VEGETATION AND LARGE CARNIVORE RESPONSES IN AN ENCROACHED LANDSCAPE

by

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A THESIS

Presented to the faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Master of Science

Major: Natural Resource Sciences

Under the Supervision of Professors Craig Allen and Dirac Twidwell jr.

Lincoln, Nebraska

June 2020

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University of Nebraska, 2020

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The Great Plains biome supports biodiverse plant and animal communities, provides a wide array of ecosystem services, and is depended upon by agricultural economies. Despite these advantages, however, Great Plains grasslands are becoming increasingly degraded by landcover changes due to agriculture and urbanization, fragmentation, loss of biodiversity and invasion by woody species. Woody encroachment is a biome-wide threat to Great Plains plant and wildlife communities and is therefore managed, though with variable success. I investigated the efficacy of invasive tree management projects in restoring tallgrass prairies in southeast Nebraska and regenerating oak gallery forests along the Niobrara River. I measured plant community species composition and frequency at 9 sites in southeast Nebraska to quantify woody reinvasion of restored grasslands. Along the Niobrara River, I surveyed oak-planted plots and quantified oak survival and plant community abundance at 7 sites to determine success of restorations. In each case, restorations had mixed, but mostly negative results. Management decisions following initial treatment of invasive trees compromised the long-term success of restorations. Management is therefore a process, not an action, and must extend beyond initial treatment if restorations are to sustain native plant communities. I also studied habitat use of the newly establishing mountain lion (*Puma concolor*) as they recolonize Nebraska. I used radio-collar locations of 2 mountain lions to evaluate habitat preferences in a use-availability design. These mountain lions selected riparian woodlands, which will provide dispersal corridors and habitat for breeding populations as mountain lions recolonize the Midwest and eastern North America.

To my family,
My friends,
My teachers,
For making learning a priority
And a joy

Acknowledgments

I would like to thank:

Craig Allen for taking a chance on his technician
Dirac Twidwell and John Benson for agreeing to be on my committee and providing me with valuable insight

The landowners, who, for no reason conceivable to me other than the kindness of their hearts, allowed me to access and survey their land
Kent Pfeiffer, for his help with research in southeastern Nebraska
Scott Wessel, for his help and instruction with research along the Niobrara River
Sam Wilson, for his help and instruction with mountain lions in Nebraska
Wilma Gerena and Caryl Cashmere, the lifeblood of the Coop unit

Hannah Birge, who took me under her wing and paved the way
Becca Bevans, who taught me plant identification
Baxter Seguin, for his compassion and inclinations toward philosophy and debate
Allie Schiltmeyer, who made a house a home
The Schiltmeyer and Benes families, for taking me in
The Ellerman family, for everything

And for all the help along the way, I would like to thank:

Dillon Fogarty
Caleb Roberts
Tori Donovan
Jessica Burnett
Zac Warren
Abigail Ellerman
Bob and Dee
And even Bones

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Multimedia objects

General Introduction

The grasslands of the world are changing. A century and a half of global scale conversion to agriculture and urbanization, loss of biodiversity, fragmentation of habitat by roads, and woody encroachment have made grasslands the most endangered biome in the world. North American grasslands are no exception. The biome of concern in North America is the Great Plains, where agricultural and urban landcover types dominate the landscape, particularly in the Midwest of the United States. These pressures on grasslands are exacerbated by management that excludes fire from grasslands. Woody species are able to mature and propagate in areas where historically patterns of frequent surface fires restricted woody growth, thus providing another method of landcover conversion that works against grasslands. This conversion of grassland to woodland is known as woody encroachment, and it is the thread that ties together the three seemingly disparate chapters of my thesis.

The loss of grasslands is a major natural resource problem in the Midwest. Livestock and agricultural economies are built on the foundation of ecosystem services provided by grasslands. Livestock and livestock feed production require intact grasslands to produce forage, especially as global demands for food production continue to increase. Pollinators that inhabit grasslands provide billions of dollars of pollination services to the agricultural industry. Game birds, many species of wildlife, and diverse communities of vegetation make their homes in grasslands. Grasslands also provide the open area necessary to harness wind energy. In Nebraska, atop the Ogallala aquifer, grasslands contribute more groundwater recharge than neighboring forested areas. Grasslands are necessary and valuable for the continued functioning of these social and natural systems, and the capacity of grasslands to contribute these ecosystem services is reduced and/or jeopardized by woody encroachment. My first chapter evaluates management of woody encroachment in grasslands.

Woody encroachment, however, is not limited to grasslands. In riparian woodlands, woody encroachment takes the form of infilling: the increase in density of woody plants beyond historical limits in a wooded area. Many of the outcomes are similar: native flora and fauna, including fish, are either displaced or destroyed, intensity of water use increases, and oak gallery forests are unable to regenerate. My second chapter evaluates the management of woody encroachment in riparian forests in relation to the survival of experimentally planted oaks.

Finally, woody encroachment alters the physiognomy of the landscape. Woody structures are present where before open grasslands dominated. This shift in vegetative structure displaces grassland associated wildlife and provides more habitat for woodland associated species. Mountain lions prefer wooded areas to open habitat and select these habitat features. Mountain lion recolonization of the Midwest and eastern North America coincides with the expansion of woody species in Nebraska. How mountain lions interact with Midwestern landscapes, which are more agricultural than western landscapes, is unknown. My third chapter evaluates habitat selection patterns of colonizing mountain lions in Nebraska.

These are the chapters that compose my thesis. To my readers who have made it this far, I hope that my thesis can provide some value, however small, to you, whatever your interest is.

Happy reading.

Chapter 1: Evaluating re-encroachment of restored grasslands in southeast Nebraska

Introduction

Grasslands, because of their high rate of conversion to other land uses and landcovers, and limited protection, are the most endangered biome in the world (Hoekstra et al. 2004). Grasslands make up the United States' largest vegetation province, and occur mostly in the Great Plains (Knopf 1988). Grasslands are threatened by several, often intertwining pathways of decline, which include landcover change to agriculture or urban development, fragmentation, loss of biodiversity, and invasion by woody species (White et al. 2000).

One pathway of decline involves invasion by woody species and eventual conversion to woodland (Van Auken 2009). This conversion occurs as the result of changes to fire dynamics and the introduction or invasion of woody species (McPherson *et al.,* 1988). Among other factors, like precipitation, patterns of frequent, low intensity fires regulate woody growth in grassland systems and when these patterns undergo major change, as they do under common practices such as fire exclusion, woody species are able to mature and propagate in grasslands (McPherson et al. 1988, Fuhlendorf et al. 2008). This propagation and expansion of woody species in grasslands is known as woody encroachment (Romme et al. 2009).

Woody encroachment changes nutrient flux and the structure of plant and animal communities in grassland systems. Soil nutrient distribution becomes more variable and patchy in encroached areas (Throop and Archer 2008). Grassland nitrogen and carbon pools shift from belowground to aboveground, where they are incorporated as biomass in woody plants (McKinley et al. 2008) and become more labile. The shift in nutrient allocation to aboveground woody biomass dramatically changes the structure of plant communities (Van Auken 2009). Encroaching woody plants can form dense monocultures that decrease diversity in plant and animal communities (Archer et al. 2017). Even when change to species richness is limited, woody encroachment strongly affects plant community structure by changing species evenness and relative abundance of plant functional groups (Archer et al. 2017). These changes extend into animal communities, where woody encroachment decreases abundance of grassland-associated animals across several taxa (Blaum et al. 2007, Block and Morrison 2010, Pike et al. 2011). As grassland-associated animals are displaced, animal community composition shifts to dominance by shrub/forest-associated species (Sirami and Monadjem 2012, Reddin and Krementz 2016).

The Great Plains ecoregion has the highest rate of woody encroachment in North America; estimates of recent increase in woody cover range from 1.1 to 2.3% per year (Briggs et al. 2002, Barger et al. 2011). In this ecoregion, the most pervasive encroaching species is eastern redcedar, *Juniperus virginiana* (Barger et al. 2011). Woody encroachment alters plant and animal communities, and hydrology. Plant communities lose herbaceous biomass to woody encroachment and reductions in herbaceous biomass beneath *J. virginiana* canopies may be as high as 80% (Smith and Stubbendieck 1990, Gehring and Bragg 1992). Woody encroachment also decreases species diversity in plant communities and is associated with increased cover of non-native plants (Pierce and Reich 2010, Ratajczak et al. 2012). Grassland birds have declined more than any other group of birds in North America (Sauer and Link 2011), due in part to the fragmentation and loss of grasslands to woody encroachment. Increased vegetative structure associated with woody encroachment displaces grassland obligate birds, some of which disappear in the beginning stages of encroachment (Fuhlendorf et al. 2002, Chapman et al. 2004). In small mammal communities, species richness increases at early stages of encroachment (woody cover ≤ 17%), where forest species and grassland species cohabitate, and then decreases sharply as woody encroachment progresses (Matlack et al. 2008). In animal communities, woody encroachment displaces grassland-obligate species and provides habitat for forest-associated species (Chapman et al. 2004, Horncastle et al. 2005, Frost and Powell 2011, Reddin and Krementz 2016).

Woody encroachment also alters grassland hydrology. Tree plantations reduce aquifer recharge by 86-94% compared to adjacent grasslands (Adane and Gates 2015). *J. virginiana* uses more water than many other woody species (Adane and Gates 2015), and may deplete water resources in encroached grasslands. *J. virginiana* woodlands have low soil moisture compared to surrounding grasslands and also decrease annual runoff due to increased water use (Qiao et al. 2017). Deep soil water uptake through root systems also increases following *J. virginiana* encroachment, as does transpiration (Acharya et al. 2017, Zou et al. 2018). The suite of problems associated with woody encroachment makes it a management concern, particularly for livestock managers who depend on forage production.

Management of woody encroachment is complicated; the extent of treatment is often limited to landowner parcels, which may be surrounded by encroached woodlands, and methods of control are often not financially feasible based on incentives to increase forage production and livestock performance (Tanaka et al. 2011). Applying prescribed fire prior to mechanical and/or herbicide treatments and at early stages of encroachment reduces costs (Ortmann et al. 1998, Simonsen et al. 2015), however many land managers are reluctant to use fire due to liability concerns and inclinations toward fire-exclusion (Weir et al. 2019).

State and federal agencies have developed cost-share programs in which the agency pays some percentage (sometimes 75%) of treatment expenses to mitigate the costs of management for landowners. These programs allocate funds to woody plant removal, however evaluation of treatment success rarely occurs beyond immediately post-treatment, there is often no management requirement following treatment, and the programs are applied without consideration that treatments may occur on small patches, or that patches surrounded by woodland are at high risk of reinvasion. These shortcomings cast doubts on the long-term effectiveness of some tree management.

