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ECOLOGY AND BEHAVIOR OF COYOTES IN URBAN
ENVIRONMENTS AT VARYING SPATIAL SCALES

by

Sharon A. Poessel

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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2015

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ABSTRACT

Ecology and Behavior of Coyotes in Urban
Environments at Varying Spatial Scales

by

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Utah State University, 2015

Major Professor: Eric M. Gese
Department: Wildland Resources

Increasing global urbanization has altered landscapes for many wildlife species, including carnivores. Some carnivore species have been able to adapt to and even thrive in urban environments, including coyotes (*Canis latrans*). As coyotes continue to settle in more urban areas, human-coyote conflicts, such as attacks on humans or pets, are also increasing. Understanding the various factors affecting space use of urban coyotes may assist wildlife officials in reducing such conflicts. We conducted three studies of urban coyotes at varying spatial scales. First, using a captive population of coyotes at a fine spatial scale, we tested whether coyotes preferred urban, natural, or a mixture of habitat structures and whether sex, behavioral profile, biological season, or food manipulation affected coyote patch choice. When investigating novel environments, coyotes, especially females and bold animals, preferred a mixture of urban and natural structures rather than uniform structure. Food had no effect on patch choice, and coyotes appeared

to be primarily motivated by the structure of the habitat rather than by the amount of food within each habitat. Second, we examined home-range size, habitat use, and resource selection of 22 coyotes at a local, population scale in the Denver metropolitan area. Mean (\pm SD) home-range size of resident coyotes ($11.6 \pm 11.0 \text{ km}^2$) was smaller than ranges of transient coyotes ($200.7 \pm 232.4 \text{ km}^2$). Home-range size did not vary by season or sex, but resident coyotes during the day had smaller home ranges than during the night. Coyotes had high percentages of developed lands ($44.5 \pm 18.9\%$) within their home ranges, but the percentage of coyote locations in natural lands ($48.9 \pm 22.4\%$) was higher than in developed lands ($20.6 \pm 11.7\%$). Coyotes selected for natural lands over developed lands, and they increased activity at night. Finally, we surveyed 105 urban areas in the United States, focusing on the occurrence of coyotes and conflicts on a national scale. Larger urban areas were more likely to contain both coyotes and conflicts, and were also more likely to have greater numbers of conflicts. Urban areas in the western regions with larger amounts of high-intensity development and less forested and agricultural areas were more likely to have conflicts. Most urban areas considered the management of conflicts to be of low priority. We conclude from these three studies that coyotes residing in urban areas prefer to spend their time in natural lands where human activity is minimized, especially forested and riparian areas that provide cover for coyotes and their native prey. Habitat management practices, such as sustainable urban planning and landscape design incorporating wildlife habitat requirements, may be an important tool in reducing human-coyote conflicts in highly urbanized environments.

PUBLIC ABSTRACT

Ecology and Behavior of Coyotes in Urban Environments at Varying Spatial Scales

Sharon A. Poessel

As urban development continues to increase throughout the world, wildlife species, including carnivores, will be affected either positively or negatively. Coyotes (*Canis latrans*) have learned to efficiently adapt to highly developed areas, and conflicts between humans and coyotes, such as attacks on humans and pets, are increasing. We conducted three studies of urban coyotes to understand the factors affecting habitat use by coyotes so that wildlife managers can reduce human-coyote conflicts. Each study was conducted at progressively larger scales, with the first study at a fine scale using captive coyotes, the second study at a local scale in the Denver metropolitan area, and the third study at a national scale. Our results suggested that coyotes prefer a mixture of urban and natural habitat, and food does not play as large a role in coyote habitat choices as does habitat structure. Coyotes residing in urban areas will spend much of their time in natural areas where human activity is minimized, especially forested and riparian areas that provide cover for coyotes and their native prey. Urban areas throughout the United States were less likely to have human-coyote conflicts if they contained large amounts of forested and agricultural areas and smaller amounts of highly developed areas. Hence, we conclude that habitat management practices, such as increasing or preserving large forested and other natural habitat patches, should be a priority of urban wildlife managers

to provide coyotes with places to live. Recreational activity by humans and their pets should be minimized in these natural areas to reduce encounters between coyotes and humans. These practices should help prevent the continued increase of human-coyote conflicts in urban areas.

ACKNOWLEDGMENTS

The completion of this project was possible only with the assistance and support of many individuals. First, I am sincerely grateful to my advisor, Dr. Eric Gese, for his support, advice, and encouragement over the last several years. I am honored that he agreed to accept me as his student and allowed me to work with such an extraordinary wildlife professional. I also thank my committee members, Dr. Julie Young, Dr. Stewart Breck, Dr. Doug Ramsey, and Dr. Jim Powell, for their advice and guidance along the way. I particularly thank Dr. Julie Young for her ideas which led to two of my research projects, and Dr. Stewart Breck for allowing me to work on the Denver coyote project and for his tremendous assistance with field work, analyses, and manuscripts. I am also thankful to Susan Durham and Peter Mahoney for their statistical advice.

I am especially grateful to the employees and volunteers at the National Wildlife Research Center Predator Research Facility, including Stacey Brummer, Jeff Schultz, Erika Stevenson, Bonnie McDonald, Mike Davis, Leila le Caro, Alexia Legros, Caley Boone, Lewis Ferguson, Emily Wright, Blair Jones, Mélodie Belz, Delphine Napoletano, Marion Mahe, Corey Wallace, Beth Orning, Linsey Blake, and Matt Stevenson. Without their help, I would not have been able to successfully complete my captive coyote project. I am also thankful to the many individuals who assisted with field work for the Denver coyote project, including Jerry Brinker, Fred Quarterone, David Lewis, Jason Kougher, Ben Massey, Eleanor Mock, Rebecca Much, and Giancarlo Ulloa. Very special thanks go to Rick Sedbrook and Rob Raker; their assistance in the field was exceptional and their knowledge of coyotes was remarkable. I thank Lisa Wolfe and Karen Fox of

Colorado Parks and Wildlife for providing necropsy services. I am also grateful to the many wildlife agencies, animal control organizations, and police departments that responded to my questions for the coyote survey project.

Finally, I would like to thank all of the sources that provided funding for this project, without whom none of this work would have been possible. These sources include the Ecology Center at Utah State University, the Quinney Foundation, and U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center.

Sharon A. Poessel

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CHAPTER 1

INTRODUCTION

Global landscapes are becoming increasingly urbanized, and the world's human population is now dominated by more individuals living in cities than in rural areas (United Nations Population Fund 2007; Seto et al. 2012). By 2030 almost 5 billion people in the world will be living in urban areas (United Nations Population Fund 2007). Urban expansion significantly affects the natural environment and, therefore, many wildlife species (McKinney 2002; McDonald et al. 2008). Urbanization is one of the leading causes of species endangerment (Czech et al. 2000) and can have a negative impact on biodiversity (McDonald et al. 2008; Seto et al. 2012). However, in some cases, urbanization can enhance wildlife species richness (McKinney 2008) and increase densities of certain animal species (Prange et al. 2003; Magle et al. 2007). These species are able to persist in urban environments by modifying their behaviors (Tigas et al. 2002), habitat use (Prange et al. 2004), and foraging strategies (Fleischer et al. 2003).

Mammalian carnivores with large home ranges and low population densities may be negatively impacted by changes in their environment caused by human development, such as habitat loss, landscape fragmentation, and increased road density (Noss et al. 1996; Crooks 2002). However, some carnivore species have demonstrated an ability to adapt to and thrive in urban environments (Gehrt et al. 2010; Bateman & Fleming 2012). Carnivores residing in urban areas range from kit foxes (*Vulpes macrotis*; Cypher 2010) and mountain lions (*Puma concolor*; Beier et al. 2010) in North America to red foxes (*Vulpes vulpes*; Soulsbury et al. 2010) and Eurasian badgers (*Meles meles*; Harris et al.

2010) in Europe. Carnivores successfully occupying urban areas generally have small to medium body sizes, are dietary generalists, and behaviorally have a tolerance for humans (Fuller et al. 2010). Coyotes (*Canis latrans*) embody these characteristics (Gese & Bekoff 2004; Morey et al. 2007) and have colonized urban landscapes throughout North America (Gehrt et al. 2009; Gehrt & Riley 2010; Magle et al. 2014).

Coyotes are highly adaptable, opportunistic carnivores and habitat generalists (Bekoff & Gese 2003; Morey et al. 2007). They are usually the top wildlife predator in urban areas and positively impact urban ecosystems through predation and competition (Crooks & Soulé 1999; Gehrt & Riley 2010). Although the majority of urban coyotes tend to utilize the landscape in ways that avoid humans (Gehrt et al. 2009), some coyotes may become involved in human-coyote conflicts, primarily through attacks on pets and, occasionally, people (Grubbs & Krausman 2009; Gehrt & Riley 2010; Poessel et al. 2013). Such conflicts have become an important consideration for urban wildlife managers (Gehrt et al. 2009; Lukasik & Alexander 2011; Poessel et al. 2013). As a result, the coyote has been identified as one of the most controversial carnivore species in urban areas in North America (Gehrt 2007; Gehrt & Riley 2010).

Coyote populations generally respond positively to urban environments. In southern California, coyote occurrence increased with both proximity and intensity of urbanization (Ordeñana et al. 2010). Because coyotes have efficiently adapted to urban life, thorough knowledge of coyote spatial and temporal use of urban environments is critical in understanding carnivore use of the landscape and the potential for human-coyote conflicts (Gese et al. 2012). Previous studies of urban coyote ecology have

determined coyotes select natural habitat patches within their home ranges and minimize activity near areas of human development (Quinn 1997; Grindler & Krausman 2001; Gehrt et al. 2009; Gese et al. 2012). Research has also shown urban coyotes will become more active at night when humans are least active (Quinn 1997; Grindler & Krausman 2001; Riley et al. 2003). Hence, although coyotes use urban areas, they generally utilize natural areas integrated into or surrounding urban development, and they are most active at times when humans are not. Although these spatial and temporal patterns suggest that urban coyotes avoid humans, conflicts between coyotes and humans continue to increase in many urban areas (Gehrt & Riley 2010).

Previous research on urban coyotes has determined they may prefer certain natural habitat types, specifically forested patches or riparian areas that provide cover. In Indiana, coyotes occupied suburban areas with high housing densities adjacent to large forested patches (Atwood et al. 2004). In metropolitan Detroit, Michigan, habitat surrounding locations with evidence of coyote use (i.e., carcasses, dens, scats, tracks, or sightings) included more forested tracts than expected in both urban and suburban areas (Dodge & Kashian 2013). In the Chicago metropolitan area, Gese et al. (2012) found home ranges of coyotes in less-developed and mixed-habitat areas contained more riparian habitats than were available in the study area; Gehrt et al. (2009) also determined water habitats (i.e., retention ponds) were consistently highly selected by coyotes in the same study area. Hence, coyotes may thrive in highly developed areas when natural habitat patches providing protective cover are nearby and readily available.

Coyote use of urban areas may also be influenced by the availability of anthropogenic foods. Although urban coyote diets are typically dominated by native small mammals, such as rodents and lagomorphs (Fedriani et al. 2001; Morey et al. 2007; Lukasik & Alexander 2012), coyotes will sometimes take advantage of anthropogenic food sources associated with humans, placing them in increasing contact with humans and their pets (Gehrt & Riley 2010). The availability and abundance of food may be an essential determinant of coyote habitat use (Knowlton et al. 1999; Morey et al. 2007; Turner et al. 2011). However, food may not always influence coyote spatial patterns. Alternative factors, including habitat features or denning sites, might be more important than food in determining space use in coyotes (Young et al. 2008).

Human-coyote conflicts in urban areas can occur spatially in a nonrandom manner. In the Denver metropolitan area of Colorado, conflicts occurred more frequently than expected in developed areas and less frequently than expected in natural and agricultural areas (Poessel et al. 2013). In addition, conflicts occurred more often than expected in suburban areas and less often than expected in exurban and rural areas. In Calgary, Alberta, the highest numbers of conflicts were in two small parks located near the urban core of the city, and the fewest conflicts were in two large, natural parks located near the city boundary (Lukasik & Alexander 2011). Furthermore, conflicts were most often reported in close proximity to a river. Management of human-coyote conflicts may be an important priority for wildlife officials in many urban areas, and appropriate tools for addressing such conflicts are becoming increasingly essential (Poessel et al. 2013; Magle et al. 2014). Predicting where conflicts may likely occur, on both local and

regional scales, as well as understanding the factors influencing coyote decision-making regarding habitat selection or patch choice, would be an important step in developing such tools.

In this dissertation, we evaluated the behavior and ecology of coyotes in urban environments at varying spatial scales, with an objective of identifying variables that could help predict, and subsequently mitigate, human-coyote conflicts. In Chapter 2, we used a captive coyote population at a fine spatial scale to experimentally test which factors, including sex, behavioral profile, and biological season, affected coyote patch choice along a gradient from natural to urban habitat structure, and how manipulation of the quantity of food might guide coyote decision-making. We hypothesized that bold coyotes would use urban patches more than shy coyotes, and that food availability would affect coyote patch choice more than habitat structure. The results of this study should allow urban wildlife officials to predict coyote behavior related to space use and, thus, assist in reducing human-coyote conflicts.

In Chapter 3, we examined the spatial ecology of coyotes in the Denver metropolitan area of Colorado in terms of home-range size, habitat use, and resource selection. This study was conducted at a local scale of one particular urban area where human-coyote conflicts have increased in the last decade (Poessel et al. 2013). We hypothesized 1) home ranges of resident coyotes would be smaller than those of transients, 2) coyotes would have large amounts of natural areas within their home ranges, 3) home-range sizes would increase as the percent of developed areas within home ranges increased, 4) coyotes would use developed areas more at night than during

the day, and 5) coyotes would select natural habitat over developed areas. Our results will increase understanding of coyote ecology in the Denver metropolitan area, elucidate differences between coyotes in our study area and coyotes in other urban areas, and supplement current knowledge of urban coyotes in North America.

In Chapter 4, we expanded our research to a national scale to assess the environmental variables influencing whether or not coyotes or conflicts may occur in certain urban areas throughout the contiguous United States. Our primary objectives were to determine why some urban areas have coyotes and why some of those have conflicts by examining geographic, demographic, and climatic characteristics of those urban areas, including human population size, geographic region, land cover, housing density, and precipitation. Additional objectives were to determine annual rates of conflicts and the management priority for handling such conflicts. We predicted that most urban areas would contain resident coyotes and that urban areas without conflicts would contain higher amounts of natural areas, higher rural or exurban housing densities, and higher precipitation levels. We further predicted that management of conflicts would be of high priority for most urban areas and that larger urban areas would have higher annual rates of conflicts. Our results will allow urban wildlife managers throughout the coyote's range to forecast the most likely areas to contain coyotes and conflicts and, accordingly, to implement habitat management practices to mitigate such conflicts.

The results of these three studies contribute to current knowledge of urban coyote ecology and human-coyote conflicts. Urban wildlife officials and resource managers of urban areas throughout North America can use our results to proactively reduce conflicts

between humans and coyotes by implementing practices such as sustainable urban planning, landscape design that incorporates wildlife habitat requirements, and citizen education. Such practices will promote coexistence between urban citizens and wildlife and maintain the biological diversity of urban ecosystems.

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CHAPTER 2
INFLUENCE OF HABITAT STRUCTURE AND FOOD
ON PATCH CHOICE OF CAPTIVE COYOTES¹

Abstract

Increasing urban development can have significant effects on wildlife species, including carnivores. Some carnivore species have been able to adapt to and even thrive in urban environments, including coyotes (*Canis latrans*). The presence of carnivores in urban areas can sometimes lead to conflicts with humans and their pets. Although coyotes may frequently use urban areas, they also inhabit natural areas surrounding urban development. Understanding the various factors affecting patch choice of urban coyotes may assist wildlife officials in managing human-coyote conflicts. Both sex and behavioral profile can influence patch choice; bold individuals are more likely to be exploratory than shy animals, which can result in increased conflicts in urban environments. Using a captive population of coyotes, we tested whether coyotes preferred urban (anthropogenic) habitat structure, natural structure, or a mixture of structures and whether sex, behavioral profile, biological season, or food manipulation affected coyote patch choice. Coyotes generally preferred the control, homogeneous structure representing their natal habitat (mean percentage of time $23.3\% \pm 19.3$ SD; $P = 0.037$). The next most preferred habitat for coyotes, especially females ($23.7 \pm 16.6\%$ for 25% urban pen; $P = 0.020$) and bold coyotes ($27.8 \pm 23.2\%$ for 75% urban pen; $P = 0.005$), was a mixture of anthropogenic and natural structures rather than uniform

¹ Co-authors are Eric M. Gese and Julie K. Young; published by Elsevier in Applied Animal Behaviour Science at <http://www.sciencedirect.com/science/article/pii/S0168159114001178>.

structure (all natural or all anthropogenic), and this preference was more strongly expressed during the non-breeding season ($25.6 \pm 23.2\%$ for 75% urban pen; $P = 0.017$). Food had no effect on patch choice ($P = 0.983$); coyotes appeared to be primarily motivated by the structure of the habitat rather than by the amount of food within each habitat. Our results suggested that urban areas containing large amounts of both natural and anthropogenic structures are more likely to be used by coyotes and, thus, could have the potential for human-coyote conflicts.

1. Introduction

Patch choice theory states an animal will choose the most profitable patch, or the patch containing the highest density of prey (Goss-Custard, 1977; Krebs et al., 1977; Stephens and Krebs, 1986). However, some studies contradict this theory, reporting that animals are willing to expend more energy even when food is freely available (Forkman, 1991; Inglis and Ferguson, 1986; MacLean et al., 2005). Inglis and Ferguson (1986) suggested animals are willing to spend more time and energy foraging in order to gather information about their environment, including knowledge of alternative food sources. This concept might apply to animals that are more certain of their survival (Forkman, 1991) or have certain behavioral profiles, such as boldness (Kurvers et al., 2012).

Studies have shown individuals within many animal species can have varying personalities, or behavioral profiles (i.e., more bold or more shy; Gosling, 2001; Sih et al., 2004). Bold individuals are more likely to be exploratory, and shy individuals may exhibit a greater degree of vigilance in unfamiliar situations (Wilson et al., 1993).

Differences in behavioral profiles can affect animal movements, including the ability to

find novel food sources (Fraser et al., 2001), and can influence patch choice. Patch choice decisions may vary between urban and natural systems because animals living in urban environments frequently display different behaviors than animals living in rural areas (Sol et al., 2013). Certain behavioral profiles, e.g., boldness, might be important in successful colonization of urban areas (Lowry et al., 2011).

Global landscapes are becoming increasingly urbanized, and the world's human population is now dominated by more individuals living in cities than in rural areas (Seto et al., 2012; United Nations Population Fund, 2007). Urban development significantly affects the natural environment and, therefore, many wildlife species (McDonald et al., 2008; McKinney, 2002). Several species are able to persist in urban environments, including those species previously associated only with rural or undeveloped landscapes (Ditchkoff et al., 2006), by modifying their behaviors (Tigas et al., 2002), habitat use (Prange et al., 2004), and foraging strategies (Fleischer et al., 2003). Certain carnivore species have also demonstrated an ability to adapt to and thrive in urban environments (Baruch-Mordo et al., 2008; Beier, 1995; Gehrt et al., 2009; Riley et al., 1998). Patch choice in carnivores can be influenced by both landscape structure and the availability of food resources in fragmented landscapes (Mortelliti and Boitani, 2008), although cost-benefit thresholds may be reached beyond which carnivores cannot use highly-urban, human-dominated patches (Baruch-Mordo et al., 2013).

Coyotes (*Canis latrans*) are highly adaptable, opportunistic carnivores and habitat generalists (Bekoff and Gese, 2003; Morey et al., 2007) and are increasingly colonizing urban areas (Gehrt et al., 2009; Grindler and Krausman, 2001). Coyotes living in close

proximity to humans and their pets may cause conflicts, which have become an important consideration for urban wildlife managers (Gehrt et al., 2009; Lukasik and Alexander, 2011; Poessel et al., 2013). Although urban coyote diets are typically dominated by native small mammals, such as rodents and lagomorphs (Fedriani et al., 2001; Lukasik and Alexander, 2012; Morey et al., 2007), coyotes will sometimes take advantage of anthropogenic food sources associated with humans, placing them in increasing contact with humans and their pets (Gehrt and Riley, 2010). The availability and abundance of food may be an essential determinant of coyote habitat use (Knowlton et al., 1999; Morey et al., 2007; Turner et al., 2011). However, food may not always influence coyote spatial patterns. Alternative factors, including habitat features or denning sites, might be more important than food in determining space use in coyotes (Young et al., 2008).

Previous studies of space use in urban areas have shown coyotes select natural habitats within their home ranges and minimize exposure to human development (Atwood et al., 2004; Gehrt et al., 2009; Gese et al., 2012; Grinder and Krausman, 2001; Quinn, 1997; Riley et al., 2003). Hence, although coyotes may use urban areas, they generally utilize natural areas integrated into or surrounding urban development. Understanding the factors influencing a coyote's decision regarding patch choice could prove beneficial in managing human-coyote conflicts in urban areas and predicting coyote behavior related to space use.

Our objective was to determine which factors, including sex, behavioral profile, and biological season, affected coyote patch choice along a gradient from natural to urban habitat structure, and how manipulation of the quantity of food might guide coyote

decision-making. We defined habitat as the resources necessary for an animal to survive; however, we only manipulated food and the structure within the habitat. We used captive coyotes, maintained for research purposes, to experimentally test these factors. We hypothesized that bold coyotes would use urban patches more than shy coyotes, and that food availability would affect coyote patch choice more than habitat type.

2. Materials and methods

2.1. Study site

We conducted the study at the USDA/National Wildlife Research Center (NWRC) Predator Research Station in Millville, UT, USA, which houses a large population of coyotes maintained individually and in pairs. For this study, we used an interaction pen system consisting of one center pen and six pens (each pen 0.1 ha measuring approximately 40 m across at the widest point) surrounding and attached to the center pen by fenced alleys with gates at each end of the alleys (Fig. 2-1); the topography was flat. Each of the six outer pens contained a den box (0.5 m high \times 0.5 m diameter) with corn cob bedding (Green Products Company, Conrad, IA, USA), an automatic water source, and a 0.7 m high wooden shade table, which were standard items placed in all coyote pens at the facility. The center pen consisted of native grasses, i.e., native habitat, but no additional structures or plants; this habitat was similar to the environment in which coyotes at the facility were raised. Five of the six outer pens were designed to simulate a gradient of habitat structure from planted shrubs and trees (defined as “natural”) to anthropogenic structures (defined as “urban”); the coyotes at the facility

were unfamiliar with these types of habitat structures. The sixth outer pen remained similar to the center pen and acted as the experimental control pen (hereafter “control”). One pen was designated as all natural (hereafter “0% urban”) and included structurally native vegetation (i.e., shrubs and trees) planted before study commencement. Another pen was designated as all urban (hereafter “100% urban”) and included anthropogenic structures made from plywood and wood pallets, trash cans, a culvert, and solar lights placed on top of certain wooden structures. The remaining three pens included a mixture of natural vegetation and urban structures, with one pen containing 25% urban and 75% natural structural habitat (hereafter “25% urban”), one pen with 50% urban and 50% natural structural habitat (hereafter “50% urban”), and one pen including 75% urban and 25% natural structural habitat (hereafter “75% urban”). We randomly chose which of the six pens would receive each habitat design before study commencement. Due to the complexity of our habitat design, we were unable to randomly reallocate habitat structure to each pen before testing each study animal; thus, each pen retained its original habitat structure throughout the duration of the study. This constant habitat design, where each type of habitat structure remained in the same location, might have influenced the pen choices of our study coyotes. We also built a fence covered with black shade cloth (approximately 1.5 m tall) surrounding two sides of the interaction pen system (at least 15 m away from the pens) to block the view of study coyotes from other coyotes at the facility. This fence was built after the first two animals tested were observed interacting with coyotes in neighboring pens. We included these two animals in our data analysis because their results were similar to the results for animals tested after the fence was built

(i.e., preferred mixed habitat pens over uniform pens, although we did not analyze these data statistically). Finally, we placed a traffic counter (TrailMaster®, Goodson & Associates, Inc., Lenexa, KS, USA) at the entrance to each of the six outer pens to determine when a coyote entered or exited each pen. Each unit consisted of a receiver and transmitter with an invisible active infrared beam between them, and the receiver recorded the date and time the infrared beam was broken by a coyote. This system allowed us to determine the amount of time spent in a pen by calculating the difference between entrance and exit times. Study animals were fed a ground meat, commercial diet (Fur Breeders Agricultural Cooperative, Logan, UT, USA), which we froze into food balls. Water was provided *ad lib* in all six outer pens via an automatic watering system. Monthly temperatures at the study site ranged from a mean low of -11° C in December to a mean high of 33° C in July.

2.2. Study design

We tested a total of 24 coyotes individually. We chose an equal number (six) of coyotes from the following categories: bold males, bold females, shy males, and shy females. We determined bold versus shy coyotes from video recordings of each coyote being exposed to a plastic coyote model placed in their pens before this study began. We categorized coyotes that quickly approached the model as bold (mean latency to approach 1:05 min \pm 0:38 SD) and those that avoided it as shy (never fully approached the model), based on the definition of bold individuals as showing exploratory tendencies and shy individuals as retreating from unfamiliar situations (Wilson et al., 1993). By including boldness/shyness as a factor in the study, we could examine the variability in patch

choice due to behavioral or personality differences. All coyotes were ≥ 1.5 years of age. We tested three of the six coyotes in each group during the breeding season (November to April) and three during the non-breeding season (June to October). Order of testing was based on the availability of individual coyotes, but predominantly followed the pattern of shy female, bold male, bold female, and shy male.

