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Research Article

Inter-population differences in coyote diet and niche width along an urban–suburban–rural gradient

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Abstract

Many generalist species thrive in urban environments by supplementing their diets with anthropogenic food, which creates numerous challenges for managing urban wildlife. Management could be advanced with more information on how spatial and temporal variation in habitat use by urban animals predicts variation in their dietary ecology. In this study, we used stable isotope analysis complemented with GPS collar location data to determine how diet composition and the dietary niche of coyotes (*Canis latrans*) varied across a sample of 169 individuals collected along an urban-to-rural gradient in Alberta, Canada. We further categorized urban individuals as either matrix (frequent use of developed areas) or greenspace (use of natural areas) via GPS locations. Matrix coyotes were isotopically distinct from all other coyote populations: they had the largest dietary niche, exhibited the most among-individual variation in diet, consumed the most anthropogenic food and fruit, and consumed the least amount of prey. Greenspace coyotes consumed more anthropogenic food than rural and suburban coyotes but otherwise exhibited similar niche width, among-individual heterogeneity, and prey consumption. We further tested for seasonal dietary variation and found that urban coyotes had a larger dietary niche during the summer, when they also consumed more anthropogenic food. Our conclusions were robust to our choice of mixing model parameters, including discrimination factors, suggesting that these methodological choices have limited effect when discerning relative trends among populations. Overall, our results suggest that management of urban coyotes should target the food sources accessible to coyotes in the urban matrix to reduce human–coyote conflict.

Key words: coyote, *Canis latrans*, dietary niche, discrimination factor, urban wildlife, stable isotope analysis

Introduction

Urbanization is one of the most rapid and widespread changes to terrestrial ecosystems, with urban areas predicted to increase in size by 1.8- to 5.9-fold by 2100 (Gao and O'Neill 2020). Although expansion of urban areas has negative effects on many species (McKinney 2008; Seto, Güneralp, and Hutyra 2012), cities can support considerable biodiversity (Ives et al. 2016; Hall et al. 2017). Successful city-dwelling animals are primarily generalists that exhibit various adaptations including temporal variation in activity patterns, changes in diet or foraging behavior, altered reproductive rates and tolerance for pollution or disease (reviewed in Ditchkoff, Saalfeld, and Gibson 2006; Lowry, Lill, and Wong 2013; Ritzel and Gallo 2020). These urban-adapted species, and the distinctive selective pressures imposed by urbanization, provide a unique opportunity for studying how behavioral and life history characteristics contribute to adaptive success. Identifying key behaviors of urban-adapted wildlife can additionally be important for managers trying to minimize human–wildlife conflict.

Stable isotope analysis is an effective tool for answering questions about variation in dietary habits among urban animals because the isotopic composition of an animal's tissue represents the isotopic composition of its diet. Corn, which is ubiquitous in processed foods in the form of corn syrup and starch, has a uniquely high δ^{13}C value, making it a reliable indicator of anthropogenic food consumption (Newsome et al. 2010). δ^{15}N correlates to trophic level and serves as an indicator of prey consumption (DeNirot and Epstein 1980). An advantage of using stable isotopes to conduct dietary analyses is that they represent dietary patterns over several days or months, depending on the type of tissue being sampled (Crawford, McDonald, and Bearhop 2008), whereas other methods (e.g. scat and stomach-based analyses) represent a single point in time and may be less representative of dietary habits in animals whose individual foraging patterns may vary widely (Petta et al. 2020). However, the accuracy of dietary estimates obtained from stable isotope mixing models can be limited by the availability of species-specific discrimination factors (Bond and Diamond 2011) and by decisions about model design, such as whether to account for the carbon and nitrogen concentrations of prey sources (Koch and Phillips 2002).

Stable isotopes have traditionally been used to examine trophic level or dietary composition within or among species and populations, but they can also provide information on population niche width and the degree of dietary variation among individuals and seasons. This information could be used to improve management of species that exhibit strong dietary changes with urbanization. Urban landscapes can be highly inconsistent, with individual patches of usable and non-usable habitat combined in different proportions and arrangements (Cadenasso, Pickett, and Schwarz 2007), and the animals that inhabit urban areas exhibit a corresponding degree of spatiotemporal heterogeneity in space use, behavior, and diet (Lowry, Lill, and Wong 2013). For example, some animals that live within city boundaries reside almost exclusively in urban natural areas and maintain diets and behaviors similar to rural conspecifics, whereas other animals are more tolerant of humans and rely heavily on anthropogenic food subsidies and the built environment (McKinney 2006; Lowry, Lill, and Wong 2013; Fischer et al. 2015; Newsome et al. 2015). More detailed evaluations of dietary niche width and among-individual variation in urban animals in relation to habitat use could enhance a general understanding of urban exploitation by these species, thereby supporting more context-specific approaches to management expected by the public (Draheim et al. 2019). Food subsidization in urban environments can also reduce seasonal dietary variation in urban animals (Larson et al. 2020), and an improved understanding of how season affects the diet and niche width of urban animals could help wildlife managers focus resources on the times of the year when anthropogenic food consumption has the highest potential to contribute to human–wildlife conflict.

Coyotes (*Canis latrans*) are one example of a highly successful urban species that has received considerable attention from urban wildlife managers. The foremost adaptations that have enabled coyotes to succeed in urban areas include broadening their diet to include more anthropogenic food (Gehrt and Riley 2010; Murray et al. 2015a; Poessel, Mock, and Breck 2017) and shifting to a more nocturnal lifestyle to avoid human activity (Grinder and Krausman 2001; Gese, Morey, and Gehrt 2012; Murray and St. Clair 2015). Anthropogenic food supplementation has created numerous challenges for urban coyote management, as food supplementation has been connected to poor health (Sugden et al. 2020), human–wildlife conflict (Murray et al. 2015a) and a higher prevalence of parasites (Murray et al. 2016). Zoonotic parasites are of particular concern; for example, after consuming infected rodents, urban coyotes can carry a helminth parasite (*Echinococcus multilocularis*) that can cause a fatal zoonosis in humans (Catalano et al. 2012; Gesy et al. 2014; Sugden et al. 2020). Understanding how coyote diet changes with urban habitat use could therefore advance management practices that reduce human–coyote conflict and disease transmission. Insights into urban coyote dietary ecology could also be applied more broadly to other urban-dwelling species that exhibit similar adaptations and face similar selective pressures.

