WOLVERINE HABITAT QUALITY, CONNECTIVITY, AND PRIORITIZATION AT THE LANDSCAPE SCALE

by

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DEDICATION

To Winston, for giving me almost a decade of unconditional love and dedication through four degrees, four moves, and countless tears. He will never read this, because he is a dog.

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VITA

Kathleen Carroll was born in 1991 in Mesa, Arizona. She has two undergraduate degrees, one in Wildlife Ecology and one in Marine Biology cum laude from the University of Maine, and a Master of Science in Environmental Sciences from the University of Tennessee at Chattanooga. Kathleen has studied wildlife in Africa, South America, and North America. She has backgrounds in wildlife conservation, marine biology, behavioral ecology, landscape ecology, statistics, education, and science communication. Her understanding spans across a broad range of disciplines and has provided her with a unique perspective on connectivity science and management strategies across a range of taxa. Kathleen is dedicated to outreach and communication. She recently completed a year as a National Science Foundation STEM Communications Fellow, presented at a TEDx event, and attends numerous conferences. Kathleen works as a Graduate Student Instructor, covering upper-level elective and required courses while Ecology Department faculty are on sabbatical. In addition to her Ph.D., Kathleen has completed a Graduate Certificate in Statistics and a Graduate Certificate in College Teaching. Her background in leadership includes serving as the secretary for MSU's Graduate Employee Organization (GEO) and The Wildlife Society's Student Development Working Group. She also helped found MSU's GEO Civil Rights Committee to prevent incidents, protect students, and provide resources regarding civil rights violations at MSU. Kathleen contributed greatly to her department and served as the co-chair of the Ecology Seminar Committee, was the graduate student representative from 2018-2019, and is one of only two graduate students to receive a department service award.

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ABSTRACT

The core of conservation biology is understanding how to mitigate the impacts of anthropogenic activities on species. These impacts are particularly detrimental to isolated and small populations, which face extirpation or extinction without immediate conservation action. For small and isolated populations, protecting connective habitat (e.g., corridors) and facilitating movement is key. Corridor identification requires rigorous planning and appropriate statistical choices to ensure that resulting conservation actions are defensible and best support ecological processes. This manuscript asks: 1) how do different, commonly used statistical methods inform our understanding of species resource selection across scale and between sexes, 2) how does landscape resistance and connectivity differ between resident and dispersing individuals, and 3) what information is important to include in a systematic conservation plan to best support on-the-ground conservation between land trusts, landowners, and other practitioners under future climate change conditions. To address each of these questions we focused on wolverines (*Gulo gulo*), which exist as isolated metapopulations across the western contiguous United States. Our key findings included that 1) the importance of habitat variables differ only slightly by sex, across selection scales, and across analysis methods, 2) dispersing animals are less sensitive to habitat quality compared to resident animals, and 3) including information that both helps mitigate potential threats and preserves ecological processes is the best approach for connectivity conservation planning. This work represents the most comprehensive wolverine connectivity conservation analyses to date. This research suggests that examining multiple approaches and validating results is critical to generating rigorous and defensible conservation decisions are being made for wolverines, although more studies are needed to validate this in other species. Taken together, this research provides land managers, policy makers, and scientists with guidance for future connectivity analyses, conservation action for wolverines, and a research framework that can be applied to additional species of conservation concern in isolated populations.

INTRODUCTION

> "That's here. That's home. That's us. On it, everyone you ever heard of, every human being who ever lived, lived out their lives. The aggregate of all our joys and sufferings, thousands of confident religions, ideologies and economic doctrines, every hunter and forager, every hero and coward, every creator and destroyer of civilizations, every king and peasant, every young couple in love, every hopeful child, every mother and father, every inventor and explorer, every teacher of morals, every corrupt politician, every superstar, every supreme leader, every saint and sinner in the history of our species, lived there — on a mote of dust, suspended in a sunbeam."
>
> — Carl Sagan, speech at Cornell University, October 13, 1994

Over the last 200 years, conservation has transitioned from being a privilege dominated by specific socioeconomic classes to being viewed as a right of the general public. Contemporary conservation is often viewed as a moral choice to protect the intrinsic value and aesthetic qualities of land (Muir 1979, Fox 1985). However, as public participation in conservation has grown, so have human impacts on biodiversity and the environment (Pimm et al. 1995, Wilcove et al. 1998, IPPC 2007). Human population growth, and the subsequent anthropogenic impacts on the environment, are the single greatest threat to biodiversity (Wilcove et al. 1998).

Increasing habitat fragmentation and habitat loss are two of the leading causes of species loss. In Canada, boreal woodland caribou (*Rangifer tarandus caribou*) rely on continuous old growth forests for food and protection (Hebblewhite 2017). Linear infrastructure from energy development has led to changes in the relationship between wolves, caribou, and moose and resulted in massive losses of caribou populations. It is estimated that caribou populations in Alberta that overlap with energy development experience 50% population loss each year and approximately half of all populations are in decline (Hebblewhite 2017). This example demonstrates the catastrophic impact human-caused habitat fragmentation can have on populations.

Increasing human land use and habitat fragmentation also have had drastic impacts on species movement and connectivity. Across Africa, African elephants (*Loxodonta africana*), a species adapted for long distance movements, have been confined to fenced or small game reserves largely to avoid human-wildlife conflicts. Since the establishment of reserves, this historic cross-continental population has been transformed into a highly discontinuous population (Blanc 2007). This has resulted in elephants becoming overpopulated in southern Africa, populations being less able to respond to stochastic events, and small reserves struggling to maintain viable genetic diversity in small populations. This is another clear example of how anthropogenic activities impact species persistence and biological processes.

With the continued increases in habitat fragmentation and habitat loss, the need for immediate conservation action has become increasingly dire. There is already a plethora of research aimed at protecting rare and high-risk species, but there is less research on designating and protecting corridors for connectivity. Connectivity specific conservation is relatively new compared to habitat, species, or ecosystem specific conservation. Protecting areas of connectivity has only been recognized as high priority by national and global organizations, practitioners, policy makers, and scientists over the last 20 to 30 years. Great advances have been made in connectivity conservation, but there are still many uncertainties. It is critical that research on connectivity conservation uses highly defensible methods that are appropriate for the study species or group and are validated to ensure that the connectivity conservation is as rigorous as possible as it advances.

The primary objective of this work is to provide managers and practitioners with conservation tools that best support ecological processes of and mitigate potential human-caused threats for wolverines (*Gulo gulo*). This introduction precedes three research chapters and a final concluding chapter.

Chapter 2 compares output from frequently used statistical approaches to output from alternative approaches used to identify how species select habitat. Traditionally, ecologists rely on logistic resource selection function (RSF) models to determine or predict habitat use by focal species based on presence only or presence/absence data. Logistic regression has the foundational assumption of independence of the observation residuals. However, most research on wildlife violates this assumption for two reasons. First, because repeated measures are taken on marked or tagged individuals, and second, because there is often high spatial or temporal autocorrelation in data from tagged individuals. There may be additional issues when these analyses are conducted on rare and wide-ranging species, whereby small sample sizes can lead to coefficient and interpretational bias (Northrup et al. 2013). We compared output from these RSF models to output from a random forest machine learning algorithm. There are tradeoffs with using either approach, while machine learning methods do not always have all of the assumptions of model-based inferential methods, they sometimes require large amounts of data and can be more computationally intensive (Shoemaker et al. 2018). We compared the output from each approach, using telemetry data from wolverines, to determine how the different assumptions impacted our results. We did this separately for each sex, as each sex has vastly different home range sizes and selection pressures driving habitat selection. We compared our results at both a first- and third-order selection scale to examine the importance of scale in habitat selection. We found that the importance of habitat covariates differed only slightly by sex, across selection scales, and across analysis methods.

Chapter 3 determines the degree to which dispersing wolverines are sensitive, or not, to differences in habitat quality outside of areas suitable for a home range. In wildlife studies, researchers typically assume that there is a negative linear relationship between habitat quality and resistance to movement, despite contrary evidence in some mammals (Keeley et al. 2017). In this analysis we generated estimates of habitat quality based on the behavior of resident wolverines, and we used this output to generate five different negative relationships (1 linear, 4 exponential) between habitat quality and resistance. We compared the resulting connectivity output from each of these five relationships to data from 9 dispersing wolverines using three different metrics to validate our results. We found that a negative linear inverse between habitat quality and resistance does not represent dispersing wolverine movement. Rather, once outside of habitat suitable for a home range, wolverines were only moderately sensitive to changes in predicted habitat quality. This chapter was particularly important in highlighting the need for validation of connectivity models before using them to inform conservation or management.

Chapter 4 focuses on how to best make management recommendations for wolverine connectivity. We solved predetermined conservation problems using a systematic conservation planning framework and integer linear programming. The output was used to prioritize areas important for wolverine habitat connectivity under future conditions (2050) across western Montana. We considered three problem sets for prioritization, including 1) an anthropogenic and ecological mode, which included genetics, high-quality habitat area, connectivity value, current flow centrality, land development, likelihood of conversion, and road density, 2) an ecological only model with genetics, high-quality habitat area, connectivity value, current flow centrality, and 3) a connectivity only model with connectivity value. After comparing the three approaches, we determined that the value of including anthropogenic threats outweighed the cost of excluding them, even when including layers that aimed to mitigate threats to wolverines (anthropogenic layers) did not align spatially with layers that aimed to maintain ecological processes. Our analysis resulted in a set of maps that can be used by land trusts to work with willing private landowners to secure the connectivity of the wolverine metapopulation over the long term in the western US.

Conclusions from the work are outlined in Chapter 5. This chapter is particularly important because it outlines recommendations for managers and policy makers based on the previous chapters. It also contains potential areas of future research that would add to both wolverine conservation and connectivity conservation moving forward.

COMPARING METHODS TO DISENTANGLE HABITAT PREDICTORS FOR WOLVERINES IN THE SOUTHERN EXTENT OF THEIR DISTRIBUTION

Contribution of Authors and Co-Authors

Manuscripts in Chapter 2

Author: Kathleen A. Carroll

Contributions: Conceived and implemented the study design, conducted the analysis, oversaw variable acquisition, and wrote the primary draft.

Co-Author: Dr. Andrew J. Hansen

Contributions: Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

Co-Author: Dr. Robert M. Inman

Contributions: Generated or acquired a few explanatory variables and the wolverine data. Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

Co-Author: Dr. Rick L. Lawrence

Contributions: Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

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Abstract

In the conterminous United States, wolverines (*Gulo gulo*) occupy semi-isolated patches of subalpine habitats at naturally low densities. Despite previous work modeling wolverine habitat, a consensus has yet to be established on what factors most strongly influence wolverine habitat use. In this analysis we aimed to determine the relative importance of human land use, snow water equivalent, high-elevation talus, landforms, elevation, and vegetation community type on wolverine habitat quality for animals collared around the Greater Yellowstone Ecosystem. This analysis was conducted at a first- and third-order selection scale to examine the importance of scale in habitat selection. We also compared output from parametric and nonparametric methods including standardized logistic regression coefficient, logistic regression variable importance, pseudo R-squared output, machine learning variable importance, and random forest machine learning mean decrease gini to determine how commonly used approaches with different assumptions produce different results. We ran these analyses separately for male and female wolverines, as each sex has vastly different home range sizes and selection pressures driving habitat selection. We found that the importance of habitat covariates differed only slightly by sex, across selection scales, and across analysis methods. Snow water equivalent, distance to high-elevation talus, and latitude-adjusted elevation were the driving selective forces for wolverines across the Greater Yellowstone Ecosystem (first-order) while more nuanced landform types also became important for movement within-home ranges (third-order). Overall, our results indicate that wolverine habitat selection is, in large part, driven by high-elevation structural features. However, we also found that snow water equivalent, which is

subject to change because of anthropogenic impacts, is an important features for habitat selection as well.

Introduction

Wolverines (*Gulo gulo*) are the largest terrestrial species of the Mustelid family in North America. In the conterminous U.S., the species occurs at naturally low densities on high-elevation public lands. Historically, wolverines ranged across the US and Canada north of the 38th parallel (van Zyll de Jong 1975, Hash 1987, Aubry et al. 2007, Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2014), but are now restricted to the northwestern US and western Canada (Aubrey et al. 2007, Inman et al. 2013, COSEWIC 2014). In the US, the current and historic wolverine population capacity has been estimated to be approximately 300 individuals across Washington, Oregon, Idaho, Montana, and Wyoming (Inman et al. 2013). Despite a growing number of studies in the US, there is limited information on wolverine ecology and behavior due to the expense associated with studying a cryptic, low-density species that occupies challenging terrain. A consensus has yet to be established on what factors most strongly drive wolverine habitat use, although there have been several studies at various scales to predict wolverine habitat (Hornocker and Hash 1981, Carroll et al. 2001, Aubry et al. 2007, Copeland et al. 2010, Inman et al. 2013, Fisher et al. 2013, COSEWIC 2014).

Wolverine habitat selection is driven by food and their ability to compete successfully for it, presence of potential mates, and possibly anthropogenic activity (Inman et al. 2012). Globally, there is agreement that wolverines exhibit intrasexual territoriality and, in the US, male home ranges are 2 to 4 times larger than female home ranges (Powell

1979, Magoun 1985, Copeland 1996, Copeland and Yates 2008, Persson et al. 2010, Inman et al 2012, Heinemeyer and Squires 2015, but see Hornocker and Hash 1981). Wolverines readily move into previously occupied home ranges of same-sex individuals when those ranges become empty, due to the dispersal or death of the previous resident (Bischof et al. 2016). This indicates that wolverines of the same sex are selecting similar habitat features to successfully establish and maintain a home range. In some populations, resident individuals of both sexes make extensive routine movements within their home range that are likely driven by seasonal diet shifts and breeding activities (Magoun 1985, Hornocker and Hash 1981, but see Inman et al. 2012). There is evidence that these within-home range movements are also impacted by human activities, such as recreation, and that movement and selection behaviors differ by sex (Heinemeyer et al 2016). Adult and juvenile wolverines of both sexes are capable of long-distance dispersal to establish new home ranges (Inman 2012). While long-distance dispersal has been documented in both sexes (Vangen et al. 2001, Flagstad et al. 2004), females often settle closer to their natal ranges compared to males (COSEWIC 2014, Moriarty et al. 2009, Inman et al. 2012). This suggests that there could be pressures driving movement by sex as well. Given the possibility that wolverines exhibit sex-specific habitat selection and dispersal, examining what factors most strongly drive wolverine habitat use and movement cannot be effectively understood without considering sex-specific differences in selection.

Multiple biotic and abiotic factors have been hypothesized to limit wolverine habitat use and drive selection, including snow cover area and duration (Schwartz et al. 2009, Copeland et al. 2010), food abundance (COSEWIC 2014), the ability to compete successfully for food (Inman et al. 2013), and human land use (Hash 1987, Laliberte and Ripple 2004, Krebs et al. 2007). While these hypotheses are not mutually exclusive, no studies have successfully disentangled and tested the impact of each of these variables across scale by sex. With the growing impacts of climate change and human land use change, it is likely that several of the factors hypothesized to drive wolverine habitat selection will change in the future, making disentangling the relative importance of each factor critically important for conservation planning. For instance, both climate change and human land use will likely shift high-quality habitats, and potentially connective pathways as well, over the long term and lead to changes in species distributions and management strategies (Pimm et al. 1995, Parmesan and Yohe 2003, McKelvey et al. 2011, Di Marco et al. 2018, Newbold 2018). Understanding these changes is particularly challenging for rare or cryptic species, like wolverines.

In rare or cryptic species, radio collar location data is often used to understand or predict habitat selection. This can be problematic because radio collar data often violates the assumptions of common statistical approaches. The inherent limitations of radio collar presence data include repeated measures on individuals and often these data have high spatial autocorrelation. Observational independence is a fundamental requirement in many statistical models, including logistic regression. Many resource selection functions (RSF) on collar data require fitting a logistic regression model with repeated measurements, using locations that are close in space and potentially correlated. Having spatial autocorrelation in the residuals is a violation of the independence assumption of logistic regression analyses and can exacerbate errors, leading to additional bias in interpretation, particularly for binary response variables (Dormann et al. 2007, Northrup et al. 2013). In telemetry datasets, observations made on the same individual are also not independent. Both of these issues are commonly ignored in RSF models and can lead to analytical and interpretational biases and untrustworthy coefficients.

An alternative to logistic models is the use of machine learning models such as random forest, boosted regression trees, maximum entropy, classifiers, and neural networks. Some machine learning methods do not have all of the assumptions of model-based inferential methods, but a portion of these require large amounts of data and are more computationally intensive than logistic regression (Shoemaker et al. 2018). Additionally, machine learning methods can be used as predictive inferential methods (e.g., random forest) or inferential methods of the difference, and selection depends on the goal of the research. In comparing logistic regression to random forest models, Shoemaker et al. (2018) found that the two modeling approaches yielded substantially different results. If researchers have the computing capacity and data requirements, machine learning tools present a strong alternative to traditional logistic regression RSFs.

In this analysis, we compared parametric and nonparametric analytic approaches to disentangle the relative importance of human land use, snow water equivalent, high-elevation talus, landform type, elevation, and vegetation on wolverine habitat quality by sex for animals around the Greater Yellowstone Ecosystem (Table S1, S2). The Greater Yellowstone Ecosystem (GYE) represents the southern extent of the wolverine distribution; long-term conservation of wolverines in this region will benefit from knowledge of and planning for changes due to climate and human land use change (Hansen and Phillips 2018). However, disentangling what variables drive wolverine selection is challenging for a few reasons. High-elevation variables are often highly collinear, wolverine data are limited, previous work often focused on a single scale of habitat use for predictive analyses, and radio collar data often violates the assumptions of common statistical approaches. We conducted our analysis at two different spatial scales, both to account for ecological processes that are scale specific and to provide decision-makers with more information for future management (DeCesare et al. 2012). By examining the output from methods with different statistical assumptions, we can compare similarities and disparities in our findings.

Based on wolverine observations and existing literature, we expected distance to high-elevation talus and snow water equivalent to be important predictors of wolverine habitat. There is evidence that wolverines use talus fields extensively for food caching, denning, microrefugia from warm temperatures during summer, and hunting (Copeland 1996, May et al. 2012, Inman et al. 2013). Wolverines are also a snow adapted species, as demonstrated by their foot-loading (Telfer and Kelsall 1984), pelage characteristics (Telfer and Kelsall 1984), general distribution (Copeland et al. 2010), and life-strategy (Inman et al. 2013). We expected other variables such as landform type and vegetation community to be important but have a weaker signal in the models. Because females require different habitat types and resources for offspring at various developmental stages, we also expected female wolverines would have more complex habitat associations compared to males, similar to findings on wolverines from British Columbia (Krebs et al. 2007). We expect our parametric and nonparametric methods to yield different results for variable importance and to have different predictive power on withheld data (Northrup et al. 2013).

Methods

Study Area

Wolverine data were collected in the Greater Yellowstone Ecosystem (GYE), an area that includes parts of Montana, Idaho, and Wyoming and encompasses Yellowstone National Park and Grand Teton National Park. Watersheds, geologic materials, vegetation, and geomorphic and hydrologic processes are often used to define the boundary of the GYE (Marston and Anderson 1991). Within the GYE, elevation, fire regime, and precipitation drive vegetation communities, including short-grass prairie, sagebrush communities, conifer forest, mixed forest, alpine tundra, and barren talus (Despain 1990). Across the GYE, elevation ranges from 500 to 3300 m. The GYE is typically dominated by steppe habitats below 1700 m and montane conifer forests and alpine tundra habitat dominating above 1700 m and 2900 m respectively (Despain 1990). There is considerable spatial variation in precipitation patterns in the GYE. The July/January precipitation ratio is lower in the southern and central portions of the GYE and at high elevation compared to the northern region (Whitlock and Bartlein 1993). The broad range of precipitation patterns, vegetation communities, and elevation in the GYE supports a rich diversity of both plant and wildlife species, including a large number of carnivores (Bailey 1930, Streubel 1989, Marston and Anderson 1991). While the GYE is considered to be one of the last intact temperate ecosystems and one of the largest areas of wildland in the contiguous US, increasing human pressures, climate change, and invasive species are having significant influences (Berger 1991, Westerling et al. 2011, Hansen and Phillips 2016).

Wolverine Data

Between 2001 and 2009, 38 wolverines (23♀, 15♂) from the GYE were fitted with intra-peritoneal VHF radio-transmitters and/or global positioning system (GPS) collars, some individuals were monitored for up to 9 years (Inman et al. 2012). Animals fitted with VHF implants were relocated every 10 days from a fixed-wing aircraft. For each resident animal, wolverine relocations were used to create 95% kernel density estimates (KDE) fit with a bivariate kernel function using a least squares cross validation bandwidth to avoid oversmoothing of the data. The KDEs were used to represent home ranges for the resource selection function (RSF) models (Calenge 2006, DeCesare et al. 2012, Carroll et al. in review). All resident animals with estimated home ranges were included in each of the coefficient comparison methods.

To determine the relative importance of human land use, snow water equivalent, high-elevation talus, landform type, elevation, and vegetation on high quality wolverine habitat quality, we used both a first-order and third-order analysis scales (Figure 2.1). For the first-order selection scale, which characterize selection of the population home range within the study area, we extracted random points within-home ranges to represent used locations and random points were selected around the study area to represent available points. For the third-order selection scale, which characterizes individual-level selection of used areas within-home ranges, random points within-home ranges were selected as available points, and telemetry data represented used points.

Ecological Variables

We collected a large number of publicly available data layers from agencies and scientists. From this collection, a subset of variables was selected to use in the modeling process based on availability and ecological relevance to wolverines, which was determined in a previous analysis (Carroll et al. in review). These variables included latitude-adjusted elevation (LAE, m), average monthly snow water equivalent (SWE, cm), distance to high-elevation talus (DHITAL, m), landform classification (LANDFORM, categorical), vegetation class (VEG, categorical) and human land use/housing density (HOUSE, houses/km^2) (Figure 2.2, Table S1; Theobald et al. 2005, Brock and Inman 2006, Bierwagen et al. 2010, Abatzoglou and Brown 2012, Inman et al. 2013, Michalak 2015). For each data layer, values at used and available locations were extracted to use as explanatory variables in each model.

Variable Comparison Method

To disentangle the relative importance of each habitat predictor, we compared results from 2 analyses — logistic regression and random forest machine learning, on a training dataset of 80% of the data for each sex and scale. For the logistic regressions we used standardized beta coefficients, pseudo R-squared values, and variable importance from the caret package in the statistical software package R, version 3.5.3 (Kuhn 2008, R Core Team, 2019). For the machine learning approach we examined mean decrease gini (MDG) from the randomForest package and variable importance from the caret package in the statistical software package R, version 3.5.3 (Liaw and Wiener 2002, Kuhn 2008, R Core Team, 2019). Multiple methods allowed for comparisons of outputs with different assumptions, including the comparison of parametric and non-parametric approaches. We compared the relative rank, importance, or explanatory power for each method to determine the relative importance of the explanatory variables at each selection scale by sex.

Logistic Regression Analyses

Beta-standardizing logistic regression coefficients offers one simple means to compare the relative importance of different variables in models (Bring 1994, Schielzeth 2010, Hosmer 2013) but can be difficult to interpret (King 1986). Previous analyses have used standardized regression coefficients from GLMM models on wolverines (Heinemeyer et al. 2019) and on other telemetry datasets (Laver et al. 2015). We generated four RSF models to compare standardized regression coefficients (herein referred to as betas) for each logistic regression model. To generate top RSF models, we started with full models for male and female separately at both selection scales. Each full model included human land use, snow water equivalent, high-elevation talus, landforms, elevation, and vegetation. Forward/backward step selection, based on the model AICc values was used to determine a single top model for each scale and sex. These beta coefficients were then ranked based on the absolute value of the standardized coefficient.

Logistic Variable Importance The caret package in R can generate model-based variable importance using the absolute value of the t-statistic for each model parameter in a linear model (Kuhn 2008). These variable importance functions can also be evaluated for models where no model-specific methods for estimating importance exist using receiver operating characteristic curves. The output from this analysis is useful because all output is generated on the same scale (0-100) and can be compared for tree methods, linear models, and a number of other analytical approaches.

Pseudo R-Squared We also wanted to examine how much variability each ecological variable explained using a coefficient of determination on the full dataset. Due to the binary nature of the response variable, true R-squared values could not be generated. However, several pseudo coefficients of determination, or pseudo R-squared metrics, do exist. Like R-squared, higher values of pseudo R-squared indicate better model fit (Cameron and Windmeijer 1997). There are many different methods to calculate pseudo R-squared metrics that all vary slightly (Veall & Zimmermann 1996). We compared three methods of calculating pseudo R-squared values, including McFadden's pseudo R-squared, maximum likelihood pseudo R-squared, and Cragg and Uhler's pseudo R-squared (Long 1997). Pseudo R-squared values can be generated to represent explained variability, improvement from null to fitted models, and the square of the correlation between predicted and actual values (Long 1997, Long and Freese 2006). McFadden's pseudo R-squared works to both explain variability and show improvement from null to fitted models, maximum likelihood pseudo R-squared works to explain variability, and Cragg and Uhler's pseudo R-squared works to show improvement from null to fitted models.

