and ask how that tool can be used most effectively.

One important impediment to the effective use of corridors is the gap between their intended purpose and actual application, which generates a dichotomy between pattern and process. By pattern, we mean the composition and spatial configuration of habitats (Wiens 1995, Turner et al. 2001) and snapshots of organism distribution derived from censuses. By process, we mean the ways animals actually move within landscapes to cause patterns of distribution and drive related ecological processes. Probability of movement then determines the functional connectivity of landscapes (Taylor et al. 1993, Tischendorf & Fahrig 2000a, b). Despite the fact that the process of animal movement provides the impetus for corridor design and application, it is the pattern of landscape structure that dictates most of the research, planning, and application of corridors (Beier & Noss 1998, Vos et al. 2002). Yet an extensive review (Beier & Noss 1998) found corroboration between corridor patterns and process-based metrics such as immigration and colonization rates in fewer than half of the studies. Since that time, dozens more observational and experimental studies have focused on corridors. A few emphasize processes (e.g., Sieving et al. 2000, Berggren et al. 2002, Levey et al. 2005). More often corridor designations are based -- as they were in Canmore -- on patterns of remaining habitat that appear (to human observers) to be connected in a simplified and binary depiction of the landscape.

The enduring bias of binary landscapes in corridor plans and studies stems partly from the ecological theory supporting corridor designs. Island biogeography (MacArthur & Wilson 1967) offered the stepping stones that others generalized to corridors (Wilson & Willis 1975, Diamond et al. 1976). Metapopulation theory (Hanski & Gilpin 1997) inferred the processes of dispersal, colonization, and local extinction in binary habitat patches with different spatial configurations (Dunning et al. 1992, Fahrig & Merriam 1994). Landscape ecology (Turner 2005) reinforced the patch-corridor-matrix paradigm by quantifying habitat configuration and composition patterns mainly with tools that juxtapose habitat and non-habitat (e.g., Turner & Gardner 1991, McGarigal et al. 2002). Together, these theories have vastly increased appreciation of the relationships between habitat patterns and populations, but they have done so in a way that promotes corridors as archetypically linear and static features (Saunders et al. 1991, Hobbs 1992, Beier & Noss 1998) in binary landscapes.

This simplistic, pattern-based view of corridors as habitats has resonated with ecologists because of its tractability (Goodwin & Fahrig 2002, Goodwin 2003) and scale versatility (Calabrese & Fagan 2004), but it has important limitations. First, it assumes that movement is categorically facilitated by corridors and impeded by the matrix (Simberloff et al. 1992, Rosenberg et al. 1997, Baum et al. 2004), whereas real landscapes create a continuum of influences on movement (Puth & Wilson 2001). Second, this simplified, categorical view of corridors homogenizes species and spatial scales for corridor planning whereas functional connectivity is inevitably species-specific (Lidicker 1999, Puth & Wilson 2001, Goodwin 2003). In fact, corridors may not be beneficial to some species (Schmiegelow et al. 1997, Schultz 1998, Collinge 2000, Hannon & Schmiegelow 2002), although there is little to support the argument that they are detrimental (e.g., Hess 1994, Boswell et al. 1998, McCallum & Dobson 2002). Thus, pattern-based approaches to corridor planning may not make appropriate provisions for all or even most of the species for which a corridor is designed, and corridor structure may be both insufficient and unnecessary to promote movement. Better integration of pattern and process is critically important to corridor design.

Several authors have distinguished the pattern and process components of corridors (Rosenberg et al. 1997, Bennett 1999) and landscape connectivity more generally (Tischendorf & Fahrig 2000b, Bélisle 2005). Others have acknowledged that corridors are more than linear structures in binary landscapes (Hobbs 1992, Beier & Noss 1998) and instead are places on the landscape that facilitate the movement of individuals, promote genetic exchange, and support ecological processes (Puth & Wilson 2001, Forman 2002). Broadening the concept of corridors to "linkages" allows them to support these processes without being linear, continuous, or even structurally distinct from the surrounding landscape (Bennett 1999). We amplify these views by suggesting that a greater emphasis on the processes of habitat selection and movement could address several fundamental questions that pattern-based approaches tend to neglect. We do not attempt to answer these questions but review new approaches and tools that can be used to identify, design, and test corridors for conservation more effectively.

First, should corridors promote certain types of movement? Corridors often are assumed to facilitate dispersal but this might not be the only movement type relevant to corridor designs. Moreover, it is frequently difficult to know the motivation of moving organisms (Lima & Zollner 1996). Instead of assuming this motivation, we could statistically identify habitats that are associated with short-range foraging movements versus longer-distance movements (e.g., Johnson et al. 2002). This approach makes it possible to separate movement into types, some of which might be targeted by corridor designs, even without identifying their underlying motivation.

Second, should corridors increase movement rates relative to movement in other habitats (Puth & Wilson 2001, Haddad & Tewksbury 2005)? Individuals have more tortuous pathways in good quality habitat and move further and faster over unfavorable terrain (Crist et al. 1992, Johnson et al. 1992, With 1994). However, individuals that move more sometimes suffer higher mortality (Biro et al. 2003, Frair et al. 2007). Moreover, high movement rates in corridors may not correlate with the functional connectivity of a landscape (Bélisle 2005).

Third, is habitat quality as important as movement characteristics in designing corridors? Even if animals use corridors only to travel between suitable patches, they are unlikely to do so if they perceive that the habitat within the corridor is unsuitable. Organisms use a wide variety of mechanisms to select suitable habitats (Stamps 2001, Danchin et al. 2001) and knowing the details of habitat selection might be as important to corridor design as it is to identifying suitable habitat for other purposes.

Fourth, if corridors result in ecological traps or sinks (e.g., Weldon & Haddad 2005), is their corridor function necessarily compromised? Only occasional movement is necessary to maintain gene flow (Mills & Allendorf 1996) and infrequent dispersal may be sufficient to sustain demographic rescue (Hanski 2001). Corridors might provide these benefits to adjacent populations over large time scales, even if they lessen the survival and reproductive success of most of the individuals that use them.

Despite over 20 years of research on corridors, few corridor studies lend insight into these questions. Rather than review the latest empirical studies that focus on corridors, we explore recent advances in technology and quantitative methods that make it easier than ever before to answer these questions by integrating pattern and process.

These tools could revolutionize our ability to design and manage corridors to ensure that they are accomplishing conservation objectives. This review is intended to identify those opportunities by showing how we can develop gradient-based habitat selection models and probabilistic movement models to identify corridors in complex, real-world landscapes.

2. Habitat Selection Processes

Habitat selection is the behavioural process used by individuals when choosing resources (Johnson 1980) and habitats. These choices occur at a variety of spatial and temporal scales that range from finding food resources within a season, to defining home ranges during a lifetime, to expansion of ranges across generations (Johnson 1980; Table 1). The motivation for habitat selection is presumably to maximize individual fitness (Garshelis 2000) with consequences for distribution and density across different habitats (Morris 2003). The behavioural mechanisms that play a role in habitat selection for residency, such as conspecific attraction, habitat imprinting (reviewed by Stamps 2001), natal home range cues (Cooper et al. 2002), and public information (Danchin et al. 2001), logically apply to the selection of habitats for movement (i.e., corridors) as well. Even during dispersal movements, animals must forage, sleep, avoid predators, and either seek out or avoid conspecifics. They do not have the omniscience that geographical information systems (GIS) provide us to visualize corridors as merely routes to better habitats and must instead continuously assess habitat for its suitability. The assumed dichotomy between patch and corridor is likely perceived by animals as a continuum.

A second false dichotomy applies to the way corridors are typically viewed as connected areas of habitat, in a "sea" of inhospitable matrix. We know that the so-called matrix is often used as habitat (Haila 2002, Rosenzweig 2003, Berry et al. 2005) and that it can increase the viability of adjacent populations (e.g., Vandermeer & Carvajal 2001). Moreover, matrix characteristics determine the use of embedded corridors and stepping stones (e.g., Baum et al. 2004) and more complex matrices may dramatically reduce the effects on movement of patch isolation (Bender & Fahrig 2005). Thus, organisms actually occupy a spectrum of habitats in nearly every landscape type. The artificial dichotomy of patch and matrix creates fundamental difficulties for understanding species responses to fragmented habitats (McIntyre & Hobbs 1999, Fischer et al. 2004). Fortunately, habitats can be described instead as probabilistic functions of multiple landscape attributes.

2.1 Resource Selection Functions

Habitats can be characterized using resource selection functions (RSFs), defined to be any function that is proportional to the probability of use of a resource unit (Manly et al. 2002). A resource unit is a sampling unit of the landscape, e.g., a pixel or grid cell. Predictor variables (covariates) are habitat attributes that can be used to predict the relative probability of use for a resource unit (Manly et al. 2002)

A number of sampling designs can be used to estimate an RSF, e.g., a random sample of resource units could be drawn and examined for the presence or absence of an organism (Boyce & McDonald 1999). Model coefficients can be estimated using logistic regression if occurrence is recorded as absence-presence (0,1), or an alternative link function might be used for count data, such as Poisson regression or zero-inflated Poisson regression (ZIP; Nielsen et al. 2005). Alternatively a sample of occupied resource units could be contrasted with a random sample of landscape locations using a logistic discriminant function (Johnson et al. 2006). Predictive ability of an RSF can be assessed using *k*-fold cross validation (Boyce et al. 2002).

Such an RSF can be applied in a geographic information system (GIS) to map the relative probability of use across the landscape, in contrast with binary maps of habitat vs. non-habitat. For most organisms, patterns of use of a landscape are much more complex than simple binary characterizations of habitat. These models can be used to identify habitat associations for animals at multiple scales (e.g., Carroll et al. 2001, Gaines et al. 2005).

2.2 Using Resource Selection Functions to Delineate Corridors

By depicting landscapes as probabilistic functions, RSF models offer an important departure from categorical representations of corridors, patch, and matrix habitat. Although RSF models tell us nothing about the movement of animals per se, they allow us to identify habitats that are likely to support occupancy. For example, we used the telemetry locations for three grizzly bears in the Canmore region of the Bow Valley, Alberta, Canada (Figure 1a) to generate an RSF that compared topographic and vegetation variables at telemetry locations with those at random locations in their combined home ranges (Figure 1b). Applying the RSF to a GIS illustrates areas of high probability of occupancy (green) and their proximity to one another as well as areas of lower probability of occupancy (red). This approach provides a powerful framework for locating potential corridors or evaluating current corridor designations (Figure 1a).

Although characterizing habitats used by organisms would appear to be a fundamental first step in identifying corridors, caveats are appropriate. Use of habitats does not necessarily mean that the habitats are productive ones, and in the worst case used habitats might be sinks or traps (Pulliam 1988, Kristan 2003). Yet, 85% of avian studies have found that habitats used more intensively by a bird species were also those in which reproductive success was highest (Bock & Jones 2004). Nonetheless, corridors may sometimes represent poor quality habitats while still facilitating movement (Haddad & Tewksbury 2005).

3. Movement Processes

Organisms are motivated to move to forage, avoid predators, find breeding opportunities, access seasonal or ephemeral resources, and expand ranges (Ims 1995, Bennett 1999), generating movements that range from foraging patches of a few cm^2 to transcontinental migrations. Ims (1995) offered four categories of movement – foraging, searching, dispersal, and migration – that are strikingly similar to a hierarchy of habitat selection described earlier by Johnson (1980; Table 1). All of these categories are relevant to corridors (Bennett 1999), but dispersal tends to be emphasized as most pertinent (reviewed by Vos et al. 2002), particularly for spatially structured populations (reviewed by Clobert et al. 2001). Yet corridors also may be critical for maintaining seasonal migrations (e.g., Powell & Bjork 1995) or for access to resources within a home range (e.g., Nielsen et al. 2004a). With so many contexts for movement and such a fundamental role in population dynamics, it is surprising that movement as a process is seldom explicit in corridor planning. This lack of emphasis has been caused, in part, by the difficulty of quantifying movement.

3.1 Techniques for Measuring Movement

Turchin (1998) identified two empirical approaches for measuring movement: Eulerian and Lagrangian. Eulerian approaches measure population metrics by recording the redistribution of large numbers of marked or unmarked individuals at specific locations. Individuals have been marked using leg-bands in birds, radioisotope labels and dyes in insects, or otolith dyes in fish (reviewed by Southwood & Henderson 2000). Subsequent recaptures, resightings, or recovery provide an estimation of movement rates (reviewed by Bennetts et al. 2001). In contrast, Lagrangian approaches characterize the magnitude, speed and directionality of individual movements with a variety of techniques. For insects, movement paths have been recorded using numbered flags (e.g., Schultz 1998) or harmonic radar systems (e.g., Cant et al. 2005), whereas movement pathways for vertebrates can be recorded using snow tracking (Whittington et al. 2005) or radiotelemetry (Millspaugh & Marzluff 2001). Movement paths are quantified by velocity, step lengths, degree of directionality, and measures of tortuosity (Turchin 1998). Eulerian and Lagrangian approaches provide different but complementary methods for understanding animal movements across a landscape.

In general, Eulerian approaches do not provide the same detail of movement information as Lagrangian approaches, but they make it possible to describe movement over much larger spatial and temporal scales. Eulerian approaches employing genetic techniques (Webster et al. 2002, Nathan et al. 2003, Nathan 2005) or stable isotopes (reviewed by Rubenstein & Hobson 2004, Hobson 2005) are rapidly evolving and offer particular promise to reveal landscape connectivity. Because individuals are "marked" with a unique genotype or isotopic signature, the frequency of various markers from different sources can be identified. Genetic techniques offer enough precision to provide an estimate of dispersal movements within one or more generations (Waser & Strobeck 1998). For example, Proctor et al. (2004) measured genetic similarity to estimate dispersal distances for grizzly bears and to show that animals moved with a series of short stepping stone like movements rather than a few long-distance dispersal movements. Genetic approaches also can be used to measure the effect of corridor patterns on gene flow (e.g., Aars & Ims 1999, Mech & Hallett 2001) or to document that some organisms moved through corridors (e.g. Coffman et al. 2001). These methods may be complemented with Lagrangian approaches to show how individual movements influence gene flow (e.g., Keyghobadi et al. 2005).

Many applications of Lagrangian approaches have involved small organisms (e.g., Schultz 1998) and experimental systems (e.g., Haddad 2000), but global positioning systems (GPS) radiotelemetry can provide detailed movement information over much broader spatial and temporal scales (reviewed by Millspaugh & Marzluff 2001). Obviously, GPS radiocollars increase the practicality of collecting movement information for wide-ranging organisms, but handheld GPS also can be combined with field observations or conventional telemetry to support equivalent spatial grain and extent for animals that are too small to wear GPS collars or to offset the relatively high costs of GPS radiotelemetry. GPS technology provides exciting new potential to use Lagrangian data to design and evaluate corridors. The ideal approach might engage both Eulerian and Lagrangian methods.

3.2 Quantifying Movement Processes

Kernohan et al. (2001) described three non-exclusive categories of quantitative approaches for characterizing movement: 1) summarizing movement pathways with turning angles, fractal dimensions, and step lengths; 2) modelling movement with random walks or their variations (Turchin 1998); and, 3) identifying patterns in movement data retrospectively to distinguish different movement types (e.g., Morales et al. 2004). The first approach, quantifying movement pathways as turning angles, step lengths (Figure 2), and fractal dimensions offers several advantages. First, these metrics can be used to associate movement types with landscape features. For example, cougars moving ≥ 100 m at any one time tended to have straighter movements and moved faster through urbanized areas (Dickson et al. 2005). Second, these metrics can be used to parameterize movement rules for spatially explicit models. Such a model was created from movement data for beetles to evaluate the effect of hedgerow width on movement rates (Tischendorf et al. 1998). A final advantage of quantifying movement pathways is they can be used to examine responses to edges or habitat boundaries. For example, eastern bluebirds (*Sialia sialis*) typically flew parallel to edges in an experimentally fragmented field system emphasizing the role of edges in directing and channelling flight pathways (Levey et al. 2005).

The second approach characterizes movements according to a mechanistic model, typically derived from diffusion theory and approximations of random walks (Turchin 1998). For example, Gustafson and Gardner (1996) simulated self-avoiding random walkers to explore the effects of landscape heterogeneity on movement patterns and identify frequently traversed portions of the landscapes that might denote corridors. In another application, a correlated random walk (CRW) diffusion model was used to simulate movements by grizzly bears and illustrate how land ownership and habitat information could reveal dispersal routes (Boone & Hunter 1996). Even if real organisms usually violate some of the assumptions of general movement models (Bergman et al. 2000), CRWs can be useful null models for distinguishing different movement types (Austin et al. 2004) and opportunities for corridors.

The third approach for quantifying movement is to identify types of movement retrospectively. An early method for achieving this was fractal dimension (fractal ***D***), but this technique was typically applied to small organisms and limited spatial scales (reviewed by Nams 2005). GPS technology makes it possible to apply similar approaches at much broader spatial and temporal scales. For example, Johnson et al. (2002) used a non-linear ("broken stick") curve-fitting procedure to define two types of movement behaviour for caribou (*Rangifer tarandus*) in British Columbia. This approach used variation in the frequency of movement rates to define a threshold value that could differentiate between intra-patch movements (short, high-frequency moves below the threshold) and inter-patch movements (larger, less-frequent moves greater than the threshold) (Figure 3). We might expect that longer-step, inter-patch movements would better characterize habitats used as corridors.

Once different movement states are identified, they can be combined with RSF-based habitat characterizations to align behavioural states with landscape features. Morales et al. (2004) used a latent model structure based on turn angles and step lengths to identify two behaviours: "encamped" (step lengths were small, turning angles were high) or "exploratory" (step lengths were several kilometers long, turning angles were low) for wapiti (*Cervus elaphus*) in Ontario. They then identified landscape features correlated with these states. Frair et al. (2005) used a similar approach to identify three types of movement behaviour in wapiti and then related these behaviours to landscape conditions including wolf (*Canis lupus*) predation risk and cover.

The three approaches to quantifying movement we have described here have two important attributes. First, all are readily applied to a variety of temporal and spatial scales. Previous use of different approaches for small and large organisms has polarized the corridor literature (Haddad et al. 2000, Noss & Beier 2000). Although generalizations that transcend spatial scales for management are challenging (Boyce 2006), it is sometimes possible to derive movement mechanisms at one scale and apply them to other scales (e.g., Ims et al. 2003). In other cases, movement processes may not generalize across scales (e.g., Fortin et al. 2005a), yet these limitations are more readily apparent when movement is emphasized (e.g., Urban 2005). For example, highway-crossing structures designed as corridors for grizzly bears are frequently used by large animals (Clevenger & Waltho 2005), but almost completely avoided by microtine rodents (McDonald & St. Clair 2004).

A second useful attribute of quantifying movement is that it provides a means of identifying important differences among individuals. For example, female grizzly bears appear much less willing to cross barriers than males (Gibeau et al. 2002). Individual variation generally has been viewed as an inconvenience in wildlife studies but might be profitably examined and incorporated in studies of both habitat selection and movement with random effects (Gillies et al. 2006). Similarly, latent class models (McCulloch et al. 2002) can be used to identify how individual motivation affects both habitat selection and movement. Understanding individual variation in movement and habitat selection may be an important aspect of corridor planning, particularly if the individuals targeted by the conservation (e.g., adult females) exhibit more specific preferences or behaviours.

4. Marrying Pattern and Process for Corridor Design

A main impediment to advancing corridor study and planning is the missing integration between patterns of landscape composition and configuration, and the processes of habitat selection and movement. In this section we review what we consider to be the most promising approaches for advancing that integration. One of the earliest applications of this sort is percolation theory (With 1997, 2002), which examines movement within spatially structured systems representing neutral landscapes. In these landscapes, a lattice grid of "habitat" cells can be connected structurally (lattice percolation) or via movement rules (bond percolation) (With 2002). Species-specific responses to real landscapes, such as gap-crossing abilities (e.g., St. Clair et al. 1998, Desrochers 2003) and responses to edges (e.g., Schultz 1998, Haddad 1999), can be used to define movement rules for percolation models (With 2002). For example, Williams and Snyder (2005) used common 'neighbor rules' from percolation theory to evaluate how habitat corridors could be restored to maintain percolating clusters, an assemblage of connected habitat cells, across the extent of simulated neutral landscapes. This application showed how landscape connectivity could be optimized to maintain percolating clusters while minimizing both corridor length and the number of nonhabitat cells that needed to be restored. Surprisingly, a meandering corridor sometimes generated lower costs (measured with both the number of restored cells and corridor length) than the shortest straight-line corridor between habitat cells. In this case, percolation theory based on movement rules identified a non-intuitive approach to corridor design.

Least-cost path analysis is a GIS-based approach similar to percolation theory except it involves estimating movement costs between two points from the suitability of intervening habitat. Parameters are based on descriptions for suitable habitats derived either from the literature or expert opinion (e.g., wolves are unlikely to occur above 1,500 m; Singleton et al. 2002), and a raster grid based on accumulated distance weighted such that suitable habitats have lower movement "costs" than unsuitable habitats. The least-cost path analysis evaluates the "costs" of moving between two habitat nodes by comparing the cumulative weighted distance between the cell and the two nodes. This approach has been used to map and visualize corridors (e.g., Singleton et al. 2004, Beier et al. 2006), but is typically based on assumptions about movement and habitat suitability, rather than empirical data. Telemetry data are not required for a least-cost path analysis. Tools like RSF and the movement analyses described above offer new ways to quantify path costs. RSFs have been estimated for three carnivores in the Rocky Mountains based on sighting data (Carroll et al. 2001) and mortality locations for grizzly bears have been used to characterize landscape features where bears died in Alberta (Nielsen et al. 2004b). If these multi-variable characterizations of habitats could be combined with movement processes, a better measure of functional landscape connectivity (*sensu* Taylor et al. 1993) would result.

Graph theory offers particular promise for measuring landscape connectivity holistically by combining the movement emphasis of percolation theory and the habitat modelling potential of least-cost path modelling. Graph theory evolved for transportation and computer networks (Cantwell & Forman 1993) and only recently has been applied to assessments of landscape connectivity (Urban & Keitt 2000). Graph-theoretic approaches combine landscape data, typically derived from a GIS, with movement data measured as either a dispersal distance (D'Eon et al. 2002) or a random draw from a dispersal kernel generated as a function of dispersal probability with distance (Havel & Medley 2006). A lattice describes the connections between pair-wise combinations of resource patches (nodes), which can be quantified as dispersal distances (edges) or weighted by other movement metrics such as tortuosity. If the distance between a pair of nodes is less than or equal to the movement threshold used, the nodes are connected. The sum of these connections can be scaled up to assess the connectivity of the entire network using a variety of metrics such as correlation length and distance to cluster edge (Calabrese & Fagan 2004). Greater correlation lengths, for example, result from an increase in the sizes of clusters suggesting greater landscape connectivity. Best of all, these process-based metrics of connectivity are readily visualized on maps to explore the effects of adding or removing connections between nodes (e.g., corridors) or resource patches (Bunn et al. 2000, Urban & Keitt 2001). For example, Urban (2005) created a graph for the wood thrush (*Hylocichla mustelina*) in North Carolina using habitat patches as defined in a GIS as nodes and movement thresholds of 2,500 m to define graph edges (Figure 4). The resulting graph effectively identified functional corridor locations by showing how the loss of two small patches would break the single connected graph into three separate components. Importantly, these locations did not fit a conventional corridor description of linear and connected habitat and their identification was driven by information about bird movement. It is less likely that they would have been identified by a pattern-based approach to corridor designation.

Although graph theory typically relies on a binary depiction of habitat (nodes), it is possible to identify these nodes probabilistically with an RSF (B.L. Schwab, C. Woudsma, S.E. Nielsen, G.B. Stenhouse, S.E. Franklin SE, & M.S. Boyce, submitted). Schwab and colleagues developed an RSF for grizzly bears in Alberta to locate areas where bears were more likely to occur (high RSF). These areas were then used to generate nodes (habitat patches) and the inverse of the RSF (i.e., 1/RSF) was used to generate a cost surface as a surrogate for movement. Least-cost path modelling was then applied to this 1/RSF cost surface and the resulting paths were compared to paths created with out-of-sample GPS location data. These data aligned with the cost surface estimated from 1/RSF showing that it performed well as a predictor of movement. This approach provides an exciting advance over previous least-cost methods such as linkage zone prediction (LZP) models. LZP models typically predict the relative probability of movement through an area by integrating qualitative scores for a number of GIS layers. For example, an LZP model for grizzly bears integrated human features, linear disturbance elements, visual cover, and riparian habitat (Singleton et al. 2004). However, an LZP model does not incorporate quantitative information about habitat or movement and generally is not validated with empirical data (Carroll et al. 2001).

