AN INDIVIDUAL-BASED MODELLING APPROACH TO ESTIMATE LANDSCAPE CONNECTIVITY: A CASE STUDY WITH BIGHORN SHEEP (*Ovis canadensis*) AND TIGER SALAMANDERS (*Ambystoma mavortium*) IN THE OKANAGAN VALLEY, BRITISH COLUMBIA

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Abstract

Preserving connectivity, or the ability of a landscape to support species movement, is among the most commonly recommended strategies to reduce the negative effects of climate change and human land use development on species. Connectivity analyses have traditionally used a corridor-based approach and rely heavily on least cost path modeling and circuit theory to delineate corridors. Individual-based models are gaining popularity as a more ecologically realistic method of estimating landscape connectivity; however, this remains a relatively unexplored approach. The overarching aim of this thesis was to assess the utility of an individual-based modeling approach as a tool for identifying species-specific functional connectivity across a landscape and to apply this approach to identify a network of wildlife corridors in the Okanagan Valley for two selected species of interest: the bighorn sheep (*Ovis canadensis)* and tiger salamanders (*Ambystoma mavortium).*

A series of computer models that simulate sheep and tiger salamanders traversing a landscape by following simple movement rules were developed. Simulations were then run to determine baseline connectivity between subpopulations of both species and the impact of various land management and environmental change scenarios on connectivity. The results of this work show how species might use the Okanagan landscape to colonize suitable yet unoccupied habitats, move in response to climate change, and breed with subpopulations that are spatially isolated. More generally, the use of an IBM in this study highlights the power of this method to identify how species might make broad use of a landscape for movement and migration. It identifies connectivity to areas that are suitable yet not currently occupied, emphasizing the importance of designing conservation plans that encompass more than just current species ranges. The individual-based approach also provided a more realistic representation of how animals perceive and move in their habitats than traditional approaches to identify corridors such as least cost path analysis. Application of this approach elsewhere can provide effective quantitative support for decision makers seeking to incorporate wildlife conservation and connectivity into land use planning.

Preface

This research was conducted at the University of British Columbia, Okanagan, in the Complex Environmental Research Lab under the supervision of Dr. Lael Parrott. For the work presented throughout this document, I was responsible for the entirety of conceiving and developing the computer models; performing experiments; displaying, interpreting, and analyzing data; and, writing and editing this thesis with Dr. Parrott's advice and feedback.

A version of chapter 2 was published in a peer-reviewed journal (Allen, C.H., Parrott, L., Kyle, C., 2016. An individual-based modeling approach to estimate landscape connectivity for bighorn sheep (*Ovis canadensis).* PeerJ. doi: 4:e2001https://doi.org/10.7717/peerj.2001). I was responsible for developing the models, performing experiments, interpreting data, preparing figures, and writing the manuscript. Mrs. Catherine Kyle and Dr. Lael Parrott assisted with conceptualizing the project, contributed to analyzing and interpreting data, and reviewed drafts of the publication. Components of the introduction and discussion of this article are included in Chapter 1, 4, and 5 of this thesis.

A version of chapter 3 will be submitted to a peer-reviewed journal (Allen, C., Parrott, L. An individual-based modeling approach to estimate landscape connectivity for amphibians in a drying environment). I was responsible for developing the computer model, running simulations, analyzing and interpreting data, and writing the manuscript. Dr. Lael Parrott contributed to conceptualizing and developing models, analyzing and interpreting data, and reviewed drafts of the manuscript.

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List of Abbreviations

BCS – Biodiversity Conservation Strategy

COSEWIC – Committee on the Status of Endangered Wildlife in Canada

IBM – Individual-Based Model

LCP – Least Cost Path

TCG – Transboundary Connectivity Group

WHCWG – Washington Wildlife Habitat Connectivity Working Group

1 Chapter: Introduction

1.1 Conceptualizing connectivity

Maintaining or restoring connectivity has become a central priority in conservation and is among the most widely recommended strategies to reduce the negative effects of habitat loss, habitat fragmentation and climate change on species (Heller and Zavaleta, 2009). The importance of connections between populations (Cushman et al., 2013), across political borders (Flesch et al., 2010; Singleton et al., 2004), or along climate gradients (Krosby et al., 2010) is widely acknowledged. To integrate connectivity into land management requires tools to identify where priority action sites are on a landscape (Beier et al., 2011). However, there is still much debate on the theory surrounding connectivity and even more so on the methods used to estimate it (Kindlmann and Burel, 2008; Tischendorf and Fahrig, 2000a). Connectivity is broadly conceived as the ability of a landscape to facilitate movement (Taylor et al., 1993; With et al., 1997). Although researchers and practitioners tend to apply a vertebrate lens to connectivity by focusing on animal movement, it is important to emphasize that it simply refers to movement. This could include the flow of wind, water, pollution, nutrients, soil, pollen, disease, or even people. For simplicity and brevity, this work will focus only on animal movement across a terrestrial landscape although much of this discussion can be applied to connectivity more generally.

Landscape connectivity was originally formalized as the degree to which a landscape promotes or impedes movement (Taylor et al., 1993). It is thus a combination of how a species perceives and reacts to its landscape and the configuration and composition of elements on that landscape. More recent definitions of landscape connectivity have become somewhat diffuse from the original meaning proposed by Taylor et al. (1993); however, it is still widely agreed that connectivity emerges from the complex interactions of a species and its landscape. For example, With et al. (1997) define connectivity as the functional relationship between habitat patches due to the landscape structure and animal movement responses of species to those features. Beier et al. (2011) describe connectivity as the ability of a landscape to support ecological and evolutionary processes requiring large geographical areas such as animal range shifts, migrations, and climate change adaptation. Some researchers further distinguish between habitat, landscape, and ecological connectivity, which characterize connectedness through habitat for a species, physical linkages across a landscape, and connectivity for ecological processes respectively (Fischer and Lindenmayer, 2007). For the purposes of this thesis, I use the term landscape connectivity to emphasize that connectivity is a landscape-scale property of a system.

Despite wide recognition that connectivity emerges from individual movement in response to landscape structure, the application of connectivity for on-the-ground conservation efforts tends to emphasize physical features on a landscape often without considering the complex interactions between a species and its environment. Many of the tools and methods used to assess landscape connectivity (discussed elsewhere in this chapter) have been criticized for poorly representing animal processes and properties such as dispersal, limited perceptual range, and non-optimal movement behavior. Further, and perhaps more importantly, connectivity is a dynamic landscape feature. As such, fluctuations in land use, natural disturbances, new species compositions, and changes in spatial and temporal scale will ultimately influence how individuals move across a landscape. Thus connectivity should be assessed and managed as a component of an adaptive system rather than a static feature of a landscape.

1.1.1 Structural versus functional connectivity

Landscape connectivity can be broadly viewed from two perspectives: structural and functional connectivity. Structural connectivity emphasizes the physical elements on a landscape and is therefore directly influenced by landscape features such as topography and land cover (Tischendorf and Fahrig, 2000b). Structural connectivity is somewhat easy to estimate and measure with tools readily available to both researchers and land use practitioners. By increasing the continuity between similar habitat patches, structural connectivity will increase. In contrast, functional connectivity considers not only the physical elements on a landscape but also how a species of interest interacts with and moves in response to those elements (Taylor et al., 1993; Tischendorf and Fahrig, 2000b; With et al., 1997). Functional connectivity therefore requires a more nuanced understanding of how a landscape increases or decreases animal flow and how behaviours such as dispersal and foraging interplay with movement.

For species that are hesitant to move through non-optimal habitats, structural and functional connectivity become somewhat synonymous. However, for species that show complex movement attributes, the distinction between structural and functional connectivity becomes more than simply semantics. By explicitly considering how individuals respond to landscape features, functional connectivity will highlight movements through non-optimal habitats that a structural connectivity assessment might dismiss (Baguette and Van Dyck, 2007; Goodwin and Fahrig, 2002; Pither and Taylor, 1998). In such cases, many of the methods used to identify landscape connections risk underestimating connectivity. Also, contiguous habitat patches that are structurally connected may not in fact be functionally connected. To provide an example, this could happen when a poorly placed habitat corridor does not facilitate movement for a particular species. With the recent wide availability of Geographic Information Systems (GIS), measuring structural connectivity has become a routine objective in land use planning. However, integrating the structural features of a landscape together with realized animal movement can contribute to a more functional, and ultimately a more resilient landscape.

1.1.2 Habitat corridors

Creating, protecting, or restoring habitat corridors are among the most common strategies to realize connectivity across a landscape. Corridors are traditionally conceptualized as swaths of a landscape that connect otherwise isolated patches of habitat. Measuring the effectiveness of corridors in conservation has proven difficult and controversial. The detection of a species' use of corridors is dependent on the response variable measured, the specific landscape, and the species studied. Moreover, corridors often cover large spatial extents and cross political borders, which can make collecting field data to validate corridor design logistically unfeasible. Albeit the value of habitat corridors as a conservation tool has been criticized (Beier and Noss, 1998; Chetkiewicz et al., 2006; Proches et al., 2005; Simberloff et al., 1992), in general, corridors have been found to increase movement in a fragmented landscape and thus contribute to connectivity (Gilbert-Norton et al., 2010; Haddad et al., 2003; Tewksbury et al., 2002). Their spatial design tends to follow one of three approaches: general corridors for many species (for example, Washington Wildlife Habitat Connectivity Working Group, 2010), corridors for a particular species or suite of similar species (for example, Rabinowitz and Zeller, 2010; Schadt et al., 2002; Ziółkowska et al., 2012), or a landscape integrity method, which focuses on maintaining existing contiguous natural areas to provide connectivity (for example, Krosby et al., 2015; Theobald et al., 2012). Moreover, recent focus has shifted from making corridors between patches of good habitat to creating corridors across environmental gradients that allow species to shift ranges in response to a changing climate (Nuñez et al., 2013).

With a generalized species approach, researchers or planners use broad-sweeping assumptions about animal movement to identify probable habitat corridors (Koen et al., 2014). A researcher might decide gentle slopes, naturally vegetated regions, and riparian areas tend to act as conduits to animal movement whereas proximity to roads, buildings, and rugged, precipitous terrain may inhibit animal movement. Homogenizing species and spatial scales with a generalized approach may be appropriate for conservation efforts that aim to facilitate connectivity without any particular species in mind or when a paucity of time and resources limits the capacity for a more inclusive assessment. However, this simplistic, pattern-based view may not support movement for all or even most of the species in a region or may even be detrimental in some cases. In contrast, species-specific habitat corridors identify how features on the landscape influence movement through the lens of a particular species (Rabinowitz and Zeller, 2010; Schadt et al., 2002; Ziółkowska et al., 2012). Species-specific assessments usually focus on a charismatic or at risk species. Many researchers express the importance of validating species-specific corridors with movement or genetic data and emphasize that land use managers should exercise caution in cases where it is not feasible to validate corridors. Finally, an ecological integrity approach to landscape connectivity identifies corridors across regions without substantial human modification (Krosby et al., 2015; Theobald et al., 2012). This highlights patterns of continuous remaining natural areas without focusing on corridors specific to any species.

Habitat corridors are often considered a solution for mitigating the effects of fragmented landscapes and have been widely integrated into conservation and land management plans. A driving factor in their broad application is the relative ease with which researchers can use GIS to identify habitat corridors. Moreover, corridors are conceptually simple and relatively easy to grasp by ecologists and land use practitioners alike. A fundamental assumption underlying the application of habitat corridors in land use planning is that a landscape can be simplified as a patch-matrix-corridor archetype and species will move through favourable habitat and will not move through poor habitat. Recent literature is shifting away from the corridor approach to connectivity by recognizing that the matrix is not such a black and white landscape feature, but rather a grayscale of varying movement permeability (Kupfer et al., 2006; Murphy and Lovett-Doust, 2004). Species likely have a nuanced perception of their landscape and patches, corridors, and the matrix intervening them fall along a continuous gradient of movement permeability. Even components of a landscape that researchers identify as movement barriers may still facilitate rare dispersal events. Corridors are often conceptualized as static, linear features on a landscape that facilitate animal dispersal. In reality, it is challenging to predict how and where species will move and even more difficult to understand the motivation underpinning their movement (Bélisle, 2005). There is a growing dialogue on moving away from a patch-corridor-matrix archetype in conservation and towards a more refined understanding of how a landscape facilitates and impedes animal movement. For example, Beier et al. (2008) coined the term “linkages” to describe those features of a landscape that facilitate movement for many species or promote other ecosystem processes. A linkage therefore expands the corridor approach to include animal movement across a landscape without requiring continuous, linear corridors (Chetkiewicz et al., 2006).

1.2 Quantifying landscape connectivity

To integrate connectivity into conservation, it is necessary to understand, or at least predict, how a landscape can facilitate animal movement and which features act as barriers to movement. Ideally, measures of connectivity should consider movement responses to landscape elements such as dispersal range, gap-crossing ability, and mortality. However, such information is often challenging to obtain from field studies, particularly when one is interested in large spatial extents or small and/or endangered animals that are difficult to track. As a result, many indirect measures of connectivity such as gene flow are often used as proxies for movement data. Recently, computer modeling has emerged as an additional tool for connectivity analyses and there exist a number of well-developed techniques for this purpose. However, there is still a lack of consensus on how to measure and estimate landscape connectivity (Calabrese and Fagan, 2004; Kindlmann and Burel, 2008). Here I will briefly discuss common direct and indirect methods along with modeling approaches to estimate landscape connectivity.

1.2.1 Direct and indirect approaches to estimate landscape connectivity

Tracking individuals in the field is perhaps the simplest method of estimating landscape connectivity. Tracking can be logistically inefficient, particularly at large spatial scales or when working with small or endangered species that are hard to find. Techniques such as mark-recapture, cameras with motion sensors, or radio tagging animals, are used extensively to overcome these challenges. Translocation studies are also commonly used to measure landscape connectivity (for example, Bowman and Fahrig, 2002; Bridgman et al., 2012). In this approach, individuals are captured and moved across a barrier of interest, such as a matrix or road, and then released. With this approach, researchers are able to test hypotheses about species-specific connectivity relative to landscape attributes by identifying the proportion of individuals that successfully find a route through novel habitat back to their original patch.

Translocation studies are appealing to researchers because it is possible to directly measure non-optimal dispersal behavior that is, at least in theory, a realistic representation of how an animal might move across a landscape. In a translocation study, researchers capture and relocate individuals across landscapes. The ability of the individuals to then travel back to their initial location is used as an estimate of landscape connectivity (Betts et al., 2015). Although translocations offer insight into functional connectivity, there are several known limitations of this approach (Betts et al., 2015). Previous work has suggested that animals in translocation studies might take large and uncharacteristic risks to reach their home patch (Gillies et al., 2011). Thus, translocation studies may overestimate functional connectivity.

Genetics have recently emerged as a powerful tool to investigate landscape connectivity. Since the term ‘landscape genetics’ was coined in 2003 (Manel et al., 2003), it has been widely applied to identify if and where connectivity exists across a landscape (see reviews by Bolliger et al., 2014; Manel and Holderegger, 2013; Storfer et al., 2007). This approach aims to describe how genetic patterns observed across a landscape correlate with barriers to movement. This can be advantageous over alternative methods of estimating connectivity because it is possible to directly infer whether functional connections exist across a landscape. Coupled with path finding algorithms such as least cost path or circuit theory (see below), landscape genetics has proven to be a powerful approach to quantify connectivity (for example, Epps et al., 2007; Shirk et al., 2010).

The first major barrier to landscape genetics is that this approach can be costly and time consuming to both gather and analyze data. This is particularly true when the organism of interest is small and elusive or covers large geographical areas. Second, genetic patterns across a landscape take generations to develop and therefore have been continuously evolving for centuries if not millennia. It therefore may be erroneous to assume that current land use information can explain genetic patterns across a landscape (Balkenhol et al., 2009). Despite this, some empirical evidence has suggested that patterns of genetic diversity across a landscape can reflect recent land use changes (Zellmer and Knowles, 2009), highlighting the importance of considering the temporal and spatial scale of a study and the ecology for the organism of interest in landscape genetic studies.

1.2.2 Modeling approaches to estimate landscape connectivity

1.2.3 Graph theory approaches

Connectivity across a landscape can be conceptualized as dynamic network where habitat patches (nodes) are functionally linked by the flow of individuals (edges). Graph theory has been extensively used to analyze spatial networks and research in landscape connectivity has benefited considerably from its application (see reviews by Urban and Keitt, 2001; Galpern et al., 2011). Graph theory has proven to be a particularly powerful approach to identify clusters of highly connected patches along with the relative importance of each patch for landscape-level connectivity (for example, Estrada and Bodin, 2008; Minor and Urban, 2008; Peterman et al., 2016; Saura et al., 2014).

Graph theory can provide insight into the overarching structure of a landscape, which is useful to explore questions related to landscape resilience (Minor and Urban, 2008). For example, network measures such as the degree distribution, centrality, and modularity provide an estimate of network resilience to events such as random and/or targeted node removal (see Rayfield et al., 2013 for a complete discussion of network metrics applied to connectivity). Also, it is possible to determine which nodes and edges are most important to connectivity, and subsequently, where to target conservation efforts. Conceptualizing a landscape as a series of nodes however can be somewhat limiting. This approach requires clearly defined nodes to connect. In landscapes with clear patch boundaries such as wetlands or clusters of individuals, it can be relatively easy to define nodes. When landscapes are composed of a gradient of poor to good habitat however, this may prove challenging. Also, it may be difficult to incorporate animal behavior or landscape elements into a network.

1.2.4 Path finding analyses

With the recent wide availability of GIS, path-finding analyses have been extensively utilized to predict how animals move across a landscape and subsequently which features of a landscape contribute to connectivity. Central in most path finding approaches is a resistance surface. Resistance surfaces are raster maps that describe the ease with which an organism travels across a landscape (see reviews by Spear et al., 2010; Zeller et al., 2012). They are commonly derived by assigning a 'movement cost' from a continuum of low to high resistance to movement for each pixel on a landscape. Cost values are usually a weighted function of several landscape features such as slope, elevation, roads, urban areas, etc. Thus, resistance layers recognize that animal movement is influenced by the physical structure of a landscape and that populations separated by high resistance are functionally more isolated than those separated by low resistance. In practice, there is considerable variation in how researchers weight resistance values such as with occurrence (Stevenson-Holt et al., 2014; Wang et al., 2008), radio telemetry (Cushman and Lewis, 2010; LaPoint et al., 2013; Richard and Armstrong, 2010; Trainor et al., 2013), or genetic data (Peterman et al., 2014; Richardson, 2012). Moreover, expert opinion is commonly used to create a resistance layer in cases where empirical data are lacking and/or there is urgency in conservation actions (Hepcan et al., 2009; Rabinowitz and Zeller, 2010). Zeller et al., (2012) found that of 96 papers that used resistance layers, 76 relied, at least in part, on expert opinion to develop weighting schemes. Although empirical data has been shown to outperform expert opinion (Shirk et al., 2015), in many cases it is logistically unfeasible to collect field data due to small, elusive species, limited timelines, or cost. Expert opinion is often the only available resource to weight costs in a resistance layer. Also, as demonstrated by Clevenger et al. (2002), resistance cost values assigned with data from expert-literature that is presumably collected, analyzed, and summarize following analytical processes, can closely match empirically parameterized models. Regardless of the data used to create a resistance layer, researchers should explore how uncertainty affects model outputs (Beier et al., 2009; Dudaniec et al., 2016).

An assumption of resistance modeling is that animals preferentially move across a landscape with the same criteria they use to select habitat that facilitates life cycle requirements such as foraging or breeding. Therefore, animal movement underpinned by motivations other than resource selection will be poorly captured with a resistance layer. This issue is particularly problematic in resistance layers validated with expert opinion. Experts are probably more familiar with a species' home range habitat than dispersal habitat and resistance layers may reflect this bias. Despite this, resistance surfaces are fundamental to path-finding approaches of identifying landscape connectivity such as least cost path analysis and circuit theory.

Least cost path analysis (LCP; Adriaensen et al., 2003) and circuit theory (McRae et al., 2008) are two widely adopted methods to identify where habitat corridors are located on a landscape. Both of these methods use path-finding algorithms to identify routes across a resistance layer. The least cost path approach is readily applicable using widely available software packages (e.g., ArcGIS), which is probably a driving factor in its popularity (for example, Creech et al., 2014; Driezen et al., 2007; Epps et al., 2007). This approach requires modellers to identify locations on the landscape to connect (i.e., an origin and a destination) and a single, best route between these locations (calculated as the route having the lowest sum of resistances) is then identified. Despite the wide application of least cost path simulations, this approach has been criticized as a poor representation of animal movement (Coulon et al., 2015; Sawyer et al., 2011). Least cost path analysis assumes that individuals have complete knowledge of their landscape and can identify optimal routes between pre-determined locations. As discussed by Fahrig (2007) however, this is a tenuous assumption. Although it is reasonable to assume animals have a general understanding of their landscape, including the location of good habitat, it is unlikely an individual is capable of discerning optimal routes between these locations. By simulating individuals as intrinsically optimal, least cost path approaches do not capture the inherent variability in natural systems, nor the heterogeneity in individual behaviour and movement decisions.

Circuit theory draws on the resemblance between random walks observed in natural systems and the flow of electrical current through a circuit (Cowley et al., 2015; McRae et al., 2008). Similar to LCP, circuit theory uses a resistance layer to quantify how impermeable each pixel is to animal movement. Software packages such as Circuitscape (McRae et al., 2013) then simulate this resistance layer as an electrical circuit to identify corridors, pinch points, or barriers to movement across the landscape. Circuit theory presents several differences to LCP modeling. First, this approach assumes that dispersing individuals have no prior knowledge of their landscape. This is in stark contrast to LCP analysis, which assumes individuals have complete knowledge. Second, unlike LCP, which will show a single, optimal route across a landscape, circuit theory can incorporate multiple pathways into results (McClure et al., 2016; Walpole et al., 2012). Moreover, circuit theory does not require predefined start and destination points on the landscape to connect as an input (Pelletier et al., 2014). Although circuit theory presents advantages over LCP modeling, it may be unrealistic to assume that only neighbouring grid cells govern animal movement, an assumption implicit in circuit theory. For example, many if not most species will have a nuanced representation of their environment and are capable of learning and adapting to their surroundings. By simulating movement as a random walk, circuit theory therefore may be as problematic as identifying optimal movement paths across a landscape.

1.3 Individual-based models

Individual-based models are emerging as a promising tool to assess, plan, and implement landscape connectivity (Baguette and Van Dyck, 2007; Beier et al., 2011; Kool et al., 2013). In general, individual (or agent) based models (hereafter IBM) create agents that interact with each other and/or their environment through prescriptive rules (Grimm et al., 2005). Individual-based models have been widely applied in ecology as a simulation tool to explore systems where individual, localized decisions play into system-level dynamics. This is a potentially powerful approach to explore landscape connectivity because researchers can simulate individuals responding to local environmental conditions to make movement decisions and allow corridors to emerge as a result of animals interacting with their landscape. An IBM therefore may provide a more nuanced estimate of connectivity than least cost path analysis or circuit theory by highlighting all components of a landscape with the potential to facilitate animal movement rather than only the least costly routes or optimal paths of least resistance. This is a potential advantage of IBMs because it results in a gradient of possible locations for conservation actions that can align with other land use objectives. Individual-based models therefore provide a compelling framework to explore how management actions will impact connectivity before investing in on-the-ground work, which is important given the paucity of resources available in most conservation projects.

There are a handful of studies that have used IBMs to explore landscape connectivity both theoretically and experimentally (Aben et al., 2014; Graf et al., 2007; Kanagaraj et al., 2013; Kramer-Schadt et al., 2011; Pe'er et al., 2011). Further, prior work has demonstrated that, compared to least cost path or circuit theory, IBMs better reflect how animals move across a landscape and thus can provide an improved estimate of connectivity (Coulon et al., 2015). Despite the potential advantages of IBMs over least cost path and circuit theory, this remains a relatively unexplored approach to identify components of a landscape that contribute to connectivity.

1.4 Study area: The Okanagan Valley

The Okanagan and Similkameen Valleys are a semi-arid landscape located in Southern British Columbia along the Canadian-American international border (Figure 1.1). The Okanagan Valley has considerable biological and ecological importance and is recognized as a biodiversity hotspot (Iverson et al., 2008). Many of the species found in this region are at the northernmost limit of their global range and have very specific habitat requirements. Further, a series of large lakes, mountains, and valleys naturally restrict access to available habitat. In addition to natural factors, considerable human land use transformations are pervasively changing the Okanagan Valley to support a high human growth rate (South Okanagan Regional Growth Strategy, 2007; Regional District of Central Okanagan Regional Growth Strategy, 2013). Many of the natural areas found at lower elevations are undergoing considerable transformation due to urbanization, industrial development, and agricultural expansion, whereas in the highland areas surrounding the valley bottom, fire suppression, logging, over-grazing and off-road vehicle damage are significantly impacting ecosystems. Collectively, these natural and anthropogenic pressures on the natural flora and fauna have resulted in the valley's designation as one of the most endangered regions nationally. Within the valley, there are 56 species assessed by the Committee of the Status of Endangered Wildlife in Canada (COSEWIC) as 'endangered' or 'threatened' and a further 309 'red' or 'blue' listed provincially (BC Conservation Data Centre, 2016). Land use managers are increasingly recognizing the importance of maintaining connectivity in the Okanagan Valley to support animal movement across the landscape.

Figure 1.1 Map of the Okanagan Valley, British Columbia, Canada. Cartography by C. Allen. Data sources: BC Geographic Warehouse and Geogratis. Imagery courtesy of ESRI Digital Globe. Used with permission. Map compiled in ESRI ArcMAP 10.2.

1.4.1 A regional perspective on connectivity

Despite agricultural and urban land use in the valley bottom, the Okanagan is unique in that it has considerable remaining habitat to preserve connectedness as human land cover change proceeds. Moreover, the Okanagan has been identified as the only low-elevation corridor between the shrub-steppe ecosystems south of the USA/Canada border with the grasslands of Central BC (Benzener et al., 2004, Figure 1.1). As temperatures warm, it is anticipated species will move North along their climatic gradients from Washington and through the Okanagan into British Columbia (WHCWG, 2011). This region is therefore important for facilitating animal range shifts in a changing climate.

Stakeholders in Washington and British Columbia have identified habitat connectivity across the USA/Canada border as a priority (WHCWG, 2013). As a result, the Transboundary Connectivity Group was formed to elicit coordinated discussions on connectivity for wildlife between British Columbia and Washington and to develop a series of decision support tools that identify key habitat corridors that facilitate movement across the international border (Transboundary Connectivity Group, 2016). This work used a "Connectivity Focus Area" approach wherein researchers identified intersection points with high connectivity value for multiple species and landscape perspectives. The perspectives used in this analysis include: a montane species model, a shrub-steppe species model, and a landscape integrity model. Finally, aggregating the results of these three models created a composite connectivity map that illustrates connectivity focus areas that likely facilitate movement between Washington and the Okanagan Valley for many species (Figure 1.2).

In addition to the transboundary work, a regional habitat connectivity analysis was completed for the North, Central, and South Okanagan as a component of the Biodiversity Conservation Strategy (hereafter BCS, Okanagan Collaborative Conservation Program, 2014; South Okanagan Conservation Program, 2012). A connectivity value was assigned to each pixel on the landscape depicting how permeable that pixel is to animal movement. To determine these connectivity values, a series of assumptions were made regarding how species respond to elements on a landscape. It was assumed that connectivity is higher with proximity to water and on gentle slopes, whereas steep rugged terrain and structures such as roads and buildings likely inhibit movement. This work therefore does not show connectivity, but rather the ease with which an animal is likely to move through different components of the landscape. Building on the work completed for the BCS, the Complex Environmental Systems Research Group used the BCS Habitat Connectivity map to create a resistance to movement layer. By applying the Circuitscape program to this resistance layer, major habitat corridors were then identified across the Okanagan Valley (Figure 1.3; Parrott et al., manuscript in preparation).

