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# Impervious surface cover and number of restaurants shape diet variation in an urban carnivore

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**Abstract**

In the past decade, studies have demonstrated that urban and nonurban wildlife populations exhibit differences in foraging behavior and diet. However, little is known about how environmental heterogeneity shapes dietary variation of organisms within cities. We examined the vertebrate prey components of diets of coyotes (*Canis latrans*) in San Francisco to quantify territory- and individual-level dietary differences and determine how within-city variation in land cover and land use affects coyote diet. We genotyped fecal samples for individual coyote identification and used DNA metabarcoding to quantify diet composition and individual niche differentiation. The highest contributor to coyote diet overall was anthropogenic food followed by small mammals. The most frequently detected species were domestic chicken, pocket gopher (*Thomomys bottae*), domestic pig, and raccoon (*Procyon lotor*). Diet composition varied significantly across territories and among individuals, with territories explaining most of the variation. Within territories (i.e., family groups), the amount of dietary variation attributed to among-individual differences increased with green space and decreased with impervious surface cover. The quantity of anthropogenic food in scats also was positively correlated with impervious surface cover, suggesting that coyotes consumed more human food in more urbanized territories. The quantity of invasive, human-commensal rodents in the diet was positively correlated with the number of food services in a territory. Overall, our results revealed substantial intraspecific variation in coyote diet associated with urban landscape heterogeneity and point to a diversifying effect of urbanization on population diet.

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## INTRODUCTION

Urban landscapes are complex mosaics of biophysical properties that have been designed to support diverse human activities and requirements (Des Roches et al., 2020). Within cities, transitions in percent cover of impervious surfaces, building density, economic activity, and biodiversity occur among city blocks or neighborhoods (Estien, Fidino, et al., 2024; Pickett et al., 2017). Such heterogeneity exposes wildlife in urban systems to diverse local conditions that vary at small geographic scales (Pickett et al., 2017; Rivkin et al., 2019). Although a growing body of literature has documented that several traits differ between urban and nonurban populations (Alberti et al., 2017), little is known about how environmental heterogeneity shapes behavioral variation across subpopulations exposed to different conditions within cities (Rivkin et al., 2019; Schell et al., 2020; Thompson et al., 2022).

Intracity studies suggest that urban–wildlife populations exhibit diverse behaviors (Caspi et al., 2022). For example, the song frequencies of Song Sparrow (*Melospiza melodia*) in Portland, Oregon, USA, varied spatially as a function of differing levels of urban noise (Wood & Yezerinac, 2006). Sulfur-crested Cockatoos (*Cacatua galerita*) in Sydney, Australia, had site-specific garbage-bin-opening behaviors, linking the onset of new foraging behaviors to spatial variation in human activity (Klump et al., 2021). These studies reveal that human-driven environmental variation within cities can promote within-population behavioral and niche differences (Caspi et al., 2022; Des Roches et al., 2020; Schell et al., 2020). One of the most common behavioral changes in urban animal populations is a shift in diet and foraging behavior (Birnie-Gauvin et al., 2017; Hallam & Harris, 2023). Urbanization alters the abundance, distribution, and quality of food sources and provides access to novel diet items including introduced species and human food (Birnie-Gauvin et al., 2017). Although few studies have considered how resource use by individuals and subpopulations within urban areas varies as a function of environmental heterogeneity, evidence of within-city dietary variation is emerging. For example, inter-individual dietary variation and specialization in coyotes (*Canis latrans*) in Chicago, USA, and red foxes (*Vulpes vulpes*) in Berlin, Germany, were extensive (Newsome et al., 2015; Scholz et al., 2020). However, the underlying drivers of

dietary variation within urban populations are not yet well understood.

Recent theoretical and empirical work suggests that individual niche differentiation is related to both the degree of intraspecific competition and the extent of “ecological opportunity,” or the diversity of available resources for foragers (Araújo et al., 2011; Costa-Pereira et al., 2019; Layman et al., 2015; West & Jones, 2022). Specifically, individuals experiencing high levels of intra-specific competition may feed on alternative resources if access to common optimal resources is constrained (Svanbäck & Bolnick, 2005, 2006). The increased landscape heterogeneity characteristic of urban environments is also predicted to increase individual niche variation by expanding foraging possibilities for individuals, which facilitates niche divergence (Araújo et al., 2011; Layman et al., 2015). In particular, the accessibility of human food in cities may expand the set of diet items available to foragers, and thus augment individual niche differences by increasing ecological opportunity (West & Jones, 2022). Conversely, if all or most individuals exploit human foods, niche differences may decrease (West & Jones, 2022). These alternative scenarios suggest that the strength of individual niche differences may be variable across urban landscapes, dependent on competition and the distribution of anthropogenic versus natural food resources. Additionally, the extent of among-individual diet variation may be subject to the scale of analysis (e.g., differentiation within social groups vs. between them). Further research is needed to better understand the mechanisms by which urbanization promotes diet differentiation within populations at different levels of biological organization (Manlick & Newsome, 2021).

