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Ecology Of Coyotes (canis Latrans) In The Greater Detroit Area Of Southeastern Michigan

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ECOLOGY OF COYOTES (*CANIS LATRANS*) IN THE GREATER DETROIT AREA OF SOUTHEASTERN MICHIGAN

by

WILLIAM B. DODGE, JR.

DISSERTATION

Submitted to the Graduate School

of Wayne State University,

Detroit, Michigan

in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

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MAJOR: BIOLOGICAL SCIENCES

Approved By:

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Advisor   Date

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DEDICATION

To my wife, Trish, for all her love and support and encouraging me to follow my dreams.

Thanks, Trish

Love,

Bill

ACKNOWLEDGEMENTS

I would like to thank the Wayne State University Graduate School and Department of Biological Sciences for providing the primary funding for this research.

I am grateful to Dr. Kashian (AKA Dan) for agreeing to take me on as a PhD student and showing interest in this project as it slowly took shape. I also appreciate his patience, which I sorely tested during the final stages of the writing of my dissertation. His insightful comments on my writing and ideas and his editing skills greatly improved my dissertation. I would like to thank my committee members, Dr. Dwayne Etter, Dr. Donna Kashian, and Dr. Chris Steiner for their support and helpful comments on my dissertation. Dwayne deserves extra thanks for filling in at the last minute on my committee, as well as providing guidance and help when I was first educating myself about trapping coyotes.

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The success of this study would not have been possible without the generous help of Holly Hadac and Mike Huntzinger, volunteers who contributed countless hours to all phases of the project. Holly adopted the first coyote we radio-collared and diligently and enthusiastically radio-tracked him for nearly two years until he was struck and killed by a motor vehicle. Holly was particularly adept at knowing where to sit and wait during tracking sessions to get an opportunity to see this coyote, and did so, on at least two dozen occasions. Mike was invaluable in helping collect and process coyote scat, assist

Cluster, Ann Arbor; Huron-Clinton Metropolitan Authority, Lake St. Clair Metropark, Harrison Twp.; Association of Animal Control Officers, Thompsonville; Seven Ponds Nature Center, Dryden; E. L. Johnson Nature Center, Bloomfield Hills; Huron-Clinton Metropolitan Authority, Indian Springs Metropark, White Lake; Seney National Wildlife Refuge, Seney; Madison Heights Nature Center, Madison Heights; Sierra Club, Southeast Michigan Group, Bloomfield Hills.

Finally, I would like to thank the numerous individuals that I talked to in the field and elsewhere that showed interest in the project and enjoyed (sometimes) telling me where they had seen a coyote in southeastern Michigan.

TABLE OF CONTENTS

vii

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Coyotes (*Canis latrans*), in the absence of larger predators that in many cases have been extirpated from landscapes (e.g., wolves; *Canis lupus*), have become the de-facto apex predator in the last several decades in most major metropolitan areas in North America (Gompper 2002, Gehrt 2004). Prior to wide-spread settlement of western North America (circa 1800), the coyote's primary range was the arid grassland and deserts of the Great Plains region (Moore and Parker 1992, Young and Jackson 1951, Seton 1929). By the close of the 20th century, however, the coyote had expanded its range to include nearly all of North and Central America (Parker 1995).

Coyotes were an original component of the native fauna of Michigan, though historically they occupied only the prairies and oak savannas of the southern Lower Peninsula (Baker 1983; Dice 1927). Coyote northward range expansion was initially limited by interference competition and direct killing of coyotes by wolves, although temporal resource partitioning may have allowed coyotes to co-exist with wolves (Berger and Gese 2007). Coyotes inhabiting southeastern Michigan may have been briefly extirpated, or at least reduced to low numbers by humans in the early part of the 19th century as industry and commerce grew in the region. By about 1850, coyotes from the Great Plains had extended into Michigan to re-occupy their historic range (Gier 1975). Extirpation of wolves from the Lower Peninsula (circa 1910; Beyer et al. 2009) allowed coyotes to utilize areas where they were previously outcompeted (Ballard et al. 2003). Coyote range expansion across Michigan was further facilitated by large-scale human disturbances (e.g., logging, farming) that created edge and seral stage vegetation that promoted the availability of communities of prey species across the landscape (Patterson

and Brown 1991). Range expansion and recent population growth (circa 1980; Frawley 2008) of coyotes in Michigan has led to their increased presence in urban environments including the greater Detroit area in southeastern Michigan. The recurrence of coyotes in Michigan and advent in northeastern North America has become a major wildlife management challenge, with extremely negative public perceptions of coyotes predominating in urban areas (Gompper 2002; Gehrt 2004).

Because coyotes have the ability to structure ecological communities through direct and indirect top-down effects, they may play a keystone role in maintaining biodiversity and ecosystem function (Crooks and Soulé 1999, Bekoff and Geese 2003). For example, predation of rodents by coyotes has been shown to promote overall biodiversity of rodents (Henke and Bryant 1999). Increases in recruitment of ground-nesting birds have also been attributed to coyote exclusion of meso-predators (Mezquida et al. 2006, Rogers and Caro 1998, Sovada et al. 1995; but see Gehrt and Clark 2003). In urban areas, coyotes may act as important bio-control agents limiting the population growth of overabundant nuisance wildlife such as Canada geese (*Branta canadensis*) (Brown 2007) and white-tailed deer (*Odocoileus virginianus* (Gehrt and Riley 2010; Piccolo et al. 2010). Despite coyotes' potential ecological and economic benefits, however, and regardless of the infrequency of adverse interactions with humans, coyote management will inevitably focus on human-coyote conflicts (Gompper 2002, Way et al. 2004, Gehrt and Riley 2010) as it has historically.

Although numerous studies of coyotes have been carried out in metropolitan areas in the western United States (e.g., Atkinson and Shackleton 1991, Quinn 1997, Grinder and Krausman 2001, McClennan et al. 2001, Tigas et al. 2002, Riley et al. 2003) only a

handful have been conducted in the East and Midwest (see Way et al. 2004, Atwood et al. 2004, Gehrt et al. 2009). How coyotes respond to urbanization in eastern and Midwestern cities is likely to be very different from western environments because the climatic conditions and plant and animal communities are dramatically different. Our poor understanding of the ecology of coyotes in eastern and Midwestern metropolitan areas makes it difficult for wildlife managers to make proactive decisions to mitigate coyote-human conflicts and for urban residents to form an educated opinion about the true risk associated with coyotes. Clearly, more knowledge of how coyotes have successfully adapted to urban environments in the eastern and Midwestern U.S. is needed to inform discussions of options and strategies to mitigate negative human-coyote interactions in urban areas.

As an attempt to gain a better understanding of how the coyote, a medium-sized carnivore, has adapted to and succeeded in the greater Detroit area of southeastern Michigan while remaining relatively unnoticed by humans, I gathered base-line ecological data on coyotes at different locations throughout the area. Specifically, I completed the following series of studies to: (1) determine how coyotes distribute themselves and use habitat across the urban landscape, (2) quantify coyote diets and foraging patterns, and (3) evaluate how coyotes use space and navigate the urban matrix.

In Chapter 1, I used a field survey for evidence of coyotes to determine how coyotes are distributed across the landscape, and a raster geographic information system (GIS) land cover layer of southeastern Michigan to quantify coyote occupancy of different land cover. Examining the distribution and habitat use of coyotes can be useful in establishing where interactions between coyotes and humans are likely to occur.

Knowing the whereabouts of coyotes living in close proximity to humans is important to avoiding and mitigating negative human-coyote interactions.

Chapter 2 was based on field studies conducted to determine if both coyote diets and prey availability varied between urban and suburban areas (urbanization level) or among important coyote biological periods and how this might affect coyote foraging patterns. Quantifying variation in the diet of coyotes and availability of prey are important for identifying periodically important prey and differences between urbanization levels in prey value. Examining the foraging patterns of coyotes is important to understanding their role as a top predator in urban environments and their potential to limit nuisance urban wildlife.

In Chapter 3, I incorporated field monitoring of radio-collared coyotes to examine use of space by coyotes. Using collected radio-telemetry data, I estimated the size and position across the landscape of coyote home ranges and core-use areas. I then used a raster geographic information system (GIS) land cover of southeastern Michigan to explore what effect urban land cover, and both fragmentation and connectivity of natural land cover, had on the home range and core-use areas of coyotes. Mapping the position of coyote core-use areas across the landscape can be used to identify habitats where important resources or aggregations of prey exist. Because of the coyotes' strong dependence on patches of natural habitat, it is important to understand how urban land cover and the contrasting landscape metrics of fragmentation and connectivity of natural land cover affect coyote space use patterns.

Collectively, these three chapters are unique because the information and data of which they are comprised is from the only field-based study of coyote ecology ever

conducted in a large metropolitan area in Michigan. The findings from this research provide a clearer picture of the ecology of coyotes in urban environments generally, and specifically in the greater Detroit area of southeastern Michigan. Understanding how coyotes respond to urbanization is an important component of efforts to manage human-coyote conflicts and to conserve urban coyotes. Dissemination of these chapters through publication in peer-reviewed journals will be useful to natural resource managers, municipal planning boards, educators, and other interested parties to help guide development and management plans to help reduce human-coyote conflicts and transform indiscriminant coyote removal and control into more ecologically justifiable coyote management.

CHAPTER 1: RECENT DISTRIBUTION OF COYOTES ACROSS AN URBAN LANDSCAPE IN SOUTHEASTERN MICHIGAN*

INTRODUCTION

Urbanization is known to fragment and/or destroy wildlife habitat and alter ecological processes that occur within it (McKinney 2002), and much of the ecological literature has focused on human encroachment and alteration of wildlife habitat. However, species classically adapted to edge habitat (e.g., white-tailed deer (*Odocoileus virginiana*)) and those that utilize human-associated food (e.g., raccoons (*Procyon lotor*)), for example, may benefit from inhabiting urban areas (Adams 2005). As such, understanding the distribution and habitat use by wildlife establishing or re-establishing in areas already populated by humans (Adams 2005) warrants additional investigation.

Coyotes (*Canis latrans*) have readily adapted to urban landscapes and have become a top carnivore in many major metropolitan areas in the last decade (Crooks and Soulé 1999; Gompper 2002; Gehrt 2004). A common result across most studies of coyotes in urban areas is that they typically avoid human activity by being nocturnal in human-dominated areas (e.g., Atkinson and Shackleton 1991; McClennen et al. 2001; Atwood et al. 2004), yet they are often active during the day in more rural or wilderness areas (Major and Sherburne 1987; Gese et al. 1989; Kitchen et al. 2000a). Studies of distribution and habitat use of coyotes in urban landscapes have provided mixed results, but coyotes are generally associated with green space (undeveloped land partly or completely covered with natural and/or naturalized trees, shrubs, grass, or other vegetation) within the urban matrix specifically for food, den sites, and diurnal resting

cover (Quinn 1997; Riley et al. 2003; Gehrt et al. 2009). Notably, some researchers have found coyote use of green space within urbanized landscapes to be less than expected based on its availability (Grinder and Krausman 2001), or that habitat was occupied regardless of the presence of humans (Gibeau 1998). Coyotes will readily move through residential and commercial areas, but they do so quickly, covertly, and usually at night to avoid humans (Grinder and Krausman 2001; Way et al. 2004; Gehrt et al. 2009). Most studies of coyotes in urban areas have been conducted in southwestern North America (e.g., Grinder and Krausman 2001; Riley et al. 2003; Grubbs and Krausman 2009) where coyotes were probably never completely extirpated from many metropolitan areas (Gehrt and Riley 2010). Coyote presence in Midwestern and eastern cities is more recent and less studied (see Way et al. 2004; Atwood et al. 2004; Gehrt et al. 2009), and likely poses a very different set of ecological and societal issues (Gompper 2002).

In Michigan, coyotes historically inhabited the prairies and oak savannas of the southern Lower Peninsula (Baker 1983; Dice 1927) because of the abundant prey species these habitats supported. Coyote populations within wolf (*Canis lupus*) range were limited by interference competition and direct killing of coyotes by wolves (Thurber and Peterson 1991; Peterson 1996; Berger and Gese 2007), although temporal resource partitioning may have allowed coyotes to co-exist with wolves (Berger and Gese 2007). Humans essentially eliminated coyotes from southeastern Michigan as the region developed into a major metropolis in the late 19th century. Coyotes from the Great Plains expanded into Michigan to re-occupy their historic range, as well as areas previously unoccupied, by the early 20th century. Human-associated disturbances facilitated coyote range expansion across Michigan by promoting the availability of communities of prey

species across the landscape (Patterson and Brown 1991). In addition, state-sponsored predator control programs that emphasized wolf removal allowed coyotes to utilize areas where they were previously outcompeted (Ballard et al. 2003). Range expansion and population growth of coyotes in Michigan since 1980 (Frawley 2008) has led to their increased presence in urban environments including the counties surrounding the metropolitan Detroit area in southeastern Michigan. The recurrence and range expansion of coyotes in Michigan and appearance in northeastern North America in general has become a major wildlife management challenge, with extremely negative public perceptions of coyotes predominating in urban areas (Gompper 2002; Gehrt 2004). For example, homeowners in the Greater Chicago Metropolitan Area rated coyotes highest among nuisance wildlife species perceived to pose the greatest threats to human health and safety (Miller et al. 2001).

Coyotes can significantly impact the abundance and community structure of flora and fauna through direct and indirect top-down effects. Coyote exclusion or predation of mesocarnivores (Rogers and Caro 1998; Sovada et al. 1995) and predation on small rodents (Henke and Bryant 1999), feral domestic cats (Crooks and Soulé 1999), and overabundant urban wildlife (e.g., white-tailed deer fawns (Gehrt and Riley 2010)) can have both ecological and economic benefits despite a largely negative public perception of coyotes. Understanding coyote distribution and habitat use in urban areas is therefore important for providing the most basic data describing how coyotes behave in close proximity with humans (Way et al. 2004). We examined the distribution of coyote evidence in metropolitan Detroit to address: (1) What habitats do coyotes utilize in a human-modified landscape? and (2) How do coyotes distribute themselves with respect

to the arrangement of land cover? We predicted that coyote evidence would more likely be found in areas with a greater proportion of green space and less urban land cover regardless of the degree of human development.

STUDY AREA

The greater Detroit area of southeastern Michigan encompasses portions of Livingston, Macomb, Oakland, Washtenaw, and Wayne counties, an area of approximately 8,600 km^2 (Figure 1.1), with a human population of approximately 4.5 million (SEMCOG 2010). In its urban core (the area where anthropogenic development and activity is greatest, impervious surfaces predominate, and green space is lacking ;Gehrt 2010), human population density of metropolitan Detroit is nearly five times greater than in the surrounding suburbs (Table 1.1). Land use in the urban core is primarily residential, commercial, industrial, and transportation oriented, with parks, recreation areas, and other green space representing only a small proportion of the landscape. In the suburbs, land use is predominately residential and agricultural (Table 1.1).

Within the urban core existing areas of natural and naturalized vegetation are extremely fragmented; most are highly altered river floodplains dominated by grassy areas and eastern cottonwood (*Populus deltoides*), or abandoned lots and old farmland dominated by non-native grasses and forbs. Forest remnants are more common in suburban areas, and are often second-growth woodlots dominated by oak (*Quercus* spp.), elm (*Ulmus* spp.), or other tree species that have become established with the reversion of former agricultural lands to more natural conditions. The urban core in the region has lost
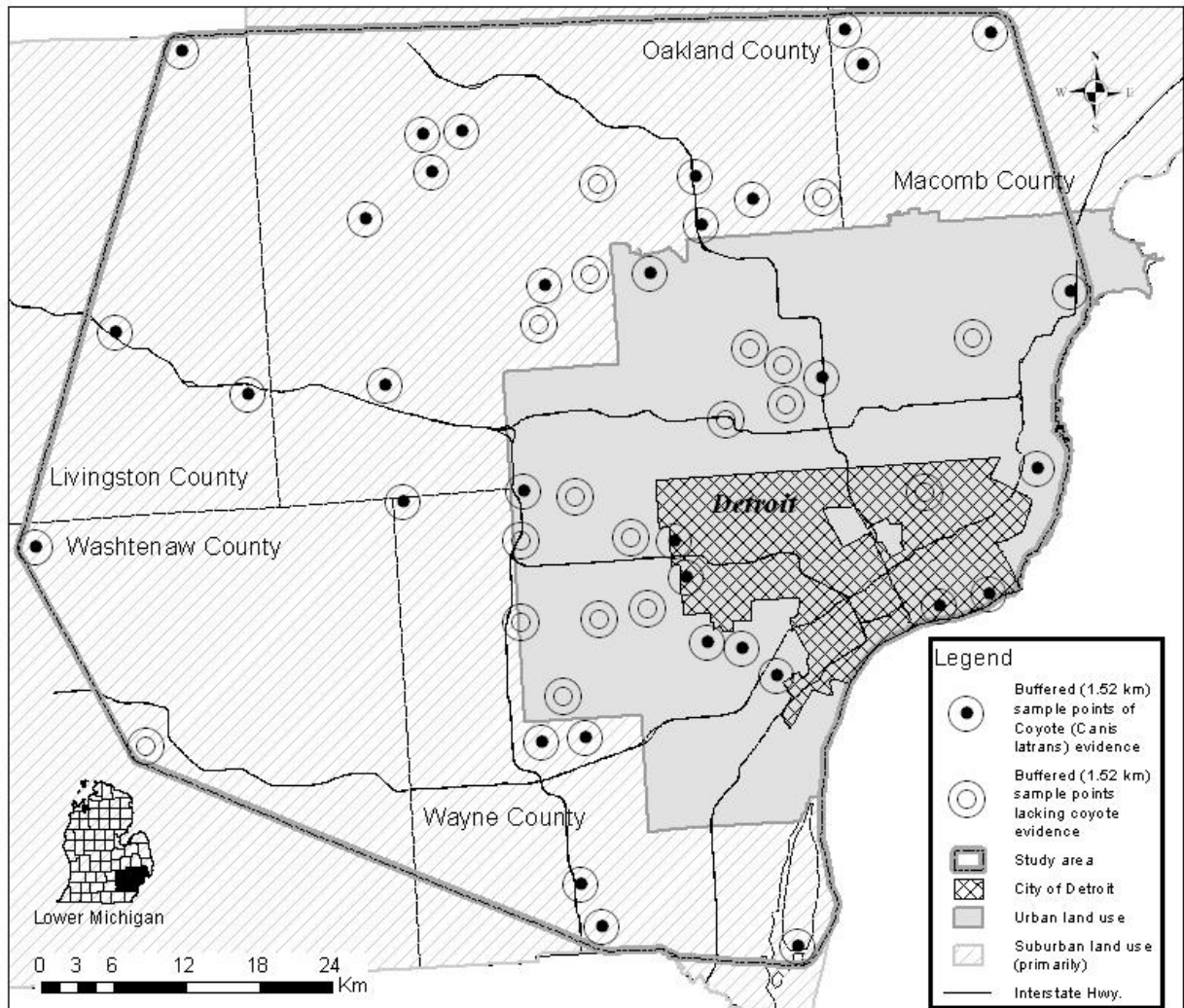
Figure 1.1. Sample points of coyote (*Canis latrans*) evidence at 34 locations (urban: n=12; suburban: n=22) and sample points lacking coyote evidence at 18 locations (urban: n=13; suburban: n=5) sampled between May-September 2009 and June-December 2010 in the Detroit, Michigan metropolitan area. Rings around each sample point signify 1.52-km radius buffers encircling each location.

Table 1.1 Comparison of urban and suburban land use in the Detroit, Michigan metropolitan area between 2009 and 2010. Data and land use classes are summarized from SEMCOG (2010).

