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Spatial and Seasonal Differences in the Diets of Urban and Rural Coyotes (*Canis latrans*) in
the Calgary, AB Vicinity

by

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Abstract

Coyotes (*Canis latrans*) can temporarily adapt to urbanization by modifying dietary habits. Since coyotes are keystone predators in urban ecosystems, more research is needed to understand how they persist in urban areas. This research explores the spatial, seasonal and diversity differences in coyote diet in the Calgary, Alberta area. Between July 2009 – July 2010, scats were collected from 8 urban sites ($n=160$) and 6 rural sites ($n=178$). Food items in scats were quantified and analyzed. Natural foods were the most voluminous food source in all spatial areas and seasons. However, urban scats presented significantly more garbage and crab apples, and significantly less deer and cattle. Diet differed significantly between seasons, especially in urban areas. There is also significantly higher diet diversity in urban areas. These findings should apply to other urban settings and inform residents and management agencies to foster co-existence.

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Dedication

I would like to dedicate this thesis

In honour of my mother,

CAROLE FORTIN

And in honour and loving memory of my father,

PERRY ROSS McCUAIG.

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Urbanization is known to affect wildlife species ecology (Drinnan 2005, Fischer & Lindenmayer 2007), but there is little research on how wildlife species adapt to such landscape modifications. As a means to adapt¹ to the encroachment of urbanized areas on wildlife habitats, some species undergo life-history and behavioural modifications (Whittaker & Knight 1998, Tigas *et al.* 2002, Ortega-Álvarez & MacGregor-Fors 2009, Ditchkoff *et al.* 2006). Some of these behavioural changes can lead to conflict between humans and wildlife. Coyotes (*Canis latrans*) exemplify species' resilience in the face of urbanization (Rose & Polis 1998, Atwood *et al.* 2004, Quinn 1997, Morey 2004).

Behavioural changes can be studied using landscape gradients as laboratories for research on urban wildlife species (Natuhara 2008). While urban areas are, in general, not considered to be natural areas, they are still part of an ecosystem that thrives and fully function when a natural equilibrium is present. Coyotes play an important role in maintaining that equilibrium (Crooks & Soulé 1999), even if this role is not quite well-understood.

¹ In the context of this research project, the term “adaptation” or its verb “to adapt” do not imply any long-term genetic modification or natural selection processes. Instead, it refers to non-permanent modifications or adjustments of behavioural traits that allow the species to survive in a new or modified environment under different constraints, stresses and/or spatiotemporal changes in climate, resource availability, inter and intraspecific competition and/or ecological processes.

Considering that coyote diet can reflect the habitat's resource availability (Morey *et al.* 2004, Quinn 1997, Atwood *et al.* 2004) and that conflict potential increases when anthropogenic food sources are consumed (Baker 2007, Lukasik 2011), it is important to evaluate the composition of coyote diet in urban areas. Decreased home-range sizes (Andelt 1985, Grindler & Krausman 2001) and increased densities (Fedriani *et al.* 2001) in urban habitats suggest that these areas may have higher carrying capacity for coyotes. Urban habitats are filled with anthropogenic resources that are energy-rich and easy-access (e.g. human refuse, pets, and crab apples). Due to the coyote's propensity to forage both opportunistically (Andelt *et al.* 1987, Van Vuren & Thompson 1982) and optimally (Hernandez *et al.* 1994, Harrison & Harrison 1984), they can exhibit prey switching behaviours, which may result in anthropogenic resources being included in the urban diet. However, individual coyotes that include human refuse in their diet may become habituated if encountering humans on a regular basis. In fact, habituation can be defined as a process that occurs gradually through time and perhaps space, and through which a wildlife species loses its natural fear of humans. Habituation can often be linked to food conditioning where, in an attempt to meet nutritional and survival needs, an individual or a pack has regularly come into rather close contact with or proximity to humans and has perhaps come to associate food with human presence (Carbyn 1989, Timm *et al.* 2004). Habituated animals can often present increasingly bold behaviours towards humans like resource guarding, and such behaviours can clearly lead to potential safety risks for humans, pets and to the coyotes themselves. For that reason, understanding influencing

factors in coyote diet is essential for the development of effective and sustainable wildlife management plans.

Quantifying urban diet can help in evaluating human-wildlife conflict potential (Baker 2007, Lukasik 2009). Indeed, attacks or aggression displays most often occur when an individual has been human-habituated (Timm *et al.* 2004). Therefore, quantifying garbage, pet remains and crab apples in scats can help in considering human/wildlife conflict risks and in informing residents and managers about how to foster a sustainable co-existence. Evaluating urban coyotes' diet divergence from the rural coyote diet may also help assess and identify the food sources on which urban coyotes rely to persist in disturbed landscapes. As such, this research investigates the dietary behaviours of the Western coyote (*Canis latrans*) in the foothills of the Rocky Mountains, AB.

My study focuses on three aspects of coyote diet: spatial, seasonal and diversity variations. A key objective of the study is to illuminate differences that exist between the diets of urban and rural coyotes of the Calgary, as well as on the temporal and diet diversity differences that occur within that space. Although Lukasik (2009) has quantified coyote diet in Calgary urban parks, coyote diet has never been investigated in the Calgary area in the context of diet differences between urban and rural habitats. By examining rural coyote diets, I hope to establish a base line of the component parts of coyote diet under less human-disturbed or less humanized landscapes than Calgary, AB area.

Herein, I tested the hypothesis of whether urban coyote scats differed significantly from rural coyote scats. I also tested for seasonal variation and whether differences in diversity would be observed between the regions, biological seasons and/or calendar

seasons. I developed a literature review of existing coyote life-history research, which provided the knowledge necessary to understand and interpret results of my research. In Chapter Three and Four, I provide a description of my study sites and methodology. In Chapter Five, I determined if significant spatial, seasonal and diversity differences exist between the diets of urban and rural coyotes in and near Calgary, AB. In Chapter Six, results are discussed and in Chapter Seven, I conclude this thesis by discussing the significance and the implications of the findings as well as by stating the contributions of this study to the existing scientific knowledge, ensuing recommendations and potential areas of future research that could aid in filling remaining knowledge gaps.

Since the 1800s, the coyote's distribution has expanded due to various factors including its high behavioural plasticity, the extirpation of wolves from extensive parts of North America, human-induced landscape changes (e.g. clearings) and anthropogenic food availability (Fox & Papouchis 2005). Coyotes are "keystone predators" (Power *et al.* 1996, Henke & Bryant 1999) that acclimatize rapidly to very diverse habitats and conditions. Through predation and competition, they "mediate faunal community structure" (Henke & Bryant 1999: 1066). Thus, they are believed to help maintain a higher biodiversity and richness in rodents and songbirds by controlling the population of meso-predators such as bobcats, foxes, feral cats, badgers and raccoons (Henke & Bryant 1999, Crooks & Soulé 1999). Although the coyote's survival is presently not threatened, it is crucial to understand its life-history traits and behaviour in order to improve our wildlife management practices and foster co-existence.

2.1 Reproduction

Coyotes can reproduce once a year between the months of January and March. Although they may change partners during their life-time, they usually mate with the same individual annually (Bekoff 1977). Three months after mating, pups that are deaf and blind are born in a den either dug out by coyotes, or by individuals of another species such as badgers (Bekoff 1977). As cited in Bekoff (1977: 4), preferred den site locations can be found in "brush covered slopes, steep banks, thickets, hollow hogs, rock ledges, often on

south-facing slopes (Gier 1968).” Litter size averages 5 to 6 pups, but its size may be influenced by coyote population densities as well as by rodent abundance (Bekoff 1977, Gier 1968). Once the pups can hear, see and move on their own, (i.e. between 2 and 3 weeks after birth) they can start exploring the world outside of the den. At 3 weeks of age, they can begin eating regurgitated foods and they will be completely weaned between 5 and 7 weeks (Bekoff 1977).

At around 9 months of age, pups reach their adult weight. Coyotes typically disperse between 6 and 9 months (Bekoff & Wells 1986). However, not all juvenile coyotes disperse. In fact, those that have not dispersed by 10 to 11 months are likely to remain with the alpha pair and/or family group, and become “betas” within the pack (Fox & Papouchis 2005, Bekoff & Wells 1986). Of those that do disperse, many do not survive. The dispersal is a process that occurs mostly during the fall and winter seasons and it is often associated with higher mortality rates (Pyrah 1984, Bekoff & Wells 1986). In central Alberta, Nellis and Keith (1976) found mortality rates to be as high as 71% for the first year of a coyote’s life, but decreased by half after the first year.

Once dispersed, the average life-span of coyotes in the wild is between 6 and 8 years (Gier 1968). Resident coyotes as well as those that are part of a pack tend to live longer than solitary and/or transient coyotes (Gier 1968, Andelt 1982). Survival can also be limited by several factors such as climate conditions, parasites and diseases, food, accidents, and predation (Gier 1968).

2.2 Social Structure

Typically, coyotes form “monogamous pair bonds” (Bekoff & Wells 1986: 264) that will either establish a territory (resident), travel together (transient) or meet annually during the breeding and pup-rearing seasons. Males often help by bringing food to their mating partner (Bekoff 1977). Packs may form when juvenile coyotes remain with the alpha pair to help in rearing the new pup litter. In a pack, usually only the alpha pair breeds, but the alpha male may occasionally breed a second time with a beta female (Fox & Papouchis 2005). While they participate in most activities together, a hierarchy exists within the pack itself (Bekoff and Wells 1986).

Coyotes living in packs typically travel less than resident pairs or solitary coyotes, especially in the case of females in a pack versus solitary females or versus females in a pair (Bekoff & Wells 1981). During winter, small prey is harder to hunt because of snow cover and snow depth. However, deer may be easier to prey upon as they can be weakened by the harsh weather conditions and be slower to escape in deeper snow or on ice (Patterson & Messier 2000, Gese & Grothe 1995). Bowen (1981) believed that prey size was a determining factor of group size of coyote packs in Alberta. In fact, packs may be more useful during the winter to hunt larger prey such as ungulates and/or to steal or defend carcasses against other competitors such as wolves. A larger pack size may help coyotes predate upon larger prey but a pack may still feed primarily on small mammals (Gese *et al.* 1996a). Furthermore, the success of the hunt is not dependent on pack size, but rather, on the hierarchy level of the individuals participating (Gese & Grothe 1995). In successful hunting attempts, alpha individuals led the pack in the hunt while betas usually remained

on the sidelines. It can likewise be influenced by other factors such as weather conditions (e.g. water, snow depth, and wind), health (e.g. nutritional condition), age, and behaviour of the prey (Gese & Grothe 1995).

Coyotes may be residents that will defend a set territory, which is often the case for bonded pairs and packs. Or, there are also “transient” coyotes that have much larger territories, and will often avoid resident coyotes (Kamler & Gipson 2000). Transient coyotes frequently have much higher mortality rates than resident coyotes (Andelt 1982), which could be due to predation or resource competition-related killing from wolves or from resident coyotes. These coyotes typically do not breed, but will move into a territory if one becomes available (Gese & Grothe 1995).

Coyotes claim their territory by direct confrontation or indirectly, by howling and scent-marking (Gese 2001). Scent-marking is done through glandular secretions, urine marking, and scat deposition (Bekoff & Wells 1986). It is done in a similar way as that of wolves, where the alpha pair seems to be the most active in scent-marking activities (Gese & Ruff 1997). Scent-marking is independent of pack size, but alpha males more frequently during the breeding season (Gese & Ruff 1997). As opposed to wolves, all coyotes in the pack will take part in scent-marking, although the alpha pair will mark more often (Barrette & Messier 1980, Gese & Ruff 1997). Coyotes living in packs and/or resident coyotes tend to mark more and use stronger means of marking than transient coyotes (Barrette & Messier 1980). Resident coyotes, especially alpha pairs, also have a habit of marking their territory more on the periphery than the interior (Gese & Ruff 1997).

2.3 Competitors

Some species share a similar ecological niche with coyotes, both spatially and temporally. They exploit similar food sources, similar habitat, and similar territory. Such competitors for resources include, mainly, foxes (Randa *et al.* 2009, Kamler *et al.* 2007, Neal & Sacks 2001, Gehrt & Clark 2003), wolves (Fuller & Keith 1981, Nowak 1978, Carrera 2008, Fox & Papouchis 2005, Gese 2001), bobcats (McKinney & Smith 2007, Crête *et al.* 2001, Arjo & Pletscher 1999), and humans. According to the available literature, a linear hierarchy among canids, seemingly ruled by body size, appears to dictate interspecific relationships. The largest of canids, the gray wolf, is one of the main competitors of coyotes. Coyotes will often tend to avoid areas inhabited by wolves. Indeed, they tend to be present mainly in areas where wolf packs were not or less present (Fuller & Keith 1981). A main driving factor of this is that coyotes living within wolf pack's home-range are more likely to be killed by wolves if encountering them (Fuller & Keith 1981). However, Paquet (1991)'s findings contradicted the previous findings, and showed that coyotes were following wolf tracks, and did not avoid wolf presence. The possibility of discovering a carcass killed by wolves could have motivated coyotes to take risks and follow wolf tracks. Although wolves have been found to kill coyotes (Peterson *et al.* 1992, Fuller & Keith 1981), it has been reported that both species can coexist successfully "through spatial and temporal separation as well as through behavioural changes" (Arjo & Pletscher 1999: 1919).

Following the eradication of wolves from many states in the United States, coyotes have thrived and are believed to have expanded their range to fill in the newly available niche (Fox & Papouchis 2005). Coyotes have been observed forming packs to hunt larger

prey such as deer and elk, as the wolves once did (Fox & Papouchis 2005). However, in some states such as Idaho and Montana where wolves have been reintroduced, coyotes which were observed prior to wolf re-colonization were either solitary or had formed bonded pairs that preyed upon lagomorphs and small mammals. It was only after the wolf reintroduction that some coyotes were seen in pairs or in small packs, also hunting ungulate mammals (Arjo & Pletscher 1999). Wolf presence can be advantageous for coyotes in the sense that there is a much increased amount of carrion, on which coyotes often rely during the winter season (Switalski 2003, Todd *et al.* 1981).

The fox is another important competitor for resources. Although smaller in size, they also feed mainly on small mammals (Neal & Sacks 2001, Kamler *et al.* 2007, Randa *et al.* 2009). Foraging strategies appear to be similar between coyotes and red foxes, although coyotes have an overall greater diversity of vertebrate prey in their diets (Randa *et al.* 2009). In the canid hierarchy, coyotes seem to be higher than foxes, probably due to body size and pair/pack territory protection. In fact, declines in red fox numbers have been reported when coyote numbers increased (Cypher 1993). Randa *et al.* (2009) acknowledged the displacement of red foxes by coyotes could be attributed to similar diets and lack of habitat space. Kamler *et al.* (2003a, b) also found similar displacement as well as high mortality rates of swift foxes in areas where coyotes are present. This could be explained by their high dietary overlap with coyotes (Kamler *et al.* 2003b). In many instances, coyotes have been reported to kill swift foxes, although they would rarely eat them (Kitchen *et al.* 1999, Kamler *et al.* 2003a). Furthermore, Kamler *et al.* (2003b: 168) found that “the displacement of swift foxes [by coyotes] was not due to behavioural

avoidance of coyotes but rather to the increased killing of swift foxes within coyote core areas.” Hence, their home ranges rarely overlapped each other (Kamler *et al.* 2003b).

Bobcats also compete for similar resources. Their home-range and diet often overlap with those of coyotes (Chamberlain & Leopold 2005, McKinney & Smith 2007). Although bobcats are more specialized predators with much lower diet diversity than coyotes, both bobcats and coyotes prey primarily upon rodents and lagomorphs. Coyotes tend to have a more diversified diet that will also include larger prey, and fruits and seeds (McKinney & Smith 2007), which makes them better suited than bobcats for short-term adaptation to urban habitats.

2.4 Dietary Habits

Coyotes have very flexible feeding habits that allow them to survive in very diverse habitats, including urban habitats. This flexibility is what enabled them to adapt to varying degrees of resource availability/scarcity. In times of resource scarcity, coyotes are able to switch their prey use towards other available resources (Randa *et al.* 2009). Depending on the term definition, coyotes can often be characterized as a “generalist species”. According to Sorace and Gustin (2008), omnivorous predators, as well as those who can feed on human food sources are “generalist predators”, while carnivorous predators are termed “specialist predators”. Coyotes differ from specialist species because they have been found to feed on anthropogenic food sources (Fedriani *et al.* 2001, Gibson 1974, Lukasik 2009, Morey *et al.* 2007). As opposed to specialist species, their survival is not directly linked to a sole crucial food source but rather to a wide variety of food sources (Cepek 2004, Gibson

1974, Korschgen 1957). This generalist trait may explain their wide-spread and expanding geographic distribution.

According to the existing literature, coyotes commonly prey upon murids (Fedriani *et al.* 2001, Lukasik 2009, Smith & Kennedy 1983, Witmer *et al.* 1995), lagomorphs (Cypher *et al.* 1996, Patterson & Messier 2001), birds (Gibson 1974, Huebschman *et al.* 1997, Lukasik 2009), vegetation (Andelt *et al.* 1987, Huebschman *et al.* 1997), fruits (Huebschman *et al.* 1997), invertebrates (Huebschman *et al.* 1997), and ungulates (mostly fawn) (Harrison & Harrison 1984, MacCracken & Uresk 1984, Patterson & Messier 2000). However, their main prey seems to be composed of small mammals, lagomorphs, ungulates, and vegetation, depending upon the habitat in which they live. Coyotes have also been known to scavenge on deer carrion, especially during the winter season or during a decline in hare abundance (Todd *et al.* 1981). Studies have also shown that coyotes will eat anthropogenic foods and domestic pets in more urbanized areas (Fedriani *et al.* 2001, Lukasik 2009, Morey *et al.* 2007, Quinn 1997), but those items are rarely a major food group in the coyote diet. Domestic poultry, livestock and farm produce can sometimes be an important part of coyote diets in areas where those industries are prominent and especially where leaving livestock carcasses out in the open is a common practice (Gipson 1974, Korschgen 1957).

Based on the literature, the coyote diet seems to vary geographically or, that is, between different climatic regions. In the southern regions of North America, it has been reported that coyotes feed on lagomorphs and rodents consistently (Sanabria *et al.* 1996) but also rely seasonally on deer fawns, and all year-round on fruits (Hidalgo-Mihart *et al.*

2001). Hernandez *et al.* (1994), Hidalgo-Mihart *et al.* (2001) and Sanabria *et al.* (1996) found that coyotes also relied quite commonly on reptiles and arthropods.

In midwestern United States, where a dry climate is characteristic of the region, coyote diet is composed of rodents, lagomorphs and ungulates in all seasons, insects, in some seasons, and wild fruits in some areas and seasons (Fedriani *et al.* 2001, Kamler *et al.* 2007). Gier (1968) also reported a high amount of carrion consumed by coyotes in Kansas. In the western United States, coyotes relied primarily on small rodents and fruits (e.g. crab apple) (Quinn 1997, Young *et al.* 2006), but lagomorphs and white-tailed deer were also important food sources (Young *et al.* 2006, Van Vuren & Thompson 1982). Lagomorphs, woodrats, and cotton rats were staple food items in coyote diet in southern Texas (Windberg & Mitchell 1990). In temperate climates such as that in eastern Canada and United States, small rodents, ungulates and lagomorphs are also staple preys, but ungulate occurrence in scats seems to be more frequent than in warmer regions (Cepek 2004, Huebschman *et al.* 1997, Patterson & Messier 2000, 2001, Toweill & Anthony 1988).

In fact, conflicting opinions exist when researching and interpreting coyote diet. Because of their plasticity in their geographically and temporally changeable behaviours (Bowen 1980, Gompper & Gittleman 1991, Patterson & Messier 2001), generalizations about coyote diet are not wise. However, a prevalent theory is that coyotes are opportunistic feeders that select their prey based on its availability (Andelt *et al.* 1987). Van Vuren and Thompson (1982) categorized coyotes as opportunistic feeders because they found that coyotes quickly responded to newly available food sources by including them in their diet. Changes in coyote diet composition have sometimes been found to

coincide with changes in prey availability throughout the seasons. For example, Windberg and Mitchell (1990) found that rodent presence in coyote diet is linked to its abundance. Meanwhile, rodent presence in coyote diet tends to decrease when alternative food sources such as fruits, insects, and fawns become available during some seasons (Andelt *et al.* 1987). This led many researchers to interpret this relationship as one of opportunistic feeding.

A second prevailing theory is that coyotes are foraging optimally (Hernandez *et al.* 2002). They have prey preferences, and will tend to select those preys when available. Optimal foraging is described in Pyke *et al.* (1977) in four ways, of which the optimal diet is that of an animal that chooses what is best to eat and when it is best to eat such items. Hernandez *et al.* (2002) provided a short summary of the theory and explained it in terms of “costs” and “gains”, where costs are the energy spent foraging and its related hunting attempts, and gains are expressed as the energy obtained from the prey (i.e. calorie content). In those terms, optimal foraging is when “the gains exceed the costs” (Pyke *et al.* 1977 in Hernandez *et al.* 2002: 613). The findings of Andelt *et al.* (1987) further support this, as they observed a decline in lagomorph occurrence in coyote scats that corresponded with the seasonal availability of deer fawns and fruits. Although Andelt *et al.* (1987) have concluded that this could in fact be opportunistic feeding, it could also be indicative of optimal foraging as higher energy demands characterize the pup-rearing season.

