Contemporary land-use change structures carnivore communities in remaining tallgrass prairie

by

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Abstract

The Flint Hills ecoregion in Kansas, USA, represents the largest remaining tract of native tallgrass prairie in North America. Anthropogenic landscape change (e.g., urbanization, agricultural production) is affecting native biodiversity in this threatened ecosystem. Our understanding of how landscape change affects spatial distributions of carnivores (i.e., species included in the Order ‘Carnivora’) in this ecosystem is limited. I investigated the influence of landscape structure and composition on site occupancy dynamics of 3 native carnivores (coyote [*Canis latrans*]; bobcat [*Lynx rufus*]; and striped skunk [*Mephitis mephitis*]) and 1 nonnative carnivore (domestic cat, [*Felis catus*]) across an urbanization gradient in the Flint Hills during 2016-2017. I also examined how the relative influence of various landscape factors affected native carnivore species richness and diversity. I positioned 74 camera traps across 8 urban-rural transects in the 2 largest cities in the Flint Hills (Manhattan, pop. > 55,000; Junction City, pop. > 31,000) to assess presence/absence of carnivores. Cameras were activated for 28 days in each of 3 seasons (Summer 2016, Fall 2016, Winter 2017) and I used multisession occupancy models and an information-theoretic approach to assess the importance of various landscape factors on carnivore site occupancy dynamics. Based on previous research in other ecosystems, I expected a negative relationship between both coyote and bobcat occurrence with increasing urban development but a positive relationship for domestic cat and skunk occurrence with increasing urban landcover. I also predicted grassland landcover to positively influence site occupancy for all carnivores except domestic cats. I expected that coyotes, the apex predator in this ecoregion, may limit domestic cat distributions through intraguild competition. Thus, I predicted a negative relationship between site occupancy of domestic cats and coyote occupancy probabilities. Because urban development results in habitat loss and fragmentation, I expected native species richness and diversity to decline with increased urban development. Coyotes had lower occupancy and colonization rates in areas with increased urban landcover. Bobcat occupancy was insensitive to urban landcover and colonization rates were greater in grassland landcover and row-crop agriculture fields. Site occupancy of bobcats was highly influence by forested areas and greater edge densities. Contrary to my hypothesis, striped skunk occupancy and colonization rates were negatively related to urban landcover. As expected, domestic cats were more likely to occur in and colonize sites with increased urban development and less likely to occur at sites with high coyote occupancy probabilities. Native carnivore species diversity and richness were negatively related to urban landcover. Occupancy dynamics of carnivores were shown to be influenced by landscape structure and composition as well as intraguild interactions. My results show urban landcover has a strong influence on the spatial distributions of carnivores in the northern extent of the Flint Hills.

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Dedication

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Chapter 1 - Introduction

Urban landscapes cover ~3% of Earth's surface, yet can affect the structure and function of ecosystems both regionally and globally (McKinney 2002, Grimm et al. 2008, McDonald et al. 2008, Liu et al. 2014). Towns and cities began appearing between 7,000 – 8,000 years ago (Davis 1955) with civilized urban life emerging ~5,000 years ago (Blackett 1957). Thus, these systems are relatively new on an evolutionary scale (Davis 1955) with a majority of urban expansion only beginning in past 200 years (Grimm et al. 2008). These novel environments are driven by human activity and have the ability to influence ecological processes both within and beyond city boundaries (Grimm et al. 2008, Warren et al. 2010). Human activities affect a multitude of natural phenomena including biotic diversity, soil quality, microclimates, air quality, and hydrology (Arnold and Gibbons 1996, Alberti et al. 2003). As urban areas continue to destroy and fragment natural habitats, distances among critical habitat areas also increases (McDonald et al. 2008). As such, humans are more likely come in contact with wildlife and influence evolutionary processes such as selection (Vitousek et al. 1997, Chapin et al. 2000, Polumbi 2001, Alberti et al. 2003). As a result of human interactions, urbanization is considered a primary driver for decline in native biodiversity and threatens rare species and ecosystems throughout the world (Czech et al. 2000, Marzluff and Ewing 2001, McKinney 2002, McDonald et al. 2008).

Urbanization continues to fragment natural landscapes, eliminating native habitat as well creating smaller isolated patches (Andren 1996, Fahrig 1999). New urban environments provide novel challenges to native wildlife (Gehrt et al. 2010), and carnivores are particularly sensitive to these changing environments because of their high trophic position, slower population growth rates, and large home range requirements (Gittleman et al. 2001, Crooks 2002). Carnivores may act as keystone species, shaping ecosystems from the top down (Terborgh and Winter 1980, McLaren and Peterson 1994, Wilmers et al. 2003) and also be effective indicators of ecosystem health (Eisenberg 1980, Noss et al 1996). Carnivores face many conservation challenges (Treves and Karanth 2003) including population declines (Treves 2009) and range constriction, which can ultimately lead to extinction (Ripple et al. 2014). Direct conflict with humans can occur in several ways: threats to human safety in terms of physical contact and disease transmission (Graham et al. 2004); extermination in response to livestock depredation (Treves and Karanth 2003); and persecution for international trading of skins and body parts (Woodroffe 2000). Other challenges in urban areas include fragmentation and loss of habitat, which contribute to reduced gene flow, local extinctions, and increased mortality due to car collisions (Clark et al. 1996, Carroll et al. 2001, Ordeñana et al. 2010). All of these challenges affect species distributions, space use, movement, and survival (George and Crooks 2006, Gosselink et al. 2007, Gehrt et al. 2009).

Cities represent a gradient of developed landcover, with intensity of development decreasing from the center to surrounding areas (McDonnell et al. 1997). This natural gradient provides an opportunity to study effects of urbanization on wildlife (Pickett et al. 2001, Randa and Yunger 2006). Urbanization can restrict carnivore distributions (Comiskey et al. 2002, Ahlers et al. 2016). Additionally, past research suggests carnivores select natural areas as compared to developed landscapes (Riley et al. 2003, Randa and Yunger 2006, Magle et al. 2016). Urban landcover may mediate intraguild competition among carnivores as these areas can function as refugia for mesopredators when apex predators are unwilling or unable to exploit these developed environments (Crooks and Soulé 1999; Lewis et al. 1999; Gosselink et al. 2003, 2007). However, published studies documenting species-specific responses to urban landcover have been contradictory (Fedriani et al. 2001, Gosselink et al. 2003, Randa and Yunger 2006, Gehrt et al. 2009, Ordeñana et al. 2010). For instance, Fedriani et al. (2001) found a positive correlation between coyote densities and highly developed areas in the Santa Monica Mountains of California, where as Gosselink et al. (2003) revealed that coyotes (*Canis latrans*) generally avoid human residential areas in east-central Illinois. Additionally, Ordeñana et al. (2010) reported coyote occurrence increased with human development in the south coast ecoregion of California, while Gehrt et al. (2009) reported that coyotes selected native habitat patches and avoided developed landscapes in the Chicago metropolitan area. These conflicting results highlight the need for more studies to elucidate the importance of urban landcover in structuring carnivore populations.

Imperiled landscapes are host to large numbers of endangered species (Noss et al. 1995) and contemporary landscape conversions (especially to urban development) may magnify extinction risks to these species (Myers et al. 2000, Ricketts and Imhoff 2003). Tallgrass prairie is one of the most critically endangered ecosystems in the world as these areas have been reduced to 4% of their historic distribution in North America (Noss et al. 1995). The largest remaining contiguous tract of tallgrass prairie is located in the Flint Hills ecoregion of Kansas and Oklahoma, USA (Knapp and Seastedt 1986, Samson and Knopf 1994, Deluca and Zabinksi 2011). Urban development is expected to increase in this ecoregion and is considered an emerging threat to native biodiversity (The Nature Conservancy 2000). Although the Flint Hills is host to a diverse carnivore community, little is known about how landscape composition or structure influences carnivore distributions in this ecoregion.

My thesis research focuses on the effects of expanding urban landscapes on the distribution and richness/diversity of native and nonnative carnivores found in the tallgrass prairie ecosystem of the Flint Hills. I used camera traps to determine presence/absence of carnivore species along an urban-rural gradient in the 2 largest cities of the Flint Hills and a multiseason occupancy modeling approach to uncover potential relationships between site occupancy dynamics and various landscape factors. To my understanding, this research is one of the first studies to investigate factors affecting carnivore distributions in the Flint Hills.