Here, we investigated how variability in the vertebrate dietary components of urban coyotes in San Francisco, California, relates to landscape features at different biological levels (population, territory/family group, and individual). Coyotes returned to San Francisco in the early 2000s (Sacks et al., 2006) after their previous extirpation in the early 20th century (Todd, 2018), and the city currently hosts a thriving coyote population, which regularly comes into conflict with urban residents (Wilkinson et al., 2023). San Francisco’s area is only 121 km<sup>2</sup>, but its human population is the second most dense in the United States (Townsend & Ellis-Young, 2018). The city is surrounded by water to the north, east, and west. In the south, San Francisco is crossed by

Interstate-280, a freeway with one of the highest levels of animal roadkill in the state (Kreling et al., 2019; Shilling et al., 2017), creating a barrier to surrounding natural areas.

Quantification of dietary variation within populations requires high-resolution data that enable comparison of the diets of individuals and their social groups. Traditional methods of dietary analysis, which typically rely on morphological identification of prey remains in scats, are not well suited to this task as many anthropogenic foods leave no macroscopic evidence in scats and individual identification is nearly impossible. Accordingly, many studies investigating how carnivore diets respond to human disturbances are based on stable isotope analysis (Hopkins et al., 2014; Kirby et al., 2016; Manlick & Pauli, 2020), which can estimate the contribution of human-provided food to the diet and allows for individual-level analyses (Newsome et al., 2015). However, stable isotope analysis cannot distinguish between food sources with similar isotopic profiles or generate species-level diet data when individuals consume many food sources, as is the case with coyotes (Phillips et al., 2014; Stock et al., 2018). In contrast, molecular analyses of fecal DNA reveal DNA from dietary items that leave no macroscopic evidence and from the animal that deposited the scat (Gosselin et al., 2017; Shehzad et al., 2012). DNA-based approaches allow identification of diet items at the species level (Alberdi et al., 2019) and can link samples to individual consumers (e.g., through microsatellite genotyping), in this case, coyotes, allowing inferences about individual-level dietary variation while accounting for repeated measures of individuals (Fedriani & Kohn, 2001; Manlick & Newsome, 2021).

We analyzed fecal samples collected in San Francisco over a period of 2.5 years to determine how urban landscape heterogeneity influenced territory- and individual-level niche variation, including coyote consumption of anthropogenic and nonnative, human-commensal (nuisance) rodents (*Rattus rattus*, *R. norvegicus*, and *Mus musculus*). We hypothesized that dietary niche variation was partitioned both among territories and among individuals within territories according to the distribution of urbanization and, consequently, anthropogenic food sources. Specifically, greater access to anthropogenic food in more urbanized areas could both ameliorate intraspecific competition within social groups, reducing niche differentiation and/or increase ecological opportunity, expanding niche differentiation. Irrespective of niche breadth, we predicted that coyotes in more urbanized locations consumed more anthropogenic food and coyotes with more access to green space consumed more natural prey. Additionally, we predicted that coyote

consumption of nuisance rodents was greater in locations with more restaurants, which are hotspots of rodent activity (Parsons et al., 2021).

## METHODS

### Sample collection

We collected scats from September 2019 through April 2022, with the majority collected in 2020 and 2021. We collected scats from urban green spaces, including parks, golf courses, and gardens across San Francisco (Appendix S1: Figure S1). We only collected scats that we estimated to be less than 1 week old given their appearance and time since last visit. We subsampled approximately 3 cm of each scat and stored the subsample in 15-mL tubes with >5:1 ethanol-to-scat ratio of 95%–99% ethanol. The subsamples of the scats for DNA extraction included both the external surface and internal matrix to capture both host and dietary DNA. As part of a companion study on the genetic structure of coyotes in San Francisco, 243 of the scats collected for this study and identified in the field as coyote were also typed to species by sequencing a portion of the cytochrome b gene (methods described by Quinn et al., 2019). Eighteen of the latter failed, but results confirmed 219 of the remaining 225 (97%) scats to be coyote, whereas the other 6 were domestic dog ( $n = 4$ ) or raccoon (*Procyon lotor*;  $n = 2$ ), indicating a low level of misclassification.

