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RESEARCH ARTICLE

Potential cougar habitats and dispersal corridors in Eastern North America

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Abstract
Context Cougars (*Puma concolor*) have been recolonizing Midwestern North America during the past 3 decades with > 950 cougar confirmations east of established populations. Due to an increase in confirmations east of current breeding populations, evaluation of cougar habitat suitability and connectivity is needed. However, few studies have assessed the habitat potential for cougar recolonization in the eastern portion of their former range.
Objectives We used various habitat quality thresholds to model potential cougar habitats and dispersal corridors throughout eastern North America.
Methods Based on expert opinion, we used landcover, slope, human density, distance to roads, and distance to water as model variables. Least-cost path methods were used to model dispersal corridors from western populations to potential eastern habitat patches.
Results Patches of suitable habitat ranged in size from 3868 km^2 (Ozark Mountains) to > 2,490,850 km^2 (central and eastern Canada). Potential habitats were predominantly forest and shrubland, contained little anthropogenic development, and had high stream densities. Dispersal corridors were present throughout the study area. Corridors largely consisted of forested and cultivated landscapes and had higher road densities than habitat patches.
Conclusions Our research provides conservationists with insights into areas suitable for cougar recolonization so they may proactively plan for potential cougar populations east of their current range. This work also provides a framework for evaluating multiple levels of landscape suitability for recolonizing species.

Keywords Range expansion · Habitat modelling · Habitat availability · Landscape structure · Wildlife corridors

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Introduction

Cougars, pumas, catamounts, or mountain lions (hereafter called cougars; *Puma concolor*) were the most widely distributed wild land mammal in the Americas

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(Sunquist and Sunquist 2002; Gill 2009; Cougar Network 2021). Their historical range spanned from northern Yukon territory to southern Chile. However, they have since been extirpated from much of their range in North America; largely due to human driven habitat loss, persecution, and overexploitation of prey species (Cardoza and Langlois 2002; Gill 2009). By the late 1800s, most cougar populations had been extirpated from the mid-Atlantic and southern coastal states (Cardoza and Langlois 20022; Gill 2009). During the early 1900s, the last few eastern populations in the Appalachian Mountains, New England, and Ontario were extirpated (Cardoza and Langlois 2002; Gill 2009). By 2000, remaining cougar populations were restricted to western North America and southern Florida. The Florida cougar population was designated as a distinct population and federally listed as Endangered in 1967 (USFWS 2008; Gill 2009).

In response to declines in predator populations and changes in wildlife management philosophy, cougars were reclassified from bounty animals to big game species during the mid-twentieth century (Ross et al. 1996; Sweanor et al. 2000; Gill 2009). In North America, bounty animals refer to species where compensation is provided for each individual killed. Big game species, however, refers to species where harvest laws such as take limits and harvest seasons are in place. Changes in cougar classification, management, and the recovery of ungulate prey increased cougar numbers throughout western North America (Knopff et al. 2014b). Cougars began recolonizing eastern portions of their historical range, with > 950 confirmations (e.g., carcasses and camera photographs) recorded east of their current range since 1990 (Nielsen et al. 2006; LaRue and Nielsen 2008, 2011; Cougar Network 2011; LaRue et al. 2012). Currently, 3 distinct breeding populations of cougars exist in the Midwest (LaRue et al. 2012, 2019) and are located in the South Dakota Black Hills, North Dakota Badlands, and northwestern Nebraska. The Black Hills population is the closest to western cougar populations. Immigration of western cougars into the Black Hills population makes the region a source for the Badlands and Nebraska populations through stepping-stone dispersal (Stoner et al. 2008; Beier 2009; Thompson and Jenks 2010; Wilson et al. 2010; LaRue et al. 2012, 2019; Hawley et al. 2016). Stepping-stone dispersal assumes dispersing animals move through a mosaic of habitats from one suitable habitat patch to another (Baum et al. 2004; Kramer-Schadt et al. 2011; Saura et al. 2014). Cougars fit the stepping-stone dispersal model as females disperse at lower rates and in shorter distances than males (Sweanor et al. 2000; Maehr et al. 2002; LaRue et al. 2012).

Cougar range expansion, however, is contingent upon the presence of these stepping-stone habitats. LaRue and Nielsen (2011) modeled potential habitat for cougars in the Midwest, finding 8% of the region contained highly suitable cougar habitat. LaRue et al. (2012) found 62% and 79% of reported cougar confirmations (Cougar Network 2011) were within 20 km and 50 km of modeled potential habitat, respectively. Given the capability of long-range dispersal, confirmed sightings east of the Rockies, and establishment of new breeding populations in previously extirpated regions, cougar recolonization in eastern North America is likely (Taverna et al. 1999; LaRue and Nielsen 2008, 2011; Henaux et al. 2011; LaRue et al. 2012). Cougars are expected to recolonize areas in the Midwest by 2040, creating stepping-stones for further dispersal into eastern North America (LaRue and Nielsen 2016; LaRue et al. 2019).

Previous research evaluating regional availability of cougar habitat east of their historical range has found evidence of cougar habitat throughout the region (Houser 2002; Thatcher et al. 2006; Laundré 2013; Glick 2014; O'Niel et al. 2014; Gantchoff et al. 2021). Although smaller-scale studies on cougar habitat suitability in this region have been conducted, no studies have modeled potential habitats and dispersal corridors for the entire cougar former range east of the Rocky Mountains. Such information is valuable to assist wildlife managers in predicting where cougar populations may become established and corridors they may use as range expansion and recolonization continues. Our objective was to model potential habitat patches and dispersal corridors for cougars throughout their historic range in eastern North America. These models provide geographical insights for managers should cougars recolonize unpopulated regions of the study area (Thatcher et al. 2006; LaRue and Nielsen 2008, 2011; Smith et al. 2015).

Methods

Study area

Our study area (Fig. 1) was all of Canada and the United States east of currently established cougar populations.

This region (> 12,263,257 km^2) included all 41 states and 10 Canadian provinces from the Rocky Mountains eastward to the Atlantic Ocean. Landscape and topography varied greatly across regions. The western portion of the study area is dominated by the Rocky Mountains. The central Midwest is dominated by plains and agriculture and the Northern Midwest is comprised of boreal forests. The eastern region

