Individual variation in the ecology of urban coyotes and implications for human-coyote conflict

by

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Abstract

As urbanization expands, many species are excluded from urban areas but others persist and even thrive. When these species overlap with humans in time, space, or resources, conflicts can arise such as vehicle collisions, loss of domestic animals, the spread of zoonotics, and concern for human safety. One species that thrives in urban areas and readily makes use of anthropogenic resources is the coyote (*Canis latrans*), an opportunistic carnivore that has attracted increasing interest by inhabiting many major cities. While coyotes typically avoid humans even in cities, they often consume anthropogenic food and exhibit a large degree of individual variation in their home ranges and use of residential areas. A better understanding of how and why coyotes vary in their overlap with people could help identify and mitigate precursors to human-coyote conflict and promote coexistence between humans and urban-adapted carnivores.

I examined whether the consumption of anthropogenic food increases diet diversity and likelihood of encounters with people for coyotes by comparing the diets of urban and rural coyotes that were or were not reported as nuisance animals by the public. I then tested whether subadult, male, or diseased coyotes were more likely to use developed areas, be more active during the day, and consume anthropogenic food by capturing and fitting 19 coyotes with Global Positioning System (GPS) collars with 3-hour fix rates. I also measured selection for residential areas within the home range and for anthropogenic resources at sites used for feeding and resting. I examined the potential for food waste in compost piles to promote disease spread in coyotes by monitoring compost piles with remote cameras and compared contact rates between coyotes and the prevalence of ectoparasites to reference sites in natural areas. Lastly, I tested whether seasonal differences in activity patterns and road crossings were associated with vehicle collisions by comparing the movements of coyotes that were or were not killed in vehicle collisions and reports of coyotes killed on roads.

Urban coyotes consumed more anthropogenic food and had more diverse diets than rural coyotes. Urban coyotes reported as nuisance animals assimilated less protein and were more likely to have sarcoptic mange (*Sarcoptes scabiei*). Among GPS-collared coyotes, those with mange used more developed areas, were more active during the day, and consumed more anthropogenic food. These coyotes were also more likely to select backyards with accessible garbage and compost piles and bed under houses. Compost piles were visited more frequently and especially by visibly diseased coyotes than urban natural areas. Most compost piles contained at least one species of fungal toxin capable of compromising consumer health. Coyotes killed in vehicle collisions crossed roads most often at dusk, which overlapped with evening rush hour in winter, whereas surviving coyotes crossed roads mainly around midnight regardless of season. My results suggest that diseased coyotes are more likely to overlap with people in space, time, and resources and piles of food waste may increase disease transmission. Also, avoidance of traffic in time may help reduce risk of vehicle collisions for coyotes. Management practices that prevent disease prevalence and transmission and promote nocturnal behaviour in urban carnivores may be more successful in preventing encounters between people and coyotes and ultimately foster greater coexistence of humans and urban carnivores.

Preface

This thesis is an original work by Maureen Murray. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Animal Care and Use Committee, Project Name "Habitat Selection, Diet, and Movement of Urban Coyotes in Edmonton", AUP00000047, May 20, 2009.

Chapter 2 of this thesis has been published as M. Murray, A. Cembrowski, A.D.M. Latham, V. Lukasik, S. Pruss and C.C. St. Clair, "Greater consumption of protein-poor anthropogenic food by urban coyotes increases diet breadth and potential for human-wildlife conflict," Ecography, in press. I was responsible for the data collection and analysis as well as the manuscript composition. A. Cembrowski, A.D.M. Latham, V. Lukasik, and S. Pruss were also responsible for data collection and contributed to manuscript edits. C.C. St. Clair was the supervisory author and was involved with concept formation and manuscript composition.

Chapter 3 of this thesis has been published as M. Murray, M. Edwards, B. Abercrombie, and C.C. St. Clair, "Poor health is associated with use of anthropogenic resources in an urban carnivore," Proceedings of the Royal Society B, in press. I was responsible for the data collection and analysis as well as the manuscript composition. M. Edwards assisted with the data collection and contributed to manuscript edits. B. Abercrombie contributed to data collection and concept formation. C.C. St. Clair was the supervisory author and was involved with concept formation and manuscript composition.

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Chapter 1

1 General introduction

For the first time in history, there are as many people living in cities as rural areas (United Nations 2008) and urban areas are currently the fastest growing land use type across the globe (Angel et al. 2011). As human development expands, circumstances by which humans and wildlife overlap will also become more likely; either because of humans encroaching upon wildlife habitat or by wildlife moving into developed areas (Sillero-Zubiri, Sukumar & Treves 2006). This overlap can lead to more opportunities for conflict between humans and wildlife such as property damage to crops (Nyhus, Sumianto & Tilson 2000) and domestic animals (e.g. Morehouse & Boyce, 2011). These conflicts can also result in human injury and mortality from collisions between vehicles and wildlife (e.g. Bissonette, Kassar, & Cook, 2008), attacks (e.g. Goodrich et al. 2011a) and the spread of zoonotic diseases (Hanisch-Kirkbride, Riley & Gore 2013). Wildlife mortality can also increase via retaliatory killings (e.g. Kissui, 2008), collisions with vehicles (Collins & Kays 2011), and removal by management (e.g. McCarthy & Seavoy, 1994).

Because of these negative consequences of conflict for both humans and wildlife, it is important to understand the causes of conflict so that it may be prevented. For example, conflicts may be more likely to arise when individual animals no longer avoid human disturbance. Animals that learn to tolerate human activity may be more likely to approach humans and their infrastructure and become nuisance animals (Rauer, Kaczensky & Knauer 2003) or killed on roads (Benítez-López, Alkemade & Verweij 2010). However, tolerance to human disturbance is likely important for the persistence of wildlife in human-dominated areas (Evans et al. 2011; Bateman & Fleming 2012; Lowry, Lill & Wong 2013) and does not guarantee an animal will come in conflict with people. What may be more problematic is when animals associate humans and their infrastructure as a source of food or shelter. Feeding wildlife – either intentionally or not – can escalate habituation, a neutral rather than negative association with people, to a positive association (i.e. food conditioning; Herrero, 1985). Once an animal is food conditioned, conflict and removal via management are much more likely (McCarthy & Seavoy 1994; Rauer, Kaczensky & Knauer 2003).

Traditional approaches to solving conflicts between humans and wildlife have typically involved removing the offending animals or even extirpating populations (Sillero-Zubiri et al. 2006). However, new tools are now needed to address conflicts for three reasons. Firstly, the increasing rate of urbanization will undoubtedly change both the scope and nature of conflicts from traditional forms (e.g. livestock depredation) to new problems (e.g. the emergence of zoonotic disease (Daszak 2000)). Secondly, a growing urban population has resulted in a shift in public attitudes against the use of lethal management for conflict-prone wildlife such as carnivores (Reiter, Brunson & Schmidt 1999). Lastly, a new appreciation for the conservation of urban biodiversity has prompted new interest in non-lethal management solutions that retain ecosystem function (e.g. McKinney 2002).

The need for lethal management of conflict-prone wildlife may be reduced with a deeper understanding of how behavioural variation among wildlife can promote conflict with people. Recent work has emphasized the importance of intra-specific variation in behaviour (Bolnick et al. 2003; Réale et al. 2007; Araújo, Bolnick & Layman 2011; Dingemanse & Wolf 2013) which may partly explain observations that only a few individual animals cause most conflicts with people (e.g., Linnell et al. 1999; Gehrt, Anchor & White 2009). Within species, certain individuals may be more likely to become nuisance animals based on physiology or experience. For example, male carnivores are often more likely to kill livestock (e.g. Cunningham 1995; Blejwas et al. 2006) and infirmed carnivores, either old, sick, or injured, are often more likely to kill and consume humans (Yeakel et al. 2009; Goodrich et al. 2011b). Similarly, species and individuals that exhibit higher levels of behavioural flexibility may be more or less willing or able to avoid humans (*sensu* Carrete & Tella 2011).

Certain species may also be more likely to come into conflict with people than others. Carnivores often come in conflict with people because they can compete with humans for food (e.g. Kissui 2008; Morehouse & Boyce 2011) and threaten human safety (Conover 2002a). Conflicts can also arise with species that use anthropogenic resources and live among people. These species tend to be generalists who have broad enough diets to consume anthropogenic food and tolerant enough of human disturbance to live near building and roads (e.g. raccoons *Procyon lotor*; Gross et al. 2011). Such generalists typify the species capable of persisting and even thriving in cities, known as urban adapters and exploiters (Blair 1996; McKinney 2002; Evans et al. 2011), which range from American crows in North America (*Corvus brachyrhynchos*; Heiss, Clark & McGowan 2009) to rhesus macaques in Southern Asia (*Macaca mulatta*; Jaman & Huffman 2013).

Many species are excluded from cities because of their high densities of people and impervious surfaces (Grimm et al. 2008), fragmentation (Riley et al. 2006), and non-native species of plants and animals (McKinney 2002). However, cities also have high densities of resources such as anthropogenic food (Contesse et al. 2004) and artificial shelter in and under buildings (e.g. Gross et al. 2011; Herr et al. 2010). In combination with reduced mortality from hunting and predation by large carnivores, these resources can enable smaller carnivores to reach higher population densities and survival rates in urban relative to rural or wilderness areas (Gehrt & Riley 2010; Bateman & Fleming 2012). However, the emergence and transmission of wildlife disease can be higher in urban areas (Daszak, Cunningham & Hyatt 2001; Bradley & Altizer 2007; Martin et al. 2010; Brearley et al. 2012). The spread of disease may be promoted in urban areas because of the higher densities of animals supported by anthropogenic resources (Fedriani, Fuller & Sauvajot 2001; Wright & Gompper 2005), lower biodiversity or altered community structure that can increase contact between parasites and hosts (Deplazes et al. 2004), the presence of environmental contaminants (Riley et al. 2007; Poessel et al.

2014) or from chronic stressors that increase disease susceptibility (Bradley & Altizer 2007; Giraudeau et al. 2014).

One species thriving in urban areas is the coyote (*Canis latrans*), a mid-sized (7 – 21 kg) canid native of North America (Bekoff 2001). Over the past two centuries, coyotes have undergone a dramatic expansion, or perhaps re-colonization, of their geographic range. Historically occupying the plains of the American Midwest, coyotes now inhabit virtually all of North America including urban areas (Gompper 2002). The reasons for this expansion are not entirely understood, but have been argued to include deforestation, agricultural expansion, and extirpation of wolves (*Canis lupus*; Kays et al. 2010). More recently, industrial expansion into forested areas (Latham et al. 2013), reduction in predator persecution in exurban areas (Timm et al. 2004) and an increase in low-density housing in suburban development (Theobald 2001) are thought to relate to changes in coyote distribution. This expansion is likely supported by the flexibility exhibited by coyotes in their ecology. Coyotes can hunt cooperatively to prey on ungulates (Pruss 2002) but mainly hunt individually for small mammals (e.g. cricetid rodents, leporids) and fruit (Bekoff 2001). Coyotes can also live as monogamous pairs and defend a territory with their offspring (Gese 2001), or live individually as transients (Kamler & Gipson 2000).

Perhaps because of their increasing prevalence, the presence of coyotes in cities has attracted increasing attention. Since 2000 there has been a steady increase in the number of news reports concerning coyote sightings and encounters with people in large American cities (Parayko, unpublished data, Figure 1.1). Although coyote attacks on people are rare (White & Gehrt 2009; Lukasik & Alexander 2011), the presence of coyotes in cities can elicit fear in urban residents for their own safety and that of their children and pets (Alexander & Quinn 2012). Many cities remove coyotes that become nuisance animals; for instance animals that exhibit aggression towards people or kill pets, and sometimes employ lethal management to reduce coyote numbers (Shivik & Fagerstone 2007). However, reducing the need for lethal management is both more palatable to residents (Reiter, Brunson & Schmidt 1999; Shivik & Fagerstone 2007) and may be more effective in the long term (Conover 2002b). Removing coyotes from the population can create opportunities for young or transient animals to establish territories and breed rather than helping their parents or remaining solitary (Wagner & Conover 1999; Conover 2002b). Also, as the largest carnivore in cities, coyotes are valued by many urbanites as a charismatic connection to wilderness (e.g. Ellison 2009) and can provide valuable ecosystem services. For example, coyotes can control populations of pest species and disease vectors (Ostfeld & Holt 2004) and the abundance of mesocarnivores, leading to higher songbird diversity (Crooks & Soule 1999).

To better understand how coyotes use the urban environment, several studies have described the diets and space use of urban coyotes. Even though coyotes can live in cities as large as Chicago, Los Angeles, and New York (Gehrt & Riley 2010), they mainly use remnant natural areas in cities (Grinder & Krausman 2001; Gehrt, Anchor & White 2009; Grubbs & Krausman 2009) and patches of green space in the urban matrix (Gese, Morey & Gehrt 2012). Coyotes tend to have smaller home ranges in cities than in rural landscapes but urban coyotes that use more developed urban areas tend to have larger home ranges (Gehrt, Anchor & White 2009). Urban coyotes also tend to be more nocturnal than rural coyotes (Grinder & Krausman 2001; Tigas, Vuren & Sauvajot 2002; Riley et al. 2003) and this is hypothesized to avoid times with higher human activity and traffic. However, collisions with vehicles can cause more than two thirds of urban coyote mortalities (Gehrt & Riley 2010). Coyotes can and do consume human food although its use varies considerably across different cities (Fedriani, Fuller & Sauvajot 2001; Morey, Gese & Gehrt 2007; reviewed in Gehrt & Riley 2010). While past studies provide useful descriptions of urban coyote ecology, a better understanding of how and why coyotes vary in their overlap with people, either in time, space, or resources could provide valuable information to prevent conflicts between people and coyotes. For example, individual coyotes are known to vary in their home ranges and habitat use and they may exhibit similar variation in their propensity to eat anthropogenic food, cross roads, and be active during the day, all of which may increase the likelihood of encounters between coyotes and humans.

I studied urban coyote ecology and behaviour in Edmonton, Alberta, Canada, the northernmost major city in North America (53.5472° N, 113.5006° W, population 812,201 in 2011 census). Coyotes have historically been present in Edmonton but reports of coyote sightings have increased dramatically in the last 20 years (Ramsey Cox and Bill Abercrombie, pers. comm.) and are currently reported at least daily throughout the year (Murray, unpublished data). The landscape of Edmonton is characterized mainly by the North Saskatchewan River valley, which bisects the city and is connected to several large ravines. Together this system of riparian habitat constitutes the largest stretch of continuous parkland in North America (City of Edmonton 2013), providing habitat for coyotes and several coyote prey species including showshoe hare (*Lepus americanus*), white-tailed jackrabbits (*Lepus townsendii*), white-tailed deer (*Odocoileus virginianus*), beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), and various small mammals.

1.1 Summary of thesis objectives and methodologies

The goal of my thesis is to better understand how behavioural variation among individual animals can promote conflict with people. More specifically, I examined how and why coyotes vary in their overlap with humans in space, time, and resources to prevent negative encounters between people and coyotes and facilitate coexistence between humans and carnivores in urban areas. To do so, I will integrate information on coyote diet, habitat selection, and movement and examine how these behaviours vary across individual animals and promote conflict with people.

Coyotes are known to consume anthropogenic food in cities, which may benefit coyotes by increasing their diet breadth but may also increase their risk of conflict with people and management action. In chapter 2, I tested whether the consumption of anthropogenic food was associated with greater diet breadth and conflict with people by comparing the diets of coyotes from urban and rural areas that were or were not reported as nuisance animals by the public. To do so, I compared the contents of 2,356 coyote scats collected in two rural areas and two urban areas. These scats included those collected in Edmonton and analyzed by Adam Cembrowski, scats collected in Calgary and analyzed by Victoria Lukasik, scats collected in the Wabasca region by Dave Latham, and scats collected in Elk Island National Park and analyzed Shelley Pruss. I also estimated the assimilated diets of 73 coyotes using stable isotope analysis of coyote hair samples.

Previous work suggests that most coyotes avoid people and that young, male, infirmed carnivores are more likely to come in conflict with people. In chapter 3 I tested whether subadult, male, or diseased coyotes were more likely to use developed areas, be active during the day, and consume human food. To do so, I measured the movements and diets of 19 coyotes fitted with Global Positioning System (GPS) collars and sampled for stable isotope analysis, eight of which had signs of sarcoptic mange (*Sarcoptes scabiei*) at capture.

Conflict with people may be especially likely for animals that seek out food or shelter in residential areas. In chapter 4, I measured habitat selection for residential areas within coyote home ranges and anthropogenic resources at feeding and resting sites. To do so, I used GPS locations from 19 urban coyotes and measured habitat variables in the field at clusters of GPS locations.

While anthropogenic food may be an abundant food source for urban wildlife, piles of food waste such as compost piles may also promote the spread of disease by aggregating foraging wildlife, attracting sick animals, and exposing foragers to contaminants. In chapter 5, I tested whether compost piles and landfills promoted the overlap between apparently parasitized and healthy coyotes in space and time and if they contained fungal toxins. To do so, I deployed camera traps at nine compost piles and 16 urban natural areas for 5,386 trap nights and compared the time elapsed between coyote visits and prevalence of parasitized coyotes. Undergraduate research student Peter Whyte analyzed 63 coyote scats for endoparasites and undergraduate research student Jesse Hill sampled 29 compost piles for the presence of mycotoxins.

Animals that live in human-dominated and fragmented areas may also be at higher risk of vehicle collisions. In chapter 6 I examined whether risk of vehicle collision increases for coyotes based on seasonal differences in movement patterns. To do so, I examined the seasonal distribution of 80 coyotes collected on roads by city employees and compared the movements of seven GPS-collared coyotes killed on roads with those of twelve surviving coyotes.

I conclude my thesis by discussing and integrating my most salient findings and management recommendations for mitigating conflict between humans and urban coyotes.

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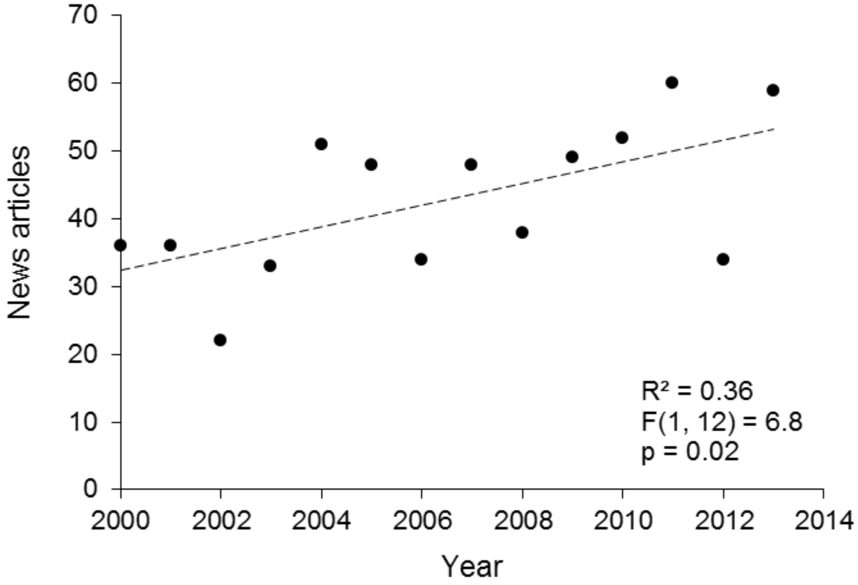
1.3 Figures

Figure 1.1 News articles archived in the NewsLibrary database that involve coyote sightings or encounters from 2000 - 2014. Articles were included if they were published in the top circulating newspaper in cities over 250,000 people in the United States. News reports were compiled by Nick Parayko.



Chapter 2

2 Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict[*]

2.1 Abstract

Reports of encounters between people and generalist urban-adapted carnivores are increasing around the world. In North America, coyotes (*Canis latrans*) are among the carnivores that appear to be especially capable of incorporating novel anthropogenic food types, including those found in cities. Consuming anthropogenic food may benefit coyotes by increasing their dietary diversity, but it may also lead to increased interactions and conflicts with humans. To test these hypotheses, we compared the diets of urban and rural coyotes from two urban and three rural sites spanning 32,200 km^2 in Alberta, Canada. We analyzed scat samples to calculate diet diversity at the level of both individuals (species per scat) and populations (Shannon index) and to determine the frequency of anthropogenic food consumption. We complemented this comparison with stable isotope analyses of hair samples taken from individual urban and rural coyotes that were or were not reported by the public for repeatedly visiting backyards and schoolyards during the day. Relative to rural coyotes, urban coyotes had more diverse diets at the level of both individuals and populations, consumed anthropogenic food more often, and animals less often, than rural coyotes. Although urban coyotes assimilated more anthropogenic food than the rural coyotes overall, the urban coyotes reported for conflict assimilated less protein and were more likely to be diseased. Our results suggest that processed anthropogenic food may contribute to the success of urban coyotes, but does not entirely correlate with conflict. Instead, some seemingly innocuous, but low-protein food sources such as bird feeders, compost, and cultivated fruit trees may contribute disproportionately to

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encounters with people for coyotes and other urban-adapted opportunistic carnivores.

2.2 Introduction

Several generalist species have increased in distribution and abundance in urban areas (McKinney 2006), leading to changes in urban biodiversity (McKinney 2002) and rates of human-wildlife conflict (Curtis & Hadidian 2010). Many behavioural changes have been documented in urban-adapted wildlife, including changes in tolerance to human activity, habitat selection, the timing of activity, and changes in diet (reviewed by Gehrt & Riley 2010; Lowry, Lill & Wong 2013). Generalist species with broad diets may be especially well-equipped at colonizing and adapting to new and highly variable habitats, such as urban areas, because they can exploit diverse food sources (Angert et al. 2011), enabling them to thrive even when natural foods are less available (Williams et al. 2006). Cities can provide many novel foods for wildlife because they contain more species of non-native flora and fauna (McKinney 2002; Grimm et al. 2008) and can contain anthropogenic food and waste year-round in the form of pet food, compost piles, bird seed, and refuse (Contesse et al. 2004; Williams et al. 2006). Species with sufficient dietary flexibility and tolerance of human activity to exploit these foods may benefit from adding anthropogenic food to a natural diet, thereby increasing diet diversity. Combined with less mortality from predators and human hunters in cities, the diversity and abundance of food in cities may explain the higher survival and reproductive rates and population densities of urban-adapted carnivores (Gehrt & Riley 2010; Bateman & Fleming 2012).

Increasing rates of encounters with people have been documented for several urban-adapted species, including red foxes (*Vulpes vulpes*; Contesse et al. 2004), raccoons (*Procyon lotor*; Prange et al. 2004) and black bears (*Ursus americanus*; Hopkins et al. 2012). It is widely understood that consumption of anthropogenic food, and resulting food conditioning, often contributes to human-wildlife conflict (Herrero 1985; Hopkins et al. 2012), but no single mechanism has been identified to predict why and which animals come into conflict with humans (Curtis and Hadidian 2010). Even when food is associated with conflict, specific links between apparent changes in diet and particular types of anthropogenic food must be identified to support specific attractant management. By removing those attractants, lethal management of urban-adapted species might be prevented or reduced. Such approaches can promote positive experiences with urban wildlife and typically are more palatable to urban residents.

Reported rates of encounters between humans and coyotes have also increased in cities across North America (White & Gehrt 2009; Alexander & Quinn 2011, 2012; Poessel et al. 2013), which coincide with increases in coyote distribution and potentially changes in coyote behaviour (Gehrt & Riley 2010). Since the early 1800s, coyotes have expanded their range from the plains of the American Midwest to most regions in North America, including urban areas (Gompper 2002). This expansion in coyote distribution is likely supported by the tremendous flexibility coyotes express in both diet and foraging behaviour; coyotes can hunt in packs to prey on ungulates but can also forage individually for rodents, leporids, insects, fruit, and vegetation (Bekoff 2001). Urban coyotes also consume anthropogenic food, however the amount varies considerably between cities (e.g. Quinn 1997, Fedriani et al. 2001, Morey et al. 2007).

Because coyotes occur over such a wide range of habitats and have broad and flexible diets, they are an ideal study species for investigating relationships between diet, urbanization, and conflicts with people. We hypothesized that coyotes in urban areas would incorporate several types of anthropogenic food into their diets, thereby increasing both dietary breadth and the proportion of diets comprised by anthropogenic food. Because the consumption of anthropogenic food has been linked to conflict with people in other contexts, we also hypothesized that coyotes that consumed more anthropogenic food would be more likely to elicit nuisance reports by people. To test these hypotheses, we compared the diets of urban and rural coyotes and of coyotes that did or did not elicit repeated nuisance complaints from the public. If supported, these hypotheses suggest that urban coyotes may be better able to respond to changes in the availability of diet items than rural coyotes and that human-coyote conflict may be successfully mitigated with targeted attractant management.

2.3 Materials and methods

2.3.1 Study Areas

To measure changes in diet with urbanization, we compared the diets of coyotes from the two major urban centres in Alberta, Edmonton and Calgary, to those of coyotes in three more natural landscapes, Elk Island National Park, the region surrounding the town of Wabasca-Desmarais, and Ministik Lake (Figure 2.1). Edmonton (53°32′N 113°30′W) centres on the North Saskatchewan River valley and has a population of 870,000 people (population density = 1,271 humans/km^2). Calgary (51°03′N 114°04′W) is situated on the Bow River valley and has 1.2 million inhabitants (population density = 1,376 humans/km^2). Located 50 km east of Edmonton, Elk Island National Park (53°37′N 112°52′W) is a fenced 194 km^2 natural area containing high densities of ungulates and comprised by aspen parkland surrounded by agricultural development. Located 48 km southeast of Edmonton, Ministik Lake (53°21'N 113°1'W) is a 109-km^2 bird sanctuary characterized mainly by aspen parkland and many small water bodies. Ministik is closed to the public and is 28 km away from the nearest town, thereby limiting the availability of anthropogenic food to coyotes. Our most remote site was an area of approximately 21,000 km^2 surrounding the town of Wabasca-Desmarais (approx. 1,500 inhabitants; 55°57′N 113°49′W) in northeastern Alberta. This area is characterized by boreal mixed-hardwood forest and scattered development resulting mainly from forestry and energy sectors (Latham et al. 2013). Although coyotes have occurred in Alberta for at least the last 100 years (Bekoff 2001), reports of coyotes by the public have become prevalent in Edmonton and Calgary only since the 1980's (Ramsey Cox, personal communication, Lukasik & Alexander 2011) and even more recently in Wabasca (Latham et al. 2013).

2.3.2 Scat collection

Coyote scats were collected on a variety of trails (i.e., game trails, gravel trails, and paved bike paths) following specified routes at least monthly. Trails were selected in areas with suspected coyote activity based on sightings, the presence of coyote tracks, and the presence of radio-collared coyotes. We collected 531 scats in Edmonton between 2009 and 2012 in parks, ravines, a zoo, and in fields at the University of Alberta South Campus agricultural research facility. In Calgary, we collected 484 coyote scats between 2006 and 2007 in parks and green spaces (Lukasik & Alexander 2012). We also collected 1,221 scats in Elk Island National Park from 1994-2000 (Pruss 2002) and collected 120 coyote scats in Wabasca from 2005-2007. Scats in Wasbasca were collected opportunistically as part of an ongoing study on wolf diet (*Canis lupus*; Latham et al. 2013) but were not collected at Ministik Lake.

