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# Coyote (*Canis latrans*) diet in an urban environment: variation relative to pet conflicts, housing density, and season

S.A. Poessel, E.C. Mock, and S.W. Breck

**Abstract:** Coyotes (*Canis latrans* Say, 1823) are highly successful in urbanized environments, but as they populate cities, conflict can occur and often manifests in the form of incidents with pets. To better understand whether coyotes view pets as prey or, alternatively, as competitors or a threat, we conducted a diet analysis of coyotes in the Denver metropolitan area (DMA) by analyzing scats. We also examined differences in diet between high- and low-density housing and among seasons. We found only small percentages of trash and domestic pets in the coyote diet. The presence of pets in the diet did not coincide with the increase of pet conflicts in the DMA in December and January, supporting the hypothesis that coyote conflict with pets is primarily driven by competition or a threat response. Coyotes relied mostly on native plant and animal species, and rodents and lagomorphs were the most prevalent diet items. Coyotes consumed rodents and non-native plants more often in high-density housing and deer, corn, and native plants more often in low-density housing. Coyotes also consumed more fruits and invertebrates during summer and autumn and more mammals and birds in winter and spring. As human–coyote conflicts increase in urban areas, understanding how coyotes and other urban-adapted carnivores use anthropogenic resources may provide insight that can be used to promote coexistence between humans and wildlife.

**Key words:** anthropogenic, *Canis latrans*, coyote, Denver, food habits.

**Résumé :** Les coyotes (*Canis latrans* Say, 1823) ont beaucoup de succès dans les milieux urbanisés, mais leur établissement dans les villes peut entraîner des conflits qui se manifestent souvent par des incidents impliquant des animaux de compagnie. Afin de mieux comprendre si les coyotes considèrent les animaux de compagnie comme des proies ou comme des concurrents ou menaces, nous avons analysé les régimes alimentaires de coyotes dans la région métropolitaine de Denver (DMA) en analysant des excréments. Nous avons également examiné les différences de régime alimentaire entre des secteurs résidentiels de forte et de faible densité et d'une saison à l'autre. Nous n'avons décelé que de faibles pourcentages de déchets et d'animaux de compagnie dans le régime alimentaire des coyotes. La présence d'animaux de compagnie dans l'alimentation des coyotes ne coïncidait pas avec l'augmentation des conflits avec ces derniers dans la DMA en décembre et janvier, ce qui appuie l'hypothèse voulant que les conflits entre coyotes et animaux de compagnie découlent principalement de la concurrence ou de réactions à la menace. Les coyotes avaient principalement recours à des espèces de plantes et d'animaux indigènes, les rongeurs et lagomorphes étant les éléments prédominants de leur régime alimentaire. Les coyotes consommaient plus souvent des rongeurs et plantes non indigènes dans les secteurs résidentiels de forte densité, et des cerfs, du maïs et des plantes indigènes dans les secteurs résidentiels de faible densité. Les coyotes consommaient également plus de fruits et d'invertébrés durant l'été et l'automne et plus de mammifères et d'oiseaux à l'hiver et au printemps. Avec l'augmentation du nombre de conflits entre humains et coyotes dans les zones urbaines, la compréhension de l'utilisation des ressources anthropiques par les coyotes et d'autres carnivores adaptés au milieu urbain pourrait fournir des renseignements utiles pour les efforts visant à promouvoir la coexistence des humains et des espèces sauvages. [Traduit par la Rédaction]

**Mots-clés :** anthropique, *Canis latrans*, coyote, Denver, habitudes alimentaires.

## Introduction

Urbanization can lead to habitat loss and fragmentation and is one of the primary causes of species endangerment (Czech et al. 2000; McKinney 2002; Markovchick-Nicholls et al. 2008). However, some wildlife species, including certain mammalian carnivores, can thrive in urban environments (Ditchkoff et al. 2006; Bateman and Fleming 2012). Carnivores that adapt to urban environments generally tend to be small to medium-sized, have high reproductive potential, can tolerate people, and are dietary generalists

(Fuller et al. 2010). The diet of these urban carnivores usually includes some anthropogenic food, such as cultivated plants, pets, garbage, and roadkill (Bateman and Fleming 2012).

Coyotes (*Canis latrans* Say, 1823) live in nearly every major metropolitan area in the United States (Poessel et al. 2017), and they exemplify the characteristics of urban-adapted carnivores (Morey et al. 2007; Gehrt and Riley 2010). Diet studies of coyotes have been conducted in several urban areas, revealing that coyotes use both natural food items (e.g., deer, rabbits, small mammals, and wild

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fruits) and anthropogenic foods (e.g., garbage, domestic pets, pet food, and cultivated plants) (McClure et al. 1995; Quinn 1997; Fedriani et al. 2001; Morey et al. 2007; Gehrt and Riley 2010; Lukasik and Alexander 2012). Some coyote diet studies have recognized temporal fluctuations in diet (e.g., Litvaitis and Shaw 1980; Crimmins et al. 2012), but no studies have evaluated diet relative to urban characteristics, such as housing density.

Increased coyote presence in more urban areas can lead to a rise in encounters and conflicts with humans (Baker and Timm 1998; Curtis and Hadidian 2010; Gehrt and Riley 2010). Reports of coyote conflicts with humans and especially domestic pets occur throughout the United States (Poessel et al. 2017). For example, in the Denver metropolitan area (DMA), conflicts with pets are now common, and behaviors that include stalking and, in rare cases, attacks on humans have become more prevalent (Poessel et al. 2013). Conflicts have been found to be particularly high in the winter months in both the DMA and Chicago (Gehrt and Riley 2010; Poessel et al. 2013), although increased conflicts during the summer months have been reported in other North American urban areas (White and Gehrt 2009; Lukasik and Alexander 2011). Questions about why pet conflicts have increased and why they fluctuate seasonally are common among natural resource managers. One question is whether coyote–pet conflict is driven primarily by the coyote’s desire to eat pets (i.e., predation) or whether conflict is primarily a product of coyotes viewing pets as competitors or as a threat. The answer to this question should allow wildlife managers to better understand coyote behavior and motivations in highly urbanized areas.

The principal goal of our study was to identify patterns in the anthropogenic portion of the coyote diet in the DMA. Our primary objectives were to (i) examine how dogs (*Canis lupus familiaris* L., 1758) and cats (*Felis catus* L., 1758) vary seasonally in the coyote diet and how this variation coincides with seasonal trends in conflicts and (ii) determine how other anthropogenic food items (e.g., trash) in the diet vary between areas of high- and low-density housing (hereafter, “high-density” and “low-density”). Our secondary objective was to describe the food habits of coyotes in the DMA and to determine how coyote diet varied in high- and low-density areas, as well as across seasons. If coyotes viewed pets primarily as prey rather than as competitors or a threat, then we expected pet consumption to be higher in the winter months, mirroring documented patterns in conflict. We also expected that consumption of trash would be more apparent in high-density housing areas, reflecting a greater influence of anthropogenic food sources in higher density areas.

