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Research article

Supplementation of seasonal natural resources with year-round anthropogenic resources by coyotes in natural fragments within a high-density urban area

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Coyotes *Canis latrans* in urban landscapes provide important food web functions and ecological services but can also trigger human-wildlife conflict when their diet includes anthropogenic resources or domestic pets. As adaptable omnivores, coyotes adjust their diet to their environment, routinely switching among food items to accommodate spatial and seasonal differences in availability. To evaluate the coyote's potential impacts within the food web of urban Long Beach, California where human-wildlife conflict involving coyotes may occur, we analyzed 115 scat samples collected once every two weeks from four open space fragments inside the urban matrix. We hypothesized that differences in scat composition would correlate with seasonal and site differences, with greater use of anthropogenic resources during the dry season supplementing lower prey availability, and with greater consumption of wild mammal prey during the wet season when fruiting plants are less abundant. We found coyote diet was predominately composed of natural prey and vegetation year-round, with seasonal variation. Mammals made up more of coyote diet in the wet season than the dry, while invertebrates and vegetation were more prevalent in dry season scats. Coyotes relied on rabbits as their main prey year-round across all sites. Domestic cats *Felis catus* were the third most common individual prey species found in coyote scats, occurring in 14% of scat samples in both seasons. Coyotes also supplemented seasonally available natural food sources with anthropogenic resources, which occurred in 13% of coyote scats overall with no significant seasonal variation. While rabbits appeared in scat from all sites, the occurrence of invertebrates, small mammals, and vegetation in scats varied between sites. While there is a potential for human-wildlife conflict in coyote's consumption of feral or domestic cats, coyotes may also be providing an ecological service by reducing cats in natural habitat fragments.

Keywords: *Canis latrans*, diet, domestic cat, *Felis catus*, human-wildlife conflict, Long Beach, seasonal, southern California

Introduction

For several hundred-thousand years, coyotes *Canis latrans* have occupied the area now known as Greater Los Angeles, California (Hody and Kays 2018). They once shared it with dire wolves *Canis dirus* and sabertooth cats (*Smilodon fatalis*; Coltrain et al. 2004, Meachen and Samuels 2012), and now share it with a human population of over 18 million (US Census Bureau 2022). Unlike larger historic predators, coyotes were omnivorous in the late Pleistocene (Coltrain et al. 2004). Their dietary flexibility, adaptability to environmental change, and ability to respond to variation in resources has enabled coyotes to thrive in the highly urbanized Greater Los Angeles region even as nearly all other native predators have declined to local or complete extinction (Bekoff and Gese 2003, Gilbert-Norton et al. 2009, DeSantis et al. 2019). In this study, we sought to explore the dietary flexibility of coyotes in Long Beach, California, within the greater Los Angeles area, as a mechanism of assessing the potential for human-wildlife conflict.

Wild carnivores are frequently involved in human-wildlife conflict (Treves and Karanth 2003, Expósito-Granados et al. 2019), with some species, such as coyotes in North America often perceived as particularly threatening (Timm and Baker 2007, White and Gehrt 2009, Poessel et al. 2013). The frequency of human-wildlife conflict is likely increasing due to expanding human populations usurping spaces previously occupied by wildlife (Madden 2004, Bateman and Fleming 2012, Conover and Conover 2022), or when wildlife is attracted to anthropogenic resources (Gehrt et al. 2010). As adaptable omnivores, coyotes adjust their diet to their environment, routinely switching to accommodate seasonal and spatial variation in resource availability (Gilbert-Norton et al. 2009). Seasonal differences in prey and vegetation consumption have been found in both rural and urban areas (Dowd and Gese 2012, Poessel et al. 2017). This may also be influenced by the biological needs of coyotes during breeding, pup-rearing, and dispersal seasons (Bekoff and Gese 2003). Anthropogenic items, including pet foods and indigestible trash, present an anthropogenic resource with year-round availability that is independent of seasonal changes. This availability may reduce natural predation by coyotes in urban areas (Rodewald et al. 2011). Conflict may disproportionately involve sick or diseased animals in poor body condition that consume anthropogenic foods (Murray et al. 2015, Sugden et al. 2020). Furthermore, unhealthy coyotes may increase their risk of conflict by relying more on anthropogenic food sources (Murray and St Clair 2017).

Diets of urban coyotes can help predict human-coyote conflict risk (Murray et al. 2015). The nature of human-wildlife conflict involving coyotes may differ seasonally as coyotes switch diets with seasonal differences in prey types. For that reason, we explored seasonal differences in the diets of urban coyotes. We were interested in understanding the roles coyotes play in urban environments, where they share limited open space fragments with human residents, feral and domestic cats *Felis catus* and dogs *Canis lupis familiaris*, and a variety of native mesocarnivores and herbivores. Interactions with each of these groups can create or exacerbate human-wildlife conflict either directly or indirectly and can influence food webs (Baker and Timm 1998, Poessel et al. 2013, Quinn et al. 2016). We used scat analyses, a proven non-invasive mechanism to quantify diet, to explore these relationships (Morey et al. 2007, Larson et al. 2020, Lingle et al. 2022).