Chapter 2 - Urban landcover affects carnivore diversity and distributions in remaining tallgrass prairie

Abstract

The Flint Hills ecoregion in Kansas, USA, represents the largest remaining tract of native tallgrass prairie in North America. However, contemporary land-use change (e.g., urbanization, agricultural production) is likely affecting native biodiversity in the ecoregion. I used presence-absence data from repeated camera-trap surveys to investigate how landscape structure, composition, and intraguild competition influenced site occupancy dynamics of 3 native carnivores (coyote [*Canis latrans*]; bobcat [*Lynx rufus*]; and striped skunk [*Mephitis mephitis*]) and one nonnative carnivore (domestic cat [*Felis catus*]) in the Flint Hills in 2016-2017. I also examined the effects of landcover composition on native carnivore species richness and diversity. I placed a single camera trap at sites (*n* = 74) on 8 transects that were positioned along urban-rural gradients in the Flint Hills. I expected to observe a negative relationship between coyote and bobcat occurrence with increasing urban development but a positive relationship for domestic cat and skunk occurrence with increasing urban landcover. I also predicted positive relationships for all species except domestic cat between grassland landcover and occupancy. As predicted coyotes had lower occupancy ($\beta = -0.60$, SE = 0.33) and colonization rates ($\beta = -3.00$, SE = 1.26) in urban areas. Initial occupancy of bobcats was not influenced by developed landcover. However, bobcats were more likely to occur in forested areas ($\beta = 0.60$, SE = 0.34) as well as areas containing high edge densities ($\beta = 0.76$, SE = 0.42). Bobcat colonization rates were greater in grassland landcover ($\beta = 1.82$, SE = 1.01 and row-crop agriculture fields ($\beta = 0.73$, SE = 0.78). Contrary to my predictions, striped skunk occupancy and colonization was negatively influenced by urban development. Domestic cats were more likely to occur (β = 1.20, SE = 0.54) in and colonize (β = 0.82, SE = 0.33) urban environments. Cats avoided areas with high coyote occupancy. As expected, urban development was seen as the most influential factor in species richness and diversity declines. Landscape structure, composition, and intraguild interactions were all observed influencing occupancy dynamics of carnivores. My results suggest urbanization has a large effect on the spatial distributions of carnivores in the northern extent of the Flint Hills.

Introduction

Urban landscapes cover ~3% of Earth's surface, yet can affect the structure and function of ecosystems both regionally and globally (McKinney 2002, Grimm et al. 2008, McDonald et al. 2008, Liu et al. 2014). Urbanization is a primary driver of biodiversity loss (Fahrig 1999, Marzluff and Ewing 2001, McKinney 2002) and has been categorized as a significant threat to native species (Czech et al. 2000). In the United States, urban areas have quadrupled in size (Lubowski et al. 2006) since 1945, as humans have increasingly relocated to and remained in these areas (Brown et al. 2005). Additionally, exurban development in the United States (lower density residential development; Hansen et al. 2005) has increased 5-fold over the past 50 years (Brown et al. 2005). These novel landscapes present unique challenges to native wildlife (Ditchkoff et al. 2006, Lowry et al. 2013) and are generally associated with reduced species' richness and diversity (Blair 1996, Marzluff 2001, Ordeñana et al. 2010, Aronson et al. 2014).

Urbanization often results in habitat loss and fragmentation (Riley et al. 2003, Randa and Yunger 2006, Ordeñana et al. 2010), which can subsequently affect species distributions, space use, and survival (George and Crooks 2006, Gosselink et al. 2007, Gehrt et al. 2009). Carnivores can be particularly sensitive to urban-dominated environments because of their high trophic position, slower population growth rates, and large home range requirements (Gittleman et al. 2001, Crooks 2002). Urban areas can mediate intraguild competition among carnivores by functioning as refugia for mesopredators when apex predators are unwilling or unable to exploit these environments (Crooks and Soulé 1999; Lewis et al. 1999; Gosselink et al. 2003, 2007). However, studies documenting species-specific responses to urban landcover have been contradictory (Fedriani et al. 2001, Gosselink et al. 2003, Randa and Yunger 2006, Gehrt et al. 2009, Ordeñana et al. 2010). For instance, Fedriani et al. (2001) and Ordeñana et al. (2010) found a positive correlation between coyote (*Canis latrans*) densities and occurrence in urban areas in the south coast ecoregion of California, whereas Gosselink et al. (2003) reported coyotes generally avoid residential areas in east-central Illinois. Additionally, Gehrt et al. (2009) found coyotes selected native habitat patches while avoiding developed landscapes in the Greater Chicago metropolitan area.

Tallgrass prairie is one of the most critically threatened ecosystems in the world (Noss et al. 1995) and has been reduced to 4% of their historic range in North America. The largest remaining tract of tallgrass prairie is located in the Flint Hills ecoregion of Kansas and Oklahoma, USA (Knapp and Seastedt 1986, Samson and Knopf 1994, Deluca and Zabinksi 2011; Figure 2.1). Urban development is expected to increase in this ecoregion and considered an emerging threat to native biodiversity (The Nature Conservancy 2000). Although the Flint Hills has a diverse carnivore community, little is known about how landscape composition or structure influences carnivore distributions in this ecoregion and this gap in knowledge is likely impeding management efforts. Previous research in the Flint Hills suggests resident coyotes select grassland-dominated landscapes (Kamler and Gipson 2000*b*). Bobcats (*Lynx rufus*) in the Flint Hills exhibited seasonal habitat-selection patterns in which forests are selected in the winter and native grasslands are selected in the summer (Kamler and Gipson 2000*a*). Our understanding of how other carnivores are distributed in the Flint Hills remains unclear. Additionally, we have limited knowledge of how land-use change, particularly urbanization, structures carnivore communities in this ecoregion.

I used multiple presence-absence surveys and an occupancy modelling approach to investigate how landscape composition, structure, and intraguild competition impact the spatial distribution of carnivore communities in the Flint Hills. Additionally, I assessed the importance of various landscape factors to carnivore species' richness and diversity in the ecoregion. Although I identified 9 carnivore species in the Flint Hills, I had adequate data to estimate occupancy and turnover rates for 4 species (coyote, bobcat, striped skunk [*Mephitis mephitis*], and domestic cat [*Felis catus*]). The relationship between coyotes and urban landcover is largely unresolved (Gehrt et al. 2010, Lesmeister et al. 2014, Poessel et al. 2016, Lombardi et al. 2017). If urban development restricts coyote distributions in the Flint Hills, I predict site occupancy and colonization rates will be negatively related to urban landcover and local extinctions would be positively related to urban landcover. Concurrent with past research in the ecoregion, I also predicted greater occupancy and colonization rates, and lower extinction rates, in areas surrounded by grassland (Kamler and Gipson 2000*b*).

Previous studies conducted elsewhere have documented negative associations between bobcat occurrence and dense urban areas, likely because of their solitary social behavior and strictly carnivorous diet (Crooks 2002, Ordeñana et al. 2010). I predicted a negative relationship between bobcat site occupancy and urban landcover. Because bobcats often utilize habitat edges as foraging areas (Clare et al. 2015), I predicted a positive relationship between bobcat occupancy probabilities and greater edge densities as well as with forested areas (Kamler and Gipson 2000*a*). I predicted that striped skunk site occupancy and colonization rates would be greater, and extinction rates lower, in urban environments because cities may provide significant amount of food resources (McKinney 2002, Ordeñana et al. 2010, Lesmeister et al. 2014) and denning sites (Larivière and Messier 1998, Gehring and Swihart 2003, Dragoo 2009). Domestic cats, often pets, are associated with urban areas (Gehrt et al. 2010, Horn et al. 2011, Elizondo and Loss 2016) but are also subject to intraguild predation by coyotes (Crooks and Soulé 1999, Grubbs and Krausman 2009). I expected site occupancy and colonization rates to be positively related to, and extinction rates to be negatively related to, the proportion of urban landcover surrounding sites. I also predicted cat occupancy and colonization rates to be negatively associated at sites with high probability of coyote occurrence. Lastly, if urban landcover constrains the distribution of native carnivore species, I expect that native carnivore species richness and diversity will be negatively related to the proportion of urban landcover.

Methods

Study area

I conducted this study along urban-rural gradients in the 2 largest cities (Manhattan and Junction City) in the Flint Hills Ecoregion (Flint Hills) of Kansas, USA (Figure 2.1; 39.1836° N, 96.5717° W). Human population censuses for Manhattan and Junction City were approximately 56,000 and 31,500 respectively (U.S. Census Bureau 2015). Fort Riley is a United States Army installation that houses approximately 7,500 residents and directly adjacent to Junction City. The study area received 40.1 cm of precipitation and average temperatures ranged from -18 - 33° C during the duration of the study (Weather Underground 2016). Along with native tallgrass prairie and expanding urban landcover, the gradient also included a mix of row-crop agriculture (e.g., corn [*Zea mays*], soybeans [*Glycine max*], and wheat [*Triticum aestivum*]), hayland/pasture, forest, and wetlands.