Characteristic	Urban	Suburban
Area (km^2)	1815	6662
Human population density (people/km^2)	1500	280
Percent residential	47	48
Percent commercial/industrial/governmental	24	11
Percent transportation/communication/utility	24	7
Percent parks/recreation/open space	5	9
Percent agricultural	0	22

about 270,000 people to net out-migration since 2000, while 80% of suburban communities situated along the urban boundary have grown in population

METHODS

Field Survey

We performed an extensive survey of urban and suburban areas in metropolitan Detroit for coyote evidence (i.e., carcasses, den sites, scats, sightings, or tracks). Exurban areas, defined as the semi-rural region beyond the suburbs, characterized by low density, large-lot (> 0.02 km^2 per unit) development (Daniels 1999) were classified as "suburban"for this analysis. Urban areas were defined as having housing density > 500 units/km^2 and human population density > 1000 people/km^2. We divided the five-county area of southeastern Michigan into 64.0 km^2 square plots (n = 163), which approximates the annual home range size of transient urban coyotes (Gehrt and Riley 2010), and randomly selected 25% of these plots (n = 41) for surveying. We visited 37 plots during May – September 2009 and 4 plots during June – December 2010. Because coyotes are generally associated with patches of natural vegetation in developed areas (Gehrt and Riley 2010; Riley et al. 2003; Quinn 1997) our survey efforts focused upon state, metro,

county, city, and local parks, golf courses, abandoned industrial and residential sites, and undeveloped lots in each plot. We used unpaved trails (i.e., hiking, biking, horse), unimproved roads, margins of roadways, paved trails, railroad beds, and utility rights-of-way as primary survey transects with start points randomized along these features, based on documented coyote propensity to travel and defecate along these features (Macdonald 1980). Field reconnaissance was based on communication with local organizations in the area (e.g., police stations, animal control centers, nature centers, and local and regional newspapers) for evidence and published articles on coyote sightings, control efforts, and attacks on pets in the last decade. We attempted to survey all patches of natural and/or naturalized vegetation (both grassland and woodland) within each plot. Universe Transverse Mercator (UTM) coordinates were recorded with a hand-held global positioning system (GPS) unit whenever coyote evidence was encountered. We also recorded UTM coordinates at the approximate centroid of areas searched where no evidence of coyotes was found.

Coyote scat was differentiated from that of other canids and raccoons by size, shape, content, and nearby sign (e.g., coyote tracks) if present (Murie 1935). Canid scat < 19-mm in diameter is difficult to distinguish between coyote, red fox (*Vulpes vulpes*; Green and Flinders 1981), or gray fox (*Urocyon cinereoargenteus*; Danner and Dodd 1982) and was excluded from our analysis. Contrasting dietary characteristics in this region make scat of raccoon, medium-sized domestic dog (*Canis familiaris*), and coyote distinguishable. Coyote scat tends to be ropelike with tapered ends and often contains large amounts of fur, bones, and teeth (Rezendes 1999). Comparatively, domestic dog scat often occurs as amorphous piles or blunt-ended tubes, is foul-smelling, and rarely

contains wild prey. Similar to coyote scat, raccoon scat often contains the remains of insects, grains, or fruit seeds due to its omnivorous diet, but rarely does it contain mammal hair. Because coyotes also consume fruit and other plant material, scat that contained only fruit was not collected unless other strong coyote evidence was nearby. For each coyote scat we recorded the maximum diameter, verifying evidence (size, shape, content, and nearby tracks), primary content, and the habitat type in which it was found.

Coyote tracks were separated from other canid tracks by size, shape, trail pattern, and other diagnostic characteristics. Paw impressions measured with a tape measure to the nearest 0.1 cm that fell within $5.7 - 8.3$ cm L x $3.8 - 6.4$ cm W (front) and $5.4 - 7.6$ cm L x $2.9 - 5.1$ cm W (rear) with trail width (straddle) > 10.2 cm and stride > 27.9 cm (Elbroch 2003) were used to differentiate coyote from fox and small domestic dog. Compared to domestic dogs, individual coyote tracks tend to be much neater, register at an angle rather than flat (i.e. the palm pad is on a much higher plane than the digit pads), the claws are sharp and pointed rather than thick and blunt, and in coyotes the leading claws (toes three and four) often register close together and point toward each other (Elbroch 2003). Trails of coyotes are also much cleaner, straighter, narrower, and their tracks direct register (i.e., the rear foot is placed exactly where the front foot had been) much more often than most domestic dogs (Rezendes 1999). Entrance holes > 33.0 cm in diameter with conspicuous throw mounds of dirt and evidence of prey and scat nearby were considered to be coyote dens (Elbroch 2003).

Evaluation of Land Cover

Coyote occupancy of different land cover was calculated using a raster geographic information system (GIS) land cover types distribution layer of Southeastern Michigan (SE Michigan Land Cover 2002; Center for Geographic Information, Michigan Department of Information Technology, Lansing, MI) consisting of three categories: urban, open space with grass and scattered trees (hereafter "grassland"), and wooded areas. These categories were selected to encompass a gradient of habitat cover across urban and suburban areas. Locations were buffered within the GIS with a 1.52-km radius circle, derived from the grand mean of estimates of annual home range size (7.3 km^2) of urban coyotes across seven studies reviewed by Gehrt (2007). To ensure that locations could be considered independent, locations whose buffers partially overlapped were removed from the analysis. When the choice between buffers to keep was ambiguous, buffers retained were those that encompassed the greatest number of evidence locations, were furthest apart if there were an equal number of locations within the buffers, and were selected to preserve the greatest total number of sample points. The study area boundary was defined by creating a minimum convex polygon using all locations and buffering the polygon with a 1.52-km buffer.

Land cover types contained within buffered locations of coyote evidence were summarized across the entire study area and by development class (suburban and urban) to determine habitat occupancy in the region. A chi-square goodness-of-fit test was used to compare the observed proportion of land cover categories within buffered locations of coyote evidence to their expected proportion calculated from the proportion of land cover across the greater study area. Chi-square analyses were performed by development class

and for the pooled data set to determine whether coyotes were selective in their use of land cover categories or whether they were located across the categories at random. We used percent deviation as a measure of the degree to which the observed proportion of each land cover category differed from the proportion expected for a random distribution. A positive percent deviation indicates that the observed frequency is greater than expected, while a negative percent deviation indicates that the observed frequency is smaller than expected.

RESULTS

We recorded evidence of coyotes on 24 of 30 (80%) suburban and 7 of 11 (64%) urban plots. Evidence included three road-kills, two den sites, eight groups of tracks, four sightings, and 285 scats. Coyote evidence was ubiquitous, but appeared more widespread across suburban plots than in the urban core, where it was more locally distributed. Coyote evidence in the urban core averaged 28 locations per plot compared to < 5 locations per plot in suburban plots, although it remains unclear whether these locations represent the same individuals or multiple coyotes. Using our criteria for considering locations to be independent, we identified 34 locations (12 urban, 22 suburban) where coyote evidence was present (Figure 1.1).

Across the study area, coyote evidence was found primarily on unpaved trails and unimproved roads within wooded areas or open grasslands often within 15 m of other land cover (i.e., edge habitat). Fifty-eight percent of independent locations of coyote evidence were found in edge habitat (Table 1.2). Den sites and tracks were the only types of evidence found strictly in non-edge habitats. All road-killed coyotes were found on interstate or state highways bordered by grasslands interspersed with shrubs and/or small

Table 1.2. Land cover and adjacent land cover within 15 m of independent 1.52 km buffered locations of coyote (*Canis latrans*) evidence in the Detroit metropolitan area, May-September 2009 and June-December 2010. Records lacking adjacent land cover are those located in non-edge habitat. "%" represents the percentage of the land cover/adjacent land cover combination within a given evidence type.

Coyote evidence				
Type	*n*	Land cover[a]	Adjacent land cover[a]	%
Road-kill	3	Urban	Grassland	100
Scat	2	Grassland	-	7
Scat	3	Grassland	Trees	11
Scat	1	Grassland	Urban	4
Scat	5	Trees	-	18
Scat	6	Trees	Grassland	21
Scat	2	Trees	Urban	7
Scat	4	Urban	-	14
Scat	5	Urban	Grassland	18
Tracks	1	Grassland	-	50
Tracks	1	Trees	-	50
Visual	1	Grassland	-	100

[a]Urban includes both urban and urban/bare soil land cover categories.

diameter trees. We observed extremely heavy concentrations of scat along a 4.5 km length of a heavily industrialized, channelized portion of the Rouge River within the urban core in Wayne County. Habitat directly adjacent to the edge created by the concrete channel consisted mostly of grassland (~32.0 m wide) and/or small irregularly-shaped wooded patches. Scats found in non-edge habitat were more often located in woodland patches (43%) compared to grassland or urban (each 29%) patches. Observations of live coyotes (4) in this study occurred in open areas (grassland or agriculture).

Land cover within the buffer around coyote evidence was occupied differently than expected across the entire study area ($\chi^2 = 3,121.2$, p < 0.0001; Table 1.3, Figure 1.2A). Compared to the greater study area, buffer areas around coyote evidence included higher than expected wooded and grassland land cover, but less urban cover (Table 1.3).

Table 1.3. Percent deviation and calculated χ^2 value for observed and expected (based on availability) proportion of land cover surrounding locations of coyote (*Canis latrans*) evidence in the Detroit metropolitan area, May-September 2009 and June-Dec 2010. A positive percent deviation signifies a higher proportion of the landscape in that category than expected at random. $P < 0.0001$ for all χ^2 values.

Land cover category	Study Area	Suburban	Urban
Grassland	+ 3.9	- 0.8	+ 42.2
Wooded	+ 18.1	+ 16.3	+ 31.7
Urban	- 12.9	- 17.0	- 10.8
χ^2	3,121.2	2,190.0	2,342.4

Specific to suburban areas, buffered areas included more wooded and less urban land cover than expected ($\chi^2 = 2190.0$, $p < 0.0001$; Table 1.3, Figure 1.2B). In urban areas, buffered areas included more wooded areas than the greater study area, as well as more grassland than expected, but less urban land cover ($\chi^2 = 2342.4$, $p < 0.0001$; Table 1.3, Figure 1.2C). Land cover surrounding areas where no evidence of coyotes was found differed from the expected amounts of land cover types across the study area ($\chi^2 = 16,012.4$, $p < 0.0001$) as well as in suburban ($\chi^2 = 2,248.9$, $p < 0.0001$) and urban areas ($\chi^2 = 323.2$; $p < 0.0001$).

DISCUSSION

Coyotes are common in both urban and suburban areas in southeastern Michigan. Coyote evidence was found in nearly all environmental settings examined in this study, including urban areas within and near the city limits of Detroit, suburban areas within neighborhoods and on the grounds of major corporations (including Ford Motor Company's World Headquarters in central Wayne County), parks and green space within the urban-suburban matrix, and rural or exurban areas in outlying counties (Figure 1.1).

Notably, coyote presence was not always predictable, as many locations within

(A)

(B)

(C)
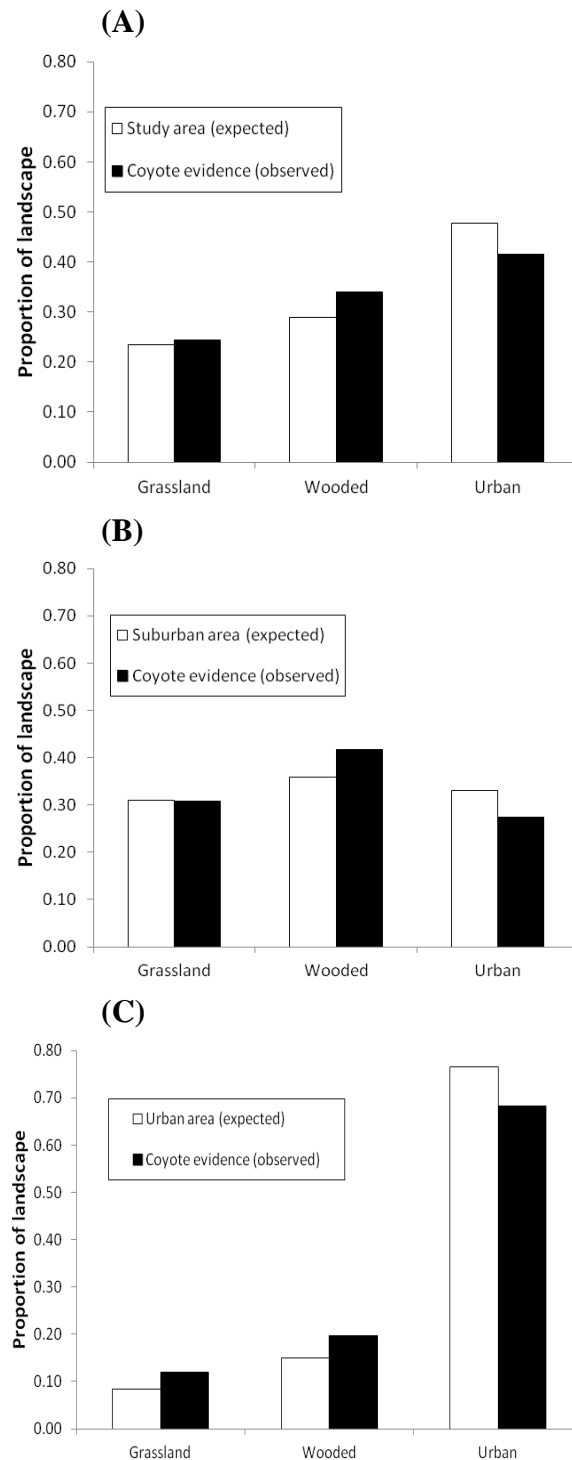
Figure 1.2. Observed proportion of land-cover types contained within buffers (1.52-km radius) of independent locations of coyote (*Canis latrans*) evidence compared to their expected proportion for (A) the greater study area, (B) suburban and (C) urban portions of the study area in the Detroit Michigan metropolitan area, May - September 2009 and June - December 2010.

the types of habitat described above contained no coyote evidence. Coyote evidence was repeatedly found in clusters, to the extent that locations in close proximity were considered to be non-independent for the purposes of statistical analysis of habitat occupancy. Genetic analysis of DNA isolated from coyote scat would clarify whether these clustered locations of coyote evidence represent transient and/or nomadic, solitary individuals, or whether we have documented resident, territorial family groups, or resident populations, and should be employed in future research. DNA analysis could also be used to unambiguously differentiate coyote scat from other sympatric carnivores (Foran et al. 1997), obtain short-term coyote population estimates (Kohn et al. 1999), and monitor long-term population dynamics of coyotes (Prugh et al. 2005) in southeastern Michigan.

The observed proportion of urban land cover surrounding coyote evidence was less than expected across the pooled study area as well as in urban and suburban areas individually (Table 1.3), consistent with other studies that show coyotes avoid more developed areas regardless of whether they are found in urban or suburban environments (e.g., Quinn 1997; Tigas et al. 2002; Gehrt et al. 2009). Landscape composition surrounding locations of coyote evidence across the study area suggests that availability and access to habitat with cover – particularly areas with trees – appears to be more important to coyotes than the presence of open space or undeveloped areas. Although coyote evidence in the field was rarely located within interior wooded areas, cover habitat provided by wooded areas is likely important for den and rendezvous sites especially in human-dominated landscapes where coyotes can avoid and remain hidden from humans except when traveling (Grinder and Krausman 2001; Way et al. 2004; Gehrt et al. 2009).

Wooded land cover was also a major component of buffer areas in both urban and suburban settings (Figures 1.2B, 1.2C). Coyote occupancy was less common in urban and open areas compared to wooded land cover and undeveloped woodlots, presumably because of the tree cover they provide, but also probably because of abundant prey available near the edges of wooded areas. The propensity for coyotes to remain near wooded areas may be one explanation for the ability of urban coyotes to avoid humans despite their prevalence in heavily-populated areas (Riley et al. 2003; George and Crooks 2006; Gehrt et al. 2009).

Land cover surrounding locations where no coyote evidence was found consisted of a greater proportion of urban and lesser proportions of wooded areas and grasslands than expected across both the pooled study area and in suburban areas. This outcome appears to support the importance of cover habitat for coyotes and their avoidance of urban areas. The outcome was more ambiguous in urban areas where the observed proportion of wooded land cover surrounding non-evidence points was greater than expected, with grassland and urban land cover occurring less than expected. Our field sampling may have been biased against finding coyote evidence in heavily urban land cover because of our focus on green space within the urban matrix, and studies tracking the movement of individual coyotes in urban environments are clearly necessary to discern where urban coyotes allocate their time.

Habitat patches in urban areas were generally smaller, more isolated and fragmented, and consisted of more non-native plant species than those in suburban areas. Competition for limited high quality habitat, particularly in urban areas, may force subordinate coyotes into more marginal habitats with a greater proportion of urban land

cover and less wooded areas and grasslands. Coyotes have naturally re-colonized the most urbanized and human-modified landscapes in the Detroit metropolitan area, probably in part due to the recent economic decline in southeastern Michigan that has resulted in the reversion of many sites into naturalized areas that are often utilized by wildlife. Like many urban areas, however, metro Detroit has long been interspersed with numerous parks, golf courses, highway interchanges, and other human-created green spaces that provide habitat for coyotes. Based on this historical land coverage alone, we speculate that coyotes were probably never limited by habitat in southeastern Michigan. The fact that coyote abundance in the region was increasing even during the height of land development in the late 1990s supports the assertion that habitat was not likely limiting. Although human-associated foods are available in urban areas, coyote diets are typically dominated by food items associated with natural areas (Morey et al. 2007; W. B. Dodge, Wayne State University, unpublished data) and human-associated foods are therefore not likely to be a primary driver of the distribution of coyotes in metro Detroit. Rather, we speculate that re-occupation of southeastern Michigan by coyotes likely occurred as a consequence of an expanding coyote population and increased competition for limited space in outlying rural and exurban areas. An accurate estimation of the coyote population is necessary to determine if current population levels in southeastern Michigan have stabilized or if coyotes will continue to expand into suburbs and cities of the area to fill unoccupied habitat.

Increased coyote abundance in southeastern Michigan may have implications from both an ecological and economic perspective. Notably, coyote presence in the Detroit area and elsewhere in Midwestern and eastern North American metropolitan areas

represents the range expansion of a native species rather than invasion of an exotic species (Gompper 2002), and thus is an important conservation issue. From a utilitarian perspective, coyotes have the potential to play a keystone role in limiting the population growth of nuisance urban wildlife. For example, coyote predation in Chicago has been considered as an important bio-control limiting the population growth rate of Canada geese (*Branta canadensis* L.; Brown 2007); reducing the growth rate of high-density urban white-tailed deer populations through predation of fawns (Gehrt and Riley 2010); and limiting the abundance of small rodents (e.g., voles (*Microtus* spp.) and mice (*Peromyscus* spp.)), which most often make up the bulk of coyote diets in urban and suburban areas (Morey et al. 2007). In rural Texas, experimental removal of coyotes to protect sheep resulted in a dramatic increase in rodent abundance and decrease in rodent diversity (Henke and Bryant 1999); coyotes may serve a similar ecological role in urban and suburban areas.

Despite the potential positive aspects of urban-dwelling coyotes, the focus of coyote management in urban areas will inevitably be on human-coyote conflicts (Gompper 2002; Way et al. 2004; Gehrt and Riley 2010) as it has been historically. The challenge for wildlife managers in urban landscapes is balancing the needs of coyotes and their coexistence with humans with preventing and mitigating conflicts with humans, typically through removal. Coyote reduction has already been a focal point for several communities in metropolitan Detroit as a response to predation on small pets (Cravens, J., City Manager, Bloomfield Hills, personal communication) and game species. Coyote populations compensate for reductions in numbers by increases in rates of immigration, reproduction, and survival of the remaining individuals, resulting in maintenance of

coyote populations in a perpetual state of colonization (Crabtree and Sheldon 1999; Knowlton et al. 1999). Efforts to reduce coyote numbers are unlikely to be effective unless >70% of the individuals in a population are continually removed on an annual basis (Connolly 1995; Connolly and Longhurst 1975) across a large geographic region (Gompper 2002). We suggest that coyotes have minimal negative impact on humans and that indiscriminant lethal control is likely to be counterproductive, given the benefits of coyote presence in urban areas (especially the reduction of undesirable prey species). Moreover, we believe the goal of coyote management in urban areas such as metropolitan Detroit should be human-coyote coexistence, as the ecosystem services provided by coyotes may increase human well-being and overall environmental quality.

