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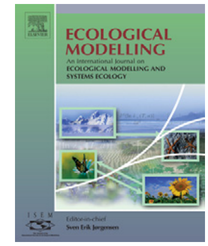

Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods

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ABSTRACT

Since 1990, cougar (*Puma concolor*) presence in midwestern North America has been increasing, with >130 confirmed cougar occurrences (i.e., tracks, photos, carcasses) being verified by professional wildlife biologists during this time. Because many of these confirmed cougar occurrences (>30%) have been carcasses of juvenile males, it is likely that cougars are dispersing into the Midwest from established western populations. Although several wildlife biologists have acknowledged the possibility of cougar presence in the region, no research has been conducted regarding potential corridors that may facilitate dispersal. Therefore, our goal was to determine potential dispersal corridors for cougars in a 9-state portion of the Midwest using a habitat suitability model and least-cost path analysis. We modelled 2-km wide dispersal corridors from established western cougar populations to (1) large areas ($\geq$2500 km^2) of highly suitable cougar habitat, and (2) locations of confirmed cougar occurrences ($n = 29$) in North Dakota, Nebraska, and Missouri. The most likely dispersal corridor to large areas of highly suitable cougar habitat originated in western Texas and branched into the Ouachita and Ozark National Forests of Oklahoma, Arkansas, and Missouri. Within this corridor, road density was low (79 m/km^2) and forests comprised 45% of land cover; these results are consistent with empirical studies that indicate dispersing cougars travel in habitat that provides cover while generally avoiding human influence. Corridor lengths from potential source populations to confirmed cougar occurrences ranged from 3 km to 1100 km, stream density (i.e., an index of riparian zones) ranged from 79 m/km^2 to 249 m/km^2, and grassland cover comprised >40% of corridors from occupied cougar habitat to confirmed occurrences. High grassland cover and riparian zones within these corridors may allow for movement between forest patches while dispersing through the highly agricultural Midwest. Our analysis provides the first description of potential dispersal corridors for cougars from established western populations into the Midwest. Primary benefits from this research include providing an understanding of landscape permeability for large carnivores in a largely unsuitable matrix, and presenting conservation agencies with useful information should cougars continue to disperse into the region.

1. Introduction

The possibility that cougars could re-colonize previously extirpated areas in midwestern North America is provocative given the implications of this phenomenon to conservation and management of large carnivore populations and their prey. Although considered extirpated for >100 years, cougars have been reported in the Midwest consistently since

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1990, with >130 confirmed cougar occurrences (i.e., tracks, photographs, or carcasses) reported by the Cougar Network (2006); one-third of these confirmations are of carcasses of juvenile male cougars killed by vehicles or hunters. Since similar re-colonization events have occurred in other carnivore populations, such as wolves (*Canis lupus*) in Wisconsin and Michigan (Mech et al., 1995; Gehring and Potter, 2005), cougar presence in the Midwest a phenomenon that warrants attention and further investigation, although male-biased dispersal in cougars may influence the rate at which re-colonization of the Midwest may occur (Maehr et al., 2003).

Given the paucity of research regarding cougar presence in the Midwest, reasons for increasing confirmations of cougar presence are unknown. However, one theory appears the most valid: since most carcass confirmation occurrences have been of juvenile males, the most plausible explanation is that juveniles are dispersing from established populations in the west (Nielsen et al., 2006). Dispersal is a permanent movement away from a natal home range to a place where an animal reproduces or would have reproduced had it survived and or found a mate (Howard, 1960; Greenwood and Harvey, 1982). In cougar populations, dispersal generally occurs between the ages of 10–33 months (Hemker et al., 1984; Maehr et al., 1991; Lindzey et al., 1994; Logan et al., 1996) and consistent with polygynous mammals, juvenile males are the primary dispersers (Anderson et al., 1992; Sweanor et al., 2000). Cougars are capable of dispersing long distances (Murphy et al., 1999; Logan and Sweanor, 2001; Thompson and Jenks, 2005); long distance dispersal is important in cougar populations, as recruitment often occurs because of immigration of juveniles from adjacent populations (Beier, 1995; Sweanor et al., 2000). Furthermore, dispersal enables cougars to expand their distributional range and can lead to gene flow between populations and re-colonization of unoccupied areas (Beier, 1995; Penrod et al., 2006). Vacant habitats may become re-colonized if they are linked geographically to populations that could provide sources of immigrants (Murphy et al., 1999).

