

VALIDATING ALTERNATIVE METHODS OF MODELING WILDLIFE
CORRIDORS USING RELOCATION DATA FROM MIGRATING
ELK AND DISPERSING WOLVERINES

by

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of

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ABSTRACT

Habitat loss and fragmentation increasingly impede wildlife movements that are essential for the long-term persistence of populations. Wildlife corridors facilitating movement have become a key component of conservation planning as a result. Models are increasingly used to identify likely corridors, but predictions are rarely validated against empirical data, resulting in uncertainty in whether corridors function as intended. This study asks: 1) What is the current state of our ability to predict corridors?, 2) How well do the most common models predict wildlife movement?, 3) Which method performs best?, and 4) How sensitive are models to parameterization decisions? I addressed these questions by synthesizing the corridor modeling literature, modeling migration paths of elk and dispersal paths of wolverines using the two most common corridor models (cost-distance and circuit theory models), validating predicted corridors against relocation data, and analyzing model sensitivity to parameterization. An additional question, 5) What drives habitat selection during long-distance migration and dispersal movements?, is also explored through these analyses. Key findings include: 1) Corridor modeling has progressed enormously in recent years, but model validation has been rare, 2) Corridor models are capable of offering valuable information, but their utility depends on conservation objectives, 3) Relative model performance depends on the match between model assumptions and focal species movement ecology, 4) Both models have similar sensitivity to model parameters, but spatial patterns of sensitivity are unpredictable for circuit theory models, and 5) The drivers of habitat selection during long-distance movements may be similar to those of primary habitat selection, but further research is needed. These studies constitute the most rigorous, comprehensive effort to validate corridor model predictions to date. They are expected to offer guidance for conservation scientists and practitioners as to reasonable expectations for corridor model performance, the importance of selecting methods appropriate to species movement ecology, and which decisions in the modeling process matter most. This work also highlights the need for further collection of data suitable for model validation, broader comparison of corridor models across diverse species and landscapes, and continued study of the ecology of long-distance movements.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

“On the eve of your birth
word of your coming
passed from animal to animal.

The reindeer told the Arctic terns,
who told the humpback whales,
who told the Pacific salmon,

who told the monarch butterflies,
who told the green turtles,
who told the European eel,
who told the busy garden warblers,

and the marvelous news migrated worldwide.”

Excerpt, *On the Day You Were Born*, Debra Frasier

From the earliest age, we learn about long-distance animal movements and develop a sense of wonder for them. Many of these movements are truly iconic. Pronghorn antelope undertake the longest seasonal migration in the contiguous United States, traveling up to 550 km round-trip between winter and summer ranges (Berger 2004). Millions of monarch butterflies make the spectacular, multigenerational trip from Mexico to breeding sites in the U.S. and Canada each year (Brower & Malcolm 1991). Pacific salmon may travel thousands of kilometers from ocean feeding grounds back to their natal rivers to spawn (Dittman & Quinn 1996). Wolverines patrol vast home ranges

and disperse alone over stunning distances in search of new territories (Inman et al. 2009; Inman et al. 2012b).

But these movements are as fragile as they are awe-inspiring. In the course of their migration, pronghorn must negotiate up to 105 fences (Sawyer & Lindzey 2000). Monarchs' migration success is dependent upon the availability of stopover sites in three countries (Brower & Malcolm 1991). Movement of salmon is increasingly threatened by hydropower and logging development (Nehlsen et al. 1991). Wolverine dispersal brings the rare, evasive carnivore into contact with roads and urban areas (Inman et al. 2009).

Habitat loss and fragmentation due to expansion of human populations are widely agreed to pose the single greatest threat to biodiversity, both within the United States (Wilcove et al. 1998) and worldwide (Hilton-Taylor 2000; Sala et al. 2000). Concern for the effects of land use change on the ability of animals to move across the landscape has grown (Theobald et al. 2011, references therein), and protection of corridors, defined broadly as regions of the landscape that facilitate movement (Chetkiewicz et al. 2006), has emerged as an important component of biodiversity conservation (Crooks & Sanjayan 2006; Hilty et al. 2006).

A growing number of national and global organizations, including Wildlife Conservation Society, The Wildlands Network, World Wildlife Fund, Yellowstone-To-Yukon, and American Wildlands, are devoted entirely or in part to preservation of connectivity for wildlife movement. Beyond the non-profit conservation world, the Freedom To Roam campaign initiated by clothing and gear company Patagonia likewise aims to conserve wildlife corridors, and the Western Governors' Association, a non-

partisan organization of the governors of 22 U.S. Western states and territories, has undertaken a Wildlife Corridors Initiative to identify and protect key linkages in the American West (WGA 2008). Corridor conservation has even gained public awareness through major news sources including the New York Times (Robbins 2008), Los Angeles Times (Kelly 2009), National Public Radio (Gorn 2009; LoMonaco 2007), and National Geographic (Ogodo 2009; Sekercioglu 2012; Ward 2012).

Given this broad enthusiasm for wildlife corridors and their expected contribution to the long-term persistence of populations, it is crucial that corridor planning is effective and defensible, making use of reliable tools and sound science to identify and conserve key areas supporting wildlife movement and ensuring that corridors function as intended. While the ecological literature has exploded with methods for identifying potential corridors based on species preferences for landscape attributes, few of these methods have been tested against empirical movement data, and then only rarely (Chapter 2). Failure to determine the extent to which predicted corridors actually align with the movements they are intended to support greatly limits confidence in and defensibility of the use of corridor modeling tools in conservation planning.

The primary objective of this dissertation is to determine how well the predictions of corridor models align with observed patterns of wildlife movement. I use two of the most commonly applied corridor modeling approaches to predict two long-distance movement processes, migration of elk and dispersal of wolverines. I then validate these predictions using telemetry data representing actual movement paths. Through these analyses, I also explore neglected aspects of focal species movement ecology. The

results of this work are expected to provide conservation practitioners with valuable information concerning the predictive capabilities of corridor models as well as key considerations in the selection of the most appropriate modeling approach for a given focal species and modeling objective, thereby supporting sound, defensible application of corridor models to conservation planning.

Organization of the Dissertation

This brief introductory chapter precedes four chapters containing the bulk of this dissertation, which are followed by a final chapter presenting conclusions and directions for future research.

Chapter 2 assesses the current status of our ability to predict locations of wildlife corridors for conservation planning purposes. I summarize and compare available methods for modeling connectivity, review the extent to which these methods have been applied to on-the-ground conservation planning, and discuss the use of genetic data and location data to validate predictions of connectivity models. This chapter establishes the dire need for connectivity model validation studies like those presented in Chapters 3-5.

Chapters 3 and 4 validate the predictive performance of connectivity models, testing the extent to which common modeling approaches are able to predict observed movement paths as represented by telemetry data. Each compares the predictive capacity of the two most common connectivity modeling approaches, cost-distance models (Walker & Craighead 1997) and circuit theory models (McRae et al. 2008).

Chapter 3 uses these models to predict and validate migration paths of elk (*Cervus elaphus*) in the Madison Valley of southwest Montana. In the course of quantifying how accurately migration movements can be predicted by connectivity models and determining which model best predicts migration paths, this chapter also considers the drivers of habitat selection during elk migration. Specifically, this chapter explores whether forage quality and availability influence selection of elk migration paths as they do other aspects of elk movement ecology.

Chapter 4 applies the connectivity models of interest to dispersal paths of wolverines (*Gulo gulo*) throughout the Greater Yellowstone Ecosystem. Similarly to Chapter 3, the ability of connectivity models to predict dispersal movements is quantified and the relative performance of cost-distance and circuit theory models is determined, with the expectation that model performance may differ substantially in this setting given the fundamental differences between the movement states of migration and dispersal. This chapter also explores the drivers of habitat selection during dispersal, providing a preliminary assessment of whether patterns of habitat selection differ between wolverine home range movements and wolverine dispersal.

Chapter 5 assesses the sensitivity of connectivity model predictions to the many parameterization decisions that must be made in the course of the modeling process. Optimal model parameterization is not always clear; it is therefore important for conservation practitioners to understand which decisions are likely to have the greatest impact on model performance and to allocate resources to data collection and model building accordingly. This chapter also explores spatial patterns in variability among

models with different parameterizations, with important implications for use of cost-distance and circuit theory models in conservation planning.

Together, these chapters constitute the most comprehensive and rigorous effort to date to validate corridor model performance, addressing an urgent need in the rapidly progressing field of connectivity conservation.

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CHAPTER 2

WHAT IS THE CURRENT STATE OF OUR ABILITY TO MODEL WILDLIFE CORRIDORS? AN OVERVIEW OF THE DEVELOPMENT, APPLICATION, AND VALIDATION OF CONNECTIVITY MODELS

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2, 3, 4, and 5

Author: Meredith M. Rainey

Contributions: Determined the scope of the synthesis. Conducted the literature review.
Wrote the manuscript.

Co-author: Dr. Andrew J. Hansen

Contributions: Provided feedback on the scope of the synthesis and comments on the
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Abstract

Habitat loss and fragmentation increasingly threaten to sever wildlife movement processes crucial to long-term species persistence, and these effects are expected to be compounded by climate change. As a result, designation of regions of the landscape that facilitate wildlife movement as corridors has emerged as a key conservation strategy. The variety of models designed to predict likely corridors has exploded in the scientific literature in recent years, and these models are increasingly applied to on-the-ground planning efforts. However, they have rarely seen validation against empirical data to determine the extent to which predicted corridors align with actual wildlife movements. This critical oversight limits the instructiveness and defensiveness of corridor model predictions in conservation planning. This review seeks to clarify the current state of our ability to predict wildlife corridors by comparing available methods of modeling corridors, summarizing application of models to conservation planning, and examining efforts to validate model predictions against empirical data. This review is intended to guide practitioners interested in using models to predict corridors, support application of corridor models to conservation and management objectives in as informed and appropriate a manner as possible, and encourage further collection and use of empirical data to investigate the predictive performance of corridor models.

Introduction

Habitat loss and fragmentation are widely agreed to constitute the single greatest threat to biodiversity, both within the United States (Wilcove et al. 1998) and worldwide (Hilton-Taylor 2000; Sala et al. 2000). Climate change is expected to progressively compound these effects (Opdam & Wascher 2004; Sala et al. 2000; Travis 2003). While protected areas such as national parks have long been the cornerstone of biodiversity conservation, it has become increasingly clear that these islands of intact habitat in a sea of human land use are not sufficient to sustain viable populations of many species in the face of these combined threats (Hansen & DeFries 2007b; Novacek & Cleland 2001). Land use intensification around reserves in recent decades (Hansen et al. 2004) has decreased their effectiveness via a variety of ecological mechanisms linking them to the degraded ecosystems in which they are embedded (Hansen & DeFries 2007a) and has increased isolation among reserves. Moreover, habitat loss beyond reserve borders may inhibit species range shifts in response to climate change, trapping them in deteriorating climatic conditions (Opdam & Wascher 2004; Travis 2003).

Conservation strategies that seek to maintain biodiversity in human-modified landscapes beyond protected area borders are now considered critical, particularly those aiming to maintain or restore connectivity between remaining habitat patches (Daily et al. 2003; Hilty et al. 2006; Miller & Hobbs 2002; Rosenzweig 2003; Taylor et al. 2006). Connectivity, defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993), is crucial for the maintenance of movement processes occurring on multiple spatiotemporal scales. Over individual

lifespans, daily and seasonal movements among patches ensure access to required resources (Dingle 1996); over generations, dispersal maintains metapopulation structure and provides rescue effects from population extinction (Harrison 1994); and over tens of generations, long-range dispersal sustains genetic diversity and the ability to respond to long-term trends including climate change (Frankel & Soule 1981).

As recognition of the importance of connectivity to biological conservation has grown, so has enthusiasm for the establishment of wildlife corridors to maintain it. Corridors have been defined most broadly as “regions of the landscape that facilitate the flow or movement of individuals, genes and ecological processes” (Chetkiewicz et al. 2006). Diverse approaches to identifying these regions have been proposed and implemented, ranging from expert workshops in which areas known to support wildlife movement are hand-selected on printed maps (e.g., Johnston et al. 2008) to computationally-intensive simulation models incorporating satellite-derived habitat data and empirical estimates of focal species movement characteristics (e.g., Hargrove et al. 2005). New methods continue to be developed, and their use in on-the-ground conservation planning and management is expanding.

It is therefore alarming that few studies have sought to validate the predictions made by corridor models against empirical data (Sawyer et al. 2011), and even fewer studies have attempted to comparatively evaluate the predictive accuracy of multiple corridor models. Failure to quantify the extent to which corridor models capture actual wildlife movements that predicted corridors are intended to maintain has thus far been a major oversight in the study of landscape connectivity. This knowledge gap must be

addressed in order for application of corridor models to conservation planning and management goals to be instructive and defensible.

The purpose of this review is to clarify the current state of our ability to predictively model wildlife corridors for conservation planning. I compare available methods of modeling corridors, summarize application of these models in conservation practice, and examine efforts to validate the models against empirical data. This review is intended to serve as a guide for those interested in using models for corridor prediction, to support application of corridor models to conservation and management objectives in as informed and appropriate a manner as possible, and to encourage further collection and use of empirical data to investigate the predictive performance of corridor models.

Approaches to Modeling Connectivity

Methods of identifying landscape elements expected to provide connectivity have progressed enormously over the past two decades. In 1991, Soule and Gilpin defined corridors very simply as linear landscape elements facilitating movement among habitat patches (Soule & Gilpin 1991). In keeping with this view, many early studies focused on monitoring the efficacy of *de facto* corridors such as fencerows, roadside vegetation, and linear remnants of logged forests (e.g., Bennett et al. 1994; Haas 1995; Lindenmayer et al. 1993; Wegner & Merriam 1990). Many researchers also pursued theoretical work on relationships between connectivity and landscape pattern in artificial landscapes composed strictly of habitat and non-habitat (Henein et al. 1998; e.g., Turner et al. 1993; With 1997; With & King 1999). These approaches' treatment of the matrix surrounding

patches and simple corridors as uniformly hostile stemmed from their roots in island biogeography (MacArthur & Wilson 1967) and metapopulation theory (Hanski & Gilpin 1991). A break from this paradigm was needed to effectively study connectivity of real landscapes exhibiting far greater complexity.

In 1996, Gustafson and Gardner demonstrated the effects of matrix heterogeneity and species-specific responses to the landscape on connectivity (Gustafson & Gardner 1996). They simulated the movement of a model species with complex habitat preferences through a real, non-binary landscape and revealed that “corridors are often diffuse and difficult to identify from structural features of the landscape”. This study illustrated the utility of Taylor’s (1993) general and now widely accepted definition of connectivity as “the degree to which the landscape facilitates or impedes movement”, which imposes no restrictions on the configuration or physical properties of what constitutes a corridor. The more recent distinction between functional and structural connectivity (Tischendorf & Fahrig 2000) further emphasizes the role of species-specific perception and behavior in determining what serves as an effective linkage.

Progress in predictive corridor modeling has relied heavily on advances in geographic information system (GIS) software, computing power, and the quality and availability of remote sensing data, which together have allowed researchers to map and analyze the combined, species-specific effects of diverse habitat factors on movement through the landscape at increasingly high spatial resolution and extent. A multitude of spatially explicit modeling approaches have now been presented, all of which are in theory capable of predicting locations of corridors in complex landscapes. However,

most have seen no validation against empirical data, and comparisons among methods have been few and cursory.

To my knowledge, no comprehensive review of existing corridor models has yet been presented. Here I summarize all known approaches to predicting locations of wildlife corridors in real landscapes. In general, these models require a resistance surface, which can be defined as a spatial layer assigning a value to each map cell representing the degree to which the characteristics of the cell impede movement of a focal species. Resistance may be estimated by either expert opinion (e.g., Adriaensen et al. 2003; Chardon et al. 2003; Larue & Nielsen 2008) or a data-based statistical model (Chetkiewicz et al. 2006; e.g., Coulon et al. 2008; Kindall & Van Manen 2007; reviewed in Zeller et al. 2012). Corridor models then quantify each cell's relative probability of movement or relative ease of movement between designated endpoints across this resistance surface. While three modeling approaches deviate from this formula, I include them here for completeness and comparison. I summarize each model's premise, core assumptions, interpretation, data requirements, and limitations (Table 2.1 and Fig. 2.1), with the goal of clarifying the range of modeling approaches available to conservation scientists and practitioners and helping to inform selection of the most appropriate model for a given application.

Connectivity Models

Cost-distance models, or least cost distance models, have been the most commonly used (e.g., Adriaensen et al. 2003; Craighead et al. 2001; Hootner et al. 2000; Larue & Nielsen 2008; Richard & Armstrong 2010; Singleton et al. 2002; Walker &

Craighead 1997) and are based on Dijkstra's algorithm, which solves the shortest path problem in graph theory by finding the path with the lowest cost-weighted distance between a source and any destination (Dijkstra 1959). Least-cost distance methods are thus able to balance travel distance among habitat patches and exposure to unsuitable habitat (Walker & Craighead 1997). Least cost paths offer the shortest cumulative cost-weighted distance between a source and destination and are thus considered optimal routes, but these single pixel-width paths alone provide minimal guidance for conservation planning. A more complete picture is obtained by produced a complete corridor surface, in which all cells are assigned the cost-weighted distance value of the least costly path passing through it, or by including all paths with cost-weighted distance values below a chosen cutoff value (Fig. 2.1a). This approach allows assessment of corridor width, identification of potential bottlenecks and alternative routes, and quantification of the contribution of any cell in the landscape to connectivity. Cost-distance models assume that dispersers have perfect knowledge of the entire landscape. Similarly, these models do not assume that cost-distance values are proportional to probability of use by the focal species; rather, paths with lower cost-weighted distance are simply predicted to offer the best chance for successful dispersal. Model outputs must be interpreted with some caution as this approach does not account for focal species' dispersal capabilities; even least cost paths may be too long to provide connectivity for poor dispersers, and long yet highly suitable routes may be overlooked even when they fall within a vagile species' dispersal range. A further limitation is that

typical application of the model requires designation of a source-destination pair of points or patches, which may be subjective and may limit the scope or scale of a study.

Circuit theory models (McRae 2006; McRae et al. 2008), which are based on electrical circuit theory, have also gained popularity since their introduction. These models make use of the intuitive analogy between movement of individuals through a landscape and movement of charge through an electrical circuit and recognize that greater redundancy in travel routes between nodes (patches) enhances flow between them. This analogy's solid grounding in random walk theory has been demonstrated (Chandra et al. 1997; Doyle & Snell 1984). Circuit theory models treat cells in a landscape as electrical nodes connected to neighboring cells by resistors, with resistance values determined by the cells' landscape resistance values. Consecutive resistors can be linked in series to create a path between two patches, and a single route's total resistance is equivalent to its cost-weighted distance (as in cost-distance models; McRae et al. 2008). Circuit theory models are unique in that when all possible paths among patches are treated as resistors connected in parallel, a measure of effective cumulative resistance is obtained that decreases with increasing numbers of paths. Circuit theory models thus account for the positive effects of path redundancy on connectivity. Resulting per-cell measures of current flow across the landscape reflect the probability of movement of individual random walkers through a given cell (Fig. 2.1b), quantitatively identifying important bottlenecks to dispersal. Conversely, this measure may discount broad swaths of highly suitable habitat because current passing through any particular cell is low. Unlike cost-distance models, circuit theory models assume that dispersers only perceive the landscape

within a 1-cell radius of their current location. The models are, however, similar in their limitations. Circuit theory models do not account for dispersal distance limits, and they require designation of source-destination pairs. Furthermore, computational intensity increases exponentially with number of cells in the landscape, limiting the size of landscapes to which this model can be applied.

Network flow models (Ahuja et al. 1993; Carroll et al. 2011; Phillips et al. 2008) are similar to circuit theory models in many ways, but their outputs are considered more analogous to the flow of water through a set of pipes (Carroll et al. 2011). Rather than quantifying the probability of movement across the landscape, they solve an optimization problem, the key objective of which is to maximize flow (of dispersers, in this case) through the landscape between a source and a destination. Network flow model outputs (Fig. 2.1c) are thus more constrained than those of circuit theory; paths that do not contribute to increasing the total flow from source to destination are given no value, whereas the random movement of current (i.e., dispersers) in circuit theory models results in all cells typically being attributed some probability of movement. One advantage of network flow models is their ability to consider landscape resistance and other cost factors (e.g., monetary cost) separately in the context of a maximum flow-minimum cost problem (Carroll et al. 2011). Flow can be maximized given the constraints imposed by landscape resistance, then the least financially costly of potentially numerous maximum flow solutions can be selected. This approach shares the limitations of circuit theory models: dispersal distance is not considered, source-destination pairs must be designated, and computational intensity increases exponentially with landscape size.

Resistant kernel models (Compton et al. 2007; Cushman et al. 2012) are a hybrid between kernel density estimation methods and least cost distance models. A kernel density function (Silverman 1986; Worton 1989) is calculated representing the probability that an individual dispersing from the focal cell will arrive at any other cell in the landscape given its estimated dispersal ability. The least cost distance algorithm is then extended to a multidirectional approach in which the functional distance from a focal cell to every other cell in the landscape is calculated. The “least cost kernel” for each focal cell representing a source of dispersers is produced by scaling these functional distances by the kernel density function. Summing across all least cost kernels produces the resistant kernel estimation, which is essentially a kernel density surface whose values are reduced in highly resistant portions of the landscape (Fig. 2.1d; Compton et al. 2007). The model assumes that probability of dispersal decreases with distance from a source location along a Gaussian dispersal curve, and, as currently applied, assumes that all sources contribute dispersers equally, failing to incorporate source-sink dynamics. This model is unique thus far in that it explicitly incorporates focal species’ dispersal capabilities and does not require (or allow) designation of individual source-destination pairs. Instead, the method is designed to capture landscape-wide patterns of connectivity considered more relevant to conservation of population-level processes.

Random walk simulation models (Gustafson & Gardner 1996; Hargrove et al. 2005; Moody et al. 2011; Tracey & Crooks 2004; Vuilleumier & Metzger 2006) imbue a set of random walkers with user-specified traits that shape their stochastic movements from source patches across a landscape in search of destination patches. Overlaying the

results of these walkers' paths produces a probabilistic corridor map emphasizing sites frequented by many individuals (Fig. 2.1e). Assigned traits may include habitat type preferences, habitat-specific mortality rates, dispersal capabilities, and directional tendencies. Walkers are generally assumed to only perceive the landscape within a 1-cell radius. While simulation models are capable of incorporating more details of focal species movement ecology than any other approach, this complexity may make them highly sensitive to model parameterization and intensive in terms of data and computational requirements. Simulation models are typically further limited in that they require a categorical rather than continuous landscape resistance surface.

The *cost-benefit approach* (Drielsma et al. 2007; Scotts & Drielsma 2003) presents an alternative solution to the problem of mapping landscape-wide patterns of connectivity. Least cost paths are calculated between source-destination pairs that are iteratively drawn at random from a pool of source and destination cells. These many pair-wise least cost paths are overlaid to produce a "link value" surface quantifying the contribution a given site makes to landscape connectivity (Fig. 2.1f). By compiling an output surface composed entirely of paths assumed to be most ecologically efficient for a given source-destination pair, this method is thought to avoid assigning value to features that do not contribute to connectivity. However, this means that the model typically does not produce a continuous surface in which the connectivity value of every cell in the landscape is quantified. Like cost-distance models, this approach assumes that dispersers have perfect knowledge of the landscape. Though this option does not yet seem to have been implemented, a maximum Euclidian or cost-weighted distance can be specified such

that least cost paths exceeding this dispersal limit do not contribute to the final model surface.

The *Universal Corridor Network Simulator* (UNICOR; Landguth et al. 2012) is formulated similarly to the cost-benefit model. It uses Dijkstra's (1959) algorithm to find least cost paths connecting every pair of source locations in the landscape, smooths these paths according to a probability density function to account for random deviation of dispersers, and combines these smoothed paths to form a density map (Fig. 2.1g). This model generally has the same assumptions and limitations as the cost-benefit approach, but differs in its application of a smoother to each pair-wise least cost path. This step may be useful in that it accounts to some extent for movements of dispersers that do not strictly follow predicted routes, but it is probably overly simplistic to assume that probability of use of least cost paths decreases as a simple function of distance.

Three additional modeling approaches are presented in the literature and pertain to identification of wildlife corridors, but they are set apart here to emphasize that they do not adhere to the general form of the methods above, and, more importantly, none of these models are capable of predicting locations of corridors in the landscape based solely on estimates of species responses to habitat characteristics. They are thus special cases presented only for completeness and for comparison with the above methods.

The *Brownian bridge movement model* (Horne et al. 2007; Kranstauber et al. 2012; Sawyer et al. 2009) is defined as a “continuous-time stochastic model of movement in which the probability of being in an area is conditioned on starting and ending locations, the elapsed time between these points, and mobility or speed of movement”

(Fig. 2.1h; Horne et al. 2007). It is used to model expected movement between known positions collected at relatively frequent intervals (e.g., by GPS collars) so as to create a continuous probabilistic path from point locations. Interpolated path surfaces for multiple individuals can also be combined to build a population-level estimate of space use (Horne et al. 2007; Sawyer et al. 2009). This approach is unique in that it does not require (nor is it currently able to utilize) a landscape resistance surface, while instead requiring relatively high quality data from animal movements. It is therefore suitable for rather different applications than the previously discussed models (e.g., estimating space and resource utilization).

Mathematical morphology (Vogt et al. 2009; Vogt et al. 2007) is not a predictive connectivity model *per se*, but rather a classification tool that can aid in differentiating landscape elements that actually contribute to structural connectivity from those that form “corridors to nowhere” or loops back to a single core patch. The method applies a series of mathematical operators (termed erosion, dilation, and anchored homotopic skeletonization; see Vogt et al. 2007 for details) to a binary habitat map to identify up to nine mutually exclusive thematic classes, including corridors (termed bridges; Fig. 2.1i). It may be useful in, for example, identifying complete dispersal paths from simulation model outputs consisting of many rather chaotic movements, but it cannot alone predict areas important for connectivity.

Graph theory models (Bunn et al. 2000; Urban & Keitt 2001) create simplified representations of landscapes in which patches are represented as nodes (points) and corridors are represented as edges (lines). The simplicity of graph representations, which

are well developed in other fields concerned with connectivity (e.g., computer science, transportation, social network theory), allows the use of highly efficient graph metric algorithms quantifying, for example, landscape- and patch-level connectivity and the importance of individual patches and corridors (e.g., Laita et al. 2011; Minor & Urban 2008). While useful for quantifying these emergent properties of patch-corridor networks, graphs are not spatially explicit and are not intended to predict *locations* of corridors in landscapes. However, they may be derived from most of the above methods by using the ‘effective’ or ‘functional’ distances calculated by these methods to define graph edge lengths rather than Euclidian distances. For example, edges may be assigned cost-weighted distance values from a cost-distance model (Fig. 2.1j; Theobald et al. 2011) or cumulative resistance values from a circuit theory model. These values are expected to be more ecologically appropriate than Euclidian distances and to yield more ecologically meaningful graph-based connectivity metrics.

This summary is intended to facilitate comparison of available corridor models in terms of their assumptions, formulation, and limitations, which is important for selecting the most appropriate approach for a proposed study or application given its questions of interest, objectives, and available data. For example, the cost-distance model assumption that individuals have perfect knowledge of the landscape may be best suited to modeling regular foraging movements among patches in a landscape that has been thoroughly explored by its inhabitants over the course of their lifetimes, while the circuit theory model assumption of no landscape knowledge beyond a 1-cell radius may be more appropriate for dispersers moving through novel environments. Similarly, cost-distance

and circuit theory models are well-suited to modeling pair-wise connectivity among defined habitat patches, a common scenario in conservation practice, while resistant-kernel methods may be more useful in cases in which patches are not well-defined, avoiding the need to subjectively define them.

What is perhaps most needed in the study and practice of connectivity conservation is the ability to compare corridor modeling approaches in terms of their ability to predict actual wildlife movements, as quantified by validation against empirical data. Comparative validation of multiple modeling approaches in many species-landscape contexts is expected to clarify which models' algorithms and assumptions tend to best capture different types of movements by different types of species in different types of landscapes. The need for these analyses becomes more urgent as the range of modeling approaches to choose from for use in conservation planning grows, and as their application becomes more frequent.

Application of Connectivity Models

As emphasis on connectivity as a critical component of biodiversity conservation has grown, so has the use of models to identify corridors expected to provide it. While most of the above models have only been developed and applied in an academic context, growing demand among conservation practitioners and decision makers for the most scientifically advanced and defensible methods available is likely to lead to increased exploration of alternative approaches for on-the-ground application. Here I summarize the extent to which the above corridor models have been applied in a conservation

planning context, reiterating the need for model validation efforts to ensure that corridor models are capable of providing sound guidance for corridor designation.

Cost-distance (least cost distance) models have seen the most extensive use in applied conservation planning, guiding many state and regional planning efforts. The state of Florida was one of the first to identify a statewide ecological network of potential corridors, using cost-distance methods to do so (Hector et al. 2000). The Western Governors' Association, which includes 22 western states and territories, has supported an initiative to identify and protect wildlife corridors across the West. California (Spencer et al. 2010), Colorado (SREP 2005), Montana (MT FWP 2011), and Washington (WHCWG 2010) have each identified corridors for a range of focal species using cost-distance methods, and given the impetus to employ consistent methodology throughout the region, many other states are likely to follow suit. Statewide corridor networks have also been identified based on cost-distance models to maintain forest connectivity in New York state (NYSDEC 2010) and lynx connectivity in Utah (Bates & Jones 2007). Other large-scale projects utilizing cost-distance methods include the South Coast Ecoregion Missing Linkages of California (SCW 2008) and a Conservation Area Design for the Cedar-Hemlock Forests of North America (Craighead & Cross 2005). Smaller-scale corridor efforts such as the Bozeman Pass corridor project in Montana (Craighead et al. 2001; Davidson 2003) and the Snoqualmie Pass linkage assessment in Washington state (Singleton & Lehmkuhl 2000), which focus on maintaining wildlife movements across an interstate highway, have relied on cost-distance methods as well.

Circuit theory models are also beginning to see use in conservation planning. The Wildlife Conservation Society (WCS; Aune et al. 2011) is in the process of prioritizing conservation action for wolverines based on circuit theory models of regional-scale wolverine connectivity. The Nevada Wilderness Project has also employed circuit theory models to guide identification of corridors (Lawler 2010).

More diverse approaches to connectivity modeling appear in recommendation reports for corridor networks that have not yet been implemented and in proposals for similar studies with application potential. Cost-distance models were used by Cypher et al. (2007) to make recommendations for connectivity components of a San Joaquin Kit Fox Recovery Plan for central California and are proposed for use in a Wildlands Network connectivity project (Sutherland et al. 2012). Recent recommendations made by the Conservation Biology Institute (Rustigian-Romsos & Spencer 2012) for maintaining fisher connectivity in eastern California were based on both cost-distance and circuit theory models. Moody et al. (2011) utilized circuit theory as well as individual-based simulation models to build recommendations and management tools for conservation of rare, threatened, and endangered species around military installations. Simulation models were also used to study large carnivore connectivity in coastal southern California and make management recommendations for the Nature Conservancy and the California Department of Fish and Game (Tracey & Crooks 2004). Circuit theory is further proposed to guide a regional conservation needs assessment for 13 northeast states, along with resistant kernel models (Anderson et al. 2011).

As connectivity models continue to see increased application to on-the-ground conservation planning, and particularly as the diversity of modeling approaches that are available and that are applied expands, it becomes ever more critical to validate the predictions of these models against empirical data to ensure that they constitute effective tools for allocation of limited conservation resources.

Validation of Connectivity Models

Validation of connectivity models using empirical data has been rare. Failure to fully validate the performance of connectivity models severely limits confidence in their application and their capacity to guide sound conservation planning. This knowledge gap is particularly alarming in that many of the above corridor models are exceedingly easy to implement without full understanding of their assumptions and limitations, potentially resulting in insufficient skepticism toward their results. Furthermore, as new modeling approaches are developed, they are often touted as the solution to limitations of existing methods, leading to confusion as to selection of the most appropriate model for a given application and demanding comparative evaluation of model predictive performance in a variety of modeling contexts.

Two broad classes of empirical data, genetic data and location data, can be used to validate connectivity models (Sawyer et al. 2011; Spear et al. 2010). Genetic data capture spatial genetic structure across the landscape by quantifying genetic relationships among individuals sampled from multiple locations, which are then correlated with modeled patterns of connectivity (Holderegger & Wagner 2008; Manel et al. 2003; Spear

et al. 2010). Location data sample use of the landscape during movements potentially relevant to connectivity, and include GPS and VHF telemetry as well as occurrence data obtained from historical records, ground or aerial observation, trapping, and noninvasive sampling via hair snares, scat collection, track plates, or remotely triggered wildlife cameras. The extent to which predictive corridor surfaces coincide with these sampled points can then be assessed. Each type of data reflects different aspects of landscape connectivity and both provide incomplete representations of connectivity, but they are incomplete in unique and often complementary ways, as discussed below. Thus, each data type is relevant to connectivity model validation in different settings. Here I contrast these data types, summarize the methods by which each is applied to connectivity model validation, review previous studies utilizing each data type for model validation, and make recommendations for selection of appropriate validation datasets.

Genetic Data

Overview: The field of landscape genetics uses genetic and statistical tools to determine spatial genetic patterns among individuals and correlate these patterns with landscape features (Manel et al. 2003). Genetic distances among sampled individuals of a focal species capture the cumulative result of movement processes over time (Spear et al. 2010). Individuals that are separated by small genetic distances, or degrees of divergence in the sequence of a given genetic locus, are assumed to have maintained this genetic similarity through high rates of gene flow via dispersal among their respective populations or subpopulations, indicating high connectivity. Individuals separated by

large genetic distances are assumed to have experienced genetic drift over time that has been counteracted with little to no gene flow, indicating low connectivity.

Genetic data capture only the subset of wildlife movements contributing to gene flow, in which individuals dispersed and survived long enough to reproduce (Spear et al. 2010). They do not capture failed dispersal attempts, completed dispersal events that were not followed by reproduction, exploratory movements, seasonal migration movements, or continuous movements among local patches. Thus, while they are not appropriate for validating models of, for example, seasonal migration corridors, they are well-suited for validating models of broader-scale connectivity among populations with applications aiming to maintain gene flow over time.

Spatial genetic patterns represent the cumulative effects of connectivity over time and are thus likely to be influenced by past demographic events and legacy effects of previous landscape conditions (Anderson et al. 2010; Harding et al. 1998; James et al. 2007). As a result, they are generally a poor representation of current relationships between landscape features and genetic connectivity in dynamic landscapes due to time lags between landscape change (e.g., construction of road barriers) and the appearance of evidence of altered gene flow (Anderson et al. 2010). Thus, again, genetic data may be best suited for validation of models intended to capture connectivity across broad spatiotemporal scales. However, the absolute time scale represented depends on the genetic loci sampled (Balkenhol et al. 2009; Holderegger & Wagner 2008). Mitochondrial loci are highly conserved, accumulating mutations slowly and thus capturing historical patterns of connectivity. In contrast, less-conserved microsatellite

loci capture more contemporary patterns and are expected to reflect responses to more recent landscape change. New approaches in which, for example, DNA is sampled from a focal species' rapidly evolving and rapidly transmitted parasites rather than the focal species itself, may further increase the temporal resolution of genetic data (Wittekindt et al. 2010).