Previous stable isotope studies have revealed how anthropogenic food consumption by urban coyotes varies both within and among cities and individuals, underscoring the difficulty in designing location- or population-specific coyote management practices. For example, anthropogenic food and domestic pets have been estimated to comprise up to 80% of the diet of urban coyotes in southern California (Larson et al. 2020), but this proportion is only 40–50% in Edmonton (Murray et al. 2015b) and 20–35% in Chicago (Newsome et al. 2015). This broad range from isotopic data parallels the 40–80% prevalence of anthropogenic food reported in scat-based analyses (Murray et al. 2015a; Poessel, Mock, and Breck 2017; Larson et al. 2020). Further variation may stem from disease status: diseased coyotes consumed more anthropogenic food and less prey than healthy coyotes (Murray et al. 2015b). General dietary patterns are also inconsistent across similar habitats, with urban habitat use increasing among-individual heterogeneity in Chicago (Newsome et al. 2015) but reducing it in Los Angeles (Larson et al. 2020). Some studies have attributed additional dietary variation to season; for example, urban coyotes in southern California exhibit less dietary variation between wet and dry seasons than rural coyotes (Larson et al. 2020). Seasonal dietary variation may be further reduced in urban environments at high latitudes, where harsh winters and heavy snowfall may promote anthropogenic food subsidization.

In this study, we used stable isotope analysis to examine spatiotemporal patterns in coyote diet composition and dietary niche characteristics across a rural–suburban–urban gradient near Edmonton, Alberta, Canada. To account for heterogeneity in coyote habitat use, we used GPS location data to discriminate between urban coyotes that relied on developed areas, which we refer to as 'matrix' coyotes, and urban coyotes that largely stayed in urban natural areas, which we refer to as 'greenspace' coyotes. We predicted that greenspace coyotes would have a similar niche width and a large degree of niche overlap with rural and suburban coyotes, whereas greater use of anthropogenic food by matrix coyotes would result in larger dietary niches and more among-individual variation. We further predicted that seasonal variation in diet, niche width, and among-individual heterogeneity would be smallest in urban environments because urban food sources are more consistently available throughout the year relative to rural or suburban prey items. Because accurate results are important in a management context and stable isotope mixing model outputs can vary substantially with input parameters (Bond and Diamond 2011), we additionally sought to determine whether our biological conclusions were affected by different mixing-model formulations.

Methods

Sample collection

We tested for differences in coyote dietary niche with urbanization by collecting coyote hair and claw samples from three separate sites, which we classified as 'urban', 'suburban' and 'rural'. Our urban sampling location was the city of Edmonton (53°32′ N, 113°30′ W), the capital city of Alberta with a population of over 1 000 000 residents (Fig. 1). For a large city, Edmonton has a relatively high amount of natural areas because it is bisected by the North Saskatchewan River valley and several large ravines, creating the largest expanse of undeveloped urban parkland in North America. Suburban samples were collected from Leduc (Fig. 1), a city of 30 000 people approximately 21 km south of Edmonton. The Leduc area is bordered by several lakes and natural areas, as well as by the regional landfill. Our rural sampling location was Ministik Lake (53°21′ N, 113°1′ W) (Fig. 1), a 109 km^2 bird sanctuary located 48 km southeast of Edmonton that is mainly comprised of aspen parkland and small water bodies. Climatically, the Edmonton area is relatively dry and is characterized by temperate summers (average high temperatures of 21°C to 23°C) and long, cold winters (average high temperatures of −3°C to −7°C).

Coyote tissue samples were collected year-round from 2009 to 2014 and again from 2017 to 2020 (Murray et al. 2015a,b; Sugden et al. 2020). Urban samples came from three sources: roadkill, lethal management, and a concurrent study on coyote movement and habitat selection (Murray et al. 2015b; Murray and St. Clair 2017). Suburban and rural coyotes were provided by fur trappers running a licensed trap line. GPS-collared coyotes were sampled while alive, and all other coyotes died or were killed for other reasons before being used for research. With few exceptions, we obtained either GPS coordinates or street intersections indicating the approximate location where each coyote was collected. Detailed methods describing our sample collection methodology are available elsewhere (Murray et al. 2015a,b; Sugden et al. 2020). During the 2009–14 sampling period, we collected at least a dozen guard hairs from the nape of each coyote. Claw samples were taken from 2017 to 2020 because several animals were provided to us without fur.

To improve the geospatial resolution in our analysis, we subdivided urban coyotes into three categories: (i) Greenspace coyotes were defined as GPS-collared coyotes that rarely, if ever, left urban natural areas (<10% of GPS fixes outside of natural areas); (ii) matrix coyotes were defined as GPS-collared coyotes that made frequent use of the urban matrix (>35% of GPS fixes in developed areas); and (iii) coyotes without GPS collar data were broadly considered 'urban' and retained separately for all analyses. These divisions were chosen because they effectively separated coyotes that frequently used developed areas (average percentage of GPS locations in developed areas for matrix coyotes = 57% ± 20; all other coyotes = 10% ± 9) and those that frequently used natural areas (average percentage of GPS locations in natural areas for greenspace coyotes = 94% ± 4; all

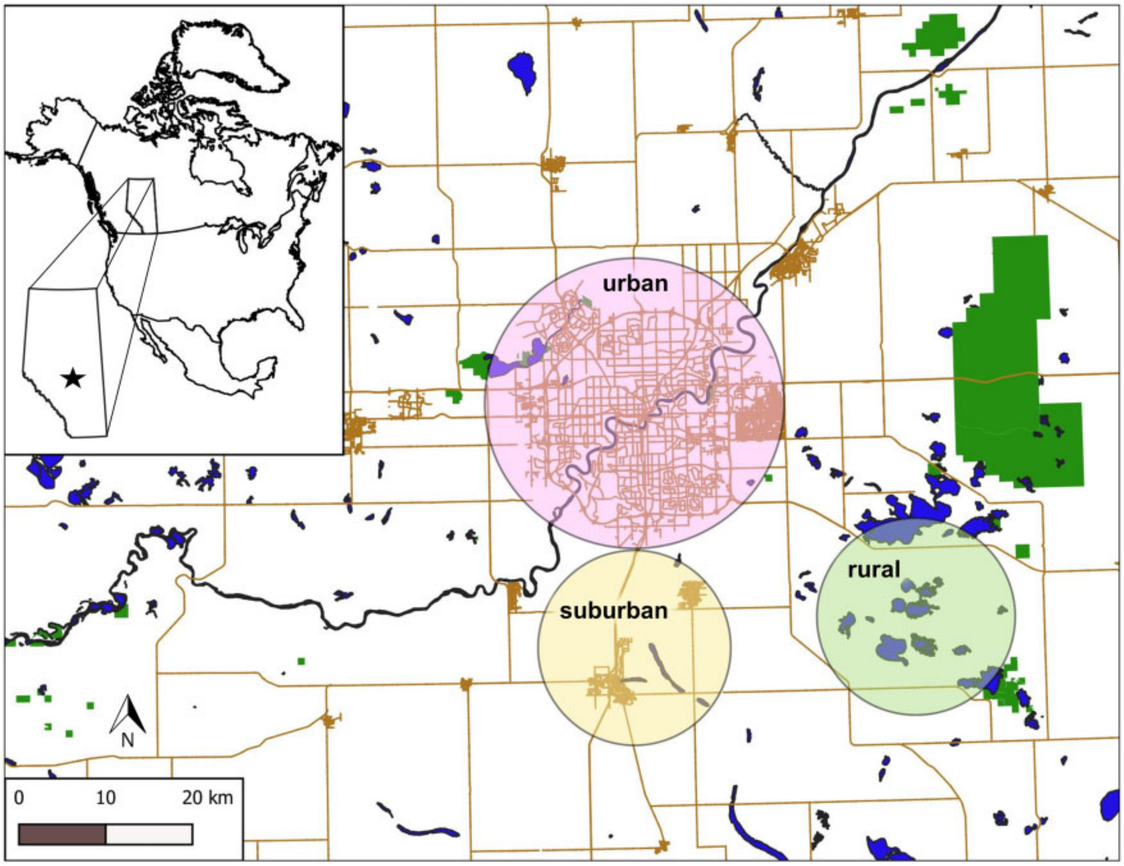

Figure 1: Map depicting sampling locations in and around Edmonton, Alberta, Canada. Colored circles indicate locations where urban (*pink*), suburban (*yellow*) and rural (*light green*) coyote samples were collected. Roads (*gold*), water bodies (*blue*) and legally designated wilderness areas or parklands (*green*) are indicated for reference.