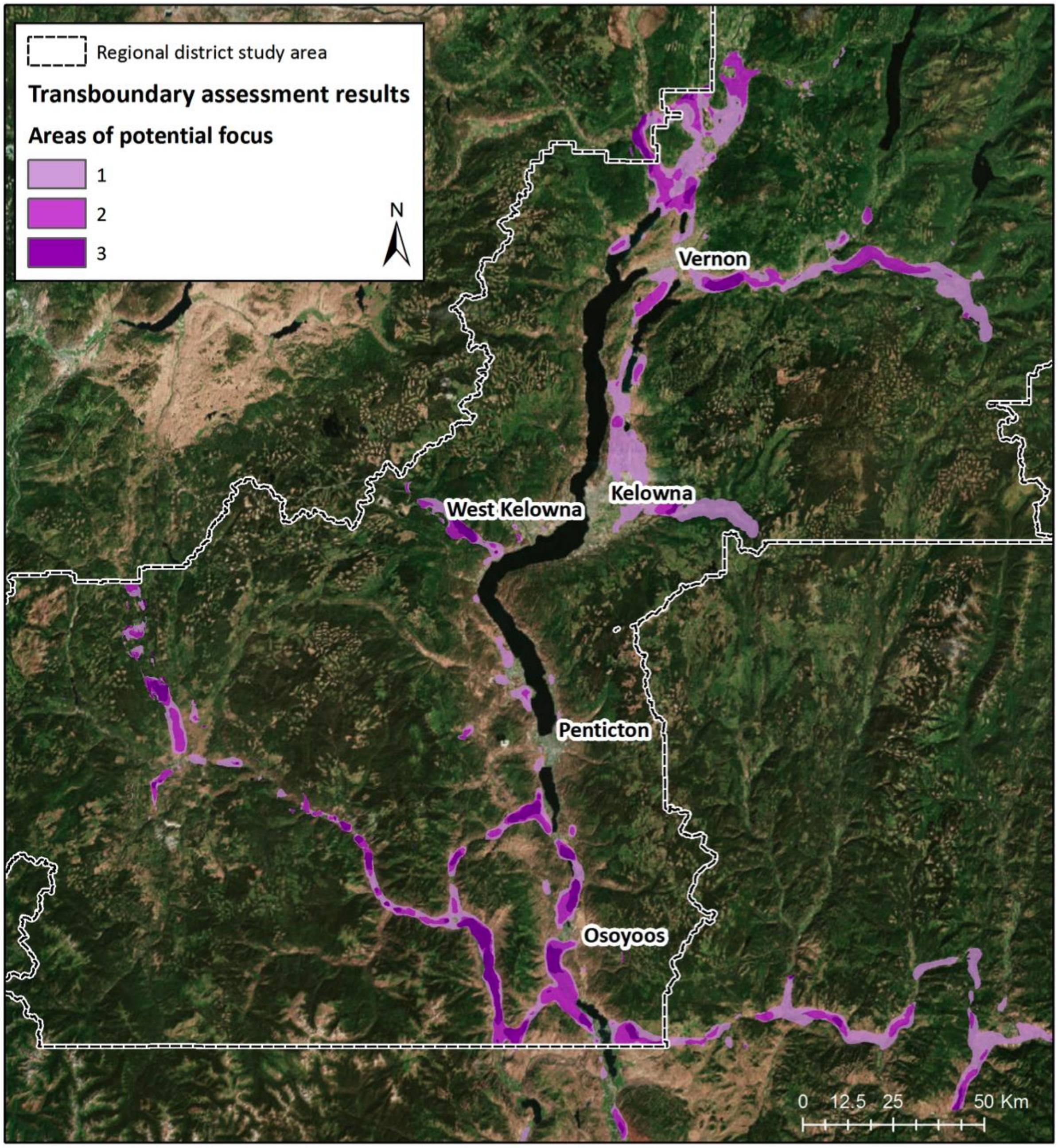

Figure 1.2 Transboundary connectivity focus areas for the Okanagan-Kettle subregion identified for shrub-steppe species, montane species, and a landscape integrity model. Possible operational areas show the degree of overlap between perspectives where dark purple (value of 3) show regions that contribute to connectivity for three of the perspectives and light purple (value of 1) shows regions that contribute to connectivity for one perspective. Cartography by C. Allen. Transboundary assessment results provided by the BC-WA Transboundary Connectivity Group. Data source: BC Geographic Warehouse. Imagery courtesy of ESRI Digital Globe. Used with permission. Map compiled in ESRI ArcMap 10.2.

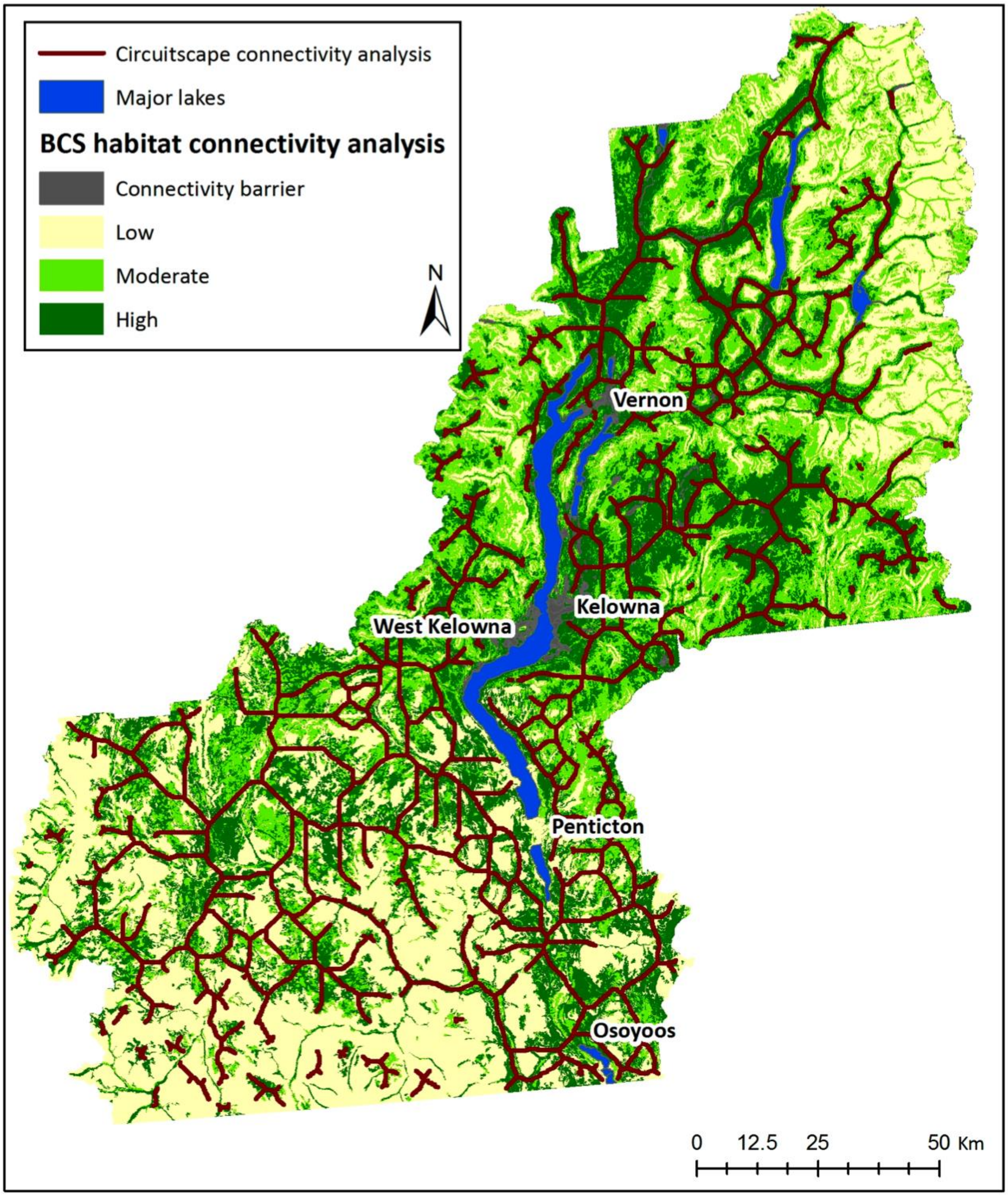

Figure 1.3 Potential wildlife movement corridors for the Okanagan Valley overlaid on the Biodiversity Conservation Strategy habitat connectivity ratings. BCS habitat connectivity maps show the relative ease with which species move throughout the landscape. Potential wildlife movement corridors were identified through Circuitscape modeling. The Circuitscape connectivity analysis builds on the BCS habitat connectivity work to establish corridors across the landscape. Cartography by C. Allen. Data sources: Biodiversity Conservation Strategy – Caslys Consulting Ltd., Complex Environmental Systems Lab, UBC, and Cardille Lab, McGill University, and BC Geographic Warehouse. Map compiled in ESRI ArcMAP 10.2.

1.5 Research objectives and thesis structure

The field of landscape connectivity has seen rapid advancement both in theory and the methods for identifying and quantifying where connectivity exists across a landscape. Researchers and land use practitioners have a sizeable toolbox of methods to identify connectivity across a landscape including circuit theory, least cost path analysis, and genetics, each with their advantages and disadvantages. Although it is well recognized that connectivity emerges from animal behavior and landscape features, as of yet, most of these methods for identifying connectivity largely emphasize the configuration and composition of a landscape. Individual-based modeling has emerged as a promising platform to incorporate a more realistic representation of how a species interacts with its landscape; however, this remains a relatively unexplored approach. The overarching aim of this thesis is to assess the utility of an individual-based modeling approach as a tool for identifying species-specific functional connectivity across a landscape and to apply this approach to identify a network of wildlife corridors in the Okanagan Valley for two selected species of interest.

Specific objectives of this work include:

1) To create an individual-based model of animal movement based on landscape characteristics and calibrate it to represent two selected species: bighorn sheep (*Ovis canadensis*) and tiger salamanders (*Ambystoma mavortium*),
2) To apply an individual-based model as an exploratory tool to simulate how land management and environmental change scenarios might impact connectivity throughout the Okanagan Valley for the selected species,
3) To explore the ease of implementation, results and implications of an individual-based modeling approach to estimate landscape connectivity, and
4) To compare the results of the IBM models to existing connectivity work and to provide prescriptive guidelines to increase landscape connectivity in the Okanagan Valley to environmental planners and land use managers.

These objectives are accomplished using the Okanagan Valley, British Columbia, as a case study area. Bighorn sheep and tiger salamanders were chosen as focal species for this study for several reasons. First and most importantly, existing connectivity modeling in the Okanagan uses a general connectivity approach that may not sufficiently represent all species. I sought to include a species that I predict will closely align with the general connectivity maps, the tiger salamander, along with a species that I predict will not align well, the bighorn sheep, to highlight the advantages and limitations of a general species approach to connectivity. Second, as of yet, connectivity for bighorn sheep and tiger salamanders has not been studied in the Okanagan Valley despite their provincial status as blue-listed and red-listed respectively. The work presented in this thesis is therefore the first site- and species-specific connectivity assessment for bighorn sheep and tiger salamanders and will contribute directly to their conservation in the Okanagan. Finally, bighorn sheep and tiger salamanders in the Okanagan are peripheral species at the northern-most tip of their global range. As a result, maintaining connectivity through this region will likely prove important to their global populations with a changing climate.

The remainder of this thesis is structured into two research chapters, a general discussion, and a conclusion. Chapter 2 and 3 present an individual-based model to identify landscape connectivity for bighorn sheep and tiger salamanders respectively. Specific land use change scenarios relevant to each species are also explored in their respective thesis chapter. Chapter 4 discusses the advantages of an IBM compared to other approaches, compares the results of the tiger salamander and bighorn sheep connectivity analyses to existing connectivity work in this region and discusses management implications of the results presented in this thesis. Finally, the conclusion addresses research objectives and more broadly highlights how this work contributes to the field of landscape connectivity.

2 Chapter: Bighorn sheep

2.1 Context

Bighorn sheep (*Ovis canadensis*) were once widely distributed across the Okanagan Valley, British Columbia Canada. However, habitat loss as a result of human and natural land use transformations along with forest fire suppression has segregated the population into three separate subpopulations with major roads, rivers and other obstacles to movement limiting dispersal ability (Demarchi et al., 2000).

There is interest in maintaining connectivity across this landscape for bighorn sheep primarily for two purposes. First, a connected landscape could facilitate dispersal between subpopulations of sheep to increase gene flow. Second, maintaining linkages between existing bighorn subpopulations and currently unoccupied yet suitable bighorn sheep habitat could promote colonization into new habitats and range shifts as a response to changing climates and to increasing human disturbances in existing bighorn sheep range. This thesis chapter presents a spatially explicit individual-based computer model of bighorn sheep movement and then applies this model to identify how land management scenarios impact bighorn sheep connectivity. Specific objectives of this chapter include:

(i) To determine if dispersal is likely to occur between present-day bighorn sheep subpopulations without management intervention;

(ii) To highlight how bighorn sheep might make broad use of this landscape to facilitate range expansions into currently unoccupied yet suitable habitat; and,

(iii) To explore how proposed land-use management options might impact bighorn sheep connectivity.

2.2 Materials and methods

This analysis followed three steps. First, to determine if dispersal is likely between subpopulations of sheep, I constructed an IBM in which virtual bighorn sheep move independently from pre-determined locations across a rasterized landscape according to behavioural movement rules. Bighorn sheep continue to wander until they either leave the landscape, become “stuck”, or the simulation terminates after 2000 time steps. By aggregating the movement paths of simulated sheep across model iterations, I identified areas of the landscape contributing to connectivity. Second, to identify how bighorn sheep might make broad use of this landscape to facilitate range shifts or expansions, I adjusted the IBM to start from any pixel with suitable bighorn habitat regardless of whether bighorns currently occupy that area or not. Third, I explored the effectiveness of two proposed management scenarios that aim to facilitate bighorn sheep dispersal in this area: restoring a more natural fire regime to remove densely forested areas and identifying optimal road crossing locations to prioritize for actions that could make roads more permeable to bighorn sheep movement.

2.2.1 Study area and study species

This study was located in the Okanagan Valley of British Columbia, Canada (Figure 2.1). Habitat isolation is regarded as the most pervasive threat to bighorn sheep persistence in this region (Demarchi et al., 2000). Despite areas of core habitat remaining largely intact, natural and anthropogenic barriers to movement surround bighorn populations and can several impede dispersal ability. These include wide valleys and plateaus, densely vegetated areas (DeCesare and Pletscher, 2006), roads (Epps et al., 2005), large urban centers (Rubin et al., 2002), and recreation trails that are frequently used by humans and dogs (MacArthur et al., 1979). Bighorns are blue-listed as "vulnerable" by the Province of British Columbia's Species at Risk Act and the existing herds are vital to maintaining the species' persistence. There is a clear need to preserve or restore physical connections between subpopulations along with connections to potential future habitats to facilitate range expansions and shifts.

Bighorn sheep occurrence data was provided by the Provincial Ministry of Forests, Lands, and Natural Resources (years 1968 – 2013; Figure 2.1). Although this data set encompasses sheep occurrences from many years, the location of bighorn sheep has not changed considerably throughout the dataset. Note that this occurrence data was sampled with a bias for areas known to have bighorn sheep rather than an inclusive search of the entire landscape. Absences of bighorn occurrences in Figure 2.1 therefore are not necessarily absences of bighorns in the real landscape.

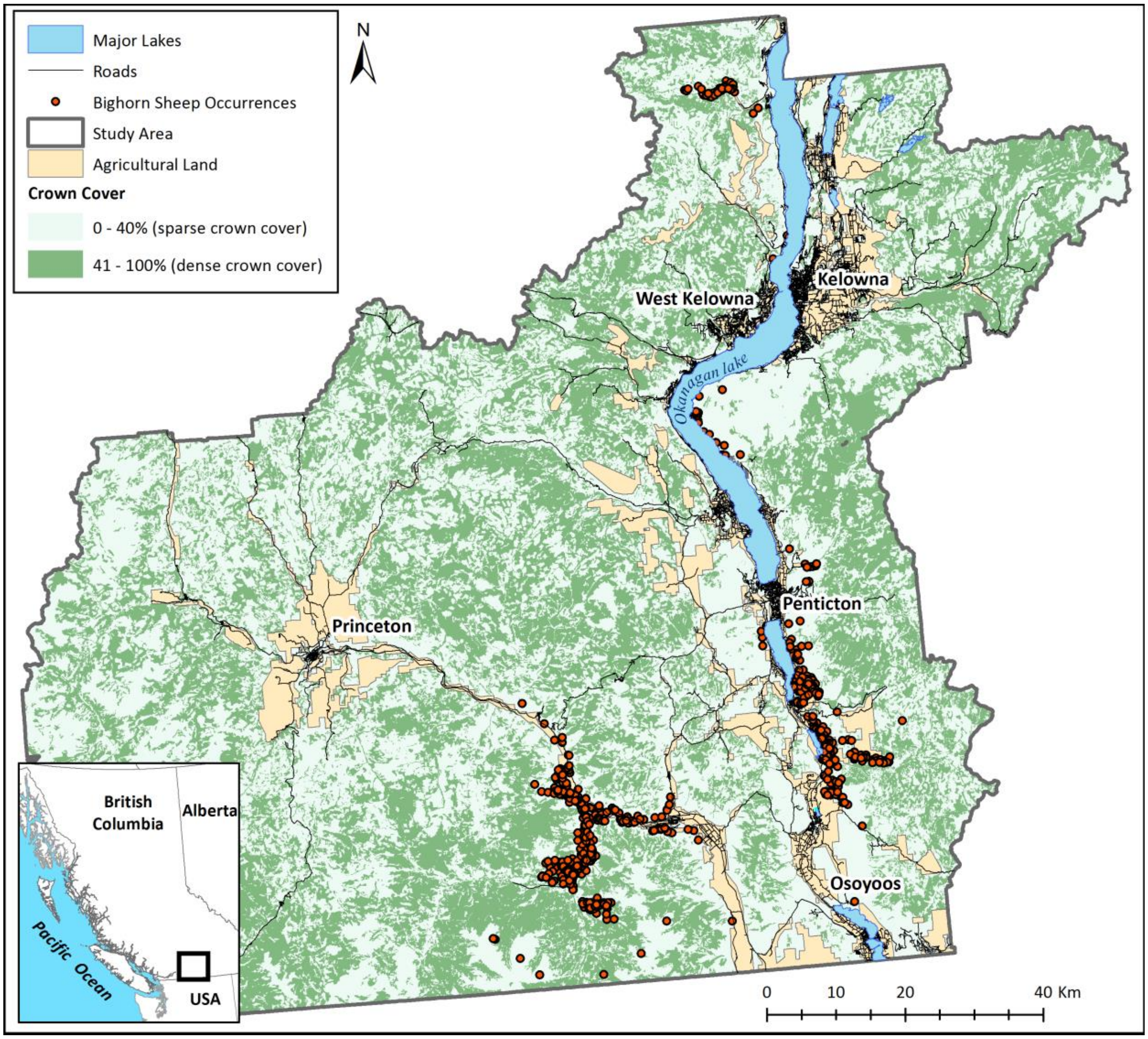

Figure 2.1 Bighorn sheep study area. The main map panel shows major land cover classes and recorded occurrences of bighorn sheep. The insert shows the position of the study area in British Columbia, Canada. Cartography by C. Allen. Data sources: BC Geographic Warehouse, BC Ministry of Forests, Lands and Natural Resource Operations, Agricultural Land Commission, and Geogratis. Map compiled in ESRI ArcMAP 10.1.

I drew extensively on site-specific government reports supplemented with literature from the greater bighorn range to profile bighorn sheep movement behaviour. The following factors have repeatedly been demonstrated as important to bighorn movement:

(i) Proximity to escape terrain – Escape terrain includes steep and rocky areas that are challenging for predators to traverse. The use of an area decreases as distance to escape terrain increases (DeCesare, and Pletscher, 2006; Demarchi et al., 2000; Shannon et al., 1975; Smith et al., 1999; Tilton and Willard, 1982), and

(ii) Preference for sparse vegetation - bighorns depend largely on acute vision to detect threats and therefore avoid densely vegetated areas or areas with a closed canopy (DeCesare and Pletscher, 2006; Demarchi et al., 2000).

Additionally, roads (Epps et al., 2005; MacArthur et al., 1979), rivers (Smith et al., 1991), and large lakes (Demarchi et al., 2000) are obstacles to bighorn sheep movement. Although sheep habitat selection has been moderately well studied in this region, there exists little information regarding dispersal behavior. However, work in the broader bighorn range has shown that sheep will, whenever possible, stay close to escape terrain and remain in areas with good visibility. Agent movement was therefore restricted to regions that satisfy the movement rules outlined in table 1 with the understanding that this likely underestimates connectivity by not including dispersal through poor habitat.

Table 2.1 Bighorn sheep movement characteristics

Movement characteristic	Description	Corresponding model rule	References
Close proximity to escape terrain	Steep terrain with interspersed rocky outcrops	Escape terrain is defined in the model as any slope greater than 40 degrees. Bighorns attempt to remain within 400 m of escape terrain with the likelihood of a sheep travelling further than 400 m from escape terrain decreasing as described by $y = 188.21e^{-0.0016x}$(Warman et al., 1998).	DeCesare and Pletscher, 2006; Demarchi et al., 2000; Shannon et al., 1975; Smith et al., 1991; Tilton and Willard, 1982
Preference for sparse vegetation	Bighorn sheep avoid densely vegetated areas or areas with a closed canopy	Sheep will not occupy a cell with more than 40% crown cover	DeCesare and Pletscher, 2006; Demarchi et al., 2000; Pittman and Semlitsch, 2013; Pittman et al., 2014; Smith et al., 1991; Smith and Green, 2005
Roads	Bighorns sheep are severely deterred by roads and highways	Sheep cannot occupy a cell with a road	Epps et al., 2005; MacArthur et al., 1979
Ability to cross rivers and lakes	Bighorn sheep rarely cross rivers and large water bodies	Sheep cannot occupy a cell with a lake or river	Demarchi et al., 2000

2.2.2 Building the individual-based model

The individual-based model presented here is designed to capture critical processes underlying bighorn sheep movement within the Okanagan Valley, British Columbia, Canada to identify where connectivity exists across the landscape. This model was constructed in the Repast Simphony programming environment (North et al., 2013). A complete description of the model following the Objectives, Design concepts and Details (ODD) protocol is included in Appendix B.

2.2.2.1 The representation of space

A virtual grid provides a physical environment where sheep agents are located and interact with their landscape. This grid is created with the following land uses: slope in degrees, percent crown cover, lakes, rivers, and roads. Each spatial data layer was collected from government open-data sites (Table A1) and registered within the coordinate system NAD_1983_BC_Environment_Albers. A spatial resolution of 75 m x 75 m was used. This resolution was selected to ensure the spatial scale over which bighorn sheep likely inform movement decisions across their landscape was captured and to allow for fast model execution. Moreover, from a management perspective, this resolution is at a fine enough scale to inform land use decision-making. The landscape is static and shows no diurnal or seasonal variation.

2.2.2.2 Bighorn sheep agents

Bighorn sheep agents are reactive to the accessibility of escape terrain and open vegetation cover that provides visibility. They also react to the presence of barriers to movement including roads, rivers, and lakes. Agents have some mental representation of their environment and know the relative locations of habitat features such as good escape terrain. They are characterized only by their current and previous locations on the raster environment stored as the x- and y- coordinate of the center of the grid cell. Bighorn agents are capable of perceiving all attributes of the cell they currently occupy, the relative location of escape terrain, along with all parameters in the eight grid cells immediately surrounding their current location. Movement is not goal orientated; instead, a simple rule-based decision-making heuristic guides bighorn movement in this model (Figure 2.2).

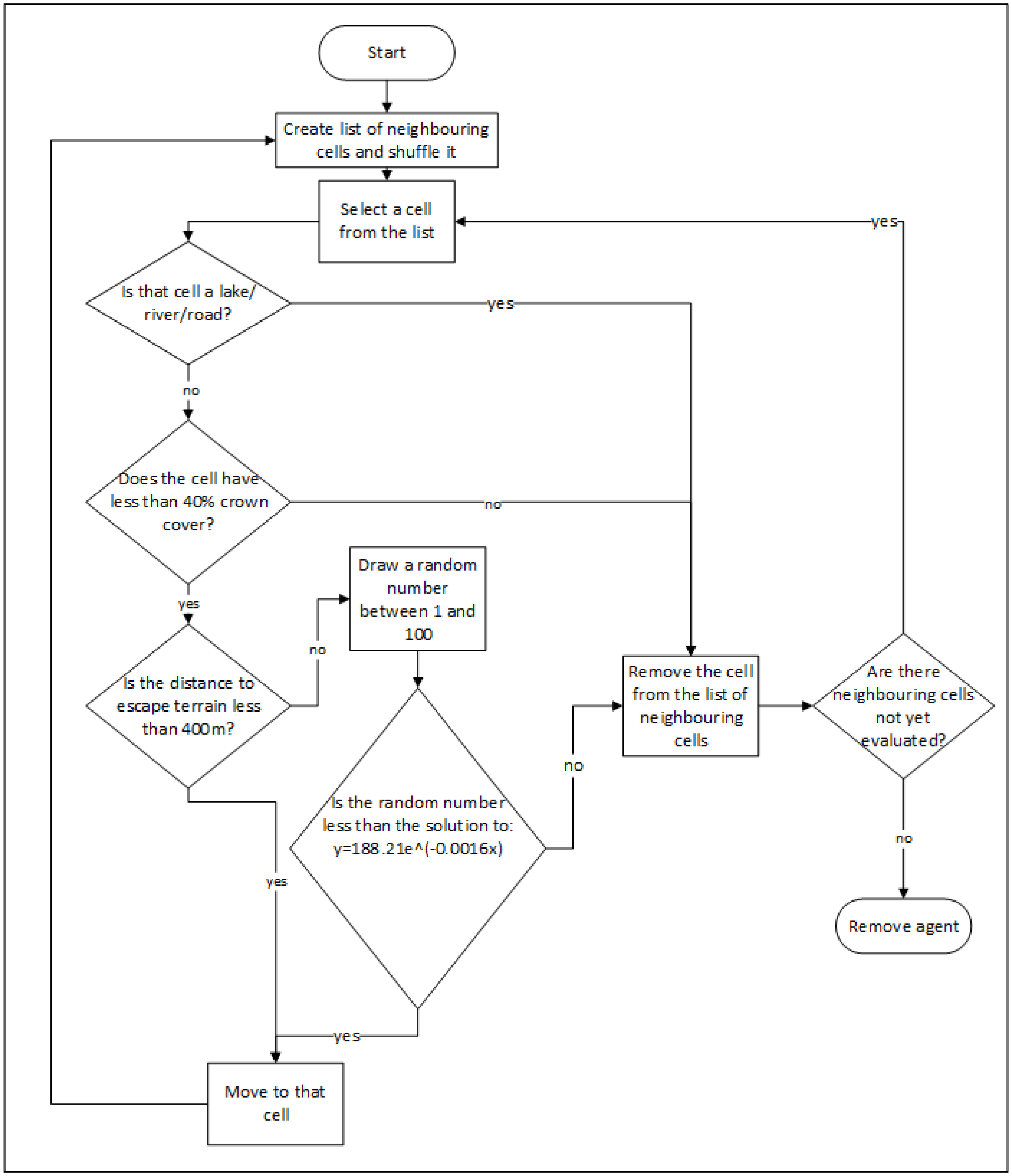

Figure 2.2 Behaviour rules of the bighorn sheep agents. For the equation used to determine the probability of a bighorn moving to a cell given its distance to escape terrain, x is the distance in meters from the cell to escape terrain, and y is the resulting probability of moving to that cell.

Bighorn sheep movement is implemented as a pseudo-biased random walk wherein agents will evaluate the quality of habitat immediately surrounding their current location and move towards favourable habitat. Each time step, the bighorn sheep agent will move from its current location to one of eight neighboring cells. Agent movement is probabilistic and driven by the type of land cover found at each cell. First a randomized list of all cells adjacent to the bighorn's current cell is generated. A cell is selected from that list and evaluated according to the movement rules summarized in Table 2.1. If the cell is located on a river, lake, or road, or has greater than 40% crown cover, it is removed as a possible cell to move to. If the cell is not on a river, lake or road and has less than 40% crown cover, the cell's distance to escape terrain is evaluated. If the cell is within 400 m of suitable escape terrain (cells with slope greater than 40 degrees), the agent will move to that cell. If the cell is further than 400 m away, the cell's distance to escape terrain is evaluated against an equation that relates the probability of movement to distance from escape terrain:

$$probability\ of\ movement = 188.21e^{-0.0016(distance)}$$

This is done by drawing a random number between 1 and 100 and if the random number is smaller than the *probability of movement*, the agent will move to that cell. Thus, as distance to escape terrain increases, it becomes less likely that a sheep agent will move to that cell. This equation was based off a habitat suitability model constructed for bighorn sheep in the Okanagan Valley (Warman et al., 1998). Note that because each grid cell is 75 m in length and width, the probability of movement effectively decreases beyond 450 m since it is not possible to be exactly 400 m from escape terrain (400 is not divisible by 75).

Each cell is iteratively evaluated against the movement requirements summarized in Table 2.1. As soon as a suitable cell is found, the sheep agent will move to that cell. The list of neighbouring cells was randomized prior to evaluating any cells. If no cell satisfies the movement rules, the agent is removed from the simulation. An agent cannot move backwards (i.e. into the cell it occupied the previous time step) to prevent agents from becoming "stuck" between small numbers of cells.

2.2.3 Running the model and management scenarios

A series of simulations were created to evaluate each of three research objectives of this chapter. Model implementation for each simulation is described below. In all cases, the simulation terminates when all agents have been removed from the simulation. Agents are removed when they become "stuck" (surrounded by only poor habitat), leave the spatial extent, or the simulation ends after 2000 time steps. Every time a sheep agent moves, its current location is stored as an x- and y-coordinate in a list. After the model terminates, the number of times a bighorn agent used each pixel on the landscape is aggregated into a single map, which is outputted into ArcMap 10.1.