Coyote scats were distinguished from domestic dog (*C. lupus familiaris*) scat based on size, morphology, contents, and location. Coyote scats were distinguished by their diameter (18-25 mm; Arjo et al. 2002) and position in the middle of trails, which coyotes likely use to demark territories (Bekoff 2001). Scats containing visible dog food (evident by flecks of grain) were rejected in the field (after Quinn 1997) to prevent overestimating the frequency of anthropogenic food consumption. Coyote scats were distinguished from wolves and foxes using tracks, the size of scats and the known locations of radio-collared coyotes. Scats collected in Edmonton, Elk Island, and Wabasca were stored at -20°C and autoclaved prior to analysis (Pruss 2002) and scats collected in Calgary were frozen at -80°C for at least 72 hours prior to analysis (Lukasik & Alexander 2012).

2.3.3 Scat analysis

We categorized the diet items found in coyote scats into 22 groups of species (Table 1) and considered anthropogenic food sources to include domestic dogs and cats (*Felis catus*), traces of garbage (e.g., plastic or paper), bird seed (i.e., sunflower seeds (*Helianthus annuus*) and millet (*Panicum miliaceum*)), and cultivated fruit (i.e., crab apples; *Malus* spp.). All other diet items were considered to be from natural sources. Mammalian hair was identified to species group by selecting hairs at random and inspecting them microscopically for medulla and scale patterns using keys (Moore, Spencer & Dugnolle 1974). Coyote hair, distinguished from domestic dog hair using colour and size, was assumed to be from self-grooming. Other identified diet components included exoskeletons (insects), feather (birds), fruit skins and seeds (fruit, but not including crab apples and bird seed), and leaves and stems (vegetation).

We measured the prevalence and relative abundance of diet items in urban and rural coyote diet by calculating the frequency of occurrence and percent occurrence for each species group. Frequency of occurrence (scats containing item / total scats x 100; Mattioli et al. 2004) calculates how often an item is consumed while percent occurrence (occurrence of item / occurrences of all items x 100; Morehouse and Boyce 2011) calculates how often each diet item is found relative to all other diet items and sums to 100. We used these metrics because they both use the presence, rather than the volume, of diet items to support comparisons across items of varying volumes and levels of digestibility (e.g., bones vs. soft anthropogenic food).

We measured the diet breadth of individual coyotes using the average number of species groups found per scat and, of coyote populations, by estimating the relative abundance (i.e., percent occurrence) for each species group and then calculating Shannon diversity index (H’) values as an index of diet trophic diversity (Fedriani, Fuller & Sauvajot 2001; Morey, Gese & Gehrt 2007). We calculated both values separately for the urban and rural sites and compared Shannon H’ values using a modified t-test (Hutcheson 1970). We also took the exponent of the Shannon index H’ values to estimate the effective number of species groups in urban and rural coyote diets (Jost 2006).

We measured differences in composition of urban and rural coyote diets by comparing the frequency of occurrence of species groups across sites and site types using replicated G tests. We also compared the frequency of occurrence of species groups in the three seasons that are most ecologically relevant to coyotes: breeding (January – April), pup-rearing (May – August), and dispersal (September – December; Morey et al. 2007).

2.3.4 Hair collection and stable isotope analysis

To overcome potential bias in diet estimated from scat samples, in which there may be few remnants of anthropogenic food, we compared the assimilated diets of individual urban and rural coyotes with known histories of conflicts with people using 13C and 13N stable isotope analysis. Stable isotope analysis can give a more accurate and long-term estimate of anthropogenic food consumption for several reasons. First, corn, as a C4 plant, has a distinctively high δ13C signature (ratio of 13C / 12C) and is present in virtually all processed food and as livestock feed (Jahren & Kraft 2008). Second, stable isotope analysis relates the diets of individual animals since their last molt to identify the cumulative effects of diet. Third, protein consumption can be estimated through δ15N signatures (ratio of 15N / 14N) because 15N is preferentially retained in consumers and higher trophic levels (DeNiro & Epstein 1981).

We collected hair samples from coyotes that were live-trapped as part of an independent study on coyote movement (Murray et al., in press a) and dead coyotes provided by others. Urban hair samples included coyotes in the live-capture study plus coyotes that had been killed by vehicles or were euthanized by provincial government wildlife officers in response to repeated complaints from people within Edmonton city limits. Rural hair samples were collected from coyotes that were killed by a private wildlife pest management company following complaints by rural residents or were harvested on a licensed trap-line in Ministik.

We considered a coyote to have exhibited conflict-prone behaviour if it had generated complaints from the public that described behaviour consistent with habituation to people (threatening behaviour or repeated, diurnal visits to backyards and schoolyards). Coyotes that were reported by the public were identified based on the reports associated with animals that were euthanized or on ear tag numbers. Thus, all coyotes could be categorized in two ways: as urban or rural, and within those categories, as whether or not they were reported for conflict by the public. When coyotes were sampled, their body condition was scored on a scale from 1 to 5 based on coat quality and body fat (Windberg, Engeman & Bromaghin 1991). We also noted whether the coyote exhibited signs of sarcoptic mange infestation, caused by the mite *Sarcoptes scabiei*, that results in hair loss, lesions, and skin thickening (Samuel, Pybus & Kocan 2001).

For both live and dead coyotes, roughly a dozen guard hairs from the back of the neck were collected and prepared for stable isotope analysis following Hilderbrand et al. (1996). During preparation, hair was sectioned where possible into two halves to estimate seasonal diet; the base of the hair contains the diet signature from the most recent months preceding collection and the tip contains diet signatures from the earliest months since the spring molt. For example, hair sampled in the fall is approximately six months old (since spring molt) and each half would contain three months of diet data. Sample δ15N and δ13C values (‰) were measured using a EuroEA Elemental Analyzer (EuroVector) and Isoprime Mass Spectrometer (GV Instruments) with a measurement standard deviation of ± 0.1 and ± 0.3‰ respectively, at the Biogeochemical Analytical Service Laboratory (Department of Biological Sciences, University of Alberta).

To quantify changes in coyote assimilation of protein and anthropogenic food with urbanization and conflict behaviour, variation in individual coyote δ13C and δ15N values was examined using linear mixed-effects (LME) models using package nlme in R (Pinheiro et al. 2012). We included coyote sex, age, body condition, presence of mange, season, site type (urban, rural), and conflict (yes, no) as well as interactions between season, site type, and conflict as covariates. We used forward selection to build our models based on the purposeful model-selection methods of Hosmer and Lemeshow (2000) using a p value of 0.05.

2.4 Results

2.4.1 Diet diversity and urbanization

Urban coyotes had more diverse diets than rural coyotes at both the population and individual levels (Figure 2.2). Urban coyotes had higher average numbers of species groups per scat than rural coyotes ($t = 10.39$, $df = 1$, $p = 0.03$; Table 1, Fig. 2.2). The number of species groups for rural coyote scats could only be calculated for Wabasca because these data were not available from Elk Island National Park. Urban coyote scats were also 90% more likely to contain more than one species group than rural coyote scats (78% of urban scats, 41% of rural scats). Urban coyote scats also had significantly higher Shannon H’ index values than rural coyote scats ($t \geq 2.35$, $df = 1$, $p < 0.01$; Table 1, Figure 2.2).

Urban coyotes consumed much more anthropogenic food, which was present in 26% ($n = 267$ of 1,015) of all urban coyote scats and <1% ($n = 11$ of 1,341) of rural scats ($G = 25.31$, $df = 1$, $p < 0.01$; Figure 2.3a). Urban coyotes also consumed animals 29% less often, relative to other items, than rural coyotes ($G = 18.62$, $df = 1$, $p < 0.01$; Figure 2.3b). Urban coyotes consumed more domestic cats and dogs than did rural coyotes, but both groups consumed domestic animals less often than other mammal species (Table 1). Urban coyotes also consumed small mammals (i.e., cricetid rodents, leporids, sciurids) 24% more often and consumed ungulates and muskrats (*Ondatra zibethicus*) 74% less often than rural coyotes ($G \geq 4.72$, $df = 1$, $p < 0.01$; Figure 2.3a). Prey use varied seasonally but the patterns were similar across urban and rural sites ($G \leq 1.21$, df = 3, $p \geq 0.45$). Coyotes did not exhibit significant seasonal changes in consumption of anthropogenic food (G = 1.93, df = 2, p = 0.39).

2.4.2 *Assimilated diet and urbanization*

We analyzed hair samples from 49 urban and 23 rural coyotes for stable isotopes. Of these, 15 urban (three adult males, five adult females, four subadult males, three subadult females) and eight rural (four adult males, one subadult female, three subadult males) coyotes were reported by the public (15/49 (urban) vs. 8/23 (rural); test for independence G = 0.12, df = 1, p = 0.72). Urban coyotes were more likely than rural coyotes to exhibit poor body condition or mange infestation (19/49 (urban) vs. 0/23 (rural); G = 12.68, df = 1, $p < 0.01$). Urban coyotes that exhibited conflict-prone behaviour were also more likely to have poor body condition or exhibit mange infestation (12/15), whereas coyotes that did not elicit complaints were more likely to be in good or very good condition (28/34; $G = 17.41$, df = 1, $p < 0.01$). None of the rural coyotes that exhibited conflict-prone behaviour had poor body condition or apparent mange infestation.

As predicted, urban coyotes assimilated more processed anthropogenic food, as measured by δ13C stable isotope signatures, than did rural coyotes (Urban: -22.6 ± 1.3‰; Rural: -23.7 ± 0.6‰; LME $\beta_{Urban} = 1.04 \pm 0.35$, t = 3.00, df = 72, $p < 0.01$; Figure 2.4). Urban coyotes assimilated similar amounts of 15N as rural coyotes, suggesting they consumed similar amounts of protein (Urban: 7.55 ± 2.35 ‰; Rural: 7.84 ± 1.03 ‰; LME $\beta_{Urban} = 0.33 \pm 0.61$, t = 0.53, df = 72, p = 0.60; Figure 2.4). In contrast to our prediction, urban coyotes that exhibited conflict-prone behaviour did not assimilate significantly more 13C, suggesting they did not consume significantly more processed anthropogenic food than other coyotes (Urban conflict: -22.4 ± 1.56‰; All other coyotes: -22.9 ± 1.06‰; LME $\beta_{UrbanxConflict} = -0.54 \pm 0.66$, t = -0.82, df = 72, p = 0.41; Figure 2.4). Rather, urban coyotes that exhibited conflict-prone behaviour assimilated significantly less protein than all other coyotes (Urban conflict: 6.3 ± 0.79‰; All other coyotes: 8.0 ± 0.22‰; $\beta_{\text{UrbanxConflict}} = -2.68 \pm 1.30$, t = -2.05, df = 72, p = 0.04; Figure 2.4).

2.5 Discussion

We assessed whether the consumption of anthropogenic food was associated with increased diet breadth and conflict with people in urban coyotes. We found that urban coyotes had more diverse diets than rural coyotes at both the population and individual levels with the addition of anthropogenic food. We also found that urban coyotes reported for conflict assimilated less protein but similar levels of processed anthropogenic food relative to other urban coyotes.

Urban coyotes had more diverse diets than rural coyotes by consuming the full complement of prey types used by rural coyotes (e.g., sciurids, beavers (*Castor canadensis*), mustelids, muskrats, and ungulates) in addition to anthropogenic food of several types. This result supports the hypothesis that coyotes, like other urban-adapted species, may succeed in cities in part because they can exploit novel food sources. In general, increased diet diversity is presumed to increase consumer survival and reproduction because consumers are less reliant on any particular diet item and can better accommodate changes in resource availability (Suryan, Irons & Benson 2000; Lefcheck et al. 2013). In addition to these benefits, anthropogenic food in cities may be more abundant (Contesse et al. 2004), and exhibit longer growing seasons (Grimm et al. 2008). All of these factors may contribute to higher survival and reproductive rates, and could account for the smaller home ranges observed in urban relative to rural coyotes (Gehrt & Riley 2010).

Increased access to anthropogenic food might be one reason that urban coyotes in our study appeared to be less reliant on consuming animals than rural coyotes. This change makes the diet of urban coyotes more similar to those of more omnivorous urban adapters like raccoons, striped skunks (*Mephitis mephitis*), stone marten (*Martes foina*), and opossums (*Didelphis virginiana*; Bateman & Fleming 2012). In general, urban adapters may even favour anthropogenic food over natural sources because it is more constantly available; sources of food like garbage cans, fruit trees, compost piles, and bird feeders are predictable in space and time, potentially lowering foraging costs (Weiser & Powell 2010; Votier et al. 2010). This predictability, in addition to high caloric content and similarity to natural food, might be one reason that cultivated fruit is the type of anthropogenic food most frequently consumed by coyotes in many cities (reviewed in Gehrt & Riley 2010; this study). Both urban and rural coyotes consumed small mammals as their primary prey source, supporting the suggestion that coyotes can control rodent populations and increase rodent diversity (Henke & Bryant 1999).

The associations between the consuming anthropogenic food and being reported by the public differed for urban and rural coyotes. Both populations contained similar proportions of conflict animals, however all urban coyotes consumed more processed anthropogenic food than rural coyotes. By contrast, protein assimilation was similar for coyotes in urban and rural areas that were not reported for conflict, but it was much lower for reported coyotes in urban areas, the majority of which had signs of sarcoptic mange. The relatively low levels of assimilated protein in the diet of coyotes reported by the public suggest that these animals may be hunting less frequently, perhaps because these animals often exhibited poor health and body condition. Animals with poor body condition or ectoparasite infestations may be less able to hunt for prey owing to lost endurance (*sensu* Alzaga et al. 2008) or intolerance to colder temperatures at peak hunting times (crepuscular or nocturnal hours, *sensu* Bekoff 2001). These coyotes may have used anthropogenic food because it could be obtained passively and is often reliable in space and time. Alternatively, they may have sought out carbohydrate-rich foods because they increase the rate of fat accumulation (Brand-Miller et al. 2002). Via either starting point, the lesser protein consumption by sick coyotes would be expected to accelerate declines in body condition (Ezenwa 2004) and these animals may fail to obtain or defend a high-quality territory (Kamler & Gipson 2000) which may promote the use of human-dominated areas.

Our results have several implications for reducing human-coyote conflict in cities. The differences in scat composition between urban and rural coyotes, combined with the lower protein assimilation by coyotes reported for conflict-prone behaviour, suggest that some attractants are more problematic than others. This difference in protein assimilation equated to over one half of a full trophic level (DeNiro & Epstein 1981), which suggests that coyotes reported for conflict consumed fewer prey and more low-protein foods such as compost, cultivated fruit, and bird seed (Van Hemert, Handel & O'Brien 2012). Our scat data supported this suggestion; cultivated fruit was the most prevalent form of anthropogenic food in Calgary and bird seed was the most common type in Edmonton. A suggestion that cultivated fruit, compost, and bird seed are highly attractive to wildlife is not new; they are already known to attract black bears in North America (Merkle, Derbridge & Krausman 2011), red foxes in Switzerland (Contesse et al. 2004), raccoon dogs (*Nyctereutes procyonoides*) in Finland (Kauhala & Kowalczyk 2011), and raccoons in both Japan (Ikeda et al. 2004) and North America (Prange, Gehrt & Wiggers 2004). By contrast, cats and dogs combined were present in less than 5% of scats and that value was even lower in most other studies (Gehrt & Riley 2010). Although consumption of dogs by coyotes was quite rare, territorial attacks on dogs may remain another important source of conflict (Lukasik & Alexander 2011).

The contribution of food conditioning to conflict behaviour is well known (Herrero 1985; Hopkins et al. 2012); less well established is the link between conflict and specific types of food and our speculation that low-protein food sources may contribute disproportionately to conflict, potentially through poor nutrition. We recommend that future studies explore this association mechanistically by comparing the long-term diets and behaviours of individual animals to identify and secure the foods that are most likely to produce conflict. This work may reveal that some kinds of anthropogenic foods, such as backyard compost piles and unharvested crab apples, have been overlooked as important contributors to conflict involving urban coyotes. As urbanization expands and rates of conflict between humans and wildlife continue to rise, coexistence will be increasingly dependent on detailed knowledge of how urban-adapted species use anthropogenic resources.

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The authors declare no conflict of interest.

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2.8 Tables

Table 2.1 Frequency of occurrence (scats containing item x 100 / total scats) and percent occurrence (scats containing item / occurrences of all items x 100; in parentheses) of food items and diet diversity found in scats collected in two urban and two rural study sites in Alberta, Canada. P values refer to replicated G tests.

		Urban			**Rural**			
	Item	Edmonton	Calgary	Mean	Elk Island	Wasbasca	Mean	p
Natural	**Cricetidae**	55.9 (22.7)	75.4 (33.1)	65.65 (27.9)	46.1 (26.5)	51.5 (35.0)	48.8 (30.8)	0.04
	Sciuridae	14.7 (6.0)	16.3 (7.2)	15.5 (6.6)	1.8 (1.0)	2.6 (1.4)	2.2 (1.2)	<0.01
	Leporidae	34.8 (14.1)	7.6 (3.4)	21.2 (17.5)	2.1 (1.2)	4.1 (2.8)	3.1 (2.0)	<0.01
	Muskrat (*Ondatra*)	15.6 (6.3)	0	7.8 (3.2)	23.3 (13.4)	37.1 (25.2)	30.2 (19.3)	<0.01
	Mustelidae	22.2 (9.0)	0.62 (0.3)	11.41 (4.7)	0	0	0	<0.01
	Ungulate	12.4 (5.0)	8.1 (3.5)	10.25 (4.3)	46.1 (26.5)	33.0 (22.4)	39.6 (24.5)	<0.01
	Beaver (*Castor*)	2.4 (1.0)	0.21 (0.09)	1.3 (0.5)	11.1 (6.4)	1.0 (0.70)	6.1 (3.6)	0.58
	Porcupine (*Erethizon*)	1.5 (0.6)	0	0.75 (0.3)	0.45 (0.26)	0	0.23 (0.13)	0.90
	Birds (Aves)	3.8 (1.5)	13.2 (5.8)	8.5 (3.7)	7.9 (4.5)	7.2 (4.9)	7.6 (4.7)	0.78
	Insects (Hexapoda)	1.7 (0.7)	4.1 (1.8)	2.9 (1.3)	8.2 (4.7)	0	4.1 (2.4)	0.66
	Woodchuck (*Marmota*)	0	0	0	0	7.2 (4.9)	3.6 (2.45)	-
	Bovidae (domestic)	0	0	0	2.7 (1.6)	2.1 (1.4)	2.4 (1.5)	<0.01
	Bovidae (wild)	0	0	0	4.4 (2.5)	0	2.2 (1.3)	-
	Natural fruit	7.9 (3.2)	12.4 (5.4)	10.2 (4.3)	14.9 (8.6)	1.0 (0.70)	8.0 (4.7)	<0.01
	Vegetation	23.9 (9.7)	44.6 (19.6)	34.3 (14.7)	4.2 (2.4)	0	2.1 (1.2)	<0.01

Anthropogenic	**Garbage**	18.5 (7.5)	12.2 (5.4)	15.4 (6.5)	0	1.0 (0.70)	0.5 (0.35)	<0.01
	Cats (*Felis catus*)	6.0 (2.4)	0.62 (0.27)	3.31 (1.3)	0.53 (0.30)	0	0.27 (0.15)	0.03
	Dogs (*Canis lupus fam.*)	0.94 (0.4)	0.62 (0.27)	0.78 (0.3)	0.15 (0.09)	0	0.08 (0.04)	0.04
	Crab apples (*Malus sp.*)	2.8 (1.1)	29.1 (12.8)	16.0 (6.95)	0	0	0	<0.01
	Birdseed	21.7 (8.8)	2.5 (1.1)	12.1 (5.0)	0	0	0	<0.01
	Species per scat	2.60	2.45	2.54	-	1.46	1.46	0.03
	Shannon's H	2.41	2.2	2.3	1.83	1.74	1.74	<0.01
	Species richness	11.2	9.23	9.97	6.20	5.73	5.73	-

2.9 Figures

Figure 2.1. Map of study sites across Alberta, Canada. We collected coyote scats from two urban sites (Edmonton and Calgary, black circles) and two rural sites (Elk Island National Park (EINP) and Wabasca, gray circles). We also collected hair samples from coyotes in one urban site (Edmonton) and one rural site (Ministik).

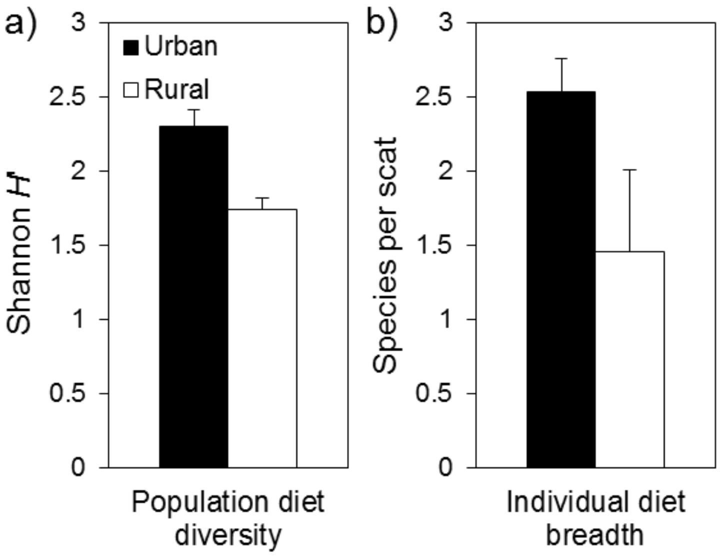

Figure 2.2 Diet diversity of urban coyote scats from two urban (black bars) and two rural sites (white bars). We measured population diet diversity by calculating Shannon's *H*' index from pooled scats (a) and measured individual diet breadth using the number of species per scat (b). Bars show mean values and error bars indicate standard error.

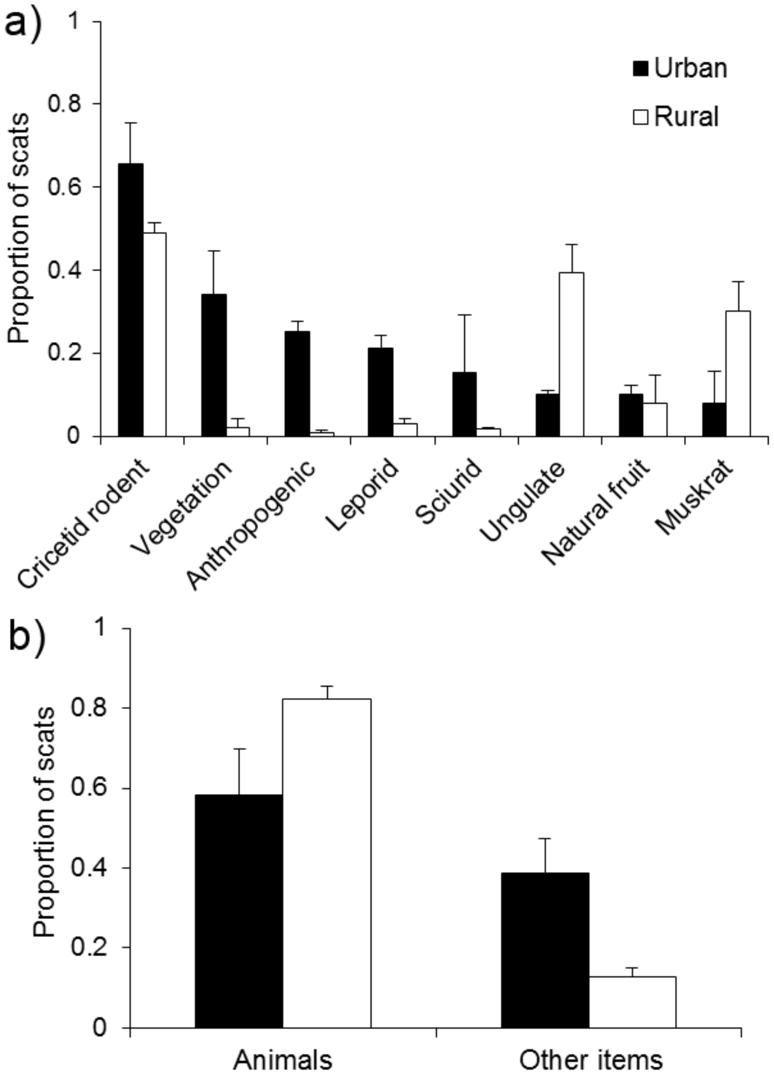

Figure 2.3 Differences in prey use in urban (black bars) and rural (white bars) coyote scats from two urban and two rural studies in Alberta, Canada. (a) The frequency of occurrence (displayed as proportion of scats that contained item) for the diet items that differed significantly between urban and rural coyotes. (b) The proportion of analyzed scats from urban or rural coyotes that contained prey remains such as hair, bones, or teeth (Animals) and all other items including anthropogenic food. Error bars show standard deviation.

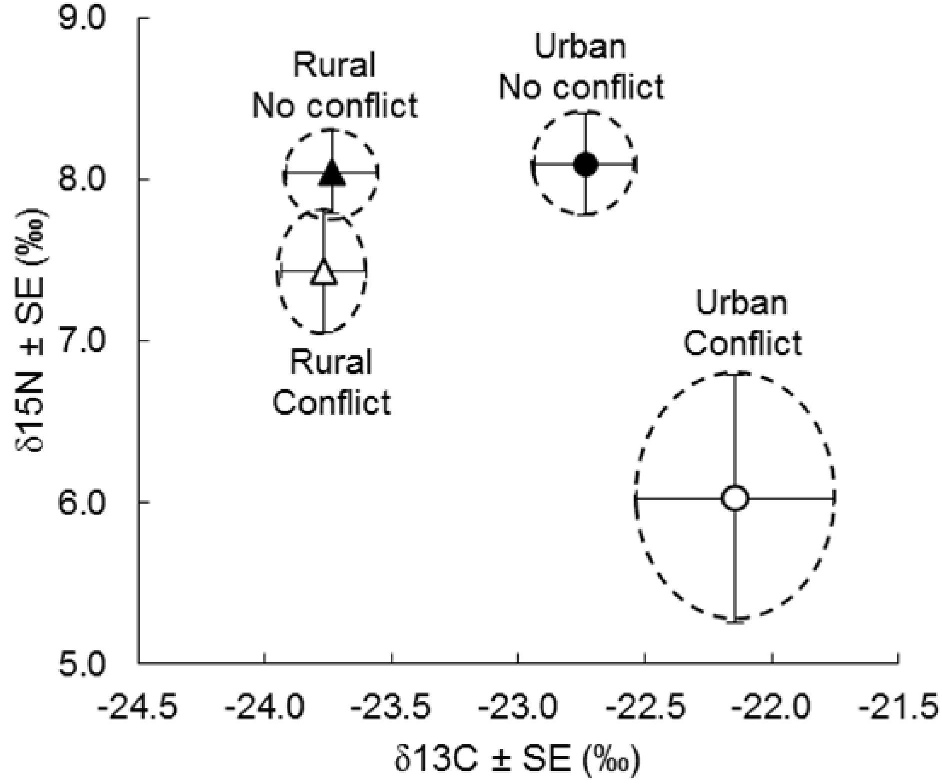

Figure 2.4 Average $\delta^{15}N$ and $\delta^{13}C$ stable isotope values of coyote hair samples. Sampled coyotes were from urban (circles, n = 49) or rural areas (triangles, n = 23) and were either reported for conflict by the public (black; n_{Urban} = 15, n_{Rural} = 8) or were not (white; n_{Urban} = 34, n_{Rural} = 15). Bars show standard deviation.