We tested each coyote for 8 days. For the first 4 days we tested coyote patch choice based on habitat structure only, and for the next 4 days we tested patch choice based on both habitat structure and food. Because coyotes at the facility generally tend to eat their food quickly, we determined that 4 days was sufficient time to detect any changes in coyote patch choice based on food. We placed each coyote in the center pen on the first day, allowing free access to all of the pens. For the first 4 days, we fed the study animal 800 g of food in the center pen; this amount was similar to the amount of food all coyotes at the facility are given on a daily basis. Towards the end of day 4, we downloaded and analyzed the data from the six counters to determine the percentage of use within each of the six outer pens, calculated by dividing the amount of time the coyote spent in each pen by the total amount of time the coyote spent in the six outer pens. On days 5–8, to determine whether food could modify the coyote's patch choices, we partitioned 1575 g of food throughout the six outer pens on a decreasing scale based on an increasing percentage of use of the pens during days 1–4. For example, we placed the highest amount of food in the pen used the least percentage of time, and the lowest amount of food in the pen used the most. We divided the 1575 g of food as follows among the six pens: 800, 400, 200, 100, 50, and 25 g, effectively doubling the amount of

food in each pen from most-used to least-used pen. We closed the coyote in the center pen while the food was distributed among the six pens each day, then opened the gates to all of the pens at the same time, allowing the coyote access to all pens. At the end of day 8, we removed the coyote from the interaction pen system and downloaded and analyzed the data from the counters for days 5–8. We then cleaned the pens (i.e., removed scats) over the next 1–2 days and readied them for the next study animal.

We conducted observations on 14 (three bold females, four shy females, four bold males, three shy males) of the 24 coyotes to determine microhabitat use within the mixed structure pens. During the first 4 days a coyote was in the interaction pen system (when we tested coyote patch choice based on habitat structure only), we observed the study animal four times per day for 5 min. When the coyote entered one of the mixed habitat pens (i.e., 25% urban, 50% urban, or 75% urban pens), we recorded which habitat, urban or natural, the coyote used. Habitat use was defined as a coyote being located within one of the eight sections of a pen (see Fig. 2-1). Resources placed in each pen (i.e., water, dens, and shade tables) were rarely used by coyotes during our observations and, thus, did not influence microhabitat use. Certain microhabitats of the same type (urban or natural) were, by design, adjacent in the 75% urban and 25% urban pens, which could have influenced coyote use. At the end of the first 4 days, we summed the number of times each coyote used urban habitats and natural habitats while in the three pens, and we then calculated the proportion of times each coyote used each habitat in these pens. Animal handling protocols were approved by the Institutional Animal Care and Use Committee at the National Wildlife Research Center (QA-1931).

2.3. *Statistical analyses*

We used data from the traffic counters to determine patch choice, measured as percentage of time spent in each of the six outer pens. Because our data were compositional, i.e., the percentages of time spent in each pen summed to 100%, we transformed the percentage of time response variable with a log-ratio transformation (Aitchison, 1986), using the percentage of time in the control pen as the reference level. Thus, the transformed response variable consisted of dividing the percentage of time in each of the 0% urban, 25% urban, 50% urban, 75% urban, and 100% urban pens by the percentage of time in the control pen, then taking the log of each ratio. We assessed the effects on the response variable by using a linear mixed model with the coyote as a random-effects factor associated with the fixed-effects factors sex (female/male), behavioral profile (bold/shy), and biological season (breeding/non-breeding). Repeated measurements on a coyote was a random-effects factor associated with the fixed-effects factor food manipulation (before/after), and multiple observations on each coyote within each food manipulation trial was a random-effects factor associated with the fixed-effects factor pen. We also analyzed all two-way and three-way interactions among the various factors. We used an unstructured matrix to model the covariance structure for the multiple pen observations, which is analogous to a multivariate analysis of variance. We estimated denominator degrees of freedom using the Kenward-Roger method. For any significant interactions or main effects, we analyzed specific pairwise comparisons of interest with *t*-tests, correcting *P*-values with a Tukey adjustment. Only adjusted *P*-values that were significant are reported.

For the microhabitat data collected from the 14 observed coyotes, we conducted a chi-square test comparing the average percentage of time coyotes used urban and natural habitats while in the mixed pens with the expected percentage of time, based on availability of 50% each. We also ran a non-parametric Kruskal-Wallis test with the observed percentage of time spent in urban habitats while in the mixed pens as the response variable and sex and behavioral profile as predictor variables. We set the significance level to 0.05 for all statistical tests, which were two-tailed. We used SAS v.9.3 for all statistical analyses (SAS Institute Inc., 2011).

3. Results

All coyotes, on average, preferred the control pen (mean percentage of time $23.3\% \pm 19.3$ SD) throughout the study, followed by the 25% urban ($18.2 \pm 18.0\%$) and 75% urban ($18.3 \pm 19.4\%$) pens, the 50% urban ($15.8 \pm 17.4\%$) pen, and the 0% urban ($13.6 \pm 17.9\%$) and 100% urban ($10.7 \pm 13.1\%$) pens. When coyotes began using the interaction pen system after release, the known mean percentage of total experiment time spent in the center pen was $6.6 \pm 2.3\%$. Because we were only interested in coyote patch choice of the six designed pens, and because the center pen was primarily used by coyotes as a funnel between the outer pens, we did not consider center pen usage further. Females and males differed in pen choice (Table 2-1, Sex*Pen interaction), as did bold and shy coyotes (Table 2-1, Personality*Pen interaction). Coyote patch choice also differed between the two seasons (Table 2-1, Season*Pen interaction). Percentage of time spent in each pen also varied within sexes and behavioral profiles, pooled across both seasons (Table 2-1, Sex*Personality*Pen interaction). One additional interaction,

Sex*Personality*Food, was significant (Table 2-1); however, we did not consider this interaction further because we were only interested in the percentage of time coyotes spent among the different pens, and this interaction did not include Pen. No other interactions were significant, including any of those with Pen and Food.

Results for each pen are reported relative to the control pen. Percentage of time in the 75% urban ($18.3 \pm 19.4\%$) pen was higher than in the 0% urban ($13.6 \pm 17.9\%$) pen for all coyotes ($t_{37} = 2.89, P = 0.049$). Males preferred the 100% urban pen more than females ($t_{35} = 2.31, P = 0.027$; Fig. 2-2). Females preferred the 75% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37} = 3.67, P = 0.007$; 100% urban: $t_{37} = 3.05, P = 0.033$; Fig. 2-2), and they also preferred the 25% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37} = 4.17, P = 0.002$; 100% urban: $t_{37} = 4.32, P = 0.001$; Fig. 2-2). Males did not show any preference among pens.

Bold coyotes chose the 75% urban pen more than shy coyotes ($t_{32} = 2.44, P = 0.020$; Fig. 2-3). Bold animals chose the 75% urban pen more than both the 0% urban and 100% urban pens (0% urban: $t_{37} = 3.59, P = 0.009$; 100% urban: $t_{37} = 3.33, P = 0.017$; Fig. 2-3), whereas shy animals preferred the 25% urban pen over the 75% urban pen ($t_{37} = 3.11, P = 0.029$; Fig. 2-3).

Coyotes in the non-breeding season preferred the 75% urban pen more than coyotes in the breeding season ($t_{32} = 3.55, P = 0.001$; Fig. 2-4). Coyotes in the non-breeding season also preferred the 75% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37} = 3.26, P = 0.020$; 100% urban: $t_{37} = 3.20, P = 0.023$; Fig. 2-4). Coyotes in the breeding season did not show any preference among pens.

Bold female coyotes chose the 75% urban pen more than the 0% urban pen ($t_{37} = 3.64$, $P = 0.008$; Fig. 2-5), and bold male coyotes chose the 75% urban pen more than the 25% urban pen ($t_{37} = 3.52$, $P = 0.010$; Fig. 2-5). Shy female coyotes preferred the 25% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37} = 3.25$, $P = 0.020$; 100% urban: $t_{37} = 3.95$, $P = 0.003$; Fig. 2-5), and they also preferred the 50% urban pen over the 100% urban pen ($t_{37} = 3.93$, $P = 0.003$; Fig. 2-5). Shy male coyotes preferred the 100% urban pen more than shy female coyotes ($t_{35} = 2.76$, $P = 0.009$; Fig. 2-5). No differences in pen choice occurred between behavioral profiles within a sex.

For the microhabitat data, coyotes in the mixed habitat pens used urban habitats 51% of the time and natural habitats 49% of the time, which was proportional to availability ($\chi_1^2 = 0.03$, $P = 0.853$). The percentage of time coyotes spent in urban habitats within each mixed pen was not affected by sex or behavioral profile ($H_3 = 1.64$, $P = 0.651$).

4. Discussion

Habitat contains multiple components, including food and water resources, cover, and denning sites. In this study, we modified two components, the structure of the habitat and food, to evaluate their effects on patch choice by coyotes. Coyotes generally preferred the control pen, then the pens with a mix of natural and urban habitat structure, over the pens with 0% urban or 100% urban habitat structure. Because the control pen consisted of similar habitat in which captive coyotes at the predator research facility are raised, our results support the idea that coyotes imprint on their natal environment (Gantz and Knowlton, 2005). Our results also indicated that coyotes, when investigating novel

environments, prefer using heterogeneous habitats. Observations revealed that, when coyotes were in the mixed habitat pens, they used habitat according to availability, i.e., the percentage of time spent in urban and natural habitats within these pens was equal to the percentage of each habitat structure that was available. Such a habitat mixture is often preferred by wild coyotes, including urban coyotes (Rashleigh et al., 2008). Riley et al. (2003) found that only 10% of coyotes they studied had no non-natural area within their home ranges. Similarly, Gehrt et al. (2009) determined that only 8% of coyotes had no natural area (i.e., less-developed areas) within their home ranges, indicating coyotes usually select habitats containing natural areas with less human use and more cover.

Both female coyotes and bold coyotes followed the same general pattern in pen preference, choosing pens with a mixture of structure over pens with uniform structure. Shy female coyotes exhibited similar preferences, indicating that our overall results were most strongly expressed in females. Grindler and Krausman (2001) determined home ranges of females followed the overall trend in habitat selection for coyotes in their study, in that home ranges included a smaller proportion of natural areas and a larger proportion of residential areas than were available in the study area. These results suggest females exhibited strong preferences that might drive habitat selection and patch choice in coyotes, whereas the preferences of male coyotes, which may follow females rather than habitat, might be more equivocal and less likely to influence overall patterns.

Bold coyotes also preferred one of the mixed pens (75% urban pen) over the homogenous pens and chose this pen more than did shy coyotes. Few studies have been conducted measuring boldness in coyotes; however, such studies have been performed on

other species. Mettke-Hofmann et al. (2002) measured exploratory behavior (i.e., boldness) in 61 parrot species (*Psittaciformes*) and determined species that were more exploratory inhabited more complex habitats, including forest edges with a rich variety of vegetation. Evans et al. (2010) investigated boldness in urban and rural song sparrows (*Melospiza melodia*) and found urban birds were bolder towards humans than rural birds and showed higher levels of territorial aggression. Our results suggested bold coyotes might be more exploratory than shy coyotes, preferring the more complex habitats of the mixed pens, possibly because of the rich environment provided by habitat edges including large amounts of structural cover. In the context of patch choice theory, bold animals also may be more likely to explore heterogeneous patches to obtain information on alternative food sources.

Coyotes in the non-breeding season selected the 75% urban pen more than the uniform pens, and they also chose this pen more than did the coyotes in the breeding season. Because of courtship behaviors displayed by breeding coyotes (Bekoff, 1977), we might expect solitary coyotes during the breeding season to seek habitats located near other coyotes. At the NWRC facility, the mixed habitat pens (25% urban and 75% urban pens) were located closest to other coyotes. However, coyotes tested during the breeding season did not choose these pens as often as the coyotes tested during the non-breeding season. Hence, the proximity of conspecifics likely was not the reason our study animals preferred the mixed pens. Hernández and Laundré (2003) found coyotes used a greater diversity of habitat types during the pup-rearing season (coinciding with the non-breeding season in our study) but concentrated their activities in a single habitat type during

gestation (coinciding with our breeding season), consistent with our results. They linked these differences in habitat use to changes in behavior between the two seasons. For example, coyotes do not travel far from den sites while raising pups when both the adult female and pups need to be provisioned with food (Harrison and Gilbert, 1985), so perhaps using a variety of habitat types increases the amount of food found within a smaller area. However, coyotes in their study also used a variety of habitats during pair formation, which also coincided with our breeding season and contradicted our results. Perhaps our delineation of breeding and non-breeding seasons was too coarse to detect fine-scale differences in patch choice through a coyote's biological seasons; instead we only found distinct differences between the breeding and non-breeding periods.

Food had no effect on coyote patch choice. Once coyotes selected a pen, they continued to use that pen even when more food was placed in less preferred pens. Observations indicated the coyotes readily brought food from the pens they did not prefer into the pens they did prefer. Hence, our results were inconsistent with patch choice theory because coyotes did not choose the most profitable patch, i.e., the pen with the highest amount of food, but instead chose patches based on some other factor, most likely habitat structure. Wild urban coyote populations are believed to exist at higher densities than those in nonurban areas at least partially because of the abundant food resources found in urban environments (Fedriani et al., 2001; Gehrt and Riley, 2010; Quinn, 1997). However, our results suggest wild coyotes may choose urban areas for reasons other than food availability. Wild urban coyotes generally use a variety of urban environments, but their diet primarily consists of native foods (e.g., rodents) rather than anthropogenic

foods found in urban landscapes (Morey et al., 2007). Hence, urban coyotes may identify attractive habitat patches containing food resources, and then reside in adjacent patches that meet other criteria, such as structural cover.

Several factors may confound the application of our results to wild coyotes. First, the captive coyotes in our study could easily carry food from one habitat patch to another, a choice not always available to wild coyotes occupying larger areas. Second, we approximately doubled the amount of food given to coyotes on days 5–8; if the coyotes had received less food, we may have seen different results, i.e., they may have been more food-motivated in their habitat choices. Finally, coyotes in captivity are more likely to have settled into a daily routine where they are fed by humans on a regular basis. Foraging is a small part of a captive coyote's activity budget, comparable to wild coyotes that may spend as little as 4% of their time on foraging (Gese et al., 1996). Hence, food may not be a principal motivator in the decision-making of a captive coyote, similar to the findings of Young et al. (2008) for wild coyotes. Additionally, our findings that patch choice theory did not apply to our captive study animals do not undermine its importance in wild coyotes; additional testing in free-ranging coyotes would be necessary to examine this theory where resident coyote home ranges (averaging from $<1 \text{ km}^2$ [Young et al., 2006] to 121 km^2 [Boisjoly et al., 2010]) can be much larger than in captivity. Nevertheless, our results suggest coyotes primarily select habitat based on the structure of such habitat rather than food, especially when food can be easily transferred to a preferred habitat.

Habitat structure can affect the expression of certain behaviors by coyotes.

Wilson et al. (2012) determined that the mesic-meadows habitat was selected by coyotes when foraging, but this habitat type had no influence on selection when generalized across all behaviors. Studies on other captive vertebrate species have noted the importance of habitat structure. Tiebout and Anderson (2001) found Florida scrub lizards (*Sceloporus woodi*) preferred sandy habitat types over habitats containing coarse woody debris that are likely too warm and thermally stressful and, therefore, impede lizard movement. Similar to our results for female coyotes, habitat preferences were expressed more strongly in female lizards than in male lizards (Tiebout and Anderson, 2001). Martinez et al. (2010) determined common redstarts (*Phoenicurus phoenicurus*) preferred habitats with sparse vegetation over dense meadows, even with a four-fold increase of food abundance in meadows. These findings demonstrated that habitat structure was more important than food for common redstarts (Martinez et al., 2010), comparable to our results for coyotes.

Our results should assist wildlife officials in North America in managing their urban coyote populations. Managers should be aware that urban areas incorporating large tracts of natural lands or open space interspersed throughout the urban matrix may be more likely to be used by coyotes and, as a result, have greater potential for human-coyote conflicts. The availability of abundant food resources in urban areas is considered to be a principal attractant of coyotes to urban environments (Fedriani et al., 2001; Gehrt and Riley, 2010; Grinder and Krausman, 2001; Quinn, 1997). However, our findings show that, at least in some cases, coyotes may be primarily motivated by the structure of

the habitat and the amount of the habitat that consists of urban versus natural lands. Hence, managing the availability of complex habitats in urban areas may warrant further consideration by urban managers. Understanding that coyote behaviors can vary greatly based on sex and personality traits should also help urban managers in mitigating conflicts by implementing specific tools that target certain individuals. We found bold coyotes had clearer patch choices than shy coyotes. Home ranges of coyotes residing in developed areas may contain large amounts of urban lands, requiring coyotes to travel through a matrix of urban and nonurban landscapes, thus facilitating increased encounters with humans and their pets (Gese et al., 2012). The exploratory behaviors of bold coyotes might lead to increased aggression and conflicts with humans during such encounters (Evans et al., 2010). Identifying and focusing management efforts on bold individuals in urban areas might reduce the prevalence of conflicts. Urban wildlife officials, as well as citizens, should appreciate that coyotes are individualistic and can express a variety of behaviors and choices, including choice of habitat.

In conclusion, coyotes preferred pens with a mixture of both urban and natural structural habitats rather than pens with uniform structural habitats. This overall pattern in patch choice was most strongly expressed in females, bold coyotes, and coyotes in the non-breeding season. Contrary to our predictions, food had no influence on coyote patch choice; instead, coyotes chose pens based solely on habitat structure. These results, as well as results from future studies focused on managing individual coyotes with specific personality traits, should assist urban wildlife officials in managing their coyotes and mitigating human-wildlife conflicts.

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Table 2-1

Tests of main effects and interactions for the model analyzing percentage of time coyotes spent in each of six pens, 2011-2012.

Effect ^a	Numerator <i>df</i>	Denominator <i>df</i>	<i>F</i>	<i>P</i> -value ^b
Sex	1	31	1.23	0.276
Personality	1	31	0.66	0.423
Sex*Personality	1	31	0.05	0.832
Season	1	31	5.59	0.025
Sex*Season	1	31	1.96	0.171
Personality*Season	1	31	0.37	0.547
Sex*Personality*Season	1	15	0.62	0.442
Food	1	22	1.02	0.324
Sex*Food	1	22	0.40	0.534
Personality*Food	1	22	0.02	0.894
Sex*Personality*Food	1	16	4.81	0.044
Season*Food	1	22	0.04	0.837
Sex*Season*Food	1	16	2.61	0.126
Personality*Season*Food	1	16	1.04	0.322
Pen	4	34	2.88	0.037
Sex*Pen	4	34	3.37	0.020
Personality*Pen	4	34	4.54	0.005
Sex*Personality*Pen	4	34	3.97	0.010
Season*Pen	4	34	3.49	0.017
Sex*Season*Pen	4	34	1.15	0.349
Personality*Season*Pen	4	34	0.85	0.501
Food*Pen	4	34	0.09	0.983
Sex*Food*Pen	4	34	0.26	0.901
Personality*Food*Pen	4	34	0.66	0.626
Season*Food*Pen	4	34	0.18	0.947

^a Predictor variables for the model included sex of coyotes, either male or female (Sex), behavioral profile of coyotes, either bold or shy (Personality), season, either breeding or non-breeding (Season), before or after food manipulation (Food), pen number (Pen), and interactions among these variables.

^b Bold denotes significance at the 0.05 level.

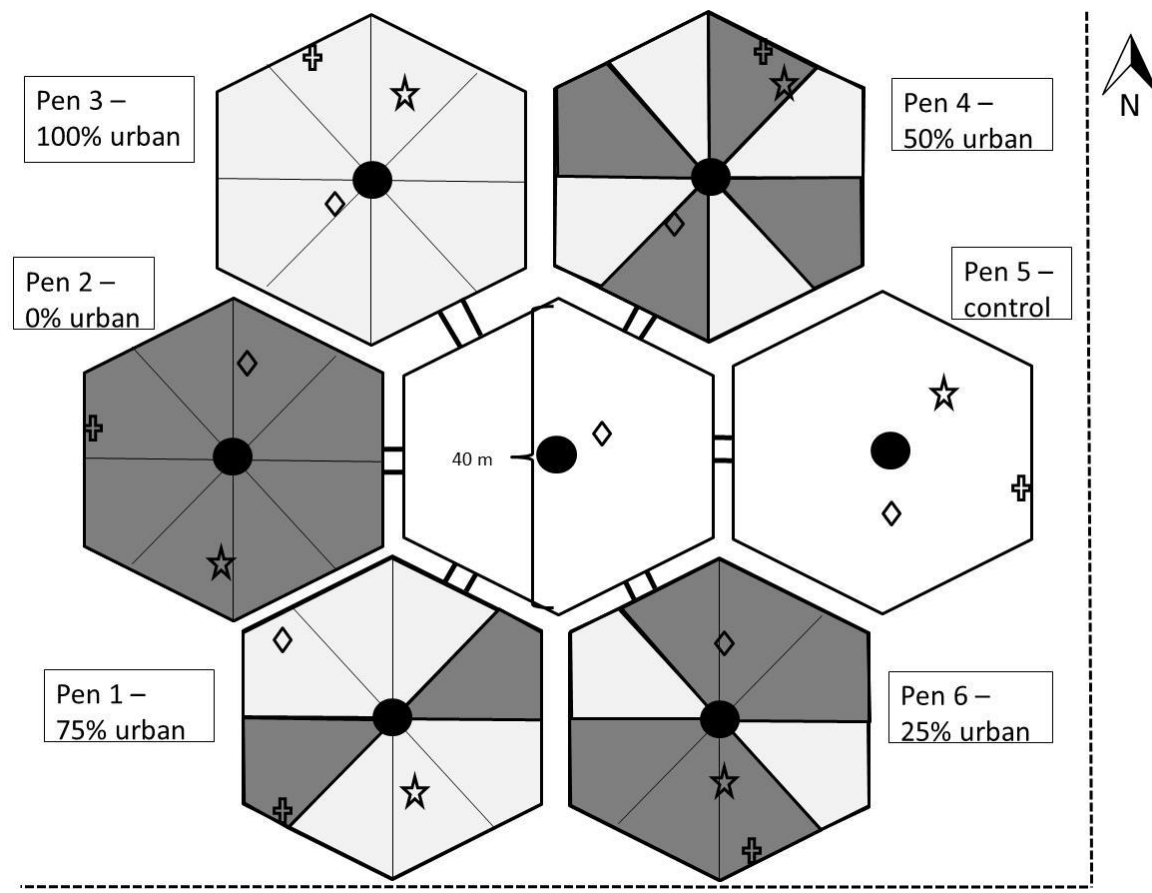


Fig. 2-1. Diagram of the interaction pen system at the USDA-WS-National Wildlife Research Center Predator Research Station. Each of five pens was divided into eight sections: urban sections (in light gray shading) included wooden structures and natural sections (in dark gray shading) included four plants. Two pens were left in an unmanipulated state. The dark circle represents where food was placed, the cross represents the placement of the watering system, the diamond represents the placement of the den, and the star represents the placement of the shade table in each pen. The dimension of a pen at its widest point is included on the center pen. The dashed line indicates the approximate location of the fence.

