A Landscape Movement and Gene Flow Model of the Fisher (Pekania pennanti) in Pennsylvania Using Circuitscape

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A LANDSCAPE MOVEMENT AND GENE FLOW MODEL OF THE FISHER

*(PEKANIA PENNANTI)* IN PENNSYLVANIA USING CIRCUITSCAPE

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The fisher (Pekania pennanti) was found throughout Pennsylvania prior to the mid-1800s but were extirpated due to habitat loss and overharvest. The fisher was reintroduced in 1996 into Pennsylvania following New York and West Virginia in 1967 and 1983, respectively. A sampling of genetic material and point locations of these and other fishers began in 2002 across Pennsylvania and were used to discern source populations using 12 microsatellite loci.

For my thesis, I used this dataset to develop a gene flow and movement models within the Isolation by Resistance theory framework. The models were built and validated using a training and testing set method with 70% and 30% of the sample points, respectively. Two results that need investigation is the role of rural development as a positive factor for fisher movement and gene flow and possible movement corridors near Scranton, PA and the Kittatinny Ridge in south eastern Pennsylvania.
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CHAPTER 1
INTRODUCTION

Background

Human development, logging, and land clearance can fragment a landscape, and this fragmentation can negatively impact the survival of animal populations within an area (Benton, Vickery, & Wilson, 2003; Fahrig & Merriam, 1985; Fahrig & Merriam, 1994). Maintaining movement corridors are valuable in counteracting the effects of fragmentation and should still be created and maintained despite the expense (Beier & Noss, 1998). A way to assist conservation corridor maintenance and identification is by modeling animal movement corridors thereby providing a likely area to investigate for actual movement pathways (Sawyer, Epps, & Brashares, 2011). I created one such corridor and movement model focusing on a species reintroduced to Pennsylvania, the fisher (*Pekania pennanti*).

The fisher (*Pekania pennanti*) was once distributed across a wide swath of North America (Powell & Zielinski, 1994). Following European settlement in the beginning of the 19th century, it’s population faced a rapid decline due to over trapping and habitat destruction (Lancaster, Bowman, & Pond, 2008; Zielinski, Dunk, Yaeger, & LaPlante, 2010). The population remained at this low point until successful reintroduction efforts began in 1947 in Nova Scotia, an area where the fisher was judged to be extirpated in 1932 (Bensen 1959; Dodds & Martell 1971). Many areas, including California, Oregon, Washington, Montana, Idaho, Wisconsin, Michigan, New York, West Virginia, and Pennsylvania followed this effort with reintroduction efforts of their own, having mixed results (Aubry & Lewis, 2003; Lewis, Happe, Jenkins, & Manson, 2011; Lewis, Powell,
& Zielinski, 2012; Powell, Swiers, Facka, Matthews, & Clifford, 2014; Vinkey, 2003; Williams, Rhodes, & Serfass, 2000).

In the west the fisher reintroduction programs were met with mixed results as the populations in Montana, Idaho and California are slowly stabilizing and expanding (Powell et al., 2014; Vinkey, 2003) while populations in Washington and Oregon have faced little success in their reintroduction programs (Aubry & Lewis, 2003; Lewis et al., 2011). It remains a species of concern in the west with a U.S. Fish and Wildlife Service species status of “warranted but precluded” for the status of endangered (U.S. Fish and Wildlife Service, 2004). This struggling population has prompted many studies into the species habitat preferences and general distribution (Carroll, Zielinski, & Noss, 1999; Weir, Corbould, & Harestad, 2004; Zielinski et al., 2004; Zielinski, Carroll, & Dunk, 2006; Zielinski et al., 2010). While the populations and reintroduction efforts have faced mixed results in the west, the reintroduced fisher populations in the east have been growing and expanding (Gibilisco, 1994). Successful reintroduction efforts were located across several eastern states and Canadian provinces including: Pennsylvania, New York, West Virginia, Vermont, Connecticut, Nova Scotia and Ontario (Bensen, 1959; Dodds & Martell, 1971; Fuller, Linden, & Royle, 2016; Koen, Bowman, & Findlay, 2007; Lovallo, 2008; Williams et al., 2000).

The successful reintroduction efforts in the east have prompted several research studies using those populations and other established, natural populations to examine habitat preferences, and other aspects of eastern fisher biology. There have been several differences found between eastern and western fisher, including western fisher selecting habitat high in coniferous forest cover (Carroll et al., 1999) and avoiding deciduous forest
cover, while eastern fishers are selective for coniferous forest in some areas, such as New York (Fuller et al., 2016), but are less selective in others, such as Pennsylvania (Gess et al., 2013). Most studies in the northeastern range have focused on local habitat selection or diet (Ellington, 2010; Ellington et al., 2017; Gess et al., 2003; McNeil, Nicks, Wester, Larkin & Lovallo, 2017). Although there have been differences in local habitat selection patterns across this region, the broad scale movement patterns and potential habitat corridors had not been studied for this region prior to this research (Ellington et al., 2017; Fuller et al., 2016; Gess et al., 2013). This is unfortunate as the region is important for the species as a while because it represents the connection of the eastern populations to the rest of the species range to the north (Powell & Zielinski, 1994). Identifying paths of movement through this area are important for maintaining gene flow and freedom of movement (Debinski & Holt, 2000).

The models resulting from this thesis are the first representation of fisher movement pathways among fisher populations in and through Pennsylvania. The goal for my thesis was to identify potential corridors used by fisher based on genetic similarity among sampled individuals. The resulting models highlight routes that appear to be frequently used by fisher and identify environmental conditions that appear most closely associated with these movements.
Literature Review

Population Decline and Reintroduction

The fisher (*Pekania pennanti*) is a mustelid that is endemic to North America (Powell & Zielinski, 1994). Prior to European settlement, *P. pennanti* once ranged across the northern section of North America (Powell & Zielinski, 1994). Then, around the turn of the 19th century, the population began to decline rapidly and was almost extirpated from its historical range (Grinnell, Dixon, & Linsdale, 1937; Powell & Zielinski, 1994; Zielinski et al., 2010). The decline can be linked to expansive logging or land clearance as the species has an exhibited habitat selection preference for a dense, closed forest canopy and has a sensitivity to forest fragmentation (Lancaster et al., 2008; Powell & Zielinski, 1994). Over trapping, incidental trapping, climate change, and accidental kills through predator control campaigns also have contributed to their initial decline (Lewis et al., 2012).