Machine Learning Analysis

Regression and classification trees (herein, tree methods) are machine learning approaches that use continuous or ordered discrete values to generate predictive or descriptive models that are ideal for analyzing complex data (De'ath and Fabricius 2000, Loh 2011). During our RSF modeling there were concerns regarding spatial autocorrelation of the residuals. Given this we chose to compare our RSF output to tree method output because tree methods generally focused on predictive inference and do not have coefficients for explanatory inference, as in traditional parametric statistical models that are adversely impacted by data violating the independence assumptions. Tree methods are incredibly flexible, can be applied to binary response data, and are easy to construct and interpret (De'ath and Fabricius 2000). Ensemble learning, which generates many trees using either boosting or bagging and then aggregates the results, are increasingly popular (Liaw and Wiener 2002). Of these methods, random forest approaches have become increasingly popular because they incorporate a bootstrapping sample to bagging, which adds additional randomness (Breiman 2001). To ensure the errors from the analysis stabilized, we generated aggregate output, variable importance from the caret package, and MDG from 500 random forest regression trees (Lawrence et al. 2006) to compare to our logistic regression results. We generated four aggregated tree outputs, one for each sex and scale, to determine if there was agreement between the different parametric and non-parametric approaches. Agreement between the logistic regression beta, logistic regression variable importance, logistic regression pseudo R-squared, machine learning variable importance, and machine learning MDG would indicate that each method is approximating the relative importance of variables for wolverines well.

Results

Our outputs indicated there was general agreement between methods, with explanatory variables being ranked similarly within sex and scale. The rank and importance of ecological variables differed slightly for males and females at both first-order and third-order analysis scales.

First-Order Analyses

Our first-order models compared locations within the population home range to available locations around the study area. The top RSF model for male wolverines was selected based on AICc scores and included all ecological variables (Table 2.1). The top female wolverine model included all variables except for human land use/housing density (HOUSE). We examined variance inflation factors (VIF) and generalized variance inflation factors (GVIF) for each of these models, and our results indicated that there was low correlation between all of the explanatory variables examined (Table 2.2).

The standardized coefficients, or ranked betas, indicated that both males (SWE, $beta_{Male}$ = 55.98, SE_{Male} = 3.84; SWE^3, $beta_{Male}$ = 51.08, SE_{Male} = 3.68) and females (SWE, $beta_{Female}$ = 55.60, SE_{Female} = 3.92) showed the strongest selection for SWE (Table 2.3, S5). For both sexes, LAE was the second highest ranked ecological variable (LAE^3, $beta_{Male}$ = 33.40, SE_{Male} = 3.96; LAE, $beta_{Male}$ = 32.26, SE_{Male} = 5.66; LAE^2, $beta_{Female}$ = 17.30, SE_{Female} = 3.61; LAE, $beta_{Female}$ = -11.34, SE_{Female} = 5.09). There was weak selection based on vegetation classes, landform classes, and increasing distance to high-elevation talus for both sexes. There was also very weak selection against increasing human land use for male wolverines (HOUSE, $beta_{Male}$ = -0.11, SE_{Male} = 0.03, Table 2.3, S5). We validated the model using previously withheld data for both males (n = 3288) and females (n = 2994). The first-order model for males correctly predicted withheld data with 77.28% accuracy and the model for females predicted withheld data with 80.23% accuracy.

Interestingly, the logistic regression variable importance, generated using the caret package in R, ranked DHITAL as the most important variable in both first-order models (Table 2.3, S6). Caret variable importance is scaled from 0-100 and no variable had an importance score > 25 in the male model and > 20 in the female model. In the first-order model for males, DHITAL was followed by SWE^3 and then SWE. In the female model, SWE and LAE^2 followed DHITAL.

There was agreement between the results from all of the pseudo R-squared approaches, including McFadden's pseudo R-squared, maximum likelihood pseudo R-squared, and Cragg and Uhler's pseudo R-squared, despite variation in how they are calculated (Long 1997, Freese and Long 2006). Unlike the results from the standardized beta coefficients, which suggested male and female selection differed slightly, the pseudo R-squared values indicated that the same variables were important, in the same order, for both sexes (Table 2.3, S7). In each pseudo R-squared calculated, DHITAL explained more variation in the response compared to any other variable, followed by SWE, and then LAE for both males and females (Table 2.3, S7).

We used random forest MDG and caret variable importance to have a nonparametric metric for comparison with our logistic output. MDG shows how important a variable is in estimating the response variable across all of the trees in the random forest. Variables with higher MDG represent variables that are more important in the model and variables with low MDG are the least important (Table 2.3, S8). The largest MDG, and most common root node (or most common first tree split), was DHITAL for males and SWE for females. This was followed by decision nodes for SWE and LAE for males and DHITAL and LAE for females (Table 2.3, S8). MDG values from both random forest models (one for each sex) on 500 trees indicated that there were similar patterns in importance for male and female wolverines at the first-order scale.

The output from the regression tree caret package variable importance indicated that the most important variables for males were SWE, DHITAL, and LAE respectively (Table 2.3, S8). For females the variables were the same but DHITAL was indicated to be of higher importance than SWE, followed by LAE (Table 2.3, S8). For the first-order male model, with 500 regression trees, the percent variation explained was 64.40% and the mean squared of the residuals was 0.07. This model correctly predicted withheld data with 90.91% accuracy, which was much higher than the logistic model. The first-order female model had a percent variation explained of 60.83% and the mean squared of the residuals was 0.07. This model predicted withheld data with 91.92% accuracy, which was also much higher than the logistic model.

There were some difference in each of the first-order selection methods, however all methods indicated that DHITAL and SWE best explained observed patterns of wolverine habitat use, and that the three most important variables were always DHITAL, SWE, or LAE (Table 2.3). Based on all of the results, snow water equivalent (SWE), distance to high-elevation talus (DHITAL), and latitude adjusted elevation (LAE) were the most important variables for explaining first-order patterns of male and female wolverine selection (Table 2.3).

Third-Order Analyses

Our third-order models compared telemetry locations within individual home ranges to random locations around home ranges where animals were not detected. The top AICc selected RSF model for male and female wolverines included all variables from the full model except for the vegetation classification (VEG, categorical; Table 2.4). VIFs and

GVIFs indicated that there was not high correlation between any of the explanatory variables examined in either model (Table 2.5).

In the ranked betas, SWE was ranked first and second, and males showed strong selection for increasing SWE (SWE, $beta_{Male}$ = 58.18, SE_{Male} = 5.40; SWE^2, $beta_{Male}$ = -21.21, SE_{Male} = 5.03 Table 2.6, S9). The third highest ranked variable for males was LAE (LAE, $beta_{Male}$ = 9.94, SE_{Male} = 6.73). Females also strongly selected for LAE and SWE, but LAE (LAE, $beta_{Female}$ = 47.34, SE_{Female} = 5.71) ranked higher than SWE (SWE, $beta_{Female}$ = 29.82, SE_{Female} = 4.59). Females also showed strong selection against local ridges in plains (LANDF6, $beta_{Female}$ = -18.31, SE_{Female} = 332.47) and plains (LANDF5, $beta_{Female}$ = -16.57, SE_{Female} = 527.75), but these variables had very large standard error values. The third-order model for males correctly predicted withheld data with 87.11% accuracy, and the model for females predicted withheld data with 78.04% accuracy.

The logistic regression variable importance, generated using the caret package in R, ranked SWE as the most important variable for males and LAE for females (Table 2.6, S10). Caret variable importance is scaled from 0-100 and no variable had an importance score > 12 in the male model and > 10 in the female model. In the first order model for males, SWE was followed by LANDF9 (steep slopes) and then DHITAL. In the female model, LAE and LANDF9 followed LANDF7 (local valleys).

Similar to the first-order analysis, there was agreement between the results from McFadden's pseudo R-squared, maximum likelihood pseudo R-squared, and Cragg and Uhler's pseudo R-squared (Long 1997, Freese and Long 2006). Unlike the results from the first-order pseudo R-squared, where both sexes had identical rankings of variables with better model fit, there were sex-specific differences at the third-order scale (Table 2.9). For each pseudo R-squared method, landform type explained more variation in the response compared to any other variable, followed by snow water equivalent for males and latitude-adjusted elevation for females, and then distance to high-elevation talus for males and snow water equivalent for females (Table 2.6, Table S11).

The largest MDG and most common root node at the third-order was SWE for male sand LAE for females (Table 2.6, Table S12). For males, the second largest MDC and decision node was LAE followed closely by DHITAL. For females, the MDG were highest for LAE, followed closely by SWE and then DHITAL. The caret package variable importance indicated that SWE, then DHITAL, then LAE were most important for males at the third-order. For females, important variables included SWE, LAE, and DHITAL (Table 2.6, S12). For the third-order male model, with 500 regression trees, the percent variation explained was 20.05% and the mean squared of the residuals was 0.10. This model correctly predicted withheld data with 86.17% accuracy, which was slightly lower than the logistic model. The third-order female model had a percent variation explained of 33.95% and the mean squared of the residuals was 0.13. This model predicted withheld data with 82.23% accuracy, which was higher than the logistic model.

There were more differences in results from each of the methods for the third-order selection scale than the first-order scale. Despite this, all methods indicated that DHITAL, SWE, LAE, and LANDF best explained observed patterns of wolverine habitat use for both sexes (Table 2.6). Based on all of the results, selection across first- and third-order scales is similar for these ecological variables in the GYE (Table 2.3, 2.6).

Discussion

There have been previous predictive analyses on wolverine habitat selection across a variety of scales (Aubry et al. 2007, Copeland et al. 2010, Fisher et al. 2013, Inman et al. 2013, Heinemeyer et al. 2019), but none have compared scales and sex-specific differences using a single dataset. Previous first-order analyses on the same data used here revealed the importance of latitude-adjusted elevation, terrain ruggedness index, April 1 snow depth, road density, interpolated human density, distance to high-elevation talus, distance to tree cover, and distance to April 1 snow > 2.5 cm (Inman et al. 2013). In that analysis, the explanatory power and rank of each variable was not examined and the model was built for predictive purposes. Other models have found late spring snowpack and high topographic ruggedness are important predictors of wolverine habitat at first- and second-order scales (Aubry et al. 2007, Copeland et al. 2010, Fisher et al. 2013, Inman et al. 2013). While these studies have used a variety of different data layers to identify important relationships between wolverine selection and rugged terrain or snow, their results suggest that both population-level and home range-level habitat selection for wolverines, across the western US, can be predicted or identified using a small number of high-elevation variables.

Fewer studies have been conducted on third-order selection for wolverines in the western US. Research on within-home range habitat selection for wolverines located primarily in and around Idaho suggests that drainage bottom topography, avoidance of steep slopes, and close proximity to forest edge is important for both sexes (Heinemeyer et al. 2019). This analysis, like ours, also found some sex-specific differences in selection.

Using ranked standardized regression coefficients, they identified that females selected for talus and smaller forest patches with more edge, while males selected for fir-dominated forests and areas close to secondary roads (Heinemeyer et al. 2019).

Each of the previously mentioned studies have added to our understanding of wolverine ecology, however, no previous study has successfully disentangled and tested the impact of environmental variables across scales for each sex. Disentangling biotic and abiotic factors that may limit wolverine habitat use and drive selection is increasingly important given the uncertain future of climate change and human land use change. We found that the importance of habitat covariates technically differed by sex and selection scales, and somewhat supported our initial hypotheses. However, even though there was variation across our methods in the order of the variables, the same suite of variables was highly ranked for both sexes. This indicated, that for our analysis, the methods we examined all had similar predictions. However, our random forest models performed 0.7% to 10% better (~6% better on average) than our logistic regression models.

Our first-order models compared locations within home ranges to random locations around the study area. At this selection scale, distance to high-elevation talus, snow water equivalent, and latitude-adjusted elevation were ranked highest in all analyses for both male and female wolverines. Our findings align well with previous wolverine research at first- and second-order selection scales (Aubry et al. 2007, Copeland et al. 2010, Fisher et al. 2013, Inman et al. 2013). However, disentangling what high-elevation variables are a stronger driving force of wolverine selection is challenging as these variables are often highly collinear. We ensured that our variables were not confounding before beginning our analyses, and we compared VIFs after generating the RSF (Table 2.2). Our results supported the hypothesis that distance to high-elevation talus and snow water equivalent would be the most important variables for wolverine habitat selection. Talus has previously been identified as important habitat structure for wolverine hunting, denning, and caching behaviors (Copeland 1996, May et al. 2012, Inman et al. 2013). Given the importance of physical habitat structure for a variety of behaviors in wolverines, including reproductive behavior, the importance of talus is logical for both sexes.

Snow water equivalent was also predicted to be important, which is not surprising as wolverines are highly snow adapted. Snow water equivalent was the first or second most important first-order variable in our analyses across sex and analysis method. While there has been debate on the obligate nature of snow denning in wolverines, snow is clearly an important habitat component for wolverines (Dorendorf 2016, Aronsson and Persson 2017).

Latitude-adjusted elevation also ranked high in our first-order models. This variable likely is explanatory because it captures the general ecological characteristics where the species niche exists. This could be a result of both current and evolutionary need to avoid competition with larger carnivores, which are less likely to hunt at high elevations on steep terrain. This behavior could also be a remnant of historic fur trapping, where wolverines living at lower elevations would have been more likely to be removed from the population, driving selection towards wolverines that spent more time in high-elevation habitats. Seasonal changes in occupied elevation are likely related to wolverine thermal requirements (higher during summer to avoid heat), food availability of both small prey and carrion, and the energetic costs of moving through snow (Hornocker and Hash 1981, Gardner 1985, Copeland 1996, Cardinal 2004, Wright and Ernst 2004).

There was slightly more sex-specific variation in our third-order models, which compared telemetry locations to random locations within home ranges where animals were not detected. At this scale, landform type (i.e., valley, ridges and peaks, etc.) was more important for both sexes, but ranked higher for females in the beta coefficients, logistic importance (caret package), and pseudo R-squared analyses. Landform predictions from the models indicated avoidance of features in valleys or plains in favor of ridges and slopes (Table 2.8). Wolverines are capable of crossing plains or valleys for dispersal (Inman et al. 2012), but resident adults are unlikely to enter these areas during routine movements. Like the first-order analysis, snow water equivalent and distance to high-elevation talus were still important predictors for both sexes. Snow water equivalent was consistently ranked higher in outputs from males, whereas latitude-adjusted elevation was ranked higher for females. There was not definitive evidence to suggest that female habitat selection was more complex than male selection, which has been observed for wolverines in British Columbia (Krebs et al. 2007). Females occupy much smaller home ranges than males, are more likely to remain stationary in their territories without abandoning or expanding their home ranges, and use smaller portions of their home ranges during reproductive periods (Magoun 1985, Aronsson et al. 2017, Dawson et al. 2010). These behaviors may lead to the more complex within-home range habitat associations of females, that other researchers have found but we did not detect. Once within their broad distributional niche, wolverines are generalist scavenger/predators. This, along with the lack of available fine-scale GIS layers mapping specific food and other resources (e.g., marmot density), makes it difficult to draw conclusions at this scale.

Conclusion

Our results indicate that distance to high-elevation talus, snow water equivalent, and latitude-adjusted elevation are the most explanatory variables regarding wolverine habitat use at the landscape scale, while more nuanced landform types become important for movement within-home ranges. This was confirmed by the fact that these variables were ranked high across all of our analytical approaches, spatial scales, and both sexes, in addition to acceptable holdback data testing scores. With the exception of the potential for climate change to influence climatic conditions (via SWE; Hosaka et al. 2005), high-elevation areas in the Rocky Mountain west are generally in public ownership and relatively well regulated. Valley bottoms generally are a far higher percentage of private land that is subject to future development. Therefore, a focus on identifying and conserving lower elevation areas used for dispersal movements would benefit wolverines. However, there is also evidence that both sexes showed strong selection for snow water equivalent, and there is some evidence against increasing housing density at both scales. While housing was not the strongest driver of wolverine selection, it is still a predictor of selection that could shift wolverine habitat in the future due to anthropogenic activity. Wolverine habitat is generally well conserved but avoiding human encroachment and other stressors in high-quality habitat is important for sustaining the current population and will only be possible through collaborative efforts of researchers, stakeholders, and land managers.

Tables and Figures

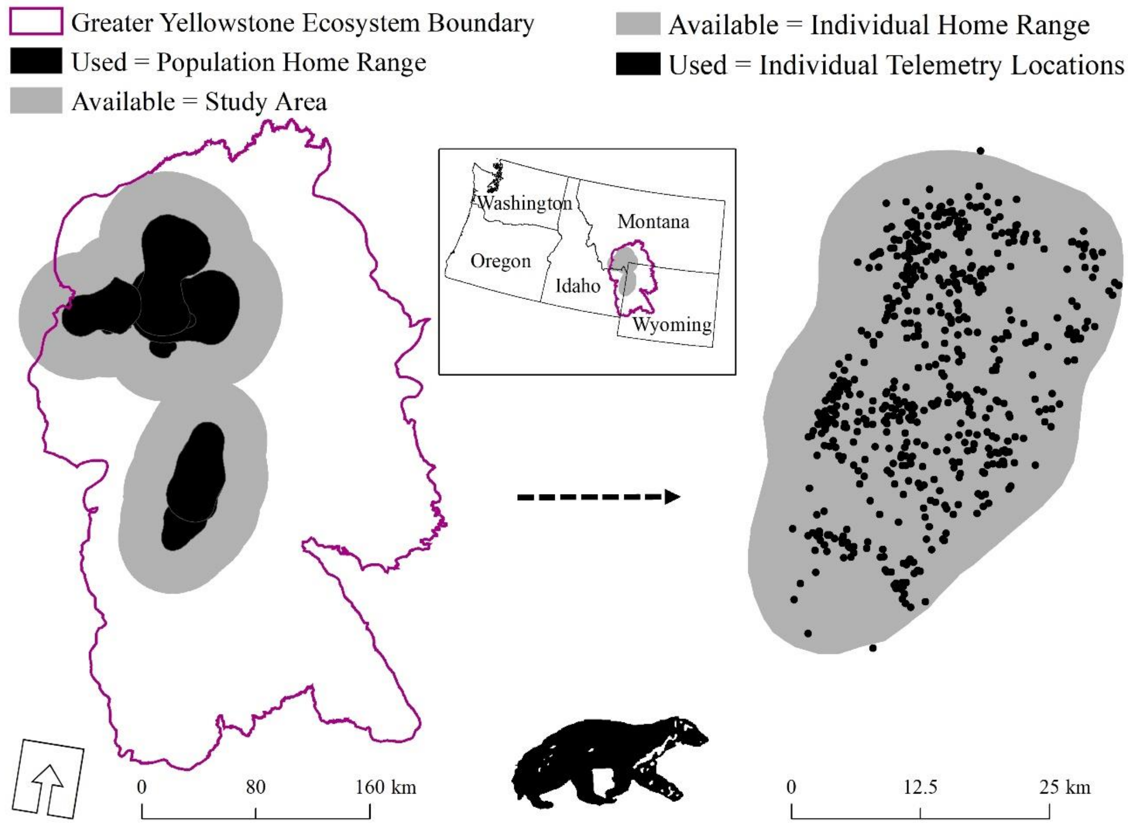

Figure 2.1 Adapted from DeCesare et al. (2012). Scales of wolverine habitat selection. For the first-order selection scale (left) available points were selected randomly within the study area (grey) and compared to used points in the population home range (black). For the third-order selection scale available points were selected randomly within an individual home range (grey) and used points were from wolverine telemetry data. Home ranges used represent 95% kernel density estimates.

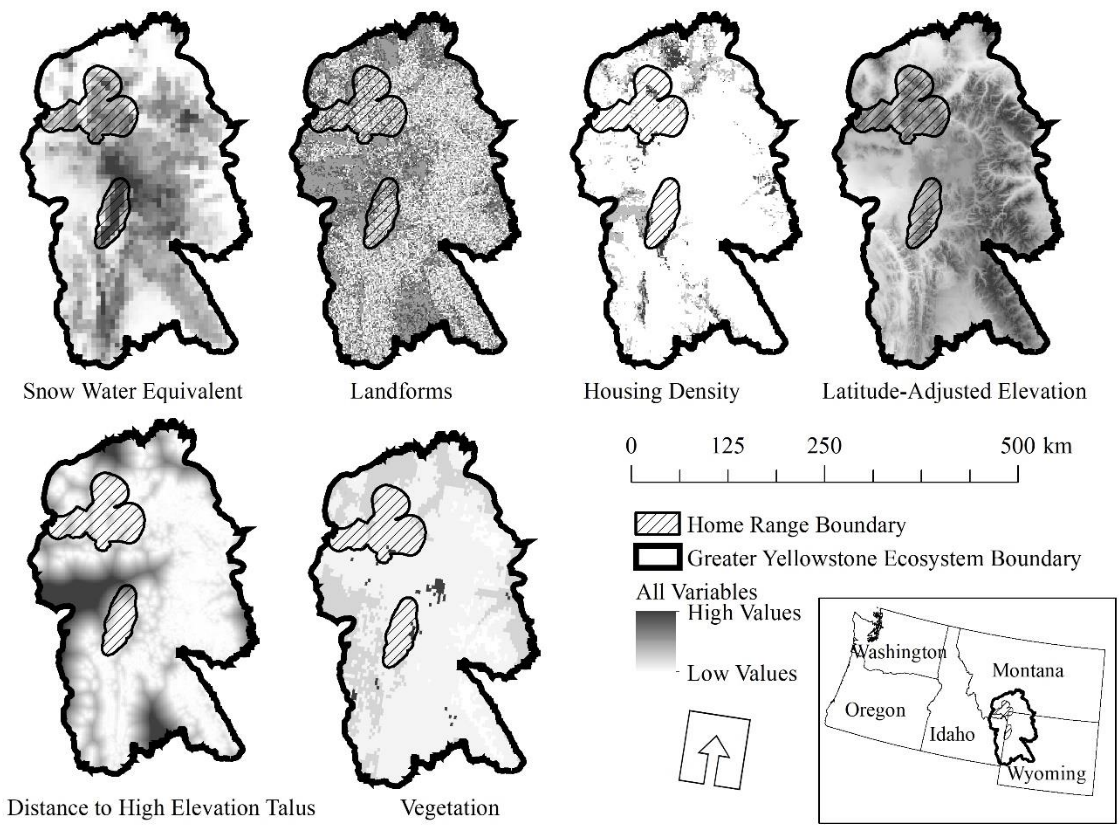

Figure 2.2 Variables used in model development for both first-order and third-order analyses. Snow water equivalent, latitude-adjusted elevation, housing, and distance to high-elevation talus are continuous. Classes for landforms and vegetation can be found in the supplementary documents (Table S2). Area with hashing represents wolverine home ranges used in analyses.

Table 2.1 AICc values from the first-order model selection used to generate beta coefficients. The top model for males included all of the same variables as the full model (latitude-adjusted elevation, vegetation class, distance to high-elevation talus, snow water equivalent, human land use/housing density, landform classification) and the top female model included all of the variables with the exception of human land use/housing density (latitude-adjusted elevation, vegetation class, distance to high-elevation talus, snow water equivalent, landform classification).

	Males		Females	
Models	AICc	DF	AICc	DF
Null Model	14886	1	13491	1
Full Model	11992	20	11273	20
Top Model	11992	20	11271	19

Table 2.2 Variance inflation factors (VIF), degrees of freedom (DF), and generalized variance inflation factors (GVIF) for each variable in the models at the first-order scale. Variables which require more than 1 coefficient and thus more than 1 degree of freedom, such as factor or polynomial variables, are typically evaluated using the GVIF. Polynomial variables are indicated with a superscript.

	Male			Female		
Variable	VIF	DF	GVIF	VIF	DF	GVIF
LAE^3	3.15	3	1.21	3.63	3	1.24
VEG	1.71	3	1.09	1.97	3	1.12
DHITAL	1.41	1	1.19	1.46	1	1.21
SWE^3	1.83	3	1.11	1.91	3	1.11
HOUSE	1.28	1	1.32			
LANDF	1.75	8	1.04	1.70	8	1.03

Table 2.3 Explanatory variable with the first, second and third highest beta rank or importance at the first order. McFadden's pseudo R-squared, maximum likelihood pseudo R-squared, and Cragg and Uhler's pseudo R-squared were combined as all three produced the same results. Variable that are listed more than once represent different polynomials (either first, second, or third order).

Rank	Beta Coefficient	Logistic Importance (caret)	Pseudo R-squared	Tree Method (randomForest)	Tree Method (caret)
			Male		
1	SWE	DHITAL	DHITAL	DHITAL	SWE
2	SWE	SWE	SWE	SWE	DHITAL
3	LAE	SWE	LAE	LAE	LAE
			Female		
1	SWE	DHITAL	DHITAL	SWE	DHITAL
2	LAE	SWE	SWE	DHITAL	SWE
3	LAE	SWE	LAE	LAE	LAE

Table 2.4 AICc values and degrees of freedom (DF) for third-order model used to obtain beta coefficients. The top model for males (n = 4810) and the top female model (n = 4893) included latitude-adjusted elevation, distance to high-elevation talus, snow water equivalent, housing, and landforms.