Urban landscapes present wildlife with unique environments where selective pressures differ from city to city and diverge from native habitats (Faeth et al. 2011, Schell et al. 2020). Urban areas may change predator avoidance behavior in coyotes' main prey. For example, rabbits in urban areas can be less vigilant to coyote activity (Gallo et al. 2019) and can have smaller home ranges and higher densities than rural populations (Hunt et al. 2013). Natural fragments, parks, and other green spaces in urban areas can host diverse plant and animal species (Angold et al. 2006), but may lack the diversity in habitat structure that rural natural areas provide (Le Roux et al. 2014). The diversity and structure of vegetation can vary greatly between habitat types available in urban areas (Threlfall et al. 2016). It is important to understand how these habitat patches are, or are not, providing coyotes with natural prey or food items.

Many previous studies have evaluated coyote diets in rural areas (Cepek 2004, Kamler et al. 2014, Lingle et al. 2022) and temperate cities (Morey et al. 2007, Lukasik and Alexander 2012, Garwood et al. 2015, Newsome et al. 2015). Here, we studied coyote diets in urban Long Beach, California, part of the Greater Los Angeles megalopolis, where high human density and semi-arid climate uniquely shape coyote diet. We tested the hypothesis that differences in scat composition would correspond with seasonal changes and differences in site characteristics of natural habitat fragments. We also predicted that coyotes would predominately rely on natural food sources. If coyotes supplemented their diet with anthropogenic foods when mammalian prey populations were lower, there should be seasonal changes in the frequency of anthropogenic resources in scats. However, if they were not relying on or supplementing their diet with anthropogenic foods, then these items would show up occasionally in their diet at a consistent rate throughout the year. We further predicted that the contents of scat would differ between different sites in urban green spaces based on their natural resources. We also predicted that natural habitat fragments that contain more vegetation and consistent water, which provide more hunting and foraging opportunities for coyotes, would contain scats with more natural prey types and less anthropogenic foods. However, if coyotes were traveling throughout the different sites in the green spaces to access and eat anthropogenic foods on the fringes, natural items would be lower and there would be less variation between sites.

Study area

Our Long Beach, California study area was in Los Angeles County, where the human population expanded from 3000

in 1850, to over half a million by 1910 and over 10 million in 2020 (US Census Bureau 2022). Los Angeles County contains highly dense urbanized areas, with a human density of 9200 people per square mile in the city of Long Beach (US Census Bureau 2022). Within this landscape, our study area along the San Gabriel River consisted of two open space fragments in Los Cerritos Wetlands, and two in El Dorado Regional Park (Fig. 1).

Figure 1. Coyote *Canis latrans* scat transects (orange dashed lines) at (A) El Dorado Nature Center and (B) Los Cerritos Wetlands in (C) Long Beach, California, USA, 2016–2017.

The Los Cerritos Wetlands sites were in a restored saltmarsh and an unrestored saltmarsh. The restored saltmarsh, east of the San Gabriel River (33.75157°N, 118.0965°W) consisted of shrub/scrub around a tidally influenced emergent herbaceous wetland restored with native vegetation bordered by residential areas, operating industrial areas, and busy roads. The unrestored saltmarsh, west of the San Gabriel River (33.75799°N, 118.1005°W), consisted of low intensity development and mixed native and invasive shrub/scrub around a tidally influenced emergent herbaceous wetland with sparse vegetation and brackish water bordered by operating oil jack pumps, shopping centers, and additional busy roads.

The El Dorado Regional Park sites were separated by a four-lane road (Willow Street) with an underpass connecting them and consisted of an irrigated open space, and an unirrigated patch of scrub/shrub. The irrigated open space, north of Willow Street (33.80837°N, 118.0901°W) received weekly water through sprinklers, was densely vegetated near public walking paths, and was surrounded by public parks and residential areas. The unirrigated scrub/shrub, south of Willow Street (33.80305°N, 118.0884°W) was less densely vegetated, lacked walking paths, and was surrounded by medium- and high-intensity development.

Material and methods

Coastal southern California has two distinct seasons demarcated by precipitation with a wet season defined by the presence of rain and lower average temperatures, and a dry season defined by the absence of rain and higher average temperatures. Wet seasons in Long Beach experience an average of 30 cm of rainfall total over 30 rainy days, and average high temperatures between 15–20°C. The 2016–2017 wet season experienced rainfall of nearly 51 cm over 43 rainy days, and daily high temperatures from 18–21°C (NOAA 2022). Dry seasons in Long Beach experience trace rainfalls accumulating to under 2 cm total, and average high temperatures of 28°C. The 2016–2017 dry season experienced trace rainfall events accumulating to less than 3 mm, and highs between 26–28°C and (NOAA 2022). Based on these criteria, we defined the wet season we studied as 17 October 2016 through 7 May 2017. We defined the two dry seasons we studied as 12 August 2016 through 16 October 2016, and 8 May 2017 through 17 August 2017. Consequently, while the surveys were conducted over a full year (12 months), they began and ended in the dry season of two calendar years. These dates are generally consistent with those of other southern California studies distinguishing wet and dry seasons (Fedriani et al. 2001, Larson et al. 2020).