Combining graph theory with RSF models offers a technique for quantifying connectivity in general and corridors in particular because it explicitly combines spatial topology with resource selection (Wagner & Fortin 2005). Because graph theory summarizes the spatial relationships between landscape elements (configuration and composition) in a concise way (Urban & Keitt 2001, D'Eon et al. 2002, Calabrese & Fagan 2004), it is especially helpful in anticipating the effects of adding or deleting particular landscape elements. Graphs also may be used to model effects of landscape on movements in two ways. First, using qualitative measures or values derived from movement data in different habitats (Manseau et al. 2002), nodes can be assigned with different weights or resistance to movement (Cantwell & Forman 1993). Second, directionality can be applied to the graph edges in the form of vectors (Urban & Keitt 2001) overcoming the enduring problem of ignoring anisotropy in landscape connectivity (Bélisle 2005). And finally, graphs can be constructed with fairly modest data (Urban 2005) to provide a useful visual tool for considering corridor placement for several species simultaneously or evaluating their associated land costs (Williams 1998).

A second new approach for integrating landscape pattern and movement processes uses conditional logistic regression to quantify movement probabilities across landscapes using step selection functions (SSF), a technique similar to RSF. Instead of characterizing telemetry locations in an RSF, Fortin et al. (2005b) paired each step (i.e., a segment between locations on the landscape) made by wapiti with random steps having the same starting point to model the effects of landscape heterogeneity on movement. They found wapiti were influenced by distance to roads, cover, and wolf predation risk. Using this approach, areas of high movement probability quantified by the SSF could be used to predict movement distance and direction in the context of a specific landscape, which is the essence of corridor design (*sensu* Haddad & Tewksbury 2006). SSF also could be used in combination with information on movement behaviour at boundaries or edges to provide stronger support for corridor designations, without reliance on categorical landscape depictions.

Graph theory and SSFs are two ways that pattern and process can be integrated better in corridor designs and studies, but many other approaches are likely possible. For example, the currency of travel cost, so extensively employed in analytical models of optimal foraging behaviour (Stephens & Krebs 1986), has barely been investigated in the context of landscape connectivity (Bélisle 2005). More generally, we advocate using behaviourally informed or process-driven methods to model habitat use and movement to identify landscape locations with high need or potential for corridor functions, rather than assuming these functions based on perceptions of habitat structural connectivity. We suggest that this approach offers several important advantages for designing and assessing corridors. First, movement processes reflect an organism's perception of landscape (Lima & Zollner 1996, Olden et al. 2004), which undoubtedly varies among individuals as well as species. Second, a focus on movement behaviour lets one identify whether or not corridors alter movement rates, a critical dimension of corridor efficacy (Simberloff & Cox 1987, Simberloff et al. 1992). Finally, a better understanding of movement processes can be used to evaluate the effect of corridors on related key processes for individuals (dispersal, reproduction and survival, e.g., Dzialak et al. 2005), populations (rates of immigration, emigration, persistence, and recolonization, e.g., Coffman et al. 2001, Berggren et al. 2002), and communities (biodiversity, predator-prey interactions, trophic cascades, e.g., Haddad & Tewksbury 2006).

5. Conclusions

"Corridors are not *the* answer to our conservation problems" (Noss 1987), but they could be used better to fulfil the promise they offer to conservation. We believe that the limitations to identifying and designing effective corridors can be traced to insufficient understanding of the processes that govern use of corridors by species of conservation interest. Behavioural processes of habitat selection and movement determine how animals use landscapes and thereby are fundamental to the identification and evaluation of corridors. We have reviewed a new generation of technological and analytical tools that allow us to quantify both habitat selection and movements with the expectation that these will allow us to approach corridors more holistically and objectively.

The Canmore example given in the introduction provides an illustration of the approach we advocate and, indeed, are attempting (C-L. Chetkiewicz, unpublished data). There, we could conduct an RSF analysis for grizzly bears using sightings, mortality locations, and data from telemetered animals (e.g., Figure 1a) to identify habitats with high probabilities of use. Then we could use SSF or graph theory to identify factors that promote movement across the landscape. RSFs would identify landscape characteristics supporting grizzly bear occurrence outside designated corridors (e.g., Figure 1a, 1b) and an SSF could be used to identify habitat characteristics that promote different movement behaviours. We could also use RSF and SSF models to explore important variation among individuals (e.g., habituated vs. non-habituated animals) in habitat selection and movement processes. Together, this information could be used to identify locations for mitigation (e.g., enhancing habitat, removing attractants, limiting human use or infrastructure) both inside and outside currently designated corridors. For example, the removal of human infrastructure and associated human use was highly successful in restoring connectivity for wolves on the outskirts of the town of Banff (Duke et al. 2001). These approaches might also make it possible to combine humans and wildlife more safely in areas that appeal to both groups because of the wild areas they still contain.

We believe that more attention to the processes of habitat selection and movement will greatly strengthen our ability to identify and design effective corridors for conservation, and we suggest that this attention will bear importantly on the four fundamental questions we posed in the introduction. There we asked (1) if certain types of movement were more pertinent to corridors, (2) if corridor designs should promote faster movement, (3) if habitat selection is as important as movement parameters in identifying corridors; and, (4) if corridors can promote gene flow and rescue effects even if they function as ecological traps and sinks? Answers to these questions are just beginning to emerge.

Unfortunately, even with these answers, we are unlikely to have general prescriptions for corridor designs for multiple species (e.g., Beier & Loe 1992). When Bunn et al. (2000) used a graph-theoretic approach to show that American mink (*Mustela vison*) perceived the landscape as connected, they could not generalize this result to prothonotary warblers (*Protonotaria citrea*) in the same landscape. By contrast, Haddad et al. (2003) found that corridors created in their experimental field system facilitated movement for a number of species. Thus, the 'best' features for corridors are unknown and, even when they can be identified, may not translate well to other species, locations, and scales. That corridors have no universal rules should not really surprise us; it is a fact of most of ecology (Lawton 1999). Habitat needs for charismatic umbrella species

(Simberloff 1998) like grizzly bears might encompass the needs of other species within the ecosystem and can be helpful in lobbying public support needed to meet those needs. A reasonable approach might be to identify the species and their source habitats that likely matter most in a given system (Beier et al. 2006), learn something about their actual processes of habitat selection and movement, and then use this information to restore, retain, or manage habitat in a way that will promote functional connectivity. This general approach appears to work well, but it could work better with more information about the critical processes with which animals use and move through habitat. In-depth study in the countries that can afford to support this level of investigation may well produce some guidelines, if not prescriptions, for the many countries in the world where biodiversity is being lost very rapidly and where there is neither time nor resources to spare.

In sum, we hope we have provided some new ideas and tools for sagacious input into the design and evaluation of corridors for conservation. Although they may seem daunting, many of the analytical techniques we described are becoming quite tractable and could be used by land managers and planners now. We hope that the more process-based examination of habitat and movement we have espoused can function to integrate humans better with other animals, particularly in the interface between urban and rural, and semi-rural and wilderness areas where many of these problems occur (McKinney 2002). Anticipating future landscapes by acknowledging how humans will directly and indirectly (e.g., climate change) affect them is critical if we are to retain our biological heritage. Conservation corridors could play an important role in ameliorating these effects and bring us closer to integrating the needs of humans and other organisms so that, at least sometimes, both parties win (*sensu* Rosenzweig 2003).

Table 2-1. Movement and habitat selection processes in relation to spatial scales and structures (adapted from Johnson 1980, Ims 1995).

Spatial scale	Habitat selection (after Johnson 1980)	Movement type (after Ims 1995)	Spatial structure
Resource Patch	Food items within the patch (4th order)	Food items search (foraging)	• Food item distribution • Food patch shape and size • Small-scale obstructions
Habitat Patch	Patches within home range (3rd order)	Patch searching, traplining, territory patrolling	• Food patch configuration • Shelter • Abiotic factors and topography
Patch Mosaic	Selection of home range (2nd order)	Dispersal	• Patch parameters • Landscape parameters
Region	Geographical Range (1st order)	Migration	• Large scale topography, Barriers

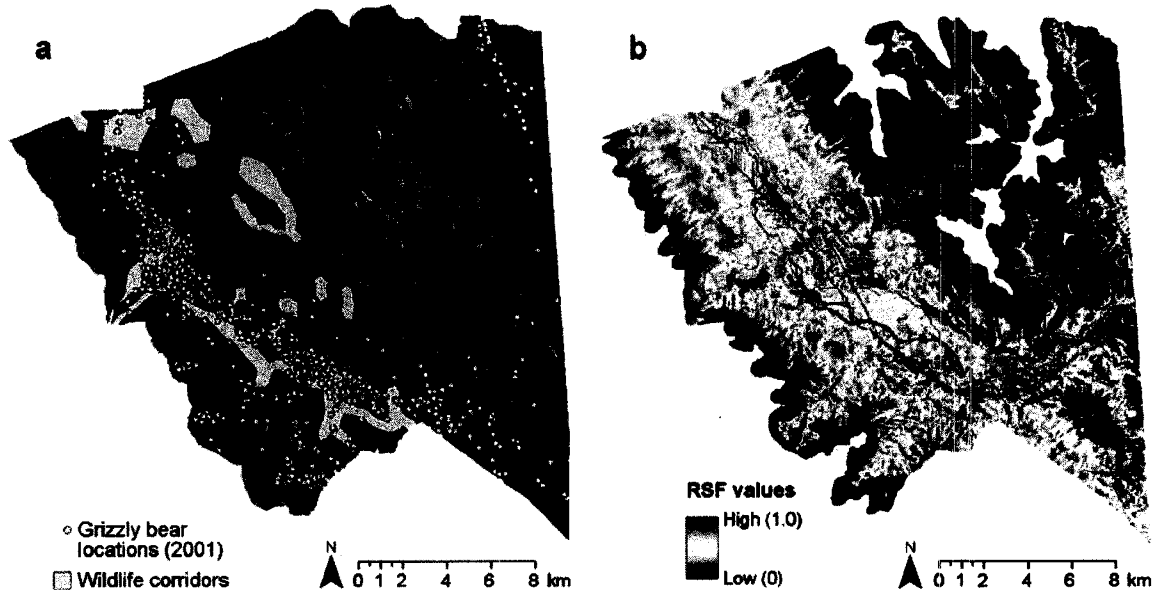

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Figure 2-1. Telemetry locations for three grizzly bears during 2001 and designated Wildlife Corridors in the Canmore region of the Bow Valley, Alberta, Canada (a) were used to generate an RSF (b) (BCEAG 1999, C-L. Chetkiewicz, unpublished data). An RSF was created using logistic regression to compare topographic and vegetation variables at grizzly bear telemetry locations obtained during 2001 with those at random points within the combined home ranges of the three bears. Applying the RSF in a GIS, illustrates areas likely to support grizzly bear occupancy based on a probabilistic function. Areas of high probability of occurrence (green) could be used to evaluate current corridor designations or guide recommendations to amend current corridor designations (a).

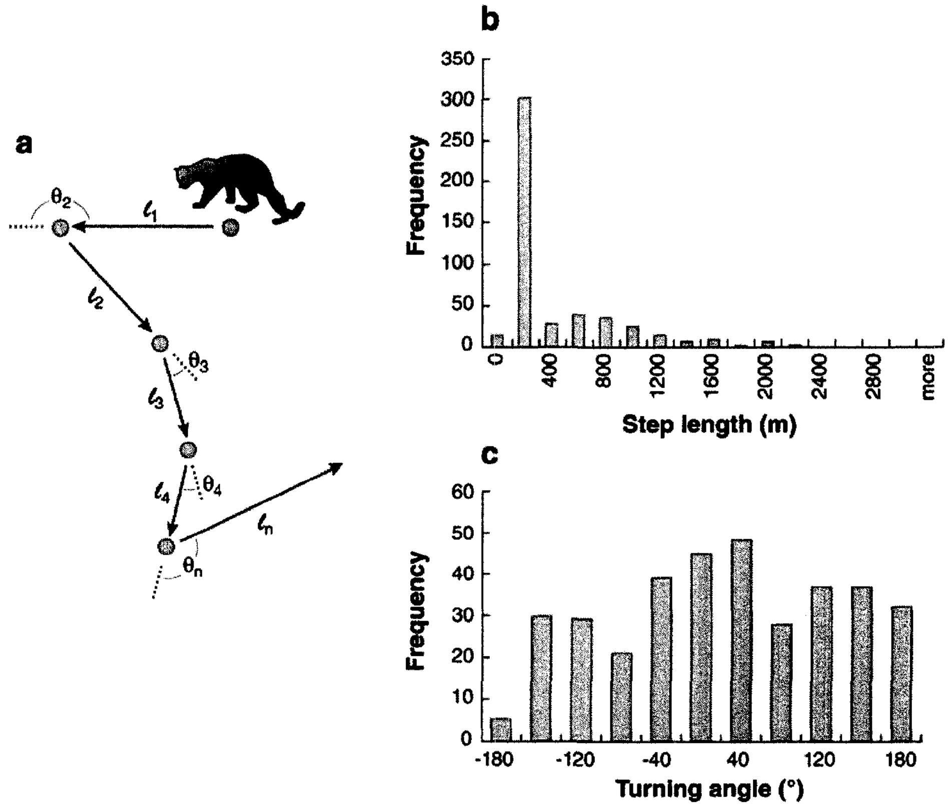

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Figure 2-2. Example of how a movement pathway (a) can be quantified into step lengths (b) and turning angles (c) for a cougar, CACO1, during 2000-2001 in the Canmore region of the Bow Valley, Alberta, Canada (C-L. Chetkiewicz, unpublished data).

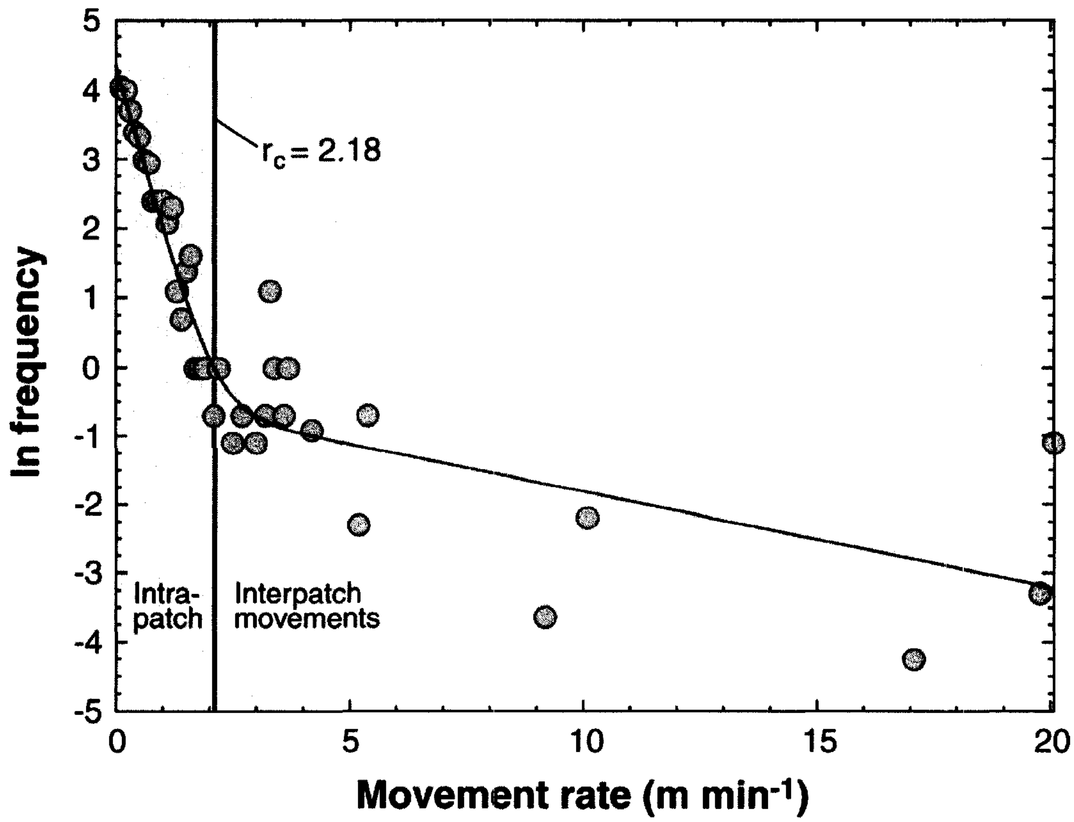

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Figure 2-3. The $\log_e$ frequency distribution of movement rates is assessed using a broken-stick method to calculate a scale criterion (r_c). Movement rates less than r_c represent intra-patch movement behaviours whereas movement rates greater than r_c represent inter-patch movement behaviours (C. Johnson, unpublished data).

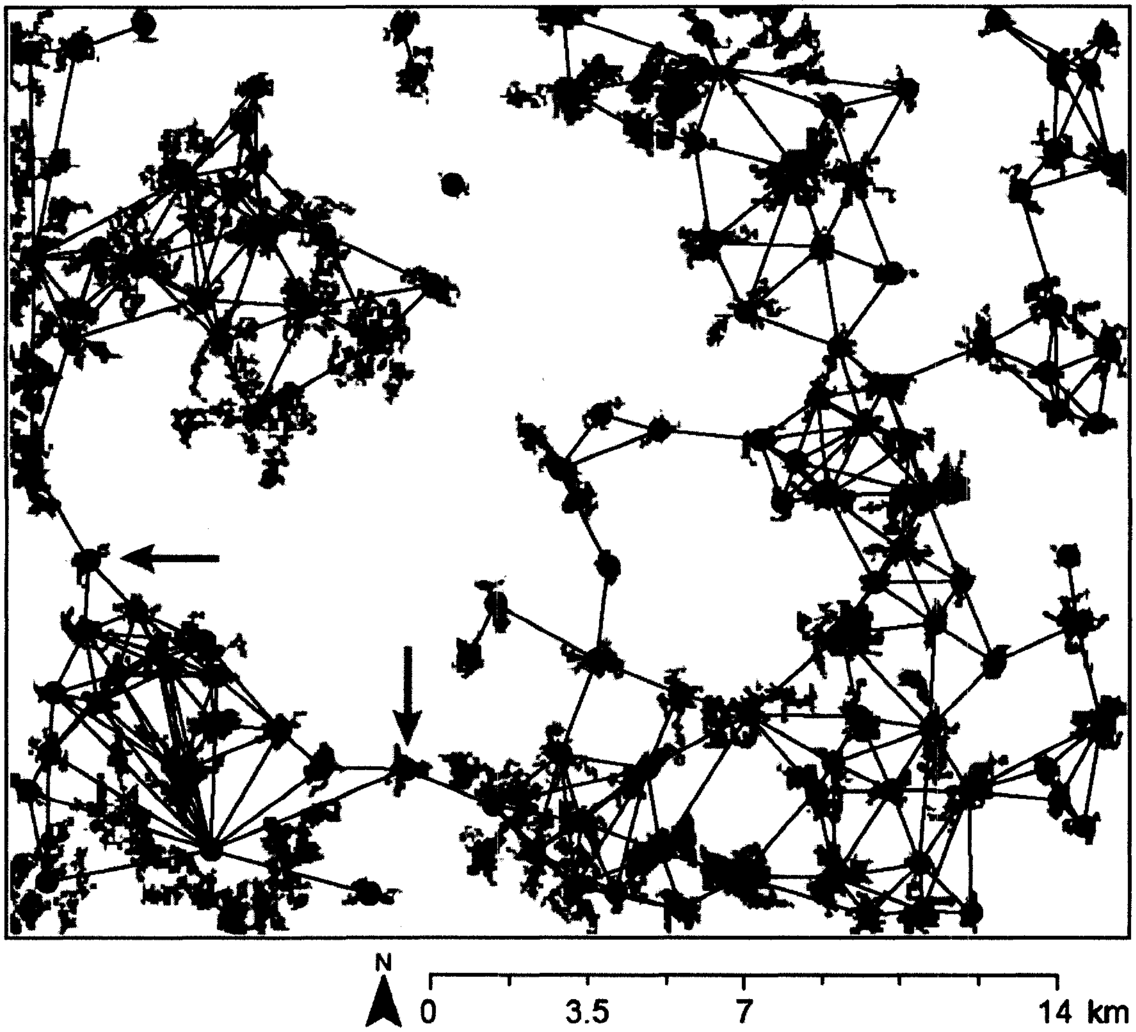

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Figure 2-4. Graph depicting connectivity for wood thrush in a North Carolina landscape. The graph was generated using nodes generated from forest patches in a GIS and edges based on a dispersal distance of 2, 500 m. Corridor locations can be visualized between nodes where the loss of a single forest patch (red arrows) would alter connectivity across the landscape by breaking the graph into separate components. Figure adapted from Urban (2005), reproduced by permission.

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CHAPTER THREE

Where to draw the line: use of resource selection functions to identify local corridors for large carnivores

1. Introduction

Large carnivores are vulnerable to extinction because they require large home ranges and have limited dispersal ability in fragmented landscapes (Weaver *et al.* 1996; Gittleman *et al.* 2001). Protected areas cannot sustain viable populations of large carnivores (Noss *et al.* 1996; Woodroffe & Ginsberg 1998) and adjacent areas often convey higher risk of mortality from roads (Clevenger & Wierzchowski 2006), hunting (Treves & Karanth 2003), competition for prey (Karanth & Stith 1999), and domestic diseases (Funk & Fiorello 2001). Hence, regional carnivore conservation strategies in North America typically rely on corridors to link protected patches of critical habitat (Noss *et al.* 1996; Soulé & Terborgh 1999; Carroll *et al.* 2003). Approaches to identify and design conservation corridors range from expert-opinion to empirical observation and predictive modelling (Noss & Daly 2006). Because expert opinions are subjective and rarely validated (Vos, Baveco & Grashof-Bokdam, 2002; Clevenger *et al.* 2002), and species-specific empirical approaches are difficult to generalize (Turchin 1998; Morales & Ellner 2002), modelling approaches predominate the corridor-planning literature.

Modelling approaches to identify and design corridors for large carnivores fall into three non-exclusive categories: 1) species-specific individual based models, 2) spatially explicit population models, and 3) models based on estimates of ecological or effective distance such as least-cost paths (LCPs). Individual based models permit evaluation of an individual's responses to a landscape through measures of landscape resistance, but they often require large amounts of data to model behavioural decisions (Tracey 2006). Spatially explicit population models can be used to evaluate the demographic consequences associated with preservation, destruction, or restoration of linkages between patches, but they encompass many individual home ranges making them unsuitable for evaluating within-home-range movements or local barriers such as roads (Carroll 2006). In terms of sophistication and data requirements, LCPs represent an intermediate modelling approach (Theobald 2006). These models evaluate potential animal routes across the landscape by estimating the "cost" of animal movement between one location (a source node or patch) and another (Rothley 2005; Theobald 2006). Source patches for carnivores typically include protected areas (Carroll & Miquelle 2006) or the largest polygons that meet some species-specific habitat criteria or area requirements (Singleton, Gaines & Lehmkuhl 2004; Beier *et al.* 2006). Least-cost path approaches have been used to examine linkages for grizzly bears (*Ursus arctos*; Servheen & Sandstrom 1993) and cougars (*Puma concolor*; Hoctor, Carr & Zwick 2000; Thorne *et al.* 2006), as well as other carnivore species (Wikramanayake *et al.* 2004; Carroll & Miquelle 2006). One limitation of the LCP approach is that it typically neglects how carnivores perceive the landscape to select resources. Understanding how animals use landscapes requires that we describe the landscape as gradients of habitat suitability along a continuum of selection (Fischer, Lindenmayer & Fazey 2004). Resource selection functions (RSF) provide a tool for achieving this (Boyce & McDonald 1999; Manly *et al.* 2002).