Since the 1960s, cougar populations in the west have increased dramatically, primarily because of management that has protected the species from indiscriminate killing (Nadeau, 2005) and because of increasing ungulate populations throughout cougar range (Berger and Weyhausen, 1991). There also appears to be healthy gene flow between several western populations, indicating that western populations are somewhat interconnected (Anderson et al., 2004). Elevated cougar populations in the west may be pushing juvenile dispersers into the Midwest (Maehr et al., 2002) in search of available habitat to establish home ranges, as relatively few vacancies may exist within western cougar range. Indeed, genetic studies of cougar populations in Wyoming discovered high migration rates across open and unsuitable habitat, as male dispersal has presumably maintained connectivity between populations (Anderson et al., 2004). Effective cougar population size in Wyoming was estimated to be 500 individuals and actual size of these populations well exceeded the minimum at nearly 4500 individuals (Anderson et al., 2004). Another study found that the age structure of cougar populations in Wyoming were primarily sub-adults (Anderson and Lindzey, 2005), which constitute most of dispersers (Anderson et al., 1992; Sweanor et al., 2000).

Populations on the eastern edge of western cougar range exist as potential sources of cougar dispersal into the Midwest. For instance, the Black Hills, South Dakota, contains a cougar population with approximately 150 individuals (Fecske, 2003), and sub-adult dispersal has been frequently documented within the past 5 years (D. Thompson, personal communication, 2006; Cougar Network, 2006). One particular male was recorded traveling 1067 km during dispersal (Thompson and Jenks, 2005) and several others have dispersed >400 km (D. Thompson, personal communication, 2006; Cougar Network, 2006). Also, populations in Texas appear to be expanding eastward, as the eastern-most counties within current Texas range have recently reported the highest cougar presence of any county in the state (Harveson et al., 2003).

Because there is a possibility that cougar range may expand into the Midwest, an investigation of potential paths of dispersal is timely. A useful method of determining dispersal corridors is through the development of least-cost paths (Meegan and Maehr, 2002; Schad et al., 2002; Larkin et al., 2004; Kautz et al., 2006; Penrod et al., 2006). This technique models the relative cost for an animal to move between two areas of suitable habitat (Penrod et al., 2006). Least-cost path (LCP) analysis is based on how the movement path of an animal may be affected by characteristics of the landscape, such as land cover, human density, roads, or slope (Singleton et al., 2002; Penrod et al., 2006). Within a GIS, each cell in a raster dataset is assigned a value for cost of movement. The model creates the most likely travel route by selecting a combination of cells that accrue the least resistance with the shortest distance between two areas of suitable habitat (Larkin et al., 2004). Least-cost paths contain the most suitable habitat and fewest movement barriers (Larkin et al., 2004), and therefore, the best theoretical route for a dispersing animal.

Although a few studies have addressed confirmations of cougar occurrence in the Midwest (Tischendorf, 2003; Nielsen et al., 2006), no research has been conducted regarding potential dispersal from western populations into the region. Our goal was to model LCP for cougars in the Midwest, using a habitat suitability model (LaRue, 2007) as the basis for analysis. We identified corridors through the Midwest where the landscape would facilitate dispersal of cougars to provide an understanding of landscape permeability for large carnivores in a largely unsuitable matrix, and to present conservation agencies with useful information should cougars continue to disperse into the region.

2. Methods

2.1. Study area

The study area covered 3,182,294 km^2 of the midwestern and western United States, including the states of North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Arkansas, Missouri, Iowa, Minnesota, Wyoming, Colorado, New Mexico, and Texas (Fig. 1). This region was selected because of the increasing numbers of confirmed cougar occurrences in the area (Fig. 1), its proximity to western cougar populations, the likelihood of potential dispersal corridors, and the scarcity of cougar occurrence confirmations east of the Mississippi River

Fig. 1 – Study area for modelling potential cougar habitat suitability and dispersal corridors in midwestern North America. Cougar confirmations in the region from 1990 to the present are shown (Cougar Network, 2006; Nielsen et al., 2006). Confirmations within the Black Hills and Badlands are not shown for clarity. Class I confirmations are carcasses, photos, or DNA verified by wildlife professionals. Class II confirmations are tracks verified by wildlife professionals.

(Nielsen et al., 2006). We also created habitat models for Texas, New Mexico, Colorado, and Wyoming because these states contain resident populations of cougars from which dispersal into the Midwest could occur.

The 13-state study area was dominated by agriculture and grasslands; 42% of the area was used for agricultural purposes and 25% was composed of grasslands. Statewide proportions of agriculture ranged from 3% in New Mexico to 81% in Iowa. Conversely, forest cover only composed 15% of the land cover of the study area; Arkansas contained the largest proportion of forest cover (51%).

Human densities ranged from <1 persons/km^2 in remote areas of North Dakota and South Dakota, to >10,500 persons/km^2 in Minneapolis and St. Paul, Minnesota. Road densities ranged from 65 m/km^2 to 189 m/km^2; these data were derived from 2000 Bureau of Transportation Statistics and included paved roads. Stream densities were lowest in South Dakota and Oklahoma (64 m/km^2) and highest in Arkansas (114 m/km^2). Stream data were derived from recent DEM data obtained from http://seamless.usgs.gov. Road and stream densities were determined by summing lengths within each state and dividing by the area of the state.