We collected scat once every two weeks along four transects, one through each of our four study sites. Transects followed established paths, roads, and walking trails within each site, resulting in lengths varying from 0.5 to 0.7 km per transect. Coyote scat may be accurately identified in the field (Prugh and Ritland 2005, Lonsinger et al. 2015), however coyote scats may also be confused with those of other

mesocarnivores, if present (Morin et al. 2016). We identified coyote scat by size, shape, and consistency following Reid (2015). We avoided collection of potential fox scat by excluding canid scats under 16 mm in diameter (Danner and Dodd 1982, Cepek 2004). We avoided collection of domestic dog scat by excluding large scat that did not have the characteristic tapered ends and did not contain visible fur, bone, or vegetative matter. We verified the reliability of our identification by identifying coyote tracks on our transects and through a concurrent remote camera study that included video-documentation of coyotes defecating (Collins 2018). Furthermore, the concurrent study did not record any occurrences of foxes, bobcat, badgers, or domestic dogs in areas where scat was collected (Collins 2018). At the beginning of the study, pre-existing scat was removed from transects to provide newly deposited scat with a timeframe within the two-week collection window (Larson et al. 2015). Thereafter, we collected samples into sealed plastic bags labeled with the location and date of collection and stored in a freezer at −20°C until processing (Morey et al. 2007). When discovered, we sampled coyote latrine areas by allowing some scats to remain as scent and visual markings.

Sample processing and analysis

We followed established protocols of bagging and washing scat samples to remove fecal materials (Cepek 2004, Morey et al. 2007, Randa et al. 2009, Larson et al. 2015). Specifically, we placed samples in two layers of new nylon stockings, soaked them in warm soapy water for 30 min, and then rinsed them under running water for 5 min. We repeated this as needed to remove all fine particles, then air-dried samples for 48 h before oven drying them for an additional 48 h at 50°C. After drying, we cooled samples for 24 h prior to dissection.

We dissected samples to separate bones, seeds, and other hard material from fur, vegetation, and other soft material. We then sorted material into six broad categories: mammalian, vegetation, invertebrate, bird, reptile, and anthropogenic. We identified mammalian remains based on the presence of fur, teeth, and dense bones. Vegetation included all plant matter (e.g. seeds, fruit husks and grasses). Invertebrates were identified by shells and carapaces of insects and snails. We identified birds by bone structure and the presence of feathers. Reptiles were recognized by scaled skin or intact body fragments. We identified the remainder of scat contents as anthropogenic items, including metals, plastics, paper, and scraps of other non-digestible materials. Damage during digestion prevented the further identification of invertebrates, birds, and reptiles to family. Vegetation was initially sorted into seeds and non-seeds, but further identification of vegetation to species or family was not completed due to project constraints.

We identified mammalian samples to more precise categories of family and species through microscopic examination of bones, claws, hair, and teeth. To do so, we used existing guides (Moore et al. 1974, Debelica and Thies 2009) and created our own catalog of images using hair samples from study skins in the Vertebrate Collections at California State

Univ., Long Beach. Sampled species from the collection were: Bailey's pocket mouse *Chaetodipus baileyi*, broad-footed mole *Scapanus latimanus*, California mouse *Peromyscus californicus*, desert woodrat *Neotoma lepida*, fox squirrel *Sciurus niger*, western gray squirrel *Sciurus griseus*, California ground squirrel *Otospermophilus beecheyi*, house mouse *Mus musculus*, agile kangaroo rat *Dipodomys agilis*, Lodgepole chipmunk *Tamias speciosus*, montane vole *Microtus montanus*, Virginia opossum *Didelphis virginiana*, Botta's pocket gopher *Thomomys bottae*, desert cottontail *Sylvilagus audubonii*, raccoon *Procyon lotor*, black rat or house rat *Rattus rattus*, ornate shrew *Sorex ornatus*, striped skunk *Mephitis mephitis*, western mastiff bat *Eumops perotis*, and white-eared pocket mouse *Perognathus alticolus*. We selected these species to reflect the broad range of possible prey or carrion that coyotes may have consumed in our study area. We also included coyote hairs from museum pelts so we could identify and remove self-grooming hairs from further analysis. In addition to the museum specimens, we collected domestic pet hairs from a variety of live individuals so we could identify cats *Felis catus* and dogs *Canis lupus familiaris*, and we collected a human *Homo sapiens* hair sample to control for contamination during processing. Hairs were wet-mounted onto slides and viewed at 200× magnification with a compound light microscope and imaged with a digital camera. These efforts led to a digital catalog of 563 images of 24 species to which we compared the contents of scat samples. Guard hairs were chosen from scat samples for magnification based on length and color, which allowed for more than one species to be identified, if present, in the same scat sample.

Statistical analyses

We considered six major categories for analysis: mammalian, vegetation, invertebrate, avian, reptile, and anthropogenic. Under the mammalian category we identified seven subcategories: rabbit, squirrel, small mammals, domestic cat, raccoon, skunk, and opossum. The small mammal category combined rats, mice, voles, and shrews. In some analyses, we consolidated cats, raccoons, skunks, and opossums into a mesocarnivore group to consider the intraguild impact coyotes may have on these species.