Scenario 1: Dispersal between subpopulations without management intervention

The purpose of this scenario is to explore how bighorn sheep might disperse from their known locations on the landscape and to assess the degree of connectivity between existing subpopulations. 100 agents were created and placed on a pixel containing known bighorn sheep occurrences from empirical sighting data. The bighorn sheep agents then disperse from their initial locations by following the movement algorithm (Figure 2.2). After a simulation ends, the model will re-initiate at a new bighorn sheep location. This is repeated iteratively through all sheep occurrence locations recorded for the real landscape.

Scenario 2: Potential bighorn connectivity across the landscape

The purpose of this scenario is to explore how bighorn sheep might make broad use of their landscape to facilitate range expansions or range shifts. One bighorn sheep agent is created and placed on the landscape. Instead of starting the simulation from pre-determined locations, its initial location is determined by selecting a random pixel that satisfies bighorn sheep movement requirements (Table 2.1). The agent traverses the landscape following behaviour rules (Figure 2.2). After a simulation ends, the model re-initiates at a new pixel on the environment. This repeats for 20,000 model iterations.

Scenario 3: Increasing connectivity by restoring a natural fire regime

Historically, frequent and naturally occurring wildfires maintained high-visibility, open forest habitats for bighorn sheep throughout the Okanagan Valley. However, considerable fire suppression in this region has resulted in widespread loss of suitable bighorn habitat with a concurrent loss in connectivity. Fire has been shown to improve and expand bighorn habitat in other regions (DeCesare and Pletscher, 2006; Smith et al., 1999). The purpose of this scenario was to explore if interventions like prescribed burns, removing trees, or allowing natural fires to burn, could increase connectivity between subpopulations and into currently unoccupied bighorn habitat. One bighorn sheep agent is created and placed on the landscape. Its initial location was determined by selecting a random pixel that satisfies bighorn sheep movement requirements (Table 2.1); however, crown cover was removed as a variable bighorn sheep select against. The agent traverses the landscape following behaviour rules (Figure 2.2). After a simulation ends, the model re-initiates at a new pixel on the environment. This repeats for 20,000 model iterations.

Scenario 4: Increasing connectivity through major road interventions

This scenario aimed to identify where roadway interventions such as removing fencing around highways and constructing animal crossing structures over major roads could increase landscape connectivity for bighorn sheep. We increased the spatial resolution to 25 m by 25 m for this analysis. This was done to provide fine enough detail to determine where sheep highway crossing points were. To identify road crossing points, roads were removed from the model to simulate where bighorn sheep would likely travel if roads were not a barrier to movement. One bighorn sheep agent was created and placed on the landscape. Its initial location was determined by selecting a random pixel that satisfies bighorn sheep movement requirements (Table 2.1). The agent then traverses the landscape following behaviour rules (Figure 2.2). After a simulation ends, the model re-initiates a sheep agent at a new pixel on the environment. This repeats for 20,000 model iterations.

2.2.4 Model validation and sensitivity analysis

Local bighorn sheep experts verified that the movement rules and preliminary corridor maps were realistic and consistent with where bighorn sheep are anticipated to disperse on this landscape (Dyer, O., BC FLNRO, pers. comm. 2014), thus providing an expert validation of the landscape level results. The model results were subsequently validated against known bighorn sheep occurrence points to ensure that predicted movement was consistent with known sheep locations. No sheep movement or genetic data were available to validate individual-level movement patterns. We therefore tested the sensitivity of the model to assumptions used in the movement rules and ran an extensive parameter search to show how uncertainty in model rules influences results (Appendix B). The selected parameter values used for the simulations described in this paper are those that gave rise to landscape level results that encompassed more than 80% of bighorn sheep occurrence points. A more detailed description of model validation and sensitivity analysis is provided in the supplementary material.

2.3 Results

Although areas of good habitat are reasonably well connected within each subpopulation, bighorn sheep agents were unable to reach other subpopulations by dispersing through secure habitat, thus confirming the isolation of existing herds in the study area (scenario 1, Figure 2.3). When the individual-based model was modified to start from any pixel that met movement requirements (scenario 2), a mosaic of corridors and stepping-stones are discernable across the landscape (Figure 2.4a). Visually, the most used areas on the map appear to follow road transportation corridors. Management interventions that reduce crown cover such as prescribed burns with timber harvest and/or allowing naturally occurring wildfires to burn in bighorn habitat could considerably increase bighorn sheep landscape connectivity in the Okanagan (scenario 3; Figure 2.4b). This increase in connectivity is most pronounced in the South Okanagan where the landscape becomes a nearly continuous swath of pixels that were used by simulated sheep. The effect of increasing road permeability was less pronounced (scenario 4; Figure 4.5). The top 10% most used road crossing sites were identified in ArcMap (ESRI Inc.) and highlighted (Figure 2.5). Additionally, two areas of interest are indicated on Figure 2.5. First, a major road that bisects the South Okanagan subpopulation has a nearly continuous range of crossing points across a stretch of several kilometers (indicated with purple rectangle (a); Figure 2.5). Second, a road that runs parallel to and between the major lakes and that isolates the Eastern sheep subpopulations was consistently crossed at one point (indicated with a purple rectangle (b); Figure 2.5). These identified crossing locations may be the object of road mitigation measures to improve bighorn connectivity in the study area.

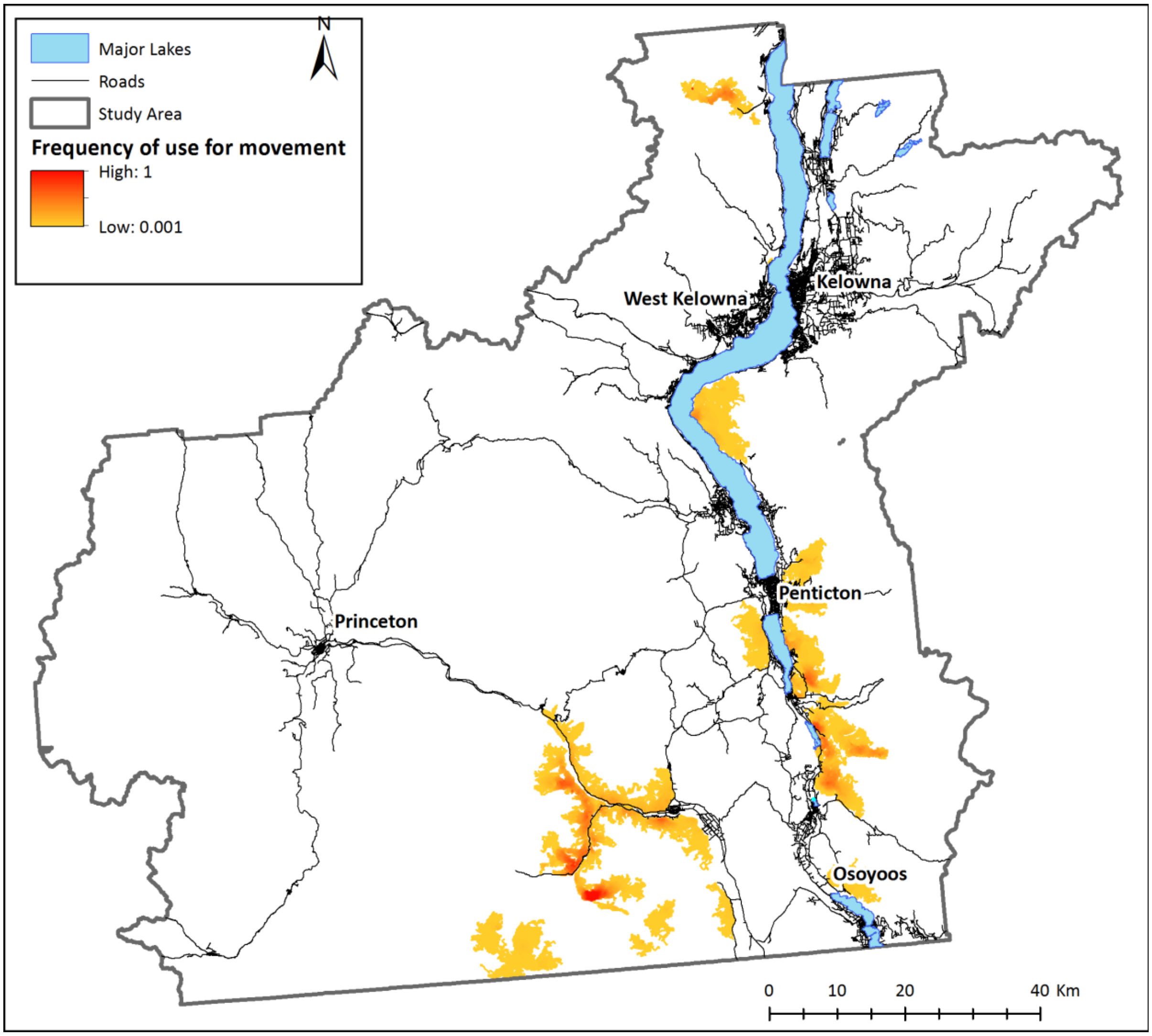

Figure 2.3 Modeled present-day frequency of use for movement by bighorn sheep, based on simulations with agents starting at known locations of recorded sheep occurrences. 100 agents were placed on the simulated environment at each known bighorn occurrence and allowed to move according to behavior rules. Relative frequency of use for movement is the number of times each pixel was used for movement by sheep agents divided by the number of times the most used pixel was crossed. White areas are pixels that were never used by a dispersing sheep. Data and Cartography by C. Allen. Data sources: BC Geographic Warehouse. Map compiled in ESRI ArcMap 10.1.

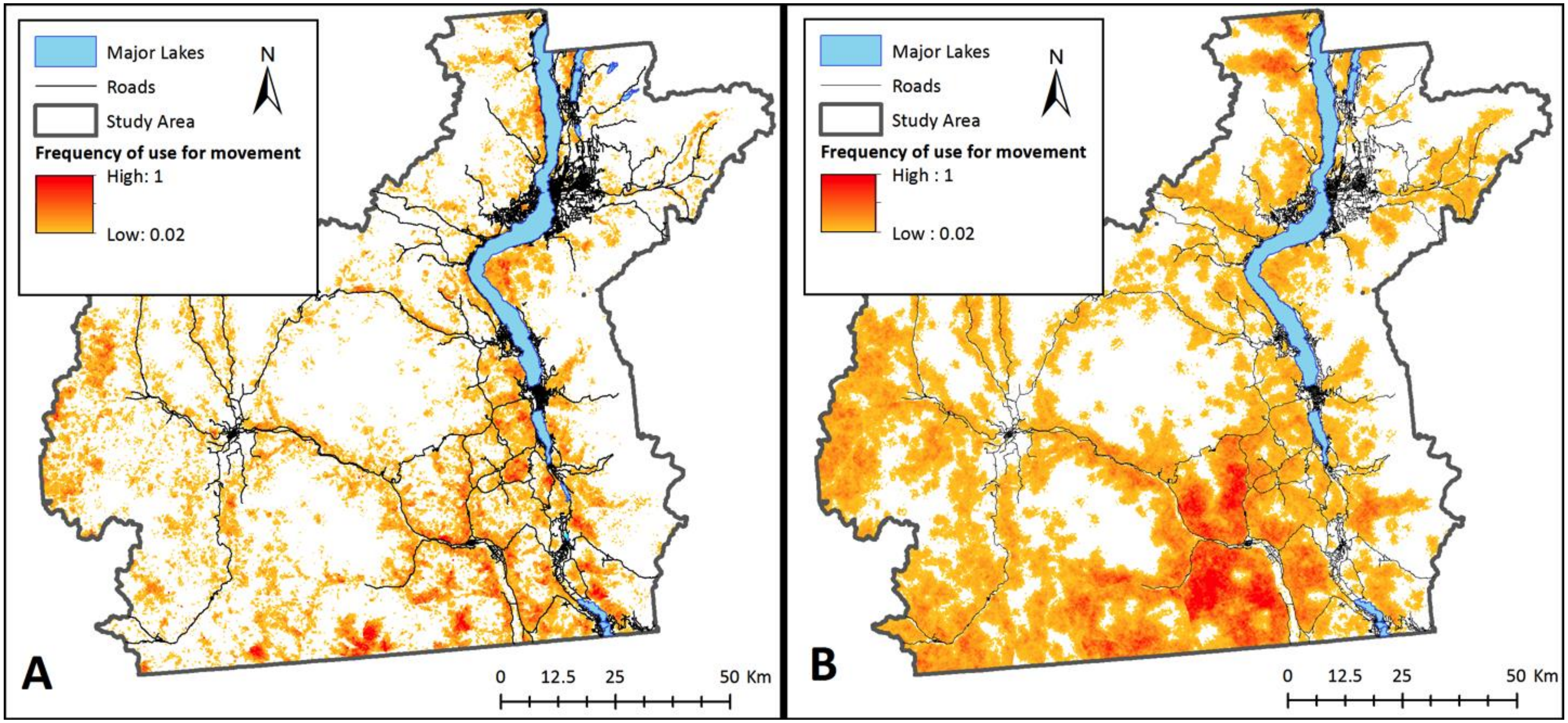

Figure 2.4 Potential relative frequency of use for movement by bighorn sheep identified by starting agents at any pixel with suitable habitat for (A) the present-day landscape, and (B) a landscape that simulates management actions that restore natural fire regimes. To simulate fire, crown cover was removed as a constraining factor on bighorn sheep movement. Relative frequency of use for movement represents the number of times each pixel was used for movement by sheep agents divided by the number of times the most used pixel was crossed based on 200000 simulations. White areas are pixels that were never used by a dispersing sheep across simulations. Data and Cartography by C. Allen. Data sources: BC Geographic Warehouse. Map compiled in ESRI ArcMap 10.1.

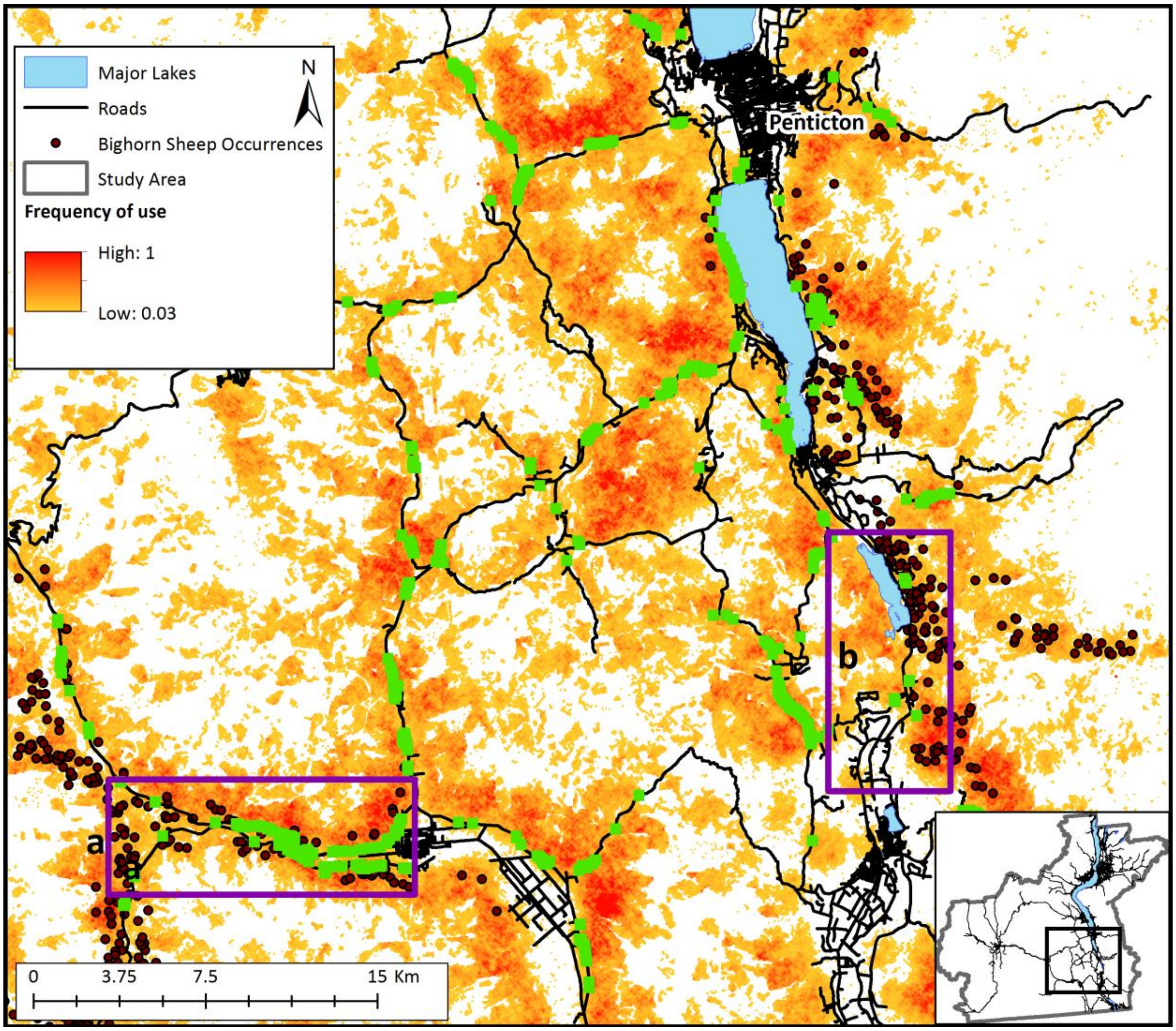

Figure 2.5 Relative frequency of use of the landscape for bighorn sheep movement and most frequently used road-crossing sites predicted by the bighorn movement model for a selection of the study area. Relative frequency of use for movement represents the number of times each pixel was used for movement by sheep agents divided by the number of times the most used pixel was crossed based on 20000 simulations. White areas are pixels that were never used by a dispersing sheep across simulations. Sections of roads highlighted in green indicate the top 10% most used locations for road crossings by simulated bighorn sheep. The dark purple rectangles (a and b) show regions of proposed highway improvements to facilitate sheep crossings based on model results. Data and Cartography by C. Allen. Data sources: BC Geographic Warehouse, Lands and Natural Resource Operations. Map compiled in ESRI ArcMap 10.1.

2.4 Discussion

Maintaining landscape connectivity has become of central importance to the conservation of many species, particularly for species that are capable of moving large distances across a landscape and have specific habitat requirements that limit their ability to disperse through poor habitat. This research chapter offers insight into the potential use of individual-based models to evaluate landscape connectivity by predicting where corridors and stepping-stones are located on a landscape. Here I have shown how a relatively simple individual-based model with behaviourally realistic movement rules can estimate connectivity across a landscape.

The results from this work suggest there are no existing continuous connections between sub-populations of bighorn sheep (Figure 2.3). Although no formal genetic work has been completed for sheep in this region, this finding supports anecdotal observations made by site- and species-experts that there has been little to no exchange of individuals between subpopulations in recent years (Dyer, O., & Reid, A., BC FLNRO, pers. comm. 2014). Despite this, the Okanagan landscape has potential to facilitate bighorn movement into currently unoccupied, yet suitable, bighorn habitats (Figure 2.4a). This is important given the anticipated re-structuring of habitat as a result of changing climates and increasing pressure on natural habitats due to human land use in the region (Nuñez et al., 2013). Many of the most used areas in Figure 2.4a follow transportation corridors. This result may have been observed because roads in this region follow the natural contours of the landscape and are thus adjacent to steep and rocky regions. By highlighting regions of high connectivity in close proximity to roads, this result re-enforces the importance of evaluating how roads can be made more permeable to sheep without increasing collision risk. Figure 2.4 also identifies stepping-stone connections between subpopulations that could provide connectivity in areas where continuous corridors were not identified in Figure 2.3. Interestingly, site experts who are familiar with historic bighorn sheep ranges in the Okanagan Valley indicated the results in Figure 2.4a highlight regions of the landscape that are known to have previously supported bighorn sheep populations (Dyer, O., & Reid, A., BC FLNRO, pers. comm. 2014).

The results of scenarios that could increase bighorn sheep connectivity demonstrate that a combination of road interventions along with restoring natural fire regimes in key areas of the study area are likely to increase bighorn connectivity. There is currently interest from various levels of government to install a wildlife bridge across a major road that bisects the Southern bighorn sheep population. The results presented here suggest that bighorn sheep are likely to use such a crossing structure at any point along that road (Figure 2.5; purple rectangle (a)). This is an important finding which provides for flexibility to the road crossing implementation process, allowing a potential structure to be located where land ownership and tenure are most amenable. In addition to road interventions, there appears to be considerable opportunity to restore dispersal ability between subpopulations by removing crown cover (either through prescribed burns or tree removal). It is, of course, unrealistic to remove crown cover across the entire landscape as was simulated here.

However, the results of this exercise show how fire or management interventions that mimic fire could positively affect bighorn sheep dispersal on this landscape. Bighorn sheep occupy a wide range in western North America extending from British Columbia, Canada to California, USA (Demarchi et al., 2000). The population of sheep we focused on in this study occupy the most northern tip of the greater bighorn range. Maintaining connectivity of these northern habitats is important on a continental scale to promote species' future range shifts in a changing climate. While this model has focused on subpopulations found in southern BC, it is easily transferable to other regions, and could be run for other landscapes with a simple adaptation of the input files describing landscape topography and vegetation cover.

There are several limitations of the results presented here. First, it is difficult to claim these results show functional connections without extensive bighorn sheep movement data. By only simulating dispersal through secure habitat, I have effectively assumed that structural connectivity is synonymous with functional connectivity. For individuals in fragmented landscapes, dispersal through insecure habitat is well recognized as a central process contributing to functional connectivity (Baguette et al., 2013). The type of habitat a species is moving through heavily influences dispersal strategies. For example, an individual attempting to cross a large area of poor habitat is likely to move quickly with a high degree of correlation in the direction of successive movements. This is in contrast to the same individual travelling through good habitat, which might result in a more circuitous and slow route. In this study, the decision to restrict simulated movement to areas of good habitat was made for two reasons. First, and most importantly, a conservation priority on this landscape is to identify, maintain and/or restore physical linkages between areas of good habitat for bighorn sheep. The model was therefore designed and implemented to identify routes that highlight how a sheep might travel through secure habitat towards subpopulations or unoccupied areas. Second, bighorn sheep are extremely cautious animals. Even while dispersing, bighorns prefer to follow rocky ridges and avoid densely forested areas. This prompted the modeling decision to identify routes that highlight how a sheep might travel through secure habitat towards subpopulations or unoccupied areas. An interesting direction for future work is to identify good gap-crossing locations through poor habitat by coupling the IBM described here with a least cost path model. Land use managers could then direct efforts to preserve crossing points or make them less hazardous for sheep.

A second limitation of this study is it captures the average behaviour of a population at the expense of individualized responses to the landscape. Dispersal is a multi-causal process with considerable variability within a population (Kokko and Lopez-Sepulcre, 2006). Individuals likely show a spectrum of behaviours in response to landscape elements; consequently, movement trajectories will differ substantially across a population (Elliot et al., 2014). This model was created by establishing a list of rules that all agents follow with no variation among individuals. Although this shows how the population as a whole might use a landscape, it does not capture individuals that show a stronger tendency to travel across barriers. We have effectively simulated the “worst-case” connectivity scenario where individuals are incapable of crossing gaps in good habitat, and thus, this model likely underestimates connectivity. In the real system, individuals may undertake rare dispersals across more difficult terrain, thus facilitating gene flow, colonizing new habitats, and expanding ranges. A priority for future work is to incorporate inter-individual variability into model assumptions. Individual-based models are an excellent platform to simulate disparate responses to landscape elements. However, to incorporate this into the model described here, we would require an extensive understanding of the variation in behaviours found in bighorn sheep, which is relatively unexplored for the study area.

2.5 Summary

By linking individual-scale movement rules to landscape-scale outcomes, this individual-based model of bighorn sheep movement allows for the exploration of how on-the-ground management or conservation scenarios may increase connectivity for sheep in the Okanagan Valley. The results presented in this chapter show spatial isolation between existing populations of bighorn sheep and highlight landscape features including corridors and stepping-stones that might facilitate movement between sheep populations and more broadly into unoccupied habitat. Further, I was able to apply this model to explore how a range of land use management scenarios might impact movement for bighorn sheep in the Okanagan. More generally, this study highlights the usefulness of individual-based models to identify how a species makes broad use of a landscape for movement. Application of this approach can provide effective quantitative support for decision makers seeking to incorporate wildlife conservation and connectivity into land use planning.

3 Chapter: Salamanders

3.1 Context

Amphibians are among the most threatened group of vertebrates globally. Habitat loss, degradation, and fragmentation have largely been credited as driving factors in declining populations (Cushman, 2006; Houlahan et al., 2000; Stuart et al., 2004). The effect of habitat loss and fragmentation is further exasperated by a complex of factors including high vulnerability to widespread pesticide use (Relyea, 2005) introduction of invasive species (Kats and Ferrer, 2003), and emergent pathogens (Skerratt et al., 2007). Further, most amphibians have a complex life cycle requiring access to aquatic habitats for breeding, larval development and metamorphosis along with terrestrial habitat for foraging and dispersing. Thus, maintaining connectivity between aquatic and terrestrial habitats is highly important to amphibian conservation (Becker et al., 2007).

Past research has highlighted the importance of small-scale connections between terrestrial and aquatic habitats. For example, Rittenhouse and Semlitsch (2007) show that amphibians use terrestrial habitats non-uniformly and that maintaining connections between terrestrial and aquatic habitats is critical to species persistence. Similarly, Guerry and Hunter (2002) found that the configuration of upland terrestrial habitat predicted wetland use for Wood frogs (*Rana sylvatic),* green frogs (*Rana clamitans)*, eastern newts (*Notopthalmus viridenscens),* and spotted salamanders (*Amhystoma maculatum).* Results such as this stress the importance of recognizing upland areas surrounding wetlands and connections between aquatic and terrestrial resources in landscape planning. Despite increasing recognition that connectivity is important for amphibian populations, existing efforts to protect amphibian habitat largely focus on the wetland breeding sites. In Canada, the Species at Risk Act protects habitat necessary for the survival or recovery of a listed species; however, this is often limited to breeding habitat. Connectivity between terrestrial and aquatic breeding sites is therefore commonly overlooked.

In addition to maintaining connectivity between terrestrial and aquatic amphibian habitat, amphibians require physical connections across the landscape to maintain dispersal between wetlands. Amphibian populations experience frequent, localized extinctions (Hecnar and M'Closkey, 1996; Trenham, 2003) and wetland suitability can vary considerably year-to-year as a result of stochastic environmental processes. Dispersing juveniles are largely responsible for re-colonizing wetlands and maintaining regional population persistence across a dynamically changing landscape (Cushman, 2006). The success of amphibian dispersal is directly influenced by a combination of landscape variables including the permeability of terrestrial habitat and the distance between neighbouring wetlands. For example, features such as forest cover (Todd et al., 2009; Popescu and Hunter, 2011) roads (Mazerolle, 2003), streambeds (Gibbs, 1998), and wetland proximity (Smith and

Green, 2005) have all been shown to influence landscape permeability for amphibians. Maintaining physical linkages across the landscape is important first for facilitating movement between aquatic and terrestrial habitats, and second, for promoting dispersal, and consequently gene flow, across the landscape. To integrate wetland connectivity into land management requires tools to identify where connectivity barriers and priority action sites are to inform conservation and recovery efforts. An individual-based model provides an excellent framework to realistically simulate amphibians emerging from wetlands and dispersing across a terrestrial landscape. Moreover, for species such as amphibians with limited ability to sense their landscape over large distances, an IBM may present advantages over LCP approaches, which implicitly assume that individuals can perceive their entire landscape.

This thesis chapter presents a spatially explicit individual-based computer model of amphibian dispersal to identify how wetlands are functionally connected across a landscape. The Western (formally Barred) Tiger Salamander (*Ambystoma mavortium*) in the Okanagan Valley of British Columbia, Canada was used for this study. Older literature often does not differentiate between the Western Tiger Salamander (*A. mavortium*) and Eastern Tiger Salamander (*A. tigrinum*). For this thesis, the most current name and classification as outlined by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) were used.

The Okanagan is a semi-arid region composed of a mosaic of permanent and ephemeral wetlands separated by a series of roads, urban areas, and other potential movement barriers. Because this valley is among the driest regions nationally, wetland inundation varies considerably year to year. The tiger salamander is provincially Red-listed as S2-emperiled (BC Conservation Data Centre, 2016) and nationally listed as endangered (COSEWIC, 2012). Loss and degradation of wetland breeding sites is repeatedly identified as the greatest factor contributing to declining amphibian populations in this region (Southern Interior Reptile and Amphibian Recovery Team, 2008). Further, predatory fish introduced to wetlands for sport fishing are known to prey on tiger salamander larvae, which can cause extirpation in breeding pools (Southern Interior Reptile and Amphibian Recovery Team, 2008). Legal and illegal stocking of wetlands remains a widespread concern for tiger salamander populations in the Okanagan area. Finally, the Okanagan is at the northern-most limit of tiger salamander distributions. Maintaining connectivity within and across the Okanagan Valley may therefore prove important for global range shifts in response to a changing climate.