Model Validation: The goal of landscape genetics is generally to understand how the landscape structures populations via patterns and processes of gene flow (Manel et al. 2003), and in these analyses the stated use of genetic data is to provide a standard against which to optimize the landscape resistance surface utilized by connectivity models (Spear et al. 2010), not to validate connectivity models themselves. However, this optimization process is generally based on effective distance metrics (e.g., least cost-weighted distance, cumulative resistance) that are defined by applying a connectivity model to the resistance surface of interest (Table 2.2). Thus, while genetic data do not directly reveal whether individuals have utilized predicted corridors in the way that location data do, they provide a test of corridor predictions in that corridors summarized by effective distances that best match patterns of genetic distances are expected to be most representative of movement paths over time.

Comparisons between patterns of genetic distance and patterns of resistance as measured by the corridor model of interest (e.g., least cost-weighted distance from cost-distance models, cumulative resistance from circuit theory models) are most often made based on Mantel tests, which measure the degree of association between two dissimilarity matrices (genetic distances and predicted effective distances; Mantel 1967; Smouse et al.

1986). Other methods such as AIC comparisons of alternative regression models also appear in the literature (Table 2.2). As these methods are well established and discussed extensively elsewhere (e.g., Manel et al. 2003; Spear et al. 2010), I do not review them in detail here. Similarly, interested readers are directed to Anderson et al. (2010) for detailed discussion of selection of sampling scales and genetic markers appropriate to questions of interest.

Challenges and Limitations: Several challenges arise in the use of genetic data for connectivity model validation stemming from difficulties in capturing all relevant influences on observed spatial genetic patterns. Depending on the genetic loci sampled and the rate of landscape change in the study area, genetic patterns may not be representative of connectivity in the time period of interest and may not match the time period represented by spatial datasets defining resistance surfaces (Anderson et al. 2010; Spear et al. 2010). Furthermore, time lags between landscape change altering connectivity and a genetic signature of this change may be difficult to estimate and require careful selection of appropriate genetic loci and statistical methods (Anderson et al. 2010). Gene flow and resulting genetic patterns are also expected to be influenced by factors other than landscape features, including population size and resulting rates of genetic drift (Hartl & Clark 1997), source-sink dynamics (Manier & Arnold 2005; Pulliam 1988), and the spatial grain of sampling and analysis (Anderson et al. 2010; Graves et al. 2012), not to mention presence of prey, predators, and competitors.

Perhaps the greatest limitation in the use of genetic data for validation of connectivity models is that patterns of genetic distances must be compared to patterns of

predicted connectivity obtained by reducing complete corridor surfaces to a single summary measure of each pairwise linkage, e.g., the least cost-weighted distance from cost-distance models or cumulative resistance from circuit theory models. Thus, in addition to providing only an indirect comparison between locations of predicted corridors and focal species' movement paths, genetic data ignore a great deal of information provided by the continuous corridor surfaces produced by most models. Still, summary measures may be sufficient and most suitable for addressing broad patterns of functional connectivity via gene flow, making genetic data a useful standard against which to validate models intended to capture this aspect of connectivity.

Location Data

Overview: Location data provide samples of animal movements that can be directly compared to landscape characteristics and predicted corridor surfaces. They may range from high spatiotemporal resolution real-time GPS relocations to historical occurrence records, potentially encompassing a broad array of movement types and varying considerably in quality and relevance. When collected in appropriate locations and at appropriate spatiotemporal scales, location data can be invaluable for connectivity model validation as they provide a transparent, spatially explicit means of assessing whether a focal species does in fact move across a landscape as predicted.

While genetic data only reflect movements that contribute to gene flow, location data may capture any movement type, including exploratory movements, seasonal migration movements, and continuous home range movements. They are therefore useful

for validation of models intended to identify corridors supporting movements that do not necessarily lead to gene flow. In turn, they may not be useful for validation of modeled corridors intended strictly to provide gene flow, because it is generally difficult to determine whether an individual breeds successfully following dispersal, and this cannot be determined from location data alone. Furthermore, given the logistics and cost often associated with collection of location data, they are likely to be of limited spatial and temporal extent, and due to the short duration of movements of greatest interest for connectivity (e.g., long-distance juvenile dispersal and seasonal migration), most location datasets are unlikely to have captured these movements unless data collection was specifically designed to do so. Therefore, location data tend to be most useful on relatively local scales, and care must be taken in selecting a validation dataset to ensure that movements of interest are in fact represented.

Location data can be thought of as falling along a scale spectrum defined by collection frequency, with high spatiotemporal resolution GPS data at one extreme and independent occurrence samples at the other. High-quality GPS data provide detailed information about movement paths with little uncertainty about an individual's position between relocations, and they are uniquely able to densely sample paths of critical movements such as long-distance migration and dispersal, providing an excellent opportunity to validate models intended to predict these components of connectivity. However, their extent may be very limited. As the time and distance between relocations increases, uncertainty about an individual's movements between relocations increases and the probability of capturing a brief, long-distance movement of interest decreases, but

assembly of many independent occurrence records may provide good spatial coverage for validation of models aimed at depicting broad-scale connectivity.

While location data may have been collected over the course of decades, each location is associated with a discrete point in time, unlike the cumulative nature of a single genetic sample. Therefore, legacy effects and time lags are not expected to be as problematic in assessing agreement between locations and predicted resistance or connectivity surfaces. Care must simply be taken to ensure that resistance surfaces are defined using spatial data that is well-matched to the time period in which location data were collected.

Model Validation: Few examples of connectivity model validation against location data are available in the literature (Table 2.3; Sawyer et al. 2011), and no consistent methodology has emerged, perhaps because quantifying performance of connectivity models using location data is not as straightforward a task as it might seem. Some models produce continuous corridor surfaces assigning a value to each cell in the landscape, while others produce only networks of paths, and few methods are applicable to both. Furthermore, alternative validation approaches test different aspects of predictive performance, and different forms of location data are best suited to different approaches to validation. In addition, some studies have used location data to validate connectivity models while others have validated underlying resistance surfaces. Here I review methods presented in the literature (Table 2.4), concluding with recommendations for selection of appropriate methods for a given application.

I begin with studies that have used location data to validate resistance surfaces rather than connectivity model outputs. Beazley et al. (2005) tested the ability of the resistance surface to predict presence/absence data using a logistic regression model, while Chetkiewicz and Boyce (2009), Pullinger and Johnson (2010), and Wang et al. (2008) assessed resistance surfaces against presence data using a Spearman rank correlation, an approach which calls for further discussion. This method determines the frequencies of locations in a withheld or independent dataset that fall within equal-area ranked bins of cell resistance values in one or more iterations (e.g., via k-fold cross-validation; Fielding & Bell 1997). It is based on the assumption that individuals will be distributed across the landscape proportionally to resistance, defined as the inverse of suitability, such that low resistance areas are occupied more densely than high resistance areas (Boyce et al. 2002; Johnson et al. 2006; Manly et al. 2002). This assumption is reasonable for assessing resistance surfaces against presence data representing habitat occupancy (i.e., home range use), but it is not reasonable for assessing connectivity model surfaces against these data, and it is not reasonable for assessing resistance surfaces against presence data collected during directional movements (as was the case in Pullinger & Johnson 2010). This is because connectivity model predictions and directional movement data are both influenced by distance from a specified source and/or distance to a specified destination, meaning that directional movement data are almost certainly not expected to be distributed across the landscape proportionally to a resistance surface, nor are occupancy data expected to be distributed proportionally to a corridor

surface. This point is critical in use of the Spearman rank correlation to validate model performance using location data.

Some studies utilizing location data for connectivity model validation have done so opportunistically and qualitatively, making general *post hoc* comparisons of model predictions with data that happened to be available from observed highway crossings (Chetkiewicz & Boyce 2009; Meegan & Maehr 2002) and radio telemetry (Epps et al. 2007). While these studies provide some knowledge about model performance and set an important precedent for model validation, future researchers are strongly urged to consciously incorporate rigorous validation of connectivity models into study designs aimed at determining whether a model adequately fulfills its intended purpose.

Only three studies have been explicitly designed to validate connectivity models with location data. Driezen et al. (2007) validated cost-distance models using radio-tracking data from homing movements of displaced hedgehogs. They compared the cumulative cost-weighted distance between an individual's origin and its current location with that of other available points of equal Euclidian distance from the origin. Pullinger & Johnson (2010) used predicted least cost paths for individual caribou migration movements captured by GPS collar data. Observed and predicted paths were compared using several tests based on a path deviation index (PDI), which gives the average distance between the observed path and least cost path. They quantified the absolute PDI, the PDI of the observed path relative to the PDI of a path from a null resistance model, and the PDI of the observed path relative to the PDIs of random paths. Poor (2011) used cost-distance models and circuit theory models to predict migration paths of

GPS-collared pronghorn antelope. Model performance was assessed by defining corridors as the 95th percentile of the connectivity model surface and calculating the percentage of GPS relocations that fell within them.

Each of these approaches has strengths and weaknesses. Driezen et al. (2007) present a rigorous method comparing points in the observed path to points in a distribution of random paths to test the null hypothesis that there is no influence of landscape features or distance on selection of movement paths, but this metric does not have clear practical interpretation indicating to a practitioner the extent to which a model accomplishes its intended purpose. Pullinger and Johnson (2010) likewise create metrics that test the above null hypothesis as well as the second null hypothesis that movements are influenced by distance but not landscape features. However, these metrics suffer from the same lack of practical interpretation and are subject to the poorly justified assumption that distance from the observed path is a good measure of corridor quality. Poor (2010) presents a measure of model performance that is sound, straightforward, and not based solely on the least cost path, but the method requires subjective choice of a corridor cutoff value.

All of these methods fail to utilize the entire connectivity model surface. I address this issue in Chapters 3 and 4 by presenting three new metrics to test the ability of cost-distance and circuit theory models to predict migration paths of elk and dispersal paths of wolverines represented by GPS collar data. After converting connectivity model surfaces to equal area percentiles, I calculate the mean percentile value of cells intersected by points in migration paths. Similarly to the above studies, I also take a

hypothesis testing approach by comparing percentile values assigned to points in observed paths by the model of interest and by a null model, and compare percentile values assigned to points in observed paths versus those in random paths.

Given the diversity of metrics available for validation of connectivity models with location data and lack of consensus in the literature on their use, I recommend applying multiple metrics when possible in order to paint a more complete picture of model performance. Some corridor model outputs consist only of networks of paths, and therefore require use of methods like those employed by Driezen et al. (2007) or Pullinger and Johnson (2010); options are more diverse for models producing continuous surfaces. Each metric has both advantages and disadvantages and captures a unique aspect of model performance, and most metrics are considered to be complementary. A growing body of literature in which comparisons among multiple metrics are made in a variety of modeling contexts is expected to greatly improve understanding of the value and utility of connectivity models and metrics for validating them against location data.

Challenges & Limitations: Due to the diversity of location data that may potentially be used for validation of connectivity models, one must ensure that selected datasets are suitable for the validation objectives at hand. The quality of location data may vary considerably, with implications for their appropriate use in model validation. GPS collar data have relatively good positional accuracy, and the time at which they were collected is known with precision. In contrast, presence data collected by other means such as reports from citizen scientists and recreationists may have poor positional accuracy, and time of observation of historical records may not be known. These

uncertainties may obscure inference when attempting to correlate location data with connectivity based on landscape features and environmental conditions that are heterogeneous in space and time.

Location data are rarely collected for the explicit purpose of capturing long-distance movements important for connectivity. Some datasets will capture these movements regardless of their original purpose; for example, ungulate GPS collar datasets typically span at least one year and thus capture spring and fall migration movements. Use of these data for connectivity model validation, however, should always take into account the purpose and intended scale of the model. A complete ungulate telemetry dataset including both home range and migratory movements may be used to validate a model intended to predict regional-scale connectivity of elk habitat, while a model meant to predict local migration corridors for a specific population of interest should only be validated against data from migration events.

Care must also be taken to ensure that properties of movements captured by location data are consistent with the assumptions of the model being tested. For example, as discussed above, data representing occupancy of home range habitat are appropriate for validation of resistance surfaces, but not connectivity models, while directional movement data are appropriate for validation of connectivity models, but not resistance surfaces.

Conclusions

Conservation scientists and practitioners now recognize the importance of connectivity for the long-term viability of wildlife populations facing habitat loss and fragmentation due to climate and land use change. In response, the diversity of modeling approaches promising to identify locations of key movement corridors has grown considerably, and application of those models to on-the-ground conservation planning appears soon to follow. Comparative validation of these models' predictive abilities is sorely needed to ensure that investment of limited conservation dollars is being guided by sound, reliable methods. While diverse sources of empirical data are available for model validation, these efforts are just beginning to take off and much remains to be learned about selection of appropriate data, how best to apply these data to validation efforts, and which data are best suited to particular modeling objectives, assumptions, and settings.

It is important to convey that not all applications of connectivity models must be validated to be considered sound and of value. Rather, by validating a sample of modeling efforts across diverse focal species, landscapes, and scales, we can begin to approximate the predictive capacity of models and to understand patterns in their relative performance that can guide expectations in other untested applications. Furthermore, validation of broad-scale models predicting connectivity of forested lands (Theobald et al. 2011) or natural landscapes (Theobald et al. 2012) may not be imperative given their primary purpose of simply focusing smaller-scale efforts on broadly-defined areas likely to be important on regional and continental scales, not prescribing precise on-the-ground corridor designation.

Ultimately, diverse validation efforts are expected to help inform conservation planning decisions, improve existing models, and set appropriate expectations concerning the predictive capacity of connectivity models in various settings. It is also hoped that existing datasets appropriate for model validation will continue to be made available for this purpose, and that new datasets tailored to model validation will continue to be collected.

Tables

Table 2.1. Summary of existing approaches to modeling connectivity.

<i>Model</i>	<i>References</i>	<i>Description</i>	<i>Assumptions</i>	<i>Input required</i>	<i>Limitations</i>	<i>Software</i>
Cost-distance	(Chardon et al. 2003; Hootner et al. 2000; Larue & Nielsen 2008; Singleton et al. 2002; Walker & Craighead 1997)	Identifies path(s) that minimize total travel cost (cost-weighted distance) between source and destination	Individuals have perfect knowledge of landscape. No limits on dispersal distance. Least cost paths are most likely to provide for successful movement.	Resistance surface, source & destination points/patches	Requires designation of source-destination pairs. Does not account for dispersal distance limitations or effects of path redundancy on connectivity.	ArcGIS Spatial Analyst (ESRI), Corridor Designer (Majka et al. 2007)
Circuit theory	(Carroll et al. 2011; McRae 2006; McRae et al. 2008; McRae & Shah 2008; Shah & McRae 2008)	Treats landscape as electrical circuit with probability of movement dependent on resistance; accounts for positive effect of path redundancy on connectivity	Individuals only perceive landscape within 1 cell of current location. No limits on dispersal distance.	Resistance surface, source & destination points/patches	Computational intensity increases exponentially with number of cells. Requires designation of source-destination pairs. Does not account for dispersal distance limitations.	CircuitScape (Shah & McRae 2008)
Network flow	(Carroll et al. 2011; Phillips et al. 2008)	Optimization problem identifying distribution of movement across landscape that maximizes flow of dispersers between source and destination	Individuals only perceive landscape within 1 cell of current location. No limits on dispersal distance.	Resistance surface, source & destination points/patches	Computational intensity increases exponentially with number of cells. Requires designation of source-destination pairs. Does not account for dispersal distance limitations.	Connectivity Analysis Toolkit (Carroll et al. 2011)
Resistant kernel	(Compton et al. 2007; Cushman & Landguth 2012)	Hybrid between kernel density estimator and multidirectional least cost distance method on continuous resistance surface	Probability of successful dispersal decreases with distance from source along Gaussian dispersal curve. All sources contribute equally to dispersal.	Resistance surface, source point(s)/patch (es), dispersal function	Models landscape-wide patterns of connectivity, not appropriate for source-destination pairs.	ArcGIS Spatial Analyst & scripts (ESRI, Cushman & Landguth 2012)

Table 2.1 Continued

Cost-benefit approach	(Drielsma et al. 2007)	Iteratively samples pairs of source/destination cells to produce link value map based on cumulative cost-weighted distance values.	Individuals have perfect knowledge of landscape. No limits on dispersal distance. Output paths are ecologically efficient.	Resistance surface, source & destination points/patches, optional dispersal distance limit.	Simplistic manner of accounting for dispersal distance limits. Poor at identifying multiple alternative paths.	Spatial links tool (Drielsma et al. 2007)
Universal Corridor Network Simulator (UNICOR)	(Landguth et al. 2012)	Applies modified least cost path algorithm to all pairs of species locations, combines to form density map	All individuals roughly follow least cost paths smoothed with user-defined probability density function.	Resistance surface, source point(s)/patch(es), dispersal function	Outputs network of (smoothed) paths, not continuous corridor surface.	UNICOR (Landguth et al. 2012)
Random walker simulation	(Gustafson & Gardner 1996; Hargrove et al. 2005; Vuilleumier & Metzger 2006)	Cumulative paths of many simulated random walkers imbued with user-specified movement characteristics produce probabilistic corridor surface.	Individuals only perceive landscape within 1 cell of current location.	Categorical resistance surface, source point(s)/patch(es), walker characteristics (habitat preferences, dispersal distance, etc.)	Intensive in terms of data and computational requirements. Tend to be highly sensitive to model parameterization.	FORTAN model (Gustafson & Gardner 1996), PATH tool (Hargrove et al. 2005), Delphi model (Vuilleumier & Metzger 2006)
Brownian bridge	(Horne et al. 2007; Sawyer et al. 2009)	Continuous-time stochastic model of movement in which probability of being in an area is conditioned on start/end points, elapsed time between points, and mobility/speed.	Movement between relocations has properties of random walk conditional on start/end points.	Movement data collected at frequent intervals, measure of relocation error.	Dependent on movement data collected at frequent intervals. Movement between relocations is assumed to be random; no consideration of focal species or landscape properties.	adehabitat R package (Calenge 2006)
Mathematical morphology	(Vogt et al. 2009; Vogt et al. 2007)	Applies series of mathematical operators to binary landscape map to identify mutually exclusive thematic classes describing geometry of landscape, including corridors.	None	Binary representation of landscape depicting movement habitat vs. nonhabitat.	Simply classification system for distinguishing structurally intact corridors from dead-ends and loops in movement habitat. Requires binary representation of landscape.	Web application (Vogt et al. 2009)

Table 2.2. Use of genetic data for connectivity model validation.

<i>Study</i>	<i>Objective</i>	<i>Use of genetic data</i>	<i>Statistical test used</i>
Stevens et al. 2006	Effects of landscape structure on natterjack toad dispersal and functional connectivity	Optimization of resistance surface based on least-cost distance	Partial Mantel tests
Epps et al. 2007	Predict connectivity and corridor locations for bighorn sheep	Optimization of resistance surface based on least-cost distance	Partial Mantel tests
McRae & Beier 2007	Test circuit theory as an alternative method of predicting patterns of gene flow	Optimization of resistance surface based on least-cost distance and circuit resistance	Partial Mantel tests
Cushman et al. 2008	Identify corridors for American black bears between Canadian border & YNP	Optimization of resistance surface based on least-cost distance	Partial Mantel tests
Wang et al. 2008	Delineate connectivity of spiny rat in a fragmented landscape	Optimization of resistance surface based on least-cost distance	Partial Mantel tests
Wang et al. 2009	Relative habitat-specific dispersal costs for tiger salamander	Optimization of resistance surface based on least-cost distance	Comparison of relative genetic and least-cost distances
Zhu et al. 2010	Influence of landscape features on gene flow in giant pandas	Optimization of resistance surface based on least-cost distance	Partial Mantel tests
Garroway et al. 2011	Landscape impacts on fisher population expansion in Ontario	Optimization of resistance surface based on circuit theory resistance	AIC comparison of linear regression models
Hagerty et al. 2011	Explain isolation patterns of threatened Mojave desert tortoise	Optimization of resistance surface based on least-cost distance and circuit resistance	Partial Mantel tests
Koen et al. 2012	Efficacy of management to maintain American marten connectivity	Optimization of resistance surface based on circuit theory resistance	Partial Mantel tests
Munshi-South 2012	Effect of urban canopy cover on white-footed mouse connectivity in NYC parks	Optimization of resistance surface based on least-cost distance and circuit resistance	Partial Mantel tests
Niedzialkowska et al. 2012	Gene flow and connectivity from translocated red deer	Optimization of resistance surface based on least-cost distance	AIC comparison of multiple regression permutation tests
Pavlova et al. 2012	Model population connectivity in fragmented landscape for Grey Shrike-thrush	Optimization of resistance surface based on circuit theory resistance	Partial Mantel tests

Table 2.3. Use of location data for connectivity model validation.

<i>Study</i>	<i>Objective</i>	<i>Model Output Validated</i>	<i>Location Data Used</i>	<i>Metric Used¹</i>
Meegan & Maehr 2002	Develop regional blueprint to enhance connectivity for Florida panther	Least cost paths	VHF telemetry	Barrier crossing comparison (qualitative)
Beazley et al. 2005	Create spatially explicit conservation design at provincial scale	Resistance surface	Presence/absence (pellets)	Logistic regression
Driezen et al. 2007	Present method to validate results of least-cost analysis	Least cost paths	VHF telemetry	Random path comparison
Eppe et al. 2007	Develop least-cost connectivity models for desert bighorn sheep	Least cost paths	VHF telemetry	Qualitative comparison
Wang et al. 2008	Incorporation of habitat suitability model into connectivity analysis for spiny rat	Resistance surface	Presence (trapping)	k-fold cross validation; Spearman rank
Chetkiewicz & Boyce 2009	Identification of potential corridors for grizzly bears and cougars in fragmented montane landscapes	Least cost paths	Highway crossings	Barrier crossing comparison (qualitative)
		Resistance surface	GPS telemetry	k-fold cross validation; chi-square, Spearman rank, linear regression
Pullinger & Johnson 2010	Prediction of woodland caribou movement paths	Least cost paths	GPS telemetry	Sinuosity, Path Deviation Index
		Resistance surface	GPS telemetry	k-fold cross validation; Spearman rank
Poor 2010	Validate seasonal pronghorn migration corridors	Corridor slices	GPS telemetry	Defined corridor

¹See Table 2.4.

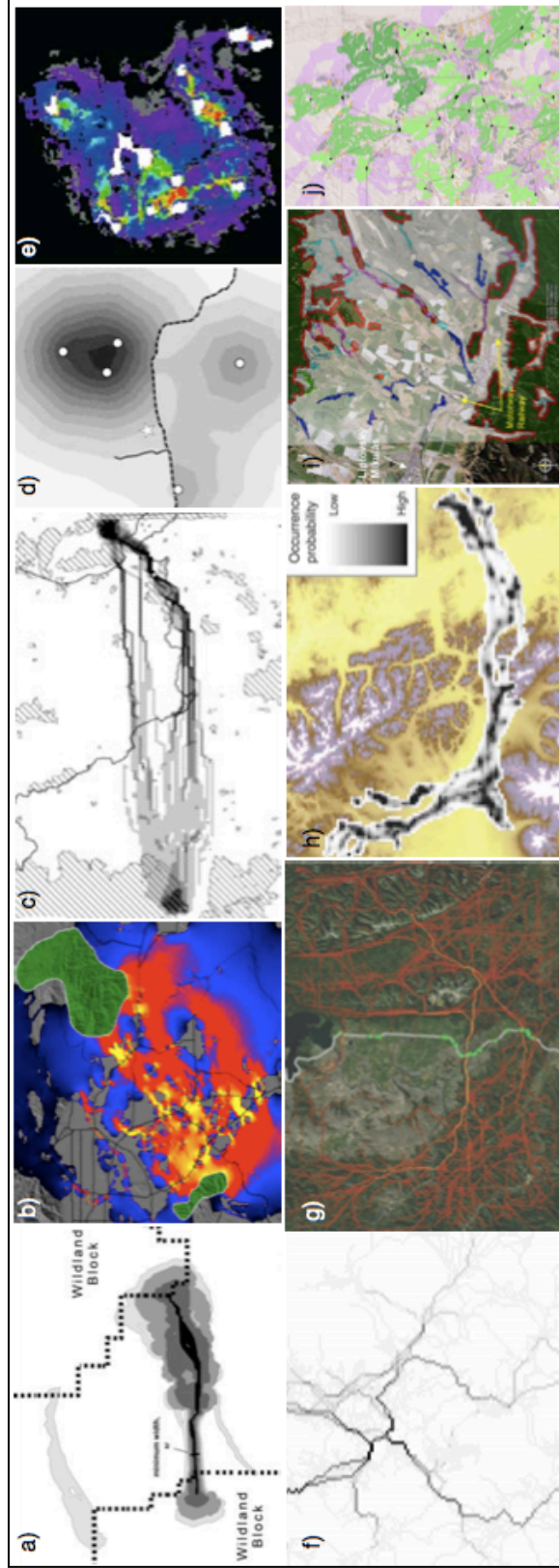
Table 2.4. Metrics for validation of connectivity models against location data.

<i>Metric</i>	<i>Description</i>	<i>References</i>	<i>Advantages</i>	<i>Disadvantages</i>
Spearman rank correlation	Frequency of observed points falling within ranked equal-area bins of modeled cell values	Chetkiewicz & Boyce 2009, Pullinger & Johnson 2010, Wang et al. 2008	Precedence in literature; Straightforward interpretation; Uses familiar statistical test	Only appropriate for validating resistance surface; should not be used with directional movement data or connectivity models
Barrier crossing comparison	Distance between observed and least cost path predicted barrier crossings	Chetkiewicz & Boyce 2009, Meegan & Maehr 2002	Relevant for barrier mitigation applications; Able to utilize highway crossing data	Highly restricted test of model performance; Requires assumption that closer to observed crossing is better
Defined corridor	Percentage of observed points falling within corridor defined by specified cutoff value	Poor 2010, Rainey Chapters 3-5	Straightforward interpretation for conservation planning	Restricted test of model performance; Choice of cutoff value is subjective/arbitrary
Path deviation index (PDI)	Average distance between observed and predicted path	Pullinger & Johnson 2010	Useful under assumption that land-use decisions focus on protecting contiguous areas surrounding used paths	Restricted test of model performance; Requires poor assumption that distance from observed path is good measure of corridor quality
Mean percentile value	Mean percentile value of modeled surface assigned to observed points	Rainey Chapters 3-5	Utilizes entire model surface; Relatively straightforward interpretation	Assignment of equal percentiles can be problematic; Absolute values dependent on total study area
Null model comparison	Paired comparison of values assigned to observed path by model of interest and null model	Rainey Chapters 3-5 (Pullinger & Johnson 2010 ¹)	Can utilize entire model surface; Hypothesis-driven test (H ₀ : no influence of landscape on mvmt, only distance)	Practical interpretation not straightforward; Doesn't directly address central question (Does model predict observed movement?)
Random path comparison	Comparison of values assigned to points in observed path and randomly generated path(s)	Rainey Chapters 3-5 (Driezen et al. 2007 ² , Pullinger & Johnson 2010 ²)	Utilizes entire model surface; Hypothesis-driven test (H ₀ : no influence of landscape or distance on mvmt)	Practical interpretation not straightforward; Doesn't directly address central question; Many methods of generating 'random' paths

¹ Compared least cost path to observed path, null straight-line path, and random path using PDI; ² Compared observed points to random points equidistant from origin

Figures

Figure 2.1. Example outputs of connectivity models: a) cost-distance (Beier et al. 2008), b) circuit theory (McRae et al. 2008), c) network flow (Carroll et al. 2012), d) resistant kernel (Compton et al. 2007), e) random walk simulation (Hargrove et al. 2005), f) cost-benefit approach (Drielsma et al. 2007), g) UNICOR (Landguth et al. 2012), h) Brownian bridge (Horne et al. 2007), i) mathematical morphology (Vogt et al. 2007), and j) graph theory (Theobald et al. 2011). In (a-h), darker or warmer colors represent higher probability of or potential for movement. In (i), corridors are classified in pink.



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CHAPTER 3

A TEST OF THE ABILITY OF CONNECTIVITY MODELS TO PREDICT
MIGRATION MOVEMENTS USING GPS COLLAR DATA
FROM MIGRATING ELK

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2, 3, 4, and 5

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Contributions: Provided feedback on the study design and analysis approach. Provided extensive comments on the structure and content of the manuscript.

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Abstract

As habitat loss and fragmentation threaten the continued ability of wildlife to move across landscapes in search of resources and mates, protection of corridors capable of maintaining these movements has become an important component of conservation planning. Models are increasingly used to identify areas of the landscape likely to serve as corridors, but their predictions are rarely validated against empirical movement data, causing uncertainty in the extent to which these corridors function as intended. I address this problem by predicting seasonal migration paths of elk (*Cervus elaphus*) using two of the most commonly applied corridor models, cost-distance (or least cost distance) models and circuit theory models, then quantifying the agreement between predicted corridor surfaces and GPS collar data representing actual movements. I found that cost distance models generally performed slightly better than circuit theory models in predicting migration paths, and that both approaches appear to provide information of potential value for conservation planning. However, in some cases models did not outperform null isolation-by-distance models, and the practical utility of corridor models ultimately depends on conservation objectives. The results of this analysis also offer insight into ungulate movement ecology by exploring the drivers of habitat selection during migration, a topic warranting further study. In sum, this study provides a rare test of corridor model performance, which is expected to inform conservation planning efforts by setting appropriate expectations for the predictive capabilities of corridor models and elucidating the importance of selecting a modeling approach that is well suited to focal species movement ecology.

Introduction

Animals exhibit a fundamental need to move. Daily movements among local patches and seasonal migration movements maintain individuals' access to resources that are patchily distributed in space and time (Dingle 1996), and dispersal movements maintain the long-term viability of populations through gene flow and rescue effects (Frankel & Soule 1981; Harrison 1994). However, as patterns of intensifying human land use continue to fragment natural habitat (Hilton-Taylor 2000; Sala et al. 2000; Wilcove et al. 1998), these critical movements become increasingly threatened.

Landscape connectivity, defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993), has emerged as a key component of biological conservation, and many research programs as well as on-the-ground conservation planning efforts now focus on the maintenance and restoration of corridors expected to provide connectivity (Crooks & Sanjayan 2006; Hilty et al. 2006).

Corridors have been defined most inclusively as “regions of the landscape that facilitate the flow or movement of individuals, genes, and ecological processes” (Chetkiewicz et al. 2006). Where empirical data representing movement processes of interest (e.g., Berger et al. 2006) are not available to identify these regions, conservation scientists and practitioners increasingly rely on connectivity models to predict regions likely to serve as corridors (Chapter 2). Connectivity models use estimates of landscape resistance to movement of a focal species to predict areas most likely to support movement and thus provide connectivity. While connectivity models hold great potential to guide conservation planning efforts, their predictions have only rarely and superficially

been validated against empirical data to determine how accurately they are able to represent actual patterns of movement (Chapter 2). Failure to validate connectivity model predictions and quantify their predictive accuracy greatly limits their capacity to inform sound conservation and land use planning decisions, which may often be costly and contentious.

The aim of this study is to validate existing methods of modeling connectivity against empirical movement data in order to quantify their predictive accuracy, offering guidance for those wishing to apply the models to conservation planning objectives, while also addressing key knowledge gaps in focal species movement ecology. I first use GPS collar data from migratory movements of elk (*Cervus elaphus*) in the Madison Valley of southwest Montana to develop rigorous, season-specific estimates of landscape resistance to migration movements. I then use the two most commonly known and applied connectivity models, cost-distance models (least cost distance models; Walker & Craighead 1997) and circuit theory models (McRae et al. 2008) to predict migration paths of individuals in a reserved dataset, and evaluate the match between their predictions and observed GPS relocations.

This analysis addresses two important questions in the growing field of connectivity conservation: 1) How well do existing methods of modeling connectivity predict observed migration movements?, and 2) Which of the two most commonly used connectivity models best predicts these movements? In the course of answering these questions, a third question pertaining to ungulate movement ecology is also presented and addressed: 3) What drives elk habitat selection during migration? Answers to these

questions are expected to support informed application of connectivity models to conservation planning and to clarify issues of compatibility between connectivity models and focal species movement ecology.

Connectivity Modeling Approach

Modeling corridors generally follows a two step process. First, resistance to movement of a focal species is estimated based on one or more landscape variables (e.g., elevation, land cover, or road density). Second, the relative probability or ease of movement between specified source and destination locations is estimated by a connectivity model, which incorporates the effects of resistance as well as distance on movement patterns. I seek to model migration corridors by applying commonly used methods in the most rigorous manner possible so as to provide an informative test of predictive capacity. I use GPS collar data to develop a data-based statistical model of landscape resistance to migration movements. I then use both cost-distance models and circuit theory models to predict movements between start and endpoints of observed migration paths across this resistance surface in order to comparatively evaluate their predictions.

Resistance is generally defined as the inverse of habitat suitability (e.g., Chetkiewicz & Boyce 2009; Walker & Craighead 1997). Suitability is often estimated through a subjective process in which focal species experts assign relative scores to categorized landscape variable values as well as relative weights to multiple landscape variables (e.g., Adriaensen et al. 2003; Chardon et al. 2003; Larue & Nielsen 2008). More recently, the use of data-based models to estimate habitat suitability has become

more common in the context of corridor modeling (e.g., Chetkiewicz et al. 2006; Coulon et al. 2008; Kindall & Van Manen 2007). Resource selection functions (RSFs; Manly et al. 2002) compare habitat characteristics at a sample of used sites (e.g., GPS relocations) and a sample of available sites (selected from the surrounding landscape) to predict the relative probability of use of a given location by a focal species based on its habitat characteristics, typically in a logistic regression framework. RSFs are based on the assumption that if sites with particular characteristics are used more often than expected by chance given the availability of these characteristics across the landscape, we can infer that these characteristics are preferred by the focal species. While other quantitative, data-based methods of estimating habitat suitability exist (e.g., Mahalanobis distance (Calenge et al. 2008; Mahalanobis 1936), MaxEnt (Phillips et al. 2006), GAMMs (Aarts et al. 2008), boosted regression trees (Friedman et al. 2000)), logistic regression RSF models are used here due to their far more frequent use in the literature relative to other approaches as well as their flexibility, accessibility, and transparency.

Cost-distance models, or least cost distance models (e.g., Adriaensen et al. 2003; Craighead et al. 2001; Hootor et al. 2000; Larue & Nielsen 2008; Richard & Armstrong 2010; Singleton et al. 2002; Walker & Craighead 1997), are based on least-cost distance methods, which minimize the tradeoff between travel distance among habitat patches and exposure to unsuitable habitat (Walker & Craighead 1997). Least cost paths offer the shortest cumulative cost-weighted distance between a source and destination and are thus considered optimal routes, but these single pixel-width paths alone provide minimal guidance for conservation planning. A more complete picture is obtained by producing a

complete corridor surface, in which each cell is assigned the cost-weighted distance value of the least costly path passing through it, or by including all paths with cost-weighted distance values below a chosen cutoff value. This approach allows assessment of corridor width, identification of potential bottlenecks and alternative routes, and quantification of the contribution of any cell in the landscape to connectivity. Cost-distance models assume that individuals have perfect knowledge of the entire landscape. Similarly, these models do not assume that cost-distance values are proportional to probability of use by the focal species; rather, paths with lower cost-weighted distance are simply predicted to offer the best chance for successful movement.