### DNA extraction and genotyping

We conducted laboratory analyses in the Mammalian Ecology and Conservation Unit of the Veterinary Genetics Laboratory at the University of California, Davis. We extracted DNA from fecal samples using a EurX Stool DNA Purification Kit (EurX, Gdansk, Poland) or a Qiagen DNeasy 96 Blood and Tissue Kit (Qiagen, Valencia, CA, USA), with modified protocols (Appendix S1: Text S1). To identify individual coyotes and to remove any dog samples, we attempted to genotype all samples at 12 canine autosomal microsatellites and one sex-typing marker, and separated coyotes from dogs using the program STRUCTURE (Pritchard et al., 2000) (Appendix S1: Text S2).

### Diet metabarcoding

Detailed diet metabarcoding laboratory methods are available in Appendix S1: Text S3. Briefly, we conducted

the study in two batches, including 370 samples in Batch 1 (342 scats and 28 controls) and 1018 samples in Batch 2 (946 scats and 72 controls). For both batches, we prepared libraries in sets of up to 96 reactions (four sets in Batch 1, 12 sets in Batch 2), each of which included up to 88 samples and up to 8 controls. Among the controls in each set, we included polymerase chain reaction (PCR)-negative controls to assess background contamination as well as positive controls to assess amplification performance and check for cross-well contamination of samples with target DNA present. To identify vertebrate species in the diet, we targeted the V5 loop of the mitochondrial 12S gene and used a blocking oligonucleotide to reduce coyote amplification (Vestheim & Jarman, 2008) (Appendix S1: Table S1). We added sequence overhangs to the 5' ends of amplicon primers to enable annealing to Illumina index sequences in the next step. We then conducted an index PCR step to anneal Illumina-compatible adapters and a unique pair of indexes to the amplicons of each sample to allow individual sequence reads to be sorted to their corresponding sample (or control) after pooling and sequencing. Finally, for each batch, we pooled 2 µL of index PCR product from each sample in each set, purified the pooled libraries, and combined them into a master pool containing the set pools at equal concentrations. The master pool for Batch 1 was sequenced and demultiplexed by Novogene Corporation (Sacramento, CA, USA) with an Illumina NovaSeq S4 PE150. Batch 2 was sequenced and demultiplexed by Admera Health (South Plainfield, NJ, USA) with an Illumina NovaSeq X Plus PE150.

Although some studies recommend the use of technical replicates for all samples (Alberdi et al., 2019), we opted to maximize the number of biological replicates (i.e., distinct scat samples) rather than technical replicates given limited resources (Mata et al., 2019; White et al., 2023). Nevertheless, to assess the repeatability of our results, we selected an arbitrary subset of 152 samples sequenced in one batch to replicate in another batch to check for consistency in recovered sequences.

## Bioinformatic processing and filtering

We used cutadapt (Martin, 2011) to trim and filter out low-quality reads. Next, we quantified amplicon sequence variants (ASVs) with DADA2 (Callahan et al., 2016), a denoising program designed to filter out poor-quality sequences, infer sample sequences, and remove chimeras. To identify the taxonomy of ASVs, we created a database of 12SV5 sequences of all vertebrate genera recovered from pilot studies to create a local reference library for the basic local alignment search tool (BLAST) command

line application (BLAST+; Camacho et al., 2009). We then used the *blastn* feature of BLAST+ to assign ASVs via the custom database and used the full nucleotide database of NCBI available online to corroborate assignments or assign newly discovered sequences not previously recovered from pilot studies. Where possible, we assigned ASVs at the species level on the basis of percent identity. Otherwise, we used the next most specific taxonomic grouping. In most cases, ASVs had 100% query coverage and matched at 99% or 100% identity; the most abundant ASV for each species had a 100% match (except *Tyto alba*, which matched at 99%). In cases where ASVs matched multiple species or ASVs were assigned to species absent from San Francisco, we used iNaturalist ([www.inaturalist.org](http://www.inaturalist.org)) and other sources of knowledge on species present in San Francisco to narrow the assignment to the locally present species. For example, some ASVs matched several *Thomomys* species, but the only species known to be present in San Francisco was Botta's pocket gopher (*Thomomys bottae*). Accordingly, we assigned all reads matching *Thomomys* spp., the most prevalent of which matched Botta's pocket gopher 100%, as Botta's pocket gopher.

