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RESEARCH ARTICLE

Mountain lions on the prairie: habitat selection by recolonizing mountain lions at the edge of their range

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Mountain lions (*Puma concolor*) have historically experienced large-scale range contractions, but are beginning to recolonize portions of their former range. To reach potential suitable habitats in eastern North America, mountain lions need to move across the grassland and agriculture-dominated habitats of the Great Plains, which are different from the forested areas associated with mountain lions in western North America. To inform restoration planning in this area, it is important to understand differences in mountain lion habitat selection in this "nontraditional" grassland habitat. We tracked GPS-collared mountain lions in the Northern Great Plains of Montana and identified movement states (localized or exploratory) using behavioral change point analysis and net-squared displacement. We compared habitat selection between the different states using step-selection functions that included several environmental covariates. Similar to elsewhere throughout their range, across both movement states, mountain lions tended to select forested environments that were farther from human development. In contrast to more traditionally occupied mountainous regions, mountain lions in the Great Plains selected areas of lower elevations. They selected areas both near and far from water, but avoided riparian areas and selected more rugged environments when in exploratory movement states. This suggests that mountain lions in the Northern Great Plains are utilizing river corridors, particularly those with rough or broken topography during exploratory phases. To enhance future recolonization and connectivity of mountain lions to the east of our study area, we encourage managers to maintain and restore forest fragments along river corridors in the Great Plains.

Key words: dispersal, habitat use, movement state, Northern Great Plains, *Puma concolor*

Implications for Practice

- The Northern Great Plains might provide the connectivity necessary for restoration of mountain lions in eastern North America.
- Mountain lions are using forested river corridors with rough or broken topography during exploratory movement phases in the Northern Great Plains.
- Maintaining and restoring riparian forest fragments along river corridors in the Northern Great Plains could improve the establishment of mountain lion populations as they recolonize.

Introduction

Over the past two centuries, large carnivores in North America have experienced large-scale range contractions (Prugh et al. 2009; Ripple et al. 2014). However, during the last several decades some large carnivores have been recolonizing portions of their historical range. One such example is the mountain lion (*Puma concolor*), which experienced one of the largest historic (73%) range contractions for large carnivores (Ripple et al. 2014), but is now recolonizing portions of its former range (LaRue et al. 2012; Hawley et al. 2016).

In western North America, provided there are areas with dense cover to allow for stalking prey, mountain lions occupy a range of habitat types (Dickson & Beier 2002; Dickson 2004), including areas at the wildlife–urban interface (Beier 1995; Kertson et al. 2011). In the past 25 years, dispersing mountain lions have been observed in eight states in the eastern United States and two eastern Canadian provinces (Cougar Network 2017). However, to reach these eastern habitats, mountain lions typically need to move across the Great Plains of central North America, which primarily contains open grassland and mixed-agricultural open habitat with only small corridors of riparian forest cover or isolated mountain forest cover.

Due to a variety of historical threats ranging from agricultural conversion to energy extraction, temperate grasslands that make up the Great Plains are one of the most imperiled ecosystems in North America (Samson & Knopf 1996). This has

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resulted in extirpation or endangerment of a wide suite of carnivores, including the black-footed ferret (*Mustela nigripes*), swift fox (*Vulpes velox*), gray wolf (*Canis lupus*), and grizzly bear (*Ursus arctos*) (Jachowski 2014; Flores 2017). Thus, while widely viewed as a system devoid of large carnivores, the potential for this region to not only host large carnivores, but serve as a conduit for connectivity has only recently become recognized (LaRue et al. 2012). The Northern Great Plains region in particular is one of the least fragmented portions of the Great Plains (Manning 2010), potentially offering suitable habitat for mountain lions. While mountain lions have been observed in this region for several decades (Berg et al. 1983; LaRue et al. 2012), there have been few studies of their habitat use patterns. Those studies that have been conducted focused on use and movement within and among isolated, forested mountain ranges (Thompson & Jenks 2010), or selection of forest patches in a complex matrix of agricultural and grassland habitats (Morrison et al. 2015). Research is needed on habitat use patterns by mountain lions on their leading edge of recolonization, the core of the Northern Great Plains, where there is an established population with unknown connectivity potential.