The region was mainly characterized by rolling plains and local changes in elevation were typically minor. However, the Ozark Mountains in southeastern Missouri, northwestern Arkansas, and eastern Oklahoma were characterized by steep topography, reaching elevations of >762 m above sea level. The Black Hills in South Dakota were also characterized by rugged terrain, with elevational changes of 914 m. Regional climate was continental and mean annual temperatures ranged from 2 °C in Minnesota to 17 °C in Oklahoma. Extreme temperatures can reach −57 °C in the north to >43 °C in the south. Average precipitation ranged from 89 cm of rain and 178 cm of snow in the north to 142 cm of rain in the south.

2.2. *Overall approach*

Our approach to modelling potential dispersal corridors was based on LCP methods and a habitat suitability model, where biological and anthropological influences were assessed by wildlife biologists to determine potential suitable habitat for cougars in the Midwest (LaRue, 2007). We were unable to use empirical data from midwestern cougars to create the habitat suitability model because such data were unavailable. The habitat suitability model for cougars represented the base layer for the LCP modelling (Kautz et al., 2006). We developed LCP (i.e., dispersal corridors) from western source populations to areas of highly suitable cougar habitat and confirmed cougar occurrences in the Midwest.

2.3. *Habitat suitability modelling*

2.3.1. *Expert-opinion surveys*

To create a habitat model, which commonly relies upon empirical data from animal space-use studies (Clark et al., 1993; Clevenger et al., 2002; Nielsen and Woolf, 2002), it was first necessary to identify specific habitat requirements for cougars. However, because cougar presence in the Midwest is relatively scant and potential habitat in this region had not been identified, acquisition of empirical data regarding habitat needs for cougars was not possible. Therefore, we used an expert-opinion survey to obtain information to rank variables for our habitat model (Store and Kangas, 2001; Clevenger et al., 2002). Our survey was approved by the Human Subjects Committee at Southern Illinois University Carbondale (protocol #06028).

We created an expert-opinion survey by first researching cougar literature and soliciting information from cougar biologists. We identified habitat factors and ecological requirements for cougars, which included cover type, distance to roads, distance to water, slope, and human density. With the assistance of two cougar experts (H. Shaw, The Juniper Institute; C. Anderson, Wyoming Game and Fish Department), we developed a survey consisting of several questions regarding pair-wise comparisons of the aforementioned habitat factors. The survey asked expert participants to score habitat variables in order of potential importance to cougars in the Midwest, based upon personal experience and knowledge of cougar ecology. The survey was then sent to 29 wildlife biologists who study cougars or furbearer biologists who work for state or federal agencies in the Midwest.

2.3.2. *Geospatial data*

We created geospatial datasets to represent midwestern landscapes by downloading 30-m digital elevation model

(DEM) data and land cover from http://seamless.usgs.gov. Human density data were obtained from the 2000 U.S. Census Bureau and converted to raster format as 90-m pixels. Road information was 2000 TIGER line data from the Bureau of Transportation Statistics. All geospatial data were processed in ArcGIS 9.0 (Environmental Systems Research Institute Inc.).

Digital elevation model data were prepared for each state in the study area using extensions in ArcToolbox for ArcGIS 9.0 (Environmental Systems Research Institute Inc.). We then resampled the mosaics to 90 m. Slope was calculated as percent rise and we classified slope based on categories in the expert-opinion survey. We further used the statewide 90-m DEM data and the Hydrology tool to create stream shapefiles by filling the DEM, calculating flow direction, and calculating flow accumulation. The stream shapefiles were buffered based on distances identified in the expert-opinion survey.

The 1992 National Land Cover Dataset contained 21 classes, but similar types were grouped together into 8 different categories: barren/developed and open water, deciduous forest, mixed forest, evergreen forest, grasslands, agricultural, wetlands, and shrublands. We then resampled all mosaics to 90 m.

Roads data, which included all major highways and interstates, were clipped by state extensions in ArcToolbox for ArcGIS 9.0 (Environmental Systems Research Institute Inc.). A multiple ring buffer was applied to all roads, according to the distances identified in the survey. All layers were then converted to raster and reclassified into categories consistent with the expert survey.

2.3.3. *Analytical hierarchy process*

The expert survey provided information necessary for calculating the relative importance (i.e., weight) of each variable in the habitat model. A popular technique for the development of relative weights is a decision-making method called the Analytical Hierarchy Process (AHP; Saaty, 1980). The AHP is a flexible, structured method that enables individuals to derive a solution to a problem based on past experience (Kovacs et al., 2004). This process utilizes pair-wise comparison matrices that clarify the relative importance of two criteria involved in determining habitat suitability. Experts then compare every possible pairing and enter ratings, which are based on a continuous scale, into the matrix.