other coyotes = 52% ± 25). For this classification, we considered 'natural areas' to be urban ravines, parks, and other unmodified open spaces, and we considered 'developed areas' to be residential, commercial and institutional land, based on publicly available land cover data (City of Edmonton 2020). Natural areas represented 7% of available habitat in our urban study area and developed areas occupied the remaining 93% (Supplementary Fig. S1) (Murray et al. 2015b).

Stable isotope analysis

Hair and claw samples were prepared for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis following previously described methods (Hilderbrand et al. 1996). In brief, samples were rinsed three times with a 2:1 solution of chloroform: methanol to remove residual lipids and then dried, and 1.5 mg subsamples were weighed for analysis. To provide better temporal resolution of coyote diet across seasons, a randomly selected subset of hair samples from each location was divided into halves to represent the most recent diet (base of the hair) and the diet 4–6 months previously (tip of the hair). To ensure that results from hair and claw samples were statistically comparable, we also prepared both hair and claw samples from a randomly selected subset of 10 coyotes. All samples were processed and analyzed using an elemental analyzer (EuroEA Elemental Analyzer, EuroVector) and a continuous-flow isotope ratio mass spectrometer (Isoprime Mass Spectrometer, GV Instruments) at the Biogeochemical Analytical Services Laboratory (Department of Biological Sciences, University of Alberta). These instruments had a measurement standard deviation of $+0.1‰$ and $+0.3‰$ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Location-based dietary shifts

To test for differences in coyote diet across an urbanization gradient, we evaluated the isotopic niches for rural, suburban, greenspace and matrix coyotes, as well as urban coyotes with no GPS-based classification. We first used the R package *SIBER* (Jackson et al. 2011) to calculate the Bayesian standard ellipse area for each group, which functions as a measure of isotopic niche width (Bearhop et al. 2004). We used the standard ellipse area rather than the total isotopic area for each group of coyotes because this measure is less sensitive to variation in group sample sizes (Jackson et al. 2011). Dietary niche overlap between rural, suburban, greenspace and matrix coyotes was quantified by calculating the percent overlap between the standard ellipses of each group of coyotes. We additionally calculated the six community isotopic metrics developed by Layman et al. (2007), which provide quantitative measures of the trophic structure of each population and include measures of within- and among-group variation. Significant differences in isotope values among populations were tested using Welch's analysis of variance (ANOVA) after confirming the data were normally distributed and heteroscedastic.

Stable isotope mixing models were used to estimate the assimilated diet of each coyote population. Diet items were grouped into seven food source categories based on previously collected isotopic data for food items consumed by coyotes in our study area: ungulates, cricetid rodents, small herbivores, insects, berries, domestic pets and anthropogenic foods (Murray et al. 2015a). A list of species included in each of these categories is provided in Supplementary Table S1. There were at least three observations for each source category, and isotopic data for anthropogenic food were supplemented with published data for fast food (Jahren and Kraft 2008). We chose to use diet-to-tissue discrimination factors of 2.0‰ for $\delta^{13}C$ and 3.5‰ for $\delta^{15}N$, which were recently determined from captive wolves at the Zoo Sauvage de St.-Félicien in Quebec, Canada (L'Hérault et al. 2018), though we also considered other published discrimination factor pairs below. Because source isotopic data were obtained from hair samples, but coyotes assimilate muscle and fat, we subtracted 1.0‰ from the $\delta^{13}C$ discrimination factor to account for the difference in $\delta^{13}C$ between prey hair and muscle, following the rationale of Newsome et al. (2015). We also included concentration dependence in our models because carbon and nitrogen concentrations varied across source items (Supplementary Table S1). All models were run in the R package *simmr* (Parnell 2019) using default parameters.

Seasonal dietary shifts

We tested the hypothesis that urban coyotes exhibit less seasonal variation than suburban and rural coyotes by classifying hair and claw isotopic samples based on the season they represented. Summer was defined as May–October and winter was defined as November–April, and samples were classified based on which season comprised a majority of the 6 months preceding sample collection. Samples taken from February–July were therefore considered to represent the winter and samples from August–January were considered to represent the summer. For the subset of hair samples that were sectioned into halves, each half was classified according to the 3-month span it represented. This classification assumes that hair or claw samples represent a 6-month dietary period, which generally agrees with documented hair and claw growth rates in carnivores (Felicetti et al. 2004; McLaren, Crawshaw, and Patterson 2015). We then calculated isotopic niche metrics and diet composition and ran mixing models for each group, as before. Mixing models were run separately for each season because one of the food sources, insects, is not available in winter. To ensure robust sample sizes, we did not discriminate between greenspace and matrix coyotes in these analyses but rather used the broader classifications of rural, suburban and urban.

Modeling procedures

We determined the best predictors of coyote $\delta^{13}C$ and $\delta^{15}N$ values by running linear models explaining isotope values from coyote habitat, age (adult or juvenile), sex (male or female) and season of collection (summer or winter). For each isotope, all model subsets were evaluated using the R package *MuMIn* (Barton 2018). Predictor coefficients were then adjusted by model weight and averaged across all models with $\Delta AIC \leq 2$. To improve the precision of our parameter estimates with a larger sample size in this analysis, urban coyotes without GPS data were reclassified into either the matrix or greenspace populations using a random forest model trained on the isotope values of the GPS-collared coyotes. Random forests were implemented with 1000 trees in the R package *randomForest* (Liaw and Wiener 2002). We confirmed that this procedure did not affect the signs or relative magnitudes of predictor coefficients by also running models excluding non-collared coyotes.

Because stable isotope mixing models can be highly sensitive to their input parameters, we also tested the results of our location-based mixing models across a suite of input values and parameters that emulate the current literature. We re-ran models using five different sets of discrimination factors for $\delta^{13}C/\delta^{15}N$: 2.0/3.0‰ (Derbridge et al. 2015), 2.0/3.5‰ (L'Hérault et al.