Circuit theory models (McRae 2006; McRae et al. 2008), which are based on electrical circuit theory, make use of the intuitive analogy between movement of individuals through a landscape and movement of charge through an electrical circuit, recognizing that greater redundancy in travel routes between nodes (patches) enhances flow between them. This analogy's solid grounding in random walk theory has been demonstrated (Chandra et al. 1997; Doyle & Snell 1984). Circuit theory models treat cells in a landscape as electrical nodes connected to neighboring cells by resistors, with resistance values determined by the cells' landscape resistance values. Consecutive resistors can be linked in series to create a path between two patches, and a single route's total resistance is equivalent to its cost-weighted distance (as in cost-distance models; McRae et al. 2008). Circuit theory models are unique in that when all possible paths among patches are treated as resistors connected in parallel, a measure of effective cumulative resistance is obtained that decreases with increasing numbers of paths.

Circuit theory models thus account for the positive effects of path redundancy on connectivity. Resulting per-cell measures of current flow across the landscape reflect the probability of movement of individual random walkers through a given cell, quantitatively identifying important bottlenecks to movement. Conversely, this measure may discount broad swaths of highly suitable habitat because current passing through any particular cell is low. Unlike cost-distance models, circuit theory models assume that individuals only perceive the landscape within a 1-cell radius of their current location.

Fundamental differences between cost-distance and circuit theory models, particularly in their assumptions concerning the extent of animals' knowledge of the landscape and whether they quantify relative ease of movement provided by paths or relative probability of use of individual cells, may result in important differences in their predictions that interact with focal species movement ecology to influence predictive performance. However, these considerations rarely appear to guide selection of methods for modeling connectivity (Chapter 2). Comparative validation of multiple modeling approaches, ultimately across a broad suite of focal species, is therefore critical to informing application of connectivity models to corridor conservation.

Movement Ecology of Elk Migration

The predictive performance of any connectivity model is strongly driven by the ability of the underlying resistance surface to accurately capture focal species responses to the landscape during movements of interest, a point that often appears to be overlooked. While the primary goal of this study is to model connectivity using common existing methods in order to test their predictive performance, novel aspects of the

resistance models developed in this study aim to provide optimal performance while also advancing understanding of elk movement ecology.

In this study, seasonal RSF models are designed to quantify habitat suitability specific to spring and fall migration movements. Previous studies develop RSFs using location data acquired from focal species' home range movements, during which animals may respond to their environments differently than during migration due to differences in motivational state, the spatiotemporal scale of movements, and seasonal environmental conditions (Ims 1995). I base RSFs in this study on data from migratory movements to ensure that elk responses to the landscape during migration are captured appropriately and to enable description of season-specific elk responses to landscape characteristics during migration.

I also explore the potential for phenology, defined as the seasonal timing of repeat natural phenomena such as vegetation green-up and snow accumulation, to influence not only the timing of seasonal migration, but also habitat selection during migration, by considering time-varying measures of primary productivity and snow conditions as candidate covariates for RSF models. As is the case with ungulates occupying spatially and temporally heterogeneous landscapes worldwide (Fryxell and Sinclair 1988), elk migrate seasonally primarily in response to shifting quality and accessibility of forage across the landscape in order to maximize nutrient intake (Irwin 2002), though migration may also reduce predation risk (Hebblewhite and Merrill 2007). In spring, migration from winter to summer ranges is triggered by snowmelt and vegetation green-up, and in fall, travel to winter ranges is instigated largely by decreasing availability of forage with

accumulation of deep snow as well as decreasing nutritional quality of vegetation as it matures (reviewed in Irwin 2002), with harvest risk playing a potential role as well (Grigg 2007). While green-up and snow conditions are known to drive the timing of ungulate migration movements as well as the use of stopover sites during migration and the duration of migration (Dalke et al. 1965; Sawyer & Kauffman 2011), there has been no quantitative study of potential phenological effects on selection of migration paths or the relative influence of habitat selection, travel distance, and habituation to historic routes (Boyce 1991; Irwin 2002) on path selection. To my knowledge, this study is the first to develop habitat suitability models specific to migration movements of an ungulate or to explore the potential effects of phenological conditions on ungulate habitat selection during migration.

This study is expected to support more informed application of connectivity models to corridor conservation and to encourage further validation of model predictions in other focal species by demonstrating a rigorous validation process quantifying the relative performance of two well-known approaches to predicting corridors. This study is also expected to shed light on knowledge gaps in elk movement ecology and the consequences of focal species ecology for connectivity model performance. It is hoped that this and future studies will serve to clarify selection of the most appropriate connectivity modeling methods for a given focal species and conservation objective, as well as to set reasonable expectations for the predictive abilities of connectivity models and thus their capacity to inform conservation planning.

Methods

Dataset

This study utilizes GPS telemetry data previously collected during a collaborative research project between Montana Fish, Wildlife and Parks (FWP) and Montana State University (K. Hamlin and R. Garrott, Principal Investigators; Grigg 2007) provided through a data sharing agreement with FWP (J. Gude, Research and Technical Services Section Chief, and K. Proffitt, Region 3 Wildlife Biologist) for model development and validation. Forty-five adult female elk (*Cervus elaphus*) in the Madison Valley area of southwest Montana were fitted with GPS collars during the winters of 2005 and 2006. Collars were worn for approximately one year, and locations were recorded every 30 minutes, providing a total of 745,432 relocations. During this period, most collared individuals in this partially migratory population completed one round trip migration between winter ranges in the valley and summer ranges in the Madison range to the east. These movements are the focus of this study.

Focal Species

Elk are the most abundant ungulate in the Madison Valley and throughout the Greater Yellowstone Ecosystem. At the time of data collection, the Madison Valley herd numbered approximately 5,000 individuals (Grigg 2007). Elk are highly adaptable mixed feeders, foraging on a variety of grasses, forbs, and shrubs (Cook 2002). The value and quantity of forage strongly influences elk nutritional condition, population dynamics, and vulnerability to predation and hunting pressure, and elk migrate seasonally primarily in

response to shifting quality and accessibility of forage across the landscape driven by seasonal changes in vegetation and snow conditions (Irwin 2002), though migration may also reduce predation risk (Hebblewhite & Merrill 2007; but see Boyce 1989; Fryxell et al. 1988; Walther 1977; White et al. 2010) and, in the fall, hunting pressure (e.g., Altmann 1956; Anderson 1958; Grigg 2007). In the Rocky Mountains, spring migration typically occurs in May but can range from April to July, and fall migration, which is more variable among individuals, may range from September to January (Grigg 2007; summarized in Irwin 2002). Migration distances of 2.4 km to 150 km have been observed, and movements may span anywhere from several days to 8 weeks, with movement rates and use of stopover sites influenced by weather conditions (Skinner 1925), rates of vegetation green-up (Dalke et al. 1965), hunting pressure (Grigg 2007), and other biological requirements such as calving (Irwin 2002).

Study Area

The Madison Valley is located in southwest Montana between the Gravelly and Madison ranges at the eastern edge of the Central Rocky Mountains (44° 58' N, 114° 36' W). The study area, defined by placing a 5 km buffer on the minimum convex polygon of all GPS relocations, includes much of the valley north to Ennis Lake and south past Henry's Lake as well as the Madison Range to the east (Fig. 3.1). Elevation ranges from 1433 m in the valley, where elk overwinter, to 3436 m with rugged topography in the Madison Range where elk summer ranges are found. Lower elevations and valleys comprising winter range are generally characterized by grasslands, sagebrush, and irrigated pastures, with willow-dominated (*Salix spp.*) riparian communities along the

Madison River and most streams (Despain 1990; Gude 2004). Slopes support grasslands at low elevations, and at higher elevations coniferous forest is intermixed with aspen stands and meadows, providing high quality forage for elk in summer. The climate is temperate, and local conditions are strongly influenced by elevation. Summers are characterized by warm daytime temperatures and cool overnight lows that can drop below freezing at high altitudes (Despain 1990; NPS 2012). Winters are long and cold, with frequent sub-zero highs. Most precipitation falls as snow, which begins to accumulate in mid- to late-October, driving fall migration of elk to lower elevation winter ranges. Snow accumulation begins earlier with increasing elevation, and snow water content is positively correlated with elevation as well. Snowmelt marks the beginning of spring, and occurs later with increasing elevation. Snow retreat and accompanying vegetation green-up trigger spring migration upslope to summer ranges (reviewed in Irwin 2002). The eastern portion of the study area extends into central Yellowstone National Park (YNP), but most of the area consists of U.S. Forest Service land, with some lands managed by other government agencies and private lands concentrated in the valley. Land ownership patterns may influence elk migration movements due to differential disturbance, habitat quality, and hunting access (Grigg 2007).

Identifying Migration Periods

GPS telemetry data were first screened to remove handling effects and poor quality relocations. The first 48 hours of data following collar placement were excluded from analysis (as recommended by K. Proffitt), along with obvious errors falling well outside the study area.

Individuals' migratory movements were distinguished from movements within home ranges using a two-step process. First, 95% kernel density contours were calculated from all of an individual's 30-minute relocations (Hawth's Tools; Beyer 2004), and locations occurring outside of these contours were selected (Fig. 3.2a). This resulted in selection of both seasonal migratory movements and short exploratory movements at edges of home ranges at other times of year. To isolate seasonal migration paths, plots of net displacement (distance from an individual's first observed location), which were generated in R (R Development Core Team 2011) with the *adehabitat* package (Calenge 2006), were used to select locations occurring outside 95% kernel density contours that also occurred during periods of sharp change in net displacement, which are easily visually identified (Fig. 3.2b). These periods correspond well with fast, highly directional migratory movements between winter ranges (low net displacement from first location) and summer ranges (high net displacement from first location).

This process results in isolation of directional movements spanning winter and summer home ranges, with use of stopover sites along migration paths excluded due to the fact that these periods of concentrated non-directional movement typically fall within 95% kernel contours. Exclusion of stopover sites from migration paths was deemed most appropriate for validation of connectivity models because a) stopover site use is considered to be a movement state more similar to home range habitat use than to migration and thus does not provide ecologically appropriate data against which to validate predictive models of directional, long-distance movements, and b) use of dense

relocations within stopover sites for model validation would have given these sites undue weight in the validation process, producing biased results.

Modeling Habitat Suitability

The migratory dataset was divided into a training set to be used in developing models and a validation set for use in validating model performance. The dataset was divided at the level of individuals rather than GPS points in order to provide complete migration paths for corridor model validation and to maximize independence between training and test data. Because migration paths overlapped considerably within four major drainages during both spring and fall migration (see Grigg 2007), individuals moving through three of these drainages (Bear Creek, Indian Creek, and Moose Creek) were selected for use in model development, while individuals moving through Raynold's Pass to the south comprised the validation dataset. This roughly maintained Huberty's (1994) rule of thumb: data from approximately $\frac{1}{4}$ of the 40 migrating individuals were withheld for model validation.

I used the training dataset to develop resource selection functions (RSFs; Manly et al. 2002) quantifying habitat suitability for migratory movements. RSFs, which typically take the form of a logistic regression model, compare habitat characteristics at a sample of used sites (GPS relocations) and a sample of available sites (randomly selected from the surrounding landscape) to predict the relative probability of use of a given location by a focal species based on its habitat characteristics. If sites with particular characteristics are used more often than expected by chance given the availability of these characteristics across the landscape, we can infer that these characteristics are preferred

by the focal species. Selection of migration routes is expected to differ between spring and fall migrations, due to seasonal climate and vegetation conditions as well as fall hunting pressure. Resource selection functions were therefore developed separately for each season.

An issue that has been discussed at length with little consensus as to appropriate solutions (Beale et al. 2010; Boyce 2006; Fieberg et al. 2010; Gillies et al. 2006; Koper & Manseau 2009; Legendre 1993) is that RSF models assume independence among observations, but GPS collar data violate this assumption in two ways: 1) positive spatiotemporal autocorrelation occurs, particularly when data are collected at frequent intervals, and 2) positive correlation may occur among data points collected from the same individual. Lack of independence causes overestimation of degrees of freedom, inflating the rate of Type I errors and invalidating quantitative inference on model coefficients. Many potential means of correcting for autocorrelation have been proposed (e.g., conditional autoregressive models: Beale et al. 2010; variance inflation: Nielson et al. 2002; rarefaction: Swihart & Slade 1985). However, autocorrelation is not generally thought to be problematic for predictive use of models because coefficient estimates are expected to be minimally affected by autocorrelation (Boyce 2006; Gillies et al. 2006; Legendre 1993). Correlation among points sampled from the same individual can bias estimates when patterns of resource selection differ among individuals and sampling across individuals is unequal, an issue that has been addressed through the use of mixed effects models (Fieberg et al. 2010; Gillies et al. 2006). However, individual differences in habitat selection are expected to be minimal in this study given the herd behavior of

elk and broad overlap among individuals' migration routes. Furthermore, the stated objective of this study is to validate common existing methods of modeling connectivity, and no previous study has taken steps to account for autocorrelation or intra-individual correlation in the context of connectivity models. Thus, although the dataset used to develop RSFs in this study violates assumptions of independence, I chose not to address this issue here given the above considerations, and instead limit inference from RSF models to qualitative discussion of selected model covariates.

Candidate habitat covariates were chosen based on input from three local elk experts as well as published literature. These covariates include topographic variables (elevation, slope, and aspect), land cover, land ownership, density of ecotones (edges between forest cover and other natural cover types), density of roads, and phenological variables related to forage quality and availability, including normalized difference vegetation index (NDVI, a measure of primary productivity), snow water equivalent (SWE), and snow cover (presence/absence) (Table 3.1). In the case of categorical explanatory variables (land cover and ownership), similar classes were grouped and assigned indicator variables (Table 3.2). Classes corresponding to water are absent because water features were not considered available habitat for elk and were masked prior to sampling of available points. Aspect, a circular variable, was transformed to produce two independent variables, Northness ($\cos(\text{aspect})$) and Eastness ($\sin(\text{aspect})$). Flat sites were assigned aspect values based on the majority of neighboring cells.

Most RSFs use ordinary logistic regression to model the relationship between the binary used/available response variable and habitat covariates, which requires all used

sites and all available sites to be pooled. I instead used a conditional sampling design and matched case-control logistic regression (Arthur et al. 1996; Compton et al. 2002; Forester et al. 2009; Johnson et al. 2002), which allows used sites (cases) to be matched with specific sets of available sites (controls) in space and time. To match case-control sets in space, for each used point, 50 available points were randomly selected from a circle with radius defined as the individual's maximum observed step length (Fig. 3.3). This sampling design is similar to the use of step selection functions (Coulon et al. 2008; Forester et al. 2009; Fortin et al. 2005a) and is equivalent to Johnson's (1980) third order habitat selection. Given the constraints imposed by migration path start and endpoints as well as rugged topography in the study area, fine-scale selection of steps along migration paths rather than broad-scale selection of a travel path from throughout the study area is expected to be most relevant to prediction of migration paths in this study. To match case-control sets in time, time-varying phenological covariates were sampled at each used point and at surrounding available points on the date that a given GPS relocation was recorded.

Habitat covariates were screened for pair-wise correlations before developing a set of 44 *a priori* candidate models. Based on published literature on elk ecology and exploratory sample logit plots, quadratic terms for elevation, slope, forest edge density, road density, and NDVI were considered. Correlations between linear and quadratic terms were minimized by performing a centering transformation on each of these covariates (centered value = observed value – mean value).

Prior to model fitting, the training dataset was further divided into five randomly selected subsets to allow assessment of RSF fit via k-fold cross-validation (Fielding & Bell 1997) and stability of coefficient estimates among subsets. Here division was at the point level to ensure equal numbers of points in each validation set. Seasonal RSFs were fitted using each possible combination of four of the validation sets, reserving the fifth for validation. Within each of these five groupings of 80% of the data, models were selected using Akaike's Information Criterion (AIC; Burnham & Anderson 2002). Model fit was then assessed based on stability of model coefficients among validation sets before fitting final predictive models using all of the training data.

RSF models were fitted in SAS 9.2 using an adaptation of the PHREG procedure, which is designed to fit Cox proportional hazards models (SAS Institute 2000). Due to the similarity between the likelihood function from the conditional logistic regression model and the partial likelihood function from the Cox proportional hazards model, the PHREG procedure is generally considered to be capable of treating matched case-control sets as strata and fitting the conditional logistic regression model appropriately (Mandrekar & Mandrekar 2004).

AIC-favored models were generally consistent between seasons and among validation sets, and they were consistently complex, with all quadratic terms represented in the set of top models. However, due to multicollinearity among explanatory variables, some model coefficients fluctuated considerably among cross-validation subsets (Fig. 3.4). Variance inflation factors (VIFs) were calculated to assess the dependence of each explanatory variable on all other variables in the model, which revealed problems

stemming primarily from quadratic terms that were moderately correlated with groups of other explanatory variables (Table 3.3). However, based on published literature and exploratory analyses supporting inclusion of quadratic terms to adequately capture the relationship between elk habitat selection and these variables, removal of these terms was deemed more problematic for model performance than moderate instability of model coefficients due to multicollinearity, and all model terms were retained.

Final predictive models were developed by selecting the subset of best models that together carried at least 95% of the total AIC weight (Burnham & Anderson 2002). AIC weights were then recalculated based only on this subset, and a model averaging approach was used to estimate final model coefficients for each season.

Each final model was used to calculate a habitat suitability map in ESRI ArcMap 9.3 in the form of

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)$$

where $w(\mathbf{x})$ gives the relative probability of use of each cell in the landscape given its covariate values, with a lower bound of zero. (The absolute probability of use cannot be calculated from a use/availability sampling design because the extent to which available sites are used is not known (Manly et al. 2002).) Suitability maps were calculated at the resolution of the coarsest input layer (SWE), with cell dimensions of 673 m (equivalent of 30 arcsec in the Madison Valley study area).

Division of the training dataset into 5 subsets enables assessment of habitat suitability models' predictive performance via k-fold cross validation (Fielding & Bell 1997). However, this procedure was not performed here because a key assumption of the

method is not justified. Validation procedures testing the ability of a habitat suitability model to capture a reserved set of relocations assume that the distribution of these relocations across the landscape is at equilibrium and is proportional to habitat suitability. This assumption is reasonable when predicting home range use, but not habitat use during migration, which is clearly also influenced by the location of migration path start and endpoints in the landscape and the distance between them. Therefore, model validation in this study focuses explicitly on connectivity model outputs, which are designed to capture the combined effects of habitat suitability and distance.

Modeling Connectivity

Both cost-distance models and circuit theory models utilize a map of resistance (cost) to predict the relative value of cells in the landscape for travel between a pair of user-defined endpoints. Resistance maps were calculated for each season as the inverse of suitability and were rescaled to be bounded by 0 and 1 using the formula

$$\text{Resistance} = 1/(1 + \text{Suitability})$$

such that highly suitable cells present low resistance to movement.

Migration paths of each individual in the withheld test dataset were predicted using both cost-distance and circuit theory models. The GPS relocations bounding migration paths were designated as the endpoints to be connected by corridor models. Cost-distance models were run as an ArcMap python script using the cost-path and corridor Spatial Analyst functions. Circuit theory models were run in CircuitScape (McRae & Shah 2008), and model outputs in the form of natural log-transformed current maps were imported into ArcMap for visualization and validation.

Model Validation

No standard methodology for corridor model evaluation has been established in previously published literature, and existing metrics fail to utilize the entire corridor map surface, instead reducing it to a binary representation of portions of the landscape that do and do not constitute a corridor or path (Chapter 2). Exploration of alternative evaluation methods was therefore required. One previously described metric and three new metrics are presented that together provide complementary views of model performance and satisfy needs for measures of model predictive success that are both statistically valid and practically interpretable (Fig. 3.5).

95th Percentile Corridors: I determined the overall percentage of observed points in the reserved test dataset that fell within the 95th percentile corridor predicted for the individual from which each point was sampled (Poor 2010) using ratio estimation for unequal size cluster samples (Lohr 2010). Individuals were considered primary sampling units, and GPS relocations nested within individuals comprised the secondary sampling units. This approach allows calculation of standard errors on overall percentages appropriate to the sampling design. This metric provides a straightforward measure of the percentage of sampled migration movements that would be protected by corridors designated using a 5% cutoff rule for each predicted migration path. While this cutoff value is admittedly arbitrary, a) it provides a reasonable starting point for corridor designation, b) there is no established method for designating corridor cutoffs that is less

arbitrary, and c) it satisfies the goal of providing an interpretable value for basic comparisons between models.

Mean Percentile Rank: I first converted the raw values assigned to each cell in the landscape by each corridor model to equal-area percentile ranks, such that the best 1% of the total study area is assigned to the 100th percentile, the next best 1% is assigned to the 99th percentile, and so on. I then determined the percentile ranks assigned to cells containing GPS relocations by each corridor model. Cross-model percentile rank comparisons were conducted through a mixed effects linear regression model, which was fit in R using the nlme package (Pinheiro et al. 2012). Percentile ranks assigned to GPS relocations were treated as the response variable, corridor model type was treated as a fixed effect, and GPS relocations nested within individuals were treated as random effects. This model estimates the relative performance of each corridor model while accounting for the nested structure of the data and providing an estimate of variance in performance among individuals. This approach avoids the introduction of biases due to unequal sampling among individuals.

Null Model Comparison: A hypothesis-driven analysis of model performance consisted of comparing predicted percentile ranks from each model that were intersected by GPS points to predicted percentile ranks from a null isolation-by-distance model, which was developed by applying corridor models to a uniform cost surface. If the percentile ranks assigned to used points by the test model exceed the percentile ranks assigned by the null model, then the null hypothesis that focal species movements are

driven only by distance and not by habitat suitability can be rejected. I generated null models by applying cost-distance and circuit theory analyses to uniform resistance maps in which all cells were assigned a suitability value of 1. Null model corridor surfaces were then converted to equal-area percentile ranks as described above, and the percentile ranks assigned to cells containing GPS relocations were determined. Differences between null and alternative model values were estimated and cross-model comparisons were again made using a mixed effects model as described above.

Random Path Comparison: A second null hypothesis, stating that there is no effect of habitat suitability or distance on elk migration path selection, was tested by comparing the predicted corridor values from each model intersected by GPS points in observed paths to corridor values intersected by points in a set of randomized paths. If observed paths are the result of an individual's response to cells' predicted corridor quality, which incorporates effects of both habitat suitability and distance, then the mean predicted quality of cells intersected by observed paths is expected to exceed the mean predicted quality of cells intersected by random paths. Random paths can be generated by a variety of methods; I chose an approach that appeared to produce paths with ecologically reasonable travel distance limits while minimizing subjective assumptions about what constitutes a plausible path. I first defined a sampling area as the circle circumscribing the start and end points of the observed path, which was then assigned a buffer corresponding to the individual's maximum observed step length. Within this circle, random points were generated, which can be thought of as samples from an otherwise unspecified path connecting migration start and end points in the same way

that GPS relocations are samples from the actual migration path. The number of sampled points in each random path equaled the number of GPS relocations in the observed path. For each individual, 99 random paths were generated. I then found the mean predicted corridor value intersected by the observed path and by each random path, and identified the rank of the observed path mean in the distribution of random path means for each individual.

Results

Identifying Migration Periods

Based on the two-step process for identifying migration periods described above, 41 out of 45 collared individuals completed a seasonal migration movement in spring and/or fall. The final migration dataset consisted of a total of 7,468 migratory relocations. Timing, duration, and distance attributes of observed migration periods are summarized in Table 3.4.

Suitability Modeling

After separating individuals into model training and validation datasets for each season, the spring training set consisted of 1,771 relocations from 29 individuals and the spring validation set contained 1,354 relocations from 12 individuals. The fall training set consisted of 2,726 relocations from 29 individuals and the fall validation set contained 1,617 relocations from 10 individuals.

The set of candidate models accounting for 95% of the AIC weight in each season is shown in Table 3.5. After averaging these model subsets, final models for both

seasons contained all covariates and all quadratic terms considered, and seasonal model covariate sets differed only in that snow effects were represented by SWE in the spring model and snow cover in the fall model. Final seasonal models are presented in Table 3.6.

Elk habitat preferences during migration at the fine spatial scales over which available habitat was sampled are broadly interpreted here based on coefficient estimates from the final RSF models along with logit plots of modeled quadratic functions over the range of values observed for these covariates (Fig. 3.6). Quantitative inference about covariate effects on habitat selection is avoided because lack of independence in the GPS collar dataset is likely to lead to inflated Type I error.

During spring migration, elk exhibit preferences for low elevations and low to moderate North and West facing slopes, while in fall, moderate elevations (~2400 m) with low to moderate slopes are preferred, with a weaker preference for North and West facing slopes. Low to moderate forest edge density is preferred in both spring and fall, and elk select for low road density in both seasons, with greater tolerance of moderate road densities in spring than in fall. In spring, migrating individuals exhibit avoidance of forested and anthropogenic cover, while in fall, forest and shrub cover are preferred. Private lands are avoided in spring in favor of forest service and park service lands. In fall, migrating elk appear to avoid both private and park service lands. Intermediate NDVI values are selected in spring, with a peak preference of approximately 0.36 NDVI units, and sites with low SWE are preferred. During fall migration, elk appear to select

for low NDVI and greater snow cover. An example of how a 95th percentile predicted corridor aligns with underlying habitat covariates is illustrated in Figure 3.7.

Connectivity Modeling

Cost-distance and circuit theory models produce broadly similar predictions of elk migration paths (Fig. 3.8). However, as expected based on differences in their formulation, their spatial patterns of emphasis differ. While cost distance models highlight complete paths spanning migration endpoints, circuit theory emphasizes areas close to path endpoints. This is because as distance from an endpoint increases, the number of possible cells that individuals may travel through en route to or from the opposite endpoint increases, resulting in a general decrease in probability of movement through any given cell. Still, areas not in close proximity to endpoints with high probability of movement in circuit theory outputs tend to align with areas of low cost-weighted distance in cost-distance models.

Six of the eight measures of model performance (Table 3.7) suggests that cost-distance models outperform circuit theory models in predicting elk migration paths. However, this trend is quite weak; most tests either do not carry statistical significance or indicate that model performance differs by a very narrow margin, and some tests (two of eight) indicate the reverse pattern in performance.

In spring, 80.32% (SE = 13.423) of migratory relocations fell within individuals' 95th percentile corridors predicted by cost-distance models, and 82.22% (SE = 7.627) fell within 95th percentile corridors predicted by circuit theory models; this difference is not statistically significant. The mixed effects model comparison of equal-area percentile

ranks indicate that relocations were assigned a mean percentile rank of 98.568 (SE = 0.6148) by cost-distance models and a mean rank of 98.345 (SE = 0.6281) by circuit theory models, constituting a mean difference of 0.223 points ($p = 0.0152$). Variability among individuals in mean percentile rank value is evident in the standard deviation on the individual random effect of 1.9508 percentile points. Cost-distance models assigned relocations percentile ranks averaging 6.34 points (SE = 0.8526) higher than those assigned by a null isolation-by-distance model, while circuit theory models assigned these points ranks that averaged 1.788 points (SE = 0.9433) lower than a null model. This mean difference of 8.128 percentile points ($p < 2.2e-16$) varied by 3.0157 (SD) points among individuals. The mean rank of individual observed paths among 99 random paths was 1 (SD = 0) for cost-distance models and 2.67 (SD = 3.869) for circuit theory models. I also report the percentage of observed paths that received ranks of 1 to account for the fact that distributions of ranks were very highly skewed. Cost-distance models assigned all observed paths ranks of 1, while circuit theory models assigned 75% of observed paths the top rank.

In fall, 95th percentile corridors predicted by cost-distance models contained 74.4% (SE = 9.85) of migratory relocations, while those predicted by circuit theory contained 73.9% (SE = 9.85) of these points; this difference is not statistically significant. Mixed effects model results indicate that cost-distance models assigned relocations a mean percentile rank of 98.304 (SE = 1.0562), while circuit theory models assigned them a mean rank of 97.125 (SE = 1.0617), a mean difference of 0.0785 points ($p < 2.2e-16$) with variability of 2.5291 percentile points among individuals. Percentile ranks assigned

to relocations by cost-distance models averaged 0.58 points (SE = 0.5766) lower than those assigned by a null model, and circuit theory models assigned relocations ranks averaging 1.339 points (SE = 0.5813) lower than a null model. These mean difference of 0.759 points ($p < 2.2e-16$) varied by 1.601 percentile points among individuals. The mean rank of observed paths among 99 random paths based on cost-distance models was 3 (SD=6.325), with 90% of paths receiving a rank of 1. For circuit theory models, the mean rank of observed paths was 1.9 (SD = 2.846), also with 90% of observed paths receiving the top rank among random paths.

Discussion

Predictive Performance of Connectivity Models

This study first sought to determine how well existing methods of modeling connectivity predict observed migration movements. By applying some of the best-supported methods available to model connectivity, utilizing a high quality GPS collar dataset capturing elk migration movements in detail for validation, and developing novel validation metrics that comprehensively assess the agreement between the models and the data, this question is addressed here with greater detail and rigor than ever before.

Validation results indicate that 95th percentile corridors predicted by both connectivity models of interest capture the great majority of GPS relocations, that GPS relocations fall within approximately the 98th percentile of modeled corridor surfaces on average, that the models are in some cases capable of improving prediction of migration paths relative to an isolation-by-distance model (though in many cases they do not), and

that elk migration movements are substantially superior to random movements with respect to predicted corridor surfaces. These findings broadly indicate that connectivity models are capable of offering information of value to identification of wildlife corridors. However, the question of whether connectivity model performance is good enough to be of use in conservation planning and whether predicted corridors are good enough to provide connectivity cannot be answered simply by this or any study. The answer depends, of course, on many factors, particularly the goals and practical limitations of the conservation or management plan at hand as well as the movement ecology of the focal species. For example, model predictions may not be accurate enough to guide parcel-level corridor designation, but may be highly informative in providing guidance as to where practitioners should focus more detailed further study of focal species movements.

There is an important disconnect between predicting *corridors* and predicting *connectivity*. Both cost-distance and circuit theory models predict areas that are expected to be optimal for movement in any given focal landscape; they do not predict whether or not the landscape is, in fact, connected for a focal species. Even the predicted least cost path may be too long, pass through habitat that is too degraded, or encounter boundary structures that are too impassable for the focal species to travel that path successfully. Similarly, both corridor models produce continuous corridor surfaces for the entire map extent analyzed; they do not incorporate any criterion for designating ecologically relevant and/or practically useful corridor boundaries. The user must decide how to extract a subset of this surface in order to define a discrete corridor, and this decision is a key determinant of the ability of a corridor to provide connectivity. Ideally, this decision

would be based on knowledge of focal species tolerance thresholds for habitat quality and corridor dimensions. However, detailed understanding of tolerance thresholds is rarely available for this purpose, and in practice, decisions may require identifying the spatial area of corridor habitat that is feasible to protect from a socioeconomic standpoint, which may lead to selection of an arbitrary cutoff value (e.g., 95th percentile of corridor surface) or involve selection of land parcels that best balance connectivity value with monetary cost.

In this study, corridors defined by a 95th percentile cutoff value resulted in most, but not all, GPS relocations falling within the designated corridor. Interpretation of this finding is species and landscape dependent. For species with some ability to generalize in their selection of suitable habitat that are traveling through areas supporting many possible travel paths of similar suitability, failure of the corridor to capture all observed relocations is not of great concern as it is likely that travel outside the predicted corridor could just as easily have occurred within the corridor. In such a case, a predicted corridor that fails to capture all portions of an observed movement is still likely to provide connectivity for the focal species. However, for species with very strict habitat requirements or very strict fidelity to particular travel paths that are traveling through highly heterogeneous areas with few suitable travel paths, failure of a predicted corridor to capture and protect the entire observed movement path may result in a loss of connectivity.

Relative Performance of Cost-Distance and Circuit Theory Models

This study also sought to determine which of the two most commonly used connectivity models best predicts migration movements. Cost-distance and circuit theory models often appear to be viewed as equally viable alternative approaches for prediction of wildlife corridors, and both are increasingly applied to conservation planning initiatives (Chapter 2). Quantifying their relative performance and elucidating sources of differences between their predictions is expected to support more informed selection of the most appropriate model for conservation practice.

Six of eight comparisons (four validation metrics in each of two seasons) indicate that cost-distance models outperformed circuit theory models in predicting elk migration paths. While absolute differences in model performance based on validation metrics seem unlikely to carry much practical significance, differences in the spatial patterns of each model's predictions that drive these differences in performance may be more important for conservation planning purposes.

While both models make spatially similar predictions and generally suggest the same routes as important for connectivity (Fig. 3.8), circuit theory models appear to overemphasize areas near path start and endpoints. This causes circuit theory models to in turn underemphasize the central portions of observed movement paths far from start and endpoints, resulting in poorer overall performance. I suggest that these differences in spatial emphasis and corresponding differences in performance may be rooted in the fit between each model's underlying assumptions and the movement ecology of migrating elk. Cost-distance models predict optimal travel paths for an individual with perfect

knowledge of the landscape, while circuit theory models predict the cumulative probability of movement across the landscape of individuals responding only to perception of local conditions. Elk migration paths are passed down through generations and route fidelity is high (Boyce 1991; Irwin 2002), which is likely to be driven by strong selection pressure to follow paths offering the best chance of arriving at seasonal home ranges in optimal condition. The assumptions of cost-distance models are therefore most appropriate to the movement ecology of elk migration, while those of circuit theory models may be better suited, for example, to dispersal movements through novel habitat.

Circuit theory model predictions may be informative for predicting elk migration movements at fine scales, where elk may respond to local habitat conditions, particularly temporally variable vegetation and snow conditions. Cost-distance and circuit theory models are generally considered to produce complementary outputs (McRae et al. 2008). Specifically, cost-distance models identify continuous paths between sources and destinations but do not differentiate among cells within these paths in terms of quality or importance. Several researchers (e.g., B. Brock and S. Bergen, pers. comm.) have suggested the utility of combining cost-distance and circuit theory model predictions by using cost-distance to delineate a continuous corridor and applying circuit theory models within these bounds to prioritize important pinch-points for conservation action. The results of this study appear to support this as a sound approach.

Value and Interpretation of Validation Metrics

The four validation metrics presented here show general agreement, which suggests that the conclusions drawn about relative model performance are robust. While

all generally point to the same conclusions, the four metrics are complementary in that they offer different perspectives on these conclusions.

Assessment of the number of relocations captured by 95th percentile corridors offers a measure of model performance that has straightforward practical interpretation. One drawback to this method, however, is that the areal extent of a corridor defined by a percentile cutoff value is dependent upon the areal extent of the study area, and for paths that are short relative to the total extent of the study area, this ‘corridor’ may be very large relative to the path and thus not very informative. For conservation applications, it is important to define a percentile cutoff value that is appropriate to the scale of movements of interest.

The mean percentile value assigned to relocations provides a more rigorous measure that is not dependent on an arbitrary choice of corridor cutoff value. Note, though, that by focusing on percentile values rather than raw corridor model output values, the distribution of raw values is masked. In other words, the 99th percentile likely contains a very different range of values than the 25th percentile. However, this conversion was necessary in order to make statistically sound comparisons between cost-distance and circuit theory model outputs, which produce different non-normal distributions of raw values, and is advantageous in that percentile values are more practically interpretable than raw values.