Following this decline and the complete extirpation of the fisher from much of their range, a concerted effort was undertaken by many states and provinces to close trapping seasons and attempt reintroduction efforts (Powell & Zielinski, 1994). This effort started in Nova Scotia, an area that has seen fisher completely extirpated in 1932 (Bensen, 1959). Twelve fishers were released in the area between 1947 – 1948, along with a second reintroduction from 1963 – 1966, and the effort has been deemed successful due to a documented increase in the population of fishers within the province (Bensen, 1959; Dodds & Martell, 1971). Other areas in North America followed suit and additional reintroduction efforts took place between 1955 and 1981 in: British Columbia, Idaho, Massachusetts, Michigan, Montana, New York, Oregon, West Virginia,

The reintroduction efforts in the western states and provinces have met with mixed success. The individuals from Oregon’s reintroduction attempts between 1961 to 1981 have only been located at two sites with one being near the 1977 and 1981 reintroduction (Aubry & Lewis, 2003). Washington initiated reintroduction efforts between 2008 and 2010 with 90 fishers from British Columbia being relocated to Olympic National Park but these populations appear to be struggling as well due to little evidence of population connectivity (Lewis et al., 2011; Lewis et al., 2012). However, in Montana and Idaho, fisher reintroductions between 1960 and 1992 have been deemed successes as the reintroduction regions experienced a large uptick in the number of captures of fishers by fur trappers in the years following these reintroduction events (Vinkey, 2003). Remnant native populations are also hypothesized to be located in the Bitterroot Mountain range, the region around Yellowstone and Glacier National Parks, and in central Idaho’s wilderness areas (Vinkey, 2003). Also, recent reintroduction efforts in California have met with some success with a reintroduced population in the northern Sierra Nevada’s having been found to have experienced high survival rates, are reproducing, and captured individual’s body condition has been deemed average (Powell et al., 2014). Fisher populations have also been generally stable in British Columbia, Canada, but they are declining in certain regions from human development (Weir, 2003). However, population trends in the province are difficult to collect and analyze (Weir, 2003). The main thoughts as to why some populations succeed while others fail are:
access to availability of habitable land, proximity to other fisher populations, impact of human development and forest characteristics (Aubry & Lewis, 2003; Buskirk & Powell, 1994; Vinkey 2003). Unfortunately, beyond some success, fisher populations in the western United States have not fared well, being considered by the United States Fish and Wildlife Service as “warranted but precluded” for inclusion under the Endangered Species Act (U.S. Fish & Wildlife Service, 2004).

While the populations in the west have been struggling, the fisher populations in eastern North America have now been characterized as stable and expanding (Gibilisco, 1994). Several states in the east have successfully reintroduced fisher populations including Vermont, Wisconsin, Michigan, and Connecticut during the 1950s and 60s (Williams et al., 2000; Williams, Gilbert, & Zollner, 2007). They have also taken place in West Virginia, New York, and Pennsylvania (Fuller et al., 2016; Lovallo, 2008; Williams et al., 2000). In West Virginia 23 fishers were reintroduced from New Hampshire in 1969 and those reintroductions were described as a success (Berg, 1982; Pack & Cromer, 1981: Williams et al., 2000). New York’s population of fisher was not completely extirpated with a few populations remaining in the region of the Adirondacks (Wallace & Henry, 1985). During 1979 thirty fishers from this region were reintroduced to the Catskills area (Lovallo, 2008). That population has been successful enough that an experimental trapping season has been opened in that region (Fuller et al., 2016; “NYSDEC 2016 Fisher Management Plan”). The fisher from New York have also been found to contribute to the stable populations in Ontario, Canada but these Canadian populations are very close to facing local declines in some regions (Koen et al., 2007).
Specifically for Pennsylvania, the last sightings of fisher were in Lancaster County in 1921 and Mifflin County in 1923 (Lovallo, 2008). However, Pennsylvania did not begin any reintroduction efforts until 1994 to 1998, when 190 fishers from New Hampshire and New York were reintroduced in several northern counties (Ellington, Larkin, Nuttle, & Hinrichsen, 2010; Lovallo, 2008; Serfass et al., 1994). Since then fisher populations have become more abundant in the state with the Pennsylvania Game Commission opening a limited fisher trapping season in 2010.

**General Description**

Fisher (*Pekania pennanti*) are of the order *Carnivora* in the family *Mustelidae* and genus *Martes* but was recently placed in its own sub-genus, *Pekania* (Koepfli et al., 2008) and it was first described in 1977 by Johann Christian Polycarp Erxleben (Powell, 1981). Males of the species can weigh between 3.5 and 5.5 kg and have a length between 90 and 120 centimeters, while females weigh between 2.0 and 2.5 kg with a length between 75 and 95 cm (Powell & Zielinski, 1994). This makes the fisher the largest species in their genus (Anderson, 1970; Powell & Zielinski, 1994). The fisher’s build is elongate, thick, and set low to the ground (Powell & Zielinski, 1994). Their fur is dark brown except for white or cream patches around the chest and genital areas (Powell & Zielinski, 1994). The feet of the fisher each have five toes, four central pads, and possess non-sheathed, retractable claws (Powell & Zielinski, 1994). Behind the central pads on the hind feet are plantar glands used for scent marking (Powell, 1981; Powell & Zielinski, 1994).
Habitat

This species has become associated with the deeper forest as it has been known to avoid open areas and reside in areas with thick forest canopy closure (Burkirk & Powell, 1994; Douglas & Strickland, 1987; Gess et al., 2013; Lancaster et al., 2008; Weir and Corbould, 2010). While canopy closure is important, the forest succession stage in their habitat can vary from late successional to mixed ages across their range as the fisher appears to select late successional forest in the western United States but inhabit a wider range of forest conditions in the eastern region of the country (Lovallo, 2008). In addition to age structure, the composition of forests used by fisher varies across their range. Fishers in the western and northern regions are often associated with riparian areas and old growth coniferous and mixed forests (Powell, Buskirk, & Zielinski, 2003; Proulx et al., 2000). In the northeastern U.S., they can reside in habitats that are primarily made up of forest cover rather than any riparian areas (Gess et al., 2013; Powell et al., 2003).

While there is a difference between eastern and western North America in the case of tree type, a commonality is that fisher in both regions select habitats that have a greater structural complexity (Lovallo, 2008; Powell et al., 2003; Proulx et al., 2000). There are several thoughts as to why this occurs such as proximity to foraging habitat (Allen, 1983; Powell, 1993) and usage for rest sites as they have been known to select features such as, tree cavities, logs, stumps, brush and rock piles, and ground burrows (Weir et al., 2004). Large deciduous trees or snags have also been used as maternal den sites (Allen, 1983).
Fishers are thought to be more sensitive to habitat differences when selecting rest sites than when moving across an area or even foraging (Powell, 1994). In areas for both the eastern and western United States, fishers prefer large trees to rest in and the forest surrounding these rest sites is typically structurally complex (Arthur, Krohn, & Gilbert, 1989; Gess et al., 2013; Zielinski et al., 2004). In the western U.S., the percentage of canopy cover and coniferous and mixed forest composition also appeared to positively associated with rest site selection (Arthur et al., 1989; Gess et al., 2013; Zielinski et al., 2004). In the eastern United States, specifically in a south-central Pennsylvania forest, neither canopy cover nor coniferous forest composition was found to be an important factor in fisher rest site selection (Gess et al., 2013). This conclusion may be a result of the high percentage of deciduous forest present in the area and a majority of the studies concluding coniferous/mixed forest preference being located in areas where those forest types are in high abundance (Gess et al., 2013). Variation in habitat selection can also be due to the fisher selecting habitat based on the preferences of the prey residing in their region (Arthur et al., 1989; McNeil et al., 2017; Powell & Zielinski, 1994).