By modelling resource selection as a probabilistic function of multiple landscape attributes, RSFs offer three important benefits for corridor applications in carnivore conservation. First, these models quantify the varying quality and composition of the matrix offering a realistic assessment of habitat fragmentation beyond a simple patch/matrix dichotomy (Fischer *et al.* 2004). A second benefit of resource selection functions is that they can be created at a variety of scales (Boyce 2006). Finally, RSFs can be used to visualize potential routes (*sensu* corridors) through the landscape, particularly when combined with other modelling approaches such as an LCP analysis. Combining RSF models with LCPs makes it possible to assess the functional connectivity of landscapes (*sensu* Taylor, Fahrig & With 2006), while providing the visual advantage of structural approaches to corridor planning (Chetkiewicz, St. Clair & Boyce 2006).

Two areas in the Canadian Rocky Mountains of Alberta present challenges to corridor planning for grizzly bears and cougars. Both areas present opportunities to explore the application of a resource selection function least-cost path to corridor identification. The Canmore region of the Bow Valley (hereafter, “Canmore”) and the Crowsnest Pass area (hereafter, “Crowsnest”) (Chadwick 2000) have been targeted for local corridor planning, particularly for grizzly bears, within the regional Yellowstone-to-Yukon Conservation Initiative that is devoted to restoring habitat connectivity throughout the Northern Rocky Mountains (Nelson, Day & Sportza 2003).

I collected location information from grizzly bears and cougars with Global Positioning System (GPS) radiocollars during 2000-2004 to estimate resource selection functions that predict their occurrence and distribution in each landscape. I combined these models in a least-cost path approach to identify local corridors in both landscapes. My objective was to provide information for managers and conservation organizations to improve corridor planning in Canmore and in Crowsnest. My approach is an example of local corridor identification that might be applicable to grizzly bears and cougars in other portions of their range, as well as for other large carnivores in human-dominated landscapes.

2. Materials and Methods

2.1 Study Areas

2.1.1 Canmore Region of the Bow River Valley

The Canmore region of the Bow River Valley (51°05', 155°22') is approximately 110 km west of Calgary, east of Banff National Park and north of Kananaskis Country (Fig. 3-1) in Alberta, Canada. The Bow River Valley, part of the Rocky Mountain Natural Region of Alberta (Natural Regions Committee 2006), is characterized by some of the best protected montane habitat for large carnivores in Alberta, including Banff National Park and a number of provincial parks (Donelon 2004). However, the quality of this habitat is undermined by a rapidly growing human population in the town of Canmore (estimated at 11 600 permanent residents; Herrero & Jevons 2000), bisection by the Trans-Canada Highway, one of the busiest transportation routes in Canada (summer traffic = 21 000 people / day; Alexander, Waters & Paquet, 2005) and its proximity to Calgary, projected to exceed 1.5 million people by 2030 (Stelfox, Herrero & Ryerson, 2005). In addition, a two-lane paved highway and a two-track transcontinental railway, operated by Canadian Pacific Railway, further challenge connectivity through the Bow River Valley for many species (Bélisle & St. Clair 2001; Clevenger & Wierzchowski 2006). To address ongoing development within the region, the Bow Corridor Ecosystem Advisory Group (BCEAG) developed a science-based framework for the design of wildlife corridors to provide connectivity between Banff National Park and other protected areas in the region

(BCEAG 1999). I focused on grizzly bear and cougar captures (see below) in Wildlife Management Unit 410 (425 km^2), which includes the town of Canmore and designated corridors. My study extent represents the composite minimum convex polygon (MCP) of grizzly bear and cougar locations collected during this study.

2.1.2 Crowsnest Pass in the Crowsnest River Valley

The Crowsnest Pass (49°37', 114°4') is a 32-km long valley of montane and grassland vegetation located along the Crowsnest River in southwestern Alberta, adjacent to the Alberta-British Columbia border, 269 km southwest of Calgary (Fig. 3-1). The Crowsnest River Valley is also within the Rocky Mountain Natural Region, but the climate is generally warmer and drier than in Canmore (Natural Regions Committee 2006). In contrast to the Canmore region of the Bow Valley, the Crowsnest River Valley is managed for multiple uses including forestry, oil and gas, recreation, and agriculture and livestock grazing. The communities of Blairmore, Bellevue, Frank, Hillcrest, and Coleman as well as the hamlets of Sentinel (Sentry) and Crowsnest comprise the Municipality of the Crowsnest Pass (population approximately 6 000). A two-lane highway (Highway 3) bisects the valley (daily traffic volume = 7 000 vehicles per day) that parallels a railroad supporting 8-16 freight trains per day (Apps *et al.* 2007). In addition to the communities located along the highway, most of the land along the Crowsnest Pass is in private or corporate ownership and potentially subject to development. Recent discussions of twinning Highway 3 through the Crowsnest Pass and ongoing residential developments have prompted concerns about carnivore movements in the Crowsnest Pass (Proctor *et al.* 2005; Apps *et al.* 2007). I focused capture efforts within the boundaries of Wildlife Management Unit 303 (1 657 km^2), that includes the three corridors identified within the municipality. The composite MCP of grizzly bear and cougar locations collected during this study defined the spatial extent of the Crowsnest Pass study area.

2.2 Data Sources

2.2.1 Grizzly Bear and Cougar Telemetry Data

During the springs of 2000-2004, four grizzly bears (2 females, 2 males) were captured and collared in the Canmore study area and four grizzly bears (2 females, 2 males) in Crowsnest, using culvert traps, standard leg and pail snares and aerial darting techniques (Cattet, Caulkett & Stenhouse 2003). During the winters of 2000 to 2004, five (4 female, 1 male) cougars were captured and collared in the Canmore study area and 13 (7 female, 6 male) cougars in Crowsnest by tracking cougars in snow with trained hounds (Hornocker 1970). Grizzly bears were fitted with Televilt-Simplex™ GPS radiocollars (Lindesberg, Sweden) programmed to acquire a fix every 1 or 2-h. Cougars were fitted with smaller, lighter Televilt collars programmed to acquire a fix every 1 or 4-h. Sampling rates were based on battery life calculations, data requirements, and ethical and logistical constraints associated with recapture operations to replace failing batteries. Capture protocols were approved by Animal Care Committees for the University of Alberta and Alberta SRD, following the Canadian Council on Animal Care guidelines.

2.2.2 Digital Data

To analyze potential explanatory variables for grizzly bear and cougar distributions across their home ranges, I developed thirteen GIS layers in four classes with a 30-m pixel size: vegetation (landcover (McDermid, Franklin & LeDrew 2005), natural subregions (Natural Regions Committee 2006), distance to water, distance to forest, percent crown closure); terrain (slope, elevation, aspect, terrain ruggedness index (Evans 2004), compound topographic index (Evans 2004); food resources (green vegetation index, elk (*Cervus elaphus*) RSF derived from annual Provincial Government surveys during the winter); and human use (road density, Mace *et al.* 1996).

2.3 Data Analyses

2.3.1 Resource Selection Functions

To address GPS fix biases due to habitat and terrain characteristics associated with early models of Televilt collars (e.g., Gau *et al.* 2004; Frair *et al.* 2004), I developed a GIS layer quantifying the probability of obtaining a fix (P_{FIX}) (Hebblewhite, Percy & Merrill 2007). The probability of obtaining a GPS fix from Televilt collars ranged from 49% to 96% in the Canmore region of the Bow Valley and 25% to 95% in the Crowsnest Pass. The P_{FIX} values were used to weight each use location during RSF model development (see below). Location error associated with Televilt collars in the Canmore study area was within the 30-m resolution of digital data used in model building (Donelon 2004). I assumed that the location error for the same models of Televilt collars was similar in the Crowsnest study area.

Following retrieval of the GPS collars, location data were imported into ArcGIS 9.0 (Environmental Systems Research Institute, Inc., Redlands, California, USA) and a minimum complex polygon home range for each grizzly bear and cougar were created using Hawth's Analysis Tools for ArcGIS (hereafter, "Hawth's Tools") (Beyer 2004). A random point generator was used to identify "available" habitat locations within each individual's home range at a sampling intensity of 5 points/ km^2 (Nielsen, Boyce, &

Stenhouse 2004). To create RSFs, I compared seasonal grizzly bear and cougar GPS locations with available locations within individual home ranges. To reflect resource selection variability by season, I partitioned the grizzly data into spring (den emergence to 15 June), summer (16 June to 10 August), and autumn (11 August to denning) seasons (Munro *et al.* 2006). Similarly, I partitioned the cougar data into two seasons: winter (15 November – 15 April) and non-winter (16 April - 14 November) (Jalkotzy, Ross & Wierzchowski 1999). Habitat selection for both species was evaluated at the third-order scale (within home ranges; Johnson 1980) and followed a "Design III" protocol where availability was sampled for each individual (Manly *et al.* 2002).

I created species-specific seasonal models following model-fitting procedures in Hosmer and Lemeshow (2000). All continuous variables were tested for collinearity using Pearson correlation coefficients. Slope, terrain ruggedness index, crown closure and elevation had $|r| \geq 0.7$ and were not included in the same models. Nonlinear relationships were tested among all continuous covariates with the addition of a quadratic term and I selected the form that resulted in the largest increase in the χ^2 statistic for the robust Wald test. Categorical variables (landcover, natural subregions) were included using dummy coding. I used robust standard errors clustered on individual animals (Nielsen *et al.* 2004a) and applied probability weights generated from the P_{FIX} layer described above to create a main-effects model. The main-effects model was refit using mixed-effects linear regression with individual animal as a random intercept (Gillies *et al.* 2006). I compared these models to five candidate models using an information theoretic approach (Burnham & Anderson 1998). I found that in all cases the seasonal models were selected, and report only these models in my results.

Model fit was assessed using a k-fold cross-validation (Boyce *et al.* 2002). I also evaluated the predictive performance of mapped RSF models to assess whether models were proportional to the probability of use (Johnson *et al.* 2006). I randomly divided the GPS locations into two groups before model development: 80% of the data comprised a "model-training" group and the remaining 20% comprised a "model-testing" group for validation. I then compared the observed (withheld model-testing sample) and expected number of GPS locations with chi-square, Spearman rank, and linear regression (Johnson *et al.* 2006). When RSF score distributions were skewed, I either re-binned the raw RSF scores or transformed them using a logistic function (Johnson *et al.* 2006). All statistical analyses were conducted in Stata 9.2 (Stata Corporation 2005).

2.3.2 Least-Cost Path Analyses

I used the RSFs to create source patches (high RSF value polygons) within each study area. I reclassified each landscape based on the top two ranked RSF bins generated from validated seasonal models. I converted the re-binned raster surface into polygons using ArcGIS and calculated the area, perimeter, surface area to perimeter ratios, and centre of each polygon using Hawth's Tools. Where possible, I selected polygons that met habitat patch guidelines of 4.5 km^2 and 1.2 km wide (BCEAG 1999).

I used the inverse of the species-specific seasonal RSF models to generate a cost surface for LCP analyses. I assumed that pixels with higher RSF values afforded lower costs to movement than those with low RSF values. I used the centre of each high RSF value polygon as the source and end points for the LCP algorithm to generate pathways on either side of the highways within the boundaries of each WMU. Because the path created is a single pixel-width (30-m) wide, I buffered each path at 350 m following guidelines specifically recommended for carnivores in Canmore (BCEAG 1999).

I merged seasonal LCPs by species to explore the overall location and extent of species-specific corridors and I compared the highway crossing locations predicted by the LCPs with actual crossings by converting the GPS locations of cougars and grizzly bears to movement paths in a GIS. I examined each species separately because cougars and grizzly bears showed differences in use of highway crossing structures in adjacent Banff National Park (Clevenger & Waltho 2005). Finally, I intersected the LCPs of both species to highlight areas where potential corridors for both species overlapped.

3. Results

3.1 Resource selection functions

3.1.1 Canmore

A total of 10 643 GPS locations (189 – 2 906 per bear) were used to develop seasonal models for grizzly bears in the Canmore region of the Bow Valley (Fig. 3-2). Canmore grizzly bears consistently selected sites with higher greenness across all seasons and lower road densities in spring and summer (Table 3-1). Selection for landcover varied seasonally, but generally grizzly bears selected herb and shrub landcovers over upland forest in alpine and subalpine subregions over montane subregions (Table 3-1). During spring, slope also had a significant nonlinear effect on grizzly bear locations whereas during summer, grizzly bears were closer to water, selected sites with intermediate soil wetness, and areas ≤ 40% crown closure (Table 3-1). Predictive accuracy for seasonal models using withheld model-testing data was excellent (spring; R^2

$= 0.971$, $r_s = 0.900$, $P < 0.05$, summer; $R^2 = 0.985$, $r_s = 1.000$, $P < 0.001$, autumn; $R^2 = 0.899$, $r_s = 0.937$, $P < 0.001$).

A total of 4 845 GPS locations (296 – 1 173 per cougar) were used to develop seasonal models for cougars in the Canmore region of the Bow Valley (Fig. 3-3). Seasonal RSF models for cougars in Canmore consistently included variables for crown closure and road density, but quadratic terms were added to these variables in the winter season (Table 3-2). Cougars consistently selected montane subregions over alpine or subalpine subregions (Table 3-2). During the winter, cougars selected intermediate crown closures (~50%), sites with road densities ≤ 3.5 km/km^2, and were more likely to be found at intermediate elevations around 1600 m in all landcover types except upland forest (Table 3-2). During the rest of the year, cougars were closer to water features, selected intermediate greenness values (~40), higher percent crown closures (i.e., more cover) and lower road densities (Table 3-2). Predictive accuracy for the seasonal models using withheld model-testing data was excellent in the non-winter season ($R^2 = 0.979$, $r_s = 1.000$, $P < 0.001$) and good in the winter season ($R^2 = 0.798$, $r_s = 0.77$, $P < 0.07$).

3.1.2 Crowsnest Pass

A total of 6 643 GPS locations (53 – 1 192 per bear) were used to develop seasonal models for grizzly bears in the Crowsnest Pass (Fig. 3-4). Similar to Canmore, grizzly bears in Crowsnest selected sites with higher greenness. Unlike Canmore, grizzly bears in Crowsnest were closer to water features, though this relationship was weak during autumn (Table 3-3). During spring, grizzly bears were also more likely to be found at intermediate elevations (~ 1 500 m) in alpine regions compared to summer when they were found at sites with drier soils in upland forest in subalpine regions. During autumn, grizzly bears selected locations with intermediate soil wetness and relatively higher elevations in upland herb landcover rather than upland forest sites. Predictive accuracy for seasonal models using withheld model-testing data was excellent (spring; $R^2 = 0.975$, $r_s = 0.943$, $P < 0.005$, summer; R^2=0.948, $r_s = 0.90$, $P < 0.05$, autumn; $R^2 = 0.924$, $r_s = 1.000$, $P < 0.001$).

A total of 5 741 GPS locations (97 – 801 per cougar) were used to develop seasonal models for cougars in the Crowsnest Pass (Fig. 3-5). Unlike Canmore, cougars in Crowsnest consistently selected sites with intermediate terrain ruggedness scores and selected upland forest over other landcover types, except during winter when they selected shrub sites compared to upland forest and montane subregions (Table 3-4). During winter, cougars were associated with drier soil sites whereas during non-winter, cougars were closer to forest cover (Table 3-4). Predictive accuracy for seasonal models using withheld model-testing data was excellent (non-winter season; R^2=0.965, r_s = 0.943, $P < 0.005$, winter; R^2=0.958, $r_s = 0.900$, $P < 0.05$).

3.2 Least-Cost Path Analyses

3.2.1 Canmore

I generated 15 polygons from the highest seasonal grizzly bear RSF models. Eighteen LCPs between polygons were then merged and identified as potential grizzly bear corridors, some of which paralleled existing corridor designations. Three bears from this study each crossed the TransCanada Highway once during spring and at least six times during summer. Two crossings were proximate to crossing locations predicted by seasonal LCPs. None of the four telemetered bears crossed during autumn.

I generated 10 polygons from the highest seasonal Canmore cougar RSF models. Eight LCPs between these polygons were then merged and identified as potential corridor locations for cougars. The LCPs generated from cougar RSFs crossed the highway and other linear features in three places. Study cougars crossed the TransCanada Highway at least 19 times and crossed Highway 1A at least twice outside winter and the TransCanada Highway at least seven times during winter. Three cougars crossed Highway 1A at least 20 times. These cougar crossings closely aligned with the LCP predicted crossing site in the central region of the study area.

Intersecting all seasonal LCPs for cougars and grizzly bears in the Canmore study area produced a number of areas of overlap. The resultant overlapped LCPs in the central portion of the valley, north of the highways, represented observed highway crossings by both species for all seasons (Fig. 3-6).

3.2.2 Crowsnest Pass

I generated 13 polygons from the highest seasonal grizzly bear RSFs in the Crowsnest. Nineteen LCPs between polygons were merged and identified as potential corridor locations for grizzly bears in the Crowsnest. The LCPs crossed Highway 3 in three different sites. None of the four study grizzly bears crossed Highway 3 during any season.

I generated 13 polygons of the highest seasonal Crowsnest cougar RSF values. Eight LCPs between polygons were identified and merged to illustrate potential corridor locations for cougars. LCPs crossed Highway 3 in two areas that were common for both seasons. During the non-winter season, three study cougars crossed Highway 3 at least 25 times and during the winter, three study cougars crossed Highway 3 at least 11 times. Some of these crossings aligned with those predicted by the LCPs.

Six intersected LCPs for cougars and grizzly bears in Crowsnest crossed the highway, including a LCP in the eastern portion of the study area that represented multi-seasonal corridors for both cougars and grizzly bears (Fig. 3-6).

4. Discussion

By describing the biological factors affecting patterns of resource use by grizzly bears and cougars in two mountain valleys of the Canadian Rockies, empirically-based corridor identification was possible. Habitat selection by grizzly bears varied by season and study area, a result consistent with other RSF studies for grizzly bears in mountainous regions (Mace *et al.* 1999; Nielsen *et al.* 2004a, b; Ciarniello *et al.* 2007). My results suggest that measures of food resources, approximated by surrogates such as greenness and soil wetness, are important predictors for grizzly bear distribution throughout the year. The importance of greenness for grizzly bears in RSFs across all seasons in both study areas is consistent with the animals' omnivorous needs for quality forage and herbaceous resources to maximize weight gain and fat deposition for hibernation (Rode, Robbins & Shipley 2001; Robbins, Schwartz & Felicetti 2004). Proximity to water sources and soil wetness indices (CTI) were important components of summer models in both Canmore and Crowsnest. Soil wetness indices were useful in describing local patterns of certain bear food items such as bearberry (*Arctostaphylos uva-ursi*) and *Equisetum* spp. (Nielsen et al. 2004b) and grizzly bears feeding on ungulates during spring and autumn often were located closer to water within forest sites (Munro *et al.* 2006).

My results suggested that road density, as a measure of human influence on grizzly bears, may not be a useful surrogate for understanding the relationship between grizzly bear occurrence and roads in these landscapes. In Canmore, grizzly bears avoided roads during spring and selected areas with low to intermediate road densities during summer, whereas in Crowsnest road density was not a reliable predictor of grizzly bear occurrence patterns. These results contrast to findings from other areas in which habitats close to roads can attract bears because of the availability of preferred plants (Munro *et al.* 2006; Roever, Boyce & Stenhouse, i*n press-a*), or as refugia for females with cubs and subadults avoiding adult male bears (McLellan & Shackleton 1989; Mattson *et al.* 1992). Roadside habitats might also be used by habituated bears (Gibeau *et al.* 2002). While habituated bears appear to successfully use habitats near humans, they also are most likely to die due to conflicts with humans (McLellan *et al.* 1999, Nielsen *et al.* 2004a). Indeed, two of the four bears in my Canmore study area were translocated due to conflicts with humans and later were shot by hunters. A better understanding of the relationship between bears and roads in human-dominated landscapes like my study areas may require finer-scale temporal and spatial measures of human use (e.g., Donelon 2004).

Cougars varied in habitat use by season and region. Cougars in both landscapes were consistently associated with montane subregions throughout the year and shrub landcover types during winter. The montane subregion, represented by river valley bottoms in both landscapes, presents optimal climate and cover relative to subalpine and alpine areas. The use of shrub landcover in winter is likely associated with prey availability. I suspect the avoidance of subalpine and alpine subregions in winter also is tied to snow accumulation and prey availability (Murphy, Ross & Hornocker 1999). In Canmore, greenness was an important predictor of cougar occurrence during the non-winter season, a finding supported by other cougar studies where greenness was considered a surrogate for ungulate prey (Jalkotzy, Ross & Wierzchowski 1999; Carroll, Paquet & Noss 2000). However, measures of terrain ruggedness were more useful in describing cougar occurrence as has been shown for cougars in other regions of Alberta (Jalkotzy, Ross & Wierzchowski 1999). Cougars require abundant horizontal and vertical cover provided by vegetation and topography to facilitate their ambush-style of hunting (Murphy, Ross & Hornocker 1999). I suspect that terrain ruggedness also may be important for providing escape habitats for hunted cougars in Crowsnest Pass. Understanding the spatial distribution of human-caused cougar mortalities (*sensu* Riley & Malecki 2001) would be valuable for refining local models of occurrence and distribution, particularly winter habitats.

Despite the link between abundance and distribution of carnivores and prey (Ross, Jalkotzy & Festa-Bianchet 1997), models of elk occurrence failed to predict cougar habitat selection in either study area. This is likely explained by the fact that the elk model was developed for elk winter ranges outside of my study area, and not well representative of elk habitat selection within studied cougar ranges. Furthermore, elk may not be the preferred cougar prey in either study area. In nearby Banff National Park, when elk were abundant, they were prevalent in cougar diets, but when elk numbers declined, cougars switched to alternative ungulate prey (Kortello, Hurd & Murray 2007). Improved data on local prey abundance and distribution, particularly for deer (*Odocoileus* spp.) during winter, would likely improve cougar distribution models in both study areas.

Cougar and grizzly bear models were more similar between species within study areas, than they were for the same species between study areas. Canmore cougar models showed a similar pattern of avoidance of roads in the non-winter season with grizzly bear seasonal models. During winter, when grizzly bears were denning, cougars still selected areas with low to intermediate road densities. I found fewer similarities between cougar and grizzly bear models for Crowsnest. While RSFs allow us to identify areas of the landscape that are likely to support occupancy by both species throughout the year, there are two challenges to using RSFs to identify and delineate corridors: 1) identifying multi-species corridors; and, 2) translating species-specific and seasonal details from RSF models into general corridor guidelines. To address these challenges I used the RSF models in a least-cost path analysis for both study areas.

The RSF-informed least-cost path analyses provided a quantitative, functionally based, and repeatable way of identifying potential corridors for conservation. LCP results depend on the location of source and end polygons and assumptions of the cost surface. By using the RSFs to identify the largest polygons of high-quality habitat as the LCP sources, my approach is an improvement over more qualitative methods that presume measures of habitat quality (Singleton, Gaines & Lehmkuhl 2004; Apps *et al.* 2007) or view only protected areas as source patches (Carroll & Miquelle 2006). Use of the inverse of the resource selection function assumes that high-quality habitat presents lower costs or friction for movement and lowest risk of mortality (Adriaensen *et al.* 2003). While this is a common assumption in many LCP-based modelling approaches for carnivores (e.g., Ferreras 2001; Carroll & Miquelle 2006), actual movement studies suggest that individuals may travel faster through human-dominated habitats of low suitability, and slower movement (which is sometimes assumed to have higher costs) in preferred habitats (Palomares 2001; Dickson, Jenness & Beier 2005). In some situations, both conditions may apply. For example, Whittington, St. Clair & Mercer (2005) found that movements of wolves (*Canis lupus*) were more tortuous (e.g., higher cost) near both predation sites (e.g., high-quality habitats) and high-use trails (e.g., low-quality habitats). They suggested that the highly tortuous movements in low-quality habitats were used to avoid contact with humans. Field validation through the increasing use and availability of GPS data for various carnivore species in different landscapes will be valuable in addressing assumptions about carnivore movement, spatial theory, and the effects of landscape structure and composition on movements (Young & Shivik 2006; Gonzales & Gergel 2007). For example, Schwab *et al.* (unpublished data) found LCPs based on an inverse RSF (as used here) cost surface aligned with out-of-sample grizzly bear GPS location data in west-central Alberta suggesting that the cost surface performed well as both a predictor of actual movement and corridor location. This lends further support to my results that the integration of RSF and LCP analyses is a useful tool in corridor identification.