2018), 2.5/3.5‰ (Roth and Hobson 2000), 3.4/3.0‰ (Rioux, Pelletier, and St-Laurent 2020) and 4.3/3.1‰ (McLaren, Crawshaw, and Patterson 2015). In all cases, we subtracted 1.0‰ from the δ^{13}C discrimination factor, as before. For each set of discrimination factors, we also tested how the inclusion of source carbon and nitrogen concentrations affected results by running concentration-independent and concentration-dependent models, as well as concentration-dependent models adjusted for source digestibility following the methods described by Koch and Phillips (2002). Model results were compared across discrimination factors and source concentration parameters using Spearman's correlation.

Results

We collected hair samples from 70 coyotes between 2009 and 2014 and claw samples from 99 coyotes between 2017 and 2020. Thirty-three randomly selected hair samples were divided into two sections to improve the resolution of seasonal analysis, and four coyotes were sampled in two separate years, resulting in 213 data points from 169 coyotes (Supplementary Table S2). Using a subset of 10 individuals, we confirmed that hair and claw samples were isotopically comparable (Supplementary Fig. S2; Hotelling's $T^2 = 0.422$, $\mathrm{df} = 2$, $P = 0.663$), supporting our decision to combine data from our two sampling periods. There were no apparent sex-based differences in isotope values after controlling for location (Supplementary Table S3).

Location-based dietary shifts

When we assessed dietary changes based on location, we found that matrix and non-collared urban coyotes had a 3.5-fold larger isotopic niche than any other coyote population, including greenspace coyotes (Fig. 2a and b). Further, matrix coyotes had 32% lower δ^{15}N values than the other populations (ANOVA $F = 12.72$, $\mathrm{df} = 4$, $P < 0.001$; Supplementary Table S3). We also compared niche overlap among matrix, greenspace, suburban and rural coyotes and found that matrix coyotes had the most distinct isotopic niche, overlapping with greenspace coyotes by only 6.9% and with suburban and rural coyotes by less than 1% (Fig. 2c). Greenspace and suburban coyotes overlapped by 16.0%, and suburban coyotes overlapped approximately equally with rural and greenspace coyotes (Fig. 2c). Matrix coyotes further exhibited the greatest trophic width (range of δ^{15}N values), the greatest trophic diversity (mean distance to centroid) and the most among-individual variation, measured as both the mean and standard deviation of the distances between neighboring samples (Fig. 2d). Greenspace, suburban and rural coyotes shared relatively similar values for these metrics.

Stable isotope mixing models indicated that both greenspace and matrix coyotes consumed more anthropogenic food and domestic pets than rural or suburban coyotes, with these two items accounting for 22.0–32.5% of estimated diet (Fig. 2e). However, matrix coyotes were distinguished from greenspace coyotes by the consumption of less total prey and more berries (Fig. 2e). Rodents, small herbivores and ungulates were among the most common dietary items for rural, suburban and greenspace coyotes, along with insects in rural coyotes. Because matrix coyotes had a higher prevalence of mange than the other coyote populations (60% vs. 20% or less; Supplementary Table S2), and mange may alter coyote dietary habits (Murray et al. 2015b), we confirmed that the results from all isotopic analyses and mixing models were preserved when infected coyotes were excluded from this analysis (Supplementary Fig. S3).

Seasonal dietary shifts

We assessed dietary changes across seasons and found that dietary niches were larger in the summer in all locations, though the difference in niche width between summer and winter was most pronounced in urban coyotes (3.6-fold increase for urban vs. 2.0-fold for suburban and 1.6-fold for rural) (Fig. 3a and b). Urban coyotes also exhibited approximately 2-fold more among-individual variation in the summer than winter, as measured by the mean and standard deviation of the nearest neighbor distances among samples (Fig. 3c). Niche overlap between seasons was approximately 21% for each of the three coyote populations (urban, suburban and rural), and patterns of niche overlap among populations were relatively similar in both summer and winter, with suburban coyotes again representing an intermediate population that overlapped both rural and urban coyotes (Supplementary Fig. S4). Notably, urban coyotes had a larger niche overlap with rural coyotes in summer (7.0%) than winter (0.7%) (Supplementary Fig. S4). Mixing models suggested that the greater niche width in urban coyotes in the summer was largely due to greater evenness among source proportions (Fig. 3d): the standard deviation of estimated dietary proportions across all source items was 4.3% for urban coyotes in the summer, compared to 9.0% in the winter and up to 13.4% in other populations. Urban coyotes also consumed more anthropogenic food and slightly more domestic pets in the summer than the winter (17.1% ± 9.0 vs. 9.1% ± 5.2 for anthropogenic food and 12.0% ± 7.4 vs. 9.6% ± 4.7 for pets).

Predictors of coyote isotope values

Models trained to predict coyote isotopic values suggested that habitat use was the best predictor of both δ^{13}C and δ^{15}N, with little to no effect of age or season on either δ^{13}C or δ^{15}N values. Greenspace and matrix coyotes both had higher δ^{13}C values than suburban coyotes (Fig. 4a), whereas matrix coyotes exclusively had lower δ^{15}N values than other populations (Fig. 4b). The random forest classification scheme that was used to categorize uncollared coyotes as either 'matrix' or 'greenspace', thus improving the sample size and precision of these models, had an out-of-bag accuracy of 82%. Habitat-based trends in niche width, overlap and mixing-model results were preserved in this new, predicted data set (Supplementary Fig. S5), and linear models predicting isotope values achieved similar results when the reclassified coyotes were excluded (Supplementary Fig. S6).

Effects of mixing-model formulation

The relative trends in assimilated diet that were revealed by stable isotope mixing models were preserved across a variety of mixing model formulations, despite numerical changes in the exact estimates of source proportions. There was greater agreement among models with the same discrimination factor but different methods for accounting for source carbon and nitrogen concentrations (mean Spearman's $R = 0.954 \pm 0.037$) than among models with different discrimination factors but the same approach to source concentrations (mean $R = 0.717 \pm 0.132$) (Supplementary Fig. S7). The discrimination factor pairs 3.4/3.0 and 4.3/3.1 produced models in which most consumers did not fall within the mixing polygon defined by the sources (Supplementary Fig. S8); all other model formulations broadly confirmed the same relative results, with matrix and greenspace coyotes both consuming more anthropogenic food but matrix coyotes distinctively consuming more fruit and less prey (Fig. 5). Despite this consistency, numerical estimates

