USING COST SURFACE ANALYSIS AND LEAST COST PATHS TO ANALYZE DISPERSAL OF GRAY WOLVES IN THE NORTHERN ROCKIES, U.S.A.

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ABSTRACT

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The recent delisting of gray wolves (*Canis lupus*) in the Northern Rockies region marks a change in the management scheme employed by state wildlife agencies. The wolf population in this region has expanded rapidly since its reintroduction in 1994 and has reached sufficient size to merit removal from the federal list of threatened and endangered species. The following study employs cost surface analysis to model wolf movements across the Northern Rockies region. An examination of wolf habitat selection in the region allows for the development of a friction surface by assigning different friction values to several landscape variables (land cover class, slope, and proximity to roads). This friction surface serves as the basis for the creation of least cost paths between known wolf territories. Buffers around these paths highlight areas of especial importance for wolf movements through the region. This model is corroborated by comparing the landscape variables in the paths and the buffered areas with known wolf habitat selection. The study found that the least cost paths closely mirrored wolf habitat selection. From the least cost paths, the study concludes that a regional perspective on wolf management will benefit the species as dispersal routes often cross political boundaries.

I. BACKGROUND INFORMATION

The Northern Rocky Mountain region is once again home to a healthy, thriving population of gray wolves (*Canis lupus)*. These creatures once thrived across the entire planet, second in extent only to *Homo sapiens* (Mech and Boitani, Wolf Social Ecology 2003). Over millennia, however, habitat destruction and persecution extirpated these creatures from a vast portion of their historic ranges. Particularly in the contiguous United States, wolves were almost entirely purged. Over the past forty years the federal government has made strides to protect the last remaining wolves and reintroduce populations to their former ranges (U.S. Fish and Wildlife Service 1987).

Wolves are a highly adaptable species, which has allowed them to spread nearly as far across the globe as humans. Typically standing a meter tall and weighing up to 70 kg, wolves are highly efficient predators. In the Northern Rockies region their diet consists mostly of elk, but they also hunt deer, bison, and moose. Their diet is, however, highly adaptable when needed; wolves consume creatures "that range in size over three orders of magnitude, from 1 kg snowshoe hares up to 1,000 kg bison" (Peterson and Ciucci, The Wolf as a Carnivore 2003).

Wolves are social creatures and live in packs typically consisting of a breeding pair and their offspring. Packs can range from two individuals up to twenty, although most packs consist of four to seven wolves. New packs are formed through dispersal of adolescent wolves out of their natal territories. Dispersing wolves occasionally travel hundreds of kilometers in order to find mates and carve out territories to form new packs. Wolves are highly territorial and will defend their home ranges vigorously from incursion by other wolves or packs (Mech and Boitani, Wolf Social Ecology 2003).

Wolves' opportunistic hunting strategies have been the cause of their conflict with humans. Wolves have taken livestock since the earliest days of domestication, but eventually humans reached a level of technology that led to a wholesale slaughter of predators. During the late 19^{th} and early 20^{th} centuries, the federal government began a massive eradication campaign to rid the West of wolves. Ranchers, hunters, and wildlife managers laced countless carcasses with strychnine to hopefully kill a scavenging wolf. By 1930, no wolves remained in the Northern Rockies, and for six decades no howls were heard in Yellowstone National Park (Mech and Boitani, Wolf Social Ecology 2003).

The passage of the Endangered Species Act (1974) changed the face of wildlife management, and wolves were one of the first species to be protected by this landmark legislation. Still, wolves were not seen for thirteen more years after they were protected, until a pack dispersed into Glacier National Park from Canada. Natural recovery is a slow process and the Fish and Wildlife Service decided to implement a reintroduction program for the region. In 1994, the Fish and Wildlife Service submitted their final plan, and in 1994 and 1996 they released 35 wolves into central Idaho and Yellowstone National Park. The Fish and Wildlife Service planned a minimum population of 300 individuals and 30 breeding pairs across the states of Montana, Wyoming, and Idaho for at least three consecutive years (U.S. Fish and Wildlife Service 1987).

Fish and Wildlife achieved this goal in 2003, but was cautious in moving to delist wolves (C. Sime, V. Asher and L. Bradley, et al. 2011). The first attempts to remove wolves from federal protection were met with criticism and litigation from environmental groups, who wished FWS to wait until the wolf population had grown beyond the minimum required level. By 2009, nearly 2000 wolves inhabited the region (C. Sime, V. Asher and L. Bradley, et al. 2011).

Current Legal Status of Wolves

Wolves have held a tenuous legal status since their reintroduction to the Northern Rockies. The original recovery plan required a minimum population of 300 individuals and thirty breeding pairs evenly distributed across the states of Montana, Idaho and Wyoming for three consecutive years. This goal was achieved in 2002, but delisting has faced litigation every time it has been proposed. The Fish and Wildlife Service and the state governments in the Northern Rockies attempted in 2003 and again in February 2008 to remove the gray wolf from the Endangered Species List and place them under state management. Both of these actions were overturned. On March 28, 2008 the gray wolf was removed from the endangered species act in the Northern Rockies. Exactly one month later, a coalition of conservation groups filed an injunction with the U.S. district court in Montana. They argued that the existing state plans did not provide adequate protection for wolves by guaranteeing genetic variation and did not provide any particular advantages over federal rules (Molloy 2008).

In the final days of his administration, President George W. Bush pushed legislation to remove wolves from the Federal Register of endangered species in these two states, but leave them under federal protection in Wyoming due to inadequate protection in that state. The Obama administration and new Secretary of the Interior, Ken

Salazar, halted the delisting before it could be written into the Federal Register in January. Ultimately, the Department of the Interior went forward with delisting wolves in Montana and Idaho, but this too was met with resistance from conservation groups. These groups filed another injunction to re-list wolves across the entire Northern Rockies region, arguing that the wording of the Endangered Species Act requires that a population be managed in its regional context, and that the population across the entire region must have the same legal status (C. Sime, V. Asher and L. Bradley, et al. 2011). The Fish and Wildlife Service was ultimately able to reach an agreement with conservation groups and move forward with delisting in Montana and Idaho, despite Wyoming's reticence, citing the wolf population's status as "experimental, non-essential." Wyoming did finally submit to FWS's requirements and developed a new management plan, and wolves are now delisted across the entire region (Wyoming Game and Fish Commission 2011). Starting at the end of 2012, wolves will be fully protected in Yellowstone and Grand Teton National Parks. In the Bridger National Forest, Gros Venture Wilderness Area, and the Wind River Tribal Land, however, wolves will be subject to seasonal hunting. Outside of these areas, wolves will be classified as a "predatory species," subject to hunting year round without permits or licenses (Wyoming Game and Fish Commission 2011).

II. PROBLEM STATEMENT

The conflict outlined above illustrates the difficulty in managing wolves in a regional context. The different management agendas of each of the states will have different effects on their respective wolf populations. In particular, Wyoming's different legal designations of wolves in different parts of the state will severely restrict their movements outside of national parks and the Wind River Reservation (Wyoming Game and Fish Commission 2011). Dispersal patterns across the region will be affected as wolves moving from one state to another will now face different legal conditions. Hunting quotas in one state or more stringent protections in another will affect survivorship across the region. Predators are more sensitive to hunting than many ungulate species, and hunting will have a greater impact on their pack structure and demographic features (Haber 1996). For this reason, it is important to measure the level of connectivity across the region to build understanding of the potential dispersal of wolves between the three states. All three states are individually committed to wolf survival, but managing a regional population in three distinct segments could lead to a lack of genetic exchange if precautions are not taken. Understanding the region's landscape and how this affects potential wolf dispersal will be instrumental in states' management efforts.

To this end, the construction of a potential dispersal map for gray wolves within the region will enhance this understanding. To model diffusion, Cost Surface Analysis

(CSA) has received special attention with the advent of GIS tools as it allows researchers to create a landscape model to map the movement of a subject across a landscape. CSA is a highly adaptable method that can be applied to highly variable landscapes and for many different subjects. The present study used CSA to develop a map of potential dispersal routes of wolves across the Northern Rockies states of Montana, Idaho, and Wyoming. CSA analyzes a landscape by creating a model based on how a subject, in this case wolves, uses or reacts to landscape features such as land cover, slope, or exposure to humans. Researchers can assign friction values to any type of landscape variable and combine each type to develop a cost value for each point across a landscape. These cost values, when aggregated across the entire study area, make up a friction surface that provides an analysis of the permeability of a landscape from the point of view of the target creature.

III. OBJECTIVES

This project aimed to develop a cost-surface map of the Northern Rockies region for wolf dispersal. By combining data on land cover and land use with biological features of *Canis lupus*, this project examines the how wolf habitat use and dispersal patterns can be :

1. Constructed using a cost surface model using GIS and remotely sensed land cover/land use, and

2. Assessed with regard to the suitability of the cost surface model.

IV. JUSTIFICATION

This study has come at an important time for wolves. The recent delisting of wolves in the Northern Rockies is a testament to the effort put forth by wildlife managers, but must also proceed with caution. All three states will henceforth implement a wolf hunting season which represents a major shift in management agenda. Instead of managing wolves as a growing population, each state will instead manage the population at its current level. Thus, it becomes important to ensure the connectivity of wolf territories across the region. Research has repeatedly shown the importance of connectivity for a species' long term viability, yet habitat fragmentation continues to increase (Proctor, et al. 2005). The Northern Rockies landscape is dominated by humans, and wolves must adapt to proximity to their bipedal neighbors. Wolves' adaptability allows them to cross many geographic boundaries, but contact with humans remains the largest source of mortality (Colino-Rabanal, Lizana and Peris 2011). A cost surface approach has allowed me to analyze potential wolf dispersal across the Northern Rockies region, and has allowed me to incorporate not only physical landscape features but also anthropogenic dimensions. The anthropogenic features of the Northern Rockies play a large role in influencing wolf spatial patterns.

To date, wildlife agencies and other initiatives have not been able to compile such a model for *Canis lupus* in the Northern Rockies. This study is timely, because of the availability of newly created datasets. Datasets exist for wolf pack territories across the

Northern Rockies, compiled by state and federal wildlife agencies. Additionally, the U.S. Geological Survey compiled a new land cover dataset for North America in 2006, providing current information on land cover and land use. Furthermore, the Census Bureau makes available current road maps of the United States. Humans represent the biggest impediment to wolf movement and survival, so this project utilized roads as a proxy value for exposure to humans.

Intellectually, this study built upon former cost surface analyses by applying CSA to a larger scale than prior studies. The detailed spatial resolution that this study employed yielded accurate results spread across a wide range. It is my hope that this study will enhance the understanding of wolf spatial patterns for wildlife managers. CSA is a highly adaptable method, and this study can be expanded on with the inclusion of new wolf pack territories.

V. LITERATURE REVIEW

Because of their symbolic value, wolves have been the subject of a vast and diverse array of studies. Using a geographic lens, these studies can be divided into several categories including, but not limited to: history/philosophy, conflict management, habitat selection/resource use, and movement. Many biological studies have been published regarding wolves' taxonomic classification and genetics, but only those studies that use genetic information as a means to determine spatial distribution shall be cited within this paper. This study focused primarily on habitat selection, resource use, and movements, as these have the strongest bearing on developing a cost surface map.

Popular accounts of wolf biology and history include Never Cry Wolf by Farley Mowat and Of Wolves and Men by Barry Lopez. These works helped change the tide of public opinion more in favor of wolves by combining ecology and naturalist philosophy. Never Cry Wolf recounts the author's experiences studying wolves in the Canadian arctic, while Of Wolves and Men combines primary documents with contemporary research in wolves to portray a rich relationship between wolves and humans.

This study drew heavily from the experience and expertise of the giants in the field of wolf studies, including L. David Mech, Luigi Boitani, Edward Bangs, and many more. Their works have discovered many of the ecological characteristics of wolves. David Mech has studied wolves since before their protection under the Endangered Species Act. Early studies in the Great Lakes region described wolf habits and behavior.

(Mech, L. D. Frenzel, et al. 1971) Using a combination of aerial reconnaissance and radio tracking, Mech and his co-authors monitored wolf movements from 1964 through 1969. This study made several conclusions about wolf habits and how they were affected by environmental conditions and seasonality. They found wolves traveling more during winter, but their hunting success increased due to the inability of prey to escape. They also found evidence of wolves' social structure, citing that packs traveled across smaller territories than lone wolves. Also, they found that wolves traveled far during dispersal before mating season (Mech, L. D. Frenzel, et al. 1971, 31). A similar study a decade later corroborated these results and added more conclusions on wolf social structure, finding a negative correlation between wolf population density and pack territory size, but found no evidence to support a former assumption that pack membership also increased with population density (Fritts and Mech 1981).

Habitat Preferences

Habitat studies of wolves have shown that they are adaptable creatures that can thrive in a wide variety of habitats (Mladenoff, et al. 1995); however, statistical analysis revealed patterns in habitat selection. At a regional level, wolves tend to inhabit mixed conifer/deciduous forest (Mladenoff, et al. 1995; Jedrzejewski, et al. 2001; Oakleaf, et al. 2006). Working with wolves in the Great Lakes region, Mladenoff showed that mixed conifer/hardwood forest represented the largest land cover classification of wolf territories, 46.7 percent in pack territories versus only 18.1 percent in non-pack territories (Mladenoff, et al. 1995, 284). Keenlance (2002) found similar results in Wisconsin wolves, which he determined selected for forested wetland, aspen, and oak vegetation types within their territories (Keenlance 2002).

Working with radio-collared wolf packs in Montana, Oakleaf et al. (2006) were able to establish a negative relationship between forest cover and shrub cover within wolf packs ($r > 0.70$, $p = 0.762$). They found that wolves lived in areas that, on average, are 68% covered by conifer forest, compared to control sites which averaged between 34% and 42%. Conversely, wolf territories only contained 11% grasslands, while control sites contained between 17% and 23%. They also found that wolves tended to live on federal versus private lands (83% compared to 13%), which tended to have lower human densities and more forest cover (J. K. Oakleaf, et al. 2006, 558). Vegetation structure differed from Mladenoff's 1995 study, however, as the Northern Rockies are dominated by coniferous forest instead of mixed forest.

European wolves have exhibited similar characteristics. Wolves in Poland exhibited similar characteristics, selecting territories with more forest cover and lower human density (Jedrzejewski, et al. 2004). This study compared sample plots where wolves were present with plots which showed no wolf signs. They found a mean of 50.5% forest cover inside wolf plots, compared to only 38% forest cover in non-wolf plots. Furthermore, wolf plots contained only 4.6 villages on average, compared with 6.6 villages in non-wolf plots. Length of roads and railways showed a similar negative correlation. A study in British Columbia found that wolves selected for forest and shrub communities but avoided conifer stands during winter (Milakovic, et al. 2011). Their models concluded that wolves selected areas which would increase their encounters with prey species and number of den sites, but that this was independent of the Normalized

Difference Vegetation Index (NDVI). They also found that wolves avoided north aspects and selected for south aspect slopes for denning purposes, and that they selected shallow slopes and low elevation (Milakovic, et al. 2011).

Fine scale studies of wolves have focused on within-range resource use. Jedrzejewski et al. (2001) postulated that wolves occupy territories with mixed forest types to increase hunting success rates (Jedrzejewski, et al. 2001). Their study was corroborated by Kunkel and Pletscher (2001), who found that wolves used forest for stalking cover. They found that wolves traveled mostly in areas of steep slope (6.4 times more common than slope on control transects) and in areas of forested cover (2.1 times more abundant along travel routes than within home ranges) (Kunkel and Pletscher 2001). Bergman et al. (2006) also found that wolves hunted along forest boundaries, finding that wolves often use the transition from open to closed space in order to hinder their prey, who suddenly find themselves forced to maneuver through a complex stand of trees (Bergman, et al. 2006).

Atwood, Gese, and Kunkel (2007) similarly found an increase in the cover complexity index at wolf kill sites over time after wolves were reintroduced to the Northern Rockies. Their study analyzed wolf kill sites over several years after wolves' reintroduction to Montana, finding that after reintroduction prey species altered browsing habits to avoid detection by predators (Atwood, Gese and Kunkel 2007). This conclusion was further supported by a study of elk vigilance patterns in Yellowstone National Park by studies by Halofsky and Ripple (2008). Halofsky and Ripple's research revealed that the biggest influence on mother elk vigilance levels was their proximity to forest edges (Halofsky and Ripple 2008).

Studies on den site selection have also revealed fine-scale patterns in habitat use, showing that wolves utilize pine forests for den sites (Norris, Theberge and Theberge 2002). Wolves have been found to utilize dense forest cover for den sites in order to avoid detection (Norris, Theberge and Theberge 2002; Trapp, et al. 2008). Wolves also select den sites near available water sources (Trapp, et al. 2008).

Anthropogenic Influences on Habitat Selection

Studies have also shown that human population density plays an important role in wolf habitat selection. Mladenoff et. al. (1995) and Oakleaf et al. (2006) both found a significant positive relationship between wolf territories and public lands. Kruskal-Wallis tests revealed a significant difference between human population densities in wolf territories versus control sites (0.43 people/km^2 compared to 2.26 people/km^2). (Oakleaf, et al. 2006)

Road density has also been widely considered a useful measure of human density, and Oakleaf et. al. (2006) found that there was a statistically significant difference between road densities in wolf territories versus non-use areas (0.44 km/km^2 versus 0.62km/km^2) (Oakleaf, et al. 2006; Boyd and Pletscher 1999). Evidence supports the reasons wolves select territory away from human populations. Boyd and Pletscher (1999) found that the leading cause of mortality in dispersing wolves was human-caused, and the majority of wolves died within 0.209 km of roads (Boyd and Pletscher 1999). Blanco, Cortes, and Virgos (2005) studied the boundary effects on wolf movements of a major highway compared to a large river in Spain and found that the highway served as a permeable barrier to wolf territory expansion. They found that four radio collared wolves crossed the highway between 4% and 33% out of the 45 to 163 monitoring days. Wolves were also able to cross the River Duero Artery, a river that spans 50 meters to 100 meters wide, but dispersal across the river was only induced after severe habitat disturbance. (Blanco, Cortes and Virgos 2005). A neighboring study found that fenced highways promoted wolf mortality by blocking possible escape routes off the road (Colino-Rabanal, Lizana and Peris 2011).

Several studies have supported the notion of a threshold road density for wolf survival, first put forth by Richard Thiel's paper (1985) on the relationship between road density and wolf habitat. Studying wolf populations from 1926-1960, he found that wolves could not survive in areas with a road density greater than 0.59 km/km^2 (Thiel 1985). Thiel postulated that higher road densities open an area to higher human infiltration, who pose a threat to wolves through either intentional or accidental killing. He also noted the mortality rates of wolves living in areas of different human densities in Minnesota. In northern Minnesota, wolves experienced 33-50% mortality, but as populations moved south and west, where human densities were higher, to 76% in central Minnesota and 78% at the Minnesota-Wisconsin border (Thiel 1985). These results were confirmed by David Mladenoff, (1995) who studied wolves in Wisconsin and Michigan. He found that wolf territories had significantly lower road densities (0.23 km/km^2) compared to the regional average (0.71 km/km^2). Further confirmation was provided by Wydeven et al. (2001) in their study of the same region, which found that wolves would not establish territories in areas with greater than 0.6 km/km^2 (Wydeven, et al. 2001).

Studies in Europe have shown a similar trend in wolves avoiding human settlement, but a higher tolerance in general of human settlement. A study in the

Bialowieza Primeval Forest found that wolves inhabited an area with road density up to 1.6 km/km^2; however, the study found that only certain roads were intensively used by humans. This study found that wolves avoided humans generally, but their avoidance was more marked during the day when humans were more likely to be present near their territories. Furthermore, they found that wolves would not use parts of the forest that were open to timber harvest (Theuerkauf, et al. 2003). Similarly, research has shown that wolves in the Canadian boreal forest were disrupted by the creation of new logging roads into their territories (Houle, et al. 2010). Their research found that wolves avoided roads during dispersal periods and altered their foraging patterns.