We carried out filtering and quality control measures on taxonomically assigned sequences. We first removed ASVs that comprised <0.001% of the sequence reads in a sequencing lane. We then removed most ASVs with <98% sequence identity to any sequence in the NCBI nucleotide database, as determined via BLAST. The exceptions were California vole (*Microtus californicus*), western deer mouse (*Peromyscus sonoriensis*), Botta's pocket gopher, and pigeons and doves (Columbidae), for which we accepted ≥97% sequence identity because intraspecific sequence variation was high among the species represented in the nucleotide database and no other BLAST hits had higher sequence identity. Next, we combined ASVs that were assigned to the same species and removed host reads (*Canis* spp.) and taxa that likely originated from a source other than coyote diet, including low-level background contaminants that were assigned to species outside the study area (e.g., *Oreortyx pictus*, *Ursus americanus*). We then used positive and negative controls (Appendix S1: Figure S2) to inform filtering parameters to avoid false positives by removing unreliable PCR amplifications and low-frequency noisy reads. From the remaining samples, we discarded most taxa comprising <0.5% reads within a scat. To avoid errors of omission, however, we manually examined removed taxa and retained rare small-bodied prey (e.g., *Scapanus latimanus*; Trochilidae) and other prey known to occur in the study area but not observed in controls. We then removed any samples that had a known non-coyote origin or did not generate any *Canis* spp. reads.

## Data analysis

We performed all analyses and produced figures in the R statistical computing environment (R Core Team, 2022; version 4.2.1). We summarized the data with both frequency of occurrence (FOO) and relative read abundance (RRA) at both the lowest possible taxonomic rank and by grouping diet items into six functional groups: anthropogenic, small mammals, medium-sized mammals, birds, herptiles, and marine mammals. To calculate FOO, we divided the number of occurrences of a diet item by the total number of samples. We calculated RRA for each diet item as the number of reads assigned to the item divided by the total number of reads in the sample.

Although both FOO and RRA are biased proxies for the quantity (or biomass) of prey consumed and are best used to represent the diet qualitatively, both measures can be compared among individuals or groups because the same biases affect all individuals equally (Ando et al., 2023; Walker et al., 2023; White et al., 2023). For such comparisons, RRA is a higher resolution measure than FOO. Otherwise, FOO is especially useful for evaluating diet composition at the population level, where the most important foods tend to be consumed frequently. Conversely, at the individual or group level, FOO may overestimate the contribution of rare food items or contaminants to the diet (Deagle et al., 2019; Mallott et al., 2018; Massey et al., 2021; Walker et al., 2023). Therefore, RRA is better suited for comparing the relative importance of diet items among groups.

We calculated and compared sample coverage, species richness, Hill–Shannon diversity, and Hill–Simpson diversity for territories and individuals on the basis of sample incidence data with the R package iNEXT (Hsieh et al., 2016). Sample coverage is the proportion of individuals (or in this case diet items) in an assemblage that belong to species represented in the sample (Chao & Jost, 2012). The three metrics of diversity differ in how they scale rarity: species richness is the most sensitive and Hill–Simpson is the least sensitive to rare species (Roswell et al., 2021). We calculated dietary rarefaction curves with iNEXT to determine whether samples within territories and individuals reached a species diversity asymptote, indicating sample sizes large enough for comparison. We were unable to obtain an equal number of scat samples per individual. Therefore, we limited our individual-level analyses to the coyotes that were sampled the most frequently and with high estimated coverage, indicating that most of their diet items were represented in their samples ( $\geq 8$  scats). We used genetic data and local observations to assign these individuals to family groups. If the majority of an individual's scats were collected in one territory over the course of the

study or the individual was observed repeatedly in a territory, we felt confident in assigning the individual to the family group associated with that territory. One frequently sampled individual was designated as transient given inconsistency in where his fecal samples were collected.