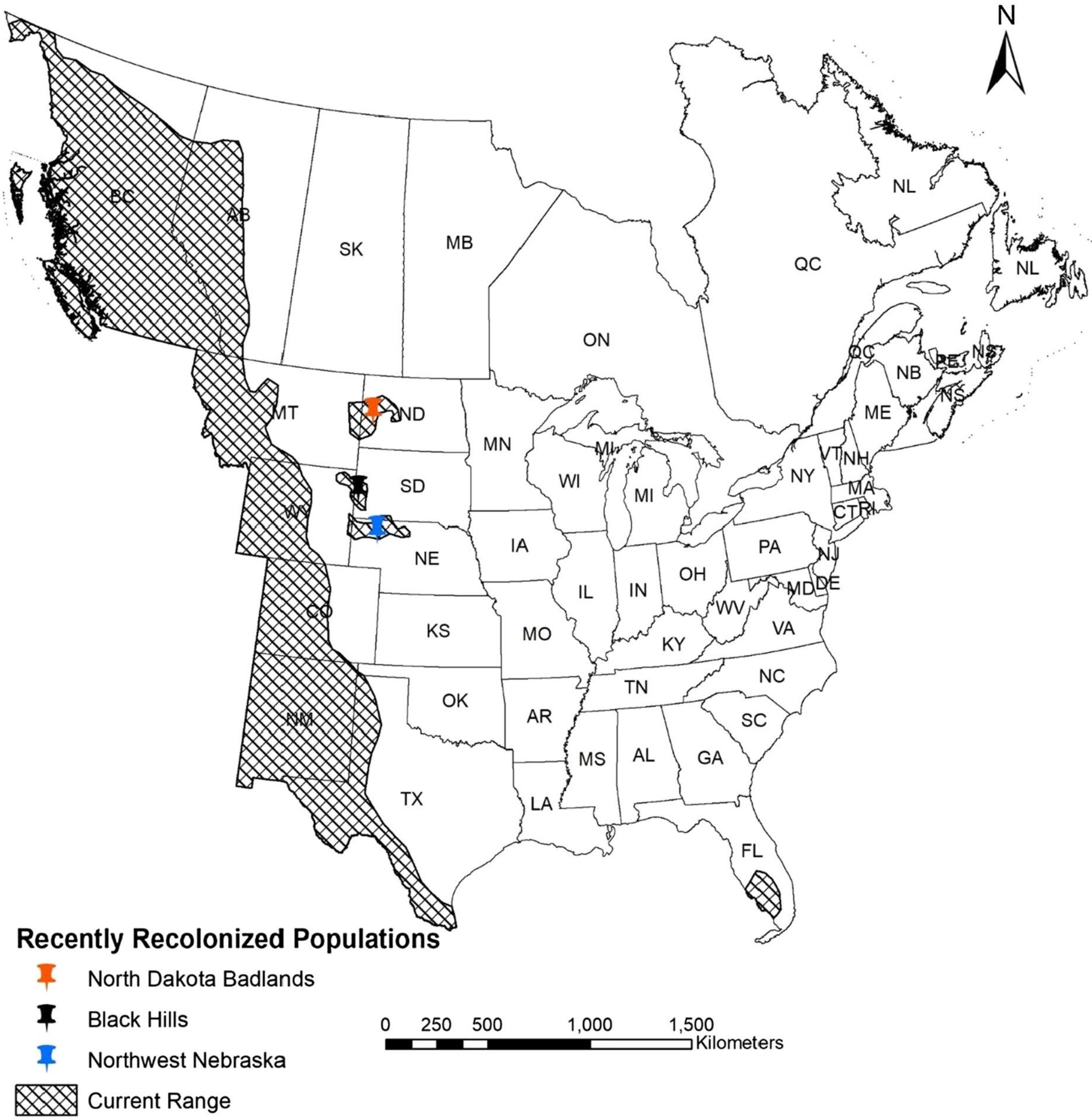

Fig. 1 Study area for potential cougar habitat and dispersal corridor modelling in eastern North America. The current cougar range is represented by black crosshatch. The recently recolonized Midwestern populations are indicated by colored pins

consists of the densely vegetated Appalachian Mountains, with Piedmont forests and coastal swamplands occurring to the east and south.

Climate also varies greatly in the study area. The northern region has harsh winters with temperatures reaching -24 °C during winter and 11 °C during summer. Mean precipitation in the northern region averages 3.2 m of snowfall and 2.5 cm of rain each year (NOAA 2020). The southern region has mild winters and humid summers with mean winter temperatures ranging from 9.3 to 1.8 °C and summer temperatures ranging from 26.7 to 23.2 °C (NOAA 2020). Mean precipitation in the southern region ranges from 40.5 cm of rainfall during summer to 0.0 to 1.58 m of snowfall during winter (NOAA 2020).

Human development is also variable across the study area. Human densities in the study area range from < 1 persons/km^2 in remote western and northern portions to > 38,000 persons/km^2 in metropolitan areas. Paved road densities range from 0.1 to 2.8 km/km^2 (Government of Canada 2016; U.S. Bureau of Transportation 2016).

Potential habitats

Methods of estimating potential habitat often rely on GPS or VHF location datasets for model building and testing (Maiorano et al. 2019; Hemmingmoore et al. 2020; Poor et al. 2020). However, when these datasets are unavailable, expert opinion surveys are used (Liu et al. 2018; Stricker et al. 2019; Crawford et al. 2020). Empirical cougar datasets are not available for the majority of our study area and inconsistencies in available cougar locations are prevalent. Some cougar sightings, DNA, and carcasses do exist; however, these may not be reliable datasets for habitat modeling. These data are often sparse across years and locations, creating a low-quality dataset. The sparseness of these data would create large uncertainty in habitats selected by animals between locations to accurately represent potential habitat and dispersal routes. Therefore, we used expert opinion survey to develop our models.

We used ArcGIS (Esri 2011, version 10.7), the Analytical Hierarchy Process (AHP; Saaty 1980), and geospatial data to model potential habitat for cougars in eastern North America (Clevenger et al. 2002; LaRue and Nielsen 2008, 2011; Laundré 2013; Glick 2014). Using cougar habitat requirement rankings from LaRue and Nielsen (2008), land cover, slope, human density, distance from streams, and distance from roads datasets were used to build the models (Houser 2002; LaRue and Nielsen 2008, 2011; Laundré 2013; Glick 2014; Smith et al. 2015; Table 1).

These datasets were converted to 5 distinct 90 m pixel raster layers. We used 90 m pixels to obtain the smallest resolution possible with the large datasets and constraints of the software used. Land cover data were collected from the 2015 North America Land Cover Dataset (CEC 2015) and reclassified from the 19 original classes into the following 8 categories based on LaRue and Nielsen (2008): barren/developed and open water, deciduous forest, evergreen forest, mixed forest, agricultural, grasslands, shrublands, and wetlands. Slope data were derived from digital elevation model (DEM) data (USGS 2007), calculated as percent rise, and ranked. The DEM dataset was used to create the streams variable for Canada using the Hydrology tool. The output Canada streams layer was combined with the 2020 USGS Hydrography dataset (USGS 2020) and buffered based on the distances associated with the expert surveys. Population density data (U.S. Census Bureau 2010; Statistics Canada 2016) were based on the most recent census surveys and added to census tract and county shapefiles. Individual province and state paved road datasets were combined into one single layer (Government of Canada 2016; U.S. Bureau of Transportation 2016) and buffered based on distances assigned by the expert opinion surveys.

To create a final weighted layer, we assigned mean weights to the 5 raster layers for each pixel (Table 1; LaRue and Nielsen 2008) using Map Algebra in ArcToolbox (Esri 2011). This base model depicted potential cougar habitat from which 4 models of potential contiguous habitat (Models A, B, C, D) were created. We developed these models using different combinations of area and suitability thresholds to better suit the variability in current cougar habitat conditions and uncertainty regarding potential habitat. For suitability thresholds, we defined cut-off percentages, ranging from 0 to 100%, for "highly suitable" habitat using existing populations as a guideline (LaRue and Nielsen 2011). Habitat suitability for the cougar population in the Black Hills region of South Dakota averaged ≥ 75% (LaRue and Nielsen 2011). Thus, we considered pixels with a suitability score of ≥ 75%

Table 1 Habitat factors for modeling potential cougar habitat in eastern North America, 2021

Factor	Variable	Rank	Weight
Land cover type	Mixed forest	4	1.8
	Deciduous	3	
	Evergreen	3	
	Shrublands	3	
	Wetlands	2	
	Grasslands	2	
	Cultivated	1	
	Barren/developed/open	1	
Human density	Low (< 5 persons/km^2)	4	1.2
	Medium–low (6–10 persons/km^2)	3	
	Medium–high (11–19 persons/km^2)	2	
	High (> 20 persons/km^2	1	
Distance to paved roads	Long (> 5 km)	4	0.9
	Medium (0.3–5 km)	3	
	Short (< 0.3 km)	2	
	Zero	1	
Slope	Steep (> 15°)	4	0.6
	Moderate (5–15°)	3	
	Gentle (< 5°)	2	
	Zero	1	
Distance to water	Short (< 1 km)	4	0.5
	Medium (1–5 km)	3	
	Long (> 5 km)	2	

Variables are ranked based on expert opinion survey results (LaRue and Nielsen 2008)

as highly favorable habitat known to support a viable cougar population. To better suit lower quality habitats used by breeding cougar populations, the northwestern Nebraska population was used to set a lower suitability threshold (Beier 1995; Hoffman and Genoways 2005; Wilson et al. 2010; LaRue and Nielsen 2011). Based on pixel values, the average habitat suitability score in the Nebraska population range was ≥ 69%. Thus, we considered pixels with a suitability score of ≥ 69% as also having favorable habitat for cougars. For area thresholds, a larger region area of ≥ 2500 km^2 and smaller area of ≥ 1100 km^2 were used. These thresholds were based on the smallest female cougar home range recorded in an existing breeding population persisting without immigration in the Black Hills and Florida, respectively (Beier 1993; Thatcher et al. 2006; Dellinger et al. 2020). Models A and B had 75% suitability scores and area sizes of ≥ 2500 km^2, and ≥ 1100 km^2, respectively. Models C and D had 69% suitability scores and area sizes of ≥ 2500 km^2, and ≥ 1100 km^2, respectively.

To generate models A–D, we reclassified the output weights as 0 and 1. Values < 75% were classified as 0 and values ≥ 75% were classified as 1. We used the Region Group tool (Esri 2011) for 1 values to identify contiguous areas at the higher threshold. Regions < 1100 km^2 were deleted from the dataset and regions ≥ 1100 km^2 were exported into a new layer to represent the lower area and upper suitability scores. Regions ≥ 2500 km^2 were exported to represent the upper area and suitability score. This process was repeated for the lower suitability score (69%) to generate the remaining threshold combinations. We calculated mean area of contiguous potential habitat patches for each model, number of distinct patches, and habitat characteristics of those patches.