Fragmentation and Island Biogeography

Many studies of habitat suitability are united in their prescription of measures to prevent habitat fragmentation. The majority of these studies focus on the causes and consequences of isolation and disturbance. Any discussion of fragmentation must be couched in the notion of island biogeography, a vast realm of literature in biology and ecology.

The tenets of island biogeography were most famously laid out by Robert MacArthur and Edward Wilson (1963), wherein they describe their eponymous MacArthur-Wilson model (MacArthur and Wilson 1963). In this publication, they described an equilibrious model of islands balancing their rates of new species immigration and species extinction. This interplay is important for islands due to their remoteness. Isolation can be measured by the geographic remoteness of an island, which would decrease the rate of immigration of new species from the mainland, thus decreasing species richness. Size of the island also plays a role in determining species richness, as larger islands are able to support larger populations due to a greater extent of potential habitat. This will increase biodiversity as the number of potential ecological niches increases.

This model spurred a new mode of thought in the world of biogeography and has had wide-reaching implications in the body of knowledge. In the realm of habitat suitability, habitat fragmentation and isolation represent some of the biggest threats to long term species richness. Due to the difficulty of recording their movements, studies of large carnivores are less common than studies on the fragmentation of habitat of smaller vertebrates. Nevertheless, the literature leads to several conclusions about the consequences of habitat fragmentation.

Perhaps nowhere is the effect of isolation on a wolf population as clear as with the wolves of Isle Royale National Park. These wolves immigrated to Isle Royal in the 1940s during a harsh winter in which portions of Lake Superior froze over, giving a single wolf pack access to the island and its moose population. Since 1948, the small Isle Royale wolf population has remained isolated from mainland wolves. Indicative of island biogeography, these wolves suffered an outbreak of parvovirus in the early 1980s which nearly wiped out the entire population (Peterson, Wolf-Moose Interaction on Isle-Royale: The End of Natural Regulation? 1999). After their decline from 50 wolves to 14, the moose population exploded. The moose’s dramatic growth put increased pressure on their food supply, and in 1996 the moose population plummeted due primarily to starvation. Moose are the wolves’ primary food source on the island, and this imbalance illustrates the fragility of isolated predator-prey interactions.

Darimont et al. (2004) found similar results studying wolves of the British Columbian archipelago. They found that wolves on more remote islands exhibited very different foraging patterns than their mainland relatives, especially regarding consumption of deer. Wolves on more remote islands further from the mainland were forced to turn to other food sources, primarily in the form of smaller prey such as mink, otter, and birds. The authors conclude that wolves living on remote islands are at risk from the same ecological imbalances as those from Isle Royale (Darimont, et al. 2004).

More terrestrial applications of island biogeography theory describe the implications of isolation and fragmentation on large carnivores. Studying three medium sized carnivores (coyote, fox, and raccoon) in Illinois, Randa and Yunger (2006) found that urban centers served as major barriers for movement of fox and coyote. Raccoons, however, were unencumbered along the urban-rural gradient, and seemed to select for more developed areas. They determined that urban and suburban development was negatively correlated with detection of the canids, and that the ecological disturbance of developed land served as a good predictor of favorable habitat (Randa and Yunger 2006).

These three species, however, do not share the wide-ranging territories of gray wolves. Several studies from the Rocky Mountains in Canada reveal the effects of habitat disturbance on large carnivores. Johnson et al. (2005) suggested that grizzly bears and grey wolves were highly sensitive to human disturbance in the Canadian arctic. They proposed that the future development of a year-round in that region road could drastically decrease the useful habitat for large predators. However, they tempered that claim by pointing out that both species may alter their foraging strategies to adapt to the disturbance (Johnson, et al. 2005).

Other studies have found that wolves rely on large, undisturbed areas for their habitat. Alexander et al. (2005) found that wolves in the Canadian Rockies were strongly associated with contiguous forested lands, and that human disturbance was negatively correlated with wolf presence. In a similar vein, Noss et al. (1996) conclude that large predators such as bears and wolves can overcome habitat fragmentation, but that interconnected networks of habitat must be maintained to ensure their long term survival. Their study suggests that because large carnivores are able to disperse greater distances to find suitable habitat then the insularization of habitat is less likely. However, due to their size large carnivores require access to greater extents of land. Thus, they propose the implementation of a management plan that incorporates a network of "core" areas, buffer zones, and dispersal corridors to aid in movement throughout the Rocky Mountains region (Noss, et al. 1996).

Michael Bader's study (2000) also prescribes a network or core areas to support large carnivores. Due to their dietary and demographic needs, Bader points out large carnivores rely on vast extents of wilderness. Bader points out that the single island method is not adequate to address the needs of most species, but especially inadequate to address the needs of large carnivores. Nowhere does there exist a large enough island to support a carnivore population entirely (Bader 2000). He emphasizes past research which states that to fully capture spatial ecological processes, 10 to 15 times as much land as the largest disturbance extent ought to be protected. Given the broad scale of wildfire in the Northern Rockies (10,460 km^2 in the 1988 Yellowstone wildfire), he concludes that between 105,000 km^2 and 157,000 km^2 needs to be protected to adequately encompass all the multitude ecological processes of the region (Bader 2000). This, he concludes, must be done through the use of core areas from which predators can disperse along suitable corridors to other areas of suitable habitat.

Thus, more studies on the effects of fragmentation of habitat of large carnivores are necessary. In instances of true island isolation, wolf populations are susceptible to inbreeding and the depletion of their food supply (Peterson, Wolf-Moose Interaction on Isle-Royale: The End of Natural Regulation? 1999). In more connected areas, anthropogenic disturbances can drastically alter foraging patterns.

Cost Surface Analysis

Many contemporary studies have taken the biological data collected from studies mentioned above and compiled habitat selection models, including cost surface analyses. Cost surface analysis builds on habitat suitability models and helps to predict future dispersal (Gonzales and Gergel 2007; Epps, et al. 2007). This analysis is especially useful for creatures that migrate or disperse and can be applied in many ways (Gonzales and Gergel 2007). Most cost surface analyses hinge on a similar structure as outlined in Spear et al. (2010): assigning costs (i.e., weights) to particular landscape features based on their suitability for a particular species' needs. Spear et al. (2010) described three means by which to do this: field data, expert opinion, and model optimization. Field data often lead to expert opinion, while model optimization is more mathematically rigorous.

Jensen and Miller (2004) conducted a simple model for dispersal without referring to cost surfaces. Instead, they used a simple logistic regression based on source population density to model wolf dispersal in Minnesota. Their project is similar to this study insofar as they assumed that the wolf population was near its carrying capacity for their region, and they would begin dispersing into subprime territory (Jensen and Miller 2004). Their study focused on genetic movement instead of landscape factors.

Many cost surface analyses examine gene flow through an environment. Epps et al. (2007) used genetic data from bighorn sheep to create a least cost habitat dispersal model. Parameters for their cost surfaces were optimized by finding statistical correlation between gene flow and effective geographic distance while controlling for anthropogenic landscape features. From this, they used a nonparametric regression test to calculate the effective geographic distance of their 26 sample bighorn sheep populations. They found that by incorporating a Digital Elevation Model (DEM), they were able to construct an accurate cost surface model, which they validated using radio-telemetry from collared sheep (Epps, et al. 2007).

The Epps et al. (2007) study benefitted from genetic data, which enhanced the reliability of their cost values. Most studies rely, instead, on expert opinion (Spear, et al. 2010). Epps et al. (2007) found that models based on expert opinion for their bighorn sheep populations did not differ far from their genetic sampling model. Models of this sort benefit from flexibility and ease of replication. Nikolakaki (2003) followed such a methodology in studying redstarts (*Phoenicurous phoenicurous*) in Sherwood Forest, England (Nikolakaki 2003). This study employed both high quality habitat and large habitat patches, since both are important to emigration of redstarts. Large woodland patches are less susceptible to isolation and disturbance and high quality habitat patches can offset their small size by promoting reproductive success or preventing mortality. Nikolakaki assigned cost values to different land cover classes obtained from remotely sensed data. Resistance values ranged from one for high quality habitat (deciduous woodland) to 25 for known barriers to redstart movement such as open bodies of water, major roads, and rail lines. The resulting cost surface map of Sherwood Forest identified high priority sites for environmental enhancement (Nikolakaki 2003).

Gonzales and Gergel (2007) employed similar techniques in their analysis of eastern grey squirrels. Their study illustrated the difference between non-spatial diffusion models and spatially explicit cost surface analyses. Diffusion models are easier to employ since they require fewer inputs, but cost surface analyses "incorporate realistic behavioral decisions" (Gonzales and Gergel 2007). Their study relied on data collected from local residents and remotely sensed land cover data.

Their first model followed the same structure as Jensen and Miller (2004), using a simple mathematical equation to plot diffusion over time. They also created two cost surfaces based on different scenarios: habitat selection versus habitat push. Habitat selection presumes that squirrels would move easily through areas of more suitable habitat and move slowly or face mortality in areas of poor habitat. The habitat push scenario presumes that squirrels would move quickly through areas of poor quality habitat and establish themselves more permanently in areas of better quality habitat (Gonzales and Gergel 2007). In both scenarios, researchers used expert opinion to assign cost values to different landscape features.

They found that their diffusion model underestimated patch size significantly (14 km^2 per year calculated versus 29 km^2 per year observed). Diffusion models have been used to predict movement of a species across a landscape, but they do not take into account the creatures preferences or needs for survival. In a diffusion model, researchers use a mathematical formula to graph movement into new territories. Gonzales and Gergel

(2007) found that their diffusion model underestimated squirrel movements into new territory because their model did not account for the favorability of certain habitat patches. They did find, to their surprise, that both habitat push and habitat selection produced similar cost surfaces, but that the least cost routes across the landscape differed markedly (Gonzales and Gergel 2007).

Rabinowitz and Zeller (2010) employed similar techniques in studying jaguars (*Panthera onca*) in South America. They created a cost surface model to highlight least cost routes across the landscape based on expert opinion. They found that their least cost routes were similar to historic data on jaguar habitat and movements. This study was unique in the scale on which they studied landscape phenomena, comprising the entire jaguar range throughout Brazil. They used their cost surface in order to develop a landscape permeability matrix in order to determine the connectivity between jaguar conservation units (Rabinowitz and Zeller 2010).

Researchers are beginning to employ graph theory into cost surface analyses. The heterogeneous nature of a landscape gives rise to a complex mosaic of land cover types, which complicates dispersal of target species. Graph analysis helps to explain how the shape and distribution of habitat patches can influence dispersal patterns. Gonzales and Gergel (2007) also analyzed the impacts of habitat patch size and distribution and linear features. To do this, they created six different models in which they changed the relative rankings of patch features and linear features. They found that by increasing the range of the absolute friction values produced dissimilar least cost paths through the landscape. Also, they found that cost surfaces were more sensitive to differences in patch values than linear values (Gonzales and Gergel 2007).

Similar studies include those conducted by Rayfield, Fortin, and Fall (2010) and Minor and Urban (2008). Graph theory employs least cost routes across a landscape to analyze the robustness of networks. According to Minor and Urban (2008), environmental networks tend to follow the scale free network model, with several high degree nodes (hubs) connected to outlying low degree nodes. Minor and Urban (2008) claim that “ideal habitat networks might resemble scale free networks with several hubs connected to multiple smaller patches.” This type of structure is resilient to random disturbance, providing a stable structure in which species may thrive (Minor and Urban 2008).

VI. STUDY AREA

The Northern Rocky Mountain region consists of portions of several states: Montana, Idaho, and western Wyoming. Isolated wolf packs have also expanded onto the Columbia Plateau in eastern Oregon and Washington as well, and also into the Southern Rockies in Utah and Colorado. Only packs with confirmed data will be considered in this study. This Northern Rockies region is a geologically distinct area marked by the unique Yellowstone National Park ecosystem. Seismic activity dominates the Yellowstone landscape, and Yellowstone National Park sits inside the caldera of an active volcano. Home to the world's largest concentration of thermal hydrologic features, and home to two-thirds of the world's geysers, the federal government set this area aside as the world's first national park in 1872. The park is home to healthy populations of elk, deer, bison, and other ungulates, hence its selection as a reintroduction site for wolves. Inside Yellowstone National Park, pine forests dominate the landscape giving way to mountain valleys and open meadows. Forests consist of lodgepole and ponderosa pine, and riparian aspen stands (National Park Service 2011).

Outside the park, the landscape consists of a mosaic of different land uses. A patchwork of federal, state, and private lands make up the region, and while wolves often reside on public lands they must also use private lands. According to Montana Fish Wildlife and Parks (MFWP) most wolf territories included about 30 percent private lands, although most wolves live in remote backcountry (Sime, et al. 2011). Similarly, most wolves in Idaho live in remote wilderness areas: the Selway-Bitterroot, Frank Church-River of No Return, and Gospel Hump, along with the Boise, Salmon-Challis, and Sawtooth National Forests. Together, these wilderness areas comprise 4 million acres representing the largest contiguous federally protected area in the lower 48 states (Holyan, et al. 2011). Southern Idaho opens to the Snake River Plain that contains primarily agricultural land and the state's large urban centers.

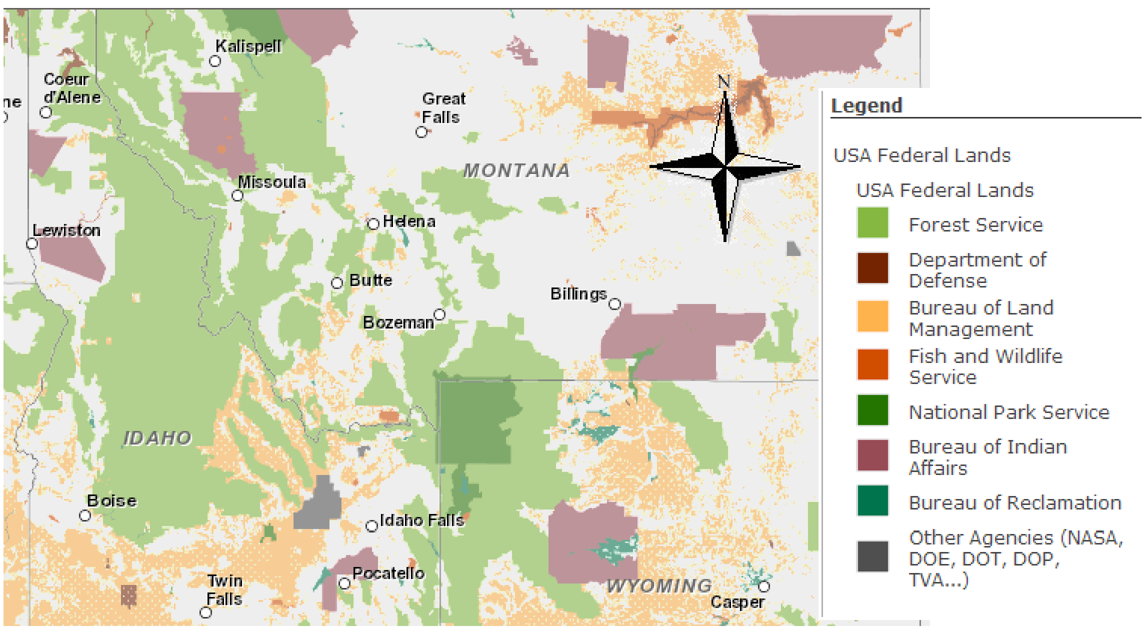


Figure 1: Federal land designations in the Northern Rockies (Esri 2012)

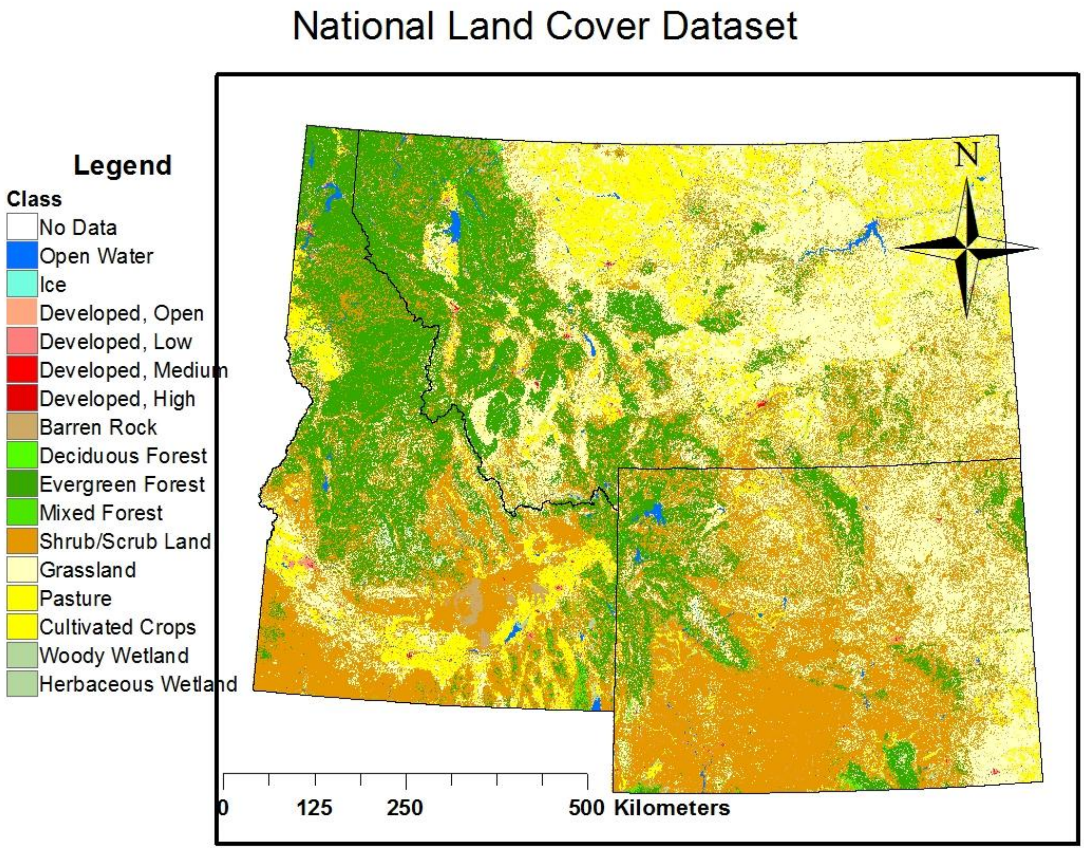


Figure 2: Multiresolution Land Cover Characteristics Consortium defined land cover classes for the Northern Rockies region

VII. SITE SELECTION

At the outset of the reintroduction project, wolves were released in the central Idaho wilderness and in Yellowstone National Park. Through dispersal, their population quickly moved into western Montana and has crossed the border in to Washington and Oregon. In 2010, the minimum estimated population of wolves stood at 1,651 individuals with 244 packs, and 111 breeding pairs (U.S. Fish and Wildlife Service 2011). The FWS considers the wolf population across the entire Northern Rockies region to be one distinct unit, and thus the study focuses on the entire states of Idaho, Montana, and Wyoming.