Nebraska, like other Great Plains states has utilized incentive programs to control woody invasive species. In Nebraska, one incentive program used to control woody encroachment was the Landowner Incentive Program (LIP). The LIP was a federal grant funding program that awarded funds to states to provide technical and financial assistance on private lands to benefit endangered, threatened, or other at-risk species (U.S. Fish and Wildlife Service 2015). The LIP was funded from 2002 to 2007, and in that time Nebraska allocated LIP funds toward habitat enhancements, management of prairie through prescribed fire and grazing, and invasive tree removal and thinning (Carr et al. 2019). More than 13,000 ha of land were managed with thinning and removal of invasive trees (Carr et al. 2019). A study that investigated the effect of woody cover and its removal on native bird communities was completed in 2007 (Forbus 2007). This study consisted of 11 sites at which trees were removed in 2005. The study found the grasslands were successfully restored and avian communities responded to reestablished grassland habitat following tree removal. However, whether these tree removal projects have led to sustained grasslands beyond the 2-year study duration is unknown since evaluation of LIP projects did not extend beyond the study period. Given the uncertainty associated with invasive woody species management programs and the lack of requirements for continued management of invasive woody species at sites treated under the LIP, I hypothesized that woody species would reestablish at LIP sites, which would be evident in the 1. Increased frequency of woody species relative to respective frequencies in the post-treatment vegetation survey and 2. Increased woody cover measured in remotely sensed imagery.

Methods

Study area and site selection

I selected nine sites in Johnson, Pawnee, Jefferson, and Gage counties of southeastern Nebraska based on participation in the LIP, participation in woody plant removals in 2005, and landowner permission to access and survey land. Prior vegetation data were available before treatment in 2005 and in 2007 after treatment as part of a previous study (Forbus 2007). This area has an approximate elevation of 350 m, with an average of 76-114 cm of precipitation per year, an average maximum annual temperature of 18.3° C, and an average minimum annual temperature of 2.9° C. Sites ranged in size from 8 to 47 ha. The main species driving woody encroachment in this area are eastern redcedar, *Juniperus virginiana*, and honeylocust, *Gleditsia triacanthos* (Schneider et al. 2011), though there are several other encroaching woody species. Information on site characteristics is summarized in Table 1.

Table 1. Characteristics of LIP tree removal sites. Species refers to invasive woody species on the site prior to tree removal in 2005.

Site	Size (ha)	Species
1	47	JUVI, GLTR
2	74	JUVI, GLTR, MAPO
3	40	JUVI, GLTR
5	41	GLTR, MAPO
6	19	MAPO
7	24	GLTR, MAPO
8	8	GLTR, MAPO
9	23	JUVI
11	19	JUVI

Key to species codes: JUVI = Juniperus virginiana, GLTR = Gleditsia triacanthos, MAPO = Maclura pomifera

Vegetation surveys

I revisited and surveyed LIP sites in the summer and fall of 2018. Sites 4 and 10 were omitted since permission from the landowner to access and survey land was not granted. Plants were identified at the species level when able (otherwise, genus). Sampling quadrats were 1 m^2. Species cover was estimated according to the Daubenmire method, by which each species was assigned a cover class value between 1 and 6 (Daubenmire 1959, Coulloudon et al. 1999). Overlapping vegetation of different species were recorded separately, allowing for more than 100% cover of plots in some cases. Transect lines were placed in approximately the same locations as in the 2007 survey (Forbus 2007). Plots, however, were not placed in the same location. Forbus 2007 sampled 100 plots per site with a 100 cm^2 quadrat. Given that vegetation could be sufficiently sampled with fewer plots, and that the larger 1 m^2 quadrat could sample a greater area per plot, I derived a sampling rate of .78 plots per ha from site 10 of Forbus 2007. Plots were equidistant from each other and the initial sample location was decided by a random number generator. When placing the sampling quadrat at the plot location, vegetation was removed as necessary to ensure the quadrat lay flat. Plants rooted within the frame were then recorded. Plant frequency was measured by dividing the number of quadrats in which a species occurred by the total number of quadrats and multiplying by one hundred to give a percentage.

I compared frequencies of woody species from the 2018 survey with corresponding frequencies in the 2007 post treatment survey to determine woody species presence, if any. Pearson’s chi-square test was used to compare frequencies of woody species (R Core Team 2019). Although Yates continuity correction factor has been found to be too restrictive (Camilli and Hopkins 1978), it was applied to chi-square tests for sites with small sample sizes ($n \leq 20$) to limit type I error (Camilli and Hopkins 1979). All chi-square tests on sites 6, 7, 8, 9 and 11 include Yates continuity correction factor.

Remotely sensed imagery

Remotely sensed imagery from the National Agriculture Imagery Project was used as a visual supplement to the surveys at the 9 sites that were resurveyed in 2018 (USDA-NAIP 2015). Imagery was taken for 2005, prior to woody plant removal, 2006, the first year following woody plant removal, and for 2018, the year in which sites were revisited and surveyed. All imagery had a 1 m resolution. I used the interactive supervised classification method in ArcGIS to specify and quantify pixels that corresponded to woody cover per site (ESRI 2019). This method uses training classes, areas of user-specified landcover composition, to define the landcover composition of imagery according to the classification model. All sites were separated into two classes: woody and non-woody. Due to variation of image quality and woody cover by year, I used different training classes to classify areas of woody and non-woody cover for imagery of different years. For the 2005 imagery, I used 123,121 woody cover pixels and 638,135 non-woody pixels to classify imagery consisting of 743,299 pixels; for 2006 imagery, I used 39,141 woody cover pixels and 1,442,438 non-woody pixels used to classify imagery consisting of 2,945,863 pixels; and for 2018 imagery, I used 42,374 woody cover pixels and 1,208,296 non-woody pixels to classify imagery consisting of 8,437,128 pixels. I removed areas of surface water from the imagery to avoid incorrect classification of these areas as woody cover. I analyzed differences in frequency of woody pixels from 2006 to 2018 using Pearson’s chi-square analysis (R Core Team 2019).

Results

Vegetation surveys

Frequency of woody species across all sites increased from 2007 to 2018 by 11% (Table 2). Four of the 7 woody species recorded increased in frequency from 2007 to 2018 (Table 2). Of these species, *J. virginiana* showed the greatest change in frequency with an increase of 4.42%, followed by *U. pumila*, which increased by 3.89% (Table 2). *R. glabra* more than tripled its frequency from 1.22% to 3.85% between 2007 and 2018, and *C. drummondii* also increased in frequency (Table 2). *G. triacanthos*, *M. pomifera* and *Symphoricarpos spp.* did not show significant changes in frequency across all sites between the 2007 and 2018 vegetation surveys (Table 2).

Table 2. Pearson's Chi-square analysis of change in woody species frequency from vegetation surveys in 2007 and 2018 across all sites (excluding sites 4 and 10). Present represents the count of plots in which the species was recorded. An * denotes a significant result at α = 0.05 level.

Species	Year	Present	Absent	Frequency (%)	X^2	P
*Cornus drummondii**	2007	15	885	1.67	7.6	0.006
	2018	11	223	4.70		
Gleditsia triacanthos	2007	101	799	11.22	0.20	0.674
	2018	24	210	10.26		
*Juniperus virginiana**	2007	14	886	1.56	15.1	< .001
	2018	14	220	5.98		
Maclura pomifera	2007	14	886	1.56	0.40	0.537
	2018	5	229	2.14		
*Rhus glabra**	2007	11	889	1.22	7.4	0.007
	2018	9	225	3.85		
Symphoricarpos spp.	2007	144	756	16.00	0.80	0.382
	2018	32	202	13.68		
*Ulmus pumila**	2007	15	885	1.67	11.7	< .001
	2018	13	221	5.56		
*Total woody spp.**	2007	314	586	34.89	10.1	0.001
	2018	108	126	46.15		

Woody species increased in frequency at 7 of the 9 sites surveyed (Table 3). *Juniperus virginiana* increased in frequency at 2 of the 5 sites where it was recorded (Table 3). At site 11, *J. virginiana* occurred in more than a quarter of quadrats (Table 3, p = 0.003). *Gleditsia triacanthos* was recorded in 6 of 9 sites; it tripled its frequency at site 7 (Table 2, p = 0.018) and greatly decreased its frequency at site 5 (Table 3, p = 0.039). *Ulmus pumila* greatly increased in frequency, becoming present in one fifth of the plots at site 6 (Table 3, p = 0.012). *U. pumila* increased in frequency nearly sevenfold at site 2 (Table 3, p = 0.041). There is also evidence to suggest an increase of *U. pumila* frequency at site 7 (Table 3, p = 0.051). *Rhus glabra* was recorded in 3 sites, including site 1 which was not recorded in prior surveys (Table 3). At site 9, *R. glabra* greatly increased its frequency from 1% in 2007 to 20% in 2018 (Table 3, p = 0.001). There is also evidence to suggest that *R. glabra* frequency increased at site 1 (Table 3, p = 0.090). *Symphoricarpos spp.* were the most widespread of woody species, occurring in all 9 of the surveyed sites (Table 3). *Symphoricarpos spp.* frequency was nearly halved at site 2 (Table 3, p= 0.041), and did not significantly change frequencies at other sites (Table 3). *Cornus drummondii* greatly increased its presence at site 9 where it occurred in a quarter of quadrats (Table 3, p = 0.023). There is also strong evidence to suggest that *C. drummondii* was more frequent at site 2 (Table 3, p = 0.051). *Maclura pomifera* frequency did not significantly change in any of the sites.

Table 3. Pearson's Chi-square analysis of change in frequency of woody species by site from vegetation surveys in 2007 and 2018. Present represents the count of plots in which the species was recorded. An * icon by the site number denotes significance at alpha = .05 level.

Species	Site	Year	Present	Absent	Frequency (%)	X^2	P
Cornus drummondii	2	2007	2	98	2.00	3.8	0.051
		2018	5	53	8.62		
	8	2007	0	100	0	2.3	0.128
		2018	1	8	11.11		
	9*	2007	6	94	6.00	5.1	0.024
		2018	5	15	25.00		
Gleditsia triacanthos	2	2007	3	97	3.00	0	0.877
		2018	2	56	3.45		
	3	2007	13	87	13.00	0	0.989
		2018	4	27	12.90		
	5*	2007	31	69	31.00	4.3	0.039
		2018	4	28	12.50		
	7*	2007	12	88	12.00	5.6	0.018
		2018	7	12	36.84		
	8	2007	27	73	27.00	0.5	0.468
		2018	4	5	44.44		
	9	2007	5	95	5.00	0	1
		2018	1	19	5.00		
Juniperus virginiana	1	2007	7	93	7.00	0.1	0.793

		2018	2	33	5.71		
	2	2007	2	98	2.00	1.3	0.263
		2018	4	54	6.90		
	3*	2007	0	100	0	6.6	0.01
		2018	2	29	6.45		
	5	2007	1	99	1.00	0.7	0.392
		2018	1	31	3.12		
	6	2007	1	99	1.00	0.3	0.613
		2018	1	14	6.67		
	11*	2007	3	97	3.00	9.0	0.003
		2018	4	11	26.67		
Maclura pomifera	2	2007	2	98	2.00	1.2	0.272
		2018	3	55	5.17		
	5	2007	2	98	2.00	0.6	0.42
		2018	0	32	0		
	6	2007	2	98	2.00	0	1
		2018	0	15	0		
	7	2007	6	94	6.00	0	0.824
		2018	2	17	10.53		
	8	2007	2	98	2.00	0	1
		2018	0	9	0		
Rhus glabra	1	2007	0	100	0	2.9	0.09
		2018	1	34	2.86		
	2	2007	6	94	6.00	0	0.823