We calculated the frequency of occurrence (FO) of food categories overall and separately for wet and dry seasons. We chose FO for our analyses because it is the most common method used for scat studies (Klare 2011, Davis et al. 2015, Larson et al. 2020), thus allowing our results to be compared efficiently with other studies. The FO of an item is expressed $FO_i = (n_i/N) \times 100(\%)$, where n_i is the number of scats in which an individual item 'i' occurs, and N is total number of scats collected (Larson et al. 2015). To allow for comparison to the widest range of studies we also calculated the percentage of occurrence (PO). The PO of an item is expressed $PO_i = (n_i/\sum n_i) \times 100(\%)$, where $\sum n_i$ is the sum of all occurrences of all food items across samples. We calculated FO and PO for each category and subcategory, and for the mesocarnivore subgroup. For our FO analysis, while scat often contained multiple food items, each sample

was only counted once for combined categories; for example, a sample containing both rabbit and squirrel remains was only counted once for the analysis of the mammalian category, and as two occurrences for our PO calculations. We focused on our FO calculations for further analyses, and used Primer ver. 7.0.21 software (Clarke and Gorley 2015) to conduct PERMANOVA tests of season, site, and an interaction between season and site, as well as pairwise comparisons among the two seasons and four sites. We visualized these relationships using non-metric multidimensional scaling (nMDS) plots using the tidyverse package ggplot2 (Wickham et al. 2019) in R Statistical Software ver. 4.2.1 (www.r-project.org). We also used χ^2 tests in R (www.r-project.org) to evaluate expected and observed FO of categories across seasons, and between limited categories and sites. We included striped skunks, opossums, and reptiles in the PERMANOVA community analysis, but due to low occurrence (once per season) we did not consider them individually in χ^2 analyses. By combining cats, raccoons, skunks, and opossums into a mesocarnivore subcategory, we were able to perform a χ^2 test to compare site and seasonal differences in this group as food sources for coyotes. We considered all tests significant at $\alpha = 0.05$.

Results

From August 2016 through August 2017, we collected 115 coyote scats, including 35 during the wet season, and 80 during the dry seasons immediately preceding and following the wet season. Of these, we collected 53 scats in restored saltmarsh (11 wet, 42 dry), 9 in unrestored saltmarsh (4 wet, 5 dry), 24 in irrigated open space (9 wet, 15 dry), and 27 in unirrigated shrub/scrub (9 wet, 18 dry). Scat composition differed between seasons (MS = 22403.0, df = 1, Pseudo-F = 8.571, P (perm) = <0.001; Fig. 2A) and sites (MS = 5221.7, df = 3, Pseudo-F = 1.998, P (perm) = 0.0282; Fig. 2B), but there was no interaction between season and site (MS = 1839.4, df = 3, Pseudo-F = 0.704, P (perm) = 0.739). Pairwise comparisons confirmed overall dietary differences between wet and dry seasons (t = 2.928, p = <0.001) and between one pair of sites, the irrigated open space and unrestored saltmarsh sites (t = 1.779, p = 0.017), but the other pairs of sites were not significantly different (all p > 0.05).