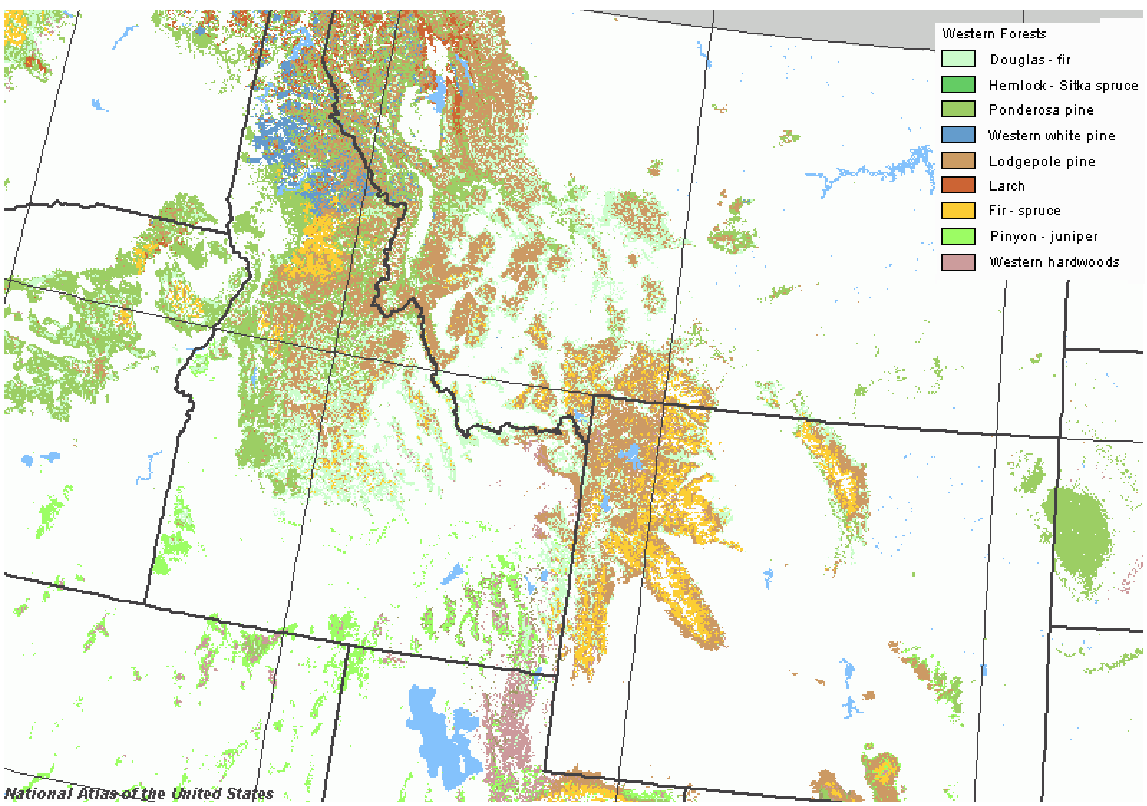


Figure 3: Forest types of the Northern Rockies (U.S. Department of the Interior 2012)

VIII. DATA COLLECTION

Wolf management is a collaborative effort between several agencies: Fish and Wildlife Service, Montana Fish, Wildlife and Parks (MFWP), Idaho Department of Fish and Game, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, and Wind River Tribes. Wildlife personnel employed several methods to monitor and manage wolves across the region. National Park Service personnel closely monitor wolf packs in order to manage visitors to the park. This is especially important during breeding season, when the park must close certain trails to prevent contact between humans and wolves (Jimenez, et al. 2011).

Wildlife personnel can track wolves year round and have acquired estimates for pack size and location using several techniques. As the wolf population has grown, it has become more difficult to accurately assess its size. Thus, recent population estimates are conservative. Radio tracking of wolves, especially in conjunction with aerial reconnaissance, yields accurate information on wolf movements and wolf territories. This is highly labor intensive. Wildlife personnel and volunteers locate wolves, either on foot or by air, using directional antennae and recording the bearing. When two or more bearings are obtained for a radio collar, its position can be triangulated with a high degree of precision. Aside from the man hours involved, the equipment for radio tracking is also expensive and thus wildlife managers attempt to distribute only one collar per pack.

Some packs are not collared, which leads to conservative population estimates (Holyan, et al. 2011).

Wildlife personnel also conduct howling and track surveys and direct observations (Holyan, et al. 2011). In order to enhance their records, Montana has created a reporting program through which the public may report wolf sightings to Montana Fish Wildlife and Parks Department (MFWP). This has proven especially useful in engaging livestock owners in wolf management as they can report cases of depredation on their animals to wildlife managers, who can then reimburse the landowner and take action to prevent further depredation. Wildlife managers deployed volunteers in areas that received repeated wolf sightings, areas of past wolf activity, or gaps in noted wolf areas despite adequate prey base (Sime, et al. 2011).

IX. SPATIAL DATA

Formed in the 1990s, the Multi-Resolution Land Characteristics Consortium (MRLC) is a collection of federal agencies with the goal of creating land cover information. The National Land Cover Dataset (NLCD) provides land cover classifications derived from remotely sensed data at a 30 meter spatial resolution. The NLCD was compiled from the Landsat initiative, a joint venture between the US Geological Survey (USGS) and NASA. The Landsat 7 system used the Enhanced Thematic Mapping+ tool with 30 meter resolution to accurately map the globe (U.S. Geological Survey 2010). Remotely sensed data from Landsat were converted into 20 different land cover classifications (U.S. Geological Survey 2011). Categories for the NLCD were modified from the Anderson Land Cover Classification System (1976), and include the following:

- Open Water
- Perennial Ice/Snow
- Developed Open Space
- Developed Low Intensity
- Developed Medium Intensity
- Developed High Intensity
- Barren Land
- Deciduous Forest
- Evergreen Forest
- Mixed Forest
- Dwarf Scrub
- Shrub/Scrub
- Grassland/Herbaceous
- Sedge/Herbaceous (Alaska only)
- Lichens (Alaska only)
- Moss (Alaska only)
- Pasture/Hay

- Cultivated Crops
- Woody Wetlands
- Emergent Herbaceous Wetlands

This project also relied on DEMs compiled by the USGS. Elevation models are available as raster files in the same 30 meter resolution as the NLCD. Road data layers are available from each state's respective transportation department, and were converted into raster format for use with the Spatial Analyst suite of tools in ArcGIS©. Past studies used road density as an adequate surrogate for human population density and exposure to humans, and this study employs the same tactic.

X. DATA PROCESSING

This study follows the same methodology employed by similar studies from Nikolakaki (2003) and Gonzales and Gerber (2007). Raster layers were created in ArcGIS© of the NLCD, elevation, distance from roads, and wolf territories. Raster layers for roads, rather than road density, were created following the methods employed by Rodriguez-Freire and Crecente-Maseda (2008), whose study found that road density across a large area did not yield a high resolution raster layer. Instead, they were able to create a different raster layer based on distance from roads, which offered more spatially explicit data. This served the study well, since roads are one of the biggest causes of mortality for wolves, and most wolves struck by cars are found less than a mile from roads. The Path Distance tool within ArcGIS© took terrain in account and more accurately represented distance from roads compared to simple Euclidean distance. Since natural land cover classes and anthropogenic land cover classes represent opposing pull and push forces on wolf habitat selection, they were treated separately in terms of landscape variables. Raster layers were created in ArcGIS© of the NLCD, slope, and proximity to roads. The Reclassify tool then assigned their associated friction values, listed in Tables 1 through 3. A review of the literature from experts in the field informed the decision on the relative costs associated with each class of landscape feature.

Each feature received a friction value to represent the amount of energy or level of risk that variable poses to wolf movements or survival. The greater risk or impediment each variable poses, the greater was its friction value. Each cell characteristic was ranked along the same scale, from 1 to 15. Sensitivity analysis then assigned weights to each landscape characteristic in the development of the final friction model. This eased any computational changes that needed to be made as the model was perfected. Still, this method is imperfect but easily adaptable to include updated information and thus makes adequate, easily replicable conclusions. Map Algebra tools were employed to compile these layers into a final friction surface. The following tables summarize the friction values I assigned to each landscape variable:

Table 1: Friction Values from National Land Cover Dataset

Conifer Forest	1	Agricultural Land	3
Shrub land	2	Developed, Open	5
Grass land	3	Developed, Low	10
Wetlands	6	Developed, Medium	12
Open Water	15	Developed, High	15

Table 2: Friction Values from Digital Elevation Model

Slope	Friction Value
0% to 5%	1
5% to 10%	5
10% to 15%	10
Greater than 15%	15

Table 3: Friction Values from Road Maps

Distance from Major Roads	Friction Value	Distance from Minor Roads	Friction Value
Less than 1 Mile	15	Less than 1 Mile	15
Between 1 Mile and 5 Miles	7.5	Between 1 Mile and 5 Miles	7.5
Greater than 5 Miles	1	Greater than 5 Miles	1

The study required two means of determining the final friction surface. First, an examination of each landscape criteria within wolf territories found which variables were present. This revealed patterns and tendencies in wolf habitat selection, and confirmed previous findings from past studies. Sensitivity analysis then followed in three stages in order to develop the final cost surface. First, equal weight was assigned to all landscape features. This allowed for the creation of several cost surfaces in which one class of landscape features had a higher relative weight than all other variables. This isolated and amplified the effects of that class of landscape features on wolf movement. Comparing this second group of cost surfaces with the original, equal-weighted cost-surface, revealed the sensitivity of the model to each class of landscape features. By examining the zonal features of each model inside wolf pack territories, I was able to minimize costs inside wolf territories. This information aided in the development of a final cost surface which adequately accounted for wolves' sensitivity to certain landscape features.

Wolf pack territories served as sources for wolf dispersal, and the starting points for least cost paths between territories. These least cost paths portrayed the connectivity between wolf packs across the region, as informed by the management agendas of the states moving forward. This resulted in a habitat graph network which identified areas of low cost (i.e., low friction of movement) for wolves, which has allowed the identification of areas important for wolf dispersal, but has also informed the analysis of the overall landscape using the techniques outlined in Rayfield, Fortin, and Fall (2010). The creation of the cost surface map has highlighted habitat patches suitable for wolves, and the paths between them have allowed me to analyze how the structure of the landscape impacts wolf dispersal.

The final friction model was used in conjunction with known wolf pack territories to create a network of potential dispersal routes throughout the region. Centroids of wolf territories served as starting points, and the least cost path tool created path routes between each centroid. These Least Cost Paths (LCPs) generated a network of paths across the landscape. The Cost Path tool in ArcGIS requires a "backlink" raster layer to determine the direction the path would follow through any given cell on the landscape. Backlink rasters for each year were created in order to develop temporally consecutive LCPs. These rasters were paired with the preceding year's pack centroids to develop LCPs between nearby packs. This provided insight into the natural dispersal of wolves across the Northern Rockies since their reintroduction.

By creating LCPs from one year to the next, the model is able to more realistically locate areas that are significant for wolf dispersal. Connectivity between wolf packs ensures genetic interchange and prevents the isolation of the species. The logic of the Least Cost Path tool is based on wolves acting rationally, taking the shortest paths across the landscape. Although wolves are capable and have proven willing to disperse distances of several hundred miles, LCPs highlight areas of especial importance for wolf movements. Thus, while wolves may move beyond the described range, the LCPs highlighted in this study illustrate a network of important corridors for wolf movements. By using centroids of wolf pack territories the LCPs developed are based on actual wolf habitat preferences. Furthermore, state wildlife management agencies have a stated interest in managing wolves as a recovered population, which means limiting wolf population growth into new areas where conflict with humans may be more common.

LCPs are useful linear features to show the most direct path across a landscape. However, in order to more accurately highlight areas that are important to wolf dispersal I needed to create a buffer around those linear features. This was done through the Cost Distance tool. Using the LCPs as the source and the Friction Model as the landscape, a threshold value of 1500 was used to create a buffer around the linear LCPs. This created a buffer around the LCPs that was based on wolves' abilities to move through the landscape, rather than a simple Euclidean distance. While any threshold value could have been chosen, a value of 1500 would provide 1 mile of buffer from the LCPs in areas of highest friction, and would thus represent a realistic model of potential wolf movement. This method creates a buffer that more accurately illustrates potential wolf movements by employing landscape features to determine areas more suitable for wolves. Wolves moving along the LCPs would be more likely to stray off that path towards areas of less friction than high friction, and the Cost Distance tool is able to accommodate this behavior.

XI. RESULTS AND DISCUSSION

Wolf Pack Territory Characteristics

Wolves have consistently expanded their territory since their reintroduction in 1994. Starting with only two wolf packs in 1994, the FWS had quality data on 189 packs across the Northern Rockies in 2009. Minimum population estimates show a population growth of only 30 wolves in 1994 to over 1700 wolves today. Since their reintroduction, pack sizes have ranged between a minimum of 2 km^2 for the Sage Creek pack in 2008, to a maximum of 5,572 km^2 for the Chief Joseph pack in 1996. Median territory size was 213.5 km^2, and the average territory size was 377.24 km^2 with a standard deviation of 513.33 km^2. These widely variable pack sizes are likely due to measurement inconsistencies. 1996 saw the rapid expansion and dispersal of reintroduced wolves into a landscape mostly devoid of these canids. The Chief Joseph pack has typically held a very large territory in the northern portion of the Greater Yellowstone Ecosystem (GYE), averaging 1,325.94 km^2 during their recorded existence. Wide ranging would have been more possible due to the lack of other established packs during the early years of reintroduction. In 2008, the Sage Creek pack straddled the Idaho/Montana border, and inconsistent measurement might underestimate pack territory size.

Total wolf extent has increased steadily since their reintroduction as young wolves disperse from their natal territories to establish new packs. The first years of wolf reintroduction saw massive expansion (over 1000% from 1994 to 1995) of the wolf population due to the reintroduction of more packs in Idaho and Yellowstone National Park, the capture and radio collaring of more wolves, and high pup survival rates in established packs. Decreases in wolf extent occurred from 1996-1997 (-4.6%), 2000-2001 (-34.24%), 2002-2003 (-11.69%), and 2008-2009 (-7.95%). An outbreak of parvovirus early in their reintroduction may explain slower growth from 1997-1999 (US Fish and Wildlife Service, et al. 2001). This period was also marked by drought, which could contribute to the availability of prey and therefore affect wolf mortality rates. In general and not including the first year of population expansion, wolf extent increased at an average rate of 26%. Excluding 1995, the largest increase in wolf extent came from 2006-2007, with a total growth of 41.71%. The final years documented in this study saw the removal and reinstatement of federal protection for wolves, and 2008-2009 saw a decrease in wolf extent due to the first wolf hunting season and control actions to remove depredating wolves, marking the first year of the more static-oriented management agenda of the states (Sime, et al. 2010; Mack, et al. 2010). We can assume that, moving forward, wildlife managers will attempt to curtail expansion of wolf territories into new areas of the Northern Rockies and through hunting and agency control wolf extent will remain mostly static. The following maps show the growth of wolf packs from 1994 through 2009.

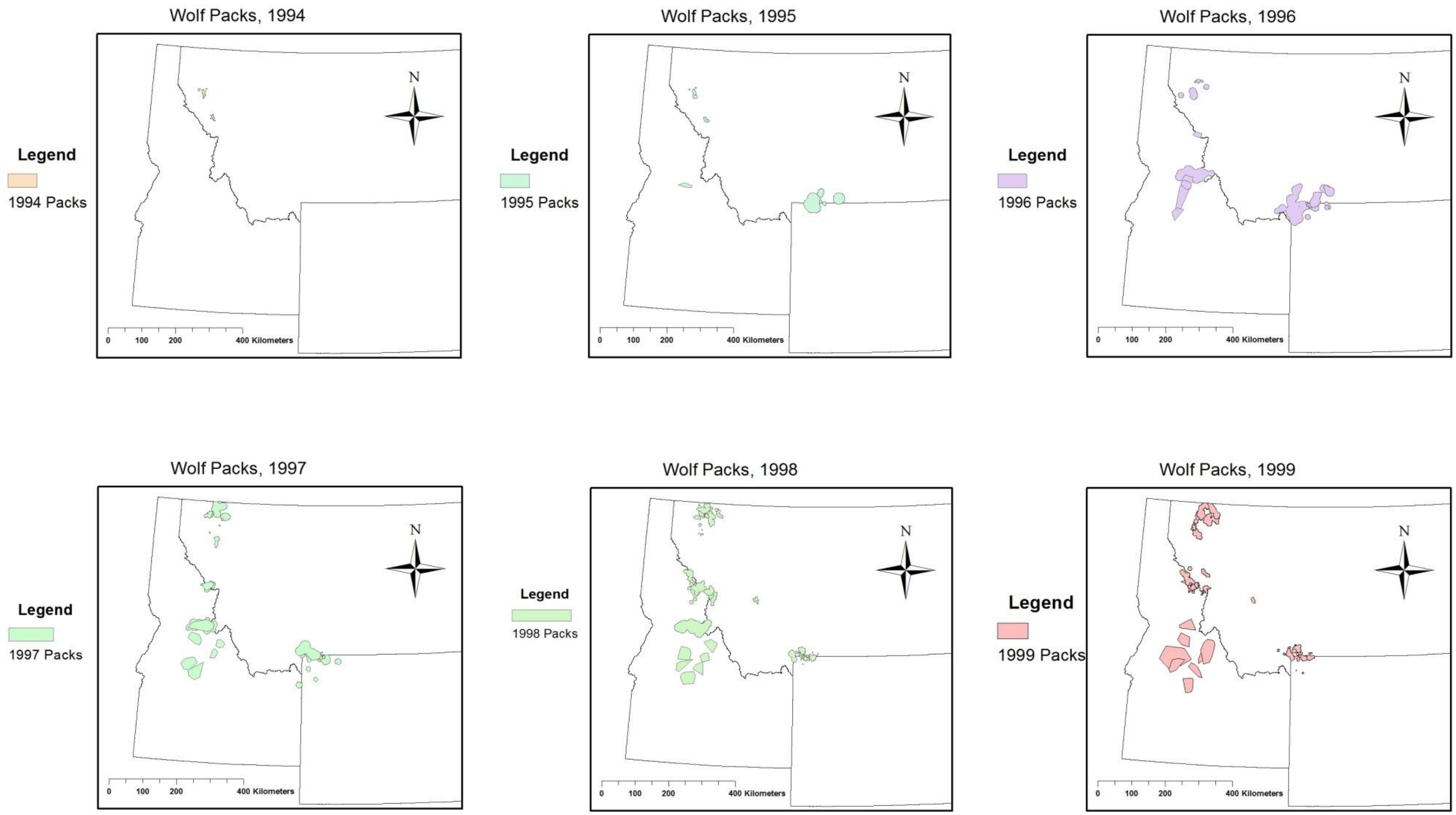


Figure 4: Wolf Pack Expansion from 1994 to 1999

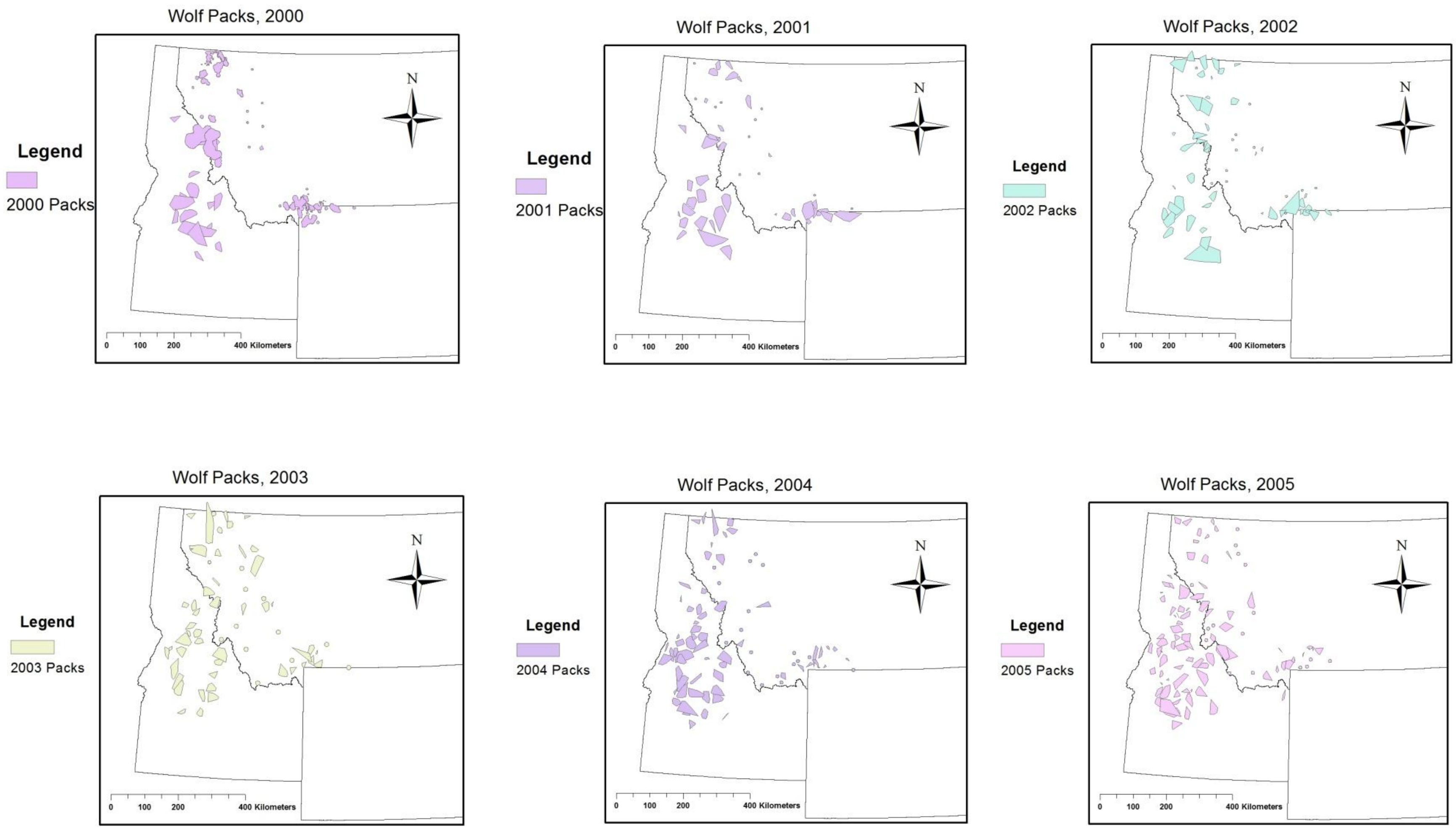


Figure 4: Wolf Pack Expansion from 1994 to 1999 (cont)