**Diet**

Fishers are opportunistic predators and their diets vary widely including fruit, vegetation, and animals (Dzialak, Serfass, Brown, & Krupa, 2005; McNeil et al., 2017; Powell & Zielinski, 1994). Of the animals in their diet, they will consume carrion, such as from white-tailed deer (*Odocoileus virginianus*), and fresh prey including small mammals of the order Rodentia, animals from the family Leporidae, and birds (Arthur et al., 1989; Giuliano, Litvaitis, & Stevens, 1989; McNeil et al., 2017; Powell & Zielinski, 1994). They have also been found to eat other mesocarnivores and porcupine (*Erethizon*)
dorsatum) (McNeil et al., 2017; Powell & Zielinski, 1994). While dietary generalists, fisher possess many features that make them well suited for predating on porcupine giving them a prey species where they have little competition with other predators (Powell & Zielinski, 1994). There have even been documented decreases in porcupine populations when fishers are present (Coulter, 1966; Hamilton, Cook, & Hamilton, 1955; Powell & Brander, 1977).

**Reproduction**

Female fishers are sexually mature and will breed at one year old (Douglas & Strickland, 1987). They give birth in late March and April and, 7 - 10 days later, will go back into estrus (Powell et al., 2003). The fisher has a delayed implantation approximately 10 months until the change in day length causes the egg to implant and actively gestate (Frost, Krohn, & Wallace, 1997; Powell & Zielinski, 1994). Before giving birth, the female fisher will select a natal den, typically a living tree or snag with a cavity high from the ground (Powell & Zielinski, 1994). They will use one to three dens per litter (Powell & Zielinski, 1994). Litter sizes range from one to six kits with an average size of two to three (Powell et al., 2003). The kit’s eyes and ears are closed upon birth and they have a coat of fine hairs (Coulter, 1966; Powell et al., 2003). By two weeks old, they are covered in a fine, grey fur, that will gradually turn into the chocolate-brown color of an adult fisher between three to twelve weeks old. Their teeth begin to erupt between 6 to 10 weeks old, but it is not until they are eight to ten weeks old that they be weaned (Coulter, 1966; LaBarge, Baker, & Moore, 1990). They will not begin to crawl until they are greater than three weeks old but when older than three months they will be good at climbing (Coulter, 1966; Powell, 1993). The characteristic intraspecific
aggression appears at around three months old and by one year old the juvenile fisher will establish their own territory (Powell, 1993; Powell et al., 2003).

After male fisher establish their own territory, marking the landscape with urine, feces, musk, and through the plantar glands on their hind feet, they will defend their territory from other males very aggressively (Coulter, 1966; Kelly, 1977; Powell, 1977; Powell & Zielinski, 1994). These cases of intrasexual aggression are encouraged by the male fisher’s tendency to expand their movement beyond their own territory, and sometimes into another male’s territory, during the breeding season, between mid-March through April (Powell & Zielinski, 1994). Some believe it is this invasion of territory and the species use of plantar glands for territory marking that cause fisher to occasionally eat the feet of dead intruding fisher, preventing their scent from marring the territory boundary, a behavior hypothesized from the finding of fisher feet in the stomachs of other fisher (McNeil et al., 2017).

Movement

Fishers are a particularly mobile species, moving on average 5 – 6 kilometers per day and have been documented to move as far as 15 kilometers in one day (Powell & Zielinski, 1994; Roy, 1991). Females will increase their movement amounts before parturition in the late spring and early summer, then the amount of movement will decline heading toward winter (Roy, 1991).

Overall, this species movement and dispersal patterns have been an object of intense scrutiny using various methods to quantify that aspect of their biology (Arthur, Paragi, & Krohn, 1993; Garroway, Bowman, & Wilson, 2011; Powell et al., 2014).

Animal Movement Pathway Modeling
Several techniques have been developed to measure animal movement pathways include Euclidean distance, Least Cost Path (LCP) modeling and Isolation by Resistance modeling. Euclidean distance is the simplest measure, just a straight-line path between locations. It is fine measure of distance however, it has three main weaknesses as an estimate of movement pathways. It is unable to account for range shape, or a varied landscape, and it has very low reliability when predicting likely movement corridors and the cost of travel between locations (McRae & Beier, 2007). A method that accounts for these weaknesses is Least Cost Path modeling, which creates a surface simulating a varied landscape in the form of values representing how difficult it is for the study species to move through that area (McRae & Beier, 2007). The model then picks the single path that provides the least resistance between two points. Unfortunately, it does not account for varied linkage widths, variations in the width of movement corridors, and only considers a single pathway between points (McRae & Beier, 2007; Sawyer et al., 2011). These deficiencies are important to account for as animals will take multiple pathways between points and having corridors of a thin, uniform width characteristic of LCP modeling result in several problems including prediction of corridors through realistically unusable habitat (Beier, Majka, & Spencer, 2008; McRae & Beier, 2007). However, this one route result can prove complementary to a multi-route method, such as Isolation by Resistance, especially when there is one extremely well known or well used path between points (Howey, 2011).

The final method, Isolation by Resistance (IBR), accounts for irregular study area boundaries and multiple pathways across a landscape (McRae, 2006; McRae & Beier, 2007). In the IBR method, the entire study area is represented as a series of cells with a
value associated with how difficult movement across that cell will be, or the resistance value, much like LCP (McRae, 2006; LaRue & Nielsen, 2008). However, all possible routes of movement are accounted for in this method, with areas of greater flow being held as less resistant (McRae & Beier, 2007; McRae, Dickson, Keitt, & Shah, 2008). Another strength of this approach is its ability to simulate an organism travelling randomly though a network due to its usage of electrical principles (Doyle & Snell, 1984; McRae et al., 2008). This method also accurately models and predicts gene flow and has been used for this purpose in studies examining species within the Mustelid family (Schwartz et al., 2009, Garroway et al., 2011).

**Circuitscape**

The software that applies the Isolation by Resistance theory to animal movement modeling is called Circuitscape (McRae, Shah, & Mohapatra, 2013). In Circuitscape, sample points are considered to be nodes connected by resistors or conductors on a simulated electrical network (represented in a raster dataset or graph). The overall resistance represents how difficult it is for the study species to move across the landscape where higher resistance value represent greater difficulty for an organism to move across the area. The relationship to movement can also be represented by the inverse of resistance, conductance. The total conductance or resistance values for the individual cells in a raster dataset is a combination of landscape variables determined by the researcher to play a role in the movement of the study species.

The three main methods to determine these total resistance values are: expert opinion, non-genetic field data, and model optimization (Spear, Balkenhol, Fortin, McRae, & Scribner, 2010). Each of these approaches have their weaknesses. Expert
opinion is limited by the researcher’s experience and resistance values in this approach tend to be arbitrarily assigned or are assumed to follow a linear relationship, resulting in a potentially erroneous relationship pattern between the variable and its effect on animal movement (Spear et al., 2010). However, the approach can be valuable depending on the experience of the expert being consulted (Spear et al., 2010). Non-genetic field data, including presence/absence data, satellite, GPS or radio telemetry tracking, and experimental movement studies, can be cost intensive, can contain detection bias, small sample sizes, and are typically constrained in the size of their study area although tracking methods and experimental studies can provide a direct measurement of movement pathways and the degree multiple environment variables impede movement (Spear et al., 2010). The final method, model optimization, is a technique that takes multiple models containing the same variables and statistically evaluates each model’s fit to genetic data (Spear et al., 2010). This approach provides an excellent way to compare multiple variables and their estimated impedance to movement although this method is dependent on the quality of the individual models being compared, and the costs associated with collecting the data for the models (Spear et al., 2010).