Site selection

I established 74 sampling sites on 8 transects (9 sites along 6 transects, 10 sites along 2 transects) that extended along an urban-rural land use gradient in the Flint Hills ecoregion (4 transects in Manhattan and 4 transects in Junction City; Figure 2.1). All transects originated from the center of their respective municipality and extended ~10 km away from the urban center. Sites were spaced ≥1 km apart along each transect and located in areas that represented the potential for wildlife use (city parks, backyards, cemeteries, woody patches within the city, pastures, and agriculture fields; Magle et al. 2016). Site selection was restricted to areas that allowed year-round access for camera maintenance and data collection. The sampling design was similar to a broader sampling scheme used by the Urban Wildlife Information Network (UWIN;

http://www.lpzoo.org/conservation-science/projects/urban-wildlife-information-network-uwin) to investigate urban landcover effects on wildlife species across the United States.

At each site, I secured a single motion-triggered infrared camera (Bushnell Trophy Cam®; Model #119436C) to a tree or abandoned power line pole ~1.0 m off the ground. Cameras were oriented away from the sun to avoid solar glare on photos. I baited sites with a fatty acid tablet (Pocatello Supply Depot, Pocatello, ID, USA), housed in a commercial tea bag, to encourage carnivores to pass in front of the camera. Bait was placed 3–5 m in front of the camera and stapled to a tree or log at a height of approximately 0.5–1.0 m (Magle et al. 2015).

Cameras were deployed for 28 days in each of 3 seasons (Summer [22 June – 21 August, 2016], Fall [10 October – 11 November, 2016], Winter [03 January – 10 February, 2017]; hereafter 'seasons'). Once cameras were activated for a particular season, I revisited each site 14 days later to exchange memory cards and batteries (if needed) and replace scent disks. I retrieved memory cards once each camera had been active for 28 days and removed remaining scent discs. Primary sampling periods were separated into 7-day sampling units providing 4 repeat surveys at each site during each season. Thus, detection histories for each site included 4 weekly sampling periods in each of 3 primary sampling periods (seasons). I archived site-specific photos in a custom database (Colorado Parks and Wildlife Photo Warehouse 4.0, Colorado Parks and Wildlife, Fort Collins, CO, USA). I identified animal species in each photo and considered species-specific photos independent if they were separated by >30 min (O'Brien et al. 2003, Johnson et al. 2006, Jenks et al. 2011, Si et al. 2014).

I chose to evaluate the relative influence of several landscape factors on site occupancy of carnivores identified as important for structuring wildlife distributions in other studies (e.g., Prange et al. 2003, Gehrt et al. 2009). I extracted site-level landscape information from the Kansas digital land-cover map (USDA NASS 2015 Cropland Data Layer; 30-m x 30-m raster cell size) using a 1-km circular buffer centered each site (Environmental Systems Research Institute, Inc., Redlands, CA, USA). I chose this scale of measurement to make this study comparable to others (Kays et al. 2008, Long et al. 2011, Gompper et al. 2016). Additionally, an *a priori* assessment of measured landscape values at alternative scales (500 m and 2-km) revealed moderate-to-high collinearity among these variables ($|r| \geq 0.61$). I used FRAGSTATS 4.2 (University of Massachusetts, Amherst, MA, USA) to calculate edge density (m/ha; sum of landcover edge lengths divided by total area) and proportions of row-crop agriculture (corn, soybeans, wheat, and milo [*Sorghum bicolor*]), grassland, urban landcover (high, medium, and low density), and forest landcover for each site. I choose not to investigate the effects of developed green space (Duggan et al. 2011, McClure and Hill 2012) because this landcover type was rare in the study area.

Species richness and diversity

I used generalized linear mixed-effects models (lme4; Bates et al. 2015) in R (R Version 3.3.2, R Core Team 2016) to investigate effects of landcover types on native carnivore species richness and diversity. I modeled species richness at each site (number of native carnivore species observed at each site; range = 0 - 7) and diversity (Shannon- Weiner) as a function of the landcover type(s) surrounding each site. I included transect location (Manhattan or Junction City) as a random effect in all models. Species richness models included a Poisson distribution, therefore, the response variable (species richness) was transformed using a log link function to meet model assumptions (Zeileis et al. 2008). Shannon-Weiner diversity estimates were natural log transformed prior to analysis. The model sets ($n = 12$) for both richness and diversity included models that incorporated 4 landcover types (Urban, Grassland, Forest, Agriculture [tillable landcover]) as single effects ($n = 4$) as well as in additive combinations ($n = 7$). A constant model (*Intercept only*) was also included in both model sets. I did not use 'Urban' and 'Grassland' in combination because of high multicollinearity ($|r| \geq 0.60$). I evaluated support for models of diversity and richness using Akaike's Information Criteria, adjusted for small sample size (AIC_c; Burnham and Anderson 2002). Support for competitive models (<2.00 ΔAIC_c) was based on their relative changes in goodness-of-fit and respective model weights (Burnham and Anderson 2002, Arnold 2010).

Site occupancy

I used multi-season occupancy models (unmarked; Fiske and Chandler 2011) in R and an information-theoretic approach (Burnham and Anderson 2003, Arnold 2010) to investigate the influence of the measured covariates on site occupancy and turnover by carnivores across an urban-rural gradient. Because of low naïve occupancy for American badger (*Taxidea taxus*), gray fox (*Urocyon cinereoargenteus*), domestic dog (*Canis lupus familiaris*), and red fox (*Vulpes vulpes*) (<0.20; Table 2.1), I was only able to model site occupancy for 4 carnivore species (coyote, bobcat, striped skunk and domestic cat). Site occupancy by raccoon (*Procyon lotor*) was extremely high (naïve occupancy across seasons = 0.93; Table 2.1), which also precluded me from modeling occupancy dynamics for this species. Because of very low detections for bobcat

(n = 5) and striped skunk (n = 4) during summer, I limited models of bobcat and striped skunk occupancy to fall and winter seasons only.

To control for seasonal effects and the potential diminishing influence of the bait attractant, I incorporated detection covariates ‘Season’ (either summer, fall, or winter primary sampling period) and ‘Scent’ (number of days since scent disk was applied or reapplied at site) into competitive models of species-specific detection while holding all other parameters (initial occupancy, colonization, and extinction) constant. For all 4 species, the candidate model set for detection included 4 models with only single effects (n = 2; Season; Scent), the additive combination of both effects (n = 1; Season + Scent), and a constant model (*Intercept Only*; n = 1). For each species, I chose the most parsimonious detection model to subsequently model remaining rate parameters.

I derived a variable, Coyote, to assess the potential intraguild influence of coyotes (the apex predator) on occupancy dynamics of bobcat and domestic cat. I did not evaluate this effect on striped skunks as previous studies have suggested habitat selection by striped skunks is not influenced by presence of coyotes (Prange and Gehrt 2007, Lesmeister et al. 2015). I used model-averaged occupancy estimates from the candidate set of coyote occupancy models (models within $\sum w_i = 0.95$, n = 13) to assign a probability of coyote occupancy at each site during each sampling season (Cosentino et al. 2011, Ahlers et al. 2016). Conditional occupancy = 1 at sites where coyotes were detected at least once. Occupancy probabilities at sites where coyotes were not detected were <1 (Ahlers et al. 2016). I chose not to use a multi-season, 2-species model to avoid overparameterization issues (Cosentino et al. 2011, Ahlers et al. 2016).

After choosing the most-supported detection model for each species, I sequentially fit species-specific models of initial site occupancy, colonization, and extinction. I did not include variables in the same model that exhibited high multicollinearity ($|r| \geq 0.60$). I limited models to combinations of ≤3 covariates for each parameter to reduce the chance of model overparameterization. Thus, for coyotes and striped skunks, the candidate model set for each parameter (*n* = 22) included single effects (*n* = 5), additive combinations of the main effects (*n* = 16), and a constant model (*Intercept only*). Bobcat and domestic cat model sets included a coyote covariate adding to the total candidate model set (*n* = 32). Because of model convergence issues, bobcat colonization models were limited a combination of ≤2 covariates, lowering the total candidate model set (*n* = 20). I was not able to model site extinction for bobcat, striped skunk, or domestic cat because of the low number of observed extinction events occurring between seasons (Table 2.1).

Results

I documented 5,125 independent observations of 9 carnivore species (raccoon, *n* = 3,809; feral cat, *n* = 445; coyote, *n* = 426; red fox, *n* = 144; striped skunk, *n* = 187; bobcat, *n* = 73; domestic dog, *n* = 33; American badger, *n* = 7; gray fox, *n* = 1) in 6,104 trap nights. I detected the presence of ≥1 carnivore species at all 74 sites during all seasons (range = 1- 9). The maximum number of species detected each season was similar (summer, *n* = 8; fall, *n* = 8; winter, *n* = 7). Species-specific naïve occupancy was dynamic across seasons (Table 2,1).