		2018	4	54	6.90		
	9*	2007	1	99	1.00	10.7	0.001
		2018	4	16	20.00		
Symphoicarpos spp.	1	2007	6	94	6.00	0.3	0.6
		2018	3	32	8.57		
	2*	2007	32	68	32.00	4.1	0.043
		2018	10	48	17.24		
	3	2007	21	79	21.00	0.4	0.552
		2018	5	26	16.13		
	5	2007	9	91	9.00	1.2	0.274
		2018	1	31	3.12		
	6	2007	31	69	31.00	0	1
		2018	5	10	33.33		
	7	2007	9	81	10	1	0.327
		2018	0	19	0		
	8	2007	15	85	15	0	0.926
		2018	2	7	22.22		
	9	2007	20	80	20.00	0.5	0.488
		2018	6	14	30.00		
	11	2007	1	99	1.00	0	1.00
		2018	0	15	0		
Ulmus pumila	2*	2007	1	99	1.00	4.2	0.041
		2018	4	54	6.90		
	6*	2007	2	98	2.00	6.3	0.012

	2018	3	12	20.00		
7	2007	5	95	5.00	3.8	0.051
	2018	4	15	21.05		
8	2007	2	98	2.00	0	1
	2018	0	9	0		
9	2007	2	98	2.00	0	1
	2018	1	19	5.00		
11	2007	2	98	2.00	0	1
	2018	0	15	0		

Remotely sensed imagery

Overall, classification of remotely sensed imagery showed reoccurrence of pixels corresponding to woody plants on LIP sites treated for invasive woody plants, though the degree of woody cover varied by site. Across all LIP sites measured, woody cover increased by 5% from 2006 to 2018 (Table 4). Increases in woody cover ranged from less than 1% to 27% where woody cover was greater than it was prior to treatment (Table 4). The most common response was an increase of less than 3% woody cover (Table 4). Another response was of more moderate increases in woody cover ranging from 5 to 7%. There were also severe increases in woody cover: site 7 increased woody cover by 41% and site 8 increased by 18% (Table 4). There was one case in which woody cover decreased by approximately 2% from 2006 to 2018, at site 2 (Table 4). Remotely sensed images of LIP sites have been included in figures 1-9 to supplement these results.

Table 4. Site number, year, number and type of pixels, and percent woody cover of LIP sites before invasive woody trees were removed in 2005, one year following invasive tree removal in 2006, and during the year sites were revisited and surveyed in 2018. Pixel counts were generated from supervised classifications of National Agriculture Imagery Program images at a 1 m resolution, and changes in the frequency of woody pixels from 2006 to 2018 were evaluated using Pearson's Chi-Square analysis.

Site	Year	Woody pixels	Non-woody pixels	Total pixels	Woody cover (%)	P
1	2005	8884	107445	116329	7.64	
	2006	12560	452614	465174	2.70	
	2018	67197	1224875	1292072	5.20	< 0.001
2	2005	84954	104383	189337	44.87	
	2006	71690	688025	759715	9.44	
	2018	153010	1950623	2103633	7.27	< 0.001
3	2005	4191	92518	96709	4.33	
	2006	6068	376388	382456	1.59	
	2018	24559	1050147	1074706	2.29	< 0.001
5	2005	15435	84426	99861	15.46	
	2006	6753	379961	386714	1.75	
	2018	26873	1082243	1109116	2.42	< 0.001
6	2005	10099	34772	44871	22.51	
	2006	2548	174975	177523	1.44	
	2018	44576	454056	498632	8.94	< 0.001
7	2005	22913	39685	62598	36.60	
	2006	9774	240497	250271	3.91	
	2018	312061	383491	695552	44.87	< 0.001
8	2005	10581	17959	28540	37.07	

	2006	9293	104844	114137	8.14	
	2018	84071	233148	317219	26.50	< 0.001
9	2005	1236	57642	58878	2.10	
	2006	626	234632	235258	0.27	
	2018	46167	607192	653359	7.07	< 0.001
11	2005	4318	41858	46176	9.35	
	2006	2340	182275	184615	1.27	
	2018	36448	476391	512839	7.11	< 0.001
Total	2005	162611	580688	743299	21.88	
	2006	121652	2824211	2945863	4.13	
	2018	794962	7642166	8437128	9.42	< 0.001

Figure 1. National Agriculture Imagery Program aerial images of site 1 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey was performed.

pretreatment post-treatment 2018

Figure 2. National Agriculture Imagery Program aerial images of site 2 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey was performed.

pretreatment post-treatment 2018

Figure 3. National Agriculture Imagery Program aerial images of site 3 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey was performed.

pretreatment post-treatment 2018

Figure 4. National Agriculture Imagery Program aerial images of site 5 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey

pretreatment post-treatment 2018

Figure 5. National Agriculture Imagery Program aerial images of site 6 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey was performed.

pretreatment post-treatment 2018

Figure 6. National Agriculture Imagery Program aerial images of site 7 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey was performed.

pretreatment post-treatment 2018

Figure 7. National Agriculture Imagery Program aerial images of site 8 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey was performed.

pretreatment post-treatment 2018

Figure 8. National Agriculture Imagery Program aerial images of site 9 at 1 m resolution. From left to right: pretreatment in 2005, post-treatment in 2006, and in 2018 when the survey was performed.

pretreatment | post-treatment | 2018

pretreatment

Figure 9. National Agriculture Imagery Program aerial images of site 11 at 1 m resolution. Top left: pretreatment in 2005. Bottom left: post-treatment in 2006. Bottom right: 2018, the same year the site was surveyed.

post-treatment

2018

Discussion

Vegetation surveys

Despite implementation of woody plant removals, woody species reestablished on LIP sites thirteen years following treatment. Reinvasion of woody species varied by species and by site, and this variation, as well as the dominant trend of reinvasion, may be explained by woody species characteristics, management shortcomings, and/or program limitations.

The characteristics of these woody plants that allowed their successful reinvasion of grasslands are the same that caused their initial success: mainly ability to rapidly recolonize and ability to resprout. The most prolific invader was *Juniperus virginiana*, whose regrowth was likely enabled by a seed bank that was established during its initial invasion, and by its characteristic rapid growth that can reach 20 cm per year (Briggs et al. 2002). The capacity of *Ulmus pumila*, *Cornus drummondii*, and *Rhus glabra* to sprout from remnant root systems after disturbance may account for their reinvasion of LIP sites (Ortmann et al. 1997, U.S. Forest Service 2014). *Maclura pomifera* and *Gleditsia triacanthos* are each capable of sprouting and did not increase in frequency across sites in the thirteen years following treatment. For *Maclura pomifera*, this result may be a sign of effective management, as its frequency did not change at any site. For *Gleditsia triacanthos*, however, the lack of change across sites is the result of opposing trends within sites. The increase of *G. triacanthos* at site 7, for example, balanced out the decrease at site 5. The high frequency of *G. triacanthos* in 2007 at site 5 was unexpected because trees had been removed in 2005, though it is likely the result of sprouting after treatment in 2005 leading to large counts of *G. triacanthos* seedlings that were effectively managed in following years.

Management shortcomings

Differences in woody species outcomes between sites resulted from the fact that, following woody plant removals, sites were managed differently, in part because different species required different management strategies, and because sites were managed by different landowners. Shortcomings in management arose because plants were not managed effectively or because follow up management was limited or absent.

In addition to its ability to grow rapidly, *J. virginiana* encroachment was also enabled by ineffective management. It is also possible that despite the technical assistance and introduction of prescribed fire, continued management following 2007 at some sites did not include prescribed fires, which are a key component in successful management efforts of *J. virginiana* (Twidwell et al. 2013a, 2013b). In addition to sprouting, *U. pumila* success following woody plant removal likely occurred due to the application of only one treatment event when *U. pumila* generally requires repeated management to be treated (U.S. Forest Service 2014). The high frequency of *R. glabra* and *Symphoricarpos spp* in the 2007 survey indicate a lack of effective management of these species during woody plant removal in 2005. Management strategies likely did not target *R. glabra* because its frequency in the pre-treatment survey was so low that it was not considered a problem (Forbus 2007), so that it was not effectively treated and sprouted as it does after mechanical removal and prescribed fire (Ortmann et al. 1997, Hajny et al. 2011). *Symphoricarpos spp* were not targeted by management either, because they are small shrubs that have some browsing value (Hauser 2007). Despite the capacity of *Maclura pomifera* for sprouting and its affinity for bare mineral soils that are abundant following woody plant removal (Locke 2011), *Maclura pomifera* did not increase in frequency from 2007 to 2018, which suggests adequate management of this species.

Program limitations

Finally, the reinvasion of restored grasslands by woody species may be the result limitations in the LIP. These limitations include management requirements that lacked enforcement following treatment, landowner and/or site selection and short-term evaluation of success. The LIP provided financial and technical assistance to landowners, which included advice on management (Nebraska Game and Parks Commission 2012). Without required management following woody plant removal, however, some landowners did not continue management following woody plant removal in 2005, which allowed the subsequent reinvasion of their properties by woody species. Contracts with strict management requirements following woody plant removal would, however, have deterred many landowners who view such requirements as overbearing, and so less area would be treated but would be managed more effectively. There is also the possibility that some landowners accepted contracts without the intention of continuing management following treatment, which is a potential shortcoming of the landowner screening process. Some treatments were applied to sites that were especially small and surrounded by stands of trees that could act as seed sources for reinvasion. These sites, such as site 8 which was 8 ha and bordered a woodland, represent high risks of reinvasion that, without the guarantee of continued management, should not have been treated. These sites were all reported as successes in management and contribute to the more than 13,000 ha of woody plant removal/invasive tree thinning reported for the LIP (Carr et al. 2019). These sites were successfully treated initially, but without evaluation beyond the short term, there is no documentation that the problem of woody encroachment in these areas persists. These challenges are not specific to the LIP program but are entrenched in many programs that place emphasis on the acreage treated or other short-term metrics while failing to account for long-term effects.

It is possible that, due to the sites surveyed all belonging to the same set of woody plant removals in 2005 (Forbus 2007), the outcomes observed were influenced by some confounding factor; for example, this subset of sites may not be representative of the whole program. Evaluating this possibility would require a broader study that considers a larger set of LIP removals around the same timeframe. The lack of significant results for site 8 despite seemingly large changes in woody plant frequency is a shortcoming of the decision to survey every site at the same sampling density, which left smaller sites with little statistical power to detect change. This problem is compounded by the application of Yates continuity correction factor, which is known to be overly conservative in conferring statistical significance (Camilli and Hopkins 1978). Paired with the classification results, however, the measured changes in frequency at site 8 are validated.

Woody encroachment has the potential to become a problem even after treatment under state and/or federal programs. Following the current trajectory, treatment of woody encroachment on private lands has a low likelihood of long-term success. The current trend suggests that treated patches in encroached areas tend to revert to woodland a decade or so following treatment. This trend does not bode well for the management of grasslands worldwide, which are already heavily degraded. If grassland restoration and conservation programs are to succeed, management on private lands must change. The risk of failure is innate in working on private lands, where the success of grasslands depends on the continued management of individual landowners who are inherently variable in their application of treatment to the land, and in the value they place in grassland management. However, tree management programs can improve by evaluating long term success of woody plant removal, incorporating requirements for continued management after removal, spatially targeted rather than haphazard enrollment, and strategic selection of landowners and treatment areas to minimize the risk of reinvasion. This study is a reminder that woody encroachment is pernicious and not solved simply.