Scats contained varied food items that we considered individually or as combined categories (Table 1). From FO analyses, mammalian remains were most common, occurring in 100% of wet season scats and 70% of dry season scats, with rabbits the most common of the mammalian category, occurring in 34% of scats. Small mammals, which included rats, mice, wood rats, voles, shrews, and unidentified rodents, were the second most common of the mammalian category, occurring in 29% of all samples. Vegetation and invertebrates were both found in more than 20% of scats. Avian remains were found in 15% of scats overall. We found anthropogenic foods in 13% of scats, and domestic cat remains in 14%. We found no evidence of coyote consumption of domestic dogs.
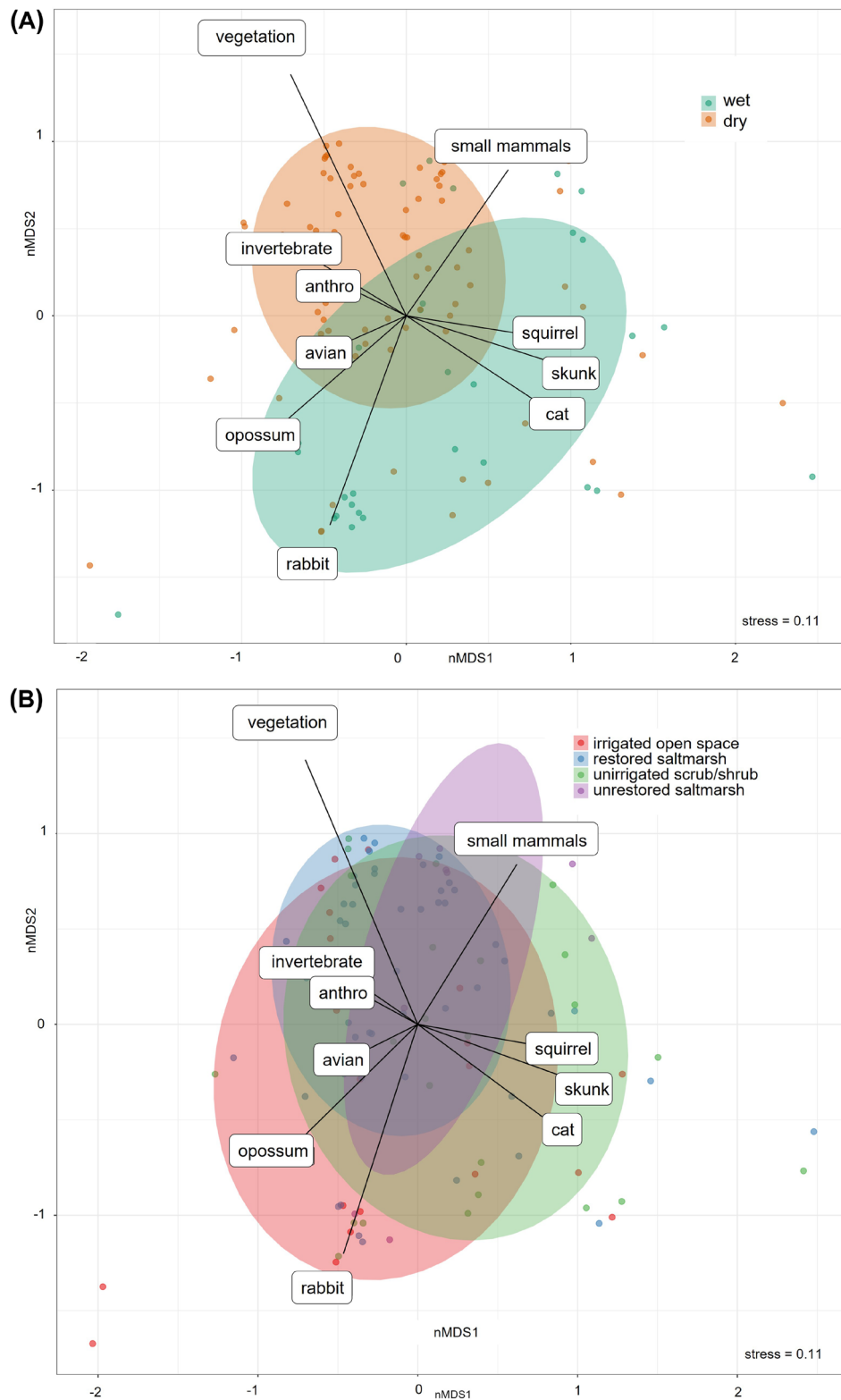
Figure 2. Non-metric multidimensional scaling plot based on the Bray–Curtis index distance method displaying a pattern of differences and similarities between seasons from 999 permutations of the contents of samples. Labeled vectors indicate where each prey type was found most commonly in the multidimensional space. (A) There is a significant difference in scat contents between the wet (more mammalian prey) and dry seasons (more vegetation and invertebrate prey). (B) We found an overall effect of site type on scat contents, but the only significant pairwise difference was between irrigated open space (e.g. opossum and rabbit) and unrestored salt marsh (e.g. small mammals).

Table 1. Counts of occurrence, frequency of occurrence (FO), percentage of occurrence (PO), and chi-square (χ^2) test results of major diet items in 115 coyote scats by season (df=1, α=0.05) collected in open spaces along the San Gabriel River in Long Beach, California, USA, 2016–2017.

| Diet item | Overall | | | Season | | | | | | Test (FO based) | |
| | | | | Wet | | | Dry | | | | |
	Count	% FO n/115	% PO n/363	Count	% FO n/35	% PO n/112	Count	% FO n/80	% PO n/251	χ^2	p
Mammalian[a,b]	91	79.1	25.1	35	100	31.3	56	70.0	22.3	13.769	<0.001
Rabbit	39	33.9	10.7	18	51.4	16.1	21	26.3	8.4	6.887	0.009
Squirrel	18	15.7	5.0	9	25.7	8.0	9	11.3	3.6	3.858	0.049
Small mammal	33	28.7	9.1	13	37.1	11.6	20	25.0	8.0	1.755	0.185
Mesocarnivore[a,b]	26	22.6	7.2	9	25.7	8.0	17	21.3	6.8	0.277	0.598
Domestic cat	16	13.9	4.4	5	14.3	4.5	11	13.8	4.4	0.006	0.939
Raccoon	7	6.1	1.9	3	8.6	2.7	4	5.0	1.6	0.543	0.461
Skunk	2	1.7	0.6	1	2.9	0.9	1	1.3	0.4	na[c]	na[c]
Opossum	2	1.7	0.6	1	2.9	0.9	1	1.3	0.4	na[c]	na[c]
Vegetation	69	60.0	19.0	9	25.7	8.0	60	75.0	23.9	24.643	<0.001
Invertebrate	26	22.6	7.2	1	2.9	0.9	25	31.3	10.0	11.218	<0.001
Avian	17	14.8	4.7	3	8.6	2.7	14	17.5	5.6	1.541	0.214
Reptile	2	1.7	0.6	1	2.9	0.9	1	1.3	0.4	na[c]	na[c]
Anthropogenic	15	13.0	4.1	3	8.6	2.7	12	15.0	4.8	0.887	0.346