To exemplify, Gipson (1974) found that coyotes were more inclined to prey upon domestic poultry during their breeding and pup-rearing season because of higher energy demands of pregnant and lactating females. In other study areas such as in that of Andelt *et*

al. (1987) and Harrison and Harrison (1984), deer fawns were the available food source that was highest in caloric content while lowest in transport energy. This could explain the preference of such food sources during certain biological seasons. In one study, coyote pup diets were primarily composed of deer fawns until their independent foraging (Harrison & Harrison 1984). “Harrison and Harrison (1984) speculated that it is either energetically or nutritionally more efficient to catch and transport deer fawns than small prey” (Huebschmann *et al.* 1997: 106), suggesting that coyote may select their prey based on preference. Hernandez *et al.* (2002) also predicted that in high-energy cost seasons such as the pup-rearing season, coyote will select even more in favour of “high-ranking” foods (i.e. high caloric gains, low energy expenditure costs). In fact, lactating females may need as much as 50% more food than non-lactating females (Gier 1975).

The two theories of opportunistic feeding and optimal foraging can be seen as two somewhat overlapping theories that attempt to explain coyote ecology and survival.² While coyotes may have prey preferences, they are known to adapt their diets to their surrounding habitats and resource availability. According to Randa *et al.* (2009: 594),

² Successful species could be described as species with a high fitness level, which are able to quickly acclimatize to new habitats (i.e. in terms of intra and inter-generational time) through varying ways such as behavioural plasticity. This acclimatization can enable those species to maintain a species abundance that allows an expanding distribution. A more extensive distribution can allow travel between populations, which in turns allows a healthy flow of genes to maintain gene diversity within populations.

coyotes emerged as a species whose foraging strategies rely on “a combination of prey selectivity and switching behaviour.”

Changes in coyote diet can also be linked to seasonal and/or annual climate variations and changes in prey availability and/or abundance. Patterson and Messier (2000) reported that snow depth had a positive influence on white-tailed deer killing rates. Hidalgo-Mihart *et al.* (2001) also reported that heavier rainfall, during one of the years of the study, allowed coyotes to have a longer access than normal to fruits during the dry season. Furthermore, Randa *et al.* (2009) found a significant decline in the abundance of their most frequent prey over time, which corresponded to an ice storm event. Consequently, coyotes relied increasingly on alternative prey after the ice storm.

2.5 Habitat, Home-Range and Activity.

As seen in Figure 1, coyotes have an extensive distribution across North America (Fox & Papouchis 2005). In fact, they can survive and thrive in a wide variety of habitats and ecosystems, including arid deserts, prairies/grasslands, deciduous, coniferous and tropical forests, and mountain habitats (Gese & Bekoff 2004, Fox & Papouchis 2005).

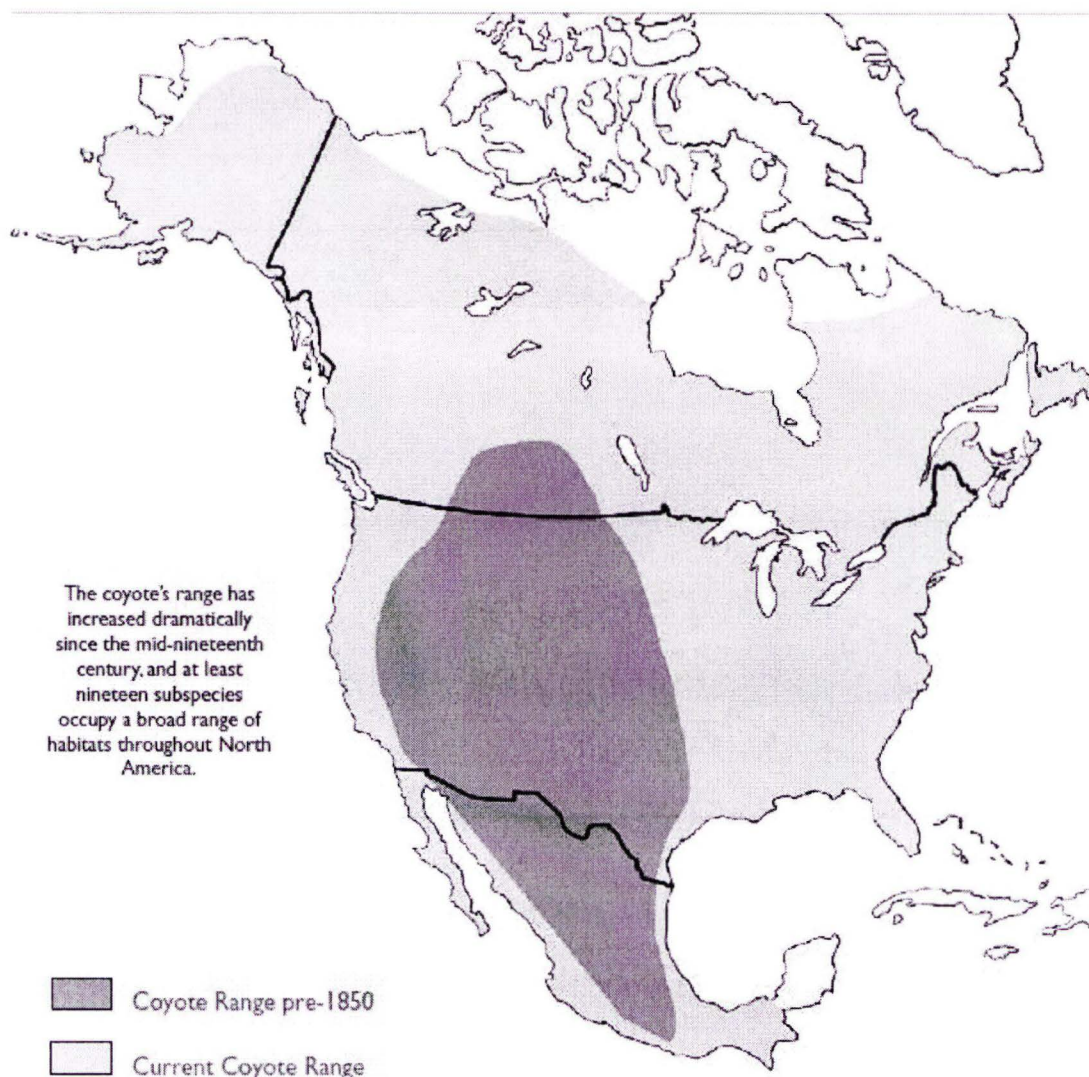


Figure 1: Current and past distribution of coyotes in North America (Fox & Papouchis 2005).

Depending on the productivity level of the habitat, individual coyote's home-range can greatly vary between one another (Gompper & Gittleman 1991, Grindler & Krausman 2001). Various studies on home-range size report average size in their study as small as 4.5 km² (Andelt 1985) and as large as 107.2 km² (Springer 1982) but most range between 30 km² and 50 km² (Andelt & Gipson 1979, Edwards 1975, Gipson & Sealand 1972, Litvaitis & Shaw 1980). Home-range size can also vary widely between coyote individuals. Grindler

and Krausman (2001) reported home-ranges in Tucson, Arizona to vary between 1.7 km² and 59.7 km². Gehrt (2007) found home-ranges varying between 3 and 30 km² and Bowen (1978) found them to vary between 5 and 78 km² in Alberta. Young *et al.* (2006) found similar home-range positions between coyote generations; they also reported that sizes varied according to the individual. Change in social dynamics of a pack can also influence a neighbouring pack's home range size as it can create possibilities to increase its boundaries (Gese 1998). Body size may also influence prey selection and diet, which may in turn affect travelling distances and home-ranges in response to prey size, distribution and abundance.

Sanderson (1966) described a home-range as "an area where use is likely determined by factors such as habitat composition, physiographic makeup, food distribution as opposed to abundance, and many factors that fulfill innate needs for survival" (Gese *et al.* 1988: 645). Such habitat characteristics and their influence on home-range size have been documented. In fact, home-range size may vary between different vegetative and topographic areas (Gese *et al.* 1988). Gese *et al.* (1988) noted that coyotes in canyons and hills had the smallest home-ranges while coyotes in prairies had the largest. As observed by Gompper and Gittleman (1991), home-range size can be dependent on diet since high biomass prey such as ungulates can be scarcer on the territory than smaller mammals, fruits and garbage. They also reported a strong correlation between home-range size and latitude, which was explained by the fact that lower latitudes tend to have more productive habitats, thus reducing the territory size needed to fulfill survival needs. In fact, in one study, territory size decreased with increased deer density and hare density

(Patterson & Messier 2001), also suggesting coyote home-range size may change according to habitat productivity, and their life-history and survival needs.

Grinder and Krausman (2001) noted that home-ranges can sometimes overlap during some seasons. However, territoriality is present because home-ranges of individuals of the same sex do not tend to overlap (Andelt & Gipson 1979, Althoff 1978). In the Welder Wildlife Refuge in southern Texas, adult coyotes travelled more during the breeding season, while females travelled less during the pup-rearing season (Andelt 1985). Some adult coyotes may also leave their home-ranges, but “coyotes with exploratory behaviours may not be involved with pup-rearing” (Laundré & Keller 1984: 136, Litvaitis & Shaw 1980). Overlapping of home-ranges and/or exploratory behaviours can be expected during the breeding season as solitary coyotes seek a mate. While some studies have found no difference between home-range size of females and males (Grinder & Krausman 2001, Laundré & Keller 1984), others have found that females often use smaller areas during the breeding season than the pup-rearing season (Laundré & Keller 1981) and/or stated differences in the average home-range size between genders (Berg & Chesness 1978, Litvaitis & Shaw 1980, Servin & Huxley 1995). However, in a bonded pair, both males and females will often “center their activities near den sites during the nursing period with females being more restricted to the den than males” (Harrison & Gilbert 1985: 712).

Habitat productivity, resource availability, distribution and diet can provide insights into coyote home-range size and use in urban areas. Indeed, Atwood *et al.* (2004) reported a negative correlation between urbanization level and home-range size, suggesting that urban habitats may be more productive for coyotes. Concentrated availability of “low cost”

food sources, such as, garbage and urban animals may reduce their needs for increased travelling distances and foraging area size. In fact, in Tucson, Arizona, coyotes spent most of their active hunting time in residential areas, which probes a speculation that residential areas may be higher in food sources (Grinder & Krausman 2001). Laundré and Keller (1981) found that coyotes seemed to travel less during the night in urban areas than they do in rural areas. Because abundance and distribution of resources in the habitats vary, Laundré and Keller (1984) argued that studies should focus on home-range use rather than size alone.

Various studies indicate that coyotes are most active during the sunset and sunrise times (Grinder & Krausman 2001, Young *et al.* 2006). Although they are active at all times of the day, their movement rates appear to generally increase during nocturnal periods, especially in urban environments (Young *et al.* 2006, McClennen *et al.* 2001, Andelt 1985, Gese *et al.* 1989, Grinder & Krausman 2001, Quinn 1995). However, some studies contradict these findings. Kitchen *et al.* (2000) found that coyotes in southeastern Colorado were most active during the day while Patterson *et al.* (1999) found that coyotes living in forested landscapes in Nova Scotia presented no diel cycle in their movement and activity rates. Furthermore, there is an acceptance that the absence of a diel cycle in coyote activity and movement rates is representative of coyotes living in a fairly undisturbed natural environment (McClennen *et al.* 2001, Andelt 1985, Kitchen *et al.* 2000). This diel cycle can be somewhat attributed to human-induced “environmental stimuli that have increased the amplitude of the circadian rhythms of the coyotes” (McClennen *et al.* 2001: 27). Their movement and activity patterns have shifted to mostly nocturnal in order to avoid human

activity. Hence, their diurnal movement rates have decreased (Andelt 1985, Kitchen *et al.* 2000), and a habit of steering clear of residential areas until night time was developed (Way *et al.* 2004).

Activity and movement patterns can affect diet in the sense that urban coyotes may need to shift their patterns to avoid human activity. By doing so, it could perhaps affect their capacity to successfully capture their usual prey. Urban areas could also have differing prey populations, such as rodent populations, which could affect coyote reproduction (Bekoff 1977). An understanding and application of our available knowledge on coyote life-history traits, such as their diet habits, can help minimize and/or prevent human-wildlife conflicts. It can also aid in our management efforts to maintain an ecological balance in human-dominated landscapes, and ensure the preservation of all ecological processes that provide all of us fundamental services and benefits.

Chapter Three: **STUDY SITES**

The study sites were divided between urban and rural areas (Figure 2). Urban areas were defined as sites within the limits of the City of Calgary. Most sites bordered on residential areas, although commercial and industrial land use types were also found within the city. In contrast, rural areas were beyond the limits of the City of Calgary, where agricultural and natural land use types predominated. The urban study sites were located in Calgary, Alberta (Figure 3) and the rural sites were located on the outer skirts of Calgary (Figures 4 & 5). Ten urban sites and seven rural sites were chosen in and around Calgary. In order to have a representative urban sample size, it was necessary to include more sampling sites within the city of Calgary. Moreover, time and limited access to private properties and the Tsuu T'ina First Nation Reserve all limited the number of rural sites that could be selected. More study sites could have been chosen, but for the scope of this Master's thesis and because of resource and time limitations, it was decided that those seventeen sites would provide ample data for my research purposes and objectives.

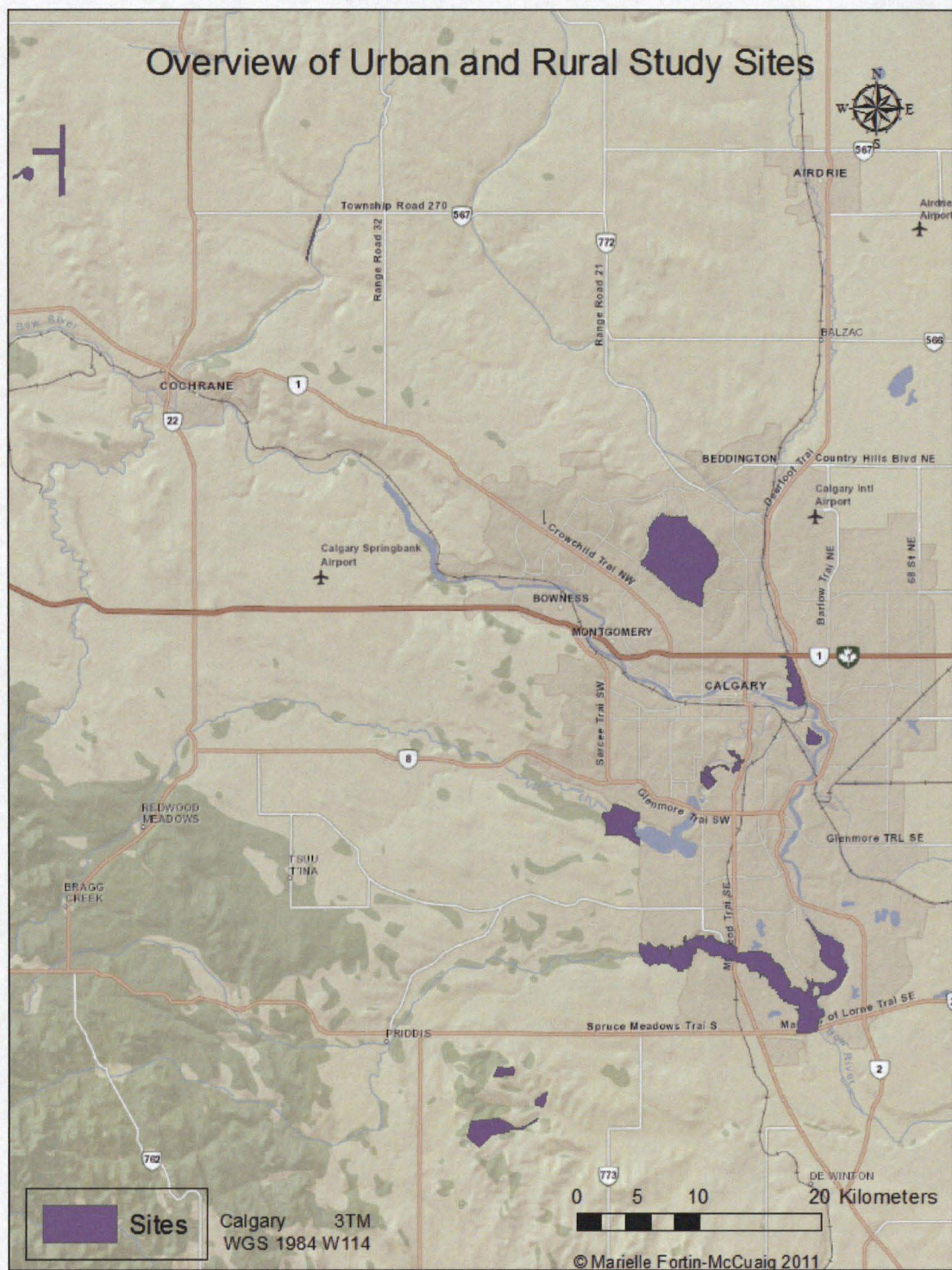


Figure 2: Map of the study area and all study sites.

3.1 Urban Study Sites

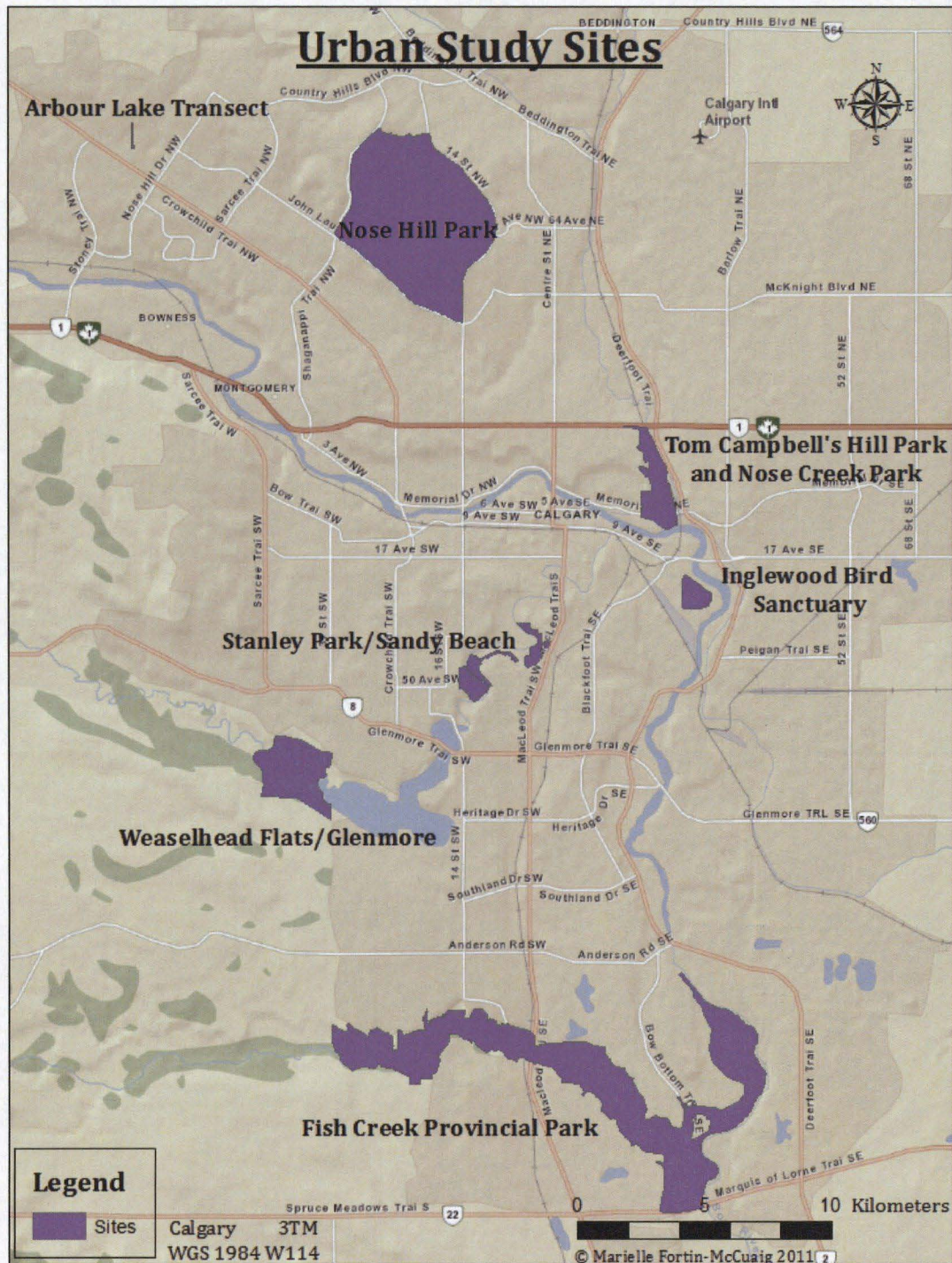


Figure 3: Focus map of all the urban study sites located in Calgary, AB.

3.1.1 Arbour Lake

The Arbour Lake study site consisted of a walking transect on a path between an urban private agricultural property and the northwestern neighbourhood of Arbour Lake. The path served as a walking path and a back road, which is adjacent to private backyards. The site was located in proximity to an elementary school. A power station, the Crowfoot train station and the Crowfoot road leading to the Highway 1A were also near the transect. Vegetation near the site was characterized by grasses and shrubs, which were located on the private agricultural land. Green turf and asphalt were on or next to the transect. Crab apple trees could be observed in some residential private backyards.