After converting the landscape into an electrical network, the researcher defines the relationship between the nodes on the network with those nodes being voltage nodes, the source of the current, or ground nodes, destinations for the current (McRae, 2006). There are three methods for representing the relationships among the nodes that represent sampled organisms in the network: all-to-one, one-to-all, and pairwise. In all-to-one setting, every node in the network except one is set as a voltage node where current begins, while the one is set to be the ground, to which the current travels. The software
rotates the setting of ground node among each node in the network and creates a new model for each. This kind of method represents movement from all sample points to a single point, this method represents the movement pattern where all animals will eventually travel to a single site, such as a breeding site. The reverse occurs in one-to-all where one node is the voltage node and every other node is the ground. Here the software again rotates the setting of single voltage node among each node in the network, producing a new model for each. The one-to-all method models the movement pattern where all animals from a single point will travel to every point in the study area. In the pairwise option one node is set as the source while another is set as the ground. Every other node in the network is set to neutral meaning it does not influence the current flowing across the network. The model then selects a new pair of nodes until the flow of current between all possible node pairs are simulated. This method models the movement pattern where only a single source and destination are considered, such as movement to find new territory, where animals will move toward a single destination without attempting to all reach a single destination or all destinations in a study area. All methods have the option of producing a cumulative current map which consists of cells with a cumulative current (I) resulting from adding the value of the current in that cell for all models (I_n) (Formula 1).

(Formula 1) \[ I = I_1 + I_2 + I_3 + \ldots + I_n \]

After the node relationship is specified, the movement of the organism is represented as a simulation of current flowing across the landscape, or resistance surface. The simulated electrical current can take all available paths across the resistance surface, but it travels most frequently along the pathways offering the least resistance or highest
conductance (McRae, 2006). This method incorporates the possibility of multiple paths an organism may use to cross a landscape (McRae, 2006).
CHAPTER 2

METHODS

Methods of Study

Study Area

This study focused on Pennsylvania, and included portions of southern New York, northern West Virginia, eastern Ohio, northern Maryland and western Delaware. The ecoregion is primarily eastern temperate forest with smaller areas in the northern and north-eastern sections of the study area being northern forests (U.S. Environmental Protection Agency, Ecological Regions of North America, Level 1). The landcover was classified as primarily forest (61%), and agriculture (20%) (U.S. Geological Survey, National Landcover Database 2011). The terrestrial elevation ranged from -85.78 to 1,453.46 meters above sea level with an average elevation of 378.26 meters above sea level (± 196.33 meters). Average temperature across multiple weather stations for the area during sample collection (2002 and 2014) ranged from -1.94°C in the winter to 21.04°C in the summer (PA State Climate, 2018).

Fisher Sample Points

Fisher samples were collected between 2002 to 2014 as part of a study conducted by Courtney Nicks (Personal communication). She used genetic and locational data from fisher hair and tissue samples that were collected between 2002 and 2014 to map the distribution of the fisher samples in Pennsylvania, West Virginia and New York along with their expected source populations. The genetic data from the 2002-2012 data were from hair snare studies, road kill samples, and trapper harvests. Data from 2013-2014 were collected through trapper harvests and samples provided by the West Virginia and
New York Game Commissions. These samples were genotyped at 12 microsatellite loci and a genetic assignment test was used to group the fisher samples into the Pennsylvania, West Virginia or New York source locations. Admixtures, individuals identified as having ancestors from two different source locations, were marked as separate groups. The microsatellite loci used were: Ma1, Tt1, Pv9 (Davis & Strobeck, 1998), Ggu 101, Ggu 216 (Flemming et al., 1999), Mer022 (Dallas & Piertney, 1998), MP59, MP144, MP175, MP197, MP200, and MP247 (Jordan et al., 2007).

Genetic assignment was completed using Program Structure, a software program that assigns individuals to a predefined number of K groups by maximizing the Hardy-Weinberg equilibrium within groups (Pritchard et al., 2000). After testing multiple values for K, K=3 was assigned as it had the highest posterior probability of the observed genotypes being present given the number of groups. These three groups represented 3 source populations: Pennsylvania, West Virginia, and New York populations stemming from separate past reintroduction efforts. The assignment of each individual to one of the three groups was determined by finding the mean estimate of the posterior probability that an individual inherited their genome from a particular group (Pritchard et al., 2000). The program indicated admixture for an individual if there was a less than a 70% posterior mean probability estimate that an individual has inherited some fraction of their genome from a particular group of ancestors (Pritchard et al., 2000). None of the samples identified as the West Virginia source population appear within the area of the samples identified from the New York source population (Figure 1). Due to this pattern, the assumption that fishers were able to move between these two areas was not supported, and each group was modeled separately. Descriptive statistics were calculated for the
dataset were: total number of alleles and expected (Nei, 1987) and observed heterozygosity using the hierfstat R package v. 0.04-22 (Goudet & Jombart, 2015), and average number of alleles per locus using rarefaction was calculated using the HP-Rare v. 1.1 program (Kalinowski, 2004; Kalinowski, 2005). Rarefaction was used to account for the variations in sampling effort and sample size (Kalinowski, 2004).
Figure 1. Map of the distribution of fisher samples. These fisher samples had estimated source populations from Pennsylvania (PA), and West Virginia (WV), and admixtures of Pennsylvania/West Virginia (PA_WV) and Pennsylvania/New York (PA_NY).

West Virginia and their admixture samples are not present in the New York admixture sample areas so assuming fisher from those areas are located in the same area is not supported by this dataset.
Landscape Variables

Six landscape variables were included in the models: percent cover of forests, percent cover of open ground, percent cover of open development and percent cover of low intensity development, distance to medium or higher intensity human development, distance to high volume roads, and terrain ruggedness. Landcover data was adopted from the National Landcover Database 2011 version through the Multi-Resolution Land Consortium (Homer et al., 2015). These data are at a 30-meter resolution derived from the Landsat 5 satellite images and cover the entire United States. The composition of the selected landcover variables in the study area were: 61% forest, 20% agriculture, 11% development, and 2% non-agriculture open fields (U.S. Geological Survey, National Landcover Database 2011). Traffic data consisted of average annual daily traffic (AADT) road layers and road polyline Geographic Information System (GIS layers) from the departments of transportation for the states surrounding Pennsylvania which are: Pennsylvania’s (PennDOT, 2017), New York’s (NYSDOT, 2015), West Virginia’s (WVDOT, 2016), Ohio’s (ODOT, 2017a; ODOT, 2017b), Maryland’s (MDOT, 2017), Delaware’s (DDOT, 2017), and New Jersey’s (NJDOT, 2015; NJDOT, 2017) Departments of Transportation. Terrain Ruggedness was calculated from 3.2 foot Digital Elevation Model data collected from the Pennsylvania Spatial Data Access PAMAP Program (PAMAP, 2006). Correlation between landscape variables was calculated using Mantel tests, Pearson method with 1,000 permutations (R Package: ecodist; Goslee & Urban, 2007).