## Materials and methods

### Study sites

We defined the DMA as the “Denver urban area” as delineated by the U.S. Census Bureau (United States Census Bureau 2015). The DMA comprises over 35 municipalities in north-central Colorado and all or parts of seven counties (Adams, Arapahoe, Boulder, Broomfield, Denver, Douglas, and Jefferson). It has a semiarid climate and, during the study, had annual precipitation of 43 cm and monthly temperatures ranging from a mean low of  $-10^{\circ}\text{C}$  in December to a mean high of  $31^{\circ}\text{C}$  in August (Weather Underground 2015). The DMA had a human population size of almost 2.4 million in 2010 and an approximate size of 1760 km<sup>2</sup>. Located along the front range of the Rocky Mountains of Colorado, the DMA lies between the foothills of the Rocky Mountains to the west and agricultural fields and grasslands to the east. Historically, the DMA was primarily dominated by grassland habitat, but now incorporates various land-cover types, including urban development, woodlands, agriculture, and grasslands (Poessel et al. 2013).

Before selecting our study sites, we first defined areas of high- and low-density housing within the DMA. Designation of these areas was based on housing-density data obtained from the Spa-

tially Explicit Regional Growth Model (SERGoM version 3; Theobald 2005), which depicts housing density for the coterminous United States at 100 m resolution. We defined high-density areas as those with a housing density of less than 0.5 acre per unit and low-density areas as those with a housing density of greater than 5 acres per unit. High-density areas contained smaller amounts of open space with housing developments extending to the borders of such open space, whereas low-density areas contained larger amounts of open space with housing developments nearby. We chose to include only high- and low-density areas (excluding medium-density areas) to compare differences in coyote diet between two distinctive types of urban habitat. We then selected 11 parks or open-space areas known to contain coyotes near neighborhoods, 5 in areas of high-density and 6 in areas of low-density housing (Fig. 1). These open-space areas consisted of natural habitat and contained both paved and dirt trails. Within each open-space area, we then selected trails that we walked to collect coyote scats. We selected trails used by coyotes (as indicated by the presence of coyote scats) that covered most parts of the open-space area.

### Scat collection and identification

We collected coyote scats every month for 1 year, beginning in June 2013. We initially walked each transect to clear all scat and then subsequently walked each transect once per month to collect scat, although we only used scat from every other collection period in the analyses. We received heavy snow in February that made collecting scat difficult, but also degraded scat when the snow melted, leaving few if any samples to be collected; thus, we were unable to analyze scat for the month of February. We were also unable to conduct genetic analyses during our study; hence, we distinguished coyote scats from dog scats based on color, shape, texture, and the amount of hair. Coyote scats tend to be 12–30 mm in diameter; red, dark brown, or gray in color; contain bones, hair, grasses, or seeds; and possess thick, segmented cords and tapered ends (Lukasik and Alexander 2012). Dog scats can be many sizes, are brown or yellow in color, tend to be smoother in shape, and lack hair, bones, and seeds. We removed any scats that looked similar to dog scats; thus, we possibly may have discarded coyote scats that may have contained a diet similar to a domesticated dog. We did not observe any foxes or bobcats (*Lynx rufus* (Schreber, 1777)) in our study sites (so we assumed they were rare), and raccoon (*Procyon lotor* (L., 1758)) scats have a different shape than coyote scats, so we were not concerned about differentiating coyote scats with those of these species. We stored scats in a laboratory at room temperature until analysis.

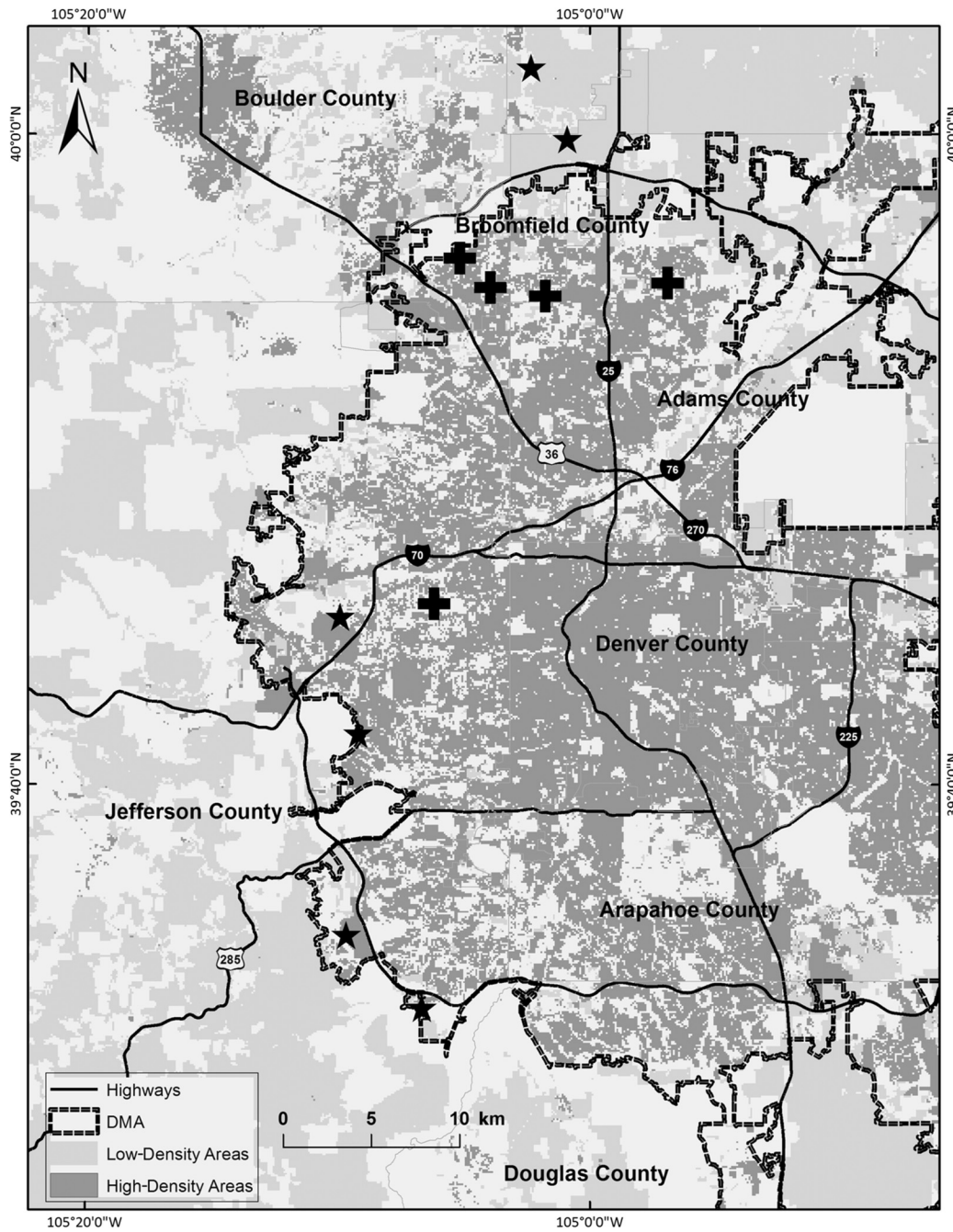
### Scat analysis

We randomly chose up to 10 scats per site for the months of August, October, December, March, April, and June and combined these scats into a single fecal sample. If we did not have 10 scats for a particular site (which frequently occurred), then we used all of the scats available. We thus had one fecal sample per site per month for analysis purposes. We chose this analysis method not only because of limited resources to process each scat individually, but also because it allowed us to address our primary question of whether the importance of anthropogenic items varied between seasons or between housing densities.