Dispersal corridors

We used least-cost path (LCP) methods to be consistent with prior cougar dispersal corridor modeling efforts (LaRue and Nielsen 2008; Menke 2008; Li et al. 2010; Kershenbaum et al. 2014) and use in other taxa (Davidson et al. 2013; Sutherland et al. 2014; Almasieh et al. 2016; Liang et al. 2018; Mohammadi et al. 2018). While other methods of modeling dispersal corridors such as circuit theory (McRae et al. 2008; Hanks and Hooten 2013; Dickson et al. 2018) exist, studies have indicated similarity between circuit theory and LCP techniques (Poor et al. 2012; McClure et al. 2016; Diniz et al. 2019). We attempted to use program Circuitscape (Gnarly Landscape Utilities 2021) to compare circuit theory and LCP model outputs. However, due to the large datasets used in this study and limitations to Circuitscape software, we were unable to successfully use the circuit theory approach.

We used the same habitat suitability requirements and original cost surface raster as our habitat model. However, instead of delineating contiguous habitats, we calculated inverse pixel values of the habitat suitability model to create a cost surface raster. Cost surface rasters associate favorable habitat with low pixel values, or cost, and unfavorable habitat with high pixel values. The cost surface raster was used to create cost-weighted distance and direction rasters. These rasters connected low-cost pixels from source areas (i.e., existing western cougar populations) to each of the individual contiguous patches, creating an LCP. This was repeated for all models. We calculated the number of routes and total length of each route for all models. We also applied a 1-km buffer around all LCPs to evaluate the habitat characteristics of each dispersal route. A 1-km buffer was used because previous research has shown 1 km is a sufficient width for cougar movement between habitats (Beier 1995; LaRue and Nielsen 2008).

Results

Potential habitats

All models consistently indicated areas of highest-suitable habitat in central and eastern Canada, the Upper Peninsula of Michigan, northern Minnesota and Wisconsin, Ouachita mountains, Ozark mountains, Great Smoky Mountains National Park, central and northern Texas, and eastern Montana and Wyoming (Figs. 2, 3).

Eastern North America was comprised of 40.2% (±6%) contiguous potential cougar habitats (Table 2).

Using the ≥ 69% suitability threshold increased available habitats by an average of 23%. Using the ≥ 1100 km^2 area threshold increased available habitats by an average of 1.6%. Model D contained the largest amount of available habitat (5,618,872 km^2) while model A contained the least (4,255,512 km^2; Table 2).

Area thresholds had a larger impact on number of potential habitat patches than suitability thresholds. Models using the ≥ 1100 km^2 area threshold increased the number of habitat patches by 54% for ≥ 75% suitability thresholds and 46% for ≥ 69% suitability thresholds (Table 2). Increasing suitability thresholds from ≥ 69% to ≥ 75% decreased the number of habitat patches by 1% for ≥ 1100 km^2 area thresholds and 16% for ≥ 2500 km^2 area thresholds (Table 2). When using the lower suitability threshold, mean habitat patch size increased by 24% for ≥ 1100 km^2 area thresholds and 35% for ≥ 2500 km^2 area thresholds (Table 2).

Landscape characteristics averaged across all models showed 64.8% (60–70%) of the identified cougar habitat was forested, 22% (21.5–22.3%) shrublands, 4.1% (2.7–5.5%) wetland, 7% (3.5–10.7%) grassland, 2.1% (1.5–2.6%) developed and 0.2% (0.1–0.2%) cultivated (Table 3).

Mean human density was 80.2 persons/km^2, road density was 8.1 m/km^2, and stream density was 282.2 m/km^2. Although individual habitat patch quality varied across all models, using the ≥ 75% suitability threshold lowered human and road densities and increased forest landcover (Table 3).

Dispersal corridors

Potential dispersal corridors to cougar habitat were found throughout the Appalachian Mountains, Oklahoma, and the northern Midwest (Fig. 4).

For all models, corridors from Florida populations to northeastern habitat followed the Appalachian Mountains. From western populations to central and northern habitats, corridors crossed Oklahoma, northern North Dakota, and Minnesota. Origins for these corridors were from the Pine Ridge region of Nebraska and Theodore Roosevelt National Park region of North Dakota populations. However, in

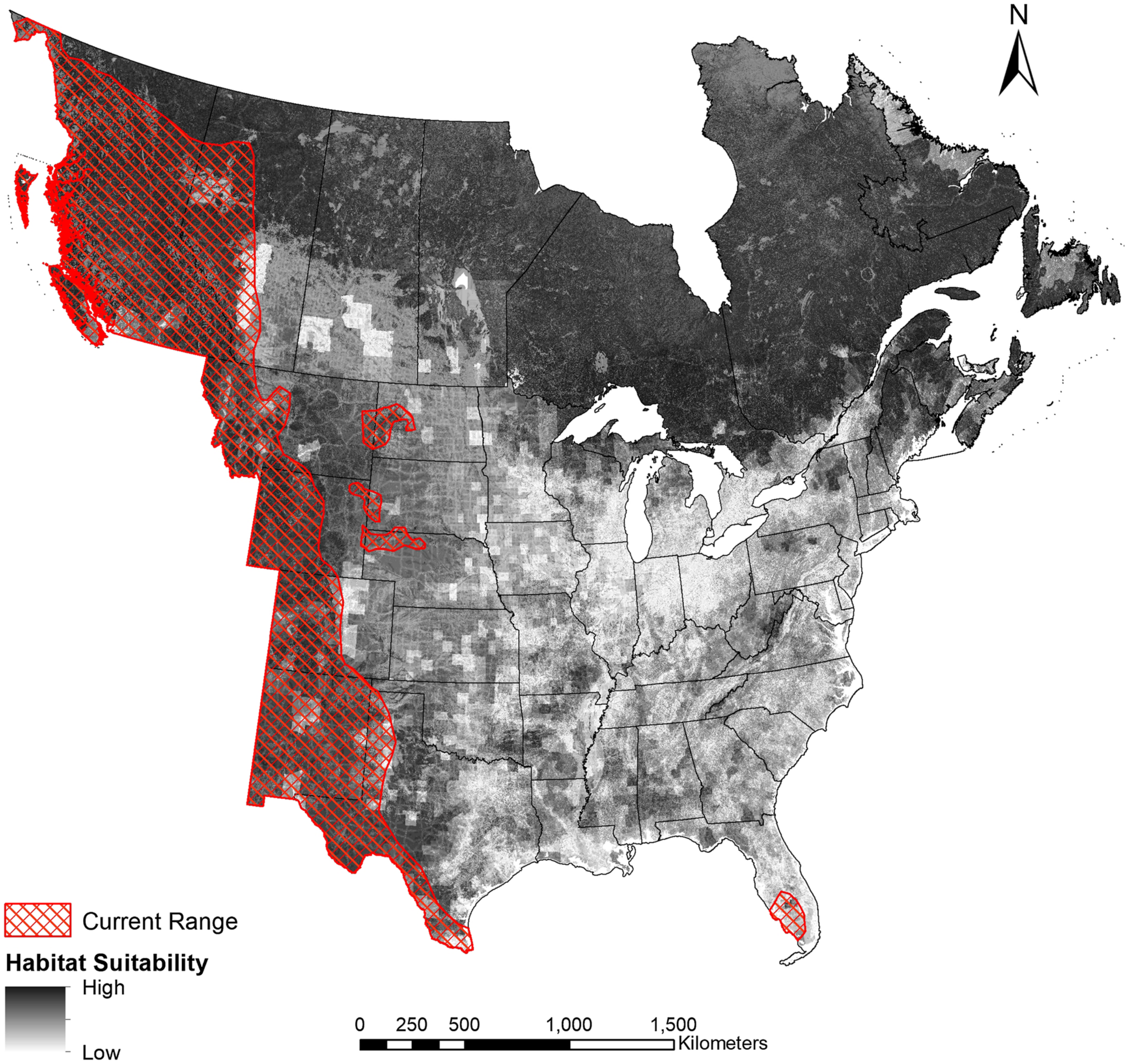

Fig. 2 Potential cougar habitat in eastern North America, 2021. Maps show expert-assisted habitat suitability scores ranging from 0% (low; white) to 100% (high; black) and current range as red crosshatch

easternmost North America, the origin for dispersal was the Florida panther population.