3.1.2 Nosehill Park

At 1127 hectares, Nosehill Park is the largest municipal park in Canada (Bullick 2007, City of Calgary 2007). Located in the northern part of the City of Calgary, it is surrounded by a road network, and suburban neighbourhoods, which contribute to its isolation within the city. Due to its size and its isolated height, it can easily be seen from a distance. As the name indicates, the park constitutes a significant hill, which reaches a plateau. It was preserved for its natural environment as well as for its native archeological features (City of Calgary 2011). It is part of a grassland habitat that is representative of the Canadian Prairies. Within the park, an extensive network of trails and pathways – paved, gravel or dirt – can be found. Small groupings of trees and shrubs can be seen in depressions and coulees as well as on the lower parts of the slopes. Large mammals, such as mule deer and coyote often take refuge in those small woods and coulees (City of Calgary

2011). Native grasses, predominantly Rough Fescue, make up most of the vegetation on the plateau (City of Calgary 2011). Porcupines, jackrabbits, Northern pocket gophers, Richardson's ground squirrels, mice and vole species as well as Northern harriers and Swainson's hawks are animal species that can be seen inhabiting the park (City of Calgary 2011).

3.1.3 Tom Campbell's Hill

Tom Campbell's Hill is located close to the downtown area, in central northeast Calgary. It covers roughly 18 hectares, and is situated in close proximity to the Bow River (City of Calgary 2011). In fact, Calgary's skyline and the Bow River Valley can be seen from the more elevated areas of the park. It is also to be noted that the park is adjacent to the busy Deerfoot Highway, sports fields and the Calgary Zoo. Also part of a grassland habitat, the park is characterized by the presence of Rough Fescue (City of Calgary 2011). Awnless Brome can also be seen (City of Calgary 2011). Planted poplars grow on parts of its grounds as well, and attract a variety of invertebrates, and insectivorous birds (City of Calgary 2011, Bullick 2007).

3.1.4 Inglewood Bird Sanctuary

The Inglewood Bird Sanctuary is a 36 hectare park adjacent to the Elbow River, not far from the downtown area of Calgary (City of Calgary 2011). It is mostly located on flat grounds spotted with lagoons and has an extensive network of paths. As the name indicates, it is a bird sanctuary, more specifically a migratory bird sanctuary that is home to

217 bird species, 21 mammal species, 27 species of butterflies, 347 species of plants, 7 species of fish, 2 amphibian species, and 2 reptile species (City of Calgary 2011).

3.1.5 Stanley Park

Stanley Park is a 21 hectare park located on the banks of the Elbow River (City of Calgary 2011). Many popular activities can be practiced in the park, including swimming in the outdoor pool. Cycling and walking paths pass through the park, which also features a notable hill often frequented during the winter for tobogganing. A school, an off-leash area for dogs, and neighborhoods are close to the park. The location of the park within the city as well as all the activities in which people participate make this park a site with high human activity. Vegetation is diverse in the park due to its varying habitats and topography. On its western part, grasses are present on flat ground while forested areas cover its much steeper northern part. Sports fields are present in its southern and eastern parts (Bullick 2007). Downstream from the Glenmore Reservoir, Sandy Beach Park borders the Elbow River on the northern side, and covers 33 hectares (City of Calgary 2011).

3.1.6 North Glenmore Park and Weaselhead Natural Wilderness Area

Glenmore Park and the Weaselhead Flats are located in southwestern Calgary. They border the Tsuu T'ina First Nation Reserve. Glenmore Park is divided into the North Glenmore, South Glenmore and East Glenmore Parks. Two samples were collected near the Weaselhead Flats and South Glenmore Park border. All other samples were collected in the Weaselhead Natural Wilderness Area and the North Glenmore Park. North Glenmore

covers an 84 hectares area on the northern part of the Glenmore Reservoir (City of Calgary 2011). It is home to the Calgary Canoe Club, Calgary Sailing Club and the Calgary Rowing Club.

The Weaselhead Flats are directly adjacent to the Tsuu T'ina First Nation Reserve. At the mouth of the Elbow River, the delta and natural wilderness areas cover 237 hectares (City of Calgary 2011). Habitats such as wetlands and marches as well as coniferous forests, deciduous forests and sandbar shrubs are located in the delta or the Weaselhead Flats. A wide array of species can be found, such as black bears, hummingbirds, crossbills, tundra swans and common loons (City of Calgary 2011).

3.1.7 Fish Creek Provincial Park

At 1,430 hectares, Fish Creek Provincial Park is the largest urban park in Canada (Foley 2006). It extends along a 19 km-long stretch of waterway between the Tsuu T'ina First Nation Reserve and the Bow River, thus linking the southwestern and southeastern areas of Calgary. Agricultural land borders its southern tip. It is adjacent to major roads and public transit stations (i.e. light rail station) as well as containing multiple water bodies such as oxbow lakes, creeks and the Bow River. An extensive network of trails and paths can be found within and beyond its boundaries. Habitats found within the park are grassland, wetlands and forests. Those different habitats provide a refuge for multiple songbirds and other animal species such as coyotes, mule deer, white-tailed deer, snowshoe hares, muskrats, beavers, porcupines, weasels, pocket gophers, Richardson's ground squirrels, red squirrels, meadow voles, shrews, little brown rats, owls,

woodpeckers, Canada geese, great blue herons, hawks, bald eagles, among others (Gov. Alberta 2011a). Two study sites were within the park. One was located in the western edge of the park while the other was located in the southeastern edge of the park, known as Sicome. These two sampling sites were walking transects on a path.

3.2 Rural Study Sites

3.2.1 North Sites



Figure 4: Focus map of the northern rural study sites.

3.2.2 Big Hill Springs Provincial Park

Big Hill Springs Provincial Park is a 31 hectare park that preserves a creek flowing in a deep valley ridges (Gov. Alberta 2011b). The sampling site was located on Big Hill Springs Road (Range Road 34A) between its intersection with the larger Township Road 567 and the parking lot at the entrance to the park. The site consisted of a transect that was located immediately outside the park limits. The transect was set deep into a narrow valley. Both sides of the transect were privately owned agricultural land. Cattle were often seen grazing on the eastern slope and deer were also a frequent sight. The main habitat was that of grasslands spotted with shrubs. The lower grounds of the valley were often flooded by an overflowing creek.

3.2.3 Kerfoot Farm (private)

Kerfoot Farm was a privately owned agricultural property. Permission to enter, travel and sample at and on the property owner was obtained prior to any sampling. It was mainly used as a cattle farm, although a herd of horses was rotated between its different fields. The sampling area encompassed the entrance road of the farm, the central field facing the housing buildings, and trails in the woods behind the main centre field. The walking transect was along fence lines, and along the entrance road. Grasses and shrubs made up the most part of the vegetation while small woods with shrubs and deciduous trees made up the rest. A coyote den was located on slope to the east of the house, and orientated on a northwestern direction. A porcupine was seen taking shelter in the den during the winter time. Mule deer and white-tailed deer were also a common sight.

3.2.4 Horse Creek Road and Township Road 272

Horse Creek Road and Township Road 272 were two intersecting roads, which served as sampling transects. Both roads pass through agricultural fields that served as cattle farms, grass crop farms or equestrian hobby farms. A canine boarding facility was located on the northwestern part of Horse Creek Road. Habitats and wildlife were the same as described in the Kerfoot Farm.

3.3 South Rural Sites

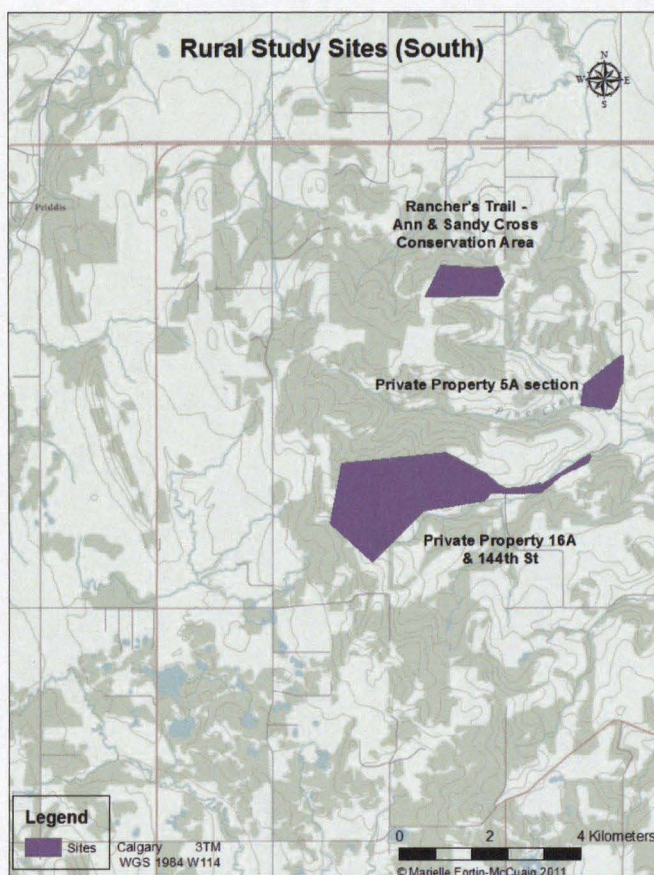


Figure 5: Focus map of the southern rural study sites.

3.3.1 Ann & Sandy Cross Conservation Area

The Ann and Sandy Cross Conservation Area is a privately owned property that was turned into a conservation area that spans over 1,900 hectares (Cross Conservation 2011). The sampling transect was specifically located on the Rancher's trail where grassland habitat reigned. Deciduous forests were also present nearby. Mule deer and white-tailed deer were a very frequent sight. Other present species were cougars, black bears, badgers, red foxes, weasels, elks, moose, muskrat, red squirrel, ground squirrel, vole and shrew species, and bald eagles, among others.

3.3.2 Private Land Parcels 5A and 16A on 144th Street

Land parcels 5A and 16A were located at the southwestern edge of Calgary, outside its city limits. These sites were being used as agricultural land and partly bordered on the Sandy Cross Conservation Area. These two sites were treated independently. In fact, different families of coyotes as well as their respective dens were spotted by the land owner. Habitats were the same as described in the Ann and Sandy Cross Conservation Area where grasslands and deciduous forests were seen.

4.1 Sample Collection

Field sampling was done in 7 sites throughout the City of Calgary (Figure 3), as well as in parks and large rural properties (with owner's permission) outside the City of Calgary limits (Figures 4 & 5). Transects consisted of sections of beaten paths, walking/cycling paths, road sides and fence lines. Transects were chosen on the basis of known coyote sightings (Lukasik 2009), presence of coyote scat during the exploration period, and especially, on the basis that coyotes tend to travel along already set paths, and will often defecate as a means of territory marking (MacDonald 1980). Existing boundaries such as paths, roads and fence lines will often serve to establish their own territory markers (MacDonald 1980, Gese & Ruff 1997). As such, roads, beaten paths, and fence lines were chosen as part of some of the rural transects, and walking transects were established on beaten paths and walking/cycling paths within the urban sites.

Samples were collected on foot. Walking was done at a speed of roughly 4-5km/h in most cases. However, in some rural sites (such as road transects), they were collected while driving through transect at a rough speed of 5-15 km/h and stopping to collect the samples. A pedal bike was also used during the summer on Nose Hill Park (rough speed of about 5-7 km/h). The use of a Jeep on road transects was safer, as well as much faster to collect scats. When the pedal bike was used, travel was done at a speed that was slow enough for the eyes to cover, visually, both sides of the path. Variable ways to collect data were chosen for logistical and safety reasons. Logistically, covering transects by car

allowed us to cover longer transects, thus yielding more scats every week. It was also used as a safety measure on sites such as Horse Creek Road, 144th St SW, and Big Hill Springs Trail Road. The car provided a barrier between the oncoming cars and me, which was especially needed during snowy and icy road conditions. The sampling could be biased towards bigger and darker scats because they may be more visible on the road than smaller and paler scats. However, only less than 1 to 2 weeks old scats were collected to ensure a good time stamp on the sample. Additionally, scats too small in diameter were not collected in order to avoid a misidentification of a scat (i.e. although smaller in size, fox scats are similar in appearance to coyote scats). The potential to miss collectable scat samples along transects was considered especially small when driving speed was lower than 15 km/h.

Fecal samples were collected weekly on established transects between the months of July 2009 and July 2010. Weekly sampling allowed for a seasonal analysis of coyote diet. Sampling on a regular weekly basis allowed for a consistent clearing from transects of present scats. It also made it possible to age the scats as “less than a week old”, and thus provided each sample with an approximate time stamp. This time stamp was found to be less accurate in winter and spring seasons. Indeed, scats were sometimes covered by a recent snow fall and/or kept frozen. Thus, they may have been conserved throughout the winter until the melting of the snow exposed them again. In order to reduce any potential sources of error or bias, weathered or very wet scats were not collected during the melting season.

When no scats were found on transects for more than two consecutive weeks, those transects were sometimes modified to follow changes in coyote habitat use and habitat

selection. This could have introduced a slight bias in the scat collection. However, I considered it valuable to modify transects within the study sites to account for the shifting nature of coyote movements through diel (McClennen *et al.* 2001), seasonal and annual time (Gese 1998), as well as the statistical need for a continued scat yield. Transects were modified and/or lengthened in Nose Hill Park, and in Weaselhead Flats when scat yield from the established transect became low to non-existent for longer than two weeks.

Scats were identified according to size, colour, shape, texture and location based on Chame (2003) and Halfpenny and Biesiot (1986) as well as with additional training received in scat identification from Dr. Shelley M. Alexander and fellow graduate student Victoria Lukasik. Scats that did not fulfill the identification criteria for coyote scat were tossed away from the transect, so as to not be confused with fresh coyote samples on the following sampling week. Table 1 describes the identification criteria used in scat identification:

Table 1: Description of identification criteria used in scat identification, which were based on Chame (2003) and Halfpenny and Biesiot (1986).

Criteria	Coyotes	Dogs
Size	55-88 x 20 mm (L=10.6 cm; < 3 cm Ø; 1.8-2.5 cm Ø)	Varies according to size of the individual
Colour	Black, dark grey, white or reddish	Brown or yellow
Shape	Cylindrical, often tapered, subdivisions	Tubular with definite ends
Texture	Firm to hard; can be porous when berries or insects are present	Soft and grainy
Composition	Undigested items are often present	Most often uniform
Location	Often on trails, roads or fence boundaries	More random and most often off of the paths

According to Chame's (2003) identification key, coyote scats are part of the group 1 (out of 9 groups). Feces of this group can be characterized and identified by their cylindrical shape along with subdivisions and tapered extremity. While misidentification is possible within this group, additional considerations such as location of the scat and ecological knowledge of the study sites can further reduce the potential for misidentification. After conducting molecular testing on carnivore species, Prugh and Ritland (2005) found that in 92% of the cases, coyote scats had been correctly identified by observers, even when wolves co-existed with coyotes. From Weaver & Fitts (1979)'s conclusions, only 4.9% of the scats were misidentified. This indicates that even in the presence of sympatric predators, coyote scats can be properly identified in most cases, or at least, with sufficient accuracy for diet studies (Prugh & Ritland 2005).

Following collection, each individual scat was placed in plastic "Ziploc®" sealable bags, and identified by taking note of the study site, the study region, the date, the time and the GPS waypoint. The geographic location was recorded with a Global Positioning System unit (GPS; Garmin E-Trex Legend HCx, Garmin International Inc., Olathe, Kansas, USA). The geographic points were documented in the form of waypoints (geographical coordinates; latitude, longitude) which provided exact collection date and time stamps. These waypoints were used as the main sample numbers for sample identification method. First, the location of the scat was noted (i.e. region and name of the study site). Second, the date (mm-dd-yyyy) was written. Finally, the waypoint number was specified as well as the GPS unit on which it was taken. Two GPS units of the same make and model were used to take waypoints. One was used by Alexander Watts and one was used by me. Alexander Watt's

GPS was named (A) and my GPS was named (M). For example, a scat collected at Big Hill Springs on November 22, 2009 would be noted as follows:

NWR (i.e. Northwest Rural)

BHS (i.e. Big Hill Springs)

NOV 22, 2009

(M) 039 (i.e. waypoint number 039 on my GPS unit)

Scat samples were then brought back to a University of Calgary Veterinary Medicine laboratory, where they were deep-frozen at a temperature of minus 80°C for four consecutive days. This freezing process ensures any potential transmission of harmful parasites and parasite eggs such as the granular tapeworm (*Echinococcus* spp.; Kennedy & Carbyn 1981) is eliminated. After deep-freezing, the scats were transported to an Earth Sciences laboratory, and stored in a commercial freezer at a temperature of approximately minus 10°C for later dissection and analysis. To allow comparisons and conclusions to be drawn between the Lukasik (2009) and this study, methods described in Lukasik (2009) were followed during scat analysis for identification of food items.

4.2 Laboratory Methods

4.2.1 Stomach Content Analysis versus Scat Analysis

Conventionally, there are three methods used to quantify and analyze coyote diet: direct observation, digestive tract or stomach content analysis and scat or fecal analysis (Smith & Kennedy 1983, Ciucci *et al.* 1996, Landry & Van Kruiningen 1979). Since in the case of coyote studies, direct observation is very time consuming, yields mostly incomplete

results, and is at best an incidental tool (Gier 1968), only the stomach content analysis and scat analysis methods will be reviewed in this chapter.

The digestive tract content analysis enables the researchers to differentiate between carrion and freshly killed prey (Landry & Van Kruiningen 1979). However, it is a much more invasive method that limits the potential sample size by requiring an animal carcass. The potential for a temporal dietary analysis or even a spatial analysis is much lower since one carcass or coyote individual represents only one sample. The digestive tract content analysis method is much more expensive and time-consuming. It also requires more preparation and organization, and it relies upon facility and equipment availability. Furthermore, a seasonal diet analysis would also not be easily feasible since the sample collection time frame may be strongly limited to the hunting season. Due to other limitations, scat analysis was the only reliable and available method of analysis that could be used. Such limitations include ethical reasons against the unnecessary killing of coyotes, the insufficient number of available coyote carcasses for diet studies, the time frame, resources, the lengthy laboratory training, and for comparative purposes (i.e. being able to compare my results with those of Lukasik (2009)).

Scat analysis is a non-invasive method of sample and data collection. Since the samples analysed have already been through the digestive tract, there may be less material to analyse. However, because of their eating habits, scat analysis remains a method that provides a representative analysis of coyote diets. In fact, Landry & Van Kruiningen (1979: 781) recognized that “carnivores masticate their prey minimally and prefer to swallow large bollets”, i.e. portions of carcasses with indigestible elements included. According to

Gier (1968), a meadow mouse would pass through the digestive system and be completely eliminated in one scat. However, food items that have passed through the digestive tract may not be representative of proportional food consumption (Gier 1968). In order to reduce biases, relative frequencies of occurrence can be combined with relative volumetric measurements of food items found in scat samples. It is important to choose analytical methods that will depict results that are as close to reality as possible so as to not disguise any possible differences or relationship, and avoid any Type I or Type II errors in interpretation. Scat analysis also has many advantages. It allows for an easier collection of samples; it is easier to collect for large sample sizes; the sampling procedure is non-destructive and non-invasive; it is also faster to produce results; and it is inexpensive

Scat removal also remains a source of bias. According to Livingston *et al.* (2005:177), "scat removal from coprophagy from other mammals can prove to be a source of bias in dietary studies based on fecal analyses if scat contents are assumed to be representative of foods consumed." In their 2005 study, they found that "rates of removal of feces from captive bobcats, captive coyotes, and free-ranging coyotes varied from 7% during spring to 50% during summer (Livingston, 2005:172)." In most cases, they found that opossums (*Didelphis virginiana*) were the coprophagy culprits and that scat removal from caching was done by Eastern woodrats (*Neotoma floridana*). Other sources of scat removal include weathering, precipitation events such as snow falls and rain storms, and removal of scat by other coyotes, accompanied by deposition of fresh scat as a means of territory marking. Coprophagy could influence diet results if scat removal was done in a

selective manner by other species. However, there is a lack of research on the influence of coprophagy on scat sampling.

Prey item identification was done through microscopic analysis, which examines the physical characteristics of the prey item (e.g. hair's phenotype). Resource availability made microscopic analysis the only available option. Microscopic analysis of macro-components such as hair, claws, teeth, bones, feathers, stems and other remains, provided a better base and background for comparison with the 2006 scat sampling results obtained by Lukasik (2009).

4.2.2 Laboratory Settings

A total of 617 scats were collected. After a secondary verification that scats met identification criteria (Table 1, p. 35), a total of 338 scats were analyzed, of which 178 were from rural sites, and 160 were from urban sites. Scats were then selected so as to have 30 samples per study site. For sites yielding over 30 scats, the least weathered samples were chosen first because they would be more representative of the diet at the specific time of collection. In certain study sites we found fewer than 30 scats were collected, which meant all samples collected for that site had to be analyzed. I assumed that only the diet of adult coyotes was analyzed, because any scats of smaller diameter that could have belonged to a coyote pup or a young juvenile would have been discarded for failing to meet the size criterion for identification. This also reduces the potential for misidentification of a scat that could have originated from another smaller sympatric predator such as foxes and bobcats.