[a]Indicates a combined category. [b]Total counts exceed sums because multiple prey types occurred in some scats. [c]No statistical analyses conducted due to small sample size

χ^2 tests indicated that rabbit and squirrel remains both occurred in greater than expected proportions in wet season scats (Table 1; rabbits: p=0.009; squirrels: p=0.049), while vegetation and invertebrates were more common in dry season scats (Table 1; vegetation: p=<0.001; invertebrates: p=<0.001). There were no seasonal differences for any other food item categories (Table 1; all p > 0.05). Across our site surveys, we found 89 scats containing mammalian remains, with 20 of these containing more than one species of mammal (Table 2; p-values reported for χ^2 tests across sites overall per category). We found 26 scats containing mesocarnivore remains, of which one contained the remains of two mesocarnivore species (raccoon and cat). While the frequency of mammalian remains did not differ across sites, scat compositions did differ across sites for all mammal prey types except rabbits. Vegetation and invertebrates were found in scats at higher than expected rates from the restored saltmarsh site (Table 2; vegetation: p=0.032; invertebrates: p=0.044); small mammals were found at higher rates at the unrestored saltmarsh site but at lower rates at the irrigated open space

(Table 2: p=0.001). Finally, in scats from the unirrigated shrub and scrub, we found mesocarnivores were present in scats at higher rates than expected (Table 2: p=0.031), but invertebrates (p=0.044) and vegetation (p=0.032) were present at lower rates than expected.

Discussion

We hypothesized that differences in scat composition would correspond with seasonal changes and with differences in the composition of open space fragments. We found that urban coyotes occupying open spaces along the San Gabriel River in Long Beach, California ate a diverse natural diet with seasonal changes in composition. Coyotes in our study area did not appear to have developed a reliance on human food sources (anthropogenic scraps or domestic animals) but apparently did consume anthropogenic foods opportunistically throughout the year.

Diet did change with season however, with coyotes consuming a higher proportion of mammalian prey in the wet

Table 2. Chi-square (χ^2) test results of major diet items as they appeared in 113[a] coyote scats by site (df=3, α=0.05) in open spaces along the San Gabriel River in Long Beach, California, USA, 2016–2017. Observed counts followed by expected values in parentheses.

| | | Sites | | | | | |
	Total	Restored saltmarsh	Unrestored saltmarsh	Irrigated open space	Unirrigated scrub/ shrub	χ^2	p
Mammalian	89[a]	37 (41.7)	9 (7.1)	20 (18.9)	23 (21.3)	5.931	0.115
Rabbits	39	18 (18.3)	3 (3.1)	10 (8.3)	8 (9.3)	0.841	0.840
Small mammal	32[a]	15 (15.0)	7 (2.8)	2 (6.8)	8 (7.6)	15.591	0.001
Mesocarnivore	26	7 (12.2)	1 (2.1)	7 (5.5)	11 (6.2)	8.899	0.031
Vegetation	67[a]	39 (31.4)	5 (5.3)	11 (14.2)	12 (16.0)	8.805	0.032
Invertebrate	26	18 (12.2)	1 (2.1)	5 (5.5)	2 (6.2)	8.083	0.044

[a]Total counts differ from seasonal data. Two samples containing vegetation and small mammals lacked specific location information and were excluded from site analyses.

season and a higher proportion of vegetation in the dry seasons. While this may have corresponded to the natural availability of mammalian prey in the wet season due to the increase in breeding activity of rodent (Nelson et al. 1995, Madsen and Shine 1999, Takele et al. 2022) and rabbit (Wells et al. 2016, Dunagan et al. 2019) populations after rains, the seasonal availability of fruiting plants, including many ornamentals, in southern California may be a more likely driver of the seasonal change in vegetation consumption. Coyote diet also varied by site. While rabbits appeared in scat from all sites, emphasizing their importance to coyote diet and availability across urban green spaces, the sites varied in other ways. Specifically, the restored saltmarsh was a source of invertebrates, in the form of snails and crustaceans, which were an important dry season protein source, while the low vegetation and surrounding human structures may have provided more small mammal hunting opportunities in the unrestored saltmarsh. Coyotes may move between sites to access a greater variety of food items.

Our findings were consistent with prior studies of urban coyotes conducted elsewhere in California. For example, Fedriani et al. (2001) also found high dietary diversity in an urban study location in the Santa Monica Mountains, and Larson et al. (2015) found mammalian remains in 80% of coyote scats in San Diego, California. Our findings were also generally consistent with studies outside of California, where rabbits were also the primary prey of coyotes in Madison, Wisconsin (Garwood et al. 2015), and the second highest prey in Denver, Colorado after rodents (Poessel et al. 2017). While researchers in Calgary, Alberta, Canada found urban coyotes ate a predominately natural diet with a similar 14% occurrence of anthropogenic food items, they only found domestic pets in less than 2% of scats (Lukasik and Alexander 2012). Our findings differed from urban Los Angeles, California (Larson et al. 2020), and Chicago, Illinois (Newsome et al. 2015), where researchers found higher levels of anthropogenic resource use and a lower reliance on rabbits or rodents. Larson et al. (2020) combined non-native animal remains, ornamental plants, pet food, and trash into their anthropogenic category for coyote scat analysis, but even considering trash and pet food alone, they had an FO of nearly 25% in their urban sites. Newsome et al. (2015), however, used stable isotope analysis, which allowed for the identification of anthropogenic sources that may be digested and more difficult to detect.