I have shown how RSF and LCP models as well as technologies such as GPS and GIS can aid conservation planning and local corridor identification for two carnivore species in the Canadian Rocky Mountains. RSFs enhance our understanding of the factors affecting cougar and grizzly bear occurrence on the landscape, while the RSF-informed least-cost path results suggest possible corridor locations. When these paths were intersected for both species, the results were rarely a linear "corridor." In Canmore, two potential "crossing" areas were outside of designated corridors or patches. In

Crowsnest, areas of intersection occurred within areas broadly outlined in draft corridor maps. While RSF-informed least-cost paths offer an important advance in addressing structural connectivity in a species- and landscape-specific way, there is no guarantee that the identified corridors provide functional connectivity on the landscape (Taylor, Fahrig & With 2006). RSFs and LCPs, though spatially explicit, are still static models, providing a snapshot of current (or recent) relationships between individuals and their habitats, rather than long-term functionality. The fundamental challenge will be linking local corridor planning with regional landscape approaches to quantify the contribution of local corridors to population persistence (Carroll 2006).

Table 3-1. Estimated seasonal model coefficients for grizzly bears in the Canmore region of the Bow Valley.

Variable	Spring				Summer				Autumn			
code	β	SE	95% CI		β	SE	95% CI		β	SE	95% CI	
CTI*					0.148	0.045	0.061	0.235	-0.055	0.041	-0.136	0.026
CTI^2					-0.007	0.002	-0.012	-0.003	0.008	0.002	0.004	0.012
Distance to water (km)					-1.617	0.150	-1.911	-1.322				
Greenness	0.033	0.003	0.028	0.038	0.050	0.002	0.045	0.054	0.074	0.002	0.070	0.078
Road Density (km/km^2)	-0.187	0.049	-0.283	-0.092	0.940	0.047	0.848	1.032				
Road $Density^2$					-0.122	0.009	-0.140	-0.104				
% crown closure					0.079	0.009	0.063	0.096				
% crown $closure^2$					-0.001	0.000	-0.001	-0.001				
slope (degrees)	0.185	0.009	0.168	0.202								
$slope^2$	-0.004	0.000	-0.004	-0.004								
Landcover [1]												
Upland Herb	1.663	0.179	1.312	2.015	-0.069	0.121	-0.306	0.167	1.687	0.093	1.505	1.870
Shrub	0.907	0.120	0.672	1.141	0.307	0.073	0.164	0.451	1.294	0.071	1.154	1.434
Water	-0.458	0.366	-1.176	0.260	-1.368	0.356	-2.067	-0.670	0.265	0.295	-0.314	0.844
Barren	1.058	0.095	0.870	1.245	-0.272	0.107	-0.481	-0.063	1.076	0.076	0.926	1.226
Subregions [2]												
Alpine	0.924	0.174	0.583	1.265	0.420	0.097	0.230	0.609	2.638	0.165	2.315	2.960
Subalpine	1.807	0.157	1.498	2.115	0.381	0.067	0.250	0.513	2.615	0.157	2.306	2.923

*CTI = Compound Topographic Index; a measure of soil wetness

[1]Landcover categories are reported with respect to Upland Forest;

[2]Subregion categories are reported with respect to Montane

Table 3-2. Estimated seasonal model coefficients for cougars in the Canmore region of the Bow Valley.

Variable	Non-Winter				Winter			
code	β	SE	95% CI		β	SE	95% CI	
Distance to water (km)	-1.649	0.190	-2.020	-1.278				
Elevation (m)					0.021	0.003	0.016	0.026
Elevation^2					0.000	0.000	0.000	0.000
Greenness	0.052	0.009	0.035	0.069				
Greenness^2	-0.001	0.000	-0.001	0.000				
% crown closure	0.025	0.003	0.019	0.031	0.113	0.016	0.080	0.145
% crown closure^2					-0.001	0.000	-0.001	-0.001
Road density (km/km^2)	-0.187	0.032	-0.249	-0.126	0.641	0.076	0.492	0.791
Road density^2					-0.090	0.011	-0.112	-0.068
Landcover [1]								
Upland Herb	0.300	0.184	-0.061	0.660	0.262	0.214	-0.158	0.681
Shrub	-0.074	0.124	-0.318	0.170	0.471	0.122	0.232	0.711
Water	-0.393	0.211	-0.806	0.021	-3.415	0.721	-4.828	-2.001
Barren	-0.336	0.157	-0.643	-0.029	0.587	0.184	0.226	0.948
Subregions [2]								
Alpine	-1.436	0.154	-1.737	-1.135	-4.010	1.019	-6.007	-2.013
Subalpine	-0.471	0.077	-0.623	-0.319	-1.163	0.109	-1.376	-0.950

[1] Landcover categories are reported with respect to Upland Forest

[2] Subregion categories are reported with respect to Montane

Table 3-3. Estimated seasonal model coefficients for grizzly bears in Crowsnest Pass.

Variable	Spring				Summer				Autumn			
code	**β**	**SE**	**95% CI**		**β**	**SE**	**95% CI**		**β**	**SE**	**95% CI**	
CTI*					0.052	0.017	0.019	0.085	0.576	0.072	0.435	0.718
CTI^2									-0.029	0.004	-0.038	-0.021
Distance to water (km)	-1.538	0.184	-1.899	-1.178	-1.498	0.262	-2.012	-0.985	0.376	0.028	0.321	0.432
Elevation (m)	0.017	0.002	0.013	0.022					0.002	0.000	0.001	0.002
$Elevation^2$	0.000	0.000	0.000	0.000								
Greenness	0.034	0.004	0.026	0.042	0.034	0.005	0.025	0.043	0.026	0.003	0.020	0.032
Landcover [1]												
Upland Herb					-0.752	0.117	-0.981	-0.523	0.165	0.060	0.047	0.283
Shrub					-0.671	0.143	-0.952	-0.390	0.011	0.085	-0.156	0.177
Water									0.605	0.571	-0.515	1.724
Barren									-0.829	0.205	-1.231	-0.427
Subregions [2]												
Subalpine					0.943	0.103	0.742	1.144				
Alpine					0.060	0.231	-0.392	0.512				

*CTI = Compound Topographic Index; a measure of soil wetness

[1] Landcover categories are reported with respect to Upland Forest

[2] Subregion categories are reported with respect to Montane

Table 3-4. Estimated seasonal model coefficients for cougars in Crowsnest Pass.

Variable	Non-Winter				Winter			
code	β	SE	95% CI		β	SE	95% CI	
CTI*					0.040	0.014	0.012	0.068
Distance to Forest (km)	-0.002	0.008	-0.018	0.013				
Terrain Ruggedness	0.031	0.006	0.020	0.041	0.064	0.006	0.052	0.076
Terrain Ruggedness^2	0.000	0.000	-0.001	0.000	-0.001	0.000	-0.001	-0.001
Landcover [1]								
Upland Herb	-1.012	0.087	-1.183	-0.841	-0.381	0.075	-0.528	-0.234
Shrub	-0.363	0.117	-0.592	-0.134	0.667	0.093	0.486	0.849
Barren	-2.678	0.722	-4.094	-1.262	-0.760	0.437	-1.617	0.098
Subregions [2]								
Subalpine	-0.465	0.060	-0.583	-0.347	-1.793	0.062	-1.915	-1.671
Alpine	-1.089	0.225	-1.530	-0.649	-2.708	0.251	-3.199	-2.217

*CTI = Compound Topographic Index; a measure of soil wetness

[1] Landcover categories are reported with respect to Upland Forest

[2] Subregion categories are reported with respect to Montane

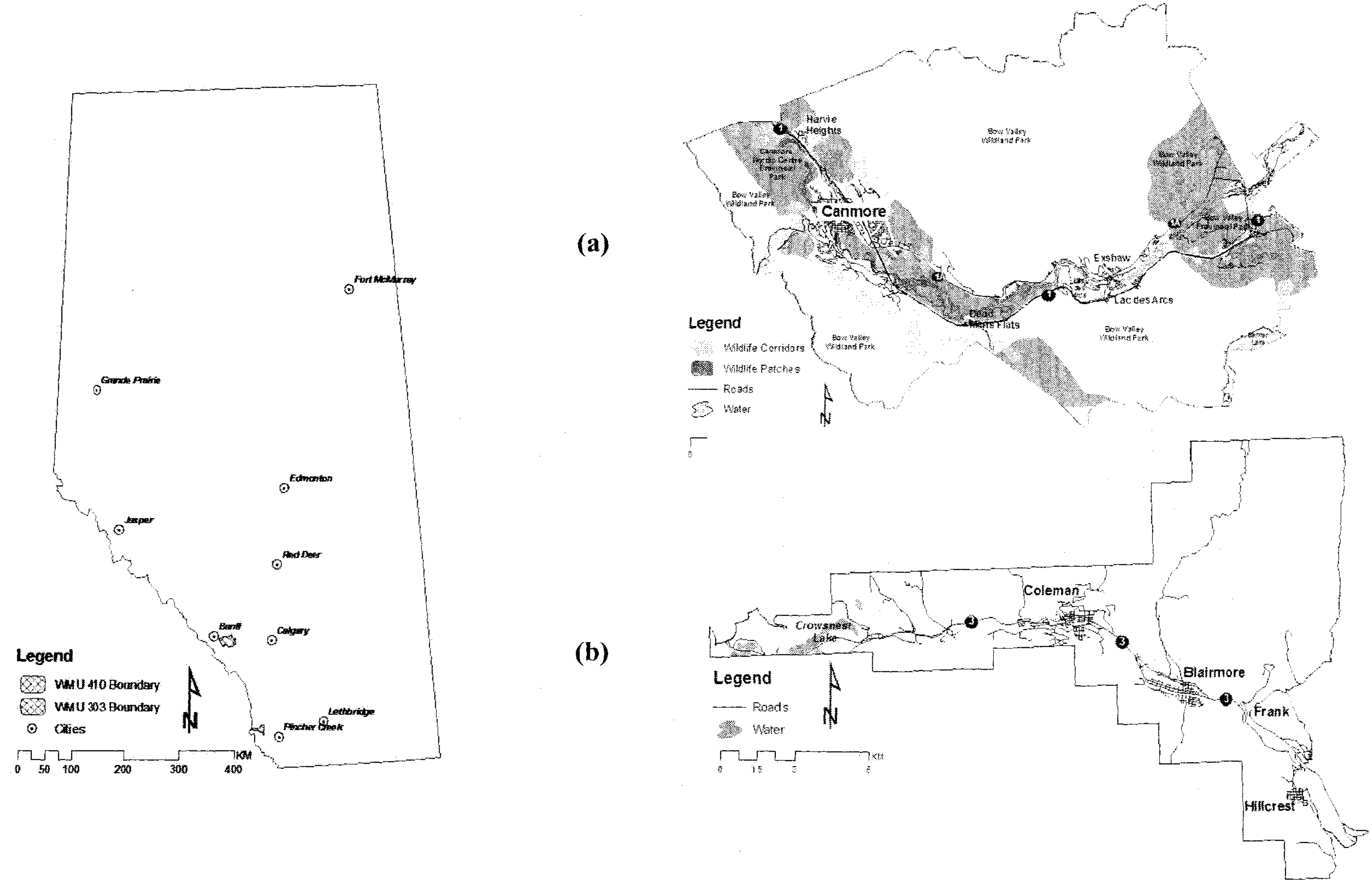


Figure 3-1. (a) The Canmore Region of the Bow Valley study area illustrating Wildlife Management Boundary (WMU) 410 as well as currently designated wildlife corridors and habitat patches. (b) The Crowsnest Pass study area illustrating WMU 303. Inset map of Alberta illustrates locations of WMUs within Alberta, Canada.

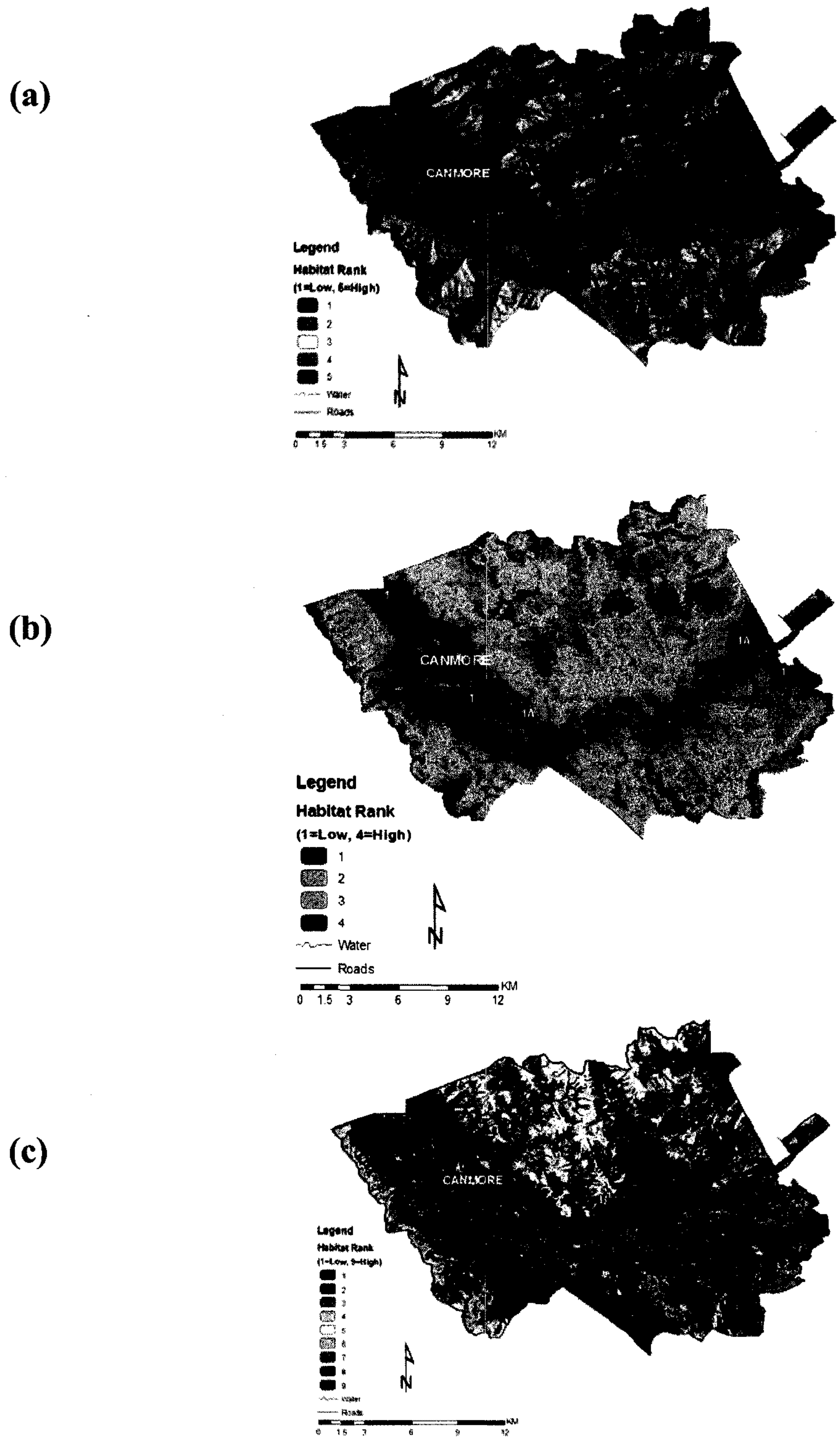
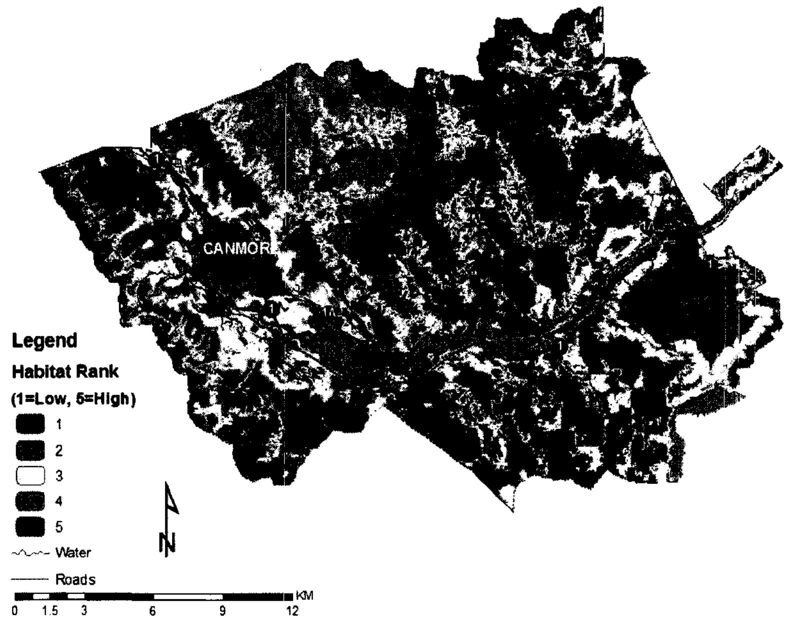


Figure 3-2. Predicted probability of grizzly bear occurrence in the Canmore region of the Bow Valley during: (a) spring – den emergence to 15 June; (b) summer – 16 June – 10 August; and, (c) autumn - 11 August to denning). Refer to Table 3-1 for description of model variables and coefficients.

(a)



(b)

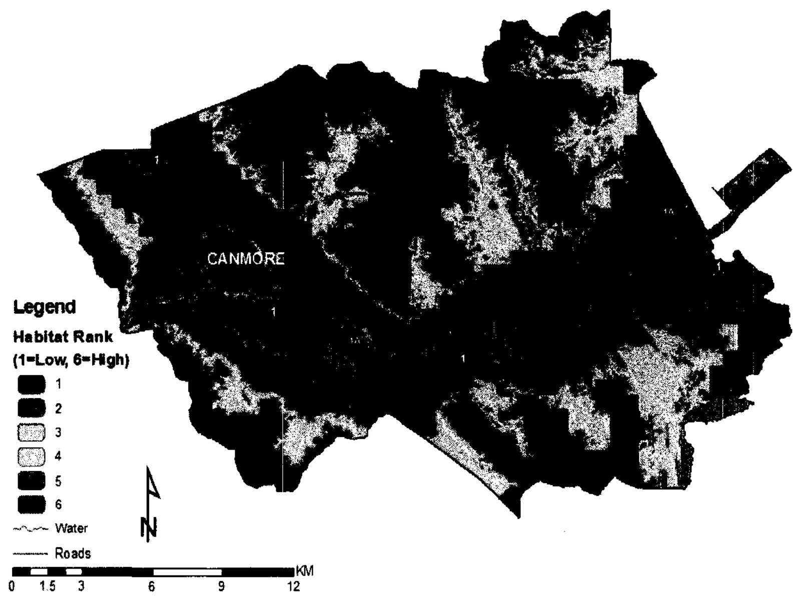


Figure 3-3. Predicted probability of cougar occurrence in the Canmore region of the Bow Valley during (a) the non-winter season; and, (b) the winter season. Refer to Table 3-2 for description of model variables and coefficients.

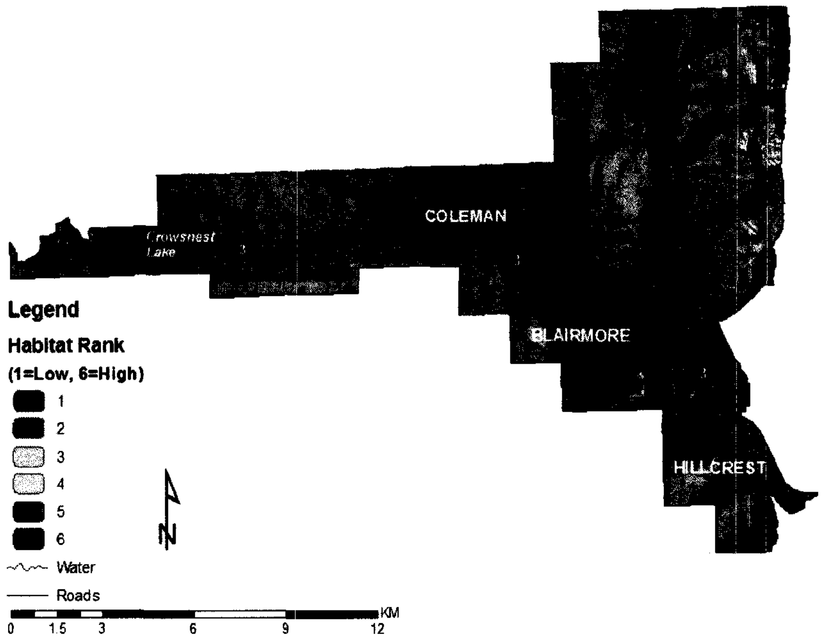
(a)

(b)

(c)

Figure 3-4. Predicted probability of grizzly bear occurrence in the Crowsnest Pass during: (a) spring – den emergence to 15 June; (b) summer – 16 June – 10 August; and, (c) autumn - 11 August to denning). Refer to Table 3-3 for description of model variables and coefficients.

(a)



(b)

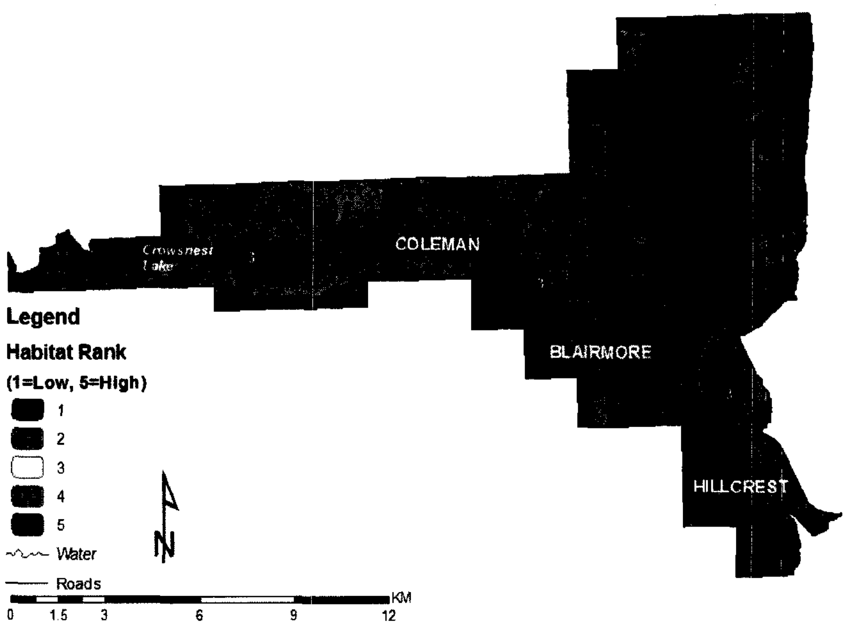
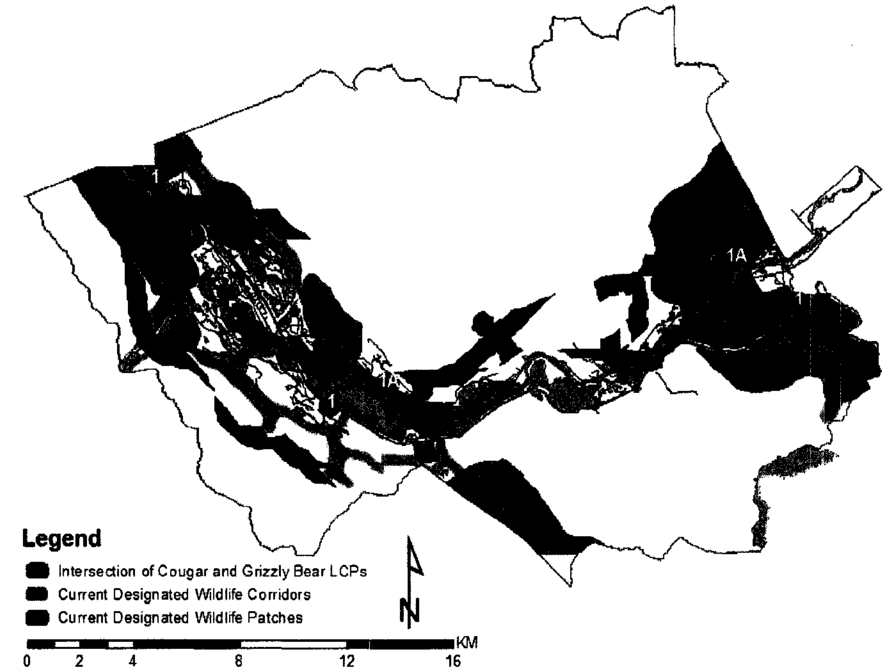


Figure 3-5. Predicted probability of cougar occurrence in the Crowsnest Pass during (a) the non-winter season; and, (b) the winter season. Refer to Table 3-4 for description of model variables and coefficients.