Chapter 3

3 Poor health is associated with use of anthropogenic resources in an urban carnivore[*]

3.1 Summary

Rates of encounters between humans and wildlife are increasing in cities around the world, especially when wildlife overlap with people in time, space, and resources. Coyotes (*Canis latrans*) can make use of anthropogenic resources and reported rates of conflict have increased in cities across North America. This increase may be linked to individual differences in the use of human food and developed areas. We compared the relationships between coyote age, sex, and health on the use of anthropogenic resources, which we defined as using developed areas over large home ranges, being active during the day, and consuming anthropogenic food. To do so, we applied GPS collars to 19 coyotes and sampled hair for stable isotope analysis. Eleven coyotes appeared to be healthy and eight were visibly infested with sarcoptic mange (*Sarcoptes scabiei*), a mite that causes hair loss. Diseased coyotes used more developed areas, had larger monthly home ranges, were more active during the day, and assimilated less protein than coyotes that appeared to be healthy. We speculate that anthropogenic food provides a low-quality but easily-accessible food source for diseased coyotes, which in turn may increase reliance on it and other anthropogenic resources to promote encounters with people.

3.2 Introduction

There is mounting global pressure to minimize negative interactions between people and wildlife while maintaining wildlife populations and functional ecosystems, emphasizing the need to understand the causes of human-wildlife conflict (Treves & Karanth 2003). Urban areas are the fastest-growing ecosystems on Earth (Angel et al. 2011) and have some of the highest rates of human-wildlife conflict because they have high densities of people,

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anthropogenic attractants, and urban-adapted wildlife (Ditchkoff, Saalfeld & Gibson 2006). Conflicts can arise when wildlife are attracted to anthropogenic resources, which can include food, shelter, and breeding sites. Common forms of conflict include damage to property, transmission of zoonotic disease and depredation on pets or livestock (reviewed by Sillero-Zubiri, Sukumar & Treves 2006). For example, raccoons (*Procyon lotor*) that den in houses in North America (Prange, Gehrt & Wiggers 2004) and Japan (Ikeda et al. 2004) can cause extensive property damage and spread raccoon roundworm (*Baylisascaris procyonis*) to humans. Carnivores may attack pets, e.g. red foxes (*Vulpes vulpes*) in Europe (Contesse et al. 2004), and even people, e.g. tigers (*Panthera tigris*) in India (Carter et al. 2012) and Russia (Goodrich et al. 2011a) and black bears (*Ursus americanus*) in North America (Baruch-Mordo et al. 2008). These actions are often preceded by behavioural cues that reveal habituation to people, such as frequenting human-dominated areas (Prange, Gehrt & Wiggers 2004), being active during daylight hours (Schmidt & Timm 2007), and eating anthropogenic food (McCarthy & Seavoy 1994). These behaviours create potential for food conditioning, wherein wildlife associate humans with food either through intentional or unintentional feeding (Mazur & Seher 2008; Hopkins et al. 2012), which often results in human-wildlife conflict, particularly when it involves carnivores (Baruch-Mordo et al. 2008).

Over the past 20 years, reports of encounters between humans and coyotes (*Canis latrans*) have been increasing in cities across North America (White & Gehrt 2009). This trend follows decades of increase in the range of coyotes (Gompper 2002), but the reasons for rising conflict are unclear (Gehrt & Riley 2010) and coyotes appear to vary in their reliance on anthropogenic resources. Many urban coyotes seldom leave natural areas (Grinder & Krausman 2001; Gehrt, Anchor & White 2009; Gehrt & Riley 2010) where they feed mainly on small mammals and berries (Gehrt & Riley 2010), but some are known to frequent developed areas where they are more likely to elicit nuisance wildlife reports (White & Gehrt 2009) and where anthropogenic food can comprise up to 30% of their diets (Mcclure, Smith & Shaw 1995). A better understanding of this variation in resource use could identify the contexts, locations, and individuals that are most likely to elicit human-coyote conflict.

The use of anthropogenic resources by coyotes could vary for many reasons, including sex, age, and health status. For example, breeding male coyotes appear to be more prone to killing domestic sheep (*Ovis aries*; Blejwas et al. 2006), perhaps to support their larger body size, which produces similar sex-biased conflict in several other carnivore species (Linnell et al. 1999). By contrast, dispersing sub-adult (Linnell et al. 1999) or transient coyotes (Gehrt, Anchor & White 2009) may be more likely to seek out human-occupied areas because they are relegated to lower quality habitat with fewer hunting opportunities (Kamler & Gipson 2000). Any age or sex class may be infected by disease, which can make animals less afraid of people (e.g. rabies virus; Randall et al. 2004), more reliant on easily-accessible food (Towns et al. 2009; Goodrich et al. 2011a) and less able to tolerate cold temperatures (Samuel, Pybus & Kocan 2001), all of which could promote interactions with humans. Rates of disease in urban-adapted species are sometimes higher than in rural areas because of higher densities of animals supported by anthropogenic resources (Wright & Gompper 2005), altered community structure that can increase contact between parasites and hosts (Deplazes et al. 2004), or from chronic stressors that increase disease susceptibility (Bradley & Altizer 2007; Giraudeau et al. 2014).

Few studies have examined multiple hypotheses for increasing conflict behavior in coyotes, or any urban carnivore, and examining the effects of disease is especially difficult in wild, free-living animals. This opportunity exists in northwestern North America, where there is a high prevalence of sarcoptic mange (Todd, Gunson & Samuel 1981), which is highly visible (Samuel, Pybus & Kocan 2001) because of associated hair loss, skin thickening, and lesions (Pence et al. 1983). This form of mange is caused by a mite, *Sarcoptes scabiei*, that causes infected animals to bite and chew at the affected areas, in turn providing entry routes for secondary infections and other parasites (Pence et al. 1983; Samuel, Pybus & Kocan 2001), reducing thermoregulatory and foraging abilities (Samuel, Pybus & Kocan 2001), can ultimately lead to emaciation and death (Pence et al. 1983).

In this study, we examined the relationships between three explanatory variables – age, sex, and health status – to four measures of anthropogenic resource use: using developed areas more frequently and having larger home ranges, being active during the day, and consuming anthropogenic food. We assumed that coyotes that made more extensive use of anthropogenic resources or increased spatial and temporal overlap with people would be more likely to elicit conflict reports, which has been linked to habituation and food conditioning (Herrero 1985; Schmidt & Timm 2007). Based on the associations reported in the literature, we predicted that coyotes that were young, male, or sick would use more developed areas, have larger home ranges, be more active during the day, and consume more anthropogenic food.

3.3 Methods

3.3.1 Study area

Our study took place within the city of Edmonton, Alberta, Canada. Edmonton is a northern city (53.5472° N, 113.5006° W) large in both area (684.4 km2) and population (812,201 in 2011 census) and characterized by warm summers (average temp: 17.5°C), and cold winters (-11.7°C). Edmonton also has a large network of contiguous parkland connected to a central river valley (Figure 3.1) which provides habitat for coyotes, white-tailed deer (*Odocoileus virginianus*), white-tailed jackrabbits (*Lepus townsendii*), snow-shoe hares (*Lepus americanus*), beaver (*Castor canadensis*), and various small mammals. The frequency of human-coyote interactions has increased in Edmonton over the past several years, now generating multiple reports per day throughout the year (Murray, unpublished data).

3.3.2 Sample collection

We captured coyotes using four-coil padded foot-hold traps (No. 3 Victor Soft Catch Coilspring; Animal Trap Co., Lilitz, Pennsylvania) and physically restrained captured coyotes using catch poles. We selected capture sites where coyote sightings had been reported to city officials and dogs were prohibited to minimize their accidental capture. Our capture sites ranged in their proximity to human development and included several urban natural areas, the natural area bordering a zoo, and an agricultural research facility surrounded by residential areas (Figure 3.1). All capture sites were well within city limits with an average distance between capture sites and the city centre of 6.2 km ± 3.1 SD in a city with a radius of 26.6 km. Captured coyotes were aged as either subadult (<1 year old) or adult (≥ 1 year old) by tooth wear (Bowen 1982), sexed, weighed, ear tagged, fitted with a Global Positioning System (GPS) collar, and a hair sample was collected for stable isotope analysis. Coyotes were fitted with collars that acquired locations every three hours that were either stored and downloaded after collars were recovered (Lotek 3300S), downloaded remotely (Lotek 4400S), or communicated via the cell phone network (Wildcell GSM collar; Lotek Wireless Inc., Newmarket, Ontario). Most coyotes were collared in the dispersal season (September – December) and wore their collars for an average of 4 months (range: 1 – 10 months, Table 3.S1). To account for different durations of monitoring, we weighted the spatial data from each coyote by the number of months the coyote was collared or used monthly averages to compare individuals. We assessed disease status (i.e. mange) by the presence of hair loss, skin thickening and lesions on the hind legs and tail at time of capture. We used an ordinal body condition score as follows: 1 = ≤ 10% of body affected, usually the back of hind legs; 2 = 10 – 25% of body affected, usually back of hind legs and tail; 3 = 25 – 50%; 4 = 50 – 75%; 5 = 75 – 100% (Figure 3.2, Table 3.S1). We also radio-tracked coyotes periodically to monitor body condition and recorded any visible changes in mange severity. The coyotes we classified as appearing healthy were not screened for other ailments, but they all exhibited good coat quality, some body fat, and no apparent health problems.

3.3.3 Space use

We calculated three metrics of space use to test whether male, sub-adult, or parasitized coyotes were more likely to overlap with people in space and time. We measured differences in habitat selection by comparing the habitat types at GPS locations used by individual coyotes to locations generated randomly (Boyce et al. 2003). We condensed six land cover classes into two habitat types based on the presence of human activity and infrastructure: developed (residential, commercial, industrial, institutional, and open areas that were undesignated and typically composed of mowed grass; 93% of available habitat) and undeveloped (urban ravines and parks; 7% of available habitat; Figure 3.1). We measured habitat selection within our study area (third order habitat selection; Johnson 1980) by comparing each used GPS fix to one available location created within a minimum convex polygon around all coyote locations using Geospatial Modelling Environment (Beyer 2012). We then used logistic regression to model the probability of a location being used or available as a function of the habitat type at the location (i.e. developed or undeveloped) and the age, sex, and health status of the associated coyote. Landcover data provided by the City of Edmonton (2010) had a spatial resolution of 10m. For those locations that occurred on an ecotone we used the land cover class covering the majority of a 10m buffer around the location to account for collar error (Rettie & McLoughlin 1999). We also estimated monthly home range sizes for individual coyotes using 95% kernel density utilization distributions generated using a plug-in bandwidth estimator in Geospatial Modeling Environment (Gitzen, Millspaugh & Kernohan 2006).

To determine whether individual coyotes were similarly active at different times of day, we measured step lengths, which we defined as the distance traveled between successive three-hour locations. We modeled step length as a function of coyote age, sex, health, and time period. Time periods were defined as day (from one hour after sunrise to one hour before sundown), crepuscular (± one hour from sunrise or sundown), and night (one hour after sundown to one hour before sunrise) with adjustment to reflect seasonal changes in day length.

3.3.4 Diet

We examined differences in the diets of individual coyotes by analyzing hair samples collected at capture using stable isotope analysis. Guard hairs were collected from the nape of the neck and prepared for δ13C and δ15N stable isotope analysis following the methods of Hilderbrand et al. (1996). We expected stable isotope analysis to provide a measure for assimilation of anthropogenic food into body tissue because corn, as a C4 plant, has a conspicuously high δ13C signature and is ubiquitous in processed food in the form of corn syrup and starch (Newsome et al. 2010). Stable isotope analysis can also provide an estimate of trophic level because δ15N correlates with protein ingestion (DeNiro & Epstein 1981). We used the results of previous studies of coyote diet based on scat contents (Pruss 2002; Morey, Gese & Gehrt 2007) to identify several food sources for inclusion in our analysis as reference samples. For each of 18 dietary items, we sampled ≥ 3 sources for their stable isotopic signatures, which we categorized a priori into three groups based on the similarity of their 13C and 15N values. We grouped mammals and insects known to be consumed by coyotes as prey; white tailed deer, beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), cricetid rodents, sciurids, lagomorphs, and insects. We also grouped several species of fruit that are common in Edmonton; crabapples (*Malus* spp.), Saskatoon berries (*Amelanchier alnifolia*), blueberries (*Vaccinium* spp.), and raspberries (*Rubus idaeus*). Lastly, we grouped several sources of anthropogenic food that are at least partly derived from corn products: human hair (which provided an estimate of human diet), domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*), pet food, food waste from compost piles, and published isotopic values for chicken and beef (Jahren & Kraft 2008) which provided estimates of scavenged meat.

To determine whether coyotes consumed relatively more prey, fruit, or anthropogenic food, we built three-source mixing models using the program SIAR (Parnell et al. 2010). Such models provide a framework for testing hypotheses about diet because they provide a deterministic solution for estimating the probability that each food item accounts for a given proportion of the consumer's diet (Moore & Semmens 2008). We assumed that fractionation rates were isotope-specific across dietary sources and accounted for digestibility following the methods of Newsome et al. (2004).

We measured the δ13C and δ15N isotope signatures of individual coyotes and diet sources using an elemental analyzer (EuroEA Elemental Analyzer, EuroVector) and a continuous-flow isotope ratio mass spectrometer (Isoprime Mass Spectrometer, GV Instruments) at the Biogeochemical Analytical Service Laboratory (Department of Biological Sciences, University of Alberta, Edmonton, Canada). These instruments had a measurement standard deviation of ±0.1 and ±0.3‰ for δ13C and δ15N measurements, respectively.

3.3.5 Model building and selection

We evaluated our hypotheses that one or more of coyote age, sex, and health status best explained variation in coyote habitat selection, home range size, activity patterns, and diet (*sensu* Burnham & Anderson 2002). For each of these four response variables, we built five candidate models: a null model, a model for each of age, sex, and health (and their interactions with habitat type for habitat selection and time period for activity patterns), and a global model that included all terms (Table 3.1). We then ranked these candidate models based on their Akaike Information Criterion scores (corrected for small sample size; AICc) and corresponding model weights. From all models in which each covariate appeared, we calculated an average parameter estimate after adjusting the contribution of each model by its weight (Burnham & Anderson

2002; Hegyi & Garamszegi 2010). We used mixed effects models of three types depending on the best-fitting distribution of the dependent variables; generalized linear mixed model (GLMM) with a logistic link for habitat selection, a linear mixed effects model for home range size and assimilated diet, and a GLMM with a Poisson distribution for diel patterns of activity via step lengths. We partitioned the effect of individual by including animal ID as a random effect and accounted for temporal non-independence of successive GPS fixes by including an autocorrelation function (function AR1 in R with a lag of one 3-hour step; Pinheiro et al. 2012) in our analysis of habitat selection and activity patterns. We assessed the fit of each candidate model using the proportion of explained deviance (D^2) because it can be used across different model types (Midgley et al. 2003).

3.4 Results

Between 2009 and 2012, we captured and sampled 21 coyotes of which 19 wore functional GPS collars and were included in our spatial analyses. Eleven of the 21 sampled coyotes had good coat quality and appeared to be healthy (hereafter 'healthy') and 10 coyotes exhibited signs of mange (hereafter 'diseased'), but only 8 of these has sufficient data for inclusion in our spatial analyses. The healthy, collared coyotes included five adult females, two subadult females, two adult males and two subadult males, and the diseased, collared coyotes included four adult females, one subadult female, two adult males, and one subadult male. Sex and age classes were balanced across healthy and diseased coyotes in the 19 collared coyotes ($G_{AgeXMange} = 0.12$, d.f. = 1, $p = 0.74$; $G_{SexXMange} = 0.28$, d.f. = 1, $p = 0.60$). Coyotes that exhibited signs of mange at their times of capture typically had mild or moderate infestations (e.g. hair loss and lesions on the hind and forelegs, Figure 3.2b and 3.2c). By monitoring collared coyotes using radio-telemetry, we found that coyotes with mild mange at capture became more severely affected over time, no coyotes with mange appeared to have recovered, and no coyotes we considered to be healthy when captured exhibited signs of mange while they were monitored (Table 3.S1). Over the study period, six of the 11 study coyotes with mange died; four from exposure (i.e. were found dead in sleeping positions in -20°C temperatures) and two were euthanized following reports of conflict by the public. Of these, three coyotes with mange were necropsied at the University of Calgary where the presence of *S. scabiei* mites and/or alopecia consistent with sarcoptic mange infestation was confirmed (University of Calgary, Faculty of Veterinary Medicine, pers. comm.). Of the 11 healthy coyotes, four were killed by collisions with vehicles.

Comparing the model-averaged parameter estimates revealed which of age, sex, or health status best explained variation in each of habitat selection, home range size, activity patterns, and diet. Health status was the most important variable for each of habitat selection, home range size, activity patterns, and δ15N (protein) assimilation (Table 3.1). Coyote age had the most support for δ13C (processed food) assimilation (Table 3.1).

The monthly home ranges of diseased coyotes were an average of 3.9 times larger than those of healthy coyotes ($U_{10,7} = 88$, $p < 0.001$; Figure 3.1 and 3.3a). The home ranges of diseased coyotes also overlapped in space and time with at least one other coyote, whereas those of healthy coyotes did not overlap in both space and time. Diseased coyotes also had 5.5 times more GPS fixes in developed areas than did healthy coyotes ($\beta_{Intercept} = 0.62 \pm 0.05$, $t_{19} = 12.28$, $p < 0.001$; $\beta_{Mange} = -0.32 \pm 0.08$, $t_{19} = -4.03$, $p < 0.001$; $\beta_{Developed} = -2.10 \pm 0.05$, $t_{19} = -45.12$, $p < 0.001$; $\beta_{MangeXDeveloped} = 1.38 \pm 0.06$, $t_{19} = 22.55$, $p < 0.001$; Figure 3.3b). Diseased and healthy coyotes were similarly active overall (mean metres traveled per three-hour step ± SD for Diseased = 618.42 m ± 925.88; Healthy = 591.91 ± 876.09; p = 0.624). Healthy coyotes were more active at night than during the day whereas diseased coyotes were similarly active during all three time periods and 2.2 times more active during the day than healthy coyotes ($\beta_{Intercept} = -0.10 \pm 0.08$, $t_{19} = -1.22$, $p = 0.22$; $\beta_{Mange} = -0.01 \pm 0.13$, $t_{19} = -0.10$, $p = 0.92$; $\beta_{Time} = -0.72 \pm 0.02$, $t_{19} = -43.72$, $p < 0.001$; $\beta_{MangeXTime} = 1.52 \pm 0.03$, $t_{19} = -5.44$, $p < 0.001$; Figure 3.3c).

Diseased coyotes assimilated only 60% as much dietary nitrogen as healthy coyotes, a difference of approximately one trophic level (DeNiro & Epstein 1981) ($U_{11,10} = 27$, $p = 0.009$; Figure 3.4a). Based on the δ15N and δ13C values of our reference samples, the SIAR mixing model estimated that diseased coyotes assimilated 32.8% more anthropogenic food and 87.2% less prey than healthy coyotes (Figure 3.4b). Coyote age had the most model support for differences in the assimilation of δ13C (processed anthropogenic food), however the difference in model support for age, sex, and health was small; all models had AICc scores ≤ 2 points from each other (Table 3.1). Adult coyotes assimilated only 5% more δ13C than did subadults ($\delta 13C_{\text{Adults}} = -22.33 \pm 0.82$, $\delta 13C_{\text{Subadults}} = -21.24 \pm 1.67$; $U_{10,9} = 113$, $p = 0.09$).

3.5 Discussion

Although rates of conflict with coyotes have increased throughout North America (White & Gehrt 2009), there is no general explanation for the mechanism. We evaluated three existing hypotheses for higher rates of conflict in other carnivores – sex, age, and health status – and related these variables to four measures of using anthropogenic resources that we considered to be precursors of conflict with people. Health status was most associated with all four of these behaviours: coyotes with hair loss and lesions consistent with mange infestation made more use of developed areas, had larger home ranges, were more active during daylight hours, assimilated less protein, and consumed more anthropogenic food (as estimated by our mixing model) than coyotes that appeared to be healthy at their times of capture.

Diseased coyotes used developed areas more frequently than did healthy coyotes, and this suggests that they had a greater tolerance of human development and human presence, both of which are indicators of habituation and precursors of conflict in many contexts (Schmidt & Timm 2007; Towns et al. 2009; Goodrich et al. 2011b). For example, debilitated tigers in the Russian Far East that were either injured or sick were more likely to use developed areas than healthy tigers, resulting in higher incidences of conflict with humans and livestock (Goodrich et al. 2011b). Similarly, polar bears (*U. maritimus*) in poor body condition in Canada's Arctic were more likely to frequent areas of human habitation in search of more easily obtainable foods (Towns et al. 2009).

Diseased coyotes also used more developed areas because they had much larger home ranges than coyotes that were apparently healthy. The home ranges of diseased coyotes were over four times larger than those of healthy coyotes and their home ranges were less exclusive, suggesting these animals have similar home ranges as transient individuals that do not maintain territories (Gese, Rongstad & Mytton 1988). The difference in home range size we observed was similar to one reported between resident and transient coyotes in more natural landscapes (Kamler & Gipson 2000). Such transient behaviour often characterizes young individuals (Windberg & Knowlton 1988), but we found no difference in age between healthy and diseased coyotes. In other areas, transient coyotes may be more likely to be in poor condition (Pence & Windberg 1994) because they typically use less suitable habitat on the fringes of resident coyote home ranges (Kamler & Gipson 2000), which may manifest as developed areas in the urban landscape (Gehrt, Anchor & White 2009). In this way, differences in health between individual coyotes may be related to their social status and habitat use. For example, healthy individuals that range widely as transients might be more likely to encounter unrelated coyotes, thereby potentially increasing their exposure to infected individuals (Altizer et al. 2003). Conversely, animals that are already sick or otherwise subordinate may be less capable of defending territories (Pence & Windberg 1994), more reliant on easily accessible food, and more likely to range widely to find it.

It is interesting that diseased coyotes had much larger home ranges than healthy coyotes considering they did not differ significantly in their activity levels. We suspect that this may be because residential and commercial areas contain relatively more unsuitable habitat such as buildings and other impervious surfaces relative to urban natural areas. Individuals with more developed home ranges may then range more widely but use proportionately less of their home range, which has been observed in other urban coyote populations (Gehrt, Anchor & White 2009).

Diurnal activity may be an especially important precursor to human-coyote conflict because temporal avoidance of humans by coyotes and other wildlife is widespread (Kitchen, Gese & Schauster 2000; Beale & Monaghan 2004; Ditchkoff, Saalfeld & Gibson 2006) and may be necessary for coexistence between wildlife and humans in developed areas (Carter et al. 2012). For example, bobcats (*Lynx rufus*; Tigas, Vuren & Sauvajot 2002; Riley et al. 2003) and tigers (Carter et al. 2012) both exhibit lower activity levels during the day where they overlap spatially with humans. The lack of nocturnal behaviour exhibited by diseased coyotes in our study corroborates anecdotes that diseased coyotes are more likely to encounter people and approach houses during the day than healthy coyotes (Samuel, Pybus & Kocan 2001; Gehrt, Anchor & White 2009) and could have resulted from compromised thermoregulatory ability, in turn caused by hair loss (Samuel, Pybus & Kocan 2001). Sub-zero temperatures in the winter months could increase the energetic costs of being active at night for diseased coyotes and encourage their use of developed areas in our northern study area by offering shelter under buildings (Lowry, Lill & Wong 2013). The costs of compromised thermoregulation may be considerable as several diseased coyotes died of exposure during the study period.

The greater proportion of anthropogenic food in the diet mixing model of diseased coyotes is an important precursor of potential conflict because it increases the likelihood an individual will become food conditioned (Conover 2002). Urban coyotes tend to be mainly reliant on small rodents and berries, however the extent to which they are reliant on human food varies across cities (Gehrt & Riley 2010) and, as demonstrated in our study, among individuals. In general, conflicts between humans and wildlife are more likely to arise when animals are reliant on human food, rather than simply tolerant to human disturbance (Herrero 1985). For example, problem bears requiring active management consume proportionately more anthropogenic food (Oi et al.

2009; Hopkins et al. 2012). In our study area, coyotes are often seen in alleys where there is accessible garbage, and composting is a common but unmanaged practice (City of Edmonton, pers. comm.). Piles of human food waste is likely one important food source for the diseased coyotes we sampled since it has conspicuously low protein content and is common in residential areas.

As with health status and habitat use, the relatively protein-poor diets exhibited by diseased coyotes could be both a cause and consequence of the lower-quality diet that anthropogenic waste provides. In general, animals eating a low-protein diet with low fat reserves or with high parasite loads can suffer from immunosuppression, poor thermoregulation, and increased energy requirements (Alzaga et al. 2008; Taylor et al. 2013). Although the diseased coyotes we observed were not significantly less active than healthy coyotes, diseased coyotes were relatively more active during the day when coyotes do not normally hunt (Bekoff 2001), which could impact hunting success. Sarcoptic mange infestation appears to compromise hunting ability in red foxes as infested individuals have reduced fat reserves and evidence of malnutrition (Newman, Baker & Harris 2002). Further, bobcats (*Lynx rufus*) and cougars (*Puma concolor*) that used more developed areas were more likely to be exposed to rodenticides, which in turn are linked to mange infestation (Riley et al. 2007) and have been detected in urban coyotes (Poessel et al. 2014). Once established, either of disease, poor nutrition, or poor hunting ability could be exacerbated by the other, creating a "vicious circle" of low-quality diet, poor body condition, and disease susceptibility (Beldomenico & Begon 2010) that has been documented in several other species (Ezenwa 2004; Blanchet et al. 2009) including humans (Ezzati & Riboli 2012).

The larger home ranges in developed urban areas, increased diurnal activity, and reliance on anthropogenic food by disease coyotes are likely to increase the rate at which they encounter people, pets, and other coyotes. By increasing encounter rates, these behaviours in turn may increase the spread of disease among coyotes and between coyotes and pets (Altizer et al. 2003) and the number of coyote sightings and encounters reported by the public. In this way, the differences in behaviour we observed between parasitized and healthy coyotes may be contributing to the rise in well-publicized reports of coyote encounters in many North American cities and the corresponding steady increase in public demand for more active coyote management (White & Gehrt 2009). If cities promote the survival of otherwise moribund animals by providing easily accessible food (Anderies, Katti & Shochat 2007), or promote the transmission of parasites at communal feeding sites (Bradley & Altizer 2007), the relationships we have observed between health and conflict behaviour may become more prevalent. This relationship between health and use of human resources in our study thus suggests a potential mechanism by which conflicts between humans and urban wildlife may increase and may partly explain why the majority of urban coyotes do not appear to exhibit conflict behaviour (Gehrt & Riley 2010) despite more frequent reports of human-coyote conflict (Garthwaite 2012).

Our results suggest that disease may be an underappreciated aspect of human-coyote conflict with two important implications for urban residents and wildlife managers. First, if wildlife disease can promote behaviours that may lead to conflict, wildlife managers should aim to reduce disease prevalence and avoid passive reliance on disease to regulate wildlife populations (e.g., Bellows 2001) in urban areas, particularly for diseases that can be transmitted to people (e.g. Liccioli et al. 2014). Second, although disease prevalence and spread could potentially be reduced by selectively removing highly diseased animals, reliance on lethal management may be reduced by identifying and securing hyper-abundant but low-quality anthropogenic food waste. Reducing coyote access to neighborhood compost, fallen fruit, birdseed, garbage, and other waste food could be achieved with a combination of education and by-law creation. Both of these management implications may generalize to other species, locations and contexts of human-wildlife conflict to promote positive experiences for urbanites with coyotes and other urban-adapted wildlife around the world.