Currently, there are 75 known breeding sites (BC Conservation Data Centre, 2016); however, these sites show considerable variation in suitability year to year and salamanders have not used many in decades (Dyer, O., BC FLNRO, pers. comm. 2016). Suitable breeding sites include perennially inundated water bodies with no predatory fish and ephemeral wetlands that retain water sufficiently long for larval development. A minimum of three months of water retention after spawning is required to support tiger salamander populations through hatching and metamorphosis; however, longer hydroperiods have been shown to increase the body size of emerging salamanders (McMenamin and Hadly, 2010). Natural and stochastic events such as the amount of rainfall a wetland receives and extended periods of drought can cause wetland suitability to vary dramatically in time. During periods of drought, temporary wetlands may not retain water sufficiently long for larval development or may even disappear completely. Moreover, human activities including draining, filling, polluting and/or introducing exotic predatory fish into breeding ponds can further impact tiger salamanders in this region (Southern Interior Reptile and Amphibian Recovery Team, 2008). Lea (2008) estimates that 84% of low elevation wetlands have been lost as a result of post-settlement activities in the Okanagan Valley. Similarly, Coelho (2015) reports a 63% decline in the number of ponds in the semi-arid grasslands of BC since the early 1990's with a concurrent 54% decrease in the surface area of remaining ponds.

Outside of the short periods tiger salamanders are found in wetlands for breeding and larval development, they use upland terrestrial habitat including grasslands, shrub-steppe, and open forests (reviewed by COSEWIC, 2012). Because they generally live in underground burrows (Loredo et al., 1996; Trenham, 2001), it is challenging to identify potential corridors through direct observation. By disrupting tiger salamander dispersal events, terrestrial habitat loss as a result of converting upland habitats into agricultural areas, roads and urban centers may have profound implications on tiger salamanders. Further, because wetlands in the Okanagan are highly dynamic and fluctuate in their ability to support tiger salamander breeding, connectivity is required not only between currently used breeding sites but also between potential breeding sites during both wet and dry years (Baldwin et al., 2006). Currently in the Okanagan, tiger salamander range is naturally constrained to low elevation wetlands in the valley bottom with considerable urban development reducing available habitat (Figure 3.1). There is clear need to evaluate if and where connectivity exists across terrestrial habitat that can facilitate tiger salamander dispersal in this region.

Understanding how the landscape facilitates movement between aquatic breeding sites and more broadly, maintains gene flow across the landscape, is necessary for tiger salamander conservation and recovery efforts. However, in the Okanagan, efforts have thus far focused primarily on aquatic breeding areas and the upland terrestrial habitat that immediately surrounds them. To conserve tiger salamanders in this region, it is critical to understand how wetlands are functionally connected, to plan for connectivity during times of drought, and to determine the impact of stocking wetlands with predatory fish on connectivity. Specific objectives of this thesis chapter are four-fold:

1) To identify if there is connectivity between documented tiger salamander breeding wetlands,
2) To identify physical connections between all wetlands on the Okanagan Valley that potentially facilitate tiger salamander dispersal,
3) To explore how connectivity changes in dry versus wet years, and,
4) To identify the impact of stocking permanent wetlands with predatory fish on connectivity.

3.2 Methods

3.2.1 Study area

Two focus areas were used in this analysis (Figure 3.1). First, a landscape-level connectivity assessment was completed for the South and Central Okanagan Regional Districts (outlined in grey, Figure 3.1). Second, a focus area bounded by existing tiger salamander breeding sites in the low elevation regions of the South Okanagan (outlined in red, Figure 3.1) was used to explore specific connectivity scenarios. Tiger salamander breeding site data were obtained from the Forests, Lands and Natural Resource Operations of British Columbia (Dyer, O., BC FLNRO, pers. comm. 2016). Because of data sharing limitations, tiger salamander breeding sites on First Nations Reserves are not included. Therefore, breeding sites may be under-represented in this study.

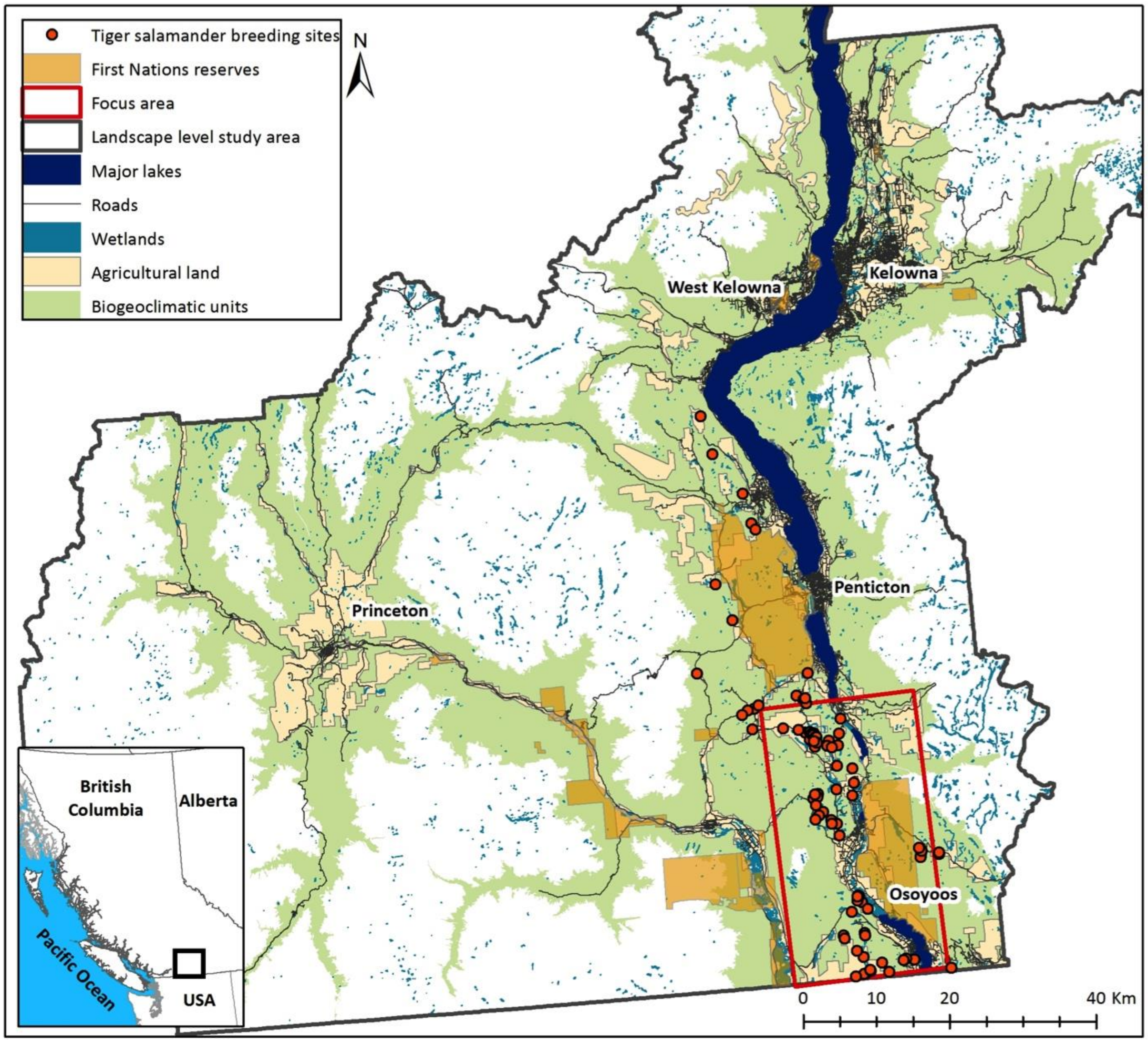

Figure 3.1 Tiger salamander study area including the spatial arrangement of wetlands and tiger salamander breeding sites. The main map panel shows major land cover classes. Highlighted Biogeoclimatic units used by tiger salamanders include Bunchgrass, Interior-Douglas-Fir, Interior-Cedar-Hemlock, and Ponderosa Pine. Biogeoclimatic units that are not known to support tiger salamanders are not included. The lower left panel shows the position of the study area in British Columbia, Canada. Cartography by C. Allen. Data sources: BC Geographic Warehouse, BC Ministry of Forests Lands and Natural Resource Operations, RDCO/Ecoscape Environmental Consultants Ltd., The Agricultural Land Commission, and Geogratis. Map compiled in ESRI ArcMAP 10.2.

3.2.2 Description of the IBM

The individual-based model described here aims to identify where connectivity exists across the Okanagan Valley for tiger salamanders. This is accomplished by simulating tiger salamanders emerging from wetlands and wandering across the Okanagan Valley following prescriptive movement rules. The model was created in the Repast Simphony programming environment (North et al., 2013) and is composed of two basic entities: a spatial landscape and tiger salamander agents. A complete description of the model following the Objectives, Design concepts and Details (ODD) protocol is included in Appendix C.

3.2.2.1 Representation of space and time

A spatial environment creates a space for agents to interact with their landscape. A discrete grid (50 x 50 m cell size) divides the landscape into a series of grid cells. Each grid cell has the following attributes: a spatial coordinate, slope (in degrees), and the presence/absence of roads, major lakes, and wetlands. Further, spatial data layers were collected from various sources (summarized in Appendix A) and converted to ASCII text files with ArcGIS 10.2. Each ASCII text file was then read in the programming environment and its values assigned to their corresponding grid cell. In addition to a spatial grid, a continuous space is used to calculate distances and directions between agents and landscape features. The landscape is static and shows no diurnal or seasonal variation. Time is abstracted to a series of time-steps, which are used to track the current state of the model. Each time-step has no equivalent real-world value.

3.2.2.2 Agents

Tiger salamander movements are governed by a pseudo-correlated random walk where their current direction of travel is +/- 45 degrees from their previous direction of travel. Each time step, an agent will move one grid cell (50 m) following the direction of travel. Movement is not biased by the salamander's local environment. Instead, when an agent encounters a barrier to movement such as roads or steep areas, there is a probability of 'dying' as a result of that barrier.

When an agent is instantiated, the following variables are initialized: a location on the grid and in the continuous space, a directional heading of travel, and a maximum dispersal distance from their wetland of emergence. The salamander's initial location is a grid cell containing a wetland and is assigned at the start of a simulation. Details on how the initial location is determined are included in "Running the model, outputs and scenarios" below. The directional heading of travel is calculated by drawing a random number between 0 and 360 inclusive. To determine the maximum dispersal distance for each individual agent, a random number is drawn from a Pareto power distribution where u is a randomly generated value between 0 and 1:

$$Maximum\ dispersal\ distance = \frac{400}{(1-u)^{\frac{1}{1.83}}}$$

8000 m was set as a maximum possible dispersal distance (Smith and Green, 2005), although because a power distribution was used, few agents will travel that far.

There were several assumptions used to derive the maximum dispersal distance equation. First, the probability of moving a distance from the initial wetland was described with an inverse power function. By a power relationship, a large number of individuals remain in proximity to a wetland and only a small proportion of dispersers travel long distances. This trend has repeatedly been observed in amphibian populations (see review by: Smith and Green, 2005). The exponent of the maximum dispersal distance function was calculated based on previously published literature of tiger salamander dispersal. Searcy et al. (2013) estimate the Euclidean distance travelled by 50%, 90%, and 95% of tiger salamanders averaged across ponds and years to be 556, 1486, and 1849 m respectively. A scatter plot was prepared with the values obtained from Searcy et al. (2013) and fitted with a power law curve (included in Appendix C). The exponent from this relationship was then used in the maximum dispersal distance function. Finally, to prevent the distribution of tiger salamander agents from dropping too quickly, the minimum distance of travel was set to 400 m. This is consistent with literature that has documented the density of juvenile tiger salamanders to initially increase with distance from the wetland before dropping off (Searcy et al., 2013; Trenham and Shaffer, 2005).

In addition to the above described instance variables, an integer variable called *toRemove* is used to store the current state of the agent. When an agent dies during a time step or moves the maximum dispersal distance, *toRemove* is set from 0 to 1.

Figure 3.2 summarizes model flow and the agent movement algorithm. At the beginning of each time step, the model first determines if the simulation is over; and second, if the simulation is not over, if the current agent should be removed from the simulation. If simulation-stopping conditions (described in “running the model, outputs and scenarios”) are not met and the agent was not removed, the agent proceeds through a two-stage movement algorithm that allows tiger salamander agents to disperse through their environment: (1) their directional heading is randomly deflected plus or minus 45 degrees, (2) the agent moves 1 grid cell following its new directional heading. If its new location is on a road, there is a 30% change of dying as a result of that road. If a randomly generated number between 1 and 100 is less than 30, *toRemove* is set to 1 marking the agent for removal during the next time step. Also, if the agent is on a steep slope (greater than 40 degrees) or a large lake, the agent dies and is marked for removal. An agent, therefore, can be removed from a simulation by two mechanisms: either moving the maximum dispersal distance assigned to that agent during instantiation, or, encountering a movement barrier. These movement rules were determined through literature and expert opinion (summarized in Table 3.1 and described in detail in Appendix C).

Table 3.1. Tiger salamander movement characteristics

Movement characteristic	Description	References
Random initial direction of emergence from wetland	Dispersing individuals have limited ability to sense terrestrial habitat. Initial direction of emergence therefore not correlated with landscape features.	(Jenkins et al., 2006; Nowakowski et al., 2013; Rothermel, 2004; Semlitsch, 2008; Timm et al., 2007)
Linear trajectory of travel	Juvenile amphibians observed using a linear trajectory of travel during wetland emergence. Correlated random walks and diffusion models proposed in literature as good methods of simulating juvenile dispersal.	(Pittman and Semlitsch, 2013; Pittman et al., 2014; Smith and Green, 2005)
Maximum dispersal distance	In the following, the maximum dispersal distance follows a power law distribution and is based off (Searcy et al., 2013)	(Searcy et al., 2013; Smith and Green, 2005)

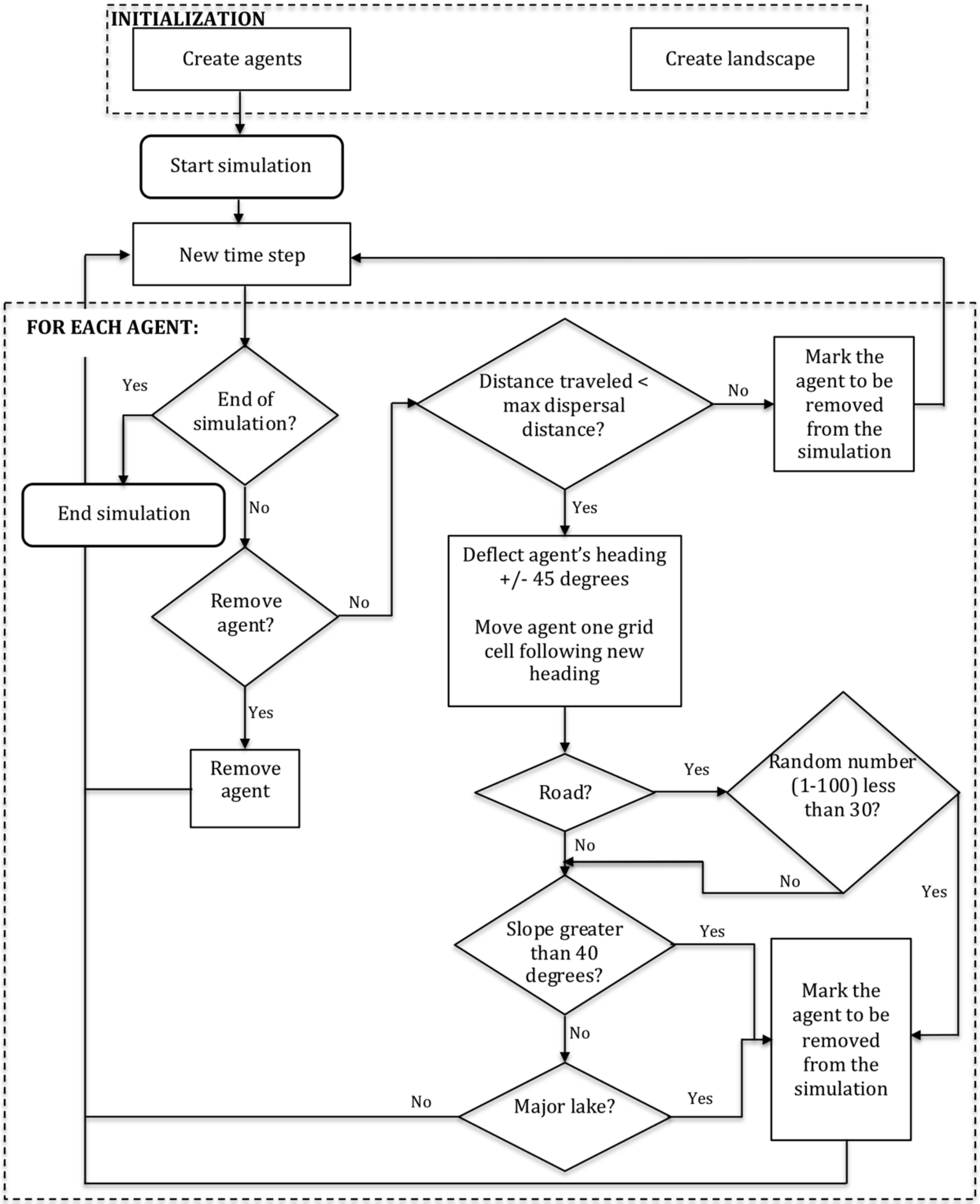

Figure 3.2 Flow chart for the tiger salamander movement model. End of simulation conditions are met when there are either no agents remaining in the simulation or 800 time steps have elapsed.

3.2.2.3 Running the model, outputs and scenarios

At the beginning of a simulation, a list is created that stores every grid cell on the landscape containing a wetland. One simulation is then run for each wetland grid cell. Note that only wetlands within biogeoclimatic zones that support tiger salamanders were included. These are: Bunchgrass, Interior-Douglas-Fir, Interior-Cedar-Hemlock, and Ponderosa Pine (Sarell, 2004). For each simulation, 100 tiger salamander agents are created and placed on a grid cell containing a wetland. Each agent will then disperse following the movement algorithm illustrated in Figure 3.2. Every time an agent moves, its new x- and y-coordinate is recorded. This movement sequence is repeated until either all of the agents have been removed from the simulation, or, a maximum of 800 time steps have elapsed. A maximum of 800 time steps was used for implementation processes only; across many simulations (>50000) no agent was able to move for 800 time steps. After the model terminates, the number of times a tiger salamander agent used each pixel on the landscape across simulations is aggregated into a single map and outputted into ArcGIS 10.2. To identify regions that contribute to connectivity, the relative frequency of use for movement (number of times each pixel was used for movement by agents/ the number of times the most used pixel was crossed) was calculated for each output layer.

A series of scenarios were used to evaluate each research objective. Modifications were made to the model for each scenario as follows:

Connectivity between known tiger salamander breeding sites:

100 agents were created and placed on a known breeding wetland (known breeding wetlands are shown in Figure 3.1). The tiger salamander agents then disperse from their initial location by following the movement algorithm (Figure 3.2). After a simulation ends, the model will re-initiate at a new tiger salamander breeding site. This is repeated iteratively through all breeding sites on the landscape.

Baseline landscape-level connectivity assessment:

To explore potential connectivity for tiger salamanders given ideal landscape conditions, the model was run from every documented wetland in the South and Central Okanagan Regional Districts (Figure 3.1 – grey outline).

Change in connectivity with variable wetland inundation:

To explore connectivity during a simulated drought year, the spatial extent was limited to low-elevation wetlands that encapsulate most known tiger salamander breeding sites (Figure 3.1 – red outline). Previous work has shown that seasonally inundated wetlands are prone to a shorter hydroperiod or may even disappear completely during extended periods of drought (Coelho, 2015); which can prevent tiger salamanders from successfully breeding and metamorphosing. For this scenario, each wetland was assigned a ‘risk of drying’. The risk of drying was determined by importing a .kmz file of wetlands into Google Earth Pro (Google Earth Pro, 2016). For each wetland in the .kmz file, I manually searched through available satellite images for that wetland over the period 2004 - 2015 and determined the wetland’s risk of drying. Risks of drying were classified as one of three easily identifiable groups (Figure 3.3): always contains water (classified as low risk of drying), sometimes contains water (classified as moderate risk of drying), and never contains water (classified as high risk of drying). To identify how connectivity changes in wet versus dry years, dispersal was simulated from wetlands with: (1) only a low risk of drying; (2) moderate and low risk of drying; and (3) low-high risk of drying. Results from these three scenarios were then compared.

Impact of stocking permanent wetlands with predatory fish:

A record of lakes currently stocked with predatory fish in the focus area (red rectangle – Figure 3.1) was retrieved from www.gofishbc.com. Because stocked lakes impact permanent water bodies, I used only wetlands previously identified as having a low risk of drying (Figure 3.3) for this analysis however with stocked wetlands removed.

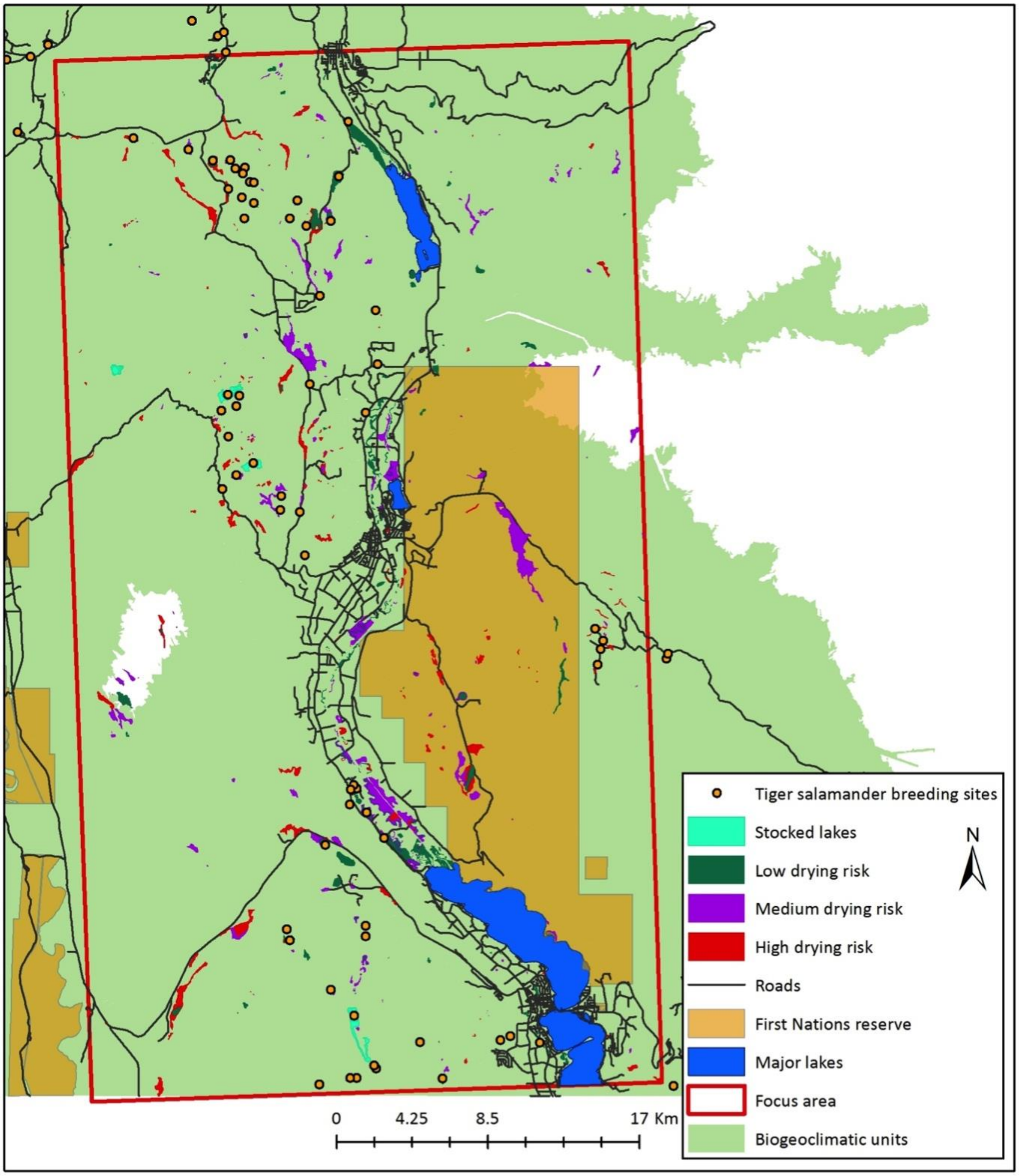

Figure 3.3 Wetland risk of drying**.** The risk of drying for each wetland was determined by visual interpretation of Google Earth Pro satellite imagery for the years 2004-2015. Wetlands that were inundated in all imagery were classified as ‘low drying risk’. Wetlands that were sometimes inundated were classified as ‘medium drying risk’, and wetlands that were never inundated were classified as ‘high drying risk’. Cartography by C. Allen. Data sources: RDCO/Ecoscape Environmental Consultants Ltd., BC Ministry of Forests, Lands and Natural Resource Operations, BC Geographic Warehouse. Map compiled in ESRI ArcMAP 10.2.

3.2.2.4 Validation and sensitivity analysis

Local Tiger Salamander experts validated that the movement rules and resulting maps were realistic and consistent with how tiger salamanders are known to interact with their landscape (Dyer, O., BC FLNRO, pers. comm. 2016), thus providing an expert validation of the landscape level results. There was no movement or genetic data available to validate individual-level movement patterns. Therefore, an extensive parameter search was run to show how assumptions used in the movement rules influence results (Appendix C).

3.3 Results

Simulations that started tiger salamander agents only from documented breeding sites resulted in clear connectivity gaps across the landscape (Figure 3.4). Specifically, there are five identifiable clusters: East of Osoyoos, Northeast of Osoyoos, Northwest of Osoyoos, East of Penticton, and a collection of isolated wetlands North of Penticton. Although connectivity is moderate to high within these groupings, no agents were able to disperse between clusters.

Simulations started from all known wetlands bounded by suitable biogeoclimatic zones for tiger salamanders, resulted in high connectedness across the Okanagan Valley (Figure 3.5). No connections are evident between Princeton and Osoyoos. Figure 3.4 also identifies connectivity within major cities that could promote tiger salamander movement.

When simulations were limited to wetlands classified as “low risk of drying”, there was a considerable loss in connectivity compared to the average and wet year scenarios (Figure 3.6). Also, Figure 3.6 shows complementarity between clusters of known tiger salamander breeding sites and areas that show high frequency of use for movement. Finally, by removing wetlands stocked with predatory fish from simulations, there was a pronounced loss of connectivity in two regions: Northwest of Oliver and East of Osoyoos (outlined with large black circles, Figure 3.7).

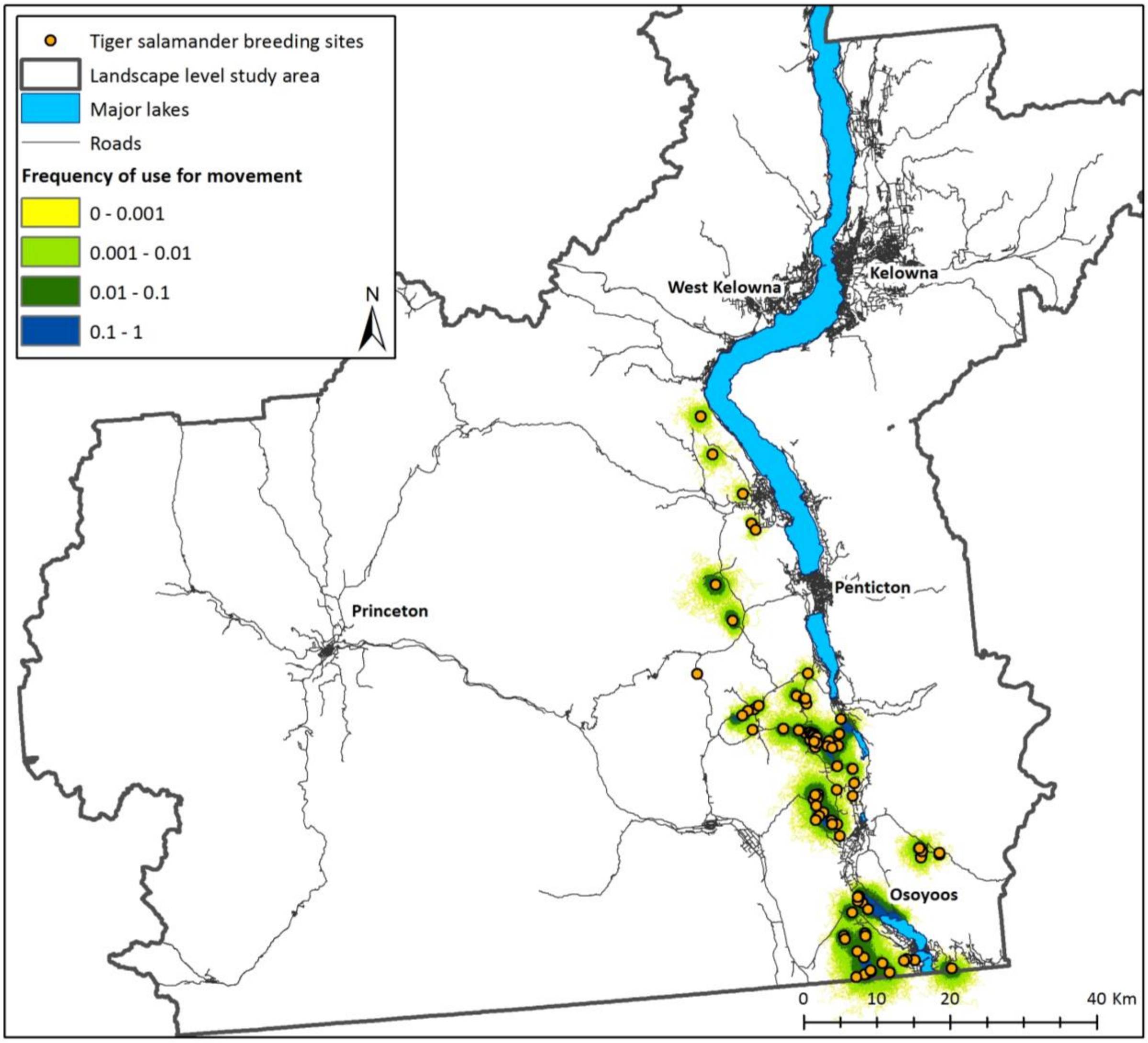

Figure 3.4 Modelled present-day frequency of use for movement by tiger salamanders, based on simulations started from known breeding wetlands. 100 agents were placed on a pixel containing a documented tiger salamander breeding pool. Agents then dispersed from the wetland following movement rules. White areas are pixels that were not used by agents. Cartography and data by C. Allen. Data sources: BC Ministry of Forests, Lands and Natural Resource Operations, BC Geographic Warehouse. Map compiled in ESRI ArcMAP 10.2.