(a)



(b)

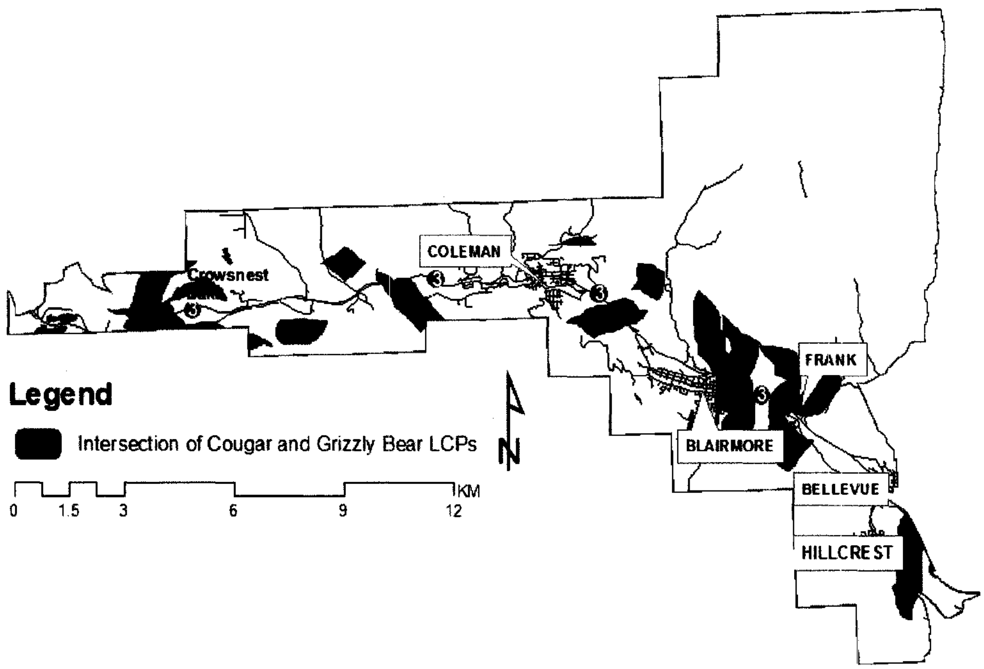


Figure 3-6. Intersected least-cost paths highlight areas of overlap for cougars and grizzly bears during various seasons in (a) Canmore Region of the Bow Valley and, (b) the Crowsnest Pass.

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CHAPTER FOUR

A step in the right direction: use of step selection functions to identify local corridors for large carnivores

1. Introduction

Because large carnivores occur at low densities and have relatively large home ranges, human activities undermine the viability of carnivore populations (Noss *et al.* 1996; Ginsberg 2001). Besides direct persecution and loss of prey, habitat loss and fragmentation due to human activities is considered the greatest long-term threat to the persistence of carnivores. This is particularly well documented as large carnivores attempt to move outside of protected areas (Woodroffe & Ginsberg 1998; Woodroffe 2000; Nielsen, Boyce, & Stenhouse 2004). Corridors (sometimes called linkages) are part of most large carnivore conservation initiatives as the most popular, albeit controversial, way to facilitate carnivore movement across landscapes (Soulé & Terborgh 1999; Sanderson *et al.* 2002). Theoretically, dispersal is the key process maintaining viability of small, spatially structured populations (Lima & Zollner 1996; Clobert *et al.* 2001). Yet corridors also may be important for maintaining daily and seasonal movements of large carnivores, particularly in areas with human development and activities. Increasingly, conservation plans will need to consider corridors and other land-use configurations that allow species to respond to climate change by supporting range shifts (Thomas *et al.* 2004; Kareiva 2006). Animal movement as a process, however, seldom has been an explicit component of corridor planning (Vos, Baveco & Grashof-Bokdam, 2002; Noss & Daly 2006), due to the difficulty of quantifying movement and measuring the effect of the landscape on movement (Turchin 1998; Chetkiewicz, St. Clair & Boyce, 2006).

The advancement of global positioning system (GPS) technology and our ability to map movements easily with geographic information systems (GIS) – allowing for more precise measurement of animal's movement over large landscapes – offer new opportunities to measure movement pathways of large carnivore and to assess the effects of landscape at spatial scales relevant to corridor identification and design. Movement pathways of large carnivores can inform corridor identification and design in several ways. First, they can be used to associate movement types with certain landscape features. For example, wolves (*Canis lupus*) had more tortuous movement pathways near high human-use trails and low-use paved roads (Whittington, St. Clair & Mercer 2004). Second, these metrics can be used to parameterize or refine movement models. For example, daily and hourly telemetric data from dispersing Iberian lynx (*Lynx pardinus*) were used to parameterize movement models across different matrix types (Revilla *et al.* 2004). In this case, movement properties of individuals in different matrix types supported population-level responses to landscape heterogeneity. Third, movement metrics can be used to examine responses to edges or habitat boundaries. For example, cougar telemetry data can be used to simulate movement pathways of cougars across habitat boundaries and edges generated in a GIS (Tracey 2006). Simulated pathways along urban and habitat edges tended to move parallel along the edge emphasizing the role of this particular type of edge in directing and channeling movements as well as creating possible barrier effects. In addition, movement of large carnivores can be characterized using mechanistic models to understand how landscape may affect movements. Characterizing grizzly bear (*Ursus arctos*) movements according to a correlated random walk (Turchin 1998), illustrated how land ownership and habitat information affected potential dispersal routes (Boone & Hunter 1996). Patterns in movement data also have been used, retrospectively, to identify behaviour at kill sites and assess predation rates (Anderson & Lindzey 2003; Franke *et al.* 2006). Despite the availability of telemetry data for many carnivore species (Young & Shivak 2006), linking landscapes and movement for the purpose of corridor design and identification remains a challenge.

One approach to integrating carnivore movement behaviour in corridor design and identification is step-selection functions (SSF, Fortin *et al.* 2005), a technique similar to resource selection functions (Manly *et al.* 2002). Step-selection functions model the selection for certain landscape features along an animal's step, i.e., lines between sequential telemetry locations, by comparing observed steps with randomly generated steps (Fortin *et al.* 2005; Coulon *et al.* 2008). By characterizing the probability of taking a step as a function of multiple landscape attributes along that step, we can use an SSF to infer what choices an animal may make during movement. Such models offer several benefits for corridor applications. Firstly, a SSF explicitly considers landscape characteristics that animals encountered between the start and end points of observed movement pathways and uses empirical movement data to generate random pathways. Secondly, a SSF can be used to quantify species-specific responses to landscape features and, by generating landscape- and species-specific movement rules for carnivores, inform corridor design and identification as well as suggest further research. Thirdly, a SSF can be generated for multiple species, often a goal in multi-species corridor plans where large carnivores are focal species (e.g., Ray *et al.* 2005; Beier *et al.* 2006). Finally, a SSF can complement other approaches that examine changes in fine-scale movement behaviour such as step length in response to landscape features. Most analyses of this kind have focused on invertebrates showing more tortuous pathways (e.g., shorter step lengths and slower movement rates) in good-quality habitats and moving further and faster over unfavorable terrain (Crist *et al.* 1992; Johnson *et al.* 1992; With 1994; Shultz & Crone 2001). An emphasis on movement behaviour, particularly in areas of human developments, may identify effects not observed in more traditional habitat selection studies (Desrochers & Fortin 2000)

I explored the application of SSF and step length models to corridor identification and design in two areas in the Canadian Rocky Mountains of Alberta. The Canmore region of the Bow Valley (hereafter, "Canmore") and the Crowsnest Pass area (hereafter, "Crowsnest") (Chadwick 2000) have been targeted for local corridor planning, particularly for grizzly bears, within the regional Yellowstone-to-Yukon Conservation Initiative that is devoted to restoring habitat connectivity throughout the Northern Rocky Mountains (Gatewood 2003). The overarching goal of my research was to illustrate what landscape features promoted movement to better local corridor identification and design for grizzly bears and cougars. I collected locations of grizzly bears and cougars fitted with GPS radiocollars in Canmore and Crowsnest during 2000-2004. My objectives were: (1) quantify what features on the landscape were selected (or avoided) by cougars and grizzly bears during different seasons using a SSF model, (2) model step length using the same variables to examine how landscape features influenced movement (e.g., shorter versus longer step lengths) of grizzly bears and cougars during different seasons; and (3) identify consistent patterns in both step selection and step length responses to identify corridors and inform corridor designs for both species and landscapes.

2. Materials and Methods

2.1 Study Areas

2.1.1 Canmore Region of the Bow River Valley

The Canmore region of the Bow River Valley (51°05', 155°22') is approximately 110 km west of Calgary, east of Banff National Park and north of Kananaskis Country (Fig. 4-1) in Alberta, Canada. The Bow River Valley, part of the Rocky Mountain Natural Region of Alberta (Natural Regions Committee 2006), is characterized by some of the best protected montane habitat for large carnivores in Alberta, including Banff National Park and a number of provincial parks (Donelon 2004). However, the quality of this habitat is undermined by a rapidly growing human population in the town of Canmore (estimated at 11 600 permanent residents; Herrero & Jevons 2000), bisection by the Trans-Canada Highway, one of the busiest transportation routes in Canada (summer traffic = 21 000 people / day; Alexander, Waters & Paquet, 2005) and its proximity to Calgary, projected to exceed 1.5 million people by 2030 (Stelfox, Herrero & Ryerson, 2005). In addition, a two-lane paved highway and a two-track transcontinental railway, operated by Canadian Pacific Railway, further challenge connectivity through the Bow River Valley for many species (Bélisle & St. Clair 2001; Clevenger & Wierzchowski 2006). To address ongoing development within the region, the Bow Corridor Ecosystem Advisory Group (BCEAG) developed a science-based framework for the design of wildlife corridors to provide connectivity between Banff National Park and other protected areas in the region (BCEAG 1999). I focused on grizzly bear and cougar captures (see below) in Wildlife Management Unit 410 (425 km^2), which includes the town of Canmore and designated corridors. My study extent represents the composite minimum convex polygon (MCP) of grizzly bear and cougar locations collected during this study.

2.1.2 Crowsnest Pass in the Crowsnest River Valley

The Crowsnest Pass (49°37', 114°4') is a 32-km long valley of montane and grassland vegetation located along the Crowsnest River in southwestern Alberta, adjacent to the Alberta-British Columbia border, 269 km southwest of Calgary (Fig. 4-1). The Crowsnest River Valley is also within the Rocky Mountain Natural Region, but the climate is generally warmer and drier than in Canmore (Natural Regions Committee 2006). In contrast to the Canmore region of the Bow Valley, the Crowsnest River Valley is managed for multiple uses including forestry, oil and gas, recreation, and agriculture and livestock grazing. The communities of Blairmore, Bellevue, Frank, Hillcrest, and Coleman as well as the hamlets of Sentinel (Sentry) and Crowsnest comprise the Municipality of the Crowsnest Pass (population approximately 6 000). A two-lane highway (Highway 3) bisects the valley (daily traffic volume = 7 000 vehicles per day) that parallels a railroad supporting 8-16 freight trains per day (Apps *et al.* 2007). In addition to the communities located along the highway, most of the land along the Crowsnest Pass is in private or corporate ownership and potentially subject to development. Recent discussions of twinning Highway 3 through the Crowsnest Pass and ongoing residential developments have prompted concerns about carnivore movements in the Crowsnest Pass (Proctor *et al.* 2005; Apps *et al.* 2007). I focused capture efforts within the boundaries of Wildlife Management Unit 303 (1 657 km^2), that includes the three corridors identified within the municipality. The composite MCP of grizzly bear and cougar locations collected during this study defined the spatial extent of the Crowsnest Pass study area.

2.2 Data Sources

2.2.1 Grizzly Bear and Cougar Telemetry Data

During the springs of 2000-2004, four grizzly bears (2 females, 2 males) were captured and collared in the Canmore study area and four grizzly bears (2 females, 2 males) in Crowsnest, using culvert traps, standard leg and pail snares and aerial darting techniques (Cattet, Caulkett & Stenhouse, 2003). During the winters of 2000 to 2004, five (4 female, 1 male) cougars were captured and collared in the Canmore study area and 13 (7 female, 6 male) cougars in Crowsnest by tracking cougars in snow with trained hounds (Hornocker 1970). Grizzly bears and cougars were fitted with Televilt-Simplex™ GPS radiocollars (Lindesberg, Sweden) and programmed to acquire a fix at intervals between 1 – 4-h. Capture protocols were approved by Animal Care Committees for the University of Alberta and Alberta Sustainable Resource Development, following the Canadian Council on Animal Care guidelines.

Following retrieval of the GPS collars, location data were imported into ArcGIS 9.0 (Environmental Systems Research Institute, Inc., Redlands, California, USA). Because I wanted to compare between species and study areas, I re-sampled locations occurring less than 4 hrs apart since 4 hours was the minimum sampling interval for cougars in Crowsnest. This also minimized autocorrelation in the datasets (Turchin

1998). Hawth's Analysis Tools for ArcGIS (hereafter, "Hawth's Tools") (Beyer 2004) were used to generate a step, a straight-line segment, between successive 4-h telemetry locations and turning angles, based on three consecutive locations (Turchin 1998). To assess how seasonality influenced step selection, I partitioned the grizzly bear telemetry data into pre-berry (den emergence to July 15) and berry (July 16 to denning) seasons (Nielsen, Boyce & Stenhouse, 2004) and the cougar telemetry data into winter (15 November – 15 April) and non-winter (16 April - 14 November) seasons (Jalkotzy, Ross & Wierzchowski 1999). Though grizzly bear and cougar movements also vary throughout the day (e.g., Donelon 2004; Beier *et al.* 1995), I chose not to segregate the dataset into further time periods. My main interest was exploring the factors that affected step selection for the purposes of describing movement of cougars and grizzly bears regardless of time of day to maximize the application of my results to corridor identification and design.

2.2.2 Predictor Variables

Habitat: Percent crown closure and a landcover classification were obtained for both study areas (McDermid, Franklin & LeDrew 2005). Mean percent crown closure was calculated for each step. Using Spatial Analyst in ArcGIS, I generated three distance grids for forested, shrub, and non-vegetated (ice/snow and rock/bare soil) landcover types. The mean distance to each landcover type and the mean percent of each landcover type on each step were estimated using Hawth's Tools (Beyer 2004). A dummy variable was created to determine whether a step ended in an open (0) or forested (1) habitat.

Terrain: A 30-m digital elevation model was used to calculate slope (degrees) in both study areas was obtained from Alberta Sustainable Resource Development. A dummy variable was created to evaluate whether steps crossed slopes greater than 45 degrees following guidelines that consider such slopes to be barriers to most carnivore movements within currently designated corridors (BCEAG 1999). The digital elevation model also was used to estimate a terrain ruggedness index (Evans 2004). The mean value of terrain ruggedness was calculated for each step using Hawth's Tools (Beyer 2004).

Roads: Road layers were obtained for the Canmore and Crownest Pass study areas from Alberta SRD and the Miistakis Insitute. Using Spatial Analyst, I calculated distance to paved roads and road density grids in each study area. Using Hawth's Tools (Beyer 2004), I calculated the minimum distance to a paved road and the maximum road density encountered along each random and observed step. Finally, a count of the number of paved roads crossed by each step was determined using Hawth's Tools (Beyer 2004).

2.3 Data Analyses

2.3.1 Step-Selection Functions

I investigated the effects of landscape features on grizzly bear and cougar movement using a step-selection function. To create a seasonal SSF, I compared observed grizzly bear and cougar steps to a matched random sample of 20 steps with the same origin as observed steps, created using custom tools for ArcGIS 9.0 (H. Beyer, personal communication). Random steps were drawn from distributions of empirical step length and turning angles obtained for each species and season in my study (total of eight distributions). Small sample sizes precluded examining step selection differences by sex and age group. Kolmogorov-Smirnov tests were used to test for differences between distributions by species and season. Distributions that were not significantly different were combined.

I selected or created landscape variables based on previous research that demonstrated their influence on cougar and grizzly bear movements (Dickson, Jenness & Beier 2005; Dickson & Beier 2007; Roever, Boyce & Stenhouse i*n press-a,b*) and resource selection patterns (Chapter 3). Using custom tools in ArcGIS 9.0 (H. Beyer, personal communication), each step was then described in relation to the encountered landscape variables (see below) using summary statistics (i.e., length-weighted mean, minimum, and maximum values). Length-weighted means (hereafter, "mean") were calculated by taking the average of each predictor variable along the step divided by the total step length.

I created species-specific seasonal models following procedures in Hosmer and Lemeshow (2000). Because I was interested in qualitatively comparing effects of landscape heterogeneity across seasons, species, study areas, and analyses, I used a full model with the exclusion of correlated and collinear variables. All continuous variables were tested for correlation and collinearity using Pearson correlation coefficients and variance inflation factor (VIF) diagnostics. All variables with correlation coefficients > 0.7 or individual VIF scores > 10 (Chatterjee, Hadi & Price 2000) were assumed to be collinear and the weaker covariate was not included in the full model. Nonlinear relationships were tested among all continuous covariates with the addition of a quadratic term and I selected the form that resulted in the largest increase in the χ^2 statistic for the robust Wald test. I used robust standard errors clustered on individual animal (Nielsen *et* *al.* 2002) to address the lack of independence between steps made by an individual. I examined autocorrelation and partial correlation plots of model residuals for each animal in each season to evaluate autocorrelation within seasonal datasets (Fortin *et al.* 2005). Statistical analyses were conducted in Stata 9.2 (Stata Corporation 2005) and R 2.6.1 (R Development Core Team 2004).

2.3.2 Step-length analyses

I used linear mixed-effect models with individual grizzly bears or cougars as a random intercept (Rabe-Hesketh & Skrondal 2008) to explore the relationship between seasonal grizzly bear and cougar 4-hr step lengths (e.g., rate of movement) and landscape variables described below. Step lengths were $\log_{10}$ transformed to normalize the right skew in the data. I built a full model using the same approach and criteria as for the SSF analyses. All statistical analyses were conducted in Stata 9.2.

3. Results

3.1 Step-Selection functions

3.1.1 Canmore

In Canmore, a total of 553 steps (56 – 239 steps per cougar) and 576 steps (85 - 324 steps per cougar) were used to develop a winter and non-winter SSF, respectively, for cougars. Step-length distributions were significantly different between winter and non-winter seasons (two-sample Kolmogorov-Smirnov test, D = 0.125, $P < 0.001$) and were analyzed separately. The distributions of turning angles were not significantly different between seasons (two-sample Kolmogorov-Smirnov test, D = 0.074, $P = 0.216$) and were combined.

During both seasons, cougars steps were closer to paved roads (Table 4-1, Fig. 4-2) and cougars avoided crossing paved roads (observed steps crossed a paved road 28 and 16 times during winter and non-winter, respectively). Cougars also avoided taking steps far from forest landcover and this response was strongest in the winter (Fig. 4-3). Cougar steps had a higher percent of non-vegetation (e.g., snow, ice, barren ground) on the step compared to random steps (Table 4-1). During winter, cougar steps occurred in areas of high road density (Table 4-1). Cougar steps had more shrubs on them compared to random paths and they avoided moving very far from shrub landcover during the winter. No observed steps crossed steep slopes in the winter. During non-winter, cougars took steps in areas with increasing crown closure and terrain ruggedness (Table 4-1), although only one observed step crossed a steep slope during this season. Cougar steps ended in forest more often than open habitat (Table 4-1).

In Canmore, a total of 900 steps (50 - 449 steps per grizzly bear) and 798 steps (50 – 589 steps per grizzly bear) were used to develop a pre-berry and berry SSF, respectively, for grizzly bears. Step-length distributions were significantly different between winter and non-winter seasons (two-sample Kolmogorov-Smirnov test, D = 0.125, $P < 0.001$). The distributions of turning angles were not significantly different between seasons (two-sample Kolmogorov-Smirnov test, D = 0.074, $P > 0.216$) and were combined.

During both seasons, grizzly bear steps ended in open habitat significantly more often than they ended in forest (Table 4-1). Selection for terrain ruggedness varied by season: during pre-berry season, grizzly bears crossed less rugged terrain compared to random steps, but during berry season they crossed increasingly rugged terrain. However, only four observed steps crossed a steep slope. Observed steps crossed paved roads 56 times during pre-berry and berry seasons, respectively, but these were not significantly different from random steps that crossed paved roads. During pre-berry season, grizzly bears took steps that were closer to forest landcovers and non-vegetated areas (e.g., snow, ice, barren ground) (Table 4-1). During berry season, grizzly bears avoided being far away from shrub landcovers (Fig. 4-4) and took steps where crown closure was less (e.g., more open forest canopy). However, steps had fewer shrubs on them compared to random steps. Grizzly bears took steps that were closer to paved roads (Fig. 4-5) and steps were taken in areas where road density was lower.

3.1.2 Crowsnest Pass

In Crowsnest, a total of 1 106 steps (59 - 253 per cougar) and 1 147 steps (113 – 308 per cougar) were used to develop a winter and non-winter SSF for cougars. Step length and turning-angle distributions were significantly different between winter and non-winter seasons (step length; two-sample Kolmogorov-Smirnov test, $D = 0.215$, $P < 0.001$, turning angles; two-sample Kolmogorov-Smirnov test, $D = 0.072$, $p = 0.014$).

During both seasons, cougars took steps that were closer to paved roads compared to random steps (Fig. 4-2) (Table 4-2). During winter, cougar steps crossed less rugged terrain and only one step crossed steep slopes. Cougar steps had more shrubs on them and they avoided moving where their steps were closer to non-vegetated areas such as ice, snow and barren ground. Cougar steps ended in forest significantly more than they ended in the open. Cougars avoided crossing paved roads (observed steps crossed paved roads 27 times), but this was not significantly different from the number of paved road crossings by random steps. During the non-winter, however, cougars avoided crossing paved roads (18 observed steps crossed paved roads). Cougar steps had less crown closure (e.g., open forest canopy) compared to random. They did not cross any steep slopes during non-winter.

In Crowsnest, 414 steps (51 – 154 steps per grizzly bear) and 655 steps (94 - 378 per grizzly bear) were used to develop a pre-berry and berry SSF, respectively, for grizzly bears. Step-length distributions were significantly different between pre-berry and berry seasons (step length; two-sample Kolmogorov-Smirnov test, D = 0.101, $P < 0.001$). Turning angles distributions were not significantly different by season and were combined.

There were no consistent significant predictors of grizzly bear step selection in both seasons (Table 4-4). However, no steep slopes were crossed by grizzly bears and steps from only one individual crossed a paved road (1 crossing in pre-berry season and 5 crossings in berry season). During pre-berry season, grizzly bears steps crossed less rugged terrain. During berry season, grizzly bear steps were closer to shrub landcovers (Fig. 4-4) and they took steps in areas with lower crown closures (e.g., more open forest canopy). Grizzly bears took steps in areas of higher road density and their steps were closer to paved roads compared to random steps (Fig. 4-5).

3.2 Step-length analyses

3.2.1 Canmore

During both seasons in Canmore, cougar step lengths increased with increasing number of paved road crossings and as road density increased (Table 4-3). Cougars had shorter steps when close to shrub landcover and increased their step lengths as terrain increased. Cougars had longer steps when the percent of crown closure was low (e.g., more open forest canopy). During winter, cougar step lengths increased when they were close to paved roads. Cougar step lengths were short when they were close to forest landcovers as well as non-vegetation (e.g., snow, ice, barren ground). During the non-winter, cougar step lengths increased as the percentage of shrubs along the step increased.