	Males		Females	
Models	AICc	DF	AICc	DF
Null Model	3184	1	4442	1
Full Model	2252	20	3234	20
Top Model	2249	17	3231	17

Table 2.5 Variance inflation factors for each variable in the third-order top models. There are no values for vegetation as this variable was dropped in both models.

	Male			Female		
Variable	VIF	DF	GVIF	VIF	DF	GVIF
LAE^3	1.85	3	1.11	1.96	3	1.12
DHITAL	1.29	1	1.14	1.21	1	1.10
SWE^3	1.30	3	1.05	1.38	3	1.06
HOUSE	1.02	1	1.01	1.01	1	1.01
LANDF	1.70	8	1.03	1.63	8	1.03

Table 2.6 Explanatory variable with the first, second and third highest beta rank or importance at the third-order. McFadden's pseudo R-squared, maximum likelihood pseudo R-squared, and Cragg and Uhler's pseudo R-squared were combined as all three produced the same results.

Rank	Beta Coefficient	Logistic Importance (caret)	Pseudo R-squared	Tree Method (randomForest)	Tree Method (caret)
			Male		
1	SWE	SWE	LANDF	SWE	SWE
2	SWE	LANDF	SWE	LAE	DHITAL
3	LAE	DHITAL	DHITAL	DHITAL	LAE
			Female		
1	LAE	LAE	LANDF	LAE	SWE
2	SWE	LANDF	LAE	SWE	LAE
3	LANDF	LANDF	SWE	DHITAL	DHITAL

TESTING LANDSCAPE RESISTANCE LAYERS AND MODELING CONNECTIVITY FOR WOLVERINES IN THE WESTERN US

Contribution of Authors and Co-Authors

Manuscripts in Chapter 3

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Contributions: Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

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Contributions: Generated or acquired a few explanatory variables and the wolverine data. Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

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Contributions: Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

Manuscript Information

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Abstract

In the conterminous United States, wolverines (*Gulo gulo*) occupy semi-isolated patches of higher elevation subalpine habitats at naturally low densities. The long-term success of the wolverine metapopulation requires open space in valley bottoms that link the mountain ranges of the western US to facilitate dispersal. No previous analysis has used empirical data to determine the degree to which dispersing wolverines are sensitive, or not, to differences in habitat quality outside of areas suitable for a home range. This sensitivity is important because it influences conservation actions. Improving wolverine habitat connectivity models among mountain ranges will benefit future wolverine conservation aimed at maintaining gene flow among populations. To determine how to most accurately model wolverine habitat connectivity, we used a resource selection function to model habitat and then generated five circuit theory connectivity maps. Each connectivity map represented a degree of sensitivity to movement within low-quality habitats. We used 3 validation metrics to compare these different connectivity layers and determine which layer best approximated observed wolverine dispersal using collar data. We found that a strong negative exponential relationship between habitat quality and resistance best described observed wolverine dispersal ($c = 8$). This suggests that once outside of habitat suitable for a home range, wolverines are only moderately sensitive to changes in habitat quality. However, we found that there is still some lower threshold of dispersal habitat quality for wolverines, as dispersing wolverines follow lower-resistance pathways that connect high-quality habitat and do not move indiscriminately across the landscape. Our results highlight the need to disentangle dispersal data from home range data through validation using

dispersal data. Our findings also indicate that validation of connectivity metrics is an essential component of conservation planning to best support the persistence of species.

Introduction

As human land use and infrastructure continue to fragment landscapes, understanding species distributions and habitat connectivity has become essential to protecting diversity globally. In the western United States, there are extensive swathes of public lands with varying degrees of protection and large areas of private land with low human modification relative to the rest of the country (Theobald 2013, Dickson et al. 2014, Belote et al. 2016). The relatively intact ecosystems in the western US, such as the Greater Yellowstone Ecosystem (GYE), serve as the last strongholds in the lower 48 for large mammalian species such as wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), and wolverine (*Gulo gulo*) (Keiter 1997, Musiani and Paquet 2004, Freese et al. 2007, Aubry et al. 2010, Inman et al. 2013, Vickers et al. 2015, Jimenez et al. 2017, Gustafson et al. 2018, Lyons et al. 2018). However, these species face growing challenges associated with increasing human population growth, exurban development, changing disturbance regimes, and climate change (Theobald 2003, Brown et al. 2005, Gude et al. 2006, Abatzoglou and Williams 2016, Hansen et al. 2016, Westerling 2016, Hansen and Phillips 2018, Adhikari and Hansen 2019, Carter et al. 2019). These and other species will continue to experience range shifts or increasing suitable habitat fragmentation in the coming decades due to anthropogenic effects (Burns et al. 2003, Pandey and Papeş 2018). Because of these habitat changes, connectivity research has become a conservation priority. In ecology, connectivity, or “the degree to which the landscape facilitates or impedes movement”

(Taylor et al. 1993) encompasses a broad range of processes that function over differing spatial and temporal scales and includes gene flow, species range expansion, and metapopulation dynamics (Hanski 1998, Coulon et al. 2004, Crooks and Sanjayan 2006, Crowl et al. 2008, Schwartz et al. 2009, Cosentino et al. 2011, Melles et al. 2011, Heard et al. 2015).

The use of connectivity modelling programs has accelerated rapidly in the past decade (Correa Ayram et al. 2016). These programs are designed to identify areas of conservation concern, opportunity, or action for wildlife connectivity in a heterogeneous landscape (McRae and Shah 2009). Given the uncertain future of how climate and human land use change will impact species, identifying pathways that allow species to move under changing conditions and facilitate gene flow across the landscape will be essential to the persistence of many species globally (Drielsma et al. 2017, Le Roux et al. 2017). These programs are essential to determine where movement between habitat patches is at risk and identify connective pathways that may disproportionally compromise connectivity (Castilho et al. 2015). The biggest challenge in connectivity modeling is examining validation methods to compare outputs from different connectivity programs (McClure et al. 2016, Zeller et al. 2018). These challenges impact managers' ability to make informed management decisions. A component of these issues is rooted in the models used to predict resistance to movement. There are inherent issues in using models like resource selection functions (RSF)– namely that resistance to movement on the landscape is inferred from point data, which confounds movement data and how animals use resources (Zeller et al. 2012). This points to a key issue in connectivity research, that resistance or connectivity must also be validated, particularly when conservation actions that could require significant financial inputs and opportunity costs may result from the products.

There is growing focus on understanding and modeling connectivity for species that exhibit large scale dispersal in the US (Beier et al. 2011, Inman et al. 2013, Wasserman et al. 2013, McClure et al. 2016). Wolverines are such a species. In the southern extent of their range in the western US, wolverines occur at naturally low densities in isolated high-elevation habitats and exhibit metapopulation dynamics (Hanski and Simberloff 1997, Inman et al. 2013). The current and historic wolverine population capacity has been estimated to be approximately 300 individuals across Washington, Oregon, Idaho, Montana, and Wyoming (Inman et al. 2013). Connective habitat is important for wolverine gene flow and dispersal events. Wolverines are capable of making extraordinarily long dispersal movements; for example, an animal collared in Wyoming in 2008 dispersed approximately 1900 km between Wyoming, Colorado, and North Dakota. While movements of this magnitude are infrequent, at maturity, individuals born in one mountain range typically disperse across valley bottoms to other mountain ranges to establish their own territory in areas with unrelated mates (Ruggiero et al. 1994).

Both wolverine habitat connectivity and multiple dispersal modeling programs have been previously examined for wolverines (Schwartz et al. 2009, Inman 2013, McClure et al. 2016). Least cost path (LCP) models and circuit theory models (Circuitscape) comparisons indicated considerably different dispersal routes (McClure et al. 2016). These differences included how pathways follow high-quality habitat and the probability of movement through small patches of high-quality habitat (McClure et al. 2016). Results from this analysis, although conducted at a finer spatial scale, indicated that circuit theory models performed better than LCP models across multiple validation metrics for wolverines (McClure et al. 2016). However, no previous analysis has examined wolverine tolerance for low-quality habitat during dispersal. Recent evidence suggests that some mammal species have lower tolerance thresholds for fragmented habitat during dispersal than when they are moving within their home ranges (Keeley et al. 2017), but this has not been examined in wolverines. In this study we aimed to 1) build a resource selection function model using resident wolverine home ranges for a connectivity analyses; 2) generate connectivity maps using circuit theory models that represent various degrees of resistance to dispersers; and 3) compare different resistance layers using several validation metrics to determine what modeled resistance value best represents observed dispersal data for wolverines. Because dispersing wolverines often move long distances through very challenging terrain (e.g., sagebrush steppe, agricultural lands; Inman et al. 2012), we hypothesized that layers that represent less sensitivity to low-quality habitat will best represent wolverine dispersal. This relationship would suggest that resistance for dispersing wolverines is likely dictated by some sensitivity threshold, where animals traveling outside of high-quality habitat have lower sensitivity to habitat quality rather than steadily decreasing sensitivity to habitat quality. To determine where this threshold may generally exist across the west, we modeled and compared different negative exponential relationships of habitat quality and landscape resistance.

Methods

Study Area

The animals used in this study were collared around the Greater Yellowstone Ecosystem (GYE; 109º49’23” W, 43º16’42” N) between 2001 and 2009 (Figure 3.1). The GYE is the southern periphery of the current distribution of wolverines and is an approximately 10.8 million ha region encompassing Yellowstone National Park and Grand Teton National Park. The GYE includes portions of Montana, Wyoming, and Idaho and less than 32% is privately owned (Gude et al. 2006). Historically, 100- to 500-year interval stand-replacing fire was the dominant form of disturbance in the GYE. Now human pressure and climate change (e.g., increased fire interval) are the dominant mechanism of change in the system (Hansen and Phillips 2018). Elevation, fire regime, and precipitation drive the dominant vegetation communities of the GYE, including short-grass prairie, sagebrush communities, conifer forest, mixed forest, alpine tundra, and barren talus (Despain 1990). The dominant characteristics of this area include high-elevation mountain ranges and past and current geothermal and volcanic activity (Parks et al. 2005).

Study Species

Between 2001 and 2009, 38 wolverines from the GYE and were fitted with intra-peritoneal VHF radio-transmitter and/or global positioning system (GPS) collars. Each animal was monitored for at least 3 years, and some individuals were monitored for up to 9 years (Inman et al. 2012). Animals fitted with VHF implants were relocated every 10 days from a fixed-wing aircraft, and location data were estimated to be accurate to within 300 m (Inman et al. 2013; Figure 3.1). Of the 38 VHF implanted animals, 9 dispersed and were excluded from resource selection models and were used to validate connectivity maps (Figure 3.1).

For each resident animal, relocations were used to create 95% kernel density estimates (KDE) and were fit with a bivariate kernel function using a least squares cross validation bandwidth to avoid oversmoothing of the data. These KDEs represented home ranges for a first-order resource selection function (RSF) (Calenge 2006, DeCesare et al. 2012). We used a first-order RSF because our goal was to characterize selection of home ranges within high-quality habitat for the species. We generated points within the KDE to represent "presence" or "observed" locations and we generated points outside the KDE to represent "available" points. All available points were selected within 34.8 km of each KDE, a distance which represents the average maximum distance resident wolverines were located from their initial point of capture (Inman et al. 2013). In order to avoid pseudoreplication, we overlaid a 1-km grid on that study area and then randomly selected 8000 grid cells within the KDEs and 24000 cells outside the KDEs to serve as the observed and available observations respectively.

Ecological Data

All abiotic or biotic variables previously analyzed in US wolverine habitat selection were considered as potential explanatory variables (Table S3; Schwartz et al. 2009, Copeland et al. 2010, Inman et al. 2012, Inman et al. 2013, McClure et al. 2016; Table S3). Available public data layers were collected from a variety of sources, which reduced the original list considerably due to some layers being unavailable or not publicly hosted. We further reduced the number of potential explanatory variables based on evidence of biological important from previous wolverine habitat studies in the US (Table S3). The ecological variables examined included: distance to high-elevation talus (DHITAL, m), latitude adjusted elevation (LAE, m), average monthly snow water equivalent (SWE, cm), landform classification (LANDFORM, categorical; Table S1, S4), vegetation class (VEG, categorical; Table S1, S4) and human land use/housing density (HUMAN, categorical, Table S1, S4; Theobald 2005, Brock and Inman 2006, Bierwagen et al. 2010, Abatzoglou and Brown 2012, Inman et al. 2013, Michalak 2015). For each data layer, information was extracted at each of the 8000 observed and 24000 available points.

Resource Selection Function

The RSF analysis was conducted in R statistical program 3.5.1 using a logistic regression, given that the logistic regression performed well on both holdback data and compared to alternative methods (Carroll unpublished, R Core Team, 2019). Exploratory data analyses revealed no first-order spatial trends and no violation of homoscedasticity. After checking model diagnostics on the full model, forward/backward step selection was used to determine a top model based on AICc selection criterion. The single top model selected included the same variables as the initial model, indicating that none should be dropped. We then assessed the assumptions for the logistics regression model. Due to concerns regarding high spatial autocorrelation of the residuals, we withheld a random test dataset of 30% of the presence/availability data to use for model validation. We also used a separate GPS collar dataset and an additional test dataset to examine model performance.

Determining High-Quality Habitat

We use the RSF model to produce a single raster layer representing the odds that wolverines could maintain a home range at any given location across the study area following Inman et al. (2013). We extrapolated this output across the western US, as there are no comprehensive wolverine datasets we could have used to generate these more extensive maps. The output from our analysis included Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming, states that either are currently or historically have been occupied by wolverines. The final raster layer was scaled from 1 to 10, where 10 represented the highest likelihood and 1 represented the lowest likelihood that a wolverine would be able to establish a home range in the area (Figure 3.2). Values 6 or greater from the RSF were considered high-quality habitat, or the areas where wolverine would be more likely than not to be able to establish a home range. These areas of predicted high-quality wolverine habitat were extracted to serve as "cores", or potential animal sources, in the connectivity analysis (Figure 3.2).

Resistance Layers

Previous work indicates that simply inversing habitat quality, or suitability, is not the best proxy for connectivity analyses (Beier et al. 2008, Keeley et al. 2017). To produce resistant surfaces layers to compare, we applied negative exponential functions to the habitat quality raster layers generated from the top model (McClure et al. 2016, Keeley et al. 2017, Zeller et al. 2018). We used five different negative exponential curves to transform habitat quality values into resistance values using equation (1), where h represents the habitat quality matrix (Keeley et al. 2017). The transformation values included c = 0.25, 1, 4, 8, and 32, in order to examine values ranging from a linear relationship (c = 0.25) to increasingly nonlinear negative exponential relationships between habitat quality and resistance (Figure 3.3; Keeley et al. 2017). In this equation, c = 0.25 results in a resistance layer where each one unit increase in habitat quality equated to a one unit decrease in resistance. Alternatively, c = 32 results in high resistance when habitat quality is very low but landscape resistance drops off very sharply as habitat quality increases (Figure 3.3). For each layer generated, resistance ranged from 1 to 100. These resistance surface outputs were used alongside the cores generated for each model in the Circuitscape analyses (Figure 3.4).

$$(1)\ 100 - 99 * ((1-\exp(-c * h))/(1-\exp(-c))) = \text{Scaled Resistance}$$

Predicting Connectivity

We only examined circuit theory models in this analysis, because previous research indicates that circuit theory models outperform cost-distance models for wolverines when resistance and habitat quality are scaled linearly (McClure et al. 2016). Unlike other movement models, circuit theory models (e.g., Circuitscape 4.0) incorporate the assumption that flow is higher in areas with redundant pathways linking destinations. Circuit theory models are also called random walk models because the circuit value at each cell represents the probability of a random walker using that cell when moving from a source to a destination. Circuit theory models are useful for evaluating the contribution of many dispersal pathways for animal movement and for their theoretical basis in random walk theory (McRae et al. 2008). However, they do have some limitations. A critical limitation of circuit theory models is the assumption that dispersing animals have no knowledge of their surroundings beyond adjacent cells, which is unlikely. Dispersing animals likely have some knowledge of surroundings based on smell and sight. Despite this limitation of Circuitscape, it has been shown to perform better than alternative methods for wolverines (McClure et al. 2016). In circuit theory models, sources and destinations are defined as “core” habitat patches. The current density estimates from Circuitscape output represent the pathways animals are likely to use and whether or not alternative pathways exist (McRae et al. 2008, McRae and Shah 2009). We ran Circuitscape analyses five times, once for each resistance layer (Figure 3.5). Cores were the same for all analyses across different resistance layers.

Testing Resistance/Connectivity Layers with Dispersal Data

Researchers have used a number of validation metrics to examine connectivity with little consensus (Driezen et al. 2007, Poor et al. 2012, Cushman et al. 2014, Keeley et al. 2017, Zeller et al. 2018). More recently, researchers have generated several complimentary validation methods to compare output generated from different methods or layers (McClure et al. 2016, Zeller et al. 2018). Based on the recommendations of McClure et al. (2016) we chose to examine three modified validation metrics to compare our different resistance layers including 1) value at observed dispersal points, 2) random point comparison, and 3) null value comparison. Our goal was to determine if any resistance layer predicted higher connectivity values at actual dispersal locations, and thus performed better, compared to the others across the three validation metrics. To compare our different connectivity layers, each layer was scaled from 1 to 100. In our analysis, high Circuitscape output values represented the highest connectivity values and low values represented the lowest connectivity values. We used the values at observed dispersal locations, which included 445 observations on 9 individuals for each of our three validation methods. We only used the VHF data for our validation metrics to 1) avoid pseudoreplication because several animals had both a VHF and GPS unit recording locations simultaneously; 2) account for the various time interval that the GPS collars collected data, some of which were at very fine scales compared to the resolution of the connectivity analysis; and 3) avoid bias against dense cover or mountainous terrain, because our GPS collars did not obtain locations on approximately 50% of attempts (D'Eon et al. 2002, Mattisson et al. 2010).

For the first metric, we compared the values at observed dispersal locations to the connectivity value generated by each of our five candidate layers. We referred to this metric as the value at observed points. We fit a mixed effect model using the connectivity values as the response, the negative exponential curves as the fixed effect, and a random effect of location number nested under animal ID to account for the nested nature of the data. We then looked at post-hoc Tukey's tests to contrast each resistance layer. This metric was intended to simply compare all connectivity layers and determine which layer had the highest predicted connectivity value at locations where wolverine dispersal was observed. If a connectivity value was high at an observed dispersal location, it suggested that the model was predicting movement well (McClure et al. 2016). In Circuitscape, connectivity values are highest along predicted routes or pathways. We determined that if our modeled pathways contained our observed dispersal locations, the connective values at each relocation would be higher. When comparing all five connectivity surfaces, low values indicated that that layer did not accurately predict dispersal.

The second test, random point comparison, was a paired comparison of randomly selected points to observed dispersal points. This allowed us to determine if dispersal movements aligned with predicted connectivity metrics better than, or the same as, by chance. Five random points were generated to compare to each observed point. Each random point was at least 6 km from a dispersal point to ensure that points were not within the same pixel as the dispersal locations but were no further than 40 km from any dispersal location. We chose the 40 km cutoff to ensure that each point was within the average daily travel distance for wolverines (Haglund 1966, Pulliainen 1968, Banci 1994). Each animal had a 1:5 ratio of observed dispersal points to random available points for this analysis. We then fit a mixed effect model with an interaction between the fixed effects point type (observed or available) and the negative exponential curve, plus a nested random effect of location number and animal ID. We subsequently conducted Tukey's post-hoc analyses to determine if there was a difference between connectivity values of observed dispersal locations and alternative locations. The second metric was designed to determine if the connectivity values predicted by any candidate layer at observed dispersal locations were higher than expected simply due to chance at random locations (McClure et al. 2016).

The third test we used, null value comparison, compared the percentile values at observed dispersal locations to a null model. To create a null resistance layer, we set all resistance values to 1. We ran Circuitscape on the null model using the same cores and then scaled the null model. We used a mixed effect model similar to the one used for the first validation method. We then conducted a post-hoc Tukey test to determine if the null model predicted higher or lower connectivity values at each dispersal location compared to each resistance layer. The intent of the third metric was to determine if connective layers predicted dispersal locations better than a null model where the resistance layer was set to 1 across the study areas. This metric indicates whether wolverines were following the corridors predicted by each of the different models or following direct pathways between patches.

Results

Resource Selection Function

The top model selected in the RSF included a landform classification (nine classes; i.e., valley, headwaters, ridges, peaks, etc.), a vegetation classification (fourteen classes; i.e., conifer forest, cool mixed forest, grassland), distance to high-elevation talus (DHITAL, m), latitude adjusted elevation (LAE, m), average monthly snow water equivalent (SWE, cm), and a housing/human land use classification (HUMAN, i.e., commercial/industrial, 1.5-3 units/square km, etc.). Unfortunately, because this model was developed for a predictive habitat quality analysis and the independence assumption was violated, coefficient estimates could not be interpreted in a meaningful way.

The predictive capability of the top model was determined using the previously withheld 30% of the data (accuracy = 77%), a GPS collar dataset (accuracy = 98%), and an additional test dataset of animals (accuracy = 99%), where accuracy represented the proportion of observations correctly predicted by the model. These results indicate that our logistic RSF model performed well and predicted wolverine presence with accuracy. This suggests that the top RSF model was useful for a predictive analysis. Additionally, to ensure that the variables included in the model performed well, the AICc value for this model was compared to a null model (response ~ 1). The top model explained variation in the dataset better than the null model (null model AICc =24779; top model AICc =20576, ΔAICc=4203; Table 1.3).

Resistance Type Validation Metrics

The first validation metric, value at observed points, indicated that there were strong differences in the connectivity values at observed locations across the resistance layer ($F_{4, 2228} = 1878.5$, $p < 0.001$). Percentile values ranged from 21.5 ± 2.2 for c = 0.25 to 57.18 ± 0.49 for c = 8. A Tukey's HSD test indicated that each layer had very different percentile values compared to each other layer and that the c = 8 layer had the highest connectivity values at dispersal locations (Table 3.2).

The second validation metric, which compared connectivity values at random points to connectivity values at observed dispersal locations, suggested an interaction between curve and the type of observation ($F_{4, 8452} = 245.41$, $p < 0.001$). The resistance layers all had different connectivity values at observed dispersal locations compared to available locations, with the exception of c = 32 (Table 3.3; Figure 3.6). For the layers where a difference was detected, the c = 0.25 layer had the lowest connectivity values for both available points (17.39 ± 0.33) and observed points (24.62 ± 0.72) and the c = 8 layer had the highest connectivity values for both observed points (42.36 ± 0.47) and available points (59.76 ± 1.02). The c = 8 layer also had the greatest difference between observed and available values (Table 3.3).

The third validation method compared connectivity values from a null resistance surface to the other five resistance surfaces we generated. The mixed effect model indicated that there was strong evidence that all resistance layer connectivity values differed from the null, c = 0.25 (t_{2785} = -6.65, $p < 0.001$), c = 1 (t_{2785} = -3.92, $p < 0.001$), c = 4 (t_{2785} = 12.06, $p < 0.001$), c = 8 (t_{2785} = 55.60, $p < 0.001$), and c = 32 (t_{2785} = 32.24, $p < 0.001$). Comparisons between each layer and the null indicated that both the c = 0.25 resistance layer and the c = 1 resistance layer had lower connectivity values than the null and did not perform well (Table 3.4). The c = 4, c = 8, and c = 32 resistance layers all performed better than the null model, with the c = 8 model having the highest connectivity values compared to the null model (Table 3.4). Together, these three validation metrics all indicated that the resistance layer c = 8 had the highest connectivity values at observed dispersal locations and was best supported by the dispersal data (Table 3.5).

Discussion

This is the first analysis to determine how well connectivity models based on resident wolverine habitat quality represent observed dispersal data. For the first part of this analysis we generated a RSF using home range data from wolverines around the GYE. Previous studies have used first-order resource selection analyses (Inman et al. 2013) and relationships between historical records and habitat conditions (Aubry et al. 2007, Copeland et al. 2010) to predict high-quality wolverine habitat in the United States. Our predicted high-quality habitat aligned well with these previous efforts. We also empirically validated our model using withheld locations and additional datasets. Together, this suggests that our model accurately estimated high-quality wolverine habitat. However, this validation only confirms that the RSF model accurately represents high-quality resident wolverine habitat. This validation does not provide any information about how useful resulting resistance or connectivity maps are. This is a major concern in connectivity modeling. Often, validation occurs in only a portion of connectivity analyses and limits the usefulness of the end product. In the future, researchers should ensure that validation occurs at every step of the modeling process to have the most accurate end products for conservation.