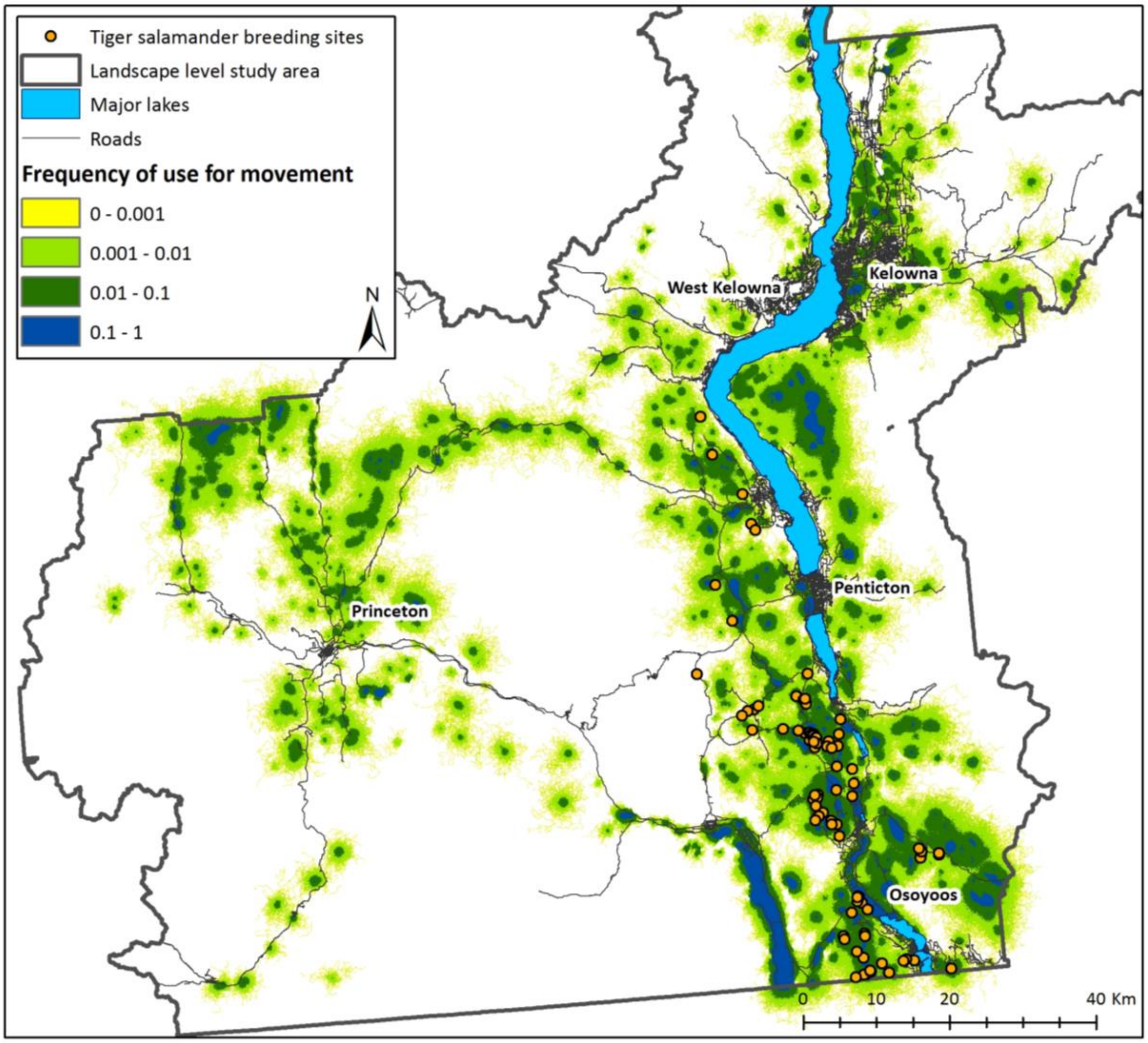

Figure 3.5 Modelled landscape-level frequency of use for movement by tiger salamanders. 100 agents were placed on a grid cell containing a wetland and then dispersed from the wetland following movement rules. The results show simulations started from each documented wetland on the landscape. White areas are pixels that were never used by an agent. Data and Cartography by C. Allen. Data sources: BC Ministry of Forests, Lands and Natural Resource Operations, BC Geographic Warehouse. Map compiled in ESRI ArcMAP 10.2

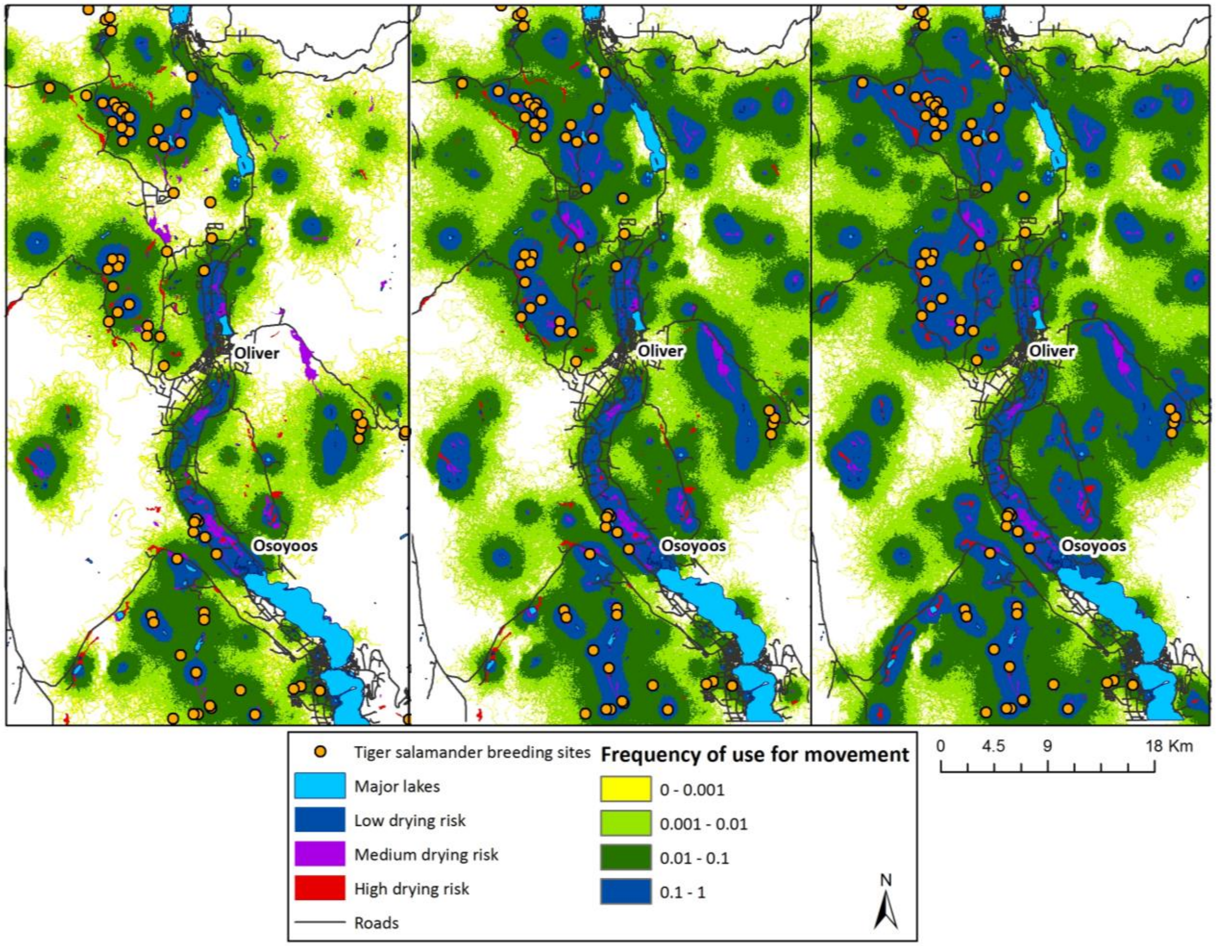

Figure 3.6 Frequency of use for movement by tiger salamanders in a simulated dry year (left panel), average year (middle panel), and wet year (right panel). The simulated dry year only considered wetlands that were identified as having a low risk of drying (always contain water); the average year considered wetlands that have a low and medium risk of drying (always or sometimes contain water); and the wet year considers all wetlands on the landscape. Data and Cartography by C. Allen. Data sources: BC Ministry of Forests, Lands and Natural Resource Operations, RDCO/Ecoscape Consultants Ltd., BC Geographic Warehouse. Map compiled in ESRI ArcMap 10.2.

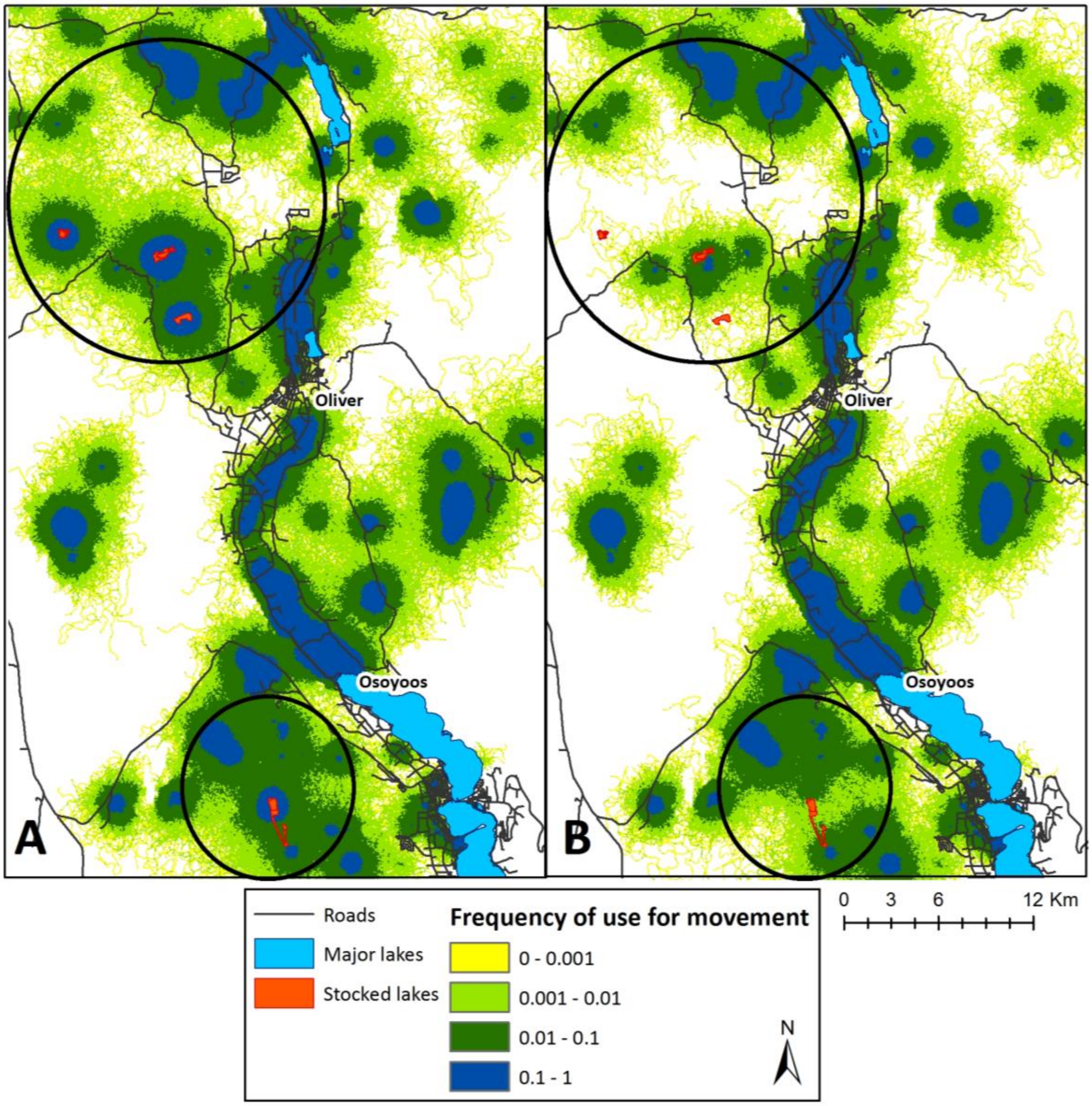

Figure 3.7. Frequency of use for movement for tiger salamanders with (A) and without (B) wetlands stocked with fish included in the simulation. Black circles show areas of difference between the two maps. Data and cartography by C. Allen. Data sources: RDCO/Ecoscape Consultants Ltd., BC Geographic Warehouse. Map compiled in ESRI ArcMAP 10.2.

3.4 Discussion

Traditionally, amphibian research has largely focused on aquatic life stages including breeding, larval development and metamorphosis, while terrestrial life stages have received considerably less attention. This is particularly true for species such as tiger salamanders that are difficult to find and track during terrestrial life stages. The work presented here aimed to increase understanding of how a landscape upholds movement between vital aquatic and terrestrial habitats, facilitates dispersal between wetlands, and more broadly, maintains connectivity across the landscape. A landscape-level connectivity assessment was used to identify all regions with the potential to facilitate dispersal between breeding sites for tiger salamanders in the Okanagan Valley. Further, I present a mechanism of exploring how connectivity dynamically changes across a mosaic of ephemeral and permanent wetlands during dry years compared to wet years and as a result of stocking fish into breeding areas. Finally, I show how existing populations of tiger salamanders are connected through dispersal.

Simulations started only from known tiger salamander breeding sites suggest that although there is good connectivity within several clusters of wetlands, there are many connectivity gaps that may prevent movement across the landscape (Figure 3.4). This is an important result because it highlights the importance of extending habitat securement past known breeding ponds. Although conservation efforts that focus on protecting known breeding areas and surrounding upland habitat are important, the results of Figure 3.4 suggest that this will not be an effective strategy for maintaining connectivity across the landscape.

The baseline connectivity assessment that considers all wetlands on the landscape (Figure 3.5) shows considerable connectivity across the study area. Since human settlement, substantial human modifications have resulted in a profound loss of wetlands in the Okanagan Valley. Further, because of a warmer and drier climate, many of the wetlands included in the landscape-level connectivity assessment have not held water for many years. Figure 3.5 may therefore be representative of how populations of tiger salamanders were historically linked in the South Okanagan rather than existing connectivity. Perhaps most interestingly, Figure 3.5 shows a clear lack of connectivity between Osoyoos and Princeton. This may provide insight into why there are no verified records of tiger salamanders in the Princeton region despite having suitable habitat (Dyer, O., BC FLNRO, pers. comm. 2016).

Exploring tiger salamander dispersal in a simulated dry year and normal year resulted in a distinctly different connectivity map compared to a simulated wet year (Figure 3.6). What is most striking in the dry year map is the complementarity between clusters of known breeding sites and areas that show good connectivity. Presumably, periods of drought can effectively isolate tiger salamanders into small clusters across the landscape. Then, during sporadic wet years, critical intermittent wetlands may become inundated and facilitate gene flow between these clusters. This clearly illustrates the importance of considering both which permanent wetlands are necessary to maintain tiger salamander populations during extended dry periods along with the intermittent seasonal wetlands that permit gene flow during wet periods.

Within the Okanagan Valley, there is widespread introduction of sport fish into permanent wetlands. Figure 3.6 shows a series of stocked wetlands have effectively isolated two populations of tiger salamanders into disjunct groups (large circle – Figure 3.7). This can also be observed south of Osoyoos as well, however it is less pronounced there (little circle – Figure 3.7). Prior to stocking, these few permanent wetlands may have maintained connectivity between populations of tiger salamanders during dry years. After stocking, the results presented here suggest this connectivity was effectively lost. Although there are no new legal stocks proposed within tiger salamander range at this time, illegal stocking of sport fish into tiger salamander breeding areas remains a pervasive concern (Southern Interior Reptile and Amphibian Recovery Team, 2008). COSEWIC (2012) predicts that all wetlands that can support sport fishing either already have or will eventually have predatory fish. The results shown in Figure 3.7 speak to the importance of carefully considering how such stocking will impact tiger salamander connectivity, particularly during periods of droughts when these permanent water bodies are essential for population viability.

Although methods such as LCP modeling have been applied to identify where connectivity exists between wetlands (for example, Wang, Savage, and Shaffer, 2009), an individual-based modeling approach was advantageous for this study because I was able to represent the movement of hundreds of juvenile amphibians emerging from a wetland and dispersing into the terrestrial habitat by following simple movement rules. As a result of small variations across agents such as the initial direction of movement and maximum dispersal distance, each individual uniquely experienced their landscape. Consequently, maps that show the frequency with which each pixel on the landscape was used reflect dispersal paths that one might expect to observe in the natural system. This not only shows successful dispersal routes between wetlands, but also unsuccessful routes. For conservation efforts that aim to reduce amphibian mortality due to roads and urban areas, it may be advantageous to know where such unsuccessful dispersal routes exist on the landscape that can be targeted for efforts to make them more permeable. Moreover, models such as the one presented here that also show sub-optimal corridors could be useful when it is not feasible to preserve optimal routes due to socio-economic or political restrictions on land use.

In addition to individual-based models, spatial networks provide an intuitive framework to explore connectivity in amphibian populations as wetlands are already organized into discrete habitat patches (nodes) connected by rare dispersal events (links; see reviews by Urban and Keitt, 2001; Galpern et al., 2011). Analyzing the topology of a wetland network provides a mechanism of quantifying the impact of habitat loss and fragmentation on the overarching network structure. Further, with a network approach it is relatively easy to identify clusters of interlinked wetlands that are effectively a single ecological unit (Peterman et al., 2016). In the IBM approach used here, it is possible to qualitatively infer where clusters occur across the landscape; however, it is difficult to conclusively show that identified clusters are in fact meaningful. An interesting line of future work could link an IBM of amphibian movement, such as the one presented here, with a spatial network. For example, Lookingbill et al. (2010) developed an IBM to simulate Delmarva fox squirrel (*Sciurus niger cinereus)* dispersal across a fragmented landscape. Graph theory was then used to assess the results of this model where the links (dispersal) between nodes (patches) were weighted by the percent of agents that successfully dispersed between patches. The methodology presented by Lookingbill et al. (2010) is highly applicable to wetlands linked by dispersing individuals and presents an interesting future research direction.

Because the model presented here was not validated against empirical field data for individual salamander movement, it carries several assumptions. First, and most importantly, these results depend largely on equations that set the maximum distance simulated tiger salamanders can disperse. Although I obtained estimates of tiger salamander dispersal buffers from literature, in doing so I assumed that these data are representative of tiger salamanders in the Okanagan Valley. It is possible that Okanagan tiger salamanders show regional variation in dispersal characteristics that we were unable to capture in this model. As a result, this modeling approach risks over- or under-estimating connectivity between wetlands. Further, I assumed amphibians dispersing from wetlands orientate randomly at the pond edge, move without goal bias, and their dispersal densities fall away from a wetland following a power law distribution. Indeed these assumptions were founded in literature; however, there is insufficient local field data to confirm these movement characteristics hold for tiger salamanders in the Okanagan region.

To identify the risk of drying for each wetland in the focus area, I relied exclusively on visual interpretation of Google Earth imagery without field validation. Therefore, it is possible that errors in this process impacted the results presented. Further, all wetlands in the study area were considered equal; characteristics such as pH, temperature, vegetation, etcetera were not included in this analysis. The results presented here therefore likely over represent suitable wetlands and subsequently the connectivity between then.

3.5 Summary

The results of this work expand on the 'pond-as-patches' approach to wetland conservation by highlighting the importance of a landscape that is functionally connected as a network of wetlands and terrestrial habitats. The 'pond-as-patches' archetype to amphibian conservation may overlook terrestrial habitats that make critical contributions to local and regional population dynamics. Provisioning habitat corridors, stepping-stones, and other landscape features that promote connectivity between wetlands can ultimately create wetland complexes that are more resilient to local extinction events and changing climates. Thus, groups of functionally connected ponds and their intervening terrestrial habitat are probably a more meaningful unit of management than single wetlands. The model presented here may guide users on where potential corridors between connected breeding pools exist to target for conservation efforts. Although managing landscapes for wetland quality and neighbouring terrestrial habitats is an important component of amphibian conservation, we argue that conservation planning should strive to extend past individual wetlands and more broadly consider how the environment facilitates landscape-level processes such as dispersal and gene flow.

4 Chapter: Discussion

The objective of this chapter is to provide an overarching discussion on the advantages and limitations of an IBM approach for estimating landscape connectivity, to compare the results of the tiger salamander and bighorn sheep connectivity analyses to existing connectivity work in this region, and finally to discuss management implications of the results presented in this thesis along with future research goals.

4.1 Discussion of the advantages and limitations of an IBM approach to landscape connectivity

Individual-based models are an excellent tool for linking animal and landscape interactions to predict how a species might move throughout their landscape. Coulon et al., (2015) demonstrate that an IBM approach provides a significantly better model of connectivity compared to other common methods including Euclidean distance, LCP, and Circuitscape. Further, Aben et al., (2014) have suggested that IBM's can stream-line land-use planning by allowing researchers and decision makers to assess the functionality of proposed corridors and stepping-stones. For example, with an IBM it is possible to directly estimate the frequency with which individuals on the landscape will use a proposed corridor or to explore how different management scenarios will impact connectivity. Despite the potential advantages of this approach, there are few examples of IBM's applied to estimate landscape connectivity and identify corridors. Here I discuss the implementation differences of an IBM compared to a LCP analysis, the advantages of an IBM, and the limitations of this approach that have perhaps reduced its uptake in the field of landscape connectivity.

4.1.1 An IBM compared to LCP analysis

To demonstrate how an IBM compares to LCP methods in implementation and results, I replicated the movement rules used to create the bighorn sheep IBM (Chapter 2) in a LCP analysis of bighorn connectivity (methods and results of this analysis are included in Appendix D). Because of model implementation differences inherent in the IBM and LCP approach used, the models do not have a one-to-one correspondence and it proved difficult to compare the results of these methods as originally intended. Therefore, this analysis serves as a basis for a general discussion of the differences of both approaches and is supplementary to the work presented in Chapter 2.

The major implementation difference between the bighorn sheep IBM compared to the LCP was simply the time required to build each model. It can take many months to a year to conceptualize, implement, and run an IBM whereas a LCP model can be completed in a single week to a few months. Despite the time required to use an IBM approach, there are many advantages to this method. For example, LCP approaches require researchers to delineate meaningful start-destination locations to connect whereas the IBM presented in Chapter 2 did not (but see Huber et al., 2012). Although there are many cases where researchers may want to use start-destination locations, it will force corridors between these locations, which might artificially connect portions of the landscape that are in actuality not connected. The IBM approach used in Chapter 2 started agents from any potential habitat. Thus, the IBM permitted corridors to emerge based on a species' potential use of the landscape rather than prescribing locations that a corridor should connect. Further, the bighorn sheep model enabled agents to wander into currently unoccupied, yet suitable habitat. This is an important difference from the LCP model because this illustrates the potential for bighorn sheep to move beyond current ranges and identifies likely places where they might do so. Maintaining potential corridors between currently unoccupied, good habitat patches could facilitate migration in response to changing habitat as a consequence of climate change or human activity. These differences are clearly illustrated in the comparison included in Appendix D. Because the LCP approach required start-destination locations and identified corridors between them, corridors cross major urban areas and roads, which are unlikely to be used by bighorn sheep. In contrast, the IBM identified circuitous routes or simply did not identify any route around urban areas. Further, the IBM shows regions that could potentially facilitate connectivity into currently unoccupied habitat.

A second distinction I identified by implementing both the IBM and LCP was the relative difference in creating rules for an IBM versus a weighting scheme for a resistance layer. Although producing a resistance layer required for LCP and Circuitscape is not necessarily a drawback to these approaches, I found it considerably easier to identify movement rules that mimic behaviours identified in literature or through expert opinion than determining the relative 'cost' of moving across different land covers.

4.1.2 Advantages and limitations of an IBM to estimate landscape connectivity

By linking individual-scale movement rules to landscape-scale outcomes, the individual-based modelling approach used throughout this thesis presents many advantages to land use decision-making. First, an IBM allows researchers to evaluate if physical linkages exist on the landscape, and if not, where major connectivity gaps are. For example, with the bighorn sheep model, I was able to start simulations from known occurrence points on the real landscape (Figure 2.3) to identify if connectivity exists between populations. Similarly, with the tiger salamander model I started simulations from breeding pools to determine if managing the landscape for only known breeding wetlands will sufficiently maintain connectivity (Figure 3.4). Although it is possible, and probably more accurate, to use genetic indices to determine whether connectivity exists between subpopulations (Hepenstrick et al., 2012; Manel et al., 2003), many conservation efforts face a paucity of resources that limits the accessibility of genetic analyses. Some researchers have applied LCP to explore connectivity gaps by incorporating a maximum cumulative cost distance such that only corridors under a threshold cumulative cost are suitable for animal movement and connect features across the landscape (for example, Epps et al., 2007). Application of LCP without considering the accumulated-cost of a least cost path may result in routes that do not reflect the ecological costs of movement across a resistance layer (Etherington and Holland, 2013). While it may be useful to identify corridors through poor habitat that could be made more useable with restoration work, LCP risks overestimating connectivity between sub-populations by showing routes through poor habitat that may be unlikely to facilitate movement. Circuit theory on the other hand, better simulates landscapes from the perspective of an individual and has proven useful for exploring connectivity questions such as edge-crossing tendencies (St-Louis et al., 2014). An IBM, such as the one for bighorn sheep presented here, could provide a reasonable indication of whether there is existing connectivity between subpopulations when a sufficient understanding of animal movement behavior is available to validate and parameterize model assumptions.

A second major advantage of the IBM approach presented here over the more traditional least cost path approach is that an IBM simulates individuals as boundedly rational (i.e., responding to local information cues without having perfect knowledge of the whole system). It is widely acknowledged that connectivity is a process that emerges as the result of how a species perceives and reacts to its landscape along with the structural composition and configuration of landscape elements (Tischendorf and Fahrig, 2000b; Walpole et al., 2012). Good connectivity indices therefore should realistically restrict the perceptual range of simulated individuals. By simulating a random walk, circuit theory also approximates individuals as boundedly rational and identifies corridors based on a limited perception of the landscape. In contrast, an assumption implicit with LCP analysis is that animals are capable of perceiving their entire landscape and identifying optimal routes between pre-determined locations. Although it is reasonable to assume animals have a general understanding of their landscape including the locations of good habitat, it is unlikely an individual is capable of discerning the most optimal route between these locations. In our approach, agent movement was informed by local landscape variables. By realistically limiting the amount of information agents use to make movement decisions, an IBM may capture non-optimal dispersal behavior ubiquitous in natural systems.