Native carnivore species richness at each site ranged from 0 – 5. The top ranked model for native species richness included a single negative effect of urban landcover (β = -0.37, SE = 0.21; Table 2.2). Grassland landcover was included in the competitive model set and showed a positive effect on richness (β = 0.37, SE = 0.27). Generally, native carnivore species richness was reduced in areas with increased urban landcover, although there was some model-selection uncertainty (Table 2.2). Native carnivore diversity varied across sites (range of Shannon-Weiner diversity estimates across sites = 0 - 1.2) The only competitive model for native carnivore diversity also revealed a negative relationship between diversity and urban landcover (β = -0.80, SE = 0.17; Table 2.2).

Coyote

Coyote detection probabilities were relatively high (0.60) as I documented coyotes at 63 sites across all seasons. The highest ranked model of detection included the negative effect of 'Scent' (β = -0.04, SE = 0.02; Table 2.3). Thus, I used this model to subsequently fit models of initial occupancy, colonization, and extinction. While holding all other parameters constant, colonization probability was 0.53 (SE = 0.10) and extinction probability was 0.14 (SE = 0.07). The most-supported model of initial occupancy included the single negative effect of urban landcover (β = -0.60, SE = 0.33) indicating that coyotes were more likely to occur at sites with a low proportion of urban landcover (Figure 2.2A). Although there was moderate model-selection uncertainty, models incorporating the variable 'Urban' accounted for 44% of all model weights for occupancy (Table 2.3). I used the top model for occupancy (Urban) to subsequently fit models of colonization and extinction.

The top-ranked colonization model for coyotes indicated that colonization probabilities were negatively related to the proportion of urban landcover surrounding sites (β = -3.00, SE = 1.26; Table 2.3). Coyotes were less likely to colonize sites that had large proportions of urban landcover (Figure 2.3A). The most-supported model of extinction included the positive effects of 'Urban' (β = 0.67, SE = 0.62; Table 2.3) and 'Forest' (β = 0.89, SE = 0.41; Table 2.3). Site extinction probabilities were greater at sites with large proportions of urban landcover and forest (Figure 2.4A, B). The positive effect of 'Forest' (β = 0.73, SE = 0.35) was also included in a competitive extinction model (Table 2.3).

Bobcat

I used the top-ranked model of detection (*Intercept Only*; Table 2.4) to subsequently fit initial occupancy and colonization parameters. the highest ranked model of initial occupancy (Forest + Edge; Table 2.4) indicated that site occupancy for bobcats was positively influenced by both the amount of forest (β = 0.60, SE = 0.34) and edge (β = 0.76, SE = 0.42) areas at sites (Figure 2.2B, C). While holding detection and initial occupancy constant, site colonization probability by bobcats was 0.21 (SE = 0.06). The top-ranked model for colonization (Grass + Ag; Table 2.4) suggested that site colonization by bobcats was positively influenced by the proportion of grassland landcover (β = 1.82, SE = 1.01, Figure 2.3B) and slightly by row-crop agriculture (β = 0.73, SE = 0.78, Figure 2.3C) at sites.

Striped skunk

The highest ranked model for detection included the single positive effect of 'Scent' (β = 0.04, SE = 0.04). The constant model (*Intercept Only*) was also included in competitive detection models (Table 2.4) but I choose to use the ‘Scent’ model to fit remaining parameters. The most-supported initial occupancy model (Urban + Forest; Table 2.5) indicated striped skunk site occupancy was negatively influenced by both the proportion of urban landcover (β = -1.40, SE = 0.41; Figure 2.3D , E) and forest areas (β= -1.05, SE = 0.44; Figure 2.3D, E) at each site. Another competitive model (Urban + Forest + Edge) also included the variable ‘Edge’. However, relative changes in model fit suggest the variable ‘Edge’ was noninformative. Predicted site colonization for striped skunks was 0.25 (SE = 0.07) while holding detection and initial occupancy constant. Of the 2 competitive models of colonization (Urban; Urban + Edge; Table 2.5), the top-ranked model included the single effect of ‘Urban’ (β = -1.80, SE = 0.67). Striped skunks were more likely to colonize sites with low proportions of urban landcover (Figure 2.3D). Minimal changes in model fit between both models indicate the variable ‘Edge’ was noninformative (Table 2.5).

Domestic cat

None of the measured covariates sufficiently explained variation in detection so I used a constant model (*Intercept only*) to fit initial occupancy and colonization models. The highest ranked initial occupancy model suggested that domestic cats were positively associated with urban landcover (‘Urban’, β = 1.20, SE = 0.54, Figure 2.2G) and negatively related to coyote occupancy probabilities (‘Coyote’, β = -0.94, SE = 0.46, Figure 2.2F) and row-crop agriculture (‘Ag’, β = -1.80, SE = 1.73; Figure 2.2H). Another competitive model (Coyote + Forest + Ag) included forest landcover. However, relative changes in model fit suggest the variable ‘Forest’ was noninformative. Holding all rate parameters constant, site colonization probabilities by domestic cats was 0.16 (SE = 0.04). The highest ranked model of colonization included the positive effect of ‘Urban’ (β = 0.82, SE = 0.33, Figure 2.3E) suggesting that domestic cats were likely to colonize areas with increased urban landcover. Again, minimal changes in model fit between the remaining competitive model (Urban + Edge; Table 2.6) suggest ‘Edge’ was noninformative.

Discussion

My results suggest that urban landcover can affect carnivore distributions in the Flint Hills. As predicted, native carnivore diversity and richness were negatively related to the proportion of urban landcover surrounding sites. These results are concurrent with other studies documenting declines in carnivore community richness with increasing urban intensity and human activities (Mathewson et al. 2008, Ordeñana et al. 2010). Moreover, site occupancy by both coyote and striped skunk (native carnivores in this ecoregion) were negatively related to the proportion of urban landcover surrounding sites. Additionally, site occupancy by domestic cat, a nonnative carnivore to this ecoregion, was positively associated with urban landcover. These results, in combination with others, highlight the effects of urban development across a wide-range of city and municipality sizes (Blair 1999, Fahrig 2003, Hansen et al. 2005, Ordeñana et al. 2010, Aronson et al. 2014).

Coyotes were less likely to occur and colonize sites with high urban landcover. Additionally, coyotes were more likely to leave sites with increased urban landcover. Although Gehrt et al. (2009) observed coyote home-ranges within urban areas, coyotes typically avoided areas of urban development and selected for natural land use. Gosselink et al. (2003) found similar results as coyotes were found to avoid urban areas. Avoidance of urban areas by coyotes in this ecoregion may stem from human avoidance behavior or lack of suitable resources (Tigas et al. 2002, Gosselink et al. 2003, Riley et al. 2003, Gehrt et al. 2009). Although coyotes generally avoided urban development in this ecoregion, I observed coyotes at some sites occurring in urban areas. These anecdotal observations may be related to increased prey resources in these areas (e.g., eastern cottontail rabbits [*Sylvilagus floridanus*; Brillhart and Kaufman 1994, 1995; Gipson and Kamler 2002]) as habitat selection by coyotes may be influenced by an interaction of land use and prey availability (Massolo and Meriggi 1998, Carroll et al. 1999, Husseman et al. 2003, Valeix et al. 2012). Unfortunately, I was unable to estimate eastern cottontail rabbit abundance at all of the sites and could not directly test this hypothesis. Future research should work towards identifying potential interactions between coyote habitat selection and prey abundances across varying levels of urban landcover.

Although the influence of urban landcover was the dominant effect for initial site occupancy by coyotes, there were seven other competitive models. Both the negative effects of ‘Urban’ and positive effects of ‘Forest’ were included in almost all remaining competitive models. Turnover rates suggested coyotes were less likely to colonize and more likely leave forested areas. Transient coyotes in the Flint Hills selected for forested areas as compared to resident coyotes selecting for grasslands (Kamler and Gipson 2000*b*) suggesting social status may influence habitat selection by this species (Person and Hirth 1991, Kamler et al. 2005, Hinton et al. 2015). Alternatively, avoidance of forest landcover by coyotes may reflect seasonal resource changes as coyotes will exploit fruit and invertebrates during the summer and then shift towards mammalian prey items during the fall and winter (Brillhart and Kaufman 1994,1995; Gipson and Kamler 2002). Edge density also had a positive effect on coyote occupancy, which is consistent with other studies (Tigas et al. 2002, Hinton et al. 2015, Lesmeister et al. 2015) and likely a result of their foraging behavior (Theberge and Wedeles 1989).