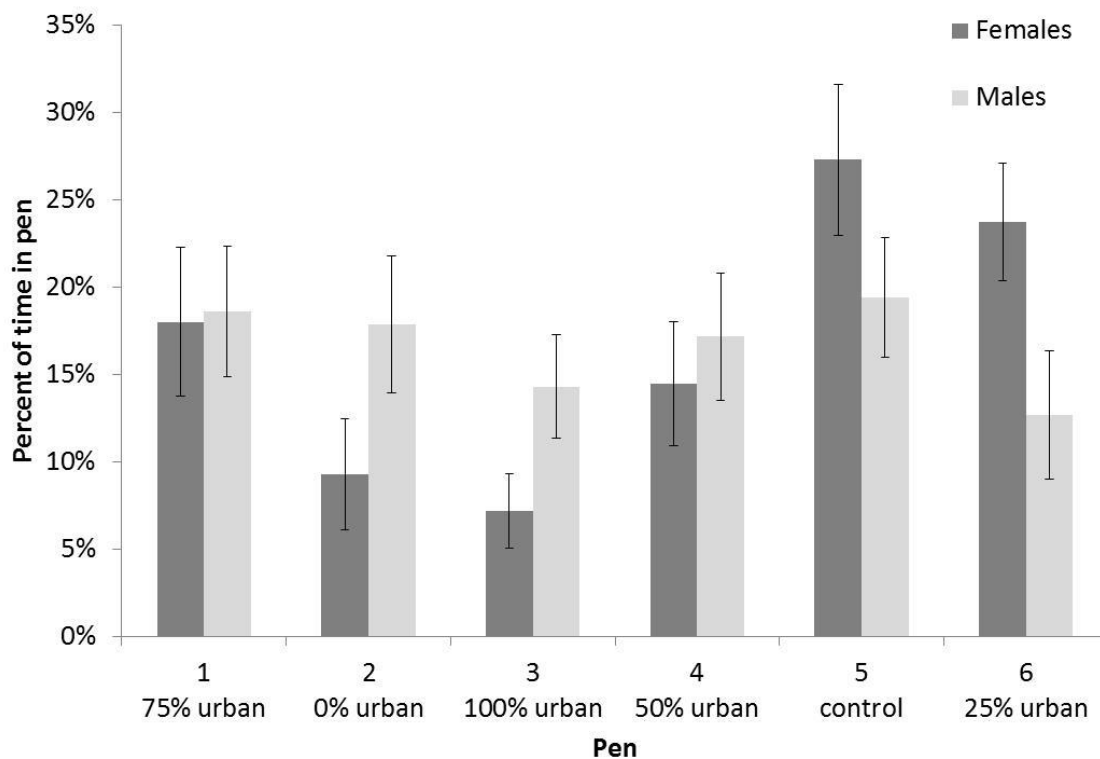


Fig. 2-2. Percentage of time spent in each pen by female and male coyotes. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

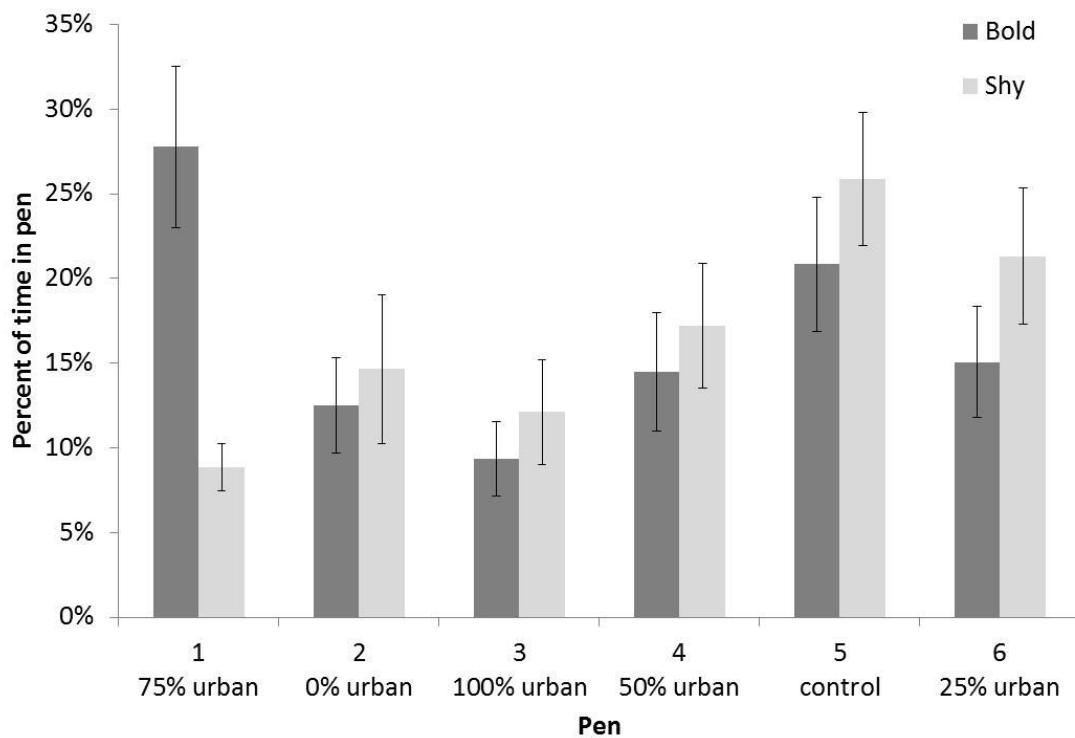


Fig. 2-3. Percentage of time spent in each pen by bold and shy coyotes. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

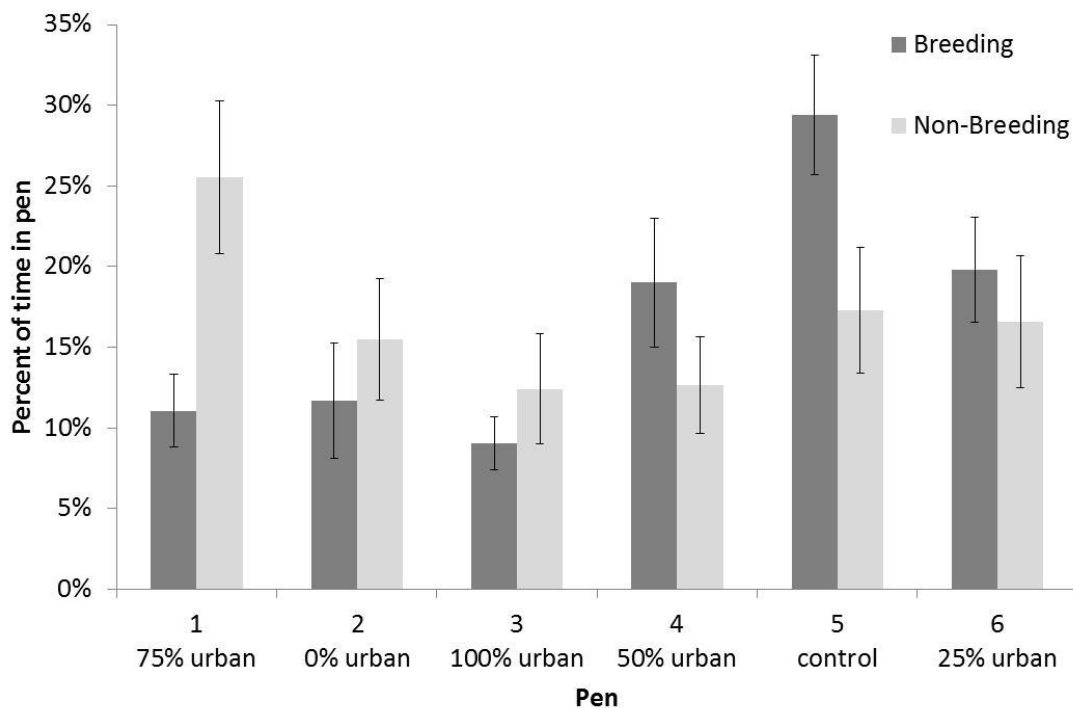


Fig. 2-4. Percentage of time spent in each pen by coyotes during the breeding and non-breeding seasons. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

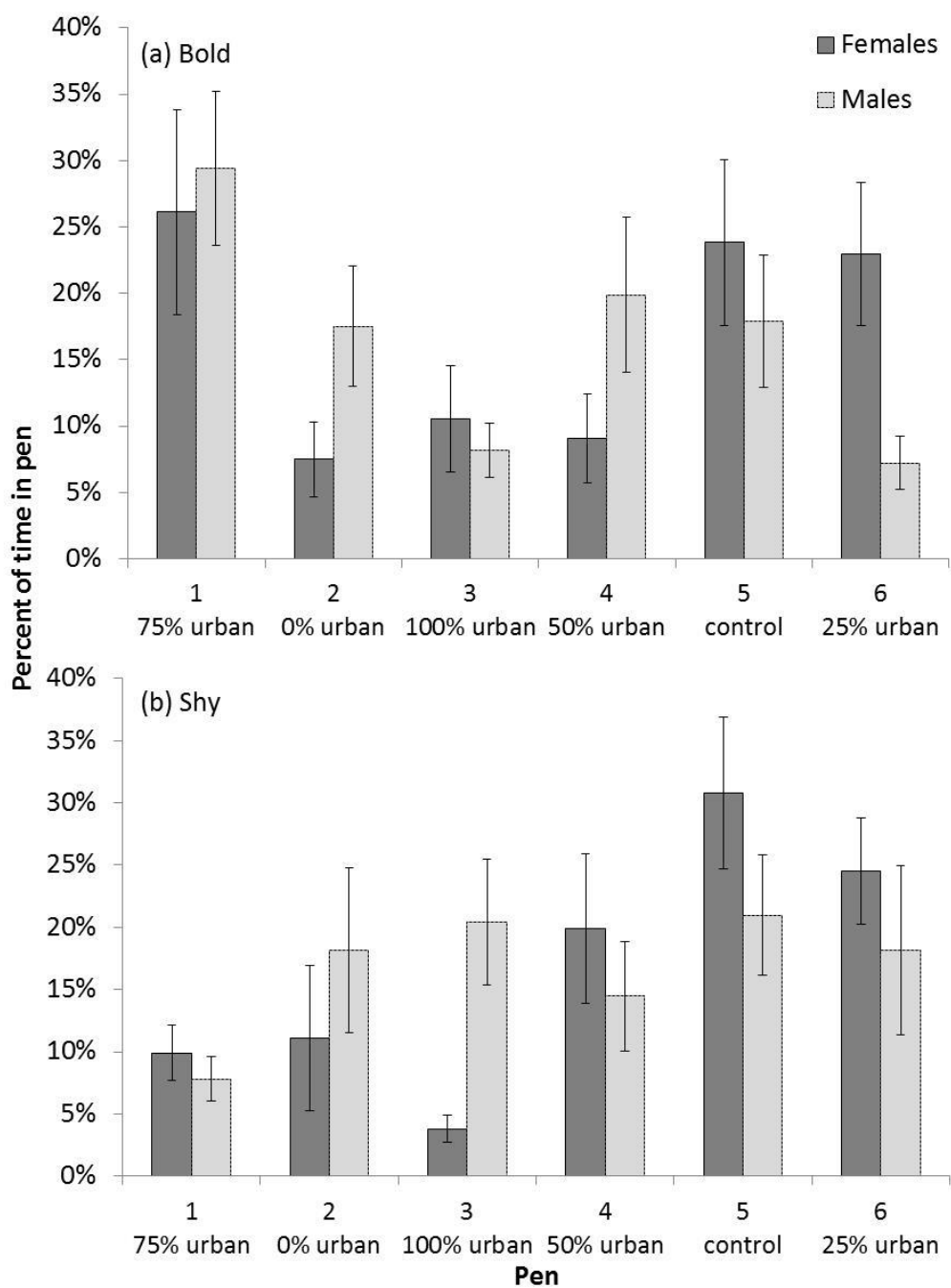


Fig. 2-5. Percentage of time spent in each pen by (a) bold and (b) shy female and male coyotes. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

CHAPTER 3

SPATIAL ECOLOGY OF COYOTES IN THE DENVER METROPOLITAN AREA: INFLUENCE OF THE URBAN MATRIX²

ABSTRACT

The increase of global urbanization has altered landscapes for many wildlife species, including carnivores. In many urban areas, carnivores may become involved in conflicts with humans and their pets. Coyotes (*Canis latrans*) are expanding into many urban areas throughout North America, and have become prevalent in the Denver metropolitan area of Colorado, where human-coyote conflicts are increasing. We examined home-range size, habitat use, and resource selection for 22 coyotes monitored with GPS collars during 2012–2014 in the Denver metropolitan area. Mean (\pm SD) home-range size of resident coyotes (11.6 ± 11.0 km²) was smaller than ranges of transient coyotes (200.7 ± 232.4 km²). Home-range size did not vary by season or sex, but resident coyotes during the day (7.2 ± 10.5 km²) had smaller home ranges than during the night (11.3 ± 10.8 km²). Coyotes had high percentages of developed lands ($44.5 \pm 18.9\%$) within their home ranges, contrary to previous urban coyote studies. However, the percentage of coyote locations in natural lands ($48.9 \pm 22.4\%$) was higher than in developed lands ($20.6 \pm 11.7\%$). Home-range size of residents was not related to either the percentage of developed lands or altered lands within home ranges. Coyotes selected for natural lands over developed lands, and they increased activity at night, similar to other urban coyote studies. Although coyotes are increasingly pervading urban

² Co-authors are Eric M. Gese and Stewart W. Breck.

landscapes and are able to thrive in home ranges containing large amounts of development, they continued to avoid areas with high human activity by primarily residing in areas with natural land cover. We conclude coyotes in the Denver metropolitan area have become efficiently adapted to a highly-developed landscape, reflecting the flexible nature of this opportunistic carnivore.

INTRODUCTION

Increasing urbanization of the world has greatly altered landscapes for many wildlife species (Czech et al. 2000; McKinney 2002). Mammalian carnivores with large home ranges and low population densities may be impacted by changes in their environment, such as habitat loss, landscape fragmentation, and increased road density, caused by human development (Noss et al. 1996; Crooks 2002). Although carnivores in urban areas can be ecologically and economically beneficial (Crooks and Soulé 1999; Hudenko et al. 2010), many carnivore species may come into conflict with humans and their pets or property (Curtis and Hadidian 2010).

Coyotes (*Canis latrans*) are opportunistic carnivores that are increasingly colonizing urban landscapes (Gehrt et al. 2009). Urban areas throughout the United States now report the occurrence of coyotes as well as human-coyote conflicts (see Chapter 4). Coyotes are usually the top wildlife predator in urban areas and positively impact urban ecosystems through predation and competition (Crooks and Soulé 1999; Gehrt and Riley 2010). However, coyotes also are involved in conflicts with urban residents, primarily through attacks on pets and, occasionally, people (Gehrt and Riley

2010; Poessel et al. 2013). As a result, the coyote has been identified as one of the most controversial carnivore species in urban areas in North America (Gehrt 2007; Gehrt and Riley 2010).

Coyote spatial and temporal use of urban environments has been studied in only a few North American metropolitan areas. These studies of urban coyote ecology have determined coyotes select natural habitat patches within their home ranges and minimize activity near areas of human development (Quinn 1997; Grinder and Krausman 2001; Gehrt et al. 2009; Gese et al. 2012). Home-range sizes of coyotes in urban environments may increase as the amount of urbanization within home ranges increases (Riley et al. 2003; Gehrt et al. 2009; Gese et al. 2012), suggesting large amounts of development may be less suitable habitat than natural areas (Riley et al. 2003). Research has also shown urban coyotes will become more active at night when humans are least active (Quinn 1997; Grinder and Krausman 2001; Riley et al. 2003). Furthermore, Gehrt et al. (2009) determined that urban coyotes, regardless of age, sex, social status, season, or activity period, were not attracted to human-associated areas within coyote home ranges. Although these spatial and temporal patterns suggested that urban coyotes avoided humans, conflicts between coyotes and humans continue to increase in many urban areas (Gehrt and Riley 2010).

Habitat use and selection in coyotes may differ between males and females and between residents and transients. Female coyotes may have stronger habitat preferences than males. Grinder and Krausman (2001) determined female habitat selection was the primary driver of the overall trend in coyote selection of habitat in their study. Poessel et

al. (see Chapter 2) also found that females exhibited strong preferences in habitat selection and patch choice, whereas males had no patterns in habitat preferences. Home ranges of resident coyotes may be more associated with natural habitats than those of transients. Gehrt et al. (2009) discovered home ranges of many resident coyotes, but not transients, in their study were almost completely contained within large natural habitat fragments, although natural land cover was nonetheless the dominant habitat type for both residents and transients.

Our objectives were to estimate home-range size, assess habitat use, and evaluate resource selection for coyotes in the Denver metropolitan area. We hypothesized 1) home ranges of resident coyotes would be smaller than those of transients, 2) coyotes would have large amounts of natural areas within their home ranges, 3) home-range sizes would increase as the percent of developed areas within home ranges increased, 4) coyotes would use developed areas more at night than during the day, and 5) coyotes would select natural habitat over developed areas. Our results will increase understanding of coyote ecology in the Denver metropolitan area, elucidate differences between coyotes in our study area and coyotes in other urban areas, and supplement current knowledge of urban coyotes in North America.

MATERIALS AND METHODS

Study area.—We conducted our study in the Denver metropolitan area, which included all or parts of 7 counties (Adams, Arapahoe, Boulder, Broomfield, Denver, Douglas, and Jefferson) and over 35 municipalities in north-central Colorado (Fig. 3-1).

The Denver urban area as defined by the U.S. Census Bureau spanned approximately 1,760 km² and had a human population size of almost 2.4 million in 2010 (United States Census Bureau 2012). Monthly temperatures during the study ranged from a mean low of -10°C in December to a mean high of 32°C in July, and average annual precipitation was 43 cm (Weather Underground 2014). The study area consisted of a gradient of urbanization and a variety of land cover types, including agriculture, grasslands, shrublands, and woodlands (Poessel et al. 2013; Magle et al. 2014).

Coyote capture and telemetry.—We captured coyotes with padded foothold traps and snares from April 2012 to May 2013, except during summer months when pups were active. We chose locations in open space parks and natural areas throughout the study area where we could gain access and minimize encountering people and pets. For trapping, we attached a tranquilizer trap device (TTD) designed to reduce injuries related to trapping (Sahr and Knowlton 2000). We also attached a trap monitor (Trap-Alert, New Frequency, Inc., Atlanta, Georgia) to the trap, which sent a text message to the researcher's mobile phone when an animal was captured in the trap, allowing us to arrive at the trap site and process the animal within 1-2 h of capture. Traps were covered during the day to minimize non-target captures. We used snares in only 1 location, and these were attached to openings in fences, did not include TTDs or trap monitors, and were checked each morning. Upon capture, we restrained coyotes with a pin stick, muzzled and blind-folded them, and used a rope to hobble their legs. We recorded sex, weight, temperature, morphological measurements, general body condition, and estimated age based on tooth wear (Gier 1968). We attached uniquely colored plastic ear tags and fitted

each coyote with a Global Positioning System (GPS) radiocollar. Once coyotes had recovered from the tranquilizer (if ingested), they were released at the capture site. Our procedures conformed to the guidelines of the American Society of Mammalogists (Sikes et al. 2011), and the Institutional Animal Care and Use Committee at the National Wildlife Research Center (QA-1972) approved trapping and handling protocols.

We used 1 of 3 types of GPS collars: 1) VECTRONIC GPS Plus (VECTRONIC Aerospace GmbH, Berlin, Germany); 2) Lotek GPS 3300S (Lotek Wireless Inc., Newmarket, Ontario, Canada); and 3) Telonics TGW-4400 (Telonics, Inc., Mesa, Arizona). We programmed VECTRONIC collars to acquire GPS positions 6 times per day every day and Lotek collars to collect GPS positions 6 times per day 4 days per week for coyotes captured in 2012 and 7 times per day every day for coyotes captured in 2013. Telonics collars were deployed only on coyotes captured at Rocky Mountain Metropolitan Airport in Broomfield, Colorado, where a separate study was conducted to determine hazing effects on coyotes located on airports (J. Kougher, USDA-Wildlife Services, personal communication, December 2012). These collars collected GPS locations 6 times per day every day until mid-October 2013, except for 1 week per month when locations were acquired every 15 min for 16 h per day to meet the objectives of that study. Beginning in mid-October 2013, the collars collected only 1 location every 11 h. For this study, we only used 6 locations per day every day, including during the weeks of intense locations, and the locations collected every 11 h. For all collars, we concentrated location acquisitions during nocturnal and crepuscular hours because urban coyotes are generally more active during these times (Grinder and Krausman 2001; Riley et al. 2003;

Gehrt et al. 2009; Gese et al. 2012). We downloaded data from collars either remotely from a receiver when the collars were still deployed (VECTRONIC collars) or directly from the collars after they were retrieved (Lotek and Telonics collars). All collars were equipped with automatic release mechanisms; we retrieved collars either when they dropped off or upon death of the animal.

Home-range size.—We estimated home-range size for each coyote by calculating 95% minimum convex polygons (MCPs) using the *adehabitatHR* package (Calenge 2006) in R (R Core Team 2014). We used MCPs rather than kernel home-range estimators because they more accurately characterized the space use of coyotes by including the areas between separate, disjunct polygons often created by kernel estimators (Riley et al. 2003; Gehrt et al. 2009; Riley et al. 2010), which could be important habitat for coyotes, especially when such habitat occurs in developed areas. These areas were also important to include within home ranges so that areas available for use by coyotes would be correctly estimated in resource selection functions. Several of our resident coyotes also exhibited exploratory movements which should not be considered part of the animal's home range, and 95% MCPs were more likely to remove these outliers than kernel estimators, which typically include all clusters of locations. Finally, our use of MCPs allowed us to more accurately compare our results to those of other urban coyote studies that used this technique to estimate home ranges.

We classified the status of each coyote as a resident or transient. A resident coyote used 1 unique area for ≥ 1 biological season, and a transient coyote did not settle in 1 area within 1 season (Gese et al. 2012). A coyote could be classified as both a resident

and a transient if the status changed over time (Gese et al. 1996); in these cases, we estimated 2 separate home ranges. We also estimated 2 different resident home ranges for any coyote that spent substantial time in 2 areas (see also Riley et al. 2003; Grubbs and Krausman 2009). We examined our data seasonally by allocating each location to 1 of 3 biological seasons (Laundré and Keller 1981): breeding (1 January–30 April), pup-rearing (1 May–31 August), and dispersal (1 September–31 December). Finally, we assigned time of day to each GPS location based on sunrise and sunset times. Day locations occurred between sunrise and sunset, and night locations occurred between sunset and sunrise.

We calculated home-range sizes by status, sex, season, and time of day. We included individual home ranges for each coyote that was monitored for at least half of 1 season. We used seasonal and temporal (i.e., day or night) home ranges for residents in analyses if area-observation curves reached an asymptote; such curves may not reach an asymptote for transients (Gese et al. 1990), so we included only those transient seasonal and temporal home ranges with at least 50 locations. For all analyses, the sampling unit was an independent home range for each individual coyote. We used *t*-tests to determine differences in individual home-range sizes between residents and transients and between males and females within each status group, and differences in temporal home-range sizes between day and night within each status group. We used analysis of variance to evaluate seasonal differences in home-range sizes by sex for resident coyotes. For each test, we log-transformed the home-range size response variable to meet distributional

assumptions. We conducted all analyses within R (R Core Team 2014), and we considered all statistical tests with $P < 0.05$ to be statistically significant.

Habitat use.—We report habitat use, in addition to resource selection, to provide descriptive data on the actual use of the landscape by coyotes, regardless of the availability of habitat. Only reporting whether or not coyotes selected a habitat type does not provide information on the animals' actual use of each habitat type, which could be important information, especially in urban areas where carnivore use of the landscape can be a concern to both residents and land managers (Riley et al. 2010). We examined coyote habitat use within home ranges by analyzing 2 variables, land-use and distance to roads. We first obtained land-use data from Landscape Fire and Resource Management Planning Tools (LANDFIRE 2013). We used ArcGIS v.10.0 (ESRI 2010) to condense this dataset, in 30-m resolution, into 11 types (Table 3-1). We further condensed 5 land-use types into a natural lands category, 2 types into an altered lands category, and 4 types into a developed lands category (Table 3-1). The natural lands category represented coyote use of natural habitat, the altered lands category represented coyote use of non-natural areas which were likely to be more attractive than developed areas but less attractive than natural habitat (Riley et al. 2003), and the developed lands category represented coyote use of developed landscapes. We then calculated the average percentage of coyote home ranges in each of the 3 land-use categories. We also assigned a land-use category to each coyote location and calculated the average percentage of locations in each of the 3 categories. Land-use association can be measured using either of these methods (i.e., percentage of home ranges or percentage of locations); we used

both methods to compare and contrast coyote actual use of each land-use type with the amount of each type in coyote home ranges.

We used simple linear regression in R (R Core Team 2014) to determine the relationship between the percentage of urbanization within a coyote's home range and home-range size. We conducted 2 regression analyses, 1 with the percentage of developed lands as the explanatory variable and 1 with the percentage of altered lands as the explanatory variable, with home-range size the dependent variable in both analyses. We log-transformed the home-range size response variable to meet distributional assumptions. For these analyses, we only used individual home ranges for resident coyotes.

We further analyzed the natural and developed land-use categories to determine how coyote land-use differed among the 5 natural and 4 developed types. We calculated the average percentage of coyote home ranges and the average percentage of coyote locations within each of the 5 natural land-use types and each of the 4 developed land-use types. We conducted all land-use analyses for the following coyote groups: all coyotes, by status, by time of day, and by time of day within status.

Next, we calculated the distance of each coyote location to the nearest highway or major road. We obtained road data from the Colorado Department of Transportation. Highways were defined as interstates, U.S. highways, and state highways. Major roads were defined as public roads classified as arterials (high-capacity urban roads that deliver traffic from collector roads to highways) or collectors (low-to-moderate capacity roads that deliver traffic from local streets to arterial roads). We combined both road types for

analysis. We used ArcGIS v.10.0 (ESRI 2010) to calculate the distance from each coyote location to the nearest road, and then averaged these distances for each of the coyote groups included in the land-use analysis.

Resource selection.—We used resource selection function models to investigate use versus availability of the 3 broad land-use categories and distances to roads. We examined 3rd-order selection only, i.e., use versus availability within a coyote's home range (Johnson 1980). We used the lme4 package in R (Bates et al. 2014) to run 3 sets of generalized linear mixed models (GLMMs) using individual, seasonal, and temporal home ranges. We included models for the seasonal and temporal home ranges to analyze resource selection by season and time of day; these 2 variables were not available in the models for the individual home ranges. For each model set, we used the coyote locations contained within each 95% MCP home range to represent use, and we generated 5,000 random points within each home range to represent availability. We used a large availability sample to ensure we adequately represented the available landscape and the logistic regression models accurately approximated point process models (Northrup et al. 2013).

All GLMMs included coyote ID as a random effect and sex, status, land-use, and distance to roads as fixed effects. We rescaled the distance to roads variable by subtracting the mean distance from each value and dividing by 2 times the standard deviation (Gelman 2008). For categorical variables, reference categories were female (sex), resident (status), and natural (land-use). The seasonal models also included season as a fixed effect, with breeding season as the reference, and the temporal models included

time of day as a fixed effect, with day as the reference. For each model set, we first ran a global model with all fixed effects and interactions between sex and land-use, status and land-use, sex and distance to roads, and status and distance to roads. We included additional interactions in the seasonal models between season and land-use and season and distance to roads, and we included interactions in the temporal models between time and land-use and time and distance to roads. We then used the MuMIn package in R (Barton 2014) to run all possible model combinations (Doherty et al. 2012) based on the global model in each model set. We used Akaike's Information Criteria (AIC) to select the best-performing models, based on $\Delta AIC < 6$, model weights, and evidence ratios, which indicate the strength of the top model relative to each model in the model set (Burnham and Anderson 2002; Anderson 2008).

Because only 1 model contained 100% of the model weights in each model set (see "Results"), we did not average models and only considered further each top model. We then used the effects package in R (Fox 2003) to calculate the effect displays, i.e., the mean probability of use, for each combination of predictors in the interactions for each top model. We used 95% confidence intervals for each effect to determine significance of contrasts between different predictor combinations. We then used these results to determine whether coyotes selected for roads or for certain land-use categories, and whether such selection differed by sex, status, season, or time of day.