Results of the remaining two validation metrics are less interpretable in a practical sense, but these metrics are useful in that they are hypothesis-driven. Comparisons between percentile values assigned to GPS relocations by models of interest and

corresponding isolation-by-distance models test the null hypothesis that movements are driven by distance but not by suitability. Based on this metric, circuit theory models performed worse than null models in spring, and in fall, both model variants performed worse than null models. This result indicates that travel distance has a very strong effect on elk migration path selection, though it is not clear whether the models perform poorly because of the relatively greater importance of distance, or because there is little conflict between suitability and distance in the study landscape. Assessment of the rank of observed paths among random paths tests the null hypothesis that movements are not influenced by distance or by suitability. This constitutes a minimum test of whether connectivity models provide any information relevant to conservation planning. Observed paths consistently rank better than the great majority of random paths, which, as expected, strongly indicates that migration is influenced by distance and/or habitat suitability as predicted by connectivity models.

Movement Ecology of Elk Migration

In the course of addressing questions of connectivity model performance, I also sought to explore what drives elk habitat selection during migration. To my knowledge, this study is the first to model habitat selection of an ungulate during migration and to consider the potential for snow and vegetation conditions to influence habitat selection during migration, though they are known to drive home range use, the timing of migration, and use of stopover sites during migration (Dalke et al. 1965; Irwin 2002; Sawyer & Kauffman 2011). Because the primary purpose of developing RSF models of habitat suitability was prediction of migration paths, spatiotemporal autocorrelation and

intra-individual correlation of GPS collar data were not accounted for, which precludes detailed, quantitative inference on RSF model coefficients. However, results of the AIC-based model selection process and qualitative assessment of final RSF models yield novel insights and point to the importance of further research in this area.

Selection of RSF models based on AIC scores (Burnham & Anderson 2002) that include covariates representing temporally variable snow and vegetation conditions suggests that these factors contribute to elk habitat selection during migration in both spring and fall. In spring, a preference for intermediate NDVI values is observed. This finding is consistent with the forage maturation hypothesis (Fryxell 1991; McNaughton 1985) stating that ungulate migration is driven by selection for forage quality. Intermediate levels of primary productivity are expected to offer the highest quality forage because nutritional quality declines as vegetation matures. This hypothesis has been supported in elk (Hebblewhite et al. 2008) and other ungulates (e.g., Mongolian gazelle: Mueller et al. 2008; mule deer: Sawyer & Kauffman 2011), but this is the first study to suggest that it may apply to selection of migration paths as well as habitat selection within home ranges and stopover sites. The spring RSF also indicates a preference for low SWE, as expected given that deep and/or dense snow impedes movement as well as forage access. Apparent preference for low NDVI and high snow cover during fall migration is not consistent with predicted patterns of selection. This relationship may be spurious or may be an artifact of tradeoffs between forage conditions and other factors.

Elk appear to select low to moderate slopes with North and West facing aspects during both spring and fall migration. This is consistent with the suggestion by Mysterud et al. (2001) that late snow melt and low temperatures on North-facing slopes retards plant maturation, thereby increasing digestibility, though their study indicated that use of a variety of aspects may provide broadest access to high quality forage as vegetation at different sites matures at different times. The models also suggest a preference for lower elevations in spring than in fall. Elk may be constrained to lower elevations in spring by persistent snow cover at higher elevations, whereas in fall, elk that migrate prior to heavy snow accumulation may be able to linger at higher elevations where higher quality forage persists.

RSFs indicate that elk prefer low to moderate forest edge density in both spring and fall. Elk demonstrate preferences for ecotones and high interspersions of cover types within home ranges as this heterogeneity provides access to diverse forage resources as well as cover for safety and thermal regulation (Geist 2002; Skovlin et al. 2002). However, use of more open habitat during migration may allow for more efficient directional movement between seasonal home ranges. In spring, elk prefer shrub and open cover types to forested and anthropogenic cover, which provide greater foraging opportunities. In fall, elk instead exhibit preferences for shrub and forest cover, which may provide safety from hunters and other predators as well as thermal cover. Elk also select for low road densities in both seasons, with greater tolerance of moderate road densities in spring. Road density is a strong indicator of hunting access (Hamlin & Ross 2002; Leptich & Zager 1991; Unsworth & Kuck 1991), and it is likely that elk are

particularly avoidant of areas accessible to hunters during the fall hunting season. Avoidance of private lands in favor of managed lands in spring may minimize exposure to human disturbance or provide higher forage quality. Apparent avoidance of park service lands in fall is likely due simply to the directionality of migration movements into the Madison Valley away from Yellowstone National Park.

While this study offers some insight into patterns of habitat selection during elk migration and the potential importance of snow and vegetation conditions for selection of migration paths, further study of these questions is needed. Development of RSF models that account for lack of independence in GPS collar data will enable quantitative evaluation of habitat selection during migration. Migration RSFs should also be compared to home range RSFs to determine the extent to which patterns of selection differ between these distinct movement states. Efforts to quantify the relative importance of habitat preferences, travel distance, and fidelity to learned paths would also greatly advance understanding of elk movement ecology.

Further comparative tests can clarify whether the fine spatial scale of habitat selection modeled here is, in fact, most appropriate for prediction of migration paths, and can determine whether phenology of snow and primary productivity not only contributes to elk habitat selection during migration, but also enables more precise prediction of migration paths. These questions are explicitly addressed in Chapter 5 by developing alternative models and comparing their predictive performance to those presented here.

Use of GPS Collar Data for Model Validation

The Madison Valley elk dataset has provided an excellent opportunity to develop and validate the predictive accuracy of corridor models for migration movements. The dataset is large and of high quality, containing movements of interest for a relatively large number of individuals (41) at very fine spatiotemporal scales (30-minute relocation intervals) with high GPS fix success rates (>95%). These features enabled development of complex habitat suitability models that presumably capture the details of elk habitat selection during migration sufficiently, while also providing a large sample size for model validation, with little uncertainty about an individual's movements between relocations due to the high relocation frequency relative to movement rates during migration.

Use of this (or any) GPS collar dataset for connectivity model development and validation also presents some limitations. As stated above, spatiotemporal autocorrelation and intra-individual correlation lead to statistical challenges in drawing rigorous, quantitative inference due to violations of independence assumptions. These challenges may be overcome through the use of more advanced forms of RSF models (conditional autoregressive models: Beale et al. 2010; mixed effects models: Fieberg et al. 2010; Gillies et al. 2006), but with potential consequences for their usability in terms of the statistical expertise required to implement and interpret them as well as extrapolation beyond the study area. When the primary goal of RSF modeling is prediction of a resistance surface for use in connectivity models, lack of independence of GPS collar data is probably of little consequence in most applications.

The validation approach presented here, which modeled individual migration paths rather than population-wide corridors, introduces an additional caveat in that it is not clear how well prediction of individual migration paths translates to prediction of corridors for migration of multiple individuals. Between any given source and destination, travel paths are likely to vary among individuals or even within the same individual over time. Validation of each of many predicted corridors against a single observed path therefore differs from validation of a single predicted corridor against many observed paths. Failure of a predicted corridor to align well with a single path may be indicative of poor model performance as has been implicitly assumed here, but misalignment may also occur if the observed path is influenced by an unusual state, condition, or event, or if many possible paths are very similar. Validation of population-level migration corridors was not possible using this dataset because the spatial distribution of individual seasonal ranges varied considerably such that many individuals' summer ranges overlapped with other individuals' winter ranges, precluding delineation of a population-level corridor between population-wide seasonal ranges. However, there is no *a priori* expectation that the ability of connectivity models to predict migration of single individuals would not be representative of their ability to predict migration of multiple individuals, particularly given the route fidelity and herd behavior of elk.

Future of Connectivity Models

It is hoped that the results of this study will serve to guide selection of connectivity modeling methods that are most appropriate to a given conservation planning application. Key take-home messages are that connectivity models are only as

good as the suitability models on which they are based, that cost-distance and circuit theory models provide complementary information, and that focal species movement ecology is likely to have an important influence on corridor model performance. Perhaps most importantly, corridor models do not provide simple solutions to the problem of conservation planning for connectivity. Rather, they are conservation planning tools capable of providing valuable information in the context of a conscious, participatory planning process. Ultimately, the quality of a connectivity model's predictions is one factor among many that will affect the success of conservation planning for connectivity, albeit an important one. The value of connectivity models is expected to increase as we begin to understand their strengths and shortcomings and how their performance varies across the diverse settings in which corridor models are utilized, and I urge the continued use of ever more available empirical movement data to expand on the currently limited array of connectivity model validation studies.

Tables

Table 3.1. Summary of candidate habitat covariates for RSF models.

Covariate	Description	Source	Spatial Resolution	Temporal Resolution
Elevation	Natl Elevation Dataset DEM	USGS	30m	--
Slope	Calculated from DEM	USGS	30m	--
Aspect	Calculated from DEM	USGS	30m	--
Land cover	2001 Natl Land Cover Dataset	USGS	30m	>1 year
Forest edge density	Calculated in 500m radius	USGS	30m	>1 year
Road density	Calculated in 5km radius	TIGER/Line data	30m	>1 year
Land ownership	Taxable parcels and public lands	MT, ID cadastral databases	varies	>1 year
NDVI	Vegetation greenness	NASA MODIS Terra satellite	250m	16-day
Snow cover	Snow presence/absence	NASA MODIS Terra satellite	500m	Daily
SWE	Snow water equivalent	NSIDC SNODAS model	30 arcsec	Daily

(NDVI = Normalized Difference Vegetation Index; SWE = Snow Water Equivalent; DEM = Digital Elevation Model; USGS = United States Geological Survey; TIGER = Topologically Integrated Geographic Encoding and Referencing; MODIS = Moderate Resolution Imaging Spectroradiometer; NSIDC = National Snow and Ice Data Center; SNODAS = Snow Data Assimilation System)

Table 3.2. Coding of indicator variables for classes of a) land cover and b) land ownership for RSF models.

a)		Availability	Indicator Variables			
Class	Description	(% sample)	Forest	Shrub/Scrub	Anthropogenic	Open*
12	Perennial ice/snow	<0.001	0	0	0	1
21	Developed: open space	0.319	0	0	1	0
22	Developed: low intensity	0.075	0	0	1	0
23	Developed: medium intensity	0.003	0	0	1	0
24	Developed: high intensity	0	0	0	1	0
31	Barren (rock, sand, clay)	1.281	0	0	0	1
41	Deciduous forest	0.526	1	0	0	0
42	Evergreen forest	49.857	1	0	0	0
43	Mixed forest	0.043	1	0	0	0
52	Shrub/scrub	33.27	0	1	0	0
71	Grassland/herbaceous	13.01	0	0	0	1
81	Pasture/hay	0.127	0	0	1	0
82	Cultivated crops	0.097	0	0	1	0
90	Woody wetland	0.422	1	0	0	0
95	Emergent herbaceous wetland	0.968	0	0	0	1

b)		Availability	Indicator Variables			
Class	Description	(% sample)	Private	NPS	USFS	Other Govt*
10000	Private	17.094	1	0	0	0
12000	Private: nonprofit	0	1	0	0	0
13000	Private: large corporation	0.005	1	0	0	0
14200	Utility: power	0	1	0	0	0
20000	US Govt miscellaneous	3.933	0	0	0	1
21000	Dept of Interior	0	0	0	0	1
21100	BLM	0.908	0	0	0	1
21400	NPS	3.441	0	1	0	0
22100	USFS	71.324	0	0	1	0
30000	State Govt	1.888	0	0	0	1
32000	State FWP	0.9	0	0	0	1
33000	State NRC	0.505	0	0	0	1
34000	Dept Transport	<0.001	1	0	0	0
36000	University	<0.001	1	0	0	0
40000	Local Govt	0.001	1	0	0	0

Table 3.3. Assessment of multicollinearity based on variance inflation factors (VIFs).

<i>Parameter</i>	<i>Spring</i>	<i>Fall</i>
Elevation [§]	2.860	3.881
Elevation ^{2§}	2.385	3.013
Slope [§]	1.662	1.697
Slope ^{2§}	1.519	1.654
North	1.000	1.000
East	1.000	1.000
Edge Density [§]	1.719	1.734
Edge Density ^{2§}	1.550	1.524
Road Density [§]	4.072	2.226
Road Density ^{2§}	2.666	1.307
NDVI [§]	5.596	3.497
NDVI ^{2§}	5.387	3.359
Land cover*		
Forest	3.272	3.232
Shrub	2.912	2.636
Anthropogenic	1.067	1.099
Ownership**		
Private	2.587	2.027
USFS	2.769	1.660
NPS	2.189	1.136
S: SWE [§] / F: Snow Cover	4.344	1.015
S: SWE ^{2§}	4.098	

[§]Centering transformation was used to minimize correlation between linear and quadratic terms.

*Reference level = open **Reference level = Other government

Table 3.4. Summary of migration movement parameters for a) spring and b) fall.

a) Spring				
	<i>Mean</i>	<i>SD</i>	<i>Median</i>	<i>Range</i>
Start date	31-May	19.2 days	25-May	5-May - 22-Jul
End date	5-Jun	20.5 days	29-May	11-May - 14-Aug
Duration (days)	5.56	9.35	2	1 - 49
Distance (km)	25.21	20.74	19.44	0.69 - 82.48
b) Fall				
	<i>Mean</i>	<i>SD</i>	<i>Median</i>	<i>Range</i>
Start date	30-Oct	28.9 days	23-Oct	16-Sep - 25-Jan
End date	4-Nov	32.7 days	31-Oct	17-Sept - 31-Jan
Duration (days)	6.67	11.35	3	1 - 57
Distance (km)	26.68	21.06	22.46	0.46 - 84.9

Table 3.5. RSF model selection and model averaging for a) spring and b) fall migration movements. Only models with sufficient weight to contribute to the final model are shown.

a) Spring

<i>Model</i>	<i>dAIC</i>	<i>AIC weight</i>	<i>Cumulative weight</i>	<i>Adjusted weight</i>
Full* - NDVI ²	0	0.3557	0.3557	0.3694
Full - Road Density ²	0.185	0.3242	0.6799	0.3367
Full	0.97	0.2190	0.8989	0.2274
Full - Edge Density ²	3.431	0.0640	0.9628	0.0664

* Full model: Elevation + Elevation² + Slope + Slope² + Aspect + Edge Density + Edge Density² + Road Density + Road Density² + Cover + Ownership + NDVI + NDVI² + SWE + SWE²

b) Fall

<i>Model</i>	<i>dAIC</i>	<i>AIC weight</i>	<i>Cumulative weight</i>	<i>Adjusted weight</i>
Full* - Aspect	0	0.6735	0.6735	0.6758
Full	1.943	0.2549	0.9285	0.2558
Full - RoadDens ²	4.582	0.0681	0.9966	0.0684

* Full model: Elevation + Elevation² + Slope + Slope² + Aspect + Edge Density + Edge Density² + Road Density + Road Density² + Cover + Ownership + NDVI + NDVI² + Snow Cover

Table 3.6. Final RSF models for a) spring and b) fall elk migration movements.

	a) Spring		b) Fall	
<i>Parameter</i>	<i>Estimate</i>	<i>SE</i>	<i>Estimate</i>	<i>SE</i>
Elevation [§]	-0.001860779	0.000170524	-5.06116E-05	0.000154179
Elevation ^{2§}	-9.9683E-07	3.94276E-07	-4.40969E-06	3.59286E-07
Slope [§]	0.000300314	0.003599336	-0.00517793	0.00283
Slope ^{2§}	-0.005456971	0.000346693	-0.00324	0.000265007
North	0.092414945	0.034300002	0.006229492	0.02764
East	-0.047670618	0.034350002	-0.011233106	0.02769
Edge Density [§]	0.009279403	0.00634831	0.009548963	0.005210684
Edge Density ^{2§}	0.001362994	0.000679177	-0.003643925	0.000721192
Road Density [§]	-0.640237876	0.247142503	1.095346003	0.201250371
Road Density ^{2§}	-0.186980769	0.254913431	-1.220579461	0.61327
NDVI [§]	-2.19077115	0.601123664	-0.821988194	0.496977062
NDVI ^{2§}	1.436606561	2.157953093	-7.888803351	2.19233095
Land cover*				
Forest	-1.026159538	0.08976319	0.211542612	0.088065642
Shrub	0.140568689	0.084000308	0.325523042	0.089567949
Anthropogenic	-1.588476998	1.009468036	0.033709913	0.537907699
Ownership**				
Private	-0.324170521	0.167960775	-0.186158998	0.137262656
USFS	0.805460848	0.101992572	0.110577867	0.069777183
NPS	0.589883831	0.256425563	-0.597235253	0.261582032
S: SWE [§] / F: Snow Cover	0.000620169	0.000326667	4.036334679	0.180196382
S: SWE ^{2§}	-8.67818E-06	9.2243E-07		

[§]Centering transformation was used to minimize correlation between linear and quadratic terms.

*Reference level = open **Reference level = Other government

a) Spring									
i)	Cost-distance			Circuit theory					
	Total	SE		Total	SE				
% in 95th percentile	80.32	13.423		82.22	7.627				
ii)									
Fixed Effects	Estimate	SE	t-value	p-value					
Intercept (Cost-distance)	98.568	0.6148	160.3363	< 2.2e-16					
Corridor model									
Circuit theory	-0.223	0.0918	-2.43062	0.0152					
Random Effects	Intercept SD			Residual SD					
Individual		1.9508							
Points in individual		1.4116		2.4025					
b) Fall									
i)	Cost-distance			Circuit theory					
Fixed Effects	Total	SE		Total	SE				
% in 95th percentile	74.40	9.908		73.90	9.850				
ii)									
Fixed Effects	Estimate	SE	t-value	p-value					
Intercept (Cost-distance)	98.304	1.0562	93.0710	< 2.2e-16					
Corridor model									
Circuit theory	-1.179	0.0785	-15.0133	< 2.2e-16					
Random Effects	Intercept SD			Residual SD					
Individual		3.0157							
Points in individual		3.6457		2.2317					
iii)									
Fixed Effects	Estimate	SE	t-value	p-value					
Intercept (Cost-distance)	-0.580	0.5768	-1.0055	0.3148					
Corridor model									
Circuit theory	-0.759	0.0522	-14.5513	< 2.2e-16					
Random Effects	Intercept SD			Residual SD					
Individual		1.601							
Points in individual		3.2023		1.4835					
iv)	Mean	SD	Prop 1	Mean	SD	Prop 1			
Random path rank	3	6.325	0.9	1.9	2.846	0.9			

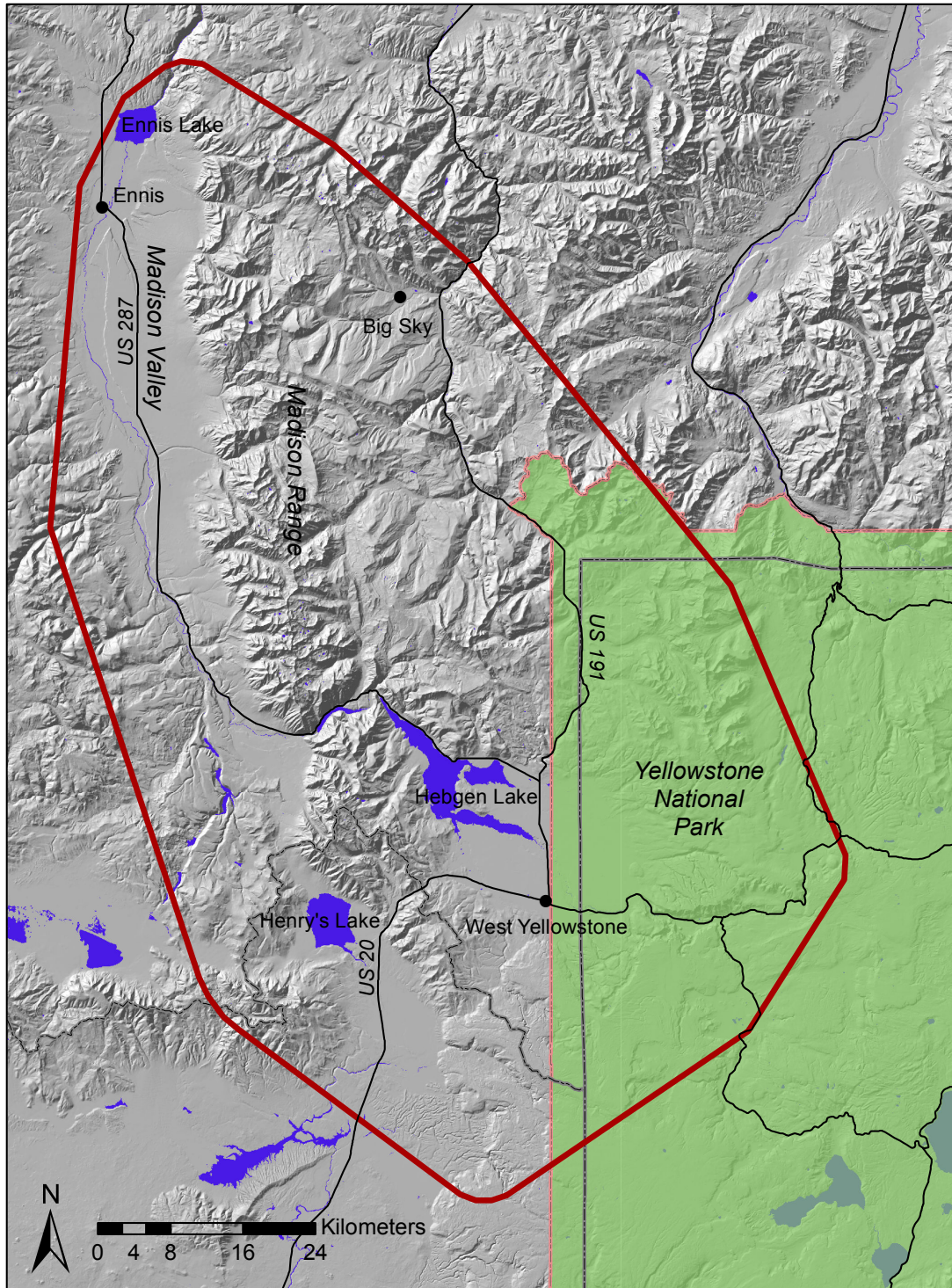
Figures

Figure 3.1. The Madison Valley study area, defined by placing a 5km buffer on the minimum convex polygon containing all GPS relocations collected from 45 female elk.

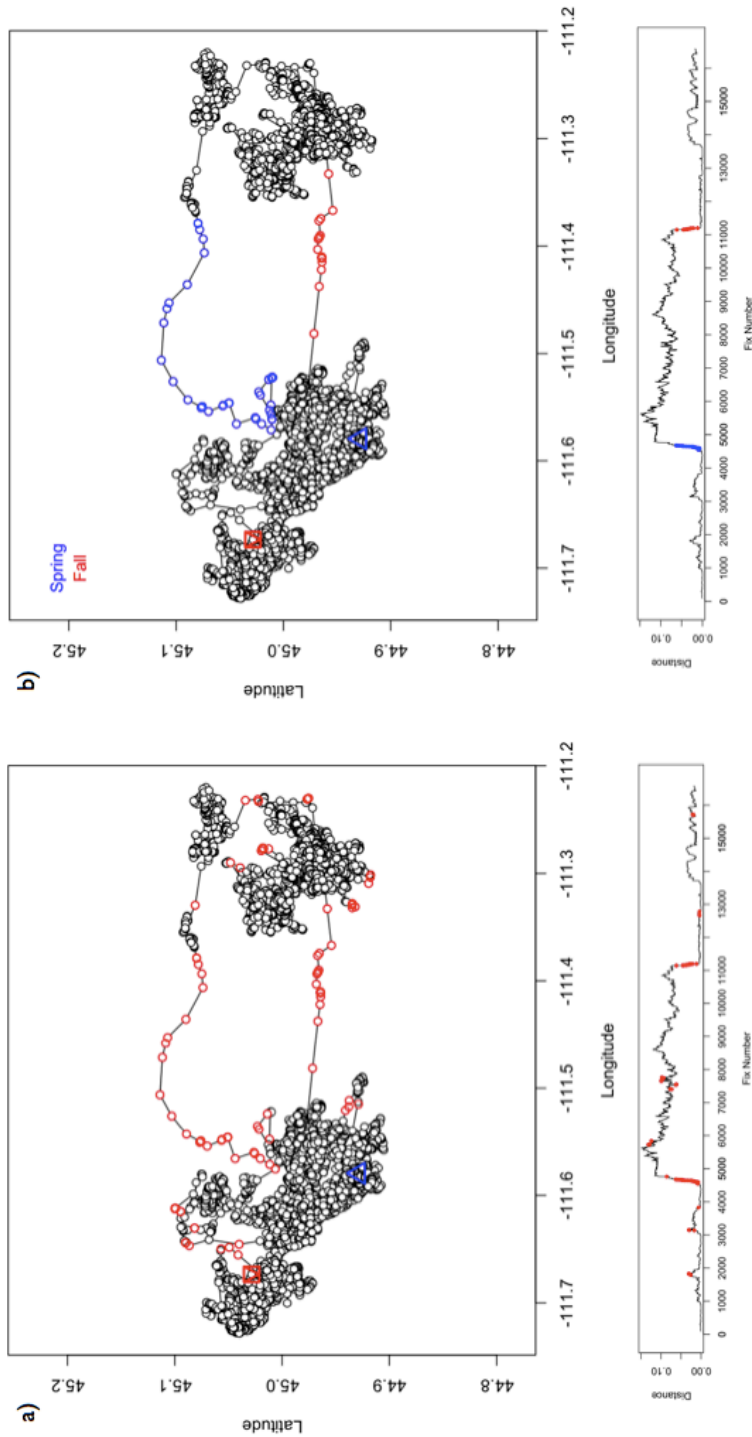
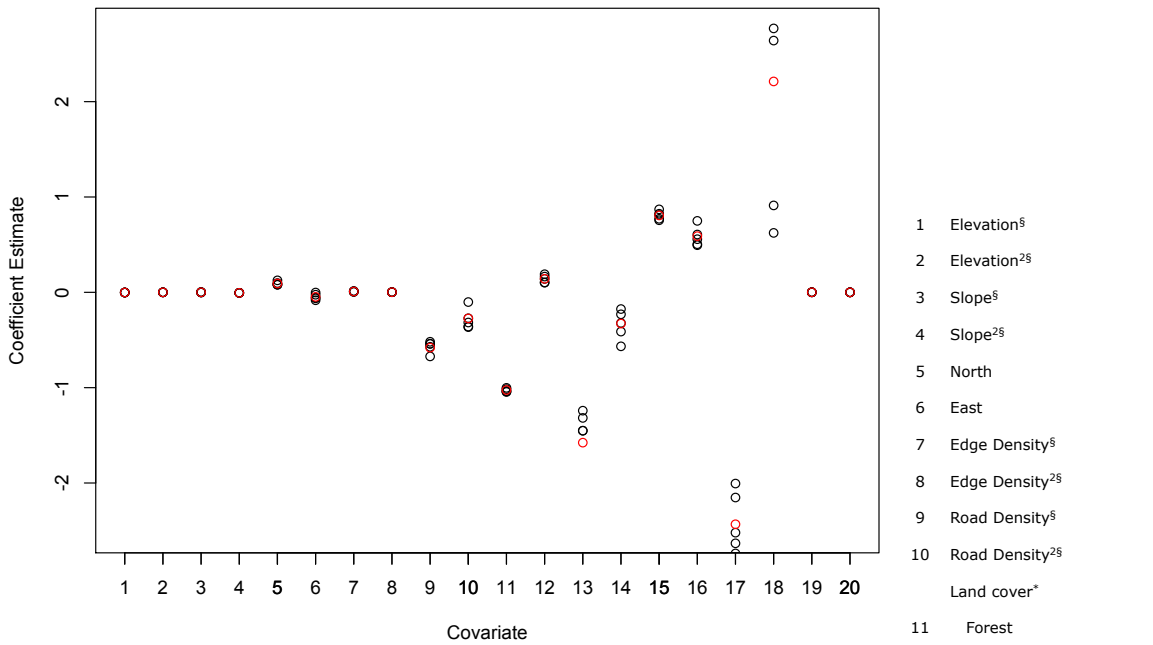


Figure 3.2. Identification of elk migration periods by a) selecting locations outside of 95% kernel contour home ranges (red), then b) selecting only points occurring during periods of high net displacement from the start point (red and blue) as indicated by steep portions of the displacement plot (bottom).



Figure 3.3. Available habitat was sampled by generating 50 random points within a circle around each observed point with radius defined by the individual's maximum observed step length between consecutive relocations. Sampled points for four GPS relocations from three individuals are shown here (middle relocations are from same individual).

a) Spring



b) Fall

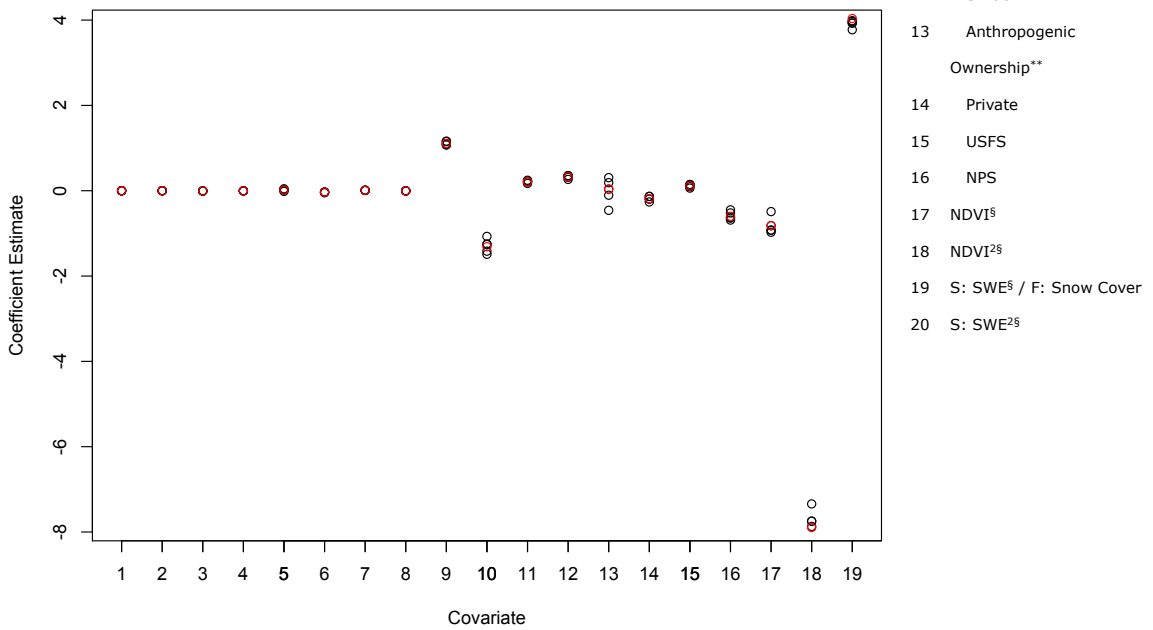


Figure 3.4. Variability in RSF coefficient estimates among five k-fold cross validation sets due to multicollinearity (black), as well as estimates based on all training data (red).

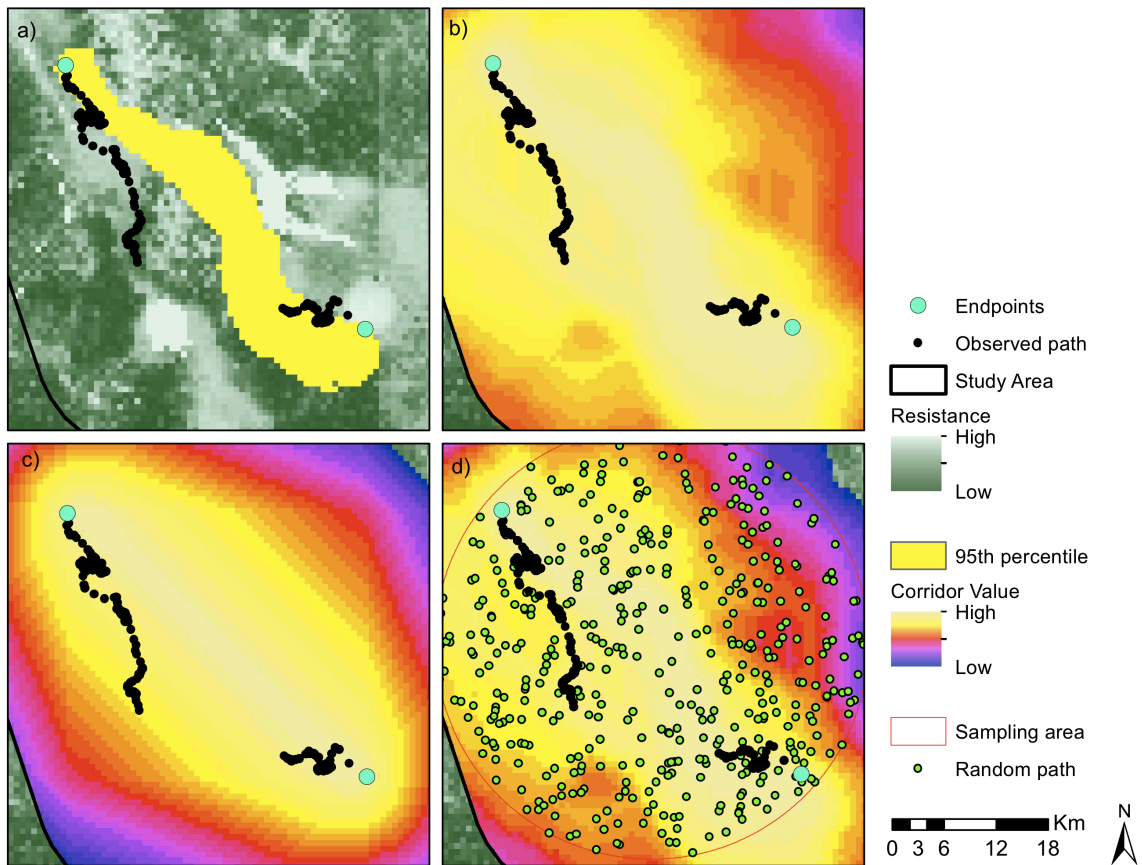


Figure 3.5. Predictive performance of corridor models was assessed based on a) percent of points found within 95th percentile corridors, b) mean equal-area percentile value assigned to points, c) comparison to a null model, and d) comparison to a set of random paths.