To understand habitat use of mountain lions in the Northern Great Plains, it is helpful to assess differences in selection based on movement. Mountain lions are known to exhibit both localized and exploratory movement states (Beier 1995; Morrison et al. 2015). Localized movements are short movements within the animal's home range, whereas exploratory movements are longer, less tortuous movements outside of an individual's home range (van de Kerk et al. 2015). During localized periods, animals use areas that meet all requirements necessary for reproduction and survival (Burt 1943; Powell & Mitchell 2012), whereas selection might differ for exploratory periods. Previous research on exploratory behavior by mountain lions has largely relied on coarse-scale location data (Beier 1995; Thompson & Jenks 2010), camera traps (Hawley et al. 2016), or expert opinion (LaRue & Nielsen 2008). These relatively coarse-scale studies are limited in predictive ability because they do not take into account complex interactions among environmental variables, internal state, navigational ability, and motion capacity that often influence individual movement patterns (Fryxell et al. 2008; Nathan et al. 2008). Animals may make exploratory movements, in which they leave an established home range but later return, because temporal variability in resources or mates might require them to search outside of their existing territory. During these exploratory periods animals might use habitat types not typically occupied, or select habitat features such as dense vegetation, roads, or corridors, which allow enhanced protection or ease of movement (Soulé 1991; Blazquez-Cabrera et al. 2016; Buderman et al. 2018).

In this study we tested the hypothesis that habitat selection of mountain lions in the Northern Great Plains region differs between exploratory and localized movement states (Beier 1995; Thompson & Jenks 2010; Morrison et al. 2015). We predicted that (1) during localized phases individuals would select forested areas near bodies of water (Morrison et al. 2015), and (2) during exploratory phases mountain lions would select habitat types not associated with their typical habitat use (Thompson & Jenks 2010; Morrison et al. 2015). By accounting for differences in habitat selection based on movement state, we evaluated habitat use of mountain lions in the Northern Great Plains, offering insight into the potential of this area to provide connectivity between established western and potential eastern mountain lion populations.

Methods

Study Area

While our study area encompassed north-central Montana to southwestern North Dakota, our focus was in the Missouri River Breaks of north-central Montana that span approximately 1.4 million ha from Fort Benton to Fort Peck, Montana (Fig. 1). The Breaks are characterized by erosive soils, topographically rugged badlands, forested coulees, and deeply incised drainages breaking off from relatively flat mixed-grass prairie and sagebrush steppe habitats characteristic of eastern Montana (Fig. 2). This region is one of the least fragmented prairie ecosystems in North America, with a majority of the land being publicly owned and managed (77%), and the remainder being privately held and primarily used for livestock production (Manning 2010). The estimated abundance of mountain lions in this part of Montana (Region 6) is lower than in the western part of the state, and the region is believed to be a population sink (Robinson et al. 2015). In the Little Rocky Mountains to the north of our study area, an estimated 10–12 adult mountain lions existed in 2010, but sustain high (50–66%) annual mortality linked to harvest (Kunkel et al. 2012). There are few recent records of mountain lions occurring in our study area. Thus, historical accounts suggest that this population is on a leading edge of mountain lion recolonization for this region.

Field Methods

We captured mountain lions in the winter months from 2010 to 2014 using a houndsman and trained dogs, focusing our trapping effort in a 48,000 ha area on the Charles M. Russell National Wildlife Refuge (CMR) north of the Missouri River in southern Phillips County, Montana, U.S.A. Patrols searched for mountain lion tracks and released dogs to chase and tree animals. When safety and other conditions were favorable, the staff darted treed animals with a medetomidine/ketamine mixture, and reversed the drugs with atipamezole after processing (Kreeger & Arnemo 2007). All animal handling and sampling procedures were approved by the University of Montana (Missoula, Montana, U.S.A.) Animal Care and Use Committee, IACUC no. FWS111209.