Dispersal corridors from model A had the largest percentage of forest landcover (53.3%) while model D had the lowest (48.4%, Table 4).

Dispersal corridors from models C and D had a higher percentage of cultivated landcover, human density, and road density than corridors made by models A and B (Table 4). All dispersal corridors passed through a matrix of unsuitable and suitable habitats with most unsuitable habitats largely found in the Midwest and East Coast. Models that used both the smaller area and ≥ 69% suitability thresholds increased available dispersal corridors by 182.6% in comparison to models using the larger area and ≥ 75% suitability thresholds. Dispersal corridors in model D had the highest total length (53,643 km) and number of corridors (77) compared to other models. Dispersal corridors in model C had the lowest total length of corridors (15,663 km) and number of corridors (25, Table 4).

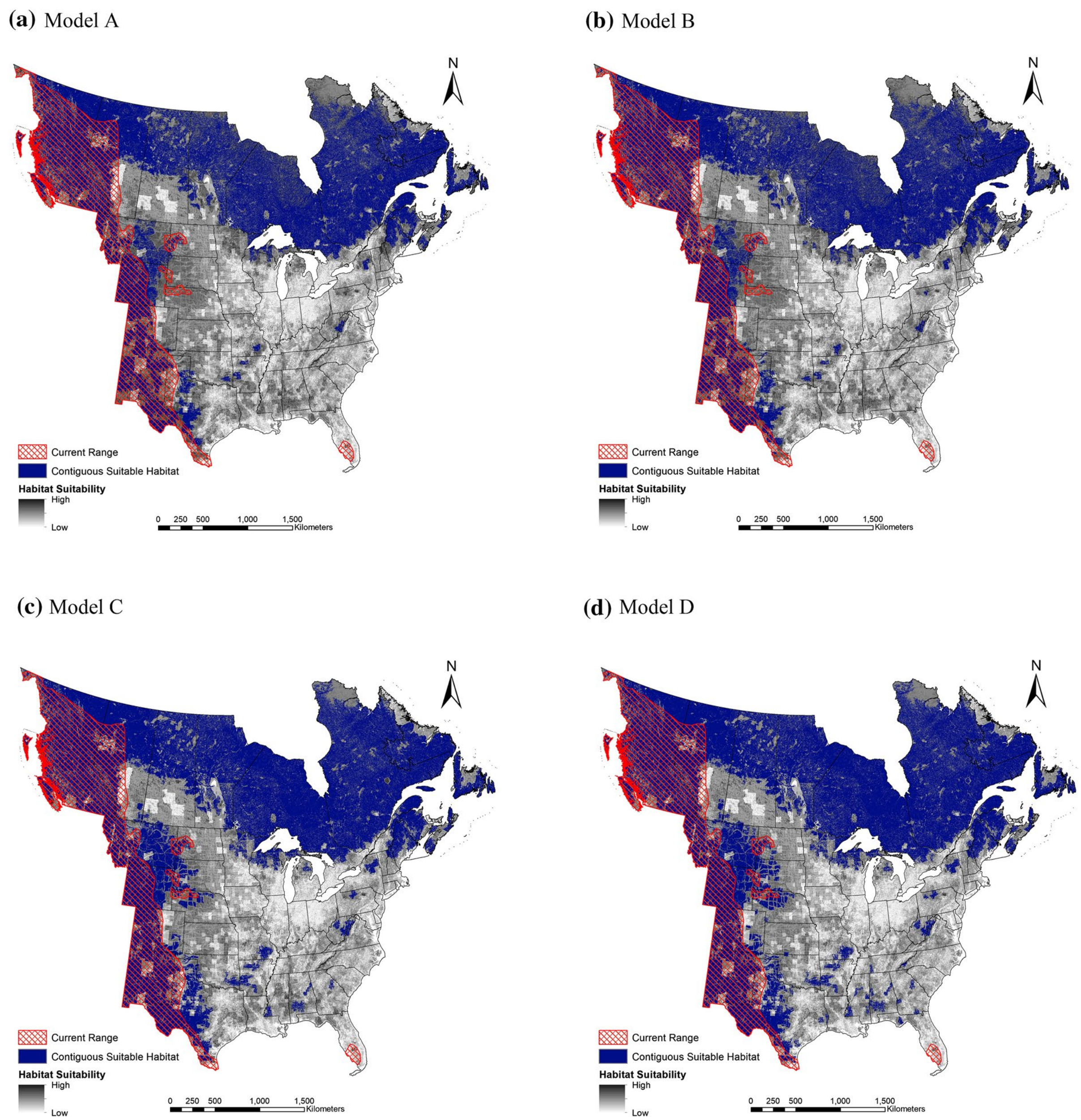

Fig. 3 Potential cougar habitat in eastern North America with **a** ≥ 75% suitability and ≥ 2500 km^2 area threshold (Model A), **b** ≥ 75% suitability and ≥ 1100 km^2 area threshold (Model B), **c** ≥ 69% suitability and ≥ 2500 km^2 area threshold (Model C) and **d** ≥ 69% suitability and ≥ 1100 km^2 area threshold, 2021 (Model D). Areas of potential habitats are in dark blue and current range is in red crosshatch

Discussion

Potential cougar habitats

We developed the first models of potential habitats and dispersal corridors for cougars in their entire former range in eastern North America. These models provide insight into potential habitat for conservationists to consider when proactively planning for potential recolonization. Central and eastern Canada

Table 2 Mean values of habitat patches and overall area for each threshold combination of contiguous potential cougar habitat in eastern North America, 2021

Model	Suitability threshold (%)	Area threshold (km^2)	Contiguous area (km^2)	Percentage (%) contiguous habitat	Number of potential habitat patches	Mean potential habitat patch size (km^2)
A	≥ 75	≥ 2500	4,255,512	34.7	56	75,991
B	≥ 75	≥ 1100	4,325,982	35.3	103	42,000
C	≥ 69	≥ 2500	5,527,310	45.1	47	117,602
D	≥ 69	≥ 1100	5,618,872	45.8	102	55,087

contained the largest portion of contiguous habitat across all models. The region is comprised of large areas of minimal anthropogenic development and dense mixed and boreal forests, making them suitable for cougars. Small cougar populations in the Cypress Hills region of Saskatchewan have recolonized in the past decade making it the easternmost Canadian population of cougars (Watkins 2005). Increased cougar confirmations in Manitoba indicate breeding populations may soon be established there as well (Maehr et al. 2002; Watkins 2005; Morrison et al. 2015; Cougar Network 2021). Increasing cougar populations, nearby source populations, and large contiguous tracts of potential habitat make central and eastern Canada likely to receive dispersing subadult cougars.

The United States also had large tracts of potential habitats across all models. However, modeled habitats were not as contiguous as in Canada. The United States has more developed lands and higher human densities than Canada, which may reduce the overall availability of potential cougar habitat relative to Canada. Despite this, recolonization events have occurred in the Pine Ridge region of Nebraska and the Badlands of North Dakota (Hoffman and Genoways 2005; Wilson et al. 2010; LaRue et al. 2019). Continued recolonization is possible from western cougar populations into potential habitats such as we have modeled (LaRue et al. 2016, 2019). Although smaller patches of potential habitats were considered too small to maintain a viable population (Beier 1993; Thatcher et al. 2006) existed throughout the study area, these small areas may still be used by dispersing cougars (Beier 1995; Kautz et al. 2006; LaRue and Nielsen 2016).

Dispersal corridors

The LCP models created may be useful predictors of general areas cougars may use for dispersal. However, due to individual behavior and small-scale barriers not accounted for by our large-scale models, these corridors are not delineations of exact cougar dispersal paths (Walker and Craighead 1997; LaRue and Nielsen 2008). Our models depict areas of low resistance in which cougars may travel through unsuitable matrices to more suitable habitat patches. These low resistant paths contain fewer barriers, thereby reducing time spent traveling and increasing survival (Taylor et al. 1993; Gloyne and Clevenger 2001). However, areas of unsuitable habitat exist within the modeled dispersal routes and were largely found in the Midwest and East Coast. These regions contained dense roadways, large cities, and agricultural landscapes which present higher mortality risk for dispersing cougars but does not fully impede movement (Lidicker 1999; Fahrig 2007). While paved roads may reduce movement and increase mortality (Maehr et al. 1991; Murphy et al. 1999), cougars may cross major roadways while dispersing (Dickson et al. 2006). Wildlife crossings and temporal variation in roadway traffic may permit cougars to move more easily across roads (Gloyne and Clevenger 2001; Dickinson et al. 2012). Cougars also do not completely avoid developed areas such as suburban housing blocks and city parks (Beier 1995; Dickson and Beier 2002; LaRue and Nielsen 2008). The LCP models appeared to have reflected this as some corridors traversed more populated areas when unsuitable habitat dominated the area. Cougar confirmations have been reported in metropolitan areas such as Chicago, Illinois (Hénaux et al. 2011), and Milford, Connecticut (Hawley et al. 2016), giving strong evidence that eastward dispersing cougars may occasionally use unsuitable habitat.