Eleven expert-opinion surveys were returned and subsequently analyzed using the AHP. Matrices of pair-wise comparisons were completed and preferences were then summarized to assign each element a relative importance value (Kovacs et al., 2004). This is a two-step process, which first involved normalizing the data, where a_{ij} was the pair-wise rating for attributes i and j:

$$a_{ij} = \frac{a_{ij}}{\sum_{i=1}^{n} a_{ij}}, \quad \text{for all } j = 1, 2, \ldots, n.$$

Weights were then calculated as follows, where w is the computed weight of an attribute (e.g., deciduous forest) within variable (e.g., cover type):

$$w_i = \sum_{j=1}^{n} a_{ij}, \quad \text{for all } i = 1, 2, \ldots, n.$$

Table 1 – Weights for variables used in development of the model of potential habitat suitability for cougars in midwestern North America (LaRue, 2007)

Variable	Weights[a] (S.E.)	Percent importance from land cover
Land cover	1.84 (0.59)	100
Human density	1.22 (0.82)	66
Distance to paved roads	0.86 (0.45)	47
Slope	0.61 (0.56)	33
Distance to water	0.47 (0.26)	26

This habitat model was the basis for least-cost path modelling procedures used for predicting dispersal corridors for cougars in the Midwest.

[a] Weights were calculated using the Analytical Hierarchy Process (Saaty, 1980) and represent the averaged, relative scores of importance of each variable to potential cougar habitat suitability in midwestern North America.

We carried out the AHP in Microsoft Excel®. All attribute and variable responses from the 11 experts were combined and averaged to depict relative weights of each attribute and variable. We then ranked attributes and assigned the averaged weights to variables. Experts indicated that land cover was the most important variable for predicting potential habitat for cougars in the Midwest, followed by human density (Table 1; LaRue, 2007). Specifically, forest cover (i.e., mixed, deciduous, and evergreen) and low human density were the most suitable for cougars (Table 2; LaRue, 2007). To complete the habitat suitability model, we reclassified all data layers based on the rankings calculated from the AHP and then assigned the averaged weights for the variables with Map Algebra within ArcToolbox in ArcGIS 9.0 (Environmental Systems Research Institute Inc.) for each 90-m^2 pixel. The model was generally accurate when validated with independent data; average habitat suitability in 66 sections containing confirmed cougar occurrences was 68% (LaRue, 2007).

2.4. *Least-cost path modelling*

Map Algebra was used to calculate reciprocal pixel values of the habitat suitability model to create a cost raster that associated favorable habitat with lower pixel values, and thus, lower cost of movement through them. We obtained information from cougar biologists in Texas (J. Young, Texas Parks and Wildlife Department, personal communication), New Mexico (R. Winslow, New Mexico Department of Game and Fish, personal communication), Colorado (K. Logan, Colorado Division of Wildlife, personal communication), and Wyoming (C. Anderson, Wyoming Game and Fish Department, personal communication), to identify the eastern-most counties that contain cougar populations in each state. The Black Hills, South Dakota, the Badlands, North Dakota, and counties of western states identified by experts served as the eastern edge of cougar range and thus, as "source areas" for LCP analysis.

Using ArcToolbox and the cost raster, we created cost-weighted distance and direction rasters for source areas for each LCP (i.e., the polygon from which all simulated movement began). The "destination" was the point or polygon

Table 2 – Weights for land cover, distance to paved roads, distance to water, human density, and slope variables used in the development of the model of potential habitat suitability for cougars in midwestern North America (LaRue, 2007)

Variable	Attribute	Weight (S.E.)	Percent importance from highest ranking variable
Land cover	Mixed forest	1.92 (0.51)	100
	Deciduous forest	1.61 (0.37)	84
	Evergreen forest	1.59 (0.62)	83
	Shrublands	1.12 (0.85)	58
	Wetlands	0.67 (0.29)	35
	Grasslands	0.61 (0.47)	32
	Agricultural	0.28 (0.17)	15
	Barren/developed	0.19 (0.05)	10
Distance to paved roads	Long (>5 km)	1.43 (0.71)	100
	Medium (0.3–5 km)	0.88 (0.34)	62
	Short (<0.3 km)	0.69 (0.73)	48
Distance to water	Short (<1 km)	1.57 (0.41)	100
	Medium (1–5 km)	0.92 (0.27)	59
	Long (>5 km)	0.52 (0.27)	33
Human density	Low (<5 persons/km^2)	2.28 (0.39)	100
	Medium-Low (6–10 persons/km^2)	1.00 (0.18)	44
	Medium-High (11–19 persons/km^2)	0.46 (0.27)	20
	High (>20 persons/km^2)	0.25 (0.07)	11
Slope	Steep (>15°)	1.17 (0.54)	100
	Moderate (5–15°)	1.17 (0.41)	100
	Gentle (<5°)	0.66 (0.53)	56

This habitat model was the basis for least-cost path modelling procedures used for predicting dispersal corridors for cougars in the Midwest.