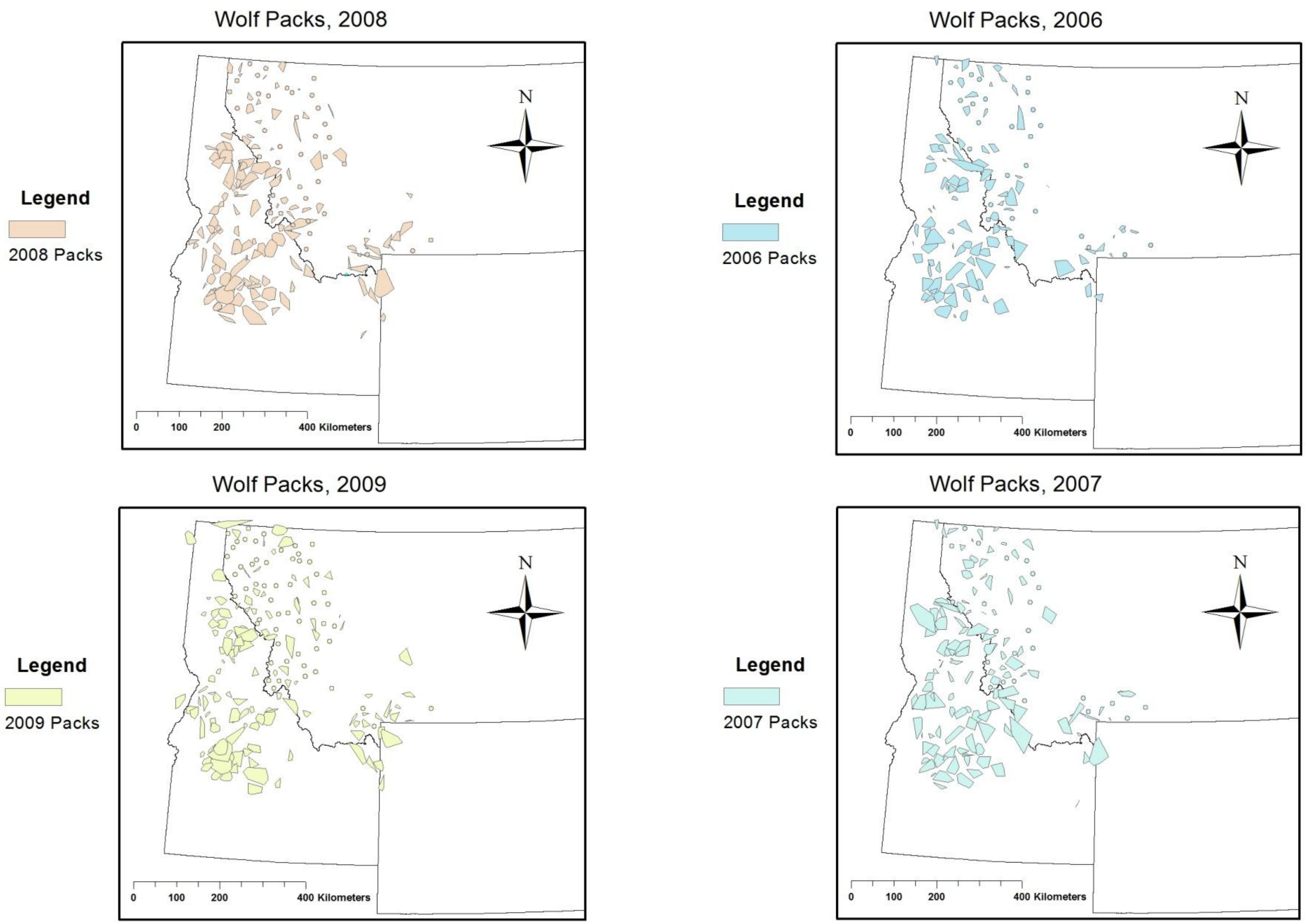


Figure 4: Wolf Pack Expansion from 1994 to 1999 (cont)

Wolf Habitat Selection

Compiling wolf pack territories revealed several interesting findings about wolf habitat selection in the Northern Rockies (Figures 5-6). Wolves in this region select strongly for forested lands, and tend to avoid human settlement. Extracting zonal statistics of land cover within wolf pack territory found that wolf pack territories contained over 300 times as much forested land as developed land. As the wolf population has grown, they have continued to occupy nearly exclusively forested lands and grasslands. Pack territories on average contained less than one tenth of one percent of developed land. Open developed land, which is marked by less than 20% impervious cover, represented the highest amount of developed land inside wolf territories but composed on average only 0.17% of wolf pack territories. Highly developed land comprised on average 0.0005% of wolf pack territories, followed by medium and low developed land classes representing 0.01% and 0.06% respectively. Agricultural land represented a similarly low percentage of total wolf territory. Pasture land represented only 0.49% of total coverage, while cultivated crops only represented 0.09%. Natural land cover classes represented vastly more of wolf pack territories. Pack territories contained on average 63.18% deciduous forest, 23.65% shrub/scrub land, and 10.20% grassland.

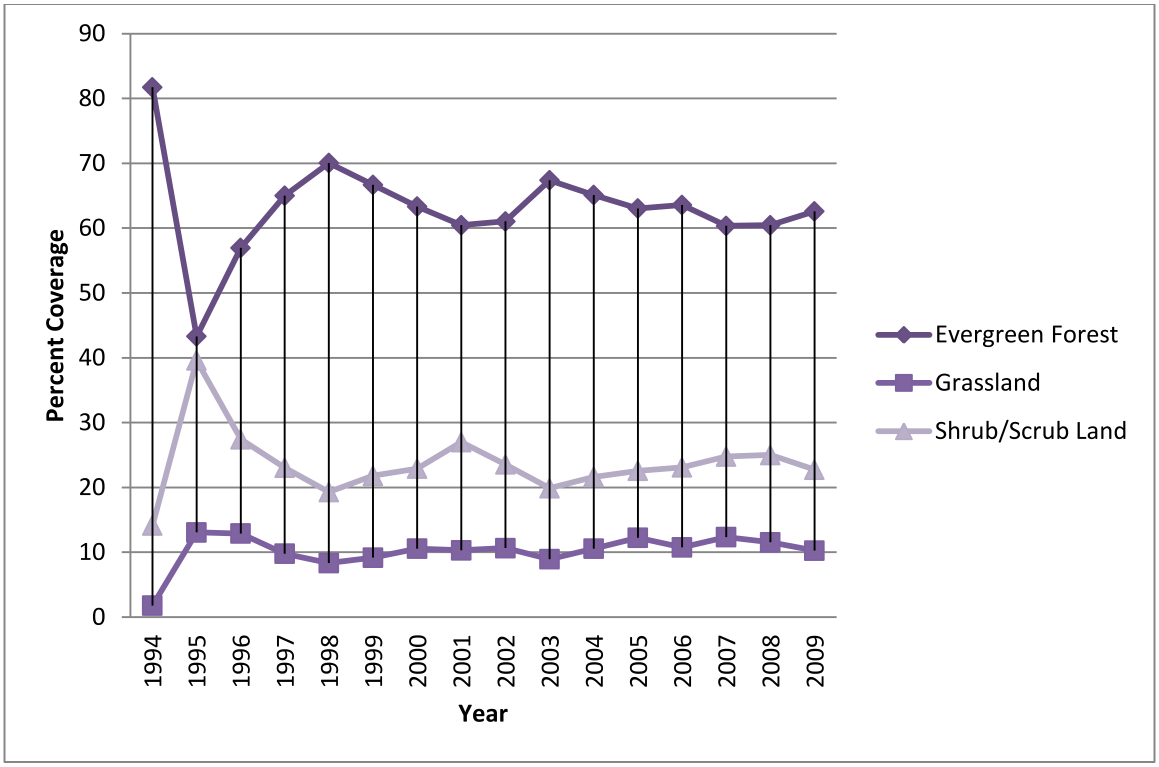


Figure 5: Evergreen forest, grassland, and shrub land in wolf pack territories

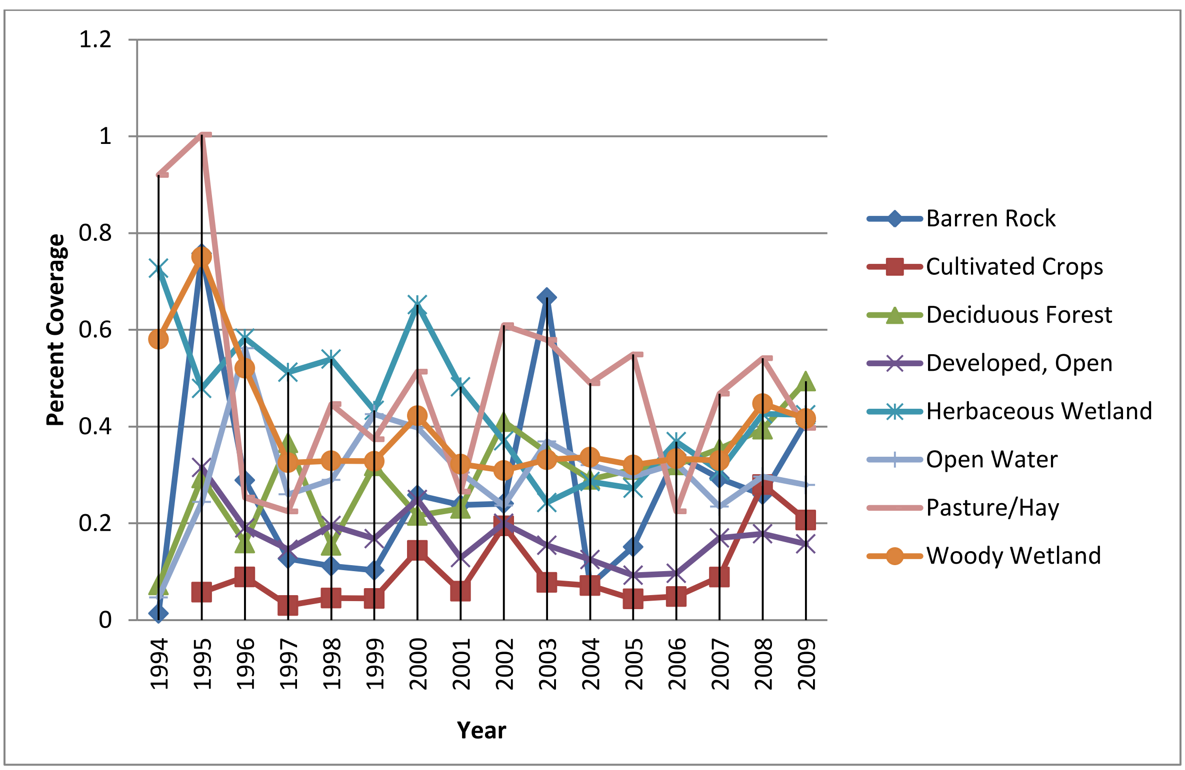


Figure 6: Other land cover classes as percent cover of wolf pack territories

Wolves were far more tolerant of steeper slope within their territories than expected. Previous studies found that wolves used areas with slope less than 5%, but wolf pack territories in the Northern Rockies contained areas with slope predominantly between 8% and 23.27%. The majority of wolf pack territories were covered by terrain between 8% to 15.25% and 15.25% and 23.27% (20.77% of total territory coverage and 21.61% of total territory coverage respectively). This suggests that the friction model will have a produce conservative cost paths regarding slope. This result was surprising until comparing land cover class with slope, and finding a strong correlation with forested lands and areas of steeper slope. Wolves are resilient creatures, and have wider paws and longer legs for faster travel over snow and rugged terrain (Mech and Boitani, Wolf Social Ecology 2003). Furthermore, this study does not examine daily wolf movements, so it remains unknown what terrain wolves use for different purposes.

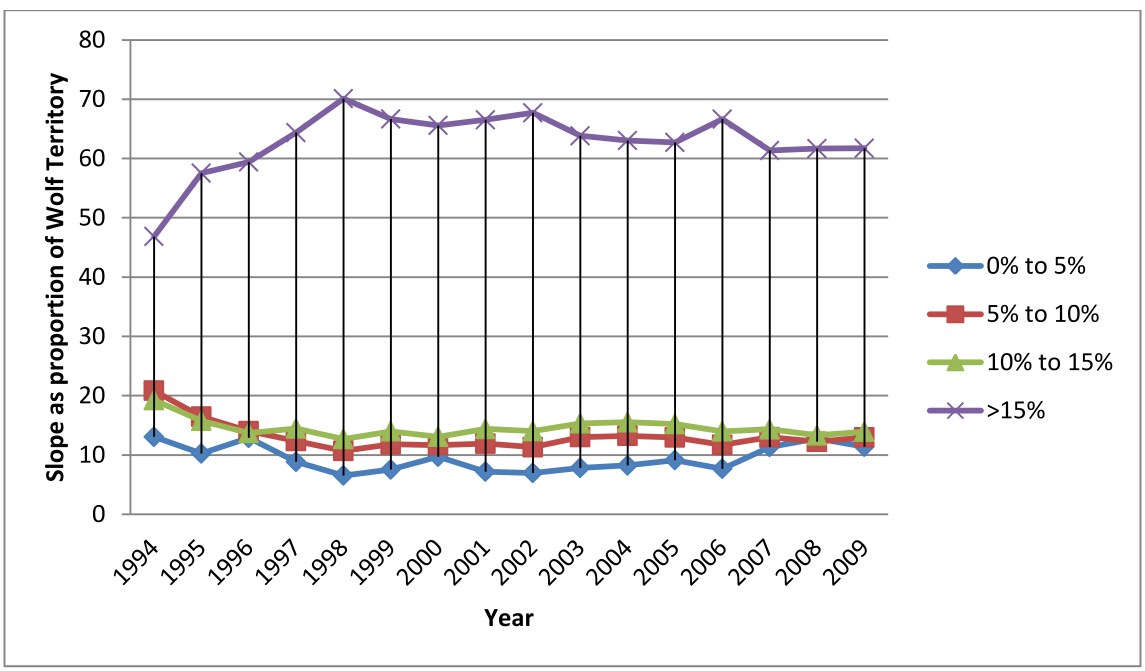


Figure 7: Percent slope found in wolf pack territories

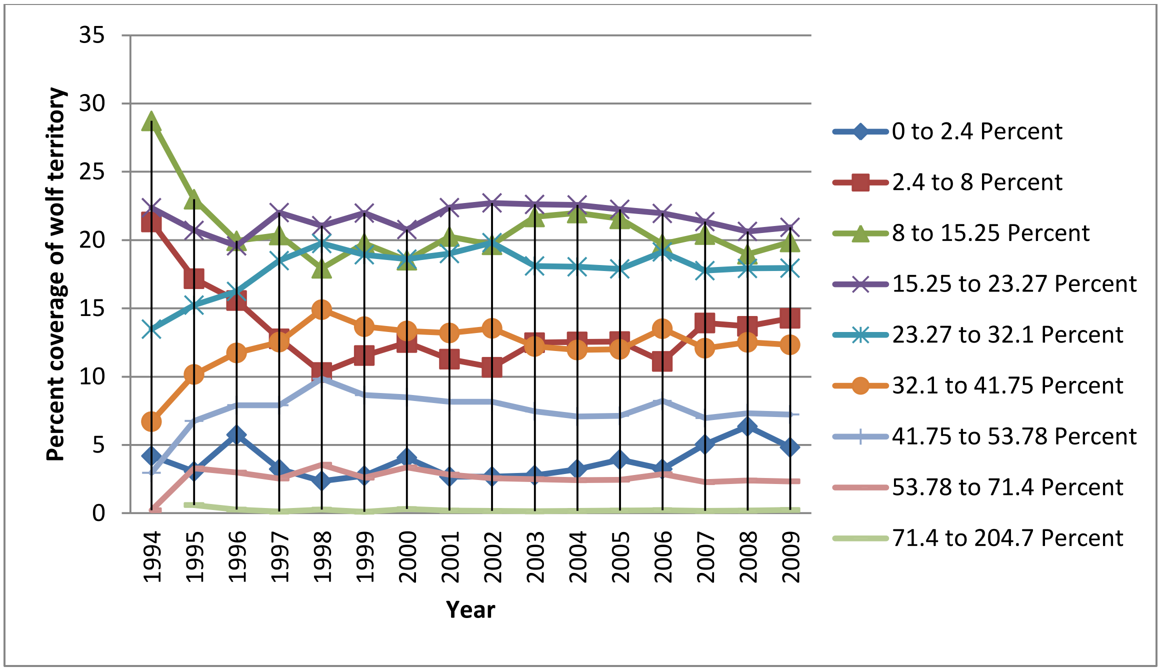


Figure 8: Further subdividsion of slope classes as percentage of wolf territory

Wolves were also more tolerant of roads that originally expected. Minor roads, in particular, were more prevalent in wolf territories than originally expected. Over 90% of total wolf territory was within 5 miles of a minor road. Major roads, however, played a much greater role in wolf habitat selection. Very few wolf territories intersected major roads, and the vast majority of wolf territory fell outside of 5 miles from major roads. About 8.5% of wolf territory in Montana was one mile or closer to a major road, while about 5% of wolf territory in Idaho was within one mile of a major road. Thirty-one percent of wolf territory in Montana was between one mile and five miles from major roads, while roughly 21% of Idaho wolf territories were between one and five miles from major roads. Thus, the friction model will overestimate cost of minor roads and cost paths and their buffers may be more underestimated.