We first brushed off each scat to remove any external vegetation or rocks that may have attached to the scat after defecation. After combining scats into fecal samples, we then placed them on a tray and dried them in an incubator at  $50^{\circ}\text{C}$  for 24 h. We recorded the total dry mass and then placed the fecal sample in a soap bath for 24 h to soften the feces for analysis.

Once softened, we broke up and washed the fecal sample through a sieve that retained all of the macroscopic material of hair, feathers, exoskeletons, bones, seeds, vegetation, and trash. We discarded the microscopic material (more than 50% of the

**Fig. 1.** Map of the western portion of the Denver metropolitan area (DMA) with high- and low-density housing. White space includes public land, undeveloped private land, and areas of housing density between 0.5 and 5 acres per unit. Black crosses represent the five high-density transects and black stars represent the six low-density transects used to collect coyote (*Canis latrans*) scats from 2013 to 2014.



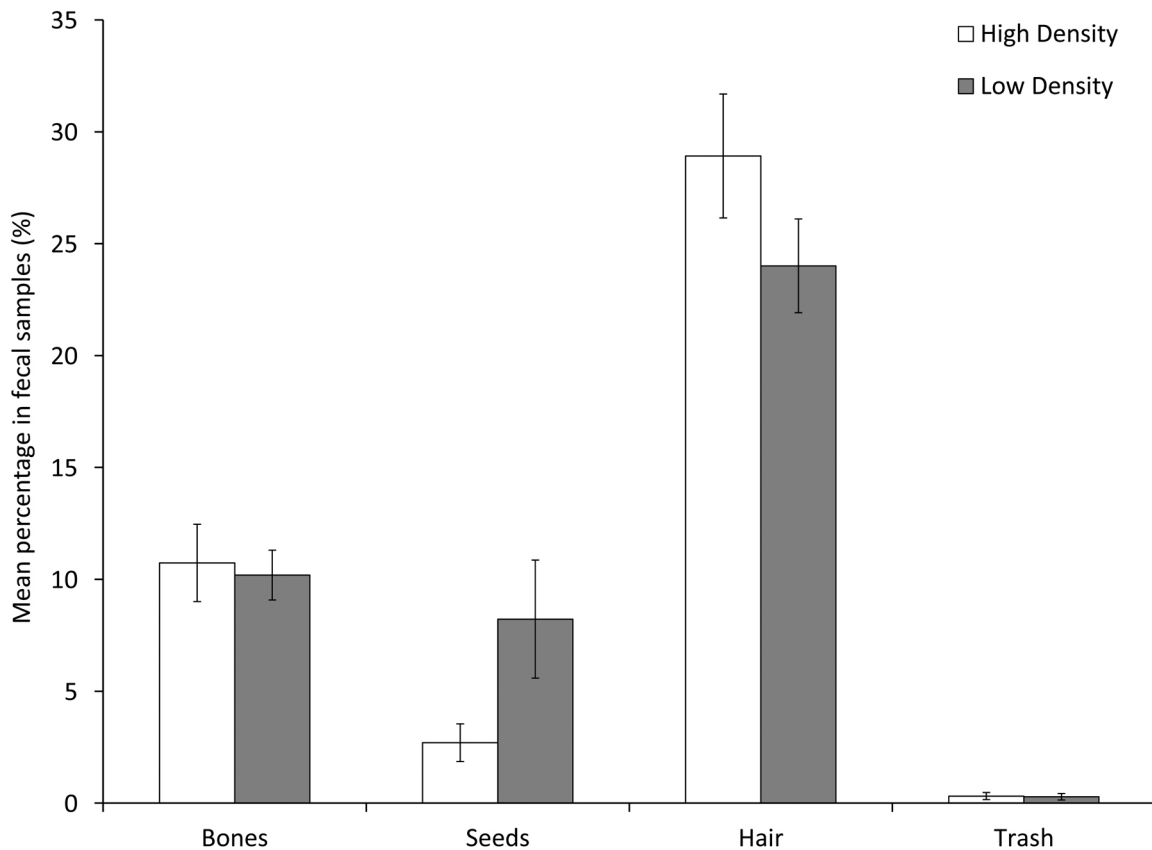
fecal sample), containing unidentifiable organic matter but also potentially earthworm chaetae and feather fragments (Reynolds and Aebischer 1991). We washed and dried the remaining material (i.e., macroscopic material) two more times after placing material in a large bucket with water and mixing it with a paint mixer. Our goal was to separate bones, seeds, and trash, which tended to sink from the hair, feathers, vegetation, and exoskeletons that tended to float. We then separated bones, hair, seeds, and trash and recorded the dry mass of each of these items. We then divided the masses of each of these components by the total mass of the fecal samples to calculate the percent composition. These percentages provided a relative index of vertebrates (bones, which could in-

clude mammals, birds, reptiles, and amphibians), mammals (hair), plants (seeds), and anthropogenic food (trash) in the coyote diet.

We subsampled hairs from each combined fecal sample to identify the mammals consumed by coyotes. For each fecal sample, we randomly selected 100 hairs using a system of gridded cells on a tray. We then laid the selected hairs parallel to one another on a slide for analysis under a microscope. Using a hair identification key, we identified each subsampled hair according to banding, medulla, and cuticle patterns and placed each hair into the following categories: rodent, lagomorph, deer, raccoon, red fox (*Vulpes vulpes* (L., 1758)), coyote, cat, dog, soricomorph, and unidentified (Moore et al. 1974). We further condensed these categories by combining



**Fig. 2.** Mean ( $\pm$ SE) percent composition of coyote (*Canis latrans*) fecal samples (mass of each item divided by mass of the fecal sample) in four diet groups (bones, seeds, hair, and trash) in high- and low-density sites in the Denver metropolitan area, from 2013 to 2014.



raccoon, red fox, and coyote into a “carnivores” category and cat and dog into a “pets” category. We recorded the frequency of each mammal category in fecal samples and calculated the percentage of hairs in each mammal category by dividing the number of hairs in each group by the total hairs analyzed for each sample (i.e., 100 hairs). We then computed mean percentages for each housing density across months and for each month across housing densities.