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3.8 Tables

Table 3.1 Summary of candidate model outputs for coyote habitat selection, home range size, activity patterns, and diet. Model weights were calculated using corrected Akaike Information Criterion (AICc) scores and used to calculate weighted-average parameter estimates.

Behavioural metric (Response Variable)	Model terms	ΔAICc	w_i	D^2	Model-averaged parameter estimate ± S.E. (Term)
Habitat selection					
(Location used or available)	Global (all terms)	0	1.00	0.24	
	Health + Health * Habitat type	110	0.00	0.21	**1.34 ± 0.28 (Health * Habitat type)**
	Age + Age * Habitat type	491	0.00	0.073	0.504 ± 0.23 (Age * Habitat type)
	Sex + Sex * Habitat type	637	0.00	0.068	0.076 ± 0.032 (Sex * Habitat type)
	Null model (Intercept)	2922	0.00	0.00	
Home range size					
(Monthly home range size)	Health	0	0.66	0.22	**1.75 ± 0.12 (Health)**

	Global (all terms)	3	0.19	0.27	
	Sex	4	0.073	0.090	0.30 ± 0.024 (Sex)
	Null model (Intercept)	5	0.057	0.00	
	Age	7	0.020	0.022	-0.052 ± 0.003 (Age)
Activity patterns (Metres traveled between GPS fixes)	Global (all terms)	0	1.00	0.26	
	Health + Health * Time period	269	0.00	0.21	**1.04 ± 0.13 (Health * Time period)**
	Age + Age * Time period	7255	0.00	0.17	-0.324 ± 0.078 (Age * Time period)
	Sex + Sex * Time period	7320	0.00	0.15	-0.0193 ± 0.021 (Sex * Time period)
	Null model (Intercept)	9421	0.00	0.00	
Changes in diet (δ^{13}C assimilation)	Age	0	0.30	0.097	**-0.23 ± 0.11 (Age)**
	Global model (All terms)	1	0.23	0.23	
	Null model (Intercept)	1	0.22	0.00	
	Health	1	0.14	0.047	0.10 ± 0.031 (Health)

	Sex	2	0.11	0.015	-0.082 ± 0.027 (Sex)
Changes in diet ($\delta^{15}N$ assimilation)	Health	0	0.49	0.19	**-0.57 ± 0.34 (Health)**
	Null model (Intercept)	2	0.17	0.00	
	Global model (All terms)	2	0.15	0.22	
	Age	3	0.11	0.027	-0.037 ± 0.061 (Age)
	Sex	4	0.082	0.0093	0.033 ± 0.022 (Sex)

Table 3.S2 Summary information for the 21 coyotes included in this study, including: age (years), sex (male (M) or female (F)), weight at capture (kg), sarcoptic mange status (ordinal scale from 1 – 5, final status was measured at time of death or end of monitoring period or study period), home range (km^2), step length (m).

Coyote ID	Age	Sex	Weight	Mange capture	Mange final	Months monitored	Cause of death	δ13C	δ15N	% Fixes in Developed	Monthly Home Range	Step length (Day)	Step length (Night)
1	0.5	F	9	1	1	10	Exposure	-20.26	-0.32				
2	3	F	12	1	3	4.6	Vehicle	-21.09	1.21	66	17.7 ± 4.3	493.6 ± 45.6	658.1 ± 66.3
3	3	M	16	1	5	5.2	Euthanized	-22.13	2.02	40	34.8 ± 13.3	484.8 ± 37.8	910.9 ± 93.6
5	1.5	F	9.5	2	4	1.5	Exposure	-21.39	2.66	31	2.5 ± 2.3	172.9 ± 40.9	271.4 ± 43.2
7	2	F	9	0	0	0	Vehicle	-23.77	0.09				
8	0.5	F	8	0	-	0		-21.86	4.78				
9	0.5	M	10	1	5	5.9		-20.56	4.83	35	52.3 ± 17.0	289.8 ± 42.1	610.9 ± 98.5

10	0.5	F	9.5	1	1	1.0		-19.49	6.62				
11	3	F	15	0	0	6.4		-20.61	6.97	7	12.6 ± 2.5	207.3 ± 21.7	1820.7 ± 68.8
12	0.5	F	9	0	0	2.0	Vehicle	-18.58	7.89	0	3.6 ± 0.5	253.3 ± 28.5	756.5 ± 65.2
13	2	F	12	1	3	10.4		-21.99	7.40	45	24.6 ± 3.9	320.2 ± 21.0	463.9 ± 38.7
14	0.5	F	11	0	0	2.0	Unknown	-20.49	7.30				
15	1.5	F	12	0	0	3.3		-22.18	8.74	4	3.3 ± 0.8	153.6 ± 15.9	674.2 ± 51.0
16	1	F	10	1	3	3.1		-21.84	6.69	25	6.9 ± 3.3	256.5 ± 30.8	554.6 ± 69.5
17	1.5	F	10	0	0	7.5		-21.81	7.54	6	4.2 ± 0.6	101.3 ± 9.6	1469.6 ± 44.3
18	2	M	12	0	0	5.1		-22.44	8.44	11	6.1 ± 0.5	122.3 ± 12.4	1477.4 ± 45.5

19	2	M	13	2	4	5.4	Exposure	-23.03	8.47	26	12.6 ± 4.9	100.4 ± 10.5	345.0 ± 22.4
20	1	M	12	0	0	1.5	Vehicle	-23.24	7.58	12	1.2 ± 0.5	201.4 ± 24.0	356.1 ± 45.1
21	2	F	10	0	0	3.3		-23.36	7.78	31	1.1 ± 0.4	237.0 ± 18.1	386.6 ± 27.9
22	1.5	F	9	0	0	0	Vehicle	-23.46	8.04				
23	2	F	12	0	0	1.2		-22.17	8.16	19	3.9 ± 1.0	122.3 ± 21.5	1031.9 ± 91.2
24	1.5	M	13	0	0	0		-23.04	7.68				
26	2	F	12	3	4	2.5	Exposure	-22.28	7.19	31	6.8 ± 1.2	758.2 ± 231.6	755.8 ± 175.8
27	3	F	13	0	0	0.9	Vehicle	-22.28	8.21	7	3.8	183.6 ± 39.3	1086.3 ± 74.5
28	0.5	M	10	0	0	2.8	Vehicle	-22.73	10.21	1	3.0 ± 0.8	178.2 ± 26.2	506.2 ± 48.6

29	0.5	F	10	0	0	3.2			-23.55	6.79	2	1.2 ± 0.8	103.7 ± 10.9	251.9 ± 21.1

3.9 Figures

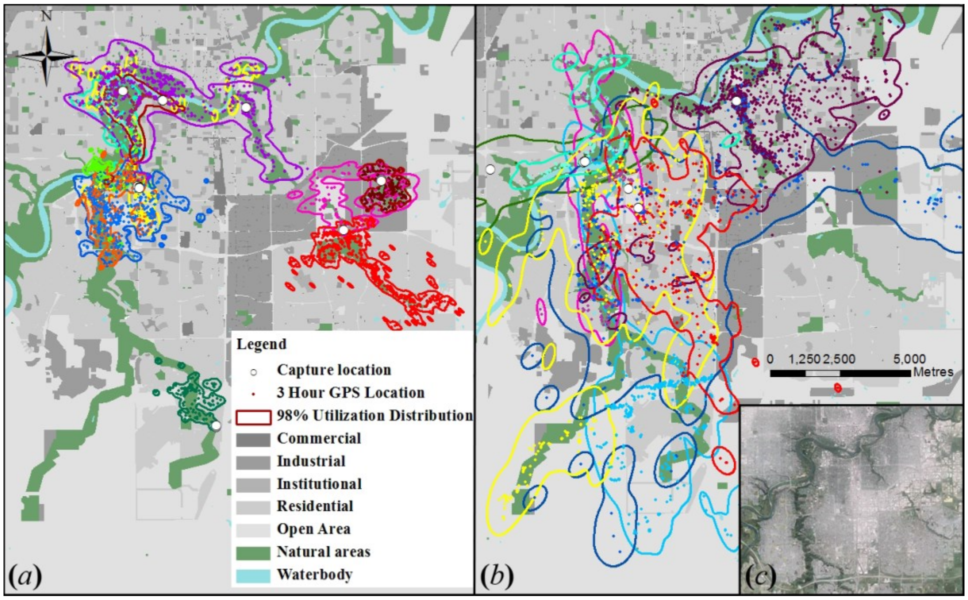

Figure 3.1. Map of the city of Edmonton showing the capture locations (white circles), 3-hour GPS locations (points), and 95% utilization distribution home ranges (polygons) for GPS-collared coyotes that were apparently healthy (n=11; a) and or classified as diseased and had visible ectoparasite infestations (n=8; b). Colors distinguish individual coyotes and land use types, either developed (gray) or urban natural areas (green). (c) Aerial photo of map section of Edmonton from Google Earth.

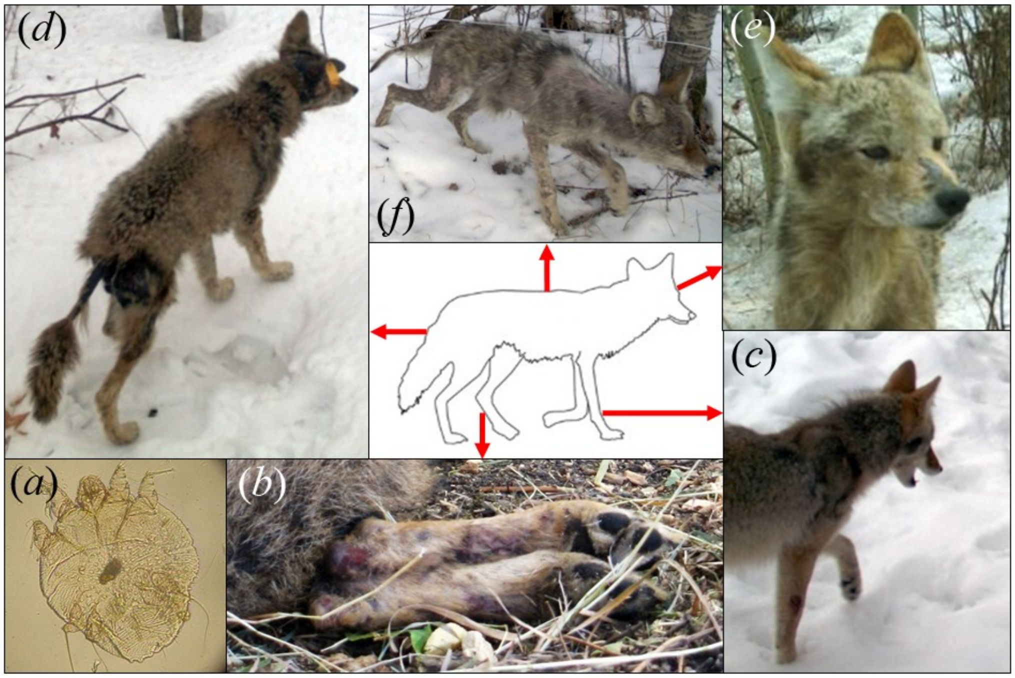

Figure 3.2. Signs of sarcoptic mange used to visually assess coyote health status at time of capture. Sarcoptic mange is caused by the mite *Sarcoptes scabiei* (a) leading to intense itching and hair loss. Coyotes we classified as exhibiting mange at time of capture had lesions on (b) hind legs and (c) forelegs. Coyotes exhibiting mild signs of mange at capture progressed to losing hair on the tail (d), and eventually on the face (e), following the typical pattern of mange spread. In the most severe cases of mange, hair loss can occur over the whole body (f). Photo credit: (a) Wikimedia, all others from authors.

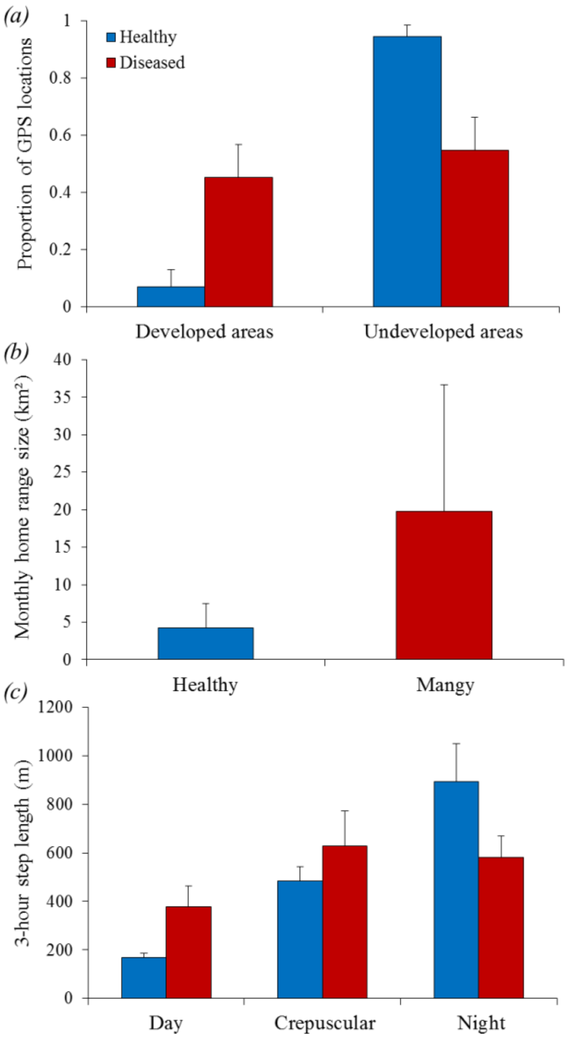

Figure 3.3. Differences in space use between apparently healthy (n = 11; blue) and coyotes with visible ectoparasite infestations (n = 8; red). We compared the habitat selection, home ranges, and activity patterns of coyotes by measuring (a) monthly home range utilization distributions, (b) use of developed (residential, commercial, industrial, institutional, and undesignated mowed areas) and undeveloped (parks and ravines) areas, and (c) metres travelled between successive 3-hour GPS fixes during three time periods. Columns show averages across individuals and bars show standard deviations.

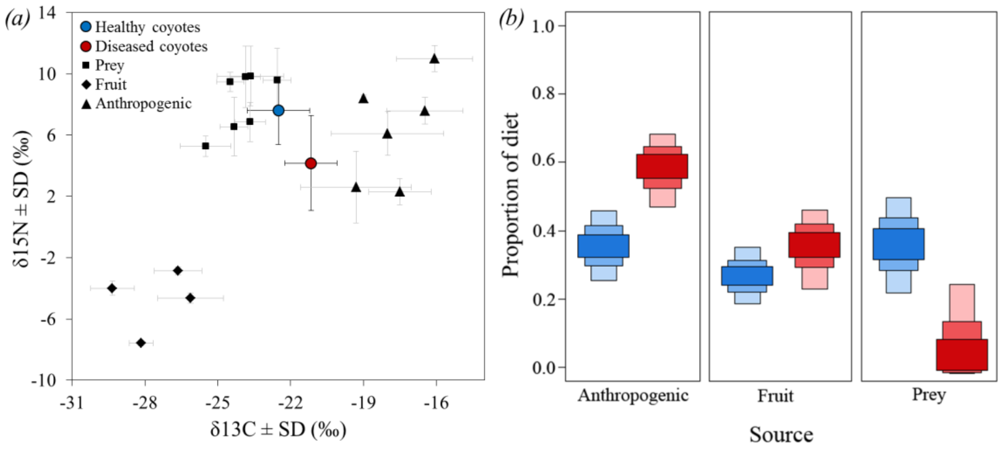

Figure 3.4. Stable isotope analysis of healthy and diseased coyote diets. (a) Isotopic δ15N and δ13C signatures for sampled healthy coyotes (n=12, blue circle), diseased coyotes (n=11, red circle), and food sources we grouped as prey (squares), fruit (diamonds), and anthropogenic food (triangles) based on the similarity of their stable isotope signatures. Bars show standard deviations. (b) Boxplots showing the proportional contribution of anthropogenic food, fruit, and prey to the diet of healthy (n=12, blue) and diseased (n=11, red) coyotes, as modeled by a three-source mixing model (SIAR). Bars show the 50%, 75%, and 95% confidence intervals respectively with lighter shades.

Chapter 4

4 Selection for anthropogenic resources varies with spatial scale and individual health in urban coyotes[*]

4.1 Summary

1. Several species of urban-adapted wildlife that make use of anthropogenic resources appear to adjust their habitat selection or timing of activity to lower the risk of encountering humans. Among these species, individuals with poor body condition may be more likely to accept greater risk to access anthropogenic resources and may, consequently, be more likely to encounter and come in conflict with people.

2. We tested this hypothesis by measuring the habitat selection of urban coyotes (*Canis latrans*) within home ranges and at habitat patches. We fitted 19 coyotes with GPS collars using 3-hour fix rates and divided our sample into 11 animals that appeared to be healthy and eight that had signs of sarcoptic mange (*Sarcoptes scabiei*). We measured selection for residential areas at different times of day and for selection of anthropogenic food or shelter in locations where individuals exhibited multiple GPS locations. We paired these sites with randomly-generated control sites and compared selection for anthropogenic areas and resources by coyotes of different age, sex, and health classes.

3. Nearly all coyotes avoided residential areas within their home ranges but those with signs of disease used residential areas more frequently, especially during the day. Within residential areas, coyotes selected for foraging or bed sites in backyards that lacked fences, contained anthropogenic food, and with higher visual cover. Diseased coyotes were

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more likely to select for sites with anthropogenic food and bed sites under houses. Outside of residential areas, coyotes selected for sites with anthropogenic food, prey sign, flatter slopes, and further away from trails but closer to buildings than available sites.

4. *Synthesis and Applications:* Our results suggest that coyotes avoided residential areas and especially during the day when they are more likely to encounter people but were attracted to locations with anthropogenic resources. Diseased coyotes exhibited stronger selection for anthropogenic resources and particularly during the day, which may promote negative encounters between humans and coyotes. Management practices that promote the removal and containment of attractants for coyotes and other urban-adapted wildlife could reduce rates of conflict with people via attraction to residential areas, supporting diseased individuals in the population, and promoting the spread of disease.

4.2 Introduction

When selecting for suitable habitat, animals must access necessary resources while minimizing various kinds of risk (Brown 1999). Wildlife that persist in human-dominated areas like cities, known as urban adapters (McKinney 2002), can make use of abundant and novel anthropogenic food and shelter but these are often in residential areas where encounters with people, and thus conflict, are most likely. These conflicts can lead to removal via lethal management, especially for species such as carnivores that are capable of threatening the security of people, their pets, or their property. To avoid this risk, carnivores in human-dominated landscapes often adjust their habitat selection in space (Whittington, St. Clair & Mercer 2005) or time (e.g. Ciucci et al. 1997) to make use of available habitat, including human infrastructure or resources, while avoiding interactions with people.

Coexistence between humans and carnivores in human-dominated landscapes may be facilitated by fine-scale avoidance of places and times with high human activity (e.g. Boitani, 1982; Ciucci et al. 1997). However this tendency is highly variable among both species (Bateman & Fleming 2012) and individuals (e.g., Knopff et al. 2014). Encounters with people and subsequent management action appear to be more likely for animals that have become highly habituated to human infrastructure, such as buildings (e.g., Rauer, Kaczensky & Knauer 2003; Elfström et al. 2014), which can be used as den sites for a variety of urban carnivores (reviewed in Bateman & Fleming 2012; Lowry, Lill & Wong 2013). Many carnivore species can also make use of anthropogenic food (e.g. Contesse et al. 2004; Newsome et al. 2010) and the development of food-conditioned animals who associate people with food usually results in conflict (e.g., Herrero 1985; McCarthy & Seavoy 1994). Although the result of food-conditioning is well-known, there is less understanding of the causes of variation among individuals in their initial propensity to approach people or their infrastructure.

Tolerance to humans and their infrastructure is one of many ways in which risk-taking behaviour may vary with individual state (McNamara & Houston 1996) whereby animals with physiological constraints are more likely to tolerate human disturbance (Gill, Norris & Sutherland 2001, Beale & Monaghan 2004b). Greater acceptance of risk with energetic need is well studied in both laboratory (e.g. Godin & Sproul 1988) and free-living animals (e.g. Beale & Monaghan, 2004a). This relationship between individual condition and avoidance of humans may in part explain why some carnivores are more likely to encounter people. Several cases in the literature of injured (e.g. lions *Panthera leo*; Yeakel et al. 2009), nutritionally stressed (e.g. polar bears *Ursus maritimus*; Towns et al. 2009) or diseased (e.g. lynx *Lynx lynx*; Ryser et al. 2002) carnivores approaching people and their houses for food have led some authors to suggest that poor physical condition is a typical cause of human-carnivore conflict (Linnell et al. 1999). This hypothesis may also explain why rates of encounters with people are increasing for several urban-adapted carnivores, including raccoons (*Procyon lotor*; Bozek, Prange & Gehrt 2007), red foxes (*Vulpes vulpes*; Contesse et al. 2004; Baker et al. 2007), and coyotes (Gehrt, Anchor & White 2009; White & Gehrt 2009; Lukasik & Alexander 2011).

The coyote (*Canis latrans*) is an opportunistic canid that is thriving in cities across North America (Gehrt & Riley 2010). Although coyote attacks on people are rare, coyote sightings are increasing in many urban areas (White & Gehrt 2009) and often elicit concern from the public, especially when coyotes inhabit residential areas. Coyotes typically avoid human activity, both by primarily using urban natural areas (reviewed by Gehrt & Riley 2010; Gese, Morey & Gehrt 2012) and shifting to more nocturnal activity cycles relative to rural coyotes (Tigas, Vuren & Sauvajot 2002; Riley et al. 2003). However, coyotes are known to consume human food (Fedriani, Fuller & Sauvajot 2001; Morey, Gese & Gehrt 2007; Murray et al., in press a) which can account for up to 30% of their diets (Gehrt & Riley 2010). Thus, coyotes may select for areas and time periods that support access to anthropogenic resources while minimizing their risk of encountering people.

Despite a general tendency for coyotes to avoid people, substantial variation exists among individuals in both diet and habitat use. For example, coyote home ranges can contain almost exclusively natural areas or residential and commercial areas (Gese, Morey & Gehrt 2012; Murray et al, in press a) and coyote consumption of prey can vary significantly across individuals (Murray et al., in press b). Others have shown that these differences can be result from social status (Kamler & Gipson 2000) and sex (Blejwas et al. 2006) but may also result from disease. For example, anecdotal evidence suggests that coyotes with sarcoptic mange (*Sarcoptes scabiei*) tend to elicit more complaints from the public in urban Chicago (Gehrt, Anchor & White 2009). Recent work has shown that coyotes reported as nuisance animals by the public are more likely to be diseased (Murray et al., in press b) and disease is associated with more frequent use of developed urban areas and consumption of anthropogenic food (Murray et al., in press a).

In this study, we extended our previous work to test the hypothesis that human-wildlife conflict associated with habitat selection is mediated by disease status. We predicted that urban coyotes would select habitat to access anthropogenic resources in ways that minimized their risk of encountering people, but diseased animals would make greater use of anthropogenic resources and in both locations and at times that were more likely to overlap with people. Specifically, we predicted that within their home ranges, coyotes would generally avoid residential areas, especially during the day, but would select for feeding or resting sites that provided anthropogenic resources. We further predicted that diseased animals would make more use of residential areas and would target anthropogenic resources, such as garbage, compost and shelter under buildings, more often.

4.3 Methods

4.3.1 Study area

We studied coyote habitat selection in the city of Edmonton, the northern capitol city of Alberta, Canada (pop: 812,2012 in 2011 census, 53.5472° N, 113.5006° W). The frequency of reports of coyote sightings in Edmonton has increased in recent decades (Ramsey Cox, pers. comm.) and are now reported multiple times per day throughout the year (Murray, unpublished data). Edmonton is bisected by the North Saskatchewan River valley which is connected to several large ravines, providing the largest area of continuous urban park land in North America (City of Edmonton, 2013). These natural areas provide habitat for several coyote prey species including showshoe hare (*Lepus americanus*), white-tailed jackrabbits (*Lepus townsendii*), white-tailed deer (*Odocoileus virginianus*), beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), and various small mammals.

4.3.2 Capture and collaring

We collected data on coyote habitat selection by trapping and fitting coyotes with Global Positioning System (GPS) collars. We captured coyotes from 2009 – 2012 in areas within city limits where coyote sightings had been reported and where dogs were prohibited. We trapped coyotes using four-coil padded foot-hold traps (No. 3 Victor Soft Catch Coilspring; Animal Trap Co., Lilitz, Pennsylvania) and physically restrained captured coyotes using catch poles. Restrained coyotes were then sexed, aged as either subadults (< 1 year old) or adults (≥ 1 year old) using degree of tooth wear (Bowen 1982), weighed, and tagged. We also noted any signs of sarcoptic mange infestation. Coyotes with visible hair loss, skin thickening, and lesions consistent with sarcoptic mange (Samuel, Pybus & Kocan 2001) were considered "diseased", whereas coyotes with no evidence of sarcoptic mange or any other ailment were considered "healthy". Coyotes with severe hair loss or emaciation were not collared. A full description of signs and evidence of sarcoptic mange is available from Murray et al. (in press a). We programmed the GPS collars to collect fixes every 3 hours and most coyotes were fitted with collars that transmitted coyote locations to us daily over the cell phone network (Lotek Wildcell SG, 17 coyotes) or could be downloaded remotely (Lotek 4400S, two coyotes).

4.3.3 Habitat selection within the home range

We measured selection for habitat types by coyotes using landcover data provided by the City of Edmonton (2010; spatial resolution = 10m). We condensed seven landcover types defined by the city into four land use categories based on the presence of vegetation and human activity. We grouped parks and natural areas as habitat with little to no human infrastructure and relatively natural vegetation (hereafter "Natural"). We grouped residential areas and schoolyards as areas with high human use and potential for conflict (hereafter "Residential"). We grouped commercial areas with industrial parks as areas with relatively high densities of human infrastructure and little vegetation (hereafter "Industrial"). Lastly, undesignated land that typically was comprised by mowed grass or impervious surfaces was defined as open areas (hereafter "Open").

We estimated habitat selection by coyotes within their home ranges (third order habitat selection; Johnson, 1980) by comparing the land use categories at locations used by coyotes to those at an equal number of available locations that were randomly-generated within individual home ranges. We estimated home ranges by generating minimum convex polygons (MCP; Mohr, 1947) around all locations for each coyote using Geospatial Modeling Environment (Beyer 2012). For GPS locations that occurred on an ecotone between two different land use types, we account for collar precision by using the land cover category that encompassed the majority of a 10m buffer around the location (Rettie & Mcloughlin 1999). We then calculated selection ratios for habitat type (used in categoryi / available in categoryi ; Manly et al. 2002) for each individual coyote with a value of 1 indicating no selection. Using these selection ratios, we used means tests to determine whether avoidance of residential areas differed for coyotes of different age, sex, or health classes.

We also tested whether coyotes preferentially avoided residential areas during the day when human activity is often higher. We compared the selection ratios of individual coyotes for residential areas during the day (one hour after sunrise to one hour before sunset) and at night (one hour after sunset to one hour before sunrise) by calculating the ratio of these two values (selection ratio for residential areas during the day / selection ratio at night). Using this day/night ratio, we used means tests to determine whether coyotes of different age, sex, and health classes significantly differed in their avoidance of residential areas during the day relative to night. We also tested whether diseased coyotes both used residential areas more frequently and also more often during the day using linear regression.