A third advantage of an IBM is that the approach allows researchers to move away from the patch-corridor archetype to conservation towards a more nuanced representation of habitat quality on a landscape. Traditional approaches to connectivity analyses distinguish between core habitat areas and corridors. Conversely, the IBM presented in this study highlights how a species might make broad use of a landscape for dispersal or migration without differentiating between habitat areas and corridors. It is important to note this type of analysis cannot replace a habitat suitability model, which considers ecological requirements of species, climate envelopes, and limiting factors to predict the likelihood of species occurrences across a landscape (Hirzel and Le Lay, 2008). However, this model provides additional insight into how a species might use a landscape over deterministic, single-best-route connectivity analyses such as least cost path (but see Cushman et al., 2009). Further, other features of a landscape such as stepping-stones have the propensity to facilitate dispersal between larger habitat patches. The individual-based model presented here identified such features of a landscape in addition to corridors.

Finally, the connectivity approach outlined here uniquely highlights all components of a landscape that contribute to connectivity, not simply the most optimal corridors or paths of least resistance. On-the-ground conservation work tends to be a balancing act between where and when opportunities for conservation present themselves alongside where efforts are most needed. Land use managers could use the methodology described in this thesis to identify where corridors fit with other conservation priorities for a particular landscape. Moreover, most conservation projects tend to have limited resources to restore and improve connectivity. In this thesis I have shown how an IBM can be manipulated to explore the impact of management scenarios on landscape connectivity before investing in expensive on-the-ground work. Thus researchers can apply an IBM approach to move from descriptive towards predictive models of landscape connectivity. With rapid and considerable habitat fragmentation as a result of human land-use and climate changes, it is critical that decision support tools guide conservation work in the most effective direction to meet the needs of species.

Despite the potential advantages of an individual-based approach, there are very few examples of IBM’s used to explore connectivity throughout the literature and even fewer examples of IBM’s applied to land use management. A major limiting factor for use of an IBM is the time required to build a computer model. For on-the-ground efforts, which often face a paucity of funding and time, it may not be feasible to invest in developing an IBM. Further, to create an IBM requires researchers to have some understanding of computer programming, which further limits the accessibility of this approach. For these reasons, well-established methods such as LCP and Circuitscape may be the only options available to many researchers and land use decision makers.

4.2 Overlay of existing connectivity models to thesis results

Partners of the Complex Environmental Research Group are working to identify corridors that provide connectivity throughout the Okanagan Valley and, more broadly, from the U.S. Columbia Basin to the B.C. Interior region. Prior work provides a general assessment of landscape connectivity across the Okanagan Valley. This includes the Transboundary focus areas analysis (TCG, 2016), Biodiversity Conservation Strategy connectivity assessment (BCS, Okanagan Collaborative Conservation Program, 2014; South Okanagan Conservation Program, 2012) and the

Circuitscape connectivity skeleton (Parrott et al., manuscript in preparation – refer to chapter 1 for a brief discussion of existing connectivity work in the Okanagan region). Although the methods used in the above listed connectivity projects differed, each model applied a general-species approach where a series of assumptions were made regarding how animals move across their landscape. The work presented in Chapters 2 and 3 of this thesis provides species-specific refinement to these existing connectivity assessments. To the best of my knowledge, this is the first species-specific connectivity estimate completed in this region. An objective of this research was to compare the results of the bighorn sheep and tiger salamander analyses to existing connectivity work. Chapters 2 and 3 include a species I predicted would closely align with the general connectivity maps, the tiger salamander, along with a species that I predicted would not align well, the bighorn sheep, respectively.

There was a surprising degree of overlap in the bighorn sheep connectivity work presented in Chapter 2 and the general species connectivity maps (Figure 4.1). Perhaps most interesting, there is high complementarity between the bighorn model, transboundary assessment, and Circuitscape skeleton in the South Okanagan, particularly between Princeton and Osoyoos (Highway 3). Further, both the bighorn sheep model and Circuitscape analysis identified the same major crossing point that links the West and East side of the landscape (above and below Vasseux Lake). East of the major lakes, the Circuitscape output follows the same general trend North and parallel to Okanagan Lake as the bighorn sheep model. Despite a surprising amount of overlap, the bighorn sheep model highlighted many areas as important to connectivity that were not identified in the Circuitscape or transboundary assessments. For example, the IBM approach identified a long corridor north of West Kelowna and parallel to the Okanagan Lake. This corridor may have important implications for a small population of bighorn sheep found North of West Kelowna. Further, the IBM approach provides information on the width and length of corridors, along with highlighting other landscape elements that may contribute to connectivity such as stepping-stones that are not included in the Circuitscape or transboundary assessment.

An overlay between the tiger salamander connectivity work presented in Chapter 3, transboundary assessment, and Circuitscape skeleton shows considerably more areas of overlap than in the bighorn sheep comparison (Figure 4.2). The majority of the Circuitscape corridors overlapped moderately well or very well with the IBM results. As with the bighorn sheep work, there is high complementarity between all three approaches in the South Okanagan along a major transportation corridor between Osoyoos and Princeton (Highway 3). In the Regional District of Central Okanagan (RDCO, Figure 4.3), the tiger salamander model also highlights potential connectivity through an urban landscape. The OCCP in collaboration with the Complex Environmental Systems Lab, UBCO, are undertaking a project to establish the East Kelowna to Okanagan Mountain Park corridor (highlighted in pink – Figure 4.3). As shown in Figure 4.3, there is good overlap between this proposed corridor and the tiger salamander modeling work.

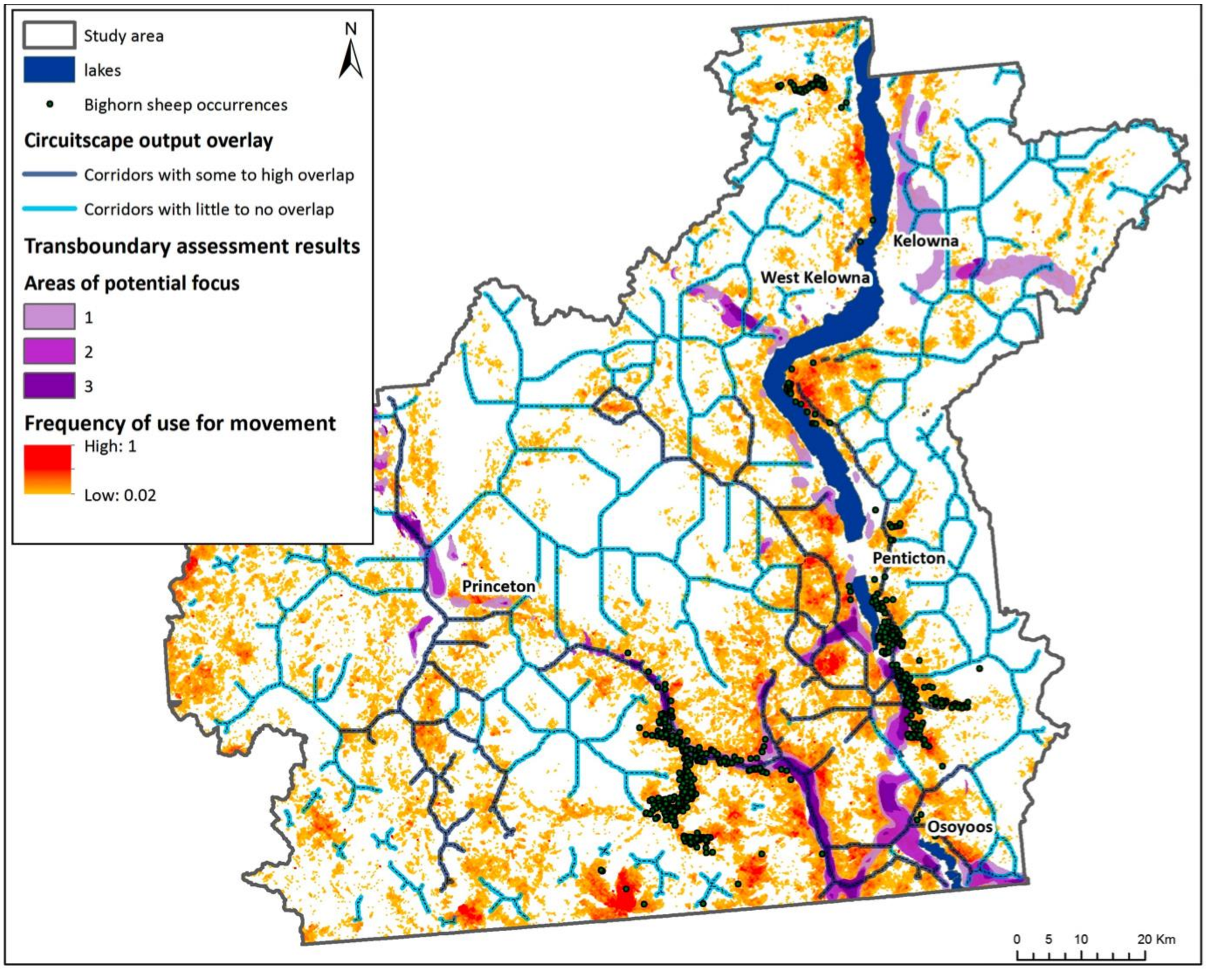

Figure 4.1 Overlay of the frequency of use for movement for bighorn sheep calculated with an IBM, Circuitscape analysis, and transboundary connectivity focus area assessment results. Potential relative frequency of movement was determined by starting bighorn sheep agents at any pixel with suitable habitat for the present day landscape. The transboundary assessment results show regions that contribute to connectivity for three species perspectives: shrub-steppe species, montane species, and a landscape integrity model identified by the BC-WA Transboundary Connectivity Group. Potential wildlife movement corridors identified by the Circuitscape analysis that had some to high overlap with the bighorn sheep output are coloured dark blue. Movement corridors with low or no overlay are coloured light blue. Data and cartography by C. Allen. Data sources: BC-WA Transboundary Connectivity Group, Complex Environmental Systems Lab, UBC, and Cardille Lab, McGill University, BC Geographic Warehouse, BC Ministry of Forests, Lands and Natural Resource Operations. Map compiled in ArcMap 10.2.

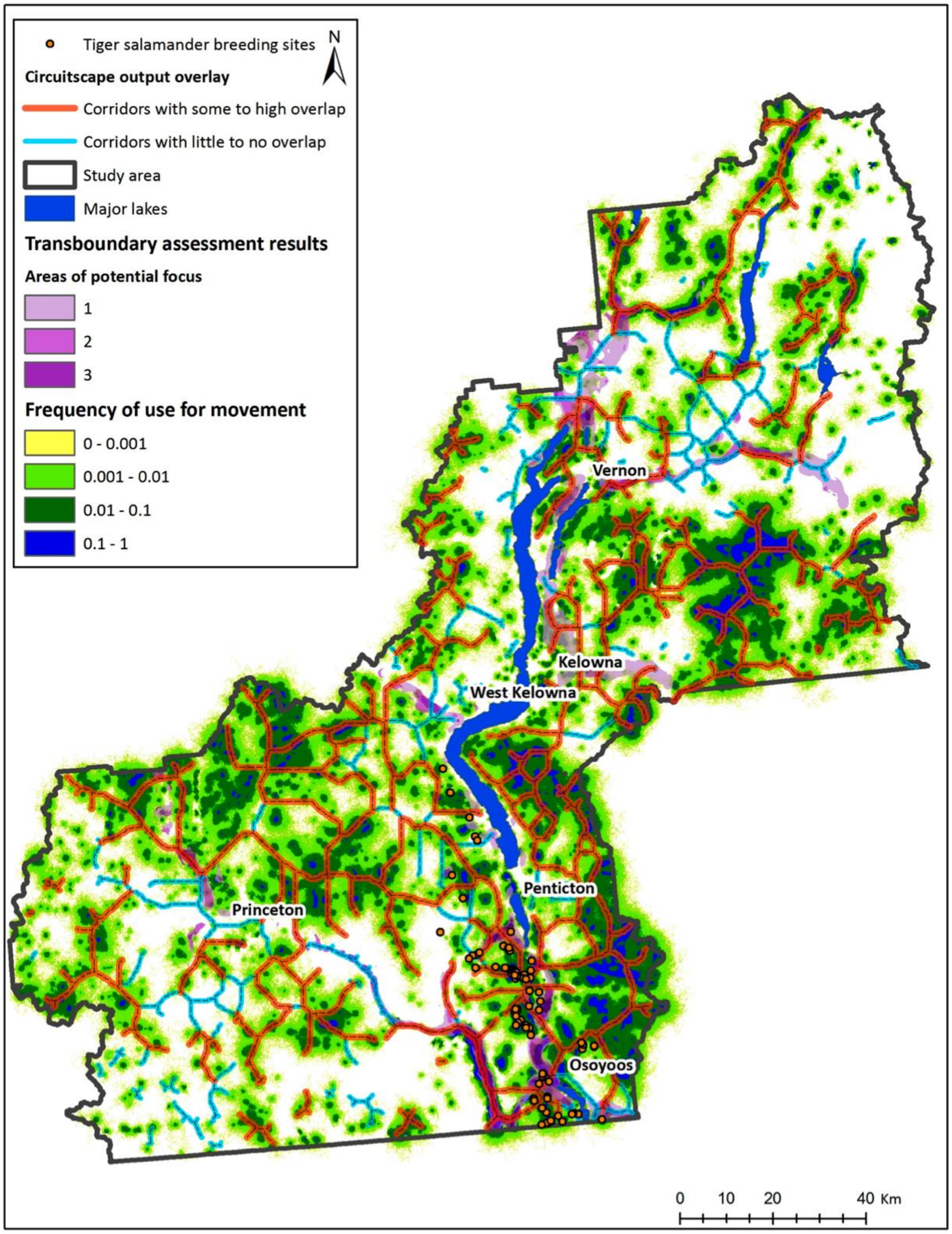

Figure 4.2 Overlay of the frequency of use for movement for tiger salamanders calculated with an IBM, Circuitscape analysis, and Transboundary Assessment Results. Potential relative frequency of movement was determined by starting tiger salamander agents at any wetland pixel. Potential wildlife movement corridors identified by the Circuitscape analysis that had some to high overlap with the tiger salamander output are coloured orange. Areas of low to no overlap are blue. Data and cartography by C. Allen. Data source: BC-WA Transboundary Connectivity Group, Complex Environmental Systems Lab, UBC, and Cardille Lab, McGill University, BC Geographic Warehouse, BC Ministry of Forests, Lands and Natural Resource Operations. Map compiled in ArcMap 10.2.

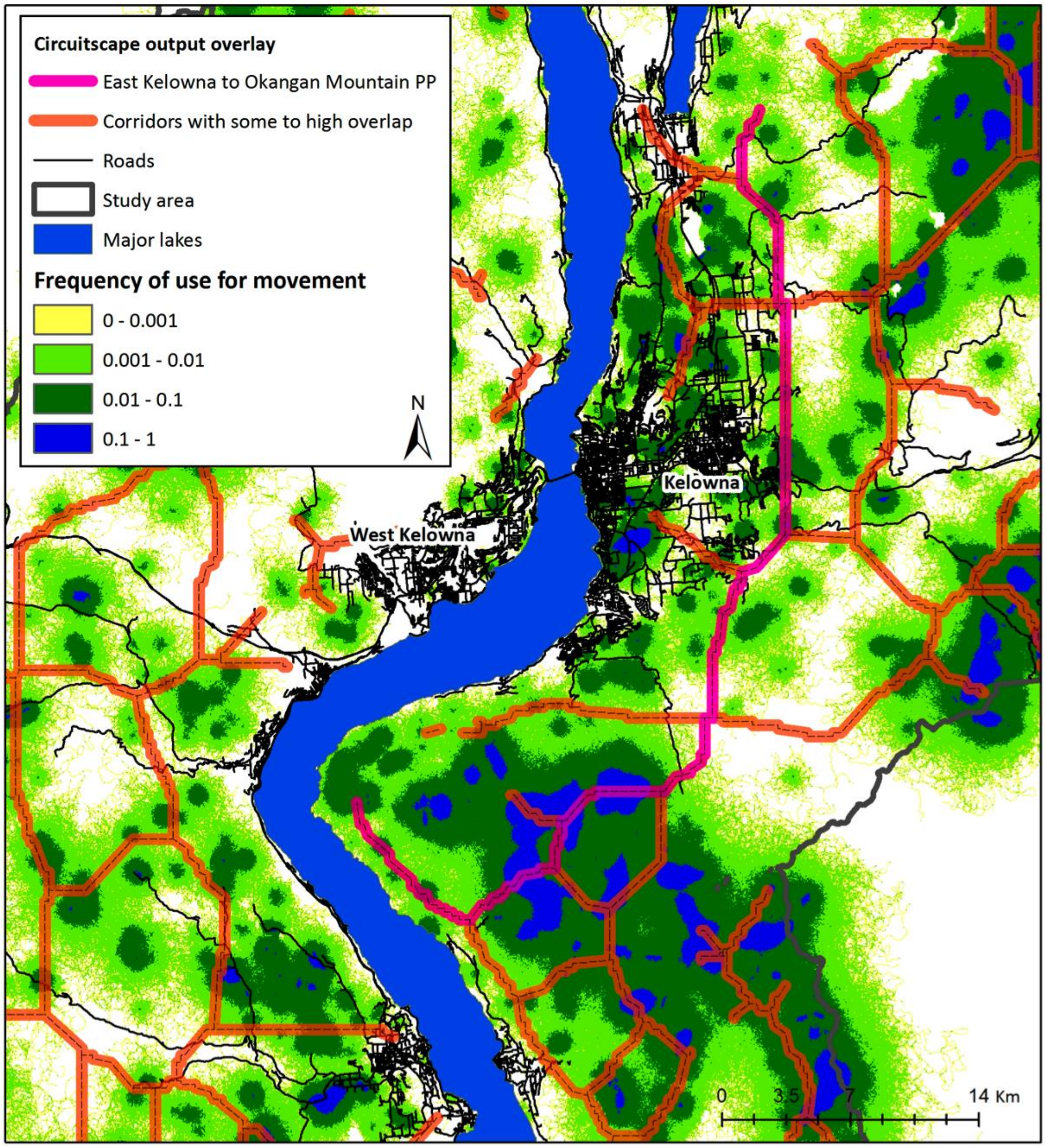

Figure 4.3 Overlay of the Circuitscape analysis and tiger salamander frequency of use for movement IBM results for the Regional District of Central Okanagan. Areas of moderate to high overlay are highlighted in orange. The East Kelowna to Okanagan Mountain Provincial Park corridor is highlighted in pink. This is a proposed corridor to preserve animal movement South to North through the Regional District. Data and Cartography by C. Allen. Data sources: Complex Environmental Systems Lab, UBC, and Cardille Lab, McGill University, BC Geographic Warehouse. Map compiled in ESRI ArcMAP 10.2.

4.2.1 Discussion of model overlay

The modeling work completed by the Biodiversity Conservation Strategy, Complex Environmental Systems Laboratory (UBCO), Washington-BC Transboundary Working Group, along with the analysis presented in this thesis, all highlight regions throughout the Okanagan Valley that promote animal movement. Although each model applied different methods with unique assumptions, it is reassuring to see areas of overlap. It is unsurprising that the tiger salamander model and Circuitscape output show many similarities. The Circuitscape output builds on the Biodiversity Conservation Strategy Connectivity maps that assigned values to each pixel on the landscape depicting how permeable that pixel is animal movement. Thus, low elevation areas in proximity to water show as contributing to connectivity whereas steep and rugged terrain is unlikely to show as important to connectivity. Although the tiger salamander model presented in Chapter 3 was based on rules specific to this species, there nonetheless are similarities between the tiger salamander movement rules and assumptions made in the general connectivity Circuitscape approach. Specific to the RDCO, a proposed corridor extending from Okanagan Provincial Park to East Kelowna shows many areas of overlap with the tiger salamander model output (highlighted in pink - Figure 4.3). Although tiger salamanders are not found as high north as Kelowna, the assumptions used in the tiger salamander model are similar to other species that breed in wetlands and disperse into their terrestrial habitat. Therefore, areas of connectivity identified with the IBM are relevant to many other species found in the RDCO. The OCCP in collaboration with the Complex Environmental Systems group at UBCO are currently working to establish this corridor through on-the-ground efforts. The results of the tiger salamander modeling work provides further evidence suggesting that the East Kelowna to Okanagan Mountain corridor is well positioned to support animal movement across the valley. Further, the tiger salamander model can complement the Circuitscape output by providing information on the potential width of this corridor along with pinch-points that cannot be discerned by exclusively using the Circuitscape output. Finally, the results of the tiger salamander work show potential connectivity through an urban environment (Figure 4.3). Although the Circuitscape output shows a handful of corridors that extend into the City of Kelowna, it is difficult to identify specific sites that are important for facilitating connectivity through the city. An approach such as the IBM presented here may provide finer-scale information on connectivity that is useful for guiding land use planning in an urban environment.

In contrast to the tiger salamander overlay, the bighorn sheep model results only had a few areas that were complementary to existing connectivity work. Further, without considering the ecology of bighorn sheep, it is easy to misinterpret these regions of overlap. For example, the bighorn sheep model, Circuitscape output and transboundary assessment all identified the transportation corridor between Osoyoos and Princeton as important to connectivity (Figure 4.1). Although this is a region of high overlap, a corridor through this region would not be useful to bighorn sheep unless it extends up from the valley bottom and into the highland areas that bighorn sheep use as habitat. Further, without exploring connectivity through a species-specific lens, many features that promote connectivity for bighorn sheep would have been completely overlooked.

In many cases, a paucity of time, data, and resources limits the availability of species-specific connectivity assessments. Further, connectivity projects often aim to preserve movement ability without particular species in mind. In such cases, a general connectivity assessment may prove useful. The results of these overlays lend support to the usefulness of general connectivity maps; however, it is important to acknowledge that such a simplistic view of a landscape will not support movement for all species in a region. The results of the bighorn sheep overlay demonstrate the importance of exercising caution when relying on general connectivity assessments. Researchers and land use practitioners should carefully evaluate the implications of proposed corridors and identify which species likely align with the model assumptions and conversely, which species will not.

4.3 Considerations for implementing landscape connectivity

Implementing connectivity in the Okanagan Valley will ultimately be a process of opportunity and compromise. Unfortunately, modelling efforts do not provide simple solutions for realizing connectivity on the landscape. Rather, developing models, such as the ones shown in this thesis, is only the first step in a much larger process of implementing landscape connectivity. Mechanisms of implementing corridors will depend on regional objectives, funding, existing and future land use, government jurisdictions, and a complex array of social, political, and economic factors. Further, ecological processes occur at scales much larger than municipal and regional land use planners will typically have jurisdiction over. A proposed habitat corridor may cross crown land, agricultural land reserves, private land, First Nations reserves, major transportation routes, or even national borders. To incorporate connectivity assessments into land use planning will therefore require collaboration across partners including academia, government, the private sector and other stakeholders who will likely have competing objectives and interests. To further complicate connectivity planning, landscapes are inherently dynamic. The spatial structure of a landscape is constantly changing as a result of human land use, climate, disturbance regimes, and the interactions between species and their landscape. To successfully implement connectivity into land use planning requires foresight into how the landscape might change and to allow opportunity for the system to adapt to these changes. Despite the array of connectivity modelling projects that have been completed, there are few examples of connectivity successfully incorporated into land use plans. In the Okanagan Valley, stakeholders are making important steps to secure habitat corridors across the landscape. As a result of the work presented in this thesis, I have identified key considerations for incorporating connectivity plans in this region and more broadly. This section is not intended to serve as a complete discussion of implementing landscape connectivity, but rather, a dialogue of key themes I identified as important. Further, these considerations are intended for a landscape with remaining natural areas to implement connectivity. For human-dominated landscapes, these considerations may not apply.

Connectivity implementation should first identify and focus on existing opportunities, not missed opportunities. There are effectively two ways to implement connectivity into land use planning: (1) identify remaining structures that contribute to connectivity and develop strategies to maintain them, and (2) identifying connectivity gaps or movement barriers and focusing resources towards making these features more permeable to animal movement (McRae et al., 2012). I argue that land use managers should first seek to take advantage of existing connections and implement measures to protect these connections into the future before looking to increase connectivity in previously fragmented regions. I argue this approach to prioritizing connectivity for two reasons: first, it is considerably easier to integrate connectivity into regional or city planning processes rather than as a post hoc addition to a landscape, particularly in areas with remaining tracks of natural vegetation; and second, without integrating existing connectivity into land use plans, it is highly likely these opportunities will disappear as land use development proceeds. After establishing existing corridors, stakeholders can then start identifying important connectivity gaps to target for restoration work. The IBM approach I used throughout this thesis highlights regions on the landscape that contribute to connectivity given existing land use conditions. As shown throughout Chapter 2 and 3, the Okanagan landscape has considerable opportunity to maintain connectivity. Although there are also regions that should be considered for restoration work as well, such as across major roads to promote bighorn sheep movement (Figure 2.5) such barriers to movement should not overshadow the need to protect existing connectivity.

I argue a second objective of connectivity implementation should be to establish multi-functional corridors with purposes that extend past simply preserving connectivity for wildlife movement. For example, preserving wetland connectivity as identified in Chapter 3 may support a suite of ecosystem services such as providing habitat for terrestrial and avian species, water quality improvement, flood abatement, and carbon management (Zedler and Kercher, 2005). Many of the areas identified as important for bighorn sheep connectivity in Chapter 2 are also important recreational areas for mountain biking, rock climbing, and hiking. Further, corridors identified with the Circuitscape work in the Okanagan Valley along with the tiger salamander modeling included in Chapter 3 cross areas important for agriculture. I argue that we should promote connectivity as a multi-functional feature on a landscape rather than trying to manage corridors exclusively for animal movement. By designing corridors as multi-functional, we can encourage the various services these landscape features already provide. Much of recent literature on connectivity paints a stark dichotomy between landscape areas dominated by human activates and areas set aside to promote animal movement. I argue that implementing connectivity requires a more nuanced representation of a landscape to identify how corridors, stepping-stones, and other features can integrate with existing land use objectives. This approach to implementing connectivity serves several purposes. First, although most ecologists accept the importance of a connected landscape, not everyone involved with land use planning will appreciate the ecological reasons to maintain connectivity. Promoting corridors as multi-functional features that provide a range of environmental, social, and economic functions may resonate with the interests and objectives of different individuals or stakeholder groups. Further, including human activities such as bird watching, hiking, and mountain biking in corridor design will engage community members in the importance of preserving natural areas for wildlife movement. By including ecologists in the land use planning processes, it is possible to identify many purposes of a wildlife corridor and subsequently to design such connectivity features to promote multiple functions.

Finally, researchers and land use planners should seek to shift away from the single-corridor archetype to connectivity and move towards building a resilient landscape with opportunity to adapt and respond to a changing environment. Resilience is most commonly applied to describe the capacity of a system to absorb disturbance (Folke, 2006). My aim here is not to provide a complete review of literature surrounding resilience, but to start a dialog on the importance of applying a complexity framework to the field of connectivity that promotes landscape resilience. Landscapes are inherently uncertain. Natural stochastic events such as wildfire, floods, droughts and invasive species along with human land use transformations can dynamically change a landscape. The impact of natural and human-caused land use transformations are further exasperated by a rapidly changing climate. A corridor approach to implementing landscape connectivity may not be resilient to such changes. Instead, I argue that researchers should adapt an approach that promotes opportunity for restructure and adaptation. For example, one strategy to increase landscape resilience is by incorporating redundancy, or maintaining multiple opportunities to reach a specific outcome, into corridor design. Perhaps the simplest method of planning for redundancy is by maintaining many ‘routes’ that promote landscape connectivity. However, redundancy can also be conceptualized as managing the matrix between areas of good habitat to promote animal movement. Second, connectivity strategies should seek to incorporate heterogeneity wherever possible. The constituents of a landscape are inherently heterogeneous. Species differ markedly in behavior, movement ability location, history, and their ability to adapt. Moreover, a landscape over which species interact will vary in soil composition, water availability, terrain, and temperature. I suggest that we promote such heterogeneity into implementing landscape connectivity. Land use planners can vary the design of corridors, stepping-stones, and other connectivity features, to further promote heterogeneity. By considering how connectivity projects will promote landscape resilience, researchers and land use planners will increase the likelihood that their efforts will promote a desirable future in the Okanagan Valley.

4.3.1 Implementing connectivity in the Okanagan Valley

The results of the work presented throughout this thesis along with previous modeling projects show many opportunities to implement landscape connectivity in the Okanagan Valley. Because land use planners in the Okanagan have access to many connectivity models, efforts can be focused on regions with the most overlap. Presumably, multiple studies that all highlight the same region as contributing to connectivity, provides good evidence that it is an important area to focus resources. For example, the Circuitscape analysis, transboundary connectivity assessment and tiger salamander/bighorn sheep models all highlighted a region in the South Okanagan between Princeton and Osoyoos as important to connectivity. In addition to focusing efforts in areas of good overlap, land use planners should also consider connectivity pinch-points and unique landscape features. For example, there were only two crossing points identified that facilitate bighorn sheep movement from the East to West side of the landscape. Although these sites may not have shown high overlap, they are nonetheless important to consider for connectivity restoration work.