We fit mountain lions with a variety of GPS collars. We deployed five store-on-board collars programmed to record a location every 5 hours (model 2110B, Advanced Telemetry Systems Inc., Isanti, Minnesota, U.S.A.), three store-on-board collars programmed to record a location every 3 hours (model WGPS, Sirtrack, Havelock North, New Zealand), and seven GPS collars with ARGOS satellite uplink capabilities programmed to record a location every 5 hours (model TGW

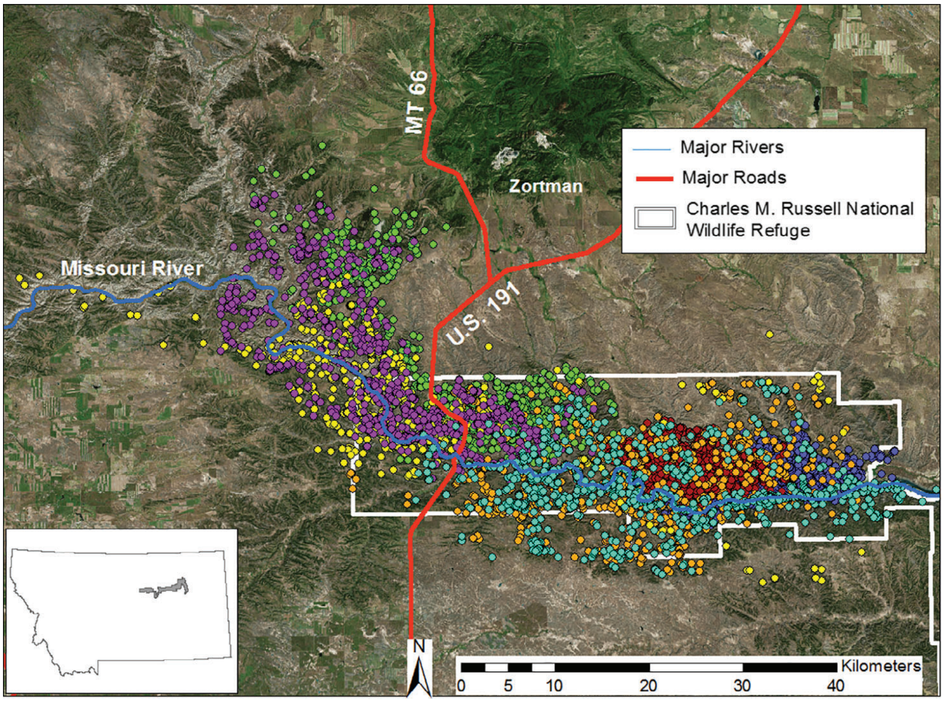

Figure 1. Satellite image of study area in the Northern Great Plains of central Montana (U.S.A.) containing point locations from all nondispersing collared mountain lions. Each animal is indicated by dots of a different color.

4580H, Telonics, Mesa, Arizona, U.S.A.). Due to collar malfunction, data from only nine of the 12 collars were retained for subsequent analysis. All collars contained a very high-frequency radio transmitter and had drop-off mechanisms programmed to release 1 to 1.5 years after deployment.

Movement States Identification

We used GPS locations and behavioral change-point analysis to distinguish among movement states for individual mountain lions (Morelle et al. 2017). To identify these states within each animal's movement dataset, we first calculated net-squared displacement (NSD; Bunnefeld et al. 2011), which is the linear distance between the initial location of a trajectory and all successive locations. We visually assessed the initial location of each trajectory to ensure that it was within the home range or natal home range of the animal. Using the NSD data, we performed behavioral change-point analysis to differentiate between movement patterns using the package *bcpa* (Gurarie 2014) in Program R (R Core Team 2016). Behavioral change-point analysis looks for pattern changes in time-series data, based on a user-defined moving window. Mountain lion movement is often extremely localized during feeding bouts. To exclude isolated predation events during an otherwise exploratory period, given that mountain lions typically make a kill every 5–10 days (Knopff et al. 2014), Morrison et al. (2015) defined localized movement periods as those lacking long unidirectional movements and demonstrating high site fidelity for at least 20 days. Therefore, we considered 20 days as the minimum duration used to identify shifts between exploratory and localized periods. We identified the movement state by fitting the NSD values to models corresponding to localized movements ($\text{NSD} = c$, where c is a constant; Bunnefeld et al. 2011) and exploratory movements ($\text{NSD} = \beta \times t$, where t is the number of days since the initial time step; Bunnefeld et al. 2011). We considered the model with the lowest Akaike information criterion value (AIC; Burnham & Anderson 2002) to best describe the data.