CHAPTER 2: ANALYSIS OF COYOTE DIETS AND FORAGING PATTERNS IN THE GREATER DETROIT AREA OF SOUTHEASTERN MICHIGAN

INTRODUCTION

Understanding the diet and foraging patterns of coyotes (*Canis latrans*) is fundamental to determining their role as a top predator and gaining insight into the dynamics of human-coyote conflicts in urban landscapes. Coyote attacks on human companion animals, particularly small domestic dogs (*C. lupus familiaris*), are a major societal and wildlife management challenge in developed areas (Gehrt and Riley 2010). Although extremely rare, coyote attacks generate sensational media coverage that often creates a public perception of increased risk (Riley and Decker 2000). Coyote habituation to humans typically through positive food conditioning is often a precursor to coyote loss of fear and aggression towards humans (Curtis and Hadidian 2010; Timm et al. 2004). Even with access to anthropogenic food sources (Gill and Bonnett 1973) however, coyotes inhabiting developed environments typically consume natural foods (Atkinson and Shackleton 1991, Quinn 1997, Fedriani et al. 2001, Morey et al. 2007). This diet reflects the coyotes' dependency on green space (undeveloped land partly or completely covered with natural and/or naturalized trees, shrubs, grass, or other vegetation) within the urban matrix (Quinn 1997; Riley et al. 2003; Gehrt et al. 2009; Dodge and Kashian 2013). In contrast, several studies have suggested that coyotes nearest urban centers tend to have diets containing a greater proportion of human-associated foods than those inhabiting exurban or suburban areas (Quinn 1997, Fedriani et al. 2001, Morey et al. 2007). Despite greater acceptance of urbanization, however, coyotes largely restrict foraging to nocturnal hours and disappear in wooded cover during the daytime in human-

dominated areas (e.g., Atkinson and Shackleton 1991; McClennen et al. 2001; Atwood et al. 2004; Dodge and Kashian 2013). Refraining from daytime activity appears to be an adaptation for avoiding humans because coyotes in natural, undisturbed areas are often most active during daylight hours (Gese et al. 1996, Kitchen et al. 2000a) and evidence indicates that coyote vision is best adapted to diurnal and crepuscular activity (Ramous and Kavanaugh 1975).

Traditionally, coyotes have been considered an archetypal example of an opportunistic, generalist predator because they have a broad food niche and consume prey in proportion to local and seasonal availability (Young and Jackson 1951, Bekoff 1978, Van Vuren and Thompson 1982, Sacks and Neale 2002). Prey switching, whereby a predator increases selection of a prey species when it is abundant and decreases selection when it is scarce, is a foraging strategy commonly associated with generalist predators (Murdoch 1969, van Baalen et al. 2001). Research in urban areas mostly supports these characterizations with both spatial and temporal variation in the occurrence of prey items in coyote diets (Atkinson and Shackleton 1991, Quinn 1997, Fedriani et al. 2001, Morey et al. 2007). Studies outside urban areas (e.g., O'Donoghue et al. 1998, Prugh 2005), however, have found coyotes to be selective predators whose foraging patterns show strong synchrony with fluctuations in snowshoe hare (*Lepus americanus*) populations (in terms of handling time, medium-sized lagomorphs are the coyote's most profitable prey; Bekoff and Wells 1986, MacCracken and Hansen 1987).

Optimal foraging theory predicts that the most energetically profitable prey will be consumed disproportionately (i.e., selectively) to availability and that feeding on less profitable prey will occur on a continuum of decreasing profitability only when the

density of the most profitable prey drops below some critical threshold (Charnov 1976, Krebs 1978). Predator foraging patterns and the rate at which they encounter prey are defined by the inherent spatial heterogeneity in prey distribution (Hansson 1989, Prugh 2005, Kauffman 2007). Widespread alteration of the spatial structure of landscapes in developed areas has dramatically changed prey aggregation patterns (Fortin et al. 2015) and hence predator foraging patterns. Outcomes from different landscapes indicate that coyotes are not strictly generalist predators that consume prey in proportion to availability, but often specialize on the most profitable prey depending on ecological conditions (Prugh 2005). Predators inhabiting landscapes where prey is spread across large, contiguous habitat patches (e.g., wilderness, rural, and to a much lesser extent suburban areas) should specialize on the most profitable prey (MacArthur and Pianka 1966). In contrast, on highly fragmented landscapes (e.g., urban) where prey are distributed in habitat patches that are small relative to the area searched during foraging, predators will feed opportunistically on the most abundant prey.

I examined coyote diets and foraging patterns in the greater Detroit area of Michigan to determine if coyotes preferentially select particular prey (i.e., forage optimally) or switch to the most available alternative prey (i.e., forage opportunistically). I specifically addressed the following questions:

1) How does coyote diet vary with level of urbanization and among important coyote biological periods in a large metropolitan area?

2) Does the density and biomass of the primary prey of coyotes within a large metropolitan area vary with level of urbanization and across biological periods?

3) How does variation in availability of prey biomass affect the foraging patterns of coyotes across a large metropolitan area?

I hypothesize that the diets of coyotes residing in urban areas will reflect an opportunistic foraging strategy, whereas those in less developed suburban areas will exhibit an optimal foraging strategy, preying specifically on eastern cottontail rabbit (*Sylvilagus floridanus*), the only lagomorph present in the greater Detroit area. Although numerous studies examining coyote diets have been conducted in developed areas, no studies have closely examined coyote foraging patterns in relation to different levels of urbanization in a large metropolitan area.

STUDY AREA

The greater Detroit area of southeastern Michigan encompasses portions of Livingston, Macomb, Oakland, Washtenaw, and Wayne counties, an area of approximately 8,600 km^2, with a human population of approximately 4.5 million (SEMCOG 2010). In its urban core (the area where anthropogenic development and activity is greatest, impervious surfaces predominate, and green space is lacking (Gehrt 2010)). Land use in the urban core is primarily residential, commercial, industrial, and transportation oriented, with parks, recreation areas, and other green space representing only a small proportion of the landscape. In the suburbs, land use is predominately residential and agricultural.

Within the urban core existing areas of natural and naturalized vegetation are extremely fragmented; most are highly altered river floodplains dominated by grassy areas and eastern cottonwood (*Populus deltoides*), or abandoned lots and old farmland dominated by non-native grasses and forbs. Forest remnants are more common in

suburban areas, and are often second-growth woodlots dominated by oak (*Quercus* spp.), elm (*Ulmus* spp.), or other tree species that have become established with the reversion of former agricultural lands to more natural conditions.

METHODS

Coyote diet

Coyote diet was assessed through identification of remains of food items (e.g., claws, fur, teeth, seeds) recovered in coyote scat collected along 12 pre-determined routes ranging in length from 5.60 – 7.60 km ($\bar{x}$ = 6.38 ± 0.19 SE) located in urban and suburban landscapes in the greater Detroit area. Relative urbanization level was quantified by land cover and mean road, housing, and human population density within a 64.0 km^2 areal area (the approximate annual home range size of transient urban coyotes; Gehrt and Riley 2010) encircling GPS locations of coyote scat collected along sampling routes (Table 2.1). Sampling routes were established along hiking/biking trails, dirt roads, road margins, and other linear features where coyote activity had been previously documented (Dodge and Kashian 2013). Sampling routes were initially cleared of all scats and subsequently traversed at approximately 5-week intervals. I used content, shape, size, and nearby sign when present to distinguish coyote scat from that of other urban carnivores (Murie 1935, Elbroch 2003). Because coyote, red fox (*Vulpes vulpes*), and grey fox (*Urocyon cinereoargenteus*) scat are difficult to differentiate based on content alone and may overlap in size, scats < 19-mm in diameter (the maximum diameter of fox scat; Elbroch 2003) were excluded from my analysis. To detect seasonal dietary differences, as recommended by Trites and Joy (2005), I collected 20 to 30 scats during the coyote breeding-gestation (Jan 1 – Apr 30), pup-rearing (May 1 – Aug 31),

Table 2.1 Land cover (%), and mean road (km/km²), housing (units/km²), and human population density (persons/km²) within a 64.0 km² areal area surrounding GPS locations of coyote scat collected along sampling routes in the greater Detroit area of southeastern Michigan. Road densities were determined from data downloaded from the State of Michigan Geographic data library. Human population and housing data derived from USGS TIGER line files and U.S. census data (U.S. Census Bureau 2012). Land cover determined from a land cover distribution layer of Southeastern Michigan (SE Michigan Land Cover 2002).

Site	Density (n/km²)			Land cover (%)				
	Human	Housing	Road	Urban	Grassland[a]	Scrub-Shrub	Wetland	Woodland
Urban	1195.6	529.5	9.0	64.3	12.7	0.4	5.2	13.6
Suburban	317.4	138.3	3.2	24.5	18.6	2.1	14.9	28.8

[a] Includes agricultural fields

and dispersal (Sep 1 – Dec 31) periods (adapted from Laundre and Keller 1981). Scats used for analysis were randomly selected in equal numbers from samples collected along each survey route then collectively segregated by biological period within urban and suburban locations.

Dried scat samples were placed individually in nylon stockings along with uniquely colored plastic disks and soaked in soapy water for 24 – 48 hours. Scats were then cleansed and rinsed through a 0.05-mm mesh sieve to remove the water soluble waste and retain the partially digested and undigested remains. Cleansed scats typically consisted of large amounts of fur intertwined with bones, teeth, and claws which were hand separated, oven dried at 60°C for two hours, and weighed to the nearest 0.10 g. Bones, claws, and teeth of mammals were identified using skeletons assembled from Wayne State University's Museum of Natural History collection, road-killed specimens, and identification manuals (Jones and Manning 1992). Plant material was identified macroscopically using a reference collection of seeds and fruits, and insects by exoskeleton remains. I created a microscopic slide reference collection of fur of potential mammalian prey that was used in conjunction with identification guides to identify fur recovered in scats (Moore et al. 1997). Fur was evenly spread over a square transparent reference grid consisting of 16 quadrants and individual hairs were chosen from the center of 10 randomly selected quadrants for identification. Fur size (length and coarseness), color, and banding pattern, presence/absence of a shield, and medulla and cuticle scale patterns were used to identify fur to species whenever possible (Moore et al. 1997). Fur identified as vole (*Microtus* spp.) and mice (*Peromyscus* spp.) were combined for statistical analysis.

Prevalence of prey items in coyote diets were examined using the calculation developed by Prugh (2005) for percent weighted occurrence:

$$\%\mathbf{WO}_i = \sum_{s}^{S} \mathbf{X}_{is}\, \mathbf{Z}_{is} \bigg/ \sum_{i}^{I} \mathbf{XZ},$$

where X_{is} = occurrence of prey i in scat s and Z_{is} = weighted proportion of prey i in scat s, divided by the total weighted occurrence of all prey items in the diet. The weighting factor (Z) scaled from 1 to 5 is based on the relative proportion of prey items found in scats, where, 1 = < 2%, 2 = 2 - 25%, 3 = 26 - 50%, 4 = 51 - 75%, and 5 = 76 - 100%. Proportional estimates of prey based on bones, claws, and teeth were made visually; those from fur were calculated by dividing the number of hairs of an identified prey species by 10.

Prey with a body mass of 10 to 108 g (the weight below which Weaver and Hoffman (1979) estimated detection of prey remains in coyote scat equaled consumption), were classified as small prey, rat- (*Rattus norvegicus;* 140 g minimum) to raccoon-sized (10,000 g maximum) mammals medium-sized prey, and white-tailed deer (> 16,000 g) large prey. Deer fur recovered in coyote scats collected during the neonatal white-tailed deer postpartum period (May – August), when deer are most vulnerable to coyote predation (Duquette et al. 2014, Vreeland et al. 2004, Ballard et al. 1999) was considered to be remains of neonates or older fawns. I assumed that small- and medium-sized prey was completely consumed, neonate and older fawn white-tailed deer 90% consumed, and adult white-tailed deer 80% (Patterson et al. 1998).

The number of small prey ($N_{prey\ i}$) in scats was estimated by:

$$N_{prey_i} = \sum_{s}^{S} W_s P_{is} \Big/ Y_i,$$

where W_s = dry weight of scat s, P_{is} = proportion of fur of species i in scat s, Y_i = average dry weight of fur of species i determined using the regression equation: $Y_i = 0.1541 + 0.0195X_i$ (where X_i = average body weight of species i) developed by Gamberg and Atkinson (1988). In instances where fur of small prey was unavailable (~20% of samples) I used diagnostic parts (mostly incisors and molars) that provided the highest count (Murie 1935). Remains of medium- and large-sized prey found in coyote scat were recorded as a single individual regardless if multiple items were recovered.

Biomass estimates of mammalian prey consumed by coyotes were calculated by multiplying counts of prey species recovered in scat by the mean body mass of the respective prey species. Mean body mass of small rodents was calculated from my trapping data (see below), and that of other species obtained from the literature (eastern cottontail rabbit, 1,120 g; Hunt et al. 2013, white-tailed deer (adult), 46,100 g; Robbins et al. 1974, white-tailed deer (neonate and older fawns), 31,100; Watkins et al. 1991, other mammals; Kurta 1995). I used different mean body mass values for biomass calculations of small rodents captured at urban ($\bar{x} = 20.92 \pm 0.34$) and suburban ($\bar{x} = 19.13 \pm 0.25$) sites because the values differed significantly ($t = 4.15$, $df = 1049$, $P < 0.001$). Biomass estimates of small- and medium-sized prey were adjusted downward by 3% to account for undigested fur. White-tailed deer biomass estimates were also reduced by 20% to account for partial consumption of deer carcasses. Relative proportion of consumed biomass within biological period was calculated by dividing site-averaged consumed

biomass of each prey species by the sum of consumed biomass of all prey species within the site.

I tested differences in relative proportion of consumed biomass of prey between urbanization level and among biological periods with a repeated-measures PERMANOVA based on Bray-Curtis dissimilarities (Anderson et al. 2008), using PRIMER-6 software (Clark and Gorley 2006), with urbanization level as the between-subject factor and period as the repeated measure. Significant results were followed by repeated-measures ANOVA within each taxon to test for the effects of urbanization level and biological period. For all statistical tests, p-values < 0.05 were considered significant. I considered p-values > 0.05 but ≤ 0.10 to be marginally significant, and present these results for the reader's interpretation.

Prey density and available biomass

Small rodent density. The density of small rodents was estimated using spatially explicit capture-recapture (SECR) models (Efford 2004). Circular trapping webs consisting of 12 radial trap lines of 80 m each were replicated at each site (Anderson et al. 1983). Trap lines included 10 Sherman live traps alternated by size (large: 8 x 9 x 23 cm; small: 5 x 6 x 15 cm) at the beginning of each line as well as along the trap line itself, the first 4 traps were placed at 5-m intervals from the center, and the next 6 traps at 10-m intervals. An additional 4 traps were placed at the web center for a total of 124 traps. The area of the trapping web (2 ha) was > 16 times as large as the average home range size of our suite of small mammal study species (Bondrup-Nielson 1983). For the two major small rodent taxa in our study (*Microtus* and *Peromyscus*), average home range area estimated from body mass using allometric equations (Harested and Bunnell 1979)

ranged from 0.02 to 0.11 ha. Trapping sessions were conducted during coyote breeding-gestation, pup-rearing, and dispersal periods to test for seasonal variation in small rodent density. Traps were baited with peanut butter and rolled oats, set in the evening of Day 1, then checked, disabled in the morning, and re-set and bait refreshed in the evening over the next four consecutive days. Small mammals captured were weighed to the nearest 0.1 g and marked with an ear-punch using a modified universal mouse numbering system (Dickie 1975). All field procedures were approved by Wayne State University's Institutional Animal Care and Use Committee and met the guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

I used likelihood-based procedures for closed population mark-recapture data in the R package secr-2.9 (Efford 2011). SECR fits a spatial model of the population and a spatial model of the detection process to the capture histories of trapped animals. The population model describes the density D of animal home range activity centers across the landscape ($\widehat{D}$, the estimated value of D, is the population density). The detection model links the probability, g0, of catching an individual at a particular trap to the distance, σ of the trap from that animal's home range activity center (Royale et al. 2014). The distribution of home range activity centers in the population is typically modelled as a homogenous Poisson point process (Borchers and Efford 2008). The decline in detection probability can be modelled using either half-normal (HN), negative exponential (NE), or hazard (H_z) detection functions. Like traditional Mark-capture-recapture (MCR) models, SECR also accommodates variations in detection probability (e.g., M(t) – "time factor" where g0 takes on a unique value at each sampling occasion). SECR fits the spatial model of the population ($\widehat{D}$) and the detection process ($\widehat{g0}$ and $\widehat{\sigma}$) to

the captured animals' detection histories by numerically maximizing the likelihood (Borchers and Efford 2008). In addition to the assumptions of closed-population MCR models (e.g., no turnover in population, marks are accurately reported; Otis et al. 1978) SECR models assume that (1) animals occupy stationary and independent home ranges, (2) home range activity centers are uniformly distributed in space, (3) the state-space (i.e., potential locations for any activity center) is defined, and (4) capture probability is a function of the Euclidian distance between an animal's activity center and the trap location (Efford et al. 2004).

Seasonal density of small rodents was estimated at each site and pooled by urbanization level. Season was treated as a covariate listed in the 'groups' argument of the R function secr.fit(). For site-specific data sets, I used the model selection procedures in the program CAPTURE, which employs multivariate discriminant function analyses to determine the "best" detection probability model (Otis et al.1978), which was subsequently used as the detection parameter in the 'model' argument of secr.fit(). For the pooled data sets, I used the R function: stepAIC() to eliminate non-significant higher-order interactions from the saturated model, to determine the "best" fit model (i.e., the model with the lowest AIC value). Models were ranked based on the difference between the lowest AIC value and the AIC value of the other i models ($\Delta_i = AIC_i - AIC_{lowest}$

Eastern cottontail rabbit density. Counts of eastern cottontail rabbit (*Sylvilagus floridanus*) fecal pellets were used to estimate rabbit density. To detect differences in pellet counts between suburban and urban sites, as recommended by Palomares (2001), I placed 15 to 20, 0.7-m diameter (0.38 m^2) plots at each site. Plots were placed at least 50 m apart (the approximate average summer foraging distance of eastern cottontail rabbits;

Janes 1959) along a 750 – 1000 m long meandering transect in edge habitat with dense cover where observed rabbit use was high. Plots were initially cleared of all existing fecal pellets and debris (e.g., twigs and rocks), and herbaceous cover and woody stems cut to the ground and discarded. Plots were subsequently re-located and fecal pellets counted at intervals so as to coincide with the coyote breeding-gestation, pup-rearing, and dispersal periods. Rabbit density was estimated using the equation:

$$\widehat{D} = \frac{\overline{p}}{tra}$$

where $\widehat{D}$ = estimated rabbit density, $\overline{p}$ = mean pellet count per plot, t = days between counts, r = rabbit defecation rate (350 pellets/day; Cochran and Stains 1961), and a = area of sampling unit (Novaro et al. 1992).

I used repeated-measures ANOVA with urbanization level as the between-subject factor and biological period as the repeated measure to test for effects of urbanization level and biological period on small rodent and rabbit density. Density estimates were transformed as $\ln(X + 1)$ to meet the assumptions of ANOVA. Normality was tested with the Shapiro-Wilk W test, homogeneity of group variances with an F_{max} test, and equality of the variances of the differences between all possible pairs of groups with Mauchly's test of sphericity. Significant differences were evaluated using pairwise t-tests with alpha error accumulation corrected with the Holm-Bonferroni method.

White-tailed deer carcass numbers. To estimate the number of deer-vehicle collisions (DVCs) in the study area, I created a geographic information system (GIS) shapefile of locations of DVCs in southeastern Michigan for June 2012 – October 2013 obtained from the Southeastern Michigan Council of Governments (SEMCOG). For each

study site, the numbers of DVCs that fell within a 64.0 km^2 areal area encircling GPS locations of coyote scat found at the site (see above) were tallied. Counts of DVCs were increased by 50% to account for those that go unreported (Decker et al. 1990). I used maximum likelihood chi-square analyses of a 2 x 3 (urbanization level x period) contingency table to determine if observed number of DVCs differed from expected among periods between urbanization levels.

Available biomass. Available biomass of small rodents, eastern cottontail rabbit, and adult white-tailed deer were calculated by multiplying density estimates and counts of DVC by the mean body mass of the respective prey (see above). I tested differences in the relative proportion of available biomass of the top three most-consumed prey between urbanization level and among biological periods with repeated-measures ANOVA. Significant results were followed by Holm-Bonferroni-adjusted paired t-tests.