Because we used hairs to identify mammal species (the most common vertebrate group in fecal samples), we did not identify the bones in the fecal samples to species or use the mass of bones in analyses. We identified birds by analyzing feathers (as described below). We only found reptile skin in one scat; thus, we did not include reptiles and amphibians as a separate category in the coyote diet.

We separated all seeds by type based on size and appearance and submitted them to the Colorado State Seed Laboratory (Colorado State University, Fort Collins, Colorado, USA) for identification. After identification of the seeds to plant species, we then recorded the masses of seeds by species and the frequency of each species in fecal samples. We then computed mean seed masses of each species for each housing density across months and for each month across housing densities. We further identified each plant species as either native or non-native.

Finally, in each fecal sample, we visually estimated the amount of feathers and exoskeletons, which were not removed from the samples. We did not identify feathers to bird species; however, exoskeletons were mostly intact and were easily identified as grasshoppers or beetles. We assigned a separate score for both feathers and exoskeletons in each sample. For feathers, we assigned a 0 when no feathers were visible, 1 when roughly 1%–20% of the sample was composed of feathers, and 2 when >20% of the sample was composed of feathers. For exoskeletons, we assigned a

0 to fecal samples with no exoskeletons present, 1 when roughly 1%–10% of the sample was composed of exoskeletons, and 2 when >10% of the sample contained exoskeletons. We inadvertently used a 10% break for exoskeletons rather than 20%; however, we proceeded with this scoring rather than simply reporting presence or absence so that we could present patterns similar to what we demonstrated for feathers. For both feathers and exoskeletons, we then calculated a weighted average of scores for each housing density across months and for each month across housing densities. To do so, for each housing density, we multiplied the number of sites within a month with a particular score by the value of that score (i.e., 0, 1, or 2), added these three products, then divided this sum by the total number of sites in a month for which we had fecal samples. These scores reflect a rough qualitative assessment of the mean consumption of birds and invertebrates by coyotes (i.e., a score of 0 reflects no consumption, a score of 1 reflects low consumption, and a score of 2 reflects high consumption).

We note that, for each food-item group described above (mammals, plants, and birds or invertebrates), we used a different analysis method to determine variation in the coyote diet between housing densities and across months. Our goal was to determine not only how frequently a food item occurred in the diet, but also how important each item was in the diet by using masses when possible. These methods may vary from other coyote diet studies.

#### Statistical analysis

We focused our statistical analysis on our primary objective of whether coyotes kill pets because of predation or because of competition or a threat response. We conducted an analysis of variance (ANOVA) test in R version 0.99.446 (R Core Team 2015) to determine if the amount of pet hair in the coyote diet varied by

**Table 1.** Frequencies and percentages of mammal hairs, as well as frequencies, masses, and percentages of seeds of plant species and trash, found in 64 coyote (*Canis latrans*) fecal samples (consisting of up to 10 scats per site per month) in the Denver metropolitan area, from 2013 to 2014.

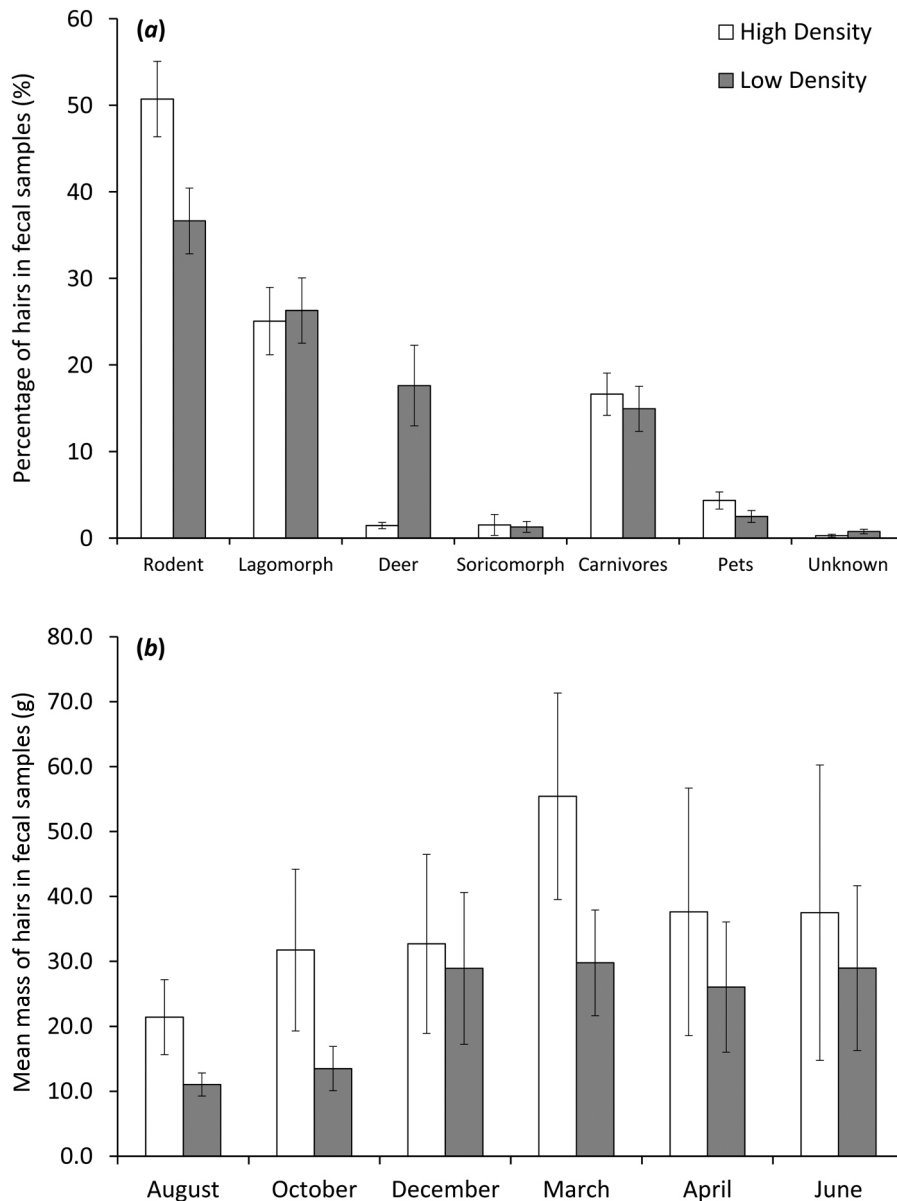
Group	Species	Frequency	Mass (g)	Percentage (%)
<b>Hair</b>				
Rodents	NA	64		43.02
Lagomorphs	NA	61		25.73
Deer	Mule deer, <i>Odocoileus hemionus</i>	35		10.29
Carnivores	Raccoon, <i>Procyon lotor</i>	40		8.98
Carnivores	Red fox, <i>Vulpes vulpes</i>	34		5.14
Carnivores	Coyote	23		1.58
Pets	Domestic cat, <i>Felis catus</i>	24		2.12
Pets	Domestic dog, <i>Canis lupus familiaris</i>	25		1.21
Soricomorphs	NA	10		1.39
Unknown	NA	14		0.54
Total by group				
Rodents		64		43.02
Lagomorphs		61		25.73
Deer		35		10.29
Carnivores		56		15.70
Pets		41		3.33
Soricomorphs		10		1.39
Unknown		14		0.54
<b>Seeds</b>				
Non-native	Russian olive, <i>Elaeagnus angustifolia</i>	17	30.05	6.48
Native	Cactus, <i>Opuntia</i> spp.	11	209.28	45.16
Non-native	Corn, <i>Zea mays</i>	8	24.47	5.28
Non-native	Field bindweed, <i>Convolvulus arvensis</i>	7	0.32	0.07
Non-native	Sorghum grain, <i>Sorghum</i> spp.	6	1.44	0.31
Native	American plum, <i>Prunus americana</i>	6	24.11	5.20
Native	Sunflower, <i>Helianthus annuus</i>	6	0.28	0.06
Non-native	Grapevine, <i>Vitis</i> spp.	5	16.60	3.58
Native	Manzanita/bearberry, genus <i>Arctostaphylos</i> Adans.	5	2.89	0.62
Non-native	Wheat, genus <i>Triticum</i> L.	5	0.40	0.09
Native	Chokecherry, <i>Prunus virginiana</i>	4	139.96	30.20
Non-native	Watermelon, <i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai	3	0.16	0.03
Non-native	Oat, <i>Avena sativa</i> L.	3	1.96	0.42
Native	Virginia groundcherry, <i>Physalis virginiana</i> Mill.	2	0.45	0.10
Native	Raspberry, genus <i>Rubus</i> L.	2	0.08	0.02
Native	Flax, <i>Linum usitatissimum</i> L.	2	1.42	0.31
Non-native	Safflower, <i>Carthamus tinctorius</i> L.	1	0.02	0.01
Non-native	Dandelion, genus <i>Taraxacum</i> F.H. Wigg	1	0.06	0.01
Non-native	Pigweed, genus <i>Amaranthus</i> L.	1	0.01	0.00
Non-native	Black bindweed, <i>Fallopia convolvulus</i> (L.) Á. Löve	1	0.47	0.10
Non-native	Hairy vetch, <i>Vicia villosa</i> Roth	1	0.02	0.01
Non-native	Alfalfa, <i>Medicago sativa</i> L.	1	3.93	0.85
Unknown	NA	19	5.05	1.09
Total mass			463.43	100.00
Total by group				
Native		27	378.47	81.67
Non-native		35	79.91	17.24
Unknown		19	5.05	1.09
<b>Trash</b>				
NA	NA	27	21.0	0.31