Similar to cougars, grizzly bears during pre-berry and berry seasons in Canmore had longer step lengths as the number of paved road crossings and road density increased (Table 4-3). Because minimum distance to paved roads was correlated with maximum road density ($r = 0.718$), I evaluated the effect of paved roads and road density on step length separately. Step lengths near paved roads varied by season: during pre-berry season, grizzly bears had shorter steps when close to paved roads, but during berry season, grizzly bears had longer steps close to paved roads. A similar pattern was found in response to distance to non-vegetated areas such as snow, ice and barren ground: during pre-berry season, grizzly bears had shorter steps when they were close to non-vegetated areas, but during berry season, step lengths were longer when closer to non-vegetation (Table 4-3). Step lengths also varied seasonally in response to percent crown closure: during pre-berry season, step lengths were longer when percent crown closure was low (e.g., more open or less cover), but during berry season, step lengths were longer when percent crown closure was high (e.g., more closed or more cover). In the pre-berry season, grizzly bear step lengths decreased as the percent of non-vegetation along the step increased (Table 4-3). During berry season, grizzly bear step lengths decreased with increasing terrain ruggedness. Grizzly bears also had shorter steps when they were closer to shrub landcovers during the berry season.

3.2.2 Crowsnest Pass

During both seasons, step lengths for cougars in Crowsnest were short when they were close to both forested and shrub landcovers (Table 4-4). Cougars had longer steps as road density increased. Cougar step lengths were shorter when steps ended in forest habitat compared to open habitats (Table 4-4). During winter, cougar step lengths decreased as the percent of non-vegetation (e.g., snow, ice, barren ground) along the step increased and steps were short near non-vegetated areas. During the non-winter, and similar to cougars in Canmore, the step lengths of cougars in Crowsnest increased with increasing number of paved road crossings and increasing terrain ruggedness (Table 4-4). During the non-winter, cougars had longer steps as the percent of shrubs along the step increased.

Similar to cougars in Crowsnest, during both seasons, grizzly bears had short steps near forested landcover and when steps ended in forest compared to open (Table 4-4). No other variables were significant predictors of grizzly bear step length during the pre-berry. During berry season, grizzly bears step lengths increased with increasing terrain ruggedness and as the percentage of crown closure and shrubs along the step increased (Table 4-4). Grizzly bear steps were short near shrub landcovers. Grizzly bear step lengths were long near paved roads and as road density increased.

4. Discussion

My results demonstrated how landscape features correlated with cougar and grizzly bear movements. My results can be used to answer two fundamental questions about selection patterns and movement responses of these large carnivores in a given landscape: what features on the landscape might promote movement?; and, how do large carnivores respond to those features? Specifically, my results showed which landscape features are correlated with cougars and grizzly bears taking relatively longer (e.g., faster) or shorter (e.g., slower) steps. Step-selection function models can quantify the relationship (e.g., promotion or avoidance) between steps, or moves, with specific landscape features. Step length analyses however can indicate how they are moving (e.g., shorter or longer) in responses to those same features. By combining these two approaches for different species and landscapes, it is possible to examine consistent patterns in selection and movement responses across seasons. As such, this empirically based, quantitative approach provides conservation planners (hereafter, "managers") with an important tool for identifying areas of the landscape that may facilitate individual movements (*sensu* corridors).

Landscape features correlated with carnivores taking longer steps.

My SSF results showed that cougar steps were closer to paved roads during winter in both study areas. Although other studies have reported that cougars generally avoid paved roads (Sweanor, Logan & Hornocker, 2000; Dickson & Beier 2002), cougars might select to move through areas closer to paved roads for a number of reasons. First, they may be following their preferred prey, primarily deer (*Odocoileus* spp.), that are attracted to roadside habitats. While data on winter deer abundance and distribution in Canmore and Crowsnest were unavailable in my study, cougars can move seasonally in response to ungulate prey (Pierce *et al.* 1999). In other studies, cougars have been shown to move to valley bottoms– where the roads tend to be located – in response to the distribution of prey and snow conditions (Jalkotzy, Ross & Wierzchowski 1999) and cougars select gentle slopes and valley bottoms for traveling and hunting (Dickson, Jenness & Beier 2005; Dickson & Beier 2007). My results supported this general trend – cougars avoided crossing steep slopes throughout the year. A second reason cougars might select areas closer to paved roads for movement in the winter is that they use these habitats as conduits for easier travel, which has been shown to be the case for their use of dirt and gravel roads (Dickson, Jenness & Beier 2005). A third reason cougars may be closer to paved roads could be the result of the geophysical properties of each landscape which are characterized by rugged mountainous terrain and narrow valleys, particularly around Canmore. Because the valley bottoms are also the areas where roads and human development tend to occur, cougars may be closer to paved roads because of the geophysical features rather than a selection for proximity to paved roads per se. Finally, cougars may have selected areas close to paved roads for movement in the winter because they are waiting for an opportunity to cross the road. Beier (1995) showed that dispersing cougars approached highways, but usually stopped 50-100 m away until an opportunity to cross, usually at night.

Similarly, my SSF results showed that in both study areas grizzly bears also selected areas close to paved roads for movement during berry season. The results are consistent with other researchers that found grizzly bears in the Banff-Bow valley consistently use areas closer to roads, particularly near low-volume, two-lane paved roads (Gibeau *et al.* 2002; Chruszcz *et al.* 2003). Grizzly bears in areas of high human development may be attracted to roadside habitats (Gibeau *et al.* 2002; Chruscz *et al.* 2003; Roever, Boyce & Stenhouse, *in press-b*). This attraction was most evident in the berry season, when grizzly bears are more likely to seek out quality forage and herbaceous resources to maximize weight gain and fat deposition for hibernation (Rode, Robbins & Shipley, 2001; Robbins, Schwartz & Felicetti 2004; Munro *et al.* 2006). A second reason grizzly bears might be using areas close to paved roads for movement is that they are habituated to traffic noise and human development on these roads and are therefore less wary (Gibeau *et al.* 2002; Chruszcz *et al.* 2003). Two of the four grizzly bears used in my study in Canmore were considered habituated and eventually translocated to avoid further conflicts with people (Honeyman 2007). As with cougars, a close correlation with paved roads may be because rugged mountainous terrain and narrow valleys, particularly around Canmore, force grizzly bears in closer proximity to paved roads (Chruszcz *et al.* 2003; Roever, Boyce & Stenhouse, *in press- b*). My results showed that in both Canmore and Crowsnest, grizzly bears avoided steep slopes and tended to cross gentle terrain, which suggests they are more likely to be in valley bottoms.

My step length results showed that in both study areas, grizzly bears and cougars had longer step lengths near paved roads during berry and winter seasons respectively. These longer steps may stem from flight responses to roads, a behaviour that has been detected in ungulate species in response to recreational vehicles (Borkowski *et al.*, 2006; Preisler, Ager & Wisdom, 2006). Grizzly bears, particularly females, tend to avoid the high-volume roads such as the Trans-Canada Highway in the Banff-Bow Valley (Gibeau *et al.* 2002; Chruczcz *et al.* 2003). Although cougars are generally thought to exhibit a higher degree of behavioural plasticity or tolerance for human development and activity (Beier 1995; Weaver *et al.* 1996), paved roads are often a source of mortality for both species regardless of traffic volumes and are likely to be avoided (Nielsen *et al.* 2004; Alexander, Waters & Paquet 2005). A second reason that both species may have longer steps near paved roads is that paved roads are actually directing or channeling carnivore movements. Cougars and grizzly bears traveling along paved roads would have longer steps if they encountered fewer impediments and straighter movement pathways. However, this response would also occur when paved roads create barriers that animals cannot cross immediately, leading them to take longer steps alongside roads until they encounter suitable crossing conditions. Determining which of these scenarios is most likely in both study areas for both species remains a challenge. Clarification could be provided by using a fine-scale (e.g., less than the 4-hr time step used here) analysis of movement near paved roads with respect to different road class, traffic volumes, and time of day. Although this approach might enable managers to fine-tune corridor design closer to paved roads in certain areas or even home ranges (i.e., to support the placement of a crossing structure), it may not be necessary for corridor identification at broader scales.

The step selection function model and step length results of this study also suggested that, during the non-winter season, cougars in Canmore and in Crowsnest avoided crossing paved roads and had longer steps as the relative number of road crossings increased. Since observed cougar steps in both study areas crossed paved roads throughout the year, paved roads do not appear to present an absolute barrier to cougar movement. The results suggested, however, that cougars cross paved roads as quickly as possible, supporting the need for mitigation structures on paved roads to address cougar movements near paved roads in both study areas. Both cougars and grizzly bears use wildlife crossing structures (Gloyne & Clevenger 2001; Clevenger & Waltho 2005). Currently, a portion of the Trans-Canada Highway near Canmore is mitigated with fencing, two underpasses, a wildlife jump-out and cattle guards (Clevenger, Maher & Hallstrom, 2006), however, there are no specific mitigation structures for paved roads along Highway 3 in Crowsnest other than two existing railroad bridges that might function as crossing structures (Apps *et al.* 2007). Understanding where to place such structures in Crowsnest would be achieved best by examining habitat variables and fine-scale movement behaviour at actual road crossings or by using these data to simulate road crossings (e.g., Dickson, Jenness & Beier 2005, Tracey 2006).

Landscape features correlated with carnivores taking shorter steps

The step-selection function results highlight differences between cougars and grizzly bears in steps selected based on their ecological requirements in each season. My results showed that during the winter, cougars in Canmore chose areas close to forest landcover for movements. Although this specific variable was not a significant predictor of step selection for cougars in Crowsnest, the response was similar. Additionally, the steps of cougars in Crowsnest ended in forest habitat significantly more often than in the open, and cougars took shorter steps when they did end in forest. Cougars in winter may be using areas close to or within forest landcovers because of their requirement for horizontal and vertical cover for hunting and predation sites, as well as resting during the day (Jalkotzy, Ross & Wierzchowski 1999; Murphy, Ross & Hornocker, 1999).

The step-selection function results also showed that during the berry season, grizzly bears in Canmore and Crowsnest selected areas with less crown closure (e.g., more open forest canopy) and shrub landcovers for movement. Although data on the spatial and temporal distribution of important bear foods such as horsetails (*Equisetum* spp.) and soopolallie or buffaloberry (*Shepherdia canadensis*) (Munro *et al.* 2006) were not available for either study area, my results generally lend support to grizzly bear step selection based on important food resources such as *Shepherdia* berries. The percent of forest crown closure has been shown to be an important predictor of in the production of *Shepherdia* berries, and berry productivity declined when forest cover exceeded 45% (Hamer 1996).

Both cougars and grizzly bears had short step lengths close to forest and shrub landcovers, respectively. Shorter step lengths in proximity to landcovers might be the result of two possible factors. First, shorter step lengths near landcover types could indicate foraging (grizzly bears), predation sites (cougars) or resting (both). Donelon (2004) examined 1-hr mean movement distances for the Canmore grizzly bears that I used in this study and attributed the significantly shorter distances during the night to bears bedding down or resting. A second possible reason for shorter step lengths near these features could be related to high levels of human use or activity that are also occurring in or near these landcover types. In the Foothills region of west-central Alberta, researchers documented that grizzly bears were bedded at night and attributed this to the low levels of human activity in their area (Munro *et al.* 2006). Donelon (2004) suggests the shorter distances traveled by Canmore grizzly bears at night could be the result of uninterrupted feeding opportunities when levels of human use on trails are low. Whittington *et al.* (2004) uses very fine-scale spatial information (< 25 m) to show that movements of wolves were more tortuous at predation sites in high quality habitat **and** near high-use human trails. They attributed the circuitous movement patterns near human-use trails as an avoidance response. Donelon (2004) concluded that the high density of human-use trails within the combined home range of the Canmore grizzly bears left few options for grizzly bears in Canmore to avoid humans during the day. Interpreting movement responses of cougars and grizzly bears in the Crowsnest relative to human use in or near potentially high-quality food habitat, would be even more speculative although some human use data collection is now underway (D. Duke, personal communication).

My results showed that SSF models combined with step length analyses are powerful tools for integrating movement data into corridor identification and design and highlight consistent and species-specific responses to landscape features. However, caveats are appropriate. First, inferences were based on small sample sizes in my study. Although the Canmore grizzly bear sample used in this study was "believed to represent a significant portion (>50%) of the total number of grizzly bears that use this area" (M. Gibeau, personal communication 2004 cited in Donelon 2004), generalizations are limited. A second caveat is that some potentially important variables were omitted from the models due to limited data availability. In my study, for example, the distribution of prey and seasonally important food resources were not available. Finally, it is difficult to know the motivation for movement, a key issue in functional connectivity (Bélisle 2005). Studies with small mammals (e.g., Rizkalla & Swihart 2007), birds (e.g., Bélisle & St. Clair 2001; Gobeil & Villard 2002), or invertebrates (McIntyre & Wiens 1999; Schooley & Wiens 2004) have been able to standardize motivation for movements through gap crossing experiments or playbacks as well as manipulate movement behaviours by varying quality and configuration of different habitats and the matrix. While large carnivores may be considered "terrible experimental subjects" (Minta, Kareiva, & Curlee 1999 p. 325), a number of approaches have been used to standardize the motivation for movement in large carnivores with respect to non-habitat features such as predators or conspecifics. For example, playbacks were used to examine predator avoidance tactics of cheetahs (*Acinonyx jubatus*; Durant 2000) and territorial responses from conspecific lions (*Panthera leo*; Spong & Creel 2004). In North American landscapes, particularly in areas with high human development or activities, another opportunity for examining movement of large carnivores where the motivation to move is clearly known is when individual animals are translocated due to their perceived threat to humans (e.g., Linnell *et al.* 1997). Translocation of individual large carnivores, particularly in areas with high levels of human activity and development, probably occurs more frequently than the rare dispersal movements corridors are assumed to facilitate. In addition, dispersal movements for large carnivores are notoriously difficult to obtain directly with conventional telemetry studies (Waser, Strobeck & Paetkau 2001; Trakhtenbrot *et al.* 2005). A combination of SSF and step length analyses as used here could be applied to these kinds of "motivated" large-scale movement opportunities for the purpose of identifying or evaluating corridors.

In this paper, I showed how seasonal SSF and step length models represent a "step" in the right direction in improving our understanding of large carnivore interactions with landscape features and the implications for corridor design. Providing safe passage for carnivores across a complex matrix dominated by human activities must avoid channelling individual carnivores into areas where they may kill people or their livestock. SSF models and step length analyses could help managers assess not only where on the landscape carnivores are showing selection, but where they are moving fast. This combination may identify corridor solutions that reduce the possibilities for conflict between people and large carnivores. Ultimately, the most effective corridors will be those areas of the landscape that can serve as both places for movement as well as habitat (Haddad & Tewksbury 2005) and a multifaceted approach to assessing connectivity makes corridor identification and design more defensible and reliable (Noss & Daly 2006). To this end, a combination of approaches like SSF and step length analyses to quantify movement choices and resource selection functions to quantify habitat selection would be a valuable addition to a manager's toolkit.

Table 4-1. Beta coefficients and robust standard errors for the final cougar and grizzly bear step-selection function (SSF) models in the Canmore Region of the Bow Valley. Separate models were generated for each season.

	Cougars						Grizzly Bears					
	Winter			Non-winter			Pre-berry			Berry		
	β	SE		β	SE		β	SE		β	SE	
Paved road crossing	-0.969	0.199	**	-0.327	0.004	**	0.246	0.156		-0.045	0.057	
Paved road crossing^2	0.068	0.017	**				-0.054	0.032				
Mean terrain ruggedness	0.002	0.003		0.007	0.001	**	-0.017	0.007	*	0.005	0.002	**
Mean percent crown closure	-0.004	0.006		0.030	0.006	**	0.007	0.012		-0.014	0.003	**
Mean % non-veg on step	2.231	1.047	*	0.822	0.326	*	0.052	0.396		-0.236	0.566	
Mean % shrubs on step	1.185	0.446	**	-0.039	0.717		-0.281	0.417		-0.623	0.156	**
Distance to non-veg landcover (km)	-0.816	0.851		-0.441	0.271		-0.781	0.160	**	-0.332	0.399	
Distance to shrub landcover (km)	-0.750	0.334	*	-0.380	0.292		-0.185	0.281		-3.716	0.385	**
Distance to forested landcover (km)	-17.038	6.960	*	-2.035	0.014	**	-2.194	1.080	*	-1.609	1.094	
Minimum distance to a paved road (km)	-0.284	0.363	*	-0.701	0.104	**	-0.263	0.197		-0.545	0.059	**
Maximum road density (km/km^2)	0.589	0.164	**	-0.497	0.461		-0.077	0.166		-0.179	0.078	*
Maximum road density^2							0.007	0.013				
Step ends in forest[a]	0.361	0.342		0.254	0.125	*	-0.424	0.105	**	-0.415	0.068	**

(*) denotes coefficients significant at the p=0.05 level and (**) denotes significance to the p=0.01 level

[a] compared to open habitat

Table 4-2. Beta coefficients and robust standard errors for the final cougar and grizzly bear step-selection function (SSF) models in the Crownest Pass. Separate models were generated for each season.

	Cougars						Grizzly Bears					
	Winter			Non-winter			Pre-berry			Berry		
	β	SE		β	SE		β	SE		β	SE	
Paved road crossing	-0.349	0.206		-0.812	0.351	*						
Mean percent crown closure	-0.004	0.008		-0.021	0.006	**	-0.001	0.015		-0.028	0.005	**
Mean terrain ruggedness	0.018	0.006	**	-0.006	0.011		-0.006	0.002	**	-0.002	0.003	
Mean % non-veg on step	0.175	1.294								0.602	0.398	
Mean % shrubs on step	1.356	0.426	**	0.772	0.598		-0.927	0.755		-0.086	0.468	
Distance to non-veg landcover (km)	0.326	0.160	*	-0.137	0.130		0.131	0.140		-0.064	0.228	
Distance to shrub landcover (km)	-0.446	0.310		-0.177	0.240		0.099	0.158		-0.609	0.232	**
Distance to forested landcover (km)	-2.093	1.229		-4.197	2.799		0.526	6.493		-0.510	0.640	
Minimum distance to a paved road (km)	-0.374	0.137	**	-0.426	0.111	**	0.070	0.089		-0.365	0.182	*
Maximum road density (km/km^2)	0.373	0.191		-0.113	0.187		0.141	0.115		0.214	0.100	*
Step ends in forest[a]	0.432	0.125	**	0.093	0.154		-0.332	0.229		0.160	0.222	

(*) denotes coefficients significant at the p=0.05 level and (**) denotes significance to the p=0.01 level

[a] compared to open habitat

Table 4-3. Beta coefficients and standard errors for cougar and grizzly bear step lengths in the Canmore region of the Bow Valley.

	Cougars						Grizzly Bears					
	Winter			Non-winter			Pre-berry			Berry		
	β	SE		β	SE		β	SE		β	SE	
Paved road crossing	0.116	0.037	**	0.431	0.119	**	0.177	0.061	**	0.106	0.030	**
Mean terrain ruggedness	0.005	0.003	*	0.009	0.003	**	0.000	0.002		-0.010	0.002	**
Mean percent crown closure	-0.011	0.004	**	-0.012	0.005	**	-0.011	0.002	**	0.010	0.002	**
Mean % non-veg on step				0.319	0.301		-0.377	0.113	**	-0.026	0.094	
Mean % shrubs on step	-0.285	0.193		0.655	0.242	**	0.058	0.136		0.128	0.096	
Distance to non-veg landcover (km)	0.710	0.164	**	0.141	0.109		0.227	0.085	**	-0.159	0.076	*
Distance to shrub landcover (km)	0.484	0.236	*	0.434	0.145	**				0.790	0.143	**
Distance to forested landcover (km)	6.377	1.712	**	0.588	0.997		0.101	0.346		0.183	0.207	
Minimum distance to a paved road (km)	-0.082	0.014	**	0.031	0.036		0.017	0.009	*	-0.040	0.012	**
Maximum road density (km/km^2)	0.091	0.034	**	0.153	0.062	**	0.149	0.035	**	0.051	0.025	*
Step ends in forest[a]	-0.041	0.112		-0.073	0.118		0.066	0.070		-0.006	0.046	
Constant	2.150	0.331		2.369	0.353		2.815	0.196		2.228	0.155	

(*) denotes coefficients significant at the p=0.05 level and (**) denotes significance to the p=0.01 level

[a] compared to open habitat

Table 4-4. Beta coefficients and standard errors for cougar and grizzly bear step lengths in the Crowsnest Pass.

	Cougars						Grizzly Bears					
	Winter			Non-winter			Pre-berry			Berry		
	β	SE		β	SE		β	SE		β	SE	
Paved road crossing	0.095	0.053		0.663	0.178	**						
Mean terrain ruggedness	0.004	0.003		0.010	0.002	**	-0.003	0.005		0.008	0.003	*
Mean percent crown closure	-0.004	0.003		0.001	0.002		-0.006	0.004		0.006	0.002	**
Mean % non-veg on step	-3.483	1.724	*									
Mean % shrubs on step	0.578	0.306		0.533	0.276	*				0.726	0.305	*
Distance to non-veg landcover (km)	0.033	0.017	*	0.019	0.013		0.019	0.022		0.002	0.015	
Distance to shrub landcover (km)	0.328	0.083	**	0.136	0.062	*	0.117	0.096		0.206	0.077	**
Distance to forested landcover (km)	9.226	1.627	**	8.028	1.521	**	11.012	2.110	**	7.275	1.163	**
Minimum distance to a paved road (km)	-0.035	0.016	*	0.003	0.007		-0.014	0.008		-0.019	0.007	*
Maximum road density (km/km^2)	0.111	0.033	**	0.204	0.028	**	0.051	0.036		0.273	0.035	**
Step ends in forest[a]	-0.321	0.095	**	-0.175	0.068	*	-0.212	0.103	*	-0.297	0.077	**
Constant	2.065	0.238		1.749	0.175		2.789	0.279		1.826	0.171	

(*) denotes coefficients significant at the p=0.05 level and (**) denotes significance to the p=0.01 level

[a] compared to steps that end in open habitats

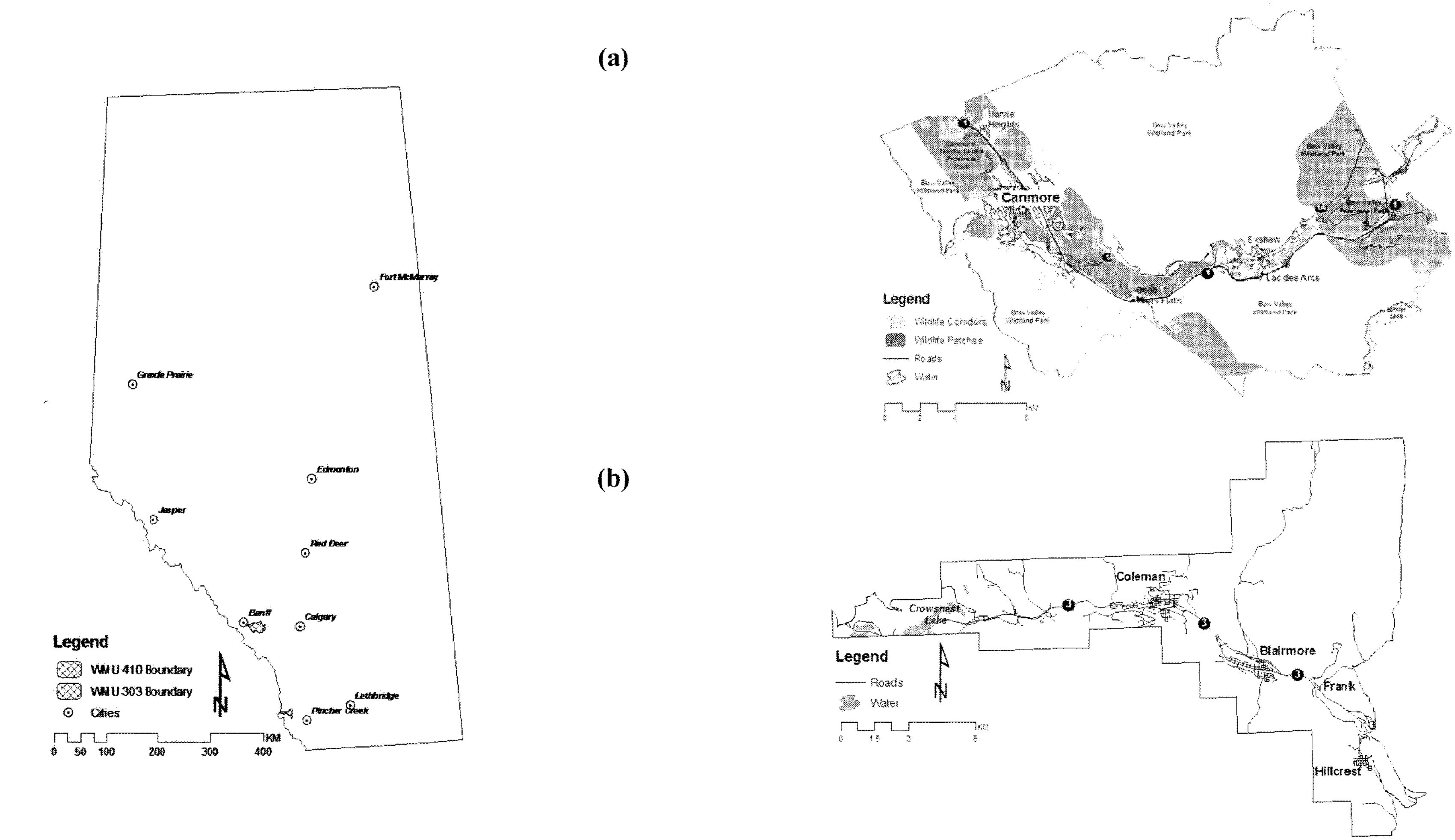

Figure 4-1. (a) The Canmore Region of the Bow Valley study area illustrating Wildlife Management Boundary (WMU) 410 as well as currently designated wildlife corridors and habitat patches. **(b)** The Crowsnest Pass study area illustrating WMU 303. Inset map of Alberta illustrates locations of WMUs within Alberta, Canada.