Coyote Prey Selection

Coyote selection of small rodents, eastern cottontail rabbit, and white-tailed deer (the top 3 prey found in coyote diets) were examined using selection ratios (relative consumed biomass/relative available biomass or $\widehat{w}$) and Manly's standardized selectivity index (Manly et al. 2002):

$$\widehat{\beta}_i = (d_i/n_i)\Big/\sum_{j=1}^{m}(d_j/n_j),$$

where d_i and d_j are the relative proportion of biomass of prey i and j in the diet, n_i and n_j are the relative proportion of biomass of prey i and j in the environment, and m is the number of different prey. The selectivity index reflects the deviation in prey use from what would be expected if use were purely random (Heisey 1985). Importantly, $\widehat{\beta}_i$ does

not change with fluctuations in prey density unless consumer behavior also changes (Chesson 1983). Manly's standardized selectivity indices were used to determine prey selection among the top 3 prey types and identify the direction in which selection occurred. $\widehat{\boldsymbol{\beta}}_{\boldsymbol{i}} > 1/m$ indicates positive selection, $\widehat{\boldsymbol{\beta}}_{\boldsymbol{i}} < 1/m$ non-selection, and $\widehat{\boldsymbol{\beta}}_{\boldsymbol{i}} = 1/m$, random feeding (Manly et al. 2002). To determine whether coyotes are selective foragers, I performed a log-likelihood chi-squared test of the null hypothesis that coyotes randomly consume prey in proportion to availability. A significant outcome was followed by conducting pairwise comparisons of differences in seasonal prey selection ratios by comparing the statistic$\left(\widehat{\boldsymbol{w}}_{\boldsymbol{i}} - \widehat{\boldsymbol{w}}_{\boldsymbol{j}}\right)^{\boldsymbol{2}}/\boldsymbol{var}\left(\widehat{\boldsymbol{w}}_{\boldsymbol{i}} - \widehat{\boldsymbol{w}}_{\boldsymbol{j}}\right)$, (where i and j are seasons), with the critical values of the chi-squared distribution with 1 degree of freedom (Manly et al. 2002). To test if joint relationships and interactions among the categorical factors urbanization level, season, and prey type affected coyote prey selectivity, I conducted a log-linear analysis using the R function glm(). Individual cell frequencies of the underlying contingency table of the log-linear model were based on the corresponding expected proportion of a particular prey-type, season, urbanization level combination (Heisey 1985). A likelihood-ratio G-test was used to test for independence of each two-way combination of categorical factors and categorical factors collectively, as well as categorical factor interactions, with a significant season\prey interaction statistical evidence of prey switching (Randa et al. 2009). Akaike's Information Criteria (AIC) was used to numerically rank the models based on the difference between the lowest AIC value of the best fitting model and the individual AIC values of the other i models ($\Delta_i = \text{AIC}_i - \text{AIC}_{low}$).

RESULTS

Coyote diet

I collected 741 coyote scats (suburban: *n* = 257; urban: *n* = 484) during August 2010 – April 2013. To insure that dietary differences between urbanization level and among biological periods could be detected, ≥ 30 scats per biological period were analyzed from urban (*n* = 102 scats) and suburban (*n* = 90 scats) sampling routes. Based on estimated biomass consumed, the two highest-ranked prey items, regardless of urbanization level, were white-tailed deer and eastern cottontail rabbit. Consumed biomass of small rodents was the third ranked item in suburban areas, whereas woodchuck was the third ranked in urban areas (Table 2.2). With the exception of raccoon in suburban areas, %WO proportions were lower for larger-sized prey and greater for smaller-sized prey compared to proportions of consumed biomass (Table 2.2). Other mammalian prey consumed by coyotes included tree squirrel (Sciuris spp.) and muskrat (*Ondatra zibethicus*). Evidence of human-associated foods (e.g., fast-food or candy wrappers, rubber, plastic, string, aluminum foil) was found only in urban areas and only during the breeding-gestation and dispersal periods. Annually, evidence of domestic cat (*Felis catus*; *n* = 3 scats) in coyote diets was < 5% regardless of method of estimation (Table 2.2, Appendix A, B).

Coyote consumption of prey biomass was significantly affected by urbanization level (*F* = 5.24 *df* = 1, 26, *P* < 0.001, repeated measures PERMANOVA), but not period, and no interaction was detected between urbanization level and period. This result is probably largely driven by the large difference in coyote consumption of white-tailed

Table 2.2. Comparison of the estimated relative proportion of biomass consumed and weighted frequency of occurrence (%WO) and corresponding overall rankings of the 7 most consumed mammalian prey recovered in coyote (*Canis latrans*) scats collected in the greater Detroit area of southeastern Michigan, August 2010 – April 2013.

| | Suburban | | | | | | | Urban | | | | | | |
| | Biomass | | | Weighted occurrence | | | | Biomass | | | Weighted occurrence | | | |
Prey item	Rel %	SE	Rank	%	SE	Rank	n scats	Rel %	SE	Rank	%	SE	Rank	n scats
White-tailed deer	46.26	6.08	1	21.55	0.08	2	38	19.44	4.45	2	8.39	0.74	5	24
Rabbit	25.98	6.80	2	39.08	1.93	1	47	20.64	4.50	1	23.74	0.74	2	39
Small rodent	9.49	3.85	3	19.34	0.91	3	42	15.33	3.65	4	37.98	1.00	1	60
Dog	6.23	2.55	4	3.14	2.44	5	7	2.83	1.29	7	0.25	0.18	7	15
Raccoon	4.50	1.84	5	6.49	2.26	4	9	14.67	4.49	5	7.01	1.40	6	20
Woodchuck	3.69	2.36	6	2.77	1.31	7	8	17.69	4.12	3	13.19	1.92	3	8
Muskrat	2.61	1.03	7	2.97	1.13	6	5	8.00	3.46	6	8.71	1.57	4	3

Figure 2.1. Estimated proportion (±SE) of biomass of the seven most consumed prey of coyotes at urban and suburban areas in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. Letters above column error bars that differ indicate significant differences ($P < 0.05$).

deer biomass between urban and suburban areas (Figure 2.1). When examining responses of individual taxa using univariate repeated measures ANOVA, there were no strong effects of period or a period-by-urbanization-level interaction of consumed biomass for any of the taxa. The exception was small rodents which showed a marginally significant period-by-urbanization-level interaction ($F = 3.06$, $df = 2, 16$, $P = 0.08$, repeated measures ANOVA). Separate analyses of suburban and urban sites produced no effect of period on consumption of small rodent biomass for suburban sites, but a marginally significant effect of period at urban sites ($F = 3.90$, $df = 2, 8$, $P = 0.07$). There was a

strong between-subjects effect (averaging over periods) of urbanization level on consumption of white-tailed deer biomass (F = 20.21, df = 2, 8, P = 0.002). Marginally significant between subjects-effects of urbanization level were also found with coyote consumption of raccoon (F = 4.44, df = 1, 8, P = 0.07) and woodchuck (F = 3.55, df = 1, 8, P = 0.096) (Figure 2.1).

Small rodent, rabbit, and deer carrion density

Small rodent density. Mice (*Peromyscus* spp.) (n = 568, 77.6%) were the most commonly captured small rodent, followed by voles (*Microtus* spp.) (n = 154, 21%). I also captured 3 eastern chipmunk (*Tamias striatus*; 0.27%), 7 meadow jumping mice (*Zapus hudsonius*; 0.64%), 40 masked shrew (Sorex cinereus; 3.6%), and 44 short-tail shrew (*Blarina brevicauda*; 4.02%). Eighty percent of masked shrews and 36.4% of short-tail shrews were captured at a single suburban site located in an old agricultural field. I did not include the shrew species in our population estimates of small rodents because shrew remains were rarely found in coyote scats (n = 2)

The model of small rodent density that best fit the pooled urbanization level data sets incorporated the hazard detection function and included time dependent capture probability (Table 2.3). Since the hazard rate (H_z) detection function best described the decline in detection probability with distance from the home-range centers for the pooled data set, it was used in the models of site-specific density estimates. The site-specific estimates of small rodent density that returned the best fit models included the equal catchability (M_0 or null) (n = 3), time variation (M_t) (n = 5), and time variation, trap response (M_{tb}) model (n = 3). Interestingly, 100% of the models of capture probability at urban sites varied with time (M_t = 4) or included time variation (M_{tb} = 1), whereas, only
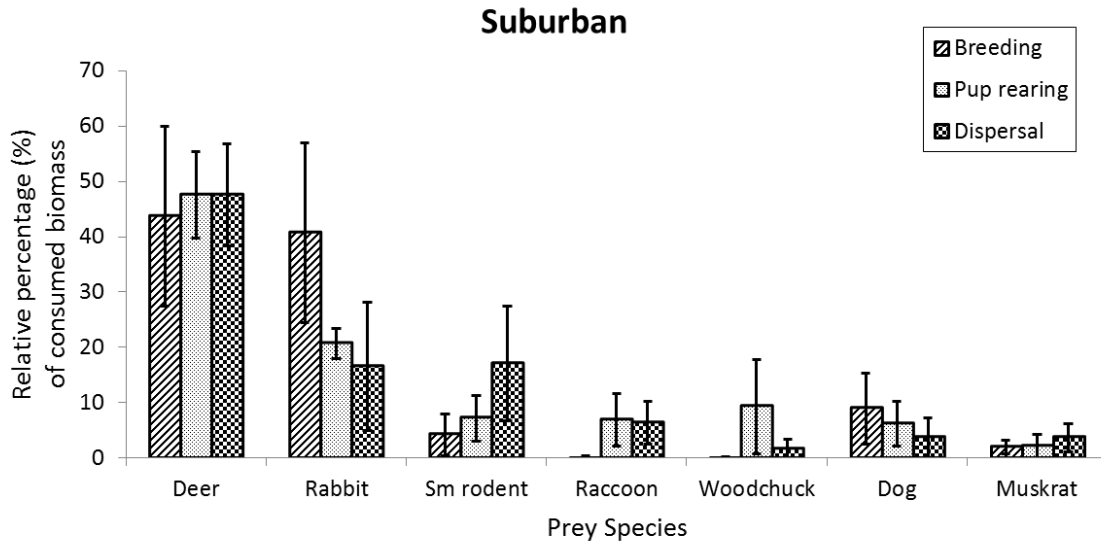
Figure 2.2A. Seasonal estimates (± SE) of the proportion of biomass of the seven most consumed prey by coyotes at suburban areas in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. Within prey species, letters above column error bars that differ indicate significant seasonal differences ($P < 0.05$). *Hibernating during the coyote breeding-gestation period; consumed biomass either from old carrion or other misidentified squirrel spp.

43% of models at suburban sites did so ($M_t = 1$, $M_{tb} = 2$, $M_0 = 4$).

Annually, small rodent density (per ha) was greater at urban ($\bar{x} = 16.17 \pm 0.69$ SE) than suburban sites ($\bar{x} = 7.38 \pm 5.89$), but the difference was not significant. Small rodent density was affected by biological period ($F = 3.50$, $df = 2, 20$, $P = 0.05$), but not urbanization level, and no interaction was found between biological period and urbanization level (Figure 2.3). I recorded the least and greatest densities (per ha) of small rodents in urban areas during the breeding-gestation ($\bar{x} = 5.37 \pm 0.95$) and dispersal ($\bar{x} = 22.86 \pm 1.8$) periods, respectively. Differences in small rodent density between the breeding-gestation and dispersal periods were marginally significantly different ($t = -2.1$ $df = 22$, $P < 0.07$) (Figure 2.3).

Eastern cottontail rabbit density. Annually, rabbit density was greater in urban
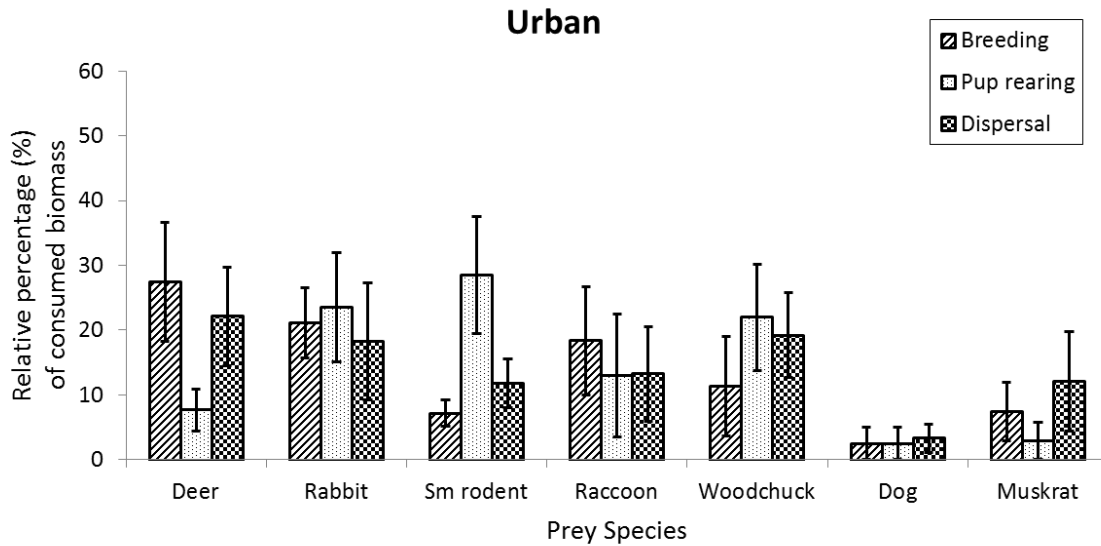
Urban

Figure 2.2B. Seasonal estimates ($\pm$ SE) of the proportion of biomass of the seven most consumed prey by coyotes at urban areas in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. Within prey species, letters above column error bars that differ indicate significant seasonal differences ($P < 0.05$). *Hibernating during the coyote breeding-gestation period; consumed biomass either from old carrion or other misidentified squirrel spp.

areas ($\bar{x} = 1.10 \pm 0.24$) than suburban locations ($\bar{x} = 0.61 \pm 0.11$), but the difference was not significant. Rabbit density was not affected by biological period or urbanization level, but a significant interaction was found between urbanization level and biological period ($F = 3.53$, $df = 2, 18$, $P = 0.05$) (Figure 2.4). I recorded the least and greatest rabbit densities in urban areas during the dispersal ($\bar{x} = 0.31 \pm 0.24$) and breeding-gestation ($\bar{x} = 1.56 \pm 0.53$) periods, respectively. Rabbit density peaked during the dispersal period in suburban habitats when rabbit density was at its lowest in urban habitats, which likely explained the significant interaction between urbanization level and biological period detected with the repeated-measures ANOVA.

White-tailed deer carcass density. Adjusted counts of available deer carcasses from DVCs were not affected by season between suburban (n = 183) or urban (n = 177)
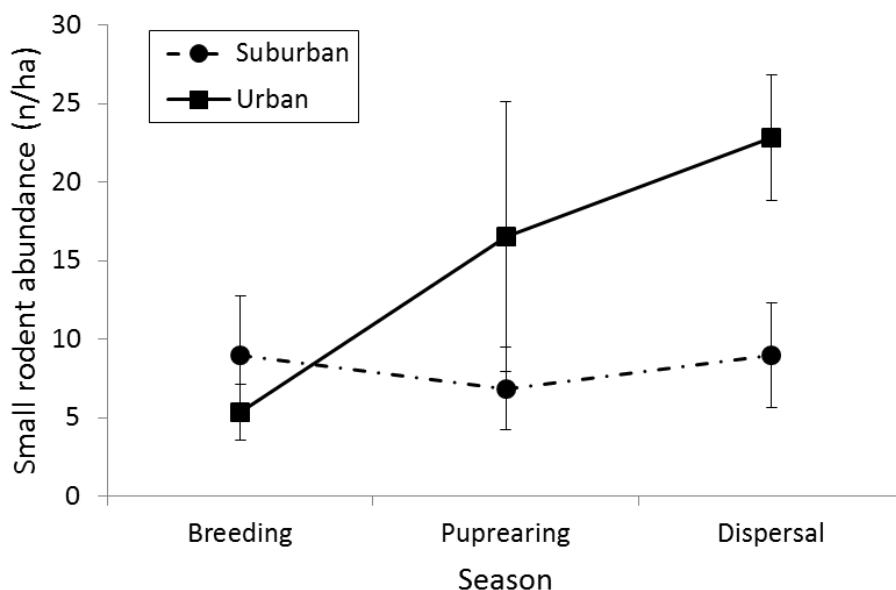
Figure 2.3. Seasonal estimates (±SE) of small rodent density (*n*/ha) derived from mark-recapture trapping data collected at urban and suburban areas in the greater Detroit area of southeastern Michigan, August 2010 – April 2013

locations. There was also no difference in the number of DVCs between urbanization levels. Mean occurrence of DVCs increased between periods, increasing 23% between the breeding-gestation and pup-rearing periods, and 100% between the pup-rearing and dispersal periods (Figure 2.5).

Available prey biomass. Relative available biomass of white-tailed deer was affected by biological period ($F = 13.473$, $df = 2, 82$, $P < 0.001$). White-tailed deer available biomass was significantly different between the breeding-gestation and dispersal periods ($t = -5.1$, $df = 21$, $P < 0.006$) as well as between the pup-rearing and dispersal periods ($t = -5.9$, $df = 10$, $P < 0.002$) (Figure 2.6A). Relative available biomass of eastern cottontail rabbit was not affected by urbanization level or biological period, and no interaction was found between factors (Figure 2.6B). Relative available biomass
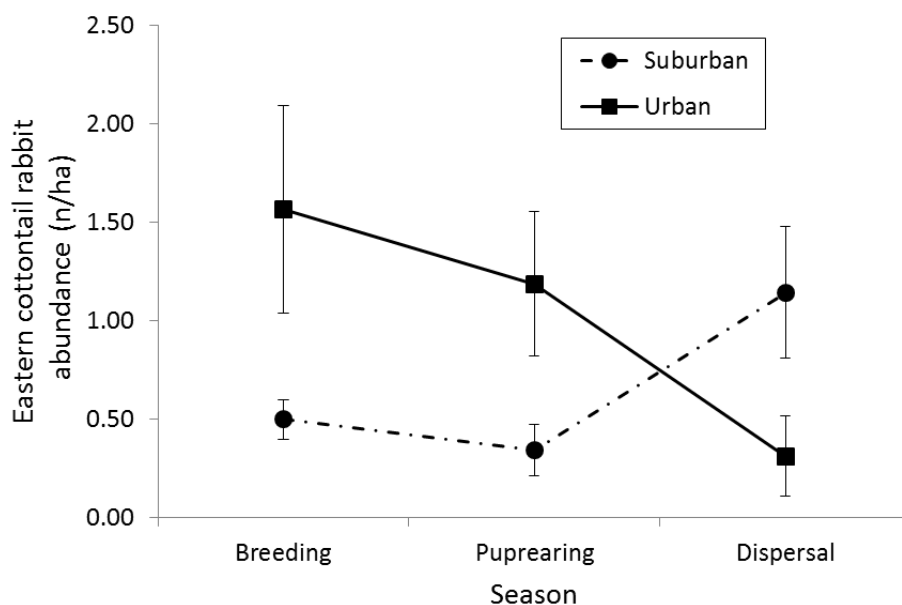
Figure 2.4. Seasonal estimates (±SE) of eastern cottontail rabbit (*Sylvilagus floridanus*) density (*n*/ha) derived from counts of fecal pellets collected at urban and suburban areas in the greater Detroit area of southeastern Michigan, August 2010 – April 2013.

of small rodents was affected by season (F = 4.536, *df* = 2, 20, P < 0.02) and there was a marginally significant interaction between urbanization level and biological period (F = 3.10 *df* = 2, 20, P < 0.07). Small rodent biomass was marginally significantly different between the breeding-gestation and dispersal periods (t = -3.2, *df* = 19, P < 0.08) (Figure 2.6C). Between the breeding-gestation and pup-rearing periods in suburban locations, available biomass of white-tailed deer increased 62.5% (z = -3.68, *df* = 2, P < 0.001; Figure 2.6A) and rabbit biomass increased 77.3% (z = -4.17, *df* = 2, P < 0.001; Figure 2.6B)

. *Coyote Prey Selection*

Log-likelihood chi-square test results indicated significant deviation from random (χ^2_{ML} = 21.06, *df* = 2, P < 0.001) areas. Significant differences in seasonal selection ratios were also found among the three most consumed prey species at both urbanization levels
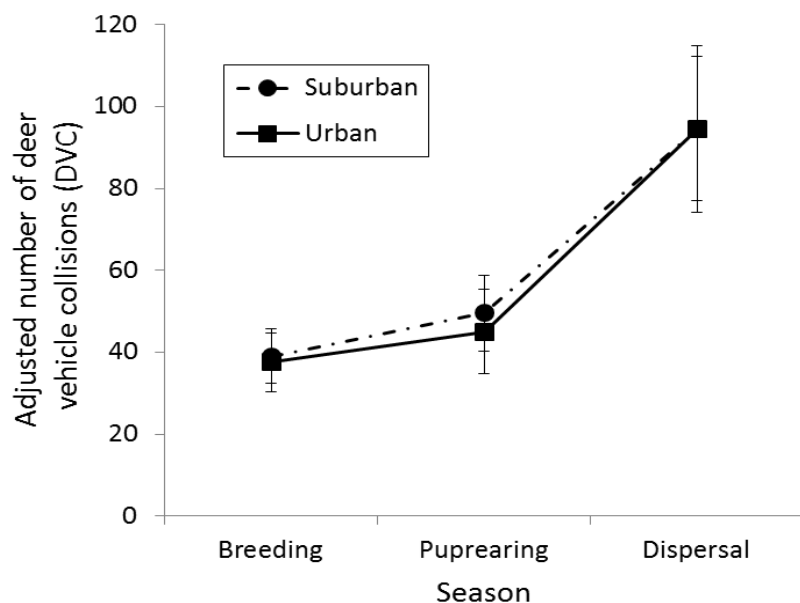
Figure 2.5. Seasonal number (±SE) of white-tailed deer–vehicle collisions (DVC) at urban and suburban areas in the greater Detroit area of southeastern Michigan, June 2012 – October 2013. Numbers adjusted +50% to account for unreported DVCs.

feeding by coyotes in both suburban (χ^2_{ML} = 63.05, df = 2, P < 0.001) and urban (Table 2.4).