Forest cover was selected as a landcover variable because many studies of fisher have indicated that the species will select high density forest cover areas for habitat and
movement (Carroll et al., 1999; Weir & Corbould, 2010). The composition of this cover, however, varies between the western and eastern United States with coniferous or mixed forest being preferred habitat by fisher in the western United States (Zielinski et al., 2010), and areas with high amount of deciduous forest cover being selected for habitat and rest sites by eastern fisher (Ellington et al., 2003; Fuller et al., 2016; Gess et al., 2013). To account for this variation in fisher selection of forest type, cells in the landcover dataset containing forest types (deciduous, conifer, mix) were combined into a single forest category. In contrast, the open field variable consisted of nearly undeveloped areas that contained agriculture or shrub land, cover types the fisher appear to avoid while moving or selecting territory (Fuller et al., 2016; Powell & Zielinski, 1994; Weir and Corbould, 2010). These areas were described as a separate category due to the lack of forest cover and the expectation of reduced human activity than human development classified areas (Anderson, Hardy, Roach, & Witmer, 1976).

To represent the variation in human development across the study area, I elected to use the percent development variables within the landcover database cell. This measure examines the percent of impermeable surface cover within a 30-meter by 30-meter cell and, if any is present, categorizes that cell into one of four categories. The lowest, rural development, is the category of cells with < 20% impermeable surface cover followed by low development with 20%-49% impermeable surface cover then medium and high development with 50 – 79% and 80% or greater impermeable surface cover, respectively (Anderson et al., 1976). Each of these levels consists of various typical development from farm houses and open lots forest rural development, to urban buildings in the high development category (Anderson et al., 1976). Low development and
medium development are made up of the intermediate types of development with low
development consisting of sparse, single family homes and medium development
consisting more of the suburban neighborhoods (Anderson et al., 1976). Additionally,
these categories also represent varying levels of vehicular traffic and road densities
characteristic of different levels of development (Holderegger & Di Giulio, 2010).

Two variables beyond cover types were chosen for this study: distance to high
traffic roads and terrain ruggedness. Some studies of fisher have included road density in
their determination of fisher habitat and movement preferences (Carroll et al., 1999;
Fuller et al., 2016; Sauder & Rachlow, 2014). Based on results from the study of
Holderegger and Di Giulio (2010) showing roads as negatively impacting population
genetic diversity and functional connectivity, I decided to measure the impact of roads as
the distance to high traffic roads due to this documented animal avoidance. Road
sections from all states in the study were classified as high volume/not high volume with
the threshold set at an AADT of 50,000 cars/year which is classified as high traffic areas
following the United States Highway Administration guidelines (FHA, 2016). This
threshold typically indicates highways, a road class that has been shown to act as a barrier
to movement to terrestrial animals (FHA, 2016; Holderegger & Di Giulio 2010).
Euclidean distance was then measured the minimum distance between each raster map
cell and a road section deemed high volume.

I measured terrain ruggedness using Vector Ruggedness Measure (VRM), a
metric that is based on a combination of aspect, slope, and change in elevation
(Sappington, Longshore, & Thompson, 2007). This metric ranges from zero,
representing flat ground, to a maximum ruggedness value based on the dataset
(Sappington et al., 2007). This approach scales a region’s topography from flat terrain to smooth hillsides to highly irregular terrain (Sappington et al., 2007). This method has already proven more accurate in identifying irregular terrain than the more common methods of Terrain Ruggedness Index and Land Surface Ruggedness Index (Sappington et al., 2007).

**Developing the Resistance Surface**

The spatial extent of all landscape data used as explanatory variables in the model were clipped to a 50-kilometer buffered polygon consisting of Pennsylvania and a minimum bounding polygon that included sampled fisher locations from outside of the state in New York and West Virginia (ArcGIS v. 10.5.1, ESRI, 2017). This geometry was created to include the samples outside of Pennsylvania and to restrict the pathway predictions to areas that led directly into the state to avoid prediction of pathways where there is no presence of fishers in the dataset (Figure 1). The 50-kilometer buffer served to reduce any edge effects that might occur in the study area (Koen et al., 2010). By extending the boundary of the modeled landscape beyond the political borders, the model would not falsely assume that fisher cannot move beyond those borders (Koen, 2010).

When preparing the landscape variables, they were resampled to a spatial resolution of 30 km² to bring the model scale to match the characteristic size of a male fisher’s territory observed in previous studies (Fuller et al., 2016). All landscape variables were also standardized on a zero to one scale to comply with Isolation by Resistance landscape formatting requirements (McRae, 2006). Before standardization, all landcover variables (forest, open field, low development, and open development) were reclassified to a binary presence/absence scale represented by a 1 for presence and a 0 for
absence of that cover type within the 30 meter by 30 meter cell. The percentage each
cover type occupied in a larger moving window was then calculated using the Focal
Statistics tool in ArcGIS 10.5. I set the moving window to a neighborhood with the same
area as the model’s spatial resolution (30 km²). This tool summed all of the presence
values for the cover type of interest within the moving window. That summed total was
then divided by the total number of cells in the neighborhood (33,489 cells) used by the
Focal Statistics tool to get the percentage of a landcover type in each cell.

Within Circuitscape, I generated the resistance maps, surfaces that represent the
potential influence of each environmental variable on the difficulty of movement (McRae
et al., 2013). Following Garroway et al. (2011), I selected the pairwise node relationship
method to generate every possible node pair combination (Table 1; McRae et al., 2013).
This method was selected because an assumption of the model was that each animal
would attempt to reach a single destination rather than all animals going to a single point
or attempting to reach every destination in the study area. The resistance surfaces of the
landscape variables were set to represent conductance, the inverse of resistance, meaning
a value of 1 would represent full ease of movement and 0 would mean no possible
movement (McRae et al., 2008). This option was selected to enable easier comparisons
and interpretability for the predicted movement pathways, resistance maps, based on each
variable. After the resistance maps were generated, an effective pairwise resistance value
for each node pairing was calculated via the software, taking into account the overall
simulated flow of individuals, and the number of pathways available between points
(McRae et al., 2008).
Modeling Methods

To accomplish the goal of modeling movement corridors parameterized by genetic distance, I followed the procedure of Garroway et al. (2011). This approach combines genetic data as the empirical input with the landscape resistance models based on potential movement pathways represented as isolation by resistance. The genetic distance represents the movements of many individuals over a long period of time and emphasizes the pathways of individuals that have successfully bred and are therefore important to the species (Dyer, Nason, & Garrick, 2010; Zeller, McGarigal, & Whiteley, 2012). Isolation by Resistance and other Matrix Selection Functions, such as least cost distance, are considered less arbitrary than other Resource Selection Functions because they avoid more arbitrary approaches where researchers define “available” and “unavailable” locations in the study area (Zeller et al., 2012). While there is debate about the performance of several Matrix Selection functions, Isolation by Resistance was selected due to it being demonstrated to improve predictions of genetic differentiation between sampled populations much more than other modeling methods, such as Least Cost Distance (McRae & Beier, 2007; Zeller et al., 2012).