For any proposed connectivity work in the Okanagan, it is important to step back and consider how a proposed feature will impact other species and ecological processes on the landscape. In some cases, such as with the tiger salamander model, species-specific plans will likely benefit a wide spectrum of plants, animals, and processes on the landscape. The habitat requirements of tiger salamanders overlap to varying degrees with the Great Basin Spadefoot (*Spea intermontana*), Pallid bat (*Antrozous pallidus*), Badger (*Taxidea taxus*), Burrowing Owl *(Athene cunicularia*), and Sage Thrasher *(oreoscoptes montanus)* (Southern Interior Reptile and Amphibian Recovery Team, 2008). Thus, it is reasonable to assume that connectivity plans targeted to tiger salamanders will benefit many other species as well. Conversely, for species with very specific habitat requirements such as bighorn sheep, identified corridors may not have such broad implications. Researchers and land use planners should carefully consider the broad implications of any proposed work.

Ultimately, maintaining connectivity in the Okanagan Valley will be a process of opportunity and compromise. Despite the best modelling efforts, when it comes to on-the-ground conservation, many factors will limit the feasibility of proposed corridors. The modelling efforts I used in this thesis identify all regions that likely contribute to connectivity across the landscape. Although areas that are more important to connectivity show as having a higher frequency of movement, this modelling approach also identifies less optimal features on the landscape. Thus, land use managers have a diverse suite of options that can be made amendable with other land use plans and objectives.

4.4 Future research goals

The results of this work highlight regions on the landscape that likely facilitate animal movement. However, an important goal for future research should be to collect the field data necessary to validate model assumptions. For the bighorn sheep connectivity model, data collected from radio-collared sheep could provide fine-scale movement data including step lengths and turning angles through different habitat types. Further, because there are so few bighorn sheep on the landscape, it could be possible to build an agent for each radio-collared sheep that captures individualized responses to landscape variables. For the tiger salamander work, inventorying wetlands for the presence/absence of salamander larvae could provide an important first step in model validation. Secondary to this, an analysis of tiger salamander genetics across the landscape could provide a fine-scale assessment of wetland connectivity. If the tiger salamander model were accurate, wetlands predicted as connected would likely have genetic evidence of recent breeding between individuals in these wetlands. As complementary to the bighorn sheep work, I would have liked to also include a generalist species such as mule deer or black bears to compare to the specialist species. Further, more broad-ranging specialist species such as the American badger would provide interesting comparison to the bighorn sheep and tiger salamander work.

5 Chapter: Conclusions

The overarching objective of this thesis was to assess the utility of an individual-based modeling approach as a tool for identifying species-specific functional connectivity across a landscape. It is difficult to claim that the results presented in this thesis do indeed show *functional* connections across the landscape. Functional connectivity requires a nuanced understanding of how species interact and respond to their landscape and how behaviours such as dispersal through non-optimal habitat, foraging, and individualized responses to movement barriers impact connectivity. In Chapter 2 and 3, I was unable to validate connectivity for bighorn sheep and tiger salamanders respectively with field data. Moreover, the modeling approach used may have oversimplified key processes in animal movement. For example, in the bighorn sheep model (chapter 2), agent movements were restricted to good habitat; however, dispersal through poor habitat is well recognized as a central process contributing to functional connectivity (Baguette and Van Dyck, 2007). In the absence of field validation, it would have proven challenging to incorporate dispersal through poor habitat into model rules without making considerable assumptions. Similarly, the tiger salamander model was too coarse to simulate individuals responding to their environment. To include localized movement decisions would have required a fine-scale model, which existing spatial data for this region simply would not support. Although I feel that the individual-based modeling approach presented here shows many advantages (discussed in the previous chapter) and has direct implications for landscape connectivity planning in the Okanagan Valley, the results of this thesis are more appropriately described as structural connectivity than functional.

The first specific objective of this work was to create an individual-based model of animal movement based on landscape characteristics and calibrate it to represent two selected species: bighorn sheep and tiger salamanders. The results of Chapter 2 and 3 of this thesis present an IBM for bighorn sheep and tiger salamanders respectively. After implementing the IBM, I explored how connectivity might change as a result of various land management and environmental scenarios for both species, thus satisfying the second objective of this work. Scenarios tested include the impact of restoring a natural fire regime to the landscape and increasing road permeability on bighorn sheep connectivity (Chapter 2) along with exploring how tiger salamander connectivity changes as a result of varied wetland inundation across years and due to stocking lakes with predatory fish (Chapter 3).

Next, I aimed to explore the ease of implementation and results of an IBM approach compared to other common approaches to assess landscape connectivity. Chapter 4 of this thesis discusses how the IBM model implemented for bighorn sheep compares to a LCP approach for the same species. Further, I more broadly discussed the advantages and limitations of an IBM approach in Chapter 4. Finally, the last objective of this research was to compare the results of the IBM models to existing connectivity work and to provide prescriptive guidelines to increase connectivity in the Okanagan Valley. Chapter 4 provides a detailed comparison of all the connectivity modeling work completed in the Okanagan region. Chapter 4 also discusses considerations for implementing connectivity into land use management plans specific to the Okanagan and more broadly.

Maintaining functionally connected landscapes is aptly important for conservation, particularly for facilitating range shifts in response to climate change (Krosby et al., 2010). While conservation and restoration of habitat to produce simple linear corridors may be effective strategies for facilitating species movement through hostile environments, achieving effective connectivity and viable animal populations at the landscape scale will require more than corridors. The use of an IBM in this study highlights the power of this method to identify how a species might make broad use of a landscape for movement and migration. It identifies connectivity to areas that are suitable yet not currently occupied, emphasizing the importance of designing conservation plans that encompass more than just current species ranges. The individual-based approach also provided a more realistic representation of how animals perceive and move in their habitats than traditional approaches to identify corridors such as least cost path analysis. I recommend further application of this approach in connectivity studies, particularly for species where facilitating range expansions is a priority.

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Appendices

Appendix A Data layers

Table A.1 Input data layers

Layer name	Source	Year	Description
Study area	BC Geographic Warehouse	2011-2015	Regional districts in British Columbia
North American Political Borders	Geogratis-Natural Resources Canada	2011	Jurisdictional areas in North America
Transboundary Overlap of three assessments	BC-WA Transboundary Connectivity Group	2015	Regions of overlap for a shrub-steppe, montane, and ecological integrity model
Biodiversity Conservation Strategy Connectivity layer	Biodiversity Conservation Strategy, completed by Caslys Consulting	2012 (South Okanagan), 2014 (Central and North Okanagan	Integration of environmental and land tenure data to model habitat connectivity, conservation values for sensitive ecosystems and relative biodiversity
Circuitscape potential wildlife movement corridors	Complex Environmental Systems Lab, UBC, and Cardille Lab, McGill University	2014	Results of circuitscape modeling based off the BCS connectivity model
Major lakes	Freshwater data atlas, BC Geographic Warehouse	2011-2015	Lake polygons in British Columbia
Roads	Digital Road Atlas (DRA) – Demographic Partially-Attributed Roads, BC Geographic Warehouse	2014	Road features in British Columbia
Agricultural Land Reserve	The Agricultural Land Commission	2016	Agricultural Land Reserve boundaries in British Columbia

Layer name	Source	Year	Description
Vegetative Resource Inventory	BC Geographic Warehouse	Unknown	Detailed information related to composition of habitat and non-habitat in British Columbia
Bighorn sheep occurrences	BC Ministry of Forests, Lands and Natural Resource Operations	1968-2012	A repository of various ungulate inventories in the study area
Indian Reserves	BC Geographic Warehouse	2014	Administrative boundaries of Indian Reserves
Wetlands	RDCO/Ecoscape Environmental Consultants Ltd.	2014	A repository of wetland mapping, inventory, classification, and other information into a single GIS database
Tiger salamander breeding sites	BC Ministry of Forests, Lands and Natural Resource Operations	2016	Known tiger salamander breeding sites in Southern BC
Basemap/ World Imagery	ESRI Digital Globe/ Map Services	2016	Satellite and aerial imagery for the study area
Digital Elevation Model	BC Geographic Warehouse	Unknown	Elevation model of study area. Derived from the B.C. Terrain Resource Information Mapping (TRIM) data.

Appendix B Bighorn sheep Overview, Design concepts and Details and sensitivity analysis

B.1 Purpose

The individual-based model presented here is designed to simulate individuals wandering across a spatially explicit landscape using simple and species-specific movement rules. The overarching purpose of this model is to identify habitat corridors on a landscape by aggregating the movement paths of individuals across multiple model iterations. This model was also designed to test the effectiveness of various management scenarios that aim to increase landscape connectivity.

B.2 Entities, state variables and scales

This model is composed of three entities: a landscape of discrete grid cells, bighorn sheep agents and a temporal scale. These are described below.

The landscape- the landscape is conceptualized as a series of heterogeneous grid cells 75 m x 75 m in size. Each grid cell has the following attributes: a spatial coordinate, slope (in degrees), percent crown cover, and the presence or absence of lakes, rivers, and roads. The landscape is static and shows no diurnal or seasonal variation.

Bighorn sheep agents – bighorn agents are characterized only by their current location and previous location within the environment. Locations are stored as the x- and y-coordinate of the center of the grid cell. Bighorn agents are capable of perceiving all attributes of the grid cell it currently occupies along with the eight grid cells immediately surrounding its current location. Furthermore, bighorn agents are assumed to have some knowledge of their surroundings and therefore know relative distances to suitable escape terrain. Movement is not goal orientated; instead, a simple rule-based decision-making heuristic guides bighorn movement in this model.

Temporal scale –A series of discrete "ticks" is used to track the current state of the model. Each tick has no real-world value.

B.3 Process overview and scheduling

The model begins when a bighorn sheep agent is placed on a landscape. The initial location of a bighorn sheep agent is randomized; however, an agent cannot start in poor habitat. After initialization, the model proceeds by iterating through the *move* sub-model until the agent either becomes "stuck" (no valid movement option exists), leaves the spatial extent, or after 2000 time steps. At this point, the simulation terminates and the spatial coordinated of every cell on the landscape used during the bighorn's route is recorded. Implementation details of the *move* sub-model are described in detail below.

B.4 Design concepts

Basic principles. This model was designed to capture critical processes underlying bighorn sheep movement behavior within the Okanagan Valley, British Columbia, Canada as a means of identifying habitat corridors. Bighorn sheep movement is implemented as a pseudo-biased random walk wherein agents will evaluate the quality of habitat immediately surrounding their current location and move towards favourable habitat. The bighorn agent will continue moving across the landscape until either becoming “stuck” or leaving the spatial extent. To identify habitat corridors, the movement paths used by agents across multiple model iterations are overlaid into a single file.

Emergence. Habitat corridors emerge as a result of overlaying the individual movement paths used by agents across multiple model iterations.

Adaptation. Bighorn sheep agents will adapt by moving towards habitat cells of good quality.

Objectives. Agents in this model have no objective. Movement is not goal orientated.

Sensing. Bighorn sheep agents are able to perceive the habitat found at their current location and in the eight grid cells immediately surrounding their current location. Moreover, bighorn sheep agents are assumed to have some understanding of their landscape and are therefore able to sense the relative distance to important landscape structures including steep terrain.

Stochasticity. Stochastic processes are used to create two sources of variability in this model. First, the initial bighorn sheep location is determined through a stochastic process wherein a random grid cell is chosen and then evaluated to determine if it meets bighorn sheep habitat requirements. If yes, the sheep agent is placed at that location. If no, the habitat at a second randomly selected grid cell is compared to the bighorn sheep habitat requirements. This process is repeated until an appropriate initial grid cell is found. Second, if during the *move* sub-model multiple cells are determined as appropriate to move towards, a random process is used to select a cell to move to out of a list of possible good cells.

Observation. Each time step, the x- and y- coordinate of the bighorn sheep is exported to a text file.

B.5 Initialization

To create the environment, an ASCII text file of each landscape layer including roads, rivers, crown cover, lakes, percent crown cover, and slope is imported into the programming environment. A matrix is then created within the programming environment for each landscape layer. The values in each ASCII text file are subsequently read and assigned to their corresponding cell within the grid. After the landscape has been created, a single bighorn sheep agent is placed on a randomly selected grid cell. The sheep agent will then evaluate the habitat at that grid cell. If the cell meets all bighorn habitat requirements, the model will execute. If not, the sheep is re-located to another randomly selected grid cell and the process repeats. This continues until a suitable grid cell is located.

B.6 Input data

An ASCII text file for each landscape layer including roads, rivers, crown cover, lakes, and slope is imported into the programming environment. We created these input files by converting raster maps of each layer into an ASCII text file in ArcGIS 10.1.

B.7 Submodels

The move sub-model defines exactly how bighorn sheep choose a neighbouring cell and subsequently move to that cell. First, the current grid cell is queried and a list of the eight grid cells immediately surrounding the current cell is created. Any cell within that list containing a lake is removed from the list (lakes are an absolute barrier to bighorn sheep movement in this model and therefore are not considered). Each cell within the list is then evaluated against the following criteria. Any cell not meeting one or more criteria is removed from the list of possible movement cells. (1) The cell cannot be the previously occupied cell; (2) the cell must be an appropriate distance to escape terrain; (3) the cell must not have more than 40% crown cover; and, (4) the cell most not be a road or a river. Once a cell has been found that meets all of the criteria, the agent will move to that cell. If no cells meet the criteria, the agent is stuck and the simulation terminates.

If a cell is within 400 m of escape terrain, it satisfies the distance to escape terrain requirement and the agent will move to that cell. If the cell is greater than 400 m from escape terrain, then its distance from escape terrain is evaluated against the function below, which relates the probability of movement to distance from escape terrain:

$$probability\ of\ movement = 188.21e^{-0.0016(distance)}$$

This is done by drawing a random number between 1 and 100 and comparing the random number to the *probability of movement.* If the random number is smaller than the *probability of movement,* the agent will move to that cell. Thus, as distance to escape terrain increases it becomes less likely that a sheep agent will move to that cell. We based the equation for probability of movement beyond 400 m off of a habitat suitability model constructed for bighorn sheep in the Okanagan Valley (Warman et al. 1998). In this study, researchers identified habitat within 400 m of escape terrain as good (a value of 1 on a 5 point scale with 1 being good habitat and 5 being poor habitat) with the likelihood of use decreasing to "greater than 1600 m" (a value of 5 in the habitat suitability model). We made the assumption that use of an area decreases exponentially with distance to escape terrain, and derived the equation used in our model based on the ranking system used in Warman et al. (1998). Note that because we were working with integer grid cells with a length of 75 m, the probability of movement effectively decreases beyond 450 m since it is not possible to be exactly 400 m from escape terrain (400 is not divisible by 75). Figure B.1 shows the likelihood of movement for a given distance from escape terrain.

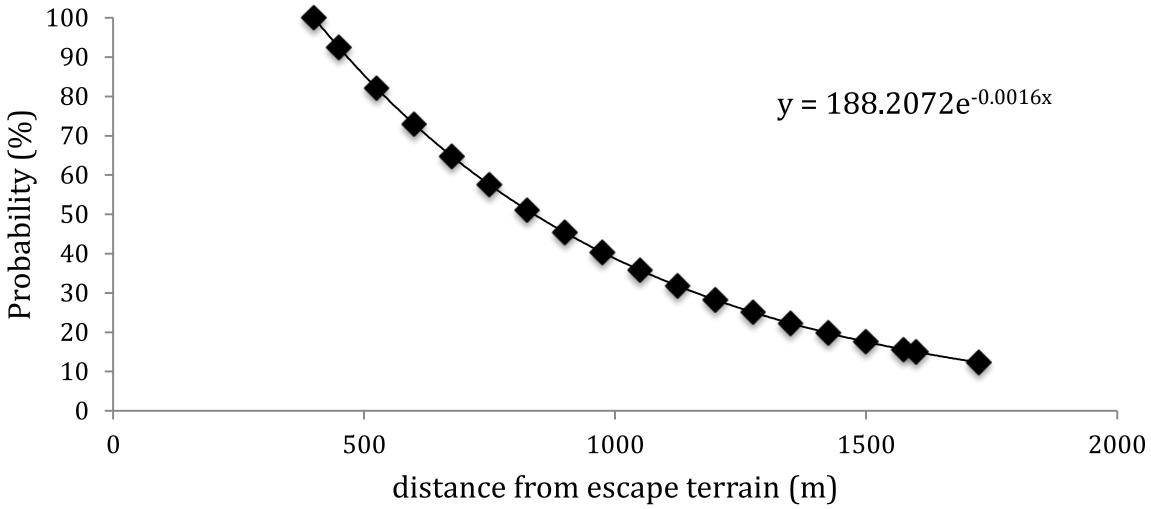


Figure B.1 The probability of movement (%) to a particular grid cell given the distance that grid cell is to escape terrain.

B.8 Model verification, justification, and sensitivity analysis

Model justification and verification

Bighorn sheep have been extensively studied in the Okanagan Valley and greater bighorn range. We therefore had a plethora of published data along with anecdotal observations from bighorn sheep experts at our disposal. Prior to creating the IBM for bighorn sheep, we preformed an extensive literature search drawing on site-specific government reports retrieved from EcoCat, the Ecological Reports Catalogue of BC, in addition to peer-reviewed literature.

From this literature search, we established a list of bighorn sheep movement criteria (Table 2.1). Prior to implementing the model, our bighorn movement criteria was verified for accuracy by site-specific, bighorn sheep experts including a representative from BC Parks, two Ecosystems Biologists and a bioterrain expert working for the Ministry of Forests, Lands and Natural Resource Operations in British Columbia, Canada. Using their feedback, the bighorn movement criteria was modified appropriately and implemented into the individual-based model. Local, bighorn sheep experts verified preliminary corridor maps were realistic and all feedback given was incorporated into the model. In addition to expert validation, we compared the simulated habitat corridors to bighorn sheep occurrence data in the Okanagan Valley. 82% of bighorn sheep occurrences were within a simulated habitat corridor. Note that we did not strive for 100% of bighorn sheep occurrences to fall within a corridor because it is possible sheep were observed in poor habitat. Moreover, some of the occurrence points documented were from several years ago; it is possible these locations were recently developed. Similarly, we didn’t limit our model to those locations because the vast majority of habitat suitable for bighorn sheep in the Okanagan is currently unoccupied. Moreover, occurrence data is not a direct reflection of habitat corridors. Although there was no bighorn sheep movement data available to compare our model results against, we are confident the corridors in this model are a realistically predict the location of potential bighorn sheep corridors for this region. Table 2.1 reflects the final version of movement rules as implemented in the model.

After finalizing model rules, we determined the optimal number of model iterations by varying the number of iterations and comparing the total number of cells visiting on the landscape across simulations. The number of cells visited did not change considerably when the number of model iterations was increased past 20 000.

Sensitivity analysis

Given the uncertainty associated with the amount of crown cover and steepness of slope bighorn sheep responds to, we preformed an extensive sensitivity analysis to explore how these two variables influence habitat corridors. The following simulations were explored:

- slope > 40 with crown cover < (0, 20, 30, 40, 50, and 60)
- Slope > 30 with crown cover < (0, 20, 30, 40, 50, and 60)
- Slope > 20 with crown cover < (0, 20, 30, 40, 50, and 60)

These sets of parameters were chosen because they are a realistic range over which bighorn sheep *could* select habitat for movement. Results from sensitivity analyses indicate that the overarching pattern of where habitat corridors were identified remains static regardless of the value given to slope and crown cover (Figure B.2). The width and connectedness of these corridors however, varies as we increased or decreased the steepness of escape terrain sheep required by bighorns or amount of crown cover. In the final model, slope greater than 40 degrees with crown cover less than 40% was used.

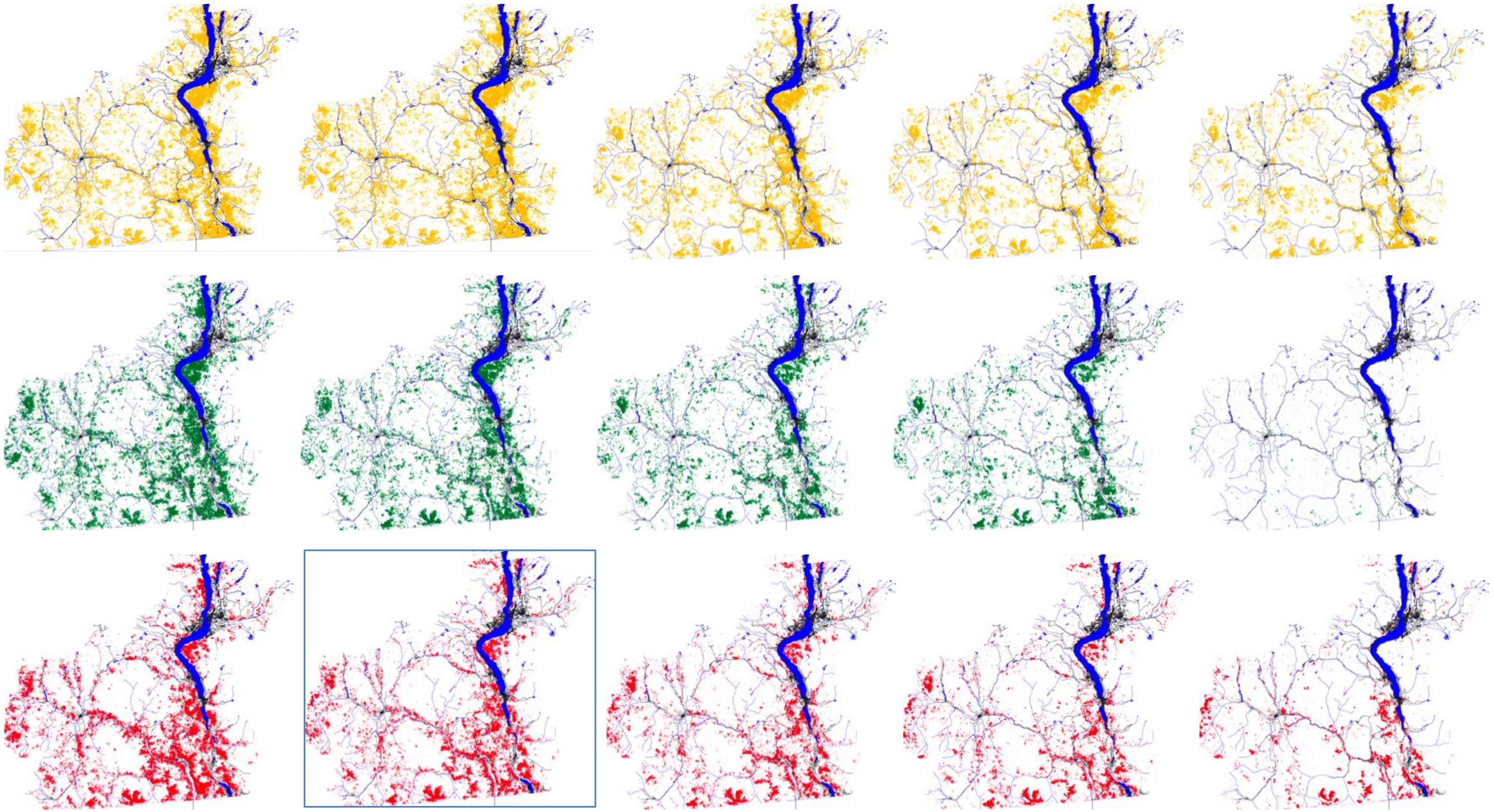


Figure B.2 Bighorn sheep model sensitivity analysis. The value of escape terrain bighorn sheep required for the model was varied from >20 degrees (top row), >30 degrees (middle row), and >40 degrees (bottom row). The amount of crown cover bighorn sheep required decreased from left to right as follows: <50%, <40%, <30%, <20%, 0%). Crown cover <40% and escape terrain >40 degrees was used in the final model (outlined in a square).

Appendix C Tiger salamander Overview, Design concepts and Details and sensitivity analysis

C.1 Purpose

The overarching purpose of this model is to identify terrestrial tiger salamander habitat corridors that functionally connect wetlands in the Okanagan Valley. This was accomplished by creating tiger salamander agents that disperse from known wetlands and wander across a spatially explicit landscape by following simple movement rules. To identify common habitat corridors, the frequency with which agents used each pixel on the landscape was recorded. This model can be used to identify physical connections that potentially facilitate tiger salamander dispersal; how connectivity dynamically changes as a result of variable wetland inundation; the impact of stocking permanent wetlands with predatory fish on connectivity; and, how currently used breeding pools are structurally connected.

C.2 Entities, state variables, and scales

The model has three components: a spatial landscape, tiger salamander agents, and a temporal scale.

The landscape: Two different spatial extents were used in this model: a regional map of the South and Central Okanagan Regional districts, and a focus area that encapsulates most known breeding sites. During model implementation, the user can select which spatial extent to run simulations from. The landscape is created with a discrete grid (50 m x 50 m cell size) and a continuous space. The grid stores values specific to each pixel on the landscape and allows agents to query and interact with their location. Each grid cell has the following attributes: a spatial coordinate, slope (in degrees), and the presence/absence of roads, major lakes, and wetlands. For the focus area spatial extent, additional attributes include the location of known breeding sites and a “risk of drying” that specifies the amount of variability in inundation across years for each wetland. The continuous space is used to calculate distances and directions between agents and landscape features. The landscape is static and shows no diurnal or seasonal variation.

Tiger salamander agents: During initialization, tiger salamander agents are placed on a grid cell containing a wetland. They then wander across the landscape following a pseudo-correlated random walk where their current direction of travel is deflected +/- 45 degrees from the agent’s previous direction of travel. Each time step, agents will move one grid cell (50 m) following their direction of travel. Salamander movement is not biased by landscape variables. This is because the spatial resolution of this model was considered too coarse for agents to perceive and react to their landscape. Instead, when an agent encounters obstacles to movement such as roads and cliffs, the agent will either have a probability of successfully traversing the obstacle, or, the obstacle will act as an absolute movement barrier and the agent is removed from the simulation. Agents will continue dispersing across the landscape until either dying as a result of a movement barrier, or moving a maximum Euclidean dispersal distance from their wetland of emergence. Agents are characterized by the following variables:

- A current location on the grid,
- The grid cell the agent was placed onto during model initialization (this will always be a wetland cell),
- The first terrestrial cell the agent emerges from a wetland and onto (this will never be a wetland cell). This variable is used to calculate the distance an agent has travelled from its wetland. This is necessary in cases where an agent was placed in the middle of a large wetland (greater than 1 cell in size) such that the distance from the middle of the wetland to the edge of the wetland is not included when calculating the distance travelled.
- The maximum Euclidean dispersal distance, which is drawn from a power law distribution,
- The current direction of travel (in degrees),
- *toRemove*: a Boolean variable that stores if an agent has died during a time step and needs to be removed from the simulation.

In addition to these variables, all agents in a simulation share a static variable "*distances*" which is a linked list that stores the Euclidean distance each agent travelled from their wetland of emergence. When an agent is removed from the simulation, the Euclidean distance they travelled from the wetland is added to this list. This list is only used during sensitivity analyses to determine how parameters influence dispersal distances and therefore has no impact on model results.

Temporal scale: a 'tick' is used to track the current state of the model. After each agent moves and updates their variables, the 'tick' will increment by one. Each tick has no real-world value.

C.3 Process overview and scheduling

The model begins by creating 100 tiger salamander agents and placing them on a grid containing a wetland. After initialization, the model will iterate through the 'step' submodel until agents either move the maximum distance away from their starting wetland, or, they are removed from the simulation because they encountered a barrier to movement. After all the agents have been removed from the simulation, the spatial coordinate of every cell on the landscape used by a tiger salamander agent is recorded. Also, the model identifies how far 50%, 90%, 95%, and 99% of the agents dispersed from the wetland. Implementation details of the 'step' sub-model are described in detail below.

C.4 Design concepts

Basic principles: The individual-based model described here aims to identify where connectivity exists across the Okanagan Valley for tiger salamanders. This is accomplished by simulating tiger salamanders emerging from wetlands and wandering across the Okanagan Valley following prescriptive movement rules. Routes that are frequently used by simulated agents that contribute to connectivity are then identified.

Emergence: habitat corridors between wetlands emerge as a result of overlaying the individual movement paths used by agents across multiple model iterations.

Sensing: tiger salamanders are able to perceive the habitat found at their current location.

Stochasticity: stochastic processes are used to create several sources of variability in this model. First, the agent's initial heading is randomly set by selecting a number between 1 and 360. Second, the maximum allowable distance of travel is randomly drawn from a power law distribution. During animal movements, their direction of travel will be randomly adjusted by 45 degrees to create a correlated random walk. Also, a random number is drawn and compared to a probability of successfully crossing various movement barriers to determine if the agent is removed from the simulation because of that barrier.

Observation: each time step, the x- and y- coordinate of the each agent is exported to a text file. Also, at the end of a simulation, the distances that 50%, 90%, 95% and 99% of the agents travelled away from their wetland is outputted to a text file.