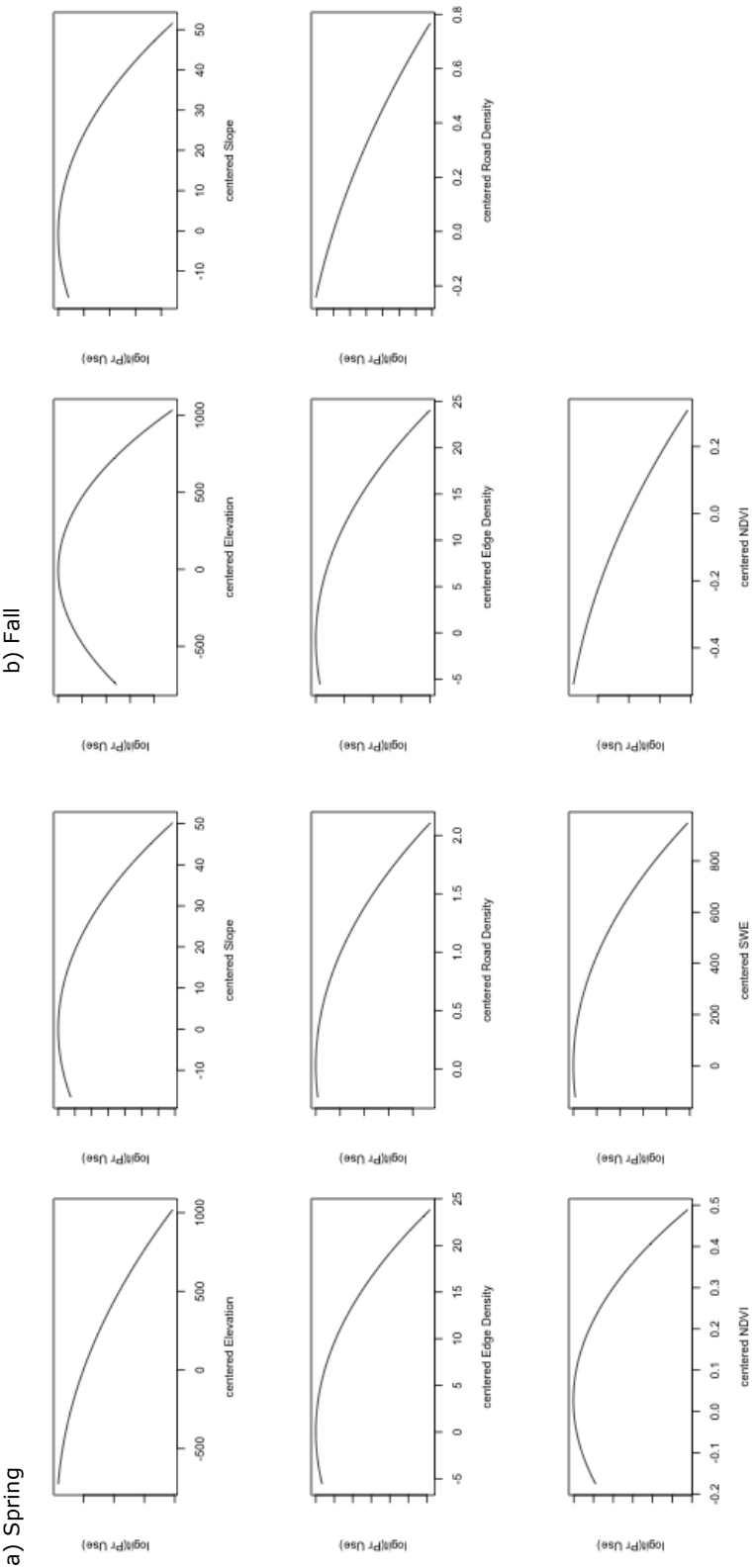


Figure 3.6. Illustrative plots of quadratic relationships between continuous explanatory variables and the logit function of the relative probability of use as estimated by final RSF models for a) spring and b) fall.

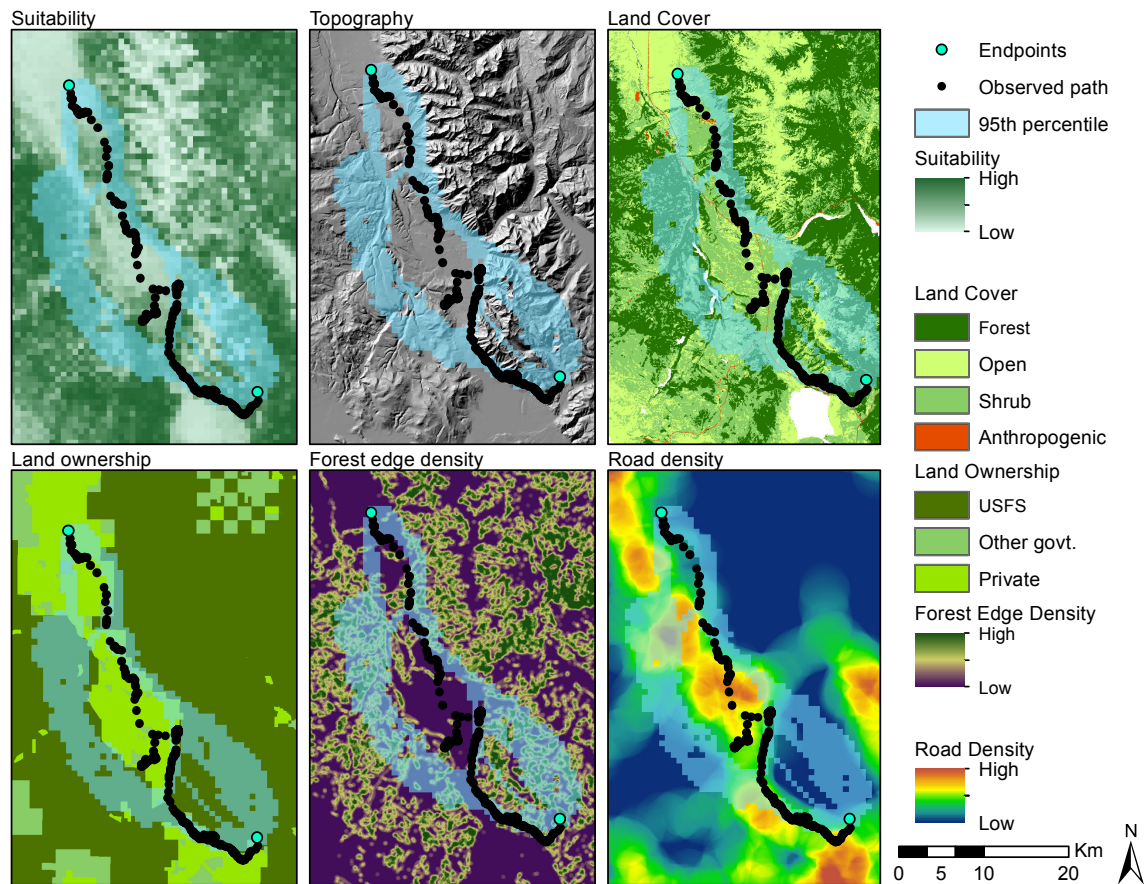


Figure 3.7. Assessment of an example predicted corridor against underlying habitat covariates.

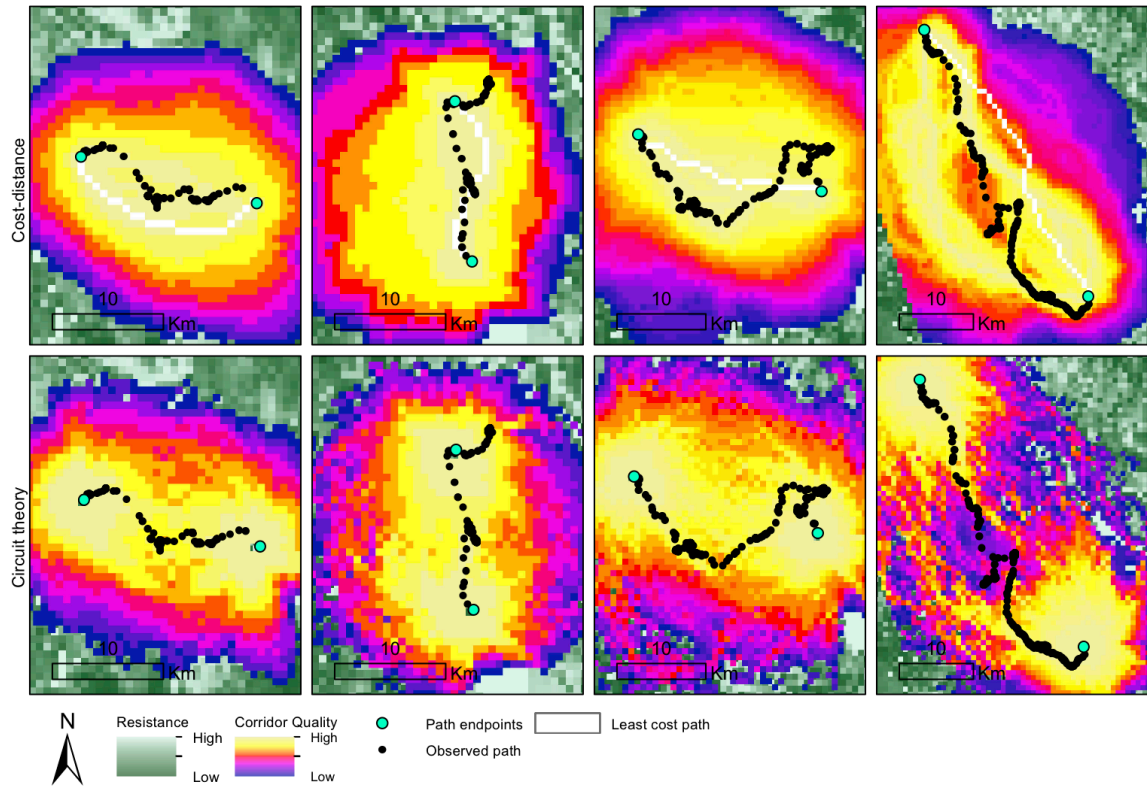


Figure 3.8. Cost-distance (top) and circuit theory (bottom) models for a representative subset of four individuals (left to right). Corridor cutoff values were defined uniquely for each individual here for visualization purposes.

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CHAPTER 4

A TEST OF THE ABILITY OF CONNECTIVITY MODELS TO PREDICT
DISPERSAL MOVEMENTS USING RELOCATION DATA
FROM DISPERSING WOLVERINES

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2, 3, 4, and 5

Author: Meredith M. Rainey

Contributions: Conceived and implemented the study design. Performed data analysis. Wrote the manuscript.

Co-author: Dr. Andrew J. Hansen

Contributions: Provided feedback on the study design and analysis approach. Provided comments on the structure and content of the manuscript.

Co-author: Robert M. Inman

Contributions: Provided the dataset and habitat suitability model. Provided input as a focal species expert on data analysis and interpretation. Provided comments on the manuscript.

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Abstract

Habitat loss and fragmentation increasingly impede wildlife movements that are essential for the long-term persistence of populations, and climate change is expected to exacerbate these effects. Protection of wildlife corridors capable of facilitating movement is therefore an important element in conservation planning. Models are now frequently used to identify areas of the landscape likely to serve as corridors, but their predictions are rarely validated against empirical movement data, limiting confidence in the efficacy of model-predicted corridors. I address this problem by predicting natal dispersal movements of wolverines (*Gulo gulo*) using two of the most commonly applied corridor models, cost-distance (or least cost distance) models and circuit theory models, then quantifying the agreement between predicted corridor surfaces and VHF and GPS telemetry data representing actual movements. Circuit theory models outperformed cost-distance models by a considerable margin and appeared to provide information of value for conservation planning, though the practical utility of corridor model predictions ultimately depends on conservation objectives. This analysis also offers a preliminary look at the movement ecology of wolverine dispersal by exploring the extent to which the drivers of primary habitat selection also drive habitat selection during dispersal. This study provides a rare test of corridor model performance in a species for which connectivity is a top conservation priority. The results presented here are expected to inform conservation planning efforts by setting realistic expectations for the extent to which predicted corridors are capable of capturing natal dispersal events, as well as

emphasizing the importance of selecting a modeling approach that is well suited to the movement ecology of the focal species.

Introduction

Natal dispersal, in which an animal leaves its place of birth in search of a breeding site, maintains the long-term genetic and demographic viability of populations through gene flow and rescue effects (Frankel & Soule 1981; Harrison 1994). These movements are increasingly threatened, however, by habitat loss and fragmentation (Hilton-Taylor 2000; Sala et al. 2000; Wilcove et al. 1998), isolating populations within islands of habitat amidst seas of human land use. Landscape connectivity, defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993), has emerged as a key component of conservation biology in response to these threats.

Climate change is expected to interact with the effects of land use intensification as land use restricts species range shifts in response to altered temperature and precipitation regimes (Opdam & Wascher 2004; Sala et al. 2000; Travis 2003). This is particularly true of cold-adapted species occupying high elevation mountain ranges separated by lowland terrain, such as Canada lynx (*Lynx canadensis*), pikas (*Ochotona princeps*), and wolverines (*Gulo gulo*). As temperatures warm and snow cover retreats, these high elevation refugia shrink (Bartlein et al. 1997; Christensen et al. 2007). Patches of sufficient quality and extent to support viable populations therefore become fewer and further between at the same time that movement among patches through lowland areas

becomes increasingly difficult and risky as dispersers encounter residential and energy development, transportation infrastructure, and associated human activity (Theobald et al. 2011).

Protection of wildlife corridors, defined most broadly as “regions of the landscape that facilitate the flow or movement of individuals, genes, and ecological processes” (Chetkiewicz et al. 2006), is now considered an important strategy for conserving species that are dependent on long-distance movements for long-term persistence. Identification of corridors amidst complex landscapes is not always straightforward, and conservation scientists and practitioners increasingly rely on connectivity models to predict regions likely to support movement. Connectivity models use estimates of landscape resistance to movement of a focal species to predict areas most likely to support movement and thus provide connectivity. Although these models hold great potential to guide conservation planning efforts, their predictions have rarely been validated against empirical data to determine how accurately they represent actual patterns of movement (Chapter 2). Failure to understand the predictive accuracy of connectivity models greatly limits their capacity to inform sound conservation and land use planning decisions that will have long-reaching effects on the persistence of vulnerable species.

This study seeks to validate existing methods of modeling connectivity against empirical movement data in order to quantify their predictive accuracy, with the goal of informing the use of connectivity models in conservation planning. I also begin to explore a key knowledge gap in the movement ecology of long-distance dispersal. I use the two most commonly known and applied methods of modeling connectivity, cost-

distance models (least cost distance models; Walker & Craighead 1997) and circuit theory models (McRae et al. 2008) to predict dispersal paths of wolverines in the Greater Yellowstone Ecosystem (GYE), then evaluate the congruence between their predictions and observed wolverine movements captured by GPS and VHF telemetry.

In this analysis, I address two key questions in the study and practice of connectivity conservation: 1) Which of the two most commonly used connectivity models best predicts dispersal movements?, and 2) How well does the best-performing method predict these movements? Answers to these questions provide a means of exploring an additional question concerning disperser movement ecology: 3) Do the key drivers of primary habitat selection in wolverines also pertain to habitat selection during dispersal? In conjunction with Chapter 3, which addressed these questions in the context of ungulate migration, this analysis is expected to further inform the use of connectivity models in conservation planning and to clarify issues of compatibility between connectivity models and focal species movement ecology.

Connectivity Modeling Approach

Modeling corridors generally follows a two step process. First, resistance to movement of a focal species is estimated based on one or more landscape variables (e.g., elevation, land cover, or road density). Second, the relative probability or ease of movement between specified source and destination locations is estimated by a connectivity model, which incorporates the effects of resistance as well as distance on movement patterns. In this study, I quantify landscape resistance to wolverine dispersal using an existing data-based statistical model (Inman et al. in review). I then use both

cost-distance models and circuit theory models to predict movements between start and endpoints of observed dispersal-related movement paths across this resistance surface in order to comparatively evaluate their predictions.

Resistance is generally defined as the inverse of habitat suitability (e.g., Chetkiewicz & Boyce 2009; Walker & Craighead 1997). Suitability is often estimated through a subjective process in which focal species experts assign relative scores to categorized landscape variable values as well as relative weights to multiple landscape variables (e.g., Adriaensen et al. 2003; Chardon et al. 2003; Larue & Nielsen 2008). More recently, the use of data-based models to estimate habitat suitability has become more common in the context of corridor modeling (e.g., Chetkiewicz et al. 2006; Coulon et al. 2008; Kindall & Van Manen 2007). Resource selection functions (RSFs; Manly et al. 2002) compare habitat characteristics at a sample of used sites (e.g., GPS relocations) and a sample of available sites (selected from the surrounding landscape) to predict the relative probability of use of a given location by a focal species based on its habitat characteristics, typically in a logistic regression framework.

Cost-distance models, or least cost distance models (e.g., Adriaensen et al. 2003; Craighead et al. 2001; Hoottor et al. 2000; Larue & Nielsen 2008; Richard & Armstrong 2010; Singleton et al. 2002; Walker & Craighead 1997), are based on least-cost distance methods, which minimize the tradeoff between travel distance among habitat patches and exposure to unsuitable habitat (Walker & Craighead 1997). Least cost paths offer the shortest cumulative cost-weighted distance between a source and destination and are thus considered optimal routes, but these single pixel-width paths alone provide minimal

guidance for conservation planning. A more complete picture is obtained by producing a complete corridor surface, in which each cell is assigned the cost-weighted distance value of the least costly path passing through it, or by including all paths with cost-weighted distance values below a chosen cutoff value. This approach allows assessment of corridor width, identification of potential bottlenecks and alternative routes, and quantification of the contribution of any cell in the landscape to connectivity. Cost-distance models assume that individuals have perfect knowledge of the entire landscape. Similarly, these models do not assume that cost-distance values are proportional to probability of use by the focal species; rather, paths with lower cost-weighted distance are simply predicted to offer the best chance for successful movement.

Circuit theory models (McRae 2006; McRae et al. 2008), which are based on electrical circuit theory, make use of the intuitive analogy between movement of individuals through a landscape and movement of charge through an electrical circuit, recognizing that greater redundancy in travel routes between nodes (patches) enhances flow between them. This analogy's solid grounding in random walk theory has been demonstrated (Chandra et al. 1997; Doyle & Snell 1984). Circuit theory models treat cells in a landscape as electrical nodes connected to neighboring cells by resistors, with resistance values determined by the cells' landscape resistance values. Consecutive resistors can be linked in series to create a path between two patches, and a single route's total resistance is equivalent to its cost-weighted distance (as in cost-distance models; McRae et al. 2008). Circuit theory models are unique in that when all possible paths among patches are treated as resistors connected in parallel, a measure of effective

cumulative resistance is obtained that decreases with increasing numbers of paths. Circuit theory models thus account for the positive effects of path redundancy on connectivity. Resulting per-cell measures of current flow across the landscape reflect the probability of movement of individual random walkers through a given cell, quantitatively identifying important bottlenecks to movement. Conversely, this measure may discount broad swaths of highly suitable habitat because current passing through any particular cell is low. Unlike cost-distance models, circuit theory models assume that individuals only perceive the landscape within a 1-cell radius of their current location.

Fundamental differences between cost-distance and circuit theory models, particularly in their assumptions concerning the extent of animals' knowledge of the landscape and whether they quantify relative ease of movement provided by paths or relative probability of use of individual cells, may result in important differences in their predictions that interact with focal species movement ecology to influence predictive performance. However, these considerations rarely appear to guide selection of methods for modeling connectivity (Chapter 2). Comparative validation of multiple modeling approaches, ultimately across a broad suite of focal species, is therefore critical to informing application of connectivity models to corridor conservation.

Wolverine Movement Ecology

Wolverines are highly mobile, solitary mesocarnivores, defending large territories and reproducing slowly, resulting in very low population densities (Golden et al. 2007; Lofroth et al. 2007; Magoun 1985; Persson et al. 2006). Their distribution is correlated with persistent spring snow cover (lasting until late May to mid-April, when den sites are

typically abandoned; Copeland et al. 2010), which may provide den sites (Magoun & Copeland 1998), thermal cover for young (Pulliainen 1968), refuge from predators (Persson et al. 2003; Pulliainen 1968), and/or food caching during critical reproductive periods (Inman et al. 2012a). While wolverines' life history strategy allows them to occupy cold, marginal habitats offering sparse resources, thus avoiding competition and predation from other carnivores occupying more productive habitats (Buskirk et al. 2000; Copeland et al. 2010; Inman et al. 2012b), it also makes them inherently vulnerable to human-induced disturbance and changing conditions. This is particularly true of wolverines in the GYE.

The GYE lies at the southern periphery of the wolverine's current global range (Cegelski et al. 2006; Copeland & Whitman 2003; Inman et al. 2012b), and suitable high elevation, snow-bound habitat occurs only as 'sky islands' that are smaller and more isolated than in more northerly portions of wolverines' distribution (Brock et al. 2007, Inman et al. in review). GYE wolverines were extirpated prior to 1930 by unregulated trapping and broadcast of poison baits for predators (Aubry et al. 2007). Many populations have since rebounded (Aubry et al. 2007; Newby & McDougal 1964; Newby & Wright 1955) but several areas of historical distribution remain unoccupied (Aubry et al. 2007; Kucera & Barrett 1993). Additionally, wolverines now face new challenges associated with habitat degradation and climate change and may have limited ability to overcome these issues due to their inherently fragile demographic characteristics. Backcountry winter recreation may increasingly encroach on critical wolverine habitat (Greater Yellowstone Coordinating Committee 1999; Copeland 1996; Krebs et al. 2007),

and expansion of human infrastructure threatens lower elevation dispersal habitat (Gude et al. 2007). Climate change threatens to considerably reduce the snow cover that wolverines depend on and to increase isolation among areas where snow persists (McKelvey et al. 2011). Wolverines are now considered warranted for protection under the Endangered Species Act, and climate change was considered to be the primary threat to U.S. Northern Rockies populations during the listing process (USFWS 2010). Maintaining connectivity via a network of open spaces among remaining patches of suitable habitat is thus considered critical for the long-term persistence of wolverines in the GYE (Inman et al. in review).

While primary habitat for wolverines appears to be constrained by persistence of spring snow cover (Copeland et al. 2010), which typically occurs in remote high elevation subalpine habitats (Aubry et al. 2007; Inman et al. 2012b), they are known to tolerate a wide range of suboptimal conditions during natal dispersal events, including open, low elevation valleys, highways, and residential developments (Inman et al. 2009). This raises the question of whether patterns of habitat selection may fundamentally differ between movement states or whether wolverines simply exhibit greater tolerance of poor habitat during dispersal movements. Animals may respond to their environments differently during dispersal than they do within home ranges due to differences in motivational state and the spatiotemporal scale at which they respond to the landscape (Ims 1995). In the case of wolverines, dispersers may be motivated to leave primary habitat in search of territories unoccupied by individuals of the same sex, and failure to encounter key features of primary habitat (i.e., snow cover, subalpine forest) during

lowland dispersal movements may necessitate habitat selection based on different sets of cues. Alternatively, dispersers may remain in primary habitat to the greatest extent possible, and, upon leaving primary habitat, may continue to seek similar conditions (e.g., tree cover, rugged terrain).

As discussed in Chapter 3, the performance of connectivity models is strongly dependent upon the quality of underlying resistance models. Potential differences in patterns of selection among movement states therefore have important implications for development of a resistance surface appropriate to prediction of long-distance movements. Chapter 3 addressed this issue by developing a resistance surface from elk migration data rather than home range movement data. In this study, as in most previous studies (Chetkiewicz et al. 2006; Coulon et al. 2008; Kindall & Van Manen 2007; but see Richard & Armstrong 2010), I instead utilize a resistance surface based on data collected within home ranges, not during dispersal. This is necessary here given the extremely limited availability of relocation data capturing dispersal movements. While this approach requires the assumption that patterns of habitat selection during home range movements are characteristic of dispersal movements as well, it also provides an opportunity for preliminary exploration of the impact of this assumption on model performance and whether it yields sufficiently accurate predictions of wolverine dispersal paths.

The central goal of this study is to quantify the ability of two commonly used corridor models to predict movements of a long-distance disperser for which connectivity is a major conservation concern. This study also seeks to clarify the extent to which

habitat selection may vary among movement states in wolverines and the importance of this potential variability for connectivity modeling. In conjunction with the work presented in Chapter 3, the results of this study are expected to provide insight into the strengths and limitations of each corridor modeling approach and how model performance may vary among focal species with different movement ecology, encouraging more appropriate, informed application of corridor models in conservation planning.

Methods

Dataset

GPS telemetry data for dispersing wolverines in the Greater Yellowstone Ecosystem (GYE) of Montana, Idaho, and Wyoming were provided by Wildlife Conservation Society (B. Inman, Wolverine Program Director). During the study period (2001 – 2009), eight wolverines fitted with VHF implants (5 males, 3 females) were identified as dispersers (Inman et al. 2012b). Four of these individuals (3 males, 1 female) were also fitted with GPS collars. Relocations from both devices were used to validate connectivity models. VHF implants provided data for up to 3.5 years with a target relocation interval of 10 days. Actual relocation intervals ranged from several hours to several weeks, with some months-long gaps present for some individuals. GPS collars collected data for 3-12 months. Although they were programmed to collect data at various intervals shorter than those typical of VHF telemetry, relocation success was

<50% (Inman et al. in review), resulting in relocation intervals ranging from one hour to one week.

Despite the fact that this dataset is limited in the total number of individuals tracked and the frequency and regularity of relocations compared to those collected from more accessible focal species capable of carrying high-capacity GPS collars, it is by far the most comprehensive dataset available on wolverine dispersal movements. This study sought to make the most extensive use possible of the dataset by applying all dispersal-related relocations from both VHF and GPS tracking devices to model validation. Despite the irregularity of relocation intervals and differences in these irregularities between devices (Table 4.1), this was felt to be defensible because no inference as to the paths that wolverines traveled between relocations is made in the validation approach presented here. Instead, each relocation represents a single sample of the traveled path, and relocation frequency and regularity is expected to have little impact on use of the dataset for validation. Potential minor impacts on interpretation are discussed below in the context of the validation results.

Study Area

The study area, encompassing much of the Greater Yellowstone Ecosystem (GYE), was defined by placing a 200 km buffer on the minimum convex polygon containing all relocations from eight dispersers. This buffer was defined by multiplying the 40 km maximum average daily travel distance reported in the literature (Cegelski et al. 2006) by this dataset's average relocation interval of 5 days (Fig. 4.1). This buffer

gave connectivity models reasonable “room to roam” in order to avoid imposing strong study area boundary effects on predicted paths.

The GYE lies at the southern periphery of the wolverine’s current global distribution (Cegelski et al. 2006; Copeland & Whitman 2003; Inman et al. 2012b) and encompasses approximately 108,000 km² across Montana, Idaho, and Wyoming. It includes the Yellowstone Plateau and 14 surrounding mountain ranges, with elevations ranging from 1400 – 4200 m. Precipitation increases with elevation and ranges from 32-126 cm per year (NOAA 2007; NRCS 2007). Snow most often falls as dry powder, and, at high elevations, may be present for at least nine months of the year, reaching depths of more than 350 cm.

Low elevation valleys are generally characterized by short-grass prairie and sagebrush communities, and lower elevation forests are typically dominated by lodgepole pine (*Pinus contorta*) or Douglas fir (*Pseudotsuga menziesii*), with Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) increasing at higher elevations (Despain 1990). All forest communities are typically interspersed with grass, forb, and shrub meadows. Above the alpine tree line, which typically occurs at approximately 2750 m, alpine tundra or talus fields are present. The GYE supports a diverse fauna, contributing both competitors and carrion food sources for wolverines (Bailey 1930; Streubel 1989).

The GYE is composed primarily of public lands and includes Yellowstone National Park and Grand Teton National Park, Red Rocks Lakes National Wildlife Refuge and the National Elk Refuge, and six National Forests. Additional public lands

are managed by the Bureau of Land Management (BLM), state wildlife departments, and other state and federal agencies.

Focal Species

Wolverines are intrasexually territorial (Inman et al. 2012b, references therein), and natal dispersal serves to move juveniles out of their maternal home range in search of territories unoccupied by the same sex. As discussed above, habitat suitable for territory establishment is constrained by persistent spring snow cover (Copeland et al. 2010), but dispersal may take wolverines through areas that do not meet this requirement. Dispersal events are often preceded by exploratory movements beyond the maternal home range (Inman et al. 2012b; Vangen et al. 2001). These movements begin at an average of 11 months of age (Inman et al. 2012b; Vangen et al. 2001), typically occurring between January and May, but exploration and dispersal may continue until at least 36 months of age. Inman et al. (2012b) observed a maximum Euclidian dispersal distance of 170 km in males and 173 km in females within the GYE. However, far greater dispersal distances are possible. A 378 km dispersal event has been observed in Alaska (Gardner et al. 1986), genetic data suggest that wolverines may disperse up to 500 km (Flagstad et al. 2004), and GPS collar data recorded a male dispersal event of 541 km (Euclidian), perhaps the longest wolverine movement ever recorded (Inman et al. 2009, included in this analysis).

Identifying Dispersal Movements

Dispersal-related movements were defined as having been initiated when an individual moved beyond two home range radii of the arithmetic center of its mother's most recent annual 95% fixed kernel home range (after Inman et al. 2012b; Vangen et al. 2001). Where maternal home range data were not available, den sites served as a proxy for the center of the mother's home range, and the mean observed female home range radius was used. In some cases neither of these information sources were available, and dispersal-related movement was identified as all relocations outside primary habitat (Fig. 4.3f) or all relocations in a highly directional observed path (Fig. 4.3d,h).

Some individuals completed a single long-distance dispersal movement, while others made multiple exploratory trips before either completing a successful move or remaining in their natal territory for the remainder of their tracking device's life. All movements outside the natal territory demonstrating directionality over a timeframe of days to months were modeled as dispersal-related movements, including both departure and return trips. Some of these movements occurred over several months and were sampled only infrequently by VHF signal, and they can therefore only be seen as strongly directional on broad spatiotemporal scales. Infrequent relocations also lead to uncertainty as to the full range of these individuals' space use during exploratory bouts. Exploratory movements were included in this analysis regardless of poor relocation frequency or lack of directionality on fine scales because a) exploratory movements are precursors to dispersal that it may be important for corridors to accommodate, and b) some non-

directional space use over fine scales is to be expected during dispersal given that dispersers are moving through novel habitat.

Habitat Suitability Model

Habitat suitability for wolverines has been previously modeled by Inman et al. (in review) using VHF telemetry data from non-dispersing individuals in the study area. Because considerable thought and effort from experts in wolverine ecology has gone into multiple revisions of this model, and because there is insufficient disperser data to develop and test a new dispersal-specific model, a suitability map based on the existing model served as the input for connectivity models in this study.

2,257 VHF telemetry relocations from 18 individuals (12 females, 6 males) were used to develop a first-order (Johnson 1980) logistic regression model (Inman et al., in review). For every used point, 3 available points were randomly sampled from a buffer with a radius of 34.8 km around wolverine trap locations, corresponding to the average maximum distance that wolverines were observed to travel from their point of capture. Data were then pooled across individuals. A full stepwise selection process was used to select among candidate models using BIC scores. The final model contained variables representing latitude-adjusted elevation, terrain ruggedness, average snow depth on April 1, road density, distance-weighted human population density, distance to high-elevation talus, distance to tree cover, and distance to April 1 average snow depth > 2.5 cm (Table 4.2). The model coefficients were used to calculate habitat quality as $w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)$. A k-fold cross validation procedure indicated good model fit ($r_s = 0.997$) and that the model was highly predictive of independent wolverine location

datasets ($r_s = 0.939 - 0.966$). Use of the linear form of the model, which gives the log of the odds ratio, rather than the exponential form as is typical of resource selection functions (RSFs; Manly et al. 2002), was necessary to prevent loss of information caused by significant digit limitations of the ArcGIS software when calculating the habitat suitability map.

Connectivity Models

A landscape resistance map was calculated as the inverse of suitability and rescaled to be bounded by 0 and 1 using the formula

$$\text{Resistance} = 1/(1+\text{Suitability})$$

such that highly suitable cells present low resistance to movement. This resistance surface served as the input map for cost-distance and circuit theory models, which were used to predict each of the 18 directional movements identified above.

For each dispersal-related movement, the last wolverine relocation inside the maternal home range limits was taken as the path start point, and the furthest point reached through continuous directional movement after departing the mother's home range (greatest Euclidian distance) was taken as the path end point, or vice versa in the case of return trips. Cost-distance and circuit theory models were run using ArcMap Spatial Analyst tools and CircuitScape (McRae & Shah 2008), respectively.

Model Validation

Relative predictive performance of each of the above model variants was assessed using four validation metrics, which are presented in detail in Chapter 3 and summarized here.

95th Percentile Corridors: After converting raw values assigned to each cell in the landscape by each corridor model to equal-area percentile ranks, the overall percentage of observed locations in the reserved test dataset that fell within the 95th percentile corridor predicted for the individual from which each point was sampled was determined using ratio estimation for unequal size cluster samples (Lohr 2010).

Mean Percentile Rank: I determined the percentile ranks that each corridor model assigned to cells containing wolverine relocations. Comparisons between cost-distance and circuit theory models were conducted using a mixed effects linear regression model. Percentile ranks assigned to relocations were treated as the response variable, connectivity model type (cost-distance vs. circuit theory) and model variant were treated as fixed effects, and relocations nested within individuals were treated as random effects.

Null Model Comparison: To test the null hypothesis that elk movements are driven only by distance and not by habitat suitability, I calculated the difference between percentile ranks assigned to relocations by each model of interest and percentile ranks assigned to points by a corresponding null or isolation-by-distance model, in which connectivity models were run on a uniform cost surface. Cross-model comparisons of these differences were conducted using a mixed effects model as described above.

Random Path Comparison: To test the null hypothesis that there is no effect of habitat suitability or distance on wolverine dispersal path selection, I compared the mean value assigned by each model to points in each observed path with the mean values assigned to points in a corresponding set of random paths. Random paths were generated by first delineating the circle circumscribing the start and end points of the observed path, buffering this circle with a radius of 40 km corresponding to the maximum average daily travel distance observed in the literature for wolverines (Cegelski et al. 2006), then generating random points within this buffered area. The number of points generated in each path equaled the number of points in the corresponding observed path. The rank of each observed path mean in the corresponding distribution of random path means was then determined for each individual. Finally, I calculated the mean observed path rank across individuals and the percentage of individuals whose observed paths received the top rank.

Results

A total of 18 directional movements outside the bounds of natal territories were identified and modeled; their parameters are summarized in Table 4.3. Six of these movements were one-way dispersal events with no documented return trip, while six were exploratory movements or failed dispersal movements and were accompanied by six return trips to the natal territory (Fig. 4.3).

While cost-distance and circuit theory models suggest some of the same routes as potentially important, their predictive surfaces differ considerably overall (Fig. 4.4).

Cost-distance models tended to favor long, circuitous paths through highly suitable habitat, while circuit theory models detected small patches of suitable habitat amidst highly resistant areas, assigning these patches high probabilities of movement by routing many possible paths through them (Fig. 4.4). A simple visual assessment of sample model outputs (Fig. 4.4) suggests that the highest quality corridors predicted by circuit theory models align more closely with wolverine relocations than do those predicted by cost-distance models.