Essential knowledge and skills for the identification of mammal hair in scat samples was acquired through training sessions with biologist John Paczkowski and fellow graduate student Victoria Lukasik (February 2010, University of Calgary). Mammal hair identification references were used to compare hair found in each sample, and support food item identification (Adorjan & Kolenosky 1969, Moore *et al.* 1974, Kennedy & Carbyn 1981). Prior to the analysis, samples were defrosted at room temperature for approximately one hour. Defrosted samples were then individually examined, and dissected. All items were separated into the dissecting dish according to its distinguishing characteristics such as hair colour, hair length, hair diameter, hair medulla and shield morphology, bone density (e.g. hollow bones in birds), teeth, claws, and all other non-animal parts (e.g. stems, seeds, insect parts, plastic, wrappers, rope, fruit skin, etc.). After all food items were identified, they were grouped into the above-mentioned food sub-categories and their depths were equalized in the dissecting tray. Their relative volume was then calculated by placing a one-inch transparent grid over the dissecting dish. Relative volume was determined by counting the number of grid squares occupied per food group items (Table 2), and dividing that number of grid squares by the total number of grid squares occupied by all prey items in the dissecting dish. This proportion was then multiplied by 100 as to obtain a percentage value.

To simplify descriptions, comparisons and analyses, prey species found in scat samples were pooled into one of eleven major diet groups or food sub-categories:

Table 2: Illustration of food groups.

Food Source		Food Groups		
Wild Mammals	Small Mammals	Medium Mammals	Large Mammals	
Vegetal	Plants & Grasses	Berries		
Human-Linked	Waste/Garbage	Cats & Dogs	Cattle	Crab Apples
Others	Birds	Insects		

For the purposes of this study, small mammals are defined as mammals whose average weight is less than 450 grams or approximately one pound. Small mammals include shrews, voles, moles, mice, rats, ground squirrels and other squirrels, gophers and ermines. Medium mammals are defined as all mammals, excluding domestic animals, whose average weight and size surpasses that of a small mammal but is less than that of an average deer. Such mammals include minks, weasels – with the exception of ermines, snowshoe hares, white-tailed jackrabbits, and muskrats. In this study, large mammals refer to white-tailed deer and mule deer, fawns included.

The reasons for grouping prey items into aggregated categories was that I believed “small mammals”, might be more precise and provide more accurate results than a species or family category, because of the nature of the analysis and samples. It is very tedious to distinguish vole, mouse, mole and shrew hair in a very compact scat because of the similarities in the diameter, length and color of their hair. Aggregated categories reduced the chances of over or under representation of a species in a scat sample. Other studies have also used food item grouping (Morey *et al.* 2007, Schrecengost *et al.* 2008). In this study, I did not examine the effects of coyote predation on specific species or on

conservation of species. In fact, the objective of this research was to quantify and differentiate anthropogenic food sources, and pet and cattle remains from natural food sources in urban and rural scats. Analysing down to species in each food group here would have been extraneous to the purposes of this study.

4.3 Statistical Analysis Methods

More often than not, parametric statistics provide results which allow more precise and powerful interpretations than nonparametric statistics while also reducing the probability of committing a Type II error (Zar 1999). However, when testing with nonparametric statistics, this difference in power can be minor with larger samples (Motulsky 2005).

4.3.1 Statistical Considerations: Sample-size and Over/Under-representation

“Sample-size issues are usually more important when it takes a lot of time to collect the data. An agricultural experiment may require a whole growing season, or even a decade, to complete. If its sample size is not adequate, the consequences are severe. It thus becomes much more important to plan carefully, and to place greater emphasis on hedging for the possibility of under-estimating the error variance, since that would cause us to under-estimate the sample size” (Lenth 2001: 7).

Trites and Joy (2005) found that a minimum of 94 samples were necessary when comparing diets over time or between areas. Thus, the sample size of 338 scats or 178

rural and 160 urban scats was large enough to have statistical power for spatial diet studies.

As suggested by Morey *et al.* (2007), small prey items can be overestimated when using the percentage of occurrence of food items in scats during statistical analyses. To reduce biases towards smaller prey items, Morey *et al.* (2007) decided that food items occurring in less than 10% in an individual scat was not counted. However, I felt that this proportion was slightly high. Prugh (2005) determined that a limit set on more than 2% of the scat volume could help reduce biases. Since volumetric proportions were also analysed, the potential for overrepresentation of small food items was reduced. Also, because canids consume their prey on the ground, the presence of low percentages of occurrence of items such as soil, pebbles, twigs, grass and insects may be incidental. For this study, I assumed that very low relative volume values (i.e. < 5%) of these food items did not represent voluntary food selection, and I did not account for these very low values when computing frequency of occurrence values. More precisely, food items that occurred in a proportion of less than 5% in an individual scat were not included in statistical analyses. Alternatively, if relative volume values were 5% or higher, I made the assumption that this food item was part of the coyote's food selection.

Food items with a much higher biomass, such as large mammals, would have been overestimated if volumetric measurements were analyzed alone (Gier 1968). Otherwise, analyzing solely results from the frequency of occurrence would have overestimated food items with a small biomass, such as small mammals, insects, birds and berries. Therefore,

volumetric measurements and frequency of occurrence data were both analyzed to allow for a less biased depiction of reality.

4.3.2 Data Analysis

To perform all diet data statistical analyses I used the statistical software IBM SPSS Statistics 19.0 (SPSS Inc., Chicago III, 2010). First, mean volumetric measurements for each prey item category were calculated. Second, relative frequencies of occurrence were calculated by re-coding all data for each food item category. A value of “1” was given for all “Present” volumetric measurement data, which was quantified as having a proportion of 5% or higher in the scat. All volumetric measurement data having a proportion of less than 5% in the scat were given the value “0” for “Absent”. Hence, each scat represented one sample or one observation. All frequencies were then categorized into their respective independent variable category (i.e. spatial area (urban or rural), biological season (breeding, pup-rearing, or dispersal) or calendar season (spring, summer, fall, or winter)). All independent variables were also re-coded with a nominal number representing one category (e.g. urban = 1, rural = 2).

The absolute frequency of occurrence was calculated as the number of scats containing the food item. The relative frequency of occurrence was computed by totalling the number of occurrences of each food type, dividing it by the total number of scats, then multiplied by one hundred:

Equation 1:

$$RF = (f_i / \Sigma_n) * (100)$$

Percent Frequency was also calculated so as to have mutually exclusive categories – which is a requirement for the Shannon-Weaver Diversity Index calculations. It represents the number of scats containing a food item from a category, divided by the total number of food items present in all scat (absolute abundance/frequency total count). When requiring a percentage value instead of a proportion, it was multiplied by 100, as shown in the equation below.

Equation 2:

$$PF = (f_i / \Sigma f_i) * (100)$$

4.3.2.1 H1: Spatial Differences in Coyote Diet

Diet was compared between urban and rural samples. To recapitulate, urban sites were those within the limits of the City of Calgary, whereas rural sites were those beyond the City of Calgary limits, where agricultural land use type predominates. The dependent variables consisted of food groups. These dependent variables were of ratio type, and were dependent on a spatial independent variable, that is, of the urban or rural category.

To test the spatial difference hypothesis, the Kolmogorov-Smirnov goodness-of-fit test was performed to determine if the data followed a normal distribution (Zar 1999). A first outcome scenario would be that the data follows a normal distribution. If so, a two-sample independent *t*-test could be appropriate in determining the significance of the differences between the urban and rural coyote diets. With a *t*-test, the statistical significance of the differences is determined by comparing the means between the two groups. In this case, separate *t*-tests would be performed for each dependent variable,

which would compare the means between the urban and rural diet data sets. Zar (1999) describes a *t*-test that can still be performed with data that is not normally distributed, providing the two samples are of approximately the same size. However, as normality is a critical assumption of the parametric *t*-test, I decided that if the data did not meet the normality assumption of the *t*-test, a non-parametric test that is analogous to the *t*-test would be performed.

In this case, a second possibility was that the data were not normally distributed. If so, the Mann-Whitney U test – also called the rank sum test – could be substituted for the *t*-test as it does not assume any distribution (Zar 1999, Hinton 2004b). Instead of comparing means, the Mann-Whitney U test ranks measurements of two unpaired samples (Zar 1999). Here, measurements used would be volume measurements of food items in the scats.

Relative frequency of occurrence or relative abundance of food items can be further compared using a Pearson Chi-Square test. Because the Pearson Chi-Square test does not have any assumptions about the shape of the underlying distribution, it is considered to be a nonparametric statistical test (SPSS 2010, Hinton 2004b). However, there are a few assumptions to consider. First, it assumes that the data come from a random sample, and second, that category expected frequencies have values of at least 1, with a maximum of 20% of the categories having expected frequencies of less than 5 (SPSS 2010, Hinton 2004b). Analysing both the volumetric measurements and the relative frequency of occurrence of food items will strengthen the spatial analysis. Spatial differences are examined between urban and rural settings, and spatial differences are also described

between study sites as to identify larger scale changes within the study areas (i.e. urban versus rural).

4.3.2.2 H2: Temporal Differences in Coyote Diet

Biological and calendar seasons were used as the independent variable in this portion of analysis. As defined by Morey *et al.* (2007), the three biological seasons are Breeding (January 1 – April 30), Pup-rearing (May 1 – August 31), and Dispersal (September 1 – December 31). Another temporal division is done following the Canadian calendar seasons, which are the spring (Mar 20 – Jun 20), summer (Jun 21 – Sep 22), fall (Sep 23 – Dec 21), and winter (Dec 22 – Mar 19). Having biological seasons as the independent variable is more relevant when describing the diet of a species that is known to exhibit different behaviours during its various life-history stages (Carbyn 1989, Morey *et al.* 2007, Markman *et al.* 2002). While biological seasons are better suited to explain diet variations due to coyote life-history traits and behaviour, calendar seasons may be more significant when describing diet variations caused by prey availability changes or resource availability changes caused by vegetative growth cycles. Hence, describing dietary differences using both types of seasons provides for a more in-depth analysis of temporal diet variations.

In a first analysis, biological seasons were used as the independent variable. Mean volumetric measurements of prey remains in scats from all sites were first pooled together to provide a general analysis of temporal variations in overall coyote diet. Frequency of occurrence data from urban and rural coyote scats were then analysed separately to

distinguish temporal differences within each spatial area (i.e. urban and rural). In a second analysis, Canadian calendar seasons were analysed using the same statistical tests as the biological season analysis.

To test the temporal difference hypothesis, an ANOVA (one way analysis of variance) can be performed to compare variances between two or more groups. If the samples are neither normally distributed nor approximately equal in size, a nonparametric statistical test can again be substituted for the parametric statistical test. The Kruskal-Wallis test can be performed as a multiple-sample ANOVA and/or MANOVA analogue when multiple samples are involved (Zar 1999). As a nonparametric statistical test, it does not assume any distribution (Hinton 2004b). A Kruskal-Wallis test was performed on a volumetric measurement data set, while in parallel; a Chi-Square can also be executed on the relative frequency of occurrence data set.

4.3.2.3 H3: Diet Diversity Differences in Coyote Diet

According to Magnussen & Boyle (1995), the Shannon-Weaver Diversity Index should be chosen over the Simpson Index because of its much higher statistical efficiency. However, the Shannon-Weaver Diversity Index tends to underestimate the diversity indices of the sampled population when faced with small sample sizes (Zar 1999). In fact, the Shannon-Weaver formula is more sensitive to variations in rare species (Peet 1974) and changes in their relative species frequency distribution (Magnussen & Boyle 1995) but the Simpson Index is more biased towards changes in common species (Peet 1974). Prugh *et al.* (2008: 323) concluded that:

“Estimates of the Shannon index (H') were substantially underestimated and highly variable for individual coyotes when the sample of scats used to construct the diet was <8-10. Estimates of H' tended to stabilize when 10-20 scats were used, and the variability dropped exponentially as sample sizes increased.”

While both indices have shortcomings, they remain useful in summarizing large data sets (Spellerberg 1991). Further measures of variations (e.g. Hutcheson's t -test for the Shannon formula) can strengthen the analysis.

For consistency within the wider research project, as well as for the sake of a higher statistical efficiency, estimates of spatial and seasonal diet diversity were calculated using the Shannon-Weaver diversity index (H'). Furthermore, the spatial and seasonal diets were all constructed with a sample of scats that was above 10-20. Therefore, based on the conclusions of Prugh *et al.* (2008) on sample size requirements for estimating H' , the sample sizes in each of my independent categories all met the minimum. The Shannon-Weaver Diversity Index can be calculated as follows:

Equation 3:

$$H' = -\sum_{i=1}^k p_i \log p_i$$

Where H' represents the food item diversity calculated with the Shannon-Weaver equation, k is the number of food item groups (categories), p_i is the relative abundance (Percent Frequency) found in the food item i . The data set of percent frequency was used in the calculations, since the relative abundance calculations must equal to one. Calculations and results of the Shannon-Weaver Diversity Index were verified with a Biodiversity Calculator

(Danoff-Burg & Xu 2003). As stated in the calculator document, “this calculator is based on the instructions given in the worked examples of Magurran (1988).”

According to Hutcheson (1970: 152), “it is shown by Bowman *et al.* (1969) that the distribution of H' is asymptotically normal.” Therefore, the H' values representing the diversity indices for each independent variable (i.e. spatial area) are compared using a t-test developed by Hutcheson (1970) for Shannon-Weaver diversity indices comparisons.

Chapter Five: RESULTS

Three key assumptions underlie my research methods and analysis. First, I assume that scat contents collected at the selected urban study sites are representative of the coyote diet in Calgary's urban areas (Figure 3, p. 24), and that scat contents collected at the selected rural study sites are representative of coyote diet in rural areas in the Calgary vicinity (Figures 4 & 5, p. 29, 31). Second, I make the assumption that all sites are independent from one another for statistical analysis purposes. Third, I assume that all scats selected for dissection and laboratory analysis were correctly identified as coyote scats. Training and experience in the field as well as reference to identification keys from Chame (2003), and Halfpenny and Biesiot (1986) were assumed to provide the necessities to be a trained observer.

A total of 338 scat samples were analyzed to estimate the relative proportion and frequency of different food items in coyote scats. These analyses were done in order to identify any spatial and seasonal variations in food groups. Volumetric measurements were first analyzed. Since they tend to over-estimate the proportions and presence of large biomass food items, relative frequency of occurrence was also analyzed. In fact, relative frequencies have opposing biases (i.e. under-estimate the presence of large food items), which could serve to moderate the bias of volumetric measurements.

In all seasons and sites (07-2009 to 07-2010), small mammals comprised the highest volume of all food groups (Figure 6). Large mammals that occurred in scats were white-tailed deer and mule deer – including fawns. While fawns were grouped with adult

deer in the large mammal category, some traces of fawn remains were found during the analysis (i.e. small hooves, shorter, thinner, lighter coloured hairs). Feathers, body parts such as beak and feet, as well as hollow bones were used to document the presence of birds in scats. Food items that were of anthropogenic source – such as plastic and aluminum wrappers, rope or string, aluminum foil, plastic bag pieces and fabric – were recorded as "garbage".

Data were analyzed using IBM SPSS Statistics 19.0 (SPSS Inc., Chicago III, 2010). I used the Kolmogorov-Smirnov goodness-of-fit test to examine whether the dependent variables were normally distributed (Hinton 2004, Zar 1999). I found that the data did not follow a normal distribution, thus failing to meet the requirements for the use of a parametric test such as a *t*-test or an ANOVA.

According to volumetric measurements (i.e. relative proportion of food groups in scats), small mammals were also the most prominent food group in overall coyote diet (53.6%). Relatively voluminous food groups were large mammals (ungulates) (10.7%), plants (9.7%), medium mammals (6.0%), and crab apples (4.89%). Least voluminous food groups (< 4%) were, overall, garbage (3.4%), birds (2.6%), cattle (2.1%), insects (1.8%), domestic pets (1.6%), and berries (0.9%) (Figure 6).

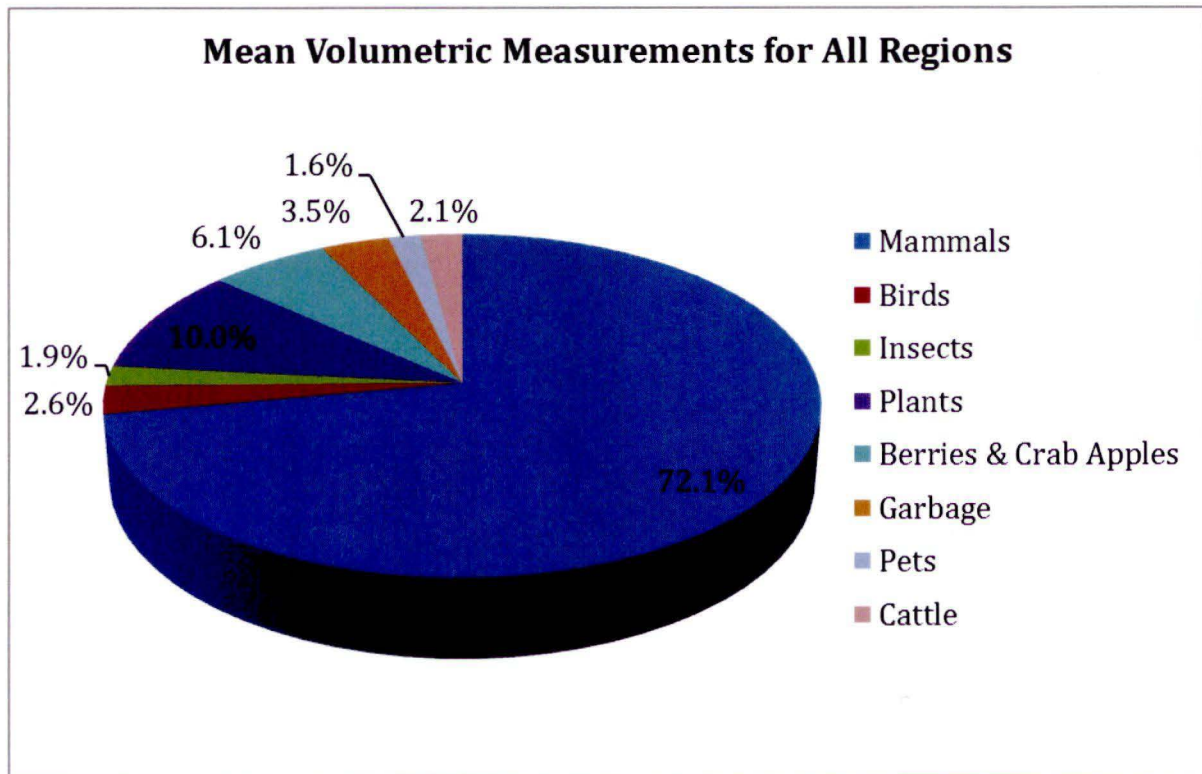


Figure 6: Illustration of the overall mean volumetric measurements and composition of coyote scats from all regions.

When examining all study sites from all regions, the most frequent food group found in scats was small mammals 76.0% relative occurrence (n=338), as seen in Figure 10 of the following section. The second most common food group in overall coyote diet was plants (39.9%). Large mammals (ungulates) were a relatively frequent food source in overall coyote diet at 16.6%. Medium mammals (9.2%), crab apples (8.6%), birds (8.6%), garbage (8.0%), and insects (5.3%) were part of overall coyote diet but in lesser proportions. Cattle (3.3%), domestic animals (2.1%), and berries (1.8%) were minor components (< 4%) of overall coyote diet.

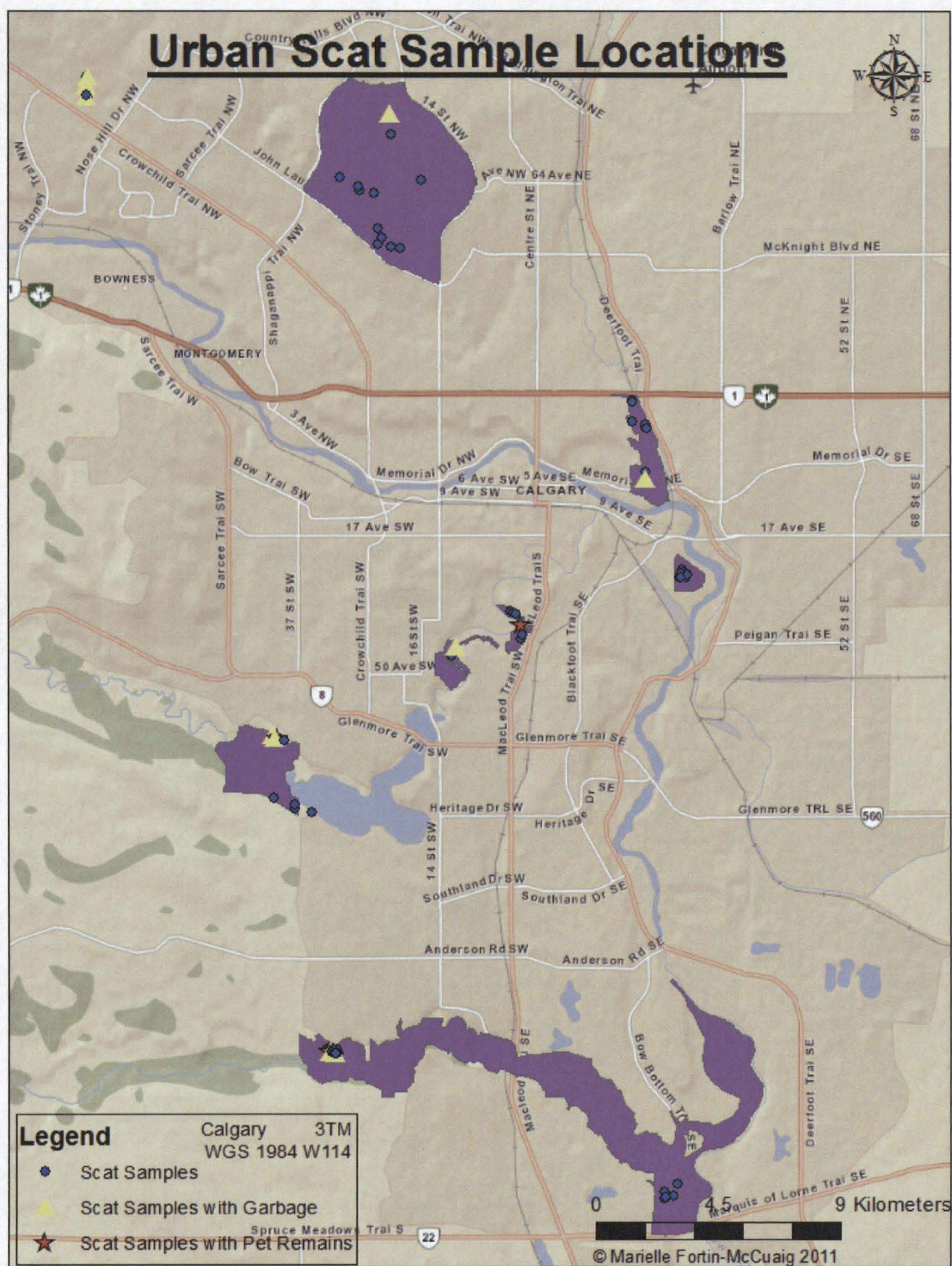


Figure 7: Location of all urban scat samples, including scat samples containing garbage and/or pet remains.