Contrary to my hypothesis, site occupancy and turnover by bobcats appeared insensitive to urban landcover. Rather, initial occupancy by bobcats was influenced positively by the amount of edge structure and forested areas surrounding sites. The Flint Hills are experiencing aggressive population expansions of eastern redcedar (*Juniperus virginiana*) into otherwise native grasslands (Briggs et al. 2002). Although I did not quantify forest composition in the analyses, many of the forested areas were dominated by eastern redcedar likely creating a very homogenous environment at sites. Bobcats often select habitats with varying forest types and areas with greater edge densities (Major and Sherburne 1987, Koehler and Hornocker 1991, Tucker et al. 2008, Donovan et al. 2011). Additionally, bobcats were more likely to colonize sites with larger proportions of grassland and row-crop agriculture. This is similar to past studies that have documented bobcats selecting grassland habitats (Kamler and Gipson 2000*a*, Tucker et al. 2008). Bobcats were likely colonizing sites with greater proportions of row-crop agriculture as these areas are largely near streams, creeks, or rivers in this ecoregion. Tucker et al. (2008) demonstrated stream densities to be a significant predictor of home range and core area sizes for bobcats; thus, bobcats in Flint Hills are likely using riparian areas as movement corridors.

Contrary to my predictions, striped skunks were less likely to occur in and colonize urban areas. This result was unexpected given their ability to use a wide range of food resources and known space-use patterns (Greenwood et al. 1999, Dragoo 2009). Lesmeister et al. (2015) reported that skunks had a positive association with anthropogenic features including greater occupancy probabilities near urban development. On the other hand, Ordeñana et al. (2010) observed that skunks were less likely to occur as the percentage of urban development increased and generally selected for native landscapes. Skunks may be avoiding urban development for multiple reasons. Skunks generally avoid crossing roads with high vehicle traffic (Gehrt 2005) and select for more open areas (Baldwin et al. 2004). Vehicle-related mortality for striped skunks is generally high (Barthelmess and Brooks 2010). Movements within urban areas may result in increased striped skunk mortality risks and preclude them from exploiting these sites. It is unclear why occupancy probabilities of striped skunks were lower in forested areas, although it may be a result of the homogenous vegetation structure seen in eastern redcedar forests. Shirer and Fitch (1970) reported that striped skunks select grassland landcover types over forested areas in northeast Kansas. Future research should focus on fine-scale habitat selection of striped skunks and also on understanding why forested areas may be underutilized in this ecoregion.

Domestic cats, the only non-native carnivore observed in my study, were more likely to occupy and colonize sites with increased urban landcover. Other studies have also documented a positive correlation between housing density and cat occupancy (Crooks 2002, Sims et al. 2008, Kays et al. 2015). Domestic cats are considered a threat to native biodiversity conservation and have been identified as a significant source of mortality for native birds and mammals (Loss et al. 2013, Kays et al. 2015). Increased housing development will likely lead to greater introductions as well as create more available habitat for domestic cats in the Flint Hills. Along with negative effects of urbanization (e.g., habitat loss, habitat fragmentation), domestic cats may pose an additive risk to native biodiversity affected by these novel land use changes.

Domestic cats were less likely to occur at sites with both high coyote occupancy probabilities and sites surrounded by agriculture. Intraguild predation of domestic cats by coyotes is common (Quinn 1997, Grubbs and Krausman 2009) and coyote presence is likely limiting domestic cat distributions in the Flint Hills (Gehrt et al. 2013, Kays et al. 2015). Indeed, apex predators can restrict mesopredator distributions (Crooks and Soulé 1999, Prugh et al. 2009, Newsome et al. 2017) and urban areas may be providing domestic cats refugia from negative intraguild interactions in this ecoregion. Albeit a moderate effect, site occupancy by domestic cats was negatively related to row-crop agriculture. Horn et al. (2011) reported that domestic cats selected row-crop fields during the summer. However, their study occurred in a landscape dominated by row-crop agriculture (85% of the region was dominated by corn and soybean production; Illinois Department of Agriculture 2000) and not representative of the Flint Hills grassland-dominated landscape. Domestic cats may be avoiding row-crop agriculture in the Flint Hills as these areas are associated with greater coyote occupancy. However, future research is needed to test this hypothesis.

Though I was unable to model habitat associations of red fox because of limited data, anecdotal evidence suggests that red foxes in the Flint Hills are more likely associated with human-modified landscapes. I detected almost twice as many independent red fox photos in areas with ≥50% urban landcover. Historically abundant in the Flint Hills (Zumbaugh and Choate 1985), red fox currently appear limited in their spatial distributions. Berry et al. (2017) found similar results, suggesting that restored grasslands in Illinois were void of red fox populations. Coyotes may be influencing red fox distributions through direct predation (Sargeant et al. 1984, Gese et al. 1996, Henke and Byrant 1999), suggesting foxes in the Flint Hills may be using areas of urban development as a refugia from coyotes. Gosselink et al. (2003) found similar results with red fox selecting human-related habitats as coyotes were generally avoiding anthropogenic features in east-central Illinois. Future studies should elucidate the cascading influence that coyotes, as an apex predator, have on prairie ecosystems.

Management Implications

My study identified landscape features having the greatest influence on carnivore distributions in the northern Flint Hills, with urban landcover being an important driver of carnivore diversity and habitat use. As urban areas and human population growth expand, understanding effects of urban development on wildlife populations will benefit conservation mitigation actions. Negative influences of urban landcover and domestic cat populations are well documented. As urban areas expand in the Flint Hills, creating available habitat for domestic cats and limiting the distribution of other carnivore species, managers may need to mitigate the potential negative cascading effects that have the potential to affect biodiversity in this critical ecosystem. These consequences are also important for city planners and developers to recognize as urban expansion will likely necessitate the need for connected native habitat patches in or surrounding urban areas. As tallgrass prairies have been reduced to < 4% of their historical range, continued biodiversity research in the Flint Hills will likely help with future conservation and management efforts.

Figure 2.1 Carnivore occupancy study area in the Flint Hills ecoregion (outlined in black shape) of Kansas, USA. Study site locations (*n* = 74) were positioned along 8 transects representing urban-rural gradients in the municipalities of Manhattan and Junction during 2016 and 2017.