In suburban areas, selection ratios for rabbits decreased significantly (35.6% lower) between the breeding-gestation and pup-rearing periods (P < 0.01). Furthermore, selection ratios in suburban areas during the dispersal period were significantly lower for white-tailed deer (62.9% lower) and rabbits (51.3% lower) compared to the pup-rearing period (P < 0.05).

In urban areas, selection ratios for white-tailed deer decreased significantly (106.5% lower) between the breeding-gestation and pup-rearing periods (P < 0.001). Selection ratios for rabbits increased 123.3% from the pup-rearing to dispersal periods (P < 0.001) while those for small rodents declined 91.9% during the same period (P < 0.001) (Figure 2.7).

Table 2.3. Model results of spatially explicit capture-recapture (SECR) analyses of small rodent density from pooled suburban and urban sites in the greater Detroit area of southeastern Michigan, August 2010 – April 2013.

Development class	Model	Detection function	K	AIC_c	Δ_i	w_i
Suburban	Time factor	Hazard rate	17	5812.51	0	0.999
	Constant	Hazard rate	6	5841.70	29.19	0.000
	Learned response	Hazard rate	7	5842.45	29.94	0.000
Urban	Time factor	Hazard rate	17	6296.62	0	0.999
	Constant	Hazard rate	6	6314.78	18.16	0.000
	Learned response	Hazard rate	7	6316.19	19.56	0.000

$AIC_c = n \text{ x } LN\left(\frac{RSS}{n}\right) + \frac{2k(k+1)}{n-k-1}$

Trends in coyote prey selection of white-tailed deer, eastern cottontail rabbits, and small rodents (the three prey most consumed) differed between urbanization levels with much wider variation seen in urban areas (Figure 2.6). In suburban areas, coyote selection of the top three most consumed prey did not change with seasonal fluctuations in prey density or available biomass. Annually, prey selection in the suburbs was positive for white tailed deer (avg. $\widehat{\beta}_i = 0.59$, range = 0.56 – 0.60), random or slightly negative for rabbits (avg. $\widehat{\beta}_i = 0.32$, range = 0.30 – 0.34), and negative for small rodents (avg. $\widehat{\beta}_i = 0.10$, range = 0.06 – 0.13) (Figure 2.6).

In urban regions, coyote selection for white-tailed deer was positive when available deer carcass biomass was low, negative as deer carcass biomass decreased slightly, then shifted to random feeding and remained negative thereafter (Figure 2.6A). A similar but opposite trend in urban areas was found with selection of eastern cottontail rabbit, whereby selection was negative when rabbit density and biomass were high and strongly positive when rabbit density and available biomass dropped to very low levels (Figure 2.6B). Coyotes residing in urban locations selected randomly for small rodents

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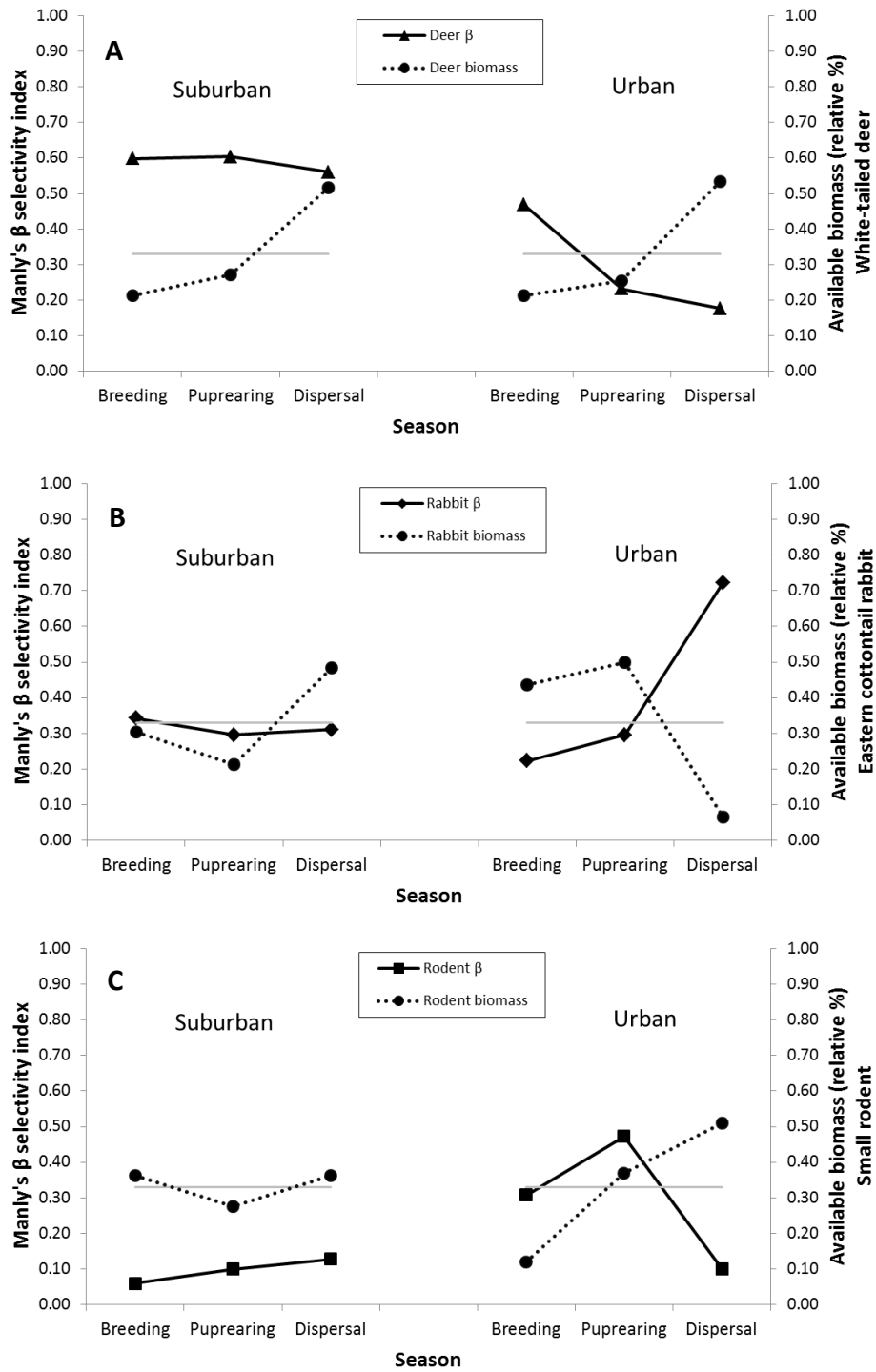
Figure 2.6. Seasonal prey selection and relative available biomass of (A) white-tailed deer carcasses, (B) eastern cottontail rabbit, and (C) small rodents consumed by coyotes at suburban and urban sites in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. Values of $\boldsymbol{\beta}$ above the horizontal gray line denote positive prey selection, below the gray line negative prey selection, and on the line random feeding.

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Table 2.6. Estimates of seasonal selectivity measures of the three most consumed prey of coyotes (*Canis latrans*), and results of comparisons of selection ratios between seasons within development class in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. The Bonferroni adjusted critical value of the chi-square distribution is 7.03. Positive prey selection ($\beta_i > 0.33$) is underlined and statistically significant differences in selection ratios between seasons ($P < 0.017$) appear in bold.

Class	Prey	Manly's β			Selection ratio			χ^2 values (Selection ratio differences)		
		Br	Pr	Di	Br	Pr	Di	Br vs. Pr	Pr vs. Di	Br vs. Di
Suburban	Deer (DVC)	0.60	0.60	0.56	2.12	1.73	0.90	6.07	**24.85**	**58.68**
	Rabbit	0.34	0.30	0.31	1.21	0.84	0.50	**8.61**	**8.25**	**28.36**
	Small rodent	0.06	0.10	0.13	0.21	0.29	0.21	1.03	1.15	0.01
Urban	Deer (DVC)	0.47	0.23	0.18	1.31	0.40	0.53	**79.10**	1.84	**46.33**
	Rabbit	0.22	0.30	0.72	0.62	0.51	2.15	0.86	**252.22**	**231.07**
	Small rodent	0.31	0.47	0.10	0.86	0.81	0.30	0.20	**21.97**	**48.63**
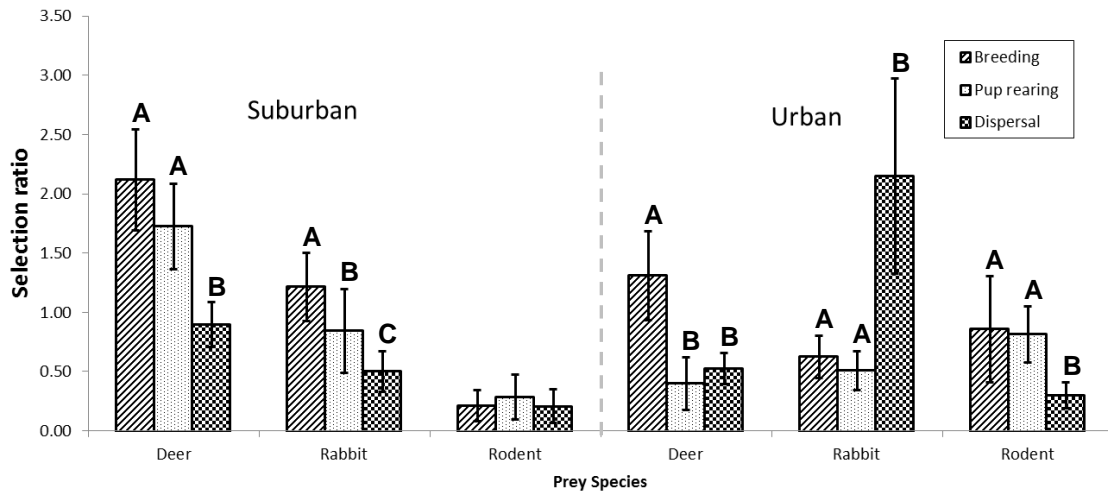
Figure 2.7. Seasonal selection ratios (±SE) of the 3 most consumed prey of coyotes at suburban and urban sites in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. For each prey species within development class, letters (A, B, C) above column error bars that differ indicate significant seasonal differences ($P < 0.05$).

when availability of small rodents was low, and strongly negative when availability was high (Figure 2.6C). The simple effects of individual categorical factors, urbanization level, season, and prey type did not adequately describe the data indicating that interactions between factors had an effect on coyote prey selection ($G^2 = 77.53$, $df = 12$, $P < 0.001$). Results of G-tests for factor independence indicated that urbanization level ($G^2 = 31.87$, $df = 2$, $P < 0.001$) and season ($G^2 = 19.96$, $df = 2$, $P < 0.001$) were not independent of prey-type. The small p-values corresponding to tests for model adequacy (i.e., H_0: the model is correct) indicate that all models are somewhat poor (Table 2.5). Based on the lowest AIC, the prey selectivity model that best fit the data, given the set of candidate models, specified conditional independence of urbanization level and season given prey-type (Model: DP,SP; Table 2.5). Closer examination of urbanization level and season while holding prey-type constant indicated that coyotes residing in suburban areas had higher, equal, and lower predicted (model fitted) levels of seasonal prey selection of

Table 2.5. Log-linear analyses of expected prey selection by coyotes (*Canis latrans*) in
the greater Detroit area of southeastern Michigan, August 2010 – April 2013.

Model[a]	G^2	df	P-value	AIC_c	Δ_i	w_i
DP,SP	17.26	6	0.008	5.26	0.00	0.85
DS,DP,SP	16.72	4	0.002	8.72	3.46	0.15
DP,S	36.53	10	0.000	16.53	11.28	0.00
DS,DP	36.11	8	0.000	20.11	14.86	0.00
SP,D	50.31	8	0.000	34.31	29.06	0.00
DS,SP	49.89	6	0.000	37.89	32.64	0.00
D,S,P	69.59	12	0.000	45.59	40.33	0.00
DS,P	69.17	10	0.000	49.17	43.91	0.00

[a]D: urbanization level (urban/suburban); S: season (breeding-gestation, pup-rearing, dispersal); P: prey type (white-tailed deer, eastern cottontail rabbit, small rodent).

deer carcasses, eastern cottontail rabbit, and small rodents, respectively, compared to coyotes in urban areas. Despite this pattern however, the null hypothesis that urbanization level and season are independent was not rejected ($G^2 = 16.71$, $df = 2$, $P = 0.763$). Therefore, I conclude that urbanization level and season are not associated when prey-type is held constant. Log-linear analysis of interactions between season and prey-type within urbanization level however, revealed a significant interaction in urban areas ($G^2 = 28.08$, $df = 4$, $P < 0.001$) indicating that prey switching was occurring. A marginal interaction between season and prey was also found in suburban areas ($G^2 = 8.03$, $df = 4$, $P = 0.091$).

DISCUSSION

Coyote diet in a large metropolitan area

Small rodents, eastern cottontail rabbit, and white-tailed deer were the primary prey of coyotes in the greater Detroit area of southeastern Michigan, a trend that agrees with other studies of coyotes in developed areas (Atkinson and Shackleton 1991, Quinn 1997, Fedriani et al. 2001, Morey et al. 2007). My results also confirm previously

reported low %WO of domestic dog in coyote diets, though estimates using domestic dog biomass were higher (Appendix A, B). I found very little evidence of fruit in coyote diets, which may reflect either lower detection of highly digestible fruits in scats or low availability of fruit in the environment. Additionally, frequency of occurrence of human-associated foods in coyote diets in the greater Detroit area was lower than those found in other studies (MacCracken 1982, McClure et al. 1995, Fedriani et al. 2001) which may reflect a higher proportion of abandoned, naturalized urban areas in the region, which would presumably increase available prey populations. Such a pattern is highly speculative, however, without further quantification of these land cover changes in the greater Detroit area compared to other regions.

Unlike most other studies of coyote diets in developed areas, raccoon and woodchuck often made up > 10% and white-tailed deer > 20% of coyote diets in my study area. These prey however are generally underestimated, because food items are often expressed as percentages (occurrence or frequency of occurrence), which has been found to considerably underestimate larger-sized prey (Klare et al. 2011). Although individual coyotes are capable of killing adult white-tailed deer unassisted (Gese and Grothe, 1995, Patterson 1994) as well as raccoon and woodchuck (Gehrt and Riley 2010), they can be formidable prey for a coyote. Consequently, though not verifiable through scat analysis, I speculate that the major source of biomass of adults of these species throughout the year is carcasses of road-killed individuals. Outside of developed areas, Gese and Grothe (1995), and Paquet (1992) found that coyotes obtain the majority of their food from scavenging carcasses of wolf-killed ungulates (also see, Ozoga and Harger 1966). Because coyotes in southeastern Michigan adapted to living in the

presence of wolves, those residing in urban areas today may have retained some beneficial behaviors of the past.

Coyote scavenging from carcasses of road-killed deer is potentially a major source of food for coyotes in metropolitan areas. This may be uniquely relevant in Michigan, which consistently records some of the highest numbers of DVCs in the Midwest, approximately 70% of which occur in the southern part of the state (Deer Vehicle Crash Information Clearing House 2015, SEMCOG 2015). In suburban areas of the greater Detroit area, the proportion of white-tailed deer biomass found in coyote diets remained steady at around 45%, whereas it fluctuated seasonally from 10% to 26% in urban areas. Noticeably in urban areas, a significant decrease in the relative proportion of white-tailed deer biomass in coyote diets occurred during the pup-rearing period (May – August) coinciding with a significant increase in small rodent biomass and appearance of woodchuck in the diet (Figure 2.2B). Frequency-based methods of estimates of white-tailed deer carrion in coyote diets ranging from 10% to 30% have been reported from other metropolitan areas in the Midwest (Bollin-Booth 2007, Morey 2007, Cepek 2004).

Woodchuck biomass in coyote diets was greatest when woodchucks were most available (i.e., not hibernating) during the pup-rearing period (May 1 – Aug 31) in both suburban and urban areas. Samson and Crete (1995) also found woodchuck to be the most important food in the summer diet of coyotes in southeastern Quebec. Woodchuck (particularly nursing females) may be at greater risk to coyote predation and (in my study area) to motor vehicle mortality during early spring because they are actively feeding on vegetation, frequently along roadsides where they are often struck and killed by automobiles. Secondly, juvenile woodchucks may be more vulnerable to coyote predation

towards the mid-point of the pup-rearing period because they are actively dispersing (Kwiecinski 1998). Woodchuck as coyote prey was somewhat surprising, given that coyotes are primarily nocturnal in developed areas and woodchuck are most active diurnally. Woodchuck may be more abundant in metropolitan areas because soils disturbed by human development are suitable for burrow construction, an important characteristic of woodchuck habitat (Grizzell 1955), and promoting growth of succulent vegetation. Woodward (1990) found very high densities of woodchuck (3.85 − 5.36 per ha) along suburban expressway interchanges in Ontario, much greater than those reported by others outside developed areas in the Great Lakes region (0.01 − 1.01 per ha). Surprisingly, little evidence of fox squirrel (*Sciurus niger*), a common roadkill in the region, was found in coyote scats. Because the fur of Sciurids is often difficult to differentiate, lack of fox or other squirrel species fur identified in scats may be a result of misidentification.

Consumption of raccoon biomass by coyotes was highest during the dispersal period (Sep 1 − Dec 31), when juvenile raccoons are vulnerable to coyote predation as well as fatal encounters with motorized vehicles because raccoons are gaining independence and dispersing during this time. Annually, the proportion of raccoon biomass in coyote diets was 9.2% (range = 6.9 − 12.0%) which was comparable to the frequency of occurrence reported by Morey et al. (2006) in Chicago, but lower than that reported by Cepek (2004) in northern Ohio. Because raccoons are a highly synanthropic species, the greater Detroit area like other urban environments (Prange et al. 2003) likely supports very high densities of raccoon.

From an energetic cost-benefit perspective there is little downside to scavenging the carcass of a road-killed animal. Because carcasses do not have to be pursued, captured, or killed, handling costs are practically non-existent, and scavenging requires no special hunting skills that less-experienced individuals may not have acquired. The spatial arrangement of roads, traffic volumes, types of roads, as well as land use, and animal densities in the greater Detroit area likely contribute to higher numbers of road-killed wildlife compared to other developed areas.

How do coyotes select their prey in a metropolitan area?

Coyotes residing in suburban areas fed randomly on eastern cottontail rabbit throughout the year, despite seasonal changes in available rabbit biomass (Figure 6B). These findings do not support my hypothesis of coyotes selectively foraging on rabbits in less-developed areas. However, year-round in suburban areas, coyote selection for road-killed white-tailed deer was positive (Figure 2.6A) and deer biomass made up the largest portion of coyote diets (Figure 2.2A, Table 2.4) regardless of the number of white-tailed deer carcasses or rabbit density. White-tailed deer appear to fulfill the predictions of optimal forging theory that a profitable prey item will be consumed regardless of its density. Assuming on average that a coyote needs to consume approximately 8.5% of its body mass per day (Mukherjee et al. 2004), the carcass of an adult white-tailed deer could provision a single 20.0 kg coyote for approximately 21 days.