All four validation metrics indicate that circuit theory models outperform cost-distance models in predicting dispersal and exploratory movements of wolverines (Table 4.4). Cost-distance models of dispersal-related movements placed a mean of 55.64% (SE = 14.867%) of wolverine relocations within corridors defined as the 95th percentile of the study area, while circuit theory models placed a mean of 86.92% (SE = 6.974%) of relocations within 95th percentile corridors. However, this difference is not statistically significant due to high variability among individuals. Due to the skewed distribution of the individual random effect estimates, the mixed model comparison of percentile ranks did not produce reliable estimates of mean ranks assigned by each model (Table 4.4b). Raw estimates indicate a mean percentile rank of 90.63 assigned to relocations by cost-distance models and a mean rank of 97.88 assigned by circuit theory models. The difference between models of 7.249 (SE = 0.6581, $p < 2.2e-16$) estimated by the mixed effects model thus appears to be unbiased, though this result should be interpreted with some caution. Cost-distance models assigned observed relocations percentile rank values that averaged 6.427 points (SE = 1.0278) lower than those assigned by a null model. In

contrast, circuit theory models assigned rank values that averaged 1.64 percentile points ($SE = 0.7023$) higher than those assigned by a null model. This mean difference of 8.067 ($p < 2.2e-16$) percentile points varied by 2.2494 (SD) points among individuals. Finally, the mean rank of observed paths among random paths was 3.61 (SD = 5.489) under cost-distance models and 2.67 (SD = 3.204) under circuit theory models ($n = 18$). With cost-distance models, 66.7% of observed paths received the top rank, while 72.2% received the top rank with circuit theory models.

Discussion

Relative Performance of Cost-Distance and Circuit Theory Models

This study first sought to determine which of the two most commonly used connectivity models best predicts observed dispersal movements. All four of the validation metrics presented here clearly indicate that circuit theory models outperform cost-distance models in predicting wolverine dispersal paths, and they do so to an extent that appears likely to carry practical significance for use of models in conservation planning. The discrepancy between circuit theory and cost-distance model predictions seems to lie primarily in their differential treatment of situations in which the least cost path is long and circuitous while more direct paths are not entirely unfavorable due to the presence of stepping stones, or series of small islands of suitable habitat found within expanses of poor habitat. In these cases, cost-distance models tend to overemphasize long, low-cost routes. Circuit theory models, in contrast, pick up on shorter routes that require travel through stretches of high-cost habitat but that also pass through relatively

low-cost stepping stones. The redundancy of many such paths that are all routed through the same stepping stones results in high probability of use of these areas, despite any single path having high cost-weighted distance relative to the least cost path.

Importantly, circuit theory models probably outperform cost-distance models in this study because their assumptions and the above tendencies align well with wolverine movement ecology. Circuit theory models assume that dispersers have incomplete knowledge of the landscape, with a perceptual range encompassing only a 1-cell radius. As natal dispersal-related movements take juvenile wolverines outside the bounds of their maternal home range into novel landscapes, this assumption is probably more appropriate than the cost-distance model assumption of complete knowledge of the landscape. Additionally, while wolverines may be capable of traveling the distances characteristic of the circuitous paths predicted by cost-distance models, they also readily cross non-primary habitat and, as observed here, appear to favor relatively direct paths even when this necessitates crossing areas of poor quality.

Cost-distance and circuit theory models are generally seen as producing highly complementary results, painting the same general picture of where a corridor is expected to lie, but with slightly different spatial emphases within that corridor. This view was well-supported in application of the models to elk migration paths in Chapter 3. However, the model results for wolverine dispersal appear to be far less complementary. In this case, use of cost-distance models to delineate a corridor followed by use of circuit theory models to identify pinch points and priority areas within that corridor, as has been suggested (Chapter 3, B. Brock & S. Bergen, pers. comm.), would lead practitioners to

miss the more direct dispersal paths often taken by wolverines in this dataset as they made use of stepping stones. It appears that relative model performance as well as the degree of complementarity between cost-distance and circuit theory models vary with focal species movement ecology.

Choice of an appropriate model (cost-distance vs. circuit theory) is clearly critical to conservation planning success. This study, in conjunction with the similar study of elk migration presented in Chapter 3, suggests that choice of a connectivity model that aligns appropriately with the movement ecology of the focal species is critical to the successful application of models to conservation planning. Circuit theory models may be best suited to predicting movements through novel landscapes by species capable of traveling through high-cost habitat in order to minimize travel distance, while cost-distance models may be more appropriately applied to movements through familiar landscapes by species that tolerate long distances in order to track high-quality habitat.

Predictive Performance of the Best-Performing Model

This study also sought to determine just how well the best-performing connectivity models predicts wolverine dispersal movements. Validation results indicate that 95th percentile corridors predicted by circuit theory models capture a considerable majority of wolverine relocations, that on average relocations fall within approximately the 97th percentile of corridor surfaces modeled by circuit theory, that circuit theory models generally improve prediction of dispersal paths relative to an isolation-by-distance model, and that wolverine dispersal movements are rather consistently superior

to random movements with respect to corridor surfaces predicted by circuit theory. Predictive success does appear to vary among individuals, as indicated by the fact that the mixed model comparison of percentile ranks assigned by each model to observed locations did not produce reliable estimates of mean ranks due to highly skewed estimates of the individual random effect. This is not particularly surprising given that many individuals' dispersal paths kept them largely within primary habitat, while a few individuals set out into suboptimal valley habitat (e.g., Fig. 4.4 Path 4). These movements were generally not predicted as well, and are discussed further below. In sum, however, these results suggest that circuit theory models, which considerably outperformed cost-distance models in predicting wolverine dispersal paths, are capable of offering information of value in identifying wildlife corridors.

The questions of whether connectivity model performance is good enough to be of use in conservation planning and whether predicted corridors are good enough to provide connectivity cannot be answered simply by quantifying predictive performance. The answers depend, of course, on many factors, particularly the goals and practical limitations of the conservation or management plan at hand as well as the movement ecology of the focal species, as discussed in more detail below. In the case of species like the wolverine, for which broad-scale conservation planning is needed and is in many ways still in its early stages, the ability of connectivity models to predict dispersal well enough that conservation focus can be limited to a relatively small percentage of the landscape and still encompass most movements is expected to be highly beneficial for guiding allocation of limited conservation resources (B. Inman, pers. comm.).

Connectivity models cannot predict whether or not the landscape is, in fact, connected for a focal species. They simply predict regions of the landscape that are expected to best facilitate movement of the focal species. It is therefore critical that focal species' dispersal capabilities and habitat tolerance thresholds are understood and accounted for in the use of corridor model outputs for conservation planning. This may be less of a concern for wolverines than for other species as they are known to be capable of extremely long-distance migration and demonstrate a willingness to cross expanses of what is predicted to be extremely poor habitat. However, wolverines may be an extreme example in this regard, and even in their case, little is known about which natural or anthropogenic landscape features may act as impassable barriers to movement beyond anecdotal observations of fine-scale avoidance of highway traffic and housing developments (Inman et al. 2009). All corridor model results must therefore be interpreted with some caution and awareness of focal species habitat needs.

The question of whether a model-predicted corridor will provide connectivity as intended will ultimately depend on how the corridor's boundaries are defined. Both corridor models produce continuous surfaces for the entire map extent analyzed; they do not incorporate any criterion for designating ecologically relevant and/or practically useful corridor boundaries. Practitioners must decide how to extract a subset of this surface in order to define a discrete corridor. Ideally, this decision might be based on knowledge of focal species tolerance thresholds for habitat quality and corridor width. In practice, however, it may require identifying the spatial area of corridor habitat that is feasible to protect from a socioeconomic standpoint, which may further involve a

subjective or algorithm-based selection of land parcels that best balance connectivity value with monetary cost. Alternatively, this decision may require selection of an arbitrary cutoff value (e.g., 95th percentile of corridor surface), depending on the context and goals of the corridor delineation effort. This choice will be an important factor in the success of any corridor initiative guided by connectivity models.

Interpretation of Validation Metrics

The complementary nature of the four validation metrics used to quantify model performance is discussed in Chapter 3, but an important additional point must be made here about the absolute values of the validation metric results. Three of the four performance metrics use area-based percentiles, which means that they are dependent on the total size of the study area. While the study area boundaries were defined as objectively as possible based on the observed and expected range of movement of the focal individuals, these are inevitably subjective criteria. Had a smaller study area been selected under different criteria, each equal-area percentile would also contain a smaller area, resulting in apparently poorer results from percentile-based performance metrics. Thus, while model comparisons based on relative values of performance metrics are valid within a given study area, absolute values are not comparable across multiple study areas. For example, mean percentile ranks assigned to wolverine dispersal locations in this study are nearly as high as those assigned to elk relocations in Chapter 3, yet visual inspection of model outputs suggests that elk migration paths are predicted with much more consistent accuracy than wolverine dispersal paths. The high absolute values of

performance metrics for wolverines are largely the result of having defined a much larger study area relative to the length of individual wolverine paths than was the case for elk.

Interpretation of model validation metrics is, in general, species- and landscape-specific. As observed in this study, an arbitrarily defined 95th percentile corridor cutoff value generally resulted in the majority of, but not all, dispersal relocations falling within designated corridors. For species like wolverines with some ability to generalize in their selection of suitable habitat that are traveling through areas supporting many possible travel paths of similar suitability, failure of the corridor to capture all observed relocations may not be of great concern as it is likely that travel outside the predicted corridor could just as easily have occurred within the corridor. This may be particularly true in the case of dispersal through novel habitat; simple lack of familiarity with path options available to dispersers would be expected to result in variability among multiple individuals dispersing from the same natal territory. In such a case, a predicted corridor that fails to capture all portions of an observed movement is still likely to provide connectivity for the focal species. In this study it therefore may not be of great concern that 95th percentile corridors predicted by circuit theory models missed over 13% of dispersal relocations. However, for species with very strict habitat requirements or very strict fidelity to particular travel routes through highly heterogeneous landscapes (e.g., Berger 2004), failure of a predicted corridor to capture and protect the entire observed movement path may result in a loss of connectivity.

Movement Ecology of Wolverine Dispersal

An additional question explored in a preliminary way in this study was the extent to which the drivers of wolverine primary habitat selection pertain to habitat selection during dispersal. It is possible that wolverines respond to the landscape differently during dispersal than they do during home range movements due to differences in the motivation behind each of these movement types and in the spatial scales over which they occur (Ims 1995). Alternatively, wolverines may continue to seek primary habitat to the greatest extent possible during dispersal, simply relaxing this preference when necessary in their search for unoccupied territories. Understanding the drivers of habitat selection during dispersal is critical for determining whether resistance surfaces developed from data on home range movements are appropriate for use in models of dispersal corridors.

The results of this study generally support the use of a resistance surface based on primary habitat selection in connectivity models for dispersal movements. Reasonably strong performance of this model is indicated by the fact that 95th percentile corridors captured nearly 87% of disperser relocations and that disperser locations ranked above the 97th percentile on average in the case of circuit theory models. Furthermore, 57.9% of relocations occurred within areas designated by Inman et al. (in review) as primary habitat (suitability values of 0.982 – 1.0), and 82.1% occurred within areas designated as dispersal habitat (0.943 – 1.0). Anecdotal support is also provided by the path of M56, the juvenile male who traveled from near Grand Teton National Park in northwest Wyoming to just south of Rocky Mountain National Park in Colorado (Fig. 4.4 Path 4, Inman et al. 2009). This individual appears to have moved through primary habitat until

reaching the southern tip of the Wind River Range, at which point he continued on into the Great Divide Basin. Although this individual chose to travel through poor lowland habitat, he passed through at least two of three small islands of mountainous habitat dotting the Basin before making his way into the Colorado Rockies, suggesting that movement through non-primary habitat is not random and that primary habitat was sought and utilized where possible. In sum, it appears reasonable to infer that patterns of primary habitat selection hold for dispersal movements, but that selection thresholds are simply relaxed when necessary in order to reach an unoccupied territory.

Caveats and Future Directions

This study highlights the need for continued collection of wolverine location data capturing dispersal movements in order to explore wolverine movement ecology and the ability of connectivity models to predict wolverine movements with more rigor and detail. Such data are extremely rare, and the locations utilized here represent the most comprehensive dataset available on wolverine dispersal movements. Using these data, this study was able to provide a rare test of connectivity models in a focal species with significant connectivity needs as well as a rare look at the movement ecology of an elusive long-distance disperser. However, this analysis was subject to some limitations, and further study is needed.

Due to wolverines' rarity in the GYE, difficulty of capture, and technical limitations of tracking devices placed on animals of this size traveling over vast areas of rugged habitat, the dataset is limited in number of individuals, total number of relocations, and the frequency and regularity of relocations. These features of the dataset

are not expected to have been particularly problematic for model validation. The use of data from few individuals requires the assumption that these individuals are representative of the population, which is probably fair considering that they constitute a relatively large sample of the small GYE population. The small number of relocations limits the precision of the analysis but is not itself expected to bias results. Irregular relocation intervals are also acceptable because no attempt is made to infer individuals' movements between relocations. Collection of data by VHF implant and by GPS collar, however, introduces device-specific sources of bias. Aerial VHF telemetry can only be conducted when conditions are suitable for flight, precluding sampling of habitat use at night and in poor weather. In addition, VHF signals may not be detected when an animal strays far from its previous locations, leading to underrepresentation of long-distance excursions. GPS collars require detection of multiple satellites to fix their position, and in dense cover or rugged terrain, satellite signals may be inaccessible. Because fix success may be habitat-dependent, a GPS fix success rate of <50% in this dataset may introduce considerable bias (Frair et al. 2004; Sawyer et al. 2009). This bias would be extremely problematic for developing habitat suitability models because use of signal-blocking habitats are likely to be severely underrepresented. However, for the purposes of model validation, biases are only a concern if the predictive accuracy of the model differs between represented and underrepresented habitats, a situation that there is no *a priori* reason to expect here. Even if such differential predictive success were present, it is unlikely that it would differentially affect cost-distance and circuit theory models.

Thus, while absolute values of the validation results presented here should perhaps be interpreted with a degree of caution, model comparisons are expected to be sound.

This study addresses an overlooked aspect of disperser movement ecology by exploring the extent to which the drivers of habitat selection may differ between home range movements and dispersal movement, but it does so in a very preliminary way. Future work to quantitatively compare patterns of habitat selection between these two movement states through formal modeling using a more extensive dataset is expected to clarify disperser responses to the landscape and whether the use of primary habitat suitability models to predict dispersal paths is truly justified. This work may, in particular, improve understanding of wolverines' perception of and response to the landscape outside of core habitat patches. Beyond areas designated as dispersal habitat by Inman et al. (in review), habitat suitability values declined sharply such that most of the intervening lowlands received scores < 0.1 . These areas differ quite drastically from the mountainous terrain occupied by wolverines in terms of the habitat covariates included in the suitability model (Inman et al, in review; Table 4.2) and were never used by non-dispersers, leading to invariable predictions of strict avoidance. Thus, very little is known about dispersing wolverines' tolerance thresholds for suboptimal habitat characteristics, particularly anthropogenic features, or about wolverines' perceptual range. It is in these areas that habitat suitability models and movement models developed from more extensive disperser location data promise to greatly improve understanding of the movement ecology of wolverine dispersal as well as prediction of wolverine dispersal corridors where they matter most.

Tables

Table 4.1. Comparison of time and distance intervals found in data for dispersal-related movements from VHF implants and GPS collars.

	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>	<i>SD</i>
Distance (km)				
VHF implant	0.02	234.89	12.58	20.25
GPS collar	0.001	67.65	3.49	6.09
Time (days)				
VHF implant	2 min	189.22	9.59	13.87
GPS collar	1 hr	7.17	0.47	0.91

Table 4.2. Summary of final RSF model for Greater Yellowstone wolverines (Inman et al., in review).

<i>Habitat covariate</i>	<i>Source*</i>	<i>Resolution</i>	<i>Reference</i>
Latitude-adjusted elevation	1	30 m	Brock & Inman 2006
Terrain ruggedness index	1	30 m	Riley et al. 1999
April 1 snow depth	2	1 km	Barrett 2003
Distance to tree cover	3	30 m	Homer et al. 2001
Distance to high-elevation talus	1	30 m	Inman et al. (in review)
Road density	4	1 km	Carroll et al. 2001
Distance-weighted human pop density	4	1 km	Carroll et al. 2001
Distance to April 1 snow depth > 2.5cm	2	1 km	Barrett 2003

* Sources: 1) National Elevation Dataset, USGS, Sioux Falls, SD, USA; 2) Snow Data Assimilation System, National Snow and Ice Data Center, Boulder, CO, USA; 3) National Land Cover Dataset, Earth Resources Observation and Science Data Center, Sioux Falls, SD, USA; 4) USGS, Reston, VA, USA.

Table 4.3. Summary of parameters describing directional movements outside maternal home range radii, which include dispersal events as well as exploratory trips and return paths.

	<i>Mean</i>	<i>SD</i>	<i>Median</i>	<i>Range</i>
Start date	11-Mar	53.72 days	10-Mar	21-Dec - 8-Jul
End date	19-Apr	68.12 days	8-Apr	11-Jan - 1-Sep
Duration (days)	59.08	81.84	13.88	1.97 - 228
Distance (km)	114.46	120.47	72.24	12.49 - 548.55

Table 4.4. Results of corridor model validation based on: a) percentages of observed points falling within predicted 95th percentile corridors, b) mixed effects model comparing percentile values assigned to dispersal locations by each model, c) mixed effects model comparing differences between percentile values assigned to dispersal locations by null and alternative models, and d) means across individuals of observed path ranks among 99 random paths.

a)				c)			
Cost-distance		Circuit theory		Fixed Effects		p-value	
Total	SE	Total	SE	Intercept (Cost-distance)	SE	t-value	p-value
% in 95th percentile	55.64	14.867	86.92	6.974	-6.427	1.0278	< 2.2e-16
b)				Corridor model			
Fixed Effects		Estimate		SE		t-value	
Intercept (Cost-distance)		93.058		1.6709		55.6934	
Corridor model		(90.63)*		1.6709		55.6934	
Circuit theory		7.249		0.6581		11.0151	
Random Effects		Intercept SD		Residual SD			
Individual		4.2189		2.2494		9.7944	
Points in individual		4.5277		0.0008		9.7944	
d)				Cost-distance		Circuit theory	
Rank in random paths		Mean rank		SD		Mean rank	
Rank in random paths		3.61		5.4899		2.83	
Rank in individual		3.204		2.83		3.204	

*Due to skew in the individual random effect estimates, the model-estimated intercept is biased. The raw estimate of the mean is shown in parentheses.

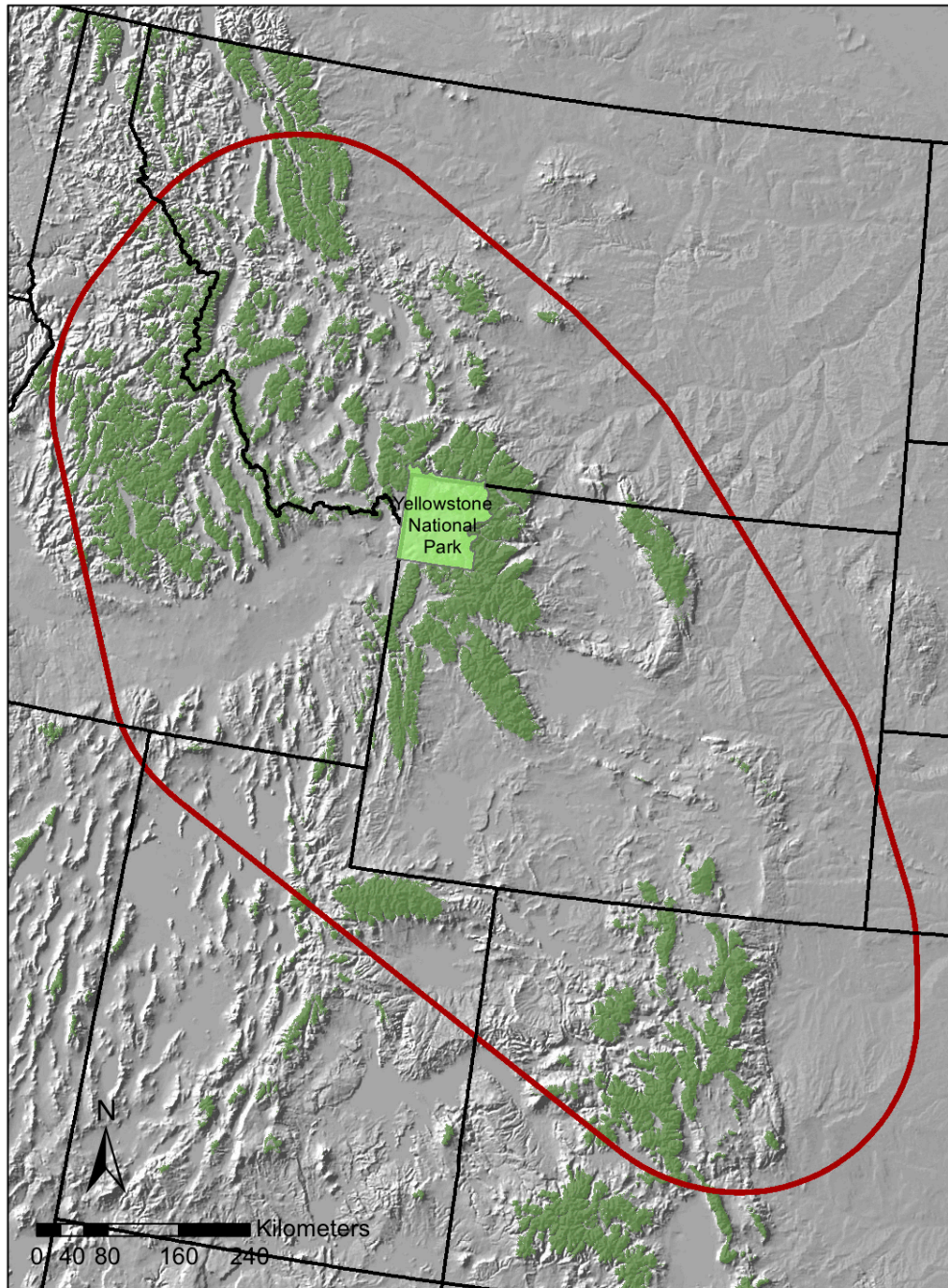
Figures

Figure 4.1. The Greater Yellowstone wolverine study area, defined by placing a 200 km buffer on the minimum convex polygon containing all GPS relocations collected from eight dispersers.

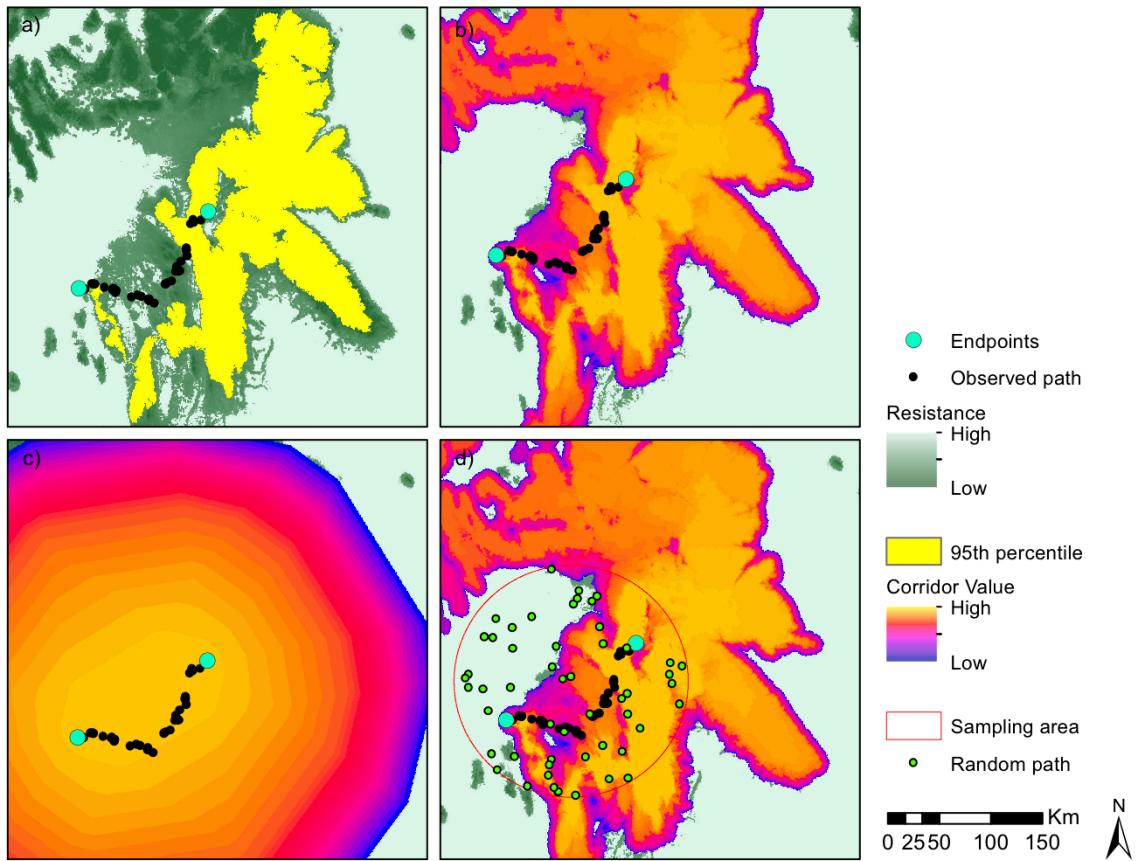


Figure 4.2. Example visualizations of validation metrics. Predictive performance of corridor models was assessed based on a) percent of points found within 95th percentile corridors, b) mean equal-area percentile value assigned to points, c) comparison to a null isolation-by-distance model, and d) comparison to a set of random paths.

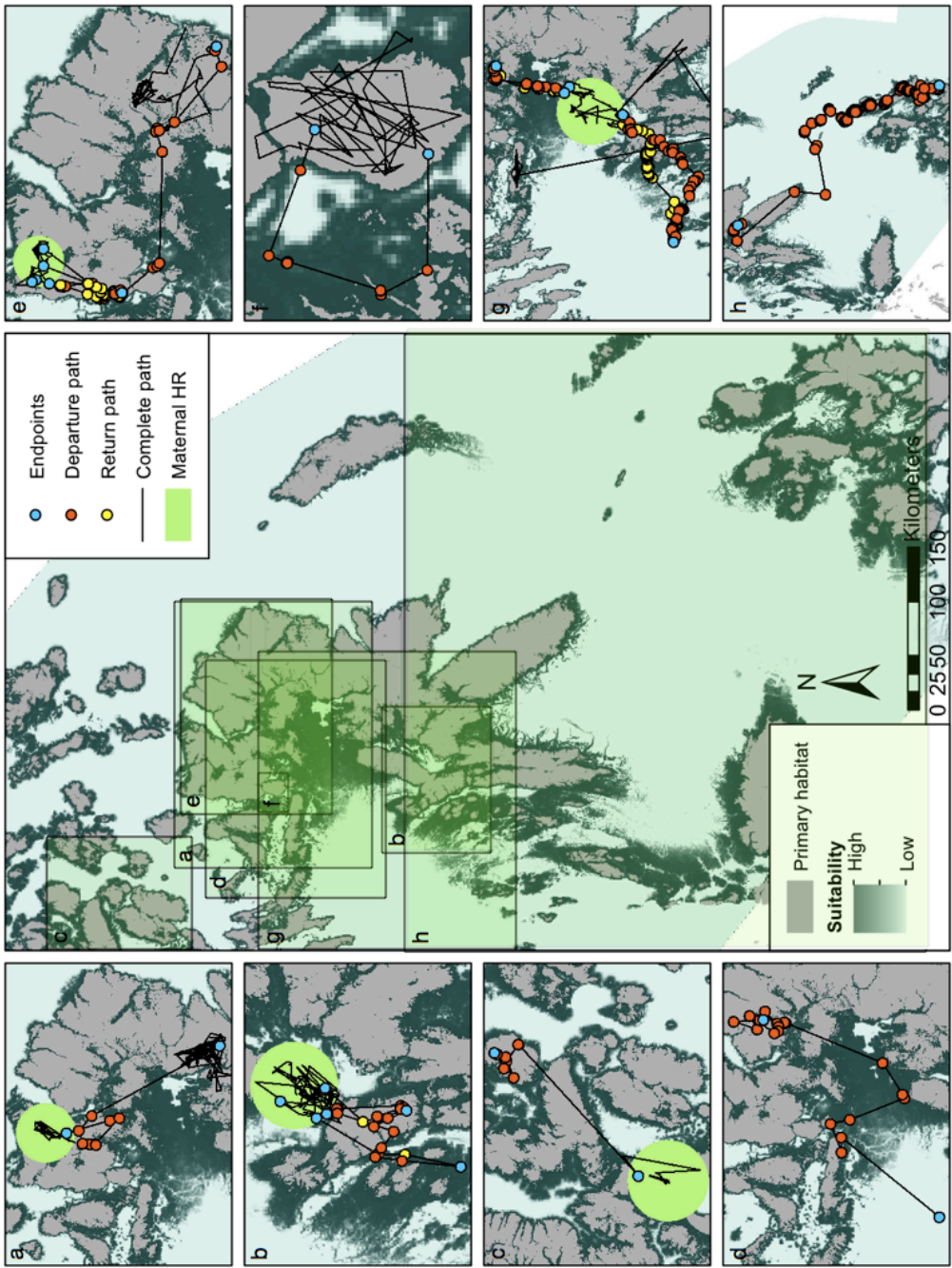


Figure 4.3. Dispersal-related movements were defined as all directional movements outside the maternal home range, outside primary habitat (f), or as the entire observed directional path (d, h). All 18 dispersal-related movements from 8 individuals are illustrated and overlaid on the study area (center) for reference.

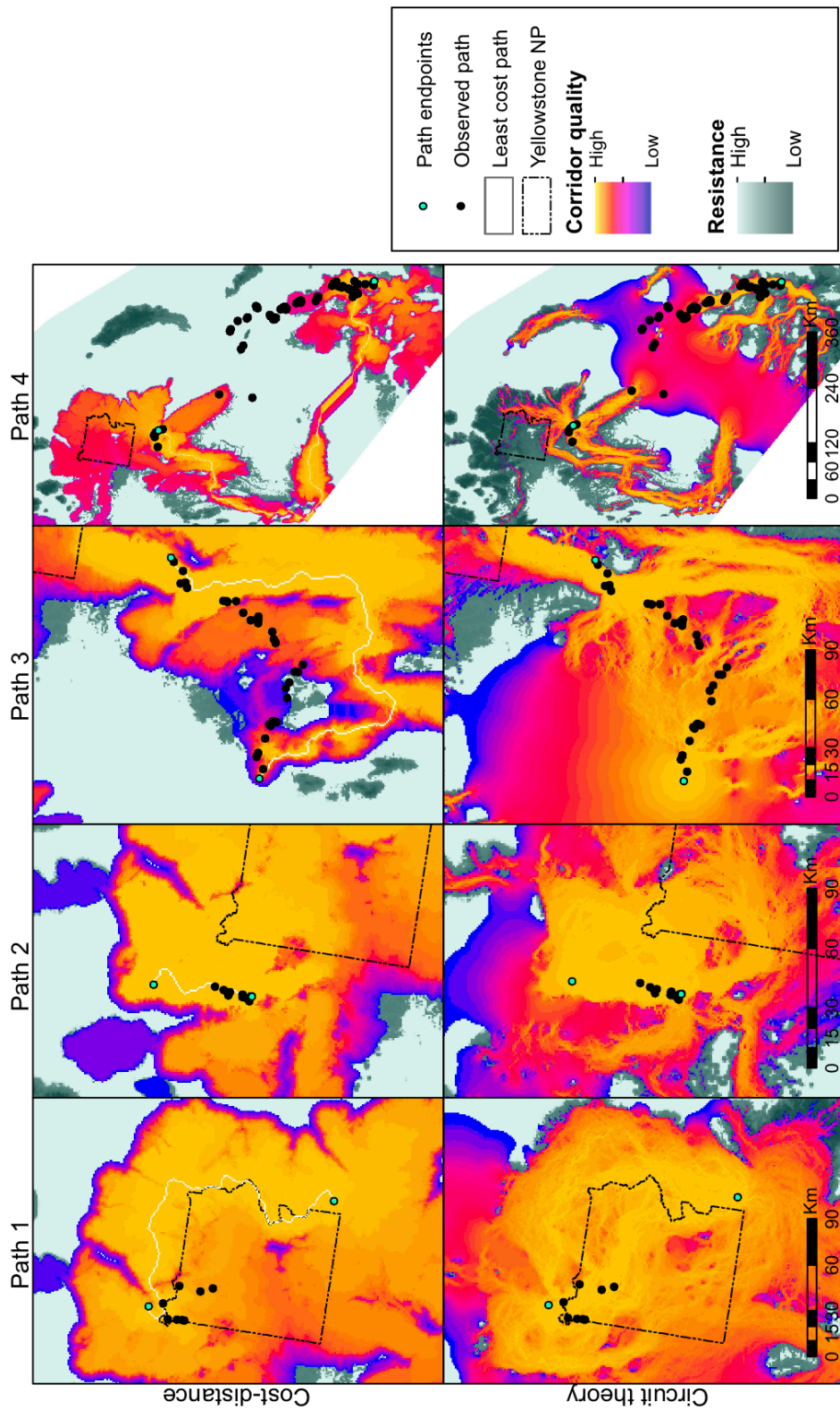


Figure 4.4. Cost-distance (top) and circuit theory (bottom) model outputs for four sample dispersal movements. The top 25th percentile of each modeled surface is shown, and the boundary of Yellowstone National Park is depicted for reference.

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CHAPTER 5

ASSESSING THE SENSITIVITY OF CONNECTIVITY MODELS TO MODEL
PARAMETERIZATION

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2, 3, 4, and 5

Author: Meredith M. Rainey

Contributions: Conceived and implemented the study design. Performed data analysis.
Wrote the manuscript.

Co-author: Dr. Andrew J. Hansen

Contributions: Provided feedback on the study design and analysis approach. Provided
extensive comments on the structure and content of the manuscript.

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Abstract

Corridors facilitating animal movements across the landscape have become important components of many conservation planning efforts as habitat loss and fragmentation increasingly threaten to sever these movements. Models are often used to identify areas likely to serve as corridors, but these models typically require many parameterization decisions, and it is currently unclear how each decision may impact predictive performance. Understanding sensitivity to model parameterization is important because few data are typically available to inform these decisions and optimal parameterization is thus unknown. This study analyzes the sensitivity to parameterization of two of the most commonly applied corridor models, cost-distance (or least cost distance) models and circuit theory models, by systematically altering key parameters of previously developed models of elk migration movements. Both models were found to be most sensitive to the spatial scale at which the focal species is assumed to respond to the landscape, as well as the complexity of the underlying landscape resistance model and uncertainty in path endpoints. An important finding was that spatial patterns of disagreement among model variants were predictable for cost-distance models but highly unpredictable for circuit theory models, with critical implications for use of circuit theory models in conservation planning. This analysis also provides insight into the potential drivers of migration path selection in elk and highlights the need for additional study of this neglected topic.

Introduction

Landscape connectivity, defined as the degree to which the landscape facilitates movement among resource patches (Taylor et al. 1993), is necessary for the long-term persistence of species. Movement provides individuals with access to resources that are patchily distributed in space and time and maintains gene flow and rescue effects among populations. However, these critical movement processes are increasingly threatened by habitat loss and fragmentation due to the spread and intensification of human land use (Hilton-Taylor 2000; Sala et al. 2000; Wilcove et al. 1998). As a result, connectivity has become a major focus of conservation biology, and establishment of corridors, broadly defined as “regions of the landscape that facilitate the flow or movement of individuals, genes, and ecological processes” (Chetkiewicz et al. 2006), is now considered a fundamental component of conservation planning (Crooks & Sanjayan 2006; Hilty et al. 2006).