Table 3 Landscape structure of suitable contiguous potential cougar habitat in eastern North America, 2021

Model	Suitability threshold (%)	Area threshold (km^2)	% Developed	% Forest	% Cultivated	% Wetland	% Shrubland	% Grassland	Stream density (m/km^2)	Human density (persons/km^2)	Road density (m/km^2)
A	≥75	≥2500	1.5	70.0	0.1	2.7	22.2	3.5	301.0	71.2	4.8
B	≥75	≥1100	1.5	69.4	0.1	2.7	22.3	3.6	298.5	71.0	4.8
C	≥69	≥2,00	2.6	60.0	0.2	5.5	21.8	10.1	264.9	89.9	11.4
D	≥69	≥1100	2.6	59.6	0.2	5.5	21.5	10.7	264.2	88.5	11.4

All modeled corridors were well within known cougar dispersal capabilities. Subadult cougars can disperse > 1340 km and travel over > 10 km/day (Beier 1995; Sweanor et al. 2000; Thompson and Jenks 2005, 2010; Stoner et al. 2008; Henaux et al. 2011). Across all models, corridors had mean lengths < 1000 km. Florida panther populations have shown reduced dispersal capability due to intense anthropogenic development in central Florida (Thatcher et al. 2006). However, they are still capable of reaching potential habitat patches in the Southeast based on distances between modeled suitable habitat patches.

Assumptions

Our models were created under multiple assumptions regarding the overall conservative nature of the models, use of expert opinion surveys, lack of competing predator and prey inclusion in the model, and model extent. The suitability thresholds we used were conservative as cougars can inhabit lower quality habitats and will cross lower quality habitat matrices to more suitable habitat (Hoffman and Genoways 2005; Wilson et al. 2010; Smith et al. 2015). For example, the Pine Ridge Region of Nebraska was initially thought to be unsuitable for sustaining viable cougar populations, however cougars successfully recolonized the region (Hoffman and Genoways 2005; Wilson et al. 2010; LaRue et al. 2019). Our dispersal corridor models are thus also conservative as dispersing animals do not always choose the most optimal path and are unaware of their destination. However, least-cost path models are still useful for providing estimates for likely dispersal routes of animals (Elbroch et al. 2016; Marrotte and Bowman 2017; Diniz et al. 2019).

We used methods adopted from LaRue and Nielsen (2008, 2011) where potential cougar habitat models were created for the Midwest based on expert surveys. Although expert surveys focused on the Midwest, we believe using similar criteria for potential habitat is valid for eastern North America. Experts surveyed were from throughout North America including Florida and western states with cougar populations (LaRue and Nielsen 2008, 2011). Also, the lower habitat suitability threshold was derived directly from existing cougar populations on the eastern edge of their range. Locations of cougar confirmations (n = 1079; Cougar

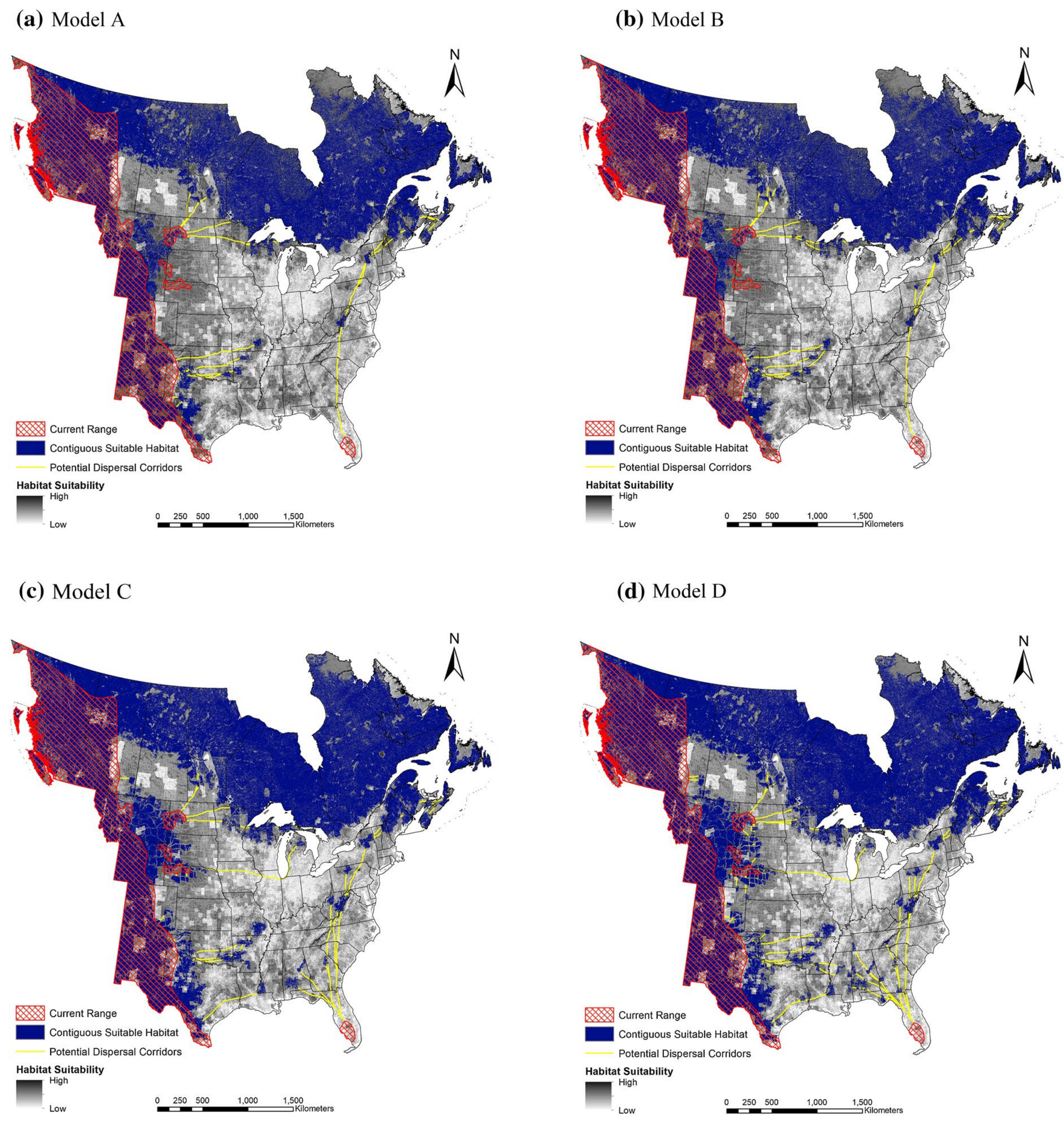

Fig. 4 Potential dispersal corridors for cougars in eastern North America from current range (red crosshatch) to identified potential habitat (dark blue) based on **a** model A thresholds, **b** model B thresholds, **c** model C thresholds, and **d** model D thresholds, 2021. Dispersal corridors shown in yellow

Network 2021) fell within suitable habitat identified by the models 26.7–68.3% of the time when buffered by mean female cougar home range size (40 km^2; Spreadbury et al. 1996; Sweanor et al. 2000; Grigione et al. 2002; Lendrum et al. 2014; Elbrock et al. 2016; Smereka et al. 2021). Identified potential habitats also aligned with current population locations. Other studies using similar ranking methods found comparable habitats in the northeastern United States (Laundre 2013; Glick et al. 2014), Upper Peninsula of the Great Lakes Region (O’Neil et al. 2014), Florida (Thatcher et al. 2006),

Table 4 Landscape structure of dispersal corridors to contiguous potential cougar habitat in eastern North America, 2021

Model	Suitability threshold (%)	Area threshold (km^2)	Corridor length (km)	Number of corridors	% Developed	% Forest	% Cultivated	% Wetland	% Shrubland	% Grassland	Stream density (m/km^2)	Human density (persons/km^2)	Road density (m/km^2)
A	≥75	≥2500	23,447	25	5.7	53.3	15.6	6.3	8.9	10.2	194.2	23.5	136.7
B	≥75	≥1100	37,195	44	7.4	52.6	14.3	6.6	9.9	9.4	196.7	22.0	129.8
C	≥69	≥2500	15,663	49	6.3	49.3	18.3	9.7	5.8	10.5	201.4	38.9	204.3
D	≥69	≥1100	53,643	77	5.7	48.4	16.0	8.5	6.7	14.7	196.8	31.1	160.3

and central Appalachians (Taverna et al. 1999) as our models, further validating our approach.