4.3.4 Selection for resources within the home range

Because we were especially interested in the fine-scale selection for anthropogenic resources by coyotes, we identified areas used for prolonged periods or visited multiple times at clusters of GPS locations that were presumably used for feeding or resting (hereafter “resource sites”; comparable to the fourth order habitat selection for feeding sites of Johnson (1980)). We defined a resource site as circular areas with a 20 m diameter in which a coyote had spent at least 18 hours (Figure 4.1). We identified these sites by calculating point density in a 20m moving window in Geographic Information System (ArcMap 10.0, ESRI, Redlands, CA) with a threshold of 0.022 locations/m^2.

To record the presence of resources that would be impossible to measure remotely, such as food attractants or use of shelter, we measured habitat variables in the field at a subset of resource sites (i.e. ground-truthing). We confirmed the previous use by a coyote at these sites using tracks in the mud or snow or the presence of scat, hair tufts, or bedding depressions. We measured variables relating to proximity to human activity or infrastructure, presence of natural or anthropogenic food attractants, and availability of cover (Table 4.1). Because we used GPS collars that transmitted locations remotely, we were able to visit most resource sites (72%) within one week of use and only these sites were used when recording the presence of attractants.

To measure selection, we compared each used resource site with a paired available site at a random bearing and a random distance between 100 – 200m (mean distance traveled by collared coyotes in one hour = 162 m). We then used conditional logistic regression to model the probability that a resource site was used or available as a function of covariates relating to habitat (Table 4.1) and individual state (age, sex, and health status) (Therneau 2014). To make our results more interpretable for management recommendations, we separated resource sites into those in backyards in residential areas (i.e. sites where coyotes would likely come in conflict with people and where residents could reduce the attractiveness of their yard) and those outside of residential areas in natural or grassy undesignated areas (i.e. sites where managers could anticipate coyote presence and use signage, attractant removal, or prohibit off-leash dogs to mitigate coyote encounters with dogs and people; Figure 4.1).

Using the covariates relating to habitat characteristics or individual state we built models following the methods of Hosmer and Lemeshow (2000). We first conducted univariate logistic regression tests for each variable and retained those that were liberally significant ($p \leq 0.25$). These liberally significant variables were then tested for collinearity and, for pairs that were highly correlated ($r^2 \geq 0.7$), we removed the variables that were less significant. The remaining variables were then combined into a main effects model and we performed a backward stepwise procedure using log-likelihood ratio tests with $\alpha = 0.05$ for variable retention. Lastly, we added relevant interactions (including interactions with coyote age, sex, and health) individually and these were retained if significant ($\alpha = 0.05$). We then calculated two measures of model fit for the top models: Nagelkirke's pseudo r^2 and D^2 (ratio of model residual deviance to null deviance).

4.4 Results

From 2009 – 2012 we captured and collared 19 coyotes. These coyotes included 11 coyotes appeared to be healthy (five adult females, two subadult females, two adult males and two subadult males) and eight diseased coyotes with signs of sarcoptic mange (four adult females, one subadult female, two adult males, and one subadult male). The collared coyotes were monitored for an average of four months (range: 1 – 10 months) and we collected on average 618 3-hour GPS locations per coyote (range: 161 – 1867 fixes). We were able to ground-truth 173 used and 173 available resource sites (sites per coyote: mean = 23 ± 9, range: 15 – 49) that were visited by coyotes up to four separate times by coyotes over five months.

All but two coyotes avoided residential areas within their home ranges (average selection ratio = 0.38 ± 0.38 SD), but healthy coyotes exhibited significantly more avoidance (0.12 ± 0.11) than diseased coyotes (0.55 ± 0.21; $t = 1.91$, $p = 0.031$; Figure 4.2). There were no significant differences in selection between coyotes of different age or sex classes ($t \leq 0.091$, $p \leq 0.49$). Coyotes that exhibited more selection for residential areas within their home ranges were also more likely to select for resource sites in residential areas ($r^2 = 0.77$, $F(17,1) = 58.78$, $p < 0.001$).

Of the 14 coyotes for which we had adequate GPS data in residential areas, all coyotes avoided residential areas more during the day than at night (average selection ratio during the day / at night = 0.52 ± 0.30 SD). However, coyotes that used residential areas more frequently also did so more often during the day ($r^2 = 0.76$, $F(1,13) = 41.16$, $p < 0.001$; Figure 4.2). Diseased coyotes (0.72 ± 0.24) exhibited less avoidance of residential areas during the day relative to at night compared to healthy coyotes (0.34 ± 0.25; $t = 2.97$, $p < 0.001$; Figure 4.2). We found no such difference between coyotes of different age and sex classes ($t \leq 0.87$, $p \leq 0.42$).

Backyards selected by coyotes were 5.4 times less likely to have fences, had 4.2 times as much visual cover, and were three times more likely to contain anthropogenic food than available yards (Table 4.2). Diseased coyotes used 73% of the resource sites in residential areas and were 2.2 times more likely to select for resource sites with accessible anthropogenic food than healthy coyotes (Table 4.2; Figure 4.3a). Of the 46 resource sites revisited by coyotes that contained anthropogenic food, the most common attractants were ripped bags of garbage (25 sites), open compost piles (17 sites), and bird seed (7 sites). Diseased coyotes were also five times more likely to occupy resource sites with bed sites under houses or decks than healthy coyotes ($\beta = 3.14 \pm 1.3$, $z = 2.39$, $p = 0.0168$; Figure 4.3b). Of the 38 backyards we ground-truthed that contained bed sites under houses or decks, 82% were used by coyotes with mange in the winter months and eight (21%) were used by more than one collared coyote. Outside of residential areas, coyotes selected for sites that were 245% more likely to contain anthropogenic food, 57% more likely to have prey sign, 22% farther away from trails, but 28% closer to buildings, and 15% less steep than available sites (Table 4.2).

4.5 Discussion

In this study, we tested the hypothesis that habitat selection by urban coyotes is mediated by disease status. We found that the coyotes in our sample generally avoided residential areas within their home ranges, but diseased coyotes used residential areas more frequently, especially during the day, relative to the coyotes that appeared to be healthy at the time of capture. Coyotes selected for feeding and resting sites in backyards without fences, with higher cover, and selected for sites with anthropogenic food both inside and outside of residential areas. Diseased coyotes were more likely to select for backyards with anthropogenic food and bed sites under houses. Together, these results support the more general hypothesis that human-wildlife conflict is disproportionately caused by animals in poor condition (Linnell 1999).

Our study also supported the finding by others that carnivores persisting in human-dominated landscapes may do so by avoiding places and times where they are most likely to encounter people. Most coyotes in our sample avoided residential areas within their home ranges and especially during the day. Although almost all coyotes avoided residential areas at the home range scale, they still selected for habitat that could provide accessible anthropogenic food when they chose resource sites. This difference in selection across spatial scales suggests that coyotes make selective use of particular anthropogenic resources while spending most of their time in natural areas where the probability of encountering people is presumably lower. Anthropogenic food tends to be more reliable in space and time than more natural food sources (Oro et al. 2013) and so the locations of accessible anthropogenic food may be easier to learn, either from parents (Mazur & Seher 2008) or from ongoing experience (Nielsen et al. 2013). Five coyotes in our sample visited the same backyards with anthropogenic food at least four times over the span of several months, suggesting that coyotes may learn to associate specific backyards with food. This association may be particularly problematic for human-wildlife conflict as it changes the neutral perception of people by habituated wildlife to a positive association between humans and food (McCarthy & Seavoy 1994).

Revisiting backyards with anthropogenic food during the day was especially prevalent among coyotes with mange, suggesting that animals in poorer physical condition are more likely to accept risk to access resources (*sensu* McNamara and Houston 1996). Diseased coyotes may be more likely to seek out anthropogenic food because it is often reliable in space and time and thus may have lower search and handling costs than hunting prey (*sensu* Rodewald, Kearns & Shustack 2011). Diseased coyotes were also especially likely to select for sites containing compost piles, either in backyards or industrial piles of animal feed. These piles may promote the spread of disease by serving as a common feeding site, thereby aggregating foragers (*sensu* Wright & Gompper 2005). Consuming compost may also promote poor body condition because it can be a substrate for mold and other toxins (Murray et al., Chapter 5), canids may be particularly vulnerable to ill health effects after consuming compost (Golden 2015). For this reason, anthropogenic food like compost could be both a response to and promoter of disease in urban coyotes.

Diseased coyotes were also more likely to seek out anthropogenic shelter than healthy coyotes. While many urban-adapted mammals use houses as bedding and den sites (e.g. raccoons (Gross et al. 2011), brushtail possums (*Trichosurus vulpecula*; Statham & Statham, 1997), and stone martens (*Martes foina*; Herr, Schley, Engel, & Roper, 2010), we found that the use of shelter under buildings was dependent on coyote condition. Coyotes with mange were much more likely to bed under houses perhaps to avoid the energetic costs of low temperatures because they suffered from poor coat quality and potentially compromised thermoregulation. Shelter under buildings appeared to be especially important in the winter months for coyotes in Edmonton, as it is for fox squirrels (*Sciurus niger*; McCleery et al. 2007). In more extreme cases of poor body condition and cold temperatures, shelter under houses may extend survival; one coyote in our sample with mange was found dead under a dryer vent in -20°C temperatures. Coyotes and other wildlife that bed in, under, or around houses may be more likely to have negative encounters with residents. They may also promote the spread of zoonotic disease to humans (e.g. raccoon roundworm *Baylisascaris procyonis*; Page, Gehrt & Robinson 2008) and conspecifics. Several of the bed sites we visited that were under houses were used by at least two coyotes in the same month, potentially promoting the spread of mange mites between coyotes if fallen mites are still viable (Arlian, Vyszenski-Moher & Pole 1989).

4.5.1 Management implications and conclusions

Taken together, our results suggest that urban coyotes avoid places and times at which they are likely to encounter humans. This was evident in our study by the avoidance of residential areas within the home range and especially during the day. Despite this avoidance, many coyotes exhibited fine-scale selection for habitat containing anthropogenic food and shelter but this tendency was much greater for diseased animals. Because human-coyote conflict is more likely when coyotes and people co-occur in space and time, our results also indicate several methods by which both residents and managers could reduce the attraction to coyotes of conflict-prone areas such as backyards, schoolyards, and parks. Residents should ensure that garbage is contained in sealed containers, bird feeders are not spilling seed on the ground, compost is kept in a covered container, yards are securely fenced, shrubs are thinned, and decks do not permit access to warm shelters. Managers should reduce practices that promote poor physical condition in urban-adapted wildlife, especially aggregations of foragers at piles of food waste that may promote reliance by animals in poor condition and associated disease transmission (Giraudeau *et al.* 2014). Following these simple steps may reduce encounters with people and carnivores in urban areas and other human-dominated landscapes around the world.

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4.8 Tables

Table 4.1 Habitat variables measured in the field at resource sites (i.e. clusters of GPS locations) visited by coyotes and at paired randomly-generated available sites in Edmonton, AB.

Covariate type	Covariate	Description
Habitat	Dominant vegetation	Vegetation class covering ≥50% of 20m area
	Canopy cover	Percent of densitometer covered
	Horizontal cover	Percent of checkerboard covered in each cardinal direction
Attractants	Anthropogenic food	Garbage, compost, bird seed (0/1)
	Fruit	Berries or crabapples on ground (0/1)
	Prey	Prey presence, tracks, or scat (0/1)
Human activity	Land use type	Residential, Industrial, Natural, Open
	Roads	Distance to nearest major road (m)
	Trails	Distance to nearest maintained trail (m)
	Buildings	Distance to nearest building (m)
	Under building	Cluster is under a house (0/1)

Table 4.2 Model outputs for coyote habitat selection at the site level in backyards or in natural and undesignated habitat. Models were built following the methods of Hosmer and Lemeshow (2000).

Habitat type	D^2	Nagelkirke r^2	Covariate	β ± SE	P
Residential backyards	0.28	0.84	Fence	-4.9 ± 2.2	0.03
			Anthropogenic food	3.4 ± 1.5	0.02
			Horizontal cover	1.09 ± 0.3	<0.01
			Mange x Anthropogenic food	3.33 ± 1.22	<0.01
Natural or open	0.82	0.29	Anthropogenic food	1.7 ± 0.7	0.01
			Prey sign	1.0 ± 0.5	0.04
			Slope	-0.5 ± 0.2	0.01
			Distance to trail	0.08 ± 0.04	0.04
			Distance to building	-0.04 ± 0.01	0.01

4.9 Figures

Figure 4.1 Aerial photograph showing a portion of a coyote home range in Edmonton, Alberta. We used GPS locations taken every three hours (red points) and defined clusters of GPS locations as sites used for feeding or resting (circles, "resource sites") to measure selection for residential areas (yellow circles) and anthropogenic resources within the home range.

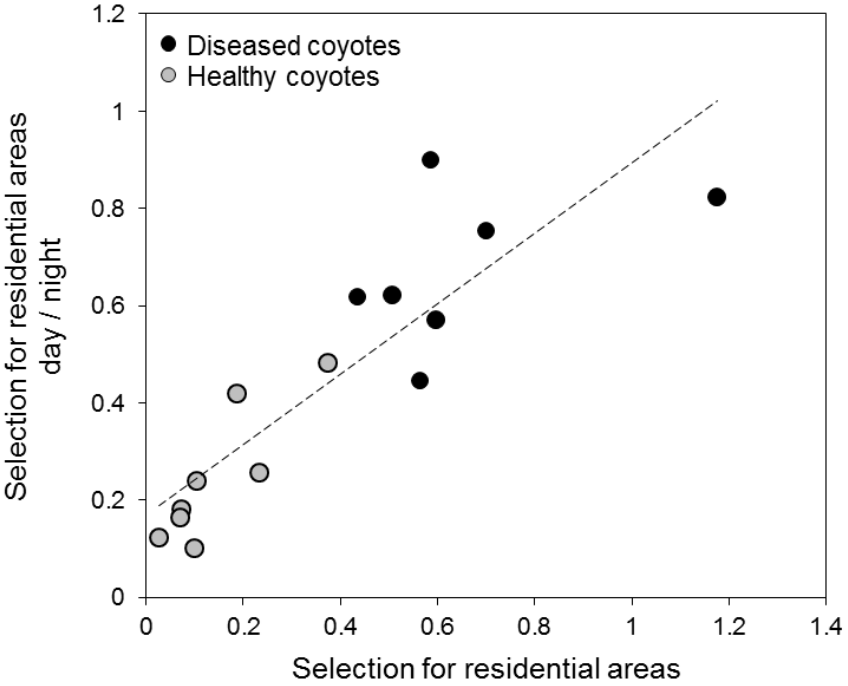

Figure 4.2 Differences among urban coyotes in their avoidance of residential areas in time and space. We measured the selection for residential areas using selection ratios and regressed these values against the ratio of using residential areas during the day relative to at night. Dashed line indicates the best-fitting linear regression line ($r^2 = 0.76$).

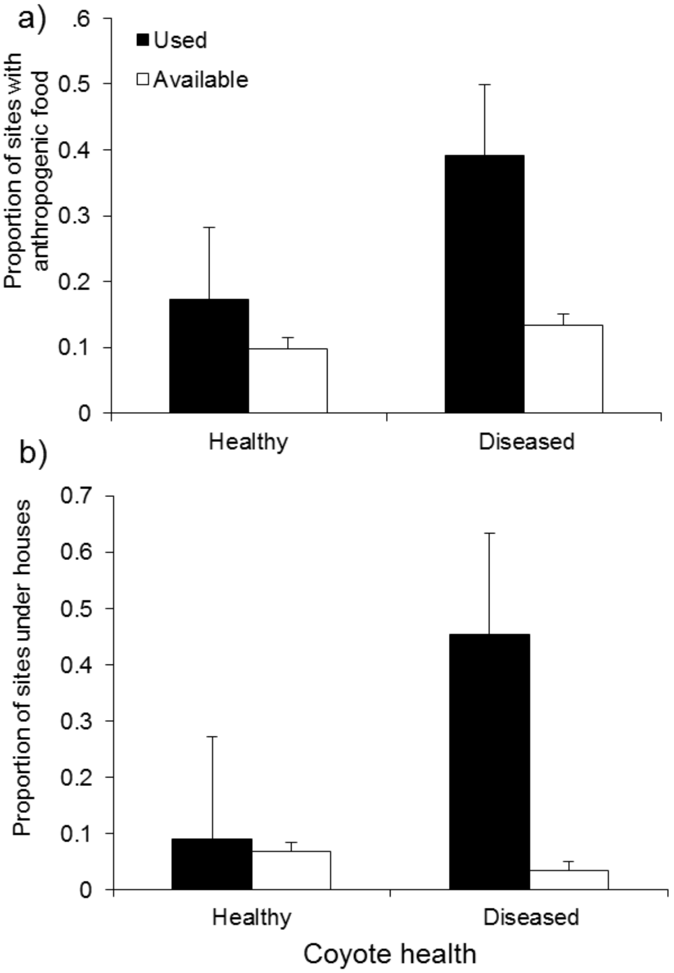

Figure 4.3. Selection for resource sites with (a) accessible anthropogenic food and (b) shelter for diseased and healthy coyotes. Proportion of used (black; n = 173) and randomly-generated available (white; n = 173) sites under houses and with anthropogenic food present averaged across healthy coyotes (n = 11) and coyotes with signs of sarcoptic mange (diseased; n = 8). Anthropogenic food included accessible garbage, compost piles, and bird seed. Error bars show standard deviation.

Chapter 5

5 You are what you eat: human food waste may promote disease spread in urban coyotes[*]

5.1 Abstract

Anthropogenic resources are often densely distributed and this can have diverse implications for wildlife. Animals that forage at feeding stations often have higher contact rates, potentially increasing disease spread, which may also occur where humans dump food waste in compost piles. Compost may also attract sick animals by providing reliable and easily accessible food and may be a suitable substrate for fungal mycotoxins that can cause numerous health problems. We tested these hypotheses in coyotes (*Canis latrans*), an opportunistic carnivore that inhabits many cities across North America. We used remote cameras to measure visitation rates by coyotes that were visibly diseased (i.e. with hair loss and lesions) and used scat analysis to measure the prevalence of endoparasites at compost piles and in urban natural areas. We also analyzed compost piles for contamination by fungal mycotoxins using mass spectrometry. We found that compost piles were visited 6.5 times more frequently, were 4.4 times more likely to be visited by visibly diseased coyotes, and 10 times more likely to have scats containing tapeworm eggs than urban natural areas. We detected mycotoxins in 86% of compost piles and several at concentrations above legal limits for animal feed. We suggest that self-reinforcing relationships between poor health and the consumption of human food waste may promote disease transmission and encounters with people in coyotes and other urban-adapted wildlife.

5.2 Introduction

One of the challenges of urban ecology is that anthropogenic resources tend to be highly concentrated in cities (Oro et al. 2013), with diverse implications for wildlife. Animals living in areas with less dispersed resources

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tend to have smaller home ranges but very dense resources patches may not be economically defensible (i.e. resource dispersion hypothesis; Macdonald 1983). Both of these factors may explain why rates of contact between individuals can be higher at landfills (e.g. raccoons *Procyon lotor*; Totton et al. 2002), bird feeders (Daszak 2000; Hosseini, Dhondt & Dobson 2004), and at feeding stations (e.g. raccoons; Gompper & Wright 2005 and white-tailed deer *Odocoileus virginianus*; Thompson, Samuel & Deelen 2008). These changes in the distribution of animals with high concentrations of anthropogenic food may partially explain why human-dominated landscapes can have higher rates of disease emergence and spread (Daszak 2000; Gottdenker et al. 2014).

Piles of anthropogenic food could also promote the transmission of disease if it is sought out by sick animals. The infirmity hypothesis (*sensu* Yeakel et al. 2009) suggests that predators in poor condition may be more reliant on easier prey based on the observations that man-eating lions often have dental injuries and deformities. Similarly, feeding on anthropogenic food may lower the costs associated with finding and killing prey for generalists in poor physical condition because it is highly predictable in time and space (Oro et al. 2013). For wildlife, some of the most accessible and reliable forms of anthropogenic food may be piles of food waste such as landfills and compost piles that are typically comprised by discarded vegetation and grain products.

Grains are consumed by many species in the form of anthropogenic food (e.g. bread), bird seed, livestock feed, and pet food but they are an excellent substrate for fungal growth (Reddy et al. 2010). These fungi can in turn produce toxic compounds known as mycotoxins which have been linked to illness in humans (Bhat et al. 1989) and animals (Hussein & Brasel 2001). Although consuming small amounts of mycotoxins can induce minor health effects (e.g. vomiting), chronic exposure or consumption of very high amounts can lead to immune suppression and organ failure (Hussein & Brasel 2001). For this reason, governments require testing of animal feeds and prohibit concentrations above which chronic exposure is harmful (i.e. Tolerable Daily Intake; EFSA 2011). Despite previous emphasis on cereal crops and livestock feed, ruminants appear to be less susceptible to mycotoxin poisoning because the rumen bacteria can degrade mycotoxins (Hussein & Brasel 2001). In addition to livestock, wild birds can be exposed to mycotoxins by consuming contaminated supplemental seed (e.g. Oberheu & Dabbert 2001) and domestic dogs appear susceptible to health problems from consuming contaminated kitchen waste (Schell 2000). A recent report of a domestic dog becoming violently ill after eating from a neighbor's compost pile has even prompted changes to municipal composting practices (Golden 2015). However, the potential for wild mammals to incur health problems from consuming anthropogenic food and compost has not been previously addressed.

Relationships between animal health and consuming anthropogenic food may partially explain rising rates of encounters between humans and several wildlife species, including coyotes (*Canis latrans*; Ellison 2009). Coyotes now inhabit many cities across North America and human food can account for 30% of their diets (Gehrt & Riley 2010). Recent increases in reports of human-coyote encounters may stem from an increase in coyote abundance or from changes in coyote behaviour. Coyotes may be more likely to approach people and their infrastructure if they learn to associate piles of food waste as an easy food source, especially coyotes in poor physical condition who may have lower hunting success. Other studies have found that nuisance coyotes are proportionately more likely to be infested by ectoparasites (Gehrt, Anchor & White 2009; Murray et al. in press b) and that diseased coyotes are more likely to use residential areas and consume human food (Murray et al. in press a).

Because compost piles contain high densities of easily-accessible anthropogenic food and are substrates for fungal growth, we hypothesized that they could promote the spread of disease and poor health for wildlife. We predicted that at compost piles, coyotes would have higher rates of contact by visiting and co-occurring at piles more frequently and would have higher prevalence of ecto- and endoparasites relative to more natural areas. We also predicted that compost piles visited by coyotes would contain fungal mycotoxins at biologically relevant concentrations.

5.3 Methods

5.3.1 Camera trapping

We used remote cameras to measure if anthropogenic food waste in compost piles (hereafter ‘compost’) was associated with higher rates of contact between coyotes and higher prevalence of visible ectoparasite infestation. We deployed remote camera traps (HyperFire HC600, Reconyx Inc. Holmen, Wisconsin) in Edmonton, Alberta, Canada at nine compost piles ranging from industrial landfills to residential compost piles and in 16 urban natural areas that served as reference sites (Figure 5.1). We chose these camera trap sites based on reports of coyote sightings or coyote sign and to be as far apart as possible within the study area to decrease the probability of detecting the same coyotes at multiple sites. We baited both types of sites with commercial coyote food lure every two weeks to increase detections.

For analysis, we grouped consecutive photographs of coyotes and defined these as visits. Using these visits we recorded three measurements: the time elapsed between coyotes, the presence of coyotes with visible ectoparasite infestations, and consumption of compost. We recorded the time elapsed between visits as a measure of indirect contact and potential for parasite transmission (i.e. mites falling off infested coyotes and attaching to new hosts). If multiple coyotes visited simultaneously, we considered that visit as potential for direct contact and recorded the time between coyotes as one second (Figure 5.2a). To minimize bias from multiple detections of the same foraging coyote, visits had to be separated by at least one hour of coyote inactivity (Rovero & Marshall 2009). As a second and more direct measure of the potential for indirect transmission of ectoparasites between foraging coyotes, we also measured the time elapsed between visits by coyotes with apparent ectoparasite infestations followed by visits by apparently healthy coyotes.

During visits, visibly infested coyotes were noted if any of the photographed coyotes were exhibiting patterns of hair loss and lesions consistent with sarcoptic mange (*Sarcoptes scabiei*) and other ectoparasites (Figure 5.2b and c). These patterns included thinning of the tail, patches of visible skin on the legs and back, and skin thickening on the face. Since apparently infested and healthy coyotes could be distinguished from each other based on hair loss, the risk of detecting the same coyote was lower and for this analysis we included visits that were less than one hour apart. We also noted any visits during which any coyotes were biting or chewing compost as a measure for potential exposure to mycotoxins if present (Figure 5.2a). Photos were coded by two independent observers to reduce observer bias. We also accounted for a potential bias of lure on the relative visitation rates to compost and natural sites by recording the proportion of visits in which coyotes approached the lure for both site types. Lastly, we recorded the season during which the visit took place. Following the designation of coyote seasons used by others (Morey, Gese & Gehrt 2007), we defined three seasons (Breeding: January – April, Pup rearing: May – August, Dispersal: September – December) based on coyote life history and seasonal changes in prey and fruit availability.

We tested for the effects of site type (compost or urban natural) on the time elapsed between visits (measured in natural log transformed hours) and the probability of a visit being made by a coyote with hair loss (as a binary variable) using a linear mixed effects model (LME) and a generalized linear mixed effects model (GLMM), respectively, in R (Pinheiro et al. 2012). We included site name as a random effect to partition the effect of site on the similarity of observations.

5.3.2 Scat analysis

We tested whether compost piles were more also more likely to be visited by coyotes with endoparasites by collecting coyote scats at four of the compost piles and four of the urban natural sites monitored with remote cameras at which we detected fresh coyote scat (coyote scats collected and analyzed by Peter Whyte). Coyote scats were discriminated from those of domestic dogs and red foxes (*Vulpes vulpes*) based on diameter (18-25 mm; Arjo, Pletscher & Ream 2002) and the presence of coyote tracks, and only scats deemed fresh based on moisture were collected. Prior to analysis, coyote scats were frozen at -80 C for a minimum of 72 hours, and subsequently stored at -20 C (Veit et al. 1995). We took three two-gram subsamples from each scat to account for variability and identified parasite eggs to family using fecal flotation (Bowman 1999). We then tested whether scats collected at compost piles were more likely to contain cestodes (Taeniidae), roundworms (Toxocaridae), or any other type of parasite. We then coded these as binary variables in a GLMM with a log link in R with site name as a random effect (Pinheiro et al. 2012).

5.3.3 Mycotoxin analysis

To determine the prevalence of mycotoxins and their concentrations in compost piles we analyzed samples of compost for three mycotoxin species: ochratoxin A, T-2 toxin, and zearalenone (compsost samples collected and analyzed by Jesse Hill). We sampled piles where coyotes were known to forage from anecdotal reports and at all piles monitored with remote cameras. Our sample sites included industrial piles of food waste, piles of decomposing animal feed, and residential compost piles and were sampled between June and September 2012. To control for heterogeneity within each pile, we took three cores (4.8 cm diameter, 30 cm length) which were then combined. We then followed the methods of Rundberget et al. (2004) to extract mycotoxins from food waste and quantified mycotoxin concentrations using high-performance liquid chromatography (Agilent 1290 HPLC system) and mass spectrometry (ABSciex Trap 400 mass spectrometer). To control for extraction efficiency, we also analyzed a reference sample containing known mycotoxin concentrations (Trilogy Analytical Labs). Lastly, we calculated the tolerable daily intake amount (in μg) for each of the three mycotoxins by taking the mycotoxin concentration (µg/kg body weight) above which health problems would be expected if an animal was chronically exposed from the literature (EFSA, 2011) and multiplied this value by the average coyote body weight (11 kg; Gehrt & Riley 2010).