Developing the Model Sets

I partitioned the fisher samples into two model sets where each fisher sample location is described as a node. The first set consisted of sample points where the source populations were from Pennsylvania and West Virginia along with their respective admixtures (WV/PA dataset, Table 1). For the second set, I used sample points with identified source populations from Pennsylvania and New York along with their respective admixtures (NY/PA dataset, Table 1). Partitioning these data into two model
sets, averts the estimation of pathways between possibly unrelated samples. Specifically, it prevented the models from assuming fisher from West Virginia or New York would be able to travel between the two areas, north-east and south-west Pennsylvania. This is required as the current dataset does not suggest any such possibility (Figure 1). The samples for each model set were then randomly subdivided into training and testing sets with 70% of the samples used in the training set and 30% in the testing set (Table 1). The training set samples for each model were used to parameterize the model while the testing set samples validate the model’s predictive ability.

Table 1

*Number of Samples Used, and all Possible Pairings in the Training and Testing Datasets*

<table>
<thead>
<tr>
<th></th>
<th>TNS</th>
<th>STrS</th>
<th>STeS</th>
<th>PTrS</th>
<th>PTeS</th>
</tr>
</thead>
<tbody>
<tr>
<td>WV/PA</td>
<td>301</td>
<td>211</td>
<td>90</td>
<td>22,155</td>
<td>4,005</td>
</tr>
<tr>
<td>NY/PA</td>
<td>149</td>
<td>103</td>
<td>46</td>
<td>5,253</td>
<td>1,035</td>
</tr>
</tbody>
</table>

Note. Lists the number of sampled fisher locations used for each movement model and the number of samples divided into the respective training and testing sets for both models. The respective movement models are samples with an estimated source population from West Virginia and/or Pennsylvania (WV/PA) and samples with an estimated source population from New York and/or Pennsylvania (NY/PA). The samples are used as departure and destination points for simulated fisher movement paths across a single variable landscape surface, one surface for each independent variable in the model. The pairings are the number of pathways that are simulated between samples. The column heading abbreviations are: TNS = Total Number of Samples, STrS = Samples in the Training Set, STeS = Samples in the Testing Set, PTrS = Pairings in the Training Set, PTeS = Pairings in the Testing Set.
**Genetic Distance and Model Building/Validation**

After partitioning the samples into testing and training sets, the genetic distance of the training set samples were compared to the effective resistance between the corresponding training samples for each environmental variable via Multiple Regression on Distance Matrices with 1,000 permutations (R package: ecodist; Garroway et al., 2011; Goslee & Urban, 2017). The result was a coefficient for each environmental variable that represented its correlation with genetic distance between fisher (Garroway et al., 2011). The MRDM technique is based on partial Mantel tests but has several advantages over a pure partial Mantel test. The advantages include being able to separate the independent factors into their multiple categories, allowing for the consideration of the effect each independent variable has on the model, and ability to handle non-linear regression methods, capturing non-linear relationships that may be present in natural systems (Lichstein, 2007).

The dependent variable of genetic distance was calculated using Genepop v. 4.7 (Raymond & Rousset, 1995). This software computes a wide array of genetics based statistics such as exact tests for Hardy-Weinberg equilibrium and estimates of $F$-statistics (Raymond & Rousset, 1995). Since these data consisted of individuals, Rousset’s $\alpha$ was the genetic distance metric selected for this dataset (Hall & Beissinger, 2014; Rousset, 2000). This statistic also features a lack of asymptotic bias and it has also performed well when compared to other measures of genetic distance (Hall & Beissinger 2014; Shirk, Landguth, & Cushman, 2017).

Independent variables that significantly contributed to the genetic distance between each pair of fisher in the training sample were selected through a forward
stepwise selection procedure. The training samples used to build the model were resampled from the overall data set 1,000 times and the forward stepwise selection procedure was repeated for each resampling resulting in a new model being “built” each time. The forward stepwise selection procedure was used because it previously has been deemed suitable for MRDM (Balkenhol, Waits, & Dezz, 2009) and other methods, such as Akaike’s Information Criterion (AIC), were recently criticized as resulting in incorrect model selection with this framework (Franckowiak et al., 2017). The stopping rule for adding a variable during stepwise selection was a Type 1 error rate threshold of 0.05. After this process, the average coefficient for each variable, and their 95% confidence intervals, were calculated and these average coefficients were used to modify the effective resistances for each independent variable.

Model validation was conducted on the remaining data not used to build the model, by comparing the effective resistance values among the testing dataset pairs to their corresponding genetic distances using a Mantel test with 10,000 permutations (R package: vegan; Oksanen et al., 2018). The null hypothesis for this test was no correlation between the pair’s average resistance values and their genetic distance. The testing datasets were also resampled 1,000 times and a Mantel test was completed for each resampling. I summarized the Mantel tests as an average R statistic along with the 95% confidence. The Mantel test has been used in other studies comparing isolation by resistance models to genetic distance and has proven to be a reliable measure for validation (McRae & Beier, 2007; Seymour, Räsänen, Holderegger, & Kristjánsson, 2013).
CHAPTER 3
RESULTS

Descriptive Statistics

Of the fisher samples that were collected in Pennsylvania, 85 were from live-trapping or hair snare studies while 104 fisher samples were collected from road-kill and accidental trap-killed fisher (Courtney Nicks, in progress). The samples from New York and West Virginia were also collected from road-kill (Courtney Nicks, in progress). The average number of alleles per individual in the West Virginia/Pennsylvania dataset was 17.545 (SD ±2.00), the average observed heterozygosity was 0.501 (SD ±0.136), and the average expected heterozygosity was 0.564 (SD ±0.152). For the New York/Pennsylvania dataset, the average number of alleles per individual was 17.866 (SD ±1.920), the average observed heterozygosity was 0.513 (SD ±0.150), and the average expected heterozygosity was 0.269 (SD ±0.081). The average number of alleles per locus for the West Virginia/Pennsylvania dataset was 1.787 (SD ±0.671) while for the New York/Pennsylvania dataset it was 1.681 (SD ±0.473).

The Mantel test examining correlations between all variables being considered resulted in the removal of the Distance to High Volume Roads variable after it was found to be positively correlated with the Percent Forest Cover variable (rM = 0.874, p-value < 0.05). The Mantel statistics for the other variables did not exceed 0.5.
West Virginia/Pennsylvania Model

The stepwise selection process for the estimated successful gene flow movement pathway models resulted in three of the variables being selected during every model run: Rural Development, Forest, and Open Field. However all variables were included in more than 75% of all trials, meaning that every variable is potentially contributing to the final genetic distance between samples (Table 2). The model predicted an increase in Genetic Distance when Low Development and Open Field coverage increased and when Distance to Medium and High Development increased (Table 2). It also predicted a decrease in Genetic Distance when Forest cover, Rural Development coverage, and Terrain Ruggedness increased (Table 2). A high Genetic Distance means the sample pair being considered are not closely related. When tested, the West Virginia/Pennsylvania model accounted for, on average, approximately 25% of the variation of genetic distance samples for all of the testing samples (R: 0.243 ± 0.001).