where all paths ended. Modelling created LCP that began at the source and ended at the defined destination, using the cost-distance and direction rasters as the environment through which to move. We modelled LCP from sources to two sets of destinations: (1) areas of contiguous (≥2500 km^2) habitat with an average suitability value of 75% (i.e., highly suitable habitat) in Minnesota, Missouri, Arkansas, and Oklahoma (LaRue, 2007); and (2) locations of 29 confirmed cougar occurrences (Cougar Network, 2006) in North Dakota ($n = 9$), Nebraska ($n = 12$), and Missouri ($n = 8$). The latter analysis simulated the most likely path through which a cougar could have moved from anywhere in western cougar ranges to the point at which the occurrence confirmation was recorded. Confirmations of cougar occurrence consisted of carcasses, photos, tracks verified by a professional wildlife biologist, or DNA evidence (Cougar Network, 2006). None of the confirmed cougar occurrences used in this analysis were radio-collared animals associated with any on-going cougar research projects (Fecske, 2003; Thompson and Jenks, 2005).

We described habitat factors in corridors associated with LCP (and statewide for states containing LCP) and determined lengths of each path. First, we buffered all LCP by 1 km, which is a sufficient width for cougar movement through a corridor (Noss, 1992; Beier, 1995), and hereafter call these "potential dispersal corridors". We then extracted all land cover, streams, and road density data within each potential dispersal corridor and determined the amount of forest, grassland, agriculture, and developed land within. We also calculated the density of streams and roads contained in each corridor by summing all road and stream segments in each LCP polygon and dividing by the area of the segment. For comparison purposes, we further calculated landscape characteristics for all states through which corridors passed.

3. Results

3.1. *Potential dispersal corridors to highly suitable cougar habitat*

We created one potential dispersal corridor to large, contiguous areas of highly suitable cougar habitat in the Midwest; this corridor originated in Kimble County, Texas, and branched to areas in the Ouachita National Forest, the Ozark National Forest, and Mark Twain National Forest (Fig. 2). Corridor length was 1113 km and road and stream densities were 79 m/km^2 and 77 m/km^2, respectively. Forest cover represented 45% of the corridor and grasslands comprised 20%. Agriculture and developed land represented 15% and 21%, respectively, of the corridor. Percent available forest cover statewide in Texas was 15%, while grasslands composed 21% of the state (Table 3). Arkansas and Missouri contained higher amounts of forest cover (37–51%; Table 3).

3.2. *Potential dispersal corridors to confirmed cougar occurrences*

We created 29 potential dispersal corridors from occupied cougar habitat to confirmed cougar locations in North Dakota, Nebraska, and Missouri (Fig. 3). Average road and stream densities were 36 m/km^2 and 143 m/km^2, respectively, in corridors (Table 4). Grasslands and agriculture combined represented

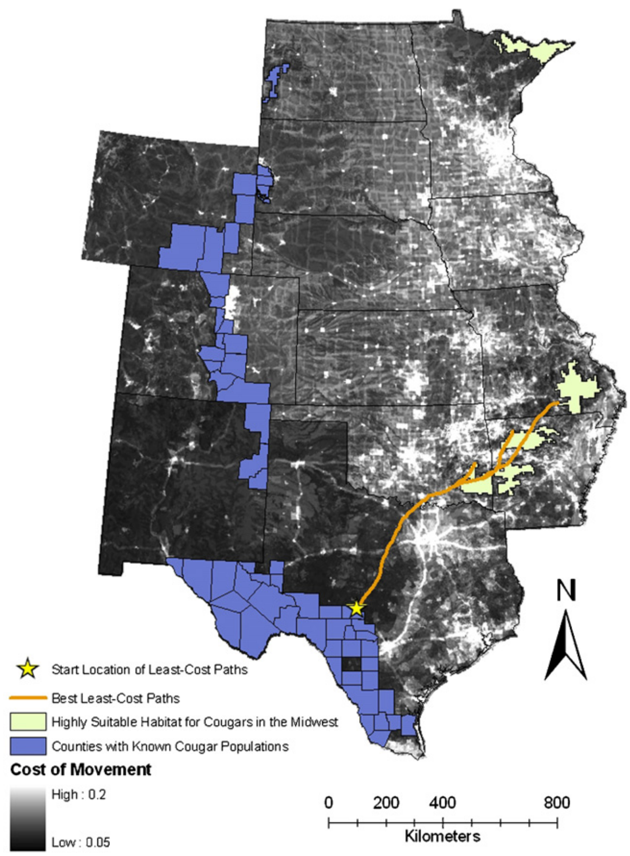

Fig. 2 – Best potential dispersal corridor from source area (i.e., easternmost areas in current western cougar ranges containing known breeding populations) to areas of highly suitable potential cougar habitat in midwestern North America.