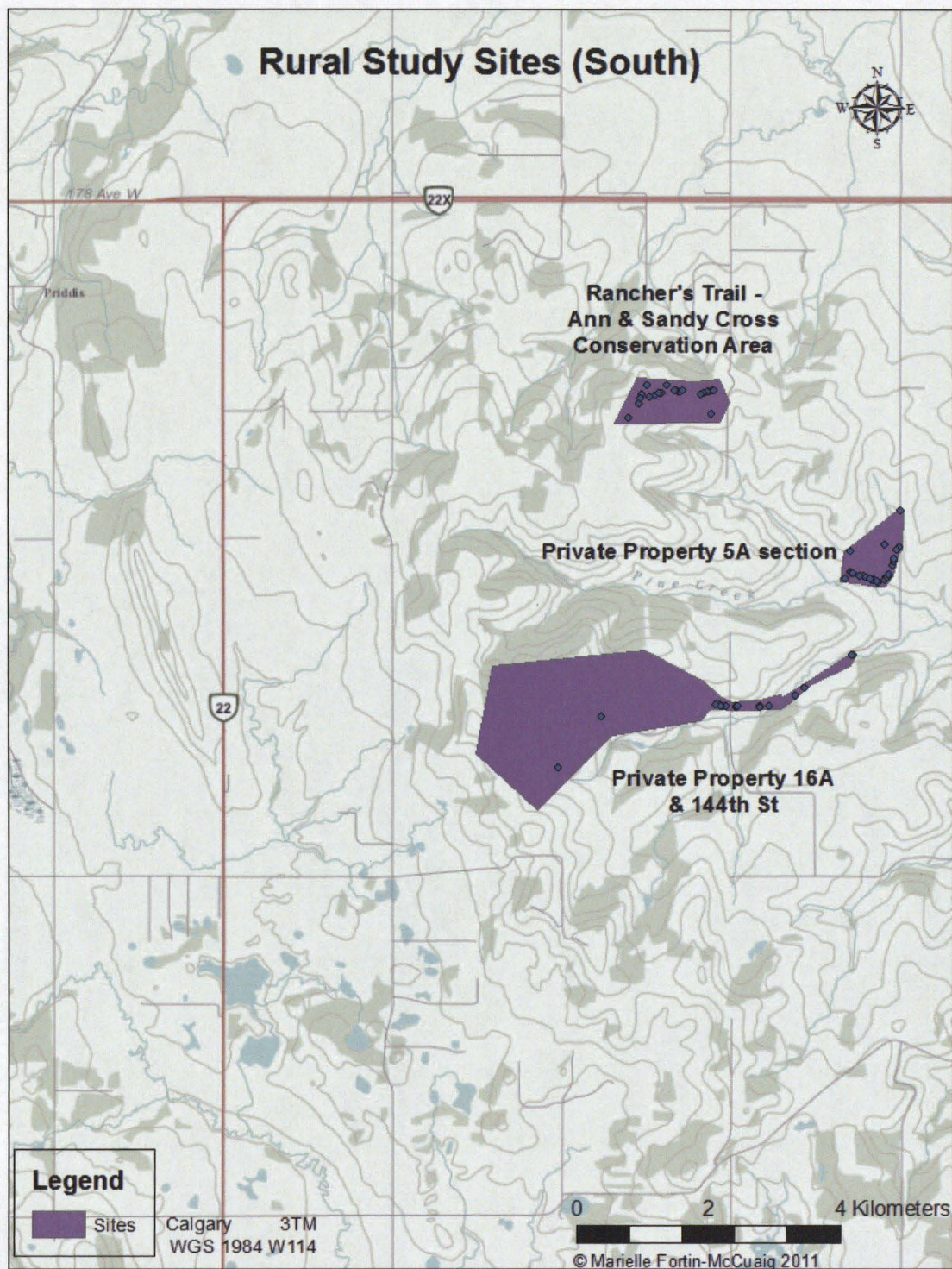


Figure 8: Location of all south rural scat samples, including scat samples containing garbage and/or pet remains.

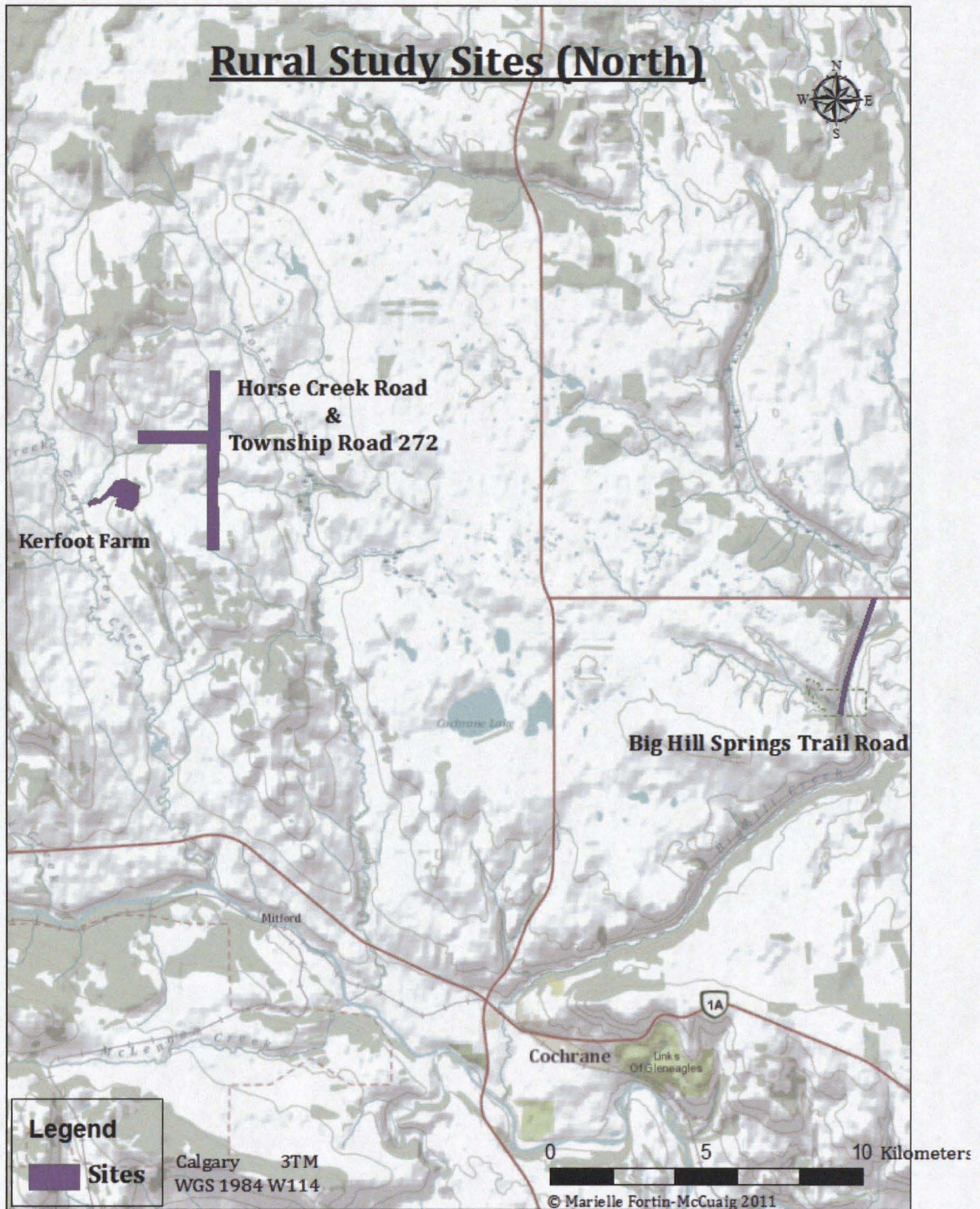


Figure 9: Location of all north rural scat samples, including scat samples containing garbage and/or pet remains.

In order to illustrate the diet variations between urban and rural coyotes, a bar graph is shown in the following section (Figure 10).

5.1 Spatial Differences

The objective of this section was to examine the spatial differences between urban and rural coyote diets in the Calgary, AB area. Consequently, the ensuing hypothesis was posed:

H₁: There is a statistically significant difference between rural and urban coyote diets in the Calgary, AB area.

H₀: There is a no statistically significant difference between rural and urban coyote diets in the Calgary, AB area.

Volumetric measurements were analyzed first. For this test, the independent variable was spatial area (urban and rural) and the dependent variables were groups of food items. The data failed to meet the normality assumption for both the two-sample independent *t*-test and the ANOVA. Consequently, I decided to use a Mann-Whitney U test to assess the significance of spatial and seasonal differences in coyote diet. This test is of a non-parametric nature since it does not assume a normal data distribution (Hinton 2004b, Zar 1999). It was used here as an analogue of the *t*-test, where volumetric measurements of food groups were measured on a continuous measurement scale or a ratio scale to meet the variable requirements for the Mann-Whitney U test.

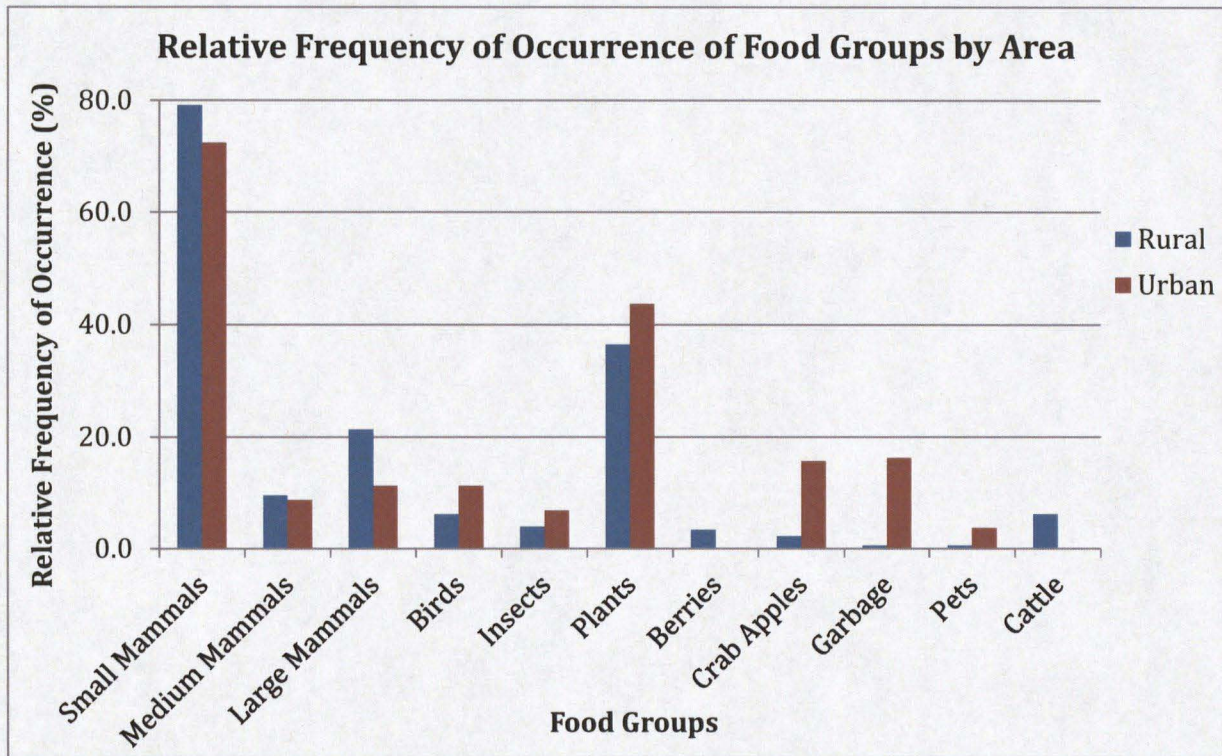


Figure 10: Comparison between urban and rural percent relative frequency of occurrence of all food groups.

Figure 11 shows mean volumetric measurement data. A pie chart was used as it shows proportions accurately as found in scats. Small mammals (57.2%) were the most voluminous food group in rural scats, followed by large mammals (14.7%) (Figure 12). Food groups of lesser prevalence included plants (8.7%) and medium mammals (6.2%). The remaining food groups can be considered to make up only a minor part of rural scats. However, the contents of urban scats (Figure 11) appeared to have a wider variety (See Hypothesis 3). While small mammals still made up most of their contents (49.6%), there seemed to be an increased number of food groups of intermediate importance. In fact, such categories included plants (10.8%), crab apples (8.4%), garbage (7.1%), large mammals (6.4%) and medium mammals (5.9%).

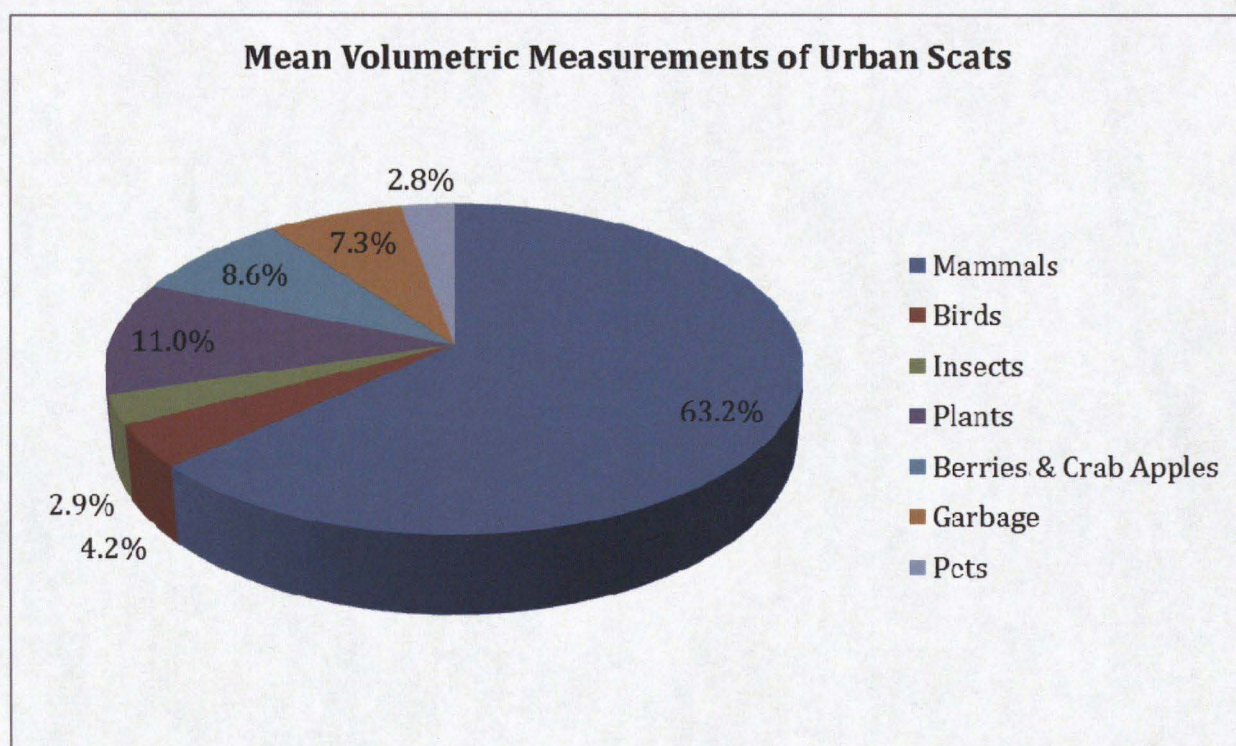


Figure 11: Illustration of the mean volumetric measurements and composition of urban scats.

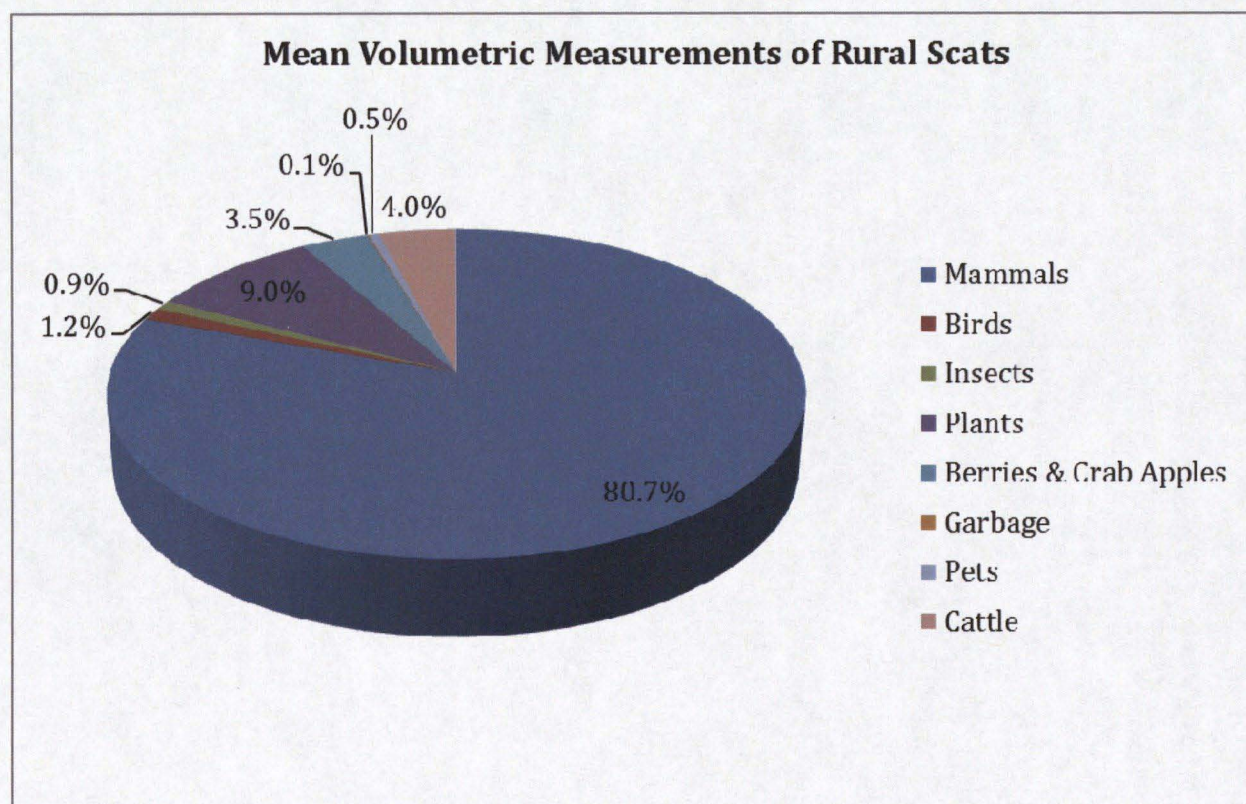


Figure 12: Illustration of the mean volumetric measurements and composition of rural scats.

Again, data were found to come from a non-normal distribution. Therefore, differences in volumetric measurements of food groups between urban and rural scats were analysed using the Mann-Whitney U Test. Significant statistical differences were detected in seven of the food groups. In fact, I rejected the null hypothesis at the α (0, 05) confidence level in the cases of domestic animals (i.e. pets) ($p = 0.040$), berries ($P_{0.045} < 0.05$), large mammals ($P_{0.011} < 0.05$), crab apples ($P_{0.000} < 0.05$), garbage ($P_{0.000} < 0.05$), and cattle ($P_{0.000} < 0.05$). No statistically significant differences were found between urban and rural scats for small mammals ($P_{0.410} > 0.05$), medium mammals ($P_{0.829} > 0.05$), birds ($P_{0.066} > 0.05$), insects ($P_{0.420} > 0.05$), and plants ($P_{0.118} > 0.05$).

The percent frequency of occurrence (Equation 2, p. 46) was calculated for all food groups (Table 3), and the relative frequency of occurrence (Equation 1, p. 45) of food groups in scat was also analysed. In relative frequency of occurrence, small mammals remained at the top of the categories for both urban (72.5%) and rural (79.2%) (Figure 10, p. 59). Large mammals were a significant food source but more so in the rural diet (21.4%) than in the urban diet (11.3%). The volumetric measurements mean, the percent frequency of occurrence and the relative frequency of occurrence show that birds and insects were present in slightly higher proportions in urban scats (11.6% (birds) and 6.9% (insects)) than in rural scats (6.2% (birds) and 3.9% (insects)).