Interestingly, in urban areas coyotes selected white-tailed deer during the breeding-gestation period, despite available rabbit biomass being 69% greater. Patterson et al. (1998) found a similar feeding pattern outside developed areas of southwestern Nova Scotia where coyotes continued to feed on deer, even in the presence of high

snowshoe hare densities. In urban areas, coyote prey selection during the pup-rearing period shifted to being positive for small rodents, negative for white-tailed deer, and random for rabbits (Figure 6). This shift occurred following a 200% increase in available biomass of small rodents. During the pup-rearing period, coyotes consumed more biomass of small rodents, less white-tailed deer and raccoon biomass, and woodchuck began to appear in coyote diets (Figure 2.2B). The decrease in white-tailed deer biomass may have been the result of coyotes shifting from scavenging carcasses of white-tailed deer to preying on neonate deer and older fawns. During the dispersal period in urban areas, coyote selection shifted markedly to rabbits despite a dramatic 87% decrease in available rabbit biomass which incidentally coincided with increases in available biomass of both deer (110%) and small rodent (38%).

The foraging patterns of coyotes in urban areas of greater Detroit do not fit neatly into an optimal foraging framework. Notably, coyote selection for road-killed white-tailed deer, a presumably optimal food source, was negative during the pup-rearing and dispersal periods (Figure 2.6A). Consumption of deer biomass during the pup-rearing season was both lower than expected and considerably lower than consumption of both rabbit and small rodent biomass (Table 2.4), characteristics not associated with an optimal foraging strategy. Moreover, except for selection of small rodents during the pup-rearing period, shifts in coyote prey selection did not follow increases or decreases in prey density as would be expected for an opportunistic predator. Quite the opposite, among the three most consumed prey items, prey selection was often positive when prey density was at its lowest and vice versa (Figure 2.6). That coyotes selected for rabbits when rabbit density was low may reflect greater vulnerability of rabbits to coyote

predation, because of overall more edge habitat in urban environments, and reduction in hiding cover, a result of plants losing their leaves during the dispersal period. Conversely, small rodents may be less vulnerable to coyote predation during the dispersal period precisely because of increased leaf cover on the ground.

I found convincing evidence of prey selection and prey switching by coyotes in the greater Detroit area (Figure 2.6, 2.7). Coyotes in suburban areas specialized exclusively on carcasses of road-killed white-tailed deer throughout the year, and deer neonates and older fawns during the spring/early summer, and did not switch to alternative prey regardless of availability of deer carrion. Outside developed areas, coyotes can be important predators of deer neonates and fawns (Duquette et al. 2014, Vreeland et al. 2004, Ballard et al. 1999), but this has not been rigorously evaluated in urban landscapes (Gehrt and Riley 2010).

In urban locations, coyotes used a foraging strategy that incorporated both prey selection and switching, without a strong discernable pattern. Both suburban and urban dwelling coyotes did, however, take advantage of the plethora of available carcasses of road-killed wildlife. My findings do not support the coyote's designation as a strict generalist predator, but suggest that its foraging strategy is very fluid in developed areas. The greater Detroit area, like all urban environments, is constantly changing, with new housing and commercial developments, road construction and repair, and constant automobile traffic. Urban environments are inherently disturbed environments, such that coyotes have to adapt their foraging patterns to the ever-changing spatial structure of the landscape and prey aggregation patterns (Fortin et al. 2015). The high plasticity in

foraging displayed by coyotes is likely a major reason they have succeeded in urban landscapes.

CHAPTER 3: MOVEMENT PATTERNS AND HABITAT USE O OF COYOTES IN THE GREATER DETROIT AREA OF SOUTHEASTERN MICHIGAN

<u>**INTRODUCTION**</u>

Understanding how wildlife responds to urbanization is a critical component of conserving and managing wildlife in developed areas and mitigating human-wildlife conflicts. For wildlife to succeed, adjustment to the loss of habitat and fragmentation that results from urbanization requires dramatic changes in behavior, habitat selection, and demographics (Adams et al. 2005). While a number of small mammalian carnivores (e.g., raccoon (*Procyon lotor*) Prang et al. 2004; red fox (*Vulpes vulpes*) Cavallini 1996; striped skunk (*Mephitis mephitis)* Rosatte et al. 1991) have thrived in urban environments, large predators considered incompatible with humans (e.g., wolves (*Canis lupus*)) typically have not (Cardillo et al. 2004, Woodroffe 2000). Characteristics of many synanthropic (ecologically associated with humans; Andrzejewski et al. 1978) species that have succeeded in urban environments include a generalist diet, high reproductive potential, and tolerance for or lack of avoidance and even affinity for humans (Fuller et al. 2010). Coyotes (*Canis latrans*) are ideal candidates for studying wildlife response to urbanization because they have traits favorable to inhabiting urban ecosystems (flexibility in habitat use, high reproductive potential), yet they retain a strong dependence on natural or remnant habitat patches (Gill and Bonnett 1973, Tigas et al. 2002, Riley et al. 2003), tend to steer clear of developed areas (Quinn 1997, Gehrt et al. 2009), and largely avoid humans.

Key for wildlife to survive in the urban landscape is the capacity to negotiate the urban matrix and exploit important resources in both natural and highly human-modified

habitats (Gehring and Swihart 2003). A major reason coyotes have persisted in developed areas is that they restrict their activities to crepuscular and nocturnal periods, specifically to avoid humans where human activity is heavy (Andelt 1980, Quinn 1997, Gehrt and Riley 2010). Under the cover of darkness, coyotes freely traverse established home ranges, which often encompass residential and commercial areas, in search of food while simultaneously patrolling territorial boundaries. Developed landscapes consist of a patchwork of human land use dissected by linear landscape features (e.g., dirt roads, utility rights-of way, highway and roadway medians, linear parks, golf courses, hike-bike trails, and active and abandoned railroad tracks) interspersed with isolated remnants of natural habitat. The resulting landscape is dominated by narrow transition zones between different types of land cover (ecotones or edge habitat). Edge habitats often support communities of animal species that are primary prey of coyotes, and linear features provide coyotes with habitat and travel corridors between natural habitat patches (Atwood et al. 2004, Tigas et al. 2002). Despite the many documented detrimental effects of fragmentation in urban landscapes, coyotes are probably more capable of exploiting small isolated habitat fragments than other large carnivores (Gehrt and Riley 2010), although there is a threshold below which coyotes will disappear as habitat patches become increasingly smaller and more isolated (Crooks 2002). Track station data indicated that the probability of coyote occurrence was at least 50% in habitat fragments >1 ha in size and an isolation distance of 883 m (Crooks 2002).

Resident coyotes form family groups or packs that establish, maintain, and generally remain within well-defined home ranges across the landscape, with little or no overlap between adjacent home ranges of other packs (Gese et al. 1988; but see Atwood

and Weeks 2003). Home range size, especially in carnivores, can be an important indicator of habitat quality and availability of resources (Gittleman and Harvey 1982). Many small urban dwelling carnivores, such as red fox (Cavallini 1996, Goszeyzynski 2002, Newman et al. 2003), raccoon (Prang et al. 2004), and badger (*Meles meles*; Davison et al. 2009) have smaller home ranges in urban areas, suggesting that, at least for these predators, urban areas provide high quality patches of discrete resources.

There appears to be a trend for home ranges of coyotes in urban areas to be smaller (Atkinson and Shackleton 1991, Person and Hirth 1991, Riley et al. 2003, Atwood et al. 2004, Gehrt et al. 2009) compared to those outside developed areas (Gosselink et al. 2003, Bekoff and Gese 2003), although there is considerable variation in home range size across the coyotes' geographic range. Estimates of the mean home range size of resident coyotes from studies in non-urban (Bekoff and Gese 2003) and urban (Gehrt and Riley 2010) landscapes, respectively were 17.5 km^2 (range 3 – 42 km^2) and 8.2 km^2 (range 5 – 13 km^2) (estimates based on n ≥ 10 individual home ranges). Coyote home ranges may be smaller in highly fragmented disturbed urban landscapes because food and cover resources are more abundant (Timm et al. 2004, Baker and Timm 1998, Quinn 1997, Oehler and Livaitis 1996, Mills and Knowlton 1991, Howell 1982). At the landscape level, small home ranges may also be an indicator of high population density (Andelt 1985, Fedriani et al. 2001) as has been reported for raccoons (Riley et al. 1998) and red foxes (Harris 1981) in urban areas. Thus home range size is correlated in some manner to the degree of urbanization, but the reasons for this are not well understood. Theoretical studies suggest that as resources become clumped across the landscape – as might occur in developed areas – animals must operate at larger spatial scales.

Researchers have found both positive (Gehrt 2007, Riley et al. 2003, Way et al. 2001) and negative (Atwood et al. 2004) relationships between coyote home range size and proportion of non-natural or developed land within the home range. The size of a coyote's home range may be constrained not only by the size, number, and distribution of natural habitat patches within the home range, but also by the connectivity linking these patches.

Coyote territories, which generally include the entire home range, are used exclusively and defended by pack members through direct confrontation and indirectly via scent marking and howling (Voigt and Berg 1999, Bekoff and Wells 1980). Resident coyotes have strong fidelity to territories and have been known to maintain them over multiple generations (Kitchen et al. 2000b). Because important habitat resources (e.g., den sites, wooded cover) and prey species are often aggregated across the home range, certain "core areas" within the home range are used with greater intensity than others (Powell et al. 1997). Although many core areas can be ephemeral in space and time, certain core areas are often used traditionally by coyotes (e.g., den sites).

Destruction of habitat and transformation of the spatial structure of landscapes caused by urbanization tends to aggregate and isolate resources onto islands or belts of habitat (Fortin et al. 2015). Loss and degradation of territories may dislocate coyotes and dramatically disrupt their space use and movement patterns. Individual coyotes may adjust to changes in resource distribution by expanding the area over which they traverse, while others may focus on smaller areas.

Studies in urban landscapes have found considerable variation in the movement and space-use patterns of coyotes, and additional research is needed to provide a clearer

picture of how coyotes utilize and travel through cities. Most studies have focused on the association between coyote home range size and proportion of urban vs. natural land cover within the home range. Fewer studies, however, have examined the relationship between specific landscape metrics (e.g., habitat fragmentation) and coyote movement patterns in developed areas. To better understand these relationships, I explored the following questions:

1)   How does urbanization (measured as the proportion of urban land cover) within the home range affect the size of coyote home ranges and core areas in a large metropolitan area?

2)   How does fragmentation and connectivity of land cover within the home range affect the size of coyote home ranges and core areas in a large metropolitan area?

Due to the extensive corridor habitat that connects patches of natural habitat in my study area, I hypothesize that the proportion of urban land cover within the home range will have little effect on the size of coyote home ranges or core areas. Further, I hypothesize that the size of coyote home ranges and core areas will be positively related to with fragmentation and inversely related to connectivity of natural land cover within the home range.

STUDY AREA

The greater Detroit area of southeastern Michigan encompasses portions of Livingston, Macomb, Oakland, Washtenaw, and Wayne counties, an area of approximately 8,600 km^2, with a human population of approximately 4.5 million (SEMCOG 2010). In its urban core (the area where anthropogenic development and

activity is greatest, impervious surfaces predominate, and green space is lacking (Gehrt 2010)). Land use in the urban core is primarily residential, commercial, industrial, and transportation oriented, with parks, recreation areas, and other green space representing only a small proportion of the landscape. In the suburbs, land use is predominately residential and agricultural.

Within the urban core existing areas of natural and naturalized vegetation are extremely fragmented; most are highly altered river floodplains dominated by grassy areas and eastern cottonwood (*Populus deltoides*), or abandoned lots and old farmland dominated by non-native grasses and forbs. Forest remnants are more common in suburban areas, and are often second-growth woodlots dominated by oak (*Quercus* spp.), elm (*Ulmus* spp.), or other tree species that have become established with the reversion of former agricultural lands to more natural conditions.

METHODS

Trapping and radio-tagging

Coyotes were live-trapped with KB Compound 5.5, 4-coiled spring, leg-hold traps with slightly offset jaws (hereafter KB 5.5) and non-powered cable restraints (e.g., Powell and Proulx 2003). These trapping devices are considered safe and effective when properly used and set correctly (Association of Fish & Wildlife Agencies 2006, Shivak et al. 2005). To minimize the capture of non-target species and juvenile coyotes, as recommended by Phillips and Gruver (1996), we set the pan tension of the KB 5.5 to 1.4 – 1.8 kg (3 – 4 lbs.) using a force gauge (Sullivan's Trap Tester). Cable restraints were secured in the ground with cable anchor stakes (Pogostick; Minnesota Trapline Products). Traps and cable restraints were typically set in the afternoon and checked the following

day at dawn, early-afternoon, and at dusk to minimize the amount of time a coyote could potentially be restrained (8 – 9 hours maximum). To reduce the possibility of inadvertent capture of diurnally active non-target species, such as domestic dogs, traps were placed in areas not frequented by humans. Additionally, the immediate area surrounding trap locations were posted with signs that included a warning of the presence of traps, a short description of the research project, and project personnel contact information. My trapping and handling protocols were approved by Wayne State University's Institutional Animal Use and Care Committee (IACUC A01-07-11).

Trapping occurred in late June after den sites were abandoned and pups are fairly independent of adults (8 – 10 weeks old) and are often left at rendezvous sites while adults make nightly foraging trips. I pre-baited trap sites with carcasses of road-killed mammals, primarily white-tailed deer (MDNRE Scientific Collector's Salvage Permit No. 1384) 7 to 10 days before setting and arming traps. Cable restraints were placed along trails and foot-hold traps near baited areas with recent evidence of coyote activity. I trapped throughout the winter and into spring several weeks before the birthing/pup-rearing season in mid-April.

Captured coyotes were initially restrained with a handheld net (0.96-m x 0.84-m x 1.2-m deep) or catch pole, then physically restrained and quickly administered a single injection of xylazine HCL (2.0 mg/kg body weight), a neuroleptic (tranquilizer) in the quadriceps muscle using a handheld syringe. Large-gauge (16 – 18) needles secured to syringes with Leur-Lok fittings were used for quick and stable drug delivery (Pond and O'Gara 1994). Tranquilized coyotes were placed in a left lateral recumbent position on a 1.8-m x 2.4-m (6-ft x 8-ft) square canvas tarp, the head and neck were extended, and the

tongue drawn-out over the incisors to ensure an open airway. I applied a bland eye ointment to prevent eye drying and loosely placed a blindfold over the eyes to reduce stress, and auditory stimulation (talking) was kept to a minimum. Heart rate (70 − 120 beats/min), respiratory rate (10 − 30 breathes/min), rectal temperature (37.8 − 39.2 °C), and capillary refill (~ < 1.0 sec) were closely monitored throughout the period of immobilization. I conducted a systematic head-to-tail physical examination of captured coyotes looking for any signs of injury, illness, or disease. Minor injuries (cuts and abrasions) were thoroughly rinsed with betadine solution and triple antibiotic ointment applied if deemed necessary. I attached uniquely numbered and colored (females - red, males – yellow) plastic ear tags (NASCO Farm & Ranch, Fort Atkinson, Wisconsin) to the pre-punched (6.25-mm diam.) ears of all adult coyotes. I recorded coyote gender, age (based on body size and tooth wear), weight and length (body and tail), and reproductive condition. Adults were outfitted with a very-high-frequency (VHF) radio-collar equipped with a 4-hour mortality sensor (model MB220B; Advanced Telemetry Systems, Insanti, Minnesota). Weight of radio-collars (160 g) was < 2% of the body weight of an average sized coyote (9 − 16 kg.), well below the 5 − 10% of body weight recommended by Gannon and Sikes (2011). After processing, coyotes were placed in a large (91-cm L x 64-cm W x 69-cm H) pet carrier and administered an IM injection of yohimbine (0.25 mg/kg body weight) to reverse the clinical effects of xylazine. Coyotes were then released.

Ground-based radio telemetry techniques were used to closely monitor radio-collared coyotes over the next 2 − 3 days for abnormalities in their typical active nocturnal and diurnal resting activity pattern. Thereafter, coyotes were tracked 1 − 3

times per week with UTM radio locations estimated via triangulation and the maximum likelihood estimator in the program LOCATE III (Nams 2006) loaded on a Personal digital assistant (PDA) (Garmin iQue™ 3600). I gathered a minimum of six crepuscular/nocturnal and one diurnal radio location per coyote per week estimated with $\geq$ 3 azimuths collected within 45 minutes of each other. I concentrated monitoring activities to crepuscular and nocturnal periods to correspond with coyote activity in urban areas (Morey 2004, Riley et al. 2003, Gibeau 1998, Atkinson and Shackleton 1991). Radio-locations with error polygons that exceeded 2500 m^2 were not used in the analyses. I attempted to collect a minimum of 30 radio locations per coyote during the breeding-gestation (Jan 1 – Apr 30), pup-rearing (May 1 – Aug 31), and dispersal (Sep 1 – Dec 31) seasons.

Analysis of home range and core areas

Coyote home range boundaries (the spatial domain) were initially defined by the 95% isopleth of the fixed kernel density estimate (KDE; Worton 1989) with reference bandwidth as the smoothing parameter (Venables and Ripley 2002). Until recently, many researchers using kernel density estimates arbitrarily chose the 50% isopleth of the KDE to describe core areas (Laver and Kelly 2008). Wilson et al (2010) introduced a novel statistical method that determines the isopleth of the KDE that optimally partitions the home range into core areas and peripheral use regions for a given point pattern. I applied Wilson et al's (2010) methodology to my radio-telemetry relocation data to delineate core areas recurrently used by coyotes. Following estimation of home range boundaries, radio-telemetry relocation points within the spatial domain are tested for deviation from spatial homogeneity (i.e., clustering) using a modification of Ripley's K function (L-hat; Ripley

69

1976). If clustering is detected (i.e., relocations are not random), a Bayesian statistical model is applied iteratively to objectively partition the spatial pattern of radio-telemetry relocation points into ≥ 2 regions (the optimal isopleths representing core areas) of completely spatially random (CSR) point patterns. Modeling and analysis was conducted in R (R Core Team 2014; code provided by R. Wilson).

To extract land cover attributes, I overlaid the boundaries of coyote home ranges and core areas on a raster data layer within a geographic information system (GIS). The raster data layer included the distribution of land cover types in southeastern Michigan (SE Michigan Land Cover 2002; Center for Geographic Information, Michigan Department of Information Technology, Lansing, MI) delineated along five broad land cover categories: urban, grassland, scrub-shrub, woodland, and wetland. I then used FRAGSTATS 4.2 (McGarigal et al. 2012) to quantify landscape metrics within coyote home range and core areas. I used PLAND (percentage of landscape) as a fundamental measure of landscape composition. Area-weighted mean patch fractal dimension (AWMPFD) was used as a measure of habitat fragmentation (Milne 1991). AWMPFD ranges between 1.0 and 2.0 with values approaching 1.0 indicative of very simple perimeters (e.g., circles or squares) and values approaching 2.0 a sign of highly convoluted, plane filling perimeters (McGarigal and Marks 1995). The connectance index (CONNECT), defined as the number of functional joinings between like land-use patches, was used to quantity habitat connectivity with a threshold distance for joinings of 1.52-km (the radius of a 7.3 km^2 circle representing the grand mean of estimates of annual home range size of urban coyotes across seven studies reviewed by Gehrt 2007). The index ranges from 0 (no like patches connected) to 100 (all like patches connected)

Finally, the largest patch index ($0 < LPI < 100$) was used as a measure of the dominant land cover category within coyote home ranges and territories.