**Note:** Group represents condensed categories for mammals and species origin for plants. Frequency represents the number of fecal samples (out of 64) containing that food item. Mass represents the total mass of each plant species and group and of all trash found in fecal samples. For hair, percentage is the mean percentage of hairs for each mammal species or group, calculated as the number of hairs for that species or group divided by total hairs analyzed (i.e., 100) in each fecal sample. For seeds, percentage is the mass for each plant species or group divided by the total mass for all plant species (463.43 g). For trash, percentage is the mass of all trash divided by the total mass of all fecal samples analyzed (6788.66 g). NA, not available or not identified.

month. Poessel et al. (2013) previously found that coyote–pet conflicts were more frequent during the winter months (specifically, December and January). If coyotes pursue pets primarily for consumption, then pet hair in scats should increase in December. If no such pattern occurs, then the hypothesis that coyotes pursue pets primarily because they perceive them as competitors or a threat is supported.

We found very little trash in the coyote diet in both housing-density areas (see Results), so statistical tests to address our second primary objective, i.e., to determine how anthropogenic food items vary between high- and low-density housing areas, were not possible or necessary. We also did not statistically analyze specific food items and how they varied by housing density or month (i.e., our secondary objective). Instead, we present these results in a

**Fig. 3.** Mean ( $\pm$ SE) percentage of hairs of mammal groups found in coyote (*Canis latrans*) fecal samples in high- and low-density sites (a) and mean ( $\pm$ SE) mass of all hairs found in coyote fecal samples by month in high- and low-density sites (b) in the Denver metropolitan area, from 2013 to 2014. The “unknown” category in panel a includes all unidentified mammal hairs found in coyote fecal samples during the study.



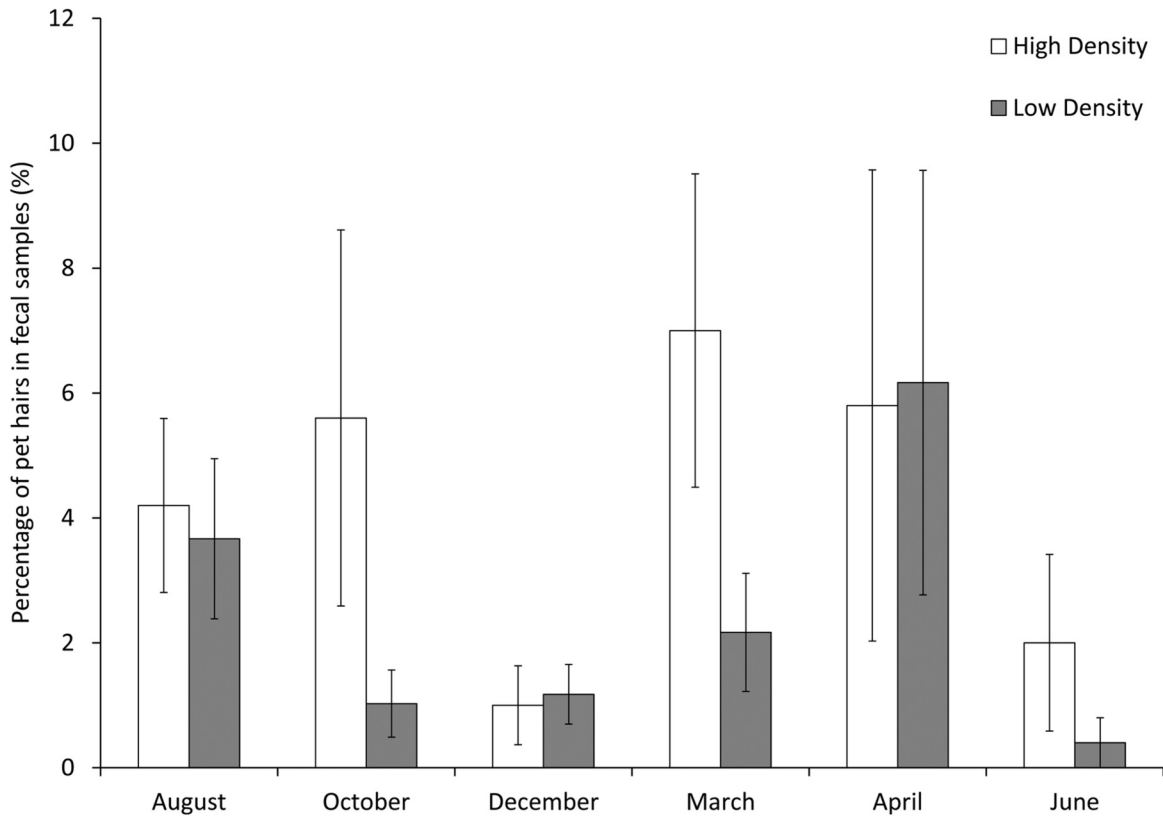
descriptive manner by graphically evaluating patterns in the data; the error bars in these graphs indicate the amount of variation between housing densities and across months.

