

Population viability of recolonizing cougars in midwestern North America



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ABSTRACT

Although cougar (*Puma concolor*) populations have been absent from most of midwestern North America for >100 years, the combination of long-distance dispersal and a significant increase in presence of cougars in the Midwest since 1990 suggests an eastward range expansion. Building on previous research on potential cougar habitat in the Midwest, we modeled two scenarios that could impact recolonization of cougars (annual harvest of cougars in western populations versus no harvest) in a spatially explicit population viability analysis (PVA). We built a stage-based demographic model for cougars using values for survival and fecundity from 40 years of published literature. We then modeled population viability of cougars in the Midwest for 25 years in RAMAS/GIS. We calculated $\lambda = 1.083$, and found that our study area comprised 9.6% highly suitable habitat patches for cougars. Our no-harvest model indicated all eight large patches of habitat in the Midwest occupied after 25 years; the harvest scenario found seven of eight large patches occupied. Both models were most sensitive to changes in dispersal rates and distances, and were least sensitive to changes in stage matrix means or deviations. We suggest that cougars are likely to recolonize habitat patches in the Midwest in the next 25 years, regardless of current harvest pressure. Our study is an important step forward in understanding cougar potential in the Midwest, as successful conservation and management strategies will require an integrated approach regarding the potential for presence of a large carnivore in the region.

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1. Introduction

Recolonization of cougars in midwestern North America is of interest to wildlife biologists given the implications to conservation and management of large carnivore populations and their prey. Although extirpated for >100 years, cougars have been reported in the Midwest consistently over the past two decades, with >170 confirmed cougar occurrences (e.g., tracks, photographs, or carcasses) during 1990–2008 (Fig. 1; LaRue et al., 2012). Approximately 76% of known-sex carcass confirmations were of subadult males (LaRue et al., 2012), a rate consistent with male-biased dispersal in cougar populations (Logan and Sweanor, 2001); though population settlement is predicated upon arrival of females in a given area. Because similar recolonization events have occurred in other carnivore populations across North America, such as wolves (*Canis lupus*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*; Pletscher et al., 1997; Wydeven et al., 1998; Gompfer, 2002; Pyare

et al., 2004; Gehring and Potter, 2005), and because humans in the Midwest have been living without cougars for >100 years, cougar presence in the region warrants attention and further investigation. Large carnivores can drastically change ecosystem function after their return (i.e., wolves in Yellowstone; Ripple and Beschta, 2004; Fortin et al., 2005; Callan et al., 2013), with the potential for trophic cascades or impacts to competitor populations through niche partitioning or competitive exclusion. Specifically, the return of cougar populations to the Midwest could have impacts on white-tailed deer population dynamics (*Odocoileus virginiana*; Thompson et al., 2009).

Research regarding the increasing occurrence of cougars in the Midwest has gained credence recently (Thompson and Jenks, 2010; Henaux et al., 2011; LaRue et al., 2012; O'Neil et al., 2014), and recolonization is occurring via dispersal from western populations and several collared animals have come from the Black Hills, South Dakota (Thompson and Jenks, 2010). The Black Hills population is at or near carrying capacity with approximately 250 individuals and frequent subadult dispersal (Thompson, 2009; Thompson and Jenks, 2010; Thompson et al., 2014), including a male that traveled >2500 km before being killed by a vehicle in

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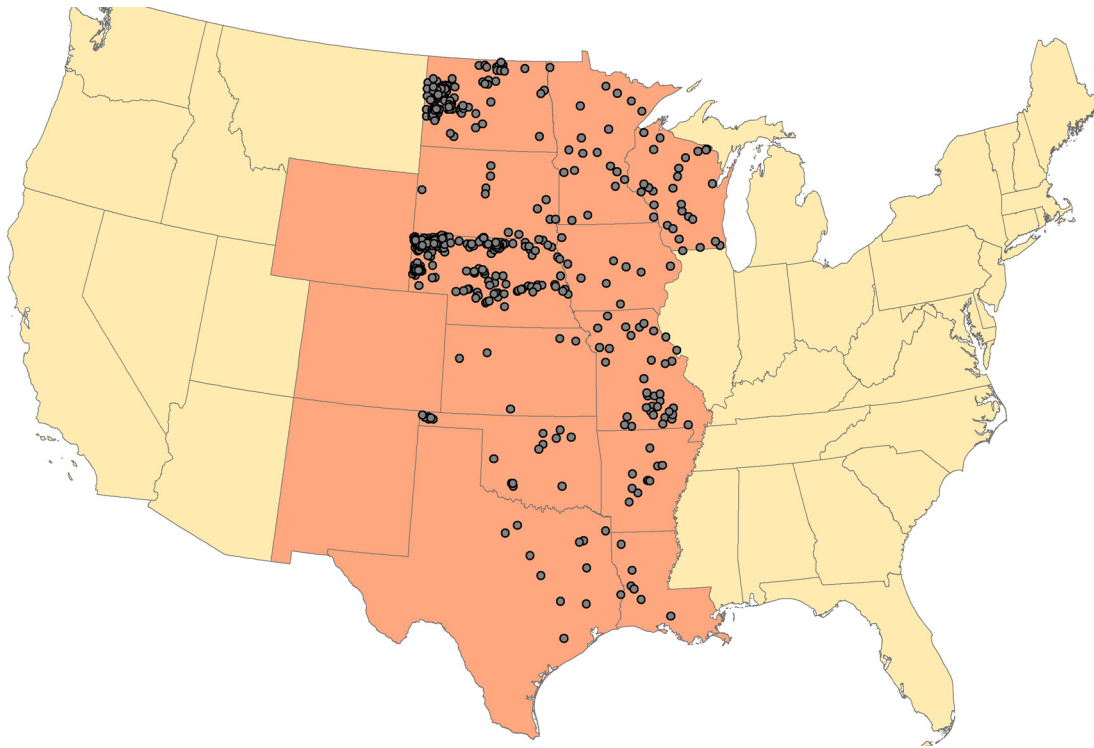