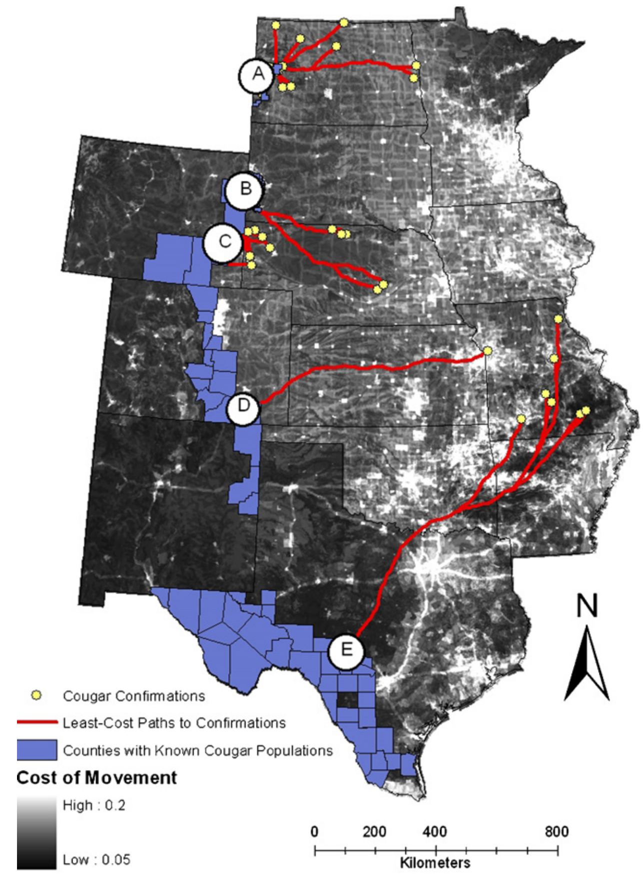

Fig. 3 – Potential cougar dispersal corridors from source area (i.e., easternmost areas in current western cougar ranges containing known breeding populations) to cougar confirmations in North Dakota, Nebraska, and Missouri. Starting points for least-cost paths were: A. Badlands, ND; B. Black Hills, SD; C. Platte and Niobrara Counties, WY; D. Las Animas County, CO; E. Kimble County, TX. Dates of confirmations range from 1990 to 2006 and confirmations are exact coordinate locations of cougars.

>80% of corridors (Table 4). Available land cover in these states was dominated by agriculture and grassland, although proportions of agriculture were higher in North Dakota and Missouri and approximately equal to proportions of grasslands in Nebraska (Table 3).

In North Dakota, all potential dispersal corridors originated in the Badlands (Fig. 3); lengths ranged from 3 km to 479 km (Table 4). For the 12 occurrence confirmations in Nebraska; 7 corridors originated in Wyoming and 5 started in the Black Hills of South Dakota (Fig. 3). The average length of corridors beginning in Wyoming was 68 km; grasslands represented >80% of corridors and only 1% of corridors contained developed land (Table 4). Average length of the 5 corridors originating in the Black Hills was 384 km, and these corridors contained a stream density of 249 m/km^2 and only 7% forest cover (Table 4). These corridors generally contained

Table 3 – Proportions of grassland, agriculture, developed, and forested cover available in states containing least-cost paths for cougars in midwestern North America

State	Road density (m/km^2)	Stream density (m/km^2)	%Forest	%Grassland	%Agriculture	%Developed
North Dakota	68	83	1	30	54	1
South Dakota	65	64	3	44	44	1
Nebraska	80	76	2	50	41	1
Kansas	85	71	3	43	50	1
Oklahoma	118	64	21	32	38	2
Texas	77	61	15	21	27	3
Arkansas	189	113	51	0	37	2
Missouri	123	85	37	3	54	2

Table 4 – Summary statistics for 29 dispersal corridors (i.e., least-cost paths) from source area (i.e., easternmost areas in current western cougar ranges containing known breeding populations) to cougar confirmations in North Dakota, Nebraska, and Missouri

Source location[a]	Paths n	Path length (km)		Road density (m/km^2) (S.E.)	Stream density (m/km^2) (S.E.)	%Forest (S.E.)	%Grasslands (S.E.)	%Agriculture (S.E.)	%Developed (S.E.)
		Mean (S.E.)	Range						
A	9	201 (59)	3–479	36 (6)	143 (29)	2 (1)	45 (6)	38 (5)	6 (1)
B	5	384 (55)	267–522	39 (2)	249 (24)	7 (1)	83 (0.4)	7 (1)	2 (0.2)
C	7	68 (12)	13–108	77 (49)	60 (24)	6 (4)	83 (3)	8 (2)	1 (0.5)
D	1	838	–	80	187	5	58	29	4
E	7	1213 (52)	1015–1455	79 (1)	78 (2)	57 (1)	13 (0.5)	16 (1)	2 (0.1)

[a] Defined in Fig. 3.

more grassland cover than states through which they passed (Table 3).