Avian prey can be underestimated in visual studies of mesocarnivore scat (Cavallini and Volpi 1995, Balestrieri et al. 2011) due to the breakdown of avian tissues during digestion (Oja et al. 2017, Shi et al. 2021). The presence of avian remains in 15% of our samples, while higher than most comparable studies, may not be unusual for urban areas of southern California where coyotes generally lack access to large mammalian prey. For example, Larson et al. (2020) found an FO of 14.5% in urban areas, and 5.5% in suburban sites around Los Angeles using scat dissection methods similar to ours. We hypothesize that we did not find statistically significant differences in avian consumption between seasons

because waterfowl were present, and presumably accessible, year-round. Future research could incorporate molecular methods to help assess this hypothesis.

The seasonal variation we observed in mammalian remains, vegetation, and invertebrates in scats was most similar to a rural population of coyotes studied by Bowyer et al. (1983) in a state park outside of San Diego. This may indicate that relatively small natural habitat patches within heavily developed urban areas allow for the maintenance of natural behaviors of opportunistic hunting and foraging. Some urban area studies have also found similar seasonal variations in mammalian and vegetation consumption, including in the Denver area (Poessel et al. 2017) and Chicago (Morey et al. 2007). In Los Angeles, Larson et al. (2020) found native fruits in less than 2% across sites and seasons, but their ornamental fruit results were higher, with an FO of up to 32% at their suburban site in the dry season. Fedriani et al. (2001) also found evidence for higher consumption of domestic fruit during the southern California dry season. Non-native, ornamental or cultivated plants likely made up much of the vegetation found in our coyote scat from our study area, although we were unable to quantify this because we did not classify seeds to species.

Intraguild predation is common in carnivores, and coyotes are among the top three canids to practice this behavior (Palomares and Caro 1999), killing bobcats *Lynx rufus*, and grey foxes *Urocyon cinereoargenteus* (Fedriani et al. 2000), as well as domestic and feral canids and felids (Gehrt et al. 2013, Kays et al. 2015, Poessel et al. 2017). After domestic cats, raccoons were the second most common mesocarnivore found in scats in this study but had low occurrence at 6% compared to 18% found in rural Ohio (Cepek 2004) or 27% in urban New York (Henger 2022). Other studies have similarly found low to no evidence of raccoon consumption (Gehrt and Prange 2007). Raccoons may not actively avoid coyotes (Gehrt and Prange 2007, Chitwood et al. 2020) and the highest causes of urban raccoon mortality may be disease and vehicle collisions (Prange et al. 2003, Kreling 2019), which provide scavenging opportunities for coyotes. This may also explain the presence of skunks and opossum in our scat samples, which occurred in trace numbers and may be attributable to scavenging (Cherry et al. 2016, Shedden et al. 2020). While coyote attacks on dogs are well documented (Timm et al. 2004), we found no evidence of the consumption of domestic dogs in our study. Other studies have also had low occurrence of domestic dogs in coyote diets (Morey et al. 2007, Murray et al. 2015, Larson et al. 2020). Cat remains, however, occurred in 14% of scats in our study year-round and from all sites except the unrestored saltmarsh (the site with the smallest overall sample size). While common in other southern California studies, the FO varies. Larson et al. (2015) found cat remains in 29% of scats collected in small natural fragments in urban San Diego, while the same study found 0% in larger natural fragments. In Los Angeles, cat remains were found in nearly 20% of urban coyote scats (Larson et al. 2020), but in only 1% of scats in the Santa Monica Mountains located outside of Los Angeles (Fedriani et al. 2001). Urban areas in other regions also vary

greatly, with cat remains found in less than 1% of coyote scats in Calgary, Alberta (Lukasik and Alexander 2012), and as much as 38% in Denver (Poessel et al. 2017). This variation may be due to some combination of sampling methods, a variation in the density of cats across urban areas, and whether coyotes perceive cats as competitors, prey, or threats (Poessel et al. 2017).

Predation of cats has the potential to trigger human-wildlife conflict when the predation event is witnessed or the individual cat is owned or fed by people, while also mediating the potential negative impacts domestic cats have on other wildlife (Poessel et al. 2013, Kays et al. 2015). Domestic cats negatively affect wildlife species worldwide and are estimated to be responsible for the loss of 1.3–4.0 million birds annually in the United States alone (Loss et al. 2013, Loss et al. 2022). In addition to direct predation, domestic cats also spread diseases like toxoplasmosis (Taggart et al. 2019, Lepczyk et al. 2020), rabies (Suzán and Ceballos 2005), and other viruses (Riley et al. 2004, Guerrero-Sánchez et al. 2022) to wildlife. Urban cats occur in higher densities in areas of intermediate human density and impervious surface cover (Bennett et al. 2021), which describes the residential areas and roadways surrounding our sites. Cats hunt predominately within and on the edges of residential areas (Kays and DeWan 2004, Kays et al. 2020), selecting more developed areas in the presence of interference competition from coyotes (Gehrt et al. 2013). Control of cats by coyotes occurs through direct killings, interference competition, and cat spatial avoidance behavior, potentially keeping cats out of natural habitat fragments (Gehrt et al. 2013, Kays et al. 2015, Suraci et al. 2016). With cat remains appearing in 14% of both wet and dry seasons scats in our study, Long Beach coyotes may be limiting cats in natural habitat fragments where the probability of urban cats hunting native prey increases (Herrera et al. 2022, Pirie et al. 2022). This further provides evidence of the potential for urban coyotes to mediate the negative effects of high urban cat density on native wildlife by preventing mesopredator release (Crooks and Soulé 1999).