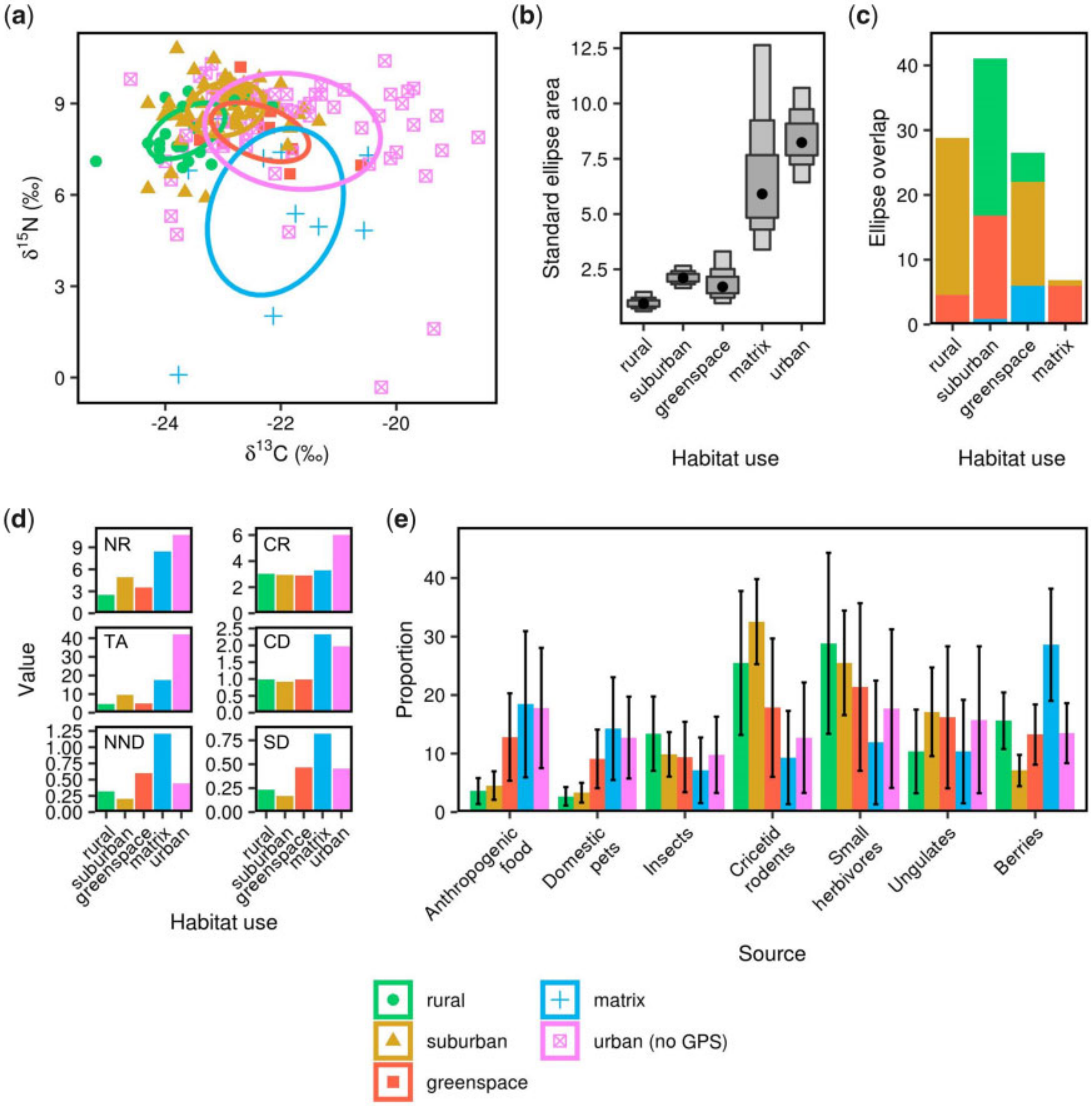

Figure 2: Habitat-based differences in the diet and isotopic niche of coyote populations in and around Edmonton, Alberta, Canada. (a) Isoscape showing δ^{13}C and δ^{15}N values for coyotes from each habitat, with standard ellipses containing 40% of the data points. (b) Standard ellipse areas for each of the coyote populations. Boxes, from largest to smallest, represent the 50%, 75% and 95% confidence intervals based on Bayesian probability densities, and central dots represent the modes. (c) Percentage overlap of standard ellipse area among coyote populations. For each habitat along the x-axis, colored bars indicate the percentage of isotopic niche shared with other populations. (d) Six isotopic niche metrics described by Layman et al. (2007): NR, range of δ^{15}N values; CR, range of δ^{13}C values; TA, total area; CD, mean distance to centroid; NND, mean nearest neighbor distance; SD, standard deviation of the mean nearest neighbor distance. (e) Results of stable isotope mixing models predicting proportions of food items in assimilated coyote diet. Bars and error bars indicate mean and standard deviation, respectively.

of assimilated dietary proportions varied by an average of 2-fold across models: for example, one model predicted anthropogenic food comprised 5.0% of the diet of matrix coyotes, whereas another model estimated 19.4% for this same proportion (Fig. 5; Supplementary Table S4).

Discussion

Understanding variation in how urban-adapted wildlife use urban areas could advance management of these species to reduce human–wildlife conflict and the spread of zoonotic disease. We found that urban coyotes generally consumed more anthropogenic food than rural or suburban coyotes; however, within urban coyotes, matrix coyotes that made extensive use of developed areas exhibited a unique dietary ecology relative to greenspace coyotes that primarily stayed in urban parklands. Specifically, matrix coyotes had a larger isotopic niche that shared little overlap with suburban, rural, or greenspace coyotes. Matrix coyotes also consumed less protein and exhibited the most dietary variation among individuals. These results suggest that matrix coyotes are broader generalists at a population level, but that individual coyotes specialize within this broader niche. We further showed that seasonal variation in niche characteristics is larger in urban coyotes (combining matrix, greenspace and non-collared coyotes) relative to rural animals, with urban coyotes having a larger niche in the summer driven by greater evenness among diet items. Coyote habitat use was the best predictor of isotopic values in individual