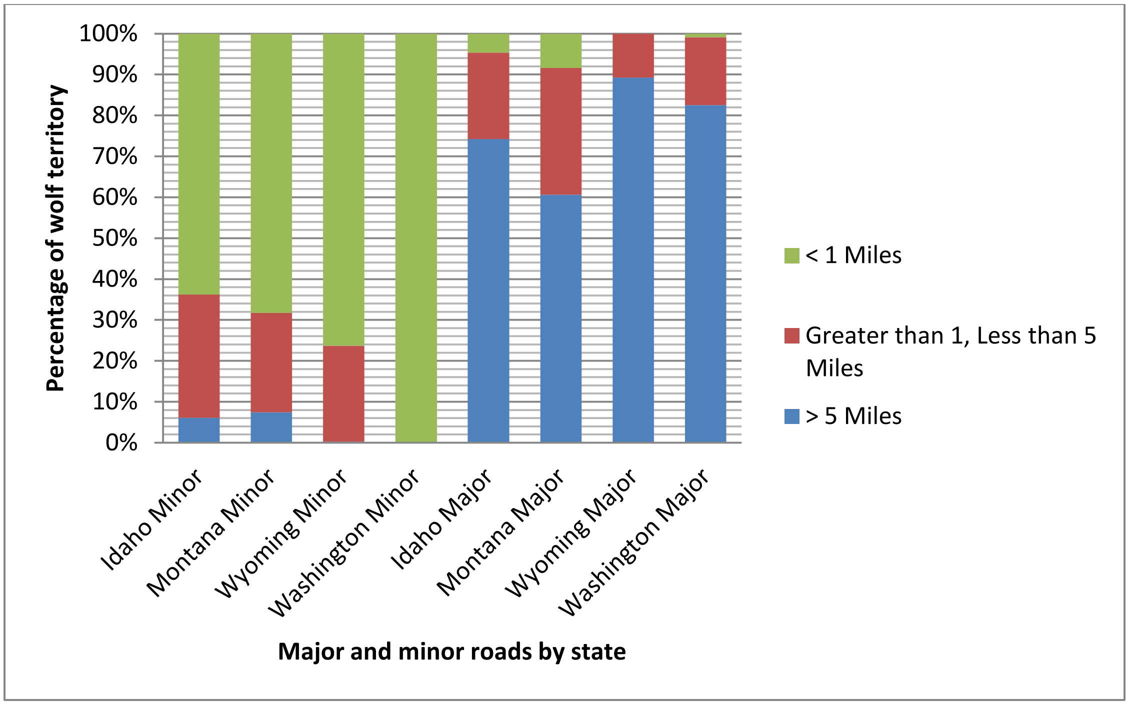


Figure 9: Proximity of wolf pack territories to minor and major roads

Other studies have focused on wolves' relationships with road density. Thiel (1985) proposed a threshold road density of 0.59 km/km^2 that wolves would tolerate, above which the establishment of a pack would be unlikely. Road density in the Northern Rockies is much higher than this proposed density. Figure 10 shows that the majority of wolf territories have existed on lands with a road density between 0 and 0.89 km/km^2. Beyond this threshold, we see a significant drop in the amount of wolf territory coverage. This pattern is strongest in Montana, where wolves are tolerant of road densities between 0.89 and 1.05 km/km^2. Figure 9 provides the distribution of road density in km/km^2 across the study unit, and we can see that in the Kalispell, MT area to the west of Glacier National Park many wolf packs have established territories in an area with higher road density. Also, Interstate 90 traverses northwest from Butte, MT through the Lolo National Forest which increases road density along the Montana/Idaho border. These findings are remarkable, since Thiel's proposed threshold (1984) has held wide approval among the literature (Jedrzejewski, et al. 2001; Jedrzejewski, et al. 2004; Mladenoff, et al. 1995) and shows that wolves of the Northern Rockies are resilient in the face of face of higher human population density. This also suggests an increase in risk exposure both for wolves and humans, as wolves appear to live in closer prosimity to human development.

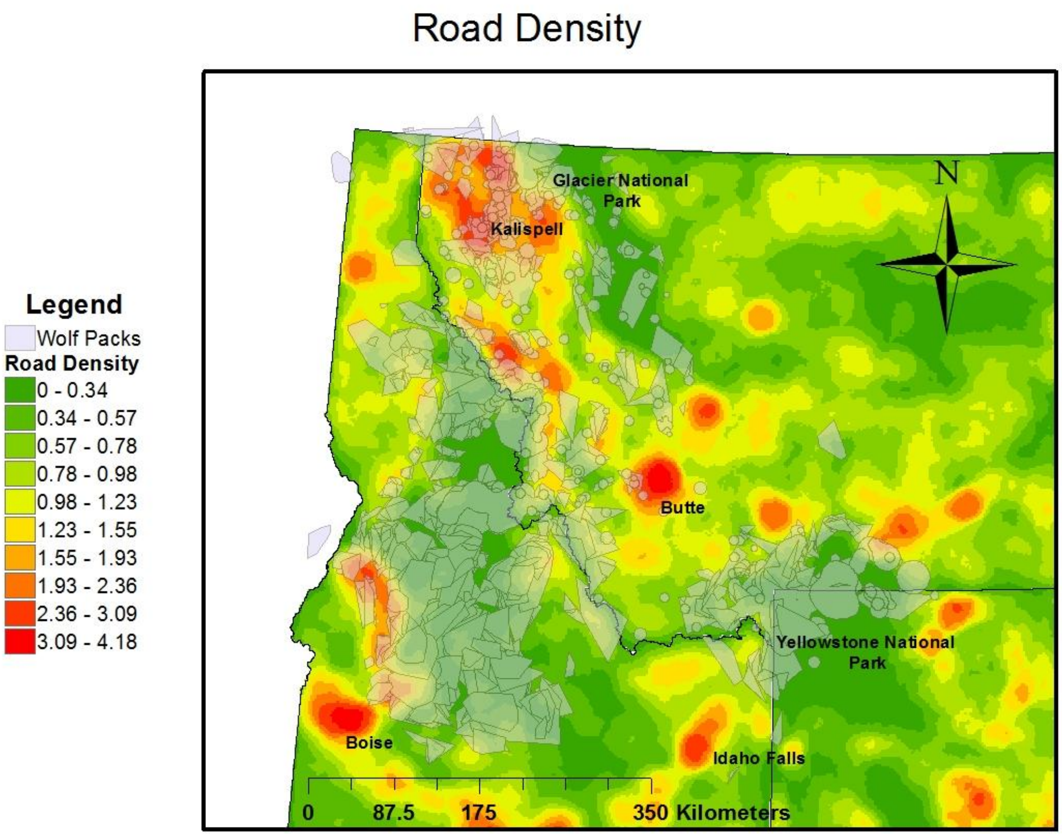


Figure 10: Road density and wolf packs in the Northern Rockies

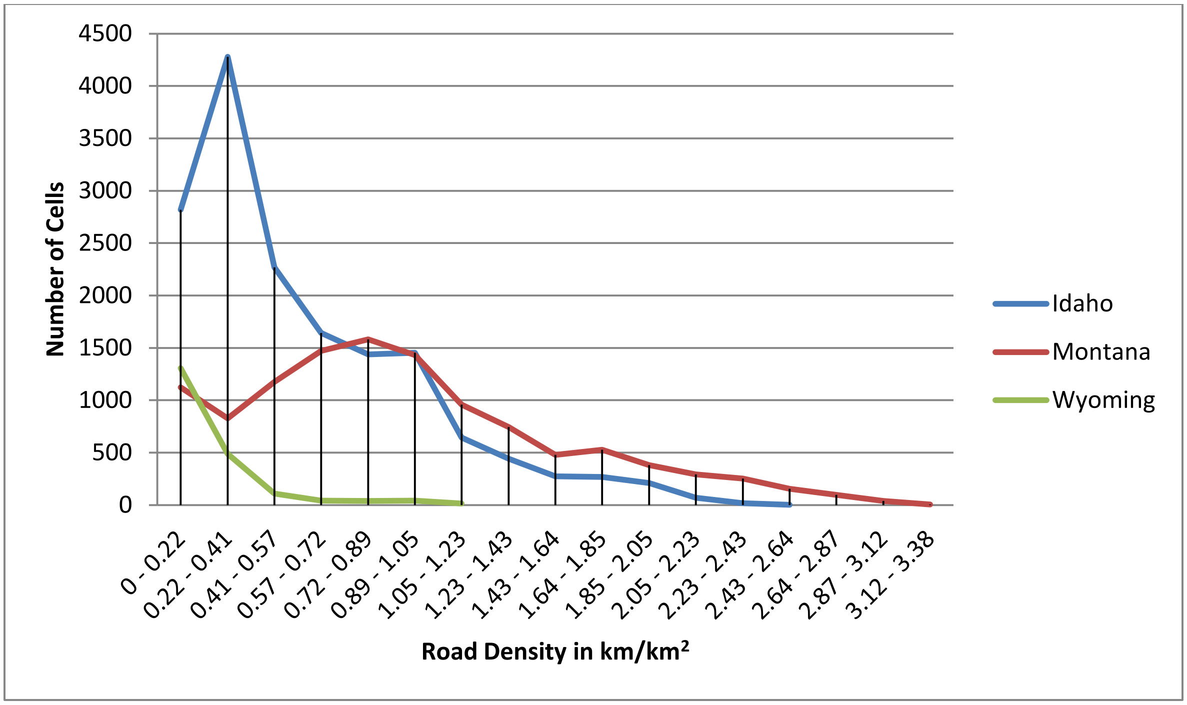


Figure 11: Road density inside wolf pack territories

Development of Friction Surface

Examining the zonal characteristics found within wolf pack territories highlighted sources of greater friction for wolf dispersal. Amplifying individual landscape variables also aided in the development of the final friction surface (figures 12 through 14).

Extraction of the zonal characteristics allowed the creation of graphic plots of landscape variables in wolf territories. Because of their abundance within wolf pack boundaries, minor roads contributed less towards wolf habitat selection and therefore accumulate lower costs for wolf dispersal. If they were a disturbance to wolf movements or habitat selection, then they would not be so prevalent throughout wolf territories. Similarly, natural land cover classes were strongly associated with wolf pack territories and therefore represented a much smaller cost. Slope appeared to be evenly distributed throughout wolf territories, and due to its association with forested land cover, slope received the lowest weight.

Several friction models were developed, but the final model consisted of the following formula:

Table 4: Weight of Landscape Variables in Final Friction Model

Landscape Variable	**Weight**
Anthropogenic Land Cover Features	60%
Distance from Major Roads	15%
Natural Land Cover Features	10%
Distance from Minor Roads	10%
Slope	5%

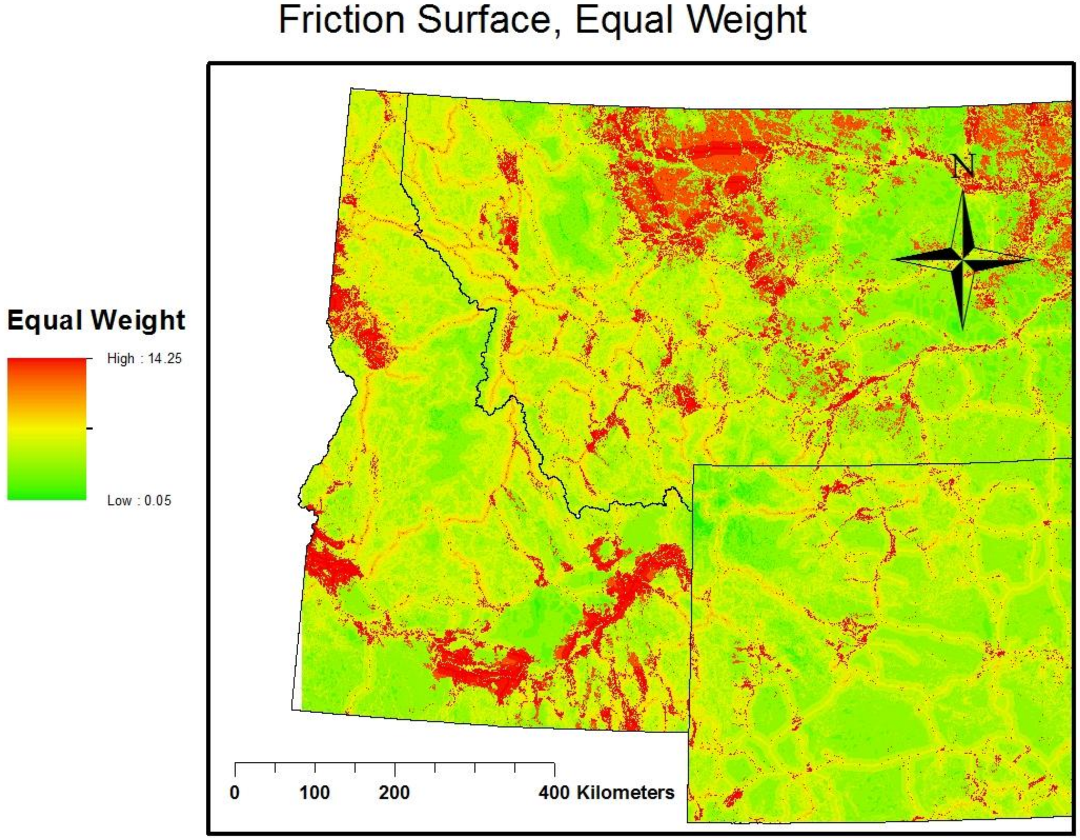


Figure 12: Equally Weighted Friction Model

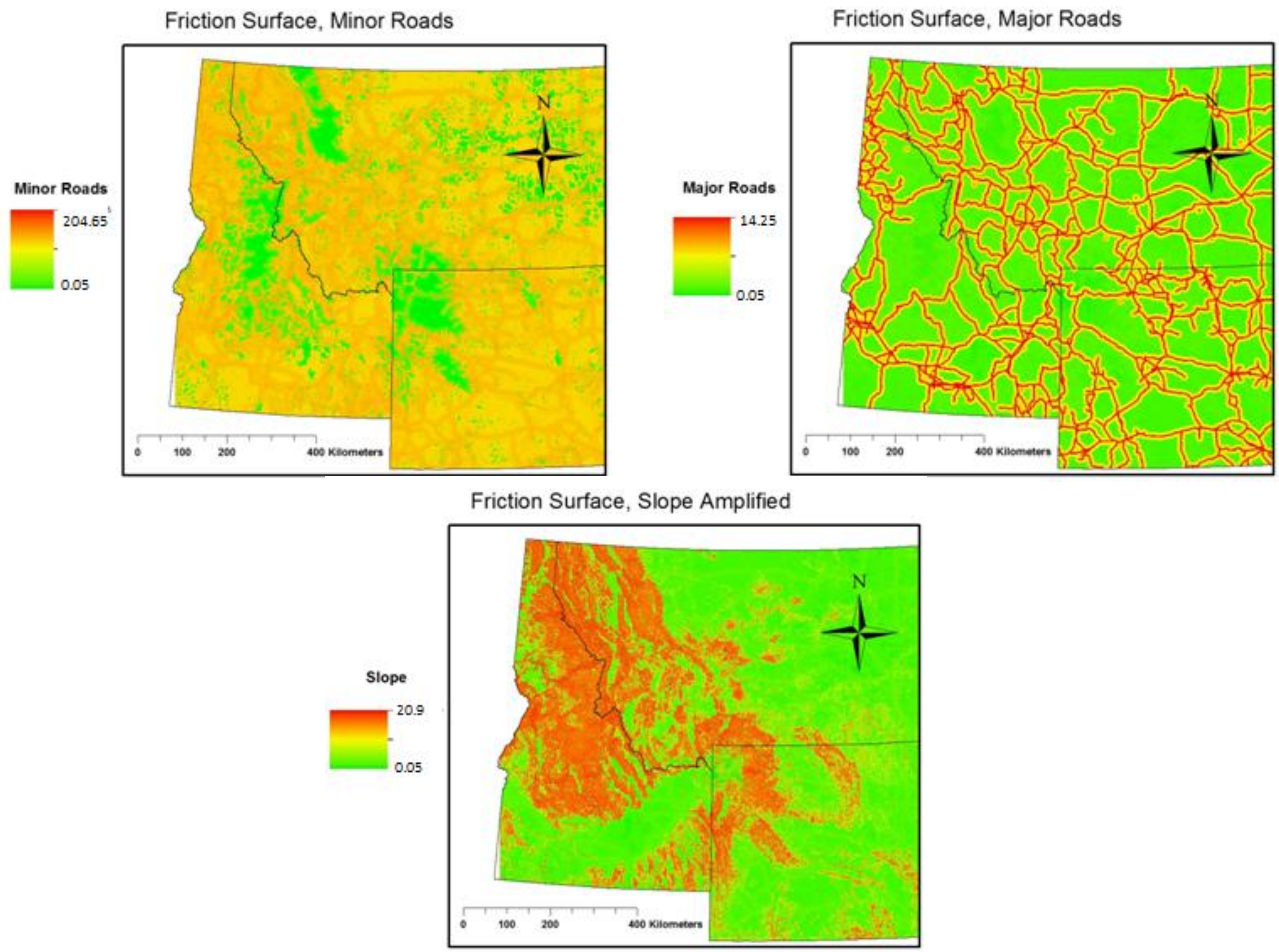


Figure 13: Friction models with each landscape variable amplified using a 95% weight

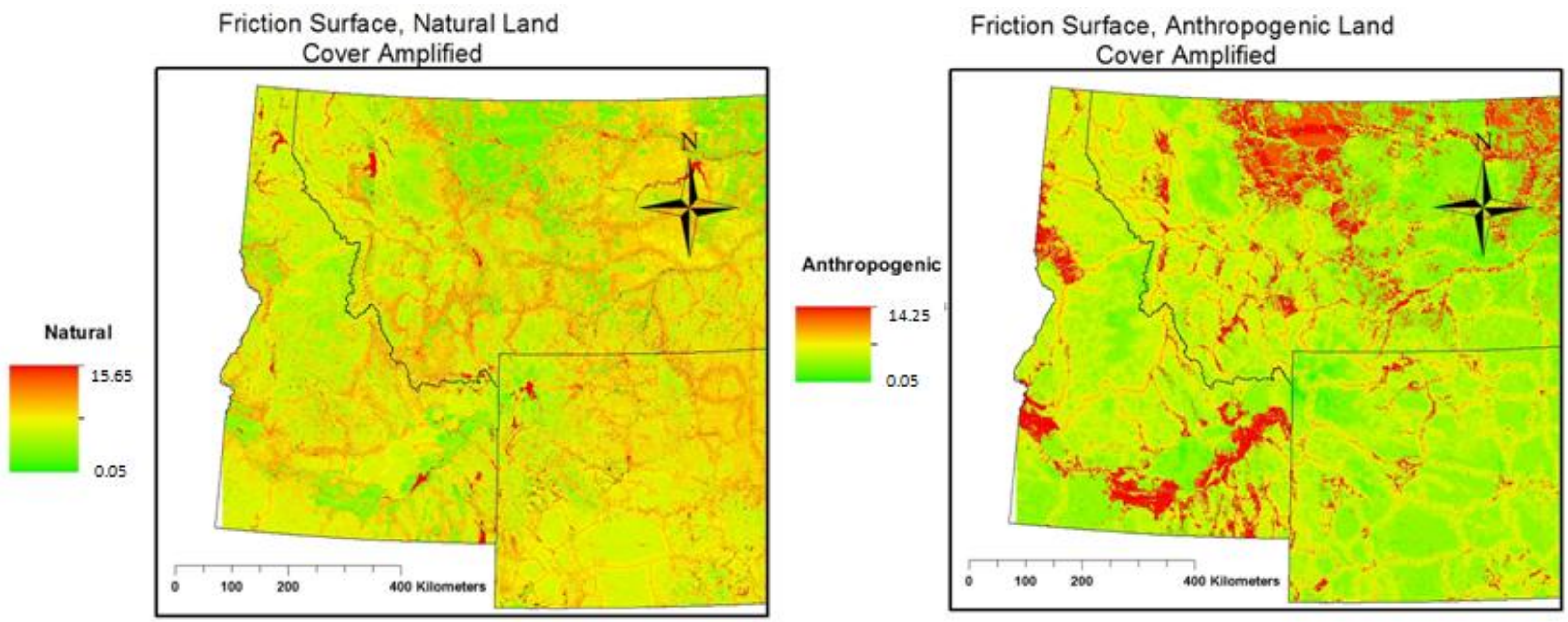
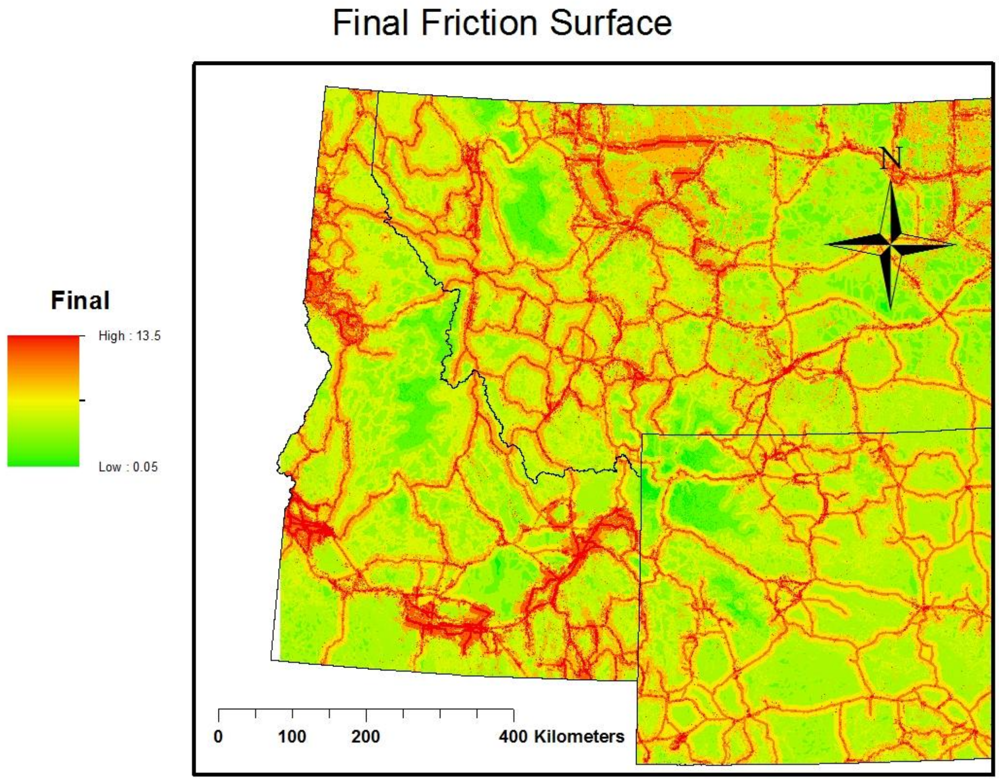