Habitat Use

We used step-selection functions to analyze mountain lion habitat use for each movement state. We resampled trajectories of all animals into 5-hour increments and only used points with successive fixes in our analysis. For each GPS location, we generated 10 random steps drawn from the distribution of observed step lengths and turning angles specific to each movement state (Fortin et al. 2005). We extracted covariates associated with the end-point of each step, and compared the covariates of the used step end-point with the covariates of the available step end-points. To analyze selection, we used mixed-effects conditional logistic regression models, with individual animal as a random effect using the *mclogit* package (Elff 2014).

We developed several a priori models containing covariates predicted to influence habitat selection based on research on habitat preferences of mountain lion in other parts of their range (Dickson 2004; Kertson et al. 2011; Morrison et al. 2015; Robinson et al. 2015). Our covariates of interest included land cover, ruggedness, elevation, distance to water, and distance to roads. All covariates were at a 30-m resolution and created from

Figure 2. Representative photograph of study area along the Missouri River within the Charles M. Russell National Wildlife Refuge, Montana, showing rough and partially forested "Breaks" topography along the side of the river.

raster layers obtained from the Montana Spatial Data Infrastructure (https://mslservices.mt.gov) and North Dakota GIS Hub (https://www.nd.gov/itd/statewide-alliances/gis). We separated land cover into seven classes based on Level 1 Anderson Land Cover codes (Anderson et al. 1976), but separated forests into coniferous forests and deciduous forests. Because mountain lions are known to select coniferous forest in other areas of their range (Dickson & Beier 2002; Kertson et al. 2011), we used coniferous forest as the reference category for the land cover covariate. We calculated distance covariates using the Euclidean distance (ArcMap 10.4). To calculate ruggedness, we used a Terrain Ruggedness Index from a 30-m digital elevation model using the *spatialEco* R package (Evans 2016). Because covariates might exhibit nonlinear relationships, we included a quadratic term for all continuous covariates in all models, but only retained these terms if they were significant. We assessed collinearity between continuous covariates using a Pearson correlation to determine if any should be excluded from analysis ($r > 0.75$).

Corresponding with our hypotheses, we ran models with single covariates (elevation, ruggedness, land cover, distance to water, distance to road), a full model with all covariates, a model to account for the effects of land cover and terrain conditions (land cover + elevation + ruggedness), and a model to account for the effects of human development (land cover + distance to road). We compared models using Akaike's information criterion corrected for sample size (AIC_c; Burnham & Anderson 2002) and considered models within 2 AIC of the top model to be competitive. For each covariate we calculated 85% confidence intervals and considered continuous variables with confidence intervals not spanning zero to be important and categorical variables with intervals not spanning zero to be different from our reference category (Arnold 2010). We validated the predictive ability of the top model for each movement state using a k-fold validation for case–control designs (Fortin et al. 2009). We randomly assigned each stratum (one observed location and 10 paired random steps) to five subsets and used an 80:20 training to testing ratio. For all points in each testing stratum, we ranked predicted values from a low of 1 to a high of 11. We summed the ranks of the observed locations and compared them to bin ranks using a Spearman-rank correlation.

Results

Habitat Use

We obtained 13,577 GPS locations from nine mountain lions (Table 1). Two individuals dispersed outside of our study area and died, and were excluded from further comparisons (see Appendix S1, Supporting Information). For the remaining nondispersing individuals, mountain lions spent 37% of time in localized phases and 63% of time in exploratory phases. During both localized and exploratory periods, habitat use was best described by our global model (Table 2).

Across both movement states, mountain lions tended to select low-elevation (Fig. 3) forested environments that were farther from human development (Table 3). We observed support for a quadratic effect of distance to water, suggesting that mountain lions tended to select areas near and far from water and avoided intermediate distances (Fig. 3). We also observed support for a quadratic effect of distance to roads, suggesting that mountain lions selected areas that were an intermediate distance from roads (Fig. 3). The primary difference we observed in selection between movement states was that in contrast to localized states, mountain lions avoided riparian areas and selected more rugged environments when in exploratory movement states (Table 2). Our top models had a high predictive ability based on the results of our k-fold cross-validation for both the exploratory ($\overline{r_s} = 0.97$, $p < 0.001$) and localized ($\overline{r_s} = 0.96$, $p < 0.001$) phase models.