C.5 Initialization

A grid is created for each landscape layer including roads, slope, lakes, and wetlands. An ASCII text file for these landscape layers is subsequently read and each value within text files assigned to their corresponding grid cell on the landscape. After the landscape has been initialized, a list is created that stores every grid cell on the landscape that contains a wetland. When the model is run in "batch" mode, which allows for many consecutive iterations of the model, it will run one simulation per grid cell in this list. When the model is not run in batch mode, the user selects which wetland cell to start the simulation from. After the landscape has been created, 100 tiger salamander agents are created and placed on the selected grid cell containing a wetland. To determine the maximum dispersal distance of travel for each agent, a random number is drawn from the following power law distribution:

$$Maximum\ dispersal\ distance = \frac{400}{(1-u)^{\frac{1}{1.83}}}$$

If the maximum dispersal distance is over 8000 m, another random number is drawn. This repeats until a value is returned that is less than 8000 m. There were several assumptions used to derive the maximum dispersal distance equation. First, the probability of moving a distance from the initial wetland was described with an inverse power function. By a power relationship, a large number of individuals remain in proximity to a wetland and only a small proportion of dispersers travel long distances. This trend has repeatedly been observed in amphibian populations (See review by: (Smith and Green, 2005). The exponent of the maximum dispersal distance function was calculated based on previously published literature of tiger salamander dispersal. Searcy et al. (Searcy et al., 2013) estimate the Euclidean distance travelled by 50%, 90%, and 95% of California tiger salamanders averaged across ponds and years to be 556, 1486, and 1849 m respectively. A scatter plot was prepared with the values obtained from Searcy et al. (2013) and fitted with a power law curve (Figure C.1). The exponent from this relationship was then used as the scaling factor in the maximum dispersal distance function. Finally, to prevent the distribution of tiger salamander agents from dropping too quickly, the minimum distance of travel was set to 400 m. This is consistent with literature that has documented the density of juvenile tiger salamanders to initially increase with distance from the wetland before dropping off (Searcy et al., 2013; Trenham and Shaffer, 2005).

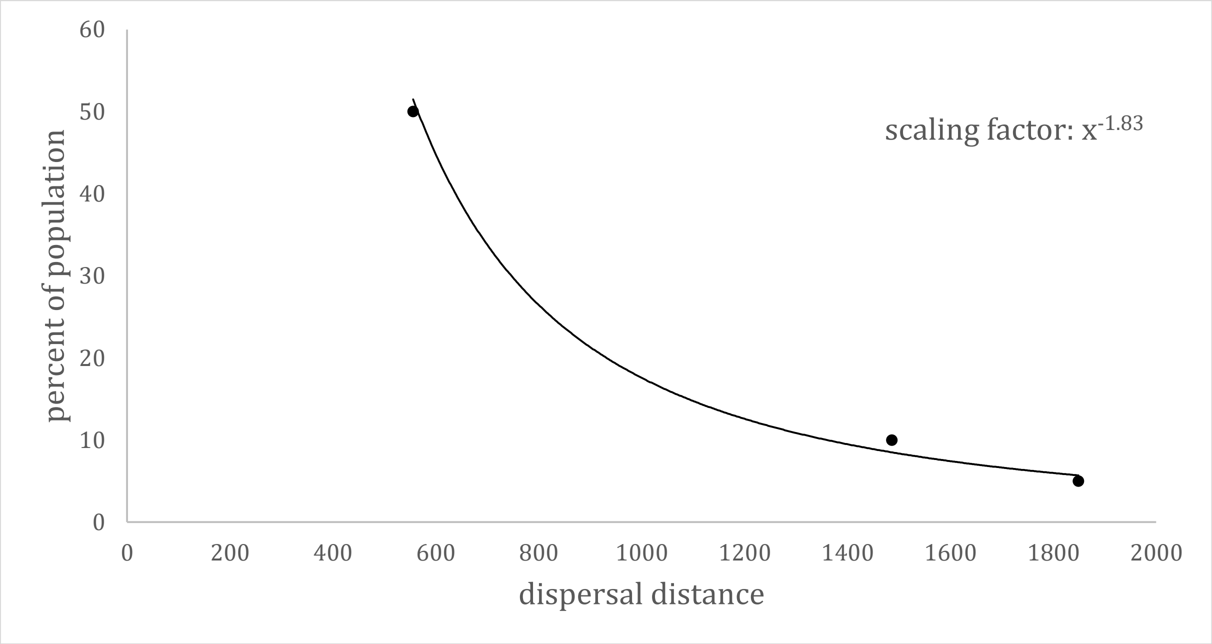


Figure C.1 The percent of a tiger salamander population that disperses *x*-distance from a wetland. Values obtained from Searcy et al. (2013). ($y = 5465461x^{-1.83}$)

To set the initial heading, a random number between 0 and 360 is drawn. Next, the location of their initial location is stored as a variable. The agent will then move following their initial heading until they reach a terrestrial grid cell. The location of the first terrestrial grid cell the agent walks across is stored and used to calculate how far the agent moves from their wetland. The agent is then returned to their initial location and the simulation begins.

C.6 Input data

An ASCII text file for each landscape layer including roads, wetlands, lakes, slope, and the wetland drying index is imported into the programing environment. For the focus area, the location of known breeding sites and wetland risk of drying is also imported. Each input file was created by converting raster maps of each layer into an ASCII text file in ArcGIS 10.2. The risk of drying for each wetland was determined by importing a .kmz file of wetlands into Google Earth Pro (Google Earth Pro, 2016). For each wetland in the .kmz file, I manually searched through available satellite image for that wetland over the period 2004 - 2015 and determined the wetland's risk of drying. Risks of drying were classified as one of three easily identifiable groups (Figure 3.3): always contains water (classified as low risk of drying), sometimes contains water (classified as moderate risk of drying), and never contains water (classified as high risk of drying). To identify how connectivity changes in wet versus dry years, dispersal was simulated from wetlands with: (1) only a low risk of drying; (2) moderate and low risk of drying; and (3) low-high risk of drying. Results from these three scenarios were then compared.

C.7 Submodels

There are two submodels in this model: "step", which controls model flow every time step, and, the "disperse", which allows agents to move throughout their landscape.

Step submodel

First, if there are no agents left in the simulation or 800 time steps have elapsed, the simulation ends. If the simulation has not ended, the current status of the agent is called (variable *toRemove*). If the agent died or moved their maximum dispersal distance from the wetland the previous time step (*toRemove = 1)*, the agent is removed from the simulation. If the agent was not removed from the simulation, the "disperse" submodel is called.

```
if → (number of agents < 1) OR (time step >= 800)
End simulation
else if → toRemove == 1
{
```

```
        -  calculate the Euclidean distance the agent moved from their wetland of emergence and
           sort it into a static linked list of all agents' distance travelled
        -  remove the agent from the simulation
}
else if → agent still exists AND (distance travelled < max dispersal distance)
        -  call submodel "disperse"
if → (distance travelled >= max dispersal distance)
        -  toRemove =1
```

Disperse submodel

The disperse model allows agents to travel across their landscape by following a two-step algorithm: (1) the agent's previous directional heading is deflected +/-45 degrees, and (2) the agent will move one grid cell (50 m) following their new directional heading. Then, if the agent's new location is one a road, there is a 30% chance the agent will be removed as a result of the road. If the agent is on a slope greater than 40 degrees or a major lake, the agent is marked for removal.

```
If → (distance travelled < max dispersal distance)
{
        -  draw random number number between 0 and 45
        -  draw random number sign between 0 and 1
        if → (sign == 1)
                - (add number to the previous directional heading)MOD 360
else
        -  (subtract number to the previous directional heading)MOD 360

        -  move 1 grid cell (50 m) following new directional heading
        if → (new location is on a road) AND (random number between 0 and 100 < 30)
        -  toRemove =1
        if → (new location is on a slope > 40 degrees steep)
        -  toRemove = 1
        if → (new location is on a major lake)
        -  toRemove =1
}
```

C.8 Model verification, justification, and sensitivity analysis

Justification

An extensive literature search was completed on tiger salamander movement behavior along with amphibian movement characteristics more broadly. Where ever possible, site- and species-specific reports were used in developing this model. It is widely acknowledged that landscape-level connectivity among breeding pools is predominately influenced by long distance dispersal events by juveniles (Berven and Grudzien, 1990; Cushman, 2006; Gamble et al., 2007). This model therefore focuses on juvenile, unidirectional dispersal from aquatic breeding sites and into terrestrial habitat. Amphibian movement from breeding ponds is a complex and multi-phase process (see review by

Pittman et al. (2014)). In the following, we simplify tiger salamander movement to two stages: emergence from a wetland and dispersal into upland terrestrial habitat. Key literature findings for these stages are summarized below.

During emergence from a wetland, previous research suggests amphibians have limited ability to sense the terrestrial habitat surrounding their wetland (Rothermel, 2004). Although studies have demonstrated the overall orientation of emerging juveniles tends to be non-random at the pond edge (for example, Walston and Mullin (2008)), studies that consider multiple years and ponds have shown this bias varies markedly and becomes more uniform over space and time, suggesting there is no innate directional bias during emergence (Jenkins et al., 2006; Timm et al., 2007). Moreover, the direction of emergence is often not correlated with landscape features past the pond perimeter. Researchers have therefore hypothesized that although juveniles likely respond to micro-habitat at the pond edge, overall their direction of dispersal is random (Rothermel, 2004; Semlitsch, 2008). Then, simply by virtue of many juveniles emerging each year, some will reach suitable habitat or colonize new breeding pools. A local study observed tiger salamanders emerging from a wetland orientated towards dry sagebrush grasslands (Richardson and Shatford, 2000), however, this study only measured directionality for one pond and for one year. It therefore is difficult to extrapolate this pattern across the landscape. In this study, tiger salamanders were simulated emerging from their initial wetland with a random initial direction.

After emerging from a wetland, juveniles will follow a relatively linear trajectory into terrestrial habitat without searching for good habitat (categorized as ‘away’ mode by Pittman et al. (2014)). This behavior is likely a result of juveniles attempting to move away from the pond edge as quickly as possible to avoid competition and a high rate of predation near the wetland. Correlated random walks and diffusion models have been suggested as good methods to simulate juvenile dispersal from a wetland (Pittman and Semlitsch, 2013; Pittman et al., 2014; Smith and Green, 2005). This model therefore applied a pseudo-correlated random walk where an agent’s current direction of travel is weighted by their previous direction of travel.

To determine the maximum distance tiger salamanders travel, we exclusively used studies specific to tiger salamanders because distance of travel can vary markedly across amphibian species. Radio-telemetry studies of 14 tiger salamanders in 1998 in the white lake area showed no individual travelled further than 150 m from their pond (Richardson et al., 2000). Studies of tiger salamander dispersal in California used pitfall trapping to estimate the buffers required around a breeding area to capture certain percentages of the breeding population. For example, Trenham and Shaffer (2005) found that 50%, 90%, and 95% of subadults are within 380, 590, and 630 m of their initial wetland respectively. Applying a more robust calculation, Searcy and Shaffer (2011) identified that 50%, 90%, and 95% of the population is encapsulated by buffers placed 562, 1501, and 1867 m from the wetland respectively. These migration distances were also determined to be within the ecophysiological capabilities of tiger salamanders (Searcy and Shaffer, 2011). Similarly, Searcy et al. (2013) identified the 50%, 90%, and 95% buffers to be 556, 1486, and 1849 m from the pond edge respectively. In the following, we base the distance tiger salamanders can disperse from their wetland off the values presented in (Searcy et al., 2013).

Validation

Movement rules (Table 3.1) were validated by local tiger salamander experts to confirm they are consistent with current knowledge of salamander populations in the Okanagan Valley (Dyer, O. Pers. communication, 2016) thus providing an expert validation of the landscape level results. Because no movement or genetic data is available to empirically validate model rules, an extensive parameter search was included.

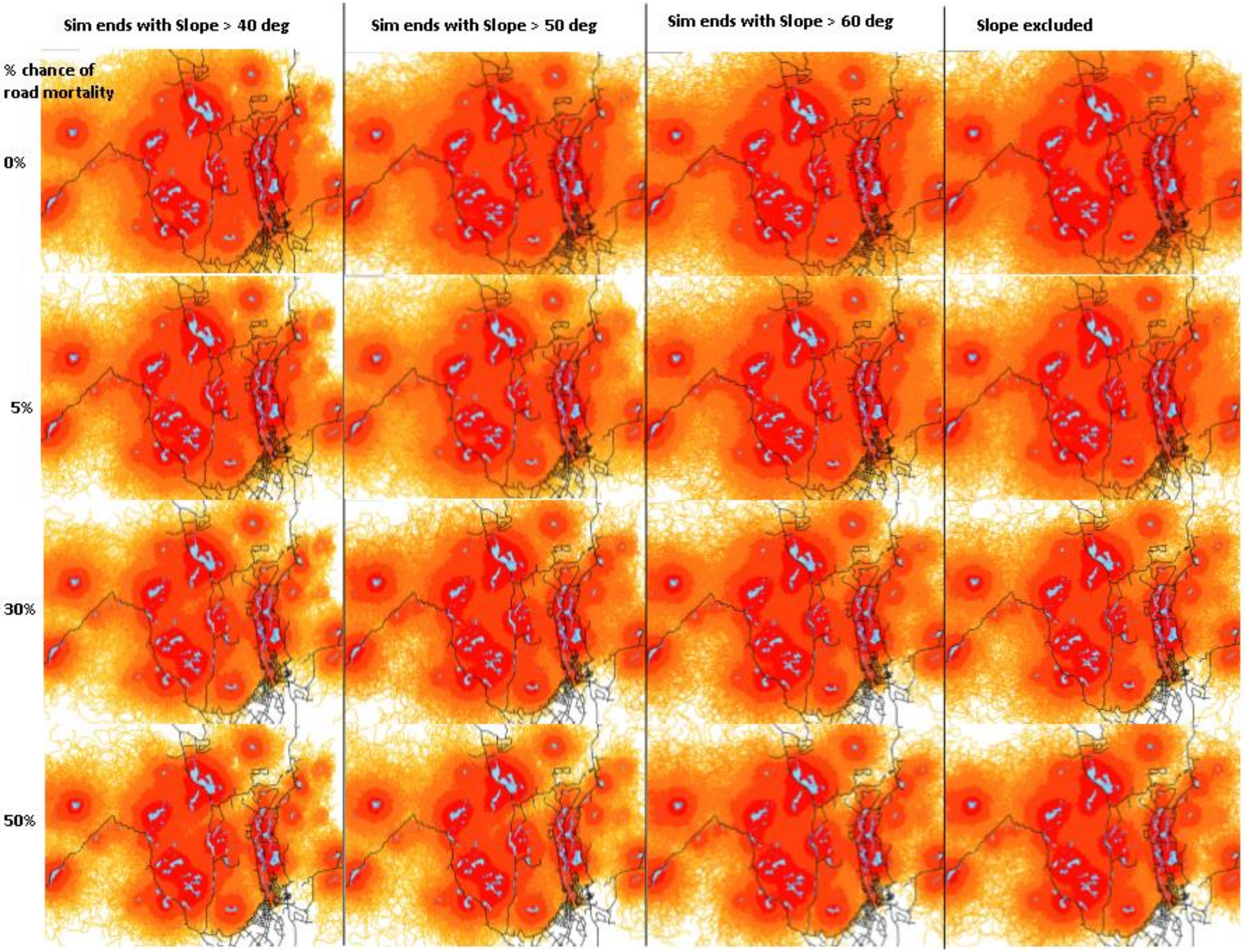
Sensitivity analysis

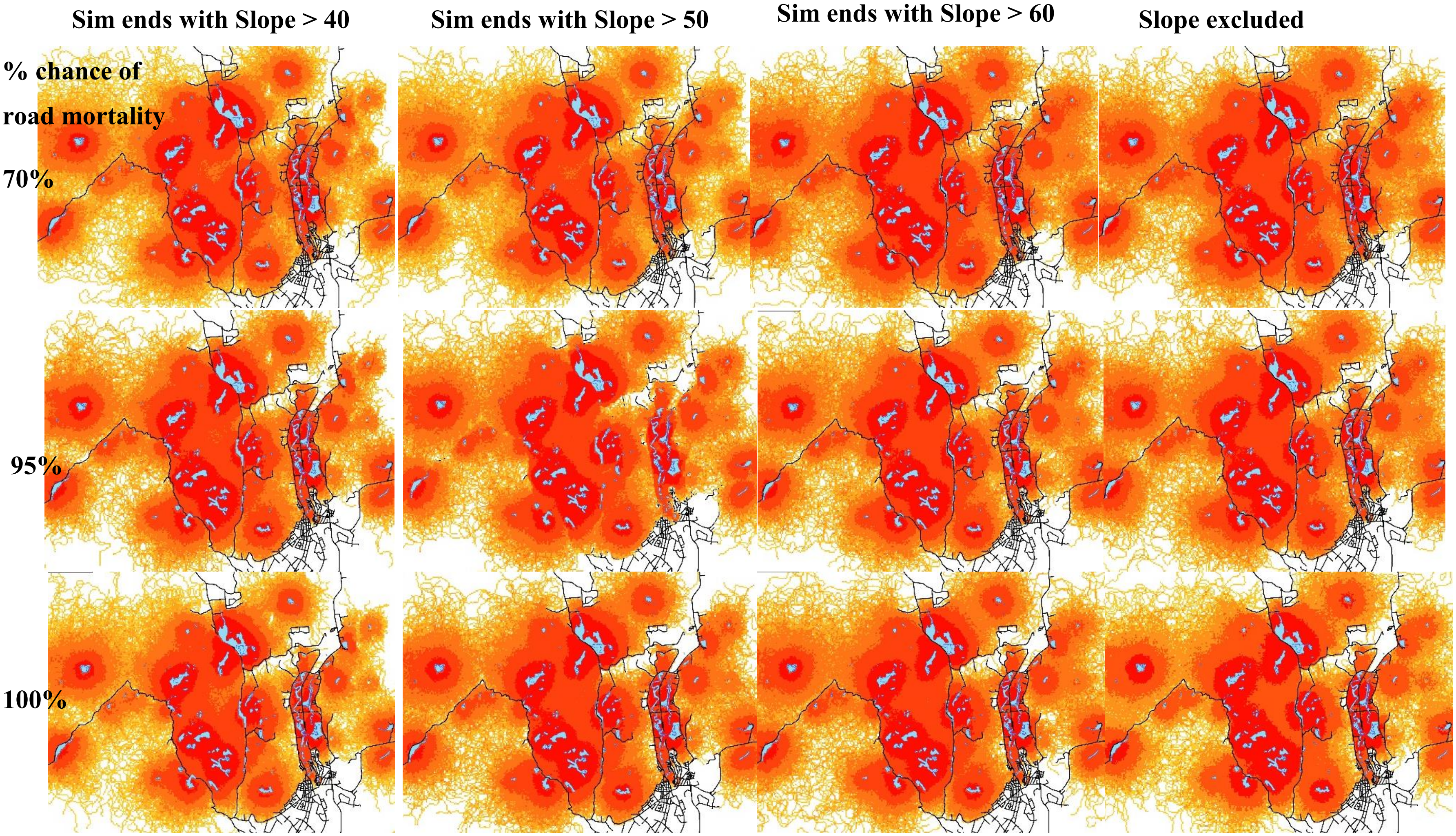
Given the uncertainty with model parameters, a sensitivity analysis was preformed to explore how values used in the model influence results. The following simulations were explored:

- slope >40 resulted in mortality with percent road mortality = (0, 5, 30, 50, 70, 95, 100)
- Slope > 50 resulted in mortality with percent road mortality = (0, 5, 30, 50, 70, 95, 100)
- Slope > 60 resulted in mortality with percent road mortality = (0, 5, 30, 50, 70, 95, 100)
- Slope excluded with percent road mortality = (0, 5, 30, 50, 70, 95, 100)

These sets of parameters were chosen because they are a realistic range over which landscape variables impact amphibian dispersal. Results from sensitivity analyses indicate that the overarching pattern of where amphibians moved across the landscape remains static regardless of these parameters (Figure C.2). In the final model, slope greater than 40 degrees resulted in tiger salamander mortality and percent road mortality was set to 30%.

Figure C.2 Tiger salamander model sensitivity analysis. The percent change of road mortality for the model decreased from top to bottom as follows: 0%, 5%, 30%, 50%, 70%, 95%, and 100%. The slope required for a salamander to die during a simulation was varied from greater than 40 degrees to greater than 60 degrees. A simulation was also run with slope excluded from the model rules. A geometric interval in ArcGIS 10.2 was used to characterize the change in connectivity.


Sim ends with Slope > 40 deg
Sim ends with Slope > 50 deg
Sim ends with Slope > 60 deg
Slope excluded
% chance of road mortality
0%
5%
30%
50%



Sim ends with Slope > 40

Sim ends with Slope > 50

Sim ends with Slope > 60

Slope excluded

% chance of road mortality

70%

95%

100%

Appendix D Bighorn sheep LCP analysis

Objective: To develop a least cost path model of the bighorn sheep work (Chapter 2) to explore how an IBM compares to a LCP model in implementation and results. To create the LCP, I converted the movement rules used in the IBM to a weighted resistance layer that describes the ecological cost of moving across each cell. Least cost corridors were identified using this resistance layer to find the 'cheapest' routes between start-destination locations. The LCP model was implemented using the same underlying assumptions as the IBM.

D.1 Methods

I used a four-step process to delineate corridors with the LCP: (1) identify start-destination locations from bighorn occurrence data, (2) create a raster resistance layer where each cell has a value depicting the cost associated with travelling across that cell, (3) calculate the accumulated travel cost and the direction of travel from all cells to each start location, and (4) calculate the least cost path from each start location to each destination. These are described in detail in the next sections.

(1) *Identifying start-destination locations:* To create start-destination locations, I qualitatively delineated bighorn sheep occurrence data into groups. Two criteria were used to pragmatically group occurrence data into start-destination points: (1) spatially segregated bighorn sheep occurrence points were grouped into a single group, and/or (2) bighorn sheep occurrences that were isolated by major dispersal barriers such as valleys, plateaus, roads, rivers, or large water bodies were separated into distinct groups. This resulted in 15 groups of bighorn sheep occurrences. To identify start-destination points from groupings of sheep, I placed a point at the center of gravity for each group. This resulted in a layer with 15 points representing the middle of each bighorn sheep occurrence grouping. These points were used as start-destination locations for the LCP analysis.

2) Creating the resistance layer: The resistance layer is a weighted composite grid created by combining a series of input grids. This produces a raster map describing the ecological cost incurred by traveling across each cell. This was done by converting five input layers, crown cover, escape terrain, lakes, rivers, and roads to a value between 1 and 10 representing high and low permeability to movement respectively (see table D1). Note that roads were used as a proxy for urban areas in this model. To combine each of the normalized input layers into a single composite resistance map, I first combined escape terrain and crown cover as described below:

$$weighted\ cell\ value = \frac{escape\ terrain + crown\ cover}{2}$$

After combining escape terrain and crown cover, lakes were identified as absolute movement barriers by setting any pixel containing a lake to *NoData*. Cells overlapping roads and rivers were then reclassified as 10 to indicate a permeable barrier albeit with high movement cost.

Table D.1 LCP resistance layer weighting scheme

Variable	*Normalization*	*Weighting*
Crown Cover	Crown cover > 40% → 10 Crown cover < 40% →1	50%
Escape terrain[1]	Within 400 m → 1 Within 650 m → 3 Within 1000 m → 5 Within 1250 → 8 Greater than 1250 → 10	50%
Lakes	Any pixel with a lake set to NoData	Any cell with a lake set to NoData[2]
Rivers	Any pixel with a river set to 10	Any pixel in composite resistance map with a river set to 10[3]
Roads	Any cell with a road set to 10	Any pixel in composite resistance map with a road set to 10[3]

[1] To identify escape terrain, we identified all cells with slope greater than 40° and calculated the Euclidean distance to escape terrain from every other cell. The function $y = 204e^{-0.036x}$ was then used to convert Euclidean distances (x) to a probability of moving to a cell (y).

[2] Cells set to NoData in composite resistance map are absolute barriers to movement.

[3] Cells with a value of 10 in composite resistance map are permeable barriers to movement.

3) Calculate accumulated cost from each destination to each start location: The cost distance tool (ArcMap 10.1) was used to create an accumulated travel cost map from each destination. The cost distance tool uses the resistance layer and start-destination locations as input fields to calculate the accumulative cost from each pixel within the spatial extent to the nearest start-destination cell. I also calculated the direction of travel from each cell to reach the nearest start-destination cell with the back link function in ArcMap 10.1.

4) Generating the least cost path: With the cost path application in ArcMap 10.1, we generated least cost paths from each start to destination location.

To explore the sensitivity of the LCP model to how the resistance layer was weighted, we created a second resistance layer where cells containing a road were given a value of 100.

D.2 Results

Figure D.1 shows habitat corridors identified with the LCP analysis overlaid on the bighorn sheep IBM of landscape connectivity presented in Chapter 2. The IBM resulted in a mosaic of landscape features that contribute to connectivity; however, corridors were not as discernable with the IBM compared to LCP results. Because the IBM did not limit movement to start-destination locations, the corridors identified encompass a much broader area than the LCP results including suitable habitat not currently occupied by sheep. Moreover, the IBM results were not limited to single-pixel-width corridors. In contrast, the LCP analysis resulted in clearly discernable corridors between bighorn populations. In the LCP model, corridors crossed major urban areas several times whereas the IBM either identified circuitous routes around urban areas or did not find any possible route through/around urban areas.

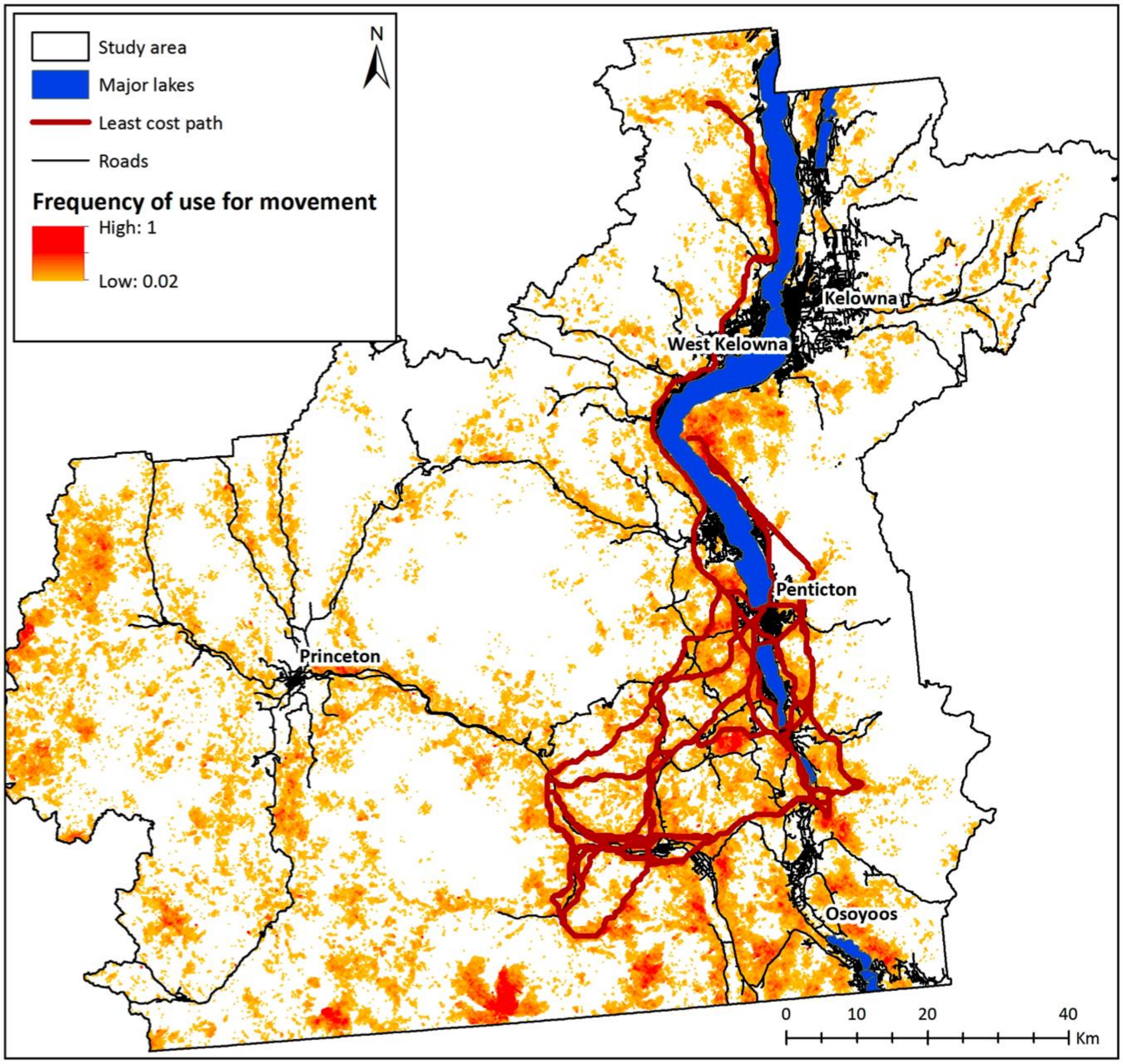


Figure D.1- Bighorn sheep LCP corridors overlaid on the frequency of use for movement. Data and cartography by C. Allen. Data sources: BC Data Warehouse. Map compiled in ArcMap 10.2.