We constructed Bray–Curtis (for RRA) and Jaccard (for FOO) dissimilarity matrices comparing each pair of fecal samples and ordinated the values with nonmetric multidimensional scaling (nMDS) to visualize dietary differences among biological seasons, territories, and individuals. We conducted nMDS over a range of dimensions ( $k$ ) and selected the minimum number of dimensions ( $k = 3$ ) in which the stress of the ordination was  $\leq 0.1$  (“metaMDS” in the vegan package in R; Oksanen et al., 2022). To evaluate the significance of variation in vertebrate diet composition among territories, biological seasons, and individuals, we conducted a series of permutation-based multivariate analysis of variance tests (PERMANOVA; Anderson, 2017) on the distance matrices (“adonis2” in vegan). To test for seasonal differences, we used the date of sample collection to group scats according to biological season: mating: (November–February), pupping (March–June), and dispersal (July–October). We first used all fecal samples to investigate differences in diet as a function of biological season and territory. Because not all scats yielded genotypes, and some samples came from the same individual, we verified that significant PERMANOVA results were not an artifact of pseudoreplication by conducting 1000 trials in which we randomly sampled a single scat per individual. Because we were interested in individual dietary variation, we investigated differences in diet at the individual level by comparing the most frequently sampled coyotes ( $\geq 8$  scats). In this test, we included individual nested within family group as the main predictor and used a sequential (Type I) sum of squares. We assessed differences in dispersion among all predictors to understand whether dietary differences could be attributed to differences in group dispersion, a proxy for dietary niche breadth (“betadisper” and “permute” in vegan). We ran all analyses with 999 permutations and conducted post hoc tests for pairwise analysis with a Benjamini–Hochberg correction for multiple comparisons (via “pairwise.adonis” in the pairwiseAdonis package for composition and via “permute” in the vegan package for dispersion; Arbizu, 2020; Benjamini & Hochberg, 1995). To assess which diet items contributed the most to observed differences in coyote diets among territories, we used similarity percentage analysis based on the dissimilarity matrix of the RRA data (“simper” in vegan).

To test whether land use and land cover affected diet, we constructed a 1-km buffer around the midpoint of the

minimum convex polygon enclosing all fecal samples collected in a territory in ArcGIS Pro 3.1.0 (ESRI, Inc., 2023) and calculated the following metrics for each buffer: mean percent impervious surface cover and mean percent urban cover from the 2019 National Land Cover Database (Dewitz & Geological Survey, 2021); mean housing density and mean population density from the 2020 US Census (Helmers, 2022); and the number of food services (e.g., restaurants, cafeterias) from the City and County of San Francisco (City and County of San Francisco, 2023). We used 1 km as our buffer distance because it was the maximum distance that did not overlap the buffers of neighboring territories and coyote territories tend to be contiguous (Gehrt et al., 2009; Larson et al., 2020). All land use and land cover covariates were highly correlated ( $r > 0.7$ ; Appendix S1: Figure S3). Accordingly, we used only one of these covariates in any single model as a proxy for several potential metrics of urbanization. We fit a beta regression for RRA (function “gam” with family *betar* in mgcv; Wood, 2011) and a quasibinomial generalized linear model (GLM) (function “glm” in stats) for FOO to test the effect of percent cover of impervious surfaces, a measure of urbanization, on the proportion and frequency of anthropogenic food in each territory. We applied these same models to test the effect of the number of food services, an attractant for rodents (Parsons et al., 2021; Sánchez et al., 2021), on the proportion and frequency of nuisance rodents in the diet in each territory.

To assess the strength of individual niche differences in the population and within family groups, we applied Roughgarden’s (1972) variance-partitioning framework, in which the total niche width (TNW) is composed of within-individual and among-individual (hereafter, “between-individual”) components (WIC and BIC, respectively). We used the Shannon–Weaver approximation to calculate the ratio BIC/TNW, which measures the proportion of the TNW explained by between-individual variation such that higher values indicate more variation attributable to between-individual differences (specialization) and lower values indicate more variation attributable to within-individual differences (generalization) (Bolnick et al., 2002). Because coyotes are territorial, it is important to consider individual niches relative to the social (i.e., family) group niche (Sheppard et al., 2018). Accordingly, in addition to calculating the population-level BIC/TNW, we calculated group-level BIC/TNW measures that represent the proportion of group-niche width explained by between-individual variation in each family group. We then used these proportions as our response variables to test the effect of impervious surface cover on within-group niche differentiation with a beta regression (function “gam” with