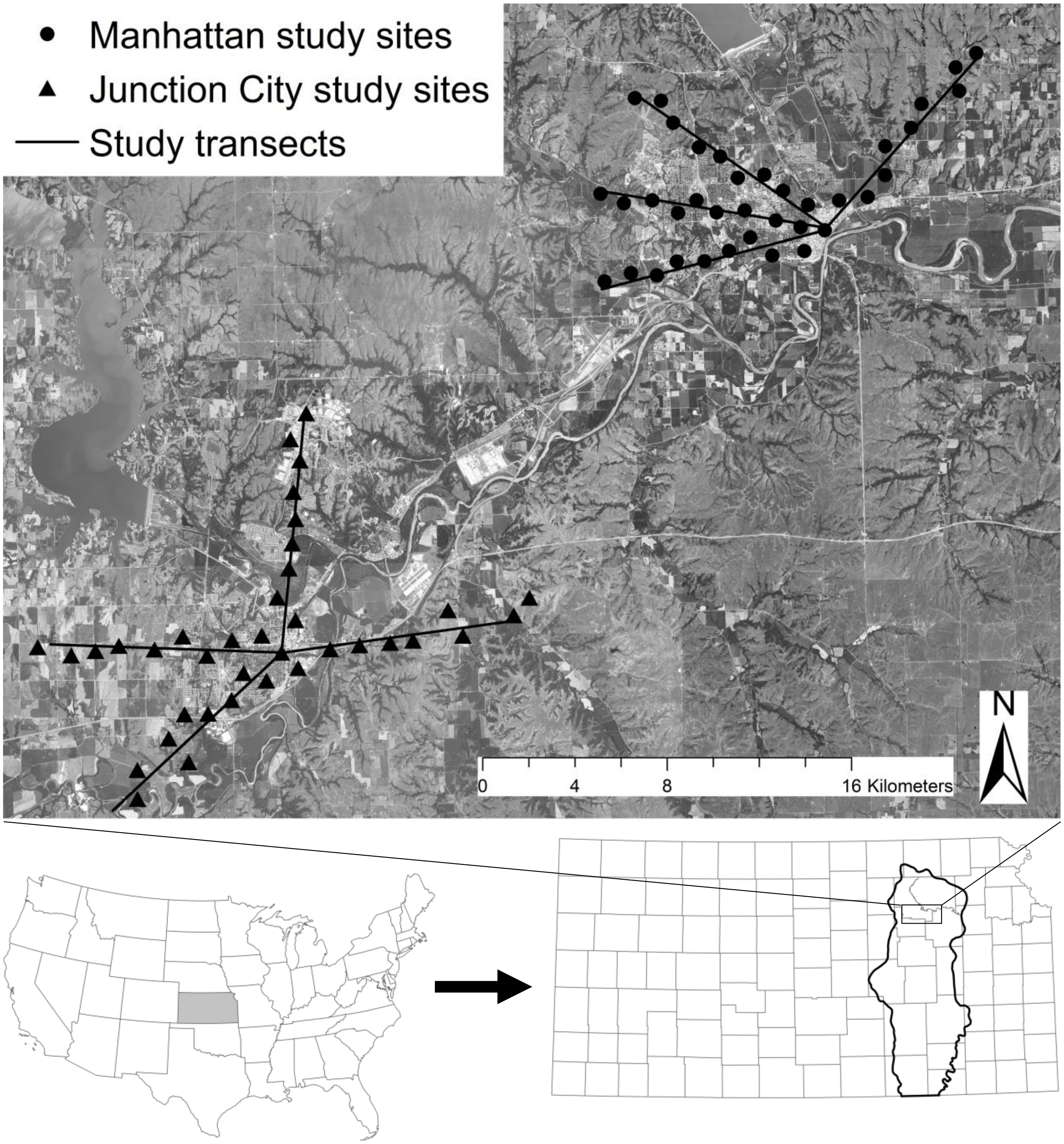

Figure 2.1 Influence of urban (A) (D) (F), forest (B) (E), edge densities (C), coyote occupancy (G), and row-crop agriculture (H) landscape covariates on site occupancy probabilities for coyote (*Canis latrans*), bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), and domestic cat (*Felis catus*) across an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. Site occupancy (n = 74) was assessed using camera traps distributed across 8 transects covering the municipalities of Manhattan and Junction City, Kansas, during 2016 and 2017. Coyote occupancy was estimated from model-averaged single-season occupancy models. Solid lines (predicted occupancy probabilities) and dashed lines (95% confidence intervals) were determined from most-supported colonization model for each species.

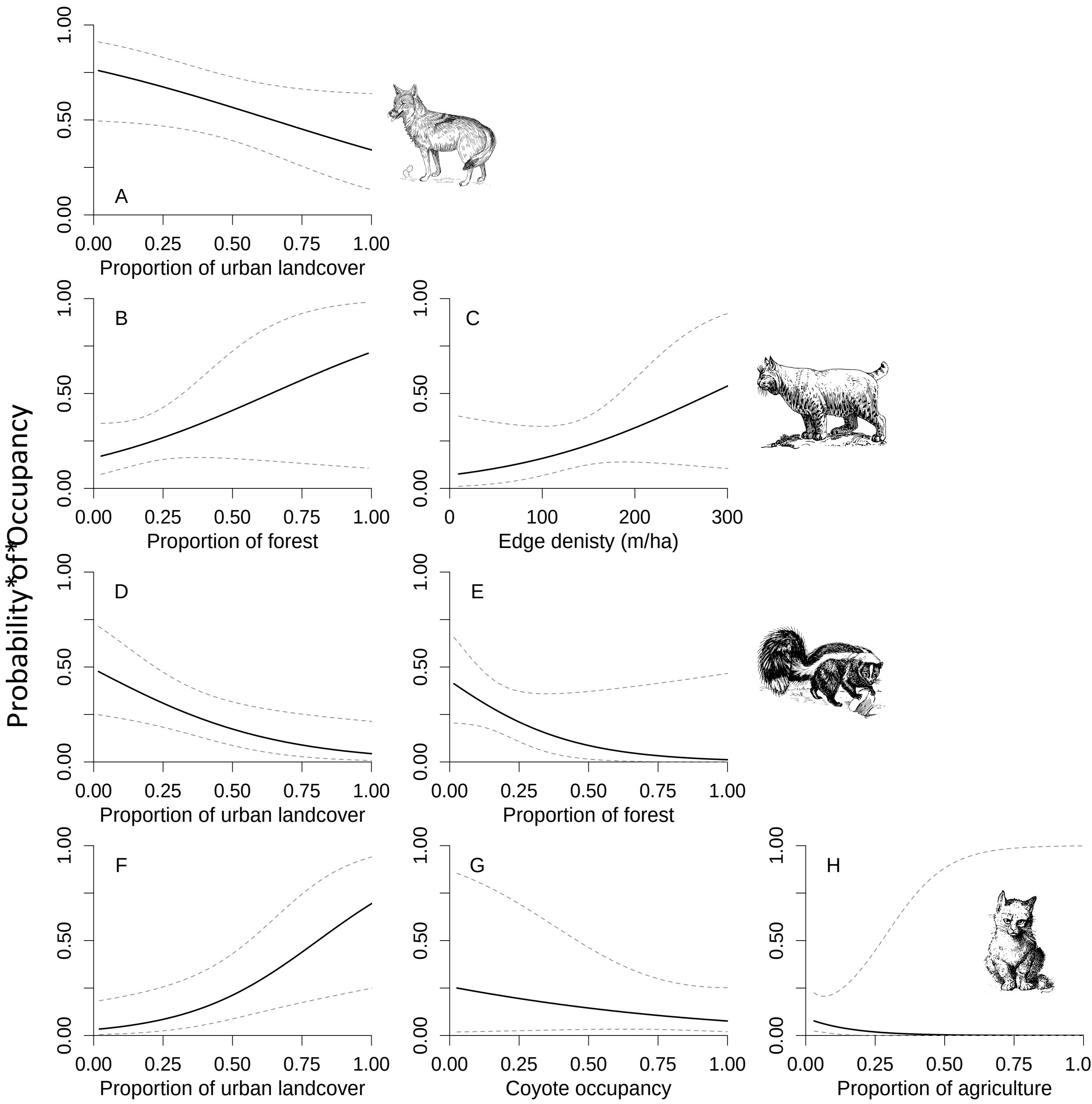

Figure 2.2 Influence of urban (A) (D) (E), grassland (B), and row-crop agriculture (C) landcover types on colonization probabilities for coyote (*Canis latrans*), bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), and domestic cat (*Felis catus*) across an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. Site occupancy (*n* = 74) was assessed using camera traps distributed across 8 transects covering the municipalities of Manhattan and Junction City, Kansas, during 2016 and 2017. Solid lines (predicted colonization probabilities) and dashed lines (95% confidence intervals) were determined from most-supported colonization model for each species.