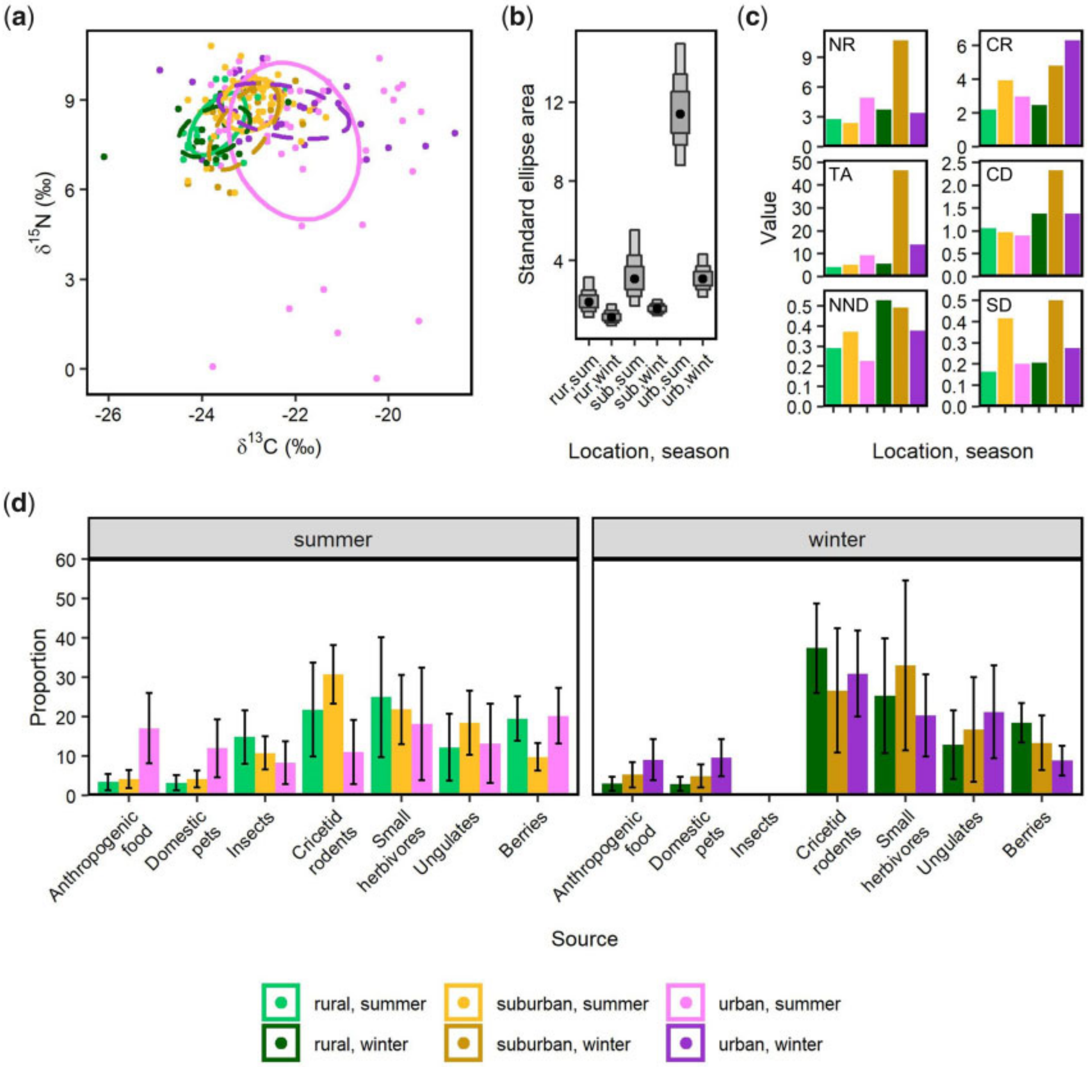

Figure 3: Seasonal differences in the diet and isotopic niche of rural, suburban, and urban coyote populations. (a) Isoscape showing δ^{13}C and δ^{15}N values for coyotes from each habitat, separated by season with standard ellipses containing 40% of the data points. (b) Standard ellipse areas for each of the coyote populations during each season. Boxes, from largest to smallest, represent the 50%, 75% and 95% confidence intervals based on Bayesian probability densities, and central dots represent the mode. (c) Six isotopic niche metrics described by Layman et al. (2007): NR, range of δ^{15}N values; CR, range of δ^{13}C values; TA, total area; CD, mean distance to centroid; NND, mean nearest neighbor distance; SD, standard deviation of the mean nearest neighbor distance. (d) Results of stable isotope mixing models predicting proportions of food items in assimilated coyote diet. Bars and error bars indicate mean and standard deviation, respectively.

coyotes, with increasingly developed areas driving increased δ^{13}C values in both greenspace and matrix coyotes and decreased δ^{15}N values exclusively in matrix coyotes.

Our results demonstrate high individual variation among coyotes in their use of urban areas, supporting similar findings in other cities across North America (Gehrt, Anchor, and White 2009; Newsome et al. 2015; Breck et al. 2019) and contradicting a common interpretation in media articles that all urban coyotes are generally dependent on anthropogenic resources. Although all urban coyotes had higher δ^{13}C values and urban habitat use was the best predictor of anthropogenic food consumption in our models, greenspace coyotes were more similar to suburban and rural coyotes than to matrix coyotes with respect to niche width and δ^{15}N values. High δ^{13}C values in greenspace coyotes, without correspondingly lower δ^{15}N values, might be expected to occur if greenspace coyotes consumed urban prey species (e.g. mice and leporids) that themselves had diets higher in δ^{13}C. The larger niche of matrix coyotes, along with lower niche overlap with other populations, suggests that matrix coyotes are broader generalists than other urban coyotes and that their prey base is ecologically distinct. Larger niches are a reliable indicator of generalist behavior (Peers, Thornton, and Murray 2012) and, for coyotes and six other carnivore species, are strongly correlated with the use of developed areas (Manlick and Pauli 2020). The increase in anthropogenic food consumption that underlies the increase in niche width further correlates with the probability of human-wildlife conflict (Manlick and Pauli 2020).

Conceptually, the large isotopic niche in matrix coyotes could be driven either by individuals within the population specializing on different resources or by large variation within individuals over time (Bolnick et al. 2002). The increased among-individual variation that we observed in matrix coyotes supports the former hypothesis, but long-term and repeated measurements within individuals are needed to assess within-individual variation over time. Individual specialization likely

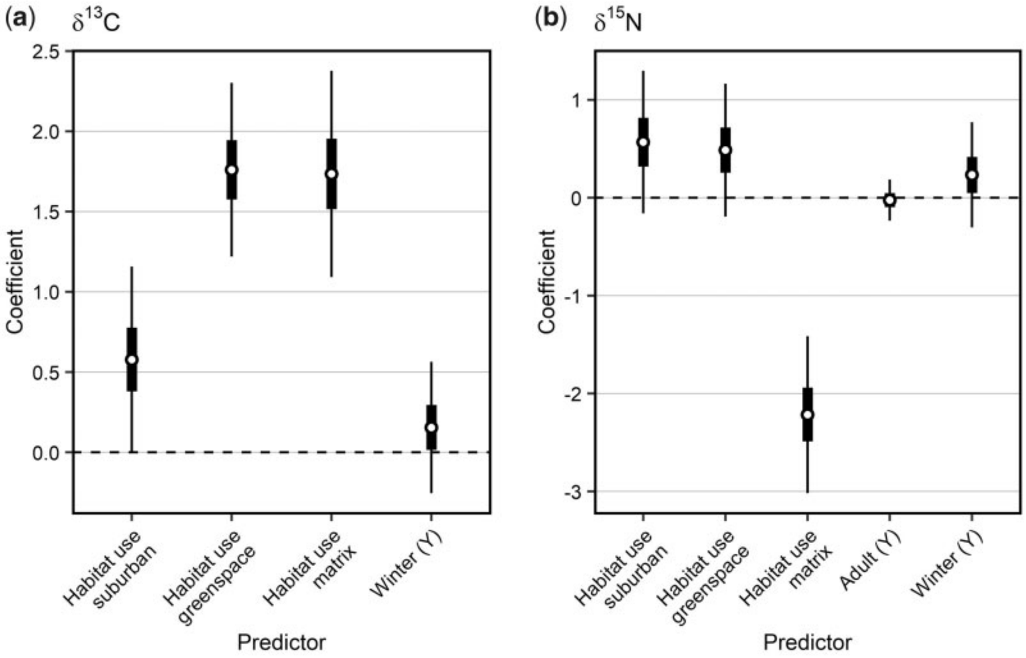

Figure 4: Model-averaged coefficients from linear models predicting (a) δ^{13}C values and (b) δ^{15}N values for coyotes collected in and around Edmonton, Alberta, Canada. Isotope values were predicted from habitat use (with rural populations as the reference), age (adult vs. juvenile), sex and season (summer vs. winter). Predictor coefficients were averaged across all model subsets with $\Delta AIC \leq 2$. Random forest models were used to classify non-GPS-collared coyotes as either matrix or greenspace coyotes. Predictors that did not appear in any models with $\Delta AIC \leq 2$ are not represented.