Fig. 1. Study area for modeling demographic matrix for cougars, and confirmed locations of cougars in the study area (midwestern United States) during 1990–2014.

Connecticut (Drake, 2011) and several other long-distance dispersals (400–1000 km; Thompson and Jenks, 2005, 2010). Importantly, female cougars are also capable of traveling long distances, as evidenced by a >1300 km dispersal in Utah (Stoner et al., 2008), and also the recent establishment of four breeding populations in North Dakota and Nebraska within 250 km of western cougar range. Genetic and isotopic evidence supports the idea of eastward expansion (Henaux et al., 2011) with dispersers originating from Colorado, Montana, and South Dakota (Cougar Network, 2015). Populations in Texas also appear to be expanding as counties in the eastern part of current Texas range have reported several confirmations (Harveson et al., 2003). Finally, LaRue et al. (2012) suggested that based on confirmed locations and the emergence of new breeding populations in the Midwest over 18 years, cougars are recolonizing the region via stepping stone dispersal.

We wished to further address cougar potential in the Midwest, specifically: (1) Which portions of the Midwest are likely to contain cougars after 25 years, and what is the likelihood of female occupancy?; and (2) Will cougar harvest influence population establishment in the Midwest? The cougar harvest question is important because of annual hunts in the American west, the Dakotas (North Dakota Game and Fish, 2015; South Dakota Game, Fish and Parks 2015) and one recent hunt in Nebraska (Nebraska Game and Parks, 2015) that could result in “short-stopping” dispersing cougars from recolonizing their former range. To address these questions, we conducted a population viability analysis (PVA), a process which has been used to predict population changes in other wide-ranging carnivores (Haines et al., 2006; Tian et al., 2014), and endangered or rare species (Akçakaya and Atwood, 1997; Akçakaya and Raphael, 1998; Brook et al., 2000). Specifically, we built a stage-based population model using >40 years of published literature, and implemented the stage matrix into a spatially explicit population model (RAMAS/GIS; Akçakaya, 2005) to understand the possibility for establishment and viability of cougar populations in the Midwest.

2. Materials and methods

2.1. Study area

We modeled cougar population viability for 3.2 million km² of western and midwestern United States including areas with established cougar populations and areas of potential cougar habitat (Fig. 1). States were similar to LaRue and Nielsen (2011), including Wisconsin, Illinois, Michigan, Minnesota, Iowa, Missouri, Arkansas, Louisiana, Texas, Oklahoma, Kansas, Nebraska, Colorado, Wyoming, New Mexico, South Dakota, and North Dakota. We selected this study area because of the increasing number of cougar occurrences there since 1990 (LaRue et al., 2012), potential for cougar dispersal (Thompson and Jenks, 2005; Henaux et al., 2011), and presence of potential dispersal corridors and habitat (LaRue and Nielsen, 2008, 2011). As recolonization eastward is occurring, the Midwest will be the first region to be occupied by cougars (LaRue et al., 2012).