Figure 13: Friction models with each landscape variable amplified using a 95% weight



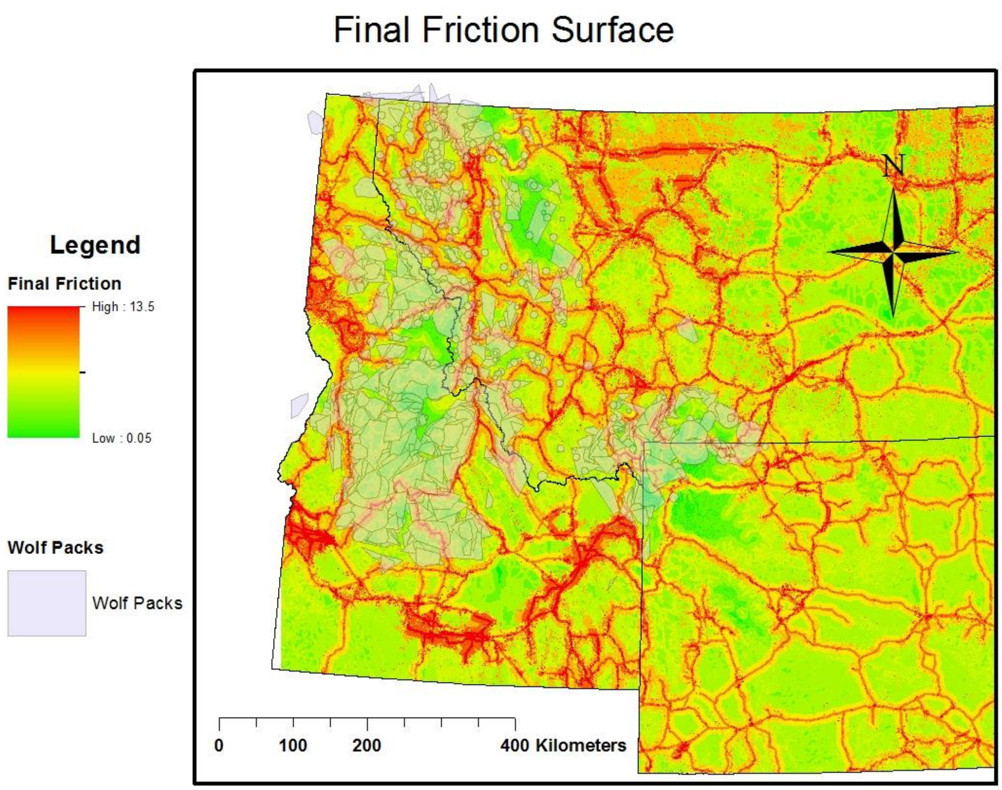


Figure 14: Final friction model, with and without wolf pack territories overlaid

The final friction model was selected because it adequately balanced major roads and land cover classes. Major roads stood out as barrier features, as evidenced by overlaying the compiled wolf pack territories across the friction surface. Most wolf packs existed in areas with fairly low friction, with occasional intersections with major roads or anthropogenic land cover. During the trial and error development of this model, I found that even significant alterations to the weight of different categories did not significantly alter the impact of major roads. Due to their strong influence, anthropogenic land cover classes needed to be assigned a higher weight in order to become apparent.

Least Cost Path Characteristics

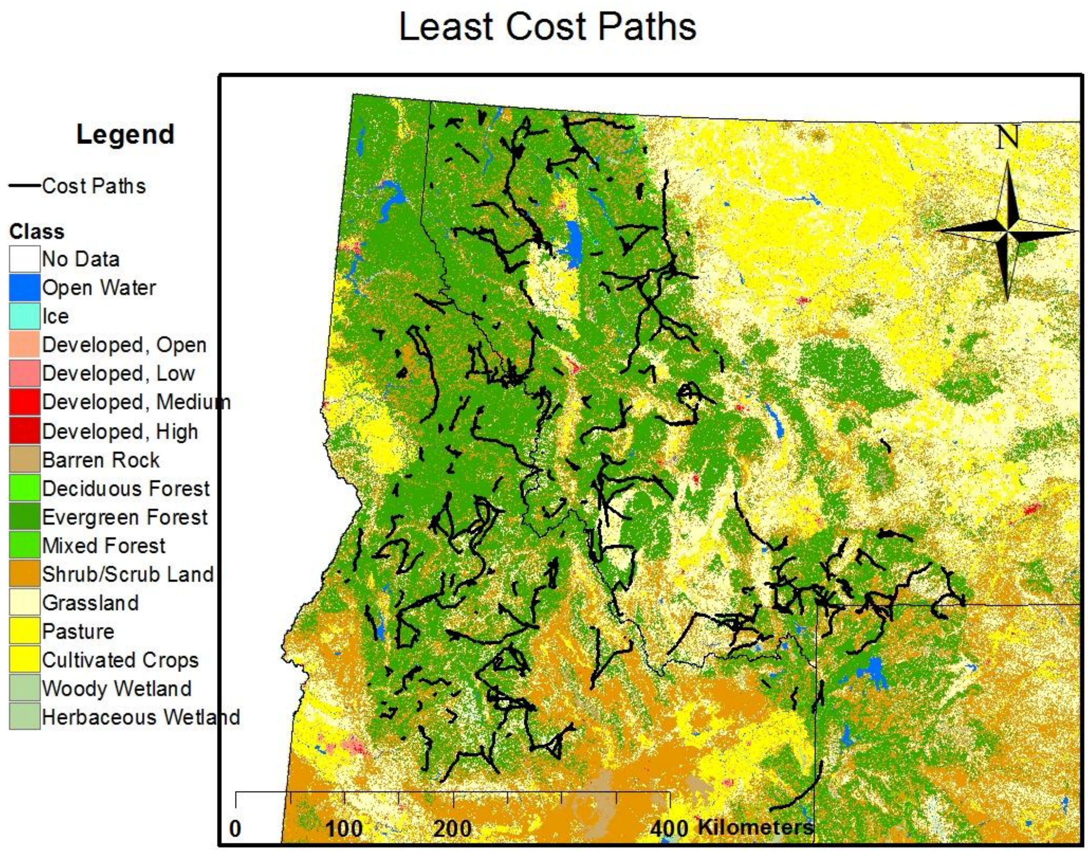


Figure 15: Least Cost Paths across the Northern Rockies

In order to be a valid model, the LCPs needed to display similar traits to the selected wolf habitats. By extracting the intersection between the LCPs from each year was able to graph the landscape variables present in each cell of the generated paths. Extraction revealed that the LCPs follow very closely the same patterns as wolf habitat selection.

LCPs crossed primarily forested land. Evergreen forest accounted for up to 75% of the land cover crossed by LCPs and averaged 65.30% of the LCPs, followed by shrub land and grassland, accounting for up to 30.00% and 14.00% respectively and averaging 21.18% and 10.56% respectively. Again, forested land vastly overshadowed developed land in LCPs. Open developed land accounted for an average of 0.069% of total LCP distance, and Low Developed and Medium Developed land accounted for only 0.033% and 0.0055% respectively. Agricultural land played a similarly vacant role in LCPs, representing an average only 1.14% of total LCP distance (combined between Pasture/Hay and Cultivated Crops).

The makeup of LCPs is likely due to two factors. The abundance of forested land is partly attributable to the fact that the Least Cost Path tool built LCPs between existing wolf pack territories, which are strongly associated with forested land. This fact is tautological, as wolves' ecological habits suggest that they will inhabit remote forested areas. Thus, we must conclude that the friction model adequately represents land cover class as a friction-causing factor. By closely mirroring measured habitat selection, we can infer that the friction model accurately represents wolf movements through more favored terrain and identifies areas that are most important to their dispersal across the landscape.

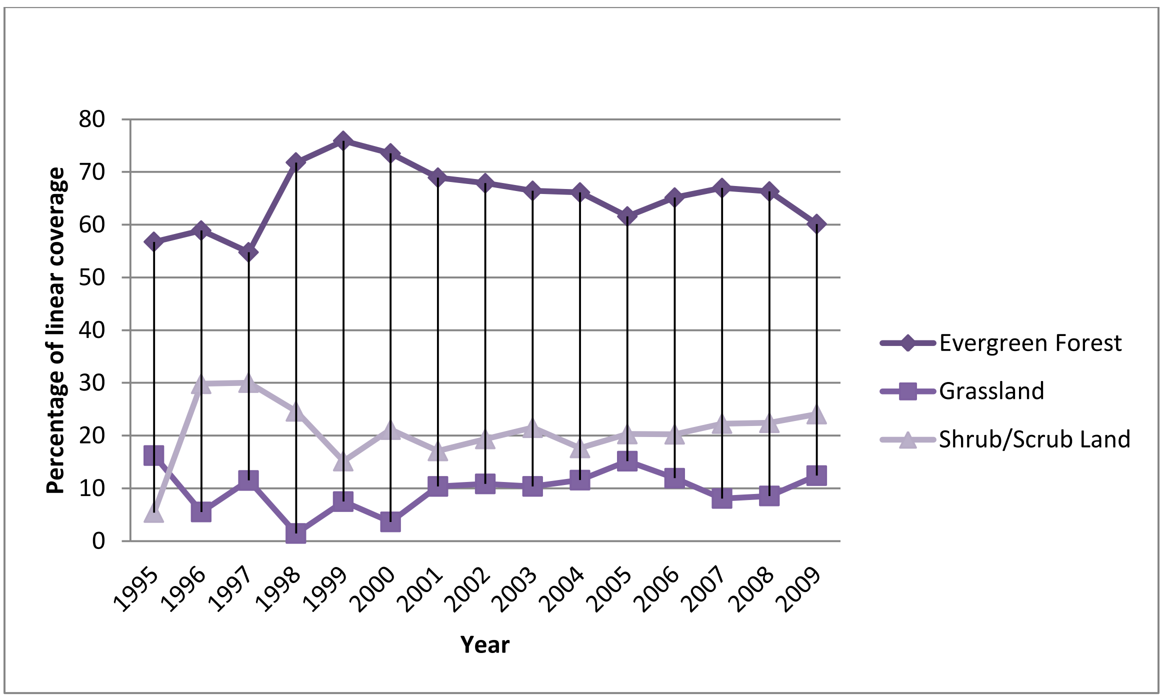


Figure 16: Predominant Land Cover Class as a percentage of LCPs by year

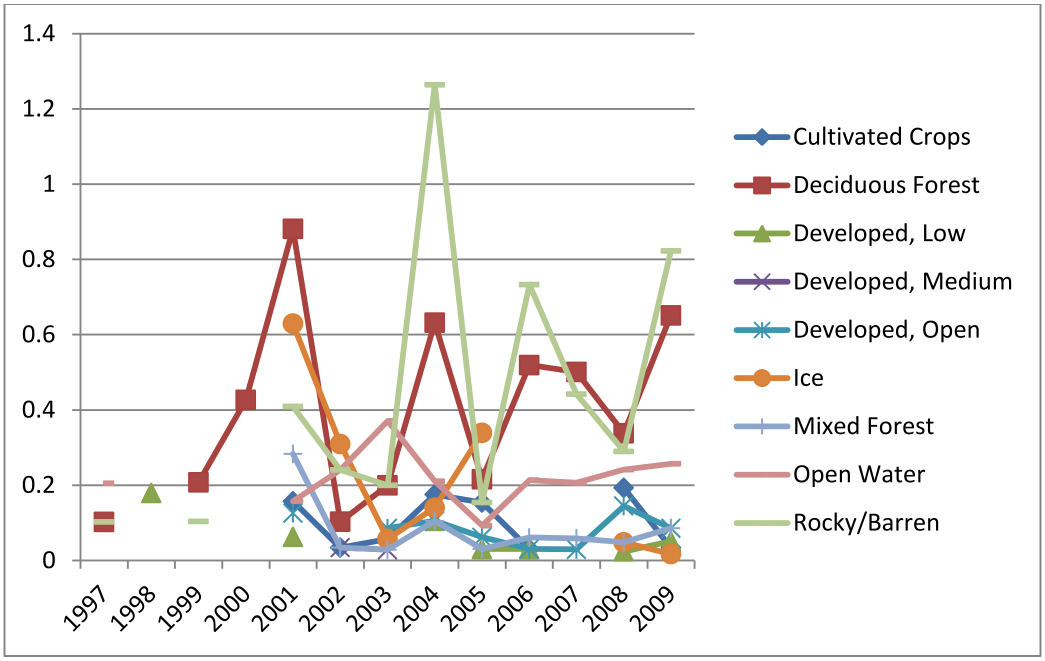


Figure 17: Land Cover Class as a percentage of LCPs by year

Patterns of slope in the LCPs also reflected wolf habitat selection. LCPs consisted primarily of slope between 2.4 % and 15.25%, although the period from 2007 to 2007 saw an increase in slope to 23.27%. Areas of steepest slope (over 71.4%) did seem to act as a barrier to wolf movements in this model, as these slopes accounted for a nearly negligible portion of overall LCP length. The lack of very shallow slopes, less than 2.4%, could partly be attributable to the low weight given to slope in the model, but will also be due to the strong relationship of shallow slopes with anthropogenic land cover classes. The fact that slopes between 2.4% and 15.25% are so highly represented, while incredibly steep slopes (over 40%) are less so, suggests that the friction model adequately implements slope as a friction-causing agent.

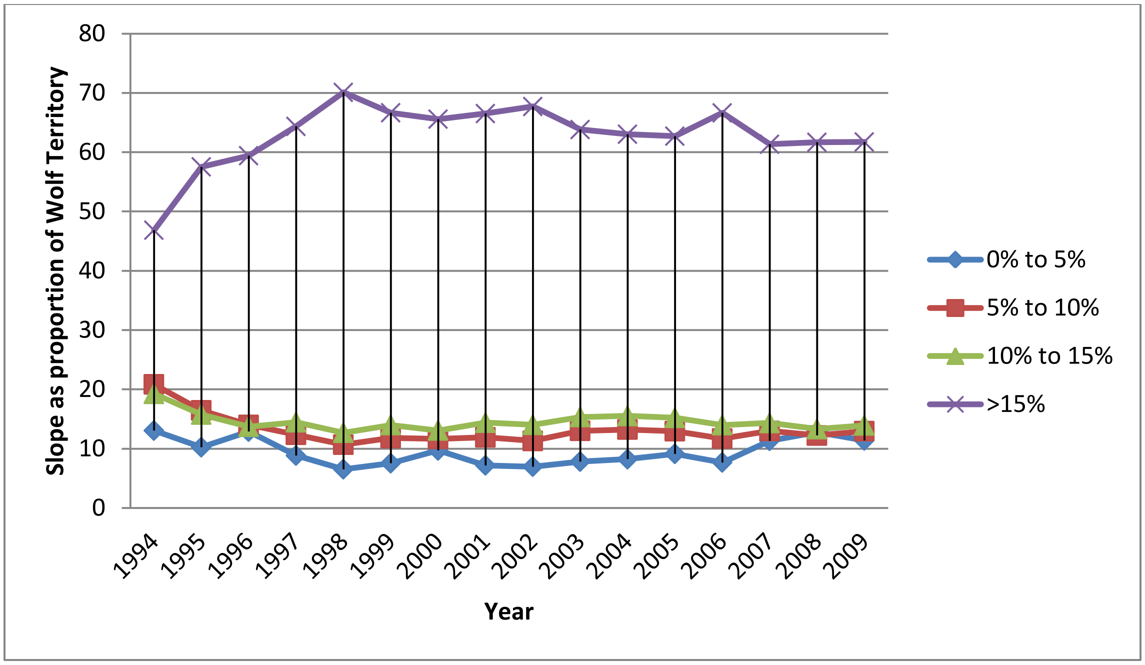


Figure 18: Least Cost Paths crossing sloped terrain

LCPs were equally proximal to minor roads as wolf pack territories. LCPs were frequently within one mile of a minor road. This was inevitable, as minor roads were so prevalent across the landscape within and around wolf pack territories. Smaller roads represent less of a risk for wolves, as they are a smaller disturbance on the landscape. Less traffic, not to mention narrower widths, means wolves can cross minor roads with less risk. Thus the proximity of LCPs to minor roads is less surprising.

Major roads, however, appear to act as more of a barrier, as most LCPs fall outside of 5 miles from major roads. Nevertheless, wolves are able to cross major highways. This result agrees with prior wolf studies that found that major roads act as permeable barriers.