family *betar* in mgcv; Wood, 2011). Quantification of niche components assumes that sampled diets are reflective of the overall diet of individuals (Araújo et al., 2011). Because carnivore gut transit times are relatively short (~48 h), DNA in a single fecal sample likely represents only a few foraging decisions. Accordingly, although these statistical approaches have been applied to herbivore diet metabarcoding data (e.g., Jesmer et al., 2020; White et al., 2023), they may overestimate the degree of between-individual differences in carnivores if there are fewer diet items in sampled diets compared with long-term diets. Nonetheless, systematic biases will similarly affect all family groups, making relative comparisons between these groups valid. To control for potentially confounding effects of sample size, however, we included sample size as a fixed effect in the model to control for differences in the number of samples collected for each family group. Prior to running analyses, we calculated the average RRA for each diet item for each individual (using all scats belonging to an individual), and multiplied proportions by 1000, the product of which we rounded to the nearest integer. It was necessary to convert the number of sequence reads into proportions so that individuals with greater total reads did not have undue influence on estimates (Jesmer et al., 2020). Finally, to quantify specialization in the most frequently sampled coyotes, we calculated the proportional similarity index ( $PS_i$ ), a measure of individual specialization that corresponds to the similarity between an individual’s diet and the population diet (Bolnick et al., 2002). Both BIC/TNW and  $PS_i$  were calculated using the package RInSp in R (Zaccarelli et al., 2013).

## RESULTS

We collected and attempted to genotype 1258 putative coyote scats. Genotyping resulted in 735 individually identifiable coyote samples, 14 dog samples, and 509 putative coyote samples that did not provide genotypes of sufficient quality for individual identification. Of the latter 509 samples, cyt b analysis confirmed that 67 originated from coyotes, one from a dog, and two from raccoons.

We attempted metabarcoding on all 1258 samples and 152 replicates. Based on the distribution of prey reads in controls and samples, as well as those of target species in positive controls, we selected minimum thresholds for numbers of prey reads of 4400 reads in Batch 1 and 150 reads in Batch 2 (Appendix S1: Figure S2). Based on these thresholds, we retained 707 samples (and 87 replicate pairs) for the analysis. Correlations between RRA in replicate samples were high, with average Pearson  $r = 94.5$

( $SD = 11.3$ ,  $n = 87$  pairs). The 707 samples used in diet analyses included 565 verified coyotes (525 with individual genotypes and 40 based on cyt b but without individual genotypes) and 142 putative coyotes without individual genotypes. From 525 individually genotyped samples, we identified 111 individual coyotes, of which 22 were sampled 8–24 times each. Overall, the fecal samples contained 59 diet items (Table 1). The average number of diet items per scat was 2.75 (range: 1–8).

## Population-level diet

The effect of season on diet composition was small, but statistically significant (RRA  $F = 7.01$ ,  $R^2 = 0.02$ ,  $p < 0.001$ ; FOO  $F = 5.65$ ,  $R^2 = 0.01$ ,  $p < 0.001$ ; Appendix S1: Table S2). Significant dispersion differences suggested that seasonal dietary differences in part could have been due to differences in diet breadth (Appendix S1: Table S2, Figure S4a). After randomly subsampling to one sample per individual, however, the effect of season on diet composition was significant only in 64% (FOO) or 31% (RRA) of 1000 PERMANOVA trials (data tabs. 1 and 2: <https://doi.org/10.5061/dryad.9s4mw6mqr>). On the basis of the 707 scats, the highest average ( $\pm SE$ ) contributor to the coyote diet was anthropogenic food (FOO = 78.1%  $\pm$  1.6, RRA = 46.6%  $\pm$  1.5), followed by small mammals (FOO = 73.8%  $\pm$  1.7, RRA = 37.1%  $\pm$  1.5), medium-sized mammals (FOO = 22.8%  $\pm$  1.6, RRA = 9.4%  $\pm$  0.9), birds (FOO = 23.6%  $\pm$  1.6, RRA = 6.84%  $\pm$  0.7), herptiles (FOO = 0.57%  $\pm$  0.28, RRA = 0.11%  $\pm$  0.07), and marine mammals (FOO = 0.28%  $\pm$  0.20, RRA < 0.01%) (Figure 1). The most frequently detected vertebrate species (and those composing the highest proportions of reads) were domestic chicken, Botta's pocket gopher, domestic pig, and raccoon (Figure 1, Table 1).

## Territory-level diet

After excluding 14 scats that were not collected in a known territory, the remaining 693 scats were included in territory-level analyses. Territory rarefaction curves based on Hill-Shannon diversity indicated sufficient sample sizes for most of the study sites. Golden Gate Park West, McLaren Park, and St. Francis Wood had sample coverage estimates of 84%, 83%, and 89%, respectively, suggesting that coyote diet diversity was slightly underrepresented at those sites (Appendix S1: Table S3). However, all rarefaction curves based on Hill-Simpson diversity reached asymptotes, indicating that the most dominant diet items were well-sampled across all territories (Appendix S1:

Figure S5). Territory-level species richness ranged from 13 to 35 (Appendix S1: Table S3).