arises from a combination of opportunistic behavioral plasticity (Lowry, Lill, and Wong 2013; Ritzel and Gallo 2020) and heterogeneous food distributions in urban habitats (Cadenasso, Pickett, and Schwarz 2007). Either mechanism could counteract potential competition within and among species of urban-adapting carnivores (Bolnick et al. 2003). Our interpretation of individual specialization is consistent with observations of increased among-individual variation in Chicago coyotes (Newsome et al. 2015) and in other urban carnivores (Robins et al. 2019; Scholz et al. 2020), but contradicts a study in the Los Angeles area, where urban coyotes exhibited less among-individual variation (Larson et al. 2020). This discrepancy could potentially arise because Edmonton and Chicago have a similar climate and more urban natural areas relative to Los Angeles (Gehrt, Anchor, and White 2009; Murray et al. 2015b; Larson et al. 2020). Greater habitat heterogeneity is likely to support greater dietary heterogeneity.

A comparison of our dietary estimates with results from other studies further supports the hypothesis that abundant urban greenspace provides a greater diversity of natural coyote prey species and associated habitats, which potentially magnifies the differences between greenspace and matrix coyotes with respect to niche width, anthropogenic food subsidization, and individual specialization. For example, our estimate of the proportion of anthropogenic food in urban coyote diets (35–40%, including domestic pets) is consistent with previous stable isotope-based studies in Edmonton (40–50%) (Murray et al. 2015b; Sugden et al. 2020) and Chicago (30–50%) (Newsome et al. 2015), but lower than estimates from a comparable study in Los Angeles (70–80%) (Larson et al. 2020), where urban density is generally higher. In addition, δ^{15}N values of coyotes in the Los Angeles area were negatively correlated with human population density (Larson et al. 2020). Conversely, coyotes in smaller developed areas with abundant access to nearby natural environments (city populations $<$ 100,000), analogous to the suburban population in our study, did not appear to consume more anthropogenic food than rural coyotes (Santana 2010). More detailed multi-city studies of urban coyotes across North America would help distinguish these effects of urban density from potential confounds such as climate (Fidino et al. 2020).

Our exploration of dietary change among seasons showed that urban coyotes exhibited greater seasonal variation in their isotopic niche compared to suburban and rural animals. We suspect this resulted from increased evenness among diet items (less population-level specialization) and increased consumption of anthropogenic food and pets in the summer. Again, our results differ from the Los Angeles area where anthropogenic food consumption increased during the dry season in suburban coyotes, but not in urban coyotes (Larson et al. 2020). We suspect that the winter decrease in anthropogenic food and pet consumption by Edmonton's urban coyotes reflects the pattern of availability of this food source. Presumably, less anthropogenic food is available in urban outdoor areas during the winter, when average high temperatures of −3°C (compared to 21°C in Los Angeles) limit horticultural food sources, outdoor pets, and garbage associated with picnics, festivals, and the temporary camps of unhoused people. Suburban and rural coyotes also had larger isotopic niches in the summer, which we attribute to the increased summer availability of a variety of prey items, including insects and fruits. Scat-based analyses have specifically shown that coyotes living in natural areas generally shift their diets to favor ungulates in winter, when other prey species (e.g. ground squirrels) are unavailable or difficult to obtain (Lingle 2000; Seamster et al. 2014; Swingen, Deperno, and Moorman 2015). There was no clear evidence for this in our mixing model results, but these models are limited in their ability to account for the seasonal availability of food sources (Phillips 2012).

Additional limitations of our study include potential dispersal among populations, variation in home range sizes, and unmeasured differences in food availability across adjacent