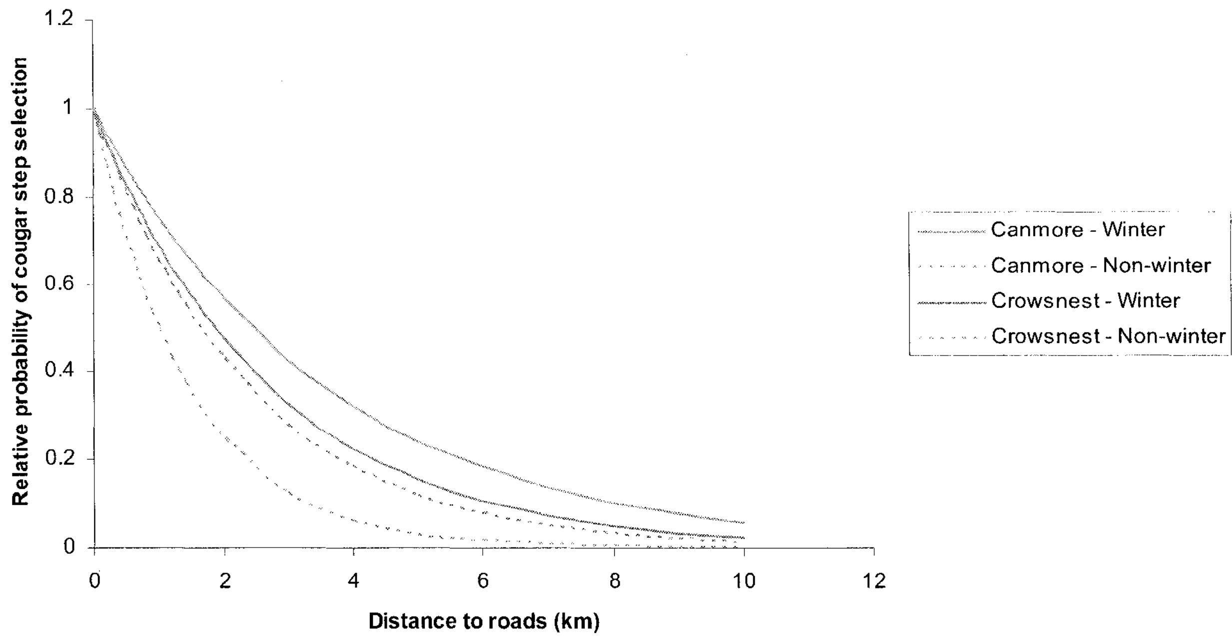

Figure 4-2. Relative probability of a step being selected by cougars during the winter and non-winter seasons in Canmore and Crowsnest given the minimum distance to paved roads along the step, as calculated from the step selection functions (SSF) models in Table 4-1 and Table 4-2. Cougars took steps that were closer to paved roads throughout the year in both study areas.

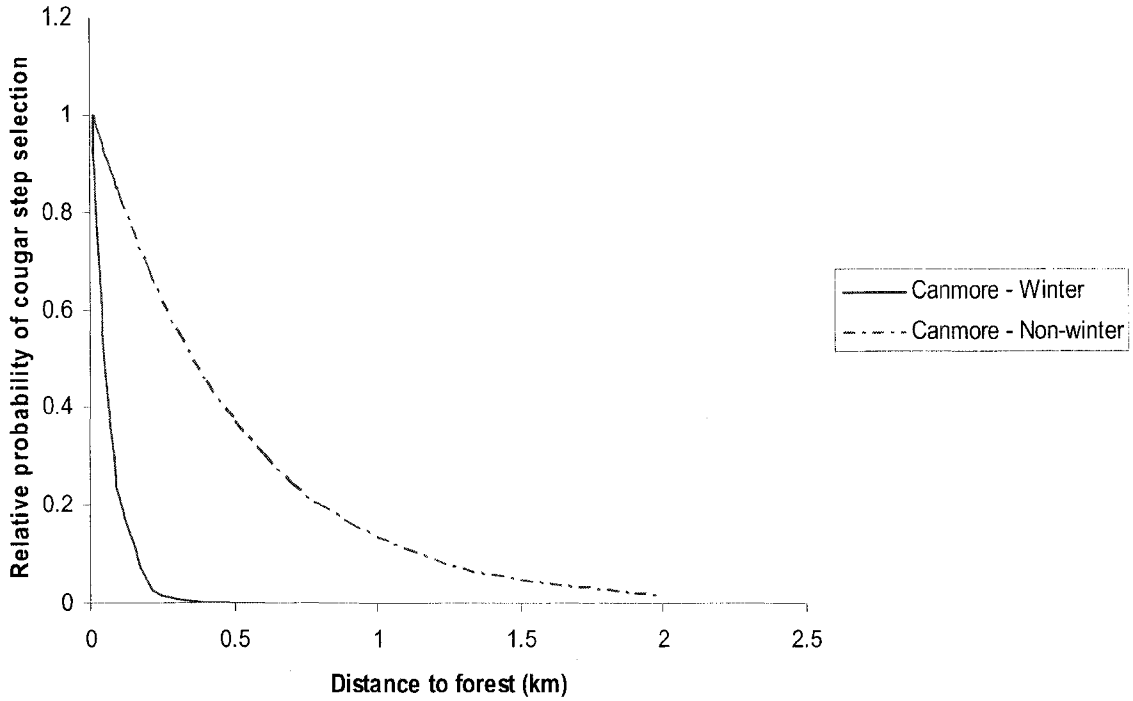

Figure 4-3. Relative probability of a step being selected by cougars during the winter and non-winter seasons in Canmore given the minimum distance to forest landscovers along the step, as calculated from the step selection functions (SSF) models in Table 4-1 and Table 4-2. Cougars took steps that were closer to forest landcovers in the both seasons.

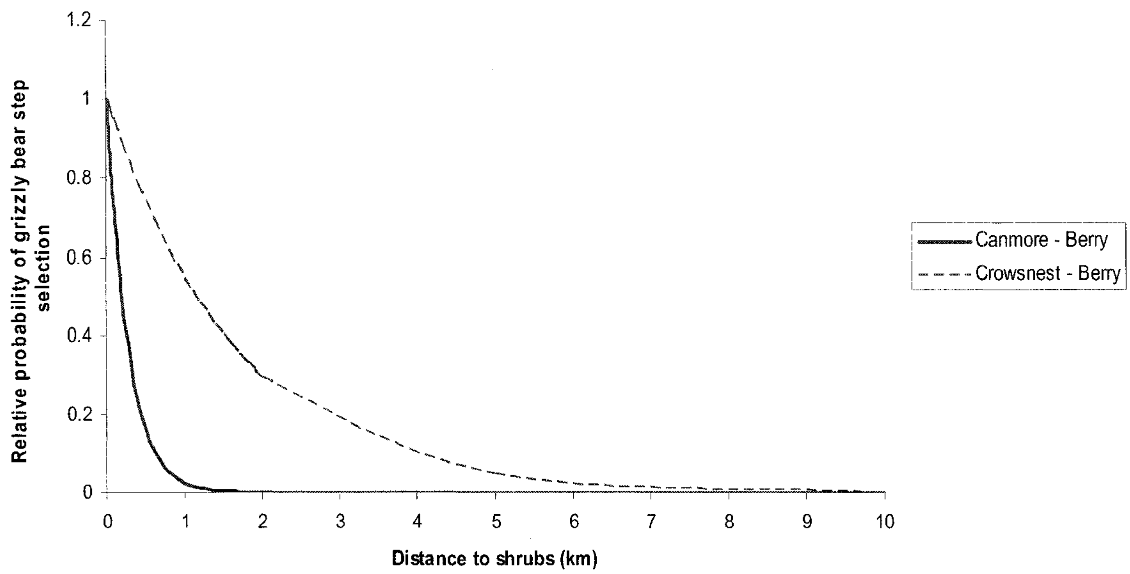

Figure 4-4. Relative probability of a step being selected by grizzly bears during the berry seasons in Canmore and Crowsnest given the minimum distance to shrub landcover along the step, as calculated from the step selection functions (SSF) models in Table 4-1 and Table 4-2. Grizzly bears took steps that were closer to shrub landcovers during the berry season.

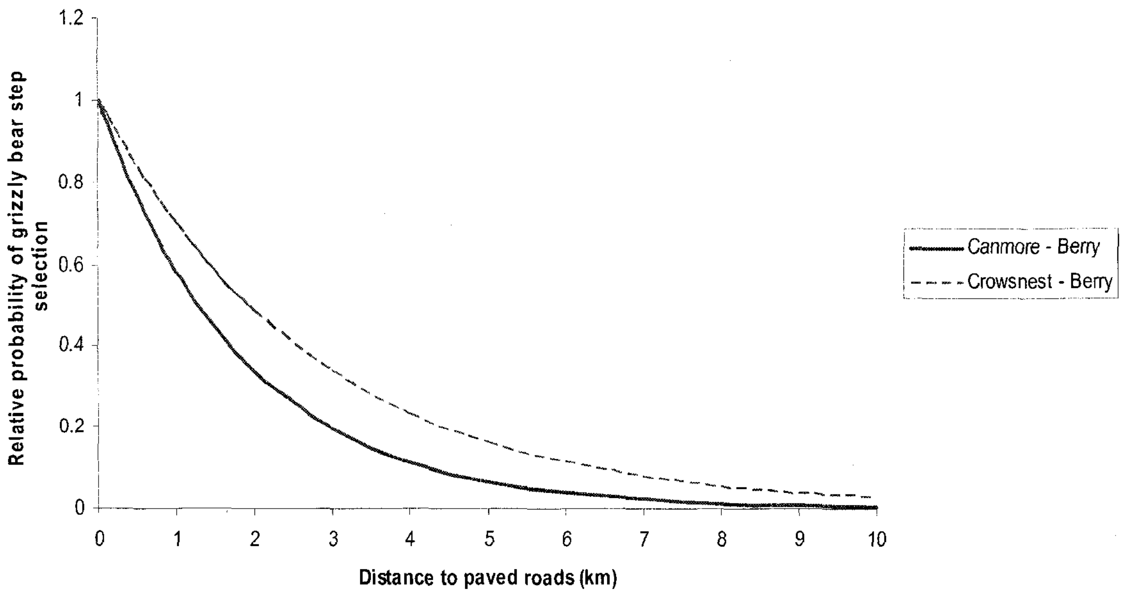

Figure 4-5. Relative probability of a step being selected by grizzly bears during the berry seasons in Canmore and Crowsnest given the minimum distance to paved roads along the step, as calculated from the step selection functions (SSF) models in Table 4-1 and Table 4-2. Grizzly bears took steps that were closer to paved roads during the berry season.

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CHAPTER FIVE

Improving the practice of corridor identification and design: an approach for large carnivores

1. Introduction

Habitat loss, fragmentation, and urbanization are major threats to large carnivores (Noss 1996; Weaver et al. 1996; Sunquist & Sunquist 2001. For most large carnivores, moving between fragments through agricultural or urban areas is problematic because they are more likely to come into conflict with humans (Woodroffe & Ginsberg 1998; Woodroffe 2001; Ginsberg 2001) or die (Noss et al. 1996). For wide-ranging and area-sensitive carnivores, conservation groups and management agencies design and create reserve networks, currently believed to offer the best solution for sustaining populations (Noss et al. 1996; Soulé & Terborgh 1999; Carroll et al. 2001). A number of conceptual frameworks used for designing reserve networks (Soulé & Terborgh 1999; Noss 2003; Beier et al. 2006, 2008) outline methods for identifying and prioritizing the basic elements of reserve networks to ensure persistence of target species.

Basic elements of reserve networks include corridors (sometimes called linkages), or portions of a landscape that are expected to facilitate movement between landscape features (also called sites, sources, patches or core areas). Various approaches have been used to identify corridors (reviewed by Noss & Daly 2006), but their effectiveness in providing connectivity has been debated (reviewed by Hilty et al. 2006). Connectivity emerges from the interaction between movement and the physical structure of the landscape (Taylor et al. 2006). Typically, assessing the physical structure of the landscape is less challenging than measuring the behavioural responses to that structure (Fagan & Calabrese 2006). Consequently, corridors identified or designed based on patterns of perceived structural connectivity (to humans at least), may not facilitate movements (Hannon & Schmiegelow 2002; Bélisle & Desrochers 2002; Selonen & Hanski 2003, but see Haddad et al. 2003). Integrating quantitative habitat selection and movement processes for focal species would be more likely to identify and support corridor designs that confer functional connectivity (Beier & Noss 1998; Vos et al. 2002; Chetkiewicz et al. 2006; Haddad & Tewksbury 2006). Moreover, a number of tools that integrate habitat selection and movement might better support corridor design and implementation (Chetkiewicz et al. 2006).

In this paper, I demonstrate how an understanding of large carnivore habitat selection and movement responses, developed from empirical data and models, can be integrated to identify and design local corridors. Specifically, I examined how resource selection functions (RSF, Manly et al. 2002), least-cost paths (LCPs, Theobald 2006), step-selection functions (SSF, Fortin et al. 2005), and movement analyses based on step lengths can inform patch or site selection and corridor designs. I applied these tools to Global Positioning System (GPS) radiotelemetry data collected for two large carnivores, grizzly bears (*Ursus arctos*) and cougars (*Puma concolor)*, in two landscapes in the Rocky Mountains, Alberta. I use my results to discuss the assumptions of different modelling approaches to corridor identification and design as well as their potential applications. Finally, I discuss species-specific patterns of resource selection and movement uncovered with the help of these tools and their application for large carnivore corridor planning.

2. Methods

Within the Yukon-to-Yellowstone Conservation Initiative (Y2Y) (Gatewood 2003), my study areas included the Canmore Region of the Bow Valley (hereafter, "Canmore") and the Crowsnest Pass (hereafter, "Crowsnest") (Fig. 5-1). These are montane river valleys (Natural Regions Committee 2006) with some of the busiest transportation networks in Canada (Alexander et al. 2005). Corridor planning efforts in Canmore includes a science-based framework for the design of wildlife corridors (BCEAG 1999). In Crowsnest, highway twinning proposals raised concerns about carnivore movements throughout the valley (Proctor et al. 2005; Apps et al. 2007).

During 2002-2004, I captured and collared four grizzly bears (2 females, 2 males) in Canmore and in Crowsnest, using standard techniques (Cattet et al. 2003). I also captured and collared five cougars (4 female, 1 male) in Canmore and 13 cougars (7 female, 6 male) in Crowsnest using standard methodology (Hornocker 1970). I used Televilt-Simplex™ GPS radiocollars (Lindesberg, Sweden) programmed to acquire a fix every 1 – 4-h.

I used 10,643 and 6643 GPS locations to model resource selection of grizzly bears in Canmore and Crowsnest, respectively. I partitioned the grizzly bear GPS data into spring (den emergence to 15 June), summer (16 June to 10 August), and fall (11 August to denning) seasons (Munro et al. 2006). A total of 4845 and 5741 GPS locations were used to model resource selection by cougars in Canmore and Crowsnest, respectively. I partitioned the cougar GPS data into winter (15 November – 15 April) and non-winter (16 April - 14 November) (Jalkotzy, Ross & Wierzchowski 1999).

I developed a seasonal RSF for both species following a "Design III" protocol (Manly et al. 2002) within home ranges (third order, Johnson 1980). Using model-fitting procedures in Hosmer and Lemeshow (2000) and logistic regression, I created RSFs using the following GIS-based predictor variables: **habitat** (landcover (McDermid et al. 2005), natural subregions, distance to water, distance to forest, percent crown closure); **terrain** (slope, elevation, aspect, terrain ruggedness index, compound topographic index); **food resources** (green vegetation index, elk (*Cervus elaphus*) resource selection); and, **human use** (road density). I used each model to identify patches of high RSF values using patch-size guidelines in BCEAG (1999). I used the inverse of the RSF to generate a cost surface, assuming high relative probability of use offered the least resistance to movement (Theobald 2006). I conducted least-cost path analyses, buffering the paths at 350 m (BCEAG 1999). Finally, I intersected species-specific LCPs to highlight potential inter-specific areas of overlap. See Chapter 3 for more details on methods.

To create the step selection function and step length models, I first re-sampled telemetry locations to 4 hr and generated steps, a straight-line segment, between successive 4-h telemetry locations and turning angles, based on three consecutive locations using Hawth's Analysis Tools for ArcGIS (Beyer 2004). I partitioned the grizzly bear telemetry data into pre-berry (den emergence to July 15) and berry (July 16 to denning) seasons (Nielsen et al. 2004a,b). A total of 900 and 798 grizzly bear steps were used to develop a pre-berry and berry SSF, respectively, for Canmore models. I used a total of 414 and 655 grizzly bear steps to develop a pre-berry and berry SSF, respectively, for Crowsnest models. I also re-sampled cougar telemetry data to 4-hr steps and used the same seasons described for RSF models. A total of 553 and 576 cougar steps were used to develop a winter and non-winter SSF, respectively, for Canmore models. I used a total of 1106 steps and 1147 cougar steps to develop a winter and non-winter SSF, respectively, for Crowsnest models.

I created a SSF model for grizzly bears and cougars using methods outlined in Fortin et al. (2005). I used model-building procedures in Hosmer & Lemeshow (2000) and using conditional logistic regression, I compared observed grizzly bear and cougar steps to a matched random sample of 20 steps using the following GIS-based predictor variables: **habitat** (mean distance to landcover types, mean percent of each landcover type on a step, mean percent crown closure, dummy variable for steps ending in forest); **terrain** (mean terrain ruggedness index along a step, dummy variable for slopes > 45 degrees); and **roads** (minimum distance to paved roads, maximum road density along each step, number of paved road crossings). Finally, I used linear mixed-effect models with individual grizzly bears or cougars as a random intercept (Rabe-Hesketh & Skrondal 2008) to examine the response of step lengths (4-hr) to the set of predictor variables described for SSF models. More detailed methods for SSF and step length (SL) models are described in Chapter 4. All statistical analyses were conducted in Stata 9.2 (Stata Corporation 2005) and R 2.6.1 (R Development Core Team 2004).

3. Results

3.1 RSF and LCP analyses

In both study areas and in all seasons, grizzly bear occurrence was positively correlated with greenness and with soil wetness and proximity to water during summer.

During spring, grizzly bear occurrence was negatively correlated with road density in Canmore, but not in Crowsnest Pass. Cougar occurrences were inversely correlated with road density in Canmore during non-winter and positively correlated with terrain ruggedness in Crowsnest Pass. Greenness was a predictor of cougar occurrence during the non-winter season in Canmore. To support corridor planning in both landscapes, I mapped species-specific seasonal RSF models in ArcGIS 9.0 (Environmental Systems Research Institute, Inc., Redlands, California, USA). I provide the RSF map for cougars in the non-winter as an example for this chapter (Fig. 5-2). Intersecting LCPs of both species highlighted areas where corridors could potentially support movement of both species (Fig. 5-3). More detailed RSF and LCP results are presented in Chapter 3.

3.2 SSF and SL analyses

Cougars and grizzly bears in both study areas, during winter and berry seasons, respectively, moved closer to paved roads than random paths. Cougars and grizzly bears also moved faster (e.g., longer step lengths) when they were closer to paved roads in the winter and berry seasons, respectively. Cougars in Canmore during both seasons and in Crowsnest during the non-winter avoided crossing paved roads and step lengths increased as the number of paved road crossings increased.

During winter, cougars in Canmore moved closer to forest landcover and took slower steps (e.g., shorter step lengths) when closer to forest. During the berry season, grizzly bears in Canmore and Crowsnest moved closer to shrub landcovers and across areas with less crown closure (e.g., more open forest canopy) compared to random paths Grizzly bears also moved more slowly near security cover, such as shrub landcovers.

Both grizzly bears and cougars in both study areas and seasons avoided crossing slopes > 45 degrees. More detailed results for the SSF and SL analyses are presented in Chapter 4.

4. Discussion

When identifying and designing large carnivore corridors, conservation planners and conservation planners often must rely on sparse species-specific data, their approaches are evaluated infrequently, and the results are rarely published in scientific journals (Vos et al. 2002; but see Beier et al. 2006, 2008). Various empirical and modelling approaches have been used to identify regional corridors (e.g., Carroll et al. 2001; Beier et al. 2006). However, these are not easy to apply to local applications, due to the species and landscape-specific nature of connectivity (Taylor et al. 2006). Using a combination of different models to understand landscape effects on cougar and grizzly bear resource selection and movement processes, I sought answers to three questions fundamental for corridor identification and design: (1) where are large carnivores most likely to occur?; (2) where are large carnivores likely to move?; and, (3) how do large carnivores move relative to landscape features?

4.1 Where are large carnivores most likely to occur?

Resource selection functions (RSF; Manly et al. 2002) represent the continuum of habitat quality that animals encounter (Fisher et al. 2004), offering an alternative to categorical representation of the landscape as corridors, patches, and matrix (Chetkiewicz et al. 2006). In my study, grizzly bear occurrence was positively correlated with greenness in both study areas across all seasons, whereas cougars in Canmore were more likely to occur where road densities were low (< 3.5 km/km^2) throughout the year. Hence, seasonal species-specific RSFs can be used to examine patterns in resource selection within and across landscapes to evaluate patch-selection guidelines. Terrain ruggedness, however, was an important predictor for cougar occurrence in Crowsnest, but not in Canmore, illustrating how it can be difficult to translate species-specific and seasonal details from RSF models into general guidelines. However, identifying habitat patches that both cougars and grizzly use within the conservation network might help conservation planners prioritize or justify patch delineations.

Mapping high RSF values (green) in a GIS (Fig. 5-2) facilitates patch delineation as stepping stones and/or as source patches within the landscape. The proximity of these areas to one another as well as to low RSF values (red) could indicate possible links between patches. A spatial representation of each RSF permits an evaluation of what corridors might look like if corridors are based soley on high habitat quality. For example, conservation planners trying to manage large carnivores in areas of high human use could evaluate the proximity of these "green links" to trails, human developments, or even current corridor designations. Conservation planners may not want corridors based on high quality habitat since large carnivores are more likely to occur there, potentially at the peril of people who may also use those areas. Consequently, corridors identified based on high quality habitat i.e., least-cost paths could lead to inappropriate land-use decisions if conservation planners do not explicitly define their assumptions regarding habitat selection and movement processes. Ideally, in the situation described above, managers would want to know where large carnivores are more likely to move through the landscape.