We did not include prey or competing predator species abundances in these models, given (1) reliable datasets that encompass the full study area were unavailable and (2) such datasets are not the best predictors for successful large carnivore recolonization (Mladenoff et al. 1995). Primary prey is strongly linked with forest cover, which was an important variable in our models. Deer (*Odocoileus* spp.) are the primary prey of cougars in North America (Ackerman et al. 1984; Cooley et al. 2010; Wielgus 2017) and white-tailed deer (*Odocoileus virginianus*) would be important prey for cougars in the East given their abundance and distribution regionally (Hirth 1977; Waller and Alverson 1997; Rooney and Waller 2003). Abundance of white-tailed deer is positively associated with forest cover (Kohn and Mooty 1971; Larson et al. 1978; Rouleau et al. 2002; Munro et al. 2012), thus we indirectly accounted for prey abundance in our analysis. Furthermore, in regions where white-tailed deer densities are low, other staples of cougar diet (i.e., raccoons [*Procyon lotor*], rabbits [*Sylvilagus floridanus*], beavers [*Castor canadensis*]) are present, providing ample prey throughout the study region (Sweanor et al. 2000; Sunquist and Sunquist 2002; Knopff et al. 2010). Abundant prey availability in eastern North America may limit cougar density, but not restrict cougar recolonization of the region (Riley and Malecki 2001; Cooley et al. 2010). Currently, cougars overlap in ranges with black bears (*Urus americanus*), grizzly bears (*Ursus arctos horriblis*), and wolves (*Canis lupus*) in western North America. While direct competition does occur, resource partitioning is known to allow coexistence (Murphy et al. 1998; Atwood et al. 2006; Kortello et al. 2007; Stahler et al. 2020). Ample prey abundances in eastern North America will likely permit similar coexistence among large carnivores should cougars recolonize the region.

Our models included regions north of historical cougar ranges in Canada (Cardoza and Langolois 2002; Sunquist and Sunquist 2002; Gill 2009). However, as climate change continues to shift the landscape over time, this region of the study area is likely to be impacted as such to improve habitat suitability and prey densities for cougars (Rustad et al. 2012; Dawe and Boutin 2016). Changes in forest composition due to warming temperatures, increased fire occurrence and severity, and timber harvest has shifted much of northern old growth forests to early seral and deciduous forest (Weber and Flannigan 1997; Wittmer et al. 2007; Gergel et al. 2017). This change in forest structure has facilitated the range expansion of white-tailed deer (Seip 1992; Dawe 2011; Dawe and Boutin 2016). White-tailed deer populations are expected to continue to advance to the north in coming years, providing higher prey abundances in regions originally not inhabited by cougars (Dawe 2011; Dawe and Boutin 2016; Knopff et al. 2014a, b). Changes in forest structure to mixed forests, which are preferred by cougars, may also improve habitat availability in regions not historically inhabited by cougars (LaRue and Nielsen 2011; Knopff et al. 2014a, b). Furthermore, human densities in the northern extent of the study area are also low, increasing cougar habitat suitability.

Conclusions

Our models inform conservationists of areas of eastern North America that may receive dispersing cougars in the coming decades (Suchant et al. 2003; LaRue and Nielsen 2011). As cougars continue to expand into previously extirpated habitat, having multiple model predictions based on habitat quality may aid in adaptive planning. Conservation agencies must be adaptive in their management practices to understand the potential for cougar recolonization (Davenport et al. 2010; LaRue and Nielsen 2011; Gilbert et al. 2017; Greenspan et al. 2021). Predicted habitats and dispersal corridors may be protected or at least monitored (e.g., via camera traps; Soria-Díaz et al. 2010; Burton et al. 2015; Alexander and Gese 2018) for cougar presence. Deciding which model best fits management objectives for local use depends on regional landscape structure. Some regions may be more isolated within highly developed and densely-populated landscapes. Thus, the higher-threshold models may prove more beneficial for localized management planning. The dispersal corridors modeled can assist with identifying barriers to dispersal. Adaptive management plans to protect these corridors may enhance gene flow among source populations and newly established populations in potential habitats. Identifying these corridors can also assist with understanding where bottlenecks for dispersal may exist as a dispersing cougar is not aware of their destination or the habitat therein (LaRue and Nielsen 2008).

All models predicted many regions in the study area will contain enough contiguous habitats to support breeding populations of cougars. Many of these regions have not had breeding populations since the emergence of modern wildlife management, which presents novel management obstacles for these regions, particularly when managing cougar-human conflict. Proactively planning for cougar recolonization may help reduce cougar-human conflict and ultimately determine the success of recolonization (Smith et al. 2014, 2015). Our models can provide managers with focal points for educational programs for the public. These programs can be focused on increasing public knowledge of how to live and recreate responsibly in large carnivore habitat (LaRue and Nielsen 2011; Smith et al. 2014) and identify focal areas to address future potential human-cougar conflict (LaRue and Nielsen 2011; LaRue et al. 2019). Adaptive management in western states has facilitated the range expansion of cougars into previously extirpated habitats (Anderson and Lindzey 2005; Cooley et al. 2009). The recovery of these populations implies when legislation is proactive in addressing both the ecological and social implications of cougar presence, recolonization can occur (Smith et al. 2015). Models that predict potential habitats that supports breeding populations of cougars can prove valuable to adaptive management practices to facilitate recolonization.

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Declarations

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References

Ackerman BB, Lindzey FG, Hemker TP (1984) Cougar food habits in southern Utah. J Wildl Manage 48:147–155

Alexander PD, Gese EM (2018) Identifying individual cougars (*Puma concolor*) in remote camera images-implications for population estimates. Wildl Res 45:274–281

Almasieh K, Kaboli M, Beier P (2016) Identifying habitat cores and corridors for the Iranian black bear in Iran. Ursus 27(1):18–30

Anderson CR, Lindzet FG (2005) Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildl Soc Bull 33:179–188

Atwood TC, Gese EM, Kunkel KE (2006) Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. J Wildl Manage 71:1098–1106

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85:2671–2676

Beier P (1993) Determining minimum habitat areas and habitat corridors for cougars. Conserv Biol 7:94–108

Beier P (1995) Dispersal of juvenile cougars in fragmented habitat. J Wildl Manage 59:228–237

Beier P (2009) A focal species for conservation planning. In: Hornocker M, Negri S (eds) Cougar: ecology and conservation. University of Chicago Press, Chicago, pp 177–189

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E (2015) Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J Appl Ecol 52:675–685

Cardoza JE, Langolis SA (2002) The eastern cougar: a management failure? Wildl Soc Bull 30:265–273

CEC (Commission for Environmental Cooperation) (2015) North American land cover. http://cec.org/. Accessed 23 Jan 2020

Clevenger AP, Wierzchowski J, Chruszcz B, Gunson K (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conserv Biol 16:503–514

Cooley HS, Wielgus RB, Koehler GM, Robinson HS, Maletzke BT (2009) Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921

Cooley HS, Robinson HS, Wielgus RB, Lambert CS (2010) Cougar prey selection in a white- tailed deer and mule deer community. J Wildl Manage 72:99–106

Cougar Network (2011) Big picture map by the Cougar Network. https://www.cougarnet.org. Accessed 1 Jan 2021

Cougar Network (2021) Expanding cougar population by the Cougar Network. https://www.cougarnet.org. Accessed 1 Jan 2021

Crawford BA, Maerz JC, Moore CT (2020) Expert-informed habitat suitability analysis for at- risk species assessment and conservation planning. J Fish Wildl Manag 11:130–150

Davenport M, Nielsen CK, Mangun J (2010) Attitudes toward mountain lion management in the Midwest: implications for a potentially recolonizing large predator. Hum Dimens Wildl 15:373–388

Davidson A, Carmel Y, Bar-David S (2013) Characterizing wild ass pathways using a non- invasive approach: applying least-cost path modelling to guide field surveys and a model selection analysis. Landsc Ecol 28:1465–1478