Seven of the eight potential dispersal corridors from occupied cougar habitat to confirmed occurrences in Missouri originated in Kimble County, Texas (Fig. 3). The average length of these corridors was 1213 km. Road and stream densities were 79 m/km^2 and 78 m/km^2, respectively (Table 4). Corridors were dominated by forest cover; developed land only represented 2% of the area. The length of the 1 corridor beginning in Colorado was 838 km (Fig. 3), stream density was 187 m/km^2 and grasslands were the dominant land cover type in that corridor (Table 4), although the highest percentage of land cover available in Kansas was agriculture (Table 3).

4. Discussion

4.1. *Potential dispersal corridors for cougars in the Midwest*

Our creation of LCP provides the first description of potential dispersal corridors for cougars in midwestern North America. The best potential dispersal corridor to highly suitable cougar habitat originated in Kimble County, Texas, and terminated in the Ouachita and Ozark Mountains of Oklahoma, Arkansas, and Missouri. Seven corridors from occupied cougar habitat to confirmed occurrences in Missouri also partially followed the best corridor. These corridors passed through areas of Texas and Missouri containing generally more forest cover than what existed statewide; corridors also passed through more developed areas than what was available, likely due to their presence near large metropolitan areas such as Dallas-Ft. Worth, Texas. This set of corridors traversed portions of Texas containing similar grassland cover as available on the landscape, but contained more grassland cover than existing statewide in the relatively forested landscapes of Arkansas and Missouri. Agricultural cover within corridors was much less than available on the larger landscape. Clearly the agricultural portions of the Midwest, which are generally devoid of plant cover for ca. 6 months of the year, would be of poor habitat suitability for dispersing cougars much of the time.

The best potential dispersal corridor to highly suitable cougar habitat and corridors from occupied cougar habitat to seven confirmed occurrences in Missouri originated in an area of Texas where eastern range expansion has already occurred (Harveson et al., 2003) and therefore, could be a realistic source of dispersers into the area. Furthermore, 12 confirmed cougar occurrences have been recorded recently in eastern Texas and 2 have been recorded in Arkansas (Cougar Network, 2006), all of which were relatively close to this particular corridor.

In the best potential dispersal corridor to highly suitable habitat and dispersal corridors originating in Platte and Niobrara Counties, Wyoming, road density was slightly higher than stream density, but this may be inconsequential as Dickson et al. (2005) noted that paved roads may constrain movement, but do not prevent movement by cougars. Other studies have shown that cougars do not necessarily avoid roads during travel (Sweanor et al., 2000) and may also disperse through corridors containing unsuitable habitat (Anderson et al., 2004) or unnatural features such as golf courses and housing developments (Beier, 1995; Dickson and Beier, 2002). However, contact with roads and other human influences clearly increase probability of mortality for cougars (Logan et al., 1986; Maehr et al., 1991; Murphy et al., 1999). For this set of corridors, road density within corridors was less than existing statewide in Arkansas and Missouri, but similar to the lower road densities prevalent in Nebraska, Texas, and Oklahoma. This indicates that the influence of roads in LCP determination is greater in states containing relatively high road densities, as reflected in the opinions of expert biologists.

Lengths of corridors predicted in our analysis were within ranges of feasible dispersal distances for cougars. The length of the best corridor to highly suitable cougar habitat was 1113 km, which is similar to the maximum straight-line distance for a juvenile male cougar during dispersal (Thompson and Jenks, 2005); a dispersing juvenile female cougar within western distributions has also been recorded traveling >1300 km (Cougar Network, 2006). Furthermore, lesser dispersal distances of <400 km are commonly reported in the literature (Anderson et al., 1992; Beier, 1995; Sweanor et al., 2000; Logan and Sweanor, 2001).

Potential dispersal corridors from occupied cougar habitat to confirmed occurrences were similar to the best corridor to highly suitable cougar habitat in that these paths also included low road density (≤80 m/km^2), low proportions of developed land (≤6%), and terminal locations were within recorded dispersal distances of cougars. However, one major difference between the best corridor to highly suitable cougar habitat and corridors to confirmation occurrences was that average forest cover was low (2–7%) and percent grass cover was relatively high (45–88%) in routes to cougar confirmation occurrences. Others have found that grasslands may play an important role in cougar movement (Dickson et al., 2005), especially in areas devoid of forest cover such as the agricultural Midwest. Dickson et al. (2005) found that grasslands were used during movement and stasis, suggesting that grasslands allow cougars to stalk and pursue prey. A study involving an expert survey found cougar presence in mixed and short-grass plains of western Oklahoma, and that prairie and grassland matrices in Minnesota were suitable habitat for cougars based on occurrences (Hutlet, 2005; Cougar Network, 2006). Grassland patches may also provide security for cougars while dispersing through areas containing more highly preferred forest or brushy cover. Furthermore, cougar populations were once widespread throughout the prairie-dominated Midwest prior to extirpation circa 1900 (Sunquist and Sunquist, 2002; Pierce and Bleich, 2003). Therefore, the resulting high grassland cover within corridors from occupied cougar habitat to confirmed cougar occurrences may in fact allow for movement between forest or riparian areas while dispersing.