5.4 Results

We deployed 25 cameras traps between January 2012 and July 2013 for a total of 5,681 trap nights (number of days deployed for all cameras). We monitored nine compost piles for 2,202 trap nights and detected 1,911 coyote visits (212 ± 56 visits per site). We monitored 16 urban natural areas for 3,479 trap nights and detected 1,155 coyote visits (64 ± 32 visits per site). We also collected 68 coyote scats for parasite analysis at four compost sites and in four urban natural areas. We collected compost samples at nine compost piles monitored with cameras and at an additional 19 piles.

Coyotes detected at compost piles had higher rates of indirect contact and a higher prevalence of visible ectoparasite infestation than coyotes detected in urban natural areas (Figure 5.3). At compost piles, the time elapsed between coyote visits was 3.6 times shorter (Figure 5.3a) and the time elapsed between visits by visibly diseased coyotes and apparently healthy coyotes was 6.5 times shorter (Figure 5.3b) than in urban natural areas in the breeding and dispersal seasons (Table 1). Relative to urban natural areas, compost piles were also 4.4 times more likely to be visited by visibly diseased coyotes exhibiting hair loss (Figure 5.3c; Table 1). Coyotes approached the lure in 12% of visits in urban natural areas but in only 2% of visits at waste piles ($G = 7.93$, $p < 0.01$) and the frequency of these visits was balanced across apparently sick and healthy coyotes ($G = 0.06$, $p = 0.90$) suggesting that the differences we observed were less likely to be increased by the use of lure.

Coyotes at compost piles also had a higher prevalence of some types of endoparasites than in urban natural areas. Coyote scats collected at compost piles did not have significantly higher parasite prevalence overall (Food waste: 95 ± 9%; Urban natural: 87 ± 16% of scats), however they were more likely to contain Taeniidae (tapeworm) eggs (Mean prevalence ± SD: 30.0 ± 15.5% (compost); 3.2 ± 5.0% (urban natural) of scats; Table 1).

We also detected mycotoxins at many of the sampled compost piles. Of the 28 sampled piles, 86% (24/28) contained mycotoxins at detectable concentrations and 22% (6/28) of piles contained more than one species. Ochratoxin A and T-2 toxin were present in 14% (4/28) and 11% (3/28) of piles, respectively, and in all but one pile at concentrations over government limits for animal feed (5 μg/kg and 100 μg/kg respectively; EFSA 2011; Figure 5.4). We detected zearalenone in 79% of piles but none at concentrations exceeding government limits (100 μg/kg; EFSA 2011; Figure 5.4).

Ochratoxin A, zearalenone, and T-2 toxin have tolerable daily intake concentrations of 0.017, 0.25, and 0.06 μg/kg body weight, respectively, for all types of animal feed including pet food (EFSA 2011). At the piles containing the highest concentrations of each mycotoxin, a coyote would exceed this tolerable daily intake amount for toxicity by eating 1.83 g of compost containing T-2 toxin (i.e. the approximate size of one peanut), 4.92 g of compost containing ochratoxin A (i.e. the approximate size of one cherry), and 20.2 g of compost containing zearalenone (i.e. the approximate size of one strawberry). On average, coyotes foraged on compost every eight days in the dispersal (0.12 ± 0.37 events per trap night) and breeding (0.13 ± 0.32) seasons and every 25 days in the pup rearing season (0.04 ± 0.07).

5.5 Discussion

Because anthropogenic food waste in compost piles is easily accessible and a substrate for fungal growth, we tested if it could promote the spread and prevalence of disease in wildlife. Relative to urban natural areas, sites with compost piles were visited more frequently by coyotes, were more likely to be visited by coyotes with signs of ectoparasite infestation, and coyote scats collected at compost piles were more likely to contain tapeworm eggs. Most compost piles contained at least one species of mycotoxin and several piles contained concentrations above regulated limits for animal feed.

Our observation that coyotes with signs of disease were more likely to be detected at compost piles supports the hypothesis that impaired animals are more likely to seek out easy and reliable sources of food. Animals with low energy reserves or compromised thermoregulation may be especially reliant on reliable food sources in the fall and winter when temperatures fall and young prey and fruit are often less abundant, supporting the seasonal patterns we observed. Combined with this higher prevalence of ectoparasites, the shorter separation between coyote visits at compost piles may also increase the likelihood of parasite spread between individuals. Mange mites can survive off the host and remain infective to new animals for several hours even in low temperatures but this risk decreases with time (Arlian, Vyszenski-Moher & Pole 1989). Food waste in compost piles appeared to attract sick coyotes and bring them in closer contact with other coyotes. However, our results suggest that consuming compost may also play an important role in disease dynamics.

The coyotes we detected at compost piles may have also had a higher prevalence of disease because they were exposed to mycotoxins. Because the health effects of consuming mycotoxins have not yet been studied in carnivores, we can only speculate from studies involving domestic dogs. At the concentrations we detected, ochratoxin A can damage kidney function and suppress immune system function (Leung et al. 2006) and we detected concentrations of T-2 toxin high enough to cause vomiting (Bhat et al. 1989). Although we detected zearalenone at relatively low concentrations, chronic consumption has been linked to decreased immune function, food intake, and body mass (Leung et al. 2007). Because of these health effects, consuming contaminated food may render carnivores and other wildlife less able to forage for more natural but less accessible food, such as animal prey. In turn, this may increase their reliance on easily accessible, but potentially harmful, food waste. This ‘downward spiral’ could be caused by either factor and could be analogous to other relationships between poor health and low-quality diet seen in other animals (Taylor et al. 2013) and even humans (Sapolsky 2004).

There are two important implications of our results for the management of urban wildlife. Firstly, if consuming mycotoxins in compost increases an animal’s reliance on easily-accessible resources, it could also increase rates of encounters between people and wildlife seeking anthropogenic food. Similar to reports of injured (Goodrich et al. 2011) or nutritionally stressed (Towns et al. 2009) carnivores approaching people and houses for food, coyotes with mange have been reported to approach houses during the day to consume compost (Todd, Gunson & Samuel 1981; this study). Not only could this bring wildlife and humans in closer proximity, it may also encourage sick wildlife to associate humans as a source of food (i.e. food conditioning; Herrero 1985).

Secondly, by promoting the spread of disease and exposure to immunosuppressive mycotoxins, compost piles may also promote the transmission of wildlife disease across species, including zoonoses. For example, sarcoptic mange can be transmitted from coyotes to domestic dogs, as can the canid tapeworm *Taenia serialis*. Moreover, the coyote tapeworm *Echinococcus multilocularis* can be transmitted to humans and cause cysts in the brain and organs (Echinococcosis; Liccioli et al. 2014). Piles of contaminated food waste may also increase the potential for spill-over of pathogens and parasites from reservoir species to those more sensitive or less abundant (Daszak 2000). Coyotes with mange can have much larger home ranges than healthy coyotes (Murray et al. in press a) and could range widely enough to encounter and transmit diseases or parasites to wolves (*Canis lupus*) in rural areas. Similarly, spotted hyenas (*Crocuta crocuta*) in Ethiopia rely heavily on human food waste but only in some seasons (Yirga et al. 2012) and may encounter lions (*Panthera leo*) in others.

Despite their ubiquity, our results suggest that piles of decomposing human food, either as compost, animal feed, or landfills, can promote the spread of wildlife disease by attracting sick animals and harbouring fungal mycotoxins. Restricting access to these types of food, either through municipal composting programs, waste containment, or restrictive fencing may reduce these negative effects. Doing so may also reduce the spread of zoonotics and wildlife pathogens and prevent negative encounters between humans and many urban-adapted wildlife species.

5.6 Acknowledgements

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5.8 Tables

Table 5.1 Mixed effects model outputs for time elapsed between coyote visits (LME), the presence of at least one coyote with hair loss (GLMM with log link), and the presence of taeniid eggs in coyote scat (GLMM with log link) at compost piles and reference sites in urban natural areas.

Metric	Model term	Parameter estimate ± SE	df	t	p
Time between coyotes	Intercept	3.93 ± 0.56	3335	7.04	< 0.01
	Site type (Natural)	2.09 ± 0.70	25	3.01	< 0.01
	Season (Dispersal)	-0.20 ± 0.15	3335	-1.40	0.16
	Season (Pup rearing)	1.94 ± 0.29	3335	6.63	< 0.01
	Site type * Season (Natural * Dispersal)	0.03 ± 0.26	25	0.09	0.93
	Site type * Season (Natural * Pup rearing)	**-1.75 ± 0.46**	**25**	**-3.76**	**< 0.01**

Time between apparently parasitized and healthy coyotes	Intercept	0.73 ± 0.21	383	3.48	< 0.01
	Site type (Natural)	0.51 ± 0.30	23	1.71	0.10
	Season (Dispersal)	-0.44 ± 0.09	383	-5.00	<0.01
	Season (Pup rearing)	0.05 ± 0.20	383	0.23	0.82
	Site type * Season (Natural * Dispersal)	**0.72 ± 0.37**	**383**	**1.97**	**0.04**
	Site type * Season (Natural * Pup rearing)	-0.80 ± 0.49	383	-1.62	0.11
Coyote with hair loss present	Intercept	-1.49 ± 0.35	2903	-4.27	< 0.01
	Site type (Natural)	-0.96 ± 0.46	25	-2.09	0.036
	Season (Dispersal)	-0.39 ± 0.13	2903	-2.90	< 0.01
	Season (Pup rearing)	0.41 ± 0.22	2903	1.85	0.064

	Site type * Season (Natural * Dispersal)	**-1.24 ± 0.47**	**25**	**-2.63**	**< 0.01**
	Site type * Season (Natural * Pup rearing)	-0.60 ± 0.50	25	-1.20	0.23
Scat contains tapeworm (taeniid) eggs	Intercept	-3.43 ± 1.04	8	-3.29	< 0.01
	Site type (Compost)	**2.59 ± 1.12**	**8**	**2.31**	**0.021**

5.9 Figures

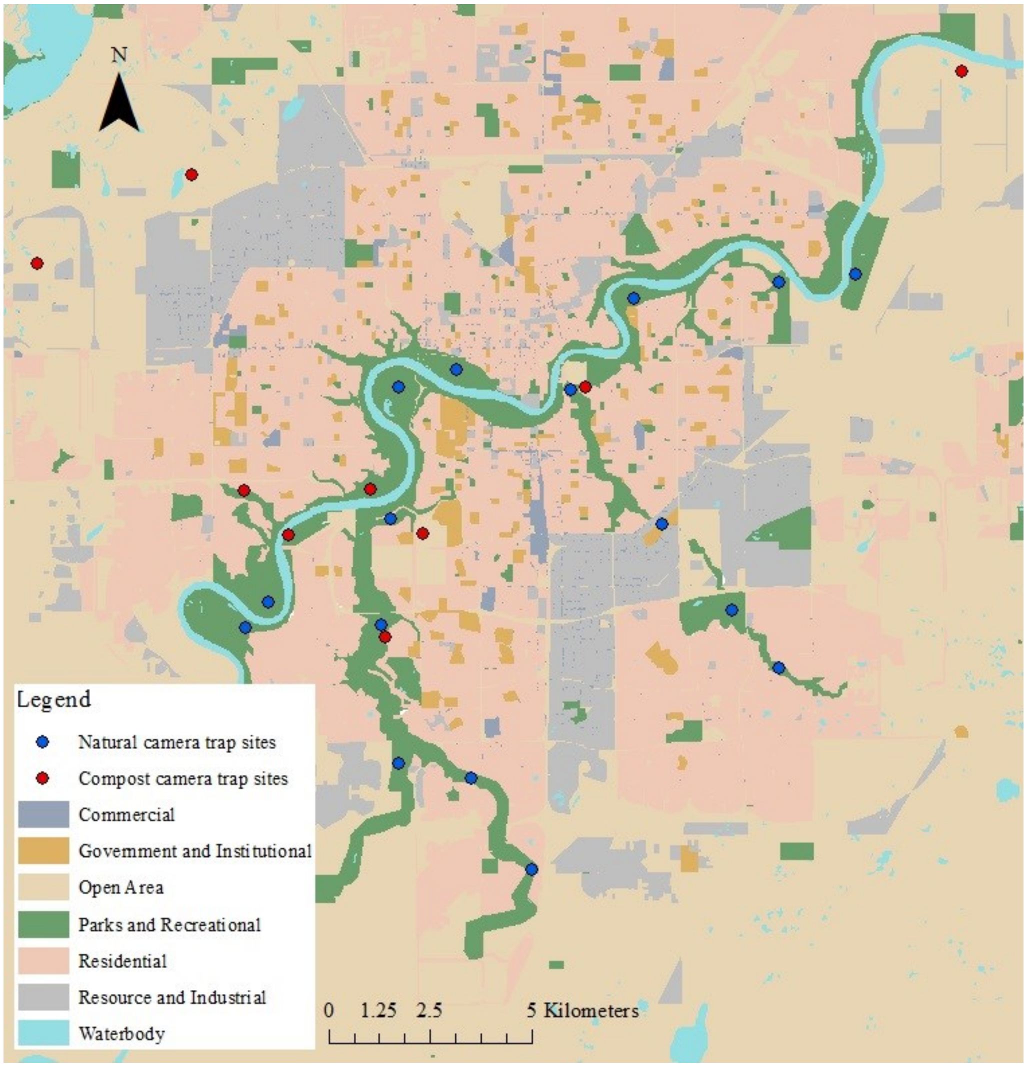

Figure 5.1 Map of the City of Edmonton showing the locations of remote cameras deployed at compost piles (red) and at reference sites in urban natural areas (blue). Land cover data provided by the City of Edmonton.

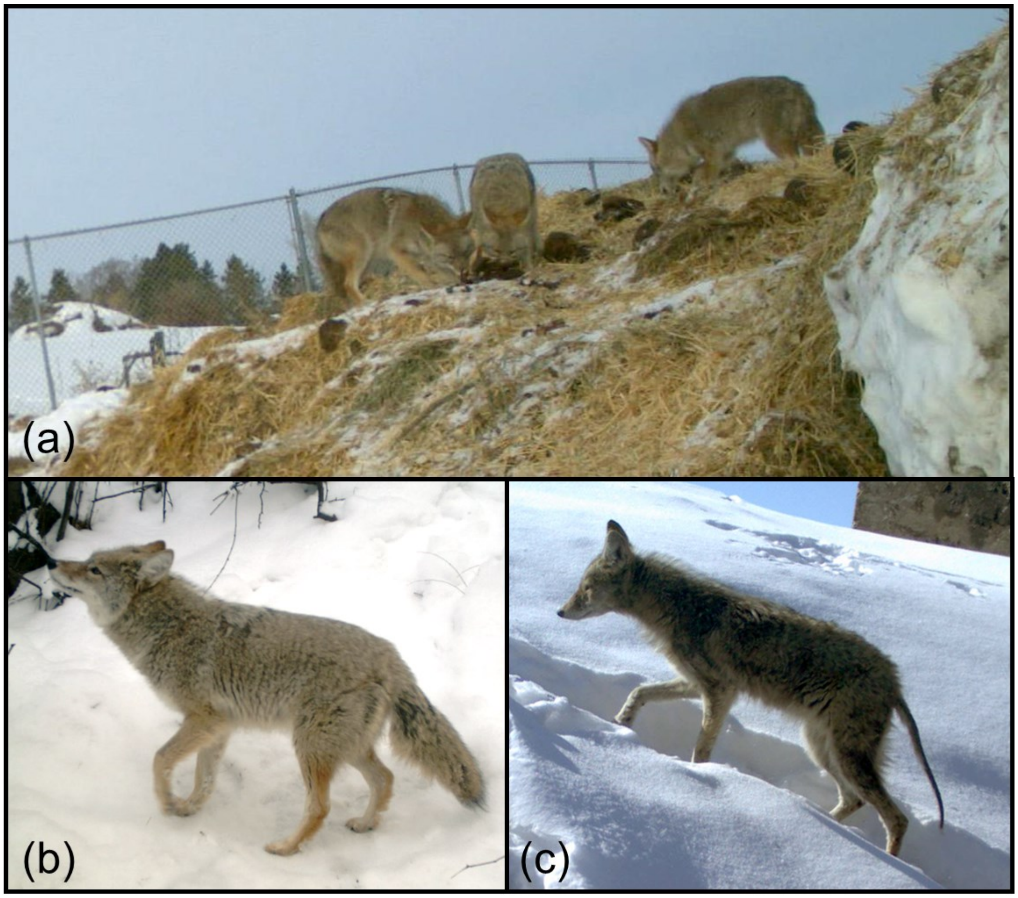

Figure 5.2 We used remote cameras at piles of compost and urban natural areas in Edmonton, Alberta, Canada to (a) monitor coyote contact and foraging rates and the relative frequency of (b) apparently healthy coyotes and (c) coyotes with hair loss consistent with ectoparasites.

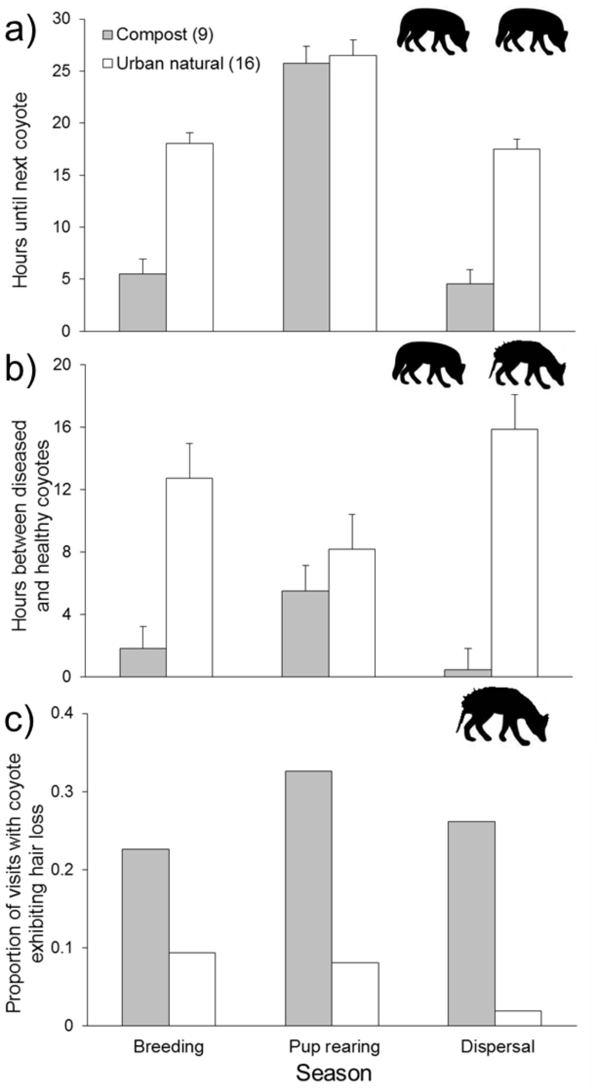

Figure 5.3 We used remote cameras to monitor coyotes at piles of compost (gray; n=9) and reference sites in urban natural areas (white; n=16). (a) Time elapsed between coyote visits to camera as a measure of contact rates (hours). (b) Time elapsed between parasitized and healthy coyotes as a measure of potential indirect parasite transmission. (c) Frequency of visits with at least one coyote showing visible hair loss consistent with ectoparasite infestation. Bars show standard deviation.

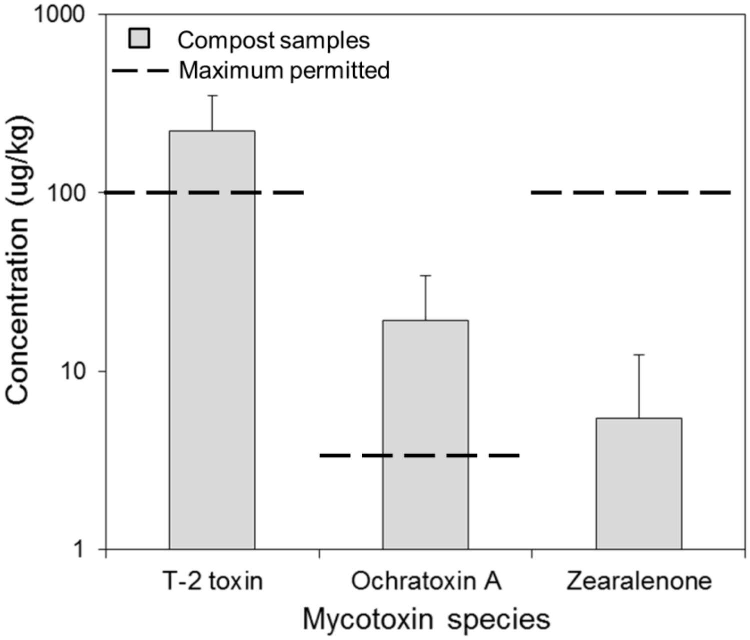

Figure 5.4. Concentrations of three species of mycotoxin detected in 29 piles of compost. Columns show mean concentration, measured in µg per kg on a logarithmic scale for display purposes, and dashed lines show the maximum concentration permitted in animal feed.

Chapter 6

6 Individual flexibility in nocturnal behaviour reduces probability of road mortality for an urban carnivore[*]

6.1 Summary

1. Many species living in developed areas adjust the timing of their activity and habitat selection to avoid humans, which may reduce their exposure to several kinds of risk. One such risk is collision with vehicles which, for many species, peaks in spring and fall annually and at dusk and dawn.

2. Understanding the adaptations to vehicles exhibited by species that thrive in urban areas could provide information relevant to the conservation of the many species that are threatened by road-caused mortality. We explored this potential by examining seasonal patterns in 80 road-killed coyotes and differences in activity and road crossings made by 19 coyotes (*Canis latrans*) we fitted with GPS collars with 3-hour fix rates, seven of which were killed on roads.

3. Collection of road-killed coyotes peaked in spring and fall, which corresponded to the most rapid changes in day length in our northern study area and when crepuscular activity overlapped with rush hour. Among collared coyotes, those that were killed on roads (n=7) were most active (measured by step lengths) in the early evening and crossed roads most frequently at dusk. By contrast, surviving animals (n=12) were most active and crossed roads most often near midnight year round. Surprisingly, coyotes killed on roads avoided crossing roads relative to road availability in their home ranges, whereas surviving coyotes crossed roads in proportion to their availability.

4. Synthesis and Applications: Our results suggest that risk of vehicle collision is lower for coyotes that restrict the times at which they cross roads but some coyotes do not or cannot. Surviving coyotes crossed roads up to

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three times more often than coyotes that were killed on roads, but they crossed mainly late at night regardless of season and day length. Such capacity to adapt to the timing of human activity relative to exogenous cues like dawn and dusk may contribute to differences both among and within wildlife species in rates of co-existence with humans. Management strategies that foster fine-scale segregation of humans and wildlife in time, for instance by deploying on-demand deterrents at dusk in spring and fall, may help to mitigate vehicle-caused mortality for many species.

6.2 Introduction

Urbanization is currently the fastest growing type of land-use around the world with concomitant increases in the density of human infrastructure that can contribute to loss of biodiversity (Shochat et al. 2010, Murphy & Romanuk 2014). One problematic type of infrastructure is road networks (Hansen et al. 2005) which can have many negative effects on wildlife, including habitat loss, barriers to movement, and road mortality (reviewed by Trombulak & Frissell 2000; Benítez-López, Alkemade & Verweij 2010). For some species, road mortality can be significant enough to cause population decline (e.g. Hels & Buchwald 2001). For humans, vehicle collisions with species such as large ungulates cause ~200 human fatalities (Langley, Higgins & Herrin 2006) and ~$8.4 billion USD in damage and injuries (Bissonette, Kassar & Cook 2008; Huijser et al. 2008) annually in the United States. Road mitigation, such as fencing and crossing structures (reviewed by Glista, DeVault & DeWoody 2009) can reduce rates of wildlife mortality but could be advanced with a better understanding of why some species thrive in human-dominated landscapes with high road densities.

Species that tolerate high densities of people are known as urban adapters and exploiters (McKinney 2002) and many are increasing in cities around the world. Urban adapters include several species of carnivores (reviewed in Bateman & Fleming 2012) that are typically generalists with high behavioural flexibility (McKinney 2002; Lowry, Lill & Wong 2013). For these species, persistence in human-dominated landscapes appears to require a complex mix of behaviours that makes use of available habitat while avoiding negative encounters with people and vehicles, often by exhibiting more nocturnal behaviour than their rural counterparts. This suite of behaviours appears to characterize urban foxes (*Vulpes vulpes*; Baker et al. 2007), urban bobcats (*Felix rufus*; Tigas, Vuren & Sauvajot 2002) and wolves near human settlements in Italy (Ciucci et al. 1997). Wary wildlife may also reduce their risk of collision by preferentially avoiding roads with higher traffic volumes, which has been observed in moose (*Alces alces*; *sensu* Seiler 2005), wolves (*Canis lupus*; Whittington, St. Clair & Mercer 2005), elk (*Cervus elaphus*; Preisler, Ager & Wisdom 2006), and grizzly bears (*Ursus arctos*; Northrup et al. 2012). Avoiding traffic in space or time may allow wildlife to avoid humans at fine scales while continuing to persist in fragmented areas. Although avoidance of human activity in time or space appears to be variable among populations (above) and individuals (e.g. Knopff et al. 2014), little is known about the effect of that flexibility on the risk of road mortality.

The ability to adjust behaviour to avoid overlap with people might be especially important at higher latitudes where there are pronounced seasonal changes in human activity in relation to day length and light levels. Several studies have found that wildlife-vehicle collisions peak in fall and spring and at dusk and dawn (e.g. Lagos, Picos & Valero 2012; reviewed by Steiner, Leisch & Hackländer 2014). These patterns in road mortality have been hypothesized to coincide with periods of high movement rates, including dispersal (e.g. foxes (Baker et al. 2007) and Eurasian badgers (Grilo, Bissonette & Santos-Reis 2009)), mating (e.g. Roe deer *Capreolus capreolus*; Lagos, Picos & Valero 2012 and Egyptian mongoose *Herpestes ichneumon*; Grilo, Bissonette & Santos-Reis 2009) and migration (e.g. moose *Alces alces*; Lavsund & Sandegren 1992). These life-history explanations do not appear to explain all seasonal peaks in vehicle collisions, which sometimes do not correspond to periods of high movement (Neumann et al. 2012) and vary by region (Steiner, Leisch & Hackländer 2014). A more general explanation for this variation might be achieved by comparing the movement and road-crossing behaviour of individuals that were or were not killed in vehicle collisions within a single species and region.

We studied seasonal patterns in vehicle mortality and individual variation in responses to roads in urban coyotes (*Canis latrans*), an opportunistic mid-sized canid with increasing prevalence in cities across North America (White & Gehrt 2009; Lukasik & Alexander 2011). Urban coyotes typically have higher survival rates (Gehrt & Riley 2010) and usually exhibit more nocturnal activity cycles than rural coyotes, which are typically crepuscular (Grinder & Krausman 2001; Tigas, Vuren & Sauvajot 2002; Riley et al. 2003). Among urban coyotes, there appears to be considerable variation among individuals in the size of home ranges, the use of developed areas (Riley et al. 2003; Gese et al. 2012), and the probability of being killed from a collision with a vehicle (Gehrt & Riley 2010). Although more than two thirds of the mortalities of urban coyotes may be caused by vehicle collisions (Gehrt & Riley 2010), coyotes often cross major roads and can occupy areas that are highly fragmented by human infrastructure (Tigas, Vuren, & Sauvajot 2002; Riley et al. 2003; Gese et al. 2012).