## Results

Across our 11 sites, we sampled 26.2 km of trails (high-density housing: 12.5 km, mean  $\pm$  SD =  $2.5 \pm 1.4$  km; low-density housing: 13.7 km, mean  $\pm$  SD =  $2.3 \pm 1.3$  km). We analyzed 64 fecal samples, 29 in high-density sites and 35 in low-density sites. These fecal samples consisted of 424 scats, 210 in high-density sites (mean  $\pm$  SD =  $7.2 \pm 3.0$ ) and 214 in low-density sites (mean  $\pm$  SD =  $6.1 \pm 2.9$ ). Among diet items, hair had the highest percentage by mass in combined coyote fecal samples (mean  $\pm$  SE =  $26.2\% \pm 1.7\%$ ), followed by bones ( $10.4\% \pm 1.0\%$ ) and seeds ( $5.7\% \pm 1.5\%$ ). Percentage of trash by mass in fecal samples was negligible ( $0.3\% \pm 0.1\%$ ). Hair percentages by mass were higher in fecal samples in high-density sites and seed percentages were higher in low-density sites (Fig. 2).

Based on the hair analysis, the most common mammal group found in fecal samples was rodents ( $43.0\% \pm 3.0\%$ ), followed by lagomorphs ( $25.7\% \pm 2.7\%$ ) and carnivores ( $15.7\% \pm 1.8\%$ ; raccoon:  $9.0\% \pm 1.5\%$ ; fox:  $5.1\% \pm 1.0\%$ ; coyote:  $1.6\% \pm 0.3\%$ ; Table 1). Carnivore consumption could have been from scavenging, predation, or in the case of coyotes, self-grooming. Fecal samples contained a small percentage of pets (i.e., cats and dogs;  $3.3\% \pm 0.6\%$ ; Table 1). Percentages of rodents and pets in fecal samples were higher in high-density sites and percentages of deer were higher in low-density sites (Fig. 3a). Mammals were more common in the diet in December, March, April, and June than in August or October and more common in the diet in high-density sites than low-density sites throughout the year, especially in August, October, and March (Fig. 3b). Pet hairs were least common in the diet in December (Fig. 4), the time of year when coyote–pet conflicts were highest in the DMA (see Fig. 3b in Poessel et al. 2013). Month was not a significant variable in the ANOVA testing for a relationship be-

**Fig. 4.** Mean ( $\pm$ SE) percentage of hairs from pets found in coyote (*Canis latrans*) fecal samples in high- and low-density sites by month in the Denver metropolitan area, from 2013 to 2014.



tween the amount of pet hair in the diet and month ( $F_{[5,58]} = 1.8$ ,  $P = 0.123$ ).

Fecal samples contained 33 different species of seeds that coyotes either fed on directly or were present in prey items of coyotes. Russian olive (*Elaeagnus angustifolia* L.), cactus (species of the genus *Opuntia* Mill.), corn (*Zea mays* L.), field bindweed (*Convolvulus arvensis* L.), sorghum (species of the genus *Sorghum* Moench), American plum (*Prunus americana* Marshall), and sunflower (*Helianthus annuus* L.) were most commonly present in fecal samples by frequency (Table 1). Russian olive and grapevine (species of the genus *Vitis* L.) were more common in high-density sites, whereas cactus, chokecherry (*Prunus virginiana* L.), and corn were more prevalent in low-density sites by mass (Fig. 5a). The presence of seeds in fecal samples also reflected seasonal availability, with more plants consumed in August and October than in December, March, April, or June. Fecal samples also contained a higher amount of seeds in August and October in low-density sites than in high-density sites (Fig. 5b), especially of native plants.

Ground beetles and grasshoppers made up the majority of exoskeletons found in scats. The presence of exoskeletons was highest in August and October and lowest in March and April (Fig. 6a). Exoskeletons were also more common in low-density sites than in high-density sites for most of the year (Fig. 6a). The amounts of feathers in scats varied across months in both high- and low-density sites and were most common in December and April (Fig. 6b). Feathers were also more common in high-density sites than in low-density sites for most of the year (Fig. 6b).

## Discussion

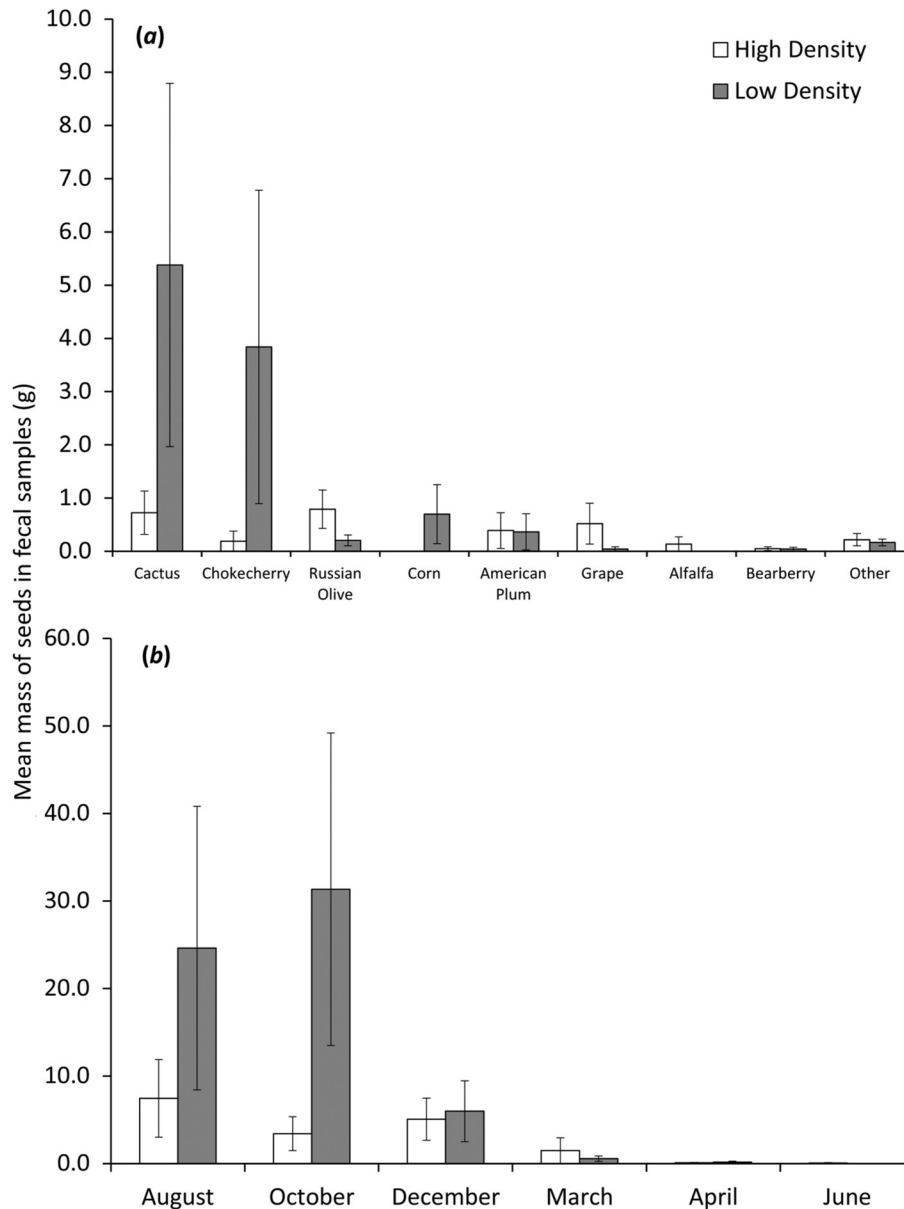
Coyotes appeared to have consumed anthropogenic food items in low amounts in our study area. Pets comprised only 3% of mammal hairs in the coyote diet, and they were more commonly found in high-density sites (Fig. 3a). This finding corroborates