The disparity in the amount of forest cover between the best potential dispersal corridor to highly suitable cougar habitat and corridors to confirmations was notable, as the former contained higher proportions of forest cover than the latter. This result was not surprising, given that most of the Midwest contains low amounts of forest cover (<15%). Corridors to confirmation occurrences generally compensated lack of forest cover with high proportions of grassland and high stream density potentially suitable for cougar dispersal. Stream density (i.e., representing riparian areas) in corridors to confirmations was much higher (up to 249 m/km^2) than the best corridor to highly suitable cougar habitat. These results were consistent with studies documenting cougar use of riparian corridors for movement (Murphy et al., 1999; Dickson and Beier, 2002; Dickson et al., 2005). The resulting high stream density also probably represents the importance of riparian corridors to cougars in a region where forest is not highly available.

4.2. *Assumptions*

We made several assumptions regarding LCP modelling. Dispersing cougars respond to the landscape at several scales (Dickson and Beier, 2002; Dickson et al., 2005). Our major assumption was that dispersing cougars would be less sensitive to microhabitat characteristics (e.g., vegetation structure) and respond to general suitability of macrohabitat for movement purposes (Walker and Craighead, 1997). To model large-scale corridor routes, we further made these assumptions:

(1) Favorable corridors were composed of primarily suitable habitat for cougars. Dispersal habitat may contain smaller areas of suitable establishment habitat, and may contain areas of completely unsuitable habitat (e.g., developed lands, agricultural fields) throughout the corridor (Beier, 1995; Kautz et al., 2006). Although cougars prefer cover (Lindzey, 1987; Belden et al., 1988; Laing, 1988; Pierce and Bleich, 2003), we assumed that a cougar could move relatively short distances without appropriate cover, as studies have found that cougars can travel over unsuitable terrain (Beier, 1995; Logan and Sweanor, 2001; Anderson et al., 2004; Dickson et al., 2005; Kautz et al., 2006).

(2) The LCP provides a greater probability of survival for a cougar while traversing the entire distance. A dispersing cougar may not choose the most optimum path for movement, as animals are likely unaware of their destination and use of a corridor is dependent on whether travel patterns of a cougar cause it to encounter the entrance (Beier, 1995). We recognize that these may not be exact paths used by cougars, due to variability in individual behavior (Walker and Craighead, 1997). If a cougar did follow the LCP, it would encounter fewer hazards (e.g., roads), spend less time traveling, and habitat through which it traveled would likely optimize food and cover, thus increasing survival (Walker and Craighead, 1997; Larkin et al., 2004; Penrod et al., 2006).

(3) Human influences on the landscape are permanent and may hinder movement of cougars. First, human development greatly influences cougar presence in an area, as cougars tend to avoid human disturbance (Van Dyke et al., 1986). Roads, in particular, may pose the greatest threat of mortality for a dispersing cougar (Beier, 1995; Murphy et al., 1999); indeed, several confirmations of cougar occurrences in the Midwest have been road-killed animals (Cougar Network, 2006). Also, because cougars are large, elusive predators and people typically do not understand cougar biology (Casey et al., 2005), innate fear by humans may cause the tendency for direct persecution. Therefore, we assumed that optimal dispersal habitat should tend to

avoid human development and disturbance, even though cougars may persist near areas of human development (Beier, 1995).

5. Conclusions

There is much utility in modelling LCP for cougars because this analysis allows for the identification of potential dispersal corridors, which is important to long-term management and planning for cougar populations in the Midwest (Sweanor et al., 2000). Identification of areas on the landscape that promote dispersal may better equip agencies to monitor cougar presence in the region. In particular, the most cost-effective and widely used method of determining cougar presence and abundance is track surveys (Smallwood and Fitzhugh, 1995; Beier and Cunningham, 1996; Mason et al., 1999; Choate et al., 2006). Camera traps may be another useful method for monitoring cougar presence as these methods have been effective for monitoring other large, elusive felids such as jaguars (*Panther onca*; Wallace et al., 2003; Silver et al., 2004) and tigers (*Panthera tigris*; Karanth, 1995; Karanth and Nichols, 1998) that typically occur at low densities. Because paths of travel for cougars through the Midwest are not yet known empirically, conservation agencies could use the potential dispersal corridors identified in this study as a guide for placement of track surveys or camera traps. Finally, conservation agencies could use our work to target areas in which to conduct surveys to better understand human attitudes and perceptions regarding cougars (Riley and Decker, 2000; Casey et al., 2005).

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