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Chapter 2: Oak survival falls to zero after removal of herbivory exclosures

Introduction

The Lower Niobrara River of northeastern Nebraska is a Biologically Unique Landscape (BUL) (Schneider et al. 2011). Conservation areas of concern within the Lower Niobrara River BUL are bur oak (*Quercus macrocarpa*) woodlands, cattail marshes, and reed marshes (Schneider et al. 2011). These communities are threatened by woody encroachment and herbaceous plant invasion, leading to natural resource concerns about degradation of wildlife habitat, changes to hydrology, and loss of native biodiversity.

Woody encroachment alters hydrology in riparian areas and wetlands by decreasing aquifer recharge (Adane and Gates 2015), increasing water use (Tabacchi et al. 2000), and interfering with nutrient runoff and streamflow (Tabacchi et al. 2000, Qiao et al. 2017). A single eastern redcedar (*Juniperus virginiana*), a common encroaching woody species in this area, can consume 62 L of water per day (Landon et al. 2008), and thereby decrease water availability for more desirable woody species. Woody encroachment and herbaceous invasion endanger bur oak woodlands by stifling oak regeneration through shading and direct competition of resources (Davis et al. 1998, Wolfe 2001, Oliver et al. 2019).

Bur oaks are important features of riparian woodlands in the Great Plains. Bur oaks are sources of habitat and food for native ungulates (Caners and Kenkel

2003), small mammals (Rumble and Gobeille 2001), and game birds (Servello and Kirkpatrick 1989, Flake et al. 2006). Bur oaks also contribute to the ecosystem services provided by riparian forests, including filtration of dissolved pollutants, improvement of fish habitat, protection from flooding, stabilization from erosion, and shelter for livestock (Dosskey 1998). Bur oaks are also economically important; bur oak acorns feed livestock (Uresk and Paintner 1985) and can be harvested for lumber. Bur oak is among the 5 most important tree species for sawtimber production in the Great Plains, though its capacity for wood production is decreasing with the lack of oak regeneration (Meneguzzo et al. 2018). Due to the array of conservation and economic benefits associated with keeping bur oaks on a landscape, bur oak regeneration is a management objective for public agencies and private landowners. Removal of invasive trees is a common first step in bur oak management as the presence of invasive trees inhibits the availability of adequate light and soil nutrients necessary for oak seedling survival.

Control efforts for woody encroachment consist of various methods, including mechanical (i.e., uprooting, clipping, or heavy machinery techniques) and chemical (i.e., herbicide application) methods, and prescribed fire. Although prescribed fire is often more cost-effective for managing woody invasives, particularly eastern redcedar (Ortmann et al., 1998, Simonsen et al., 2015), mechanical and chemical methods are more commonly used due to perceptions of risk (Weir et al. 2019a). Due to the cost of managing woody encroachment, many federal cost-share programs aid land managers who wish to implement tree removals on their land. Due to the cost of mechanical and chemical methods, federal cost-share programs such the Wetlands Reserve Program aid land managers who wish to protect or restore their wetlands. The Wetlands Reserve Program is a federal program that protects and restores native systems on eligible, private land by supplying technical and financial assistance to landowners who, in exchange, retire their land from agriculture (Nelson et al. 2011). The goal of the Wetlands Reserve Program along the Niobrara is to restore native plant communities in natural systems, including wetlands and gallery oak forests. One of the ways that the Wetlands Reserve Program restores plant communities is by assisting with non-native and invasive tree removals.

Long term restoration of riparian plant communities depends on the persistence of native vegetation and successful regeneration of native woody species following tree removal. It is unknown, however, whether increased light and bare ground, decreased competition, and disturbed soil caused by tree removal will restore plant community species composition or leave it susceptible to herbaceous plant invasion (McPherson and Weltzin 1998, Dulohery et al. 2000, Diamond et al. 2018). This concern is especially relevant because smooth brome (*Bromus inermis*), reed canary grass (*Phalaris arundinacea*), and other invasive herbaceous species threaten this BUL by forming dense, monotypic stands that exclude desired plant species and degrade habitat for desirable wildlife species (Schneider et al. 2011).

This project addresses the efficacy of an oak regeneration project following tree removal and the response of vegetation to tree removal in riparian areas, which are critical unknowns in restoring and preserving riparian plant communities. Given the uncertainty associated with the success of oak plantings following tree removals, and with vegetative response to tree removals in riparian forests, my goal was to 1) quantify oak survival 7 years following tree removal and 2) determine vegetation response of riparian wetlands following tree removal at experimental oak plantings. I hypothesized that 1) oak survival would be subsequently greater with more herbivory protection and 2) tree removal sites would have greater numbers of introduced species.

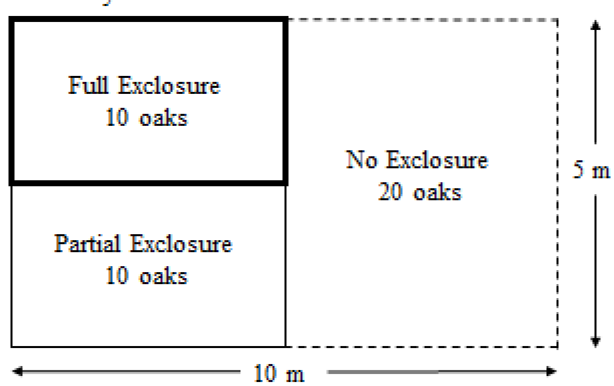
Methods

The Lower Niobrara River BUL consists of a 3.2 km buffer along the portion of the Niobrara River from central Brown County in northern Nebraska to the confluence with the Missouri River (Schneider et al. 2011). This area consists of the Niobrara River which is flanked with woody and herbaceous wetlands and riparian woodlands. Beyond the valley itself is a mixed landscape of agriculture and grasslands. This area has an average high temperature of 16.7 °C, an average low temperature of 3.2° C, and approximately 63.5 cm of precipitation annually.

Sites were selected according to landowner willingness and Wetland Reserve Program enrollment, except for two sites which were not enrolled in the Wetland Reserve Program. All woody vegetation was removed between July 2012 and April 2013 at all but 2 sites (sites 6 and 7), which experienced a wildfire in 2012 and therefore did not require tree removal. Sites consisted of woodlands in which woody vegetation was removed or, in the case of control sites, left standing. Tree removal consisted of mechanical removal with heavy machinery followed by herbicide application to stumps. Within the greater tree removal area, oak exclosures (described below) were built and oaks planted following tree removal. At each site, one exclosure was built within the boundary of the tree removal and another was built nearby under woody cover to control for tree removal effect.

Oak seedlings were planted in April of 2013, spaced 1 m apart in 5 m x 10 m plots, half of which consisted of an herbivore exclosure (Figure 1). Herbivore exclosures were divided into two parts: a partial exclosure (5 m x 2.5 m) that consisted of 1.5 m high fencing to exclude large herbivores, and a full exclosure (2.5 m x 5 m) built in the same way with an additional layer of poultry wire to exclude small mammals (unpublished, Fricke). Forty oaks were planted at each exclosure: 10 in the partial herbivory exclosure, 10 in the full herbivory exclosure, and twenty adjacent to the exclosure to gauge herbivory effect. Exclosures were removed when the initial project ended in 2014 from all but the burn sites.

Figure 1. Oak planting plot set up. 40 Oaks were planted in 5 x 10 m plots. Half the plot was enclosed to either partially or fully prevent herbivory.



Vegetation surveys were conducted in 2012 to measure canopy and understory vegetation composition and cover at tree removal areas prior to tree removal. Understory vegetation was separated into native status. These surveys were conducted using the line-intercepts (Hormay 1949), in which vegetation cover is measured by the length of area in which the plant overlaps with a transect. Vegetation censuses were conducted at each 50 m^2 oak planting site in August, 2019. Censuses consisted of plant identification at the species level when able (otherwise identified to genus) and counts of individuals belonging to that species to measure abundance. Plants were excluded if they were shorter than 30 cm tall. This height was selected to exclude tree seedlings and small herbaceous species that were not of interest. Bur oaks that were 30 cm in height or shorter were considered seedlings. I assigned native status to species according to the USDA plant database designations as either native, introduced, or both. Both refers to species that are native invasives and to entries at the genus level in which the genus contains both native and introduced species (USDA 2020).

Vegetation community metrics

Vegetation community metrics were assessed using species frequency and relative abundance. Frequency represents the percentage of plots in which a given species is present. Relative abundance was calculated by taking the proportion of individuals represented by a given species out of the total number of individuals at each site, treatment, and/or total project.

Two-way ANOVA was used to determine whether treatment type and exclosure type influenced oak survival (O’Brien and Kaiser 1985, Fox 2016). Tukey’s honest significant differences test was used to detect differences in mean oak survival between different treatment types and between different exclosure types

(Yandell 1997). Significance of differences in species richness between treatment types was calculated using a one-way paired t-test in R studio (R Core Team 2019).

Results

Oak survival

Oak sapling survival was 0 across all sites in 2019 except sites 6 and 7 (Table 1), where there were herbivory exclosures. Oak sapling survival was highest at site 7 where 18% of oaks survived and matured into saplings (Table 1). A tenth of oaks planted matured into saplings at site 6 (Table 1). Oak seedlings survived to 2019 at only slightly more than half the sites (Table 1). Oak seedlings were most abundant at sites that kept herbivory exclosures, especially site 7 (Table 1). Of the sites that removed herbivory exclosures in 2014, oak seedlings were only present in woodland (control) sites, and in each case only a tenth survived (Table 1).

Table 1. Percent survival of oak seedlings and, for 2019, saplings. Forty oaks were planted for each treatment in April of 2013 and measured in July/August of 2013, 2014, and 2019. Survival of mature oak saplings is included for 2019. Saplings were defined as oaks that were greater than or equal to 30 cm in height.

site	*treatment*	*2013 (%)*	*2014 (%)*	*2019 (%)*	*2019 (sapling)*
1	removal	92	92	0	0
	control	85	35	0	0
2	removal	95	92	0	0
	control	80	52	0	0
3	removal	100	90	0	0
	control	85	45	10	0
4	removal	92	78	0	0
	control	82	62	0	0
5	removal	100	70	0	0
	control	95	68	10	0
6	burn	100	75	26	10
	control	50	10	0	0
7	burn	92	78	50	18

Of the two sites that had herbivory exclosures in 2019, oak survival was highest in the full exclosures and lowest in the open areas beside the exclosures, although oak survival between partial and full exclosures was equal at site 6 (Table 2). In 2019, oak survival was highest in the full exclosure of site 7, where 80% of oaks survived (Table 2). Site 6 had the only oak sapling to survive without an exclosure, and the only sapling to survive in the partial exclosure (Table 2). The full exclosure at site 7 was the only subplot that showed greater oak survival in 2019 than in 2014 (Table 2).