We hypothesized that urban coyotes adjust their activity to reduce overlap with people as a means of reducing risk, but that the degree of this adjustment would vary among individuals. We predicted that, in general, coyotes that exhibit more overlap with humans in space or time would experience higher rates of conflict. Specifically, we predicted that coyotes that were more active and more likely to cross roads when or where traffic volumes were highest would be more likely to be killed by vehicles. We also predicted that this variation among individuals would be most pronounced in the seasons – spring and fall – when day length changes most quickly.

6.3 Methods

6.3.1 Study area and road characteristics

We studied coyote movement in Edmonton, Alberta, Canada, (population 812,201 in 2011 census) one of the northernmost major cities in North America (53.5472° N, 113.5006° W) where day length varies from 7.5 hours in December to 17 hours in June (NRC 2014). Reports of coyote sightings by the public in Edmonton have increased steadily over the past 20 years (Ramsey Cox, personal communication) and now occur almost daily. Collisions between coyotes and vehicles are reported almost weekly throughout the year (City of Edmonton, pers. comm.). The city contains several large and contiguous riparian natural areas that may facilitate animal movement, but these are bisected in several locations by highways that contain up to seven lanes of traffic.

To examine the road-crossing behaviour of coyotes (below), we designated major roads as those with at least four lanes of traffic because these roads likely pose the greatest barrier to movement (Riley et al. 2006) and because they were typically at least five kilometres long, increasing the likelihood that a coyote crossed rather than circumvented them when successive coyote GPS locations occurred on either side. Traffic volume on these roads peaks at 0800 h and 1700 h and does not vary significantly with season (AAWDT 2013). We designated morning and evening rush hours as being 0500 h – 0800 h and 1700 h to 2000 h because these time periods contain 41% of daily traffic flow (AAWDT 2013) and because they maximize the seasonal changes in day length.

6.3.2 Road mortality

To determine the annual distribution of coyote-vehicle collisions in our study area, we requested mortality records from the City of Edmonton collected in 2013 – 2014. We received the total number of coyote mortalities for each month, which be binned into four seasons based on changes in day length. We defined winter as November – January (Day length = 8.1 ± 0.5 hours/day, Change in day length = 2.3 ± 0.7 SD minutes/day), spring as February – April (11.9 ± 2.1 SD hours/day, 4.1 ± 0.1 SD minutes/day), summer as May – July (16.4 ± 0.5 SD hours/day, 2.2 ± 0.7 SD minutes/day), and fall as August – October (12.7 ± 2.1 SD hours/day, 4.0 ± 0.1 SD minutes/day). We then tested whether collisions were more frequent during the spring and fall relative to summer and winter using a G test of independence.

6.3.3 Coyote capture and collaring

Coyotes were captured from 2009 – 2012 in areas within city limits where coyote presence was previously reported, and where dogs were prohibited, using four-coil padded leg-hold traps (No. 3 Victor Soft Catch Coilspring; Animal Trap Co., Lilitz, Pennsylvania) and physically restrained using catch poles. Once captured, coyotes were sexed, aged as either subadults (< 1 year old) or adults (≥ 1 year old) using degree of tooth wear (Bowen 1982), weighed, ear tagged, assessed for body condition, and fitted with a GPS collar. We programmed the GPS collars to collect fixes every three hours that, depending on the collar, were stored until the collar was retrieved (Lotek 3300S, two coyotes), were remotely downloaded (Lotek 4400S, three coyotes), or were sent to us daily over the cell phone network (Lotek Wildcell, 14 coyotes). We calculated movement metrics for each of our collared animals (below) and related these metrics to whether or not the animal was killed by a vehicle collision during the study period.

6.3.4 Spatial and temporal analyses

We tested whether coyotes killed in vehicle collisions were more likely to overlap with human activity in their activity and road crossings by creating steps between consecutive three-hour GPS locations. Using these steps, we calculated four movement metrics for each three-hour period of the day: step length (i.e., the distance between successive GPS locations) and the number, locations, and times of road crossings. We inferred the locations and times of road crossings by intersecting each three-hour step with major roads using a Geographic Information System (ArcMap v10.1, Redlands, CA).

We first tested for seasonal differences in the timing of activity and road crossings between coyotes that were and were not killed on roads. We compared coyote activity (i.e. step length) during rush hour across seasons using a two-factor ANOVA with a weighted means analysis for unequal sample sizes and log-transformed step length to normalize its distribution. Because we did not have 12 months of GPS data per coyote, we calculated the average log-transformed step length for at least five coyotes in each survival category per season. We compared the step lengths and frequency of road crossings at different times of day and how these patterns differed across seasons using circular statistics (Oriana 4; Kovach, 2013). We tested for skewness in the distributions of both step lengths and crossing frequency over the day using Moore's Modified Rayleigh test (Zar, 1999) for uniform circular distributions and tested for differences in the mean time of step lengths and crossings using a Waston's U^2 test. Finally, we determined whether the diel timing of road crossings was correlated with step lengths and compared this relationship between seasons. To increase sample sizes within survival status categories, we condensed the four calendar seasons into two seasons based on day length and defined summer as March 22 – September 21 when day length was longer than average (day length = 15.2 ± 1.7 hours SD) and winter as September 22 – March 21 when day length was shorter than average (day length = 9.4 ± 1.7 hours SD).

We also tested whether surviving coyotes exhibited relatively more avoidance of roads or traffic in space or time relative to coyotes that were killed in collisions. To account for differences in road density in coyote home ranges, we compared each coyote movement step with available steps that started at coyote locations using logistic regression (i.e. Step Selection Function (SSF); Fortin et al., 2005; Roever, Boyce, & Stenhouse, 2010). For each used step, we generated 10 available steps randomly using the same distribution of step lengths and turning angles as the used steps made by collared coyotes. At each used or available step, we measured whether the step did or did not cross a major road (0/1). If a step did cross a road, we measured the relative traffic volume at the time of crossing (% of daily traffic flow) and the traffic volume of the road section that was crossed (average number of cars per hour). Traffic information for each hour of day and on individual road sections was provided by the City of Edmonton (AAWDT 2013). Using these data from used and available steps, we calculated selection ratios (used in category_i / available in category_i ; Manly et al. 2002).

We evaluated the importance of avoiding traffic in time vs. space by constructing three candidate models and ranking them using model AICc scores (Table 6.1). Specifically, we used the characteristics of used steps to distinguish between killed and surviving coyotes after adding a variable that described avoidance of road crossings (a) in general, (b) only when traffic volume was high and (c) only where traffic volume was high. We compared used and available steps using a Generalized Linear Mixed Model that included coyote ID as a random effect to account for non-independence of steps made by the same individual (Pinheiro et al. 2012).

6.4 Results

We received reports of 80 coyotes collected as vehicle-caused mortalities on roads and we captured and collared 19 coyotes. The collared coyotes were monitored for an average of 5 months (range: 1 – 10 months) and we collected on average 639 3-hour GPS locations per coyote (range: 161 – 1867 fixes). Seven of the 19 collared coyotes were killed in vehicle collisions during the study period; the other 12 were presumed not to have died from vehicle collisions (hereafter, “survived”).

Of the 80 reports of coyotes killed on roads, 73% were collected in spring or fall, significantly more than the other seasons ($G = 14.0$, d.f. = 1, $P < 0.01$; Figure 6.1). These two seasons also exhibited larger average changes in day length, ($t = 4.39$, d.f. = 1, $P < 0.01$). Although there were no differences among seasons in the average step length during rush hour for all coyotes (2 factor ANOVA F(1,1) = 0.86, P = 0.19; Figure 6.1), road-killed coyotes were significantly more active during rush hour in the spring and fall (mean = 231.21 ± 64.86 m (spring and fall), 115.02 ± 56.28 m/h (summer and winter); 2 factor ANOVA F(1,1) = 4.74, P = 0.036; Figure 6.1). There were no seasonal differences in the rush hour movement rates of surviving coyotes (mean = 123.81 ± 38.34 SD m/h (spring and fall), 103.89 ± 44.07 m/h (summer and winter)). Five of the seven road-killed collared coyotes were also collected in spring and fall.

Coyotes killed on roads also exhibited different daily patterns in activity across seasons than surviving coyotes. In summer, surviving coyotes had three times longer step lengths at night with peaks near midnight (Moore's R* = 2.35, P < 0.001), but road-killed coyotes exhibited no such peaks in activity (Moore's R* = 0.55, P = 0.62; Figure 6.2). In the winter, coyotes of both survival categories were slightly, but not significantly, more active at night (Survived: R* = 0.935, P = 0.39; Road killed: R* = 0.29, P = 0.75; Figure 6.2).

Corresponding to their more even diel patterns of activity, road-killed coyotes were more likely to cross roads throughout the day (Moore's R* ≤ 1.65, p ≥ 0.57; Mean crossing time: 19:34 ± 4:32 95% CI (Summer); 17:22 ± 3:49 95% CI (Winter)), whereas the surviving coyotes crossed roads mainly late at night (Moore's R* ≥ 9.58, P < 0.001; Mean crossing time: 23:17 ± 1:36 95% CI (Summer); 23:14 ± 1:03 95% CI (Winter); Figure 6.3). On average in both summer and winter, road-killed coyotes crossed roads most frequently at dusk (Summer: average time of sunset = 20:04, peak crossings = 20:00; winter: average time of sunset = 17:17, peak crossings = 17:00). Because of this change in the timing of road crossings, road-killed coyotes crossed roads most often when traffic volume was 57% higher in winter than in summer and 343% higher in winter than when surviving coyotes crossed roads (Watson's U^2 = 23.56, P = 0.034).

The likelihood of a coyote being killed in a collision was most associated with crossing roads during the day when traffic was higher compared to crossing roads more frequently overall or crossing roads with higher traffic loads (Table 6.1). Surviving coyotes avoided crossing roads at the times when traffic volume was higher and neither group significantly selected or avoided roads with higher traffic loads (Figure 6.4). Surprisingly, coyotes killed in collisions exhibited more avoidance of crossing roads than surviving coyotes, which crossed roads in proportion to their availability and three times more often than killed coyotes (Figure 6.4).

We did not find any relationship between the survival status of our 19 collared coyotes and any other metric by which we could categorize them. Specifically, road-killed coyotes were not of different age and sex classes (Road-killed: two adult males, three adult females, two subadult males; Not Killed: two adult males, seven adult females, two subadult males, and one subadult female; G = 1.70, d.f. = 3, P = 0.64). Similarly, road-killed coyotes were not more likely to have ectoparasites that were visible at capture (Road killed: three diseased, four apparently healthy; Not Killed: four diseased, eight apparently healthy; G = 0.171, d.f. = 1, P = 0.68). Finally, road-killed coyotes were no more or less likely to exhibit large home ranges that overlapped with other animals and which might be indicative of transient social status (Road killed: four residents, three transients; Not Killed: seven residents, five transients; G = 0.003, d.f. = 1, P = 0.96; see Murray et al., in press a for methods).

6.5 Discussion

In this study, we tested the hypothesis that coyotes adjust their activity to reduce overlap with people in time and / or space as a means of reducing risk of conflict and that this behaviour would vary among individuals. Our results support our prediction that conflict, as measured by road-kill, is higher for coyotes that overlap with humans, as measured by traffic volume, in time but not in space. The importance of avoiding overlap in time was also supported by our analysis of a database of 80 road-caused mortalities, in which we found that coyotes were more likely to be killed on roads in spring and fall. We found that road-killed coyotes were most active and crossed roads most often at dusk, whereas surviving coyotes were active and crossed roads much later at night, especially in summer. We also found that road mortality was more associated with avoidance of times with higher traffic than avoiding roads or locations with higher traffic volume.

The shift by surviving coyotes to more nocturnal activity cycles is one of several behavioural changes exhibited by wildlife in other human-dominated landscapes. Areas with high human densities are associated with more nocturnal activity by several carnivores, including wolves (Boitani 1982; Ciucci et al. 1997), grizzly bears (Kaczensky et al. 2006; Northrup et al. 2012), leopards (*Panthera pardus*; Odden et al. 2014) and coyotes (Grinder & Krausman 2001; Tigas, Vuren & Sauvajot 2002; Riley et al. 2003). Such shifts to nocturnal activity have been interpreted as avoidance by animals of activity at times with high traffic volumes (reviewed by Ditchkoff, Saalfeld & Gibson 2006 and Lowry, Lill & Wong 2012), but existing studies of this relationship report population-level changes. For example, urban foxes in the UK preferentially cross roads at night when traffic is lower (*Vulpes vulpes*; Baker et al. 2007) and urban barn owls (*Tyto alba*) are more likely to be killed on roads when traffic is high (Grilo et al., 2012).

Inferring a causal relationship between nocturnal activity and vehicle mortality requires knowledge of variation in and consequences of this shift within a population. Our data provide both components; peaks in both activity and road crossings late at night characterized surviving coyotes, whereas peaks for activity and crossings around dusk, and corresponding more often with rush hour, characterized road-killed coyotes. It is especially interesting that the surviving coyotes did not avoid crossing roads overall and did so up to three times more frequently than coyotes killed in collisions. These differences among individuals suggest that temporal avoidance of high traffic is important, but also complex; most coyotes were killed on roads in spring and fall and so vulnerability might be higher in these periods. Coyote vulnerability to collision could be higher in spring and fall because there is a rapid change in the relationship between traffic volume and the exogenous cue provided by dusk.

The seasonal changes in the timing of activity and road crossings suggest that some coyotes, like many other species (e.g. Georgii 1981; *sensu* Hill et al. 2004), vary their activity based on day length. Darkness may be a fairly reliable cue for human disturbance more generally, for example to minimize the risk of encountering people in natural areas (Arnberger 2006) or being seen in backyards. However, natural cues such as daylight can become mismatched and unreliable as predictors of travel risk in locations where the timing of sunset and sunrise, but not traffic, vary throughout the year. Even in the absence of people, many mammalian species are nocturnal owing to a combination of evolutionary, sensory, and ecological factors (Gerkema et al. 2013).

The ubiquity with which dusk serves as an exogenous cue for biological activity makes its interaction with post-industrial human activity a potential ecological trap (*sensu* Gates & Gysel 1978; Robertson, Rehage & Sih 2013). For wildlife, the lack of a consistent relationship between the timing of traffic volume and the cues of dawn and dusk may impose the need for behavioural flexibility to successfully avoid traffic, particularly at higher latitudes where changes in day length are more pronounced. For example, studies of roe deer (*Capreolus capreolus*) in more northern countries (e.g. Scotland, Netherlands and Denmark) found peaks in collisions in spring (April and May) or fall (October) while studies in more southern countries (e.g. Italy, Slovenia, and Germany) found no such pattern (Steiner, Leisch & Hackländer 2014). Others have speculated that the ability for wildlife to avoid high traffic volumes is compromised by the rapid changes in this relationship in spring and fall (Hardy & Seidler 2014). In some species, these peaks may also stem from higher movement rates associated with breeding and dispersal in (e.g., Grilo et al. 2012), but those do not appear to provide a compelling explanation for coyotes. Coyote dispersal typically occurs most between November and April (Gese, Ruff & Crabtree 1996; Way 2007) and their home ranges tend to be either smaller during the breeding season in early spring (Gese, Rongstad & Mytton 1988) or similar among seasons (Gehrt, Anchor & White 2009). Thus, for coyotes and potentially many other species the spring and fall peaks in road mortality may be more associated with the rapid changes in overlap in those seasons between rush hour and twilight.

The ability for some coyotes to restrict the timing of their road crossings suggests a strong role behavioural flexibility in this species, which may generalize to other urban-adapted wildlife. The coyotes that shifted their activity patterns to be more nocturnal especially in summer crossed roads late at night when traffic was lower and also exhibited higher rates of subsequent survival. Interestingly, our data do not suggest that this difference was associated with age, sex, or body condition, but such flexibility could potentially drive further behavioural changes in urban wildlife because plasticity itself can be partly heritable (e.g. Nussey et al. 2005) or taught to offspring by parents (e.g. Mazur & Seher 2008; Nielsen et al. 2013). Regardless of cause, the behavioural flexibility that enables some coyotes to delay activity, and associated road crossings, until late at night may partly explain why coyotes and other species are able to thrive in urban areas.

6.5.1 Management implications

Other authors have successfully identified spatial hot-spots of wildlife-vehicle collisions for the purposes of advancing mitigation (Ramp et al. 2005) and we advance that framework by suggesting that identifying hot-spots in time could be just as important. In particular, we have shown that an overlap between high traffic volume and activity may explain patterns of vehicle-caused mortality for urban coyotes when measured at the level of both individuals and populations. These relationships suggest that animals may be misled by changing relationships between traffic volume and dusk, but some animals reduce their risk of mortality by concentrating their activity late at night when traffic volumes are consistently low. Managers could address the vulnerability stemming from the mismatch in light cues in several ways. For example, they could add devices that detect and signal the arrival of either vehicles (via headlights; e.g. DeerDeter 2015) or wildlife (via thermal cameras; e.g. Crosstek 2012). Managers could also encourage populations of urban wildlife to become more nocturnal (Lowry, Lill & Wong 2013). Hazing programs (HSUS 2009) of carnivores that are active during the day might be one way to accelerate a shift to nocturnal activity for many species, potentially encouraging wildlife movement and survival while decreasing the probability of vehicle collisions and encounters with people. However achieved, an increased emphasis on temporal segregation of humans and wildlife might support complementary approaches based on spatial segregation, ultimately fostering greater coexistence of humans and wildlife.

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6.8 Tables

Table 6.1 Model outputs from candidate GLMM models for three alternative hypotheses testing differences in the road crossings between GPS-collared coyotes that were or were not killed in vehicle collisions during the study period.

Model	ΔAIC	Model weight	Nagelkirke r^2	Model covariates	β ± SE	z	p
Avoided crossing roads *when* traffic volume was higher	0	1.0	0.35	Intercept	-2.98 ± 0.31	-9.50	<0.01
				Coyote killed in collision	-0.45 ± 0.50	-0.91	0.37
				Traffic (time of crossing)	-0.45 ± 0.027	-16.47	<0.01
				Traffic (time) x Coyote killed	1.52 ± 0.26	10.45	<0.01
Avoided crossing roads	295	0.0	0.12	Intercept	-2.88 ± 0.32	-9.14	<0.01
				Step crossed road	-1.3 ± 0.29	-6.21	0.023
				Coyote killed in collision	0.16 ± 0.54	0.43	0.65
				Crossed road x Coyote killed	-0.54 ± 0.51	-1.06	0.28
Avoided crossing roads *where* traffic	296	0.0	0.11	Intercept	-2.89 ± 0.32	-9.10	<0.01

volume was higher				
	Coyote killed in collision	-0.54 ± 0.51	-1.05	0.29
	Traffic (crossing location)	0.015 ± 0.030	0.53	0.60
	Traffic (location) x Coyote killed	-0.14 ± 0.066	-2.06	0.055

6.9 Figures

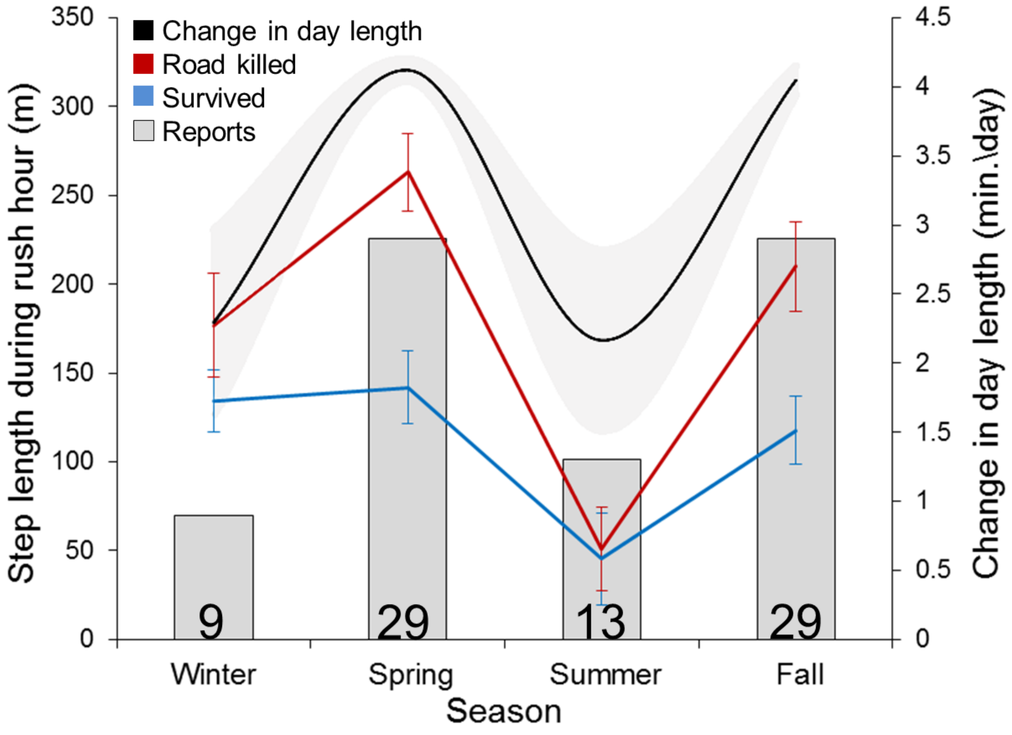

Figure 6.1 Seasonal values for civic reports of coyote mortality on roads (relative size of gray bars and the numbers within them), average change in day length (black line ± SD shaded gray area), and 3-hour step lengths during rush hour (5:00 – 8:00 and 17:00 – 20:00) for road-killed (red line, n = 7) and surviving (blue line, n = 12) coyotes (± SD as error bars). Mortalities summarized monthly by the City of Edmonton in 2013 and 2014 were categorized as winter (November – January), spring (February – April), summer (May – July), and fall (August – October).

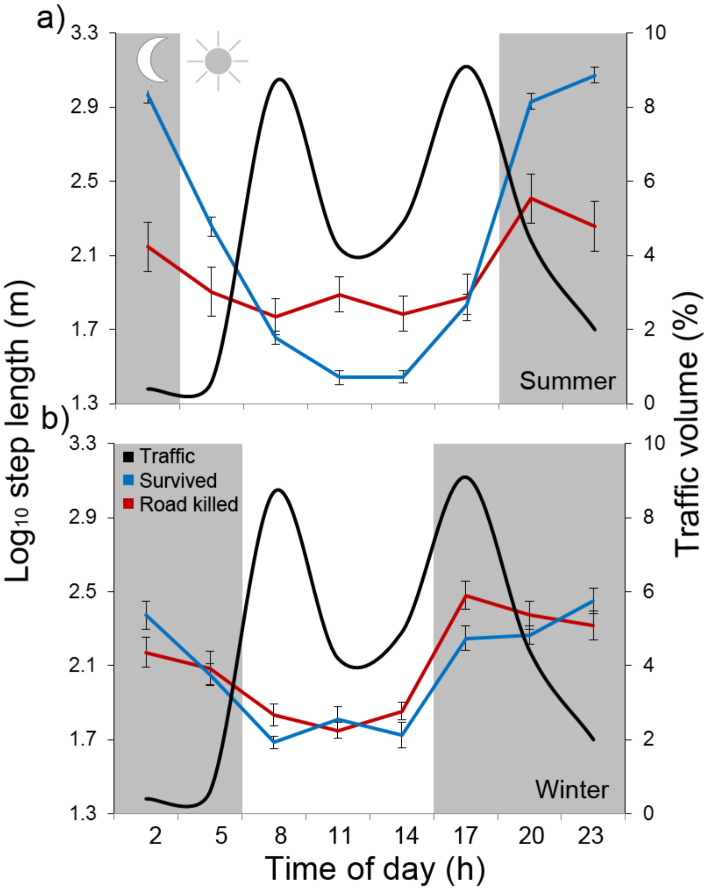

Figure 6.2 Diel distribution of activity for coyotes that were killed in vehicle collisions (red; n=7) or presumed to have survived (blue; n=12). Blue and red lines show the weighted average of log-transformed step lengths between GPS locations taken every three hours. Black lines show percent of daily traffic flow over time, provided by the City of Edmonton. Gray areas indicate times after sunset and before sunrise. Bars show standard deviation.

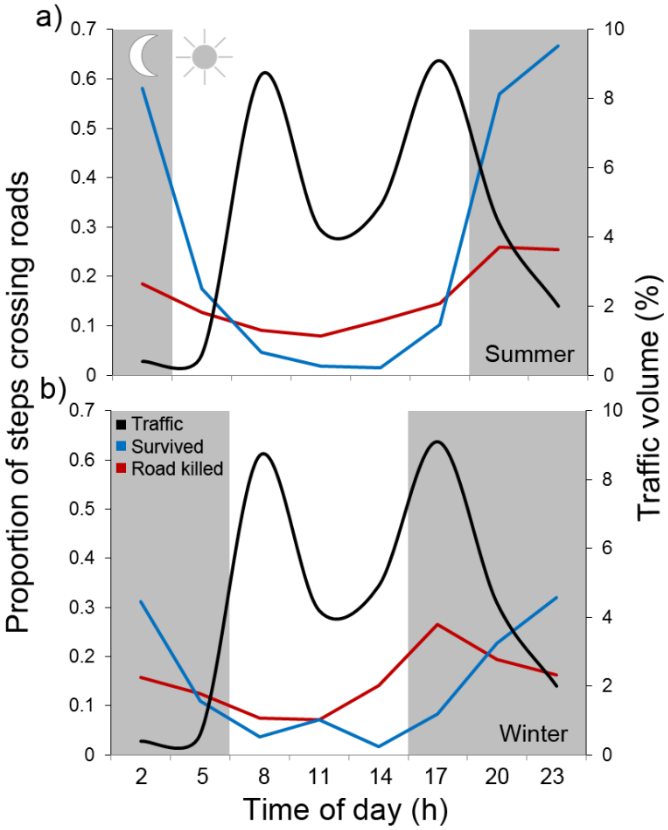

Figure 6.3 The timing of road crossings made by coyotes that were killed in vehicle collisions (red; n=7) or presumed to have survived (blue; n=12) in (a) summer (March 22 – September 21) and (b) winter (September 22 – March 21). Blue and red lines show the weighted average proportion of coyote movement steps between successive 3-hour GPS locations that crossed major roads. Black lines show percent of daily traffic flow over time, provided by the City of Edmonton. Gray areas indicate times after sunset and before sunrise.