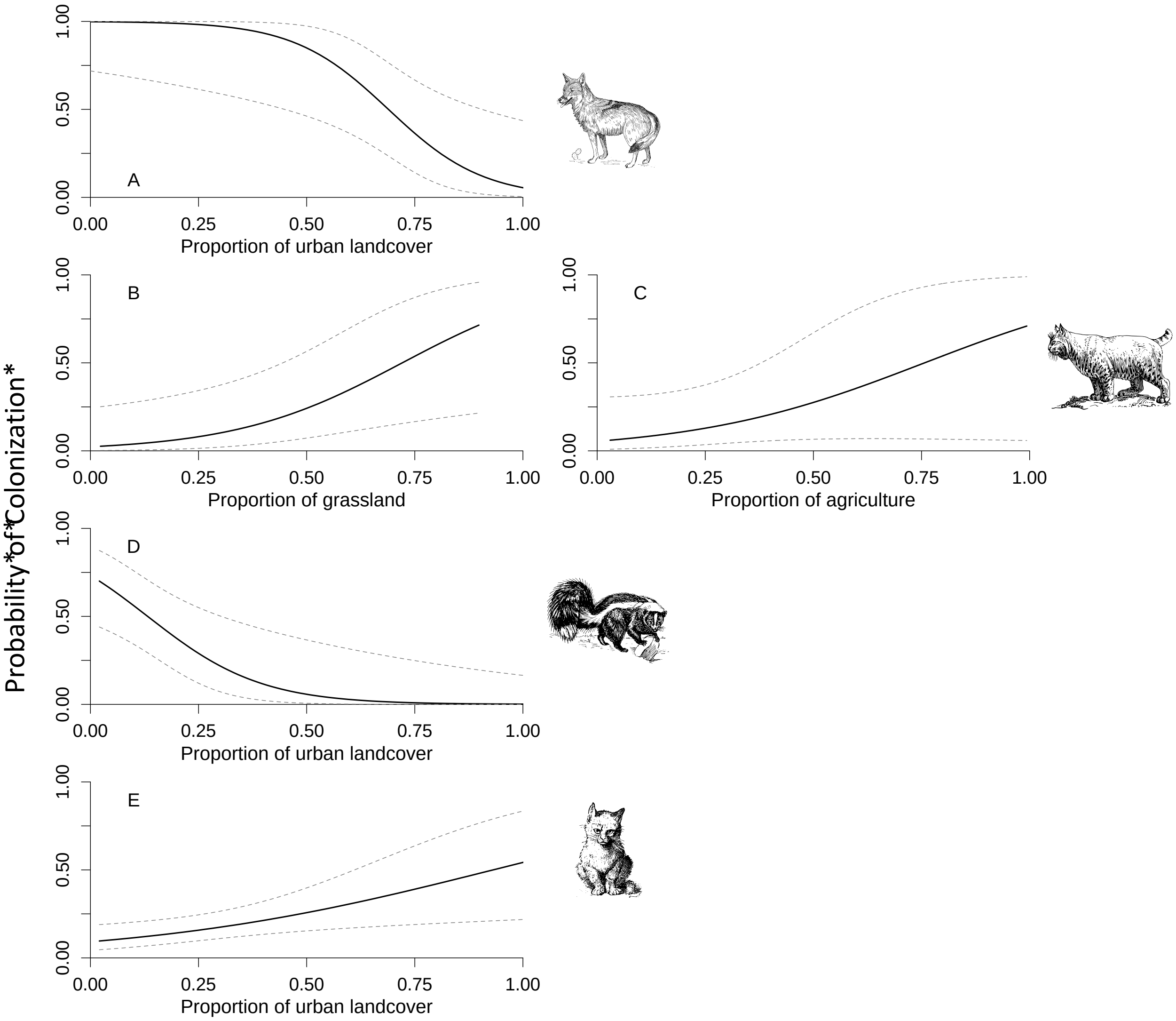

Figure 2.3 The effects of urban (A) and forested landcover (B) on extinction probabilities for coyote (*Canis latrans*) across an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. Site occupancy (*n* = 74) by coyotes was assessed using camera traps distributed across eight transects covering the municipalities of Manhattan and Junction City, Kansas, during 2016 and 2017. Solid lines (predicted extinction probabilities) and dashed lines (95% confidence intervals) were estimated from the most-supported extinction model (Urban + Forest).

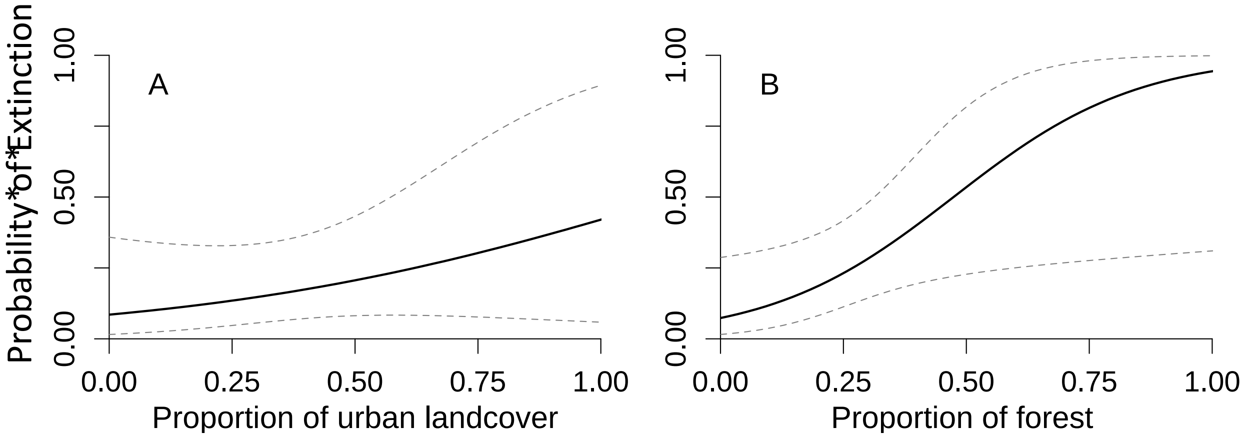

Table 2.1 Site occupancy, colonization, and extinction dynamics of coyote (*Canis latrans*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), domestic cat (*Felis catus*), domestic dog (*Canis lupus familiaris*), and American badger (*Taxidea taxus*) across Summer (July 2016), Fall (October 2016), and Winter (December 2017) seasons in the Flint Hills ecoregion of Kansas, USA. Presence of species at each site (n = 74) was determined using camera traps distributed across 8 urban-rural transects occurring in the Manhattan and Junction City municipalities.

Species	Season	Naïve occupancy[a]	Ψ^b (SE)	Naïve colonization[c]	Naïve extinction[d]
Coyote	Summer	0.50	0.61 (0.07)		
	Fall	0.57	0.73 (0.05)	21	14
	Winter	0.70	0.77 (0.06)	18	4
Bobcat	Summer	0.08	0.14 (0.06)		
	Fall	0.20	0.30 (0.06)	14	4
	Winter	0.26	0.38 (0.08)	10	6
Red fox	Summer	0.09			
	Fall	0.14		9	5
	Winter	0.19		11	7
Gray fox	Summer	0.01			
	Fall	0.00		0	1
	Winter	0.00		0	0
Raccoon	Summer	0.79			
	Fall	0.89		11	3
	Winter	0.74		1	10
Striped skunk	Summer	0.07	0.18 (0.10)		
	Fall	0.30	0.33 (0.05)	17	0

	Winter	0.39	0.42 (0.06)	13	6
Domestic cat	Summer	0.18	0.19 (0.05)		
	Fall	0.31	0.30 (0.05)	14	2
	Winter	0.36	0.39 (0.06)	7	4
Domestic dog	Summer	0.08			
	Fall	0.09		6	4
	Winter	0.09		6	5
American badger	Summer	0.00			
	Fall	0.05		4	0
	Winter	0.00		0	4

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[a] Naïve occupancy = number of sites where the target species was detected/ total number of sites

[b] Ψ is the estimate of occupancy by target species after controlling for detection

[c] Naïve colonization is the number of sites that a species was detected during a given season but not the previous season

[d] Naïve extinction is the number of sites that a species was not detected during a given season but was detected the previous season.

Table 2.2 Competitive generalized mixed models explaining native carnivore species richness and diversity across sites (*n* = 74) distributed along an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. I used camera traps to document the presence of native carnivore species at each site during the summer (July 2016), fall (October 2016), and winter (January 2017) seasons. Covariates ‘Urban’, ‘Grass’, ‘Forest’, and ‘Ag’ represent proportions of landcover types within a 1-km buffer surrounding camera sites. Models are ranked by descending ΔAIC_c values (Akaike’s Information Criteria, adjusted for small sample size). w_i = model weight. -2*l* = -2(Log likelihood); *K* = number of parameters in each model.

Category	Model	ΔAIC_c	w_i	-2*l*	*K*
Richness	Urban	0.00	0.27	250.74	3
	Intercept Only	0.85	0.15	253.77	2
	Grass	1.11	0.13	251.85	3
	Urban + Forest	1.74	0.10	250.25	4
Diversity	Urban	0.00	0.52	368.87	3
	Intercept Only	13.19	0.00	384.30	2

Table 2.3 Competitive species specific multi-season occupancy models explaining detection, initial occupancy, colonization, and extinction of coyote (*Canis latrans*) across sites ($n = 74$) distributed along an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. I used camera traps to document the presence of coyotes at each site during the summer (July 2016), fall (October 2016), and winter (January 2017) seasons. Detection covariate 'Scent' represents the number of days since a fatty acid tablet disk was applied. Covariates 'Urban', 'Forest', and 'Ag' represent proportions of landcover types within a 1-km buffer surrounding camera sites. 'Edge' also represents edge densities within the same buffer. Models are ranked by descending ΔAIC_c values (Akaike's Information Criteria, adjusted for small sample size). w_i = model weight. $-2l$ = -2(Log likelihood); K = number of parameters in each model.