The final current map predicted an area of high gene flow along the thick forest corridors through Cambria, Clearfield and Indiana counties (Figure 2). The majority of the map, however, predicted a moderate to low amount of gene flow across the rest of the state (Figure 2).
Table 2

Percent Coefficients Were Selected From all Model Building Trials and Final Average Coefficients for the West Virginia/Pennsylvania Model

<table>
<thead>
<tr>
<th>Variable</th>
<th>Selection %</th>
<th>Coefficient</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>DMDHV</td>
<td>78.5%</td>
<td>-0.009</td>
<td>(-0.0092, -0.0086)</td>
</tr>
<tr>
<td>Forest</td>
<td>100%</td>
<td>0.023</td>
<td>(0.0222, 0.0230)</td>
</tr>
<tr>
<td>Low Dev.</td>
<td>93.1%</td>
<td>-0.007</td>
<td>(-0.0075, -0.0071)</td>
</tr>
<tr>
<td>Rural Dev.</td>
<td>100%</td>
<td>0.037</td>
<td>(0.0368, 0.0376)</td>
</tr>
<tr>
<td>Open Field</td>
<td>100%</td>
<td>-0.019</td>
<td>(-0.0193, -0.0186)</td>
</tr>
<tr>
<td>Terrain Ruggedness</td>
<td>96.7%</td>
<td>0.011</td>
<td>(0.0105, 0.0112)</td>
</tr>
</tbody>
</table>

Note. Percentages out of the 1,000 trials each coefficient was selected for the forward stepwise selection procedure in the West Virginia/Pennsylvania model. Includes the final coefficients for the model, along with their 95% confidence intervals. The Rural Development variable was predicted to have the strongest relationship to genetic distance, followed by the Forest variable. The abbreviations Low Dev. = Low Development, Rural Dev. = Rural Development, and DMDHV = Distance to Medium and High Development.
Figure 2. Cumulative current map for the West Virginia/Pennsylvania model. Areas of a high current amount indicate high predicted gene flow while a low current amount is the opposite. The predicted high gene flow areas follow the thick forest corridors within Cambria, Clearfield and Indiana counties.
New York/Pennsylvania Model

Only one variable was selected for every trial in the model selection process, Open Development (Table 4). The Forest variable was also selected over 90% of the time but the other variables were selected around 30% of the time or less (Table 3). The model predicted an increased in Genetic Distance as Rural Development and Forest cover amounts decreased (Table 3). This model accounted for around 19 percent of the variation in the genetic distance between samples within the entire set of testing samples (R: 0.194 ± 0.001).

The map of the gene flow predicted by the model indicates two corridors of high flow in Luzerne and Dauphin counties (Figure 3). The upper corridor in Luzerne county has the highest amount of predicted movement and gene flow, represented by the red color on the map (Figure 3). This corridor also extends into Sullivan and Lycoming counties before there is a large amount of dispersal, represented by the light blue color on the map in Lycoming county (Figure 3). The lower corridor through Dauphin count, following the Kittatinny Ridge, is only indicated to be highly concentrated in an area at the border of Dauphin and Perry counties (Figure 3).
Table 3

Percent Coefficients Were Selected From all Model Building Trials and Final Average Coefficients for the New York/Pennsylvania Model

<table>
<thead>
<tr>
<th>Variable</th>
<th>Selection %</th>
<th>Coefficient</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>DMHDHV</td>
<td>11.8%</td>
<td>-0.009</td>
<td>(-0.0095, -0.0090)</td>
</tr>
<tr>
<td>Forest</td>
<td>98.9%</td>
<td>0.015</td>
<td>(0.0144, 0.0160)</td>
</tr>
<tr>
<td>Low Dev.</td>
<td>28.2%</td>
<td>0.010</td>
<td>(0.0090, 0.0117)</td>
</tr>
<tr>
<td>Rural Dev.</td>
<td>100%</td>
<td>0.032</td>
<td>(0.0304, 0.0332)</td>
</tr>
<tr>
<td>Open Field</td>
<td>4.9%</td>
<td>-0.004</td>
<td>(-0.0050, -0.0027)</td>
</tr>
<tr>
<td>Terrain Ruggedness</td>
<td>5.6%</td>
<td>-0.008</td>
<td>(-0.0092, -0.0075)</td>
</tr>
</tbody>
</table>

Note. Percentages out of the 1,000 trials each coefficient was selected for the forward stepwise selection procedure in the New York/Pennsylvania model. Includes the final coefficients for the model, along with their 95% confidence intervals. The Rural Development variable was predicted to have the strongest relationship to genetic distance, followed by the Forest variable. The remaining variables were only considered significant in the final Genetic Distance determination in less than 30 of the 1,000 trials. The abbreviations Low Dev. = Low Development, Rural Dev. = Rural Development, and DMDHV = Distance to Medium and High Development.
Figure 3. Cumulative current map for the New York/Pennsylvania model. Areas of a high current amount indicate high predicted gene flow while a low current amount is the opposite. The predicted areas of high flow in Luzerne and Dauphin counties directly follow the thick corridors of forest cover. The samples are also found within a semi-urban landscape in places and high current flow has been predicted in some of these areas.
DISCUSSION

Discussion

The maintenance of predator populations, and the reintroduction of extirpated populations, has become the goal of many conservation organizations. Healthy predator populations are able to apply top-down controls on prey populations, thus assisting in maintaining the biodiversity in a region, including species the predators do not directly consume (Baggio, Salau, Janssen, Schoon, & Bodin, 2011; Beschta & Ripple 2016; Terborgh et al., 1999). The effect can even move into the realm of abiotic effects such as increasing in-ecosystem carbon cycling (Wilmers & Schmitz, 2016). After reintroduced predator populations are initially established, the maintenance of corridors is essential to providing avenues of dispersal for genetic exchange between populations and avoiding long-term reintroduction failure (Jamieson & Lacy, 2012; Richardson, Doerr, Ebrahimi, Lovegrove, & Parker, 2015). These corridors also allow predators to move between habitat patches that have satisfactory prey abundances, enabling a predator population to grow even if some patches fluctuate in prey abundance (Baggio et al., 2011).

The western portion of Pennsylvania appeared to lack distinct corridors and explains, in part, why the fisher reintroductions was so successful in this state. The lack of distinct paths of movement indicates that many areas of the region are considered acceptable to move through. These many avenues of movement in turn, provide an interconnected landscape which is helpful to maintaining populations (Baggio et al., 2011). The large amount of genetic flow predicted at the large cluster in south-eastern Cambria county (Figure 2) may be the effect of disproportionate sampling and, while
Isolation by Resistance theory is unaffected by spatial autocorrelation of sample points, the disproportionate sampling cluster may be influencing these results (Marrotte & Bowman, 2017).

In the northeastern section of the state, two corridors were evident near Scranton, PA and along the Kittatinny Ridge in eastern Pennsylvania (Figure 3). These corridors represent areas of high movement surrounded by areas of limited movement indicating potential “pinch points,” or areas where the species have a high likelihood of traveling through (McRae et al., 2008). The identification of these features is particularly important for conservation professionals and area planners because the loss of these pinch point corridors could isolate the eastern most fisher populations from other areas of the state (McRae et al., 2008). Eventually this could lead to a loss of genetic diversity of both fisher populations and could be a detriment to the long-term recovery of fisher populations (Jamieson & Lacy, 2012).