Coyote diet composition varied significantly across territories (PERMANOVA: RRA  $F = 8.06$ ,  $R^2 = 0.10$ ,  $p < 0.001$ ; FOO  $F = 7.85$ ,  $R^2 = 0.10$ ,  $p < 0.001$ ; Appendix S1: Table S2). Even after randomly subsampling to a single sample per individual, the effects of territory on diet composition were significant in 98% (FOO) and 78% (RRA) of 1000 PERMANOVA trials (data tabs. 1 and 2: <https://doi.org/10.5061/dryad.9s4mw6mqr>). Diet overlap among individual fecal samples within territories was substantial, but the location of group centroids indicated different diet composition among territories (Appendix S1: Figure S4b). For example, 95% ellipses for Coit Tower and Presidio overlapped very little. SIMPER analysis indicated that most of the dissimilarity across territories was attributed to differences in the proportion of pocket gopher (27.7%) and chicken (22.5%) reads (Appendix S1: Table S4).

The RRA of detected diet items varied across territories (Figure 2a; data tabs. 3 and 4: <https://doi.org/10.5061/dryad.9s4mw6mqr>). For example, the average RRA of anthropogenic food was lowest at Presidio (RRA = 20.6%  $\pm$  4.6) and highest at Bernal Hill (RRA = 68.0%  $\pm$  3.3). Similarly, small mammals comprised a much greater percentage of the dietary reads at Presidio (RRA = 64.0%  $\pm$  10.3) than at Coit Tower (RRA = 17.1%  $\pm$  3.2), primarily driven by differences in the representation of pocket gopher RRA (RRA = 55.7%  $\pm$  5.5 vs. 2.1%  $\pm$  1.4, respectively). Conversely, the RRA of birds was higher in scats from Coit Tower (RRA = 13.3%  $\pm$  3.0) than from other sites, and primarily reflected pigeons and doves, which were recovered in nearly a quarter of the scats from Coit Tower (FOO = 23.3%  $\pm$  4.6; RRA = 9.5%  $\pm$  2.7). Two marine mammals—Fin whale (*Balaenoptera physalus*) and California sea lion (*Zalophus californianus*)—were detected in scats from Merced. We detected nonnative rats (*R. rattus*, *R. norvegicus*) in scats from most territories at relatively low percentages (RRA < 2%) and frequencies (FOO < 10%). Exceptions were Coit Tower (FOO = 45.3%  $\pm$  5.4, RRA = 12.4%  $\pm$  2.8), Corona Heights Park (FOO = 24.3%  $\pm$  7.1; RRA = 7.7%  $\pm$  3.6), and Glen Canyon (FOO = 15.1%  $\pm$  3.5, RRA = 4.5%  $\pm$  1.8). Domestic cats were detected in the scats from most territories, but at low percentages (RRA  $\leq$  3.2%).

The percent impervious cover in a territory ranged from 17.7% to 80.9% and the number of food services ranged from 5 to 328 (Appendix S1: Table S3). The RRA of anthropogenic food in the territory-level samples was positively correlated with the percent cover of impervious surfaces in the territory (Figure 3;  $\phi = 21.0$ ,  $\beta = 0.02$ ,  $z = 3.360$ ,  $p < 0.001$ ). The FOO of anthropogenic food was similarly correlated with impervious surface cover

**TABLE 1** Number of detections, frequency of occurrence (FOO), and average relative read abundance (RRA) for each vertebrate diet item at the finest taxonomic resolution detected among 707 coyote scats in San Francisco, California, USA.