Table 3: Percent frequency of occurrence of food groups in urban and rural areas, and in all regions.

Food Group:	Urban n=160		Rural n=178		Total n=338	
	%	n	%	n	%	n
Small Mammals	38.2	116	46.7	141	42.4	257
Medium Mammals	4.6	14	5.6	17	5.1	31
Large Mammals	5.9	18	12.6	38	9.2	56
Birds	5.9	18	3.6	11	4.8	29
Insects	3.6	11	2.3	7	3.0	18
Grasses	23.0	70	21.5	65	22.3	135
Berries	0.0	0	2.0	6	1.0	6
Crab Apples	8.2	25	1.3	4	4.8	29
Garbage	8.6	26	0.3	1	4.5	27
Pets	2.0	6	0.3	1	1.2	7
Cattle	0.0	0	3.6	11	1.8	11
TOTAL	100	304	100	302	100	606

Based on the frequency data, plants seemed to have a much stronger presence in coyote diets at 36.5% in rural sites and 43.8% in urban sites. Cattle was completely absent from urban scats, while its frequency of occurrence in rural scats remained fairly low (6.2%). Berries were also absent from urban scats while they were present in 3.4% of rural scats. Although crab apples, garbage and pets were present in very low numbers in rural scats (respectively, 2.3%, 0.6%, and 0.6%), their presence in urban scats was much stronger for crab apples (15.6%) and garbage (16.3%), and fairly stronger for pets (3.8%).

In fact, the Chi-Square test results provided further evidence that the null hypothesis can be rejected because they also revealed statistically significant differences for large mammals ($\chi^2_1 = 6.216$, $P_{0.013} < 0.05$), cattle ($\chi^2_1 = 10.220$, $P_{0.001} < 0.05$), crab apple ($\chi^2_1 = 18.036$, $P_{0.000} < 0.05$) and garbage ($\chi^2_1 = 29.513$, $P_{0.000} < 0.05$). I found a statistically significant difference for pets ($\chi^2_1 = 4.223$, $P_{0.040} < 0.05$) and berries ($\chi^2_1 = 5.491$, $P_{0.019} < 0.05$) but both variables had two cells with expected counts of less than 5, thus violating one of Chi-Square's assumptions. No statistically significant spatial differences were found for small mammals ($\chi^2_1 = 2.470$, $P_{0.116} > 0.05$), medium mammals ($\chi^2_1 = 0.065$, $P_{0.799} > 0.05$), birds ($\chi^2_1 = 2.762$, $P_{0.097} > 0.05$), insects ($\chi^2_1 = 1.447$, $P_{0.229} > 0.05$), and plants ($\chi^2_1 = 1.838$, $P_{0.175} > 0.05$).

Upon closer look, there were differences between study sites. In fact, Stanley Park/River Park had the most scats with pet remains present (16.7%) and only one rural site (5A) had pet remains present in scats. Garbage was most present in Arbour Lake (38.9%) – followed by Tom Campbell's Hill (27.3%), Nose Hill Park (20.0%), and Fish Creek Provincial Park-West (15.4%). Only one rural site, private property 16A, had scats (1) in which garbage was present (3.8%). Crab apples were detected most in Stanley Park/River Park (58.3%), followed by Tom Campbell's Hill (36.4%). Albeit in lower amounts, crab apples were also found in Arbour Lake (16.7%) and Nose Hill Park (16.7%). Only one rural site, Rancher's Trail, had crab apple presence (13.8%). Berries had the highest dietary contribution at the Kerfoot Farm (9.4%) and Horse Creek Road (7.1%) sites but the overall presence of crab apples in rural diet remained fairly low compared to major categories such as small mammals. Plants (grasses and leaves) seemed to be a food source in all sites but

even more so in Fish Creek Provincial Park-East (66.7%), Tom Campbell's Hill (63.6%), the Kerfoot Farm (62.5%), Stanley/River Park (58.3%), which all had values of over 50%. Inglewood Bird Sanctuary stood out when looking at both insect (38.1%) and bird remains (42.9%) frequency in scats.

Birds were present in scats from Fish Creek Provincial Park-East (25.0%). Although large mammals were most common in 16A (50.0%), 5A (38.5%) and Fish Creek Provincial Park-West (34.6%), they were completely absent from the Kerfoot Farm, Arbour Lake and Inglewood Bird Sanctuary. Medium mammals were also most common in 5A (19.2%) and Fish Creek Provincial Park-West (15.4%) but were completely absent from Tom Campbell's Hill. Highest relative frequency of small mammals in rural sites was in 16A (88.5%) while the lowest was in 5A (65.4%). In urban sites, the highest relative frequency of small mammals was found in Nose Hill Park (83.3%) while the lowest relative frequency was found in Tom Campbell's Hill (54.5%) and Stanley/River Park (58.3%).

5.2 H2 Seasonal

H₂: There is a statistically significant seasonal difference in coyote diet.

H₀: There is a no statistically significant seasonal difference in coyote diet.

5.2.1 Biological Seasons

Since the data were not normally distributed, the Kruskal-Wallis H test was used as an ANOVA analogue test. Statistically significant seasonal differences were found between biological seasons as well as between calendar seasons. First, in the case of biological

seasons, I rejected the null hypothesis for three food groups: birds ($P_{0.032} < 0.05$), insects ($P_{0.000} < 0.05$) and crab apples ($P_{0.000} < 0.05$). Berries ($P_{0.054} > 0.05$) and cattle ($P_{0.059} > 0.05$) were slightly outside of the confidence level.

Moreover, volumetric means of food groups in scat seemed to differ on different levels. Small mammal importance in scat seemed to be lowest during the pup-rearing season (49.9%) while medium mammal volume in scats (8.8%) was slightly higher during that same season. Large mammal consumption appeared to increase (14.1%) during the pup-rearing season as well, while decreasing (7.9%) during the dispersal season. Bird volume in scats also differed between the biological seasons, and it was highest during the pup-rearing season (3.6%) and lowest during the breeding season (1.4%). There didn't appear to be a strong demarcation in insect volumetric measurements in scats between the pup-rearing (2.5%) and the dispersal (2.9%) seasons. However, the Kruskal-Wallis test indicated that there was a significant difference between seasons. This difference could point to a significantly lower volume of insects in scats during the breeding season (0.1%), which also corresponds to the winter season. There were no significant differences in plant volumetric measurements between seasons, but it was at its lowest during the pup-rearing season (7.5%). There could be a difference in berry volume in scats between seasons, passing from an average volume of 0% during the breeding season to an average volume of 1.88% during the dispersal season. Volumetric measurements of crab apples in scats were significantly higher during the dispersal season (9.6%) than during the breeding (2.2%) and pup-rearing (1.7%) seasons.

Although there was no significant temporal variation in garbage content in scats, it was highest during the breeding season (4.0%) and lowest during the dispersal season (2.7%). As for volumetric measurements of pet remains in scats, it was highest during the pup-rearing season (3.2%) and lowest during the breeding season (0.0%) but no significant difference was detected. From the test results, there could be a temporal difference in cattle content in scats but it is not considered significant. It was highest during the breeding season (4.3%) and lowest during the dispersal season (0.8%).

Relative frequency of occurrence of food groups was also computed. However, a high number of variables (i.e. food item data) violated the Chi-Square assumptions (i.e. over 20% of cases with expected count less than 5 for the categories of cattle ($\chi^2_2 = 11.025$, $P_{0.004} < 0.05$), berries ($\chi^2_2 = 5.716$, $P_{0.057} > 0.05$), and pets ($\chi^2_2 = 4.894$, $P_{0.087} > 0.05$)). Thus, those Chi-Square test results were unreliable, which prevented their use in the analysis. Other results that showed significant seasonal differences were those of the bird category ($\chi^2_2 = 8.101$, $P_{0.017} < 0.05$), insect category ($\chi^2_2 = 8.535$, $P_{0.014} < 0.05$), and crab apple category ($\chi^2_2 = 13.256$, $P_{0.001} < 0.05$).

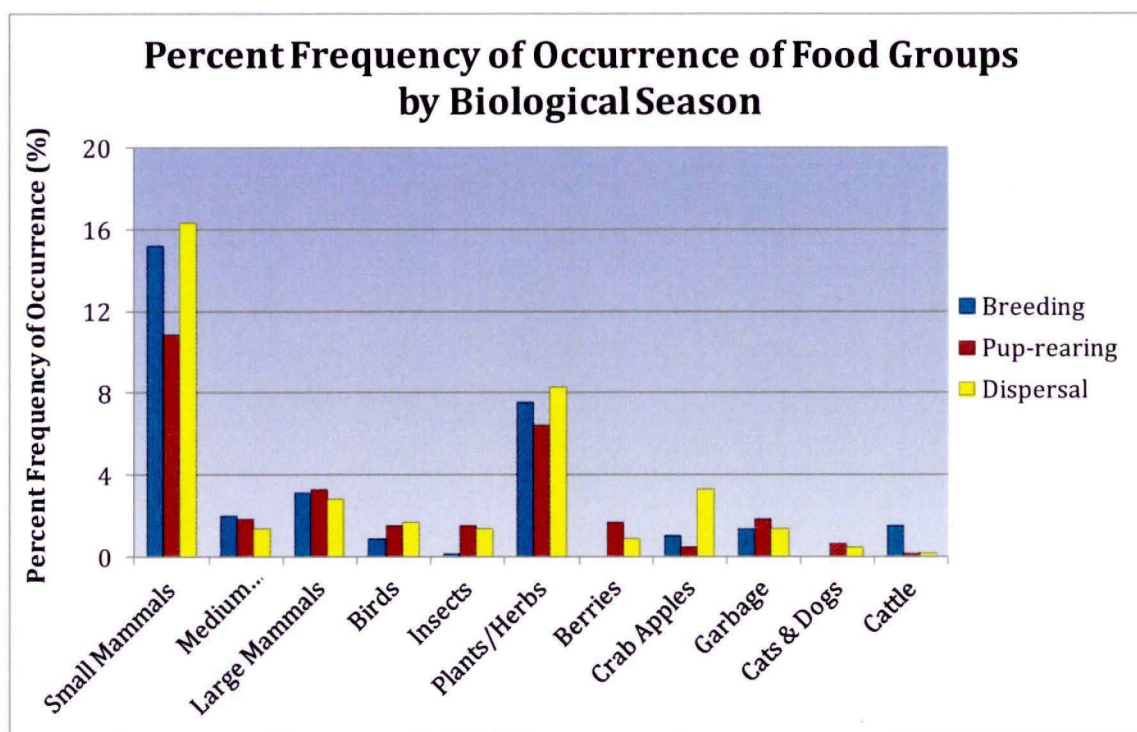


Figure 13: Comparison between biological seasons of percent frequency of occurrence (%) of food groups in all areas.

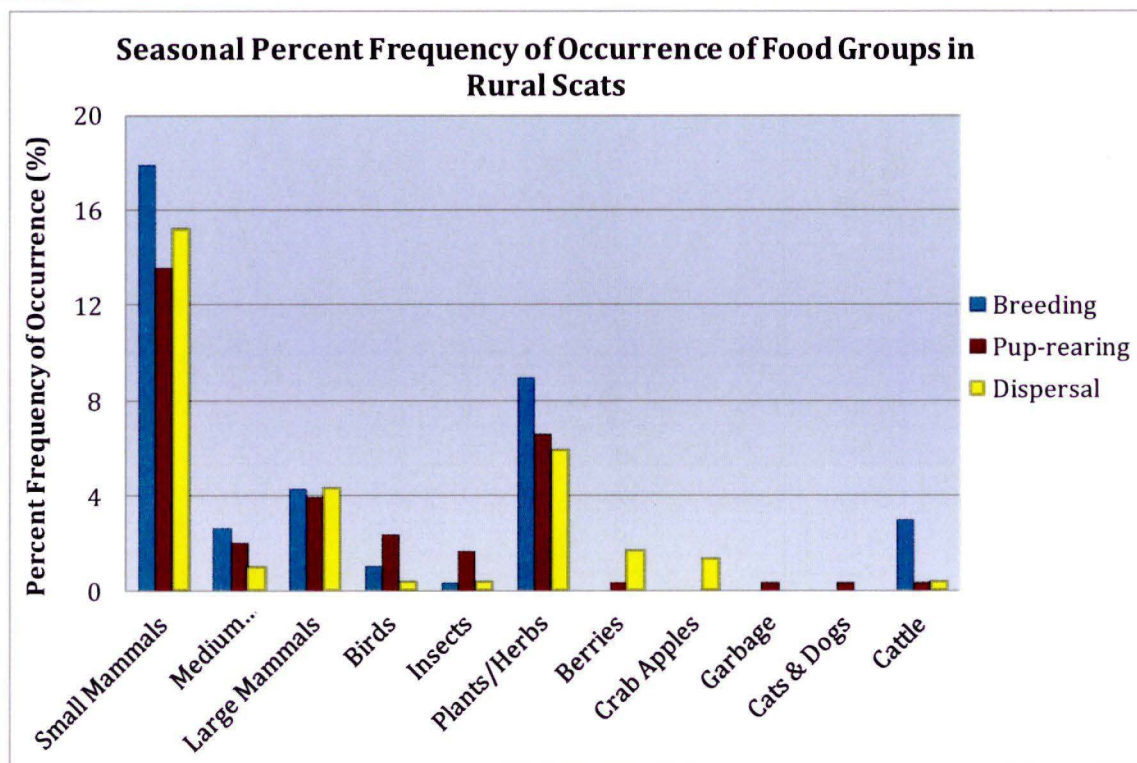


Figure 14: Comparison between biological seasons of percent frequency of occurrence of food groups in rural scats.

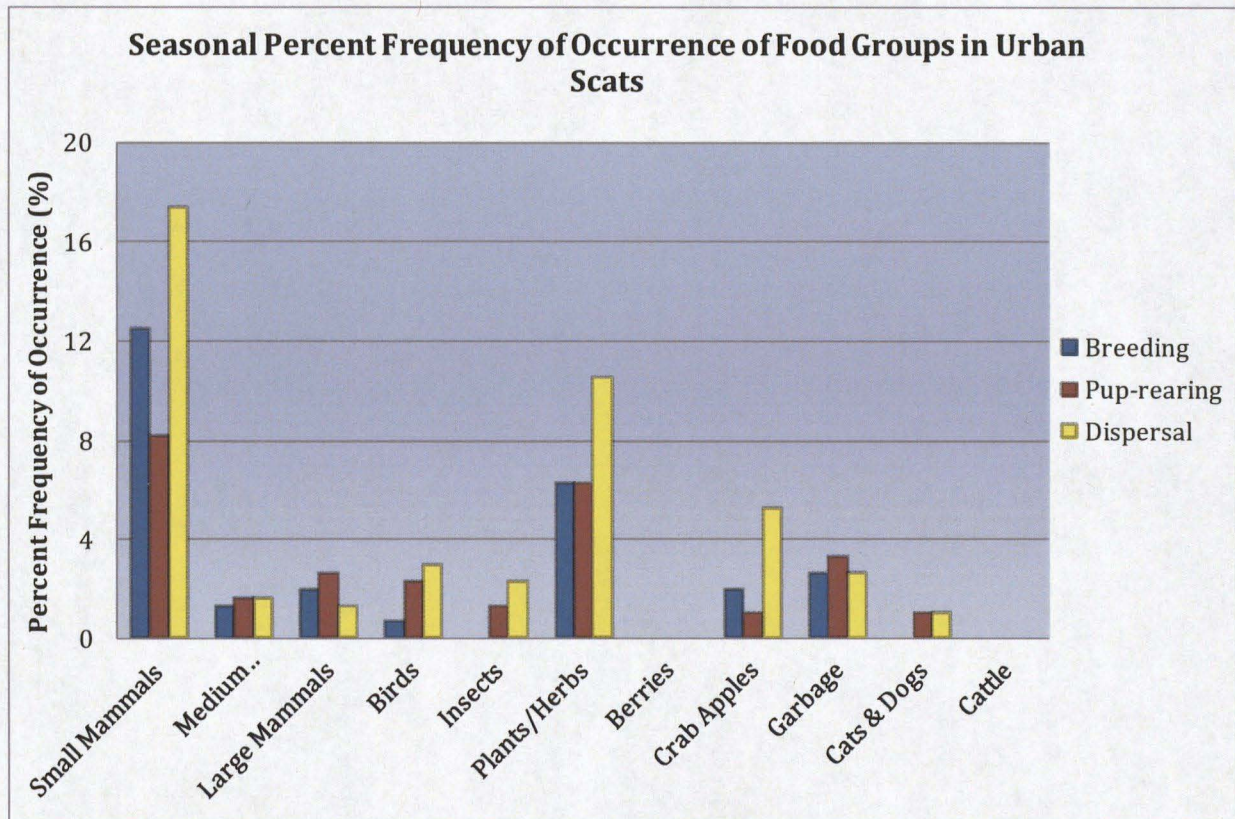


Figure 15: Comparison between biological seasons of percent frequency of occurrence of food groups in urban scats.

A summary of the relative frequency of occurrence values can depict their value variations over the seasons. During the pup-rearing season, a few food groups appeared to be more frequent in scats: large mammals, birds, insects and pets (Figure 13). A temporal difference could be seen in cattle remains relative frequency in scats as it was higher during the breeding season (7.6%) than the pup-rearing (1.1%) and dispersal (0.8%) seasons. During the dispersal season, berries (3.9%) and crab apples (15.6%) definitely seemed to have a higher relative frequency in scats as well. There also looked as if there was a stronger difference in urban diet during the dispersal season (Figure 15). Furthermore, crab apples frequency in scats seemed to peak during that season.

5.2.2 Calendar Seasons

Variations can also be seen during calendar seasons in volumetric measurements and relative frequency of occurrence. The Kruskal-Wallis test results indicated statistically significant differences for birds ($P_{0.030} < 0.05$), insects ($P_{0.000} < 0.05$) and crab apples ($P_{0.000} < 0.05$) as well as for berries ($P_{0.028} < 0.05$) and cattle ($P_{0.008} < 0.05$).

Therefore, I rejected the null hypothesis at $\alpha < 0.05$ confidence level for these five food groups. Volumetric measurements showed that birds constitute significantly higher proportions in summer scats (3.6%) and/or significantly lower proportion of in spring scats (2.0%) than other scats from other seasons. Insects were significantly more voluminous in summer scats (6.1%) than in scats from any other season (0.01%_{winter}; 0.6%_{spring}; 0.8%_{fall}). Crab apples volumetric measurements also showed a significant difference with a much higher proportion of crab apples in fall scats (16.8%) compared to other seasons (1.1%_{summer}; 2.0%_{spring}; 3.6%_{winter}). The occurrence of cattle varied significantly between seasons (6.1%_{winter}; 2.0%_{spring}; 0.01%_{summer}; 1.0%_{fall}), as well as the berries category (0.0%_{winter}; 0.0%_{spring}; 2.9%_{summer}; 0.6%_{fall}). Although no other significant seasonal differences were found, there appeared to be some seasonal variation in other categories. Large mammals appeared more frequently in spring scats (14.9%) than in those from other seasons (9.85%_{winter}; 9.0%_{summer}; 9.4%_{fall}), and garbage was slightly higher during the spring (5.3%) and winter (4.3%) seasons than during the summer (2.16%) and fall (2.3%) seasons.

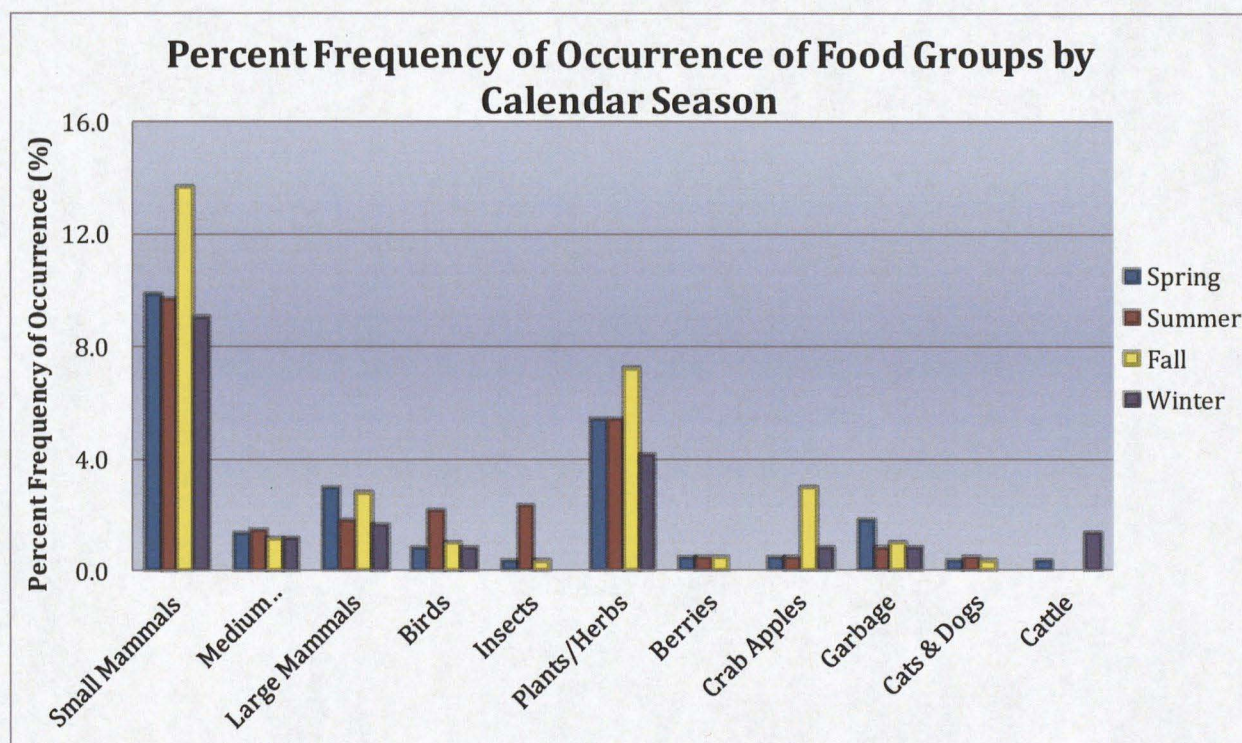


Figure 16: Comparison between calendar seasons of percent relative frequency of occurrence (%) of main food groups.