RESULTS

Capturing and locating coyotes.—We captured and radiocollared 32 coyotes (18 males, 14 females). Of these, we were able to retrieve data from the collars of 24 coyotes (14 males, 10 females). Of the 8 coyotes for which we did not retrieve data, 6 coyotes either dispersed from the study area or the collars malfunctioned so we could not receive a signal, 1 coyote was killed by a vehicle and the collar was too damaged to retrieve the data, and 1 coyote had a collar that did not drop off as scheduled. We had a sufficient number of locations from 22 coyotes (13 males, 9 females) to estimate home-range sizes (mean \pm *SD* = 1,236 \pm 712 locations, range = 217–2,449 locations); these coyotes were monitored an average of 316 \pm 163 days (range = 57–569 days) between April 2012 and June 2014.

Home-range size.—We estimated 28 individual coyote home ranges, including 2 home ranges (1 resident and 1 transient) for 4 coyotes (2 males, 2 females) and 2 separate resident home ranges plus 1 transient range for 1 female coyote. Two of the 4 coyotes with 2 home ranges were juveniles whose status switched from resident to transient as they dispersed from their natal home ranges, 1 coyote was a transient when captured who then settled into a resident home range, and 1 coyote was a resident male who lost his mate, dispersed in search of a new mate, then returned to his original home range with his new mate. The female coyote with 3 home ranges dispersed from a resident territory then settled into a different resident home range. We estimated 54 temporal home ranges (26 day and 28 night) and 65 seasonal home ranges (20 breeding, 21 pup-rearing, and 24 dispersal). Mean (\pm *SD*) home-range size of resident coyotes (11.6 \pm 11.0 km²) was

smaller than transient coyotes ($200.7 \pm 232.4 \text{ km}^2$; $t_{10} = -6.70$, $P < 0.001$). Resident home-range size for males ($11.3 \pm 4.8 \text{ km}^2$) was not different than females ($11.9 \pm 16.1 \text{ km}^2$; $t_{11} = 1.00$, $P = 0.337$), nor was transient range size different between males ($288.9 \pm 315.5 \text{ km}^2$) and females ($112.6 \pm 75.9 \text{ km}^2$; $t_6 = 1.03$, $P = 0.342$). Home-range size for resident coyotes during the day ($7.2 \pm 10.5 \text{ km}^2$) was smaller than during the night ($11.3 \pm 10.8 \text{ km}^2$; $t_{33} = -2.61$, $P = 0.014$), but home-range size for transient coyotes was not different between day ($202.8 \pm 214.2 \text{ km}^2$) and night ($191.6 \pm 228.7 \text{ km}^2$; $t_{13} = 0.37$, $P = 0.716$). Seasonal coyote home ranges of residents did not vary by season ($F_{2,48} = 1.54$, $P = 0.226$) or sex ($F_{1,48} = 1.07$, $P = 0.306$).

Habitat use.—Percentages in each land-use category and type are reported for the all-coyote group, unless otherwise indicated; statistical analyses of coyote habitat selection are reported in the resource selection section below. For the land-use analysis using the 3 broad categories, home ranges of each coyote group, except resident coyotes during the day, had the highest mean ($\pm SD$) percentages in the developed lands category ($44.5 \pm 18.9\%$), the next highest mean percentages in the natural lands category ($32.5 \pm 22.9\%$), and the lowest mean percentages in the altered lands category ($23.1 \pm 14.6\%$). Home ranges of resident coyotes during the day had a higher mean percentage of natural lands ($40.7 \pm 29.7\%$) than developed lands ($34.2 \pm 20.9\%$; Fig. 3-2). In contrast, the mean percentage of coyote locations in natural lands ($48.9 \pm 22.4\%$) was highest for every coyote group, the mean percentage of locations in altered lands ($30.5 \pm 19.5\%$) was intermediate for each coyote group, and the mean percentage of locations in developed lands ($20.6 \pm 11.7\%$) was lowest for every coyote group (Fig. 3-2). Each of the 3 land-

use categories was included in every coyote's home range, and each coyote had locations in each category. Home-range size of residents was not related to the percentage of developed lands within home ranges ($F_{1,18} = 0.003$, $P = 0.959$, $R^2 = 0.0001$; Fig. 3-3a) or the percentage of altered lands within home ranges ($F_{1,18} = 1.042$, $P = 0.321$, $R^2 = 0.0547$; Fig. 3-3b).

For the natural lands analysis, home ranges of each coyote group, except transients, had the highest mean percentages in riparian ($37.9 \pm 28.1\%$) and the lowest mean percentages in sparse ($1.6 \pm 1.5\%$). Home ranges generally contained low average percentages of forest ($8.0 \pm 9.7\%$) and intermediate average percentages of shrubland ($25.3 \pm 19.5\%$) and grassland ($27.2 \pm 15.0\%$; Fig. 3-4). For transient coyotes, the mean percentages of home ranges in riparian ($32.5 \pm 24.9\%$) and shrubland ($32.6 \pm 17.4\%$) were similar. Similarly, the mean percentage of coyote locations in riparian ($41.6 \pm 28.7\%$) was highest, and in sparse ($0.7 \pm 1.2\%$) was lowest, for every coyote group except transient coyotes during the night. The mean percentages of coyote locations in forest ($12.7 \pm 13.9\%$), shrubland ($21.4 \pm 19.3\%$), and grassland ($23.7 \pm 11.8\%$) were low to intermediate for each coyote group (Fig. 3-4). Transient coyotes in the night had higher mean percentages in shrubland ($31.4 \pm 14.6\%$) and grassland ($33.3 \pm 15.5\%$) than in riparian ($26.2 \pm 23.7\%$). One coyote had no riparian habitat and 5 coyotes had no sparse habitat within their home ranges. Three coyotes had no locations in forest, 1 coyote had no locations in shrubland, 1 coyote had no locations in riparian, and 8 coyotes had no locations in sparse habitat.

For the developed lands analysis, home ranges of each coyote group had the highest mean percentages in areas of low development ($44.1 \pm 7.0\%$), the next highest mean percentages in roads ($35.7 \pm 8.0\%$), the next highest mean percentages in areas of medium development ($17.0 \pm 6.2\%$), and the lowest mean percentages in areas of high development ($3.2 \pm 3.0\%$; Fig. 3-5). Similarly, the mean percentage of coyote locations was highest in either areas of low development ($47.2 \pm 17.0\%$) or in roads ($45.6 \pm 19.2\%$), the next highest in areas of medium development ($6.8 \pm 5.5\%$), and lowest in areas of high development ($0.4 \pm 1.0\%$), for each coyote group (Fig. 3-5). Two coyotes had no areas of high development in their home ranges, and 15 coyotes had no locations in areas of high development.

The average ($\pm SD$) distance for coyote locations to the nearest road was 355 ± 235 m for all coyotes, 351 ± 189 m for residents, 365 ± 349 m for transients, 378 ± 271 m for day locations, 338 ± 204 m for night locations, 370 ± 230 m for day locations of resident coyotes, 401 ± 380 m for day locations of transient coyotes, 341 ± 172 m for night locations of residents, and 332 ± 288 m for night locations of transients. Three of the 4 coyotes with the largest nearest distances to roads (i.e., farthest from roads) also had the smallest percentages of developed lands within their home ranges.

Resource selection.—In each of the 3 model sets, the fully-parameterized global model with all interactions was the top model with 100% of the model weights (Table 3-2). In the individual model, females and males had no differences in their use of all 3 land-use categories (Fig. 3-6a). Within females and males, both groups used natural and altered lands the same, but used developed lands less than both natural and altered lands

(Fig. 3-6a). Resident coyotes used natural lands more than transients, but use of altered and developed lands was similar between the 2 groups (Fig. 3-6b). Within residents and transients, both groups used natural and altered lands the same, but used developed lands less than both natural and altered lands (Fig. 3-6b). Female coyotes (Fig. 3-6c) and transient coyotes (Fig. 3-6d) selected for roads, with higher probability of use of habitat closer to roads. Male coyotes (Fig. 3-6c) and resident coyotes (Fig. 3-6d) had no selection for or against roads.

In the seasonal model, females used natural and altered lands more than males, but use of developed lands was similar between the 2 groups (Fig. 3-7a). Within females and males, both groups used natural and altered lands the same, but used developed lands less than both natural and altered lands (Fig. 3-7a). Resident coyotes used natural lands more than transients, but use of altered and developed lands was similar between the two groups (Fig. 3-7b). Within residents, coyotes used natural lands more than both altered and developed lands, and they used developed lands less than altered lands (Fig. 3-7b). Within transients, coyotes used natural and altered lands the same, but used developed lands less than both natural and altered lands (Fig. 3-7b). Female coyotes (Fig. 3-7c) and transient coyotes (Fig. 3-7d) selected for roads, with higher probability of use of habitat closer to roads. Male coyotes selected against roads, with higher probability of use of habitat farther from roads (Fig. 3-7c). Resident coyotes had no selection for or against roads (Fig. 3-7d). We found no seasonal patterns in habitat selection. Coyotes did not use natural, altered, or developed lands any differently among the 3 seasons (Fig. 3-7e), nor did they have any selection for or against roads within any season (Fig. 3-7f). Within

each season, coyotes used natural and altered lands the same, but used developed lands less than both natural and altered lands (Fig. 3-7e).

In the temporal model, females and males had no differences in their use of all 3 land-use categories (Fig. 3-8a). Within females and males, both groups used natural and altered lands the same, but used developed lands less than both natural and altered lands (Fig. 3-8a). Resident coyotes used natural lands more than transients, but use of altered and developed lands was similar between the 2 groups (Fig. 3-8b). Within residents and transients, both groups used natural and altered lands the same, but used developed lands less than both natural and altered lands (Fig. 3-8b). Female coyotes (Fig. 3-8c) and transient coyotes (Fig. 3-8d) selected for roads, with higher probability of use of habitat closer to roads. Male coyotes (Fig. 3-8c) and resident coyotes (Fig. 3-8d) had no selection for or against roads. Between day and night, coyotes used all 3 land-use categories more during the night than in the day (Fig. 3-8e). During the day, coyotes used natural lands more than both altered and developed lands, and they used developed lands less than altered lands (Fig. 3-8e). During the night, coyotes used natural and altered lands the same, but used developed lands less than both natural and altered lands (Fig. 3-8e). Coyotes selected for roads at night, but coyotes during the day had no selection for or against roads (Fig. 3-8f).

DISCUSSION

Home-range size.—We found considerable individual variation in home-range sizes of both resident and transient coyotes in the Denver metropolitan area. Among

residents, females had high variation, with the largest home-range size for a female (53.6 km²) being more than 2.5 times greater than the largest home-range size for a male (19.9 km²). Home-range sizes of resident coyotes in our study were no different than those reported for residents in a rural area in southeastern Colorado (mean size 11.3 km²—Gese et al. 1988), contrary to the trend for smaller home ranges in other urban landscapes (Gehrt and Riley 2010). Resident home ranges were smaller than those of transients, consistent with other coyote studies in both urban areas (Gehrt et al. 2009; Gese et al. 2012) and rural areas (Gese et al. 1988). Resident coyotes also had smaller home ranges during the day than at night, similar to findings by Gese et al. (1990) and Smith et al. (1981) in rural areas. Coyotes near Seattle, Washington (Quinn 1997), Los Angeles, California (Riley et al. 2003), and Tucson, Arizona (Grinder and Krausman 2001; Grubbs and Krausman 2009), increased their activity at night, although Grinder and Krausman (2001) found no differences in coyote home-range sizes by time of day. In contrast, sizes of ranges for transients did not differ between day and night. Transients likely maintained persistent movements regardless of time of day due to their search for unoccupied territories, to swiftly pass through low-quality habitats (Gese et al. 2012), or to quickly move through resident territories with minimal chance of encountering the resident pair.

We found no differences in home-range sizes between males and females or among the 3 seasons. Similarly, Gehrt et al. (2009) and Grinder and Krausman (2001) determined home-range sizes were similar by sex and among seasons, and Gese et al. (2012) reported no differences between sexes within each season. Conversely, Tigas et

al. (2002) found female home ranges were larger than those of males, but Riley et al. (2003) reported males had larger home ranges than females in the same Los Angeles study area. Way et al. (2002) also found larger home ranges of resident males than resident females in an urban environment in the eastern United States. These mixed results suggest little consistency in home-range size comparisons for urban coyotes.

The largest area used by a transient coyote was 745.8 km². This coyote was a male transient captured at Rocky Mountain Metropolitan Airport on the western side of the study area who initially established a resident home range near the airport, then dispersed to the Denver International Airport on the eastern side of the study area, where he was subsequently removed. He additionally spent time at Front Range Airport, approximately 13 km southeast of Denver International Airport, indicating this particular coyote was attracted to airports. All 3 airports were in close proximity to large grasslands, and small mammal populations have been found to support raptors at airports (Baker and Brooks 1981), so coyotes may be drawn to airports because of abundant food resources. Coyotes are considered one of the most hazardous mammalian species at United States airports (Biondi et al. 2014), and although fencing appears to be effective in reducing coyote numbers inside airports (DeVault et al. 2008), further research on the relationship between coyotes and airports is warranted.

Habitat use.—Across the study area, on average, developed lands comprised 44% of the coyote home range, although we found considerable variation among individuals. This result differs from our hypothesis and from other urban coyote studies. Gehrt et al. (2009) and Riley et al. (2003) both reported coyote home ranges in their study areas

contained the highest percentages in natural areas, rather than developed landscapes. However, the Denver urban area contained 62% developed lands, compared to 19% each in natural and altered lands (Table 3-1), so coyotes likely were compelled to include large amounts of developed areas at the home range scale. In contrast, the highest frequency of coyote locations was in natural lands, indicating that although their home ranges included considerable development, coyotes chose to spend the majority of their time in natural, undeveloped areas (finer locational scale). We predominantly observed this pattern on a temporal scale, in which coyotes, particularly residents, tended to rest in natural areas during the day then venture out into the surrounding neighborhoods at night, likely to forage (Tigas et al. 2002). However, coyotes still spent more time in natural lands than in developed lands at night, indicating foraging bouts into developed areas did not persist throughout the night, and coyotes continued to use natural areas for feeding.

Contrary to our predictions, home-range size of resident coyotes was not related to the percentage of altered or developed lands within the home range, which conflicts with other studies. Gehrt et al. (2009) found home-range size was positively related to the amount of development within home ranges, and Riley et al. (2003) reported a positive relationship between home-range size and the amount of non-natural land-use (i.e., altered and developed lands combined). Further, Gese et al. (2012) determined coyote home ranges in developed areas were twice the size of those in less-developed areas. These results suggested a consequence of coyotes living in highly-developed environments was they required larger home ranges to meet energetic requirements (Gehrt and Riley 2010). Because we found no such relationship between home-range

size and the amount of development, coyotes in our study area appeared to have adjusted to the urbanized landscape and were able to efficiently procure resources in highly-developed areas without expanding their home ranges. Additionally, every coyote in our study had all 3 of the broad land-use categories within their home ranges, indicating these coyotes were flexible and capable of adapting to the urban landscape of the Denver metropolitan area.

Within the natural land-use category, both coyote home ranges and coyote locations contained the highest mean percentages in riparian habitat, suggesting coyote preference for habitat associated with water. Similarly, Gese et al. (2012) found home ranges in less-developed and mixed-habitat areas consisted of more riparian habitats than were available in the study area. In the same study system (Chicago, Illinois), Gehrt et al. (2009) determined water habitats (i.e., retention ponds) were highly selected by coyotes within home ranges. Riparian areas usually comprise large amounts of vegetation, including trees, providing cover for coyotes, especially during the day. Coyote home ranges generally consisted of low percentages of forest, but only 1.6% of the Denver urban area was in non-riparian forested habitats (Table 3-1), resulting in a reduced ability of coyotes to include forest patches in their home ranges.

Within the developed land-use category, both coyote home ranges and coyote locations contained the highest mean percentages in areas of low development and roads and the lowest mean percentages in areas of high development. This result was not surprising, as coyotes tend to avoid high-density areas in an urban landscape (Grubbs and Krausman 2009). Fifteen of the 22 coyotes (68%) never ventured into the most highly-

developed patches, which included apartment complexes and industrialized areas. The use of areas of low development and roads indicated when coyotes were in developed patches, they preferred residential neighborhoods with low-traffic roads; coyotes also likely used roads for traveling (Grinder and Krausman 2001; Way et al. 2002). We found individual variation in the average distances of coyote locations to the nearest highway or major road. Some coyote home ranges bordered a major road, suggesting the road was a barrier, whereas other home ranges crossed a major road. For those coyotes consistently crossing major roads or highways, they may have used either a stream crossing under the road or one of the under- or over-passes designed for vehicle use located within their home ranges. One transient coyote appeared to use a highway as a travel corridor; she was subsequently killed by a vehicle on this same road. Three of the 4 coyotes with locations farthest from major roads also had the lowest mean percentages of their home ranges in developed lands, indicating that some of our study animals were less urbanized than others and preferred not to use developed landscapes.

Resource selection.—Coyotes in our study area, regardless of sex, status, season, or time of day, selected for natural lands over developed lands, consistent with our habitat use findings in which the majority of coyote locations were in natural lands even though home ranges consisted of large amounts of development. Similar selection patterns have been found in other urban coyote studies (Quinn 1997; Grinder and Krausman 2001; Gehrt et al. 2009; Gese et al. 2012). Coyotes also selected altered lands over developed lands. Coyotes likely perceived urban vegetated systems (e.g., city parks, golf courses, and cemeteries) and agricultural areas as intermediate in nature, non-natural but used less

by humans than developed lands. These results confirm that coyotes in urban environments will choose to spend their time in natural or semi-natural habitat patches within their home ranges and avoid the most developed areas.

Both females and males had no selection preference between natural and altered lands. Within seasonal home ranges, females used natural and altered lands more than males, but use was no different between the 2 sexes in the individual or temporal home ranges. Females also selected to be closer to roads, whereas males selected to be farther from roads in seasonal home ranges but had no selection for or against roads in individual or temporal home ranges. These findings suggested female coyotes in urban environments may have stronger habitat selection preferences than males, a result supported by Grinder and Krausman (2001) and Poessel et al. (see Chapter 2). Females may drive habitat selection in urban coyotes, whereas males may follow females rather than habitat (see Chapter 2).

Residents within individual and temporal home ranges and transients within all home ranges had no selection preference between natural and altered lands. Residents within seasonal home ranges selected for natural over altered lands. Residents also used natural lands more than transients in all home ranges. These results confirmed our observations of resident coyotes resting in natural areas, especially during the day, whereas transients were more likely to move through all habitat types in search of vacant territories. Resident coyotes had no selection for or against roads, whereas transients selected to be closer to roads. Transient coyotes may use roads as travel corridors and to familiarize themselves with their surroundings while moving through the urban landscape

(Way et al. 2002), or they may be compelled to use roads when traveling to avoid resident territories.

We found no seasonal patterns in resource selection. Within each season, coyotes had no selection preference between natural and altered lands. Among seasons, coyotes did not use any land-use category any differently, and coyotes did not select for or against roads in any of the 3 seasons. Gehrt et al. (2009) also found no difference in selection among seasons, whereas Gese et al. (2012) and Grinder and Krausman (2001) both determined coyotes preferred certain habitat types in at least 1 season more than in other seasons. Although not statistically significant in the resource selection models, coyotes in our study tended to increase use of all 3 land-use categories during the pup-rearing season (Fig. 3-7e), which may be biologically significant. Because coyotes usually do not travel far when raising pups (Harrison and Gilbert 1985), they may increase their use of all habitat types within home ranges during this season to find food for their pups (see Chapter 2).

Coyotes during the day selected for natural lands over altered lands, but coyotes at night had no selection preference between the 2 land-use categories, further confirming coyotes prefer to spend most of their time during the day resting in patches of natural habitat. Coyotes also used all 3 land-use categories more at night than during the day, reflecting the higher activity levels of urban coyotes at night. Additionally, they selected for roads at night, but had no selection for or against roads during the day. Coyotes may have used roads for traveling at night, when roads have less vehicular traffic. These

results provide evidence of the nocturnal nature of coyotes in urban environments and that they prefer to be most active at times when human activity is minimized.

Conclusions.—Coyotes in the Denver metropolitan area have efficiently adapted to this highly-developed urbanized landscape and effectively used all habitat types. However, coyotes preferred to spend most of their time in patches of natural habitat where humans were less active, and they expanded their home ranges and use of all habitats at night when humans were less active, suggesting they attempted to avoid human activity. By utilizing these strategies, coyotes were able to exploit urban environments and survive within them. Despite their attempts to avoid human activity, coyotes in our study area increasingly have become involved in conflicts with humans (Poessel et al. 2013), a situation that may be impossible to circumvent in such a highly-developed urban area.

Coyotes in our study area had similar habitat preferences to coyotes in other urban environments. They selected natural habitat over developed areas, and they increased their activity at night. However, we also discovered unique results in our study. Coyote home ranges, on average, contained more developed lands than natural lands, and home range sizes did not increase with higher amounts of urbanization. Further, every coyote in our study incorporated all 3 land-use types in their home ranges, whereas previous studies reported some coyotes had either no natural or no developed areas within home ranges (Riley et al. 2003; Gehrt et al. 2009). These results suggest coyotes in the Denver metropolitan area have become highly adapted to an urbanized landscape with large

concentrations of developed areas, reflecting the flexible nature of this opportunistic carnivore.

The adaptation of coyotes to human development has ecological implications for urban landscapes. As the top predator and competitor in most urban areas, coyotes are capable of influencing the abundance and behavior of many wildlife species, and they may have a strong influence on urban systems through their role in trophic cascades (Crooks and Soulé 1999; Gehrt and Riley 2010). Coyotes may limit domestic cat (*Felis catus*) populations by restricting their use of natural habitat patches through both predation and cat avoidance of coyotes (Crooks and Soulé 1999; Gehrt et al. 2013). Coyotes may also displace red foxes (*Vulpes vulpes*; Gosselink et al. 2003) from urban areas. As coyotes continue to increase their use of urban areas throughout North America, future research should attempt to evaluate the relationships between coyotes and other wildlife species in these urbanized environments.

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TABLE 3-1.—Land-use types, categories, and descriptions used to evaluate coyote land-use in the Denver metropolitan area, 2012–2014. The percentage of the Denver urban area in each land-use type is also shown.

Land-use type	Land-use category	Description	% of Denver urban area
Forest	Natural	Dominated by trees (non-riparian)	1.6
Shrubland	Natural	Dominated by shrubs (non-riparian)	6.5
Grassland	Natural	Dominated by herbaceous/non-vascular plants (non-riparian)	5.7
Riparian	Natural	Dominated by water or water-dependent vegetation (i.e., wetlands, floodplains, swamps, marshes, riparian systems, and open water)	4.7
Sparse	Natural	Barren and sparsely-vegetated areas with no dominant life form	0.4
Open space	Altered	Urban vegetated systems (i.e., city parks, golf courses, and cemeteries)	12.9
Agriculture	Altered	Croplands, pasture and hay fields, orchards, and vineyards	6.0
Low development	Developed	Areas with a mixture of constructed materials and vegetation; impervious surfaces account for 20-49% of the total cover; most commonly include single-family housing units; does not include roads	24.1
Medium development	Developed	Areas with a mixture of constructed materials and vegetation; impervious surfaces account for 50-79% of the total cover; most commonly include single-family housing units; does not include roads	11.5
High development	Developed	Highly-developed areas where people reside or work in high numbers; impervious surfaces account for 80-100% of the total cover; include apartment complexes, row houses, and commercial/industrial; does not include roads	4.4
Roads	Developed	All roads	22.2

TABLE 3-2.—Top 2 models in AIC model selection in each of 3 model sets used to determine coyote habitat selection in the Denver metropolitan area, 2012–2014. Each model set represents resource selection within individual, seasonal, or temporal coyote home ranges. *K* refers to the number of parameters (including intercept) in a model plus 1 for the error term. The evidence ratio represents the strength of the top model relative to the second model in each model set.