Parameter	Model	ΔAIC_c	w_i	$-2l$	K
Detection	Scent	0.00	0.68	964.85	5
	Intercept only	2.72	0.18	969.87	4
Occupancy	Urban	0.00	0.16	960.87	6
	Forest	1.03	0.09	961.90	6
	Intercept only	1.60	0.07	964.85	5
	Edge	1.64	0.07	962.51	6
	Forest + Ag	1.78	0.06	960.21	7
	Urban + Forest	1.78	0.06	960.21	7
	Forest + Edge	1.83	0.06	960.26	7
	Urban + Edge	1.89	0.06	960.32	7
Colonization	Urban	0.00	0.34	949.61	7
	Urban + Forest	1.97	0.13	949.05	8
	Intercept only	8.82	0.00	960.87	6
Extinction	Forest	0.00	0.23	944.76	8
	Urban + Forest	1.33	0.12	943.49	9
	Forest + Ag	1.48	0.11	943.65	9
	Intercept Only	4.29	0.03	949.05	8

Table 2.4 Competitive species specific multi-season occupancy models explaining detection, initial occupancy, colonization, and extinction of bobcats (*Lynx rufus*) across sites ($n = 74$) distributed along an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. I used camera traps to document the presence of bobcats at each site during the fall (October 2016) and winter (January 2017) seasons. Detection covariate ‘Scent’ represents the number of days since a fatty acid tablet disk was applied and ‘Season’ represents the effect of different trapping seasons (October) (January). Covariates ‘Urban’, ‘Grass’, ‘Forest’, and ‘Ag’ represent proportions of landcover types within a 1-km buffer surrounding camera sites. ‘Edge’ also represents edge densities within the same buffer. Coyote occupancy covariate was estimated from model-averaged single-season occupancy models. Models are ranked by descending ΔAIC_c values (Akaike’s Information Criteria, adjusted for small sample size). w_i = model weight. $-2l$ = -2(Log likelihood); K = number of parameters in each model.

Parameter	Model	ΔAIC_c	w_i	$-2l$	K
Detection	*Intercept only*	0.00	0.51	278.57	4
	Scent	1.80	0.21	278.07	5
	Season	1.83	0.20	278.09	5
Occupancy	Forest + Edge	0.00	0.15	271.28	6
	Edge	0.62	0.11	274.27	5
	Forest	1.22	0.08	274.88	5
	Edge + Urban	1.41	0.07	272.68	6
	Intercept only	2.61	0.04	278.57	4
Colonization	Grass	0.00	0.31	257.82	7
	Grass + Ag	0.70	0.22	256.00	8
	Grass + Coyote	1.55	0.14	256.85	8
	Intercept only	11.02	0.00	271.28	6

Table 2.5 Competitive species specific multi-season occupancy models explaining detection, initial occupancy, colonization, and extinction of striped skunk (*Mephitis mephitis*) across sites (*n* = 74) distributed along an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. I used camera traps to document the presence of striped skunk at each site during the fall (October 2016) and winter (January 2017) seasons. Detection covariate ‘Scent’ represents the number of days since a fatty acid tablet disk was applied and ‘Season’ represents the effect the different trapping season (October) (January). Covariates ‘Urban’, ‘Grass’, ‘Forest’, and ‘Ag’ represent proportions of landcover types within a 1-km buffer surrounding camera sites. ‘Edge’ also represents edge densities within the same buffer. Models are ranked by descending ΔAIC_c values (Akaike’s Information Criteria, adjusted for small sample size). w_i = model weight. $-2l$ = -2(Log likelihood); K = number of parameters in each model.

Parameter	Model	ΔAIC_c	w_i	$-2l$	K
Detection	*Intercept only*	0.00	0.47	448.29	4
	Scent	1.28	0.25	447.27	5
	Season	1.88	0.18	447.87	5
Occupancy	Urban + Forest	0.00	0.39	430.11	7
	Urban + Forest + Edge	1.99	0.14	429.59	8
	Intercept only	12.34	0.00	447.27	5
Colonization	Urban	0.00	0.37	416.77	8
	Urban + Edge	1.87	0.14	416.05	9
	Intercept only	12.82	0.00	429.59	8

Table 2.6 Competitive species specific multi-season occupancy models explaining detection, initial occupancy, colonization, and extinction of domestic cat (*Felis catus*) across sites (n = 74) distributed along an urban-rural gradient in the Flint Hills ecoregion of Kansas, USA. I used camera traps to document the presence of free ranging cats at each site during the summer (July 2016), fall (October 2016), and winter (January 2017) seasons. Detection covariate 'Scent' represents the number of days since a fatty acid tablet disk was applied. Covariates 'Urban', 'Forest', and 'Ag' represent proportions of landcover types within a 1-km buffer surrounding camera sites. 'Edge' also represents edge densities within the same buffer. Coyote occupancy covariate was estimated from model-averaged single-season occupancy models. Models are ranked by descending ΔAIC_c values (Akaike's information criteria, adjusted for small sample size). w_i = model weight. $-2l$ = -2(Log likelihood); K = number of parameters in each model.

Parameter	Model	ΔAIC_c	w_i	$-2l$	K
Detection	*Intercept only*	0.00	0.63	530.76	4
	Scent	1.91	0.24	530.37	5
Occupancy	Urban + Coyotes	0.00	0.16	502.30	6
	Urban + Coyotes + Ag	0.25	0.14	500.11	7
	Coyotes + Forest + Ag	0.78	0.11	500.64	7
	Urban + Edge	1.24	0.08	503.54	6
	Urban	1.62	0.07	506.30	5
	Intercept only	23.79	0.00	530.76	4
Colonization	Urban	0.00	0.24	494.37	8
	Urban + Edge	1.85	0.09	493.62	9
	Intercept only	2.96	0.05	502.30	6

Chapter 3 - Conclusion

Tallgrass prairie is one of the most critically endangered ecosystems in the world (Noss et al. 1995). Native tallgrass prairie has been drastically reduced to 4% of its historic range in North America with the last largely contiguous tract occurring in the Flint Hills of Kansas and Oklahoma, USA (Knapp and Seastedt 1986, Samson and Knopf 1994, Deluca and Zabinksi 2011). Although relatively safe from conversion to row crop agriculture, urban development is expected to increase in the Flint Hills and is considered an emerging threat to native biodiversity (Hamilton et al. 2000). Urban land development fragments natural landscapes and destroys native habitats (Andren 1996, Fahrig 1999). Along with native tallgrass prairie and expanding urban landcover, this ecoregion also includes a mix of row-crop agriculture (e.g., corn [*Zea mays*] and soybeans [*Glycine max*]), hayland/pasture, forest, and wetlands. Relatively little research has been done to increase our understanding of the potential effects that urbanization has on carnivore communities in this imperiled ecosystem. Carnivores have high trophic posititions, slower population growth rates, and large home range sizes (Gittleman et al. 2001, Crooks 2002). These new urban environments may have a greater effect on carnivores because of their ecological traits.

I used 3 seasons of presence-absence data to elucidate occupancy dynamics of 4 carnivore species occurring in this ecoregion. Using camera traps distributed along an urban-rural gradient, I quantified effects of urban landcover on carnivore communities in the Flint Hills. I detected 9 different carnivore species including 7 native carnivores; coyote (*Canis latrans*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), American badger (*Taxidea taxus*), red fox (*Vulpes vulpes*), and gray fox (*Urocyon cinereoargenteus*), and two nonnative species; domestic cat (*Felis catus*) and domestic dog (*Canis lupus familiaris*). Species-specific detection varied throughout the year, but I was able to observe ≥1 carnivore species at 97% of the camera sites across 3 seasons. Unfortunately, due to limited data, I was unable to analyze habitat associations for all species observed. Low numbers of detection for 5 of the species limited my analyses to a subset (coyote, bobcat, striped skunk, and domestic cat) of all detected species. My results suggest that coyotes and skunks tend to avoid urban landscapes and populations may be restricted by urban development. A non-native carnivore, domestic cat, appeared to use habitats in or close to urban development. My results, in combination with others, suggest that effects of urban development occur in a range of urban sizes and are not restricted to low or highly developed areas.

My study uncovered a decrease in native carnivore richness and diversity as urban development increased. This result agrees with other research reporting that urban landcover has a negative effect on species diversity (McKinney 2002, Aronson et al. 2014). Urbanization has eliminated many native species and accounts for high extinction rates around the world (Blair 1996, Marzluff 2001, McKinney 2002). Mathewson et al. (2008) and Ordeñana et al. (2010) had similar findings where carnivore richness declined with increased urban intensity and human activities. Nonnative species have also been shown to increase as urban development increase (Blair 1996). Although not included in the most-supported model of native carnivore richness, it is interesting to note that grasslands or prairie landscapes had a positive effect on species richness.

Tallgrass prairie is a critically endangered ecosystem, and home to many imperiled plants and animals (Samson and Knopf 1994, Noss et al. 1995). The Flint Hills represent the largest remaining tract of tallgrass prairie in North America, though this ecoregion is currently threatened by urban expansion (The Nature Conservancy 2000). My research has provided the first look into how urban expansion is affecting carnivore communities in this threatened ecosystem. Using presence-absence data and multi-season modeling approaches, I uncovered support for landscape variables that had the greatest influence on carnivore distributions through the northern Flint Hills. Understanding how wildlife populations are distributed across landscapes could potentially benefit management efforts targeted at restoring/maintain biodiversity or reducing negative human conflicts. Continued research focused on understanding fine-scale factors influencing species' movements may provide additional insight into how carnivore communities are structured in the Flint Hills.

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