2.2. Habitat suitability model

2.2.1. Expert-opinion surveys

Habitat suitability models commonly use empirical data as a basis for the model (Clark et al., 1993; Carroll et al., 1999; Clevenger et al., 2002; Fecske, 2003; Haines et al., 2006). Because collection of field data to inform suitable habitat for cougars in the Midwest was not possible, our model of habitat suitability relied on a combination of expert-opinion surveys, decision-making techniques, and geospatial data layers (as per LaRue and Nielsen, 2011). We created an expert-opinion survey that included five habitat variables: cover type, slope, human density, distance to water, and distance to roads, and sent our survey to 29 cougar or wildlife biologists from the study region. The 11 expert surveys we received back provided data to appropriately weight each variable and rank variable attributes for our habitat model, using the Analytical Hierarchy Process (AHP; Saaty, 1980; LaRue and Nielsen, 2011). The resulting habitat model, which

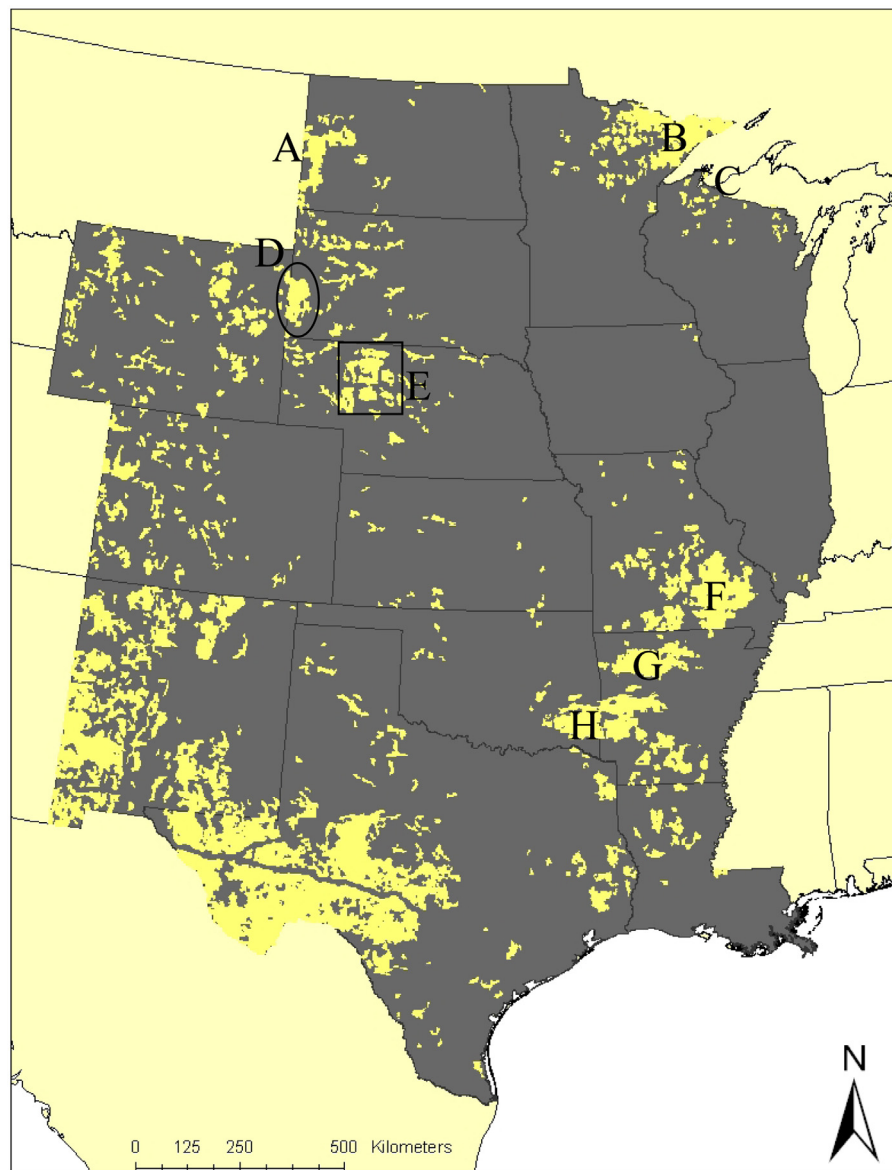


Fig. 2. Patches of suitable habitat ($\geq 64 \text{ km}^2$, lighter tone) for cougars in the Midwest study area (in dark grey) derived from the habitat model in LaRue and Nielsen (2011). (A) North Dakota; (B) Northern Minnesota; (C) Northern Wisconsin; (D) Black Hills; (E) Nebraska; (F) Southern Missouri; (G) Ozarks; (H) Ouachita Mountains.

suggested dense forest cover and low human densities as most suitable for cougars (LaRue and Nielsen, 2011), was then used as the basis for a spatially explicit population model in RAMAS/GIS 5.0 (Akçakaya, 2005).