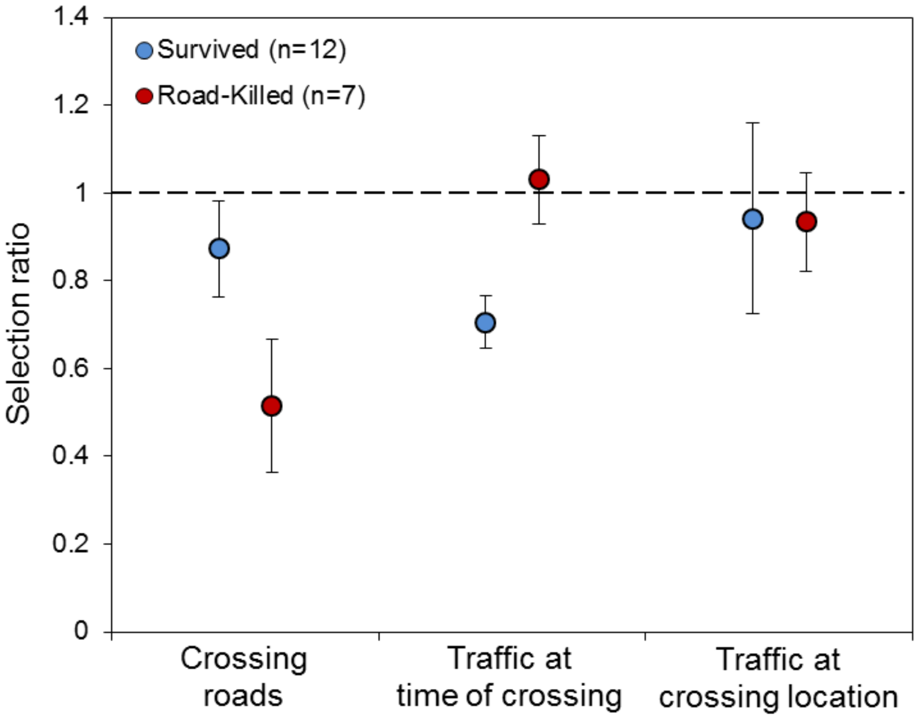

Figure 6.4 Selection ratios for the 3-hour movement steps of 19 coyotes fitted with GPS collars, seven of which were killed in vehicle collisions during the study period (red) and twelve that were not (blue). The selection ratios were calculated using the ratio of value of used steps / value of available steps for the following metrics: the proportion of steps crossing roads; the percent of daily traffic flow at time of road crossing; and the traffic at crossing location (cars/hour).

Chapter 7

7 General discussion

The overall objective of my thesis was to improve our understanding of how and why coyotes vary in their diet, movement, and habitat selection and how these behaviours can promote encounters with humans that could generate conflict. By identifying factors that promote conflict, I aimed to provide information that improves coexistence between humans and carnivores in urban areas and address the challenges for maintaining wildlife and biodiversity in cities. In this final chapter, I will summarize the specific objectives and results of each of my thesis chapters and discuss their broader implications for wildlife ecology, management, and conflict with people.

7.1 Summary of results

Changes in diet by wildlife in human-dominated areas, either through increased use of livestock, crops, or food refuse, may benefit animals by increasing diet diversity but may also promote conflict with people. In chapter 2, I examined whether greater consumption of human food by urban coyotes increased their diet diversity relative to rural coyotes and whether coyotes that consumed more human food were more likely to be reported as nuisance animals by the public. I found that urban coyotes consumed more anthropogenic food and had higher diet diversity, both as populations and individual animals, than rural coyotes. I also found that coyotes reported as nuisance animals by the public did not assimilate more processed anthropogenic food than other coyotes, but instead assimilated less protein. Reported coyotes were also more likely to have signs of sarcoptic mange than other coyotes.

While the use of anthropogenic food and habitat is often linked to conflict with wildlife, little is known about why some individual animals are more likely to use these resources than others. Based on anecdotes in the literature and our own experience that most coyotes reported by the public had signs of disease, in chapter 3 I examined whether coyotes that were young, male, or diseased were more likely to eat human food and exhibit more overlap with humans in space and time. I found that coyote health was most associated with use of human resources; coyotes with signs of sarcoptic mange used more developed areas, had larger home ranges, were more diurnal, and assimilated more human food and less protein than the outwardly healthy coyotes in our sample.

Coyotes appeared to vary substantially in their use of anthropogenic food and developed areas and especially with respect to body condition. In chapter 4, I tested whether coyotes selected habitat to avoid humans but access anthropogenic resources, and whether diseased coyotes would accept more risk to access these resources. Most coyotes avoided residential areas but diseased coyotes used them more frequently, especially during the day. Coyotes selected for backyards without fences, with higher cover, and with anthropogenic food, and diseased coyotes were more likely to select sites with anthropogenic food and bed sites under houses.

The backyards selected by coyotes, and especially coyotes with mange, were more likely to contain accessible garbage and piles of food waste for composting. In chapter 5 I examined whether industrial and residential compost piles could promote the spread of disease in coyotes by testing whether these piles increase indirect contact between coyotes, attract sick coyotes, and contain harmful fungal toxins. At landfills and compost piles, the overlap between visibly parasitized and healthy coyotes was greater in both time (time elapsed between visits) and space (higher proportion of visits by parasitized coyotes) than at reference sites in natural areas. At least one species of mycotoxin was found in 86% of compost piles, and two of the three mycotoxins we quantified were found at concentrations above regulated limits for animal health.

Coyotes and other wildlife in human-dominated areas can also come in conflict with people through collisions with vehicles, which can increase rates of mortality for wildlife and people. To better understand why risk of collision may be higher for some animals and in certain seasons, in chapter 6 I compared frequency of dead coyotes collected on roads across seasons and the movement patterns of GPS-collared coyotes that were or were not killed in collisions. Coyotes were more likely to be collected on roads in the spring and fall and during these seasons, road-killed coyotes were more active during rush hour than were surviving coyotes. Coyotes killed in collisions were active and crossed roads throughout the day and most often at dusk, which in winter overlaps with evening rush hour when traffic volume is highest. By contrast, surviving coyotes were nocturnal and crossed roads most often around midnight regardless of season.

7.1.1 Relationships between coyote health and use of anthropogenic resources

A core contribution of my research is the association I found between poor coyote health and the use of anthropogenic resources. Coyotes with signs of sarcoptic mange were more likely to be reported by the public, consume anthropogenic food, use developed areas, select for foraging sites with accessible garbage or compost and bed sites under houses, and more likely to be detected at piles of food waste. In the following section I will integrate the results from chapters 2 – 5 and discuss why animals in poor condition may be more likely to use anthropogenic resources and how using anthropogenic resources may negatively impact the health of those individuals and, more generally, the health of urban wildlife.

There appear to be complex and potentially self-reinforcing relationships between poor health and the use of anthropogenic habitat or food. For carnivores, finding and catching prey often requires a combination of acute senses of sight, smell, or hearing, and high degrees of speed, agility, and endurance (e.g. Thibault & Ouellet 2005). The predation success of individual carnivores may be affected by reduced mobility (reviewed in Linnell et al. 1999) or low energy reserves from disease or depletion of body resources by parasites (*sensu* Alzaga et al. 2008). For these animals, finding food that is highly reliable in space and time may be more important than food quality, particularly if it increases the likelihood of accessing the calories necessary to survive over the short term (Oro et al. 2013). One or both of reliability and ease of access may explain why several studies have noted a marked increase in the use of developed areas or human-associated food in injured or diseased carnivores across many species (Table 7.1). Humans have been providing such resources in the form of dump piles of food waste and carcasses for thousands of years, and the exploitation of dumps near human settlements has even been implicated in the domestication of dogs from wolves (*Canis lupus*; Axelsson et al. 2013). Currently, the amount of edible food discarded as waste ranges from 95 – 115 kg per year per capita in Europe and North America (Parfitt, Barthel & Macnaughton 2010). While consuming anthropogenic food could decrease risk of starvation during times of low food availability (Rosatte et al. 2010), it can be of poor quality if it is nutritionally deficient or contaminated.

I found that diseased coyotes had assimilated diets that were isotopically similar to anthropogenic food and almost one full trophic level lower in protein than coyotes that were apparently healthy. Diets higher in anthropogenic food have also been linked to low protein assimilation in urban crow nestlings (*Corvus brachyrhynchos*; Heiss, Clark & McGowan 2009) and ring-billed gulls (*Larus delawarensis*; Caron-Beaudoin et al. 2013). Dietary protein is important to maintain the body's supply of essential amino acids (that cannot be produced by the body), non-essential amino acids (produced from essential amino acids or formed by breaking down other proteins), and conditional amino acids (for which synthesis is limited in times of illness or high stress) all of which are critical for the formation of muscle and regular body function (Hill, Wyse & Anderson 2012). In animals, diets low in protein have been linked to lower immunity (Taylor et al. 2013) and higher gut parasite loads (Ezenwa 2004).

Diet quality can also cause or exacerbate health problems because of the presence of contaminants and toxins in decomposing food waste. My results suggest that compost piles may be an underappreciated and problematic attractant for coyotes and potentially other wildlife. The diseased coyotes I sampled had diets lower in protein, indicating that they consumed more vegetation or fruit than other coyotes, and they selected backyards with compost piles and visited them multiple times. I also detected a higher prevalence of visibly-diseased coyotes at landfills and compost piles than in urban natural areas using remote cameras. Piles of compost either landfills or in backyards were often contaminated with mycotoxins at concentrations high enough to cause chronic or acute health effects in domestic dogs (Bhat et al. 1989; Leung et al. 2006; Leung et al. 2007). Mycotoxins can cause health problems via a number of mechanisms, including by damaging kidney function (e.g. ochratoxin A; Szczech, Carlton & Tuite 1973), elevating hormone levels such as tryptophan and serotonin, thereby inducing food refusal and vomiting (e.g. T-2 toxin; Smith 1992), and by binding to DNA and interfering with normal protein synthesis and consequently cell immunity (e.g. aflatoxins; Raisuddin 1993). Wildlife that feed at waste dumps may also suffer the effects of toxins by consuming other poisonous substances such as battery acid (Lunn & Stirling 1985).

Regardless of whether health problems arise from poor nutrition or exposure to toxins, these negative physiological effects likely decrease energy levels required for successful hunting. In turn, lower hunting success may increase the reliance of an individual on easily-accessible and reliable food at waste piles. In this way, animals may consume low-quality diets because they are injured or sick, or they may be sick or reliant because they consume poor-quality diets that are low in protein or high in contaminants.

The ambiguity of direction in the causal link between diet and disease in the coyotes I studied was also evident in their habitat selection; diseased coyotes were also more likely to use developed urban areas. It is possible that coyotes in poor condition were more likely to use developed areas because they were seeking anthropogenic resources, but it is also plausible that coyotes that frequent developed areas were more likely to become diseased. In developed areas, coyotes might also be more likely to consume rodents that have consumed anticoagulant rodenticides, which have been linked to higher susceptibility to notoedric mange in cougars (*Puma concolor*) and bobcats (*Lynx rufus*; Riley et al. 2007) and have been detected in urban coyotes in Denver, Colorado (Poessel et al. 2014).

The large home ranges of the diseased coyotes in my study suggest that they were transient animals that did not maintain home ranges. If true, coyotes living in developed areas were perhaps excluded from natural areas, which is consistent with observations by others that transient coyotes typically occupy sub-optimal habitat (Kamler & Gipson 2000; Gehrt, Anchor & White 2009). If coyotes that inhabit developed areas are more likely to be transients, they may also be more likely to encounter other transient coyotes to which they are not related, increasing their risk of encountering diseased coyotes (Altizer et al. 2003). Alternatively, the home ranges of coyotes in developed areas might be larger because home ranges tend to increase in size when resources are further dispersed, as they may be in residential and commercial areas with large amounts of impervious surfaces (Gehrt, Anchor & White 2009; Newsome et al. 2013).

For the reasons listed above, poor health may be both a cause and consequence of using anthropogenic resources. Indeed, individuals who consume large amounts of protein-poor or contaminated anthropogenic food or frequent developed areas may become reliant on these resources and consequently have difficulty breaking this cycle (Figure 7.1). Regardless of whether diseased coyotes are attracted to or relegated to developed areas, the resources present there may promote the spread of disease by increasing contact between sick and healthy coyotes. For example, I found that the average time elapsed between diseased and healthy coyotes at compost piles was well within the time period that mites can remain infective off the host (Arlian, Vyszenski-Moher & Pole 1989), and several diseased coyotes shared bed sites under houses. Preventing such opportunities for disease spread may in turn decrease the prevalence of animals in poor condition that may be more reliant on anthropogenic resources and more likely to come in conflict with people.

7.1.2 Temporal avoidance of human activity

Another core contribution of my research highlights the importance of temporal separation between coyotes and human activity. Other studies have shown that carnivores can be flexible in the timing of their activity and more nocturnal when closer to human activity or infrastructure (Boitani 1982; Ciucci et al. 1997; Kaczensky et al. 2006; Northrup et al. 2012). This is especially true for coyotes (Grinder & Krausman 2001; Tigas, Vuren & Sauvajot 2002; Riley et al. 2003), bobcats (Tigas, Vuren & Sauvajot 2002; Riley et al. 2003), and foxes (*Vulpes vulpes*; Baker et al. 2007) in urban areas where the intensity of human activity is highest. Temporal separation from human activity may be especially important to urban wildlife because some individuals may not be able to avoid developed areas in space.

My findings support several observations of human avoidance by others who have studied urban coyotes, but add understanding about how this avoidance varies among individuals. Most coyotes in my study were nocturnal, crossed roads most often at night, and avoided residential areas especially during the day. However, some coyotes did not or could not do so, potentially because of physiological constraints. Coyotes with mange were more diurnal and were more likely to use residential areas during the day, perhaps because they were less able to tolerate cold temperatures at night because of poor coat quality or because they were no longer wary of human activity (e.g. Todd, Gunson & Samuel 1981). Similarly, some coyotes, equally likely to be diseased or healthy, were less willing or able to shift the timing of their activity and road crossings, potentially because of inherent differences in behavioural flexibility. Coyotes that were killed in vehicle collisions were most active and crossed roads most frequently at dusk, suggesting that their activity levels were based on day length, as it is for many species (Georgii 1981; Hill et al. 2004). By contrast, surviving coyotes were most active and crossed roads most often around midnight. This variation in the timing of activity among individual coyotes may be due to differences in behavioural flexibility (Nussey et al. 2005) or the ability to learn new movement cues such as traffic volume (Sih, Ferrari & Harris 2011). These abilities may be especially important for urban wildlife that must be flexible enough in their behaviour to accommodate anthropogenic noise (e.g. Slabbekoorn & Peet 2003; Proppe, Sturdy & St. Clair 2011) and light (e.g. Miller 2006).

7.2 Implications for conflict between humans and wildlife in human-dominated areas

The results of my thesis support of a number of recommendations to mitigate conflict between humans and wildlife in human-dominated areas, which I summarize below.

What promotes encounters between coyotes and people?

My results suggest that most coyotes strongly select for natural areas, both in the placement of their home ranges and the habitats preferred within their home ranges, and are nocturnal. Some coyotes exhibited less avoidance of humans in both space and time and consumed more anthropogenic food and these behaviours were most associated with signs of sarcoptic mange. Some coyotes also failed to avoid traffic in time and were more likely to come in conflict with people (i.e. killed in vehicle collisions). Taken together, my results support the observations of others that conflict tends to mostly arise from a few individual animals (Linnell et al. 1999; Gehrt, Anchor & White 2009) and may be promoted by disease and diurnal activity.

Do animals thrive by exploiting anthropogenic resources?

Some authors hypothesize that animals move in to urban areas and do well there because they can exploit anthropogenic resources (e.g. Prange, Gehrt & Wiggers 2004; Newsome et al. 2010). My results support a more complex picture. The urban coyotes I sampled that appeared healthy and had small home ranges typical of resident animals strongly avoided developed areas and consumed more anthropogenic food than coyotes in rural areas. However, the coyotes that used developed areas most frequently and consumed the most anthropogenic food tended to be in poor condition and had very large home ranges similar to those transient animals. Thus, anthropogenic food and habitat were used most by animals that typically have fewer options for alternative food or habitat.

How can coexistence with wildlife be improved?

Based on my results, a greater emphasis on managing the prevalence and spread of disease may mitigate conflict between humans and wildlife in human-dominated landscapes. This could be achieved by restricting access to piles of food waste that appear to aggregate sick and healthy coyotes and expose foraging animals to harmful mycotoxins. Evidence is growing that urban areas can alter disease dynamics and that urban wildlife can have higher rates of disease (Daszak, Cunningham & Hyatt 2001; Bradley & Altizer 2007; Martin et al. 2010). While some consider disease to be an important source of mortality to regulate wildlife populations (Almberg et al. 2012) it may be less effective in urban areas if survival is extended for infectious animals because of food subsidies and artificial shelter. Because most coyotes in my sample avoided humans in time and space, indiscriminate removal of coyotes would likely be ineffective at reducing encounters between coyotes and people. My results also suggest that techniques that promote nocturnal behaviour (e.g. hazing and aversive conditioning) could also reduce the frequency of collisions between coyotes and vehicles.

My results also provide evidence for targeted attractant management and habitat modification. Coyotes in Edmonton and Calgary frequently consumed crabapples and bird seed and the removal of these attractants could be emphasized to residents as a means of supporting coexistence with coyotes. Coyotes also selected backyards without fences and with high cover, suggesting simple steps for residents to prevent encounters with coyotes.

More generally, my results provide insights to solutions for conflict between humans and wildlife of several types. My results suggest the consumption of anthropogenic food by wildlife can increase both the transmission and spread of wildlife disease and that diseased individuals may exhibit greater overlap with people. All three of these factors have important implications for the spread of zoonoses and may explain why urban areas can have higher rates of disease emergence and spread (Bradley & Altizer 2007). My results also suggest that limiting support for diseased animals such as easily-accessible food or shelter in cold temperatures could alleviate nuisance wildlife and property damage to homes and buildings. Many carnivores come into conflict for the destruction of livestock or pets (Treves and Karanth 2003), but I found that pets were relatively unimportant in urban coyote diet relative to other food types, including more natural prey. Instead, my results suggest that attractants with lower protein content, such as cultivated fruit, bird seed, or compost, could be more problematic, similarly to nuisance black bears (Merkle et al. 2011). For conflicts with large carnivores wherin humans can be maimed or even killed, my findings that diseased coyotes were more likely to seek out residential areas and human food support those of others that carnivores in poor body condition are more likely to seek out easy sources of food, including man-eating tigers and lions (Yeakel et al. 2009, Goodrich et al. 2011b). Lastly, my findings that crossing roads when traffic was higher increases the risk of vehicle collisions for coyotes suggest that collision mitigation may be most successful if in place when dusk overlaps with rush hour. This has important implications for the timing of collision mitigation efforts for many species, including threatened wildlife and human mortality.

7.3 Considerations and future work

In the section below, I summarize the most important limitations of my study and suggest directions for future work.

The conclusions I have drawn were based on a small sample of animals. Many of the results in my thesis are based on the diets and movements of 19 coyotes captured in Edmonton from 2009 – 2012. While this sample of individuals is not as large as some studies, it is complemented by other data sources including 2,356 coyote scats across Alberta, hair samples from 53 other urban and rural coyotes, reports of road-kills from 80 coyote carcasses, and remote camera photographs from 5,132 trap nights. Further, in my thesis research, I focussed on coyote behaviours that increase their overlap with people in space, time, or resource use. Other kinds of conflict between people and coyotes such as coyote attacks on humans (White & Gehrt 2009) or aggressive interactions with domestic dogs (Alexander & Quinn 2011) were not addressed and could be motivated by different factors (e.g. territoriality; Lukasik & Alexander 2011).

My results showed clear associations among coyote health, habitat use, and diet, but the direction of causation was difficult to determine and likely included multiple mechanisms. Because of the ethics involved in experimentally manipulating wildlife health, there is little information on these mechanisms and most reports of changes in behaviour with health or infirmity are anecdotal cases (Table 7.1). The high proportion of coyotes with mange in our sample is unusual and perhaps because of a mild mange epizootic in Edmonton during most of the study period (2009 – 2012) as the prevalence of coyotes with mange was lower before and after this period (Ramsey Cox and Bill Abercrombie, pers. comm.). This increase in mange prevalence enabled me to test the effects of disease on the use of anthropogenic resources more directly. In future, studies following the health of individual animals over long periods, perhaps during a disease treatment baiting program or from birth, could elucidate the relationships I have observed among health, diet, and habitat use.

The two core limitations of my study, sample size and ambiguous causation, could be resolved in future studies of urban wildlife by applying more quantitative measures of health in relation to variation in use of anthropogenic food and habitat. I was fortunate to observe a parasite with such visible signs, enabling me to confirm health status after capture using visual observations or photographs from the public, and was able to confirm the presence of mange mites on several coyotes necropsied at the University of Calgary. However, my diagnosis of sarcoptic mange could have been confirmed and complimented with methods such as skin scrapings or combing for fleas (Monello & Gompper 2010). More invasive methods, such as blood collection, could have also provided more direct measures of immunity and nutrition.

There are numerous applications for a better understanding of the effects of consuming anthropogenic food. The health effects of eating food contaminated with mycotoxins on health are well studied in humans, livestock, and domestic dogs and cats (reviewed in Hussein & Brasel 2001; Edite Bezerra da Rocha et al. 2014), which support testing regimes and regulations that limit exposure. Unfortunately, almost no similar work has been done on wildlife (but see an example on Northern Bobwhites *Colinus virginianus*; Oberheu & Dabbert 2001; Moore et al. 2013), especially wild mammals. Such work is highly relevant for urban-adapted omnivores and generalist carnivores such as black bears (*Ursus americanus*), raccoons (*Procyon lotor*), foxes, and coyotes that can consume rotting vegetation, fruit, and bread from landfills. It could also be important for increasing the disease susceptibility of ungulates that aggregate at feeding stations (Thompson, Samuel & Deelen 2008).

7.4 Summary

Taken together, my results suggest that examining how and why individual animals overlap with humans in space, time, and resources can help identify factors that promote conflict between humans and wildlife. The most important factor in my own study appeared to be wildlife health; diseased coyotes were more likely to be reported as nuisance animals and approached houses for food and shelter. Another factor appears to be inflexibility in the timing of wildlife activity, which may or may not correlate with disease. Although diseased coyotes that used developed areas were also more active during the day, road-killed coyotes were less nocturnal than their surviving counterparts but did not exhibit an association with disease. Identifying the generality of these mechanisms is made more urgent by the rapidity which with urban development is expanding globally. With it, prevalence of urban-adapted wildlife and potential conflicts will undoubtedly increase. Coexistence may be facilitated by promoting fine-scale separation between humans and urban carnivores in space and time, which in turn may be promoted by reducing diurnal activity and rates of disease. In combination, restricting access to low-quality anthropogenic food while promoting nocturnal activity by urban carnivores may mitigate conflict using non-lethal management practices and promote the coexistence of people and urban carnivores. This goal of greater coexistence with coyotes contributes to a broader societal challenge imposed by increasing rates of urbanization that correspond to the decline of many species, including carnivores, world-wide. Decreasing the likelihood of negative encounters between people and urban-adapted wildlife may be an important step in slowing these declines and maintaining biodiversity in human-dominated areas.

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7.6 Tables

Table 7.1. Examples in the literature of associations between the use of human-associated food or habitat with poor health or injury in carnivores.

Family	Species	Country	Anthropogenic resource	Impairment	Reference
Ursidae	Polar bear (*Ursus maritimus*)	Canada	Closer to settlements	Nutritional stress	Towns et al. 2009
	Polar bear (*U. maritimus*)	Canada	Feeding at landfill	Poisoned by consuming batteries	Lunn & Stirling 1985
Canidae	Wolf (*Canis lupus*)	United States	Eating more carrion, euthanized in garage	Sarcoptic mange	Shelley & Gehring 2002
	Coyote (*C. latrans*)	United States	Developed urban areas	Rodenticide poisoning	Poessel et al. 2014
	Coyote (*C. latrans*)	Canada	Compost in stomach, approaching houses during the day	Sarcoptic mange	Todd, Gunson & Samuel 1981
	Coyote (*C. latrans*)	United States	Reported for conflict	Sarcoptic mange	Gehrt, Anchor & White 2009

	Coyote (*C. latrans*)	Canada	Developed areas, human food	Sarcoptic mange	Murray et al., in press a
	Raccoon dog (*Nyctereutes procyonoides*)	Japan	Use of urban and suburban areas	Sarcoptic mange	Ninomiya & Ogata 2005
Felidae	Lion (*Panthera leo*)	Kenya	Eating humans	Jaw deformities, tooth breakage, abscesses	Patterson 1925; Yeakel et al. 2009
	Lion (*P. leo*)	Zambia	Eating humans	Broken jaw	Yamakazi & Bwalya 1999
	Asiatic lion (*P. leo persica*)	India	Living on farms	55% rescued on farms had various injuries or illnesses	Vijayan & Pati 2002
	Tiger (*P. tigris*)	India	Eating humans	Arthritis, broken claws, injured limbs, gunshot wounds	Corbett 1946, 1955, 1957
	Tiger (*P. tigris*)	Russia	Eating humans	Tooth breakage, injuries	Goodrich et al. 2011a

Leopard (*P. pardus*)	India	Living on farms	60% rescued on farms had various injuries or illnesses	Vijayan & Pati 2002
Snow leopard (*P. uncia*)	India	Livestock depredation	Injured	Fox & Chundawat 1988
Jaguar (*P. onca*)	Belize	Livestock depredation	Injured from shotgun pellets	Rabinowitz 1986
Jaguar (*P. onca*)	Venezuela	Livestock depredation	Injured from shotgun pellets	Hoogessteijn, Hoogesteijn & Mondolf 1993
Cougar (*Puma concolor*)	United States	Developed urban areas	Notoedric mange from rodenticide exposure	Riley et al. 2007
Eurasian lynx (*Lynx lynx*)	Switzerland	Near houses during the day, killed sheep in stable	Notoedric mange	Ryser et al. 2002
Bobcat (*L. rufus*)	United States	Developed urban areas	Notoedric mange from rodenticide exposure	Riley et al. 2007

7.7 Figures

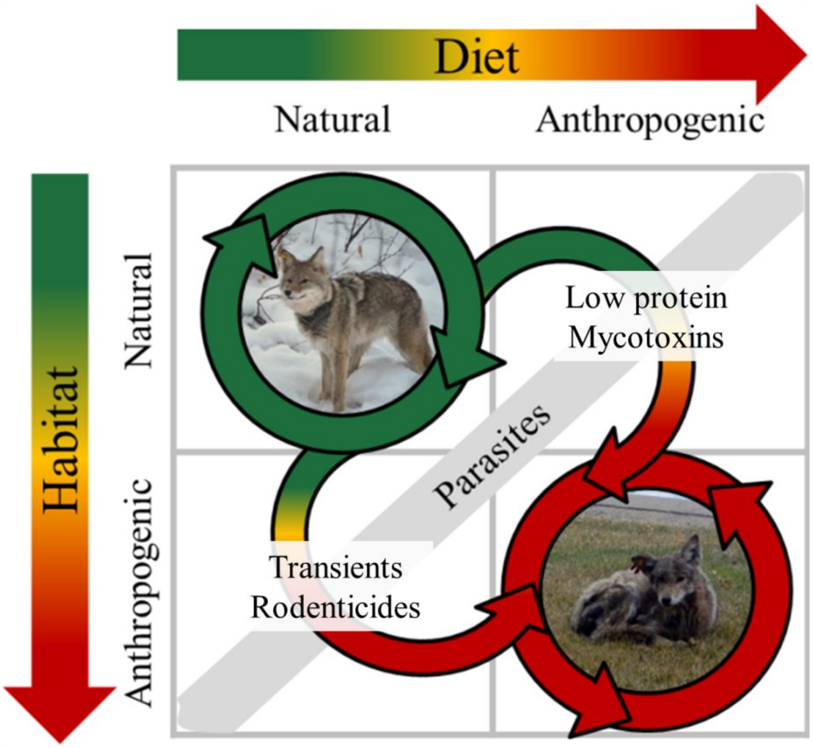

Figure 7.1. Conceptual depiction of the complex and potentially self-reinforcing relationships between wildlife health and the use of anthropogenic food and habitat.

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