Our findings suggest that coyotes may also contribute to the control of non-native rodent species. Evidence of black rats *R. rattus*, a non-native, global, and urban-adapted invasive species, was found in 7% of scat samples overall and accounted for 24% of the small mammal category, occurring in scats from all sites except the unrestored saltmarsh. Rats are potential predators of native birds and their eggs, and are competitors with native small mammals (Moore et al. 2022). The role of pest control played by urban coyotes may save urban areas thousands of dollars, an ecological service hampered by the use of anticoagulant rodenticides that kill coyotes, other rodent predators, and non-target wildlife (Erickson and Urban 2004, Moriarty et al. 2012).

Although our study provides useful information on the diet of coyotes in Long Beach, California, it is limited in scope to a single wet season and portions of two dry seasons within a specific urban area. We also only collected scats from a single, relatively short, transect at each site; multiple, or longer transects, per site in future studies could increase

sample size. These factors limit our sample size and our scope of inference. While visual analysis of scats collected in the field remains one of the most common means of diet analysis for mammalian carnivores (Klare 2011), more sophisticated methods such as genotyping scat samples to individuals (Sugden et al. 2020, Kluever et al. 2022) and stable isotope analysis of food items (Larson et al. 2020, Newsome et al. 2015) may alleviate some potential biases that scat-based studies suffer. For example, these methods could address biases from overrepresentation of resident coyotes and alpha pairs, and underrepresentation of highly digested food items, respectively. Molecular methods also reduce error in field identification of predator species, as well as scat contents, which can further illuminate predator prey relationships by providing exact species identification (Morin et al. 2016, Shi et al. 2021), and identification of anthropogenic sources (Larson et al. 2020, Henger et al. 2022). Despite their benefits, these methods are more costly, which can critically limit sample sizes. Nevertheless, in future studies where confusion regarding the origin of scats may occur, the use of mtDNA can improve confidence in identifying the origin of scats. Both scat-based and molecular methods fail to differentiate between depredated and scavenged prey items, which could provide further valuable insights into conflict risk. Future research could consider incorporation of more multifaceted methods, including behavioral observations and resident/ transient comparisons.

Management implications

At the turn of the 21st century, 39% of houses in the United States were within wildland-urban interfaces, with California containing the highest number of housing units in the United States (Radeloff et al. 2005). This situation creates substantial potential for humanwildlife conflict. Willingness and ability to make behavioral changes on the part of humans is the most direct way of alleviating or avoiding human-wildlife conflict (Treves and Karanth 2003, Miller et al. 2016). The management, and ideally prevention, of human-wildlife conflict can be facilitated through studies such as this one that expand our understanding of wild carnivores in urban settings (Messmer 2000, Schell 2020). While most urban encounters with coyotes are benign (Quinn et al. 2016, Drake et al. 2020), coyotes may perceive domestic pets as threats or competitors (Poessel et al. 2017), leading to non-benign outcomes (Timm et al. 2004, Poessel et al. 2013). Our study demonstrates that in the areas around our study sites in urban Long Beach, California, coyotes do not appear to depredate domestic canids with any substantial frequency. However, they do consume cats. While free-roaming domestic cats operate in and around natural fragments in the role of mesocarnivores, if actively hunted by urban coyotes they may be limited primarily to residential areas. An increased reliance on domestic cats as a food source outside of natural fragments and natural fragment boundaries could lead to increased presence of coyotes in residential areas and increased risk of human-wildlife conflict. While coyotes tend to avoid residential areas when

humans are active (Grinder and Krausman 2001), the likelihood of conflict increases if resources like domestic pets and pet food are available after dark (Lukasik and Alexander 2011, Murray and St Clair 2017). To avoid this, and thus indirectly to reduce the potential for conflict, human residents in Long Beach, California should be encouraged to avoid feeding pets outside, keep domestic cats indoors, especially at night, and work with local authorities and organizations to manage feral cat populations.

Author contributions

Peregrin M. Reed: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Project administration (equal); Writing – original draft (lead); Writing – review and editing (equal). **James F. Dwyer**: Conceptualization (supporting); Resources (supporting); Validation (supporting); Writing – review and editing (equal). **Theodore Stankowich**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (equal); Resources (lead); Supervision (lead); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: DOI https://doi.org/10.5061/dryad.mkkwh7140 (Reed et al. 2023).

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