2.2.2. Patch structure

We prepared the habitat suitability model for use in RAMAS/GIS by resampling cell size to 1 km to reduce the number of cells for analysis and extracted all patches of highly suitable habitat ($\geq 75\%$ suitability) that were $\geq 64 \text{ km}^2$ to create a raster comprised of suitable and non-suitable habitat (Fig. 2). Briefly, highly suitable habitat for cougars in the Midwest included dense forests, far from roads with low human densities (LaRue and Nielsen, 2011). We chose a minimum area threshold of 64 km^2 for habitat patches, as this was the smallest documented post-parturition home range of female cougars (Ross and Jalkotzy, 1992; Stoner et al., 2008). We assumed 64 km^2 would be the smallest area in which a female could reproduce and raise offspring, though perhaps too small for population establishment. Cougar home range and carrying capacity were defined as functions of patch size from several cougar

studies in North America (Ashman et al., 1983; Maehr et al., 1991; Spreadbury et al., 1996; Dickson and Beier, 2002; Fecske, 2003; Lambert et al., 2006). Initial abundance for all western patches (i.e., potential source populations) was based on patch size and known cougar density for the area, and population size of all midwestern patches were initially set to zero.

2.3. Cougar stage matrix

We then built a stage-based demographic model (Crouse et al., 1987; Haines et al., 2006) for cougars that included stage fecundities (F_x), and survival rates (G_x); we calculated the averages of these data from the literature (Tables 1 and 2). Because population establishment is predicated on female presence, we modeled only females for this analysis. We built stage matrices (Leslie, 1945) within the PopTools extension, which combine demographic and reproductive parameters to calculate population growth. We defined three stages (kitten, disperser, and adult) and dispersers (23–30 months) were the first stage that reproduced (Ross and Jalkotzy, 1992; Lindzey et al., 1994; Logan et al., 1996). We

Table 1

Fecundity of female cougars reported in peer-reviewed literature and mean fecundity calculated from these studies for use in the stage matrix for the population viability model to determine cougar viability in the Midwest.

Study	Location	Kittens/litter
Maehr and Caddick, 1995	Florida	1.9
Ross and Jalkotzy, 1992	Alberta	2.2
Hemker et al., 1986	Utah	2.4
Lindzey et al., 1994	Utah	2.4
Lambert et al., 2006	Pacific Northwest	2.5
Anderson, 1983	Colorado	2.6
Hornocker, 1970	Idaho	2.6
Hemker et al., 1984	Utah	2.8
Logan et al., 1986	Wyoming	2.9
Logan and Sweanor, 2001	New Mexico	3.0
Spreadbury et al., 1996	British Columbia	3.1
	Mean	2.5

conservatively assumed 41% of adult females would reproduce in any given year (Robinette et al., 1961; Toweill et al., 1988; Ross and Jalkotzy, 1992).

Finally, because the range of observed values of cougar fecundities is 1–3 kittens per litter, we modeled constant fecundity based on the averaged value calculated from the literature (Table 1). We also modeled a relatively short time horizon of 25 years with 5000 replications per simulation to minimize error propagation, and to allow for the evaluation of conservative models (Akçakaya, 2005; Haines et al., 2006).

2.4. Dispersal

To model female dispersal between patches, we used density-dependent dispersal functions, where the dispersal rate between the *i*th and *j*th populations (M_{ij}) is defined as:

$$M_{ij} = a \exp(-D_{ij}^c/b) \quad , \text{ if } D_{ij} = D_{\max}$$

$$0 \quad , \text{ if } D_{ij} > D_{\max}$$

where *a*, *b*, *c*, and D_{\max} are input parameters (Akçakaya, 2005). We defined D_{\max} as 1341 km, based on a record long-distance dispersal of a subadult female (Stoner et al., 2008), and we calculated average dispersal distance from several cougar studies (Table 3). Assumptions of the dispersal model equation are: (1) dispersal is a one-way movement between two populations, (2) rates are only for dispersal from one population to another, and (3) number of migrants depends on dispersal rate and individuals in the source population (Akçakaya, 2005). We also allowed for random dispersal between

Table 2

Reported and calculated means of adult (*n* = 13) and kitten (*n* = 7) cougar survival rates in North America reported in the peer-reviewed literature used to determine population viability of cougars in the Midwest using RAMAS/GIS.

Study	Location	Kitten survival	Adult survival
Cunningham et al., 2001	Arizona	n/a	0.6
Lambert et al., 2006	Pacific Northwest	0.57	0.6
Lindzey et al., 1988	Utah	n/a	0.7
Beier and Barrett, 1993	California	n/a	0.8
Stoner et al., 2006	Utah	n/a	0.8
Spencer et al., 2001	Washington	n/a	0.8
Logan and Sweanor, 2001	New Mexico	0.6	0.8
Ruth et al., 1998	New Mexico	n/a	0.9
Anderson et al., 1992	Colorado	n/a	0.9
Maehr et al., 1991	Florida	0.8	n/a
Hemker et al., 1986	Utah	0.7	n/a
Robinson et al., 2008	Washington	0.59	0.74
Cooley et al., 2009	Washington	n/a	0.71
Thompson, 2009	South Dakota	0.67	0.87
Ruth et al., 2011	GYE	0.46	0.88
	Mean	0.63	0.76

Table 3

Studies reporting straight-line dispersal distances for female cougars in North America (*n* = 6) and mean dispersal distance used in a spatially explicit population model to determine recolonization of cougars in the Midwest.