There were also many variables violating the Chi-Square assumptions (i.e. over 20% of cases with expected count less than 5 for insects ($\chi^2_3 = 31.917$, $P_{0.000} < 0.05$), cattle ($\chi^2_3 = 19.125$, $P_{0.000} < 0.05$), pets ($\chi^2_3 = 2.747$, $P_{0.432} > 0.05$), and berries ($\chi^2_3 = 5.249$, $P_{0.154} > 0.05$)). However, other results provided evidence of significant seasonal changes. That evidence was seen in the bird category ($\chi^2_3 = 8.265$, $P_{0.041} < 0.05$) and the crab apple category ($\chi^2_3 = 14.241$, $P_{0.003} < 0.05$).

Within calendar seasons, relative frequency of occurrence values showed that birds were in fact significantly more frequent during the summer (16.5%) than during any other season (7.0%_{winter}; 6.2%_{spring}; 5.6%_{fall}) (Figure 16). This was also the case for the insect category as they had a relative frequency of occurrence of 17.7% during the summer that decreased to 0.0% during the winter. Berries were also more frequent during the summer

(2.5%_{spring}; 3.8%_{summer}; 1.9%_{fall}; 0.0%_{winter}), as were pet remains in scat. Cattle seemed to be more frequent in winter scats (11.27%) compared to scats from other seasons (2.5%_{spring}; 0.0%_{summer}; 0.9%_{fall}). Crab apples appeared more common in scats during the fall season summer (3.7%_{spring}; 3.8%_{summer}; 16.9%_{fall}; 7.0%_{winter}), while garbage (13.6%_{spring}; 6.3%_{summer}; 5.6%_{fall}; 7.0%_{winter}), and large mammals (22.2%_{spring}; 13.9%_{summer}; 15.9%_{fall}; 14.1%_{winter}) seemed more recurrent during the spring season.

5.3 H3 Diet Diversity

Diet diversity was calculated using the Shannon-Weaver Diversity Index formula (Shannon & Weaver 1948), as demonstrated previously in the Methods Chapter (section 5.2.3.2). A low value indicates a low diversity (e.g. 1.5) while a higher value (e.g. 3.5) indicates higher diet diversity (MacDonald 2003). Index values will be stated for each category of analysis.

H₃: There are statistically significant spatial and seasonal differences in the diversity of coyote diets.

H₀: There is a no statistically significant difference in the diversity between coyote diet.

There was relatively low diet diversity for both urban and rural sites. However, diet diversity in urban sites was higher (1.80) than that in rural sites (1.61) and Hutcheson's *t*-test indicated that there was a significant statistical difference between the two spatial area diets ($P_{0.016} < 0.05$). Diet diversity was much lower during the breeding season (1.56), than during the dispersal season (1.75), and especially lower than during the pup-rearing season (1.85) ($P_{0.006} < 0.05$). During calendar seasons, diet diversity was highest during the

summer season (1.83) and lowest during the winter season (1.64), but no statistically significant differences were found between those seasons.

On closer investigation, within each spatial region (urban/rural), seasonal changes could also be observed. There was a statistically significant diversity difference in urban areas between the breeding season (1.54) and the pup-rearing season (1.93) ($P_{0.0007} < 0.05$), and between the breeding season and the dispersal season (1.76) ($P_{0.052} < 0.05$). Such differences can also be seen in rural areas where diet diversity was at a high of 1.67 during the pup-rearing season, while reaching its lowest value during the breeding season (1.46). However, no statistically significant diversity differences existed between biological seasons in rural sites. Further, statistically significant spatial differences could be observed when comparing urban and rural areas at the (biologically) seasonal level. In fact, there were significant spatial differences during the pup-rearing season ($P_{0.025} < 0.05$), as well as during the dispersal season ($P_{0.035} < 0.05$) (Table 4).

Table 4: Seasonal (biological seasons) diet diversity indices (Shannon-Weaver index) for coyotes in 2 spatial areas, and overall region of the Calgary area, AB, July 2009–July 2010.

	Urban H'	Rural H'	<i>t</i> value	Df	<i>P</i> value
Breeding	1.54	1.46	0.631	179	0.529
Pup-Rearing	1.93	1.67	2.255	171	0.025
Dispersal	1.76	1.50	2.125	164	0.035
Annual	1.80	1.61	2.410	585	0.016

Diet diversity also varied within both urban and rural areas and between calendar seasons. In urban areas, the largest gap in diversity values was seen between the summer season (1.86) and the winter season (1.60) ($P_{0.053} < 0.05$) while in rural areas, the gap was

largest between the summer season (1.66) and the spring season (1.39) ($P_{0.045} < 0.05$).

However, when comparing both spatial areas at the seasonal level, I found that there was a statistically significant spatial difference during the spring ($P_{0.003} < 0.05$), whereas the urban area had an H' value of 1.79 compared to 1.39 in rural areas (Table 5).

Table 5: Seasonal (calendar seasons) diet diversity indices (Shannon-Weaver index) for coyotes in 2 spatial areas and overall region of the Calgary area, AB, July 2009–July 2010.

	Urban H'	Rural H'	t value	Df	P value
Spring	1.79	1.39	3.019	144	0.003
Summer	1.86	1.66	1.643	153	0.102
Fall	1.69	1.47	1.592	172	0.113
Winter	1.60	1.46	1.026	116	0.307
Annual	1.80	1.61	2.410	585	0.016

6.1 Diet

Coyotes have recurrently different diet compositions when foraging in different habitats (Quinn 1997, Morey *et al.* 2007). Differences in prey availability, human-induced stresses, and habitat fragmentation can account for these variations (Bowler *et al.* 1983, Gipson 1974, Kamler *et al.* 2007, Lukasik 2009). However, diet composition findings differ considerably throughout the literature, possibly due to study area, prey availability, as well as analysis methods and techniques used by the researcher(s) in question. For instance, lagomorphs were found to be a major food source for coyotes in various studies (Windberg & Mitchell 1990, Cypher *et al.* 1996, Patterson & Messier 2001). However, I found that medium mammals, under which category lagomorphs would fall, were a relatively low contributor in coyote diet. Although not frequent in coyote scats, lagomorphs were readily observed in Calgary by Lukasik (2009). They were also frequently observed during the time of my study, even more so in residential neighbourhoods than surrounding parks. As stated previously in this thesis (p. 20), abundance and distribution of resources in the habitats vary. Therefore, Laundré and Keller (1984) stated that home-range studies should focus on home-range use rather than size alone. Similarly, diet studies should consider variations in abundance and distribution of food sources across the study region as study site locations, as well as abundance and distribution of food sources across habitats may affect results.

In this study, known coyote presence was a good indicative of scat yield potential, and since coyotes were observed more frequently in parks, the majority of the selected study sites were located in urban parks. As jackrabbits were often seen in residential neighbourhoods but rarely seen in parks, it is possible that jackrabbits were avoiding coyote presence and taking advantage of a habitat where the coyote's optimal food selection was focused on other resources (e.g. garbage). Hence, I suspect that the lack of medium mammals in urban coyote diet could be attributed to food selection. If the statement that jackrabbits were more abundant in residential areas as opposed to parks is true, coyotes foraging in residential areas could be selecting food sources that provide higher energy gains and are easier to access (e.g. garbage). It would be energetically more demanding for a coyote to hunt a jackrabbit than it would be to scavenge on garbage. As jackrabbits were rarely seen in rural areas, their low presence in scats could possibly be explained by resource availability (or scarcity) rather than food selection.

6.2 Spatial Differences

Within urban areas, Inglewood Bird Sanctuary seemed to be dissimilar in the sense that birds and insects were a much more voluminous food source than in other urban sites. Another interesting result is that rural site 16A had the highest small mammal consumption, while nearby adjacent field 5A had the lowest consumption of all rural sites. Plants were a major food group in all sites but especially in Fish Creek Provincial Park-East, Tom Campbell Hill, Kerfoot Farm, and Stanley Park, which all had a relative frequency of occurrence of over fifty percent. It would be interesting to assess whether scats containing

high proportions of plants (i.e. grasses), and sites with elevated relative frequency of plants also had high parasite counts. Stanley Park had the most frequent pet remains and crab apples in scats, while Arbour Lake scats were most abundant in garbage.

Although no significant difference was found between spatial areas, small mammal consumption was lower in urban areas than in rural areas. This may be due to the fact that urban coyotes have greater diet diversity than rural coyotes. Similar findings were reported in Andelt *et al.* (1987), where rodent presence in coyote diet tended to decrease when alternative food sources such as fruits, insects, and fawns became available. In the case of urban areas, anthropogenic food sources, crab apples, and birds may be more abundant and easier prey for coyotes.

Results from other studies showed that coyotes consume farm animals (Gipson 1974, Gier 1968). In fact, research in the United States revealed that coyotes do prey on farm animals and most often, on small farm animals such as poultry and sheep (Grinnell *et al.* 1937, Landry & Van Kruiningen 1979). According to the results of this study, the diet of rural coyotes near Calgary, AB does contain relatively little cattle, even though the cattle industry is important in Alberta (Alberta Beef Producers 2011). In light of Gier (1968) and Gipson (1974)'s findings that most of the livestock consumed by coyotes was in the form of carrion, it may be possible that differences between studies be attributed to animal husbandry management methods. Leaving calves or expecting cows unattended for long periods of time or leaving cattle carcasses in the field may attract coyotes (Gier 1968). Animal husbandry practices and/or the availability of other food sources in the Calgary region could potentially explain the relatively low presence of cattle remains in scats.

Therefore, when comparing rural diets between studies, it would be prudent to account for regional economic differences, and assess regional industries and practices of the study sites. In other words, it would not be wise to generalize the diet of coyotes.

As previously mentioned, coyotes may consume carrion as well. However, the limitations of the chosen scat analysis methods made it impossible to test this statement. As an example, Gier (1968) has found that carrion was consumed in 37.5% of the cases where domestic animals including livestock and chickens were eaten and in 41.5% of the cases for rodents. These findings could suggest that while urban coyotes in Calgary, AB have consumed a total of seven cats and dogs over a period of twelve months, they may not have preyed upon all seven. Instead, they may have scavenged on road killed animals in some or in all of the cases. The consumption of carrion may also reflect the availability – or scarcity – of their chosen preys and foods. In other studies, domestic cats were more frequent in urban coyote diet (Morey *et al.* 2007, Quinn 1997, Grubbs & Krausman 2009). Likewise, I found domestic cats or domestic dogs to be more frequent in urban areas than in rural areas, albeit in lesser frequency and volume than that found in the above-cited studies. Grouped together, they made up less than three percent of the urban diet composition, and less than four percent in relative frequency of occurrence. Thus, domestic animals were not a main food source in urban coyote diet. Similarly, Lukasik (2009) found that in Calgary, domestic animals made up less than one percent of urban scats in relative frequency of occurrence.

There was significantly more garbage remains found in urban versus rural scats. Garbage remains were only present in urban scats, with the exception of one rural scat that

contained some remains. Typically, higher human-wildlife conflicts arise in urban areas where garbage consumption by coyotes is greater (Baker 2007). As coyote densities can be higher in urban areas (Fedriani *et al.* 2001, Riley *et al.* 2003), intra-specific competition for food, resources and territory may drive stressed or starved individuals to prey on easier prey such as domestic animals and/or anthropogenic foods. In fact, spatial variations are likely reflecting human density, land-use as well as geographic variations in the availability of food resources. Also, as stated in Prugh *et al.* (2008b: 327), “fine-scale heterogeneity in the distribution of prey is an important cause of intraspecific diet variation, particularly for spatially structured predator populations.” Differences in experience and learning could further account for diet variations between social groups (Prugh *et al.* 2008b).

Furthermore, there was very little evidence of berries being present in the urban diet. Rural scats did contain more berries than urban scats but their presence still remained low. Lukasik (2009) found Saskatoon berries to be an important food source in the diet of coyotes in Calgary. Their near absence in this study’s scat samples could very likely be due to weather conditions being remarkably unfavourable for berries during my sampling period. In fact, during the summer 2009, a major hail event occurred in southern Alberta, which affected the City of Calgary (CBC News 2009, 2010). As a consequence, berry crops were either destroyed or left badly damaged (CBC News 2010). This could be indicative of food stress during that time.

While coyote diet may be subject to variations, and influenced by different factors and stresses, coyotes in this study still relied most heavily on natural foods, even in disturbed landscapes. Some studies indicate that even in urban landscapes, coyotes still use

predominantly natural habitats (Grinder & Krausman 2001a, Tigas *et al.* 2002, Riley *et al.* 2003). Conversely, Grinder & Krausman (2001)'s findings show that while coyote home ranges cover both natural habitats and residential areas, some coyotes will be increasingly active in residential areas during their hunting hours. Studies on coyote activity and movement patterns combined with diet studies could also indicate the level of human habituation and conflict potential. These could potentially indicate whether coyotes have become accustomed to traveling in residential areas, and perhaps also to consuming anthropogenic food sources.

6.3 Seasonal Differences

Seasonal changes seen in coyote diets may reflect prey availability, prey abundance, and inter and intra-specific competition (Prugh 2005, Windberg & Mitchell 1990, Randa *et al.* 2009, Arjo & Pletscher 1999). Snow cover and depth can affect coyote diet. Due to limitations in funding, this aspect was not measured. However, results from other studies show that snow cover may also affect coyote diet because it may be more difficult for coyotes to locate and capture smaller prey (Bekoff & Wells 1986). Alternatively, it is less difficult for coyotes to hunt larger prey such as deer when the snow cover is deeper (Patterson & Messier 2000). Following heavy snow falls, deer populations may become weaker because of the increased difficulty and energy used in finding and eating vegetation. In fact, Patterson & Messier (2000) studied factors influencing killing rates of white-tailed deer by coyotes in Nova Scotia, Canada. They reported that deer abundance, relative abundance and vulnerability of alternate prey, winter severity, and coyote social

behaviour all influenced killing rates. Furthermore, they concluded that the outcomes of pursuits of white-tailed deer were also increasingly positive when snow depth was greater. In this study, higher proportions of deer in spring and pup-rearing scats may be due to a greater abundance of fawns. It may also indicate that coyotes prey upon deer most often during the pup-rearing season, because of higher energy needs for either a lactating female and/or young pups to feed (Bekoff 1977, Gipson 1974, Gier 1975).

As seen in the results, coyotes are not strictly carnivores. Coyotes in urban areas took advantage of the availability of crab apples during the dispersal season (Figure 15, p. 68). In fact, crab apple presence in scat was dramatically affected by seasonal variation, which could be explained by the fact that crab apples are only available during the tree's fruiting season. Its fruiting season further corresponds with the coyote's dispersal season. Dispersing coyotes could be additionally stressed by their need to fulfill nutritional requirements combined with their need to find an available territory. Without an established territory, dispersing coyotes could be foraging opportunistically. However, already dispersed and established coyotes could rather be engaging in optimal foraging.

The integration of crab apples in urban coyote diet during its fruiting season suggests that coyotes could be foraging optimally in Calgary. Crab apple fruits are high in energy (high gains) and easy to obtain (low costs). Such resources could be of greater importance in dispersing juveniles and transient coyotes. Most juvenile coyotes rely on easy prey until they have established a viable territory (Carbyn 1989). Thus, their diet could be lacking in other preferred food sources, but energy needs can still be fulfilled with food sources such as the crab apple fruit. Crab apples could also be used optimally by

resident coyotes, which could need all their time and energy to defend their territory against transient and dispersing coyotes.

Presence of crab apples in scats during winter months could be due to cooler temperatures that could have led to the preservation of some late fall apples. However, it is most likely that snow and ice preserved scats against normal decay. This could be a source of bias because scats that remained frozen in snow and ice could have emerged once warmer temperatures melted the snow and/or ice cover. Warmer temperatures are common in the Calgary area in the event of a Chinook (Foley 2006). Chinook winds bring warm, spring-like conditions that last several days. This weather event occurs several times throughout the winter (Foley 2006). Such temperatures melt all or part of the snow cover, which could have uncovered scats from weeks before.

Results also showed a statistically significant difference in bird and insect consumption throughout both biological and calendar seasons. Intake of birds and insects was especially lower during the breeding season, which corresponds mostly with the winter season (Figures 13 & 16, p. 67, 70). Insects were barely consumed during the fall and winter seasons (Figure 16, p. 70), presumably because of the colder temperatures, which do not promote insect presence.

In rural areas, berries and cattle were present in significantly different proportions throughout calendar seasons, where proportions were lower during the winter and spring seasons for berries, and higher during the winter season for cattle (Figure 16, p. 70). This can be expected as the fruiting and growing season of berry-bearing plants and shrubs coincides with the summer and fall seasons. Thus, berries would not have been available

during the winter and spring seasons. As for cattle intake, it could have been in the form of carrion as harsh winter conditions can either make some cattle individuals more vulnerable to weakness and illness as well as to predation by other species. Cattle intake would have likely resulted from carrion scavenging. However, this statement cannot be tested due to the limitations of scat analysis.

During the pup-rearing season, small mammal consumption was at its lowest while large mammal consumption was at its highest (Figures 13 & 15, p. 67-68). In rural areas, cattle consumption was also highest during the pup-rearing season (Figure 14, p. 67). Higher energy needs during the pup-rearing season may drive coyotes to hunt larger biomass prey such as deer (Gipson 1974, Harrison & Harrison 1984). Demands of pup-rearing also limit time spent away from the den, and since small mammal hunting is much more energy and time-consuming, predation on large mammals could be beneficial at that time of year. Additionally, the pup-rearing season also coincides to the fawning season. This would translate into a higher abundance of deer fawns during the corresponding coyote pup-rearing season. It is unknown whether deer remains found in scats originated from carrion or fresh prey but fawn hair (i.e. shorter, light fawn-coloured, thinner deer hair) was readily observed during the analysis.

Lastly, garbage intake was also at its highest during the pup-rearing season. These findings would also support the belief that coyotes requiring higher energy intakes during the pup-rearing season will opt for energy rich foods that are easier and faster to access. This could be of management significance since food intake and behaviour of parents will likely influence the behaviour of the young pups.

Consumption of domestic pets was lowest during the breeding season and was higher during both the dispersal and pup-rearing seasons. The low frequency of occurrence of pet remains in scats from the breeding season could be attributed to a lower number of pets roaming the city during the colder months. In all but one of the samples, pet remains in scats belonged to felines. Domestic cats may stay indoors for longer periods of time during the colder months, which also happen to correspond to the coyote breeding season. During the pup-rearing season, pets could have been killed by coyotes defending a den. Pet remains present in scats during the dispersal season could be a result of coyotes that are stressed for food and territory, thus seeking easy-access prey. Hence, this would be suggestive of offensive predatory behaviour, rather than defensive behaviour. There is also the strong possibility that many or all of those pets had been killed previously, and that coyotes took advantage of the presence of carrion. Again, this could not be tested because of the limitations of scat analysis.

In urban areas, the diet during the dispersal season seemed to diverge the most from that of other seasons. Noticeable differences could be seen in small mammal consumption. During the fall season in all sites (Figure 16, p. 70) and during the dispersal season in urban sites (Figure 15, p. 68), small mammal consumption also seemed higher than in other seasons. It is interesting that plant intake was correspondingly higher during those seasons (Figures 15 & 16, p. 68, 70). This could be explained by the fact that plants could help in the digestion of the small mammals, which are increasingly consumed during the same periods. This supposition can be strengthened by the fact that in rural areas, small

mammal intake was highest during the breeding season with a correspondingly highest plant intake for the same season.

In urban areas, bird and insect intakes were also highest during the dispersal season. Reliance on a greater variety of foods may suggest that dispersing coyotes will engage in opportunistic feeding until they have found a viable territory, after which they can engage in optimal foraging (i.e. such as dietary behaviour shown during the pup-rearing season). Hence, feeding strategies of coyotes could also vary seasonally, spatially, and/or according to varying stress levels and stress nature (i.e. anthropogenic or natural).