Discussion

While there were similarities, we found that mountain lions in the Northern Great Plains exhibited differences in habitat selection from more traditional high-elevation mountainous habitat to the west. Similar to mountain lion habitat use patterns in other portions of their range, mountain lions used forests and selected against open habitat types (grassland, barren, shrubland; Beier 1995; Dickson & Beier 2002; Dickson 2004; Zeller et al. 2014). However, the forested environments selected by mountain lions in our study area were not in the mountains, but at low elevation. The preference for low-elevation forested areas regardless of movement state suggests that in contrast to other studies in this region, mountain lions are not primarily utilizing isolated forested mountain ranges (Thompson & Jenks 2010), and that low-elevation forested environments are of critical importance for maintaining connectivity among mountain lion populations in this area and facilitating future recolonization (Morrison et al. 2015).

The differences we observed in selection in relation to proximity to water further highlight the complex resource selection decisions mountain lions make in grassland-dominated systems. Studies to the north (Morrison et al. 2015) and south (Blake & Gese 2016) of our study area have documented a preference by mountain lions for areas in close proximity to water, and rivers are more generally known to be corridors for mountain lion movement (Beier 1993, 1995). We similarly observed a positive effect of decreasing distance to water, but the response was not linear and we also observed a positive effect for areas far from water. In our study area, riparian areas near the Missouri River are associated with dense vegetation where large herbivore prey such as mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and elk (*Cervus canadensis*) are more abundant (Proffitt et al. 2016). Areas far from water were typically associated with more mountainous terrain that was typically forested, and areas at intermediate distances typically represented open (i.e. unforested) grassland and agricultural habitats. Therefore, mountain lions probably selected areas both near and far from water because they contain relatively high prey densities and offer the cover needed for hunting and thermoregulation (Bleich et al. 1996; Laundré & Hernández 2003; Blake & Gese 2016).

Our finding that mountain lions selected for areas that were an intermediate distance from roads was likely the result of mountain lions balancing avoiding contact with humans while ensuring access to prey. Previous research has observed differing patterns in the response of mountain lions toward human disturbance, with mountain lions residing near urban areas showing tolerance by spatially or temporally overlapping with areas of human disturbance, whereas mountain lions in rural areas more generally avoid human disturbance (Kertson et al. 2011; Knopff et al. 2014; Vickers et al. 2015; Wang et al. 2015). A majority (77%) of our study area was federally managed lands with no major urban development, and other than a single major north–south paved highway (U.S. 191) through our study area, most roads in our study area were infrequently traveled dirt roads. Thus, mountain lions in our largely undeveloped study area likely infrequently encountered humans, and when they did, were most likely to encounter them near roads. Similar to mountain lions, large herbivore prey in our study area similarly avoid areas near roads (Proffitt et al. 2016). However, areas farthest from roads in our study area were primarily in open rangeland with little forest cover for stalking prey. Thus, mountain lions likely selected areas that were intermediate distances from roads because the risk of encountering humans was relatively low, and these areas contained suitable forested conditions near prey resources.

The primary difference we observed in selection between movement states was that in contrast to localized states, mountain lions avoided riparian areas and selected more rugged

Table 1. Sample sizes and movement characteristics of each behavioral state (mean ± SE) for all mountain lions included in analyses, Charles M. Russell National Wildlife Refuge, Montana, 2011–2015. Note that dispersing individuals were excluded from this analysis (but see Appendix S1).

ID	*Sex*	*Dispersal Status*	*Days Collared*	*GPS Fix Success*	*Number of Localized Locations*	*Number of Exploratory Locations*	*Exploratory Step Length (m)*	*Exploratory Turning Angle (°)*	*Localized Step Length (m)*	*Localized Turning Angle (°)*
F2	F	N	540	93.4%	997	1,333	742 ± 27	0.57 ± 2.86	905 ± 35	0.57 ± 3.34
F3	F	N	371	86.0%	513	590	976 ± 47	0.57 ± 4.01	805 ± 45	8.02 ± 4.58
F5	F	N	464	97.7%	784	1,276	552 ± 21	4.58 ± 2.86	678 ± 35	5.73 ± 4.01
M2	M	N	373	74.3%	42	683	1,525 ± 68	3.44 ± 4.01	1,364 ± 201	2.86 ± 17.19
M4	M	N	344	80.1%	180	598	1,102 ± 61	4.58 ± 4.58	951 ± 98	1.72 ± 7.45
M5	M	N	373	72.9%	242	420	1,194 ± 66	3.44 ± 5.16	1,177 ± 92	6.30 ± 6.88
M6	M	Y	275	94.1%	232	826	1,208 ± 65	0.00 ± 3.44	964 ± 77	6.88 ± 9.17
M7	M	Y	113	98.4%	66	406	906 ± 60	0.00 ± 4.58	1,366 ± 247	10.31 ± 10.89
M8	M	N	320	95.8%	743	585	1,441 ± 79	4.58 ± 4.58	1,438 ± 65	0.57 ± 4.01