Study	Location	Female dispersal (km)
Maehr et al., 2002	Florida	20
Beier, 1995	California	48
Thompson and Jenks, 2010	South Dakota	48
Wilson et al., 2010	Nebraska	80
Hemker et al., 1984	Utah	120
Stoner et al., 2008	Utah	357
	Mean	112

patches, meaning that we did not set parameters to model cougars traveling only from the West into the Midwest. We assumed dispersal out of source populations was density-dependent and we modeled stepping-stone type dispersal in currently unoccupied patches in the Midwest. Also, because hunting influences movement and survival between populations, we also modeled scenarios with and without hunting mortality, and assumed that hunting pressure did not change from year to year. We set harvests in western populations (i.e., North Dakota Badlands, Black Hills, Wyoming, Colorado, New Mexico, and southwestern Texas) based on the most recent harvest data available (primarily 2010–2012), and did not allow harvest in any other unoccupied patches in the Midwest.

2.5. Data analysis

We input the cougar stage matrix into RAMAS/GIS, assuming a 1:1 sex ratio for litters (Logan et al., 1986; Spreadbury et al., 1996; Lambert et al., 2006) and density dependence was set to contest competition, as cougars are territorial (Pierce and Bleich, 2003; Logan and Sweanor, 2001; Sunquist and Sunquist, 2002). We further calculated proportion of suitable habitat in the study area, mean patch size, local patch occupancy (i.e., number of years out of 25 that a particular patch is occupied), and metapopulation occupancy (i.e., total number of patches occupied at least once in the study region during the 25-year simulation). Eight large areas (>2500 km²) of potential habitat for cougars exist in the Midwest (Fig. 2; LaRue and Nielsen, 2011), so we focused our efforts on whether these patches were likely to be occupied. Because females are more philopatric than males (Sweanor et al., 2000; Logan and Sweanor, 2001) and because population establishment requires female dispersal into the Midwest, we tested model sensitivity of the harvest model to density-dependent dispersals, dispersal distance function *b* (i.e., mean dispersal distance) and D_{\max} . We also calculated mean female abundance and tested model sensitivity to stage matrix means. Each parameter was altered ± 50 –100% to understand how variation in these biological factors may influence cougar population viability in the Midwest after 25 years.

3. Results

3.1. Stage matrix

Based on the varying number of studies (*n*), mean fecundity was 2.50 ± 0.49 (SE throughout) kittens/year (*n* = 15; Table 1) and we estimated λ to be 1.083. Survival rates varied by stage: mean kitten survival rate was 0.63 ± 0.08 (*n* = 7), dispersing female survival rate was 0.60 (Thompson, 2009) and female adult survival rate was $\bar{x} = 0.76$ (± 0.11 , *n* = 13).

3.2. Habitat patches and occupancy

We found 9.6% of the study region was suitable habitat, comprised of 136 habitat patches ≥ 64 km² (Fig. 2). Approximately 35%

Table 4

Local occupancy (in number of years occupied out of 25 years) of female cougars in eight large habitat patches in the Midwest modeled within RAMAS/GIS in two scenarios: (1) no hunting allowed in the source populations in the west; and (2) current hunting levels allowed in source populations in the west.

Map label ^a	Habitat area	No hunt		Hunt	
		Mean	Max	Mean	Max
A	North Dakota	25	25	10	22
B	Northern Minnesota	1	24	1	22
C	Northern Wisconsin	1	20	0	20
D	Black Hills	25	25	17	25
E	Nebraska	25	25	25	25
F	Missouri	2	25	2	25
G	Ozarks	7	25	6	25
H	Ouachita	15	25	13	25

^a Map label is in reference to the labels for habitat patches in Fig. 2.

of patches were located east of established cougar populations. Total patch area available in the Midwest was 120,960 km² and mean patch size was 606 ± 96 km². Large patches in Texas, New Mexico, Minnesota, and Missouri accounted for >50% of total patch area. We found the mean dispersal distance of female cougars to be 112 km (±124 km, *n* = 6; Table 3).

In the no-harvest scenario, 82% of patches (\bar{x} = 112 ± 3 patches) in the study area were occupied at some point during 25 years, and maximum number of patches occupied was 126 (93% of available patches; Table 4). Occupancy varied by location: large patches in North Dakota, Nebraska, and the Black Hills were occupied for all 25 years, whereas areas farther east were occupied for fewer time steps (Table 4). Of the eight large habitat patches in the Midwest, the Nebraska patch contained the greatest abundance (54 females), followed by the Ouachita Mountains (12 females). Wisconsin and Minnesota patches had one and three females, respectively, after 25 years (Table 5). In the harvest scenario, we found 75% (\bar{x} = 102 ± 5) of patches occupied after 25 years, and the maximum number of patches possible to be occupied was 118. Nebraska patches contained the greatest abundance after 25 years and patches farthest east (Minnesota and Wisconsin) contained the fewest.