In some cases, corridors may be easily identified based on empirical data capturing movement processes of interest (e.g., Berger et al. 2006). When such data are unavailable, however, reliance on connectivity models to predict regions likely to serve as corridors is necessary (Chapter 2). Connectivity models use estimates of the resistance to movement of a focal species offered by landscape elements to predict areas most likely to support movement and thus provide connectivity for the focal species. While connectivity models hold considerable potential to inform conservation planning efforts, their predictions have rarely been validated against empirical data to determine how

accurately they are able to represent actual patterns of movement, and these tests have generally been superficial in nature (Chapter 2).

In Chapters 3 and 4, I addressed this issue by rigorously evaluating the ability of existing methods of modeling connectivity to predict GPS collar relocations representing observed movements of migrating elk and dispersing wolverines. Here, I address an important additional component of model validation: assessment of the sensitivity of models to model parameterization. In this study, I evaluate the influence of key decision that must be made in the modeling process on model performance by systematically altering the parameterization of connectivity models presented in Chapter 3, then quantifying the effects of these alterations on the agreement between predicted corridors and GPS collar data from elk migration movements.

Connectivity Modeling Approach

Many alternative approaches to modeling connectivity have been developed (Chapter 2), but all approaches follow a general two-step process. First, resistance to movement of a focal species is estimated based on one or more landscape variables (e.g., elevation, land cover, or road density). Second, the relative probability or ease of movement between specified source and destination locations is estimated by a connectivity model, which incorporates the effects of resistance as well as distance on movement patterns. To develop the connectivity models upon which the sensitivity analysis presented here is based, I first used the most well-known data-based, quantitative method available to estimate resistance (Chapter 3). I then applied the two most

commonly used connectivity models, cost-distance and circuit theory models, to the resulting resistance surface to predict elk migration paths.

While resistance is often defined through a subjective process relying on expert opinion (e.g., Adriaensen et al. 2003; Chardon et al. 2003; Larue & Nielsen 2008), the use of data-based models to estimate resistance has begun to see increased use in the context of corridor modeling (e.g., Chetkiewicz et al. 2006; Coulon et al. 2008; Kindall & Van Manen 2007). In the most common quantitative approach, resource selection functions (RSFs; Manly et al. 2002) predict the relative probability of use of a given site by a focal species by comparing habitat characteristics at samples of used sites (e.g., GPS relocations) and available sites (selected from the surrounding landscape), typically in the form of a logistic regression model. A habitat suitability map is calculated by applying the RSF equation to each cell in the landscape, and resistance is then defined as the inverse of suitability (e.g., Chetkiewicz & Boyce 2009; Walker & Craighead 1997).

Cost-distance models, or least cost distance models (e.g., Adriaensen et al. 2003; Craighead et al. 2001; Hootor et al. 2000; Larue & Nielsen 2008; Richard & Armstrong 2010; Singleton et al. 2002; Walker & Craighead 1997), minimize the tradeoff between travel distance among habitat patches and exposure to unsuitable habitat (Walker & Craighead 1997). Least cost paths offer the shortest cumulative cost-weighted distance between a source and destination and are thus considered optimal routes. A complete corridor surface can also be generated, in which each cell is assigned the cost-weighted distance value of the least costly path passing through it, or by including all paths with cost-weighted distance values below a chosen cutoff value. This approach allows

assessment of corridor width, identification of potential bottlenecks and alternative routes, and quantification of the contribution of any cell in the landscape to connectivity. Cost-distance models assume that dispersers have perfect knowledge of the landscape. Similarly, these models do not assume that cost-distance values are proportional to probability of use by the focal species. Instead, paths with lower cost-weighted distance are simply predicted to offer the best chance for successful dispersal.

Circuit theory models (McRae 2006; McRae et al. 2008) make use of the intuitive analogy between movement of individuals through a landscape and movement of charge through an electrical circuit. Circuit theory models treat cells in a landscape as electrical nodes connected to neighboring cells by resistors, with resistance values determined by the cells' landscape resistance values. Consecutive resistors can be linked in series to create a path between two patches, and a single route's total resistance is equivalent to its cost-weighted distance (as in cost-distance models; McRae et al. 2008). In contrast, when all possible paths among patches are treated as resistors connected in parallel, a measure of effective cumulative resistance is obtained that decreases with increasing numbers of paths. Circuit theory models thus account for the positive effects of path redundancy on connectivity. Resulting per-cell measures of current flow across the landscape reflect the probability of movement of individual random walkers through a given cell, quantitatively identifying important bottlenecks to dispersal. Conversely, this measure may discount broad swaths of highly suitable habitat because current passing through any particular cell is low. Unlike cost-distance models, circuit theory models

assume that dispersers only perceive the landscape within a 1-cell radius of their current location.

The complexity of this quantitative approach relative to expert opinion methods requires many decisions about model parameterization that may affect predictive performance. Statistical uncertainty in RSF model coefficients may also affect prediction. Furthermore, cost-distance and circuit theory models may differ in the extent and nature of their sensitivity to these sources of variability in model outputs, making sensitivity analysis an important component of connectivity model validation.

Assessing Sensitivity to the Modeling Process

In this study, I quantify the sensitivity of connectivity model predictions to six key sources of variability in the modeling approach described above. Using the connectivity models presented in Chapter 3 as base models, I systematically alter six model parameters to produce a total of nine variants of each connectivity model, and assess the effects of these alterations on model performance by validating migration path predictions against reserved GPS collar data.

(1) Spatial Scale of Availability Sampling: Habitat selection is understood to occur on multiple spatial scales (Johnson 1980). For example, individuals make broad-scale decisions to establish a home range before making continuous fine-scale decisions about selection of resource units within the home range. Boyce et al. (2003) have demonstrated that RSFs are sensitive to the spatial scale on which available sites are sampled for comparison with used sites. When available sites are sampled from

throughout a large study area, preferences for habitat characteristics that vary over broad scales (e.g., elevation) are apparent, but when available site samples are localized, preferences for habitat characteristics that vary over fine scales (e.g., percent cover of a particular vegetation type) may emerge. Sampling availability on the scale that is most relevant for habitat selection by the focal species in the movement state of interest is expected to be critical for accurately capturing responses to the landscape and predicting movement paths.

(2) Spatial Resolution of Analysis: There is potential for spatial resolution, or grain, to influence the outcome of spatial analyses (Wiens 1989). As grain (i.e., cell size) increases, more of the landscape's heterogeneity is contained within each cell and lost to the resolution of the analysis. Meanwhile, between-grain heterogeneity decreases. This may result in important differences between the heterogeneity that is represented in map surfaces and the heterogeneity that is perceived by the focal species during travel, and may influence the capacity for predicted corridors to match observed travel paths.

(3) Selection of Habitat Covariates: In order for RSFs to accurately quantify habitat suitability, the covariates that they include must be representative of the major drivers of the focal species' response to the landscape. By considering time-varying measures of primary productivity and snow conditions as candidate covariates for RSF models, Chapter 3 began to explore the hypothesis that phenological conditions (i.e., the timing of natural phenomena such as vegetation green-up and snow accumulation) may influence habitat selection during migration, as they are known to influence home range

habitat selection (Hebblewhite et al. 2008), timing of migration (reviewed in Irwin 2002), and use of stopover sites during migration (Sawyer & Kauffman 2011) under the forage maturation hypothesis (Fryxell 1991; McNaughton 1985). Model selection procedures based on information theory (Burnham & Anderson 2002) suggested that these factors do in fact contribute to elk habitat selection during migration, but it is not clear how inclusion of these covariates influences connectivity model performance. Comparing the performance of models including these variables to models that exclude them provides a more explicit test of the capacity for these factors to improve prediction of migration paths as well as a test of the sensitivity of connectivity models to selection of RSF model covariates.

(4) Model Uncertainty: Fitting RSF models involves a series of potentially influential choices, including selection of candidate covariates, construction of candidate models, choice of a model structure, decisions concerning adjustment of model fit, and procedures for final selection of an inferential model. All of these choices ultimately influence statistical error estimates on final RSF model coefficients, and their overall effect on connectivity model performance can be assessed by modeling corridors across the range of uncertainty in coefficients as quantified by their confidence limits.

(5) Model Complexity: RSF models can be complex, somewhat difficult and tedious to fit, and require many subjective parameterization choices. These features may make RSFs sensitive to uncertainty and parameterization details, and may render them intractable for some applications. It is therefore important to determine whether a

simpler approach may produce similar results. One simple model of habitat suitability is based on the Mahalanobis distance statistic (Mahalanobis 1936), a multivariate measure of dissimilarity between the mean covariate values associated with observed locations and the covariate values found at a given location in the landscape (Clark et al. 1993). Areas that are similar to those used by the focal species have small Mahalanobis distance values and are predicted to be more suitable than those with large distance values, which differ greatly from used locations. Mahalanobis distance models are advantageous in that no sampling of available sites is necessary, removing a major source of subjectivity in RSF model development, and they are not sensitive to multicollinearity among habitat covariates.

(6) Uncertainty in Path Endpoints: In most applications of corridor models, individual travel paths are not known with certainty, and corridor endpoints cannot be specified as the sites where an individual leaves a source patch and enters a destination patch. In Chapter 3, use of precise path endpoints from GPS collar data allowed evaluation of a best-case scenario of connectivity model performance, but does not necessarily represent a realistic application of the models. It is therefore important to understand how less precise specification of corridor sources and destinations as patches rather than points influences model performance.

While previous studies (Newell 2006; Rayfield et al. 2010) have performed limited sensitivity analysis of the effect of uncertainty in relative resistance values assigned by expert opinion approaches, this study is the first to comprehensively assess sensitivity of a rigorous, data-based approach to connectivity modeling. The goal of this

study is to quantify the relative importance of key choices that must be made in the modeling process. This analysis is expected to be of value to researchers and conservation practitioners wishing to understand the relative importance of these decisions and to allocate time and resources appropriately in connectivity modeling efforts.

Methods

Dataset

This study utilizes previously collected GPS telemetry data (Grigg 2007) provided through a data sharing agreement with Montana Fish Wildlife and Parks (J. Gude, Research and Technical Services Section Chief, and K. Proffitt, Region 3 Wildlife Biologist) for model development and validation. Forty-five female elk (*Cervus elaphus*) in the Madison Valley area of southwest Montana were fitted with GPS collars during the winters of 2005 and 2006. Collars were worn for approximately one year, and locations were recorded every 30 minutes, providing a total of 745,432 relocations. In Chapter 3, migration periods were quantitatively identified as highly directional movements occurring outside of 95% kernel density contours that resulted in marked displacement from one seasonal home range to another. Based on these criteria, 41 of 45 collared individuals in this partially migratory population completed spring and/or fall migration, and these movements form the basis of model development and validation.

Focal Species

Elk are the most abundant herbivore in the Madison Valley and throughout the Greater Yellowstone Ecosystem. At the time of data collection, the Madison Valley herd numbered approximately 5,000 individuals (Grigg 2007). Elk are highly adaptable mixed feeders, foraging on a variety of grasses, forbs, and shrubs (Cook 2002). As is the case with ungulates occupying spatially and temporally heterogeneous landscapes worldwide (Fryxell and Sinclair 1988), elk migrate seasonally primarily in response to shifting quality and accessibility of forage across the landscape in order to maximize nutrient intake (Irwin 2002). In spring, migration from winter to summer ranges is triggered by snowmelt and vegetation green-up, and in fall, travel to winter ranges is driven largely by decreasing availability of forage with accumulation of deep snow as well as decreasing nutritional quality of vegetation as it matures (reviewed in Irwin 2002). In the Rocky Mountains, spring migration typically occurs in May but can range from April to July, and fall migration, which is more variable among individuals, may range from September to January (Grigg 2007; summarized in Irwin 2002). Migration distances of 2.4 km to 150 km have been observed, and movements may span anywhere from several days to 8 weeks, with movement rates and use of stopover sites influenced by weather conditions (Skinner 1925), rates of vegetation green-up (Dalke et al. 1965), hunting pressure (Grigg 2007), and other biological requirements such as calving (Irwin 2002).

Study Area

The Madison Valley is located in southwest Montana between the Gravelly and Madison ranges at the eastern edge of the Central Rocky Mountains (44° 58' N, 114° 36' W).

W). The study area, defined by placing a 5 km buffer on the minimum convex polygon of all GPS relocations, includes much of the valley north to Ennis Lake and south past Henry's Lake as well as the Madison Range to the east (Fig. 5.1). Elevation ranges from 1433 m in the valley, where elk overwinter, to 3436 m with rugged topography in the Madison Range where elk summer ranges are found. Lower elevations and valleys comprising winter range are generally characterized by grasslands, sagebrush, and irrigated pastures, with willow-dominated (*Salix spp.*) riparian communities along the Madison River and most streams (Despain 1990; Gude 2004). Slopes support grasslands at low elevations, and at higher elevations coniferous forest is intermixed with aspen stands and meadows, providing high quality forage for elk in summer. The climate is temperate, and local conditions are strongly influenced by elevation. Summers are characterized by warm daytime temperatures and cool overnight lows that can drop below freezing at high altitudes (Despain 1990; NPS 2012). Winters are long and cold, with frequent sub-zero highs. Most precipitation falls as snow, which begins to accumulate in mid- to late-October. Snow accumulation begins earlier and lasts longer with increasing elevation, and snow water content is positively correlated with elevation as well. Accumulation of deep snow at high elevations drives fall migration of elk to lower elevation winter ranges, and spring migration upslope follows snowmelt and vegetation green-up (reviewed in Irwin 2002). The eastern portion of the study area extends into central Yellowstone National Park (YNP), but most of the area consists of U.S. Forest Service land, with some lands managed by other government agencies and private lands concentrated in the valley. Land ownership patterns may influence elk

migration movements due to differential disturbance, habitat quality, and hunting access (Grigg 2007).

Base Models

The base models upon which sensitivity analysis is conducted in this study are presented in detail in Chapter 3 and summarized here. Using a subset of the migratory GPS collar data, habitat suitability for migration was modeled using season-specific resource selection functions (RSFs; Manly et al. 2002) in the form of matched case-control logistic regression models (Arthur et al. 1996; Compton et al. 2002; Johnson et al. 2002). These models compared characteristics of used sites (cases in the form of GPS relocations) with those of available sites (controls sampled from the surrounding landscape) to estimate the relative probability of use across the landscape. Available sites were spatially matched to used sites by sampling them from within an individual's maximum observed step length between GPS relocations, and they were temporally matched by sampling time-varying covariates (vegetation greenness and snow conditions) on the same date at which their corresponding GPS relocation occurred. This allowed assessment of habitat selection at fine spatial scales and assessment of the effect of temporally variable environmental conditions on selection of migration paths. Habitat covariates included in final RSF models (Table 5.1) included topography (elevation, slope, and aspect), land cover, land ownership, density of edges between forest cover and other natural cover types, density of roads, and phenological variables related to forage quality and availability, including normalized difference vegetation index (NDVI), snow water equivalent (SWE; spring model), and snow cover (presence/absence; fall model).

Final seasonal models are summarized in Table 5.2. Each final model was used to calculate a habitat suitability map in ESRI ArcMap 9.3 in the form of

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)$$

where $w(\mathbf{x})$ gives the relative probability of use of each cell in the landscape given its covariate values and has a lower bound of zero. (The absolute probability of use cannot be calculated from a use/availability sampling design because the extent to which available sites are used is not known (Manly et al. 2002).) Suitability maps were calculated at the resolution of the coarsest input layer (SWE) with cell dimensions of 673 m (equivalent of 30 arcsec in the Madison Valley study area).

Both cost-distance models and circuit theory models use a map of resistance (cost) to predict the relative value of cells in the landscape for travel between a pair of user-defined endpoints. Resistance maps were calculated for each season as the inverse of suitability and were rescaled to be bounded by 0 and 1 using the formula

$$\text{Resistance} = 1/(1 + \text{Suitability})$$

such that highly suitable cells present low resistance to movement.

Migration paths of each individual in a withheld test dataset were then predicted using both cost-distance and circuit theory models. The GPS relocations bounding migration paths were designated as the endpoints to be connected by corridor models. Cost-distance models were run in ArcMap using the cost-path and corridor Spatial Analyst functions. Circuit theory models were run in CircuitScape (McRae & Shah 2008), and model outputs in the form of natural log-transformed current maps were imported into ArcMap for visualization and validation.

Sensitivity Analysis

I test the impact of six key parameterization decisions in the connectivity modeling process through alterations of the base models described above, which produce a total of nine connectivity model variants.

(1) Spatial Scale of Availability Sampling: In base models, available habitat was sampled from within an individual's maximum observed step length. Here, available habitat is instead sampled from throughout the study area. Available points were again matched by date with used points to enable appropriate use-availability comparisons of time-varying covariates.

(2) Spatial Resolution of Analysis: I developed habitat suitability maps with 250 m and 1 km cell dimensions for comparison with the original map (673 m). These maps were calculated by applying a bilinear resampling algorithm to the original covariate layers, then recalculating the habitat suitability map.

(3) Selection of Habitat Covariates: To determine the effect of phenological habitat covariates on connectivity model performance, I compared the performance of base models, which included these covariates, to alternative models fitted without them.

(4) Model Uncertainty: To test the effects of uncertainty in RSF model coefficients, I calculated habitat suitability maps using the upper and lower 95% confidence limits of each coefficient in base RSF models for comparison with those calculated from coefficient estimates.

(5) Model Complexity: Corridor predictions from base RSF models of habitat suitability were compared with those from a simpler Mahalanobis distance model (Mahalanobis 1936). Mahalanobis distance maps were calculated using the mahasuhab() function in the R package adehabitat (Calenge 2006). All covariates were rescaled prior to model fitting such that their variance was approximately equal to ensure that each received equal weight in the analysis. Maps were then imported to ArcMap for further analysis.

(6) Uncertainty in Path Endpoints: Base models defined corridor endpoints precisely as GPS relocations spanned by observed migration paths. Here, 95% kernel contours containing the bulk of summer and winter home range movements were treated as connectivity model source and destination patches, with habitat suitability specified by base seasonal RSF models.

Model Validation

Relative predictive performance of each of the above model variants was assessed using four validation metrics, which are presented in detail in Chapter 3 and summarized here.

95th Percentile Corridors: The overall percentage of observed points in the reserved test dataset that fell within the 95th percentile corridor predicted for the individual from which each point was sampled was determined using ratio estimation for unequal size cluster samples (Lohr 2010).

Mean Percentile Rank: After converting raw values assigned to each cell in the landscape by each corridor model to equal-area percentile ranks, I determined the percentile ranks assigned to cells containing GPS relocations by each corridor model. Cross-model percentile rank comparisons were conducted using a mixed effects linear regression model. Percentile ranks assigned to GPS relocations were treated as the response variable, connectivity model type (cost-distance vs. circuit theory) and model variant were treated as fixed effects, and GPS relocations nested within individuals were treated as random effects.

Null Model Comparison: To test the null hypothesis that elk movements are driven only by distance and not by habitat suitability, I calculated the difference between percentile ranks assigned to GPS relocations by each model of interest and percentile ranks assigned to points by a corresponding null model, in which connectivity models were run on a uniform cost surface. Cross-model comparisons of these differences were conducted using a mixed effects model as described above.

Random Path Comparison: To test the null hypothesis that there is no effect of habitat suitability or distance on elk migration path selection, I compared the mean value assigned by each model to points in each observed path with the mean values assigned to points in a corresponding set of random paths, identifying the rank of the observed path mean in the distribution of random path means for each individual. I calculated the mean rank of individuals' observed paths and the percentage of individuals whose observed paths received the top rank.

Spatial Patterns of Uncertainty

Evaluations of the above model variants quantify *how much* each of choice in the modeling process influences the overall predictive performance of corridor models, but they do not provide information about *where* these choices most influence performance. Ideally, uncertainty among models will be low surrounding a generally agreed-upon best travel corridor, where model predictions are most critical for conservation planning decisions, with uncertainty among models increasing with distance from this corridor. Awareness of typical spatial patterns in model uncertainty is important given that in most modeling applications, optimal model parameterization may not be obvious. To illustrate spatial patterns in disagreement among model variants, I calculated and mapped the inter-quartile range (IQR) of predicted values from each of the nine model variants in each grid cell for both cost-distance and circuit theory models (after Kissling et al. 2010).

Results

Sensitivity Analysis

Habitat suitability maps produced by each variant of the base suitability model are compared in Figure 5.2. Most maps are qualitatively similar, but altering the scale at which available habitat is sampled (coarse-scale model) and reducing the complexity of the suitability model (Mahalanobis distance model) result in considerable change to the map surface, apparently missing a great deal of fine-scale variability in habitat suitability that appears in other maps.

Corridor predictions among connectivity model variants are spatially similar (Figs. 5.3, 5.4), tending to emphasize the same routes. However, fine-scale variation is evident, and the relative weights given to alternative routes vary. As seen in Chapter 3, cost-distance and circuit theory models produce broadly similar predictions of elk migration paths, but as expected based on differences in their formulation and assumptions, their spatial patterns of emphasis differ. Cost-distance models highlight complete paths spanning migration endpoints, while circuit theory emphasizes areas close to path endpoints and highlights finer-scale variability within corridors broadly identified by cost-distance models.

All four metrics of model performance produce qualitatively similar results (Tables 5.3 – 5.6), in most cases indicating that cost-distance models outperform circuit theory models in predicting elk migration paths, though typically by a narrow margin. The scale at which available habitat is sampled had the greatest impact on corridor model performance: the coarse-scale model exhibited a substantial decrease in predictive accuracy compared to the base model. Model performance also drops considerably when the habitat suitability model is simplified (Mahalanobis distance model) and when endpoints are uncertain (home range model). In comparison, the grain of analysis and uncertainty in RSF model coefficients had relatively minor effects on connectivity model performance. These performance rankings generally hold across seasons, although the magnitude of differences among alternative models varies between spring and fall (Tables 5.3 – 5.6).

In spring, 95th percentile corridors predicted by base cost-distance models contained 80.32% (SE = 13.423) of GPS relocations, while 95th percentile corridors predicted by base circuit theory models contained 82.22% (SE = 7.627) of relocations. Scores ranged from 54.15% (SE = 12.543) for the cost-distance model based on coarse-scale availability sampling to 87.68% (SE = 9.176) for the cost-distance model based on upper confidence limits of RSF coefficients. The base cost-distance model assigned GPS relocations a mean percentile rank of 98.645 (SE = 0.6083), and the base circuit theory model assigned a mean percentile rank of 98.235 (SE = 0.6094). Coarse-scale availability sampling reduced mean percentile ranks by an average of 1.509 (SE = 0.0577) points, while models excluding phenological covariates had mean ranks averaging 0.659 (SE = 0.0577) points higher than base models. Base cost-distance models assigned relocations percentile rank values that averaged 6.394 (SE = 0.8467) points higher than those assigned by a null model, while the base circuit theory model assigned percentile rank values that averaged 1.921 (SE = 0.8539) points lower than those assigned by a null model. Coarse-scale availability sampling reduced performance relative to null models by 1.509 (SE = 0.1682) points, while models excluding phenological covariates increased relative performance by 0.659 (SE = 0.1682) points. Under the base cost-distance model, observed paths had a mean rank among random paths of 1 (SD = 0), with all observed paths receiving ranks of 1, and under the base circuit theory model, observed paths had a mean rank of 2.67 (SD = 3.869), with 75% of observed paths receiving ranks of 1. Mean ranks of 1 (SD = 0) were received by cost-distance models run at 250 m resolution, with upper and lower confidence limits on RSF

coefficients, and excluding phenological covariates. The maximum mean rank of 10.75 (SD = 18.543) was received by the cost-distance model variant in which home ranges defined corridor endpoints.

In fall, 95th percentile corridors from base cost-distance models included 74.4% (SE = 9.908) of GPS relocations, with 73.9% (SE = 9.850) of relocations contained by 95th percentile corridors from base circuit theory models. Scores ranged from 31.48% (SE = 17.222) for the cost-distance model based on coarse-scale availability sampling to 78.97% (SE = 8.894) for the corresponding circuit theory model. Relocations were assigned a mean percentile rank of 98.508 (SE = 1.2211) by the base cost-distance model and a mean rank of 97.897 (SE = 1.2240) by the base circuit theory model. Models based on coarse-scale availability sampling had mean percentile ranks averaging 4.483 (SE = 0.1309) points lower than base models, while exclusion of phenological variables increased mean ranks by an average of 1.161 (SE = 0.1309) points. The base cost-distance model assigned relocations percentile rank values that averaged 0.412 (SE = 0.6679) points lower than those assigned by a null model, while the base circuit theory model assigned them rank values averaging 0.604 (SE = 0.6718) points lower than a null model. Models based on coarse-scale availability sampling reduced performance relative to null models by 4.483 (SE = 0.1270) points, while models excluding phenological covariates increased relative performance by 1.161 (SE = 0.1270) points. Observed paths had a mean rank among random paths of 3 (SD = 6.325) under the base cost-distance model, with 90% of observed paths received ranks of 1, and under the base circuit theory model, observed paths had a mean rank of 1.9 (SD = 2.846), also with 90% of observed

paths receiving ranks of 1. Mean ranks of 1 ($SD = 0$) were received by cost-distance models excluding phenological covariates and based on Mahalanobis distance, and the maximum mean rank of 16.2 ($SD = 15.674$) was received by the circuit theory model in which home ranged defined corridor endpoints.

The consensus across the four metrics presented is that the model variant excluding phenological covariates produces the best corridor model predictions in both spring and fall. The 95th percentile corridor metric ranks this model variant second among cost-distance models and first among circuit theory models in spring, and vice versa in fall. The mean percentile rank and null model comparison metrics rank this variant first across both connectivity models in both spring and fall, and the random path comparison metric indicates that it is tied for the top rank among cost-distance models in spring and fall, with inconclusive ranking results among circuit theory models due to the skewed distributions of random path ranks.

Spatial Patterns of Uncertainty

Assessment of spatial patterns of uncertainty in corridor predictions among suitability model variants reveals unexpected results. Maps of interquartile ranges of corridor values assigned to map cells by suitability model variants provides a measure of uncertainty among model predictions (Fig. 5.5). The interquartile range map for cost-distance models illustrates the desirable case in which uncertainty is low in the areas of highest predicted corridor value and increases with distance, with the highest levels of uncertainty located far from the focus of any potential conservation action. The interquartile range map for circuit theory models, however, indicates that spatial patterns

of uncertainty among models are chaotic, with sites of high disagreement among models found in areas of potential importance for corridors.

Discussion

Relative Sensitivity to Model Parameters

Many decisions about model parameterization must be made in the process of constructing rigorous, data-based connectivity models, but these choices must often be made subjectively due to lack of information, and the relative impact of each choice on predictive performance has thus far not been clear. Analysis of the sensitivity of corridor predictions is therefore a key component of connectivity model validation with the potential to guide allocation of time and resources in the application of connectivity models to conservation planning. All connectivity model variants explored in this analysis tended to produce spatially similar corridor predictions emphasizing the same general routes as optimal corridor components (Fig. 5.3, 5.4). However, predictive performance varied among models, with some choices in the modeling process affecting performance considerably more than others (Tables 5.3 – 5.6). The relative magnitude of these impacts have important implications for applied use of connectivity models.

The most drastic drop in model performance resulted from modeling coarse-scale rather than fine-scale habitat selection. The difference in connectivity model performance based on fine-scale versus coarse-scale RSF models strongly indicates that elk are selecting migration paths based on fine-scale assessments of local habitat and that corridor models are sensitive to the ability of underlying habitat suitability models to

capture the dominant scale of habitat selection appropriately. This is an important lesson given that the habitat suitability maps underlying most existing connectivity models have been based on expert opinion or standard logistic regression RSF models (in which all available sites are pooled and are thus typically sampled from throughout the study area), both of which overlook the potential importance of fine-scale habitat selection during long-distance movement processes. Maxent (Phillips et al. 2006), an increasingly popular method of modeling habitat suitability that is now being applied to large scale connectivity planning efforts (e.g., Montana's recent statewide connectivity analysis; Montana Fish Wildlife & Parks, 2011), also samples availability at broad scales by default, though it is capable of accommodating other sampling designs.

The use of a much simpler habitat suitability model based on Mahalanobis distance (Mahalanobis 1936) also resulted in a substantial drop in predictive performance. This approach offers practical advantages: it is straightforward to implement using a free, widely available statistics package (R; R Development Core Team 2011), it is robust to multicollinearity among habitat covariates, and it does not require subjective sampling of availability. However, this simplicity appears to lead to its failure to capture important details of elk movement ecology and thus to a substantial loss of predictive accuracy. This approach is therefore not recommended.

A third parameter with relatively strong influence on predictive performance was the precision with which path endpoints were defined. In most applications of connectivity models, corridor sources and destinations are defined broadly as primary habitat patches or protected areas. While defining endpoints in this way negatively

affected the ability of connectivity models to predict migration paths of single individuals in this study, these corridors may in fact be good representations of the average route that would be taken by many individuals over time.

Effects of Phenology on Migration Path Selection

Exclusion of phenological covariates representing snow conditions and primary productivity from RSFs appears to yield the best predictive accuracy in both spring and fall and for both cost-distance and circuit theory models. This result was unexpected given that model selection based on information theory indicated that RSFs containing these covariates were much more strongly supported than RSFs excluding them (Chapter 3), and phenology is known to be a strong driver of other aspects of elk movements.

Improved predictive performance of models excluding phenological covariates may stem from the movement ecology of elk migration. In Chapter 3, phenology of vegetation green-up and snow accumulation were hypothesized to influence fine-scale habitat selection during migration, but habituation to learned paths constrained by more permanent landscape features may in fact be the sole or predominant driver of migration path selection. Selection of RSF models containing phenological covariates may have been due to correlations between these covariates and other unobserved factors associated with elk migration paths, or autocorrelation in the GPS collar dataset used to develop RSFs may have lead to selection of overly complex models (Beale et al. 2010; Burnham & Anderson 2002; Legendre 1993).

Alternatively, the hypothesized influence of phenology on migration path selection may be correct, and inclusion of phenological covariates may have failed to

improved prediction simply due to technical details of the modeling process. First, the matched case-control design of the RSF model accommodated temporal variability in NDVI and snow data, but the resistance surface calculated from this model for use in connectivity models was necessarily static and was calculated with seasonal average values of these covariates. Thus, while the matched case-control design is presumed to have improved coefficient estimates for time-varying NDVI and snow condition covariates relative to standard models not capable of handling temporal variability, much of the heterogeneity in these conditions as experienced by elk on the ground was lost prior to corridor prediction.

Second, the NDVI and snow datasets used in this study appear to be quite noisy, particularly in the low ranges of NDVI and SWE values at which elk are likely to initiate movements, and have coarse resolution (250 m – 675 m; Table 5.1) relative to the fine scales at which elk are likely to respond to forage conditions (Anderson et al. 2005; Christianson & Creel 2009; Fortin et al. 2005b). The ‘signal’ of elk responses to these factors is perhaps present but only minimally detected due to a low signal-to-noise ratio. This problem may be compounded if elk are responding to relative values across space and time rather than absolute values, making comparisons among the conditions present along alternative paths over time rather than seeking specific levels of primary productivity or snow cover, as these relationships may largely be lost in the noise.

Finally, the relevance and accuracy of NDVI and snow data vary with cover type, which was not addressed here. Vegetation greenness as a measure of primary productivity of grass and shrub cover is relevant to elk foraging decisions, but greenness

of forest cover is not. Similarly, SWE and snow cover estimates are expected to be considerably more accurate in grass and shrub cover types than in forest, where ground snow characteristics are largely hidden by the forest canopy. It was not possible to simply exclude these covariates from forested areas because matched case-control logistic regression models do not accommodate missing values. Furthermore, I sought to determine whether these datasets had value for practical application of connectivity models in conservation planning settings without the need for extensive screening and processing. Data representing phenological covariates were thus sampled in raw form for all cover types. Hypothesized selection for intermediate NDVI was accommodated in RSF models by including a quadratic NDVI term, and selection against high NDVI values associated with forest cover was not expected to be problematic because it is consistent with this relationship. Selection for low snow cover is expected regardless of cover type, and this pattern may simply have been captured less precisely due to poor quality of snow data in forest cover.

For the purposes of these studies, treatment of data representing phenological conditions was not particularly refined. Future work exploring the use of more sophisticated means of incorporating these data into habitat suitability models may overcome some of the problems discussed here. A clearer signal can be extracted from NDVI data by using time series of raw data to construct smooth curves depicting each map cell's growing season (Jonsson & Eklundh 2002, 2004). The start of the growing season, which is known to be strongly associated with the start of elk migration (Christianson & Creel 2009; Irwin 2002), can then be identified on a cell-by-cell basis

(Piekielek 2012). Using this smooth curve, a measure of days before or after the start of the season can be derived for use in RSF models rather than raw NDVI values, which is expected to minimize the problem of noise in the raw dataset. A model interaction term between this growing season indicator and cover type would allow the importance of vegetation conditions to vary with cover type and thus to deemphasize irrelevant values for forest cover.

Implications of Spatial Patterns of Sensitivity

Perhaps the most novel finding of this study is that circuit theory models are considerably more sensitive to spatial patterns of uncertainty among model variants than are cost-distance models. Interquartile range maps depicting the degree to which model variants differed in their predicted values for a given map cell (Fig. 5.5) indicate that spatial patterns of uncertainty are predictable in cost-distance models, with low uncertainty near the least cost path radiating out to highest uncertainty at the edges of the study area. In contrast, circuit theory interquartile range maps exhibit chaotic patterns, with sites of low uncertainty intermixed with sites of high uncertainty throughout the map surface.

This critical difference between models in spatial patterns of sensitivity has important implications for use of cost-distance versus circuit theory models in conservation planning. Given that many choices in the modeling process must often be made subjectively due to lack of information to guide them, cost-distance models may offer predictions that are more robust to this uncertainty than those from circuit theory models, offering greater confidence in resulting plans for corridor initiatives. As

suggested by Chapter 3 and other researchers (B. Brock and S. Bergen, pers. comm.), cost-distance and circuit theory models could be combined to take advantage of their complementary attributes by first delineating a continuous corridor using a cost-distance model, then applying circuit theory models within these bounds to prioritize important pinch-points for conservation action, an approach that is further supported by these findings. However, this method may only be sound for predicting corridors intended to support movement processes that are compatible with the cost-distance model assumption of complete knowledge of the landscape; cost-distance models performed poorly relative to circuit theory models in the case of dispersal movements through novel landscapes (Chapter 4). In the case of dispersal corridor prediction, it may be advisable to test multiple model parameterizations and to target areas of agreement among models for conservation planning.

Tables

Table 5.1. Summary of habitat covariates included in base RSF models developed in Chapter 3.