Table 2. Model selection results for resource selection of nondispersing mountain lions during temporary localized and exploratory periods, Charles M. Russell National Wildlife Refuge, Montana, 2011–2015. [a]Log-likelihood; [b]Akaike model weight; [c]Number of model parameters.

Behavioral State	*Model*	*AIC*	*ΔAIC*	$-2 \times ln(L)^a$	*Model Likelihood*	w^b	k^c
Localized	Full	16,571.57	0.00	16,547.57	1	1	12
	Land cover + elevation + ruggedness	16,593.19	21.62	16,573.19	0.00	0.00	10
	Land cover + distance to road	16,617.27	45.70	16,599.27	0.00	0.00	9
	Land cover	16,621.52	49.95	16,605.52	0.00	0.00	8
	Elevation	16,750.57	179.00	16,746.57	0.00	0.00	2
	Distance to road	16,765.67	194.10	16,761.67	0.00	0.00	2
	Distance to water	16,781.49	209.92	16,777.49	0.00	0.00	2
	Ruggedness	16,794.04	222.47	16,790.04	0.00	0.00	2
Exploratory	Full	25,901.54	0.00	25,877.54	1	1	12
	Land cover + elevation + ruggedness	25,939.50	37.96	25,919.50	0.00	0.00	10
	Land cover + distance to road	26,002.02	100.48	25,984.02	0.00	0.00	9
	Land cover	26,006.10	104.56	25,990.10	0.00	0.00	8
	Elevation	26,247.54	346.00	26,243.54	0.00	0.00	2
	Distance to road	26,258.51	356.97	26,254.51	0.00	0.00	2
	Distance to water	26,302.64	401.10	26,298.64	0.00	0.00	2
	Ruggedness	26,303.06	401.52	26,299.06	0.00	0.00	2

environments when in exploratory movement states. This suggests that riparian areas immediately adjacent to water sources in this grassland system were primarily utilized when individuals were exhibiting localized or home range-type behaviors, but exploratory movements typically took place outside of these riparian corridors. However, similar to localized movement states, exploratory movement was still greatest near and far from water and in forested environments. Collectively, this suggests that exploratory movements were primarily limited to forested environments within the Breaks habitat along the Missouri River valley as it transitions to upland grassland habitat. The Breaks are typified by rugged terrain, containing more evergreen and shrub cover and higher large herbivore prey densities than upland grassland habitats (Proffitt et al. 2016), and are largely protected and undeveloped, likely providing suitable exploratory habitat for mountain lions. This is further supported by our two dispersing individuals, which traveled long distances (straight-line distances of 135.7 and 365.2 km) but largely traveled along and remained in the Breaks along the Missouri River (see Appendix S1).

Our results are consistent with other studies that found differences in habitat selection based on movement states (Roever et al. 2014; Morrison et al. 2015; Gastón et al. 2016), suggesting a more nuanced understanding of animal movement decisions can be used to inform restoration connectivity planning (Squires et al. 2013; Zeller et al. 2014; Vasudev et al. 2015). Past research has shown that focusing exclusively on localized home range periods of movement behavior to analyze landscape connectivity can underestimate connectivity potential (Blazquez-Cabrera et al. 2016). For species such as the mountain lion that are recolonizing large areas through dispersal (Hawley et al. 2016), focusing on habitat selection during dispersal could help improve restoration decision-making. While we generally observed resident mountain lions using forested habitats, mountain lions in the Great Plains have been documented to use and forage in agricultural and grassland habitats (Thompson et al. 2009), particularly during dispersal (Thompson & Jenks 2010; Morrison et al. 2015). Similarly, two individuals dispersing eastward during our study period utilized open habitats temporarily (see Appendix S1). Thus, while forested areas might ultimately provide better cover and food resources for long-term habitat use by resident individuals (Kertson et al. 2011), we encourage future research to assess how dispersing individuals could be utilizing nontraditional habitat to facilitate recolonization outside of these forested corridors.