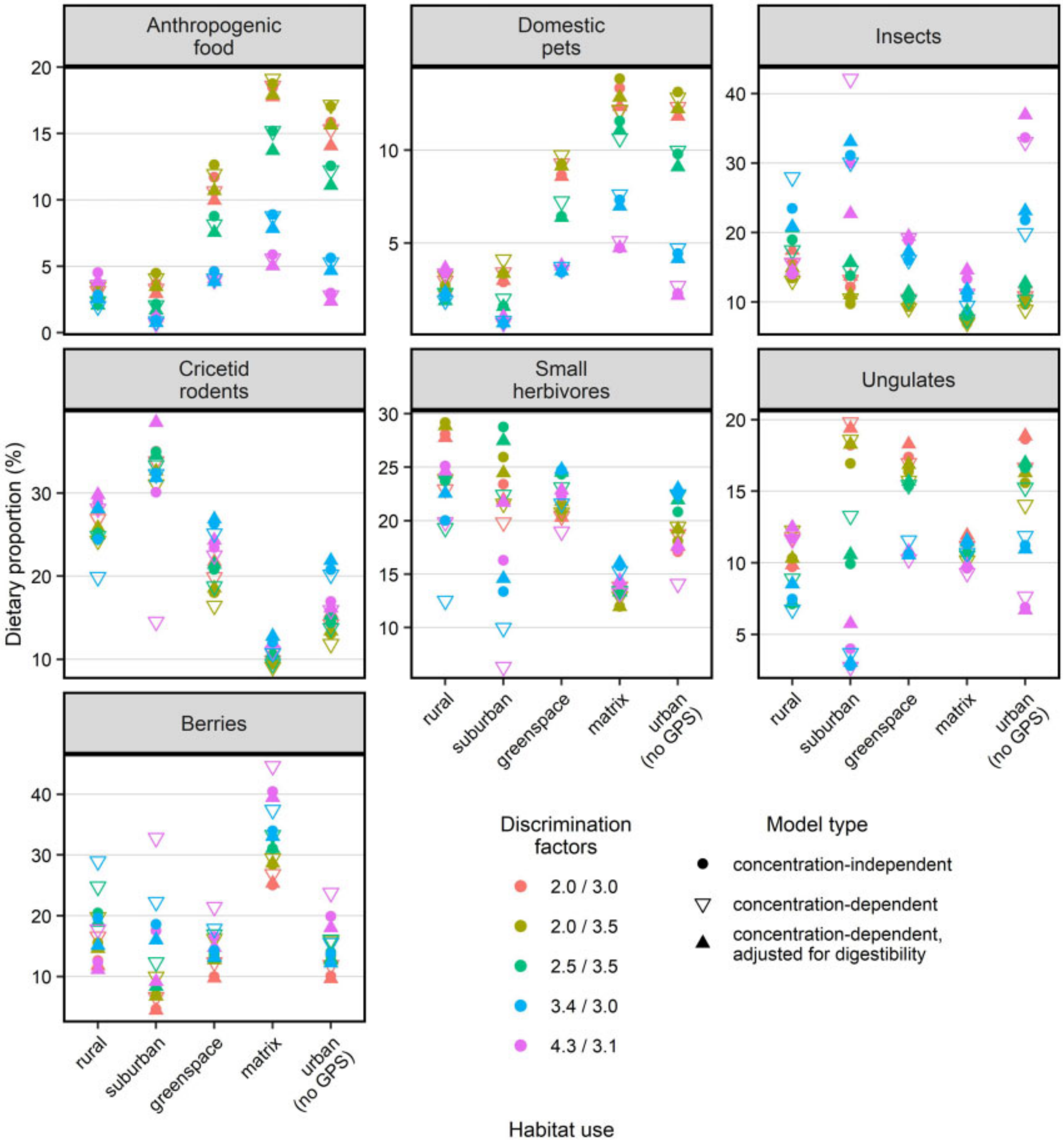

Figure 5: Results of stable isotope mixing models run for five pairs of $\delta^{13}C/\delta^{15}N$ discrimination factors (2.0/3.0, 2.0/3.5, 2.5/3.5, 3.4/3.0 and 4.3/3.1). For each discrimination factor pair, models were run independent of source C and N concentrations, dependent on source C and N concentrations, and dependent on the digestible proportions of C and N. Figure shows the mean estimated dietary proportions for each source item in each coyote group, with colors and symbols used to distinguish different mixing-model formulations.

habitats. Our study design assumed that coyotes belonged to separate populations, but coyote dispersal distances, especially in undisturbed habitat, can occasionally exceed the distances between our different study areas (Harrison 1992; Sasmal et al. 2019). However, most coyotes that disperse from their natal home range come from urban environments and travel <20 km (Zepeda et al. 2021), and none of the GPS-collared urban coyotes in our study traveled to our suburban study site. One urban animal traveled to suburban areas on the other side of the city, indicating the potential for among-population dispersal, but overall, we suspect that few coyotes in our sample dispersed between study areas. Variation in home range sizes among subpopulations could additionally contribute to variation in dietary ecology (Ward et al. 2018); home range size generally decreases along the rural-suburban-urban continuum (Atwood, Weeks, and Gehring 2004) but increases in matrix relative to greenspace coyotes (Gese, Morey, and Gehrt 2012; Murray et al. 2015b). Thus, larger home range sizes may have contributed to the wider isotopic niche of matrix coyotes in our study. Lastly, food and prey availability may vary among adjacent habitats that were not included in our study, which could increase within- and among-population variation relative to what we were able to detect. Despite these limitations, we believe our results broadly reflect coyote dietary ecology along our urbanization gradient.

We repeated our analyses with intentional variation in input parameters to determine the effects of these often-overlooked methodological choices on our biological conclusions. Previous studies of canid diet based on stable isotopes have used a variety of published discrimination factors (Roth and Hobson 2000; Derbridge et al. 2015; McLaren, Crawshaw, and Patterson 2015; L'Hérault et al. 2018; Rioux, Pelletier, and St-Laurent 2020) and differed in whether they account for source carbon and nitrogen concentrations (Reid, Gifford-Gonzalez, and Koch 2018; Larson et al. 2020), which may influence model results (Bond and Diamond 2011; Morgenthaler et al. 2021). The challenge in identifying an appropriate discrimination factor for coyotes is compounded by substantial variation in published values for δ^{13}C for canids, ranging from 2.0‰ (Derbridge et al. 2015) to 4.3‰ (McLaren, Crawshaw, and Patterson 2015). We found that, although quantitative estimates of dietary proportions differed by over 2-fold, relative relationships among source proportions were preserved in every model formulation. This finding supports the contention that discrimination factors are less consequential to model results than other parameters (Derbridge et al. 2015; Swan et al. 2020), provided that the chosen discrimination factors meet key mixing-model assumptions. In our study, using the discrimination factors determined by Rioux, Pelletier, and St-Laurent (2020) or McLaren, Crawshaw, and Patterson (2015) produced models that violated the assumption that all consumers fall within the mixing space defined by the sources (Supplementary Fig. S8). As a result, the model produced results that were biologically untenable by overemphasizing the sources, such as berries and insects, that remained within the mixing space of the consumers.

Accounting for food source C and N concentrations can also affect results (Phillips et al. 2014) and has been recommended in omnivorous species where there are large disparities in elemental concentrations in food sources (Phillips and Koch 2002). Our results were robust to incorporating source concentrations in our models and accounting for source digestibility, both of which had a smaller effect than the choice of discrimination factor and changed estimated dietary proportions by only ±2%. This effect could become more pronounced if the ranges of source element concentrations were larger; for example, the ranges among sources in this study were 16.0% and 4.8% for carbon and nitrogen, respectively, lower values than in other studies that used concentration-dependent models (Woodcock and Walther 2014; Matsubayashi et al. 2015). Although more thorough reviews of mixing model approaches are provided elsewhere (Ben-David and Flaherty 2012; Phillips et al. 2014), we suggest that, for the purpose of comparative analyses among species or populations, the choice of mixing-model formulation may not greatly affect the key biological results. More work is still needed to improve confidence in exact estimates of dietary proportions.

Conclusions

Overall, the connections we found between diet and space use in urban coyotes have important implications for urban wildlife management. Our results suggest that greenspace coyotes residing in urban natural areas exhibit none of the unique dietary ecology that may be predictive of conflict with humans, such as a larger niche and a protein-poor diet. Management efforts associated with food conditioning in coyotes should therefore focus on the highly heterogeneous population of coyotes that depend on developed urban areas. In addition to having a larger and more distinct niche, these coyotes are more likely to depend on anthropogenic food subsidization, which has been shown to be both a cause and consequence of poor health in diverse species of wildlife (Beldomenico and Begon 2010; Murray et al. 2016, 2019; Sugden et al. 2020).

Given the large degree of among-individual variation within the matrix coyote population that we observed, we suggest that broad, proactive managerial approaches designed to make anthropogenic food sources (including compost, garbage, pet food and birdseed) less accessible to coyotes and discourage coyotes from using developed areas may be more practical and effective than targeted approaches for individual problem animals (Swan et al. 2017). Our results further indicate that managers should specifically aim to reduce anthropogenic food access during times of the year when urban wildlife species are consuming more of it. Managerial efforts could be complemented with public education campaigns (Mueller, Drake, and Allen 2019) encouraging citizens to appropriately manage food waste, pets and other potential attractants in developed areas and city parks. Overall, these proactive approaches have the potential to reduce human–wildlife conflict in urban areas, with the additional benefits of promoting animal health and minimizing the spread of zoonotic diseases.

Supplementary data

Supplementary data are available at *JUECOL* online.

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Conflict of interest statement. None declared.

Data availability

The raw data and the R scripts and workspace required to reproduce all analyses are available in the GitHub repository https://github.com/sasugden/coyote_diet.

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