Model	<i>K</i>	Delta AIC	Model weight	Evidence ratio
<u>Individual model set:</u>				
Sex, Status, Land-use, Roads, Sex*Land-use, Status*Land-use, Sex*Roads, Status * Roads	13	0.00	1.0000	---
Sex, Status, Land-use, Roads, Sex*Land-use, Status*Land-use, Sex*Roads	12	27.22	0.0000	813,960.97
<u>Seasonal model set:</u>				
Sex, Status, Season, Land-use, Roads, Sex*Land-use, Status*Land-use, Season*Land-use, Sex*Roads, Status*Roads, Season*Roads	22	0.00	0.9975	---
Sex, Status, Season, Land-use, Roads, Sex*Land-use, Status*Land-use, Season*Land-use, Sex*Roads, Status*Roads	20	12.42	0.0020	498.83
<u>Temporal model set:</u>				
Sex, Status, Time, Land-use, Roads, Sex*Land-use, Status*Land-use, Time*Land-use, Sex*Roads, Status*Roads, Time*Roads	18	0.00	1.0000	---
Sex, Status, Time, Land-use, Roads, Sex*Land-use, Status*Land-use, Time*Land-use, Sex*Roads, Status*Roads	17	21.14	0.0000	39,000.35

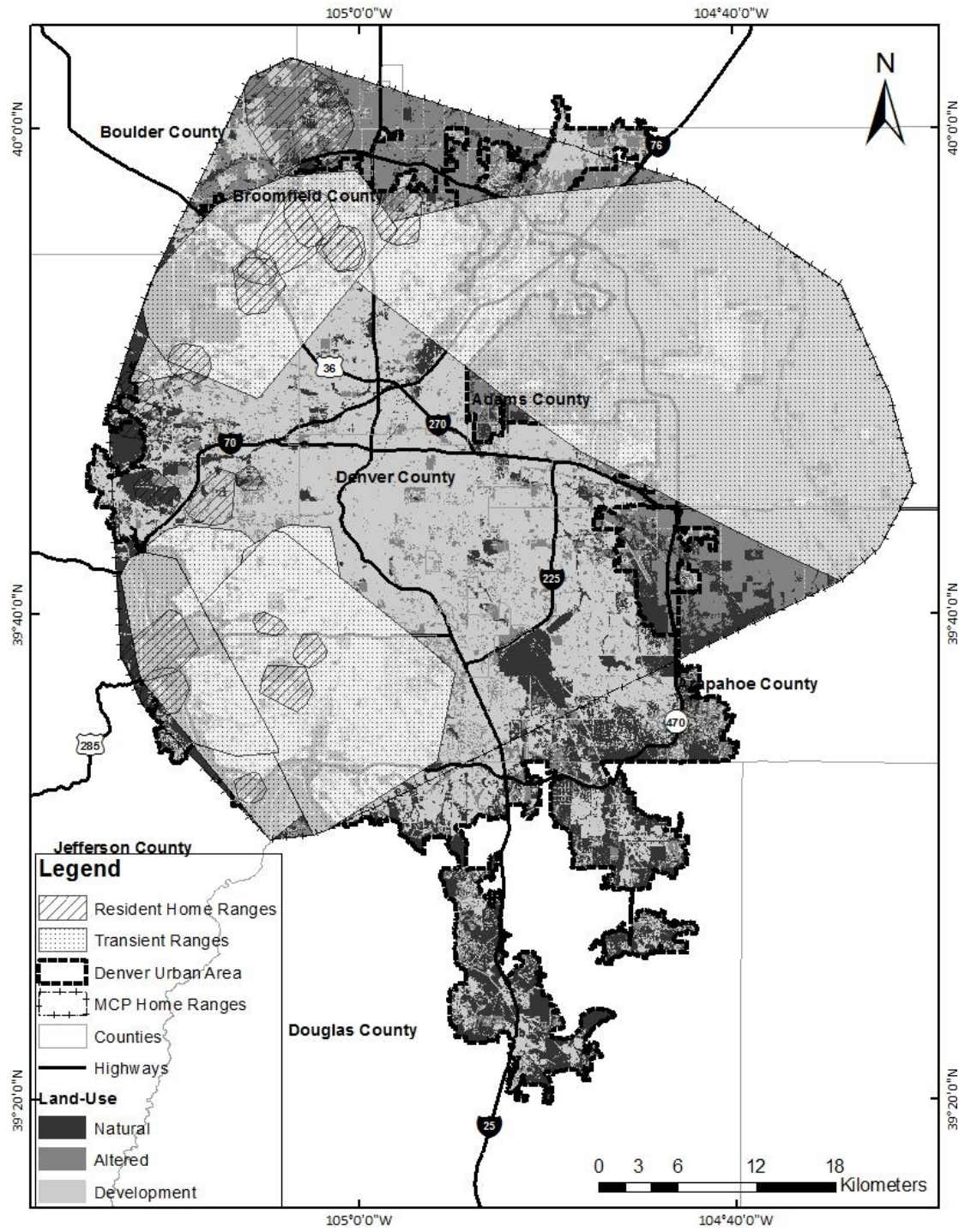


FIG. 3-1.—Map of the Denver metropolitan area with the 3 broad land-use categories and resident and transient coyote home ranges, Colorado, 2012–2014. The Denver urban area as defined by the U.S. Census Bureau is outlined with the thick dashed line. A minimum convex polygon outlining the coyote home ranges is represented by the line with hash marks.

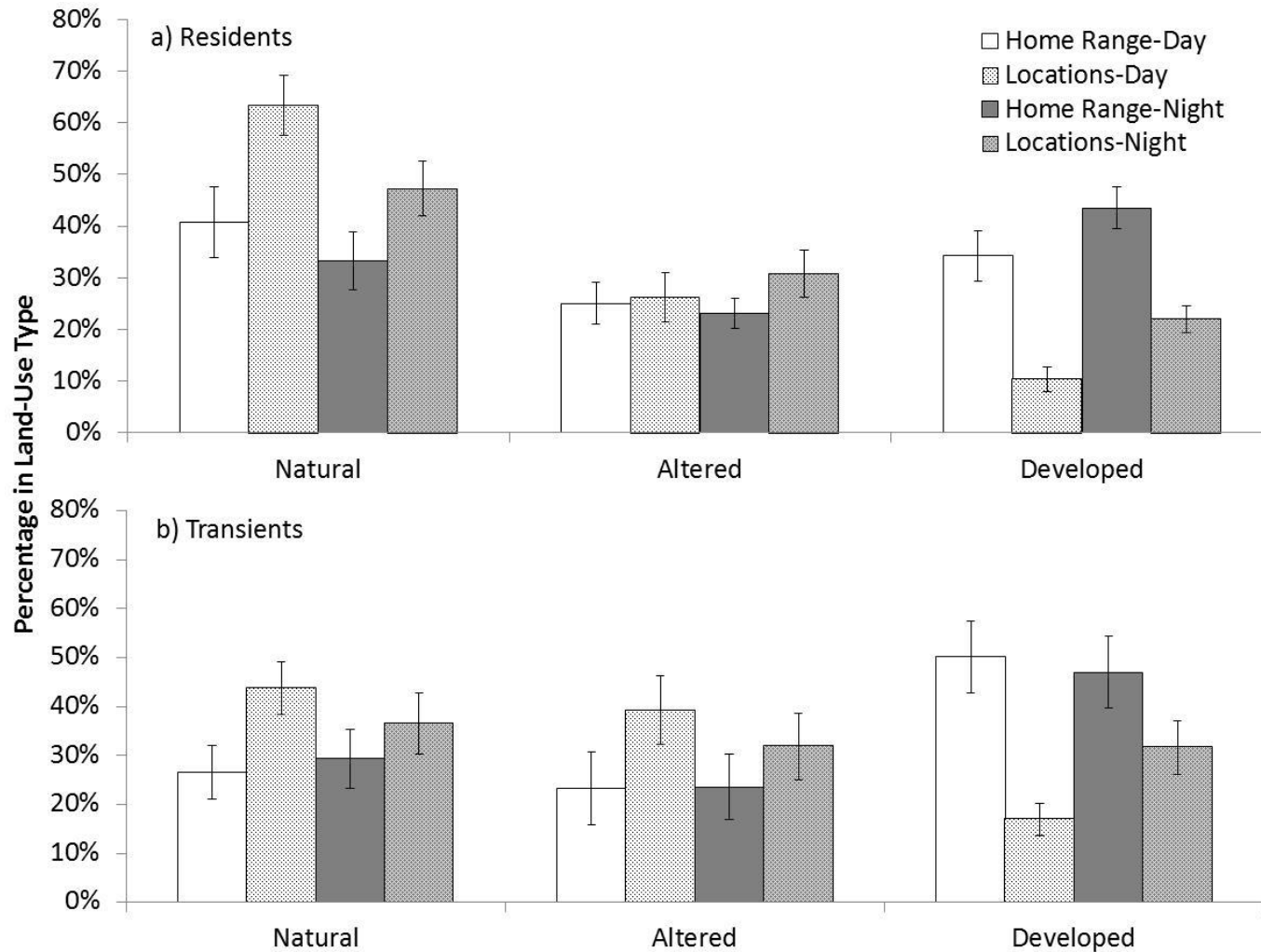


FIG. 3-2.—Percentages of coyote home ranges and locations during the day and night within each of the 3 broad land-use categories for a) residents and b) transients, Denver, Colorado, 2012–2014.

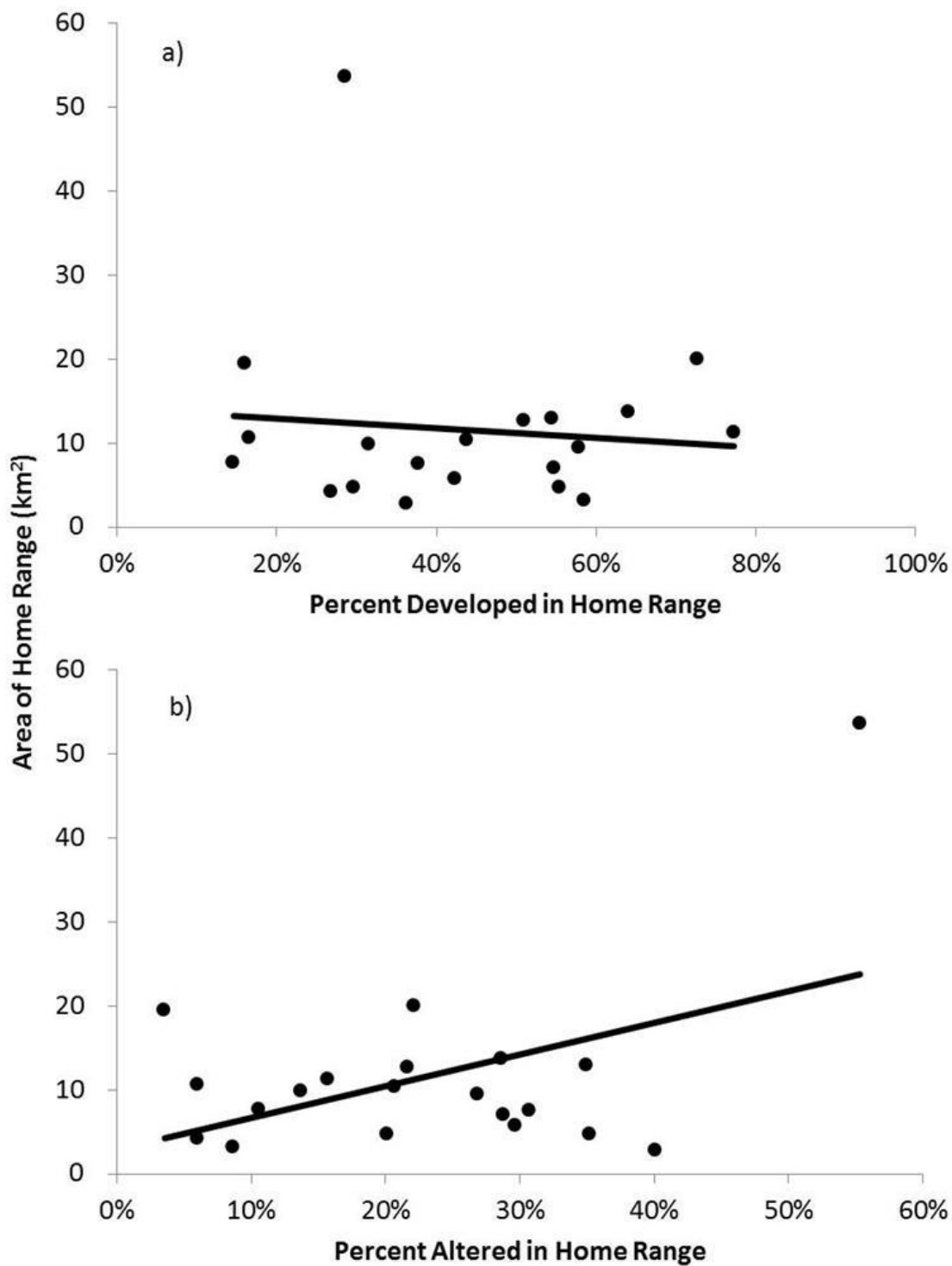


FIG. 3-3.—Linear regression of average home-range sizes for resident coyotes on percentage of urbanization within coyote home ranges for a) developed land-use and b) altered land-use, Denver, Colorado, 2012–2014.

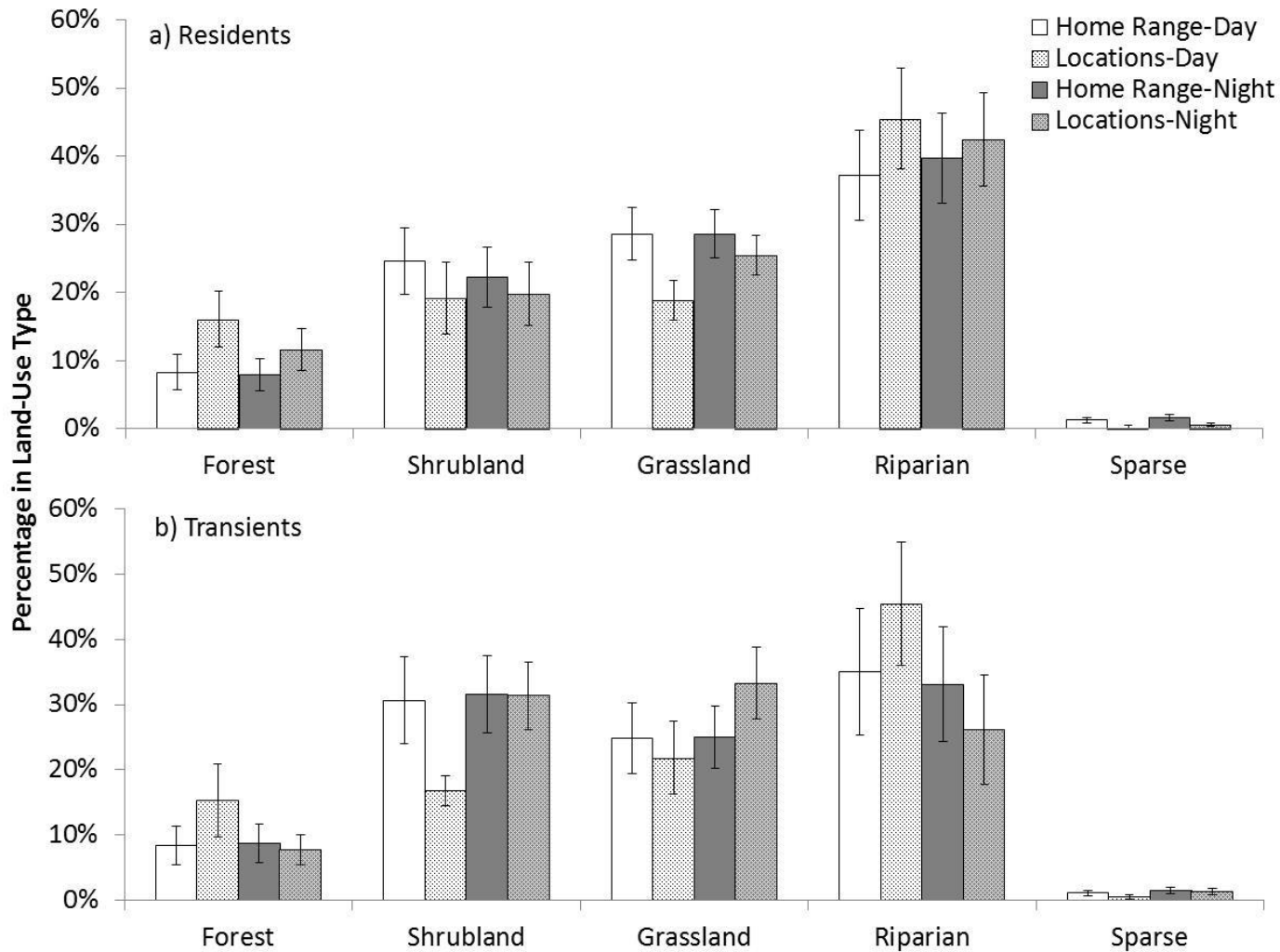


FIG. 3-4.—Percentages of coyote home ranges and locations during the day and night within each of the 5 natural land-use types for a) residents and b) transients, Denver, Colorado, 2012–2014.

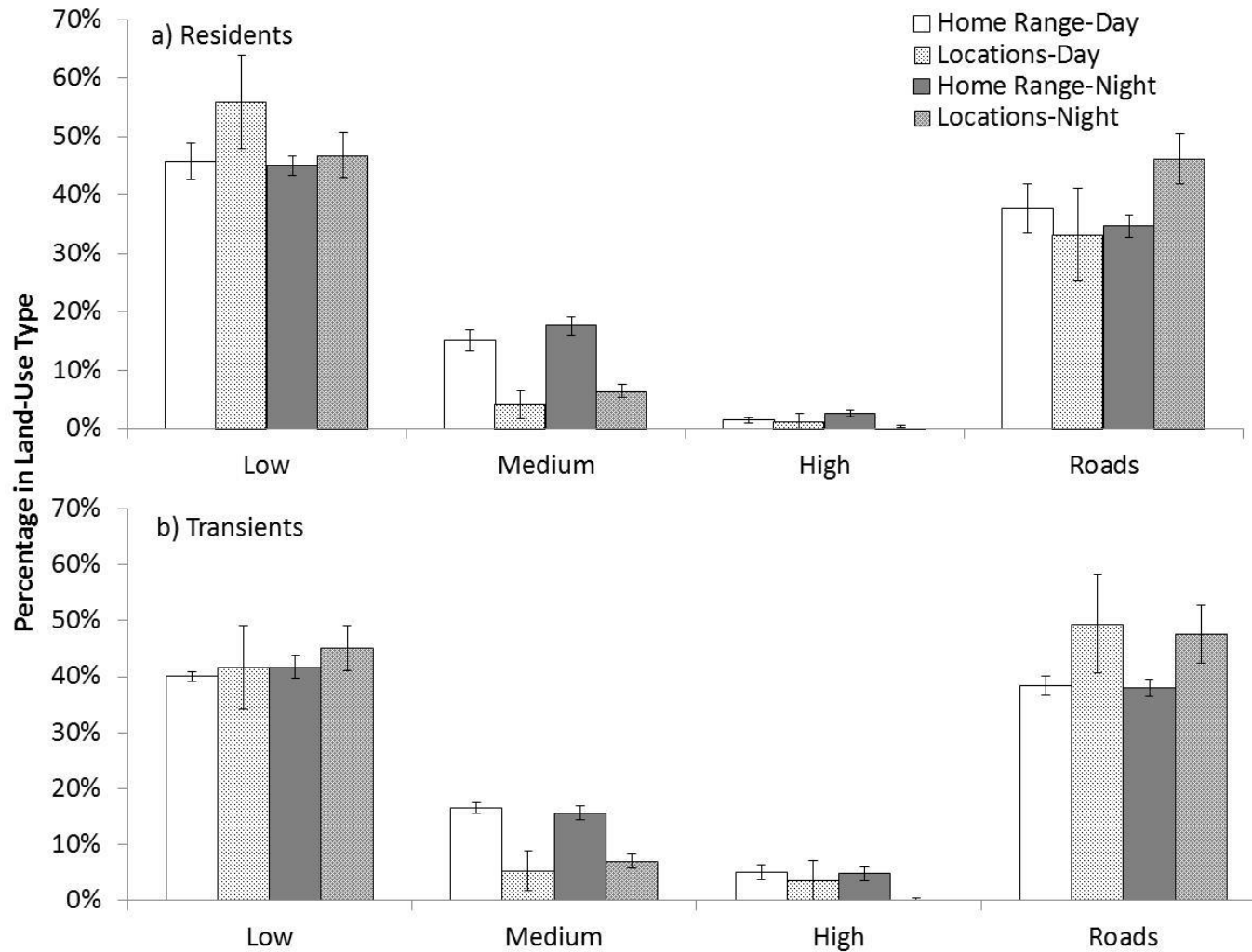


FIG. 3-5.—Percentages of coyote home ranges and locations during the day and night within each of the 4 developed land-use types for a) residents and b) transients, Denver, Colorado, 2012–2014.

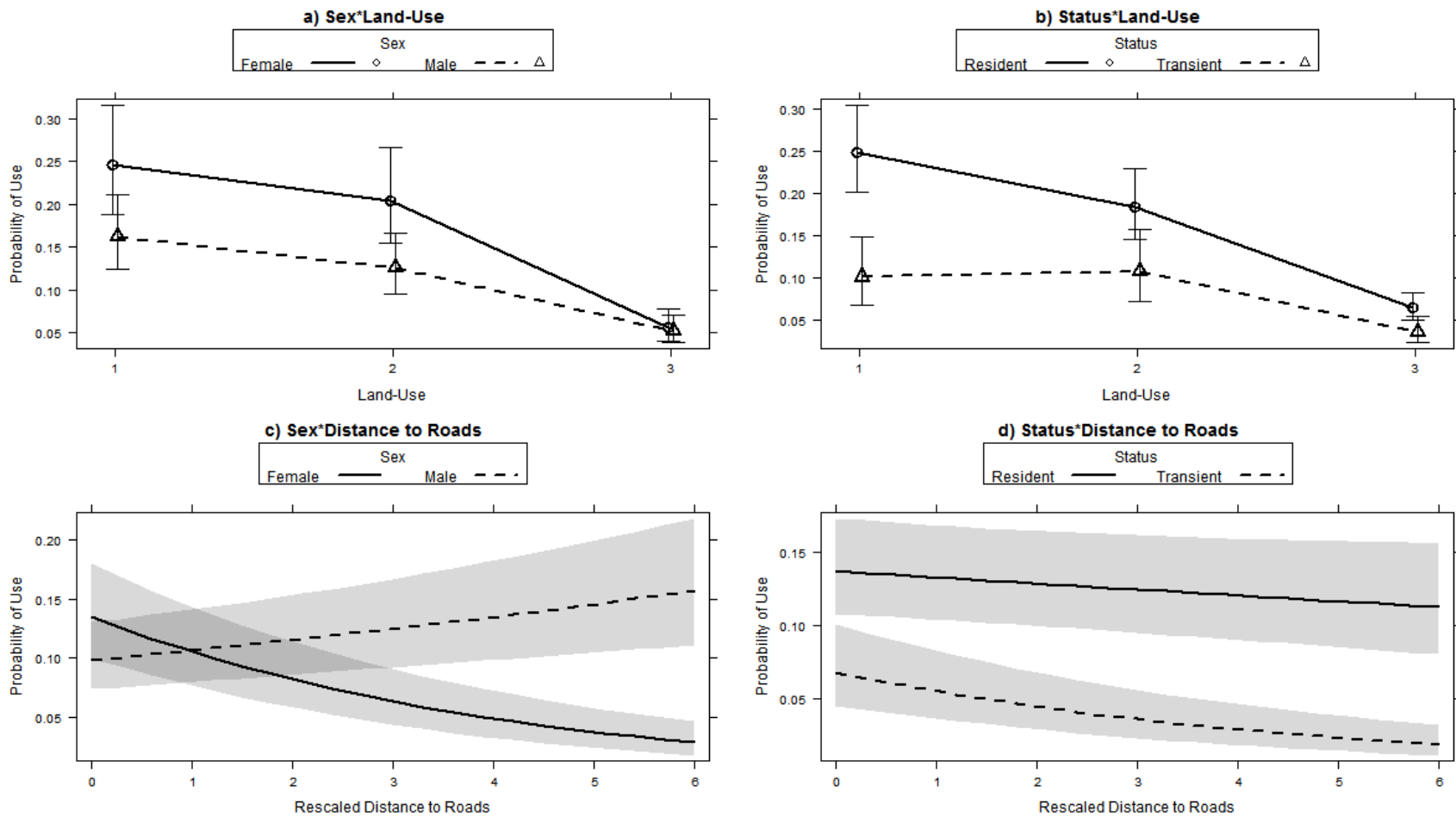


FIG. 3-6.—Interaction plots of a) Sex*Land-Use, b) Status*Land-Use, c) Sex*Distance to Roads, and d) Status*Distance to Roads for the top model in the individual home ranges model set, Denver, Colorado, 2012–2014. Land-use factors are 1 = natural, 2 = altered, and 3 = developed. Bars on the land-use plots and bands on the distance plots represent 95% confidence intervals.

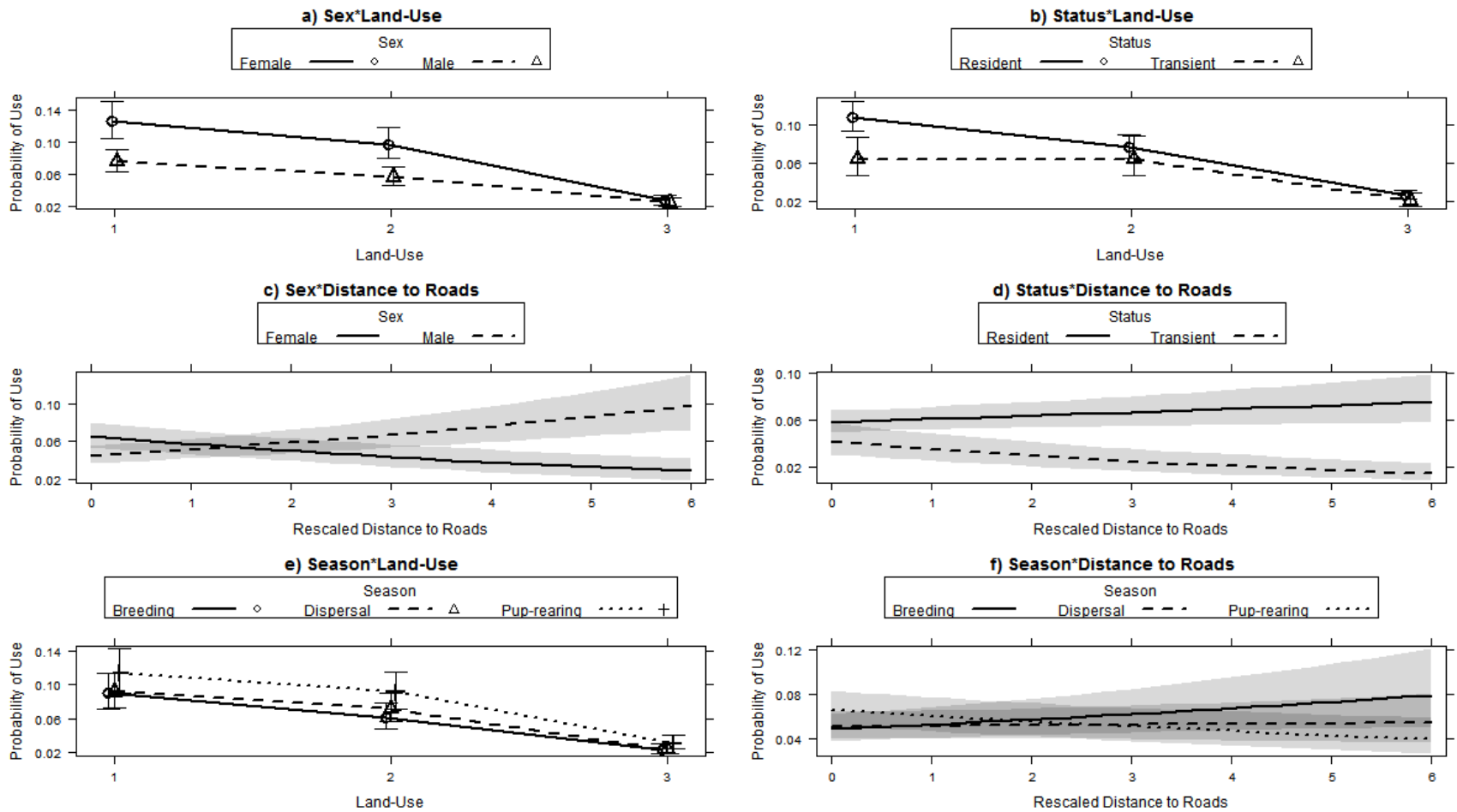


FIG. 3-7.—Interaction plots of a) Sex*Land-Use, b) Status*Land-Use, c) Sex*Distance to Roads, d) Status*Distance to Roads, e) Season*Land-Use, and f) Season*Distance to Roads for the top model in the seasonal home ranges model set, Denver, Colorado, 2012–2014. Land-use factors are 1 = natural, 2 = altered, and 3 = developed. Bars on the land-use plots and bands on the distance plots represent 95% confidence intervals.