By 2014, treatment type ($p < 0.001$) and the interaction between treatment and exclosure ($p = 0.007$) were important determinants of oak survival, while there is moderate evidence to suggest that exclosure type was important as well ($p = 0.060$) (Table 4). Removal of woody vegetation contributed to oak survival in 2014, whether it came by mechanical removal ($p < 0.001$) or burn ($p < 0.001$) (Table 4). Oaks also survived better in exclosures that fully excluded herbivory compared to partial exclosures ($p = 0.036$) and open areas ($p < 0.001$) (Table 4). There is also moderately strong evidence to suggest that oak survival was greater in partial exclosures than in open areas ($p = 0.056$) (Table 4). Conversely, oaks did not survive as well in woodlands (controls) or outside of herbivory exclosures. These factors worked additively (Table 4), and oaks performed worst when outside an herbivory exclosure at a control plot, as evidenced by the 70% decrease of oaks from 2013 to 2014 at the site 2 control plot, and the complete failure of oaks to survive at the site 6 control plot (Table 2). Overall oak survival by exclosure type is summarized in Table 3.

Table 2. Percent survival of oak seedlings in herbivory exclosures for 2013, 2014, and 2019 organized by site number and type of treatment. Treatment refers to whether trees were removed in 2012. NAs indicate sites in which herbivory exclosures were removed after 2014. Oaks were planted in 2013 after tree removal and measured in the summers of 2013, 2014, and 2019. Due to their close proximity, sites 6 and 7 shared a control site.

site	*treatment*	*exclosure*	*2013 (%)*	*2014 (%)*	*2019 (%)*
1	**removal**	full	100	100	NA
		no	95	95	NA
		partial	80	80	NA
	control	full	90	80	NA
		no	80	10	NA
		partial	90	40	NA
2	**removal**	full	100	90	NA
		no	90	90	NA
		partial	100	100	NA
	control	full	90	90	NA
		no	75	35	NA
		partial	80	50	NA
3	**removal**	full	100	90	NA
		no	100	90	NA
		partial	100	90	NA
	control	full	100	100	NA
		no	80	20	NA
		partial	80	40	NA
4	**removal**	full	100	90	NA
		no	95	80	NA
		partial	80	60	NA
	control	full	70	70	NA
		no	90	50	NA
		partial	80	80	NA

5	**removal**	full	100	90	NA
		no	100	50	NA
		partial	100	90	NA
	control	full	100	100	NA
		no	90	45	NA
		partial	100	80	NA
6	**burn**	full	100	70	50
		no	100	75	5
		partial	100	80	50
	control	full	70	40	0
		no	40	0	0
		partial	50	0	0
7	**burn**	full	100	70	80
		no	90	80	30
		partial	90	80	60

Table 3. Percent oak survival by exclosure status. Oaks were planted within herbivory exclosures in April of 2013. Tree removals occurred in 2012 and oak survival was measured in July of 2013 and 2014.

exclosure	*2013 (%)*	*2014 (%)*
full	94	83
no	87	55
partial	87	67

Table 4. Statistical analyses of factors that influenced oak survival in 2014. Oaks were planted in April of 2013 and measured in July of 2013 and 2014 after trees were removed in 2012. Analyses include a two-way ANOVA and two Tukey honest significant differences tests. No results for 2013 were significant at that early stage of the experiment.

Two-way ANOVA of the effect of treatment type, exclosure type, and the interaction between treatment and exclosure type on oak survival in 2014.

variables	*sum sq.*	*df*	*F value*	*p*
(Intercept)	18.225	1	106.062	< 0.001
treatment	9.867	2	28.711	< 0.001
exclosure	0.612	1	3.564	0.060
treatment:exclosure	1.707	2	4.966	0.007
Residuals	102.585	597	NA	NA

Tukey honest significant differences between treatment types for oak survival in 2014.

Interaction	*diff*	*p*
control-burn	-0.314	< 0.001
removal-burn	0.112	0.087
removal-control	0.426	< 0.001

Tukey honest significant differences between exclosure types for oak survival in 2014.

Interaction	*diff*	*p*
no-full	-0.258	< 0.001
partial-full	-0.143	0.036
partial-no	0.115	0.057

2012 survey results

Woody plants

In the 2012 pretreatment survey, woody cover of sites ranged from 40-86% (Table 5). *Juniperus virginiana* had for the most cover of any species and accounted for nearly a quarter of all woody cover (Table 5). *J. virginiana* comprised more than half of the canopy at site 4 and was the most abundant species at 4 of the treatments surveyed (Table 5). Dogwood species and European Buckthorn (*Rhamnus cathartica*) were the next most prominent species and together over a third of canopy cover across all sites (Table 5). Mean woody cover was 66.5% across all sites prior to tree removal in 2012.

Table 5. Percent cover of each site and species measured in the 2012 pretreatment survey. Cover was measured using the line intercept method. Sites 1 and 2 were part of the same tree removal and therefore have the same woody plant composition prior to tree removal. Sites 6 and 7 were not added to the study until after a wildfire in July of 2012 and were not surveyed.

Site	Treatment	Woody Cover (%)	Species	Canopy Cover (%)
1 & **2**	Removal	**40**	*Cornus spp*	15.1
			Juniperus virginiana	9.1
			Juglans nigra	6.8
			Ulmus americana	3.0
			Rhus glabra	2.6
			Ulmus spp	2.0
			Morus rubra	1.7
	Control	**58**	*Juniperus virginiana*	23.8
			Cornus spp	9.5
			Elaeagnus angustifolia	9.3

			Juglans nigra	5.3
			Morus rubra	4.5
			Ulmus americana	3.0
			Rhus glabra	1.9
			Rosa acicularis	0.5
3	Removal	**86**	*Cornus spp*	43.2
			Rhamnus cathartica	26.3
			Juniperus virginiana	7.0
			Zanthoxylum americanum	3.8
			Fraxinus pennsylvanica	3.5
			Ulmus americana	1.9
			Ribes uva-crispa	0.3
	Control	**71**	*Juniperus virginiana*	25.4
			Cornus spp	20.0
			Rhamnus cathartica	17.1
			Fraxinus pennsylvanica	2.9
			Tilia americana	2.4
			Ulmus americana	2.0
			Morus rubra	0.8
4	Removal	**65**	*Juniperus virginiana*	58.0
			Ulmus thomasii	3.0
			Ulmus americana	2.2
			Cornus spp	1.9
	Control	**83**	*Juniperus virginiana*	55.4
			Ulmus americana	19.3
			Morus rubra	5.8
			Cornus spp	2.8

5	Removal	**79**	*Cornus spp*	32.0
			Rhamnus cathartica	16.6
			Juniperus virginiana	11.4
			Zanthoxylum americanum	4.8
			Morus rubra	3.9
			Fraxinus pennsylvanica	3.6
			Ulmus americana	3.6
			Celtis occidentalis	2.7
	Control	**55**	*Cornus spp*	27.5
			Rhamnus cathartica	10.0
			Zanthoxylum americanum	9.8
			Ulmus pumila	4.1
			Juniperus virginiana	3.0
			Ulmus spp	0.2

Percent cover of the 10 woody species with the most canopy cover across all sites.

Species	Canopy Cover (%)
Juniperus virginiana	24
Cornus spp	19
Rhamnus cathartica	17
Elaeagnus angustifolia	9
Zanthoxylum americanum	6
Juglans nigra	6
Ulmus americana	5
Ulmus pumila	4
Fraxinus pennsylvanica	3
Morus rubra	3

Understory survey

The understory vegetation survey in 2012 showed the vegetation communities prior to treatment were composed mostly of native species, which account for over a half of vegetation at removal sites and over a third of species at control sites (Table 6). Introduced species made up the minority of plant communities in 2012, accounting for less than 5% of cover. Of the problem species recorded, Canary reedgrass (*Phalaris arundinacea*) had the highest average percent cover with 0.89% cover throughout all sites (Table 7). Smooth brome (*Bromus inermis*) and cheatgrass (*Bromus tectorum*) together accounted for 1.23% of understory cover (Table 7).

Table 6. Percent cover of understory vegetation by treatment before tree removal in 2012. Vegetation is separated into native status. Native status (NIS) was determined by referencing the U.S. Department of Agriculture plant database. Sites 6 and 7 were not added to the project until after the pretreatment survey, after a wildfire had occurred later in 2012. Cover was measured using the line intercept method. Values do not include bare ground and leaf litter do not sum to 100%.

Treatment	NIS	Cover (%)
Control	Both	34.99
	Introduced	4.77
	Native	40.65
Removal	Both	22.31
	Introduced	4.43
	Native	52.22

Table 7. Mean cover estimates of three problem herbaceous species from the 2012 understory vegetation survey. Vegetation was measured using the line intercept method.

Species	Mean Cover (%)	SD
Bromus inermis	0.74	1.23
Bromus tectorum	0.49	0.51
Phalaris arundinacea	0.89	0.91

2019 Vegetation census results

Woody plant response

10 species of woody plants (shrubs or trees) were detected in the 2019 vegetation surveys of oak planting sites. Woody species accounted for 6% of all vegetation measured (Table 8). Of these species, western snowberry (*Symphoricarpos occidentalis*) was the most abundant, accounting for 3.5% all vegetation recorded in this project (Table 8), and was the 10th most abundant species overall. *Juniperus virginiana* and dogwood species were present in twice as many plots as were oaks (Table 8). Eastern redcedar and dogwood did not appear in control sites (Table 3). European buckthorn (*Rhamnus cathartica*), American elm (*Ulmus americana*), plums (*Prunus spp.*) and hackberry (*Celtis occidentalis*) each appeared in only 1 site.

Table 8. Woody plant species frequency and relative abundance. Woody plant species were counted in 2019 at each plot following tree removal in 2012. Frequency measures the percentage of all plots in which the species is present. Relative abundance is the number of individuals of that species relative to the total number of individuals observed for the entire 2019 vegetation survey.

Species	Frequency (%)	Relative abundance (%)
Amorpha fruticosa	15	0.29
Celtis occidentalis	8	0.10
Cornus spp.	31	0.70
Juniperus virginiana	31	0.57
Prunus americana	8	0.06
Prunus virginiana	8	0.10
Quercus macrocarpa	15	0.35
Rhamnus cathartica	8	0.03
Symphoricarpos occidentalis	23	3.50
Ulmus americana	8	0.06

Herbaceous community response

The herbaceous communities in burn sites had particularly high native species abundance (Table 9). Removal sites and control sites had roughly equal species composition (Table 9). Smooth brome (*Bromus inermis*) was the most abundant species at 9.9% relative abundance (Table 9), and occurred in dense, monotypic clusters. Smooth brome dominated the site 4 removal plot (rel. abundance = 72.11%) and was abundant at the site 2 control plot (rel. abundance = 21.67%). Cheatgrass (*Bromus tectorum*) also formed dense clusters, but was infrequent; it was the 4th most abundant species overall (Table 10), despite being present in only 1 plot where it was dominant (46.26% relative abundance, site 4 control). Canada thistle (*Cirsium arvense*) was the 2nd most abundant species (9.62%) and occurred in more than half of all plots (53.85%) (Table 10). Together, smooth brome, Canada thistle, and cheatgrass accounted for more than a quarter of all individuals recorded (rel. abundance = 26.02%) (Table 10). The three most common native species, black raspberry (*Rubus occidentalis*), common milkweed (*Asclepias syriaca*), and Canada wild rye (*Elymus canadensis*) accounted for nearly one fifth of all individuals recorded (18.41% relative abundance) (Table 10). Ragweeds (*Ambrosia spp.*), Canada thistle and Virginia pepperweed (*Lepidium virginicum*) were the most frequently occurring species (53.85%), followed closely by smooth brome and Canada wild rye which occurred in nearly half of the plots (46.15%) (Table 10).