In the second part of this study, we generated three validation metrics and found that the c = 8 layer best approximated observed wolverine dispersal (Table 3.5). This layer was one of the strongest negative exponential curves we examined. This result suggests that resistance for dispersing wolverines should be modeled using a negative exponential function, rather than a linear function, as a negative exponential function best represented observed wolverine dispersal patterns. This finding supported our hypothesis that resistance and connectivity layers that represent less sensitivity to changes in habitat quality, once within low-quality habitat, will best represent wolverine dispersal. This alternatively could be interpreted to mean that wolverines are less sensitive to changes in habitat quality once they begin dispersing. Our results align with previous findings that inversing habitat quality is not the best proxy for resistance when modeling dispersal pathways in mammals (Keeley et al. 2017). Our results also demonstrate the disconnect between using telemetry data from resident animal and observed dispersal behavior. Wolverines are considered high-elevation conifer forest habitat specialists within their home ranges. However, dispersing animals must leave high-elevation habitats and move through lower elevation areas. If dispersing animals did not have a lower threshold for habitat quality, dispersal would not occur. Thus, it is very intuitive that the selection behavior of dispersing and resident wolverines would be different and should require different modeling approaches.

While our results suggest that wolverines, like several other species, are more willing to move through low-quality habitat during dispersal, there is still some degree of habitat selection occurring during dispersal, indicating that some form of habitat quality threshold exists for dispersing individuals. If wolverines moved indiscriminately through low-quality habitat, the null model would have explained movement as well as, or better, than any other model. Our results suggest that dispersing wolverines move readily through low-quality habitat but do still follow lower-resistance pathways that connect high-quality habitat (Figure 3.5). Our results align well with observed movements of wolverines between high-elevation habitats. For example, the animal that moved from Wyoming to Colorado in 2008 crossed habitat that would be considered extremely low-quality for wolverines, including sagebrush steppe, for several hundred kilometers, but also deviated from a least cost dispersal path to stop in smaller patches of high-quality habitat. While rare, this large dispersal event was not an isolated incident – wolverines have been recorded crossing state lines through low-elevation lands in several studies (Vangen et al. 2001, Inman et al. 2013). The location data from our dispersing animals suggests that wolverines have far more flexibility in what they can disperse through compared to what they move through during routine within home range movements, but that some level of selection is occurring.

Our finding, that dispersing wolverines are less sensitive to habitat quality than resident wolverines, was a critical step forward for connectivity modeling. Without the ability to compare different models, and without dispersal data on wolverines, the end product and any subsequent management decisions would be less than optimal. Our findings also have important implications for the long-term success of the wolverine metapopulation, which requires open space in valley bottoms that links the mountain ranges of the Western US. We found that there may be more flexibility in the location of these low-elevation open spaces than previously thought for wolverines. However, this does not mean that the task of protecting areas linking wolverine habitat will be easy. While wolverines were the focus of this analysis, connectivity conservation in the western US is becoming increasingly important. The western US contains some of the most relatively intact ecosystems remaining in the contiguous US (Belote et al. 2016). However, these ecosystems continue to face growing threats from human population growth, exurban development, changing disturbance regimes, and climate change (Theobald 2003, Brown et al. 2005, Gude et al. 2006, Abatzoglou and Williams 2016, Hansen et al. 2016, Westerling 2016, Hansen and Phillips 2018, Adhikari and Hansen 2019, Carter et al. 2019). Fortunately, these areas also present the greatest opprotunity for connectivity-based land use planning and conservation (Belote et al. 2016), but without accurate models of species distributions and connectivity, conservation planning will not be complete. Connectivity modeling is an important step in protecting connectivity between isolated wildlife populations and in planning for anthropogenic impacts on species. Modeling, validating, and protecting connectivity will be critical to the future of conservation action in the western US for a variety of species. Identifying and protecting land that are important for connecting high-quality wolverine habitat will also help connect the public lands of the western US. Inman et al. (2013) found that 96% of wolverine habitat is located on federal land with some degree of protection. Protecting connectivity for wolverines could help facilitate a network of connected wildlands in the west and benefit numerous species (Belote et al. 2017).

Scientific advancement in ecology depends on our ability to empirically test the accuracy of our research products. Ecological systems are already incredibly complex, and failure to validate conservation product output could lead to, at worst, poor decision making that results in worthless investments and detrimental impacts on the study species. For this reason, comparing both linear and negative exponential curves when modeling resistance surfaces is important, to ensure that connectivity layers output accurately reflect the movement for species of interest and the question(s) being addressed in the research. This does not mean that all unvalidated connectivity products are useless. For some data-poor species and systems, the necessity of conservation action may outweigh the ability or time needed to validate connectivity models. However, unvalidated models should be considered with caution for large or expensive management decisions until validation can occur. In the western US, and globally, it is essential that future connectivity analyses undergo a series of explicit validation tests to determine how well the connectivity surface represents actual animal movements. Each step in the process of modeling animal movement, from software selection to generating resistance layers, comes with a set of assumptions that may risk the utility of the end product if not addressed and analyzed. Program type and modeling approach should be carefully selected based on the questions being addressed and the species of interest, so that conservation planning can advance.

These considerations are also critical for transparency when sharing science and repeatability in future analyses. Using validation metrics to compare different connectivity models is essential to ensure that conservation planning best supports the successful persistence of species globally.

Conclusions

One of the biggest challenges facing connectivity modeling is how to validate and compare different connectivity programs and surfaces in order to make informed management decisions. Connectivity actions such as conservation easement purchases or road crossing structures require significant financial investments. Because wolverines are spread over a large geography, the costs and opportunity costs for limited conservation dollars require these types of detailed analysis. In this work, we used validation metrics and discovered that dispersing wolverines are more likely to move through low-quality habitats during dispersal events compared to resident animals. These results highlighted the need to disentangle dispersal data from home range data and to validate connectivity models so that conservation best reflects reality. Using validations metrics to compare different connectivity models is essential to ensure that conservation planning best supports the successful persistence of species of interest globally.

Future Directions and Improvements

Additional sampling of wolverine movements from across the study area is particularly important when considering the variety of conditions occupied by wolverine and our limited sample size. For instance, the habitat and dispersal predictions in the Pacific Northwest may be greatly improved, and prove more robust, by including presence data from the region. This is a very critical limitation for our study because all high-quality habitat predictions were made based on extrapolations far beyond the geography of the data. Our analysis was based on a small number of observations on 9 animals but would be more robust with additional animals. Combining data sources across the study area would reduce extrapolation and lead to a more robust and precise model of wolverine habitat quality and connectivity. Other researchers may be able to test these maps using additional datasets outside the GYE in the future, and maps that have been validated in some geographical areas are an improvement on existing maps with no validation. Despite the limitations of predictive models and our limited dataset, our analysis constitutes substantial progress towards the difficult goal of predicting wolverine habitat and connectivity in the western United States.

Tables and Figures

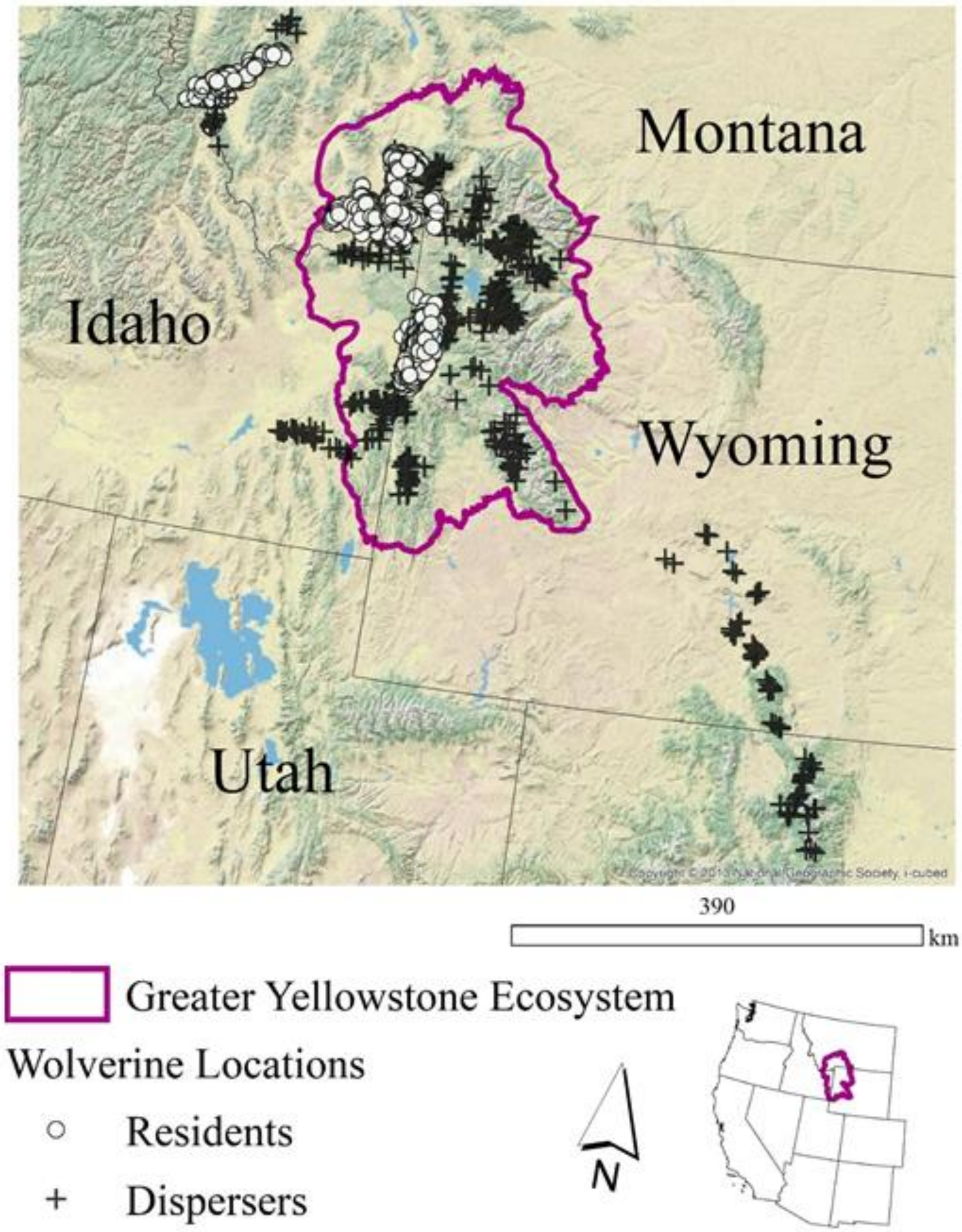

Figure 3.1 Map of resident wolverine locations (circles) and disperser wolverine locations (pluses) used to build the model for the resource selection function and in validation statistics.

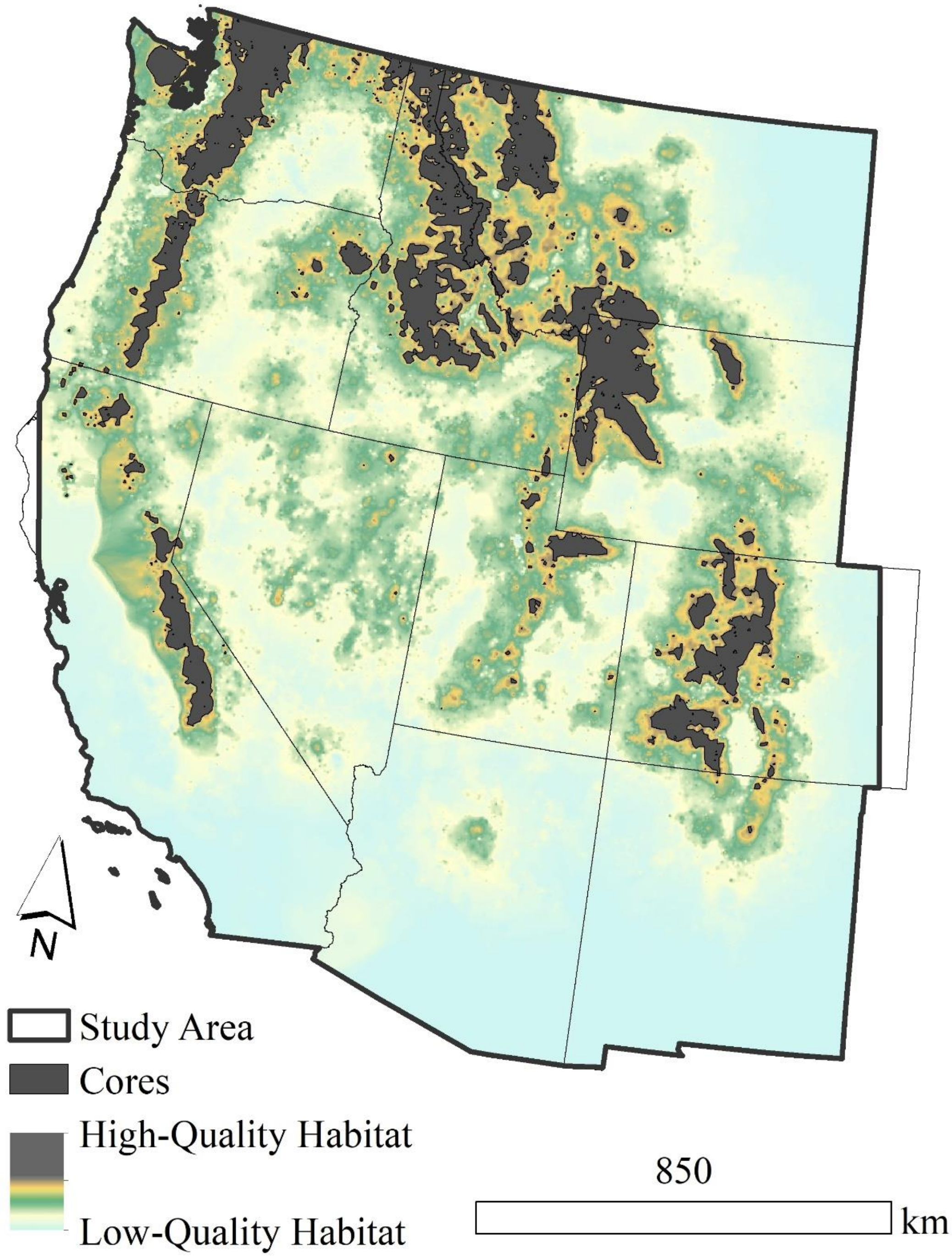

Figure 3.2 Predicted habitat quality and core wolverine habitat from the top model. The model covers portions of 11 states including Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming.

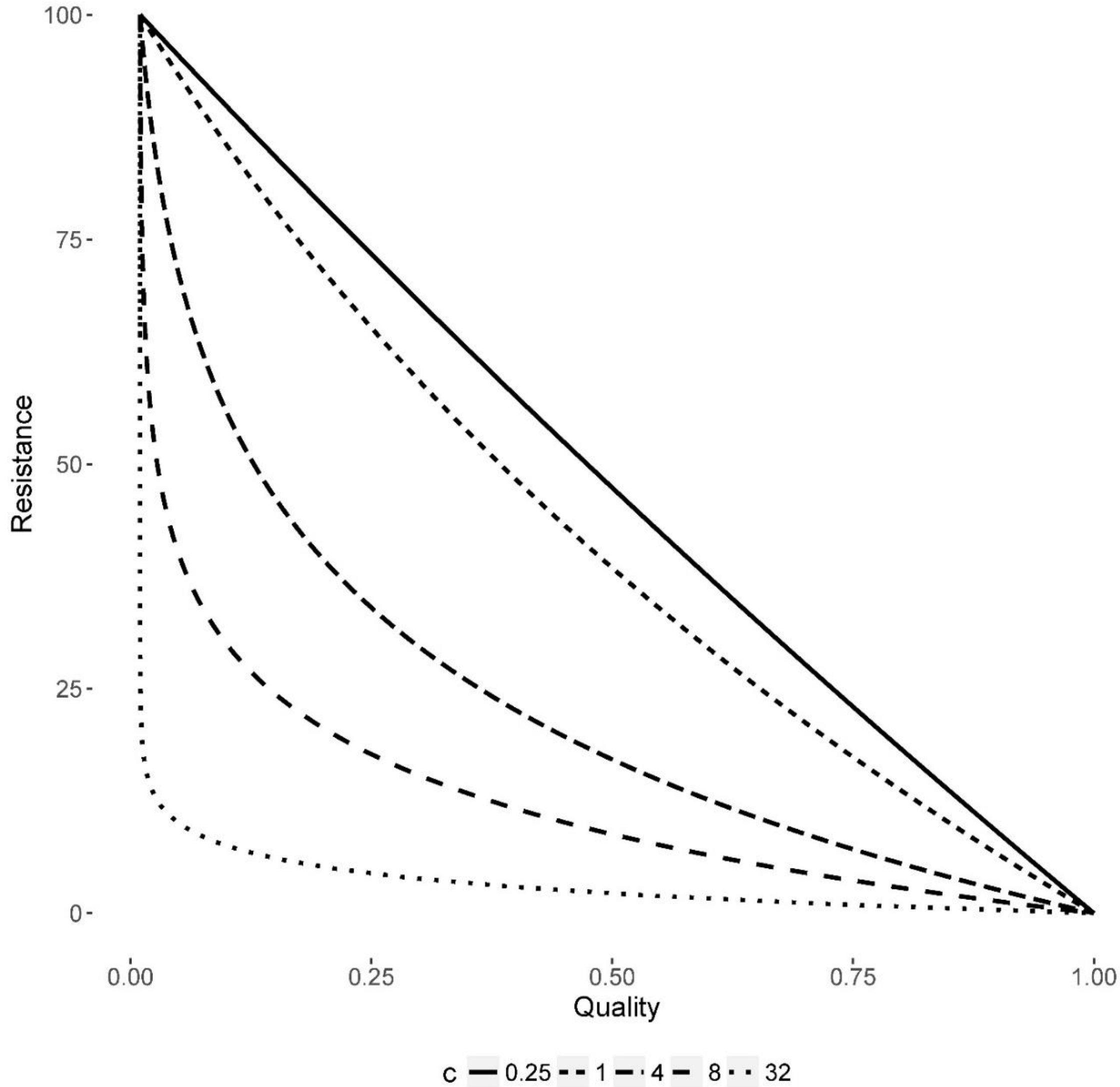

Figure 3.3 The relationship between habitat quality and resistance for each of the five transformations (c = 0.25, 1, 4, 8, 32) examined.

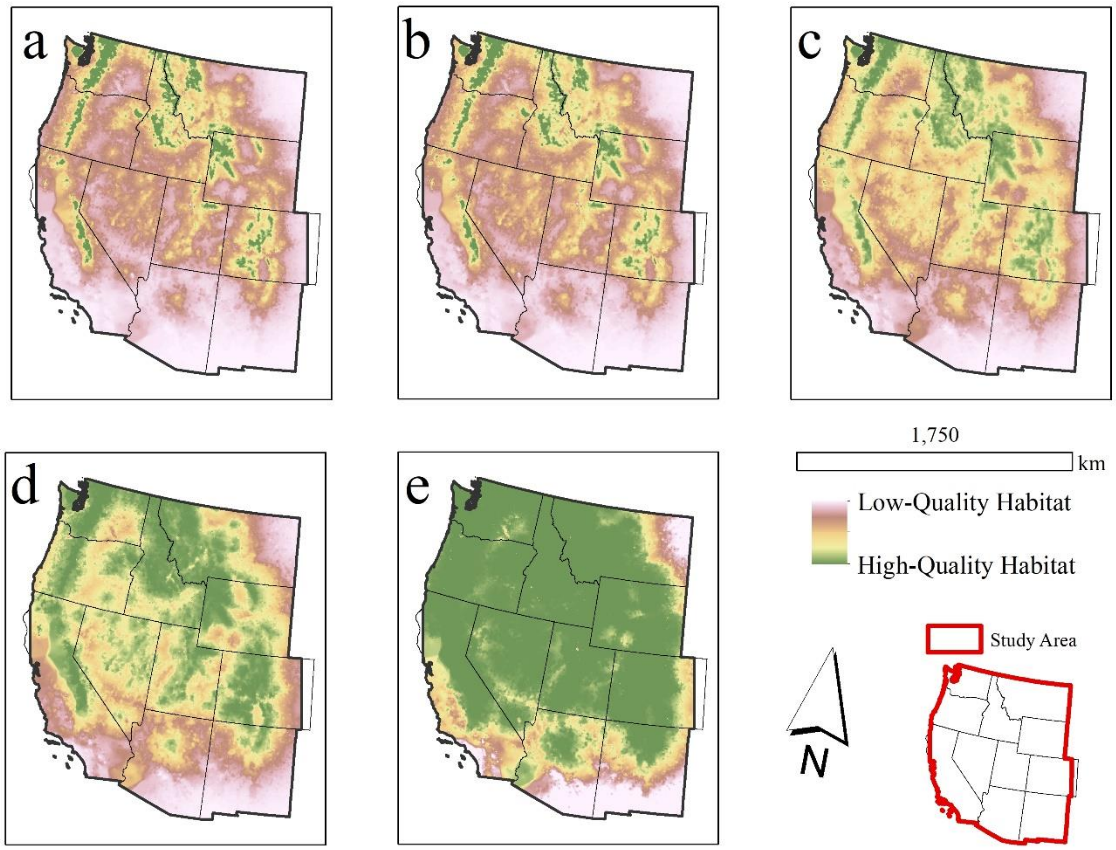

Figure 3.4 Model predictions of habitat resistance where a) c = 0.25, b) c = 1, c) c = 4, d) c = 8, and e) c = 32. Areas of lower resistance, or higher predicted permeability to movement are shown in green and areas with higher resistance are shown in red to white. Here, c = 0.25 represents the greatest degree of sensitivity to changes in habitat quality once outside of core habitat whereas c = 32 represents the least sensitivity to changes in habitat quality once outside of core habitat.

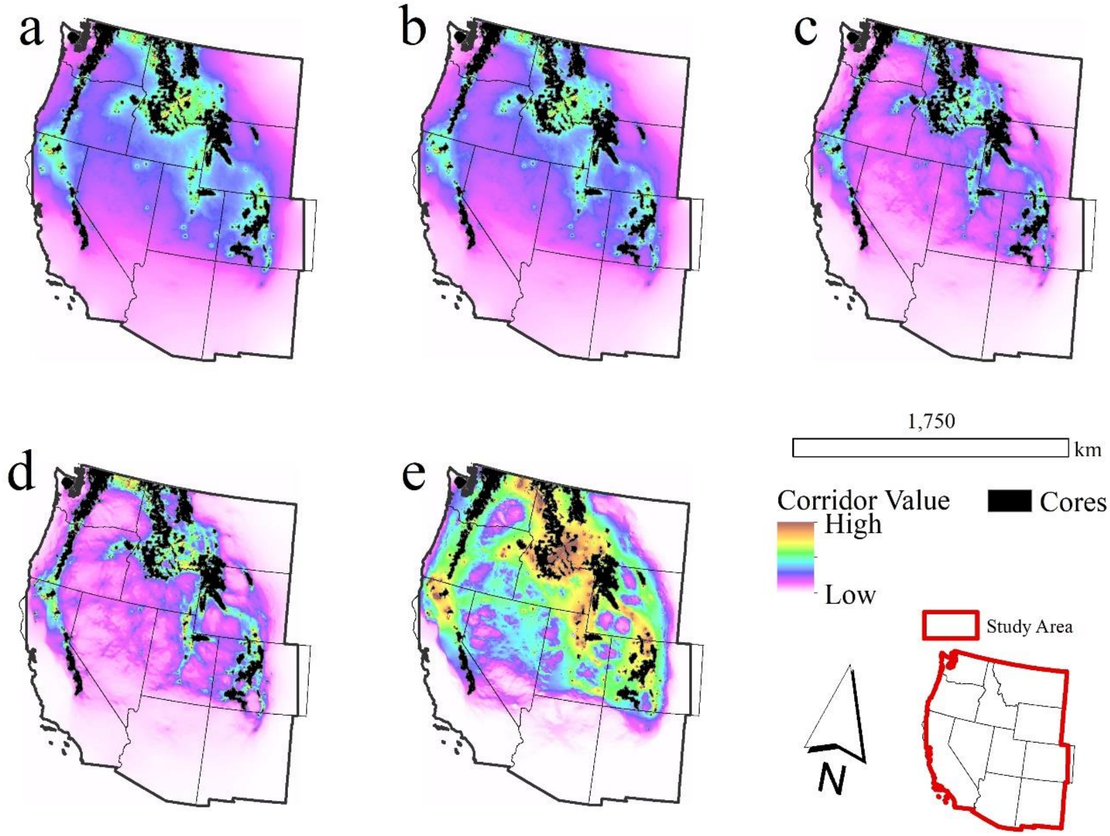

Figure 3.5 Model predictions of connectivity where a) c = 0.25, b) c = 1, c) c = 4, d) c = 8, and e) c = 32. Areas of higher connectivity value are shown in red and lower connectivity values are shown in white. Here, c = 0.25 represents the greatest degree of sensitivity to changes in habitat quality once outside of core habitat whereas c = 32 represents the least sensitivity to changes in habitat quality once outside of core habitat.