other studies that have determined that coyotes consume domestic cats and dogs in low quantities (Fedriani et al. 2001; Morey et al. 2007; Gehrt and Riley 2010; Lukasik and Alexander 2012). Murray et al. (2015) also found that coyotes in higher density (urban) areas consumed more pets than did coyotes in lower density (rural) areas. In Tucson, Arizona, Grubbs and Krausman (2009) observed 19 cats that were killed by coyotes, 18 of which were consumed. However, they did not report a dietary analysis for these coyotes, so the importance of cats in the coyote diet in this study area is unknown.

In the DMA, over 92% of coyote–human conflicts reported between 2003 and 2010 were incidents with pets (471; Poessel et al. 2013). These included injuries and deaths of cats and dogs caused by coyotes, although we did not have information on how many of these pets were killed. Hence, coyotes can be a serious threat to the safety of domestic pets. Furthermore, coyote conflicts with pets were more frequent during the winter months (December and January; see Fig. 3b in Poessel et al. 2013). However, pets comprised only a very small percentage of the coyote diet in our study, and pet hair did not increase in the diet during winter, possibly indicating that coyotes usually do not consume the cats and dogs that they kill. These results support the hypothesis that coyote conflict with pets is primarily driven by competition or a threat response, rather than predation. Coyotes may view cats as competitors because cats will hunt rodents, a primary component of the coyote diet, similar to the finding that coyotes also perceive other canids, such as dogs and foxes, as competitors for food and habitat (Gosselink et al. 2003). Winter months coincide with coyote breeding season, so during this time of year, coyotes may view dogs as potential competitors for mates, leading to increased conflicts with pets (Poessel et al. 2013). Additionally, pets increased in the coyote diet in March, the time of year when births of pups



**Fig. 5.** Mean ( $\pm$ SE) mass of seeds found in coyote (*Canis latrans*) fecal samples in high- and low-density sites of the most common plant species (a) and all plants by month (b) in the Denver metropolitan area, from 2013 to 2014. The “other” category in panel a includes all other plant species consumed by coyotes during the study.



begin, so coyotes may perceive dogs as a threat to their pups and pets killed during this time also may be consumed.

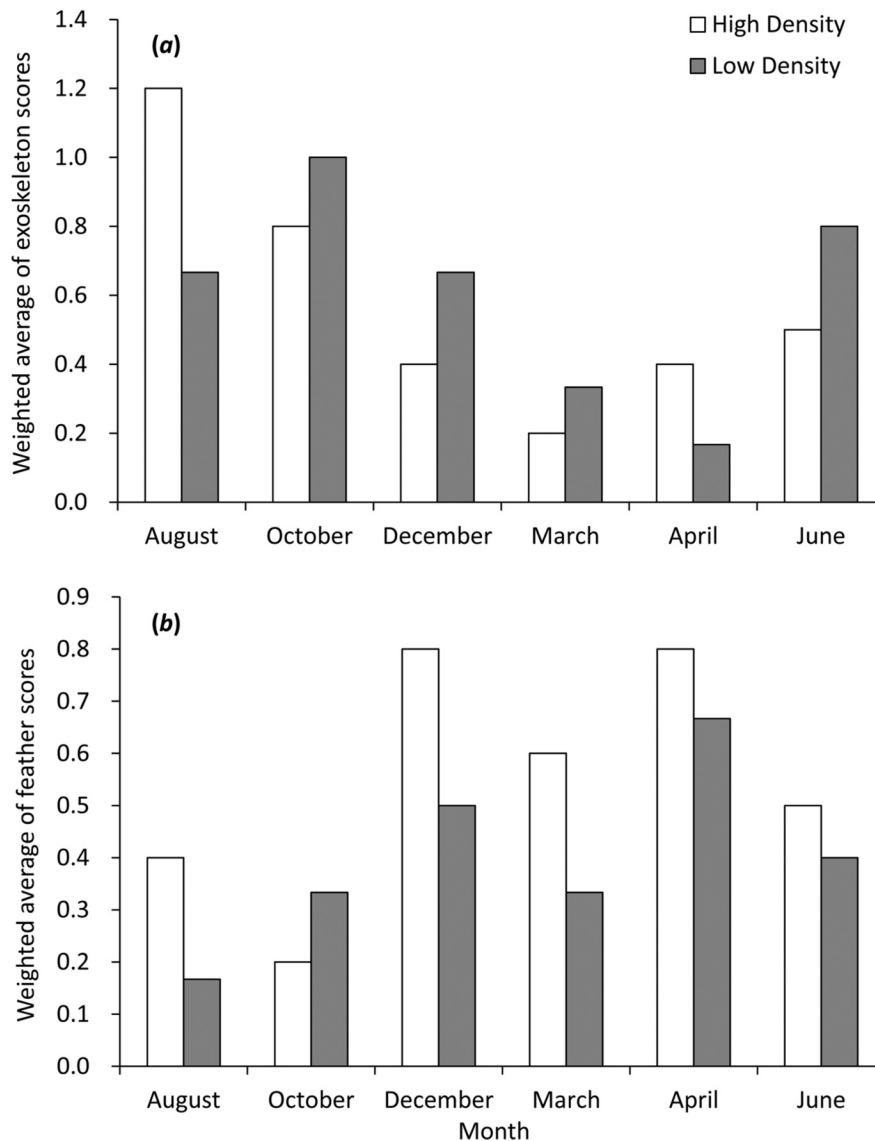
We found only a small amount of trash in the coyote diet. Only 0.3% of fecal sample masses consisted of trash in both high- and low-density sites. However, 27 of 64 fecal samples (42%) contained trash items (Table 1), although we do not know how many individual scats contained trash. Hence, although coyotes do not appear to be consuming large amounts of garbage, they may be accessing it frequently, even though during our study we did not observe coyotes eating curbside trash or entering trash dumpsters.