Table 9. Relative abundance and native or introduced status (NIS) of vegetative species by treatment type. Native status was determined by referencing the U.S. Department of Agriculture plant database. Vegetation surveys were conducted in 2019 following tree removal in 2012 at sites in which oaks were experimentally planted.

Treatment	NIS	Relative Abundance (%)
Burn	Both	14
	Introduced	11
	Native	75
Control	Both	22
	Introduced	35
	Native	43
Removal	Both	17
	Introduced	33
	Native	49

Table 10. Relative abundance and frequency of the 10 most abundant plant species surveyed in 2019 following tree removal in 2012. Frequency measures the percent of all plots in which the species was present. Surveys were conducted in August of 2019.

Species	Relative abundance (%)	Frequency (%)
Bromus inermis	*9.90*	*46.15*
Cirsium arvense	*9.62*	*53.85*
Rubus occidentalis	7.68	30.77
Bromus tectorum	*6.50*	*7.69*
Asclepias syriaca	*5.48*	*30.77*
Elymus canadensis	5.25	46.15
Poa pratensis	4.01	30.77
Ambrosia spp	*3.95*	*53.85*
Bouteloua curtipendula	*3.54*	*15.38*
Symphoricarpos occidentalis	*3.50*	*23.08*

Discussion

Oak survival is negligible following tree removal in riparian areas without protection from herbivory. Oak survival was 0 across all sites except sites 6 and 7, where survival is attributable to the presence of herbivory exclosures, which have been shown to greatly increase survival with other oak and deciduous woodland species (Muick 1991, McCreary and Tecklin 1997, Clements et al. 2011). The lone oak sapling that occurred outside of an exclosure (site 6) was covered by deep litter and a fallen tree that acted as a barrier to herbivory despite being outside of an actual exclosure. Low vegetation density may also promote oak survival, as seen in the survival of oak seedlings at the control plots of sites 3 and 5, where vegetation counts were exceptionally low (site 3: control n = 25; site 5: control, n = 21). Oaks did not survive on other sites, likely due to the combined pressure of herbivory and competition with herbaceous vegetation for soil water and light, which is a consistent result with other studies (Davis et al. 1998, 1999). The ability of oaks to persist in control sites despite oak survival dropping in these sites between 2013 and 2014 highlights the importance of competition with herbaceous vegetation in limiting oak regeneration. In addition, land management changed after 2014 to prioritize removal of encroaching eastern redcedar, which led to mulching woody species where oaks had been planting and could have compromised surviving oak saplings at some tree removal sites.

My results suggest that tree removal leaves sites vulnerable to re-encroachment or reinvasion by invasive woody and herbaceous species. Eastern redcedar and dogwood were exclusively located at tree removal sites and burn sites. Burns do not seem to encourage re-encroachment, since woody species at burn sites were found only within herbivory exclosures that provided protection. Tree removal sites, however, were prone to re-encroachment by eastern redcedar and dogwood as was seen by the presence of these species in tree removal sites despite lacking the protection of an exclosure. Western snowberry may also readily encroach following tree removal, which would be consistent with the tendency of shrubs to increase in density following overstory removal (Brudvig and Asbjornsen 2007). It is less clear, however, since western snowberry also appeared in a control site (site 4: control), and may be abundant in the area due to grazing interactions (Bailey et al. 1990). Unexpectedly, European buckthorn and Russian olive were nearly or completely absent from sites where other woody species were present, despite the abundance of these species in the pretreatment survey, and the ability of Russian olive to re-encroach following removal (Espeland et al. 2017). This result suggests that these species were either effectively managed, have a slower successional mechanism than that of eastern redcedar, and/or were not detectable in the smaller oak plantings surveyed in 2019.

The application of tree removals did not have a clear effect on the overall herbaceous community and neither encouraged the re-establishment of native species nor facilitated invasion by introduced ones. Native species abundances in 2019 were lower in both control and removal sites than might have been expected considering as context that the majority of understory cover came from native species in the pretreatment survey. This seeming difference in native species composition is more likely attributable to the different survey methods and extents than to any actual change of species composition. The disturbance associated with tree removal may, however, have increased vulnerability to reestablishment of undesirable woody or herbaceous species at some sites more than others, however, as smooth brome and Canada thistle dominated some of the sites in which they were present. Site 6 was the only site that had no vegetation, only duff. It was also the only site to occur within a full-canopied homogeneous eastern redcedar woodland, which may have been the cause of its barrenness due to the severe shading and changes to soil hydraulic properties known to come with eastern redcedar (Smith and Stubbendieck 1990, Wine et al. 2011).

There are possible confounding variables in this study. Excluding vegetation under the height of 30 cm may have led to the undercounting of surviving bur oaks, which are known to invest in root growth before growing tall (Hodges and Gardiner 1993). Undercounting would likely not have occurred outside herbivory exclosures, however, since non-enclosed seedlings were immature due to persistent herbivory and lacked the leaf size and maturity of some of the enclosed seedlings. Flooding occurred at several sites in March 2019, which could have influenced oak, European buckthorn, and Russian olive presence. However, the presence of seedlings at flooded sites, the lack of standing dead oak saplings, the presence of western snowberry, which cannot withstand prolonged flooding (Hauser 2007), and the documented flood-resistance European buckthorn (Kurylo et al. 2015) make flooding an unlikely factor in determining woody species presence.

In summary, this study demonstrates the dependence of oak survival on protection from herbivory and supports current knowledge that resource competition with herbaceous species limits oak survival. Single applications of management are insufficient to restore oaks to the canopy. The connection between tree removals and herbaceous community composition is unclear. This study has described the response of oak survival and vegetation communities to tree removals in riparian areas. This study enables land managers to better anticipate and manage vegetation changes after woody plant removal and to encourage survival of desirable woody vegetation with herbivory exclosures for future restoration projects.

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Chapter 3: Mountain lion movement and habitat use in a grassland dominated landscape at the edge of the species geographic range

Introduction

Mountain lions (*Puma concolor*) are recolonizing the Midwest, populating grassland-dominated landscapes that have not been inhabited by mountain lions for nearly a century (LaRue et al. 2012, Gigliotti et al. 2019). Mountain lions are native to the Midwest, but were extirpated due to management that prioritized mountain lion removal (Kellert et al. 1996). Management of mountain lions has since changed to regulate hunting and conserve mountain lions as game or conservation species, allowing mountain lion populations to grow and expand (Pierce and Bleich 2003, Schwartz et al. 2003). As a result, mountain lions are dispersing from western populations into unoccupied, suitable mountain lion habitat in Midwestern states (LaRue et al. 2012).

The Midwest has large amounts of suitable habitat to offer mountain lions (LaRue and Nielsen 2011), however agricultural land uses dominate this landscape and human densities are higher than in much of the “west”. The Midwest has the easternmost breeding populations of mountain lions and represents the colonization front of mountain lions in North America. Understanding movement decisions and resource selection in habitat fragmented by agriculture will be critical for predicting and understanding factors that facilitate and limit dispersal and colonization of Midwestern and eastern North America.

One critical concern regarding the expanding mountain lion range is the potential for increased human-mountain lion conflicts, which could in turn threaten the likelihood for re-establishment of mountain lions in the Midwest. Human-mountain lion conflict would likely take the form of damage to property, such as livestock, since mountain lions tend to be more of a hazard to livestock than to humans (Aune 1991). Some risk factors for livestock damage include the scarcity of alternative prey (e.g. mule deer, *Odocoileus hemionus*) and the age and sex characteristics of the mountain lion (young males more often attack livestock) (Aune 1991, Hiller et al. 2015). Dispersing mountain lions are particularly hazardous to livestock since the demographic of mountain lions that are more likely to disperse is the same as that which is more likely to attack livestock (Sweanor et al. 2000). Identifying landscape features that can act as corridors for mountain lions to reach suitable habitat, or to access livestock populations, will be critical in mitigating this conflict.

Mountain lions are considered habitat generalists due to the variety of ecosystems they inhabit; however sufficient abundance of prey and the presence of rough topography and/or vegetation to use as cover for hunting and caching prey, raising cubs, and avoiding humans are considered preconditions for use (Logan and Irwin 1985, Dickson and Beier 2002, Dickson et al. 2005, Kertson et al. 2011). An expert opinion survey identified presence of woody vegetation, long distance from paved roads, low human density, close proximity to water, and steep slopes as important characteristics for mountain lion habitat (LaRue and Nielsen 2008). These features also seem important for mountain lion movement, as they prefer to move through riparian vegetation and tend to avoid more urban and open areas (Dickson et al. 2005). This tendency may not apply to dispersing males, however, which will travel over large expanses of unsuitable habitat (Sweanor et al. 2000). Mountain lions generally avoid anthropogenic features (paved roads and buildings), but may tolerate some amount of these features in rural areas (Knopff et al. 2014). Mountain lions also avoid open areas since they lack the dense stalking cover that facilitates the mountain lion’s ambush hunting strategy (Dickson and Beier 2002). Despite the wealth of studies understanding mountain lion habitat use, empirical evidence of mountain lion habitat use in the Midwest is sparse and whether this novel landscape will elicit different behaviors from mountain lions is unknown. Nebraska is one of the few Midwestern states with a breeding population, and of these states, has the highest number of mountain lion confirmations outside of breeding populations (LaRue et al. 2012).

The first confirmed sighting of a mountain lion in Nebraska following their extirpation in the 19th century occurred in 1991 in the Pine Ridge of northwestern Nebraska (Genoways and Freeman 1996). Mountain lions have since established breeding populations in Nebraska in the Pine Ridge, Wildcat Hills, and Niobrara River (Wilson et al. 2010, Nebraska Game and Parks Commission

2020). Mountain lion activity continues to increase and is concentrated along Nebraska's river systems (Nebraska Game and Parks Commission 2020). Nebraska has a different landscape than other mountain lion-inhabited states; it has the most river miles of any state and is heavily agricultural with a generally flat and open topography. Despite the increased presence of mountain lions in Nebraska, their habitat preferences and movement through this landscape are undocumented. Nebraska has the easternmost breeding population of mountain lions that are recolonizing from western populations. Understanding mountain lion movement in Nebraska is essential for understanding recolonization of the Midwest and eastern North America. Furthermore, better understanding mountain lion movement will play a role in mitigating human-mountain lion conflict for livestock managers and communities in Nebraska.

My goal in this study is to determine movement and resource selection of mountain lions in Nebraska. Because mountain lions select natural landscape features associated with dense vegetation and rugged topography, and avoid open natural and human-altered features, I hypothesize that mountain lions will 1. select riparian areas and dense vegetation, 2. select steeper slopes, 3. avoid open grasslands, and 4. avoid human development and paved roads.

Methods

Study area

The study area was defined by GPS locations of the 2 mountain lions studied and occurred within Dawes, Sheridan, Cherry, Keya Paha, Brown and Rock counties of northern Nebraska, which includes the Pine Ridge ecoregion and much of the Niobrara River valley. The Pine Ridge is a rocky, pine-dominated escarpment that is raised several hundred meters from the surrounding prairie (Schneider et al. 2011). The Niobrara River is located east of the Pine Ridge, southeast of Rushville, Nebraska. The river is approximately 900 km long and runs eastward across northern Nebraska to its confluence with the Missouri River. Much of the area surrounding the Niobrara River is in cropland, though there are also wet meadows and marshes, mixed-grass prairie, and mixed woodlands (Schneider et al. 2011). This area has an average high temperature of 16.7 °C, an average low temperature of 3.2° C, and approximately 63.5 cm of precipitation annually.