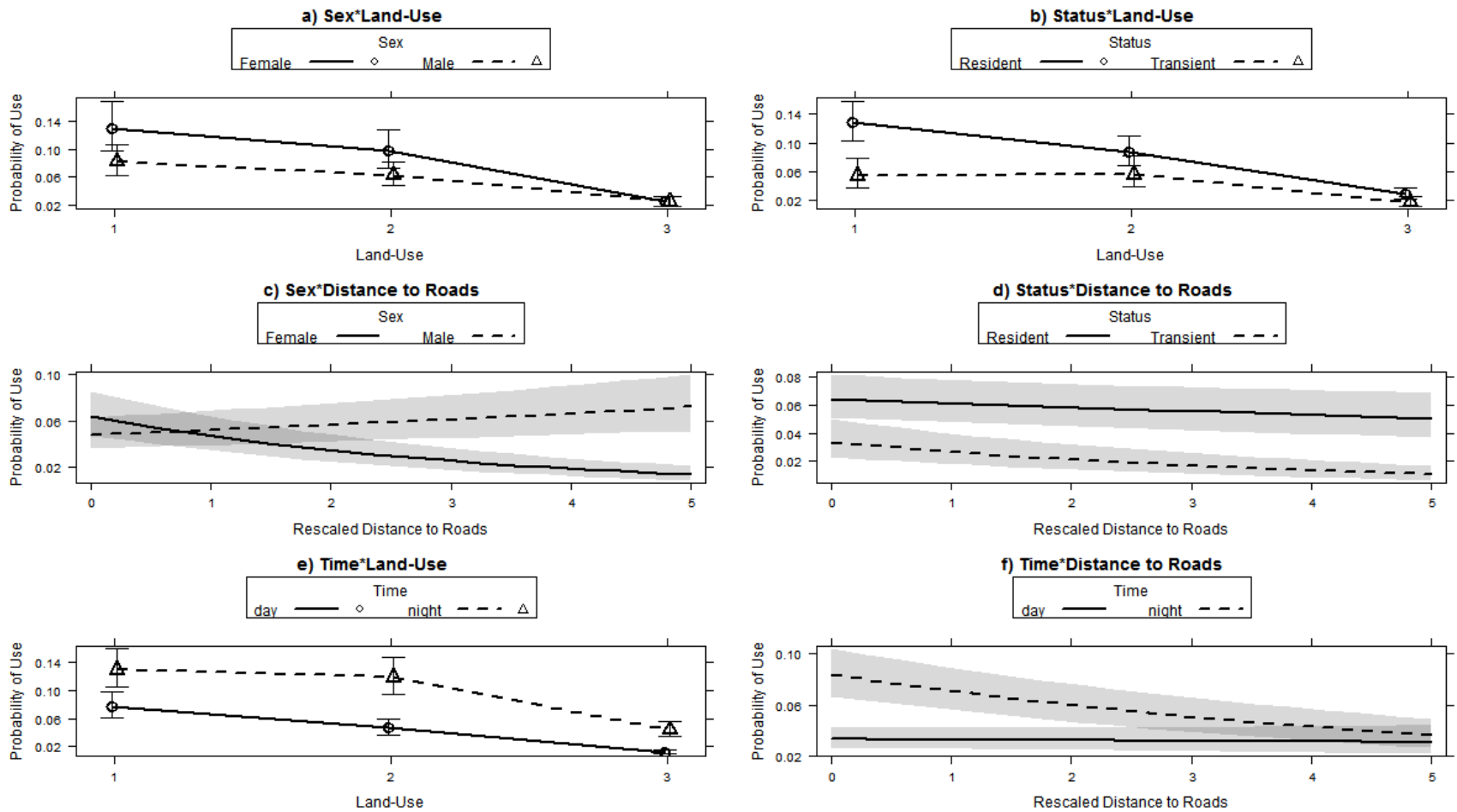


FIG. 3-8.—Interaction plots of a) Sex*Land-Use, b) Status*Land-Use, c) Sex*Distance to Roads, d) Status*Distance to Roads, e) Time*Land-Use, and f) Time*Distance to Roads for the top model in the temporal home ranges model set, Denver, Colorado, 2012–2014. Land-use factors are 1 = natural, 2 = altered, and 3 = developed. Bars on the land-use plots and bands on the distance plots represent 95% confidence intervals.

CHAPTER 4

**ENVIRONMENTAL FACTORS INFLUENCING THE OCCURRENCE
OF COYOTES AND CONFLICTS IN URBAN AREAS³**

Abstract

The increase of global urbanization can have strong impacts on wildlife species, including carnivores such as coyotes (*Canis latrans*). As coyotes continue to settle in more urban areas, human-coyote conflicts, such as attacks on humans or pets, are also increasing. Understanding environmental variables that might influence whether or not coyotes and human-coyote conflicts will occur in certain urban areas may assist wildlife officials in creating management plans for urban wildlife. We conducted a survey of 105 urban areas in the United States requesting information on the occurrence of coyotes and human-coyote conflicts. We analyzed the responses with data on human population size, geographic region, land cover, housing density, and precipitation. Larger urban areas were more likely to contain both coyotes and human-coyote conflicts, and were also more likely to have greater numbers of conflicts. Urban areas in the western regions with larger amounts of high-intensity development and less forested and agricultural areas were more likely to have conflicts. Precipitation did not predict conflicts, although precipitation was highest in eastern urban areas where conflicts were less likely to occur. Most urban areas considered the management of conflicts to be of low priority and emphasized education of citizens rather than removal of individual coyotes. Our results may assist urban wildlife managers in using geographic and demographic factors to

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forecast the occurrence of coyotes and human-coyote conflicts. Practices such as sustainable urban planning and landscape design incorporating wildlife habitat requirements may reduce human-carnivore conflicts in urban ecosystems.

1. Introduction

Urbanization is increasing on a global scale, and by 2030 almost 5 billion people in the world will be living in urban areas (United Nations Population Fund, 2007). Urban expansion leads to significant changes in the landscape, including habitat loss and fragmentation (Markovchick-Nicholls et al., 2008; McKinney, 2002), which can alter the structure of ecosystems (Niemela, 1999). Urbanization is one of the leading causes of species endangerment (Czech, Krausman, & Devers, 2000) and can have a negative impact on biodiversity (McDonald, Kareiva, & Forman, 2008; Seto, Güneralp, & Hutya, 2012). However, in some cases, urbanization can enhance wildlife species richness (McKinney, 2008) and increase densities of certain animal species (Magle et al., 2007; Prange, Gehrt, & Wiggers, 2003). To accommodate these species, resource managers in some urban areas have begun incorporating wildlife habitat requirements into landscape planning and design (Adams, 2005).

Some carnivore species are increasing their use of urban environments (Bateman & Fleming, 2012; Gehrt, Riley, & Cypher, 2010). Carnivores residing in urban areas range from kit foxes (*Vulpes macrotis*; Cypher, 2010) and mountain lions (*Puma concolor*; Beier, Riley, & Sauvajot, 2010) in North America to red foxes (*Vulpes vulpes*; Soulsbury, Baker, Iossa, & Harris, 2010) and Eurasian badgers (*Meles meles*; Harris, Baker, Soulsbury, & Iossa, 2010) in Europe. Carnivores successfully occupying urban

areas generally have small to medium body sizes, are dietary generalists, and behaviorally have a tolerance for humans (Fuller, DeStefano, & Warren, 2010). Coyotes (*Canis latrans*) embody these characteristics (Gese & Bekoff, 2004; Morey, Gese, & Gehrt, 2007) and have colonized urban landscapes throughout North America (Gehrt & Riley, 2010; Gehrt, Anchor, & White, 2009; Magle, Poessel, Crooks, & Breck, 2014).

Coyote populations generally respond positively to urban environments. In southern California, coyote occurrence increased with both proximity and intensity of urbanization (Ordeñana et al., 2010). In Indiana, coyotes occupied suburban areas with high housing densities adjacent to large forested patches, suggesting coyotes can tolerate high levels of human activity when protective cover is nearby (Atwood, Weeks, & Gehring, 2004). Similarly, in metropolitan Detroit, Michigan, habitat surrounding locations with evidence of coyote use (i.e., carcasses, dens, scats, tracks, or sightings) included more forested tracts than expected in both urban and suburban areas (Dodge & Kashian, 2013). Other studies have found urban coyotes selected natural habitat patches within their home ranges and minimized activity in developed areas (Gehrt et al., 2009; Gese, Morey, & Gehrt, 2012; Riley et al., 2003). Coyotes in captivity selected habitat patches with a mixture of both natural and urban (i.e., developed) habitat structure, indicating coyotes preferred heterogeneous environments (see Chapter 2). Hence, coyotes may thrive in highly developed areas when natural habitat patches are nearby and readily available.

Habitat selection by coyotes also may be influenced by the availability of water, in both arid sites, where coyotes primarily use water for drinking, and in moister

environments, where coyotes use riparian areas for cover. In the Chicago metropolitan area, Gese et al. (2012) found home ranges of coyotes in less-developed and mixed-habitat areas contained more riparian habitats than were available in the study area; Gehrt et al. (2009) also determined water habitats (i.e., retention ponds) were consistently highly selected by coyotes in the same study area. In a desert site in west Texas, Atwood, Fry, and Leland (2011) found coyote activity near water features (i.e., stock tanks and impoundments) increased as the number of days since the last rainfall increased. In another arid site in Arizona, DeStefano, Schmidt, and deVos (2000) determined coyote sign (e.g., scats and tracks) was seven times greater near water than away from water. These results indicated the importance of water to coyotes and that precipitation might influence coyote movement patterns.

Although the majority of urban coyotes tend to utilize the landscape in ways that avoid humans (Gehrt et al., 2009), some coyotes may become involved in human-coyote conflicts (hereafter, “conflicts,” defined in Table 4-1; Grubbs & Krausman, 2009; Poessel et al., 2013). Such conflicts might occur spatially in a nonrandom manner. In the Denver metropolitan area of Colorado, conflicts occurred more frequently than expected in developed areas and less frequently than expected in natural and agricultural areas (Poessel et al., 2013). In addition, conflicts occurred more often than expected in suburban areas and less often than expected in exurban and rural areas. In Calgary, Alberta, the highest numbers of conflicts were in two small parks located near the urban core of the city, and the fewest conflicts were in two large, natural parks located near the city boundary (Lukasik & Alexander, 2011). Furthermore, conflicts were most often

reported in close proximity to a river. Management of conflicts may be an important priority for wildlife officials in many urban areas, and appropriate tools for addressing such conflicts are becoming increasingly essential (Magle et al., 2014; Poessel et al., 2013; see Chapter 2). Predicting where conflicts may likely occur on a regional basis would be an important step in developing such tools.

Although conflicts (specifically, coyote attacks on humans) have been analyzed throughout North America to determine victim demographics and seasonality of conflicts (White & Gehrt, 2009), to our knowledge no study has assessed the environmental variables influencing whether or not coyotes or conflicts may occur in certain urban areas on a national or regional scale. Our primary objectives were to determine why certain urban areas in the United States have coyotes and why some of those have conflicts by examining geographic, demographic, and climatic characteristics of those urban areas, including human population size, geographic region, land cover, housing density, and precipitation. Additional objectives were to determine annual rates of conflicts and the management priority for handling such conflicts. We predicted that most urban areas would contain resident coyotes and that urban areas without conflicts would contain higher amounts of natural areas, higher rural or exurban housing densities, and higher precipitation levels. We further predicted that management of conflicts would be of high priority for most urban areas and that larger urban areas would have higher annual rates of conflicts. Our results may assist urban wildlife managers throughout the coyote's range to forecast the most likely areas to contain coyotes and conflicts and, accordingly,

to consider implementing habitat management and educational programs to mitigate such conflicts.

2. Methods

2.1. Data collection

We surveyed 105 urban areas within the contiguous United States, focusing on coyotes and conflicts. We used the U.S. Census Bureau's definition of an urban area: "a densely settled core of census tracts and/or census blocks that meet minimum population density requirements, along with adjacent territory containing non-residential urban land uses as well as territory with low population density included to link outlying densely settled territory with the densely settled core. To qualify as an urban area, the territory identified according to criteria must encompass at least 2,500 people, at least 1,500 of which reside outside institutional group quarters" (U.S. Census Bureau, 2014). Although coyotes are found throughout North America, we limited our survey to United States urban areas to maintain consistency in the datasets used in our analyses, each of which was obtained from a single source at a national scale. We selected 105 urban areas based on 2010 human population size in three categories: (1) high, the largest 35 urban areas based on human population size (range 1,368,035–18,351,295); (2) middle, the 35 urban areas beginning at a population size of 500,000 and up (range 507,643–953,556); and (3) low, the 35 urban areas beginning at a population size of 100,000 and up (range 100,868–119,911). We then assigned a geographic region to each urban area, i.e., Northeast,

Southeast, Midwest, Southwest, or West, based on maps from the National Planning Network and the U.S. Federal Highway Administration (Fig. 4-1).

Next, we contacted the state or district wildlife agency overseeing each urban area and asked four questions regarding coyotes in that urban area. First, we asked whether the urban area contained resident coyotes. If so, we next asked whether the urban area had conflicts and if conflicts were a high, low, or no priority for the agency. Finally, we asked for an estimate of the annual numbers of conflicts (see Table 4-1 for the full text of the four questions). If the wildlife agency did not have all of the information requested, we next contacted the local animal control office for the urban area. In some cases, the wildlife agency directed us to contact the local United States Department of Agriculture-APHIS-Wildlife Services office or the local police department for answers to the questions. If the response to question 1 was “no,” then the responses to the remaining three questions were “NA.” If the response to question 2 was “no,” then the responses to questions 3 and 4 were “NA.” For some urban areas, the wildlife official could not provide an answer to question 4 due to a lack of data. Hence, possible responses for each of the four questions included for question 1, yes or no; for question 2, yes, no, or NA; for question 3, high, low, no, or NA; and for question 4, 0, 1-10, 11-40, 41-100, >100, no answer, or NA.

After collecting the responses, we then used land cover, housing density, and precipitation data for each urban area, as well as the human population size category and geographic region assigned to each urban area, to compare responses. We obtained land cover data from Landscape Fire and Resource Management Planning Tools

(LANDFIRE), a program producing national geospatial datasets that provide information for landscape strategic planning for fire and natural resource management activities (LANDFIRE, 2013). We used ArcGIS v.10.0 (ESRI, Redlands, California) to condense the land cover dataset, in 30-m resolution, into eight types: (1) forest (naturally-occurring areas dominated by trees); (2) shrubland (naturally-occurring areas dominated by shrubs); (3) grassland (naturally-occurring areas dominated by herbaceous/non-vascular plants); (4) riparian (naturally-occurring areas dominated by water or water-dependent vegetation, i.e., wetlands, floodplains, swamps, marshes, riparian systems, and open water); (5) sparse (barren and sparsely-vegetated areas with no dominant life form); (6) open space (urban vegetated systems, i.e., city parks, golf courses, and cemeteries); (7) development (commercial and residential developed areas and roads); and (8) agriculture (croplands, pasture and hay fields, orchards, and vineyards). We attained housing density data from the Spatially Explicit Regional Growth Model (SERGoM v3; Theobald, 2005), which depicts housing density for the coterminous United States at 100-m resolution. We used ArcGIS to classify private developed land into four classes: (1) rural (>16.18 ha per unit); (2) exurban (0.68-16.18 ha per unit); (3) suburban (0.1-0.68 ha per unit); and (4) urban (<0.1 ha per unit plus industrial and commercial development; Theobald, 2005). For each of the 105 urban areas, we then calculated percentages of each land cover type and housing density class contained within the urban area. Finally, we obtained 30-year average annual precipitation values for each urban area from the National Oceanic and Atmospheric Administration (<http://average-rainfall.findthebest.com>). We included

precipitation in the analysis as a metric for water in arid urban areas and as a proxy for primary productivity of vegetation in moister urban areas.

2.2. *Data analyses*

We analyzed the responses to the coyote conflict question (question 2) with univariate logistic regression models. Because of the low number of “no” responses (Table 4-2), we could only include one covariate at a time in a model. We ran models with human population size category, geographic region, each land cover type, each housing density class, and precipitation separately as covariates. We used $P < 0.05$ to determine significant variables. We could not run models for the responses to each of the other three questions because of the low number of responses in ≥ 1 response category. We also used analysis of variance (ANOVA) to separately analyze the differences in each land cover class, housing density type, and precipitation among the three human population size categories and five geographic regions. For all models with category or region as predictor variables, we analyzed pairwise comparisons for any significant effects, correcting P -values with a Tukey adjustment. For the ANOVA land cover models, we logit-transformed the grassland and sparse land cover response variables to meet distributional assumptions. For the ANOVA housing density models, we logit-transformed the rural and urban housing density response variables. We used R in all statistical analyses (R Core Team, 2014).

3. Results

We received responses from all 105 urban areas (100% response rate). Ninety-six urban areas (91%; based on $n = 105$) contained resident coyotes, and 71 areas (68%) had conflicts (Fig. 4-1). Officials from 58 urban areas (55%) considered conflicts to be a low priority, and only 11 areas (10%) regarded management of conflicts as a high priority. Fifty-two urban areas (50%) had either 1-10 or 11-40 conflicts occurring on an annual basis, whereas four urban areas (4%) had >100 annual conflicts. These four areas were Denver-Aurora (Colorado), St. Louis (Missouri), Portland (Oregon), and Colorado Springs (Colorado). Wildlife officials from nine urban areas (9%) could not answer the question regarding numbers of conflicts, and three urban areas (3%) reported they have conflicts, but had none in 2013, the year for which data were requested (see Table 4-1).

For responses by human population size category, every urban area (100%; based on $n = 35$ for each category) in the high and middle categories had coyotes, but only 26 urban areas (74%) in the low category had coyotes (Table 4-2). Thirty urban areas (86%) in the high category, 28 (80%) in the middle category, and 13 (37%) in the low category had conflicts (Table 4-2). Human population size category was a significant predictor of whether or not urban areas had conflicts ($\chi^2 = 9.97$, $P = 0.007$). The low category had fewer conflicts than both the high ($P = 0.011$) and middle ($P = 0.043$) categories (Table 4-2). Most urban areas in all three categories considered management of conflicts to be a low priority (Table 4-2). Three of the four urban areas reporting >100 annual conflicts were in the high human population size category (Table 4-2).

For responses by geographic region, all urban areas in the Southwest (100%; based on $n = 14$), $\geq 90\%$ of the urban areas in the Northeast (based on $n = 20$), Southeast (based on $n = 23$), and Midwest (based on $n = 24$), and 83% of the urban areas in the West (based on $n = 24$) had resident coyotes (Table 4-2). Conflicts occurred in 86% of urban areas in the Southwest, 79% of urban areas in the West, $>60\%$ of urban areas in both the Southeast and Midwest, and 50% of urban areas in the Northeast (Table 4-2). Geographic region was not a significant predictor of whether or not urban areas had conflicts ($\chi_4^2 = 7.71$, $P = 0.103$); however, the region logistic regression model may have been over-parameterized (with four parameters estimated) for the number of responses. A direct comparison of urban areas with conflicts between the Northeast and West regions indicated urban areas in the West were more likely to have conflicts ($\chi_1^2 = 5.80$, $P = 0.016$). Three of the four urban areas reporting >100 annual conflicts were in the West (Table 4-2).

Urban areas with and without coyotes had high percentages of development, intermediate percentages of forest, open space, and agriculture, and low percentages of other land cover types (Fig. 4-2a). Forest ($\chi_1^2 = 4.17$, $P = 0.041$), development ($\chi_1^2 = 8.52$, $P = 0.004$), and agriculture ($\chi_1^2 = 4.30$, $P = 0.038$) were significant predictors of whether or not urban areas had conflicts; urban areas containing more forested and agricultural areas and less developed areas had fewer conflicts (Fig. 4-2b). Shrubland ($\chi_1^2 = 0.35$, $P = 0.552$), grassland, ($\chi_1^2 = 2.49$, $P = 0.115$), riparian ($\chi_1^2 = 1.41$, $P = 0.235$), sparse ($\chi_1^2 = 0.03$, $P = 0.865$), and open space ($\chi_1^2 = 0.10$, $P = 0.753$) did not predict whether or not urban areas had conflicts (Fig. 4-2b).

Urban areas with and without coyotes had high percentages of exurban, suburban, and urban housing density classes and low percentages of rural housing density (Fig. 4-3a). Exurban ($\chi_1^2 = 7.82, P = 0.005$) and urban ($\chi_1^2 = 7.11, P = 0.008$) housing densities were significant predictors of whether or not urban areas had conflicts; urban areas containing higher percentages of exurban housing density had fewer conflicts, and those containing higher percentages of urban housing density had more conflicts (Fig. 4-3b). Rural ($\chi_1^2 = 0.03, P = 0.874$) and suburban ($\chi_1^2 = 0.72, P = 0.395$) housing densities did not predict whether or not urban areas had conflicts (Fig. 4-3b).

Average annual precipitation (\pm SD) in urban areas containing resident coyotes was 91 ± 35 cm and in urban areas without coyotes was 77 ± 45 cm. Average annual precipitation in urban areas with conflicts was 89 ± 38 cm and in urban areas containing coyotes but without conflicts was 97 ± 23 cm. Precipitation was not a significant predictor of whether or not urban areas had conflicts ($\chi_1^2 = 1.04, P = 0.308$).

Sparse ($F_{2,102} = 4.07, P = 0.020$), development ($F_{2,102} = 10.43, P < 0.001$), and agriculture ($F_{2,102} = 9.68, P < 0.001$) land cover types differed among the three human population size categories (Fig. 4-4a). Percentages of sparse land cover were higher in the high category than the low category ($P = 0.015$), percentages of development land cover were higher in the high category than the middle ($P = 0.010$) and low ($P < 0.001$) categories, and percentages of agriculture land cover were higher in the low category than the high category ($P < 0.001$; Fig. 4-4a). Forest ($F_{2,102} = 0.452, P = 0.638$), shrubland ($F_{2,102} = 0.203, P = 0.816$), grassland ($F_{2,102} = 0.324, P = 0.724$), riparian ($F_{2,102} = 0.105,$

$P = 0.900$), and open space ($F_{2,102} = 0.318$, $P = 0.728$) land cover types did not differ among human population size categories (Fig. 4-4a).

Every land cover type except agriculture ($F_{4,100} = 1.08$, $P = 0.372$) differed among the five geographic regions (forest: $F_{4,100} = 29.02$, $P < 0.001$; shrubland: $F_{4,100} = 15.80$, $P < 0.001$; grassland: $F_{4,100} = 16.09$, $P < 0.001$; riparian: $F_{4,100} = 6.79$, $P < 0.001$; sparse: $F_{4,100} = 2.86$, $P = 0.027$; open space: $F_{4,100} = 5.87$, $P < 0.001$; development: $F_{4,100} = 21.56$, $P < 0.001$; Fig. 4-4b). Percentages of forest land cover were higher in the Northeast than the Midwest ($P < 0.001$), Southwest ($P < 0.001$), and West ($P < 0.001$), higher in the Southeast than the Midwest ($P = 0.001$), Southwest ($P < 0.001$), and West ($P < 0.001$), and higher in the Midwest than West ($P = 0.043$). Percentages of shrubland land cover were higher in the Southwest than the Northeast ($P < 0.001$), Southeast ($P < 0.001$), Midwest ($P < 0.001$), and West ($P = 0.003$), and higher in the West than the Northeast ($P = 0.009$), Southeast ($P = 0.013$), and Midwest ($P = 0.015$). Percentages of grassland land cover were higher in the Southwest than the Northeast ($P < 0.001$), Southeast ($P = 0.001$), and Midwest ($P < 0.001$), and higher in the West than the Northeast ($P < 0.001$), Southeast ($P = 0.001$), and Midwest ($P < 0.001$). Percentages of riparian land cover were higher in the Northeast than the West ($P = 0.019$) and higher in the Southeast than the Southwest ($P = 0.002$) and West ($P < 0.001$). Although the region effect was significant for sparse land cover, none of the pairwise comparisons among geographic regions was significant. Percentages of open space land cover were higher in the Midwest than the Northeast ($P = 0.012$) and West ($P = 0.002$) and higher in the Southeast than the West ($P = 0.015$). Percentages of development land cover were higher

in the Midwest than the Northeast ($P < 0.001$) and Southeast ($P = 0.001$), higher in the Southwest than the Northeast ($P = 0.005$) and Southeast ($P = 0.013$), and higher in the West than the Northeast ($P < 0.001$), Southeast ($P < 0.001$), Midwest ($P = 0.003$), and Southwest ($P = 0.009$; Fig. 4-4b).