Whether shifts in prey selection occur because of food scarcity stress or food preference is not known in the case of this study but findings showed spatial and seasonal differences, with seasonal differences more pronounced in urban habitats (Figures 14 & 15, p. 67-68). Differential seasonal diets can indicate either stress due to resource scarcity, optimal foraging or opportunistic consumption due to varying availability of food sources. However, more data on prey availability and abundance would be needed to understand further coyote prey selection factors in the Calgary area. Generally, diets of urban and rural coyotes vary from one another and their seasonal variations also seem to differ in their nature. Coyotes in rural habitats seem to have less seasonal variation (Figure 14, p. 67) than coyotes in urban habitats (Figure 15, p. 68). When observing and comparing Figures 14 and 15, the dispersal season in rural habitats seems to be less divergent from the other seasons, than it is in urban habitats. This could perhaps be explained by a combination of increased intra-specific competition and inter-specific competition with humans for limited resources as well as limited space and territory. As urban habitats may be more productive

they may support higher densities of coyotes (Grinder & Krausman 2001, Fedriani *et al.* 2001), thus potentially increasing intra and inter-specific competition. Finally, Figure 15 also seems suggestive of greater diet diversity in urban coyotes as it seems to show decreased food item abundance but increased food item diversity. Changes in garbage content in scats would likely originate from an increased or decreased access to garbage. Garbage output from humans is likely similar year-round, except during periods when food consumption by humans is higher such as during holiday seasons.

6.4 Diet Diversity Differences

Significant differences were found between diet diversity indices between spatial areas and between seasons. Therefore, the null hypothesis that no difference exists was confidently rejected ($\alpha < 0.05$). Diet diversity was significantly higher in urban areas than in rural areas (Tables 4 & 5, p. 72, 73). Diet diversity was also significantly higher during the pup-rearing season than during the breeding season for all spatial areas (Table 4, p. 72). While the significant difference lies in the pup-rearing season for both spatial areas, the nature of the difference seems to be somewhat different. In fact, in urban areas, diet was least diverse during the breeding season but in rural areas, it was the diet during the pup-rearing season that was much more diverse than in the other two seasons. Morey *et al.* (2007) as well as Lukasik (2009)'s study of urban coyotes also found that diet diversity was much lower during the breeding season.

A less diverse diet during the breeding season could be explained by the fact that coyotes may have to rely on a decreased number of preys. Prey diversity and availability

may itself be lower during the winter season as no insects or fruits can be found and birds are less available. The pup-rearing season also coincides with the “young-rearing” season of various other prey species such as deer and birds. It also overlaps with the fruiting season, and thus the availability period of many berry species. Insects also become readily available at the start of the warming temperatures. Hence, a greater abundance and availability of deer fawns, berries, insects and birds could explain the more diverse diet of the pup-rearing season.

All diversity indices ranged between 1.46 and 1.93 (Tables 4 & 5, p. 72, 73). These indices are much higher than those found in Lukasik (2009)’s study whose indices ranged between 0.86 and 0.96. However, they sit closer to Morey *et al.* (2007)’s indices, which spanned between 1.36 and 2.15. According to their calculated diversity index values, coyote diet was also more diversified during the pup-rearing season, with the exception of one of their study sites.

Significant differences were also observed in both spatial areas between calendar seasons. In urban areas, diet diversity was significantly higher during the summer than during the winter, while in rural areas, diet diversity was significantly higher during the summer than during the spring (Table 5, p. 73). Overall, diet diversity seemed higher during the summer seasons, as well as during the pup-rearing season. Additionally, the indices for the dispersal and pup-rearing seasons were both high compared to rural indices for the same seasons (Table 4, p. 72). Diet compromises could explain the higher diet diversity in urban areas. However, selecting towards easy-access, energy-rich foods could also be explained by the optimal foraging theory (Stephens *et al.* 1987).

6.5 Conclusion

The prediction that urban coyote diet differed from rural coyote diet was accurate. It was to be expected that urban coyote scats would contain more anthropogenic food sources because of their increased availability in urban areas. Overall, it could be said that coyote diet is highly reliant on small mammals but that in urban habitats, it is perhaps maintained by the availability of diverse food sources such as anthropogenic food sources.

Coyotes are likely adapting to spatiotemporal variations in prey availability and land-use change by including seasonally available prey and easily accessible foods. Coyote dietary behaviour could potentially be explained by a combination of two existing theories. When resource stress is higher, such as during the dispersal season, coyote foraging activities could be explained by opportunistic feeding (Andelt *et al.* 1987, Van Vuren & Thompson Jr. 1982). Intra-specific competition for territories and resources may subject coyotes to increased resource stress, especially for dispersing juvenile coyotes. This opportunistic feeding that is enabled by the coyote's plastic behaviour may assist coyotes in adapting more easily to increased resource stress and disturbed habitats. This resource stress may drive coyotes to rely on easy-access foods such as crab apples, garbage and pets. Conversely, those easy-access foods are also coincidentally energy-rich, which may justify their choice, according to the optimal foraging theory (Stephens *et al.* 1987).

Crête and Larivière (2003) found that coyote locomotion is hardest in deep snow. Thus, it may require much energy for coyotes to hunt large prey during the winter/breeding seasons. However, as mentioned above, Patterson and Messier (2000) concluded that snow depth had a positive influence on the success rates of deer pursuits.

Moreover, the Calgary area is not known to have a deep snow cover throughout the winter season. Chinook warm winds bring spring-like climate that melts the snow cover several times a year (Foley 2006). Therefore, in the Calgary area, the decreased presence of deer in winter/breeding scats is likely not dictated by the cost of locomotion in snow. Hunting hibernating small mammals in the shallow snow cover of the Calgary region may prove to be more efficient for coyotes during that time.

Furthermore, unless a small fawn is hunted – which typically does not occur during the breeding/winter seasons - a carcass of a large prey such as a deer will likely not be entirely eaten on the same day. Hence, the hunting of large prey often requires coyotes to remain close to the carcass location to keep benefiting from the hunted prey as well as to be able to defend it against competitors. However, breeding coyotes tend to have increased movement rates and activity levels during the breeding season as they are actively looking for a mate (Roy & Dorrance 1985). Hunting small mammals would likely require less tracking activity, and may be more suitable for moving and traveling coyotes. Small mammals were, in fact, main food source in all spatial regions and all seasons but even more so during the breeding and dispersal seasons.

6.6 Potential Limitations

Identification of coyote scats was more difficult during seasons where crab apples were available for intake because of the resulting change in texture of the scat. This change in texture combined with the lack of prey remains such as bones, fur, claws and/or teeth, combined with the increased digested matter in the scat and variations in colour could have increased the likelihood of scat misidentification in the field. It could have been more

likely in such occasions that a dog scat could have been wrongly identified as a coyote scat. Therefore, when in doubt, the scats were picked up, and brought back to the lab along with the other samples. Once examined closely at the lab, identification could be done with greater confidence. Upon closer examination, dog scat could easily be differentiated from coyote scat because of the presence of commercial dog food and its resulting grainy texture, and yellow-brown coloration. Shape was also significantly different between dog and coyote scats. Therefore, any scats without subdivisions or a tapered end that presented a grainy, yellow texture and colour was discarded.

According to Marucco *et al.* (2008), collecting scat samples from established transects can cause over-representation of a certain species in groups of scats collected on transects. However, carnivores that generally consume prey with smaller body sizes (i.e. coyotes) produce fewer scats per prey item, which likely will not result in problems of independence (Marucco *et al.* 2008).

Additionally, it was difficult at times to collect weekly samples from the most urbanized, less natural study sites (i.e. Tom Campbell Hill, Stanley Park, Inglewood Bird Sanctuary and Arbour Lake). Drifting territoriality could perhaps explain the inconsistent scat outputs of some sites. Increased pressures and stresses in urbanized landscapes leading to resource disparity, scarcity and heterogeneity may drive urban coyotes to shift their territories both in time and space. In fact, Doncaster and MacDonald (1991) observed pronounced and continual drifting of territories in urban red foxes (*Vulpes vulpes*), when compared to that of suburban foxes. Kruuk (1972) thought that food supplies could determine the nature of territoriality in hyenas. Further studies would be necessary to test

whether a similar territorial drift can be observed in urban coyotes, along with examining the nature of their territoriality. Such studies could also have the potential to elucidate some uncertainties regarding offensive and defensive behaviour towards humans and domestic animals, as well as to target some higher conflict neighborhoods for further public education on local coyote behaviour.

Additionally, scats collected during the pup-rearing season could be biased. For example, because female coyotes have been known to remain in closer proximity to the den during that season while males commonly hunt for the family unit (Bekoff & Wells 1986), scats collected during that time of year could be have increasingly originated from male coyotes.

I suspect my laboratory methods could have under-estimated the proportions of bird remains in scats. As bird remains suffer more fragmentation than mammals during digestion, they may not be as readily discernible as macro-components (Reynolds & Aebischer 1991). Most of the time, birds did not make up the bulk of the scat. By including relative frequency of occurrence data in addition to volumetric measurements, bird importance in scat may not be as biased because any presence over 5% in the scat was accounted for. Furthermore, by grouping all bird species together in one diet category, it also allowed small bird remains to be represented together as over 5%, and thus included in the frequency analysis. If birds were quantified down to each species, the volumetric measurement results for each species would often have fallen in the "below 5%" category, and thus not included in the volume or frequency analysis.

The analysis of volumetric measurements of food items in scats has an incorrect assumption that food items have equal densities. This assumption may result in some categories being overestimated while others may be underestimated (Reynolds & Aebischer 1991). Not all diet items are digested at the same rate and intensity. Some diet items such as garbage and larger biomass prey may have increased proportions of digestible matter. In this study, presence of wrappers, plastic, and anything undigested from human refuse was considered to be garbage presence. Anything that was highly digestible would have passed on as micro-components and thus not be analyzed. Moreover, any highly digestible garbage items that were present without any other indigestible matter would have been omitted in the analysis. Explicitly, there is another assumption that artificial and non-natural items must be present in the scat to account for garbage presence. As Reynolds and Aebischer (1991:106) state, this “gives no indication of the size of the meal.” However, due to the nature of human garbage, most undesirable digestible items are mixed with highly indigestible items such as wrapping, plastic, textile, rope, etc. Whereas volumetric measurements may be biased, relative frequency of occurrence data could have helped in partly countering that bias.

Volumetric measurements were analyzed, but they tend to over-estimate the proportions of small biomass food items, while also under-estimating the proportions of large biomass food items. In fact, small biomass food items have a higher proportion of indigestible matter than does larger biomass food items (Floyd *et al.* 1978). Likewise, relative frequency of occurrence data has its draw-backs as it tends to over-estimate the presence of large biomass food items, while under-estimating the presence of small

biomass food items. Consequently, both data sets were analysed to avoid disguising the importance of certain food groups in the coyote diet. Figure 17 shows how results varied according to data sets.

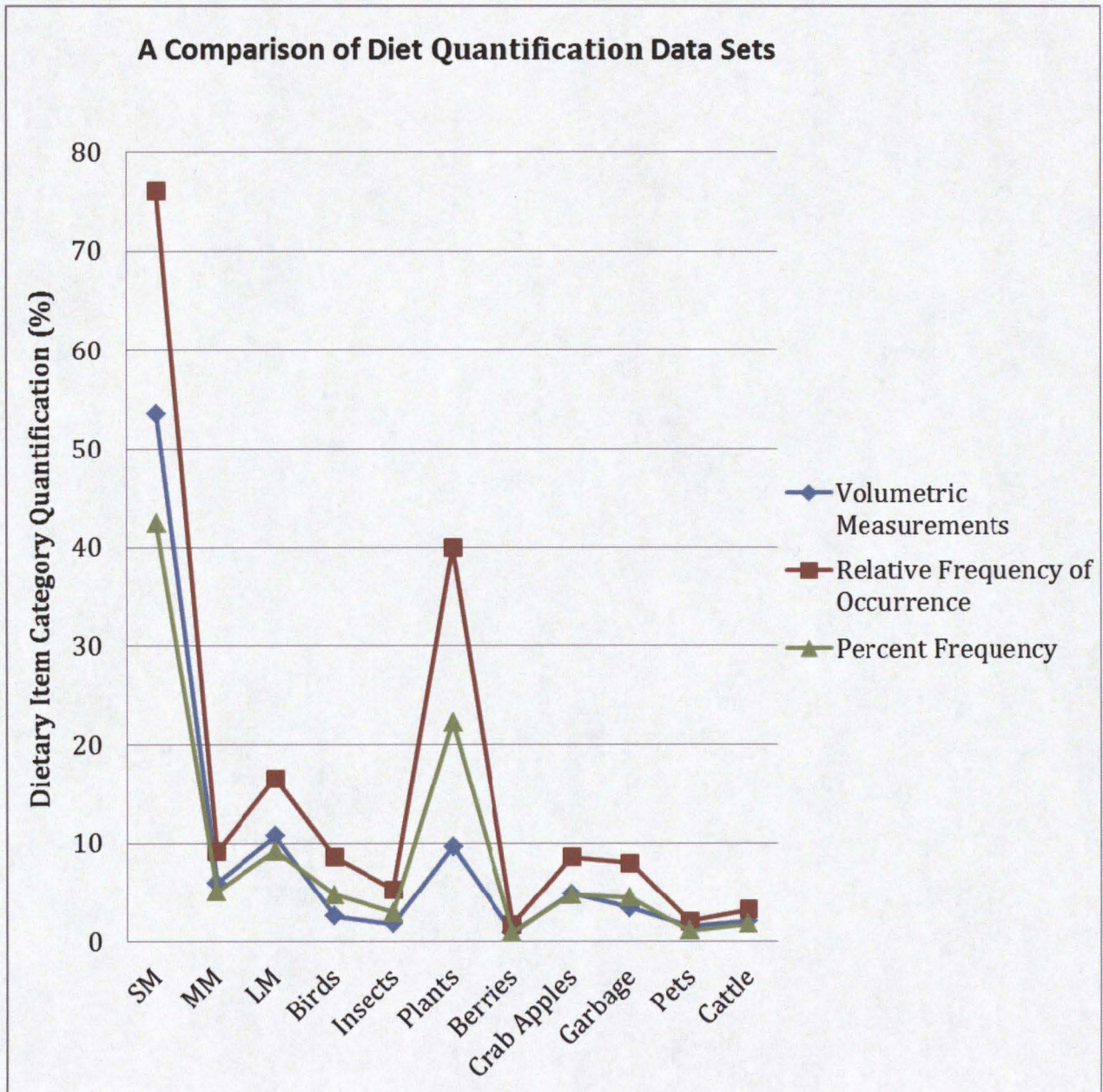


Figure 17: Comparison of the three quantification methods used to analyze coyote diets.

Finally, the choice of non-parametric statistics could have influenced the level of significance of the differences found, and whether differences were found or not. Non-significant results were still reported, and where some data violated the assumptions of the Chi-Square test, their proportions and relative frequency data were still reported. Since non-parametric have less power than parametric statistics, there could have been some underlying differences that were not detected. Raw data such as volumetric measurements and relative frequencies still have a descriptive value, and can still show some variations. Hence, by describing even non-significant results, potential or non-significant differences were not entirely dismissed.

7.1 Summary

Finally, the results of this study revealed that natural foods (i.e. food sources excluding garbage, domestic animals, crab apples and cattle) made up the vast majority of coyote diets, and virtually all of the rural diet. While all diets were widely composed of natural foods, they did differ significantly. Both habitats and seasons affected coyote diet. Anthropogenic food sources were significantly more frequent and abundant in urban scats, as were crab apples. Although urban scats did contain significantly more pet remains than rural scats, pet remains were only a very minor component of urban coyote diet. Hence, the common belief that coyotes frequently depredate on pets is misguided, and is not supported in the case of this study on Calgary area coyotes.

In retrospect, the establishment of a baseline diet in rural areas allowed us to distinguish how diet varied between less urbanized areas and urban areas. Results showed that diet did in fact significantly differ in urban areas. In all aspects of spatiality, seasonality and diversity, diet varied significantly between urban and rural areas. This could suggest that urban coyotes in Calgary, AB are already exhibiting the plastic and flexible behavioural shifts of disturbed populations that allow them to adapt to urban habitats.

In the case of the coyote, an increasingly diverse diet could potentially reflect more resource-stressed coyote populations. This higher diet diversity may suggest that coyotes from urban populations need to supplement their diet with alternative food sources such as anthropogenic food sources. Their rural counterparts can, however, rely on fewer more

abundant species that meet their dietary and energetic needs. As urban landscapes can be more unstable environments in the sense that land-use change occurs more frequently and at a faster pace, urban coyotes often have to unveil behavioural and spatial plasticity to thrive. Young *et al.* (2006: 581) found that “this plasticity is not expressed in coyotes that experience relatively stable conditions.”

As suggested by Baker (2007) and Lukasik (2009), using scat analysis to quantify anthropogenic food contents in coyote scats could be used as an indicator of attack risk or conflict risk with humans. I also advance that monitoring coyote diet diversity could also provide further indication of coyote health and resource-related stress levels. This could be of significance in human-wildlife conflict studies since elevated resource-related stresses could lead to the need for diet compromises towards anthropogenic food sources, ensuing increased human habituation, and human-wildlife conflict.

7.2 Contributions

In this comparative study between urban and rural coyote diets, we gained further knowledge on food compromises in the urban coyote diet. In fact, if the quantification of anthropogenic food contents can be used to assess human-wildlife conflict potential, as suggested and emphasized by Baker (2007) and Lukasik (2009), then it could be a possibility that conflict potential could have somewhat increased in the past 5 years. Indeed, garbage and pet remains have both slightly increased in relative frequency of occurrence in urban Calgary, AB habitats since Lukasik (2009)’s study. While pet remains have increased, and are still present in urban coyote scats, they are not a common

occurrence, and they are definitely not a central food source in the diet of Calgary coyotes. The diet of urban coyotes is composed of mostly natural foods but they still consume human-related foods. As for the rural diet, it is composed of virtually all natural foods, and especially small mammals.

This thesis can potentially help wildlife management projects, and perhaps help in the protection and preservation of resources that are of natural importance to coyotes. In fact, by learning more about the coyote's resource utilization and behaviour, city planners and decision-makers can develop programs and methods to keep urban coyotes away from the more densely populated areas in cities. For example, ensuring connectivity between larger more naturalized parks could help in reducing the need for diet compromises, as urban coyotes would have natural resource availability and access from those larger parks. As suggested by Lukasik (2009: 48), "large naturalized parks are able to sustain a sufficient natural prey base for coyotes." For less densely populated areas such as sparse suburbs, public education campaigns about coyote survival needs and behaviour, and how to live at peace with wildlife could prove to be very useful.

7.3 Recommendations

Coyotes have been known to be very resilient and show behavioural plasticity, especially in their diet. Hence, coyote diet is most likely to vary between cities, areas, landscapes and habitats. For that reason, coyote-centric diet studies cannot be generalized to all habitats, and I would recommend city planners, decision-makers and wildlife officials to conduct tailored diet studies in their respective areas in order to make wildlife

management and development planning decisions that are based on accurate and current scientific knowledge on local coyote populations. Enlightened decision-making and planning may help manage local ecosystems, and promote sustainable conditions for both wildlife and citizens while helping to reduce human-wildlife conflicts.

Reducing garbage access in cities could reduce human conflict (Baker 2007). In the case of Calgary, reducing garbage access for coyotes could be an effective way of controlling jackrabbit populations in residential areas as coyotes would be forced to find alternative food sources such as jackrabbits to maintain their food intake.

Furthermore, I would also advise managers to be wary of making generalizations of research not pertaining to the local subspecies in question when establishing management guidelines. Coyote behaviour is highly variable between spatial areas, landscapes, climate and habitats, and even between individuals and family packs (Randa *et al.* 2009, Morey *et al.* 2007, Bowen 1980, Gompper & Gittleman 1991, Patterson & Messier 2001, Andelt *et al.* 1987, Prugh *et al.* 2005, 2008a,b).

7.4 Future Research

Prugh *et al.* (2008b: 318) stated that “spatiotemporal variation in snowshoe hare availability explained 70% of the variation in hare consumption among groups, indicating that variation in local prey availability may be the primary cause of diet variation among coyotes.” If diet is in fact linked to epizootiology and conflict levels, further studies on prey availability around the study sites may prove to be useful since it may affect coyote diet.

Hence, prey availability could potentially be influencing coyote epizootiology and human-coyote conflict levels.

It would be of scientific interest to combine a diet study and a population dynamics study as well as studies of behaviour and social organization in coyotes. The size and composition (i.e. age, gender) of their group may have the potential to affect their diets by changing their predation habits. Conversely, prey availability and distribution in time and space can also affect group size, and diet (Prugh 2005, Kruuk 1972).

Population density studies of the various prey species combined with a diet analysis would also allow us to distinguish relationships between quantity of one prey species hunted, and density of that available prey. This would theoretically identify preferred food items, but it would have to be compared with the availability of other food sources as well. For example, if coyotes were to consume more garbage than is represented by the availability and quantity of garbage in the city, it could mean that garbage is a preferred food, but it could also mean that their preferred food or another vital food source has become scarce. This lack in other food sources may be driving them to rely more strongly on other food sources such as garbage and pets.

In addition, genotyping techniques would allow the determination of a coyote individual's gender and an estimate of age from a single scat sample (Prugh *et al.* 2005). Genotyping studies comparing diets of denning females, companion males, and coyote pups between biological seasons could potentially reveal further information on sex-specific trade-offs during denning and pup-rearing seasons. A similar research idea was developed and researched by Markman *et al.* (2002). Although they did not use genotyping

techniques, their research on parent Palestine sunbirds (*Nectarinia osea*) revealed life-history trade-offs between parental self-feeding and investment in current young.

This research project ties into a larger coyote project encompassing different dimensions of coyote ecology. In light of the findings of Baker (2007) and Lukasik (2009), dietary analysis is very pertinent to the human-coyote conflict. Furthermore, it could also be intrinsically linked with coyote epizootiology. Relationships between coyote diet and coyote epizootiology are likely to be paralleled and further investigated within the broader coyote research project.

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