Table 3.1 AICc and delta AICc scores from the full model, top model, and null model. The full and top model were the same model.

Model	AICc	ΔAICc
Full	20576	0
Top	20576	0
Null	24779	4203

Table 3.2 Validation results from comparisons of mean percentile value at observed VHF points across all layers. Bold p-values are < 0.05.

Contrast Resistance Layers	Estimate	p-value
0.25 – 1	-1.56	**0.0124**
0.25 – 4	-10.72	< **0.001**
0.25 – 8	-35.67	< **0.001**
0.25 – 32	-22.29	< **0.001**
1 – 4	-9.16	< **0.001**
1 – 8	-34.11	< **0.001**
1 – 32	-20.72	< **0.001**
4 – 8	-24.95	< **0.001**
4 – 32	-11.57	< **0.001**
8 – 32	13.39	< **0.001**

Table 3.3 Validation results from of random point comparison. The differences between available points (A) surrounding observed dispersal locations (O) were compared for each layer.

Contrast Resistance Layers	Location Type	Estimate	p-value
0.25 –0.25	A – O	-9.20	< **0.001**
1 – 1	A – O	-10.30	< **0.001**
4 – 4	A – O	-14.73	< **0.001**
8 – 8	A – O	-19.38	< **0.001**
32 – 32	A – O	1.98	0.1733

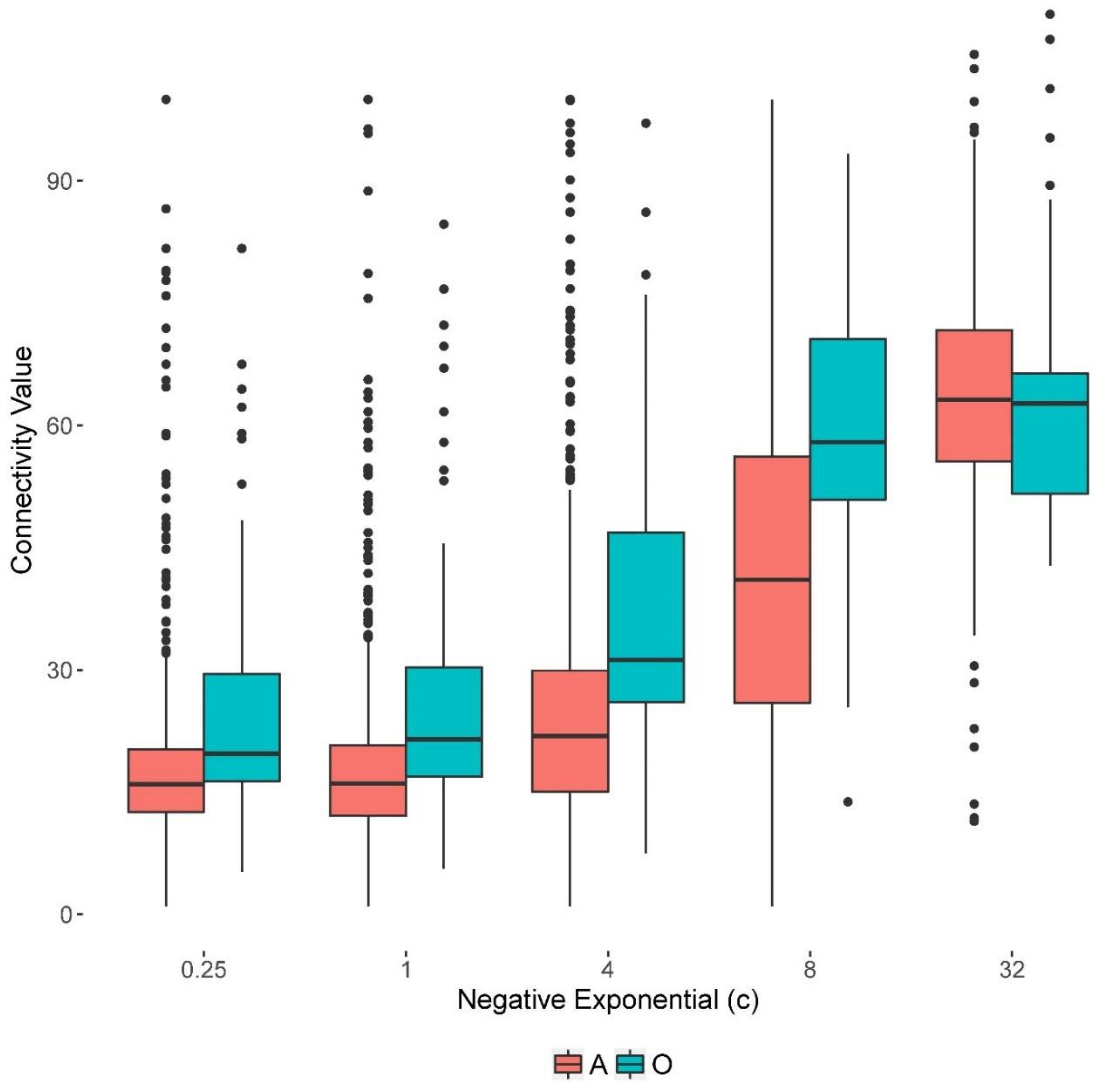

Figure 3.6 Comparison of the connectivity value for observed dispersal locations (O) and available dispersal locations (A) for each negative exponential curve c value.

Table 3.4 Validation results from comparison of mean percentile value at observed VHF points against a null layer.

Contrast Resistance Layers	Estimate	p-value
0 – 0.25	3.81	< **0.001**
0 – 1	2.25	**0.001**
0 – 4	-6.91	< **0.001**
0 – 8	-31.86	< **0.001**
0 – 32	-18.48	< **0.001**

Table 3.5 The best supported negative exponential from validation of wolverine dispersal points.

Test	Test Metric	Best Supported	Source
Value at Observed Point	Percentile value at observed points	c = 8	Table 3.2
Random Point Comparison	Percentile value between observed points and random points	c = 8	Table 3.3
Null Value Comparison	Percentile value compared to null percentile value	c = 8	Table 3.4

PRIORITIZING METAPOPULATION CONNECTIVITY FOR WOLVERINES

Contribution of Authors and Co-Authors

Manuscripts in Chapter 4

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Contributions: Conceived and implemented the study design, conducted the analysis, oversaw variable acquisition, and wrote the primary draft.

Co-Author: Dr. Robert M. Inman

Contributions: Generated or acquired a few explanatory variables and the wolverine data. Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

Co-Author: Dr. Andrew J. Hansen

Contributions: Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

Co-Author: Kevin Barnett

Contributions: Helped conceive the study, contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

Co-Author: Dr. Rick L. Lawrence

Contributions: Contributed to manuscript revisions and provided comments on the structure and content of the manuscript.

Manuscript Information

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Abstract

Wolverines in the western United States exist as a high elevation metapopulation that depends on successful dispersal through lower elevations that are often private lands. Given the potential for development of these lands, efforts to identify and conserve open space to facilitate dispersal would benefit and may be necessary for the long-term persistence of the population. Proactive work is necessary given that it is virtually impossible to walk back developments once they have occurred. However, prioritizing areas of connectivity for wolverine conservation presents several challenges: 1) the scale that the wolverine metapopulation functions over is large, 2) high-quality and connective wolverine habitats may shift in the future due to climate and human land-use change, and 3) there are many frameworks for approaching prioritization but none have been applied to wolverines across the western US. We prioritized areas important for wolverine habitat connectivity under future conditions (2050) across western Montana. Criteria for prioritization included 1) a connectivity only model with connectivity value, 2) an ecological only model with genetics, high-quality habitat area, connectivity value, and current flow centrality, and 3) an anthropogenic and ecological model, which included all of the ecological parameters and land development, likelihood of conversion, and road density. Each of these scenarios represented a systematic conservation planning problem and were solved using integer linear programming. Model output was generated by optimizing 10, 15, and 20% of each variable in the study area in each model while minimizing cost, which resulted in three sets of output for each model. We determined which counties in Montana had the highest number of selected parcels and how

irreplaceable each of these parcels were in each solution. We found high agreement between our models at the county level, and identified specific areas that would benefit from conservation action. Our analysis resulted in a set of maps that can be used by land trusts to work with willing private landowners to secure the connectivity of the wolverine metapopulation over the long term in the western US.

Introduction

Human-caused habitat loss and fragmentation have been linked to local population extinctions and global biodiversity loss (Pimm et al. 1995, Wilcove et al. 1998, Ceballos and Ehrlich 2002, Fahrig 2003, Pereira et al. 2010). However, increasing anthropogenic fragmentation does not impact all species equally and has serious consequences for metapopulations that rely on dispersers for establishment, recolonization, and genetic connectivity (Hanski 2011). As dispersal decreases between metapopulations, genetic diversity decreases, and the likelihood of extinction increases. Some of the negative repercussions of anthropogenic change for metapopulations can be alleviated using connectivity conservation. Connectivity conservation can include designating corridors, building structures to facilitate the movement of organisms (e.g., road crossing structures, fish ladders), removing barriers (e.g., dams), protecting stepping stone habitat, and protecting stopover habitat for migratory species (Crooks and Sanjayan 2006). While each of these strategies may be appropriate depending on study design and focal species, each strategy requires conservation planning and a rigorous framework for locating and managing connectivity areas.

Triage conservation provides a framework for connectivity conservation planning. Triage conservation is focused on protecting areas that face the highest risk, have the highest likelihood of success, and are of the greatest biological value (Hobbs and Kristjanson 2003). By identifying areas that have high ecological value for processes like dispersal, and will be the most resilient to climate change and human activities, researchers and practitioners can ensure that conservation actions protect areas in a systematic and defensible way. There is some disagreement about the utility of a triage approach for conservation. These disagreements are based on whether or not conservation resources are truly limited and what ecological features should be prioritized for selecting areas (Bottrill et al. 2008, McCarthy et al. 2012, Goswami and Vasudev 2017, Vucetich et al. 2017). Despite these disagreements, triage conservation can provide a rigorous framework for realizing conservation goals in a timely manner.

Designing a triage-based connectivity study necessitates obtaining a plethora of information and using a systematic conservation planning (SCP) approach. There are six distinct characteristics of SCP, which include 1) deciding what features should be used to represent the conservation target (e.g., diversity, connectivity), 2) explicit conservation goals, 3) identifying the extent to which those goals are currently represented by areas of conservation, 4) having simple, yet explicit, methods for locating and designing protected areas, 5) providing criteria for on-the-ground implementation, and 6) adopting explicit objectives and mechanisms for monitoring and adaptive management (Margules and Pressey 2000). While these six characteristics are challenging to implement together, they are critical for effective, flexible, and defensible conservation planning (Margules and

Pressey 2000). Steps 1 through 5, which are the core steps for designing a systematic conservation approach using triage conservation, can be done in several ways.

The first step of SCP, deciding what features should be used to represent the conservation target, often requires having up-to-date spatial data on specific species of interest or surrogates for biodiversity. In connectivity conservation, this step can be implemented by generating connectivity maps or metrics for species of interest (functional connectivity) or habitat types of interest (structural connectivity). The second step of conservation planning is detailing specific conservation goals (Margules and Pressey 2000). For species-specific connectivity, these goals can include avoiding barriers to connectivity (e.g., roads), protecting modeled dispersal or migration pathways, protecting habitats at risk of loss or fragmentation, and considering future climate change or human land use change scenarios that may impact modeled connective habitat. If possible, this step should incorporate cadastral data. Most organizations have limited resources for conservation. Thus, including property values for private lands simplifies step 5 (providing criteria for on-the-ground implementation) by eliminating areas from a conservation framework that may be cost-prohibitive for any organization. After obtaining species/biodiversity/land data, establishing goals, and comparing the goals to current conservation initiatives and protections, step 4 requires locating and designing protected areas. This step becomes increasingly complex as additional species, conservation targets, or variables are considered.

Identifying what areas require the most immediate conservation action, particularly when cadastral data is available, naturally lends itself to an optimization problem (Beyer et al. 2016). Like SCP, mathematical optimization provides a clear and defensible framework for designating areas that require immediate conservation action. Optimization models and software allow researchers to maximize efficiency and identify areas that, if protected, allow practitioners and policy makers to meet conservation goals for the least cost (Beyer et al. 2016). Beyer and colleagues (2016) outline the two common approaches for conservation optimization, integer linear programming (ILP) and heuristic methods like simulated annealing or ranking procedures. These approaches differ in their efficiency, computation time, capability to handle large problems, and how often they find an optimal solution. Additionally, through all of these approaches, balancing multiple conservation needs can complicate the output. Often mitigating potential human-made threats and preserving ecological processes are difficult to integrate in models. Furthermore, models with both processes can provide different results than models that only include ecological processes (Goswami and Vasudev 2017). Recent research on migration connectivity has used ILP with both ecological processes (migration) and human-made threats (conversion), because ILP provides more efficient and higher quality solutions (Tack et al. 2019).

Here, we determined what private lands are the most important and attainable for practitioners focusing on wolverine (*Gulo gulo*) connectivity conservation using ILP optimization. In the 1800s, wolverines ranged broadly across at least 18 states in the northern and western US (Aubry et al. 2007). Reliable evidence suggests that the wolverine population was drastically reduced by the mid-1900s, with extirpations in many states due to extensive trapping and habitat loss (Hornocker and Hash 1981, Aubry et al. 2007). The current range that wolverines occupy is now limited to Idaho, Montana, Washington, and

Wyoming, but suitable habitat has been identified in several other western states (Inman et al. 2013, Carroll et al. in review). The current wolverine population is likely still rebounding from historic human pressures like intensive trapping, and there is evidence of natural range expansion into historically occupied territories in southern Washington and Wyoming. Because wolverines occur at naturally low density as a high-elevation metapopulation, connectivity is essential for the persistence of this species over the long term.

To ensure that on-the-ground conservation efforts for wolverines are conducted as efficiently as possible and to prevent isolation of the current metapopulation, we employed a SCP approach and ILP optimization for future wolverine connectivity conservation. This work builds upon previous multispecies efforts, to identify areas important for wolverine connectivity. This previous work used wolverine genetic flow alongside current snow cover, housing development, and forest edge for optimization (Dilkina et al. 2016).While this previous effort provided an important baseline for wolverine conservation efforts, we chose to use future projections. This allowed us to provide additional, complementary information and also ensured our findings should be valuable over the long term for conservation planning. While the initial goal of this analysis was to maintain connectivity, we also wanted to prioritize private parcels important for connectivity that connected large cores with female occupants and were at risk of being converted from rural landscapes to exurban landscapes. We set these additional goals to identify areas that may require immediate protection from human development to maintain a highly connected wolverine population. However, in order to determine if balancing multiple conservation needs complicated or changed our optimization results, we designed multiple models with different goals. We generated three different optimization modeling approaches to determine what areas were of highest priority, including an anthropogenic and ecological model (A&E), an ecological only model (E), and a connectivity only model (C). For the A&E model, we used connectivity value, road density, core size, 2010 land development, genetics, land conversion from 2010 to 2050, and centrality of linkages. The E model included connectivity value, core size, genetics, and centrality of linkages to determine if the anthropogenic layers were drastically impacting our results. We also included the C model to determine how much our additional ecological variables were impacting our results. All three models were used in an optimization analysis for Montana, where land value data was available, and across five western states where land value data was not available. The outputs from these models were used to generate maps that identified areas requiring immediate conservation action for wolverines. The ultimate aim of this analysis was to generate connectivity maps for the western US wolverine metapopulation that can eventually be used to generate a successful network of connected public-private lands and be shared with land trusts, landowners, and other partners.

Methods

Study Area

We conducted our analyses both across five northwestern states (Idaho, Montana, Oregon, Washington, and Wyoming) and within western Montana. The western US is characterized by seasonal streamflow from mountain snowmelt, conifer forests at higher elevations, historic human settlement in valley bottoms, large extents of public lands, relatively intact historical species presence, and increasing ecotourism, recreation, and exurban development (Hansen et al. 2005, Parks et al. 2005, Hammitt et al. 2015, Li et al. 2017). Our western study area was comprised of 2-5 broadly defined ecoregions, each with unique combinations of soil, land surface form, natural vegetation patterns, land use, and climate patterns (Omernik 1987, Omernik and Griffith 2014). These ecoregions can be categorized as the Cascades, Sierran Steppe, Middle Rocky Mountains, and Northern Rocky Mountain, and Southern Rocky Mountain Steppe Ecoregions. The Cascades Ecoregion is characterized by large extents of productive and economically valuable conifer forests, north to south oriented mountain ranges, a maritime climate, high precipitation, and extensive human land use (Parks et al. 2005). The Sierran Steppe Ecoregion, in Oregon, is dominated by mountains oriented east-west, conifer forests, high botanical diversity, and warmer and drier conditions than the Cascades. The Middle Rocky Mountains Ecoregion, in Idaho, is dominated by granite mountain ranges, historically glaciated reaches, mild climates, variations in temperature and snowfall based on altitude, extensive federal land holdings, a mix of arid grasslands and shrub steppe vegetation at lower elevations, and conifer forests at mid to high elevations. The Northern Rocky Mountain Ecoregion is characterized by rugged, high-elevation mountain ranges, historical glaciation, heavy snowfall, well-marked elevation zones of vegetation, tree-free alpine habitats, and mixed-conifer-deciduous forest (Parks et al. 2005). The Southern Rocky Mountain Steppe Ecoregion, which includes a large proportion of the Greater Yellowstone Ecosystem (GYE), is the product of past and current geothermal and volcanic activity and is characterized by rugged mountains with broad valleys, historic glaciation, a cold, moist continental climate, shrub steppe and conifer forests, long historic fire intervals, and human pressures from tourism and exurban development (Parks et al. 2005).

Western Montana contains the continental divide and thus includes a broad range of forest types and climatic regimes. Areas west of the divide, including northwestern Montana are considered more mesic and receive abundant rainfall and snowfall along with relatively moderate temperatures (Pfister et al. 1977). Alternatively, areas east of the divide are considered more xeric and have a continental climate. Areas east of the continental divide include grasslands, shrublands, conifer forests, montane conifer forests, subalpine conifer forests, and alpine vegetation (Hansen and Phillip 2015). West of the divide there is more continuous forest coverage of mesic tree species. Large portions of this area include federally owned lands administered by the National Park Service, Forest Service, Bureau of Land Management, Fish and Wildlife Service and Department of Defense (Hansen and Phillip 2015). Exurban growth and development, climate change, and changing fire regimes are some of the biggest threats across this area (Parks et al. 2005, Gude et al. 2006, Hansen and Phillip 2018).

Overview of Approach

For this analysis, we used collar data from resident wolverines to predict wolverine habitat based on current snow water equivalent (SWE), generated a future habitat quality layer for wolverines using 2040 to 2069 Representative Concentration Pathway (RCP) 8.5 SWE projections (Abatzoglou and Brown 2012), identified future core (high-quality) wolverine habitat, modeled future connectivity among cores using a negative inverse of the habitat-quality layer (Carroll et al. in review), and used the resulting model output as variables in our optimization, or prioritization, models. We then used connectivity value and centrality of linkages from our connectivity models, along with road density, core size, 2010 land development, genetics, and land conversion from 2010 to 2050 in different combinations for three models. Our models included both anthropogenic and ecological variables (A&E), ecology only variables (E), and connectivity only variables (C). Each model was analyzed using ILP to optimize 10, 15, and 20% of each variable in the study area while minimizing cost. We then looked at which counties in Montana contained the highest number of parcels and how irreplaceable these parcels were in each solution.

Resource Selection Function, Resistance, and High-Quality Habitat

Between 2001 and 2009, 38 wolverines from a known population around the Greater Yellowstone Ecosystem (GYE) were fitted with intra-peritoneal VHF radio-transmitter and/or global positioning system (GPS) collars; some individuals were monitored for up to 9 years (Inman et al. 2012). Animals fitted with VHF implants were relocated every 10 days from a fixed-wing aircraft between 2001 and 2009. All resident animals with estimated home ranges around the GYE were used to develop habitat quality and connectivity estimates using a resource selection function (RSF; Carroll et al. in review).

Our RSF included a third-order polynomial term for average monthly SWE. The SWE model was chosen because snow cover area and duration has previously been shown to be a strong predictor of wolverine habitat (Schwartz et al. 2009, Copeland et al. 2010, but see Stewart et al. 2016). Additionally, this data layer also included a portion of southern Canada, which is ecologically important to consider for connectivity of the wolverine population. There is evidence of gene flow of wolverines between the US and Canada, and collared animals have been recorded moving across the border (Cegelski et al. 2006, COSEWIC 2014). High-quality habitat is also contiguous across the border, and northern habitat would be underweighted if Canada were excluded in a prioritization framework. However, other variables of interest could not be obtained for both the US and Canada. Before moving forward with this analysis, we compared a SWE only model to a previously analyzed model that included distance to high-elevation talus, latitude adjusted elevation, average monthly SWE, landform classification, vegetation class, and human land use (Theobald et al. 2005, Brock and Inman 2006, Bierwagen et al. 2010, Abatzoglou and Brown 2012, Inman et al. 2013, Michalak 2015, Carroll et al. in review). The SWE predicted presence and absence of 3 withheld datasets with 76%, 98%, and 99% accuracy. These scores were all within 5% of the accuracy scores of the previously analyzed model. Thus, this model was considered appropriate to use to model wolverine connectivity.

We then used the SWE model to predict future wolverine habitat across the western US states based on a 2040 to 2069 RCP 8.5 SWE projections (Abatzoglou and Brown 2012). The RCP 8.5 model predicts average temperatures to rise by approximately 3.7 (2.6-4.8) degrees Celsius on the same timescale. This projection currently aligns most closely with the current warming trend. The output from this analysis was used to represent future habitat quality for wolverines.

We extracted areas of high-quality wolverine habitat (values > 6 on a scale from 1 to 10) from the future projection to serve as “cores”, or potential animal sources, in a connectivity analysis (McRae and Shah 2009, Carroll et al. in review). We also produced a resistant surface layer by applying a previously validated negative exponential function to the 2050 SWE habitat quality layer (Carroll et al. in review). We used the future cores and resistant surface to analyze connectivity using both Linkage Mapper 2.0.0 and Circuitscape 4.0 (McRae and Shah 2009, McRae and Kavanagh 2011). When generating current maps in these programs "core" habitat patches serve as locations where animals are moving to or from. Circuitscape provided current density estimates that represent both the paths animals are likely to move, as well as how tenuous movements between cores are. This metric can be used to determine areas that are highly valuable to individual movement. Linkage Mapper can be used to generate a centrality metric, which identifies paths between cores that are critical to the maintenance of connectivity. These two outputs, current density and centrality of linkages, were later used for our prioritization analyses.

Characterizing Variables and Layers for Prioritization

Seven variables were originally selected to identify important land that connected large cores with female occupants, and were at risk of being converted from rural landscapes to exurban landscapes. These variables including connectivity value, road density, core size, 2010 land development, genetics, land conversion from 2010 to 2050, and centrality of linkages (Table 4.1). These variables were all included in the A&E model. A subset of these variables was selected for the E and C models. Different models were generated to ensure that the prioritization problem could be solved and that the more complicated model did not identify areas that were better for all variables at the expense of protecting important wolverine connective habitat. Variable selection was based on evidence in the literature that the variable was important for either connectivity between populations or population persistence of wolverines. All model variables were linearly scaled from 0 to 1, where 1 represented the highest value or most important category (Table 4.1).

The first variable, connectivity value, is a metric generated by Circuitscape 4.0 for connectivity analyses (McRae and Shah 2009). In Circuitscape, connectivity values are highest along predicted routes or pathways when many random walkers pass through them. It is essential to protect areas with high connectivity values for species that exhibit long distance dispersals, because these areas represent pathways that would disproportionately compromise connectivity if they were lost (Castilho et al. 2015). Identifying important pathways between areas of high-quality wolverine habitat is critical to producing a framework for future connectivity conservation. We ranked areas with higher connectivity values as more valuable in our prioritization framework.

We also considered road density in our analysis using 2018 TIGER/Line road data (U.S. Census Bureau 2018). The permeability of roads differs by taxa of mammal (Assis et al. 2019), but carnivores, including the family Mustelidae, are expected to have higher contact with roads than other mammals (Ceia-Hasse et al. 2017). During natal dispersal, wolverines can move immense distances (Inman et al. 2012, Higgins 2019), and roads have been identified as a barrier that contributes to genetic isolation in this species (Sawaya et al. 2019). We prioritized areas that had low road densities to identify areas that could be protected from future road development and facilitate wolverine movement.

Core size is also an important habitat feature for wolverine conservation. Globally, there is agreement that wolverines exhibit intrasexual territoriality (Powell 1979, Magoun

1985, Persson et al. 2010). Territorial behavior dictates how individuals partition space in areas with limited resources (Haenel et al. 2003). In the western US, where suitable and unsuitable conditions for wolverines exist in close proximity and wolverines regularly patrol territorial boundaries, areas of high-quality habitat can only support a limited number of home ranges (Inman et al. 2012). We considered patches (and their surrounding areas) that were larger extents of high-quality habitat to be more likely to support a larger number of individuals. We ranked patches of high-quality habitat based on their area (core size), to prioritize the protection of larger extents of high-quality wolverine habitat.