RESULTS

I captured eight coyotes (five adult males, two adult females, one male pup) and outfitted six adults (four males, two females) with radio-collars during July 2011 – April 2012 (Table 3.1). Four individuals were captured in foot-hold traps and four in non-powered cable restraints. My sample of radio-collared coyotes was small and precludes any quantitative statistical analyses, but I chose to continue the study with the idea that the data still provide qualitative insights into coyote movement patterns. Furthermore, because individual coyotes perceive and use landscapes differently and space-use patterns I recorded 438 relocations (range = $1 - 263$ locations per coyote) for all radio-collared coyotes during August 2011 – October 2012 (Table 3.2). I was only able to gather enough radio-telemetry location data to adequately estimate the home range boundaries of two adult male coyotes (CL02 and CL06) to conduct analyses of core areas and land cover. These two individuals were likely resident coyotes based on several observations near and during the breeding season of the individuals travelling with other un-collared coyote. Mean number of seasonal locations for these two individuals was 43.17 ($\pm$ 23.5 SE). Mean size of error polygons from triangulations were 630.98 m^2 ($\pm$ 660.86) and 590.34 ($\pm$ 598.1) m^2 respectively for coyote CL02 and CL06.

Shortly after coyote CL02 was radio-tagged he moved 27.24 km (straight-line) northwest over a period of 75 days and established a 34.1 km^2 home range which he maintained for 177 consecutive days (27 November 2011 – 22 May 2012). Thereafter I

Table 3.1. Coyotes (*Canis latrans*) captured in the greater Detroit area of southeastern Michigan, July 2011 – March 2012.

Id	Frequency	Capture date	Capture Location	Age	Sex	Weight (kg)	Ear tag no. left/right[a]
CL01	N/A	16-Jul-11	Bloomfield Hills	Pup	M	3.1	N/A
CL02	163.720	6-Aug-11	Rochester Hills	Adult	M	12.9	1Y/
CL03	N/A	27-Sep-11	Dearborn	Adult	M	12.8	3Y/
CL04	163.744	20-Feb-12	Rochester Hills	Adult	M	11.2	4Y/4Y
CL05	163.856	20-Feb-12	River Rouge	Adult	F	12.0	1R/1R
CL06	163.543	20-Mar-12	Waterford	Adult	M	17.7	5Y/5Y
CL07	163.556	23-Mar-12	Dearborn	Adult	M	14.4	6Y/6Y
CL08	163.843	24-Mar-12	Dearborn	Adult	F	10.3	2R/2R

[a] Y – yellow (males), R – red (females).

was unable to locate CL02 until 26 Jul 2012 when he was found approximately 3.0 km southeast from his previous location. He then established a new home range (size = 11.37 km^2) which he maintained for 314 days until he was struck and killed by a motor vehicle on 6 June 2013. This was likely to be a permanent home range change rather than a shift or expansion in home range boundary because coyote CL02 was never relocated within his prior home range or core areas. Furthermore, during the necropsy of CL02, his stomach contained large pieces of undigested deer flesh and fur totaling 2.1 kg, a strong indication that he was provisioning pups. Coyote CL06 was captured within his home range, estimated at 10.49 km^2. Interestingly, at their nearest edge, the home range boundaries of these two coyotes were within 4.0 km of one another and despite the short distance I never detected any incursions into the adjacent home range by either coyote. Coyote CL02 and CL06 exhibited clustering in the spatial point pattern of their respective radio-telemetry point relocation data (Figure 3.1). The southern home range of coyote CL02 (Figure 3.2) and the home range of CL06 (Figure 3.3) were adequately modeled by partitioning into two CSR regions, whereas the northern home range of CL02 required

Table 3.2. Coyote (*Canis latrans*) radio-telemetry monitoring data in the greater Detroit area of southeastern Michigan, August 2011 – March 2014.

Id	Frequency	Capture date	Age	Sex	Days monitored[a]	No. locations	Status	Last known alive
CL02	163.720	6-Aug-11	Adult	M	594	135	Mortality	4-Jun-13
CL04	163.744	20-Feb-12	Adult	M	197	7	Radio-collar recovered	18-Mar-12
CL05	163.856	20-Feb-12	Adult	F	802	15	Unknown – missing	2-May-14
CL06	163.543	20-Mar-12	Adult	M	734	130	Unknown – missing	25-Mar-14
CL07	163.556	23-Mar-12	Adult	M	68	19	Unknown – missing	30-May-12
CL08	163.843	24-Mar-12	Adult	F	53	19	Unknown – missing	16-May-12

[a] Total number of days from initial capture until contact was lost.
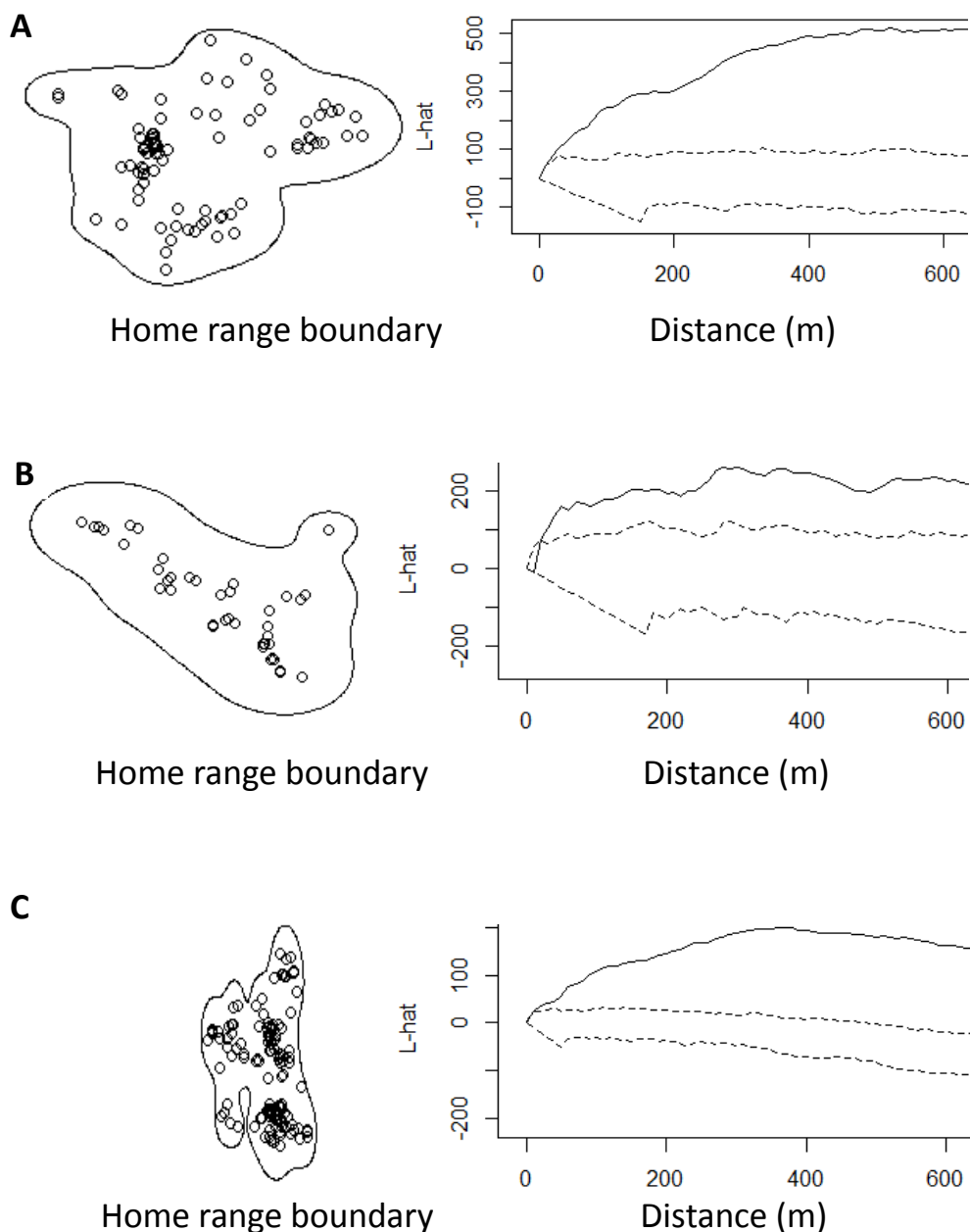
Figure 3.1. Home range boundaries defined by the 95% fixed-kernel density isopleth and radio-telemetry relocation data (left column) of coyote CL02 (A – northern) and (B – southern) and coyote CL06 (C) in the greater Detroit area of southeastern Michigan, August 2011 – March 2014. L-hat functions describing corresponding radio-telemetry relocation point patterns (right column) indicate significant departure from complete spatial randomness (CSR) as indicated by the observed L-hat rising above the envelope created by the 2 broken lines.
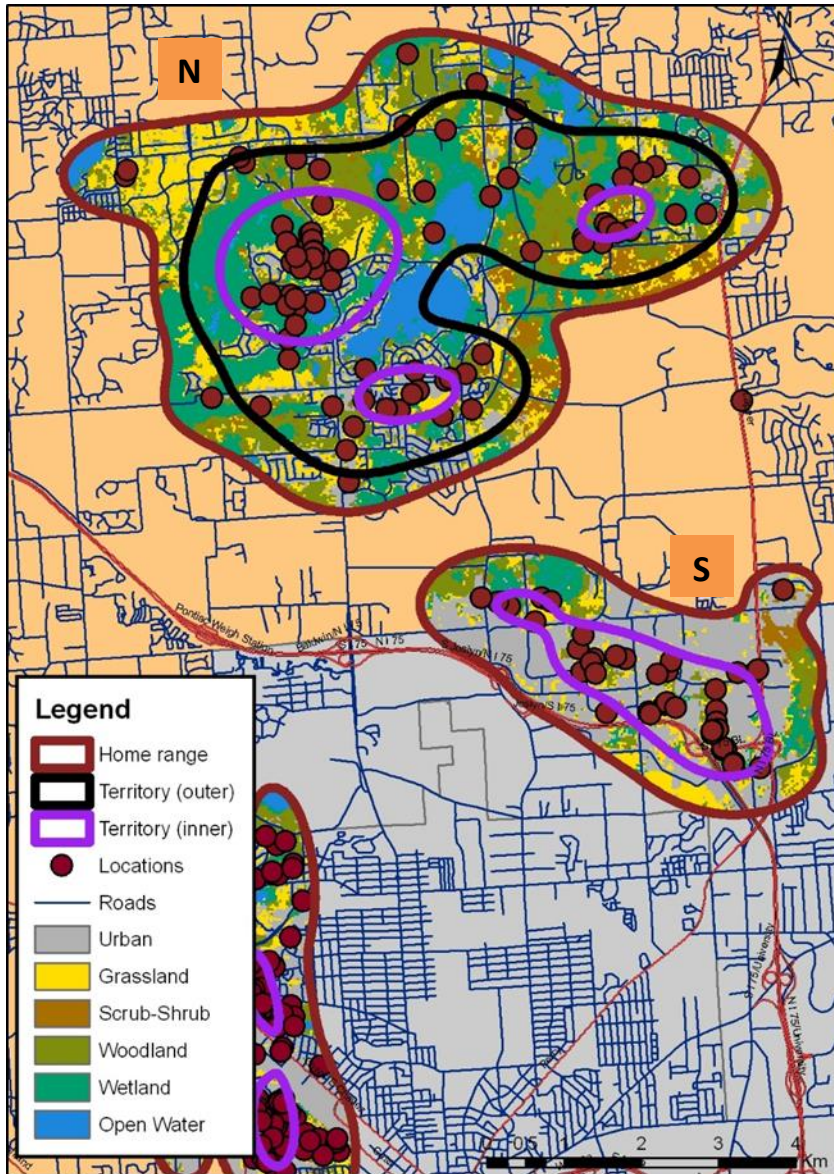
Figure 3.2. Northern (N) and southern (S) home range boundaries derived from the 95% isopleth of the fixed kernel density estimate and optimally partitioned isopleths of territorial boundaries of coyote CL02 in the greater Detroit area of southeastern Michigan, August 2011 – June 2013.

three CSR regions (Figure 3.2). The optimal isopleth for delineating the core areas of

CL06, was 23.1% which resulted in areas of 0.49 and 0.29 km^2 (Figure3. 3). The southern

core area of coyote CL02 was described by an optimal isopleth of 55.5% (49.3-56.3%)

corresponding to an area of 3.41 km^2 (Figure 3.2). The optimal isopleth for describing the
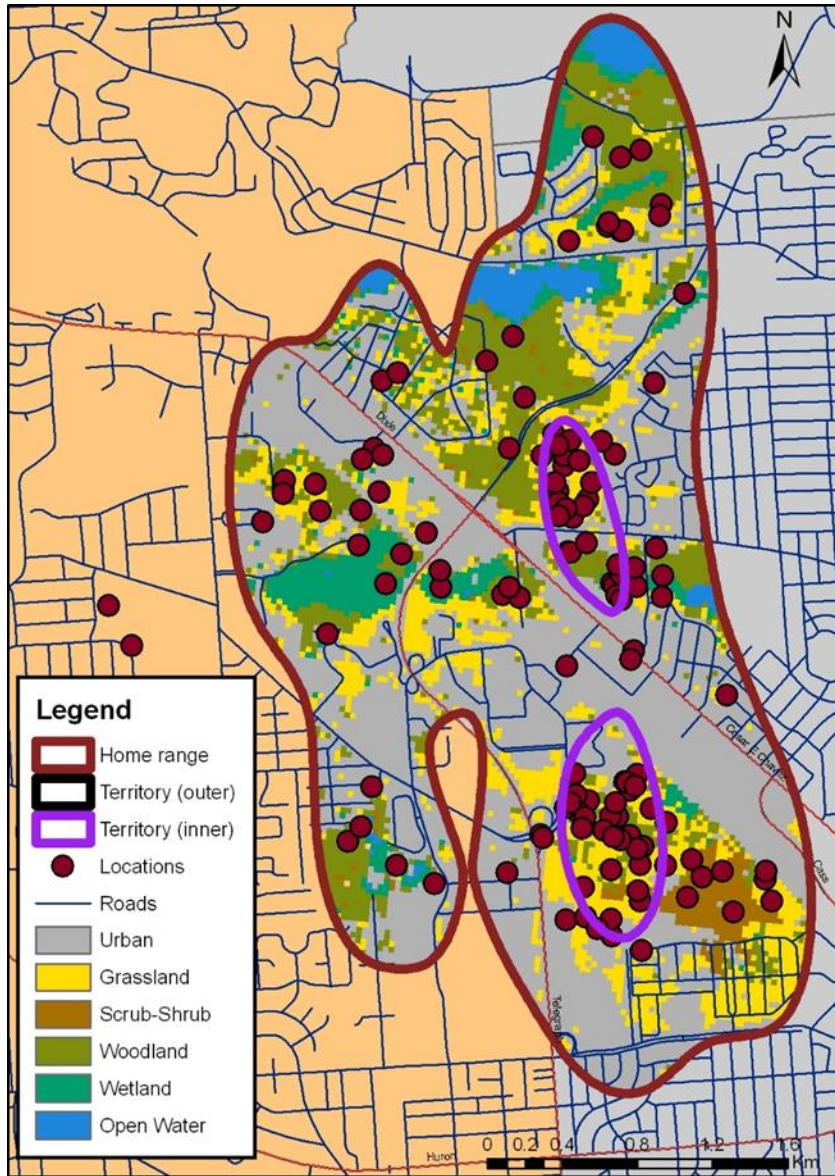
Figure 3.3. Home range boundaries derived from the 95% isopleth of the fixed kernel density estimate and optimally partitioned isopleths of territorial boundaries of coyote CL06 in the greater Detroit area of southeastern Michigan, August 2011 – March 2014.

northern inner core area of CL02, was 34.0% (30.6 – 37.3%) resulting in areas equaling 3.47, 0.66, and 0.42 km^2 (Figure 3.2). Although natural land cover (i.e., grassland, scrub-shrub, wetland, and woodland) was proportionally the most prevalent category at the home range and core area level, urban land cover was the predominant type at both

spatial scales (Table3.3, 3.4). Furthermore, at both the home range and core area, natural land cover was less fragmented and more connected than urban land cover (Tables 3.3, 3.4; Appendix C).

Compared to home ranges, core areas consisted of 13.2% more natural and 15.1% less urban land cover, were less fragmented (AWMPFD: natural 4.0% less, urban 9.3% less), had greater overall connectivity (CONNECT: natural 45.2% greater, urban 36.0% greater), and although urban land cover was still the dominant type, it was 53.8% less so. On an individual basis I found variation in the degree of fragmentation and connectivity in home ranges and core areas. Urban, both in terms of proportion and dominance, was the most prominent land cover within the southern home range and core areas of coyote CL02 (Figure 3.2, Table 3.3, 3.4) and the home range of coyote CL06 (Figure 3.3, Table 3.3). Within the core area of coyote CL06, grassland replaced urban as the dominant type of land cover (Figure 3.3, Table 3.4). Proportionally, natural land cover was the most common within the northern home range and territories of coyote CL02 with wetlands being the dominant type (Figure 3.1, Appendix C).

The long-distance movements made by the four adult (two male, two female) radio-collared individuals for whom I had insufficient location data to conduct home range analyses suggest that they were either transient individuals or dispersers. The sum of the straight-line distances travelled between successive relocations by these individuals from when they were radio-tagged until I lost contact ranged from 6.2 to 42 km (= 22.37).

Table 3.3. Proportion of land (PLAND), largest patch index (LPI), area weighted mean patch fractal dimension (AWMPFD), and connectivity (CONNECT) measures of natural and urban land use within the home ranges of coyotes in the greater Detroit area of southeastern Michigan, August 2011 – May 2012.

Coyote	HR (km²)	PLAND (%)			LPI			AWMPFD			CONNECT		
		Natural	Urban	% diff	Natural	Urban	% diff	Natural	Urban	% diff	Natural	Urban	% diff
CL06	10.49	44.03	53.19	-20.81	10.74	51.36	-378.39	1.14	1.29	-13.07	48.11	43.59	9.40
CL02S	11.37	38.37	61.29	-59.76	8.81	59.06	-570.62	1.11	1.26	-13.42	37.95	36.81	3.00
CL02N	34.10	73.57	18.91	74.29	17.57	8.33	52.59	1.15	1.25	-9.20	18.43	20.38	-10.53
Mean	18.65	51.99	44.47	14.47	12.37	39.58	-220.00	1.13	1.27	-11.89	34.83	33.59	3.56
SE	7.73	10.91	12.99		2.66	15.78		0.01	0.01		8.71	6.89	

Table 3.4. Proportion of land (PLAND), largest patch index (LPI), area weighted mean patch fractal dimension (AWMPFD), and connectivity (CONNECT) measures of natural and urban land use within the core areas of coyotes in the greater Detroit area of southeastern Michigan, August 2011 – May 2012.

Coyote	Core (km^2)	PLAND (%)			LPI			AWMPFD			CONNECT		
		Natural	Urban	% diff	Natural	Urban	% diff	Natural	Urban	% diff	Natural	Urban	% diff
CL06	0.78	71.00	28.88	59.32	31.07	13.81	55.56	1.13	1.14	-0.96	84.02	58.24	30.68
CL02S	3.41	35.06	64.87	-85.04	6.64	63.07	-849.60	1.07	1.26	-17.41	66.73	63.40	4.99
CL02N	4.55	73.68	22.13	69.96	1.89	0.34	82.29	1.07	1.08	-1.33	39.94	35.94	10.00
Mean	2.91	59.91	38.63	35.53	13.20	25.74	-94.96	1.09	1.16	-6.47	63.56	52.53	17.36
SE	1.12	12.45	13.26		9.04	19.07		0.02	0.05		12.82	8.43	1.12

DISCUSSION

It remains unclear whether resources are more available and of higher quality in smaller home ranges or larger ones, particularly if there is wide variation in the size of the home range, which is certainly true for coyotes in urban environments. Occupying a smaller home range suggests that resources occur in discrete, narrowly dispersed patches, whereas occupying a large home range indicates that resources are more widely dispersed. There is a prevailing trend for coyotes inhabiting urban landscapes to occupy smaller home ranges (Gehrt and Riley 2010), but habitat fragmentation resulting from urbanization may force coyotes to increase the area over which they search for resources. Access to important resources may be the primary driver of coyote home range size in urban landscapes. Because coyotes perceive habitat at large spatial scales they can assess the distribution of resources across the landscape (Atwood et al. 2004). Further,because of their high gap-crossing ability coyotes are capable of exploiting the small isolated resource patches often present in urban landscapes.