<i>Covariate</i>	<i>Description</i>	<i>Source</i>	<i>Spatial Resolution</i>	<i>Temporal Resolution</i>
Elevation	Natl Elevation Dataset DEM	USGS	30m	--
Slope	Calculated from DEM	USGS	30m	--
Aspect	Calculated from DEM	USGS	30m	--
Land cover	2001 Natl Land Cover Dataset	USGS	30m	> 1 year
Forest edge density	Calculated in 500m radius	USGS	30m	> 1 year
Road density	Calculated in 5km radius	TIGER/Line data	30m	> 1 year
Land ownership	Taxable parcels and public lands	MT, ID cadastral databases	varies	> 1 year
NDVI	Vegetation greenness	NASA MODIS Terra satellite	250m	16-day
Snow cover	Snow presence/absence	NASA MODIS Terra satellite	500m	Daily
SWE	Snow water equivalent	NSIDC SNODAS model	30 arcsec	Daily

(NDVI = Normalized Difference Vegetation Index; SWE = Snow Water Equivalent; DEM = Digital Elevation Model; USGS = United States Geological Survey; TIGER = Topologically Integrated Geographic Encoding and Referencing; MODIS = Moderate Resolution Imaging Spectroradiometer; NSIDC = National Snow and Ice Data Center; SNODAS = Snow Data Assimilation System)

Table 5.2. Summary of final RSF models for a) spring and b) fall elk migration movements. See Chapter 3 for details of covariate derivation and model development and selection.

<i>Parameter</i>	a) Spring		b) Fall	
	<i>Estimate</i>	<i>SE</i>	<i>Estimate</i>	<i>SE</i>
Elevation [§]	-0.001860779	0.000170524	-5.06116E-05	0.000154179
Elevation ^{2§}	-9.9683E-07	3.94276E-07	-4.40969E-06	3.59286E-07
Slope [§]	0.000300314	0.003599336	-0.00517793	0.00283
Slope ^{2§}	-0.005456971	0.000346693	-0.00324	0.000265007
North	0.092414945	0.034300002	0.006229492	0.02764
East	-0.047670618	0.034350002	-0.011233106	0.02769
Edge Density [§]	0.009279403	0.00634831	0.009548963	0.005210684
Edge Density ^{2§}	0.001362994	0.000679177	-0.003643925	0.000721192
Road Density [§]	-0.640237876	0.247142503	1.095346003	0.201250371
Road Density ^{2§}	-0.186980769	0.254913431	-1.220579461	0.61327
NDVI [§]	-2.19077115	0.601123664	-0.821988194	0.496977062
NDVI ^{2§}	1.436606561	2.157953093	-7.888803351	2.19233095
Land cover*				
Forest	-1.026159538	0.08976319	0.211542612	0.088065642
Shrub	0.140568689	0.084000308	0.325523042	0.089567949
Anthropogenic	-1.588476998	1.009468036	0.033709913	0.537907699
Ownership**				
Private	-0.324170521	0.167960775	-0.186158998	0.137262656
USFS	0.805460848	0.101992572	0.110577867	0.069777183
NPS	0.589883831	0.256425563	-0.597235253	0.261582032
S: SWE [§] / F: Snow Cover	0.000620169	0.000326667	4.036334679	0.180196382
S: SWE ^{2§}	-8.67818E-06	9.2243E-07		

[§]Centering transformation was used to minimize correlation between linear and quadratic terms.

*Reference level = Open

**Reference level = Other government

Table 5.3. Percentages of observed points falling within predicted 95th percentile corridors, calculated across all individuals.

a) Spring				
	Cost-distance		Circuit theory	
<i>Suitability model</i>	<i>Total</i>	<i>SE</i>	<i>Total</i>	<i>SE</i>
Base	80.32	13.423	82.22	7.627
Coarse-scale	54.15	12.543	64.80	8.853
250 m resolution	82.58	13.007	83.24	7.769
1 km resolution	82.22	12.884	83.38	7.872
Mahalanobis D	76.60	15.779	65.23	8.226
Lower 95% CL	77.84	14.860	79.45	7.320
Upper 95% CL	87.68	9.176	83.02	7.532
Home ranges	75.00	12.120	75.66	8.857
No phenology	86.37	8.840	84.48	8.583
b) Fall				
	Cost-distance		Circuit theory	
<i>Suitability model</i>	<i>Total</i>	<i>SE</i>	<i>Total</i>	<i>SE</i>
Base	74.40	9.908	73.90	9.850
Coarse-scale	31.48	17.222	78.97	8.894
250 m resolution	75.08	9.671	71.61	10.377
1 km resolution	72.91	10.836	72.85	10.564
Mahalanobis D	69.64	11.493	58.87	15.322
Lower 95% CL	71.74	10.237	74.64	9.094
Upper 95% CL	75.20	11.208	73.16	11.246
Home ranges	61.72	14.305	57.58	13.927
No phenology	78.73	10.036	78.48	8.729

Table 5.4. Summary of mixed effects model comparing percentile values assigned to GPS relocations by each model in a) spring and b) fall.

<i>Fixed Effects</i>	a) Spring				b) Fall			
	<i>Estimate</i>	<i>SE</i>	<i>t-value</i>	<i>p-value</i>	<i>Estimate</i>	<i>SE</i>	<i>t-value</i>	<i>p-value</i>
Intercept	98.6452	0.60834	162.1556	<0.0001	98.5081	1.221096	80.6719	<0.0001
Corridor model								
Circuit theory	-0.4102	0.027203	-15.0785	<0.0001	-0.6112	0.061728	-9.9017	<0.0001
Suitability model								
Coarse-scale availability	-1.5088	0.057707	-26.1449	<0.0001	-4.4830	0.130945	-34.2357	<0.0001
250 m resolution	0.3418	0.057707	5.9236	<0.0001	0.2938	0.130945	2.2433	0.0249
1 km resolution	0.2445	0.057707	4.2375	<0.0001	0.0668	0.130945	0.5101	0.61
Mahalanobis distance	-0.3141	0.057707	-5.4437	<0.0001	-1.9307	0.130945	-14.7446	<0.0001
Lower 95% CL	-0.0095	0.057707	-0.1642	0.8696	0.2511	0.130945	1.9175	0.0552
Upper 95% CL	0.4344	0.057707	7.5277	<0.0001	0.1219	0.130945	0.9304	0.3522
Home range endpoints	-0.4709	0.057707	-8.1592	<0.0001	-4.3238	0.130945	-33.0195	<0.0001
No phenology covariates	0.6589	0.057707	11.4179	<0.0001	1.1608	0.130945	8.8647	<0.0001
<i>Random Effects</i>								
Individual	<i>Intercept SD</i>		<i>Residual SD</i>		<i>Intercept SD</i>		<i>Residual SD</i>	
	1.93123				3.52884			
Points	2.13724		2.13707		3.20183		5.26465	

Table 5.5. Summary of mixed effects model comparing differences between percentile values assigned to GPS relocations by null and alternative models in a) spring and b) fall.

<i>Fixed Effects</i>	a) Spring				b) Fall			
	<i>Estimate</i>	<i>SE</i>	<i>t-value</i>	<i>p-value</i>	<i>Estimate</i>	<i>SE</i>	<i>t-value</i>	<i>p-value</i>
Intercept	6.394146	0.8467076	7.55178	<0.0001	-0.4117	0.6678758	-0.61641	0.5376
Corridor model								
Circuit theory	-8.31471	0.079292	-104.8624	<0.0001	-0.1919	0.059886	-3.2047	0.0014
Suitability model								
Coarse-scale availability	-1.50875	0.168203	-8.9698	<0.0001	-4.4830	0.127038	-35.2886	<0.0001
250 m resolution	0.34184	0.168203	2.0323	0.0421	0.2938	0.127038	2.3123	0.0208
1 km resolution	0.24453	0.168203	1.4538	0.146	0.067	0.127038	0.5258	0.5991
Mahalanobis distance	-0.3141	0.168203	-1.8676	0.0618	-1.9307	0.127038	-15.1981	<0.0001
Lower 95% CL	-0.00948	0.168203	-0.0563	0.9551	0.2510	0.127038	1.9764	0.0481
Upper 95% CL	0.43440	0.168203	2.5826	0.0098	0.1218	0.127038	0.9590	0.3376
Home range endpoints	-0.47085	0.168203	-2.7993	0.0051	-4.3238	0.127038	-35.2886	<0.0001
No phenology covariates	0.65889	0.168203	3.9173	0.0001	1.1608	0.127038	9.1374	<0.0001
<i>Random Effects</i>								
Individual	<i>Intercept SD</i>				<i>Residual SD</i>			
	2.53906				1.88589			
Points	4.81068				2.32839			
	6.22906				5.10757			

Table 5.6. Means and standard deviations across individuals of observed path ranks among 99 random paths. Because ranks are not normally distributed, percentages of individuals receiving the top rank are also reported. Observed and random paths were compared in terms of raw predicted corridor values assigned to points.

Suitability model	a) Spring						b) Fall					
	Cost-distance			Circuit theory			Cost-distance			Circuit theory		
	Mean	SD	Prop 1	Mean	SD	Prop 1	Mean	SD	Prop 1	Mean	SD	Prop 1
Base model	1	0	1	2.67	3.87	0.75	3	6.33	0.9	1.9	2.85	0.9
Coarse-scale	2.83	4.78	0.83	3.67	7.24	0.75	3.2	6.96	0.9	2.5	4.74	0.9
250 m resolution	1	0	1	2.83	3.64	0.75	2.1	3.48	0.9	3.9	9.17	0.9
1 km resolution	1.83	1.85	0.75	1.58	1.16	0.75	3.7	8.54	0.9	2.6	5.06	0.9
Mahalanobis dist.	2.58	5.48	0.92	4.58	7.95	0.58	1	0	1	2.9	6.01	0.8
Lower 95% CL	1	0	1	2.67	3.28	0.75	2.9	31.22	0.9	2.5	4.74	0.9
Upper 95% CL	1	0	1	4.42	9.41	0.67	2.3	4.11	0.9	3	6.32	0.9
Home ranges	10.75	18.54	0.58	9.75	15.67	0.58	2.3	4.11	0.9	16.2	4.11	0.8
No phenology	1	0	1	4.25	6.96	0.75	1	0	1	3.4	7.59	0.9

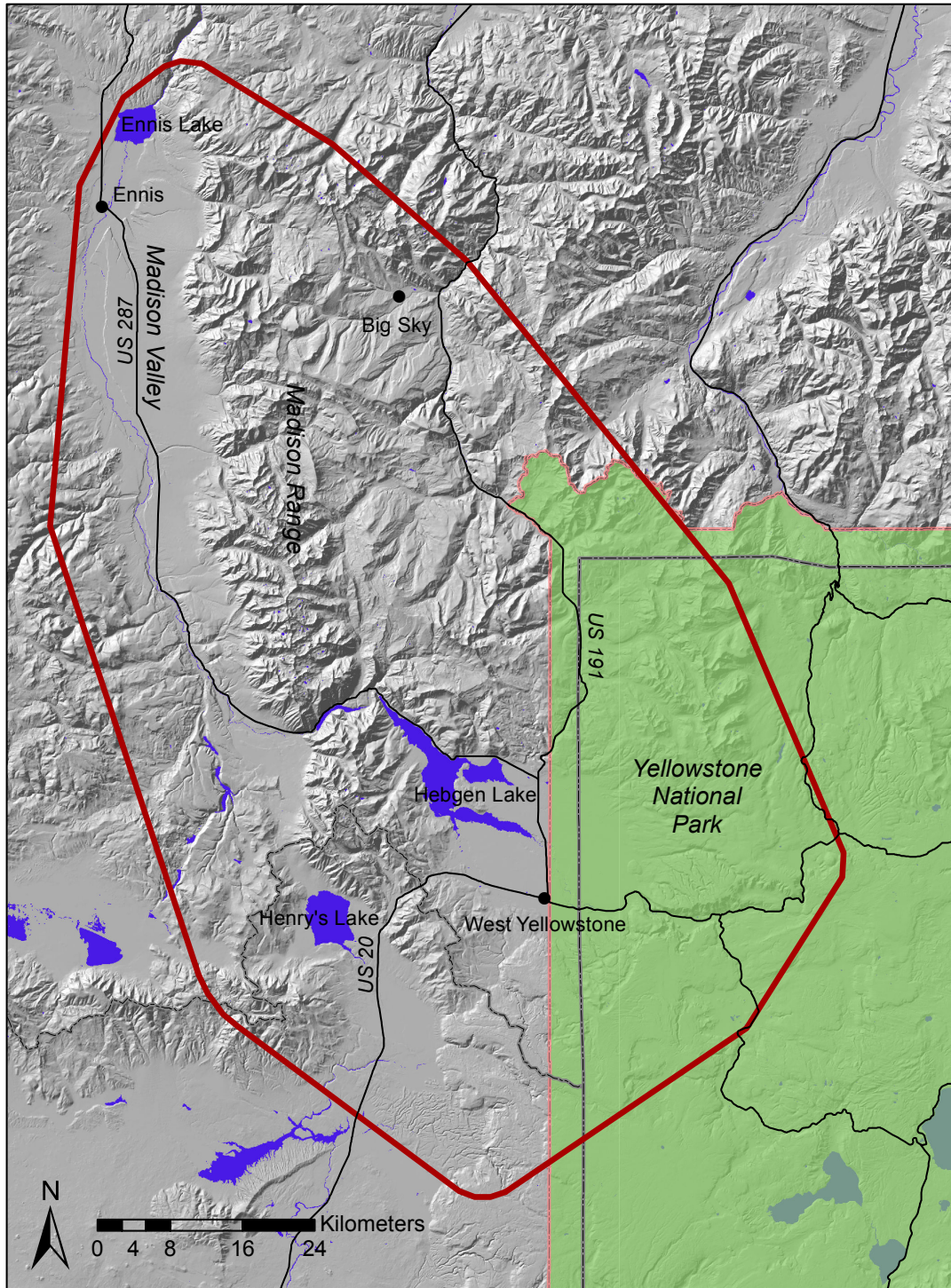
Figures

Figure 5.1. The Madison Valley study area, defined by placing a 5km buffer on the minimum convex polygon containing all GPS relocations collected from 45 female elk.

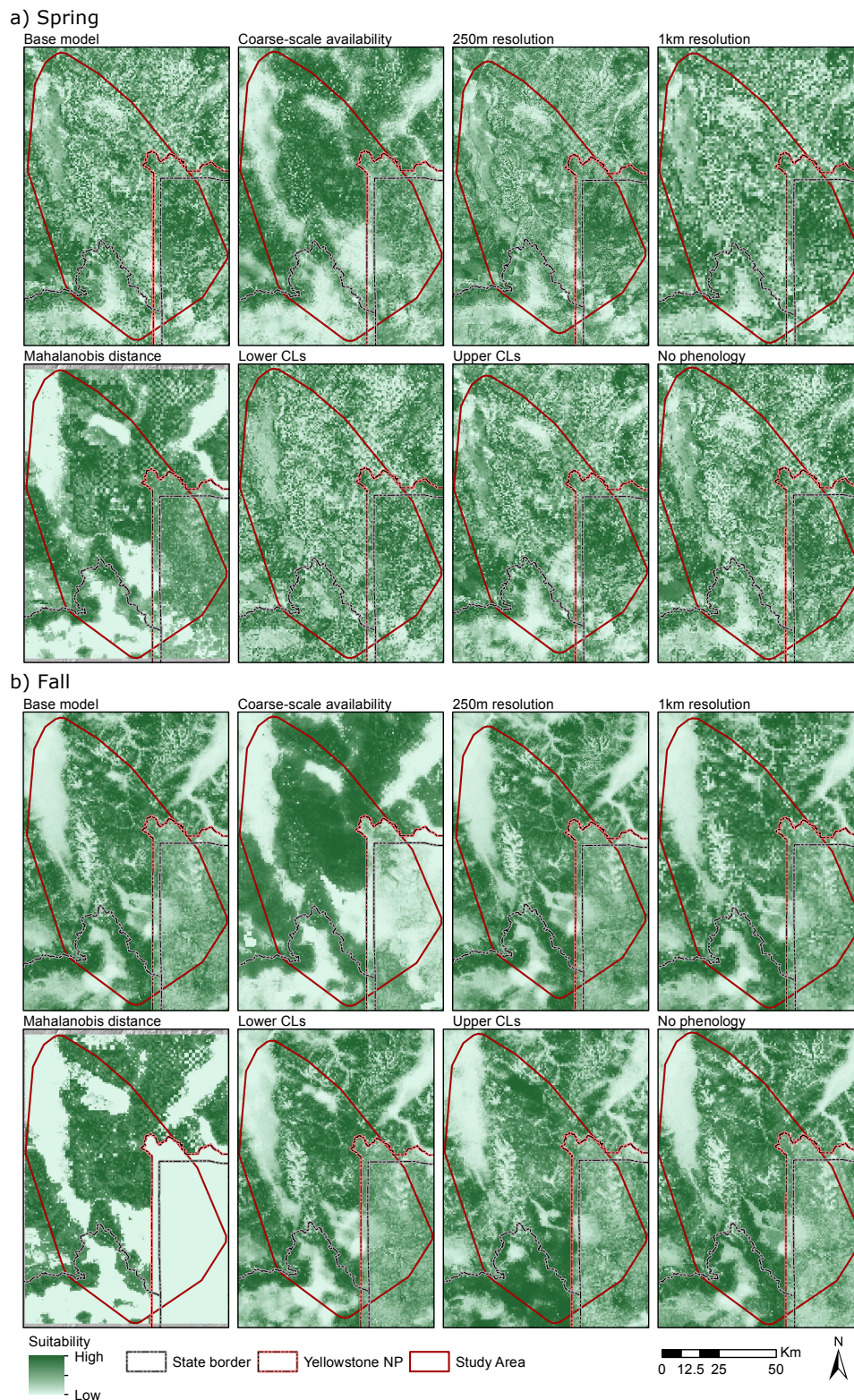


Figure 5.2. Comparison of habitat suitability maps produced by all suitability model variants in a) spring and b) fall.

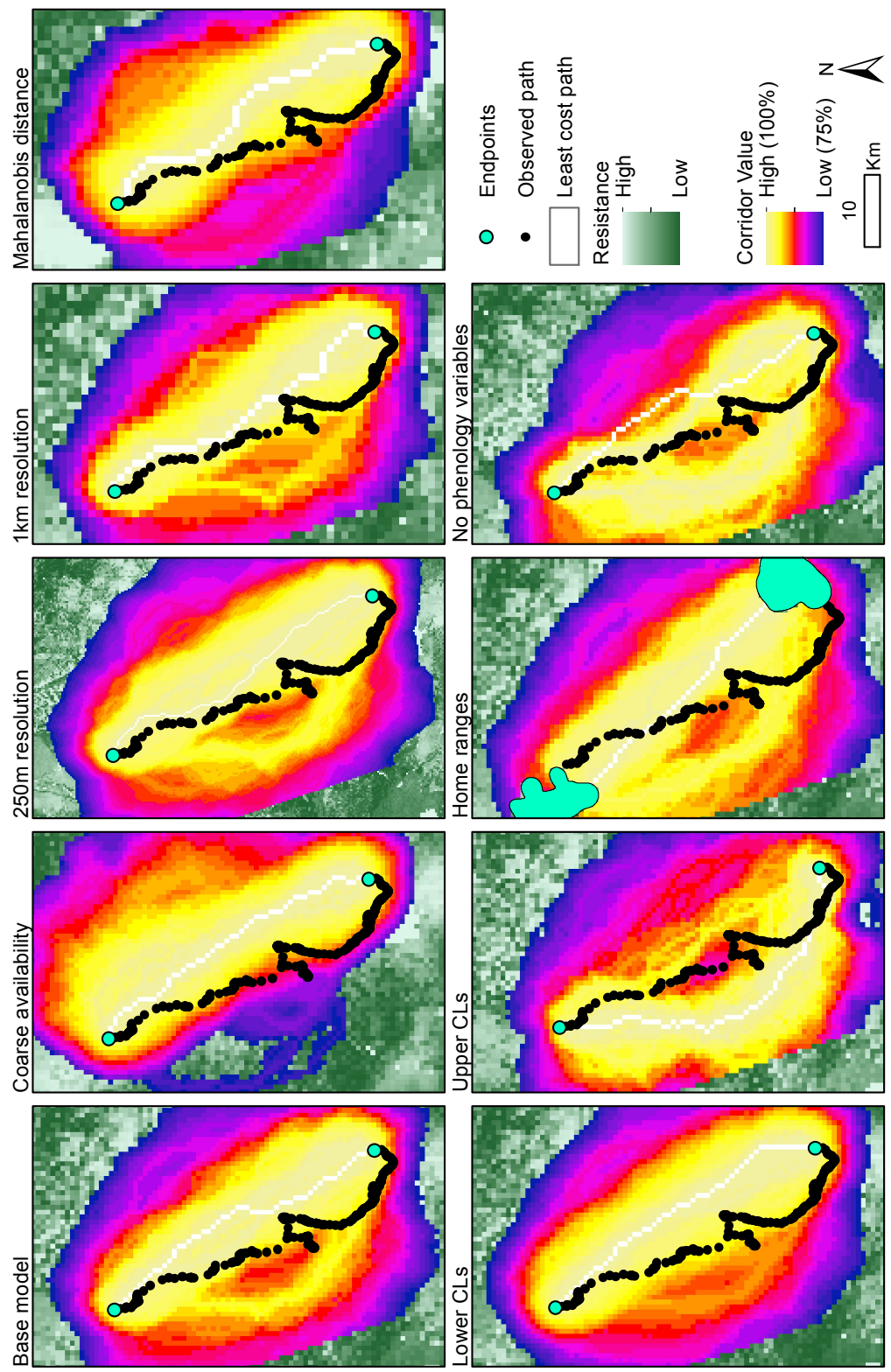


Figure 5.3. Variability in corridors generated by cost-distance model variants for an example individual.

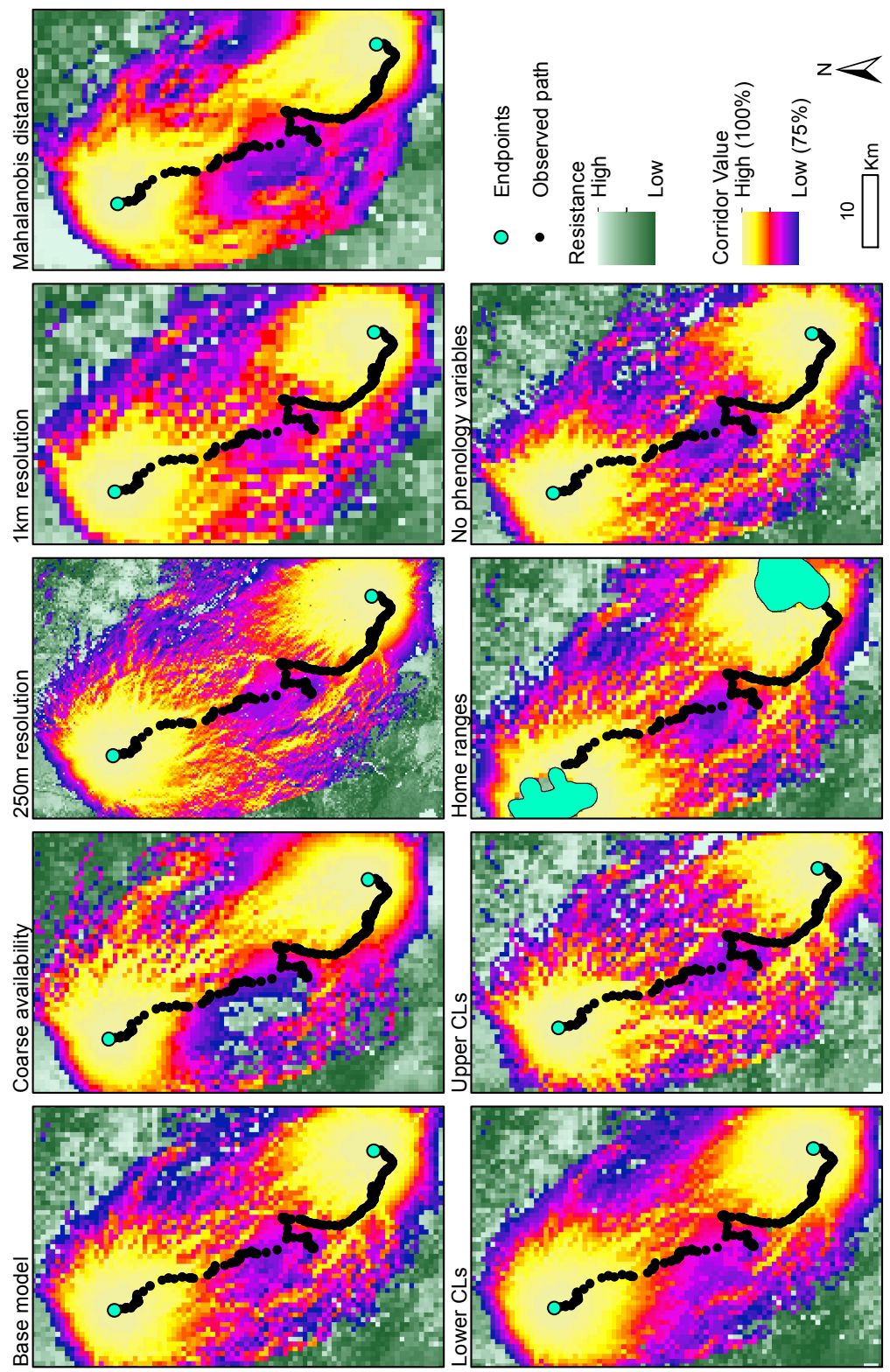


Figure 5.4. Variability in corridors generated by circuit theory model variants for an example individual.

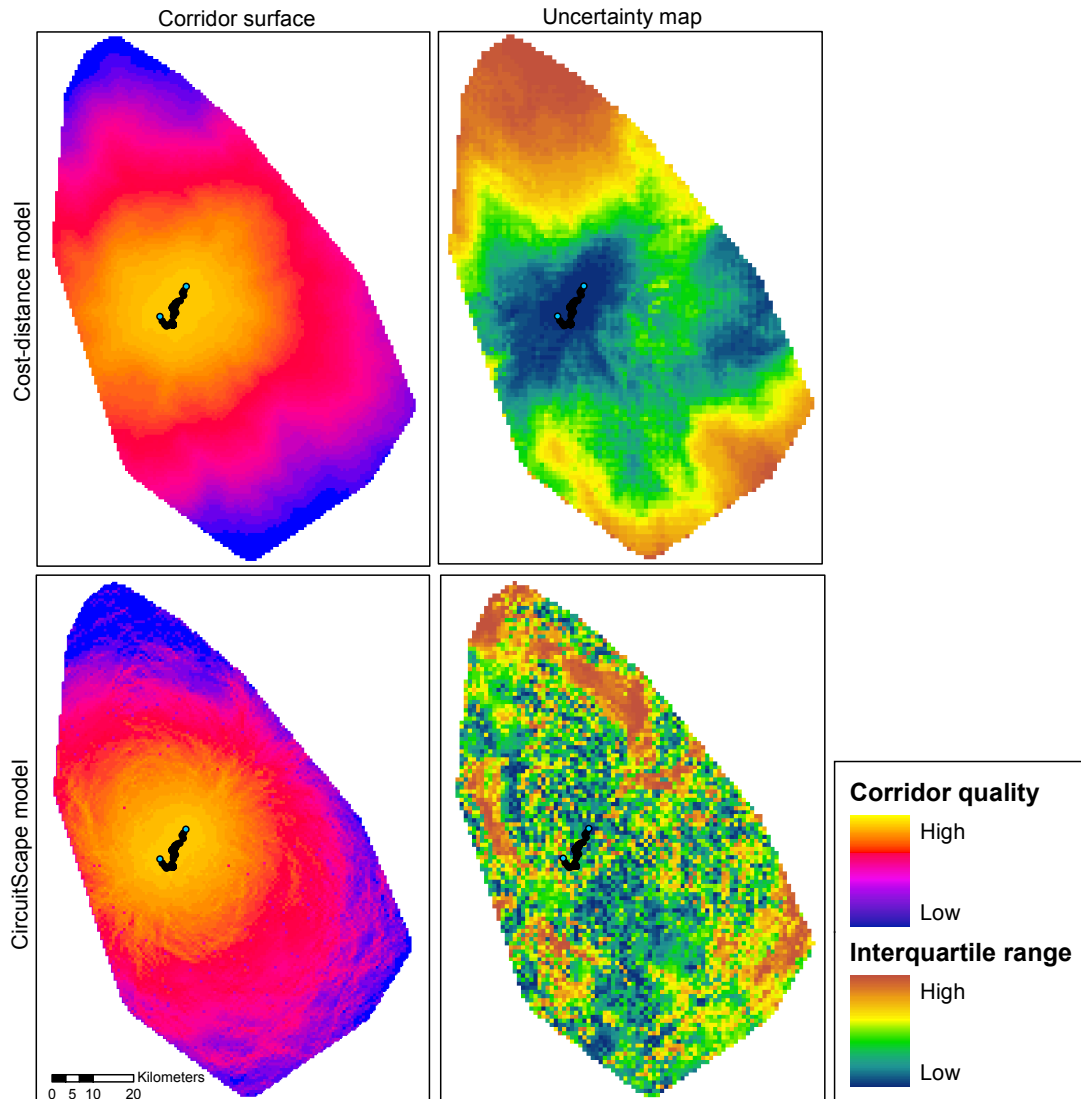


Figure 5.5. Study area-wide corridor surfaces (left) produced by cost-distance (top) and circuit theory (bottom) models for an example individual, and spatial patterns of uncertainty (right) among suitability model variants. High interquartile range values indicate high levels of disagreement among models.

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CHAPTER 6

CONCLUSIONS AND FUTURE RESEARCH

Directions for Future Research

These studies highlight the dire need for more extensive validation of corridor model predictions in support of sound conservation planning as well as important unanswered questions concerning the ecology of long-distance movements.

Corridor model validation against empirical data is needed across a broad range of focal species, landscapes, and scales in order to paint a more complete picture of model performance. A broader range of corridor modeling approaches must also be compared; only two of the 7-10 methods currently available have been validated against empirical location or genetic data (Chapter 2). The studies presented here have also indicated the importance of underlying resistance models to corridor model performance. Many methods of modeling resistance are available (e.g., Aarts et al. 2008; Calenge et al. 2008; Friedman et al. 2000; Phillips et al. 2006) and are known to vary in their ability to predict patterns of habitat selection (e.g., Elith & Graham 2009; Elith et al. 2006; Guisan et al. 2007). It is therefore important to comparatively assess performance of corridor models utilizing resistance surfaces derived from these alternative methods, particularly MaxEnt models (Phillips et al. 2006), which are beginning to see more frequent use in conservation planning applications (e.g., MFWP 2011). A critical requirement for widespread validation of corridor models is, of course, more extensive collection of data representing wildlife movements of interest, and a move toward making these datasets

more widely available to researchers and conservation practitioners for the purpose of model validation.

These studies explored the movement ecology of focal species in rather preliminary ways. More targeted, rigorous study of the ecology of long-distance movements and how it may differ from that of home range movements is important both for modeling these movements appropriately and for establishing management practices that best support them. Quantitative comparison of resource selection function (RSF) models for home range movements and long-distance migration or dispersal movements would clarify the extent to which habitat selection differs among movement states. In this context, future research can explore the potential for differences among movement states in the landscape attributes driving habitat selection, the relative weight of preferences for landscape attributes, the relative overall strength of selection, tolerance thresholds for disfavored attributes, and the spatial scale of response to the landscape (Boyce 2006). Such studies would greatly clarify whether use of resistance surfaces based on home range movements is appropriate for modeling migration and dispersal movements and guide selection of appropriate cutoff values for extracting discrete corridors from continuous modeled surfaces. They would also provide invaluable information for on-the-ground conservation and land use planning decisions seeking to balance the needs of humans and wildlife by, for example, limiting housing and road density to within the tolerance thresholds of species of interest.

Chapters 3 and 5 together produced inconclusive results as to the role of vegetation and snow conditions in driving selection of migration paths; Chapter 3

suggested that these factors contributed to habitat selection during migration, but Chapter 5 indicated that inclusion of these covariates in resistance surfaces detracted from prediction of migration paths. Further study of the relative influence of phenology, other landscape attributes, distance, and habituation to learned paths on migration movements is therefore called for. Field-based studies of fine-scale phenological conditions available to elk during migration may provide a more appropriate means of addressing this question than the use of coarse-resolution, potentially error-prone NDVI data (Christianson & Creel 2009). Alternatively, or in conjunction with these studies, use of derived phenology metrics based on growing season curves (Jonsson & Eklundh 2002, 2004; Piekielek 2012) as covariates in resistance models as discussed in Chapter 5 may offer a more appropriate means of capturing the potential relationship between vegetation phenology and selection of migration paths.

Chapter 4 suggested that a resistance model based on movements of resident wolverines (Inman et al. in review) may be appropriate for use in predicting corridors for wolverine dispersal. However, these models indicate that open, lowland habitat is almost uniformly hostile to movement, but this is an artifact of the complete absence of resident relocations in these areas. Resident-based resistance models therefore offer virtually no information as to potential differential habitat selection in these areas during dispersal. Targeted modeling of disperser habitat selection outside of core habitat areas is needed to clarify the potential effects of landscape attributes such as housing and road density on landscape permeability to wolverine dispersal, with important implications for land use planning decisions in areas that may provide connectivity between core patches.

Continued collection of disperser relocation data is needed to support these studies. Additional data may also enable studies of wolverine perception of the landscape during dispersal, and whether navigation of novel habitats is guided by sight, smell, or other drivers, as well as the perceptual range achieved by dispersers. Improved understanding of the drivers of and constraints on wolverine dispersal movements is expected to support more informed designation and management of corridors that may be crucial to the persistence of wolverines in the U.S. Northern Rockies (Inman et al. in review).

Conclusions

This body of work constitutes a rare and comprehensive effort to validate corridor model predictions and demonstrates rigorous methods for doing so that can be applied to other species and landscapes. They indicate that corridor models do indeed provide information on patterns of wildlife movement that may be useful for conservation planning, though they also make clear that the utility of corridor models must be assessed relative to a defined conservation objective. Ultimately, corridor models do not provide simple solutions to the problem of conservation planning for connectivity. Rather, they are best thought of as conservation planning tools capable of providing decision support for a conscious, participatory planning process.

Importantly, these studies are the first to clearly demonstrate that the performance of connectivity models is dependent on the compatibility of their assumptions and algorithms with the movement ecology of a focal species. Here, cost-distance models, which assume complete knowledge of the landscape, best predicted migration, while

circuit theory models, which assume only local landscape knowledge, best predicted dispersal. This pattern seems likely to hold across species and landscapes given its clear ecological basis, with important implications for selection of the modeling approach that is most appropriate for a given application.

Both models were found to exhibit similar patterns of sensitivity to key decisions in the modeling process, and both were most sensitive to the scale at which focal species are assumed to respond to the landscape. This is an often overlooked model attribute deserving more thoughtful treatment. Perhaps the most novel finding of these studies is that despite similar overall patterns of sensitivity, spatial patterns of sensitivity for circuit theory models were highly unpredictable, while those of cost-distance models were orderly, with lowest sensitivity in areas likely to be the focus of conservation planning. This drawback of circuit theory models must be weighed against their higher predictive accuracy in modeling dispersal corridors, and may call for comparison of multiple parameterization scenarios to determine sites of highest agreement.

Finally, this work offers preliminary insights into the ecology of long-distance movements and opens the door for further study of how responses to the landscape may differ among movement states. This surprisingly neglected topic is not only of interest in and of itself, but also has important ramifications for the development of sound corridor models for conservation planning.

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