With proper population management, our results suggest that the Northern Great Plains region could be a potential corridor for mountain lion recolonization to easterly portions of its historical range. LaRue et al. (2012) suggested that mountain lions in the western United States are likely to take a "stepping stone" approach to recolonization of the Midwest and eastern North America. In the Northern Great Plains, sustained long-distance dispersal needed for species range expansions of large carnivores such as mountain lions might require patches of suitable habitats, or "stepping stones," along the dispersal route (Kramer-Schadt et al. 2011; Fattebert et al. 2013; Saura et al. 2014). These stepping stones provide resources sufficient for short-term residence and facilitate movement through an unsuitable habitat matrix (Leidner & Haddad 2011; Saura et al. 2014). Our study suggests riparian forest fragments likely serve as stepping stones along movement corridors for mountain lions. In particular, given their importance to localized periods when an animal is establishing a home range, we suggest that conserving forested riparian corridors should be a priority for restoring connectivity in this region. At the same time, to enhance future eastward recolonization and connectivity, it is likely that public outreach and policy change is needed to reduce harvest of these recolonizing animals. Previous eastward recolonization attempts by populations to the south have been limited by harvest protocols in South Dakota and Nebraska (LaRue & Nielsen 2008; Hawley et al. 2016). Similarly, a majority of the state of North Dakota to the east of our study area has no limit