We also based our prioritization on 2010 human development level, or whether areas were considered rural, exurban, or urban (Theobald et al. 2005). While it has proven difficult to test whether wolverines avoid human infrastructure (due to the general lack of infrastructure within otherwise suitable wolverine habitat), we believe it reasonable to assume that habitat quality lowers with increasing levels of human activity and infrastructure. Wolverine movement within-home range is impacted by human activities, such as recreation (Krebs et al. 2007, Hienemeyer et al 2016). There are also reports from Aboriginal knowledge holders in Canada that wolverines avoid areas with human development (Cardinal 2004). We chose to include current human land use in the analysis and to prioritize rural landscapes.

We included information from a recently completed genetic analysis of wolverines across the five-state area (Lukacs et al. in review). There is genetic evidence of sex-biased dispersal and female philopatry in wolverines, which limits recolonization of previously occupied habitat (Rico et al. 2015). The contiguous US wolverine population in the Rocky

Mountains has been identified as needing at least two effective migrants per generation to avoid the effects of genetic drift (Cegelski et al. 2006). Given that female wolverines are less likely to disperse, areas that currently have female occupants are more valuable to ensure population persistence and reproduction. These areas were prioritized over areas with only males, unknown animals, or no detections respectively (Table 4.1). This ensured that priority was given to areas where female wolverines are more likely to be reproducing and supporting population growth.

We also prioritized areas at risk of land conversion between 2010 and 2050 (Theobald et al. 2005). We previously discussed that wolverines avoid areas with human development, and the western US is experiencing unprecedented development (Hansen et al. 2005). There is extensive exurban development around important intact wildlands, like the GYE (Hansen et al. 2005), that may further or permanently isolate wolverine populations. To capture areas that may require immediate protection, we determine what pixels had varying degrees of human development (rural, exurban, urban) at 2010 and predicted to change by 2050 by Theobald et al. (2005) to prioritize areas at highest risk of converting from rural to exurban and may be important for wolverine movement (Table 4.1).

The last variable we consider was the centrality of linkages, or current flow centrality, which is a metric generated in the Linkage Mapper 2.0.0 Centrality Mapper (McRae and Kavanagh 2011, McRae 2012). Linkage Mapper is based on least-cost corridors, which estimates the shortest distance based on the cumulative cost-weighted distance between them. After generating least cost corridors, the centrality of each linkage can be generated. The centrality of linkage values allowed us to identify how important any corridor between patches was in maintaining connectivity between areas of high-quality wolverine habitat. We prioritized areas that were more important in maintaining connectivity, or areas with higher centrality.

Land Tenure for Montana

We analyzed three prioritization models in western Montana on private land (Figure 4.1). To determine the boundaries of private land (herein 'parcels') for optimization in Montana, we used the US Public Land Survey System data (www.cadastral.mt.gov). Parcels were aggregated based on ownership. We also removed parcels without ownership or value data. The aggregation and cleaning of the data reduced the number of parcels from 848,376 to 375,564. We used the US Public Land Survey System data on lakes, conservation easements, and federal land tenure to determine "fixed" parcels. These "fixed" parcels were excluded from the optimization analysis and assumed to be invulnerable to loss or conversion relative to private land with no protection. Each parcel had a unique property value from the US Public Land Survey System data that was incorporated into the prioritization framework (Figure 4.2). We considered federal land to be land owned by the Forest Service (FS), the Fish and Wildlife Service (FWS), Bureau of Land Management (BLM), National Park Service (NPS), United States Department of Agriculture (USDA), Department of Energy (DOE), Department of Defense (DOD), and the Bureau of Reclamation (BOR).

Prioritization Approach and Tools

We analyzed prioritization across the five-state area in three ways. We considered all seven anthropogenic and ecological (A&E) variables equally weighted, the four ecological variables equally weighted (E), and only connectivity value (C; Figure 4.1). We chose to examine the five-state region output for several reasons. Ecologically, the current wolverine distribution of breeding individuals includes these states, thus the metapopulation functions over this extent. While we could not obtain cadastral data from all of these states to optimize each variable in the study area while minimizing cost, we could still gain some valuable insight into wolverine conservation from these data. This analysis provided some initial insight into how our A&E, E, and C models differed and helped us identify areas that may be important to consider when cadastral data is available across the five-state region. We examined the resulting maps and compared areas identified as highest priority (top 10% of output) to core, or high-quality wolverine habitat, current conservation easements, and federal lands to determine what areas were important for residence versus dispersal and already protected respectively. We also compared differences in outputs from each model to determine how the addition of anthropogenic variables and different ecological variables impacted high priority areas.

In the Montana specific analysis, we prioritized private parcels with high connectivity and centrality values that connected large cores with female occupants and were at risk of being converted from rural landscapes to exurban landscapes. We did this to identify areas that may require immediate protection to maintain a highly connected wolverine population. We analyzed our three conservation planning problems (A&E, E, and C), following the methods of Tack et al 2019, by using the prioritizR package in program R (Hanson et al. 2019) with a Gurobi optimization solver (Gurobi 2016). The prioritizR package uses ILP techniques to build conservation problems (Hanson et al. 2019). This package can interface with a number of solver software algorithms. We selected the Gurobi solver because of the speed at which it generates solutions. This same approach (combination of prioritizr with Gurobi) has been successfully used to identify private parcels for conservation of pronghorn (*Antilocapra americana*) and greater sage-grouse (*Centrocercus urophasianus*) migratory pathways (Tack et al. 2019). Using this software, we analyzed three optimization targets, 0.10, 0.15, and 0.20, for each of our variables using our three prioritization schemes while minimizing cost (A&E, E, and C). These targets allowed us to identify the 10, 15, and 20% of high value areas of each variable in the study area while minimizing cost. Each variable was scaled from 0 to 1, so the solver attempted to select parcels that protected either 10, 15, or 20% of the highest value parcels for each variable. Using three optimization targets enabled us to compare a hierarchy of important parcels across Montana. When shared with practitioners and land managers, this output will allow them to develop a conservation schedule for working with willing private landowners to protect the top 10, then 15, then 20% of parcels identified in the output.

After analyzing all nine planning problems (A&E, E, and C at 0.10, 0.15, and 0.20), we compared the parcels identified as important at the county level using maps and a Friedman Test to see if they differed across models. We also analyzed the irreplaceability of each parcel. The irreplaceability score of a parcel was generated using the planning unit score, or the value of that parcel in the solution, assigned during the optimization modeling using a replacement cost method. If a parcel, or planning unit, had a low score it was considered replaceable and not important to meeting the conservation goals, but as parcel scores approached infinity in the model output, they were considered to be increasingly critical to meeting the conservation targets. Irreplaceability could only be analyzed for Montana because this metric is based on the planning unit score from the optimization models, which are not possible to obtain without property value data.

Results

We mapped high priority conservation areas using 1) an anthropogenic and ecological (A&E) model, 2) an ecological only (E) model, and 3) a connectivity (C) model across the western US (Figure 4.4). In all three of the multi-state prioritization approaches, the areas of the highest priority included the Cascades in Washington, central Idaho, western Montana, and northwestern Wyoming. We found that the highest A&E priority areas (values > 0.9; range 0 to 1) overlapped 74% with predicted 2050 core wolverine habitat, 0% with conservation easements, 60% with Forest Service (FS) land, and 6% with Bureau of Land Management (BLM) land (Table 4.2). When only the ecological variables, including genetics, connectivity values, centrality, and core size, were included, the areas of the highest priority (values > 0.9; range 0 to 1) differed slightly from A&E model (Figure 4.4). We found that the highest E priority areas overlapped 70% with predicted 2050 core wolverine habitat, 2% with conservation easements, 70% with FS land, 1% with BLM land, and 2% with NPS land (Table 4.2). The highest C priority areas overlapped 45% with predicted 2050 core wolverine habitat, 0% with conservation easements, 62% with FS land, 5% with BLM land, and 5% with NPS land.

We also compared agreement and disagreement between the A&E and E models (Figure 4.5). This allowed us to determine how the anthropogenic variables were impacting our results. Unsurprisingly, model agreement was highest in the Cascades in Washington, central and northern Idaho, northwestern Montana, and around the GYE (Figure 4.5). This result makes sense, as these areas have large extents of public land with little human land use and high values for the ecological variables. We also compared the E and C models (Figure 4.5). This comparison was conducted to determine how including genetics, centrality, and core size influenced the E model compared to connectivity alone. Model disagreement was highest around the Wind River Range in Wyoming, around the border of the Cascades in Washington, in northern Montana, and in central Idaho. This disagreement likely stems from the disparity between prioritizing areas that were only important for connectivity and dispersal (C model) and prioritizing areas important for establishment and reproduction adjacent to large, central core areas with female wolverines (E model) (Figures 4.4, 4.5).

We also generated map output from three Montana prioritization models using all seven variables (A&E, Figure 4.6), just ecological variables (E; Figure 4.7), and connectivity only (C; Figure 4.8). Each model was used to determine the 10, 15, and 20% best parcels across variables and property values. The A&E model identified between 364 and 732 parcels for the three optimal solutions, the ecological only model identified between 328 and 661 parcels across the three optimal solutions, and the connectivity only model identified between 286 and 576 parcels across all three optimal solutions (Table

4.3). These parcels were all located on private land with no conservation easements, per the model specifications.

We used the model output to determine how irreplaceable each parcel was in each model (Figures 4.6, 4.7, 4.8). Because of the large extent of the analysis, we examined irreplaceable parcels on a county by county basis (Figure 4.9). Determining irreplaceability is key to making triage-based management decisions because parcels deemed highly irreplaceable are critical to meeting conservation targets. For each model, parcels with planning unit scores > 0.8 (on a scale of 0 to 1) were considered irreplaceable. Our models predicted between 9 and 30 irreplaceable parcels per model, with 154 parcels identified across all three models. A majority of these parcels were located in Lewis and Clark, Glacier, and Sanders counties (Figure 4.9). When the number of irreplaceable parcels were averaged by the private land area of each county, Glacier, Sanders, Lewis and Clark, Ravalli, Silverbow, and Beaverhead counties had the highest number of irreplaceable parcels.

Like the irreplaceability of parcels, we also examined which parcels were selected by the optimization criteria on a county by county basis. The number of identified parcels in any given county ranged from 0 to 55 across all models. When averaging across the 10%, 15%, and 20% outputs, the A&E and E model identified the same five counties as containing the greatest number of high priority (values > 0.9; range 0 to 1) parcels, including Cascade, Lincoln, Carbon, Toole, and Hill (Table 4.4; Figure 4.10). The connectivity only model identified the greatest number of high priority parcels in Cascade, Gallatin, Yellowstone, Fergus, and Lewis and Clark counties. When we looked at the number of parcels per private land area, Mineral, Ravalli, Carbon, Rosebud, and Treasure counties had the greatest number of high priority parcels in the A&E model (Table 4.4; Figure 4.10). In the E model Mineral, Ravalli, Carbon, Gallatin, and Stillwater counties had the greatest number of high priority parcels per area. The C model identified the greatest number of high priority parcels per area in Mineral, Ravalli, Jefferson, Gallatin, and Stillwater counties. When comparing all of these summaries, Carbon, Mineral, Cascade, Gallatin, and Ravalli counties were ranked highest the most frequently in the models. While it was difficult to compare parcel locations and counts across models, a Friedman test indicated that the three models were not different for either the per area (Friedman $\chi^2 = 0.46$, df = 2, p = 0.80) or counts (Friedman $\chi^2 = 0.60$, df = 2, p = 0.74) of parcels at the county level.

Discussion

In 2015, the Western Association of Fish and Wildlife Agencies (WAFWA) initiated work to define and implement a multi-state conservation strategy for wolverines. WAFWA's major priorities were to 1) connect, 2) restore, and 3) monitor the wolverine metapopulation of the western US. This work focused on achieving the first priority, connectivity. Our intention, along with the WAFWA work initiated in 2015, was to design a collaborative conservation strategy for wolverines across multiple states for 2050. By implementing collaborative conservation efforts between state agencies and land trusts, the goal of maintaining a highly connected and interbreeding population can be facilitated. We met the ultimate goal of this analysis – we created a set of maps that can be used to advance wolverine connectivity conservation.

Identifying areas important for wolverine connectivity conservation using optimization software provided valuable insight into how to best approach wolverine conservation. Securing a network of open space for wolverine dispersal is even more important than short-term presence of the species because it will facilitate natural species recovery and reestablishment. However, our models each yielded slightly different results. This illustrates an important problem in triage conservation research – how to balance mitigating threats to species with maintaining ecological processes (Goswami and Divya 2017). Similar to findings from connectivity conservation research on Asian elephants (*Elephas maximus*) that used an optimization approach, we found that balancing multiple conservation needs complicated our results when comparing our different models.

We chose to compare three models, an A&E, E, and C model. The A&E model was used to understand what areas/parcels were most important for mitigating potential threats and preserving ecological processes, the E model was used to understand what areas/parcels were best for maintaining the ecological processes of dispersal, establishment, and reproduction, and the C model was used to understand what areas/parcels were most important for maintaining the ecological process of dispersal. Each of these models produced different results, both across the five-state area (Figure 4.4, Table 4.2) and in Montana (Figures 4.6, 4.7, 4.8; Tables 4.3, 4.4). Despite the disparities in model output, the irreplaceability metric provided insight into what areas are most important for immediate conservation action (Figure 4.9). Regardless of what model is considered for conservation planning, the irreplaceability scores provide a starting point for conservation action.

Selecting whether to use the A&E, E, or C model still presents challenges. Wolverines, like many other species, face a number of threats associated with human-caused habitat fragmentation and human-related barriers to dispersal. While these threats are important to consider when making conservation or policy decisions, determining how to incorporate data on these threats into conservation analyses requires a deep understanding of wolverine ecology and adequate information about where important ecological processes and human-related threats have conflicting conservation requirements. For example, by including the road density layer in the A&E model, parcels in rural eastern Montana, where road density is lower, were prioritized more frequently than in the E and C model. This result can be misleading because, while those parcels could be important for a few wolverines dispersing east or southeast, these parcels are far less likely to receive dispersing animals and contribute to population persistence and growth based on current wolverine occupancy patterns and historic dispersal compared to areas in western Montana. Overall though, we believe that the value of including anthropogenic threats outweighs the cost of excluding them. Thus, we believe that the best prioritization model is the A&E model because it included both anthropogenic and ecologically important data. Our results provide a novel and valuable toolset for wolverine conservation action, but it is critical that managers and policy makers make intelligent and informed decisions when using these conservation resources. We highly recommend that practitioners using these approaches select parcels based not only on the framework provided, but also based on their best judgement. We also highly recommend that users focus on irreplaceable parcels for immediate conservation action, when possible.

Conclusions

Our analysis resulted in a set of maps that can be used by land trusts to work with willing private landowners to secure the connectivity of the wolverine metapopulation over the long term in the western US. Connectivity is essential for metapopulation persistence and increases the odds that a species is capable of withstanding catastrophic events. In light of threats associated with climate change, human-caused habitat loss, and human-caused habitat fragmentation, connectivity conservation is the most important action that can be taken to protect wolverines in the western US. However, connectivity conservation is also most valuable when considering whether the areas being protected can support multiple individual home ranges, are currently occupied by females that can produce dispersers, and may be lost due to immediate anthropogenic threats.

Connectivity conservation is critical to not only ensuring connectivity between populations, but for planning for anthropogenic impacts on species. Protecting areas that connect high-quality wolverine habitat will also help connect the public lands of the western US. Previous models indicate that 96% of modeled wolverine habitat is located on federal land (Inman et al. 2013) and thus, connecting wolverine habitat could help facilitate a network of connected wildlands in the west that would benefit numerous species and create a more resilient system of protected areas (Belote et al. 2017).

Future Directions and Improvements

There are still a number of improvements that could be made to our analysis. One potential improvement is additional data for our optimization variables. Our genetic data was based on a single winter occupancy study and could be improved with additional years of data (Lukacs et al. in review). Additionally, our core size layers were also based solely on future SWE projections. The SWE model performed slightly worse than our alternative habitat model, but the SWE layer was the only data layer that included important wolverine habitat in Canada. Without this information, we would have under-weighted the core size for habitat patches that span the US-Canada border. However, this means that our core sizes and weights were only as accurate as the future projections they were based on. The accuracy of these projections for modeling true future conditions were the best available to us, but could change if national and international emissions policy changed projected warming.

We made a number of assumptions in our optimization model and output. One assumption was treating federal public lands and conservation easements as “fixed” and excluding them from our models. These areas were excluded because the land was considered “protected”. However, depending on ownership, each of these areas have varying degrees of protection. Generally, large portions of protected areas do have some level of human impact that could negatively influence wolverines, such as reclamation. Given the evidence that wolverine avoid human activity, it is more likely that some level of protection from development is better than no protection (Krebs and Lewis 1999).

Tables and Figures

Table 4.1 The variables considered for prioritization analyses on private lands. Each variable was scaled from 0 to 1, where 1 always represents the "best case" for that variable (e.g., large cores, both sexes present, low road density). The first four variables are our ecological variables and the final three are anthropogenic variables.

Variable	Interpretation
Genetics	Proxy for reproductive potential based on genetic data from 2016 (Lukacs et al. in review). Values range from no known animals (0) to unknown/males only (0.33) to females (0.66) to known animals of both sexes (1).
Connectivity Value (Circuitscape)	Scaled connectivity values from Circuitscape output. High values represent high connectivity potentials (1) and low values represent low connectivity (0).
Core Area	A proxy for reproductive potential and resident animal potential of cores. Large cores support more female home ranges. Values of 1 represent largest cores. Zeros represent areas with no data.
Current Flow Centrality (Linkage Mapper)	Measures of network centrality (Mallory and Boyce 2018). High values represent pixels around paths of high centrality (1) and lower values represent increasingly low centrality. Zeros represent areas with no data.
2010 Development	The level of development in any pixel (Theobald 2005, Bierwagen et al. 2010). Low (0) is urban, moderate (0.5) is exurban, and high (1) is rural/undeveloped.
Conversion Values	Landscape conversion risk from 2010 to 2050 (Theobald 2005). Lowest values (0) represent pixels or parcels that were identified to remain Urban or Exurban; low values (0.33) pixels or parcels that were identified to remain Rural; moderate values (0.66) represent pixels or parcels that are expected to transition from Exurban to Urban; and high values (1) represent pixels or parcels that are expected to transition from Rural to Exurban.
Road Density	Scaled road density in each pixel (US Census TIGER 2018). Areas with the highest values have the lowest road density (1) and areas with the lowest scores have the highest road density (0).

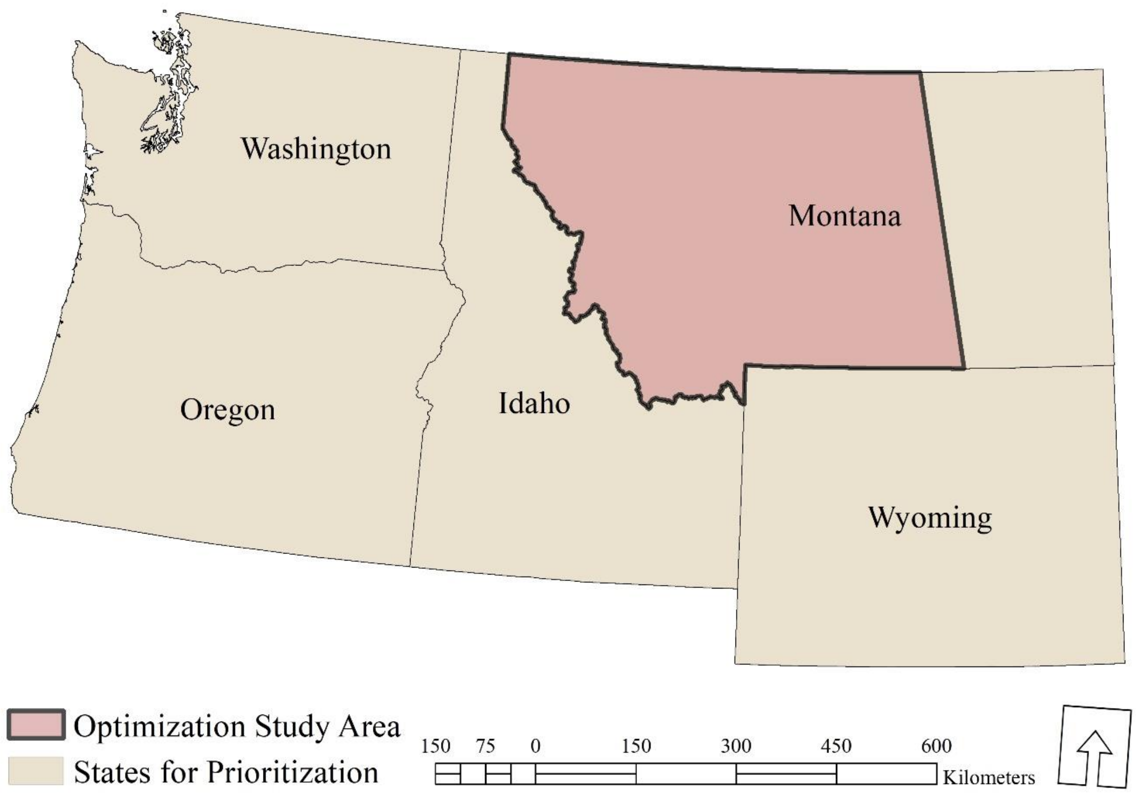

Figure 4.1 The two study areas for this research.

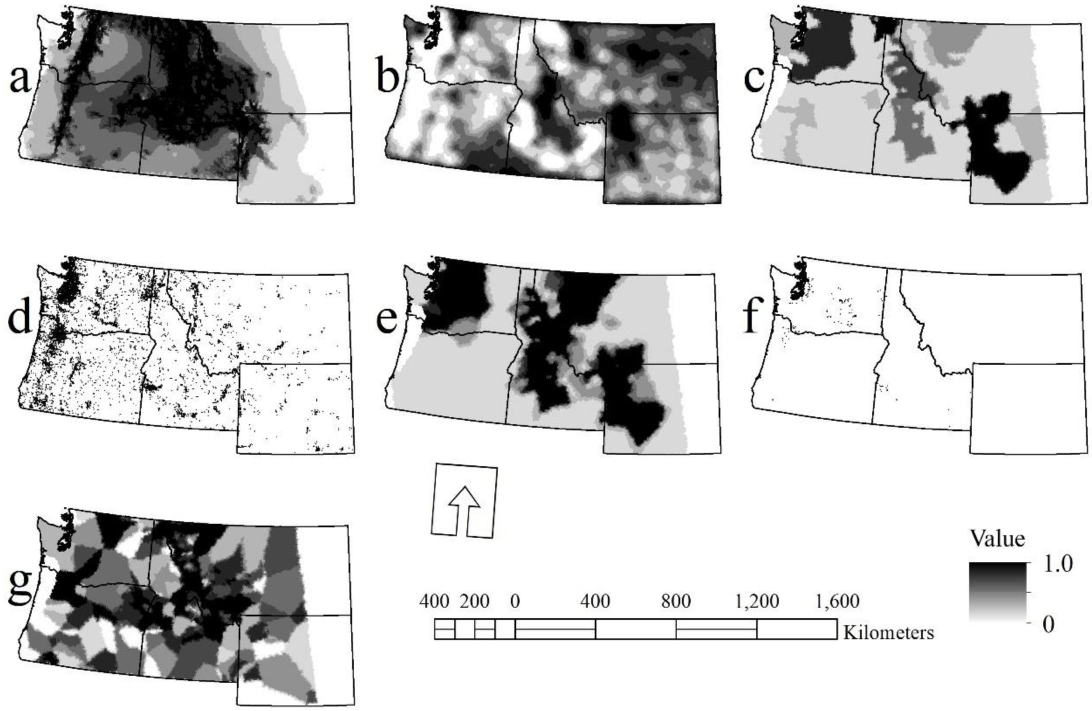

Figure 4.2 Distribution of the values for each variable used in the prioritization analyses. Variables include a) connectivity value, b) road density, c) core size, d) housing in 2010, e) genetics, f) housing conversion from 2010 to 2050, and g) centrality of linkages. Each variable is scaled from 0 to 1.