3.3. Sensitivity and model comparison

We found that both the harvest and no-harvest models were most sensitive to dispersal parameters (dispersal rate and average distance; Table 6). Changing the deviation of the stage means ±100% resulted in similar occupancy and abundance estimates in comparison to the base models across both scenarios, though the no-harvest scenario resulted in more occupied patches and increased abundances across all patches.

Table 5

Comparison of abundance of female cougars (mean and maximum) in eight large habitat patches in the Midwest after 25 years as a result of population viability modeling within RAMAS/GIS. Two models were considered to determine population viability in the eight habitat patches in the Midwest: (1) no hunting allowed in western, source populations; and (2) current hunting levels allowed in western, source populations.

Map label	Habitat area	No hunt		Hunt	
		Mean	Max	Mean	Max
A	North Dakota	20	180	1	6
B	Northern Minnesota	1	9	1	11
C	Northern Wisconsin	3	39	0	24
D	Black Hills	40	154	1	8
E	Nebraska	54	127	26	89
F	Missouri	1	14	1	20
G	Ozarks	2	23	1	24
H	Ouachita	12	70	4	34

Table 6

Comparison of mean habitat patches for cougars occupied in the Midwest versus +100% and −100% changes to model parameters (dispersal rate, mean dispersal distance, and stage matrix deviations) in the population viability model within RAMAS/GIS.

Model parameter	Mean patches occupied	
	Base model	+100%, −100%
Dispersal rate		
No hunt	112	112, 39
Hunt	102	103, 24
Mean dispersal distance		
No hunt	112	128, 39
Hunt	102	118, 24
Stage matrix deviations		
No hunt	112	111, 113
Hunt	102	99, 103

4. Discussion

It has long been known that cougars are structured in metapopulations and previous research has shown that movement occurs across large basins of open habitat in New Mexico, Wyoming, and Utah (Sweaner et al., 2000; Anderson et al., 2004; Stoner et al., 2006, 2008). The Midwest is similar in that it contains variably sized patches separated by poor habitat (in this case, row-crop fields, prairies, and pastures; though we recognize that row-crops represent suitable dispersal habitat for short periods during the year when they may provide cover and prey), and so we further suggest that a metapopulation of cougars across large expanses may emerge in the Midwest. We found that regardless of harvest scenario, female cougars are likely to recolonize large patches of habitat in midwestern North America within 25 years, with seven of eight large patches occupied in the harvest scenario. Recolonization was dependent on dispersal rates and distances, and not on variation in demographic rates; this suggests that despite harvests in western populations, female cougars are likely to disperse far enough to encounter large habitat patches in the Midwest such that these patches are likely to be recolonized. Even patches as far east as Minnesota and Wisconsin were predicted to contain at least one female cougar during this time, though such a population could suffer from the Allee effect and therefore could remain effectively extinct (Allee et al., 1949; Lande, 1987). Our work is an important step forward in understanding the potential ecological impacts of a region devoid of cougars, and can be applied to understand the potential societal values and attitudes toward these wide-ranging carnivores (Davenport et al., 2010; Smith et al., 2014).

Because cougars are habitat and prey generalists (Sunquist and Sunquist, 2002; Pierce and Bleich, 2003), the best option for accurately modeling cougar demographics and population viability in our large study area was to draw from the literature across North America: >40 years' worth of published literature (>30 studies) on cougar demographics and space use. Because the Midwest has been devoid of cougars for >100 years and because of the differences in habitat and prey distributions across western North America, no one cougar study site would be an appropriate surrogate for our models. Field studies on cougar populations are typically limited by logistical resources and therefore necessarily constrained to small geographic areas relative to the size of the Midwest region (Anderson et al., 1992; Sweaner et al., 2000). By gathering data across time and space in North American cougar populations, we were able to capture more variability than if we had simply used one population (e.g., the Black Hills population; Fecske, 2006; Thompson and Jenks, 2009, 2010) as a surrogate for the behavior and demographics in all habitat patches in our model. Indeed, our calculated population growth rate was comparable to recent research (Robinson et al., 2008; Cooley et al.,