Every housing density class except rural ($F_{2,102} = 0.17$, $P = 0.842$) differed among the three human population size categories (exurban: $F_{2,102} = 17.58$, $P < 0.001$; suburban: $F_{2,102} = 9.39$, $P < 0.001$; urban: $F_{2,102} = 10.55$, $P < 0.001$; Fig. 4-5a). Percentages of exurban housing density were higher in the middle category than the high category ($P = 0.001$) and higher in the low category than the high category ($P < 0.001$). Percentages of suburban housing density were higher in the high category than the low category ($P < 0.001$) and higher in the middle category than the low category ($P = 0.017$). Percentages of urban housing density were higher in the high category than the middle ($P = 0.007$) and low ($P < 0.001$) categories (Fig. 4-5a).

Every housing density class except suburban ($F_{4,100} = 0.55$, $P = 0.699$) differed among the five geographic regions (rural: $F_{4,100} = 12.25$, $P < 0.001$; exurban: $F_{4,100} = 13.46$, $P < 0.001$; urban: $F_{4,100} = 20.50$, $P < 0.001$; Fig. 4-5b). Percentages of rural housing density were higher in the Southeast than the Northeast ($P = 0.013$), higher in the Midwest than the Northeast ($P < 0.001$), higher in the Southwest than the Northeast ($P < 0.001$), Southeast ($P = 0.009$) and West ($P = 0.042$), and higher in the West than the Northeast ($P = 0.002$). Percentages of exurban housing density were higher in the Northeast than the Midwest ($P = 0.040$), Southwest ($P = 0.003$), and West ($P < 0.001$), higher in the Southeast than the Southwest ($P = 0.004$) and West ($P < 0.001$), and higher

in the Midwest than the West ($P = 0.011$). Percentages of urban housing density were higher in the Midwest than the Southeast ($P < 0.001$), higher in the Southwest than the Northeast ($P = 0.007$) and Southeast ($P < 0.001$), and higher in the West than the Northeast ($P < 0.001$), Southeast ($P < 0.001$), and Midwest ($P = 0.001$; Fig. 4-5b).

Precipitation values did not differ among the three human population size categories ($F_{2,102} = 0.10$, $P = 0.904$), but they did differ among the five geographic regions ($F_{4,100} = 45.73$, $P < 0.001$). Precipitation was higher in the Northeast than the Southwest ($P < 0.001$) and West ($P < 0.001$), higher in the Southeast than the Midwest ($P < 0.001$), Southwest ($P < 0.001$), and West ($P < 0.001$), higher in the Midwest than the West ($P < 0.001$), and higher in the Southwest than the West ($P = 0.006$).

4. Discussion

Most (91%) of the urban areas in our study contained resident coyotes, confirming coyotes are ubiquitous throughout North America and have learned to adapt to and thrive in one of the most extreme habitats for wildlife species, urban development. Every urban area in both the high and middle human population size categories had coyotes, compared to only 74% of urban areas in the low category. Additionally, 80% or more of urban areas in each of the high and middle human population size categories reported conflicts, whereas only 37% of urban areas in the low category reported such conflicts. These results suggest coyotes may be drawn to areas with larger numbers of humans because of the refugia they provide; trapping or hunting of coyotes usually does not occur in larger cities, so coyotes may be more protected in these urban areas (Gehrt &

Riley, 2010). Alternatively, these larger urban areas might be expanding into coyote range, thus increasing the potential for conflicts.

Coyotes may be attracted to anthropogenic food sources commonly found in urban areas, and they will consume foods that are easier to procure, such as human-related foods, as substitutes for more natural foods, such as rodents, increasing dietary diversity (Fedriani, Fuller, & Sauvajot, 2001; McClure, Smith, & Shaw, 1995).

However, in a study of captive coyotes, Poessel et al. (see Chapter 2) found habitat structure, rather than food, was the primary motivator of coyote patch choice, with coyotes preferring a mixture of anthropogenic and natural habitat found only in urban areas. In contrast, Gehrt et al. (2009) did not find evidence that coyotes were attracted to human-associated areas, but this finding was at the finer scale of the coyote's home range, rather than at the broader scale of the urban area. Our results indicate coyotes might be attracted to larger urban areas not only because they provide refugia, but also due to the heterogeneous habitats and anthropogenic food sources provided by such areas, which in turn may lead to increased conflicts.

The occurrence of conflicts also appeared to have a regional bias, with more conflicts occurring in western urban areas, consistent with White and Gehrt's (2009) analysis of coyote attacks on humans. In the Northeast region, only 50% of urban areas reported conflicts, the lowest percentage among the five regions. Further, 58% of urban areas in the Northeast and Southeast regions combined had conflicts, compared to 74% of urban areas in the other three regions combined. Coyotes began to expand into the eastern United States only during the 20th century and reached the Northeast region by

the 1950s and the Southeast region by the 1960s (Parker, 1995). This relatively recent occupation might explain the reduced level of conflict in the eastern regions if coyote densities are lower than in other regions. Coyotes unfamiliar with urbanized environments may require a period of adjustment before they can thrive in these areas, as Bogan (2004) discovered in an urban coyote study near Albany, New York where annual survival was low (20%). However, other factors may also contribute to fewer coyote conflicts. First, many eastern coyotes in the Northeast region are hybrids between coyotes and eastern wolves (*C. lycaon*; Kays, Curtis, & Kirchman, 2010; Way, Rutledge, Wheeldon, & White, 2010) and have been labeled coywolves (*C. latrans* × *C. lycaon*; Way, 2013; Way et al., 2010). Perhaps the presence of wolf DNA in these animals has influenced their behavior to be less bold towards humans, as wolves, especially in forested areas, are generally shy and avoid people (Fritts, Stephenson, Hayes, & Boitani, 2003), although coyote conflict levels in eastern rural areas have been high (Mastro, Gese, Young, & Shivik, 2012). Hybridizing with wolves also has contributed to the development of larger coyotes (Parker, 1995), so perhaps coyotes are more dependent on larger prey and less likely to occur in highly developed areas. Second, harsh winters in the Northeast region (Parker, 1995; Way et al., 2010) might reduce the likelihood of coyote encounters with pets if residents and their pets do not venture outside as much during this time of year, which coincides with the breeding season of coyotes when conflicts might be more likely to occur (Poessel et al., 2013). Finally, white-tailed deer (*Odocoileus virginianus*) densities are high in the Northeast region, including urban areas (Lund, 1997; Stromayer & Warren, 1997), and eastern coyotes are known to rely upon

deer as a primary food source (Gompper, 2002; Parker, 1995). Perhaps the high availability of natural prey reduces conflicts between humans and coyotes in the northeastern urban areas, as has been documented in a western urban area (Magle et al. 2014).

Urban areas with conflicts contained lower percentages of forested and agricultural areas and higher percentages of developed areas. Additionally, urban areas with conflicts contained lower percentages of exurban and higher percentages of urban housing densities. Several urban coyote studies have determined the importance of natural cover, including forests, for coyotes. Gehrt et al. (2009) and Riley et al. (2003) both found coyotes were predominantly associated with natural land use, with smaller percentages of development in coyote home ranges. Gese et al. (2012) determined coyotes preferred less-developed areas with low levels of human activity. Dodge and Kashian (2013) found availability and access to tree cover was more important for coyote occupancy than the presence of open space. Poessel et al. (2013) determined conflicts were greater in developed land cover than in natural and agricultural land cover, and they occurred less often than expected in exurban housing densities. These results are consistent with our findings and suggest the cover provided by forests may help reduce encounters between coyotes and humans and their pets, whereas coyote encounters and conflicts are more likely to occur in developed areas, especially areas with dense concentrations of humans and pets.

We found several patterns among land cover types, housing density classes, precipitation, human population size categories, and geographic regions. As might be

expected, development, including suburban and urban areas, was higher in the high human population size category, whereas agriculture and exurban development were highest in the low category, likely contributing to reduced conflicts in urban areas with lower concentrations of people. Forested and riparian areas were higher in the eastern regions, which may further explain why the Northeast region had fewer conflicts.

Development, especially urban housing densities, was higher in the western regions, and exurban housing densities were higher in the eastern regions, additionally clarifying the difference in conflicts between eastern and western urban areas. Although precipitation did not predict whether or not urban areas had conflicts, annual precipitation was higher in eastern urban areas, so the presence of water might mitigate conflicts to a certain extent.

Contrary to our predictions, management of conflicts was a low priority for the majority (55%) of urban areas, and only 10% of urban areas considered this issue to be a high priority. Many wildlife managers stated they provide education to the public and advice on how to reduce conflicts, rather than active management of individual coyotes. However, for many urban areas, conflict management would become a high priority if a coyote attacked a person or if human safety became a concern. We emphasize that, although conflict management was a low priority for wildlife managers, it is likely a high priority for urban residents, especially for those directly involved in conflicts with coyotes. Citizens experiencing a coyote attack on a pet or an interaction with an aggressive coyote may have a reduced tolerance for wildlife (Poessel et al., 2013). Wildlife managers should recognize these differing perceptions of conflicts and be more

proactive in their urban wildlife policies rather than reactive, i.e., only prioritize conflicts when they have reached unacceptable levels, such as attacks on humans. Both human and coyote populations will continue to grow in North American urban areas, thus contributing to escalating conflicts. By implementing proactive policies, such as landscape design that considers coyote habitat requirements and targeted education campaigns, wildlife managers may be able to prevent conflicts from becoming a high priority.

Most urban areas reported annual numbers of conflicts in the 1-10 or 11-40 ranges. Only seven (7%) urban areas reported annual conflicts in the 41-100 or >100 ranges, with six of these in the high human population size category (17% of this category) and four of these in the Southwest and West regions (11% of these two regions combined). These results indicate large urban areas, especially those in the western United States, not only are more likely to have conflicts, but they also are more likely to have greater numbers of conflicts.

We emphasize that some bias may be present in our results. Wildlife managers based their responses to the coyote conflict questions (questions 2 and 4) on conflict reports received from their citizens, which may introduce reporting bias (Poessel et al., 2013). Conflicts may occur at a reduced level in the low human population size category simply because of fewer numbers of people to report conflicts, which may also explain why some urban areas in this category reported they did not have resident coyotes. Bias may also occur if people in this category are less likely to report conflicts with coyotes if they do not perceive coyotes as a threat. The low human population size category

contained higher percentages of agriculture and exurban housing development than the other categories, so perhaps humans residing in these low-density urban areas observe coyotes more often and are more tolerant of them than people residing in more densely-populated urban areas (Poessel et al., 2013). Residents of these low-density areas may also be more likely to remove coyotes, resulting in a refuge effect for coyotes in larger urban areas (Gehrt & Riley, 2010), leading to more conflicts in these large areas.

Additional biases in all urban areas may include socioeconomic factors. For example, people with higher incomes whose properties contain more resources for coyotes (e.g., food or cover) may be more likely to encounter a coyote and, thus, report the coyote sighting or conflict (Wine, Gagné, & Meentemeyer, 2015). Additionally, urban areas with lower perimeter-area ratios may have less contact with the urban-wildland interface and, hence, a lower probability of residents encountering and reporting coyotes.

5. Conclusions

We identified multiple factors influencing the occurrence of coyotes and conflicts in urban areas of the United States. Coyotes and conflicts were more likely to occur in larger urban areas with higher concentrations of humans, and conflicts also were more likely to occur in western regions with larger amounts of high-intensity development and less forested and agricultural areas. These results should allow urban wildlife managers to predict whether or not conflicts between humans and coyotes will arise or increase based on the geographic and demographic factors in place within their cities. An assessment of such factors may allow wildlife officials to identify the most appropriate tools to prevent or mitigate conflicts, including education of citizens and certain habitat

management practices. As coyotes continue to expand into North American urban areas, proactive management could assist in reducing conflicts in increasingly urbanized regions.

Although our results were specific to coyotes, we emphasize these carnivores are an indicator of escalating human-wildlife interactions in urban ecosystems. As carnivore populations continue to increase in urban areas throughout the world, encounters and conflicts with humans also will inevitably increase (Ditchkoff, Saalfeld, & Gibson, 2006). We determined conflicts with carnivores in urban landscapes can be predicted based on environmental factors. These results have important implications for urban ecology, and future research should be focused on determining which factors predict conflict with other urban carnivore species. By implementing practices such as sustainable urban planning (Tanner et al., 2014), landscape design that incorporates wildlife habitat requirements, and citizen education, wildlife and urban managers may be able to proactively reduce human-carnivore conflicts, promote coexistence between urban citizens and wildlife, and maintain the biological diversity of urban ecosystems.

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Table 4-1

List of questions included in the survey of 105 urban areas in the contiguous United States.

Number	Text of Question
1	Does the [city name] urban area currently have coyotes residing within it? This would not include an occasional, nomadic coyote coming into the city. Rather, this would include coyotes permanently living or residing within the metro area, either in urban areas or in open spaces contained within the metro area.
2	If coyotes do reside in the [city name] urban area, do you have human-coyote conflicts? A conflict is defined as either 1) a physical attack by a coyote on a human or pet; or 2) a coyote showing aggressive behavior toward a human or pet, e.g., baring teeth, growling, stalking, or other behavior that could potentially endanger human or pet safety.
3	If the [city name] urban area does have human-coyote conflicts, do you consider this to be an issue of high priority, low priority, or no priority? High priority would indicate a critical need to address or manage the conflict issue, no priority would indicate no concern and no management taken to address the issue, and low priority would be between these two, i.e., concern over coyote conflicts but little action is taken.
4	If the [city name] urban area does have human-coyote conflicts, can you provide an estimate of the number of conflicts during the last year (2013) or for the most recent year for which you have data? a) 1-10 b) 11-40 c) 41-100 d) >100

Table 4-2

Percentage of responses to each of four questions included in the survey of 105 urban areas in the contiguous United States, by human population size category and geographic region. Human population size categories were high, the largest 35 urban areas based on human population size; middle, the 35 urban areas beginning at a population size of 500,000 and up; and low, the 35 urban areas beginning at a population size of 100,000 and up. Geographic region refers to the geographic area of the contiguous United States. Numbers in parentheses refer to the question number from Table 1.

Category	Coyotes (1)		Conflicts (2)			Management Priority (3)				Number of Conflicts (4)						
	Yes	No	Yes	No	N/A	High	Low	No	N/A	0	1-10	11-40	41-100	>100	No Answer	N/A
High	100	0	86	14	0	17	66	3	14	0	37	20	9	9	11	14
Middle	100	0	80	20	0	9	71	0	20	6	29	31	0	3	11	20
Low	74	26	37	37	26	6	28	3	63	3	14	17	0	0	3	63
Region	Yes	No	Yes	No	N/A	High	Low	No	N/A	0	1-10	11-40	41-100	>100	No Answer	N/A
Northeast	90	10	50	40	10	15	30	5	50	10	35	5	0	0	0	50
Southeast	91	9	65	26	9	0	65	0	35	0	17	35	4	0	9	35
Midwest	96	4	63	33	4	8	54	0	38	0	21	17	4	4	17	37
Southwest	100	0	86	14	0	22	57	7	14	7	36	22	7	0	14	14
West	83	17	79	4	17	12	67	0	21	0	29	33	0	13	4	21

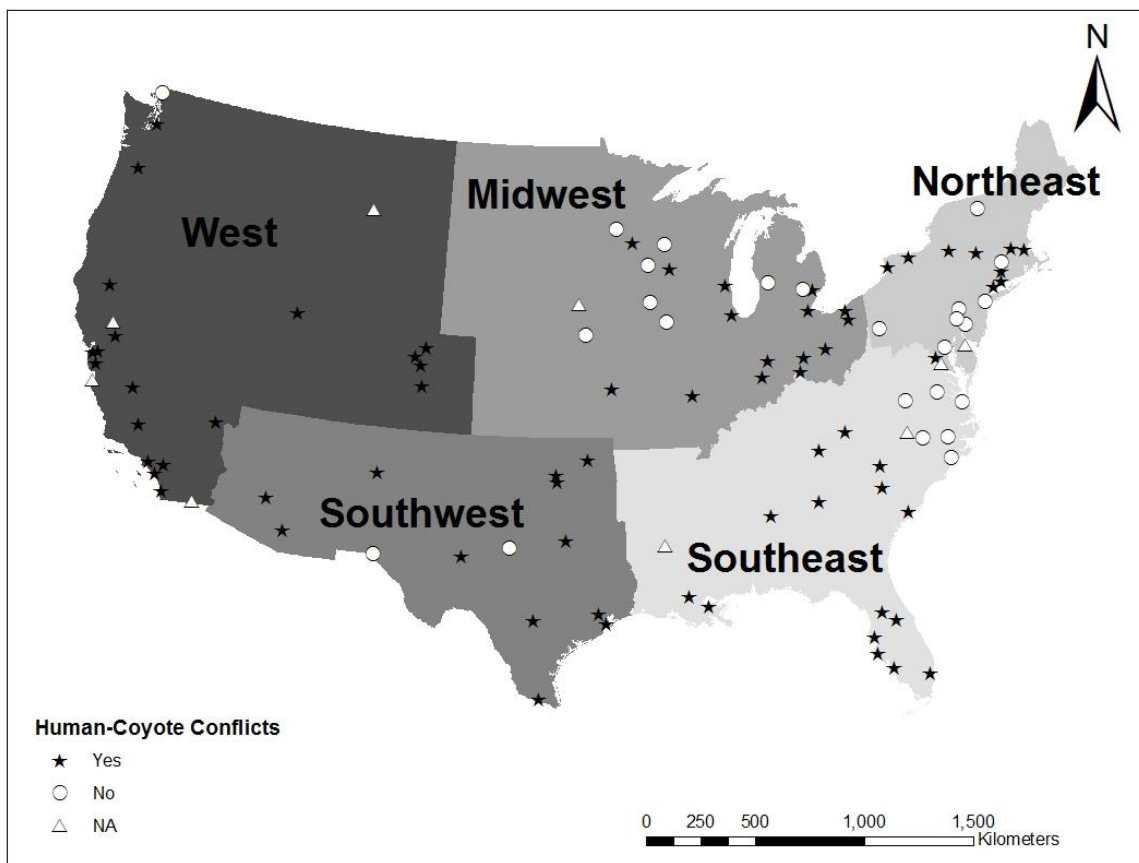


Fig. 4-1. Map of the contiguous United States divided into five geographic regions. Black stars represent urban areas that have both coyotes and human-coyote conflicts, white circles represent urban areas that have coyotes but do not have human-coyote conflicts, and white triangles represent urban areas that do not have coyotes or human-coyote conflicts.

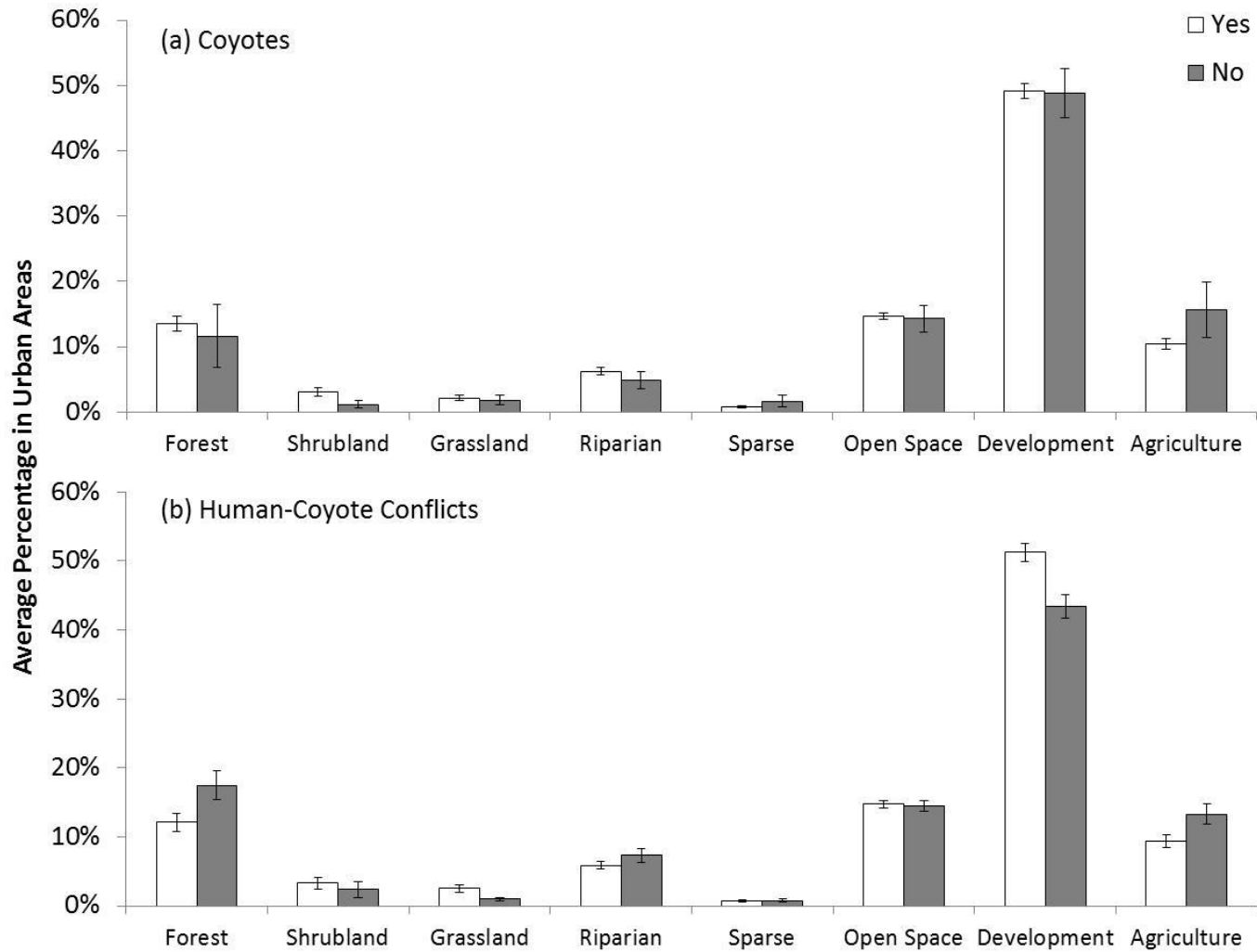


Fig. 4-2. Average percentages of each of eight land cover types in United States urban areas with (yes) and without (no) (a) resident coyotes ($n = 105$) and (b) human-coyote conflicts ($n = 96$). Bars represent standard error around the mean.

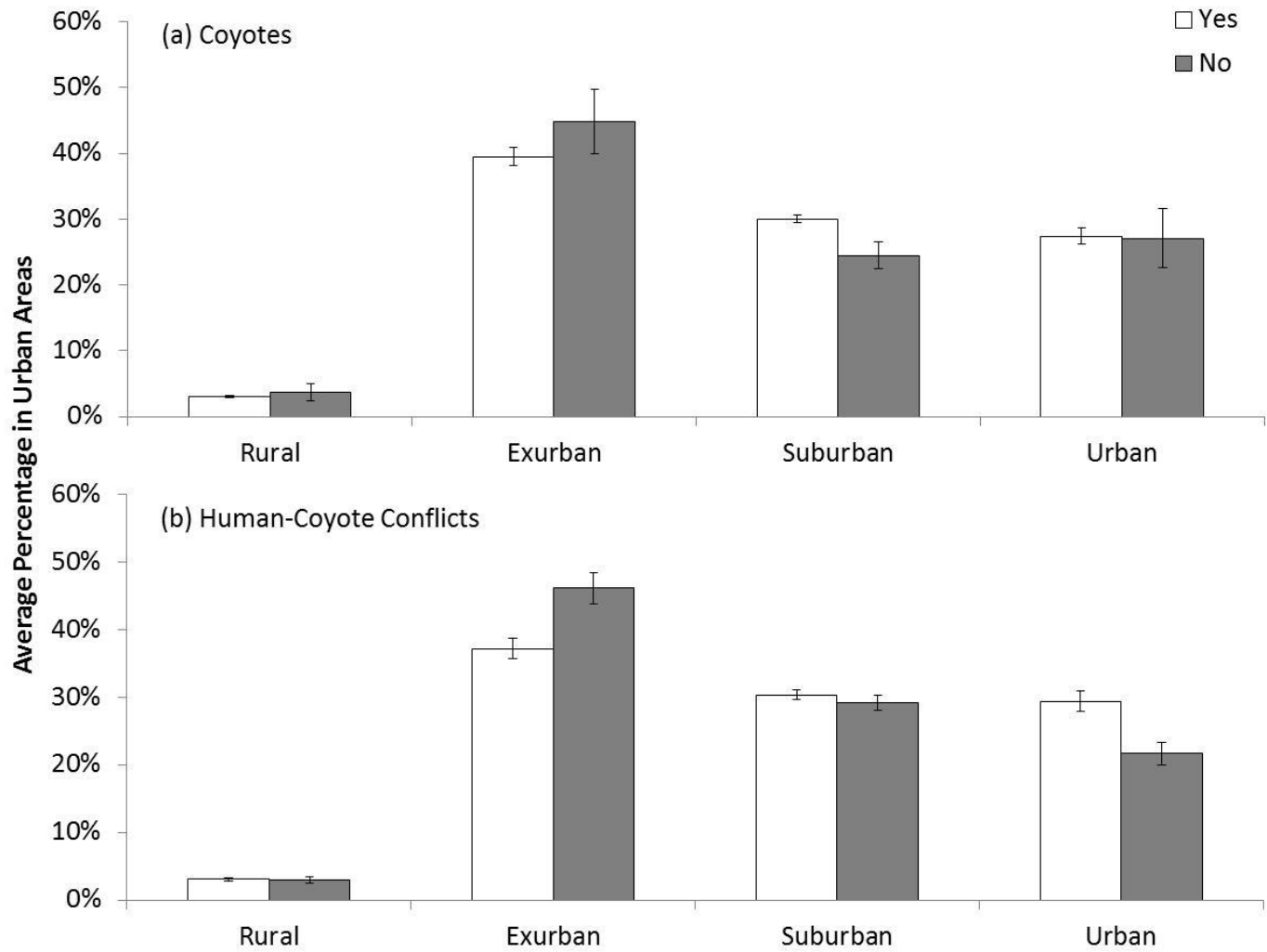


Fig. 4-3. Average percentages of each of four housing density classes in United States urban areas with (yes) and without (no) (a) resident coyotes ($n = 105$) and (b) human-coyote conflicts ($n = 96$). Bars represent standard error around the mean.