4.2 Where are large carnivores likely to move?

Numerous corridor designs based on LCPs use cost algorithms that assume that movement is more likely where habitat quality is higher (e.g., Beier et al. 2006, Carroll & Miquelle 2006). In this study LCPs highlighted areas of overlap where both species might favor moving across the landscape, assuming that high RSF values (e.g., good habitat) offer less resistance (e.g., more conducive) to animal movement (Theobald 2006). While this underlying assumption seems reasonable, actual movement data of some species suggest that more rapid movements are associated with unfavourable (Palomares 2001) or low quality (Haddad & Tewskbury 2005) habitats. Notwithstanding these limitations, areas of overlap in LCP could help further our understanding of carnivore responses to landscape. Areas of overlap might warrant fine-scale movement analyses or be assessed for mitigation such as restoration. They also could be used to evaluate existing corridor designations. However, as mentioned above, they may be inappropriate in areas where conservation planners are trying to manage high human use and large carnivore movements with corridors since corridors based on high habitat quality might create conflicts. Step selection function models provide conservation planners with some answers.

Results of SSF analyses in this study showed that throughout the year in Canmore cougars took steps closer to paved roads and they avoided crossing paved roads. During the berry season in Canmore, grizzly bears took steps closer to paved roads. No large carnivore paths crossed steep slopes in this study, supporting slope metrics used in current corridor guidelines (BCEAG 1999). Finally, cougars and grizzly bears took steps closer to shrub and forest landcovers. Because step selection functions can identify large carnivore selection and avoidance patterns near paved roads, terrain, and food resources, they can provide a set of guidelines for conservation planners about where movement is more likely. Building species-specific models permits conservation planners to consider places or features that promote movement for either carnivore species. As such, SSF models offer an important advance over traditional resource-based approaches. Using different time steps may also provide more scale-relevant information with respect to certain features. For example, in my study I used 4 hr time steps. The selection patterns near roads may require a shorter time step to determine if large carnivores are closer to paved roads because of attraction to food resources or if they are trying to cross paved roads.

Using SSF models for corridor planning and land-use decisions pose similar challenges to those described for RSF applications. First, available GIS data layers are often indirect proxies for the actual mechanisms driving step selection. How strongly these derived variables correlate with actual selection is generally unknown (Beier et al. 2008). Second, sample sizes are often limited, as in this study, and inferences are based on correlative patterns. Third, there can be biases in fix rate due to habitat types or terrain and animal behaviour (Graves & Waller 2006; Heard et al. 2008). Though corrections can be made to RSF-based models through probability weights for example (e.g., Hebblewhite et al. 2007), this is not possible for SSF that are based on conditional logistic regression models (e.g., Coulon et al. 2008). Finally, a selection for habitats or certain features on the landscape measured by the RSF or SSF does not mean these areas are automatically suitable for conservation. Instead they might be attractive sink habitats and large carnivores may die there whether they are moving there or not (Nielsen et al.

2006). While results of RSF modelling can be applied in a GIS, results of SSF models presented as a set of guidelines are not easily converted to maps except using computer-intensive simulations.

4.3 How are large carnivores moving through landscapes?

Landscape features that promote faster movement of large carnivores and funnel the animals through areas of high human use or development can be important to corridor designs where human activity is high and conflicts are likely. In Canmore, for example, a number of currently designated wildlife corridors and patches potentially increase grizzly bear-human interactions since they include golf courses that may provide attractant vegetation as well as high levels of human recreational use due to their proximity to human developments (Honeyman 2007). Quantitative movement analyses on small animals suggest that movement is faster and straighter in risky or low cover habitats (Crist et al. 1992; Schultz 1998; Schultz & Crone 2001; Haynes & Cronin 2006). Modelling step lengths of large carnivores permits evaluation of species-specific movement responses to landscape features. In this study, Canmore grizzly bears had shorter steps close to paved roads during the pre-berry season, but during the berry season they had longer steps close to paved roads. These results highlight the need to better understand fine-scale movements of bears near paved roads to inform land-use management near paved roads. One management response, for example, could be to limit human use in corridor areas near paved roads during the pre-berry season when grizzly bears may be more likely to forage there.

Combining SSF approaches with step length analysis can help to identify areas that promote certain kinds of movement for corridor planning. Some consistent patterns emerged in this study. In both study areas, grizzly bears during berry season took steps that were closer to shrub landcovers, while cougars in Canmore took steps closer to forest landcovers during winter. Both species moved slower (e.g., shorter step lengths over 4-hr period) when closer to these landcovers. This finding suggests that movement might be directed to certain landcovers for foraging, resting, or predation sites. Also, grizzly bears and cougars in both landscapes took faster steps near paved roads during the berry and winter seasons, respectively, suggesting a variety of mechanisms such as flight response to traffic or the use of roadside areas for faster travel. Another application of combined SSF and step length analyses is to evaluate effects of specific landscape features, such as barriers (e.g., steep slopes) or semi-permeable features (e.g., paved roads in Canmore) on carnivore movement. My study indicated that cougars in Canmore took steps that were closer to paved roads. Though cougars crossed paved roads, they generally avoided them. When they did cross paved roads, they took longer steps. These results support inclusion of mitigation structures such as underpasses for cougars near roads (Gloyne & Clevenger 2003). Areas on the landscape identified with SSF models, that promote grizzly bear and cougar steps, but where they tend to be slower, as per step length analyses, also could be combined with patches identified with RSF to support residency, foraging, or resting behaviours. While the application of LCP, RSF, SSF, and step length analyses advance large carnivore corridor identification and design, the underlying behavioural mechanisms are likely to remain elusive for large carnivores without more detailed behavioural or experimental studies on movement (Bélisle 2005).

5. The future of corridor planning for large carnivores

A number of guidelines exist for designing conservation networks and corridors for large carnivores and other species (Beier & Loe 1992; Noss 2003; Beier et al. 2006, 2008). Although numerous approaches have been developed for assessing structural and functional landscape connectivity for large carnivores (e.g., Noss & Daly 2006; Fagan & Calabrese 2006; Carroll & Miquelle 2006; Tracey 2006; Theobald 2006), the tools and metrics continue to be refined for different landscapes and species. My results showed advantages for several specific modelling tools, and their combination, for corridor planning. However, other opportunities to assess connectivity for large carnivores would also support corridor planning. Conservation planners will need to be creative and make use of adaptive management approaches to examine large carnivore movement and habitat selection patterns (Walters & Holling 1990). For example, carnivore "before-and-after" responses to large-scale landscape manipulations, typical in forestry management scenarios (e.g., Nielsen et al. in press; Roever et al. in press-a,b), or in association with road closures around industrial activities, might present such opportunities. When done in cooperation with industry, academia, and government agencies, such settings may provide long-term research opportunities to assess how resource selection and movement patterns vary to support corridor designs in different landscapes (Haddad & Tewksbury 2006). Similar opportunities could come from systematic "before-and-after" monitoring of grizzly bear resource selection and movement responses near human-use trails when trails are closed or food resources such as berries are removed. Such small-scale experiments could offer important local insights to support corridor planning and land-use management.

In lieu of experimental designs, comparing resource selection and movement patterns across a range of landscapes (e.g., different matrix types) for different large carnivores, would permit an assessment of when corridors would be the best solution. Similar responses to paved roads of cougars and grizzly bears might be the result of the geophysical landscape constraints directing large carnivores closer to paved roads because roads were built in the same narrow montane valleys that contain food resources for both cougars and grizzly bears (e.g., Gibeau et al. 2002; Chruszcz et al. 2003). Comparative data from less rugged landscapes might allow us to better evaluate this relationship. Also, taking advantage of situations where animal motivation to move is known (i.e., translocated "problem" carnivores) can provide opportunities to examine how large carnivores move across broader landscapes. Because large carnivores rarely remain within the boundaries of protected areas (Woodroffe & Ginsburg 1998), managing connectivity in human-dominated landscapes will always involve many sectors of society – agriculture, mining, forestry, municipalities, and land-use planning. As protected areas increasingly become habitat islands within a "hostile" human-dominated matrix, the transfer of knowledge and tools regarding connectivity and conservation corridors needs to occur more systematically between stakeholders (e.g., Beier et al. 2006). In addition, protected areas may become less suitable in the face of climate change (Hannah 2008), making connectivity even more relevant. The gaps between the generation of scientific information and implementation measures should be addressed more explicitly (e.g., Pierce et al. 2005; Knight et al. 2006). Adaptive management frameworks that share lessons learned more effectively would be particularly useful for corridor planning for large carnivores given limited resources for large carnivore research (e.g., Salafsky et al. 2002). While it is evident that we can improve corridor design and implementation with various technological, analytical, and methodological refinements, it is important, not to lose sight of the real challenge to large carnivore conservation – ourselves. Developing new technological or policy fixes always has been easier than addressing the fundamental causes of biodiversity losses as we tend to "interpret all difficulties and impediments as merely problems that are solvable with enough money, research, and technology" (Orr 2008). Given our relatively short and rather violent history of living with large carnivores (Kellert et al. 1996), it seems unlikely that the future of large carnivores will be ensured by yet another study, more research funding, or advances in model development. As conservation biologists passionate about conserving large carnivores, we need a positive and inspiring vision for their conservation (Redford & Sanjayan 2003). Ultimately, we could serve them better by understanding our own behaviour in addition to the behaviour of the remaining cougars and grizzly bears (Kaplan & Kaplan 2008).

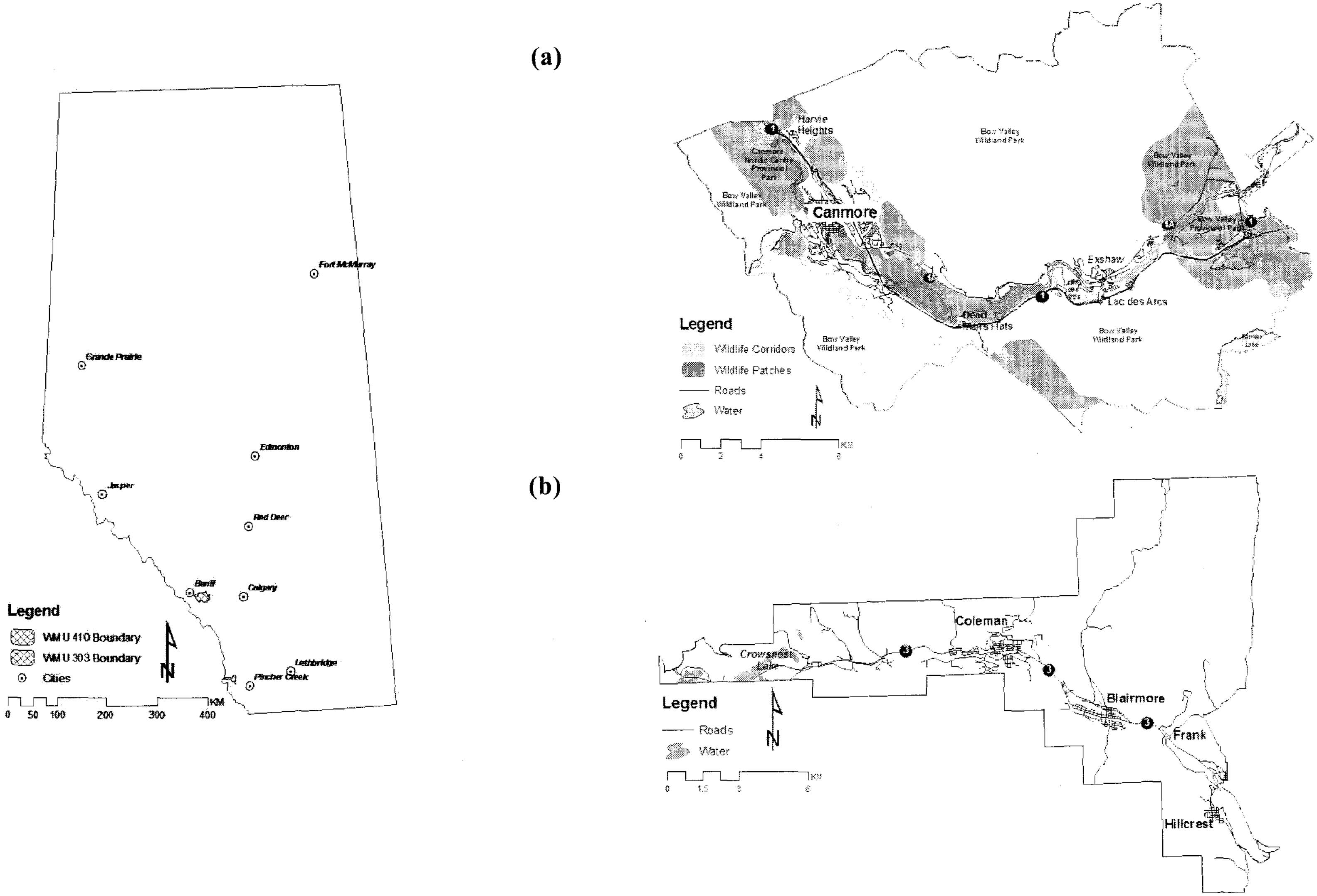


Figure 5-1. (a) The Canmore Region of the Bow Valley study area illustrating Wildlife Management Boundary (WMU) 410 as well as currently designated wildlife corridors and habitat patches. (b) The Crowsnest Pass study area illustrating WMU 303. Inset map of Alberta illustrates locations of WMUs within Alberta, Canada.

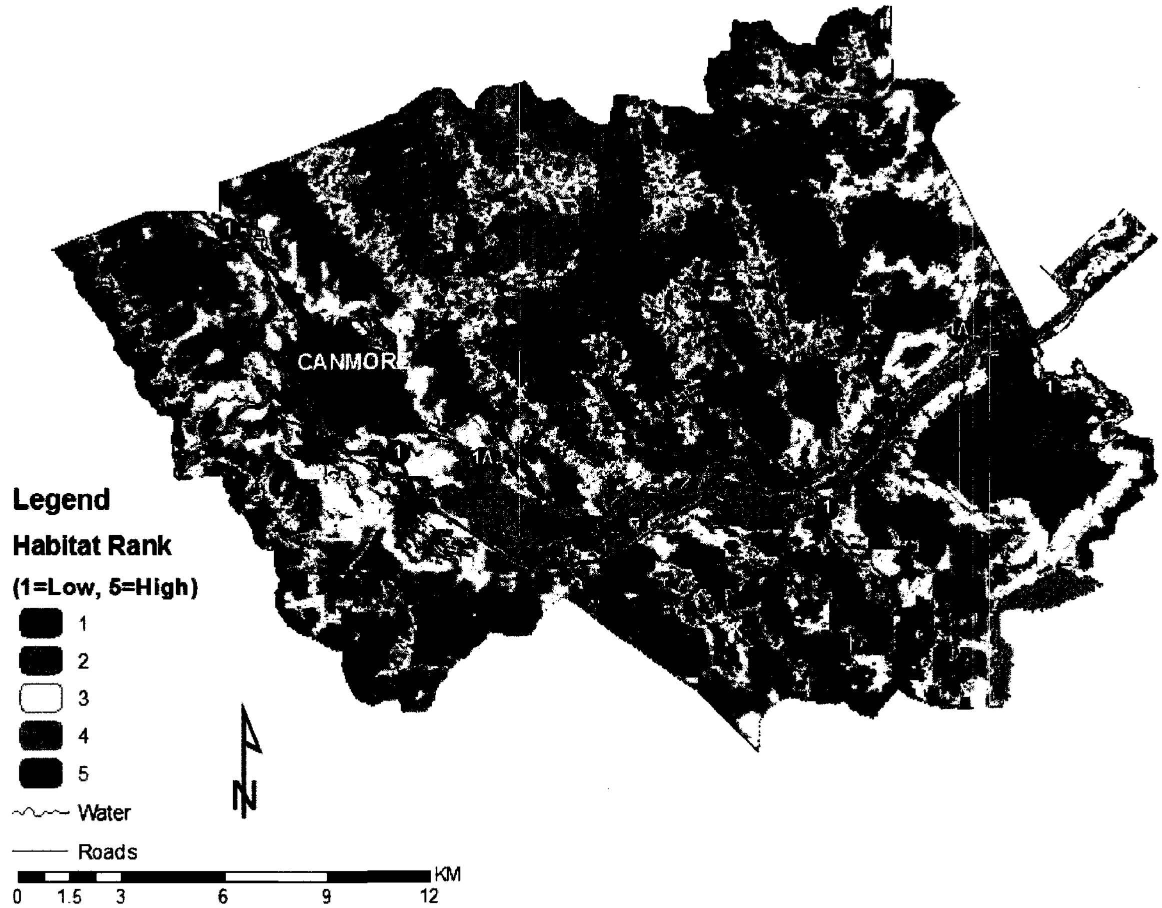
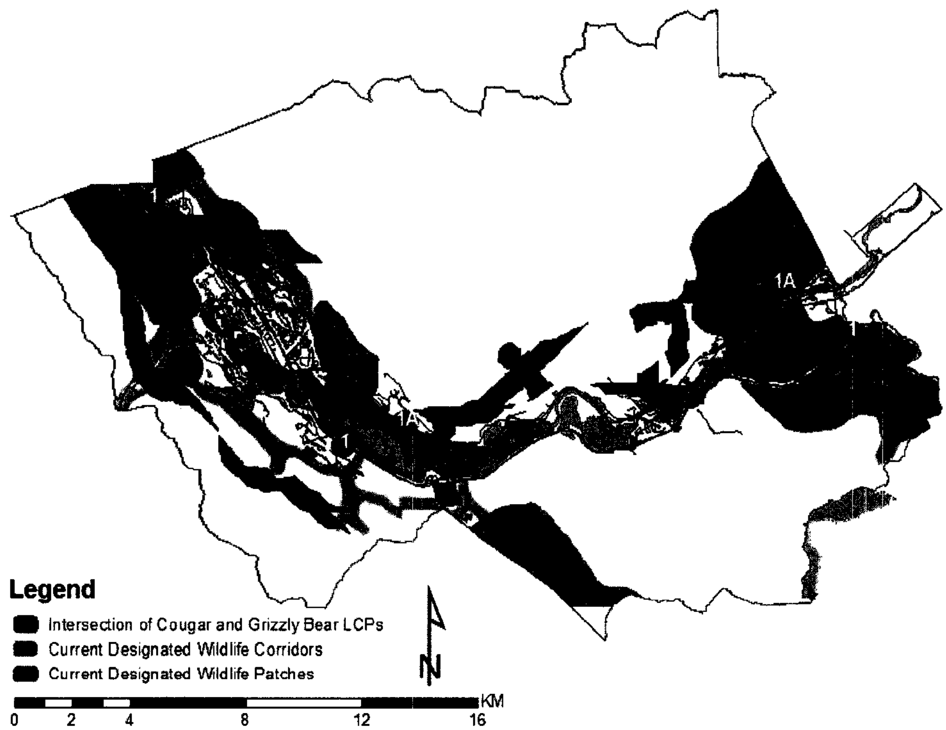


Figure 5-2. A resource selection function (RSF) was created using logistic regression to compare topographic and vegetation variables at Canmore cougar telemetry locations during the non-winter in 2001-2004. Applying the RSF in a geographic information system, illustrates areas likely to support cougar occupancy based on a probabilistic function. Areas of high probability of occurrence (green) could be used to identify potential corridor locations.

(a)



(b)

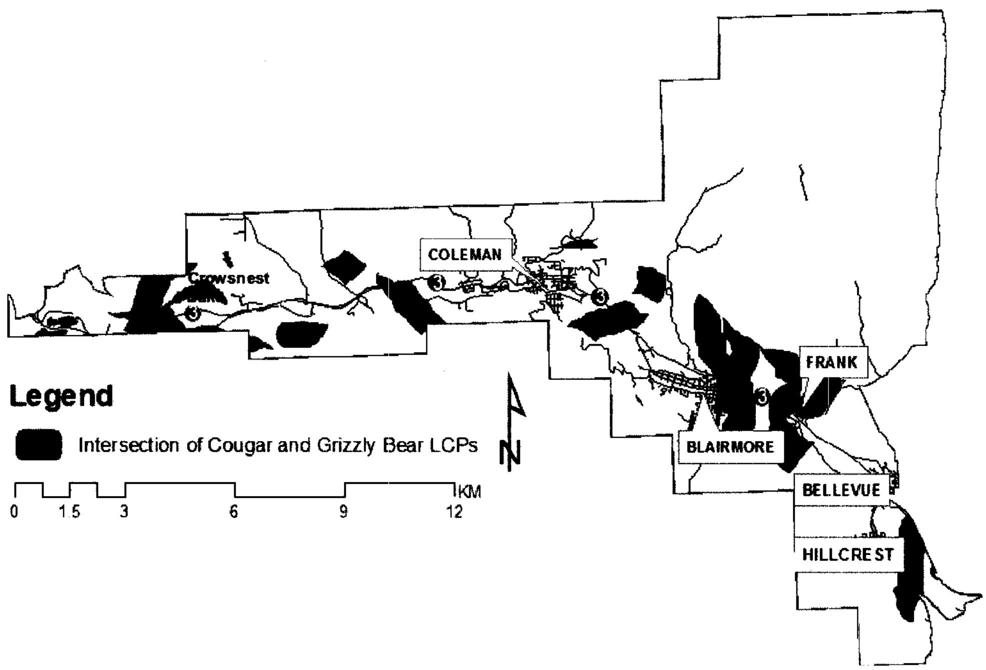


Figure 5-3. Intersected least-cost paths highlight areas of overlap for cougars and grizzly bears during various seasons in (a) Canmore Region of the Bow Valley and, (b) the Crowsnest Pass.

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CHAPTER SIX

Conclusions

Noss and Daly (2006) identify a number of guidelines for improving the methods used for connectivity design based on their review of different approaches. Firstly, corridors identified and designed on the basis of several approaches will be more defensible than those based on a single approach. Secondly, corridor designs based on quantitative models as well as field studies might create a more reliable corridor plan. Thirdly, because connectivity is a species- and landscape-specific property, corridor designs need, as much as possible, to focus on those particular species targeted for corridor planning. They also reminded us that corridors need not be the only solution – managing the matrix or a series of stepping stones may be more appropriate for some species and landscapes. Overall, this dissertation is an attempt to improve local corridor planning for grizzly bears and cougars in two landscapes by following these guidelines.

Specifically, I used two different approaches to corridor identification. I considered a least-cost path (LCP) approach that generated potential corridors based on where cougars and grizzly bears were most likely to occur as determined by a resource selection function (RSF). In addition, I used a step-selection function (SSF) to examine what habitat features were more likely to promote movements or cause avoidance across each landscape. Taken together, the mapped RSF and LCPs as well as the specific selection patterns identified in the SSF and the step length analyses provide tools for corridor planning that offer alternatives to current practices. In combination or separately, they can be used to explore important variation among individuals (e.g., habituated versus non-habituated animals) as well as consistent responses across species and landscapes. Taken together, this information could be used to identify and support land-use decisions about mitigation (e.g., enhancing habitat, removing attractants, limiting human use or infrastructure). In Canmore, where guidelines currently exist and corridors have been designated, these results provide an opportunity to evaluate current designs, make revisions, or adapt models. In Crowsnest, where local corridor planning has been less formal and systematic, these results provide a place to start. In these two landscapes where conservation planners are responsible for managing human use and the large carnivores, my results offer useful tools for answering questions about how best to accommodate both.

From a biological point of view, we know fairly well what needs to be done to conserve large carnivores. We need to reduce human-caused mortality, particularly for grizzly bears, and we need to permit some dispersal movements to afford genetic connectivity (Kareiva 2006). However, in a world also facing dramatic changes in climate, species will likely need to move more than ever, creating greater need for connectivity to our existing protected areas (Hannah 2008). This lends both support and priority to the landscapes with increasing human development and large carnivores attempting to move through them. While large carnivores may not be the umbrella for biodiversity that originally spurred much of the corridor planning on their behalf (e.g., Noss et al. 1996, Ray et al. 2005), now more than ever they offer an evocative challenge to our capacity to conserve them (Redford 2005). Schaller (2007) aptly noted, "Conservation problems are social and economic, not scientific, yet biologists have traditionally been expected to solve them. Research is easy; conservation most decidedly is not. Since conservation cannot be imposed from above, it must ultimately be based on local interests, skills, and traditions.... Instead of just being a biologist, something for which I have been trained, I must also be an educator, diplomat, fundraiser, politician, anthropologist...". Ultimately if we wish to conserve carnivores, we need good science to understand why they behave the way they do and, perhaps, how we could modify it, but we might serve them better by trying to understand and change our own behaviour (Orr 2008).

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