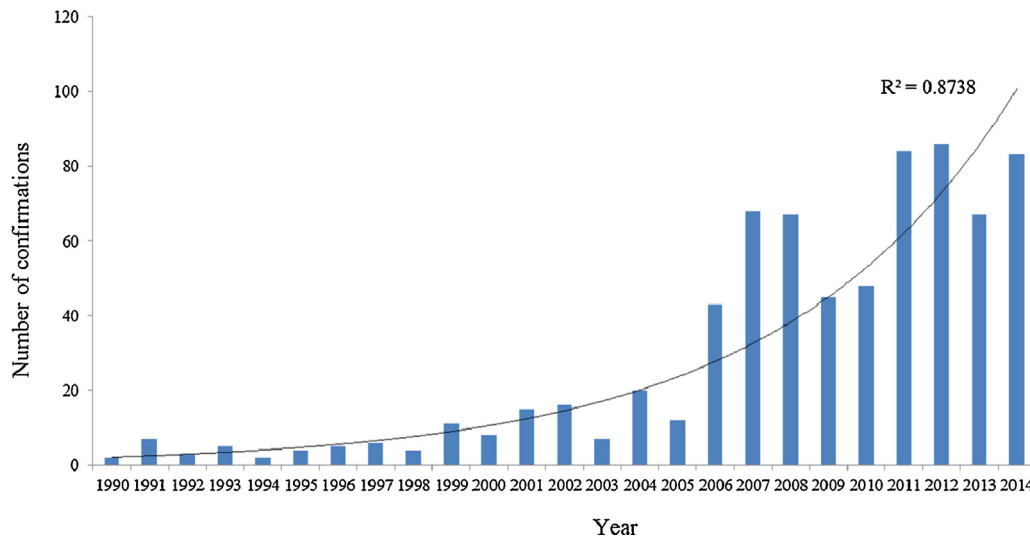


Fig. 3. Number of confirmed occurrences of cougars outside of established range in the North American West and southern Florida collected by the Cougar Network during 1990–2014 (Cougar Network, 2015).

2009), a finding that lends credibility to this particularly important part of our approach. In fact, our calculated growth rate is lower than that of than in the published literature (Cooley et al., 2009; Robinson and DeSimone, 2011; Beausoleil et al., 2013), and perhaps an even more conservative estimate of potential cougar population growth. To further account for the fact that some of the populations used to build our model were hunted, we included environmental and demographic stochasticity, and further ensured correlations between fecundity, survival, and carrying capacity. We are confident that the demographic parameters that influenced the population modeling portion of our study reflects observed demographic parameters in cougar populations across North America, and are applicable to modeling recolonization and population viability in the Midwest.

Both the harvest and no-harvest models were most sensitive to dispersal rates and distances, and were least sensitive to changes in stage matrix means, deviations, or growth rate. Changing demographic parameters $\pm 100\%$ resulted in minimal differences in patch occupancy and abundance (Tables 5 and 6), whereas a 100% decrease in the dispersal rates and mean distances resulted in 73 and 79 fewer patches being occupied in the no-hunt and hunting scenarios, respectively. Therefore we can conclude that these large areas of habitat in the Midwest are likely to have breeding populations of cougars in the next 25 years.

Given that cougars dispersing into the Midwest are likely coming from hunted western populations (LaRue et al., 2012) it is possible that “short-stopping” of dispersers into the interior Midwest could occur. However, our results do not support that hypothesis. We found that more patches were occupied in the no-harvest model than when a harvest was implemented in western populations, and that makes sense: constantly taking a proportion of the population through managed harvests would certainly decrease the number of females available to colonize any given patch. However, we found that despite model type, most large habitat patches in the Midwest (LaRue and Nielsen, 2011) were occupied after 25 years. The model that implemented harvest in western populations resulted in lower cougar abundance, but still indicated that some females were likely to disperse into the interior Midwest.

We found that two relatively large patches of habitat in Nebraska (though $<600 \text{ km}^2$ each – an area smaller than what

previous research suggested as the minimum patch size for cougars; Beier, 1993; Thatcher et al., 2006; LaRue and Nielsen, 2008, 2011) contained cougars for most of the 25-year period, regardless of harvest scenario. Indeed, substantial physical evidence supports our findings and further suggests that cougar range is expanding via stepping stone dispersal (LaRue et al., 2012). First, the number of confirmed occurrences of cougars (i.e., “cougar confirmations”) in the Midwest has continually increased since 1990 (Fig. 3; Cougar Network, 2015). Second, populations in Nebraska are continually expanding (S. Wilson, Nebraska Game and Parks Commission, personal communication). In 2007 Nebraska Game and Parks Commission confirmed kittens on a trail camera photo in the Pine Ridge area (Hoffman and Genoways, 2005; Wilson et al., 2010), which is in northwestern Nebraska and only $\sim 90 \text{ km}$ from the Black Hills. Since then, the Pine Ridge population has grown to ~ 22 animals (S. Wilson, personal communication), and two additional areas in Nebraska contain breeding populations of cougars as of 2013: Wildcat Hills, which is approximately 90 km to the south of Pine Ridge; and the other patch of habitat is $\sim 100 \text{ km}$ to the east in the Niobrara River Valley (Nebraska Game and Parks, 2015). The gradual establishment of populations of cougars in Nebraska is the clearest evidence that cougars are recolonizing the Midwest via stepping stone dispersal. Our results are congruent with the empirical evidence and suggest continual viability and growth of these populations and further expansion into the remainder of the Midwest.