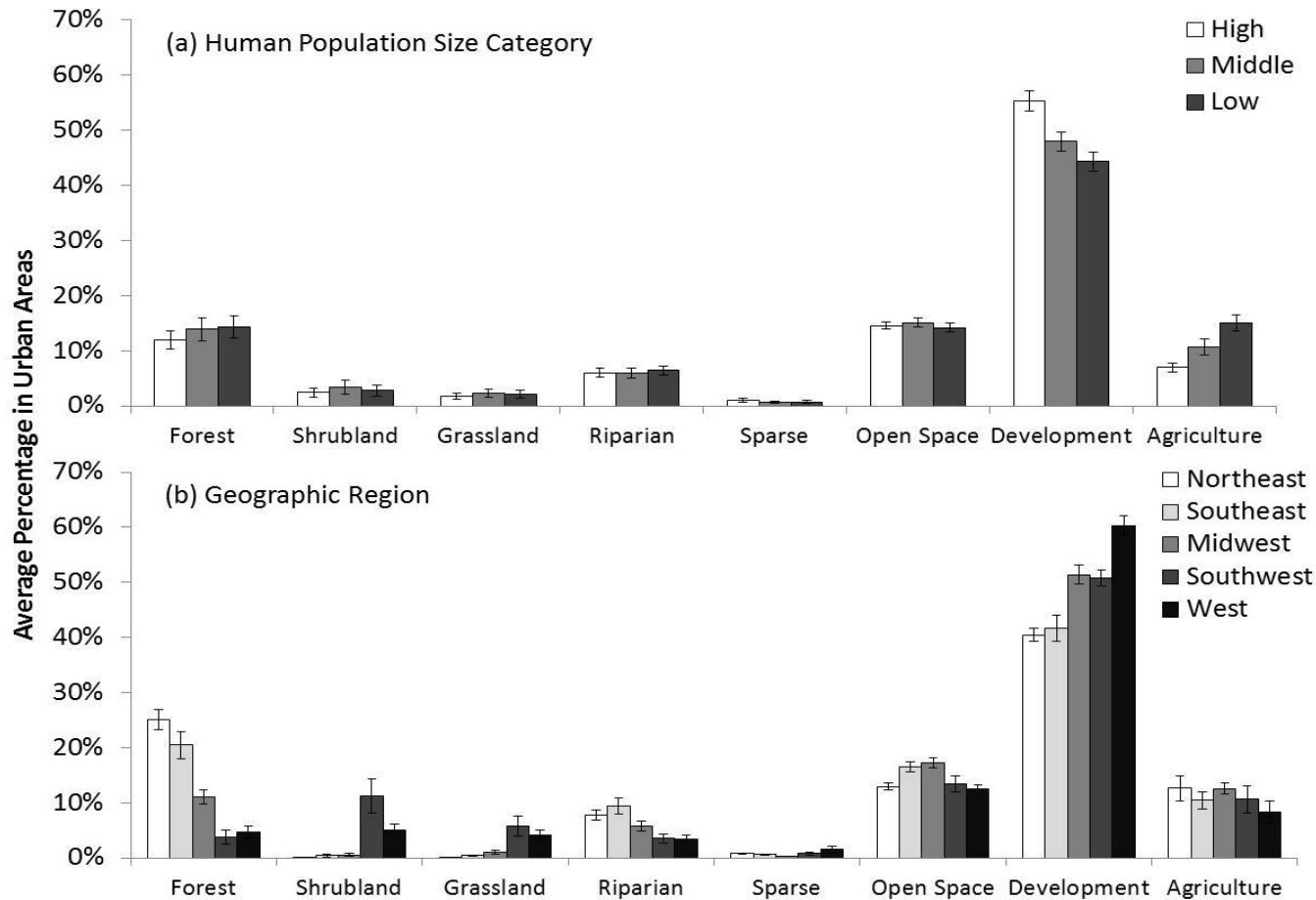


Fig. 4-4. Average percentages of each of eight land cover types in United States urban areas by (a) human population size category and (b) geographic region. Human population size categories were high, the largest 35 urban areas based on human population size; middle, the 35 urban areas beginning at a population size of 500,000 and up; and low, the 35 urban areas beginning at a population size of 100,000 and up. Geographic region refers to the geographic area of the contiguous United States. Bars represent standard error around the mean.

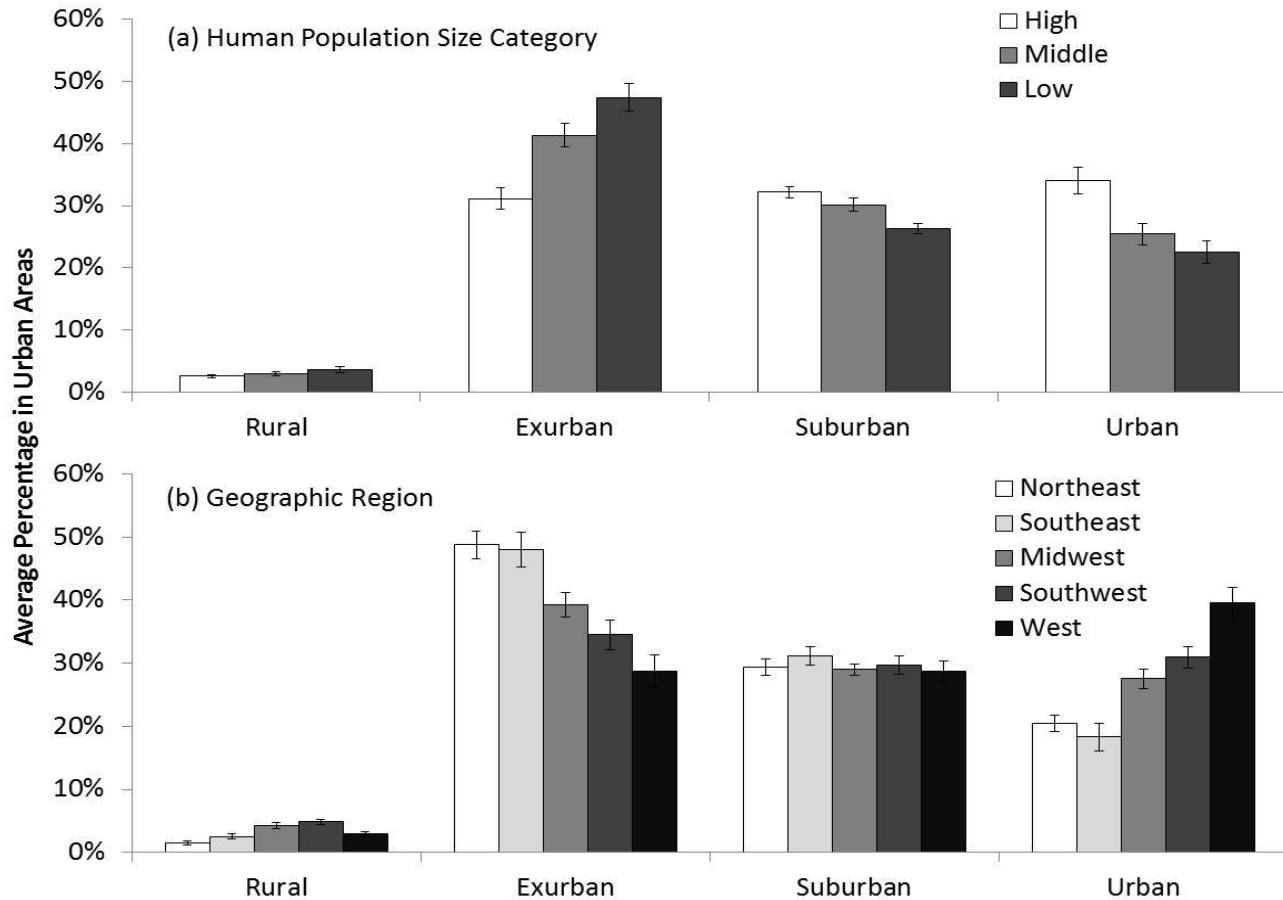


Fig. 4-5. Average percentages of each of four housing density classes in United States urban areas by (a) human population size category and (b) geographic region. Human population size categories were high, the largest 35 urban areas based on human population size; middle, the 35 urban areas beginning at a population size of 500,000 and up; and low, the 35 urban areas beginning at a population size of 100,000 and up. Geographic region refers to the geographic area of the contiguous United States. Bars represent standard error around the mean.

CHAPTER 5

CONCLUSIONS

This dissertation evaluated the behavior and ecology of coyotes in urban environments at varying spatial scales, with an objective of identifying variables that could help predict, and subsequently mitigate, human-coyote conflicts. Each chapter examined this issue at progressively larger scales. Chapter 2 focused on a captive coyote population at a fine spatial scale, Chapter 3 examined a coyote population in one particular urban area at a local, metropolitan scale, and Chapter 4 focused on coyotes and human-coyote conflicts at a national scale.

In Chapter 2, coyotes preferred the grassland habitat in which they were raised, supporting the idea that coyotes imprint on their natal environment (Gantz & Knowlton 2005). However, when investigating novel environments, coyotes preferred heterogeneous habitats, i.e., habitat structure consisting of both urban and natural habitat types. Such a habitat mixture is often preferred by wild coyotes, including urban coyotes (Rashleigh et al. 2008). Both female coyotes and bold coyotes followed the same general pattern in pen preference, choosing pens with a mixture of structure over pens with uniform structure. Shy female coyotes exhibited similar preferences, indicating that our overall results were most strongly expressed in females. These results suggest females exhibited strong preferences which might drive habitat selection and patch choice in coyotes, whereas the preferences of male coyotes, which may follow females rather than habitat, might be more equivocal and less likely to influence overall patterns. Bold coyotes also preferred one of the mixed pens over the homogenous pens and chose this

pen more than did shy coyotes. Bold coyotes might be more exploratory than shy coyotes, preferring the more complex habitats of the mixed pens, possibly because of the rich environment provided by habitat edges including large amounts of structural cover. Finally, coyotes in the non-breeding season selected one of the mixed pens more than the uniform pens, and they also chose this pen more than did the coyotes in the breeding season. Coyotes do not travel far from den sites while raising pups (coinciding with the non-breeding season) when both the adult female and pups need to be provisioned with food (Harrison & Gilbert 1985), so perhaps using a variety of habitat types at this time increases the amount of food found within a smaller area.

Contrary to our predictions, food had no effect on coyote patch choice. Once coyotes selected a pen, they continued to use that pen even when more food was placed in less preferred pens. Our results suggest wild coyotes may choose urban areas for reasons other than food availability. Wild urban coyotes generally use a variety of urban environments, but their diet primarily consists of native foods (e.g., rodents) rather than anthropogenic foods found in urban landscapes (Morey et al. 2007). Hence, urban coyotes may identify attractive habitat patches containing food resources, and then reside in adjacent patches that meet other criteria, such as structural cover.

Our results should assist wildlife officials in North America in managing their urban coyote populations and human-coyote conflicts. Managers should be aware that urban areas incorporating large tracts of natural lands or open space interspersed throughout the urban matrix may be more likely to be used by coyotes and, as a result, have greater potential for human-coyote conflicts if humans also use these lands. Hence,

managing the availability of complex habitats in urban areas may warrant further consideration by urban managers.

In Chapter 3, we captured and monitored 22 coyotes in the Denver metropolitan area to examine their spatial ecology in terms of home-range size, habitat use, and resource selection. Home-range sizes of resident coyotes in our study were no different than those reported for residents in a rural area in southeastern Colorado (Gese et al. 1988), contrary to the trend for smaller home ranges in other urban landscapes (Gehrt & Riley 2010). Resident home ranges were smaller than those of transients, and resident coyotes also maintained smaller home ranges during the day than at night. In contrast, sizes of ranges for transients did not differ between day and night. We found no differences in home-range sizes between males and females or among the three seasons; however, we found considerable individual variation in home-range sizes of coyotes in our study area.

On average, developed lands comprised 44% of the coyote home range, a result that differs from our hypothesis and other urban coyote studies (Riley et al. 2003; Gehrt et al. 2009). In contrast, the highest frequency of coyote locations was in natural lands, indicating that although their home ranges included considerable development, coyotes chose to spend the majority of their time in natural, undeveloped areas. On a temporal scale, coyotes, particularly residents, tended to rest in natural areas during the day then venture out into the surrounding neighborhoods at night, although they still spent more time in natural lands than in developed lands at night. Contrary to our predictions, home-range size of resident coyotes was not related to the percentage of altered or developed

lands within the home range, indicating coyotes in our study area were able to efficiently procure resources in highly-developed areas without expanding their home ranges. When using natural lands, coyotes preferred riparian habitat that provided cover, and when using developed lands, coyotes preferred low-density residential neighborhoods with low-traffic roads.

Based on resource selection models, we concluded coyotes in our study area, regardless of sex, status, season, or time of day, selected for natural lands over developed lands, consistent with our habitat use findings in which the majority of coyote locations were in natural lands even though home ranges consisted of large amounts of development. Coyotes also selected altered lands over developed lands. These results confirm that coyotes in urban environments will choose to spend their time in natural or semi-natural habitat patches within their home ranges and avoid the most developed areas. Female coyotes had stronger habitat selection preferences than males. Resident coyotes used natural lands more than transients, confirming our observations of residents resting in natural areas, especially during the day, and transients moving through all habitat types in search of vacant territories. We found no significant seasonal patterns in resource selection, although use of habitat tended to increase during the pup-rearing season, when coyotes increase activity to find food for their pups. Finally, coyotes during the day selected for natural lands over altered lands, whereas coyotes at night increased activity in all habitat types and also selected for roads, providing evidence of the nocturnal nature of coyotes in urban environments and their preference of being most active at times when human activity is minimized.

Coyotes in the Denver metropolitan area have efficiently adapted to this highly-developed urbanized landscape and effectively used all habitat types, although they preferred to spend most of their time in patches of natural habitat where humans were less active. Despite their attempts to avoid human activity, coyotes in our study area increasingly have become involved in conflicts with humans (Poessel et al. 2013), a situation that may be impossible to circumvent in such a highly-developed urban area. Although some of our results were consistent with the results of other urban coyote studies, e.g., selecting natural habitat over developed areas and increasing activity at night, other results were unique to our study. Coyote home ranges, on average, contained more developed lands than natural lands, and home range sizes did not increase with higher amounts of urbanization. Further, every coyote in our study incorporated all 3 land-use types in their home ranges, whereas previous studies reported some coyotes had either no natural or no developed areas within home ranges (Riley et al. 2003; Gehrt et al. 2009). These results suggest coyotes in the Denver metropolitan area have become highly adapted to an urbanized landscape with large concentrations of developed areas, reflecting the flexible nature of this opportunistic carnivore.

In Chapter 4, we found 91% of the urban areas in our study contained resident coyotes, including every urban area in both the high and middle human population size categories, compared to only 74% of urban areas with low population size. Additionally, 80% or more of urban areas in each of the high and middle human population size categories reported conflicts, whereas only 37% of urban areas in the low category reported such conflicts. These results suggest coyotes may be drawn to areas with larger

numbers of humans because of the refugia they provide; trapping or hunting of coyotes usually does not occur in larger cities, so coyotes may be more protected in these urban areas (Gehrt & Riley 2010). Alternatively, these larger urban areas might be expanding into coyote range, thus increasing the potential for conflicts. The occurrence of conflicts also appeared to have a regional bias, with more conflicts occurring in western urban areas than in eastern urban areas. Additionally, urban areas with conflicts contained lower percentages of forested and agricultural areas and higher percentages of developed areas, especially urban housing densities. These results suggest the cover provided by forests may help reduce encounters between coyotes and humans and their pets, whereas coyote encounters and conflicts are more likely to occur in developed areas, especially areas with dense concentrations of humans and pets.

As might be expected, development, including suburban and urban areas, was higher in the high human population size category, whereas agriculture and exurban development were highest in the low category. Forested and riparian areas were higher in the eastern regions, which may further explain why the eastern urban areas had fewer conflicts. Development, especially urban housing densities, was higher in the western regions, and exurban housing densities were higher in the eastern regions, additionally clarifying the difference in conflicts between eastern and western urban areas.

Contrary to our predictions, management of conflicts was a low priority for the majority of urban areas. However, conflict management is likely a high priority for urban residents, especially for those directly involved in conflicts with coyotes. Wildlife managers should recognize these differing perceptions of conflicts and be more proactive

in their urban wildlife policies so they can prevent conflicts from becoming a high priority. Most urban areas reported annual numbers of conflicts in the 1-10 or 11-40 ranges. Most urban areas reporting higher numbers of conflicts were in the high human population size category or were located in the western regions, so urban areas more likely to have conflicts also were more likely to have greater numbers of conflicts.

Our results should allow urban wildlife managers to predict whether or not conflicts between humans and coyotes will arise or increase based on the geographic and demographic factors in place within their cities. An assessment of such factors may allow wildlife officials to identify the most appropriate tools to prevent or mitigate conflicts, including education of citizens and certain habitat management practices, such as landscape design that incorporates wildlife habitat requirements. As coyotes continue to expand into North American urban areas, proactive management could assist in reducing conflicts in increasingly urbanized regions.

Although each of the three studies in this dissertation was independent, the ecological results of each study were consistent. We determined coyotes in urban environments prefer natural habitat patches, but will also use developed patches. Within natural habitat, coyotes prefer forested and riparian areas that provide cover for both coyotes and their native prey. Conflicts between coyotes and humans increase in the most highly-developed areas where encounters between coyotes and humans and their pets also increase. Other similarities between studies include the finding that females drive habitat selection in urban coyotes, and coyotes increase their use of multiple habitat types during the pup-rearing season. These results suggest habitat management and

landscape design, as well as continued education of citizens, in urban areas may be an effective method for reducing human-coyote conflicts and promoting coexistence between urban citizens and wildlife.

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APPENDIX

Permission for Chapter 2 to be reprinted in dissertation:

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EDUCATION

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 Utah State University – Department of Wildland Resources and the Ecology Center
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- 2007-2009 M.S. in Ecology
 Colorado State University – Department of Fish, Wildlife and Conservation Biology and Graduate Degree Program in Ecology
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RESEARCH EXPERIENCE

- 2010-Present **Graduate Research Assistant**, Department of Wildland Resources and the Ecology Center, Utah State University. Dissertation objectives include the analysis of: 1) the influence of habitat structure and food on coyote patch choice in urban and natural environments; 2) the influence of environmental covariates on the presence of coyotes and the occurrence of human-coyote conflicts in United States urban areas; and 3) the ecology, home ranges, spatial and temporal patterns of habitat use, and resource selection of urban coyotes in the Denver metropolitan area.

- 2009-2010 **Research Associate**, Department of Fish, Wildlife and Conservation Biology, Colorado State University. Analyzed road selection of bobcats in southern California in collaboration with the U.S. Geological Survey; mapped and analyzed coyote conflict data in the Denver metropolitan area.
- 2007-2009 **Graduate Research Assistant**, Department of Fish, Wildlife and Conservation Biology and Graduate Degree Program in Ecology. Thesis objectives included the analysis of: 1) stress responses measured in the feces of black-footed ferrets based on the provision of environmental enrichment and 2) the effects of landscape features utilized by predators on the survival and habitat selection of black-footed ferrets.

OTHER FIELD EXPERIENCE

- 2011-Present **Volunteer**, National Wildlife Research Center Predator Research Station, USDA. Assist with moving, handling, and monitoring coyotes.
- 2009 **Field Assistant**, Department of Forestry, Rangeland, and Watershed Stewardship, Colorado State University. Measured production of willow trees in Yellowstone National Park.
- 2009 **Biological Technician**, Department of Biology, Colorado State University. Captured tadpoles and cared for them in boreal chorus frog project.
- 2006-2007 **Biological Science Technician**, National Black-footed Ferret Conservation Center, USFWS. Care of black-footed ferrets in endangered species breeding program.
- 2004-2006 **Volunteer**, Society for Conservation Biology Student Chapter, Colorado State University. Projects included animal tracking, bird counts, repairing fences, collecting seeds of native plants, and removing weeds and invasive plants.
- 2004-2006 **Volunteer**, Colorado Parks and Wildlife. Projects included Track Survey for Lynx Program, Bats/Inactive Mines Project, Burrowing Owl Survey, Eagle Roost Watch, River Otter Survey, and Herpetofaunal Atlas Project.
- 2004-2006 **Volunteer**, W.O.L.F. Sanctuary. Cared for wolves and wolf-dogs and participated in Wolf Ambassador Program, providing outreach and education of wolves through public events.
- 2003-2004 **Texas Master Naturalist**, Texas Parks and Wildlife Department. Projects included endangered species surveys, bird counts, maintenance of nature trails, and participation in the Texas Amphibian Watch Program.
- 1998-2004 **Docent and Volunteer**, Houston Zoo. Assisted with care of multiple carnivore species, observed animal behavior of carnivores, primates, and elephants, handled animals, gave presentations to guests, and assisted in classrooms.

2001 **Field Assistant**, Bat Conservation International. Captured, identified, and handled multiple species of bats in Kenya, Africa in a bat survey project.

SKILLS

Field

Mammal capturing, terrestrial and aerial radio telemetry, use of remote cameras, den monitoring, nocturnal spotlighting, use of GPS technology, participating in bird counts and endangered species surveys, and attaining extensive experience with captive wildlife

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PUBLICATIONS

- Poessel, S.A.**, E.M. Gese, and J.K. Young. *In preparation*. Environmental factors influencing the occurrence of coyotes and conflicts in urban areas.
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PRESENTATIONS

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- Poessel, S.A.,** S.W. Breck, T.L. Teel, S. Shwiff, K.R. Crooks, and L. Angeloni. 2011. Spatial and temporal patterns of coyote conflicts in the Denver Metropolitan Area. Urban Wildlife Management and Planning Conference, Austin, Texas. *Oral presentation*
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Teaching Assistant

Introduction to Evolution (BZ 220), Department of Biology, Colorado State University, Spring 2009, Spring 2009, and Fall 2007.

Principles of Wildlife Management (FW 260), Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fall 2008.

Conservation Biology (FW 555), Department of Fish, Wildlife and Conservation Biology, Colorado State University, Spring 2008.

Conservation and Management of Large Mammals (FW 469), Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fall 2007.

PROFESSIONAL ACTIVITIES AND SERVICE

Member

Society for Conservation Biology, The Wildlife Society, American Society of Mammalogists

Manuscript Reviewer

Biological Conservation, Journal of Wildlife Management, Wildlife Society Bulletin, The Prairie Naturalist, Western North American Naturalist, Urban Naturalist, Mammalia, Herpetological Conservation and Biology

Conference Organizer

- 2002 Association of Zoo and Aquarium Docents national conference-Papers and Programs committee
- 2015 International Urban Wildlife Conference-carnivore symposium

ACADEMIC HONORS

Dean's List – Warner College of Natural Resources, Colorado State University, each semester from Fall 2004 to Spring 2007

Robert Davis Honor Senior Memorial Award – Warner College of Natural Resources, Colorado State University, April 2007. Awarded to recognize an outstanding senior in the College.

Outstanding Senior in Wildlife Award – Department of Fish, Wildlife, and Conservation Biology, Colorado State University, April 2007. Awarded to recognize a senior in the Department who has shown exceptional capabilities both academically and professionally.

GRANTS AND FELLOWSHIPS

- 2010-2014 Quinney Foundation Fellowship, Utah State University
- 2011-2014 Ecology Center Graduate Research Support Award, Utah State University
- 2012 Ecology Center Travel Grant, Utah State University
- 2008-2009 Hill Memorial Fellowship, Warner College of Natural Resources, Colorado State University
- 2008 Women in Natural Sciences Fellowship, College of Natural Sciences, Colorado State University
- 2008 Bill Burtness Fellowship, Rocky Mountain Goat Foundation
- 2007-2008 Graduate Fellowship, Department of Biology, Colorado State University
- 2007-2008 Graduate Fellowship, Department of Fish, Wildlife and Conservation Biology, Colorado State University
- 2007-2008 Oscar and Isabel Anderson Graduate Scholarship, Warner College of Natural Resources, Colorado State University
- 2006-2007 Florence K. and Robert M. Boughton Scholarship, Warner College of Natural Resources, Colorado State University
- 2005-2006 Oscar and Isabel Anderson Undergraduate Scholarship, Warner College of Natural Resources, Colorado State University
- 2005-2006 Clinton H. Wasser Scholarship, Warner College of Natural Resources, Colorado State University