Figure 19: Least Cost Paths' proximity to Minor Roads

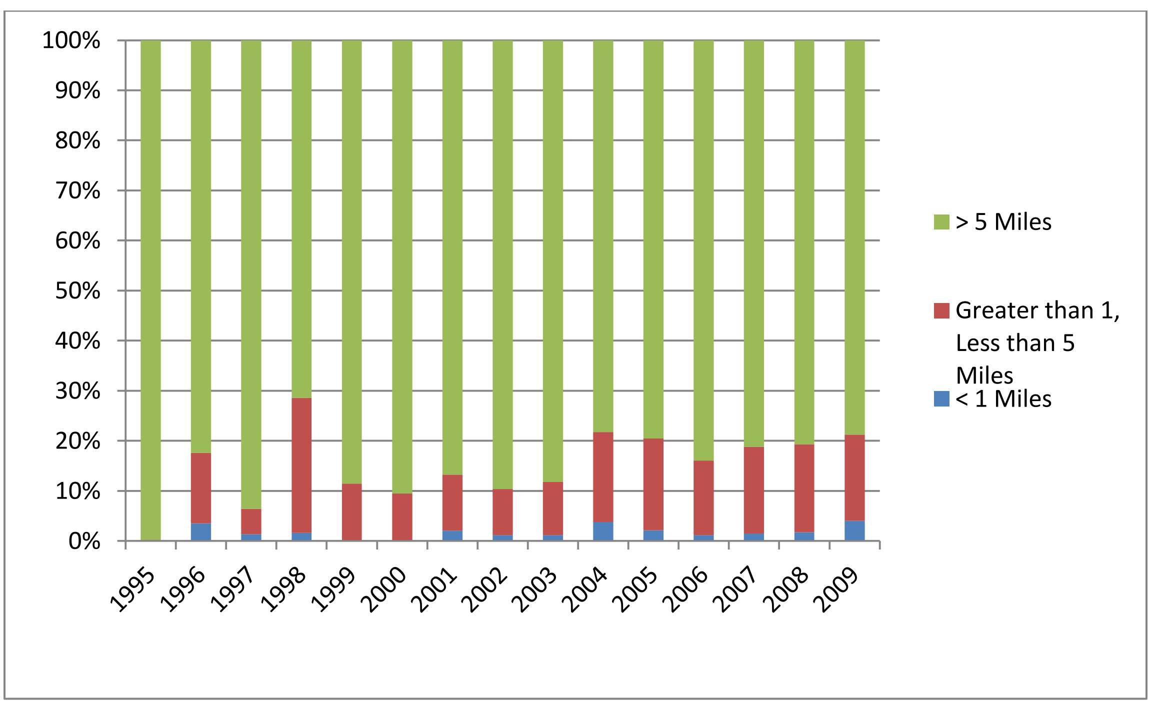


Figure 20: Least Cost Paths' proximity to Major Roads

Buffering Least Cost Paths

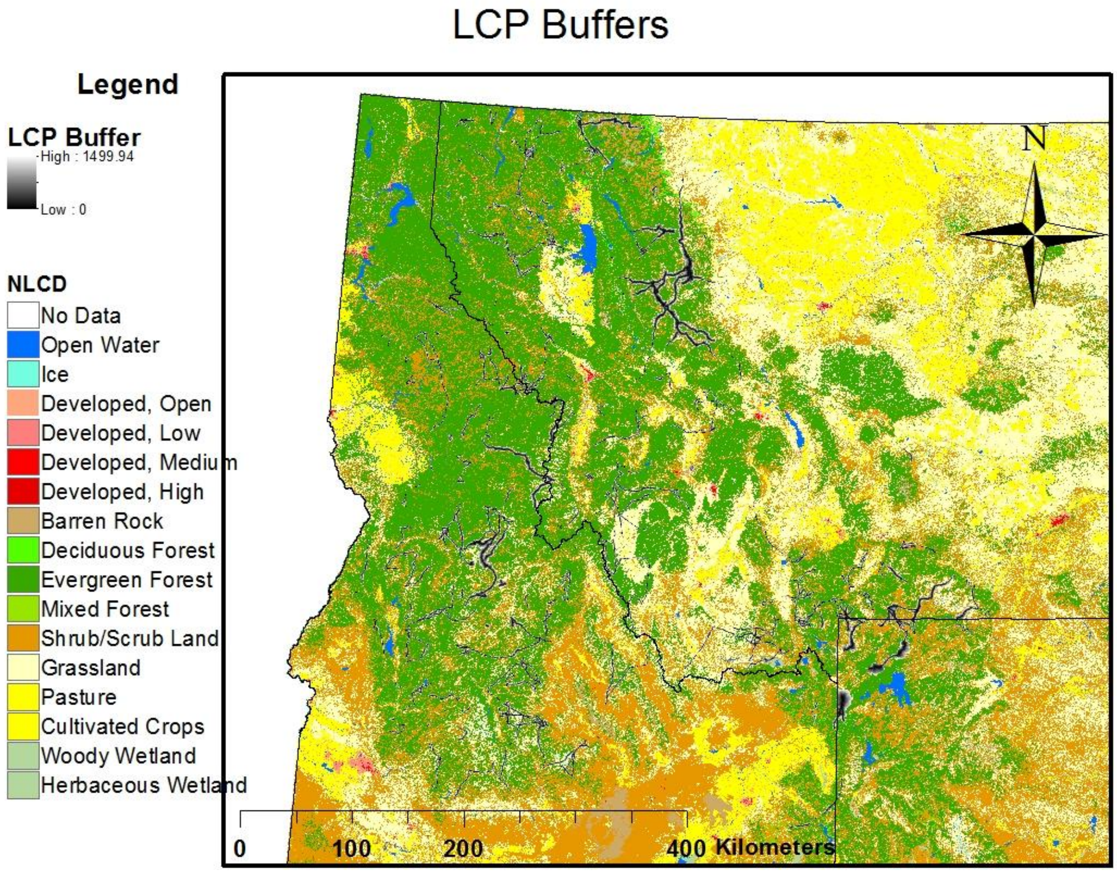


Figure 21: Least Cost Path buffers across the Northern Rockies

The buffers around the LCPs followed similar trends as the LCPs, expanding greatly into more forested areas and avoiding major roads. The largest buffers around LCPs unexpectedly occurred inside the boundaries of Yellowstone National Park. This area represents one of the largest protected habitats for wolves in the Northern Rockies, with the lowest road density and prime habitat by way of forests and availability of prey. This area was also a starting point for wolf reintroduction, as some of the first Northern Rockies wolves were released in the park. The park is surrounded on all sides by protected lands, including the Grand Teton National Park and the Custer, Gallatin, and Targhee National Forests. These areas had similarly large buffers surrounding LCPs, representing areas of wide wolf habitat.

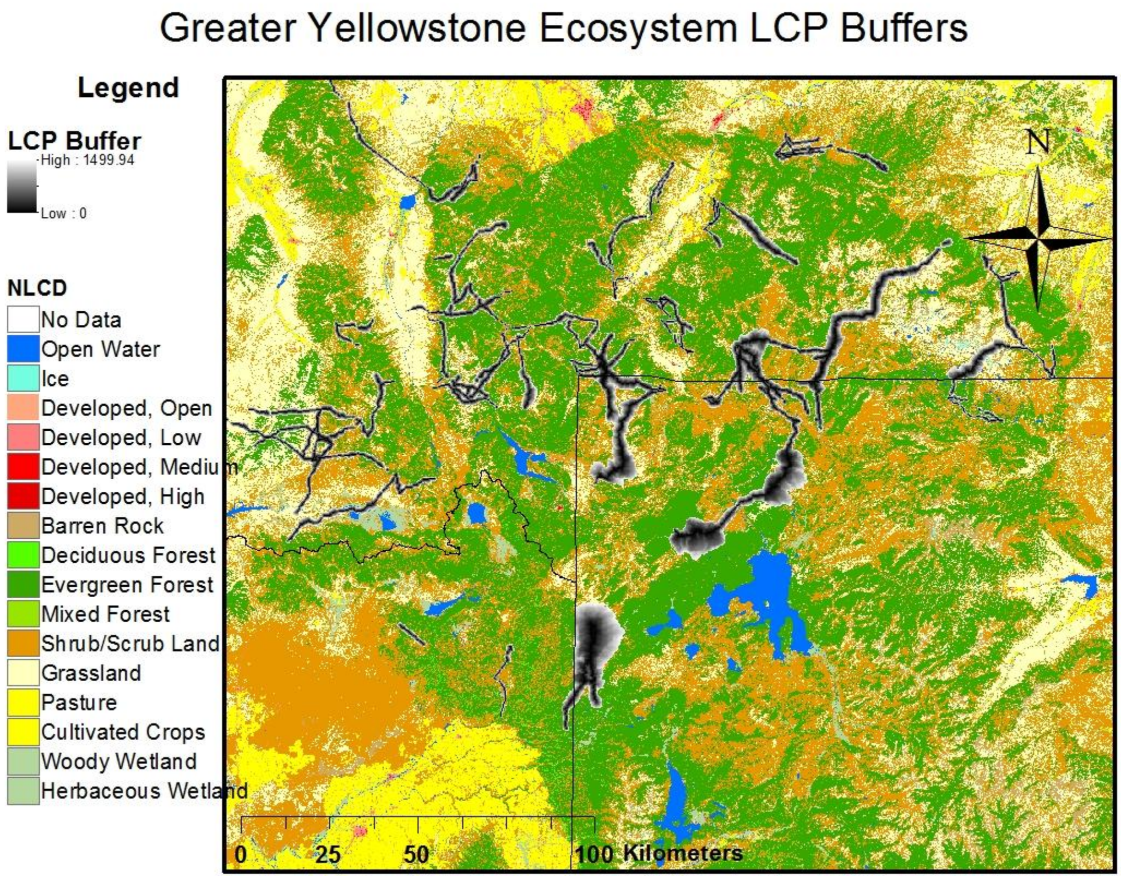


Figure 22: LCP Buffers in the greater Yellowstone ecosystem

Similarly large buffers were found in the Flathead National Forest in Montana, just south of Glacier National Park. This heavily forested area is bound on its eastern and western sides by agricultural and developed land, but Glacier National Park to the north opens wolf dispersal towards Idaho through the Kootenai National Forest, while wolves can disperse south and southwest into Bitterroot and Lolo National Forests respectively. While wolves have been found outside of these areas, this zone along western Montana represents the most vital areas for wolves in that state. Central Idaho also contained large buffer zones around LCPs due to the extensive national forests in that area. The Nez Perce National Forest contained the largest number of LCPs, along with the widest buffers. Central Idaho contains the longest LCPs in the region, suggesting that this zone represents the lowest friction for wolf movements.

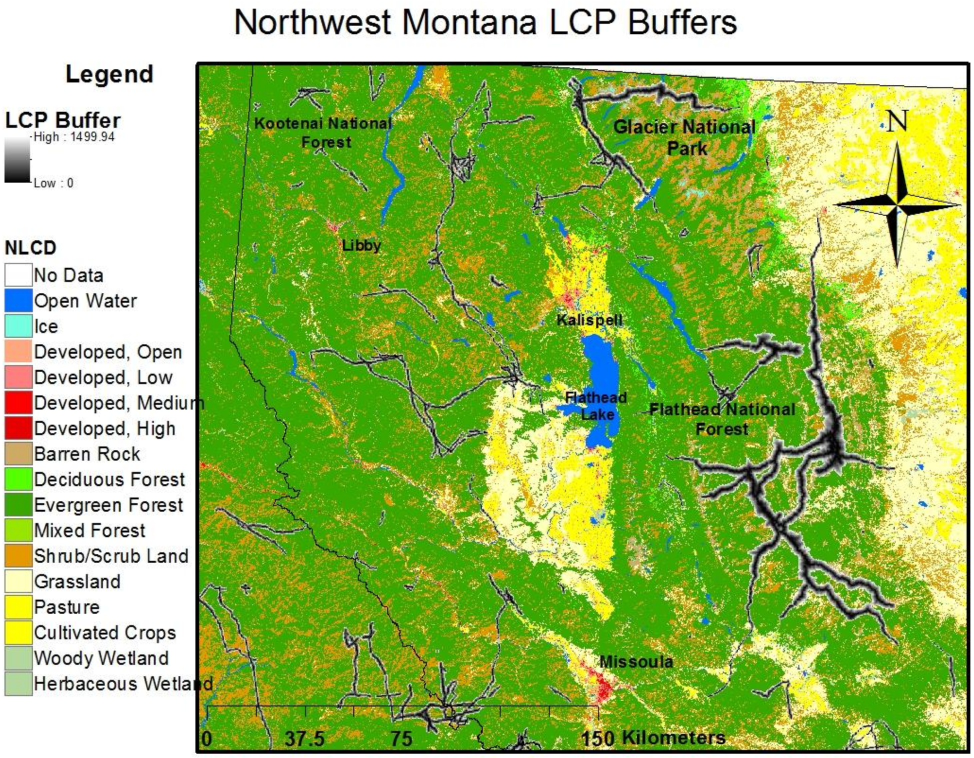


Figure 23: LCP Buffers in Northwestern Montana

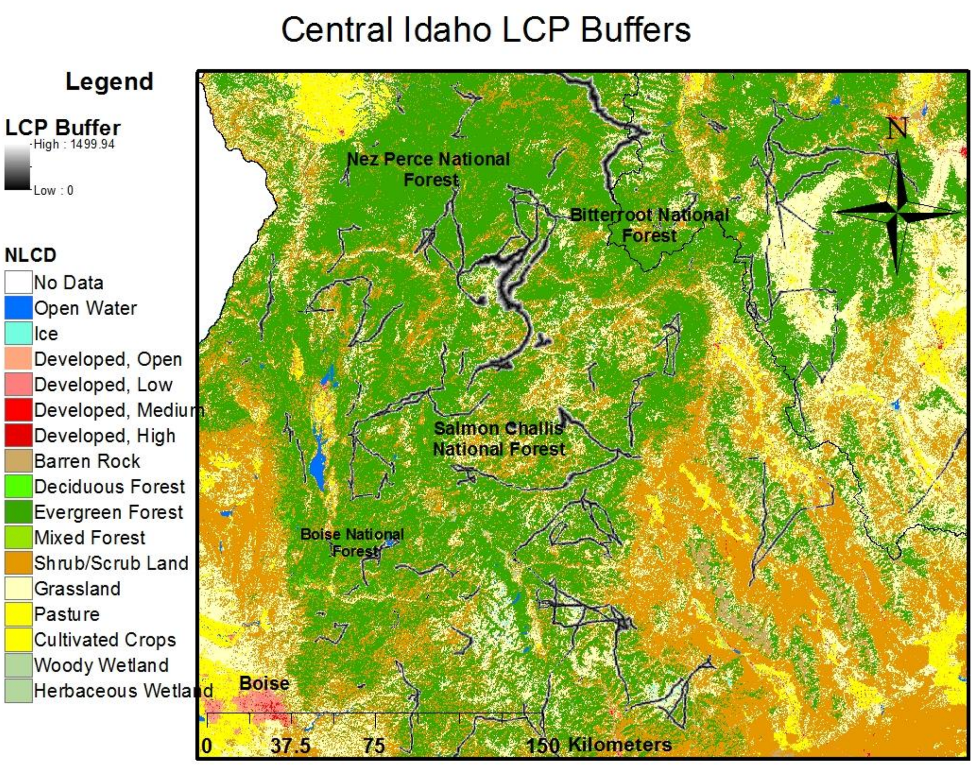


Figure 24: LCP Buffers in Central Idaho

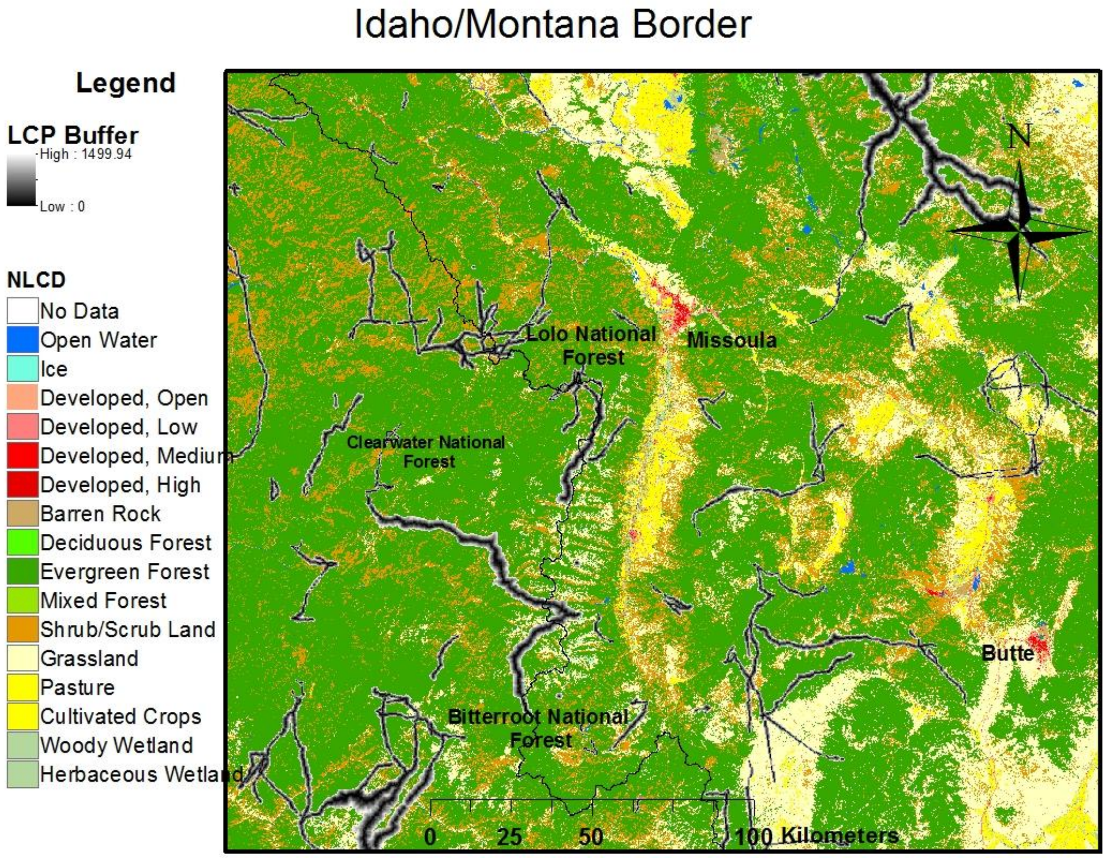


Figure 25: LCP buffers along the Idaho/Montana border

Implications for Wolf Management

The wolf population of the Northern Rockies has displayed several spatial relationships with the landscape features involved in this study. The most dominant predictor of wolf habitat selection was land cover class. Wolves selected for forested landscapes to the nearly complete exclusion of human modified lands. As expected, land cover classes modified by humans as a percentage of wolf territories decreased with increasing human presence. Highly developed land accounted for a negligible portion of wolf territories, while agricultural land accounted for just over 1% of total wolf territory.

This correlation holds with our prior understanding of wolf habits. Wolves are wary of humans and limit their exposure to risk, and thus select lands removed from human presence. In the Northern Rockies, this means selecting lands in the forested areas of central Idaho and western Montana and Wyoming. In general, the Northern Rockies wolf population has followed the patterns in land cover selection established by past studies. Furthermore, this suggests that conflict between wolves and humans will be isolated and infrequent.

The core Northern Rockies areas where wolves are most common are remote and densely forested, and are also strongly correlated with more mountainous terrain. Thus, wolves appear to have adapted to much steeper slope than originally expected. Wolf territories contained slopes over 70% grade, which is nearly impassable for many creatures. Wolves tend to have much longer legs and larger paws than domesticated canines, making them better suited for rugged mountainous terrain and allowing them to flourish in the Northern Rockies. Unfortunately, this study did not have the ability to examine fine scale wolf habitat selection. It would be beneficial to follow this study with a more intensive daily monitoring study to determine landscape use patterns for wolves on a daily, monthly, and seasonal basis.

While forested land was the greatest predictor of wolf habitat use, there are inevitably some packs that existed near agricultural and developed land, which often led to conflict with humans. However, this study shows that conflict with humans is not widespread, and will be limited to certain areas. The area around Kalispell, MT, for instance, is an agricultural area in close proximity to wolves. The Bozeman, MT, area, as well, has several wolf packs and LCPs in the vicinity. In Idaho, people living nearest the national forests will be most at risk for conflict with wolves.

In 2009, livestock loss, the most direct form of conflict between humans and wolves, was limited to 192 cattle, 721 sheep, 24 dogs, 4 llamas, and 4 goats. In 2010, cattle losses amounted to 199, while sheep and dog losses dropped significantly to 249 and 2 respectively. Cattle losses again held steady in 2011 (193 losses), and sheep losses dropped to 162. These trends show us that wolf depredation on livestock is limited, and wolves have largely remained isolated from humans.

Wolves' interactions with roads revealed the most interesting patterns. Surprisingly, roads were not as strong of an indicator of exposure to humans as originally hypothesized. Road densities were mostly on par with expectations based on prior studies. I expected proximity to roads to play a larger role in wolf habitat selection, but minor roads were more abundant than anticipated and thus wolves had no recourse. Portions of northern Montana showed unusual landscape characteristics for wolf habitat. This area between the Montana/Idaho border and Glacier National Park has long been home to wolf packs. Glacier National Park was home to naturally reintroduced wolves dispersing from Canada into the US in the 1980s, and the reintroduced population quickly dispersed into the region from Yellowstone National Park in 1995 (U.S. Fish and Wildlife Service 1987). Surprisingly, this area shows a much higher density of roads yet has still been home to several packs and serves as a dispersal corridor between Idaho and Montana.