Our model contained several assumptions, and was intentionally conservative and relatively simple. First, we chose a short 25-year timeline, as we wished to limit error propagation that increases during longer time frames (Haines et al., 2006) especially given that individual cougars have relatively long life spans (~ 13 years; Robinson et al., 2008; Cooley et al., 2009). Second, we assumed that the harvest rates used in source populations would not change and also that remaining patches in the Midwest never implemented a harvest. These assumptions likely are not to be the case, as Nebraska has already implemented and subsequently halted harvests in the state (Nebraska Game and Parks, 2015). It is impossible to predict management strategies for all 136 patches of habitat in the Midwest. Furthermore, acceptance of cougar presence and harvest in any given area is also subject to the social values and attitudes toward the species (Davenport et al., 2010). Like many

carnivores, existence of suitable habitat for cougars within a state does not mean the species can reestablish the area without the potential for human conflict; attitudes toward cougars varies spatially and by age (Davenport et al., 2010; Smith et al., 2014) and state wildlife agencies are responsible for providing input to legislators regarding harvested species in their states.

We were also unable to account for competition between existing or recolonizing predators (Smith et al., 2015) or changes in prey distributions, both of which could impact the success of cougar recolonization. Furthermore, competition for resources is likely to be different across our study region. For example, northern Minnesota has a stable population of wolves and black bears, both of which prey upon white-tailed deer (Pimlott, 1967; Nelson and Mech, 1986; Kunkel and Mech, 1994). Although there are currently no gray wolves in the southern United States, suitable habitat is plentiful in portions of that region (Smith et al., 2015). Though our models suggest that females will likely be present in Minnesota and Wisconsin after 25 years, it is possible competition among other large carnivores may have too large an impact on their success, survival and ability to breed, in comparison to the southern part of our study area.

We did not account for emigration from populations farther to the west (i.e., at the eastern edge of cougar expansion) that will almost certainly continue to occur. Our model assumed that our source populations were closed to populations farther to the west, but that clearly is not the case as cougars can and do disperse among western populations (Sweaner et al., 2000; Logan and Sweaner, 2001; Anderson et al., 2004; Stoner et al., 2008). This result is evidenced by the fact that in the hunting scenario, source populations in North Dakota and the Black Hills, South Dakota dropped substantially during the modeling period (Table 5). While sustained hunting may result in decreased abundance of cougars, it is also likely that emigration from western populations in Wyoming and Montana could partly replenish those populations (Robinson et al., 2008), but we were unable to account for that. We chose to keep our model within a 14-state region for simplicity and to avoid an unwieldy and difficult-to-interpret model, though we recognize that in reality cougar populations are not closed.

Our intention was to predict whether cougars could recolonize the Midwest in the next 25 years. Despite the above assumptions, our results suggest that the primary difference between models was the number of animals per habitat patch: more cougars were present in the no-harvest scenario than in the harvest scenario. However, almost all large patches of habitat in the Midwest were occupied by ≥ 1 female cougar during the modeling period.

5. Conclusions

We suggest that cougars are likely to recolonize the large patches of habitat in the Midwest within the next 25 years based on the results of our model, with the potential to sustain populations regardless of current harvest levels in the West. While observations remain to be seen, our results indicating relatively stable populations despite hunting scenarios are congruent with Robinson et al. (2008) and Cooley et al. (2009): hunting in cougar populations results in a compensatory immigration sink, where removal of cougars from an area results in increased emigration from adjacent areas and a shift toward a younger animals (Robinson et al., 2008). Thus, once populations in the Midwest become established, it is possible that the metapopulation will remain stable. To caution, however, stability and growth of populations is dependent on the recruitment of female progeny (Sweaner et al., 2000). Finally, recent evidence suggests that cougars adhere to source-sink dynamics (Stoner et al., 2013), so proper management in the

Midwest may require knowledge of source versus sink populations (Robinson et al., 2008; Maletzke et al., 2014), realizing that these types of population dynamics have the potential to be substantially different in newly established populations with different terrain and topography. Indeed, monitoring of cougar occupancy (e.g., Lesmeister et al., 2015) in this previously extirpated area is crucial for setting appropriate management and conservation strategies once cougars begin to recolonize an area.

What was lacking prior to our study was predictions of where cougars may be should they recolonize the Midwest, and at what population levels, that could forward education, management, and further research efforts. We have now provided the information necessary for states and federal agencies to plan for ecosystem-based management that recognizes the potential for addressing competition between cougars and existing large predators and societal attitudes toward this recolonizing predator. Given large habitat patches in the Midwest are likely to have cougars in the future this will undoubtedly pose considerable challenges to wildlife managers (Poessel et al., 2013).

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