Data collection and demographics

Data were collected on 2 mountain lions, m27 and m26, both of which were subadult males. M27 was a dispersing mountain lion, while m26 occupied a homerange. The mountain lions were collared by Nebraska Game and Parks Commission personnel. The first mountain lion, m27, wore a W300-GTX collar made by Advanced Telemetry Systems, Inc. Data recorded for m27 had a 12 h fix interval, taken at different times of the day. Data for m27 were recorded from

May of 2017 to December of 2018 and consisted of 456 locations. The second mountain lion, m26, wore a VERTEX Plus collar made by Vectronic Aerospace GmbH. This collar had a 12 h fix interval, recorded at 6:00 am and 6:00 pm. Data for m26 were recorded from February to September of 2019 and consisted of 209 locations. The collars did not record fixes when the signal was too poor to connect to a satellite. As a result, there are gaps of greater than 12 h in the data where the fix was missed. The fix success rate was 98% for m27 and 89% for m26.

Delineation of environmental covariates

I considered land use, water, elevation, slope and road as environmental covariates in this analysis. I extracted land use types from the 2016 National Landcover Database raster dataset at 30 m resolution (U.S. Geological Survey 2019) and aggregated them into groups that were relevant to mountain lions. These groups consisted of TREE – deciduous forest, evergreen forest, mixed forest, and shrub/scrub; OPEN – barren, herbaceous, pasture/hay, developed open space; WETLAND – woody wetlands, emergent herbaceous wetlands; DEVELOPED – low, medium, and high intensity development; and CROP – cultivated crops (Yang et al. 2018, U.S. Geological Survey 2019). I acquired shapefiles for water from the National Hydrography Dataset (U.S. Geological Survey 2018). I obtained 30 m digital elevation models at the county level from the U.S. Geological Survey National Elevation Dataset (U.S. Geological Survey 2020). I calculated slope from elevation data using the percent rise method of the slope tool in ArcGIS Spatial Analyst Tools (LaRue and Nielsen 2008, ESRI

2019). I acquired road shapefiles from the U.S. Census Bureau and filtered the dataset to include only paved roads (2018). I projected all layers into NAD83 UTM Zone 14 N to match the projected data. Layer information is summarized in Table 1.

Table 1. Layer information for environmental covariates. All NLCD, slope, and elevation layers had a 30 m resolution, and all layers were projected to NAD83 UTM Zone 14N.
Acronyms used: National Landcover Database (NLCD), United States Geological Survey National Hydrography Dataset (USGS NHD), United States Geological Survey National Elevation Dataset (USGS NED)

layer	*Definition*	*Source*
crop	NLCD classification for cultivated crops	NLCD 2016
open	binned NLCD classifications for barren, herbaceous, pasture/hay, and developed open space	NLCD 2016
tree	binned NLCD classifications for deciduous forest, evergreen forest, mixed forest, and shrub/scrub	NLCD 2016
developed	binned NLCD classifications for low, medium, and high intensity development	NLCD 2016
wetland	binned NLCD classifications for emergent herbaceous wetlands and woody wetlands	NLCD 2016
water	Shapefiles of water features including rivers, streams, and lakes	USGS NHD 2018
road	Shapefiles of paved roads	U.S. Census Bureau TIGER/LINE shapefiles
slope	gradient of incline (%)	calculated in ArcGIS
elevation	distance above sea level (m)	USGS NED

Step selection functions

I evaluated mountain lion habitat selection using step selection functions since these allow one to quantify movement decisions with respect to resources as animals move through the landscape. Step selection functions are thus well suited to understand resource selection of dispersing animals and animals in novel landscapes more generally. In a step selection function, availability for the animal is determined for each unit of movement, known as a step. Steps occur at regular time intervals, known as fixes. In this analysis, I sampled step lengths and turning angles from the empirical distribution of step lengths and turning angles to generate locations that were considered available to the animal (Fortin et al. 2005). These available points served as a null hypothesis of random movement that I compared to used steps (i.e., recorded animal locations) to determine whether the animal selected, avoided, or was indifferent to environmental covariates. I used distance-based variables rather than classification-based variables for landcover types to mitigate location error and take habitat edge into account (Conner et al. 2003). I determined the number of available steps generated per used step by testing different numbers of available steps until coefficients of use for environmental covariates stabilized. I used this method to avoid incorrectly estimating habitat use patterns since availability may not be accurately estimated when too few available locations are included (Benson 2013).

M27 displayed two modes of behavior: one in which he moved along the Niobrara River, and another in which he ventured away from the Niobrara River. I subsetted the data to include only the animal locations that occurred along the Niobrara River since movement away from the river consisted of too few points to be usable for analysis. Because the vast majority of animal locations occurred along the Niobrara River, I decided to assimilate the river turning angle into the estimation of availability. I calculated offset turning angles to account for animal movement relative to the river. For each location, the line that connects the previous location forms an angle with the line that connects the following location: this angle is the animal turning angle. For each location, I calculated the nearest point on the river using the near function in the proximity category of the analysis tools in ArcGIS (ESRI 2019), and calculated the turning angles for the river that corresponded to the animal turning angles. I calculated offset turning angles by subtracting the mountain lion turning angles from the angle of the river at the nearest point to the mountain lion.

$$\theta_{\text{offset}} = \theta_{\text{river}} - \theta_{\text{mountain lion}}$$

By using the offset angle, the estimate of availability becomes constrained by the river: available locations occur closer to the river than they would if sampling from animal turning angles. In this way, the offset angle estimates availability for an animal that is moving with respect to the river, which seems to more accurately describe this mountain lion's behavior. For the river analysis, forty available steps were generated for each used step because it was at this number of available steps that estimation of availability stabilized.

I also used step selection functions to evaluate use of environmental covariates for m26. Since all locations for m26 occurred on one side of the river, and since m26 seemed to occupy a homerange, I sampled turning angles from the empirical distribution of animal turning angles, as is typical in step selection functions (Fortin et al. 2005, Thurfjell et al. 2014). One hundred available steps were generated for each of the forty-two used steps because it was at this number of available steps that estimation of availability stabilized.

For all step selection functions, I used conditional logistic regression to analyze differences in environmental covariates between used and available locations, which is typical of step selection functions (Thurfjell et al. 2014). I centered covariates and rescaled them by subtracting observed values from the mean, then dividing by 2 standard deviations (Gelman 2008). Pearson's correlation coefficient was calculated for each pair of covariates. I considered covariates to be correlated at $r > 0.50$. In the case of correlated covariates, I discarded the covariate that seemed less relevant to mountain lion movement. I compared conditional logistic regression models using Quasi-likelihood under Independence Criterion (QIC) (Pan 2001). QIC is well suited to ranking case-control longitudinal models, and is therefore suited to evaluate step selection functions (Craiu et al. 2008).

Resource selection functions

In addition to the step selection functions, I used resource selection functions to analyze habitat use for m26. Resource selection functions are appropriate since m26 occupies a homerange. I estimated homerange by calculating the adaptive localized convex hulls using the LoCoH.a function in the adehabitatHR package in R (Calenge 2006, Getz et al. 2007). I determined availability using the systematic approach (Benson 2013), in which distances to each environmental covariate were calculated from the center of every 30 m pixel within the homerange. As with the step selection functions, covariates were centered and rescaled. I analyzed selection/avoidance of environmental covariates using conditional logistic regression models. I then compared these models using corrected Akaike's Information Criterion (AIC_c) to evaluate best of fit to the data and simplicity.

For each analysis, I used a model selection criterion of ΔQIC/ΔAICc < 2 to select models to average (Burnham and Anderson 2004). I averaged models with the model.avg function in the MuMIn package of R to produce a final model that contained β values that were averaged from all models within the model selection criterion (Lukacs et al. 2010, Barton 2020). Negative β values indicate selection of landscape features measured by distance, in this case the landcover classes (open, water, tree, etc.), and avoidance of classification-measured landscape features (slope and elevation). Conversely, positive β values indicate avoidance of landscape features measured with distance and selection of classification-based landscape features. I calculated 95% confidence intervals for β values by adding and subtracting 2 standard errors from the β values (Venables and Ripley 1997).

Results

Step selection functions

The models that offer the most empirical support for the movement of m27 identify cropland, woody vegetation, slope, and open areas as the most important factors influencing movement (Table 2). Wetland, developed, and road landcover classes were not considered for this analysis due to correlation between tree and wetland (r = 0.65), elevation and developed (r = 0.62), and water and road (r = 0.60). Tree, elevation and water were selected as model parameters because they are more plausibly driving mountain lion habitat use. M27 avoided cropland (β = 2.312), selected woody vegetation (β = -6.624), and selected steeper slopes (β = 1.241) (Table 3). Open areas were retained in a plausible competing model; however, the averaged β value showed a trend of no selection (β = -0.044, SE = 0.194).

Table 2. Number of parameters (K), qausi-likelihood under independence criterion value (QIC), ΔQIC, and model weight for all models within 2 QIC of the top model in the river-constrained step selection function of m27. Models were calculated with conditional logistic regression. Wetland, developed, and road parameters were not considered in this criterion due to correlation with other parameters.

Model		*K*	*QIC*	*ΔQIC*	*Model wt (%)*
1	Crop + tree + slope	3	372.96	0.00	43
2	Crop + tree + slope + open	4	374.22	1.26	23

Table 3. Variables important to mountain lion habitat use, β estimates of variables, standard errors, 95% confidence intervals, mean used distances, and behavior for the m27 step selection function of mountain lion habitat use along the Niobrara River of Nebraska. β values are the result of model averaging for conditional logistic regression within 2 QIC of the top model. A “+” in the behavior column indicates selection, a “-” indicates avoidance, and an “=” indicates proportional use. All models that were weighted within the 95% confidence set were averaged. Models were ranked with quasi-likelihood under independence criterion.

Variables	*β value*	*SE*	*95% CI*	*Mean distance (m)*	*Behavior*
Crop	2.312	0.659	(3.631, 0.994)	1860	-
Tree	-6.624	2.591	(-1.441, -11.806)	119	+

Slope	1.241	0.164	(1.569, 0.913)	NA	+
Open	-0.044	0.194	(0.343, -0.432)	18	=

The step selection function of m26 retained all parameters tested in plausible models except slope (Table 4). The parameter for developed areas was not included due to correlation with roads (r = 0.60). M26 strongly selected woody vegetation (β = -42.611) and also selected areas with close proximity to water (β = -1.382) (Table 5). The models showed a large effect size for m26 (β = 0.568), however this result was highly variable (SE = 0.507) and its biological relevance is therefore difficult to ascertain (Table 5). While the parameters for road, open, elevation, and crop appeared in the averaged model because they were retained in some plausible models, it is difficult to ascertain how they were associated with m26's movement due to the high standard errors of these landscape features, and the averaged β values show a trend of no selection (Table 5).