There are only two variables from our models that appear to be driving movement patterns in the corridors from the New York/Pennsylvania model set: percent cover of rural development and percent cover of forest. The percent cover of forest follows current literature in that fisher are known to prefer closed canopy forests in their selection of habitat and rest sites (Fuller et al., 2016; Gess et al., 2003; Powell & Zielinski, 1994). The indication of a greater ease of movement through these high forest cover areas confirms this region is similar to the other study areas in the literature in that regard (Powell & Zielinski, 1994). This support extends to both models as that variable was selected many times in the West Virginia/Pennsylvania model as well (Table 2).
The rural development variable was also shown to be a strong driver of these patterns, being selected many times for both of the models (Table 2, Table 3). This finding is consistent with recent studies that concluded fishers are potentially not deterred from moving through an area when encountering low density human development, characteristic of the rural development cover type (Anderson et al., 1976; Ellington et al., 2017; LaPoint, Gallery, Wikselski, & Kays, 2013). One study in Albany, New York found that only a few of their predicted movement corridors were used by GPS collared fisher, concluding that fisher can potentially move through a semi-urban landscape (LaPoint et al., 2013). Additionally, the top model of a study in Pennsylvania indicated a positive correlation between fisher patch use and proportion of developed land, meaning their studied fisher were not deterred by human development up to a certain point (Ellington et al., 2017). This is quite interesting for conservationists and planners since it means some types of low density rural development does not present a barrier, and may even facilitate, movement of this species across a landscape. The true utility of this type of landcover for supporting fisher movements and populations will require further study.

While the New York/Pennsylvania model only selected two variables as being strong drivers of that region’s movement patterns, the West Virginia/Pennsylvania model indicated that many landcover types play a role in determining movement patterns (Table 2). Of the variables not already covered, Terrain Ruggedness was the only one with a positive correlation to gene flow (Table 2). This positive relationship to gene flow is not surprising as the current body of literature also supports a positive association between fisher occupancy and increased terrain ruggedness (Davis, Seo, & Zielinski, 2007). This supporting result could be due to fisher using the more rugged areas of south-western
Pennsylvania, such as the Allegheny and Appalachian Mountains, as main routes of movement but that also needs to be investigated.

The remaining relationships described in the models are supported to some degree in the literature. The decrease in gene flow as the proportion of open fields in an area increased is strongly supported by the literature as that indicated the cover type as a barrier since the decrease in gene flow would indicate that individuals that successfully survived and reproduced do not go through that particular cover type often (Fuller et al., 2016; Powell & Zielinski, 1994). The negative relationship for low development is not as strong as with open fields and may reflect an inconsistent impact due to the variable nature of this landcover type as it has also been shown that semi-urban landscapes do not always represent a complete barrier to fisher movement (LaPoint et al., 2013).

Another variable that is should be examined is the apparent negative relationship between gene flow and distance to medium and high human development (Table 2). However, this relationship could be due to the completely urbanized landscape characteristic of medium and high development can act as a barrier to animal movement (Anderson et al., 1976; LaPoint et al., 2013). Some studies point out that this landscape type can act as a barrier to movement with negative impacts on individuals, while others have found it to be a semi-permeable barrier (Holderegger & Di Giulio, 2010; Keyghobadi, 2007; LaPoint et al., 2013; Powell & Zielinski, 1994). The varied effect this landcover type is indicated to have on fisher movement needs to be further investigated.

While these models resulted in several conclusions of note for fisher conservation, there were some limitations of this study including the use of stationary samples as
opposed to direct movement data, the limited number of variables that were examined, relying on a single spatial scale, and the potential sampling distribution bias. Stationary samples only provide data on the location of an individual and any predictions from this model should be tested via direct movement data such as from a GPS or radio collaring study (Spear et al., 2010). Although this can be costly (Spear et al., 2010), it is a necessary next step in understanding fisher movement patterns across the region.

Additionally, it is recommended to examine the landscape on multiple spatial scales or even initially determine the spatial scale where fisher make movement decisions. This initial study quantified the landscape at a 30 km$^2$ cell resolution because that was the approximate size of a male fisher’s territory (Fuller et al., 2016). However, animals consider their landscapes on multiple levels and incorporating multiple spatial scales could result in a more realistic prediction of their movement preferences (Mayor, Schneider, Schaefer, & Mahoney, 2009). The other limitation was related to the high density of sampled points located in south-western Pennsylvania (Figure 1). We expect that this clump of sampling points resulted in an overrepresentation of these landscape features in our model for western PA. A process of thinning these sample points while accounting for the removed sample’s genetic information should be included as these models are refined.

The most important determination of the models is the presence of two movement corridors in eastern Pennsylvania, one south-west of Scranton, PA and another along the Kittatinny Ridge, that are identified constricted areas of movement which must be prioritized in conservation and research. A particular concern is the position of these two corridors in north-eastern Pennsylvania. Both are strips of forest bordered by agriculture
and human development (Appendix A) and, since both the open field and low
development cover types act, at the very least, as a partial barrier, if those cover types
should overtake the forest then two main routes for movement connecting the eastern and
western side of the state will be lost. These corridors are important in maintaining
landscape continuity as there are no other main routes between the eastern and western
side of the state (Figure 3). The expansion of the open field and low development land
cover types could sever the linkage between eastern and western Pennsylvania and
greatly reduce the movement of fisher between these two sides of the state. This can
have a drastic effect on the health of the populations that would be separated
(Keyghobadi, 2007).

The determination of these movement paths was most strongly driven by the
presence of forest cover within an area and the presence of rural development. This
supports the conclusions that fisher movement is correlated to increased forest cover and
that the species can move through areas with limited human development unhindered.
This should mean a prioritization of conserving forested land, especially for the areas
identified as constricted movement corridors to maintain a regular exchange of
individuals across the landscape. This should be combined with a limitation of human
development in the areas identified as important corridors as these variables have been
determined to act as movement barriers.

The maintenance of corridors between patches is important for the survival of
predator species and for the success of reintroduced predator populations. Because of the
distinct points of origin from reintroduction and the great expansion of fisher populations
in the region, I was able to identify likely movement pathways for fisher and potentially
other species throughout the region. I also identified eastern populations as experiencing restrictions to their movement. We believe that this is primarily due to higher densities of human land use in the area, and reduced forest cover. In order to maintain populations in these areas, further research, such as direct movement studies, would provide more detail as to how fisher make use of these areas. Of special concern are the two corridors identified: south-west of Scranton, PA and the Kittatinny Ridge corridor. These corridors are likely to represent tenuous connections for a variety of wildlife species. Fisher would serve as an excellent model organism for understanding land use by wildlife in this area because they are medium sized animals and prone to relatively long distance movements.
References


Appendix A

Landcover Map of Fisher Samples and Surrounding Area
Appendix B

Map of NY/PA Fisher Samples and Terrain Ruggedness