Dawe KL (2011) Factors driving range expansion of white-tailed deer, *Odocoileus virginianus*, in the boreal forest of northern Alberta, Canada. Dissertation, University of Alberta

Dawe KL, Boutin S (2016) Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. Ecol Evol 6:6435–6451

Dellinger JA, Gustafson KD, Gammons DJ, Ernest HB, Torres SG (2020) Minimum habitat thresholds required for conserving mountain lion genetic diversity. Ecol Evol 10:10687–10696

Dickson BG, Beier P (2002) Home-range and habitat selection by adult cougars in Southern California. J Wildl Manage 66:1235–1245

Dickson BG, Jenness JS, Beier P (2012) Influence of vegetation, topography, and roads on cougar movement in Southern California. J Wildl Manage 69:264–276

Dickson BG, Jenness JS, Beier P (2006) Influence of vegetation, topography, and roads on cougar movement in Southern California. J Wildl Manage 69:264–276

Dickson BG, Albano CA, Anantharaman R, Beier P, Fargione J, Graves TA, Gray ME, Hall KR, Lawler JJ, Leonard PB, Littlefield CE, McClure ML, Novembre J, Schloss CA, Schumaker NH, Shah VB, Theobald DM (2018) Circuit-theory applications to connectivity science and conservation. Conserv Biol 33:239–249

Diniz MF, Cushman SA, Machado RB, Júnior PDM (2019) Landscape connectivity modeling from the perspective of animal dispersal. Landsc Ecol 33:239–249

Elbroch LM, Lendrum PE, Quigley H, Caraglulo A (2016) Spatial overlap in a solitary carnivore: support for the land tenure, kinship or resource dispersion hypotheses? J Anim Ecol 85:487–496

ESRI (2011) ArcGIS 10. Environmental Systems Research Institute, Redlands, California, USA. https://www.arcgis.com/index.html Accessed 15 Dec 2021

Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. Funct Ecol 21:1003–1015

Gantchoff MG, Erb JD, MacFarland DM, Norton DC, Tack JLP, Roell BJ, Belant JL (2021) Potential distribution and connectivity for recolonizing cougars in the Great Lakes region, USA. Biol Conserv 257:109144

Gergel D, Nijssen B, Abatzoglou J, Lettenmaier D, Stumbaugh M (2017) Effects of climate change on snowpack and fire potential in the Western USA. Clim Change 141:287–299

Gilbert SL, Sivy KJ, Pozzanghera CB, DuBour A, Overduijn K, Smith MM, Zhou J, Little JM, Prugh LA (2017) Socioeconomic benefits of large carnivore recolonization through reduced wildlife-vehicle collisions. Conserv Lett 10:431–439

Gill RB (2009) To save a mountain lion: evolving philosophy of nature and cougars. In: Hornocker M, Negri S (eds) Cougar: ecology and conservation. University of Chicago Press, Chicago, pp 5–16

Glick HP (2014) Modeling cougar habitat in the Northeastern United States. Ecol Modell 285:78–89

Gloyne CC, Clevenger AP (2001) Cougar *Puma concolor* use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. Wildl Biol 7:117–124

Gnarly Landscape Utilities (2021) Circuitscape 4. The Nature Conservancy, Fort Collins, Colorado USA. https://circuitscape.org/ Accessed 15 Dec 2021

Government of Canada (2016) Transportation Networks in Canada. http://open.canada.ca/. Accessed 23 Jan 2020

Greenspan E, LaRue MA, Nielsen CK (2021) Attitudes of social media users toward mountain lions in North America. Wildl Soc Bull 45:121–129

Grigione MM, Beier P, Hopkins RA, Neal D, Padley WD, Schonewald CM, Johnson ML (2002) Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). Anim Conserv 5:317–324

Hanks EM, Hooten MB (2013) Circuit theory and model-based inference for landscape connectivity. JASA 108:22–33

Hawley JE, Rego PW, Wydeven AP, Schwartz MK, Viner TC, Kays R, Pilgrim KL, Jenks JA (2016) Long-distance dispersal of subadult male cougar from South Dakota to Connecticut documented with DNA evidence. J Mammal 97:1435–1440

Hemmingmoore H, Aronsson M, Åkesson M, Persson J, Andrén (2020) Evaluating habitat suitability and connectivity for a recolonizing large carnivore. Bio Conserv 242:108352

Henaux V, Powell LA, Hobson KA, Nielsen CK, LaRue MA (2011) Tracking large carnivore dispersal using isotopic clues in claws: an application to cougars across the Great Plains. Methods Ecol Evol 2:489–499

Hirth DH (1977) Social behavior of white-tailed deer in relation to habitat. Wildl Monogr 53:3–55

Hoffman JD, Genoways HH (2005) Recent records of formerly extirpated carnivores in Nebraska. PNAT 37:225–244

Houser RS (2002) The use of geographic information systems to model habitat for *Puma concolor cougar* in the Northern Blue Ridge of Virginia. Dissertation, Virginia Commonwealth University

Kautz R, Kawula R, Hoctor T, Comiskey J, Jansen D, Jennings D, Kasbohm J, Mazzotti F, McBride R, Richardson L, Root K (2006) How much is enough? Landscape-scale conservation for the Florida panther. Biol Conserv 103:118–133

Kershenbaum A, Black L, Sinai I, Merilä J, Blaustein L, Templeton AR (2014) Landscape influences on dispersal behaviour: a theoretical model and empirical test using the fire salamander, *Salamandra infraimmaculata*. Behav Ecol 175:509–520

Knopff KH, Knopff AA, Kortello A, Boyce MS (2010) Cougar kill rate and prey composition in a multiprey system. J Wildl Manage 74:1435–1447

Knopff AA, Knopff KH, Boyce MS (2014a) Flexible habitat selection by cougars in response to anthropogenic development. Biol Conserv 178:136–145

Knopff KH, Webb NF, Boyce MS (2014b) Cougar population status and range expansion in Alberta during 1991–2010. Wildl Soc Bull 38:116–121

Kohn BE, Mooty JJ (1971) Summer habitat of white-tailed deer in North-Central Minnesota. J Wildl Manage 35:476–487

Kortello AD, Hurd TE, Murray DL (2007) Interaction between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. Ecoscience 14:214–222

Kramer-Schadt S, Kaiser TS, Frank K, Wiegand T (2011) Analyzing the effects of stepping stones on target patch colonization in structured landscapes for Eurasian lynx. Landsc Ecol 26:501–513

Laundré JW (2013) The feasibility of the North-Eastern USA supporting the return of the cougar *Puma concolor*. Oryx 47:96–104

Larson TJ, Rongstad OJ, Terbilcox FW (1978) Movement and habitat use of white-tailed deer in Southcentral Wisconsin. J Wildl Manage 42:113–117

LaRue MA, Nielsen CK (2008) Modelling potential dispersal corridors for cougars in Midwestern North America using least-cost path methods. Ecol Modell 212:372–381

LaRue MA, Nielsen CK (2011) Modelling potential habitat for cougars in Midwestern North America. Ecol Modell 222:897–900

LaRue MA, Nielsen CK (2016) Population viability of recolonizing cougars in midwestern North America. Ecol Modell 321:121–129

LaRue MA, Nielsen CK, Dowling M, Miller K, Wilson B, Shaw H, Anderson C (2012) Cougars are recolonizing the Midwest: analysis of cougar confirmations during 1990–2008. J Wildl Manage 76:1364–1369

LaRue MA, Nielsen CK, Pease BS (2019) Increases in Midwestern cougars despite harvest in a source population. J Wildl Manage 83:1306–1313

Lendrum PE, Elbroch LM, Quigley H, Thompson DJ, Jimenez M, Craighead D (2014) Home range characteristics of subordinate predator: selection for refugia or hunt opportunity. J Zool 294:58–66

Li H, Li D, Li T, Qiao Q, Yang J, Zhang H (2010) Application of least-cost path model to identify a giant panda dispersal corridor after the Wenchuan earthquake: case study of Wolong Nature Reserve in China. Ecol Modell 221:944–952

Liang J, He X, Zeng G, Zhong M, Gao X, Li X, Li X, Wu H, Feng C, Xing X, Fang Y, Mo D (2018) Integrating priority areas and ecological corridors into national network for conservation planning in China. Sci Total Environ 626:22–29

Lidicker WZ (1999) Responses of mammals to habitat edges: an overview. Landsc Ecol 14:333–343