Like other studies of urban dwelling coyotes, I found variation in the size of coyote home ranges. The smallest home range that I estimated was 53% larger than that

reported by Gehrt et al. (2009) in Chicago, Illinois, and the largest was similar to thatreported by Way et al. (2002) in Cape Cod, Massachusetts. Home range size appeared to be inversely associated with urbanization, but the relationship was weak. The size of core areas, in contrast, appeared to be unrelated to urbanization, but there was a trend for smaller core areas to be associated with proportionally larger patches of natural land cover (Table 3.4). Close examination of the point pattern of radio-telemetry data revealed clusters of points in natural land cover and few scattered points in urban land cover

(Figure 3.2, 3.3). These results do not support my first hypothesis of no relationship between level of urbanization and size of coyote home ranges or core areas. Atwood et al. (2004) also found that coyote home range size was inversely correlated with urbanization and that core areas (50% KDE isopleths) contained proportionately more forested and corridor habitat than other available types. My results contrast with those reported by Gehrt et al. (2009) and Riley et al. (2003), however, who found a positive correlation between coyote home range size and proportion of urban land cover within the home range. Despite these disparate results, which potentially point to the coyotes' behavioral plasticity in navigating the urban matrix, coyotes consistently avoid urban areas regardless of the make-up of land cover within the home range (Gehrt and Riley 2010). Further investigation of behavioral plasticity in coyote movement should be a point of emphasis in future research.

Fragmentation, as measured by AWMPFD was low across all land cover categories and appeared to have little impact on the size of coyote home ranges or core areas. Fragmentation would likely have to be much greater before it negatively affected movement patterns of coyotes. Habitat fragmentation in urban landscapes can actually benefit coyotes by promoting the availability of communities of edge-adapted species that often serve as coyote prey (Patterson and Brown 1991). Although roads are a major source of fragmentation in urban environments, most roads, including freeways that receive high volumes of traffic, are not barriers to coyote movement (but see Riley et al. 2006). I often obtained separate locations of radio-collared coyotes on opposite sides of secondary roads within several minutes of each other. Roads can benefit coyotes by providing a nearly endless supply of carcasses of road-killed animals in a metropolitan

area. This may be uniquely relevant in southeastern Michigan where roughly 10% of the estimated 70,000 statewide deer-vehicle collisions occur (Deer Vehicle Crash Information Clearing House 2015, SEMCOG 2015).

Structurally, corridor habitats by definition increase fragmentation, but functionally can be very important for coyotes in urban environments. Vegetated corridors (utility rights-of-ways, e.g.) may provide coyotes with temporary or permanent habitat as well as connect and facilitate movement between natural habitat patches. Attwood et al. (2004) found disproportional use of corridor habitats (fence rows and ditches) by coyotes in west-central Indiana. Although my small sample size of radio-collared coyotes did not permit quantitative analysis of coyote habitat selection, I often found coyotes using corridor habitats. On numerous occasions radio-collared coyotes would move rapidly between isolated patches of natural habitat using corridors that bridged or by-passed the urban matrix. Coyotes will also use secondary roads, particularly in high-density residential areas, to move between nocturnal foraging areas (Grubbs and Krasuman 2009, Way et al. 2004).

Consistent with my second hypothesis, coyote home range and core areas increased in size as connectivity decreased (Table 3.3, 3.4). This result is curious because connectivity is inversely related to fragmentation. I would have expected to find a positive relationship between fragmentation and the size of coyote home ranges. The reason for this discrepancy is that AWMPFD weights patches based on size while CONNECT treats patch size equally and simply uses the number of functional joinings between like land-use patches. A more appropriate analog to AWMPFD would be the proximity index (PROX) which considers the size and proximity of all patches whose

edges are within a specified radius of the focal patch (McGarigal et al. 2012). I speculate that lack of connectivity at the home range level is less important than at the landscape scale, where it is critical for both transient and dispersing coyotes.

This study is unique in its opportunity to document a permanent home range shift by an individual coyote as it was occurring. Reasons for this shift are unclear; it is possible that the individual was usurped from his position of dominance in his family group, or perhaps his mate died. Notably, this coyote moved from a home range in which the land cover was > 70% natural to one where > 60% of the land cover of the home range was urban (Figure 3.2). In stable environments where coyote populations are naturally regulated and not trapped or hunted by humans, researchers have documented constancy in the size and position on the landscape of home ranges and territories among coyote pairs and packs between years (Althoff and Gipson 1981, Bowen 1981, Bekoff and Wells, Andelt 1985) over multiple generations (Kitchen et al. 2000b) and for extended periods of time (Young et al. 2006). Shifts in boundaries and fluctuations in territory size have been documented in coyote populations that experienced die-offs associated with a disease outbreak (Camenzind 1978) or high levels of human exploitation (Mills and Knowlton 1991), respectively. Gese (1989) documented the temporary abandonment of a territory by an alpha female after the death of her mate and subsequent permanent loss of a portion of her territory to an adjacent pack, even after she returned with a new mate

Urban areas may serve as de-facto refuges for coyotes because recreational hunting and trapping (except for removal purposes) are typically not lawful within municipal boundaries. Yet landscapes dominated by human development and activities

are very unstable, with natural land covers having habitat potential for wildlife developed over time into heavily human-dominated cover types. Shifts in the boundaries and fluctuations in the size of home range and territories of coyotes are often difficult to detect, but may occur more frequently in urban areas given the concomitant shifts in cover types that occur there.

Urban landscapes are fundamentally disturbed environments, such that coyotes have to adapt their space use patterns to shifts in cover types, loss of habitat, and the ever-changing spatial structure of the landscape. Despite a small sample size, I documented coyotes to use a variety of strategies to navigate the urban landscape. Coyotes whose home ranges consisted of more urban land cover than natural were three times smaller than the largest home range which consisted of 75% more natural land cover than urban, suggesting that food and cover resources were less dispersed in smaller home ranges. Coyote core areas tended to be concentrated in natural land cover. Movements of the lone coyote, whose core area consisted of more urban land cover than natural, were concentrated in natural land cover. These size/land cover relationships, and individual movement patterns suggest coyote avoidance or at least tolerance of urban land cover. The greater Detroit area is unique in that the landscape consists of substantial corridor habitat that probably facilitates coyote occupancy of areas with relatively high human activity, although this is speculative without quantifying the amount of corridor habitat and tracking coyotes.

SIGNIFICANCE AND CONCLUSIONS

Overview

My project is the first to investigate the ecology of coyotes in the greater Detroit area, and one of only a handful of studies on urban wildlife being conducted in southeastern Michigan. This study is unique because it explores the ecology of a native wildlife species re-occupying an urban landscape undergoing de-urbanization (physical decline of human population) and naturalization of many abandoned areas. The primary goal of my research was to gather baseline data on coyote ecology in the greater Detroit area to: (1) better understand how urbanization affects the distribution and habitat use of coyotes, (2) quantify coyote diets and foraging patterns, and (3) examine how urbanization, and fragmentation and connectivity of natural land cover affects the size of coyote home ranges and core areas. Fundamental to understanding the behavior of coyotes living in close proximity to humans is knowledge of how coyotes distribute themselves and use habitat across the landscape. To understand the coyotes' role as a top predator in urban environments requires knowledge of its diet, prey base, and mode of foraging. Finally, because of the coyotes' reliance on natural habitat, it is important to identify how urbanization affects coyote space use patterns.

Habitat use by coyotes in the greater Detroit area was similar to those residing in other human-developed areas. Coyotes preferred natural or naturalized habitats and tended to avoid developed areas. Areas surrounding locations of coyote evidence included greater than expected wooded and grassland land cover, but less urban. Fifty-eight percent of coyote evidence was collected in woodland-grassland edge habitat, despite equal effort to collect evidence in urban habitat, a strong indication of importance

edge habitat as foraging areas for coyotes. Cover habitat, particularly areas with trees, appeared to be more important than just the presence of open space or undeveloped areas. Within both urban and suburban areas, buffers surrounding locations of coyote evidence included more wooded habitat and less urban land cover than expected. Importantly, treed cover provides den site and daytime resting cover for coyotes.

Diets of coyotes inhabiting the greater Detroit area differed somewhat from those in other developed areas. Like the majority of other studies, white-tailed deer, eastern cottontail rabbit and small rodents were the three most consumed prey in both urban and suburban locations. Compared to other dietary studies, however, the proportion of biomass of white-tailed deer, raccoon, and woodchuck in coyote diets in my study was higher, particularly in suburban areas. I suggest that coyotes are scavenging more on road-killed animals in southeastern Michigan compared to other areas. This is speculative however because it is not possible to determine whether prey are killed or scavenged using scat analyses (Litvaitis (2000). Examination of the stomach contents of harvested and road-killed coyotes for the presence of fly larvae as an indication of scavenging may provide more information.

Michigan consistently records some of the highest numbers of deer-vehicle collisions (DVC) in the Midwest and numbers of road-killed raccoons, and woodchuck, as well as other wildlife may also be greater than in other developed areas. In suburban areas, coyotes foraged selectively on white-tailed deer throughout the year, regardless of numbers of DVC. In urban areas, coyotes appeared to forage both selectively and opportunistically with frequent switching among the top three prey. Further investigation

of coyote use of road-kill as a major food source should be a point of emphasis in future research.

The size of coyote home ranges as well as patterns relating home range size to proportion of urbanization within the home range varied; a result consistent with other studies in urban environments. Although my small sample size (n = 3) of home ranges precluded any rigorous statistical analyses my results were nevertheless interesting. There appeared to be an inverse relationship between home range size and proportion of urban land use within the home range, suggesting that coyotes reduce their use of space in urban areas. It is noteworthy, that I documented the permanent shift in the location of a radio-collared coyote's home range. Although, dramatic shifts in coyote home ranges are not uncommon, few have been documented in urban areas. Extreme shifts in coyote space use appear to occur after some type of major disturbance (e.g., heavy human exploitation, loss of a mate, disease outbreak). Because dramatic changes in land cover occur regularly in developed areas, shifts such as what I documented, likely occur regularly but may go undetected because of the difficulty of tracking coyotes in developed areas.

The reappearance of coyotes in the greater Detroit area and their appearance elsewhere in eastern North American metropolitan areas is an important conservation issue because coyotes are endemic to North America and their range expansion occurred naturally. Existence of coyotes near humans is a major challenge of wildlife management and an experiment in how modern society responds to the presence of a top carnivore. . . Although progress has been made in better understanding the coyotes' relationship to urbanization there is still a great deal that we do not know. Future research in urban

landscapes should further explore the importance of corridor habitats as travel routes and valuable areas for foraging and cover for coyotes. Coyote removal experiments could provide a wealth of knowledge about the coyotes' role as a top predator in urban environments and their potential to limit nuisance urban wildlife and how coyote space use patterns change in response to a shake-up in coyote social structure. Quantification of the density of carcasses of road-killed wildlife and use of physical biomarkers (e.g., metallic flakes, plastic bits or beads, Microtaggant® identification particles) sprinkled over carcasses and subsequently recovered in scat would provide data on the importance of road-kill as a major coyote food source.

APPENDIX A

Weighted frequency of occurrence of prey items (%WO) recovered in coyote scats in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. n = number of scats containing food item.

Food item	Breeding				Pup-rearing				Dispersal				Annual			
	Suburban		Urban		Suburban		Urban		Suburban		Urban		Suburban		Urban	
	%WO	n	%WO	n	%WO	n	%WO	n	%WO	n	%WO	n	%WO	n	%WO	n
Odocoileus virginianus	21.78	12	10.87	9	20.98	13	4.30	3	21.89	13	10.01	12	21.55	38	8.39	24
Sylvilagis floridanus	54.02	19	23.37	14	31.06	16	28.41	11	32.15	12	19.45	13	39.08	47	23.74	38
Small rodent[a]	14.67	17	36.85	17	25.65	12	46.15	18	17.72	13	30.94	25	19.34	42	37.98	60
Procyon lotor	0.09	1	10.00	6	7.42	2	1.18	3	11.95	4	9.84	7	6.49	7	7.01	16
Marmota monax	0.09	1	9.25	4	7.29	6	23.06	8	0.92	2	7.27	7	2.77	9	13.19	21
Ondatra zibethicus	0.13	2	8.69	3	2.33	1	4.26	1	6.44	5	13.17	4	2.97	6	8.71	10
Sciurus spp.	0.29	1	0.00	0	0.00	0	0.00	0	1.02	1	0.00	0	0.44	0	0.00	0
Rattus spp.	0.00	0	0.76	2	0.32	1	0.00	0	0.06	1	0.56	1	0.13	1	0.44	3
Canis lupus familiarus	8.76	3	0.00	1	0.66	2	0.60	1	0.00	0	0.17	2	3.14	3	0.25	5
Felis catus	0.00	0	0.00	2	0.00	0	0.82	0	0.00	0	0.00	0	0.00	0	0.27	2
Birds	0.13	4	0.00	0	0.76	2	0.00	0	0.01	2	0.00	0	0.30	8	0.00	0
Vegetation/fruit	0.03	1	0.00	2	3.53	1	2.32	1	7.22	7	6.48	2	3.58	8	2.93	5
Human	0.00	0	0.20	1	0.00	0	0.00	0	0.11	1	2.02	3	0.04	1	0.74	4

[a] *Microtus* spp. and *Peromyscus* spp.

APPENDIX B

Relative proportion (%) of biomass of prey items recovered in coyote scats in the greater Detroit area of southeastern Michigan, August 2010 – April 2013. n = number of occurrences of prey item, which for all prey except small rodent equals number of scats containing the prey item.

Prey item	Breeding				Pup-rearing				Dispersal				Annual			
	Suburban		Urban		Suburban		Urban		Suburban		Urban		Suburban		Urban	
	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n
Odocoileus virginianus	43.67	14	27.42	9	47.57	14	7.68	3	47.53	14	22.13	12	46.26	42	19.44	24
Sylvilagus floridanus	40.73	19	21.11	14	20.67	17	23.56	11	16.55	11	18.22	13	25.98	47	20.64	38
Small rodent[a]	4.16	100	7.17	184	7.20	114	28.52	148	17.12	39	11.75	156	9.49	252	15.33	488
Procyon lotor	0.22	1	18.34	6	6.90	2	12.99	3	6.39	3	13.26	7	4.50	6	14.67	16
Marmota monax	0.16	1	11.34	4	9.25	6	21.92	8	1.67	1	19.21	9	3.69	8	17.69	21
Ondatra zibethicus	2.03	2	7.40	3	2.18	1	2.86	1	3.66	5	12.11	6	2.61	8	8.00	10
Sciurus spp.	0.11	1	0.00	0	0.58	0	0.00	0	0.00	1	0.00	0	0.21	2	0.00	0
Rattus spp.	0.00	0	0.15	2	0.40	1	0.00	0	0.05	1	0.01	1	0.14	2	0.06	3
Canis lupus familiarus	8.90	3	2.50	1	6.13	2	2.47	1	3.63	1	3.31	3	6.23	6	2.83	5
Felis catus	0.00	0	2.80	2	0.99	0	0.00	0	0.00	1	0.00	0	0.30	1	0.98	2

[a] *Microtus* spp. and *Peromyscus* spp.

APPENDIX C

Proportion of land (PLAND), largest patch index (LPI), area weighted mean patch fractal dimension (AWMPFD), and connectivity (CONNECT) measures of land use within the home range (HR) and core areas of coyotes in the greater Detroit area of southeastern Michigan, August 2011 – May 2012.

Coyote	Land use	PLAND (%)		LPI		AWMPFD			CONNECT		
		HR	Core	HR	Core	HR	Core	% diff	HR	Core	% diff
CL06	Grassland	18.34	44.65	1.98	17.15	1.16	1.17	0.86	43.63	94.17	115.85
	Scrub-Shrub	2.72	3.45	2.13	2.99	1.13	1.09	-4.02	56.14	60.00	6.87
	Wetland	6.04	3.11	2.02	1.61	1.11	1.10	-0.97	48.19	100.00	107.50
	Woodland	16.93	19.79	4.61	9.32	1.17	1.17	-0.38	44.49	81.90	84.08
	Urban	53.19	28.88	51.36	13.81	1.29	1.14	-13.20	43.59	58.24	33.61
CL02 (South)	Grassland	13.54	13.81	2.19	2.29	1.08	1.06	-1.60	42.36	72.36	70.81
	Scrub-Shrub	2.65	0.16	1.83	0.05	1.13	1.01	-12.85	37.21	60.00	61.27
	Wetland	9.26	7.99	2.82	2.00	1.12	1.10	-2.17	35.65	64.43	80.74
	Woodland	12.92	13.10	1.97	2.29	1.11	1.12	0.26	36.59	70.13	91.68
	Urban	61.29	64.87	59.06	63.07	1.26	1.26	-0.37	36.81	63.40	72.22
CL02 (North)	Grassland	17.70	17.68	4.00	0.45	1.13	1.06	-6.73	17.41	32.95	89.26
	Scrub-Shrub	6.80	4.83	0.93	0.14	1.11	1.03	-8.04	19.83	42.68	115.25
	Wetland	24.67	32.59	9.28	0.69	1.17	1.11	-4.67	18.88	43.98	133.01
	Woodland	24.40	18.58	3.37	0.61	1.17	1.06	-10.13	17.62	40.13	127.68
	Urban	18.91	22.13	8.33	0.34	1.25	1.08	-15.70	20.38	35.94	76.38
Mean	Grassland	16.53	25.38	2.72	6.63	1.12	1.10	-2.38	34.47	66.49	48.16
	Scrub-Shrub	4.06	2.81	1.63	1.06	1.13	1.04	-8.19	37.72	54.23	30.43
	Wetland	13.32	14.56	4.70	1.43	1.13	1.10	-2.61	34.24	69.47	50.71
	Woodland	18.08	17.16	3.31	4.08	1.15	1.12	-3.26	32.90	64.05	48.63
	Urban	44.47	38.63	39.58	25.74	1.27	1.16	-9.34	33.59	52.53	36.05

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111

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ABSTRACT

ECOLOGY OF COYOTES (*CANIS LATRANS*) IN THE GREATER DETROIT AREA OF SOUTHEASTERN MICHIGAN

by

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Coyote distribution and habitat use, diet and foraging behavior, and space use patterns were investigated in the greater Detroit area of southeastern Michigan. We found evidence of coyotes on 24 of 30 (80%) suburban and 7 of 11 (64%) urban plots. Overall fifty-eight percent of coyote evidence was found within edge habitats, with den sites and tracks the only types of evidence found strictly in interior habitats. Land cover around evidence points included more wooded land cover than expected in suburban areas, suggesting the importance of tree cover for coyote occupancy, and more open space and wooded land cover than expected in urban areas, highlighting their avoidance of heavily populated areas. Coyote diet was assessed through identification of remains of food items recovered in coyote scat. White-tailed deer, eastern cottontail rabbit, and small rodents were the most consumed prey in both urban and suburban areas. Coyote consumption of white-tailed deer biomass was 7.2% greater than expected in suburban areas and 10.0% less than expected in urban areas and the difference was significant ($P < 0.004$). More white-tailed deer, raccoon, and woodchuck biomass was consumed compared to other

studies, likely due to high use of road-kill. In suburban areas, coyote selection for road-killed white-tailed deer was positive regardless of white-tailed deer or rabbit abundance. Coyotes in urban areas used a foraging strategy that incorporated both prey selection and switching, with no strong discernable pattern. Radio-telemetry technology was used to gather relocations of coyotes for analysis of home range and cores areas frequented by coyotes. Smaller home ranges were made up of greater proportions of urban land than natural land cover, although there was variation. Core areas were dominated by relatively large patches of natural land cover and had greater connectivity compared to home range areas. Radio-telemetry data suggested that coyotes were selective in their use of space, avoiding urban land in favor of natural land cover.

AUTOBIOGRAPHICAL STATEMENT

William (Bill) Dodge earned a B.A. (1983) in computer Science from Wilkes College (now University), and B.S. (1998) and M.S. degrees (2002) in wildlife management from Michigan State University. His M.S. thesis examined the survival, reproduction, and movements of moose (*Alces alces*) in the western Upper Peninsula of Michigan. He worked as a Computer Specialist with U.S. Fish & Wildlife Service, a Mapping Specialist with the Michigan Department of Environmental Quality, a Deer Management Assessment Assistant for the Michigan Department of Natural Resources, and a White-tailed deer Research Assistant with the Department of Fisheries and Wildlife at Michigan State University, and an Interpretive Naturalist with The Huron-Clinton Metropolitan Authority. His research interests include the ecology of mammalian carnivores, and predator prey interactions in both natural and urban environments.