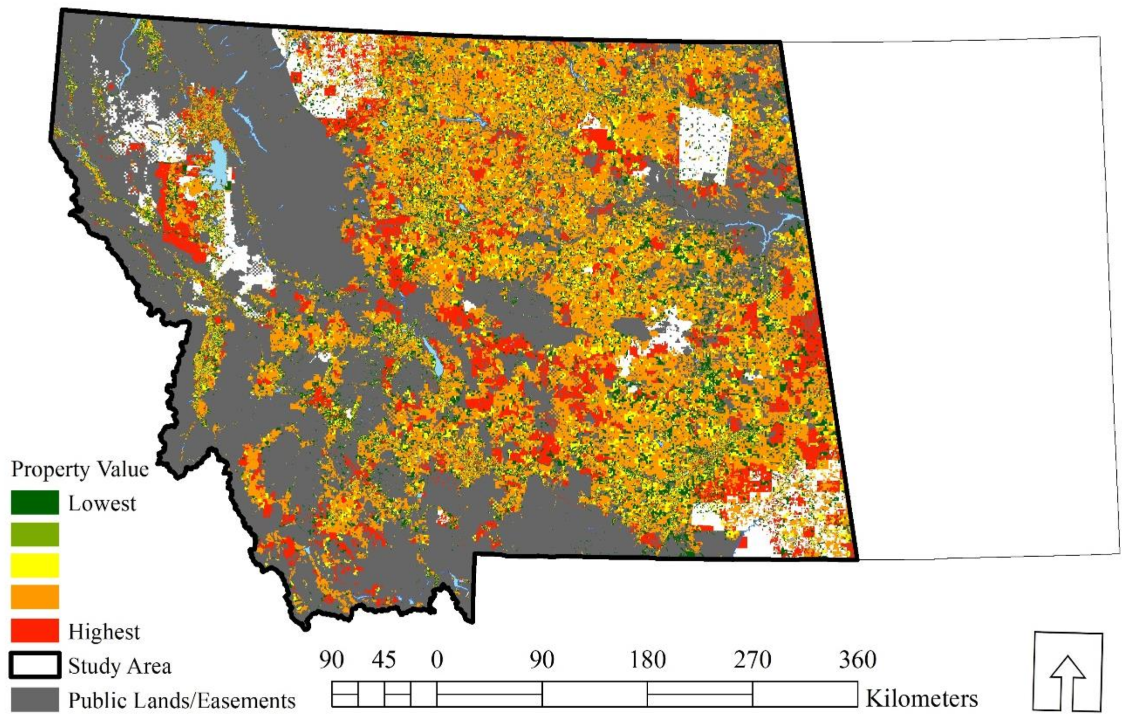

Figure 4.3 Montana 2018 cadastral data property values (www.cadastral.mt.gov). Excluded properties either did not have sufficient information or were publicly owned. The study area for Montana was based on availability of the features used for prioritization, which did not include eastern Montana.

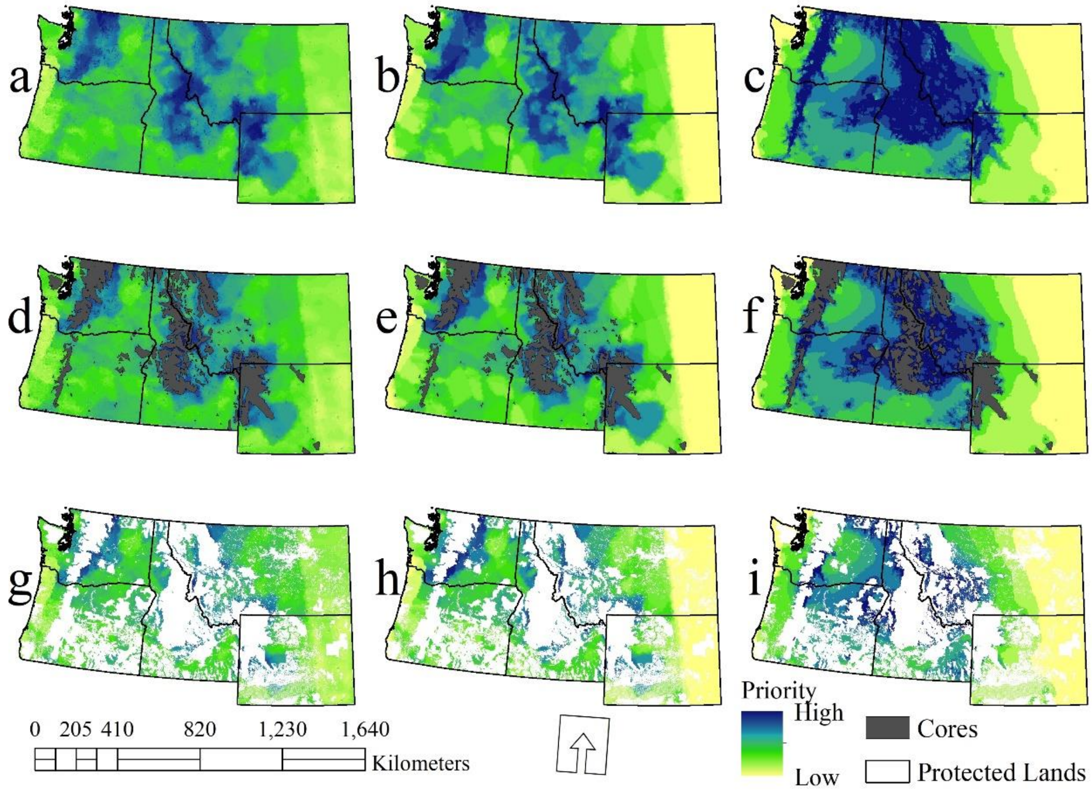

Figure 4.4 a) Anthropogenic and ecological priority based on connectivity value, road density, core size, housing in 2010, genetics, housing conversion from 2010 to 2050, and centrality of linkages. Each variable was equally weighted and scaled from 0 to 1. b) Ecological only priority based on connectivity value, core size, genetics, and centrality of linkages. Each variable was equally weighted and scaled from 0 to 1. c) Priority based on connectivity value. Each variable was equally weighted and scaled from 0 to 1. d) Anthropogenic and ecological priority with predicted 2050 core or high-quality wolverine habitat. e) Ecological only priority with predicted 2050 core or high-quality wolverine habitat. f) Connectivity output priority with predicted 2050 core or high-quality wolverine habitat. g) Anthropogenic and ecological priority with protected land, which included federal land (FS, FWS, BLM, NPS, USDA, DOE, DOD, BOR) and conservation easements. h) Ecological only priority with protected land. i) Connectivity priority with protected land.

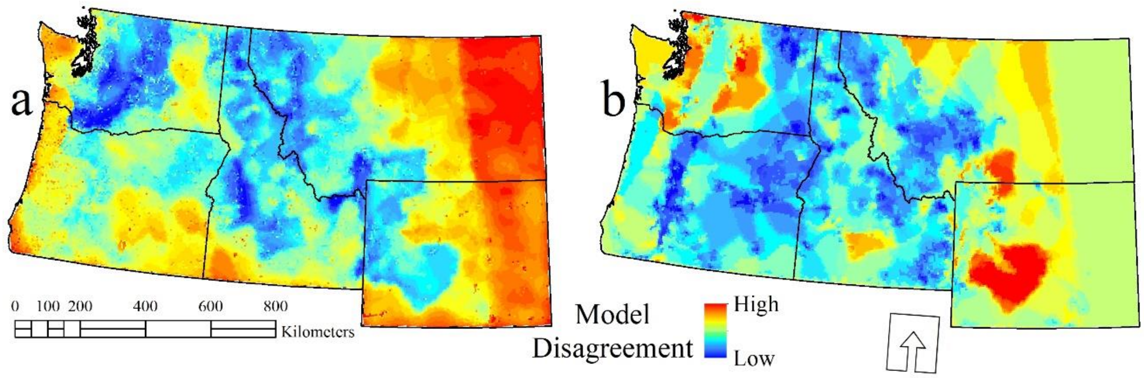

Figure 4.5 Areas of disagreement between a) the A&E and E models to determine the impact of the anthropogenic variables, and b) the E and C models to determine the impact of the additional ecological variables on connectivity. In both maps, red areas represent where model disagreement is highest and blue areas represent areas where model disagreement is lowest.

Table 4.2 Proportion of the highest priority areas (values > 0.9; range 0 to 1) in cores (high-quality wolverine habitat); conservation easements (CE); Forest Service land (FS); Fish and Wildlife Service land (FWS); Bureau of Land Management land (BLM); National Park Service land (NPS); and United States Department of Agriculture, Department of Energy, Department of Defense, Bureau of Reclamation (Other) for the whole study area, the anthropogenic and ecological model, the ecological only model, and the connectivity model.

Proportions	Cores	CE	FS	FWS	BLM	NPS	Other
Whole Study Area	0.15	0.01	0.25	0.01	0.16	0.02	0.01
Anthropogenic and Ecological	0.74	0.00	0.60	0.00	0.06	0.00	0.00
Ecological	0.70	0.02	0.70	0.00	0.02	0.02	0.00
Connectivity	0.45	0.00	0.62	0.00	0.05	0.05	0.00

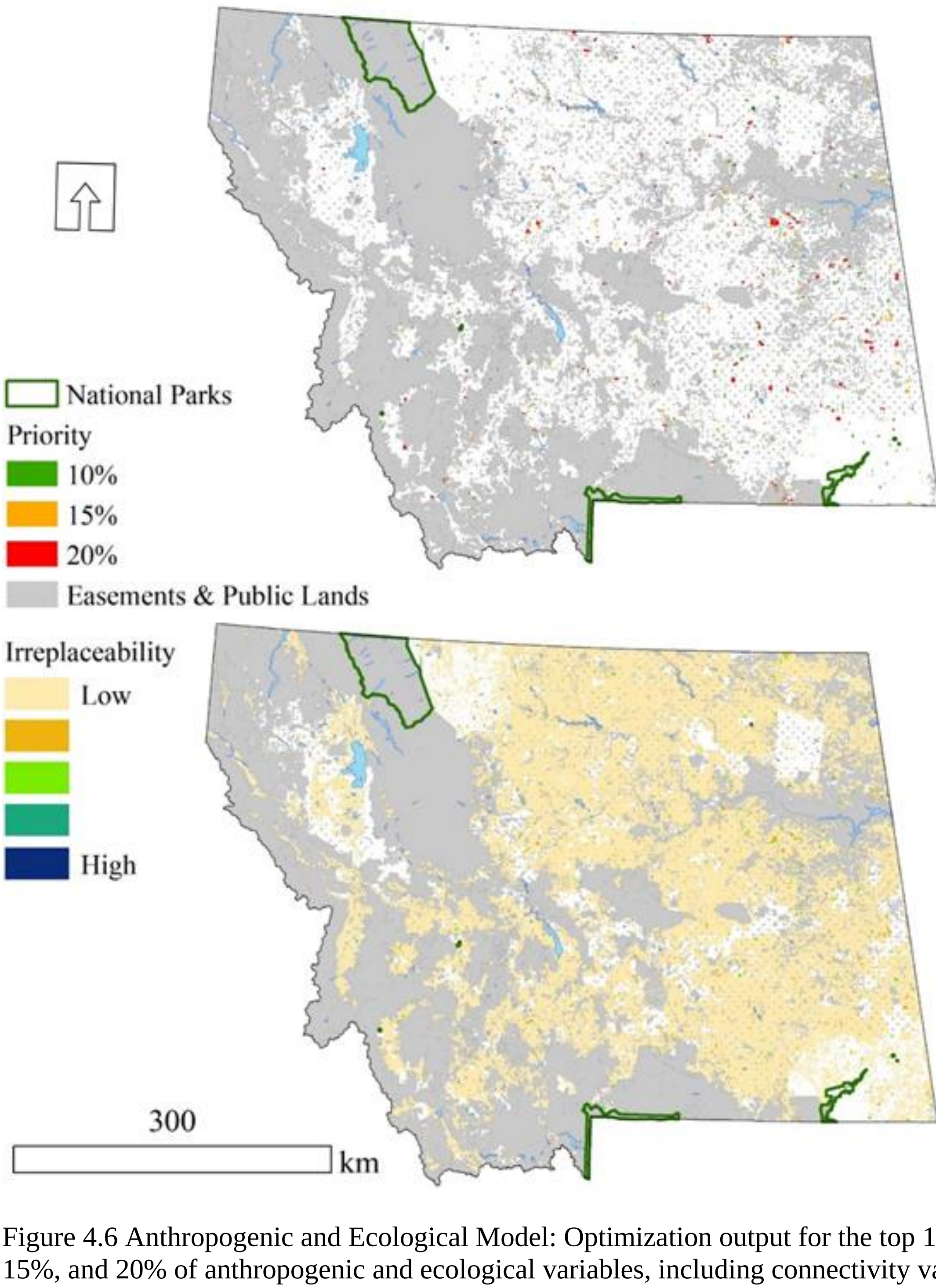

Figure 4.6 Anthropogenic and Ecological Model: Optimization output for the top 10%, 15%, and 20% of anthropogenic and ecological variables, including connectivity value, road density, core size, housing in 2010, genetics, housing conversion from 2010 to 2050, and centrality of linkages (top). The irreplaceability values are also presented (bottom).

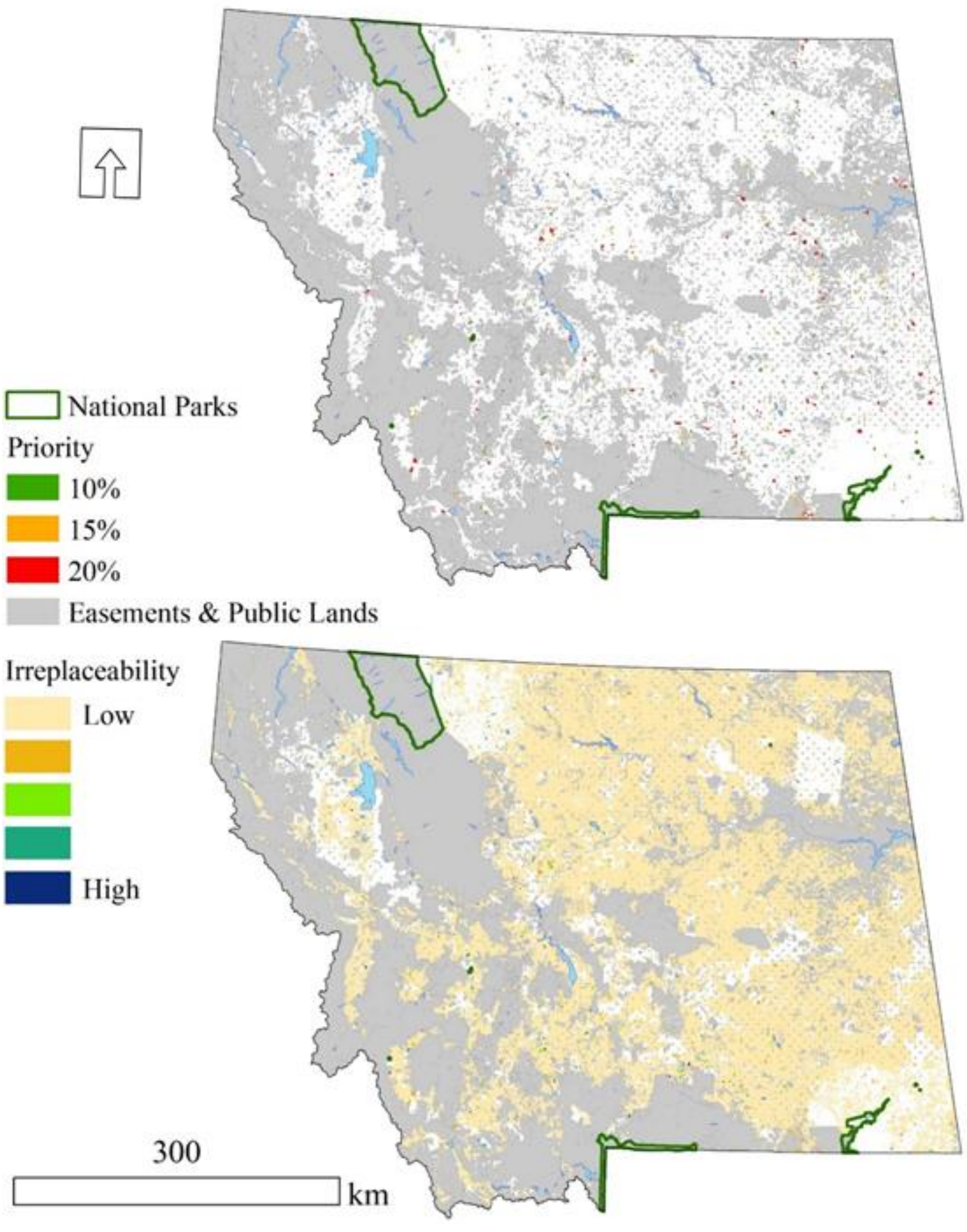

Figure 4.7 Ecological Model: Optimization output for the top 10%, 15%, and 20% of ecological variables, including connectivity value, core size, genetics, housing and centrality of linkages (top). The irreplaceability values are also presented (bottom).

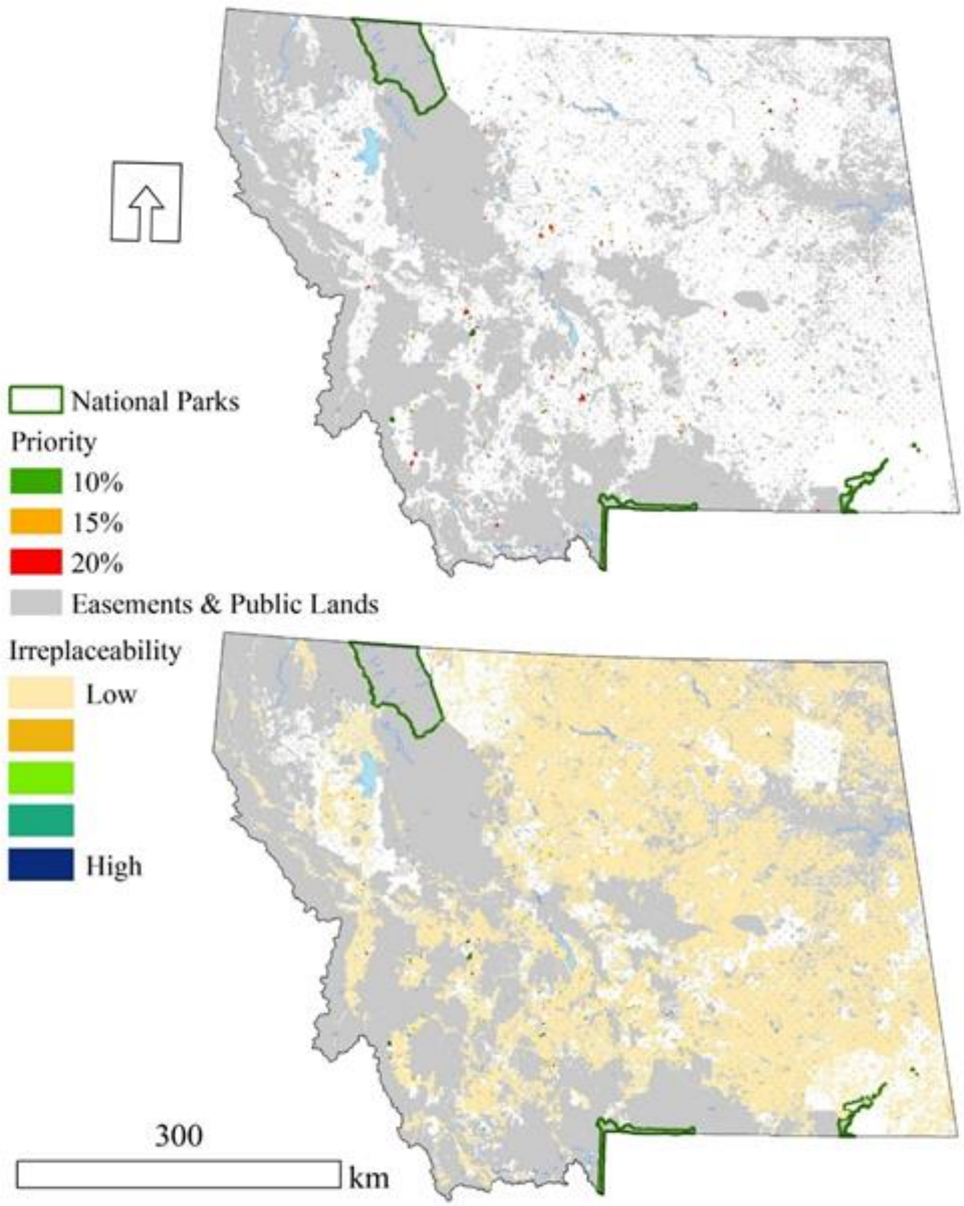

Figure 4.8 Connectivity Model: Optimization output for the top 10%, 15%, and 20% of connectivity (top). The irreplaceability values are also presented (bottom).

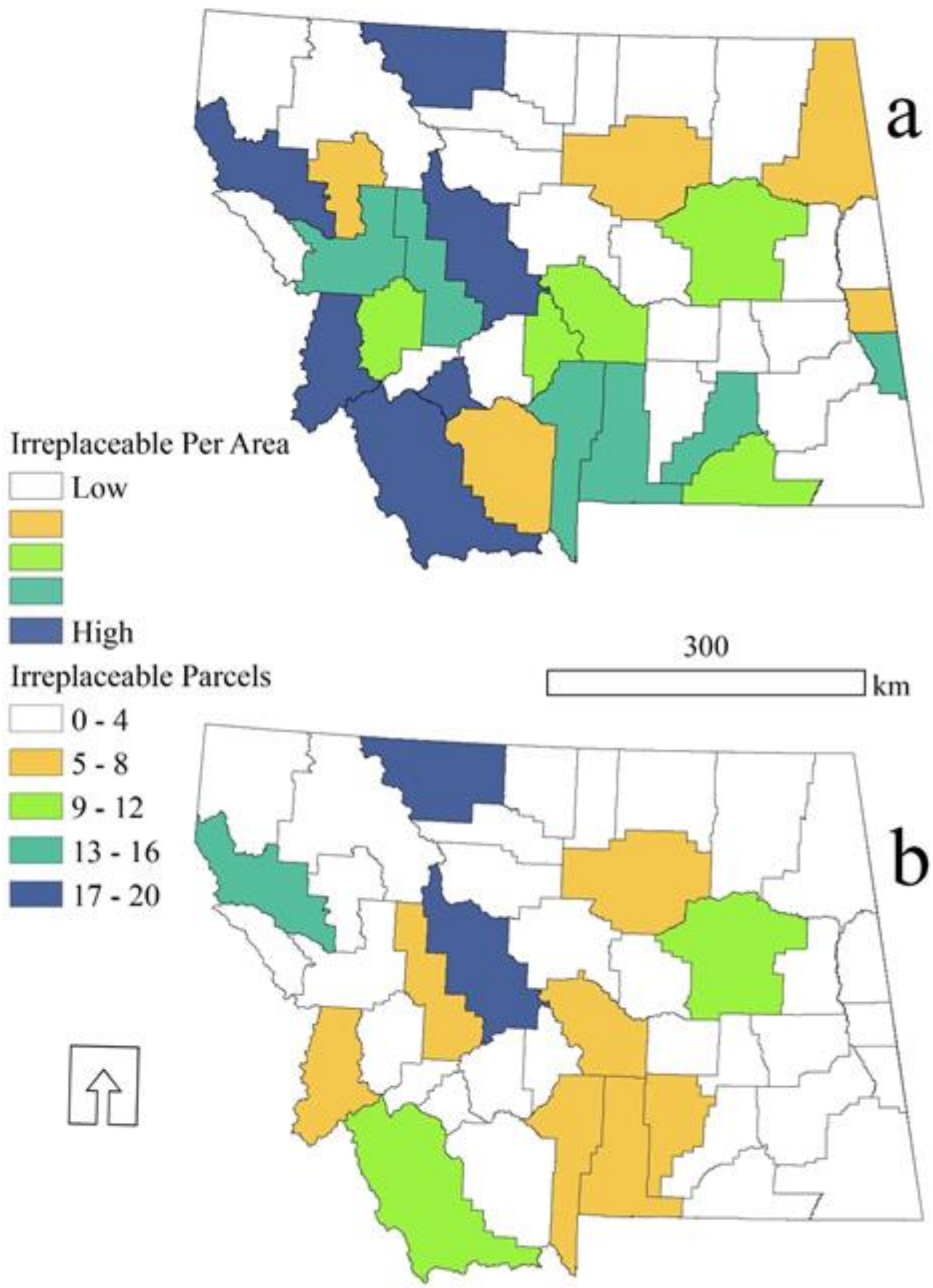

Figure 4.9 The number of irreplaceable parcels in each Montana counties by a) area of private land and b) counts.

Table 4.3 Number of parcels identified as important by the optimization framework in each model output.

Optimization Framework	Number of Parcels		
	10%	15%	20%
Anthropogenic and Ecological	364	548	732
Ecological	328	494	661
Connectivity	286	432	576

Table 4.4 Counties in each set of models with the highest number of identified parcels per area of private land and highest count values. Highest parcel values were averages across the 10, 15, and 20% models.