Liu C, Newell G, White M, Bennett AF (2018) Identifying wildlife corridors for the restoration of regional habitat

connectivity: a multispecies approach and comparison of resistance surfaces. PLoS ONE 13:e0206071
Maehr DS, Land ED, Roof JC (1991) Social ecology of Florida panthers. Nat Geo Resol Expl 7:414–431
Maehr DS, Land ED, Shindle DB, Bass OL, Hoctor TS (2002) Florida panther dispersal and conservation. Biol Conserv 106:187–197
Maiorano L, Chiaverini L, Falco M, Ciucci P (2019) Combining multi-state species distribution models, mortality estimates, and landscape connectivity to model potential species distribution for endangered species in human dominated landscapes. Bio Conserv 237:19–27
Marrotte RR, Bowman J (2017) The relationship between least-cost and resistance distance. PLoS ONE 12:e01742412
McClure MA, Hansen J, Inman RM (2016) Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. Landsc Ecol 31:1419–1432
McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724
Menke K (2008) Locating potential cougar (*Puma concolor*) corridors in New Mexico using least-cost path corridor GIS analysis. Albuquerque, New Mexico: wildlife final project report, Bird's Eye View.
Mladenoff DJ, Sickley TA, Haight RG, Wydeven AP (1995) A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Great Lakes Region. Conserv Biol 9:279–294
Mohammadi A, Almasieh K, Clevenger AP, Fatemizadeh F, Rezaei A, Jowkar H, Kaboli M (2018) Road expansion: a challenge to conservation of mammals, with particular emphasis on the endangered Asiatic cheetah in Iran. J Nat Conserv 43:8–18
Morrison CD, Boyce MS, Nielsen SE (2015) Space-use, movement, and dispersal of sub-adult cougars in a geographically isolated population. PeerJ 3:e1118
Munro KG, Bowman J, Fahrig L (2012) Effect of paved road density on abundance of white-tailed deer. Wildl Res 39:478–487.
Murphy KM, Felzien GS, Hornocker MG, Ruth TK (1998) Encounter competition between bears and cougars: some ecological implications. Ursus 10:55–60
Murphy KM, Ross PI, Hornocker MG (1999) The ecology of anthropogenic influences on cougars. In: Curlee AP, Minta SC, Karevia PM (eds) Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, pp 77–101
National Oceanic and Atmospheric Administration (NOAA) (2020) http://www.noaa.gov/. Accessed 23 Jan 2020
Nielsen CK, Dowling M, Miller K, Wilson B (2006) The Cougar Network: using science to assess the status of cougars in easter North America. Proc Eastern Cougar Conf 2004:82–86
O'Neil ST, Rahn KC, Bump JK (2014) Habitat capacity for cougar recolonization in the Upper Great Lakes Region. PLoS ONE 9:e112565
Poor EE, Loucks C, Jakes A, Urban DL (2012) Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. PLoS ONE. https://doi.org/10.1371/journal.pone.0049390
Poor EE, Scheick BK, Mullinax JM (2020) Multiscale consensus habitat modeling for landscape level conservation prioritization. Sci Rep 10:17783
Riley SJ, Malecki RA (2001) A landscape analysis of cougar distribution and abundance in Montana, USA. Environ Manage 28:317–323
Rooney TP, Waller DM (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. For Ecol Manag 181:165–176
Ross IP, Jalkotzy MG, Gunson JR (1996) The quota system of cougar harvest management in Alberta. Wildl Soc Bull 24:490–494
Rouleau I, CrÊte M, Ouellet JP (2002) Contrasting the summer ecology of white-tailed deer inhabiting a forested and agricultural landscape. Écoscience 9:459–469
Rustad, L, Campbell J, Dukes JS, Hunttington T, Lambert KF, Mohan J, Rodenhouse N (2012) Changing climate, changing forests: the impacts of climate change on forests of the northeastern United States and eastern Canada. Proceedings U.S. Forest Service, Northeast Forest and Experimentation Station
Saaty TL (1980) The Analytical Hierarchy Process: planning, setting priorities, resource allocation. McGraw-Hill, New York
Saura S, Bodin O, Fortin MJ (2014) Stepping stones are crucial for species' long-distance dispersal and range expansions through habitat networks. J Appl Ecol 51:171–182
Seip D (1992) Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Can J Appl Ecol 70:1494–1503
Smereka CA, Frame PF, Edwards MA, Slater OM, Frame DD, Derocher AE (2021) Space use of cougars at the northern edge of their range. J Mammal 102:1042–1053
Smith JB, Nielsen CK, Hellgren EC (2014) Illinois resident attitudes toward recolonizing carnivores. J Wildl Manage 78:930–943
Smith JB, Nielsen CK, Hellgren EC (2015) Suitable habitat for recolonizing large carnivores in the midwestern USA. Oryx 50:555–564
Spreadbury BR, Musil RRK, Musil J, Kaisner C, Kovak J (1996) Cougar population characteristics in Southeastern British Columbia. J Wildl Manage 60:962–969
Soria-Díaz L, Monroy-Vilchis O, Rodríguez-Soto C, Zarco-González MM, Urios V (2010) Variation of abundance and density of *Puma Concolor* in zones of high and low concentration of Camera Traps in Central Mexico. Anim Biol 60:361–371
Stahler DR, Wilmers CC, Tallian A, Anton CB, Metz MC, Ruth TK, Smith DW, Gunther KA, MacNulty DR (2020) Competition and coexistence among Yellowstone's meat eaters. In: Smith DW, Stahler DR (eds) Yellowstone wolves. University of Chicago Press, Chicago, pp 223–241
Statistics Canada (2016) National population statistics. http://www.statcan.gc.ca/. Accessed 23 Jan 2020
Stoner DC, Rieth WR, Wolfe ML, Mecham MB, Neville A (2008) Long-distance dispersal of a female cougar in a basin and range landscape. J Wildl Manage 72:933–939

Stricker HK, Gehring TM, Donner D, Petroelje T (2019) Multi-scale habitat selection model assessing potential gray wolf den habitat and dispersal corridors in Michigan, USA. Ecol Model 397:84–94
Suchant R, Baritz R, Braunisch V (2003) Wildlife habitat analysis—a multidimensional habitat management model. J Nat Conserv 10:253–268
Sunquist ME, Sunquist F (2002) Wild cats of the world. University of Chicago Press, Chicago
Sutherland C, Fuller AK, Royle JA (2014) Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. Methods Ecol Evol 6:169–177
Sweanor LL, Logan KA, Hornocker MG (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation. Conserv Biol 14:798–808
Taverna K, Halbert JE, Hines DM (1999) Eastern Cougar (*Puma concolor couguar*): habitat suitability analysis for the central Appalachians. Proc Appalachian Restoration Campaign
Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68:571–573
Thatcher CA, Van Manen FT, Clark JD (2006) Identifying suitable sites for Florida panther reintroduction. J Wildl Manage 70:752–763
Thompson DJ, Jenks JA (2005) Long-distance dispersal by a subadult male cougar from the Black Hills, South Dakota. J Wildl Manage 69:818–820
Thompson DJ, Jenks JA (2010) Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. Ecosphere 1:1–11
U.S. Bureau of Transportation (2016) TIGER/Line® shapefiles: roads. http://www.census.gov/. Accessed 23 Jan 2020
U.S. Census Bureau (2010) National population statistics. http://www.census.gov/. Accessed 23 Jan 2020
USFWS (United States Fish and Wildlife Service) (2008) Florida Panther recovery plan. Third Revision. U.S. Fish and Wildlife Service
USGS (United States Geological Survey) (2007) 30 arc-second DEM of North America. http://www.sciencebase.gov/. Accessed 23 Jan 2020
USGS (United States Geological Survey) (2020) National Hydrography Dataset (NHD). https://www.usgs.gov/. Accessed 23 Jan 2020
Walker R, Craighead L (1997) Analyzing wildlife movement corridors in Montana using GIS. Proceedings of the 1007 ESRI user conference
Waller DM, Alverson WS (1997) The white-tailed deer: a keystone herbivore. Wildl Soc Bull 25:217–226
Watkins B (2005) Cougars confirmed in Manitoba. Wild Cat News 1:6–8
Weber MG, Flannigan MD (1997) Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Enviorn Rev 5:145–166
Wielgus RB (2017) Resource competition and apparent competition in declining mule deer (*Odocoileus hemionus*). Can J Zool 95:499–504
Wilson S, Hoffman JD, Genoways HH (2010) Observations of reproduction in mountain lions from Nebraska. West N Am Nat 70:238–240
Wittmer H, McLellan B, Serrouya R, Apps C (2007) Changes in landscape composition influence the decline of a threatened woodland caribou population. J Anim Ecol 76:568–579