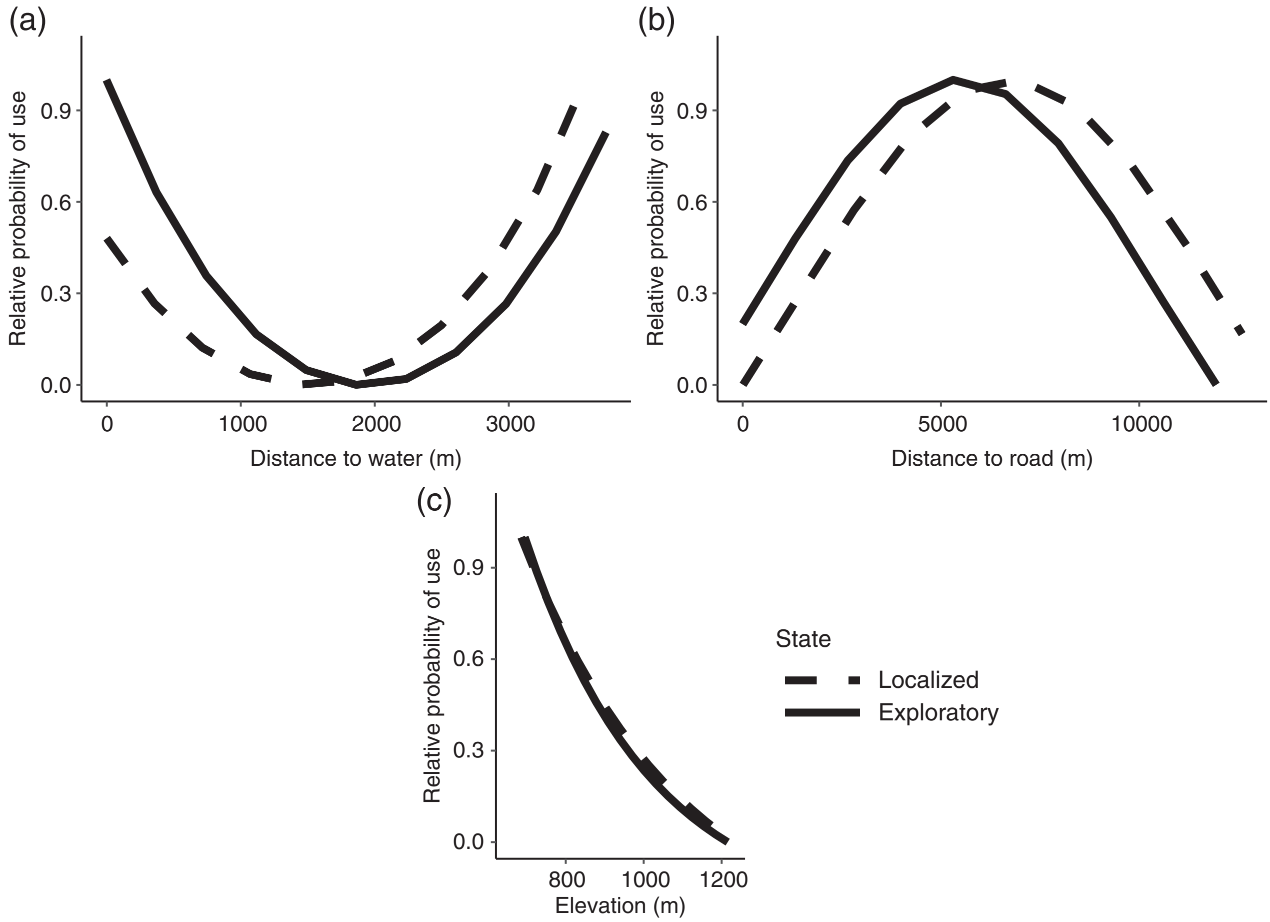

Figure 3. Probability of mountain lions during localized (dashed lines) and exploratory (solid lines) periods in relation to (A) distance to water, (B) distance to roads, and (C) elevation, Charles M. Russell National Wildlife Refuge, Montana, 2011–2015.

Table 3. Parameter estimates and associated 85% confidence intervals (CI) of mountain lion step selection function models, Charles M. Russell National Wildlife Refuge, Montana, 2011–2015.

	Localized				*Exploratory*			
Covariate	*Estimate*	*SE*	*85% CI lower*	*85% CI upper*	*Estimate*	*SE*	*85% CI lower*	*85% CI upper*
Developed	−1.05	0.59	−1.90	−0.19	−0.55	0.32	−1.01	−0.09
Barren	−0.27	0.08	−0.38	−0.15	−0.54	0.07	−0.63	−0.44
Deciduous forest	0.80	0.25	0.44	1.15	0.15	0.24	−0.20	0.50
Shrubland	−0.50	0.05	−0.57	−0.43	−0.59	0.04	−0.65	−0.54
Grassland	−1.38	0.25	−1.74	−1.02	−1.43	0.22	−1.75	−1.12
Riparian	0.05	0.09	−0.08	0.17	−0.20	0.07	−0.29	−0.10
Elevation	−0.18	0.05	−0.24	−0.11	−0.19	0.03	−0.23	−0.15
Ruggedness	0.01	0.02	−0.02	0.04	0.03	0.02	0.01	0.06
Distance to road	0.27	0.06	0.18	0.36	0.24	0.05	0.17	0.31
Distance to road^2	−0.13	0.04	−0.19	−0.08	−0.15	0.03	−0.19	−0.11
Distance to water	−0.08	0.04	−0.13	−0.03	−0.07	0.03	−0.11	−0.03
Distance to water^2	0.05	0.02	0.02	0.08	0.03	0.02	0.003	0.05

on the number of mountain lions that can be harvested, apart from the extreme western portion of North Dakota (hunting Zone 1) adjacent to Montana where annual harvest is limited to 15 individuals (https://gf.nd.gov/hunting/mountain-lion). Thus, harvest regulations just to the east of our study area could limit successful establishment of resident populations, and indeed the lone dispersing individual who made it to North Dakota was shot near the border (see Appendix S1). At the same time, dispersal is often density dependent where young animals are likely to leave their natal range when densities are high to enhance access to food and mates (Morrison et al. 2015). To facilitate recolonization, policy changes might also be needed within the core of our study area to enhance the number of dispersing individuals in a region of Montana currently believed to be a population sink (Robinson et al. 2015). While the observation of two of our nine study animals dispersing suggests that this region is a potential source population, we lack an understanding of how current harvest rates influence the processes of dispersal and population establishment at this current edge of the range of this species.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Dispersing individuals.

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