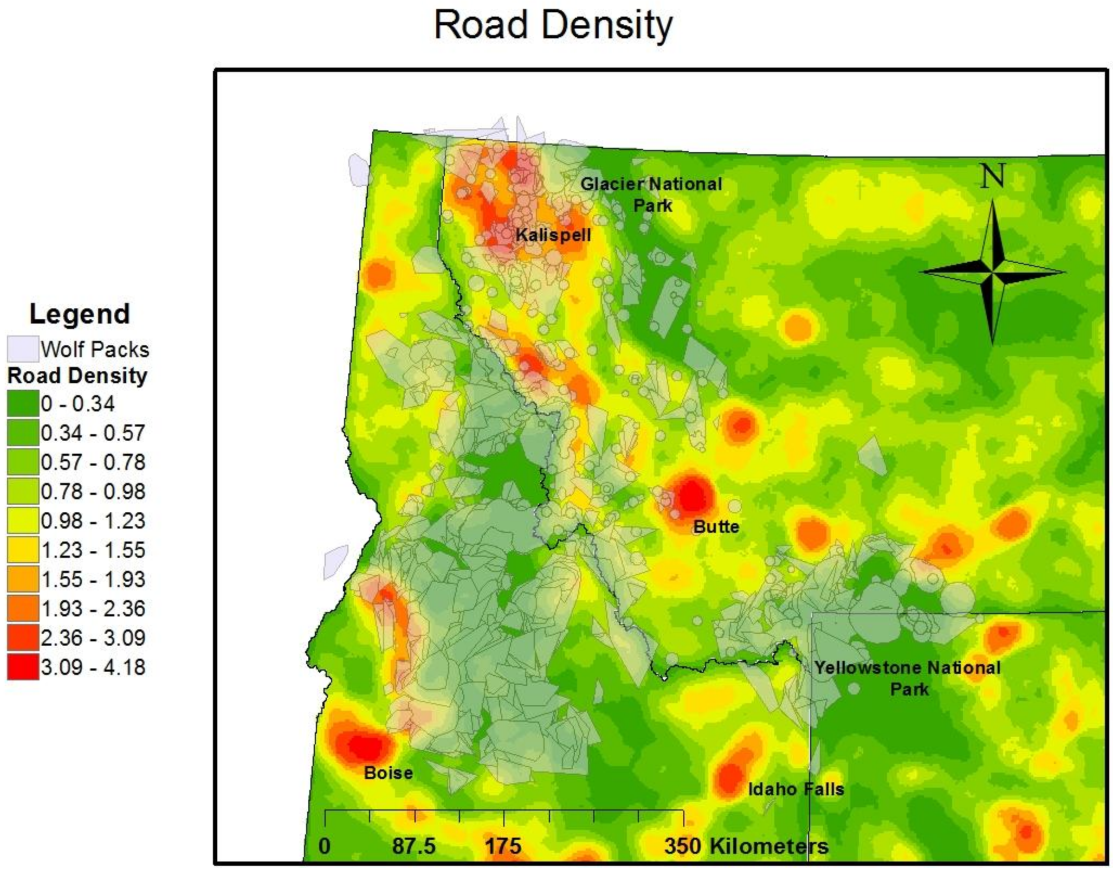


Figure 26: Road density and wolf packs in the Northern Rockies

Major roads did serve as a strong predictor of wolf territory selection. Wolf pack territories tended to be greater than 8 km from major highways, and LCPs rarely crossed major roads. This supports the notion that major highways serve as permeable barriers. Research in Spain has come to the same conclusion (Colino-Rabanal, Lizana and Peris 2011), finding that major highways are a major source of mortality for wolves. Indeed, on average 3 wolves are killed by vehicle collisions each year (U.S. Fish and Wildlife Service 2010).

Certain roads stood out as barriers, while others appeared more permeable. The national forests of central Idaho open southwards onto plains of grassland, which is dominated by agriculture. Along this plain, Interstates 86 and 84 run east to west connecting the major cities of Idaho Falls, Pocatello, Twin Falls, and Boise. Due to its surrounding area, this road acts as a barrier to wolf dispersal southward. In Montana, however, Interstate 90 seems to be far more permeable. This road runs west through Billings and Bozeman, connecting with Interstate 15 and then curving northwest towards Missoula and crossing into the northern Idaho panhandle. Several wolf packs exist near this major road and many LCPs cross over it, showing it to be a permeable barrier.

The buffer created around LCPs revealed several areas of interest for wolf movements, and also highlighted areas of potential conflict. As expected, southern Idaho remained mostly devoid of wolf dispersal corridors. However, Yellowstone National Park serves as a source for wolf dispersal westward. A large cluster of LCPs and their buffers were located on the northern and western sides of Yellowstone National Park.

Wyoming's management plan designates Yellowstone National Park, the surrounding National Forest, and the Wind River tribal land as designated wolf habitat where hunting wolves will be seasonal. Outside of this area, wolves can be shot on sight. Thus, this area is thus the most important wolf habitat in the state of Wyoming, and will prove vital to establishing wolf populations in the Southern Rockies states of Utah and Colorado. Wolves are able to disperse into Washington and Oregon from the forested lands of northern Idaho, but southern Idaho is dominated by larger urban centers and agricultural land which runs along Interstate 84. The Wind River Tribal Lands and Bridger National Forest, however, extend south near the border of Wyoming and Utah. This will provide wolves with a potential route around the more populated areas of Idaho into northern Utah and the Southern Rockies.

In Figure 26, a cost path extends from the Grand Teton National Park southwest into Idaho, showing a route that circumnavigates the developed swath along Interstate 84 in Idaho. Wolves following this path could disperse into northeastern Utah towards Bear Lake and the Uinta-Wasatch-Cache National Forest. This is not guaranteed to occur, nor is their dispersal into Utah guaranteed to result in the establishment of a large population. This corner of Utah is cordoned off by interstate freeways, and the national forest extends towards the metropolitan areas of Ogden and Salt Lake City. Nevertheless, wolves have shown that they can and will cross major highways, so this may not halt their expansion entirely.

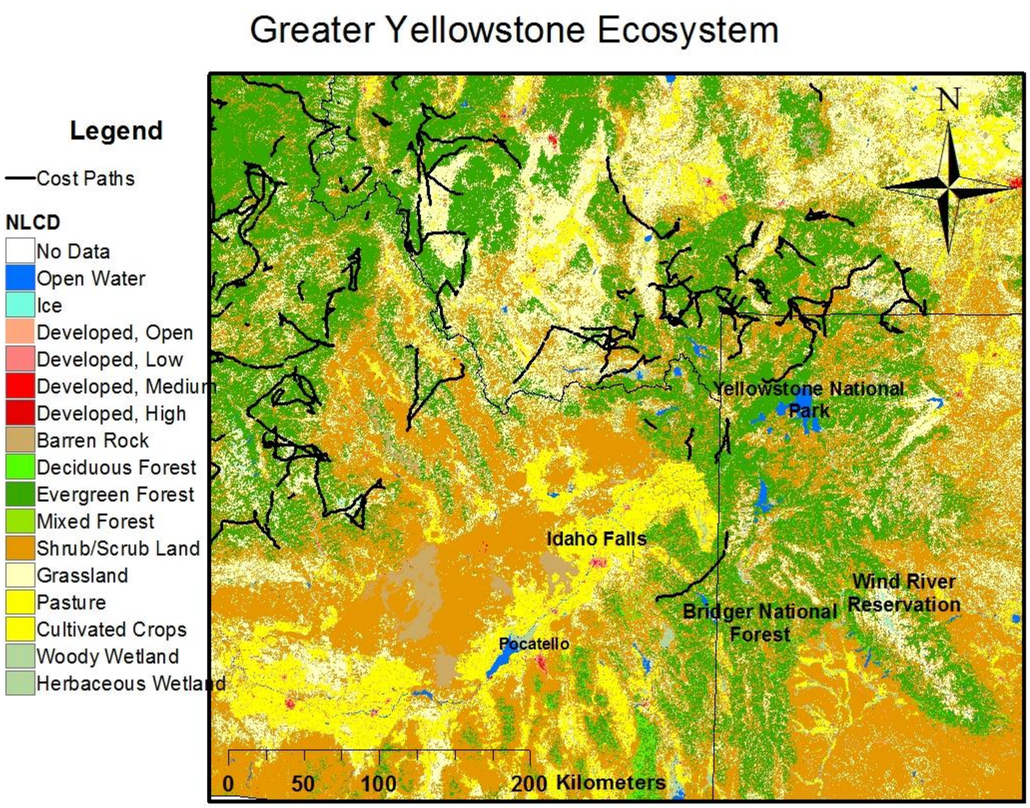


Figure 27: Least Cost Paths in the greater Yellowstone ecosystem

Cost analysis has also shown central and northern Idaho to be the most connected and accessible of the three states. Wolves have occupied western Montana and the northwestern corner of Wyoming, but agricultural land to the east acts as a barrier to their dispersal. In Montana, lands east of Glacier National Park open to plains land, which is used primarily for ranching and agriculture and would not be ideal habitat for wolves both in terms of conflict with humans but also availability of prey. This same pattern is particularly strong in Wyoming, where protecting agriculture was the impetus for the classification of wolves as a predatory species, which under Wyoming law allows people to hunt and kill wolves without license in a majority of the state (Wyoming Game and Fish Commission 2011). Wolves in these states therefore will rely on dispersal into and out of Idaho in the future.

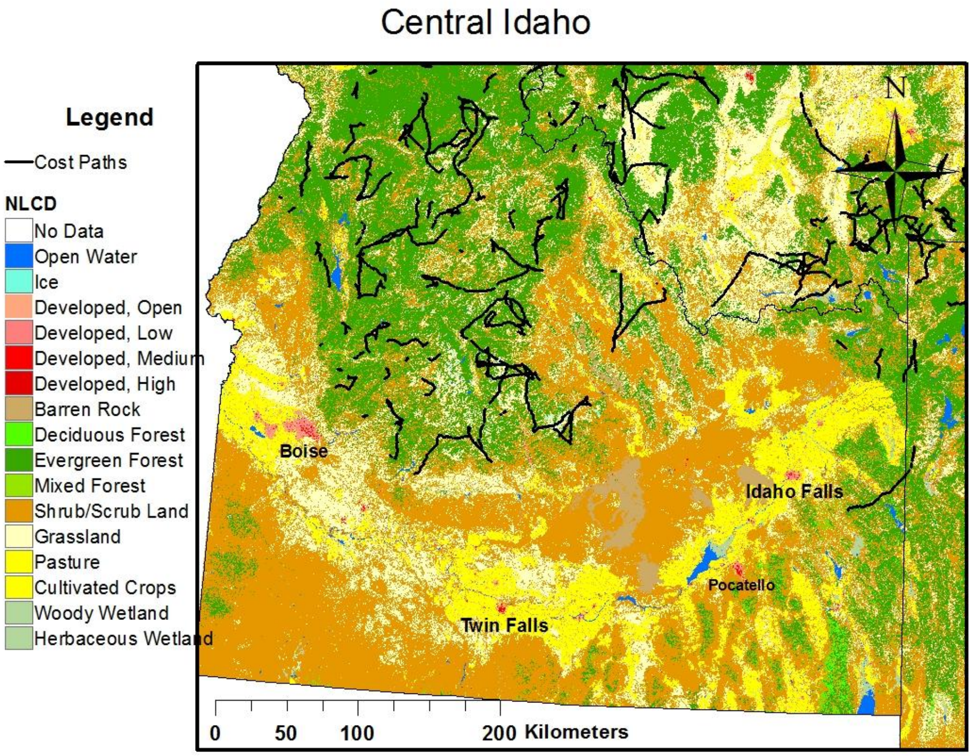


Figure 28: Least Cost Paths in Central Idaho

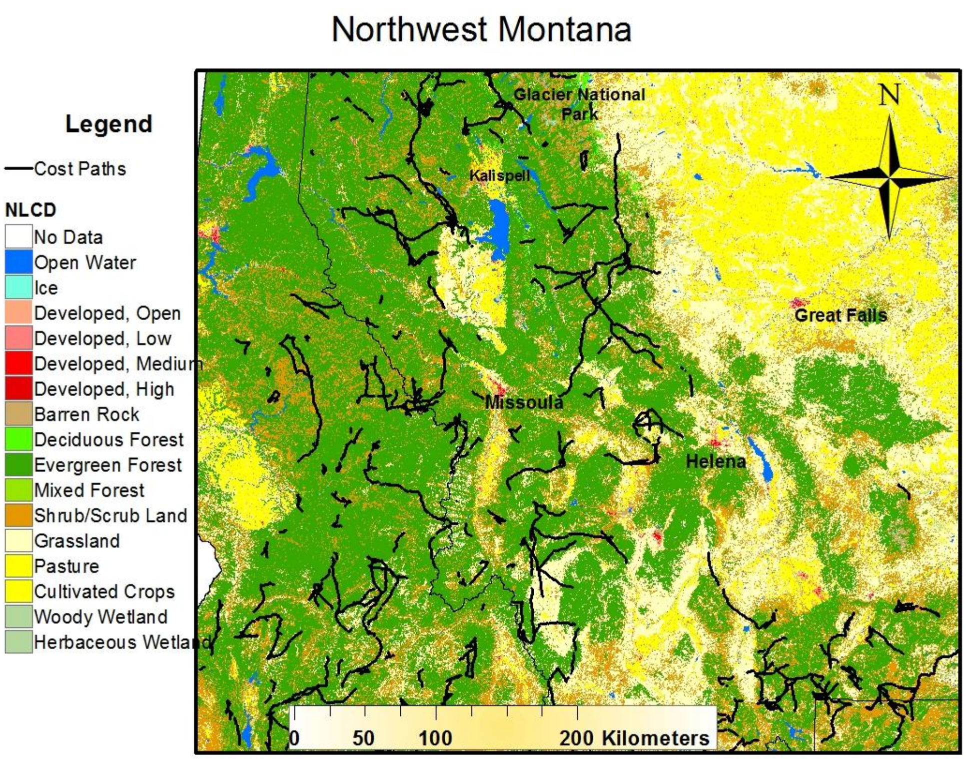


Figure 29: Least Cost Paths in Western Montana

The border between Montana and Idaho is marked by extensive national forests. The Lolo, Clearwater, and Bitterroot National Forests possess several LCPs. Yellowstone and Grand Teton National Parks, the Gros Venture Wilderness area, and the Bridger National Forest in Wyoming contain the largest LCP buffers. These areas all abut the Idaho border, and LCPs from these states frequently cross into Idaho. In central Idaho, the Nez Perce, Sawtooth, and Salmon-Challis National Forests are home to the greatest clustering of LCPs.

Thus, Idaho wildlife policy will to a large extent determine the long term viability of wolves in the region. Idaho and Montana have taken similar approaches to wolf management. Both states allow wolf hunting, but only during fall and winter to avoid mating season and states set a quota of how many wolves can be taken. Both states also monitor several Game Management Units (GMUs) in which hunting can be halted if hunters meet wolf harvest quotas for that area. Still, pressure from elk hunting groups has of this year forced wildlife managers to revise hunting seasons and increase quotas. This was largely in response to a shortfall in the number of wolves removed in the first wolf hunting season in 2011. Harvest quotas were not met within the hunting season, and the wolf population actually increased from 2011 to 2012. Still, the looming shadow of public pressure reminds us that wolves are vulnerable to shifts in policy.

For this reason, the three states will need to actively collaborate on wolf management. The fact that the core wolf habitats for the three states exist along the borders means that wolves will frequently cross state lines. Federal guidelines mandate a minimum of 30 breeding pairs across the region, and all three states have outlined plans to manage for a minimum of 10 breeding pairs in their respective states. Barring ecological catastrophe the wolf population is safe and stable for the near future, but shifts in policy could threaten wolves in the future. Idaho's wolf management program will be vital in maintaining connectivity among the three states. The national forests in central Idaho represent the largest area of suitable wolf habitat. Hunting in Idaho, if unchecked, could isolate that core from wolves in Montana and Wyoming. A healthy wolf population depends upon the continued exchange of genetic information that will only be preserved if wolves from all three states are capable of dispersing and interbreeding.

The study presented here gives wildlife managers additional information to guide their management efforts, and illustrates the importance of a regional outlook for the wolf population. It is not adequate to manage wolves on a state by state basis, as the regional population is a cohesive, dynamic unit. The LCPs developed in this study show that wolves depend on crossing state borders for their movements and dispersal. The dominant limiting factor to wolf population growth is conflict with humans, and the spatial constraints imposed by humans on the Northern Rockies population make the preservation of the LCPs shown in this study all the more important. Wolves are unable to safely disperse into eastern Montana and Wyoming, making movements in and through Idaho vital to those states' wolves' dispersal.

XII. CONCLUSION

This study has found that wolves of the Northern Rockies follow many of the patterns found in past research efforts, with the exception of their tolerance of roads. Northern Rockies wolves have adapted to live in an area with a greater human population. Many wolf territories were within less than 8 km from minor roads, though major roads were less represented within wolf territories. The dominant factor determining wolf habitat selection was land cover class. Wolves strongly selected for forest land cover classes, while developed and agricultural lands represented a nearly negligible portion of land cover inside wolf territories. Steep slope did not serve as a strong indicator of wolf habitat. Prior studies showed that wolves utilized areas of shallow slope, but in the Northern Rockies forested areas tended to be associated with steeper mountainous terrain, and thus slope was more evenly distributed in wolf territories. Shallower slopes tended to be more dominated by agricultural and developed land, where human presence would exclude wolves.

The friction model developed for this study closely reflected wolf habitat selection. Friction values inside wolf territories were lower than outside territory boundaries, and the LCPs developed from the friction surface closely mirrored wolf habitat selection. The LCPs also highlighted several areas that are vital to wolf movement and survival. Central Idaho and the Montana/Idaho border were the most interconnected areas of the Northern Rockies. The buffering methods employed highlighted several areas important to wolf movements. Buffering found that northwestern Montana and the greater Yellowstone ecosystem contain the largest buffers, representing some of the lowest friction in the region. Central Idaho, Northwest Montana, and Yellowstone National Park represent three distinct core areas for wolf dispersal, but all three of these regions are highly interconnected, and the corridors found in this study need to be protected in order to ensure wolf movements across the landscape.

Wolves of the Northern Rockies have shown remarkable resilience since their reintroduction. They have reasserted themselves as the dominant predator of the Northern Rocky Mountains. The cascade effect they have had on the ecosystem has fundamentally altered the landscape. Despite continued persecution, wolves have proven they can exist in a region dominated by humans. These wolves have surprised and inspired wildlife managers and the public alike and serve as a symbol for wild spaces in the imagination of the country. They also serve as a reminder for how far conservation has come, representing a major victory for the Endangered Species Act. State management is the logical progression of wolves' recovery, but there are still threats to their long-term survival and their role in the Northern Rockies' political structure.

With so much symbolic value tied into wolf conservation, it is vital for wildlife managers to have the best information at their disposal. This study has highlighted regions of especial importance and located areas of greater concern for wolf management. We have found that Idaho sits at the forefront of wolf conservation as the most cohesive habitat for wolves. Central Idaho serves as a nexus for wolf dispersal, connecting many paths from Montana and Wyoming. East of the national parks and forests in Montana and Wyoming, the landscape becomes less habitable for wolves.

These plains are dominated by ranching and agriculture, with less wild prey for wolves. Montana wildlife managers will seek to limit wolf dispersal into eastern Montana, while landowners in Wyoming will be actively persecuting wolves who venture out of the western fifth of the state.

For this reason, knowledge of least cost paths through the Northern Rockies region will become increasingly important. The coming years will mark a change for wolves in the Northern Rockies as the states begin to limit the wolf population's growth. Dispersal among the three states' prime wolf habitat will be the only recourse for young wolves, which will begin competing with established packs for territory. It is my hope that this study will enhance wildlife managers' knowledge of wolf movements in their respective territories.

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