Per Area			
Anthropogenic and Ecological	Ecological Only	Connectivity Only	Rank
Mineral	Mineral	Mineral	1
Ravalli	Ravalli	Ravalli	2
Carbon	Carbon	Silverbow	3
Rosebud	Gallatin	Gallatin	4
Treasure	Stillwater	Jefferson	5
Count			
Anthropogenic and Ecological	Ecological Only	Connectivity Only	Rank
Cascade	Cascade	Cascade	1
Lincoln	Lincoln	Gallatin	2
Toole	Carbon	Yellowstone	3
Carbon	Toole	Fergus	4
Hill	Hill	Lewis and Clark	5

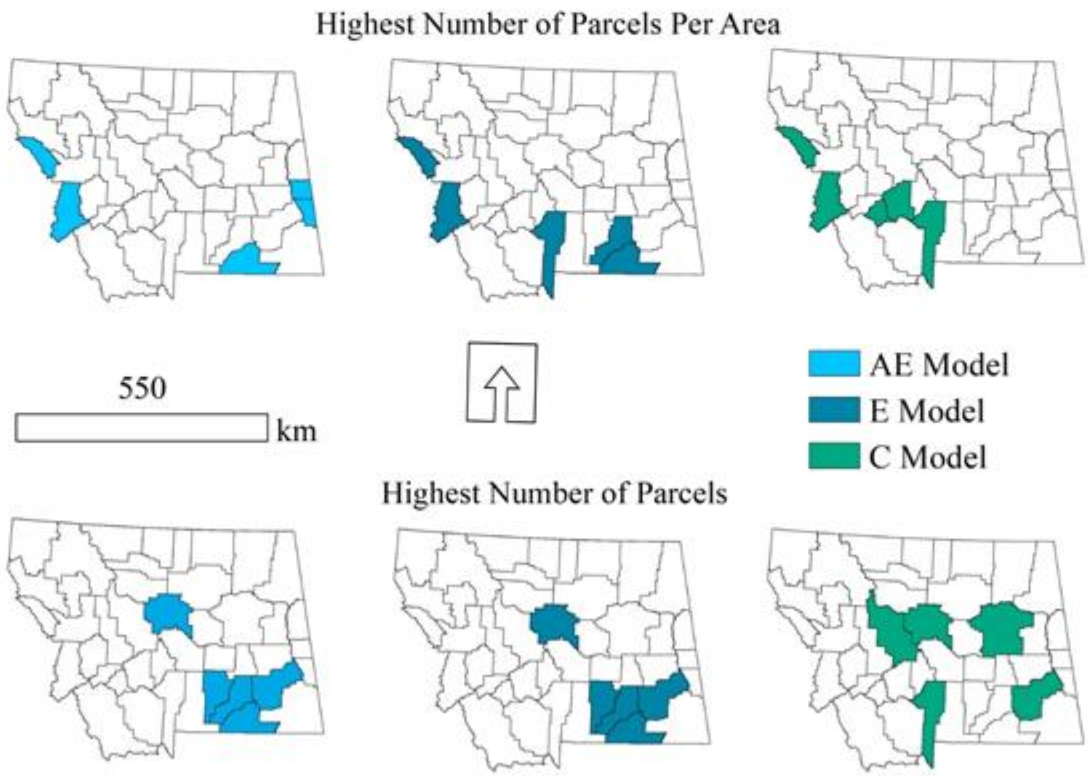

Figure 4.10 Counties with the highest number of parcels per area (top) and the highest parcels numbers (bottom) for the anthropogenic and ecological model (A&E), the ecological only model (E), and the connectivity only model (C).

CONCLUSIONS AND FUTURE DIRECTIONS

> “She asked another question: ‘What does it matter if the rhinos die out? Is it really important that they are saved?’
>
> ‘..to be honest, it doesn't matter. No economy will suffer, nobody will go hungry, no diseases will be spawned. Yet there will never be a way to place a value on what we have lost. Future children will see rhinos only in books and wonder how we let them go so easily. It would be like lighting a fire in the Louvre and watching the Mona Lisa burn. Most people would think 'What a pity' and leave it at that while only a few wept.’”
>
> — Peter Allison, Whatever You Do, Don't Run

> "If I have seen further, it is by standing upon the shoulders of giants"
>
> — Isaac Newton, Letter to Robert Hook

The original impetus for this work was to produce wolverine habitat and connectivity maps that could be used to generate a successful network of connected public-private lands and be shared with land trusts, landowners, and other partners. However, the results and implications of this work extend far beyond the initial goals of the project. The studies included herein represent the most comprehensive wolverine connectivity conservation analyses to date, and across these studies, several themes emerged.

One important conclusion I drew from this work was not to assume that commonly used approaches are the best or most appropriate for every question or focal species. The second and third chapters illustrate that common statistical approaches or assumptions in ecology do not always withstand the rigors of validation. There are many studies that justify the use of specific approaches or metrics based off of previous studies. However, this often precludes the consideration of alternative approaches and a defensible explanation of why that decision was made. It is important that every ecologist can justify their own reasoning for each decision. These studies allowed me the opportunity to practice questioning why methods were used and test alternatives.

Another important conclusion I drew from this work was that looking at fields outside ecology is critical for improving our understanding of ecology. Ecology is not a discipline that exists in isolation. Few, if any, ecologists today can succeed without understanding additional fields, especially statistics, and the greatest advances in scientific knowledge occur when ecologists learn about other disciplines (Kuhn 1962). Without some understanding of social science, economics, behavioral ecology, landscape ecology, and statistics, this work would not be possible. Diversifying beyond ecology can be done both through studying in other fields and collaborating with individuals from other disciplines. I think these two approaches are key to producing work that advances scientific knowledge. Relying on both knowledge from other fields and collaboration was critical in my approach to connectivity modeling.

Future Directions

One of the biggest challenges in connectivity modeling is making informed management decisions by validating output and comparing different methods. This research suggests that using multiple statistical approaches and validating results is a crucial step in ensuring rigorous and defensible conservation decisions for wolverines. Taken as a whole, this work provides land managers, policy makers, and scientists with guidance for future connectivity analyses and conservation action for wolverines, and it provides a research framework that can be applied to additional species of conservation concern in isolated populations.

Given the uncertainty of how climate and human land use change will impact species, identifying pathways that allow for species to move under changing conditions and allow gene flow across the landscape will be essential to the persistence of many species globally. In light of these challenges, I believe novel analyses and conservation approaches, alongside interagency collaboration, are essential to the protection of all levels of biodiversity and individual species. The statistically rigorous approaches I used herein should ensure that the land protections recommended are as useful and feasible as possible into the future. Moving forward, I firmly believe that without transdisciplinary efforts, clear communication, and collaboration with stakeholders conservation biology will not progress at the rate that is possible.

There are also many areas of scientific research where this connectivity conservation can be applied in potentially novel ways. One is in invasive species management. Modeling habitat and movement of invasive species provides insights into how we can predict sensitive areas at risk of invasion. For instance, the techniques I use could be applied to invasive wild boar (*Sus scrofa*) to determine where they may cause the most damage. This analysis could subsequently lead to conservation interventions before further destruction of at-risk habitats occur. This research is also applicable to disease transmission. Pathways of transmission could be predicted using some of the approaches in this work. One example is modeling how pneumonia is transmitted from captive nonnative sheep to protected and isolated bighorn sheep (*Ovis canadensis*) populations. A novel strand of pneumonia can lead to bacterial infections that decimate an entire cohort, or year of offspring, for a herd of bighorn sheep. By predicting where these animals are and their movement pathways, we could minimize the risk to native species. The techniques I used in this research, and similar techniques, are incredibly flexible and applicable across a wide range of scales from parcel level to landscape level analyses.

If researchers commit to finding rigorous, defensible, and collaborative conservation solutions, the future trajectories of many species could be improved. While these systematic conservation approaches have been somewhat neglected in ecology, there is a growing number of scientists recognizing that using systematic conservation planning and continuously questioning and validating methods and results are essential to conservation research implemented in conservation solutions.

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APPENDIX A

SUPPLEMENTAL TABLES

Table S1. Type, source, relevance, predicted association, and resolution of all variables used in the 2000-2010 resource selection function analysis to determine high-quality habitat and connectivity models.

Habitat Covariate Type	Covariate	Relevance	Predicted Association	Spatial Resolution	Source
Human Land Use	Housing Density	Human avoidance	-	30 m	Theobald 2005
Geomorphology	Latitude Adjusted Elevation	Low temperature and alpine meadows for prey; caching behavior	+	30 m	Brock & Inman 2006
	Landforms	Categorical; certain terrain should indicate advantageous thermal features, presence of prey, and structure	+	100 m	Land Facet*
	Distance to High-Elevation Talus	Farther from familiar feature and feature that may provide food source	-	30 m	Inman et al. 2013
Snow	Snow Water Equivalent	Competition benefit – wolverine move over snow better than competition and can avoid predators, however too much snow could mean a lack of prey. Indicative of lower temperatures and shorter growing season where have competitive advantage	+	1 km	Integrated Scenarios Group**
Vegetation	Land Cover	Alpine meadow/grassland for prey; cliff, talus, and rock and veg for denning or caching	+	30 m most areas	Conservation Biology Institute***

* https://adaptwest.databasin.org/pages/adaptwest-landfacets **https://climate.northwestknowledge.net/IntegratedScenarios/ ***https://consbio.org/

Table S2. Levels of categorical variables, including landform (LandFacet) and vegetation (Conservation Biology Institute used in Chapter 2.

Variable	Category Identifier	Categories
Landform	Value	Type
	1000	Valley
	2000	Hilltop in Valley
	3000	Headwaters
	4000	Ridges and Peaks
	5000	Plains
	6000	Local Ridge in Plain
	7000	Local Valley in Plain
	8000	Gentle Slopes
	9000	Steep Slopes
Vegetation	Value	Type
	0	Undefined
	1	Barren
	2	Tundra
	3	Taiga Tundra
	4	Conifer Forest
	5	Cool Mixed Forest
	6	Deciduous Forest
	7	Warm Mixed Forest
	8	Topical Broadleaf Forest
	9	Woodland/Savannah
	10	Scrubland/Woodland
	11	Grassland

Table S3. Type, source, relevance, predicted association, and resolution of all variables possibly considered for the 2000-2010 resource selection function analysis. Any variable with a * is listed twice, once with a potential predicted positive association and once with a potential predicted negative association.

Habitat Covariate Type	Covariate	Relevance	Predicted Association	Spatial Resolution	Source
Human Land Use	Strava Recreation	Behavioral changes linked to backcountry recreation in Heinemeyer et al. 2019	-	Unknown	STRAVA LABS
	Road Density*	Avoid roads to avoid human and predators that use roads (wolves)	-	30 m	TIGER/Line, US Census
	Road Density*	More efficient travel in winter on less frequently used roads (most roads in wolverine habitat)	+	30 m	TIGER/Line US Census
	Housing Density	Human avoidance; farther from familiar features; behavioral shifts in human used habitat	-	30 m	Bierwagen et al. 2010
	Landscape Integrity	Continuous habitat; intact systems with predators to produce carrion and prey variety	+	90 m	Theobald 2013; USGS (Homer et al 2011)
	Land Cover*	Human avoidance; farther from familiar features; behavioral shifts in human modified habitat (using disturbed	-	30 m	National LC Dataset; GAP LC/ecosystem classification

Habitat Covariate Type	Covariate	Relevance	Predicted Association	Spatial Resolution	Source
		or agricultural classes)			
	Interpolated human density	Human avoidance; behavioral shifts in human used habitat	-	30 m	TIGER/Line, US Census
Geomorphology	Latitude Adjusted Elevation	More low temperature and alpine meadows for prey; caching behavior	+	100 m 30 m	Land Facet Brock & Inman 2006
	Landforms	Categorical landform type, certain terrain (i.e. ridges and peaks) should indicate advantageous thermal features, presence of prey, and structure	+	100 m	Land Facet
	Terrain Ruggedness Index	Similar to landforms	+	30 m	Evans 2004
	High-elevation talus	More cold, rocky terrain, denning and caching structures more common; marmots	+	30 m	Inman 2013
	Distance to HET	Farther from familiar feature	-	30 m	Inman 2013
	Soil Order (or parent material)	Coarse filter of habitat for prey? Such as high-elevation meadows? May only be important in combination with LAE or Landforms	+	1 km	Land Facet

Habitat Covariate Type	Covariate	Relevance	Predicted Association	Spatial Resolution	Source
Climate	Modified Heat Load Index	More lower temperatures	+	100 m	Land Facet
	Cold Day Index	Less cold days could negatively influence kits during early denning (melting at dens when young could lower survival of young) and more cold days could impact plants leading to fewer food resources for prey	-	800 m	NOAA
	PPT	Increase in prey in summer; caching locations in winter?	+	800 m	PRISM
Snow	Distance to April 1 Snow > 2.5 cm	Further from habitat for caching/ distance to food storage; further from potential competitive advantage	-	1 km	Barrett 2003 NOAA SNODAS, NOHRSC 2004
	SWE	Competition benefit – wolverine move through snow better than competition and can avoid predators, however too much snow could mean a lack of prey.		800 m	NASA TOPS, NOAA SNODAS; Integrated Scenarios Group

Habitat Covariate Type	Covariate	Relevance	Predicted Association	Spatial Resolution	Source
	Snow Melt	Further from habitat for caching; distance to food storage;		800 m	NOAA SNODAS, NOHRSC 2004
	Snow Cover	Familiar feature, cooler temperatures, and potential reduction in competition/predators		800 m	NOAA SNODAS, NOHRSC 2004
	Average snow depth	Deep snow reduces large carnivores	+	800 m	NOAA SNODAS, NOHRSC 2004
Vegetation	Tree Cover	Escape cover from predators; potentially den structure	+		Homer et al. 2001
	NDVI	Increased prey abundance (maybe more competition?)	+	250 m	Robinson et al. 2017; Landsat
	Seasonality (GPP/annual GPP)	Is there a balance between prey abundance and limited competition for food?	+		MODIS or Robinson et al. 2017; Landsat
	Inter-annual variation in GPP	Potentially informs us about variability in prey (may be a lag year)		250 m	Robinson et al. 2017; Landsat
	Land Cover* aka Forest type and variation	Alpine meadow/grassland for hunting; cliff, scree, and rock veg for denning or caching	+	30 m most areas	GAP USGS; Conservation Biology Institute

Habitat Covariate Type	Covariate	Relevance	Predicted Association	Spatial Resolution	Source
	Distance to tree cover*	Access to prey (alpine meadows, talus fields)	+	30 m	2006 National Land cover database
	Distance to tree cover*	No escape cover from predators; further from familiar feature	-	30 m	2006 National Land cover database
	Forest Edge	Access to more prey (i.e., marmots)	+	30 m	GAP USGS
	Disturbance Vegetation Transition magnitude	Access to small prey, predator avoidance, ease of travel	+	30 m	LandFire
	Existing Vegetation Type	More trees = familiar feature, escape cover and potential areas for prey (meadows) ; potentially den structure	+	30 m	LandFire
	Existing Vegetation Height	Predator avoidance; potentially den structure	+	30 m	LandFire

Table S4. List of all levels in categorical variables, including landform (LandFacet), vegetation (Conservation Biology Institute), and human land use (Theobald 2005, Bierwagen et al. 2010).

Variable	Category Identifier	Categories
Landform	Value	Type
	1000	Valley
	2000	Hilltop in Valley
	3000	Headwaters
	4000	Ridges and Peaks
	5000	Plains
	6000	Local Ridge in Plain
	7000	Local Valley in Plain
	8000	Gentle Slopes
	9000	Steep Slopes
Vegetation	Value	Type
	0	Undefined
	1	Barren
	2	Tundra
	3	Taiga Tundra
	4	Conifer Forest
	5	Cool Mixed Forest
	6	Deciduous Forest
	7	Warm Mixed Forest
	8	Topical Broadleaf Forest
	9	Woodland/Savannah
	10	Scrubland/Woodland
	11	Grassland
Human Land Use	Value	Type
	1	Undeveloped
	2	<1.5 units/square km
	3	1.5-3 units/square km
	4	4-6 units/square km
	5	7-12 units/square km
	6	13-24 units/square km
	7	25-49 units/square km
	8	50-145 units/square km
	9	146-494 units/square km
	10	495-1234 units/square km
	11	1235-2470 units/square km
	12	> 2470 units/square km
	13	Commercial/Industrial

1nd Order

Table S5. Rank of first-order standardized beta coefficients for male (n = 13153) and female individuals (n = 11976). Negative estimate values indicate selection for lower values of the covariate. Ranks are based on the absolute value of the standardized coefficient (estimate). For both sexes, the variable name, estimate, and standard error (SE) are provided.

Male			Female			Variable
Variable	Estimate	SE	Variable	Estimate	SE	Rank
SWE	55.98	3.84	SWE	55.60	3.92	1
SWE^3	51.08	3.68	LAE2	17.30	3.61	2
LAE^3	33.40	3.96	LAE	-11.34	5.09	3
LAE	32.26	5.66	SWE2	10.77	3.49	4
SWE^2	31.79	3.61	SWE3	6.90	3.41	5
VEG11	-2.93	0.18	VEG11	-2.41	0.19	6
LANDF4	-1.83	0.07	VEG10	-2.09	0.12	7
LANDF3	-1.80	0.10	LANDF5	-2.07	0.11	8
VEG10	-1.64	0.09	LANDF8	-1.86	0.14	9
LANDF2	-1.58	0.13	LANDF4	-1.82	0.07	10
LANDF7	-1.52	0.08	LANDF7	-1.77	0.07	11
LANDF9	-1.51	0.11	LANDF3	-1.76	0.09	12
LANDF6	-1.50	0.08	LANDF6	-1.66	0.08	13
LANDF1	-1.49	0.06	LANDF2	-1.65	0.13	14
VEG2	-1.47	0.29	LAE3	-1.58	2.97	15
LANDF5	-1.40	0.09	LANDF1	-1.54	0.06	16
VEG4	-1.33	0.06	LANDF9	-1.53	0.11	17
LANDF8	-1.11	0.11	VEG4	-1.44	0.06	18
DHITAL	-0.98	0.04	DHITAL	-1.38	0.07	19
LAE^2	-0.57	4.09	VEG2	-0.59	0.26	20
HOUSE	0.11	0.03				21

Table S6. Caret package logistic regression importance for the first-order for male (n = 13153) and female models (n = 11976).

Males		Females		Overall Variable Rank
Variable	Overall Variable Importance	Variable	Overall Variable Importance	
DHITAL	22.56	DHITAL	19.93	1
SWE^3	14.26	SWE	14.44	2
SWE	14.21	LAE^2	5.12	3
SWE^2	8.40	LANDF5	4.90	4
LAE^3	7.47	VEG11	4.86	5
LAE	5.34	VEG10	4.38	6
LANDF8	4.38	SWE^2	3.17	7
HOUSE	4.19	VEG4	2.84	8
LANDF4	3.81	LANDF7	2.65	9
VEG11	2.98	SWE^3	2.63	10
LANDF3	2.95	LANDF4	2.48	11
VEG4	1.86	LANDF3	2.35	12
LANDF5	1.74	LANDF8	1.88	13
LANDF2	0.31	LAE	1.60	14
VEG10	0.28	LANDF6	0.65	15
LAE^2	0.20	LANDF2	0.32	16
LANDF9	0.13	LAE^3	0.29	17
LANDF7	0.10	LANDF9	0.14	18
LANDF6	0.08			19

Table S7. Pseudo R-squared values for the first-order analysis. In this output, McFadden represents McFadden's pseudo R-squared, r2ML represents maximum likelihood pseudo R-squared, and r2CU represents Cragg and Uhler's pseudo R-squared (Long 1997). For each pseudo R-squared, higher value represent indicating better model fit but should not be interpreted in the same way as traditional R-squared values.

	Males			Females		
Variables	McFadden	r2ML	R2CU	McFadden	r2ML	R2CU
DHITAL	0.1151	0.1221	0.1802	0.120	0.1264	0.1870
SWE	0.1045	0.1115	0.1646	0.079	0.0851	0.1259
LAE	0.0871	0.0939	0.1386	0.0736	0.0795	0.1177
VEG	0.0681	0.0751	0.1108	0.0488	0.0535	0.0792
LANDF	0.0237	0.0237	0.0391	0.044	0.0481	0.0711
HOUSE	0.0180	0.0212	0.0297	0.010	0.0114	0.0169

Table S8. Variable importance randomForest from both the importance function in the caret package (Caret) and the randomForest package (RF).

Males				Females				Overall
Variable	Caret	Variable	RF	Variable	Caret	Variable	RF	Variable Rank
DHITAL	68.54	SWE	991.37	DHITAL	57.55	SWE	951.20	1
SWE	57.10	DHITAL	564.90	SWE	56.88	DHITAL	486.63	2
LAE	46.11	LAE	487.38	LAE	32.56	LAE	426.58	3
LANDF	27.87	LANDF	165.80	LANDF	20.84	LANDF	140.73	4
HOUSE	26.06	VEG	68.43	HOUSE	14.79	VEG	37.12	5
VEG	18.50	HOUSE	50.20	VEG	11.54	HOUSE	27.90	6

Table S9. Rank of standardized beta coefficients for male and female individuals from the third-order analysis. Negative estimate values indicate selection for lower values of the covariate. Ranks are based on the absolute value of the standardized coefficient (estimate).

Male			Female			Variable
Variable	Estimate	SE	Variable	Estimate	SE	Rank
SWE	58.18	5.40	LAE	47.34	5.71	1
SWE^2	-21.21	5.03	SWE	29.82	4.59	2
LAE	9.94	6.73	LANDF6	-18.31	332.47	3
LAE^2	-6.71	5.50	LANDF5	-16.57	527.75	4
LANDF6	-5.32	0.72	SWE2	-13.58	4.43	5
SWE^3	-4.88	3.64	LAE3	-5.17	3.57	6
LANDF7	-4.87	0.51	LANDF7	-4.78	0.51	7
LANDF5	-3.96	1.01	LAE2	4.63	4.81	8
LANDF4	-2.71	0.14	SWE3	-4.41	3.54	9
LAE^3	-2.62	4.49	LANDF8	-2.86	1.02	10
LANDF3	-2.44	0.19	LANDF4	-1.84	0.10	11
LANDF2	-2.14	0.24	LANDF3	-1.82	0.14	12
LANDF8	-2.12	0.45	LANDF2	-1.64	0.21	13
LANDF1	-2.04	0.12	HOUSE	-1.42	0.56	14
DHITAL	-0.83	0.10	LANDF1	-0.99	0.09	15
LANDF9	-0.43	0.16	DHITAL	-0.37	0.09	16
HOUSE	-0.29	0.16	LANDF9	0.21	0.14	17

Table S10. Caret package logistic regression importance for the third-order for male (n = 13153) and female models (n = 11976).

Males		Females		Overall Variable Rank
Variable	Overall Variable Importance	Variable	Overall Variable Importance	
SWE	11.11	LAE	8.53	1
LANDF9	9.35	LANDF9	7.47	2
DHITAL	7.94	LANDF7	7.06	3
LANDF7	5.48	LANDF4	7.03	4
SWE^2	4.85	SWE	6.70	5
LANDF6	4.68	LANDF3	4.87	6
LANDF4	3.59	DHITAL	3.54	7
LANDF5	1.87	SWE^2	3.40	8
LANDF3	1.70	LANDF2	3.24	9
LAE	1.14	HOUSE	2.45	10
LAE^2	0.61	LAE^3	2.26	11
LANDF2	0.48	LAE^2	1.23	12
LAE^3	0.44	SWE^3	0.91	13
LANDF8	0.30	LANDF6	0.05	14
SWE^3	0.18	LANDF5	0.03	15
		LANDF8	0.02	16

Table S11. Pseudo R-squared values for the third-order analysis. In this output, McFadden represents McFadden's pseudo R-squared, r2ML represents maximum likelihood pseudo R-squared, and r2CU represents Cragg and Uhler's pseudo R-squared (Long 1997). For each pseudo R-squared, higher value represent indicating better model fit but should not be interpreted in the same way as traditional R-squared values.

	Males			Females		
Variables	McFadden	r2ML	R2CU	McFadden	r2ML	R2CU
LAE	0.0732	0.0587	0.1044	0.1260	0.1331	0.1963
VEG	0.0317	0.0317	0.0563	0.0494	0.0545	0.0803
DHITAL	0.1092	0.0864	0.1535	0.0595	0.0653	0.0962
SWE	0.1379	0.1078	0.1916	0.1110	0.1183	0.1744
HOUSE	0.0167	0.0137	0.0244	0.0257	0.0288	0.0428
LANDF	0.1397	0.1091	0.1939	0.1448	0.1515	0.2233

Table S12. Variable importance randomForest from both the importance function in the caret package (Caret) and the randomForest package (RF).

Males				Females				Overall
Variable	Caret	Variable	RF	Variable	Caret	Variable	RF	Variable Rank
SWE	19.00	SWE	131.09	SWE	31.45	LAE	218.23	1
DHITAL	13.77	LAE	123.04	LAE	29.12	SWE	217.71	2
LAE	10.06	DHITAL	114.75	DHITAL	20.40	DHITAL	158.53	3
VEG	4.63	LANDF	30.12	LANDF	7.78	LANDF	45.17	4
LANDF	2.59	VEG	6.45	VEG	7.34	VEG	11.60	5
HOUSE	0.41	HOUSE	1.61	HOUSE	1.62	HOUSE	1.64	6