We used trash to measure anthropogenic food in the coyote diet because this human-associated item was indigestible and easily recovered in fecal samples. However, coyotes could have consumed other anthropogenic food items, such as pet food or human food that is digested and cannot be measured in scats. Thus, fecal analysis has limitations for examining the diet of wildlife species in urban environments. Stable isotope analysis is an alternative method that has been used in urban systems to examine

coyote diets (Murray et al. 2015; Newsome et al. 2015). This technique is better able to discriminate between natural prey items and anthropogenic resources by estimating the isotopic composition of each food item and of coyotes, measured in hair or vibrissae. Previous studies using this method have shown that some coyotes in urban areas will consume anthropogenic food (Murray et al. 2015; Newsome et al. 2015), and stable isotope analysis can report a higher prevalence of anthropogenic foods in coyote diets than scat analysis. Therefore, if assessing anthropogenic food resources in the urban coyote diet is a primary objective, then future studies should include this technique or others like it (e.g., fatty acid analyses) in conjunction with fecal analysis to obtain a more accurate assessment of coyote diets in urban areas.

The diet of coyotes in our study area varied both spatially and temporally, and coyotes showed evidence of opportunistic foraging. Generally, coyote diets consisted of more mammals in high-density sites and more plants in low-density sites, although some individual animal and plant species varied from this pattern. Like-

**Fig. 6.** Weighted average scores of exoskeletons (a) and feathers (b) found in coyote (*Canis latrans*) fecal samples by month in high- and low-density sites in the Denver metropolitan area, from 2013 to 2014.



wise, mammals and birds were more common in winter and spring (December–June), whereas plants and invertebrates were more prevalent in late summer and autumn (August–October), likely due to seasonal food availability. Coyotes in our study area preferred natural habitat over developed landscapes, although they did use residential areas, especially at night (Poessel et al. 2016); however, we do not know where coyotes were primarily foraging.

Specifically for animals, mammal hair, particularly that of rodents and rabbits, was the most prevalent diet item in coyote fecal samples. Coyotes consumed rodents more often in high-density sites and deer more often in low-density sites (Fig. 3a). Mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) require large amounts of space, are dependent on natural areas, and therefore were more readily available in the low-density sites than in the high-density sites. Thus, coyotes may have increased rodents in their diet in high-density areas because deer were not as available.

Coyote consumption of rodents followed the seasonal pattern of higher prevalence in winter and spring, although rodents were common in the diet throughout the year. Because every one of the 64 fecal samples contained rodent hair, this mammal group influ-

enced the overall seasonal pattern for all mammals. Deer hair was most common in fecal samples in June, after the birthing period of fawns when they are vulnerable to coyote predation. However, coyotes fed on deer throughout the year, likely available as carrion from roadkill. Lagomorphs were more prevalent in the diet in late autumn and early winter than in spring and summer. Morey et al. (2007) also found that lagomorphs occurred in coyote diets in lower frequencies during the summer, suggesting that rabbits are better able to avoid capture by coyotes during a time of increased vegetation growth. Furthermore, fruit is more available during summer, so coyotes may be switching from animals to plants during this time.

Specifically for plants, coyotes consumed Russian olive (non-native) and grapevine (non-native) more often in high-density sites and cactus (native), chokecherry (native), and corn (non-native) more often in low-density sites (Fig. 5a). Russian olive, a highly invasive species, has become naturalized throughout the western United States and is primarily found in riparian areas (Shafroth et al. 1995). The high-density sites in our study area were located near riparian areas, and coyotes used riparian areas frequently (Poessel et al. 2016), leading to a high prevalence of this

plant in coyote scats at these sites. Grapevines are widely cultivated in gardens, likely resulting in a large number of these plants in residential areas and a high occurrence of these seeds in coyote scats at high-density sites. Cactus and chokecherry are both native species to Colorado and were common in low-density sites where coyotes were more likely to consume native fruits. Finally, corn may have been more common in low-density sites because of the higher presence of deer in these areas; we speculate that residents in these sites may be placing corn outside to feed deer, which can be accessed by coyotes. Corn fields also are present near the low-density sites, and we occasionally observed coyotes in these fields.

Coyote consumption of most plant species followed the same seasonal pattern of high prevalence in summer or autumn. Russian olive was found in the coyote diet in higher masses in August, October, and December. However, corn was most commonly found in the diet in early winter (December), a time of year when coyotes might be more food-stressed (Bekoff and Wells 1981). Corn, as well as sorghum, is found in different brands of birdseed, and residents of the DMA may be leaving out dried or cracked corn and birdseed in bird feeders. Thus, coyotes likely were utilizing this food source to supplement their diet in the winter. Although we can only speculate, the presence of corn in the coyote diet is likely anthropogenically driven, whether from residents feeding deer, placing corn in bird feeders, or cultivating corn plants.

Russian olive was the most frequently consumed plant, occurring in 17 of 64 fecal samples (27%; Table 1). Although coyotes consumed 14 different non-native plant species, the largest volume of seeds in the coyote diet consisted of native species (82% of total seed mass, although the majority of this mass was from only two species; Table 1). Hence, coyotes may be an important disperser of not only Russian olive, but also a variety of native plant species in this highly urbanized area.

## Conclusions

Our scat analysis revealed that pets consisted of only a small percentage of the coyote diet, and pet consumption decreased when coyote–pet conflicts increased, which supports the hypothesis that coyote conflict with pets is primarily driven by competition or a threat response, rather than predation. Coyotes in urban areas have a wide variety of foods available to them, so they do not need to consume pets. However, territoriality in coyotes is strong and they will remove perceived threats to their ability to survive and reproduce. Hence, pet owners should be diligent in their efforts to protect their pets by not letting pets outside unsupervised, including in their yards, by keeping pets on leash when walking them in natural areas, and by being especially aware of coyotes during winter. Our work further revealed that trash did not constitute a significant portion of the diet of coyotes, but our analysis technique was not sensitive to detecting certain anthropogenic food sources that are difficult to detect with scat analysis. Urban residents can reduce the amount of such food available to coyotes by securing trash and removing pet food from outdoor areas. As reports of wildlife conflicts in urban areas continue to increase, understanding how urban-adapted species, such as coyotes, use anthropogenic resources may provide insight that can be used to promote coexistence between humans and wildlife.

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