Table 4. Number of parameters (K), qausi-likelihood under independence criterion value (QIC), ΔQIC, and model weight for all models within 2 QIC for the step selection function of m26. The parameter for developed areas was not considered due to collinearity. Models were calculated with conditional logistic regression.

Model		K	QIC	ΔQIC	Model weight (%)
1	Tree + wetland + water	3	313.86	0.00	28
2	Tree + water	2	314.52	0.66	20
3	Tree + wetland + water + road	4	315.00	1.14	16
4	Tree + wetland + water + open	4	315.35	1.49	13
5	Tree + wetland + water + elevation	4	315.45	1.59	12

Table 5. Variables important to mountain lion habitat use, β estimates of variables, standard errors, 95% confidence intervals, mean used distances, and behavior for the m26 step selection function of mountain lion habitat use north of the Niobrara River of Nebraska. β values are the result of model averaging for conditional logistic regression within 2 QIC of the top model. A "+" in the behavior column indicates selection, a "-" indicates avoidance, and an "=" indicates proportional use. All models that were weighted within the 95% confidence set were averaged. Models were ranked with quasi-likelihood under independence criterion.

Variables	*β value*	*SE*	*95% CI*	*Mean distance (m)*	*Behavior*
Tree	-42.611	9.725	(-23.161, -62.061)	5	+
Wetland	0.568	0.507	(1.583, -0.446)	1042	=
Water	-1.382	0.519	(-0.344, -2.421)	1191	+
Road	0.020	0.132	(0.283, -0.244)	1086	=
Open	0.032	0.150	(0.331, -0.267)	88	=
Elevation	0.004	0.185	(0.374, -0.367)	NA	=
Crop	-0.006	0.172	(0.339, -0.351)	949	=

Resource selection functions

M26 responded to five of the recorded landscape features in the resource selection function (Table 7). The averaged model showed that m26's habitat use could be predicted by avoidance open areas (β = 0.286) (Table 7). M26 selected areas with woody vegetation (β = -5.334), close proximity to water (β = -0.59), relatively steep inclines (β = 0.339) and low-lying areas (β = -0.682) (Table 7). Road, wetland, developed areas and cropland were retained in plausible models, however the averaged β values of these landscape features show a trend of no selection.

Table 6. Number of parameters (K), corrected Akaike's information criterion values (AICc), ΔAICc, and model weight for all models within 2 AICc of the top model in the resource selection function for m26. The resource selection function was used to analyze habitat selection of the mountain lion m26 within a homerange that was estimated with adaptive localized convex hulls. Models were calculated using generalized linear mixed models.

Model		K	AICc	ΔAICc	Model wt (%)
1	Open + tree + developed + water + road + slope + elevation	7	2988.15	0.00	24
2	Crop + open + tree + developed + water + road + slope + elevation	8	2988.37	0.22	21
3	Crop + open + tree + developed + water + slope + elevation	7	2989.28	1.13	14
4	Open + tree + developed + water + slope + elevation	6	2989.35	1.20	13
5	Open + tree + water + elevation + slope	5	2989.98	1.83	10
6	Crop + open + tree + water + elevation + slope	6	2990.01	1.86	9
7	Wetland + developed + road + open + tree + water + elevation + slope	8	2990.12	1.97	9

Table 7. Variables important to mountain lion habitat use, β estimates of variables, standard errors, 95% confidence intervals, mean used distances, and behavior for the m26 resource selection function of mountain lion habitat use north of the Niobrara River of Nebraska. Models were ranked with corrected Aikaike's information criterion. β values are the result of model averaging for conditional logistic regression within 2 AICc of the top model. A “+” in the behavior column indicates selection, a “-” indicates avoidance, and an “=” indicates proportional use.

Variables	*β value*	*SE*	*95% CI*	*Mean distance (m)*	*Behavior*
Open	0.286	0.121	(0.529, 0.043)	72	-
Tree	-5.334	1.073	(-3.188, -7.479)	38	+
Developed	0.295	0.222	(0.739, -0.149)	1106	=
Water	-0.590	0.184	(-0.222, -0.958)	1375	+
Road	-0.191	0.232	(0.272, -0.655)	1266	=
Slope	0.339	0.148	(0.634, 0.044)	NA	+
Elevation	-0.682	0.165	(-0.351, -1.013)	NA	-
Crop	-0.114	0.179	(0.244, -0.472)	1014	=
Wetland	0.002	0.052	(0.106, -0.101)	1003	=

Discussion

My results support the conclusions of prior studies that mountain lions select areas with abundant cover (woody vegetation, steep topography) and close proximity to water (Logan and Irwin 1985, Kertson et al. 2011). The step selection function of m27 did not detect selection for water, not because water was unimportant to m27, but because of the method by which availability was estimated, which was predicated on the selection of the Niobrara River. It is difficult to determine the role of cropland in mountain lion dispersal. While the results of the step selection function for m27 indicated avoidance, this mountain lion also recorded many locations within or bordering cropland (Figure 1). I excluded many of the cropland locations because they did not fall within the subset of points near the river, and the data of points away from the river were too sparse to be analyzed. These cropland locations might, however, reflect a functional response toward cropland that changes from avoidance to selection as alternative forms of cover are less available in the landscape (Mysterud and Ims 1998), similar to mountain lion tolerance of urban development recorded in rural Canada (Knopff et al. 2014). Mountain lion selection of cropland may change seasonally and with crop type since availability of cover varies with these variables, and cover is likely what draws m27 to cropland when it is away from riparian areas. This hypothesis would be testable with additional data; however, the current dataset was sparse and of limited temporal extent so that it was not sufficient to test seasonality. It is difficult to discern whether this behavior is the result of individual variability or the relative availability of cover, however, since m26 did not also show this behavior.

The resource selection function of m26 differed slightly from the results of the step selection function, which can be seen in the responses toward open areas and elevation. Differences in the outcomes of resource selection functions and step selection functions are common, however, and are due to the difference between the singular estimation of availability in resource selection functions and the sequential estimation of availability in step selection functions, as well as differences in scale (Avgar et al. 2016).

These tendencies in mountain lion habitat selection indicate that future mountain lion establishment in Nebraska will be strongly tied to riparian areas, particularly those with abundant woody vegetation, as these have the requisite combination of cover and proximity to water, which has also been documented in Montana (Gigliotti et al. 2019). Mountain lion movement becomes less predictable, however, when dispersing individuals move out of contiguous expanses of suitable habitat and change habitat selection priorities. Figure 1 shows how m27 used patches of woody cover or cropland to move through otherwise open or developed habitat.

Figure 1. Locations of the mountain lion m27 when moving away from the Niobrara River. Blue circles indicate m27 locations. **Top left:** M27 appears to have taken refuge in the windbreak near a house when moving through an urban area. **Bottom left:** A windbreak that m27 stayed in for 4 days. This windbreak was located 11 km away from the Niobrara River. **Top right:** Row crop field where m27 stayed from late August to early October of 2018. **Bottom right:** A windbreak surrounded by grassland where m27 was recorded. It was located 6 km away from the Niobrara River and 5 km away from the nearest mountain lion location.

Windbreaks and, more surprisingly, cropland seem to serve a role as islands of cover in an otherwise open habitat and may act as mediating points between areas of suitable habitat, though this statement is speculation and was not tested in this study. Great Plains grasslands are not as open as they once were, however, and are steadily being encroached by woody species, particularly eastern redcedar (*Juniperus virginiana*) (Archer et al. 2017). As my results have shown, woody cover is strongly associated with mountain lion habitat use, and even in open areas mountain lions will select more complex vegetative structures for cover (Elbroch and Wittmer 2012). Over time, woody encroachment will provide greater areas of woody cover that may provide cover, as well as access to areas and wildlife or livestock prey populations of the Great Plains that, without woody encroachment, would be inaccessible.

Potential for human-mountain lion conflict will increase as populations become more established due to an increased mountain lion population and a larger number of dispersing males. Human-mountain lion conflict may more frequently occur in rural areas, and may be exacerbated by human use of mountain lion habitat, especially in evenings (Burdett et al. 2010, Morrison et al. 2014). Due to the sparse dataset and coarse time intervals, our glimpse into mountain lion habitat use in Nebraska is at a coarse resolution, and inference is limited, but offers insight into how subadult male mountain lions select resources in this habitat. The role of small patches of cover (e.g. cropland and windbreaks) in facilitating mountain lion dispersal merits further investigation. This study addresses the habitat use of two subadult male mountain lions in northern Nebraska, which is a foothold for mountain lion recolonization of the Midwest and eastern North America.

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Management implications

Woody encroachment in Nebraska is far from solved. For the restoration of grasslands, invasive tree removals are an appropriate start, and are a management success in the short term. Tree removals are too costly, however, for subsequent removals on sites reinvaded by trees to be a tenable solution. Long term success of grasslands, therefore, depends on successive management of woody encroachment following tree removal with applications of herbicide and/or prescribed fire as is most appropriate for the encroaching species. Successive management was lacking in the grassland sites that I evaluated. In part, the lack of management following tree removal was due to landowners. Tree management programs, however, would benefit from evaluating long term success of woody plant removal, incorporating requirements for continued management after removal, spatially targeted rather than haphazard enrollment, and judicious selection of treatment areas (e.g., not treating small patches, or patches surrounded by woodland) to minimize the risk of reinvasion.

My study of oak regeneration in the Niobrara River of Nebraska suggests that oak regeneration requires protection from shading and herbivory. Treating sites with fire and/or mechanical removals to decrease shading from canopy cover will also encourage oak survival. If herbivory exclosures are used, they should include poultry wire or a similar barrier to restrict access of small mammals to oak saplings. Land managers trying to preserve understory vegetation along the Niobrara River should be aware that it is difficult to predict invasive herbaceous species response to tree removals, and that species in the *Bromus* family can invade and dominate sites treated with tree removals.

Mountain lion movement across Nebraska is concentrated around riparian areas. Colonization of the Midwest will likely start with breeding populations in wooded riparian habitat, like the Niobrara River of Nebraska. Mountain lions seem to avoid cropland and open areas, though one of the mountain lions in my study used cropland and windbreaks to traverse areas of unsuitable habitat before reaching wooded riparian areas. Livestock managers along these riparian corridors should be aware that risk of predation of livestock will increase, particularly from young male dispersers, as mountain lions further establish breeding populations in the state. As for woody encroachment, the relationship between mountain lions and encroached woodlands is unclear for the time being but standing vegetation may facilitate mountain lion use of historic grasslands and increase access to otherwise inaccessible grassland prey populations. Future research could investigate the relationship between mountain lion habitat use and windbreaks, encroached woodlands, and seasonal use of croplands.

Nebraska’s natural resources are tremendously valuable: numerous economies, including food production, are important for the socio-economic well-being of Midwestern America, and for meeting the food and energy demands of a growing world; water resources are filtered by riparian vegetation, the highly demanded Ogallala aquifer relies on grasslands for adequate aquifer recharge to meet agricultural and residential water demands; pollinators and wildlife of many taxa require intact habitat to provide hunting, fishing, pollination, and viewing services; and the mountain lion, Nebraska's newly returned large carnivore, is recolonizing a landscape that has greatly transformed since its extirpation a century ago. Management in response to woody encroachment must change, as I have addressed in the previous chapters, to allow the sustainable use of these natural resources and the ecosystem services they provide.