Functional group	Scientific name (common name)	Detections	FOO (%)	Average RRA (%)
Anthropogenic	<i>Gallus gallus</i> (Domestic chicken)	509	71.99	39.80
	<i>Sus scrofa</i> (Domestic pig)	250	35.36	5.88
	<i>Bos taurus</i> (Domestic cattle)	32	4.53	0.22
	<i>Salmo salar</i> (Atlantic salmon)	15	2.12	0.11
	<i>Brevoortia</i> spp. (Menhaden)	13	1.84	0.05
	<i>Oncorhynchus</i> spp. (Salmon and trout)	7	0.99	0.12
	<i>Ovis aries</i> (Domestic sheep)	5	0.71	0.01
	<i>Capra hircus</i> (Domestic goat)	3	0.42	0.06
	<i>Engraulis</i> spp. (Anchovy)	3	0.42	0.13
	<i>Merluccius</i> spp. (Merluccid hake)	3	0.42	0.02
	<i>Cyprinus carpio</i> (Eurasian carp)	2	0.28	0.03
	<i>Acipenser</i> spp. (Sturgeon)	1	0.14	0.01
	<i>Chanos chanos</i> (Milkfish)	1	0.14	0.01
	Clupeidae (Herrings and sprats)	1	0.14	0.00
	<i>Gadus morhua</i> (Atlantic cod)	1	0.14	0.01
	<i>Morone chrysops</i> (White bass)	1	0.14	0.004
	<i>Numida meleagris</i> (Domestic guineafowl)	1	0.14	0.09
	<i>Sebastes</i> spp. (Rockfish)	1	0.14	0.01
	Tilapiini (Tilapia)	1	0.14	0.01
Birds	Columbidae (Pigeons and doves)	50	7.07	2.01
	Anatidae (Ducks)	49	6.93	1.42
	Passeriformes (Passerines)	35	4.95	1.33
	<i>Corvus</i> spp. (Crows and ravens)	17	2.41	0.60
	<i>Junco hyemalis</i> (Dark-eyed Junco)	15	2.12	0.39
	<i>Cairina moschata</i> (Muscovy Duck)	8	1.13	0.17
	<i>Turdus migratorius</i> (American Robin)	6	0.85	0.30
	Anserinae (Swans and geese)	3	0.42	0.16
	<i>Buteo</i> spp. (Hawks)	2	0.28	0.05
	<i>Catharus</i> spp. (Nightingale-thrushes)	2	0.28	0.08
	<i>Trochilidae</i> (Hummingbirds)	2	0.28	0.002
	<i>Aythya</i> spp. (Diving ducks)	1	0.14	0.14
	<i>Fulica americana</i> (American Coot)	1	0.14	0.02
	<i>Passer domesticus</i> (House Sparrow)	1	0.14	0.13
	<i>Psaltriparus minimus</i> (Bushtit)	1	0.14	0.01
	<i>Sturnus vulgaris</i> (European Starling)	1	0.14	0.04
	<i>Tyto alba</i> (Barn Owl)	1	0.14	0.00
Herptiles	<i>Batrachoseps attenuatus</i> (California slender salamander)	2	0.28	0.03
	<i>Lithobates catesbeianus</i> (American bullfrog)	1	0.14	0.07
	<i>Plestiodon skiltonianus</i> (Western skink)	1	0.14	0.02
Marine mammals	<i>Balaenoptera physalus</i> (Fin whale)	1	0.14	0.00
	<i>Zalophus californianus</i> (California sea lion)	1	0.14	0.00
Medium-sized mammals	<i>Procyon lotor</i> (Raccoon)	113	15.98	6.55

**TABLE 1** (Continued)

Functional group	Scientific name (common name)	Detections	FOO (%)	Average RRA (%)
Small mammals	<i>Felis catus</i> (Domestic cat)	32	4.53	0.96
	<i>Mephitis mephitis</i> (Striped skunk)	22	3.11	1.84
	<i>Didelphis virginiana</i> (Virginia opossum)	3	0.42	0.00
	<i>Thomomys bottae</i> (Botta's pocket gopher)	401	56.72	28.96
	<i>Microtus californicus</i> (California vole)	89	12.59	1.92
	<i>Rattus norvegicus</i> (Norway rat)	60	8.49	1.80
	<i>Mus musculus</i> (House mouse)	58	8.20	1.75
	<i>Rattus rattus</i> (Black rat)	40	5.66	1.30
	<i>Sciurus carolinensis</i> (Eastern gray squirrel)	21	2.97	0.39
	<i>Sylvilagus bachmani</i> (Brush rabbit)	18	2.55	0.63
	<i>Peromyscus sonoriensis</i> (Western deer mouse)	14	1.98	0.14
	<i>Otospermophilus beecheyi</i> (California ground squirrel)	8	1.13	0.06
	<i>Neotamias</i> spp. (Chipmunks)	5	0.71	0.04
	<i>Sorex</i> spp. (Long-tailed shrews)	4	0.57	0.06
	<i>Cavia porcellus</i> (Domestic guinea pig)	2	0.28	0.07
	<i>Oryctolagus cuniculus</i> (European rabbit)	2	0.28	0.01
	<i>Scapanus latimanus</i> (Broad-footed mole)	2	0.28	0.01

Note: Diet items are arranged by functional group and sorted in decreasing order of number of detections within a functional group.

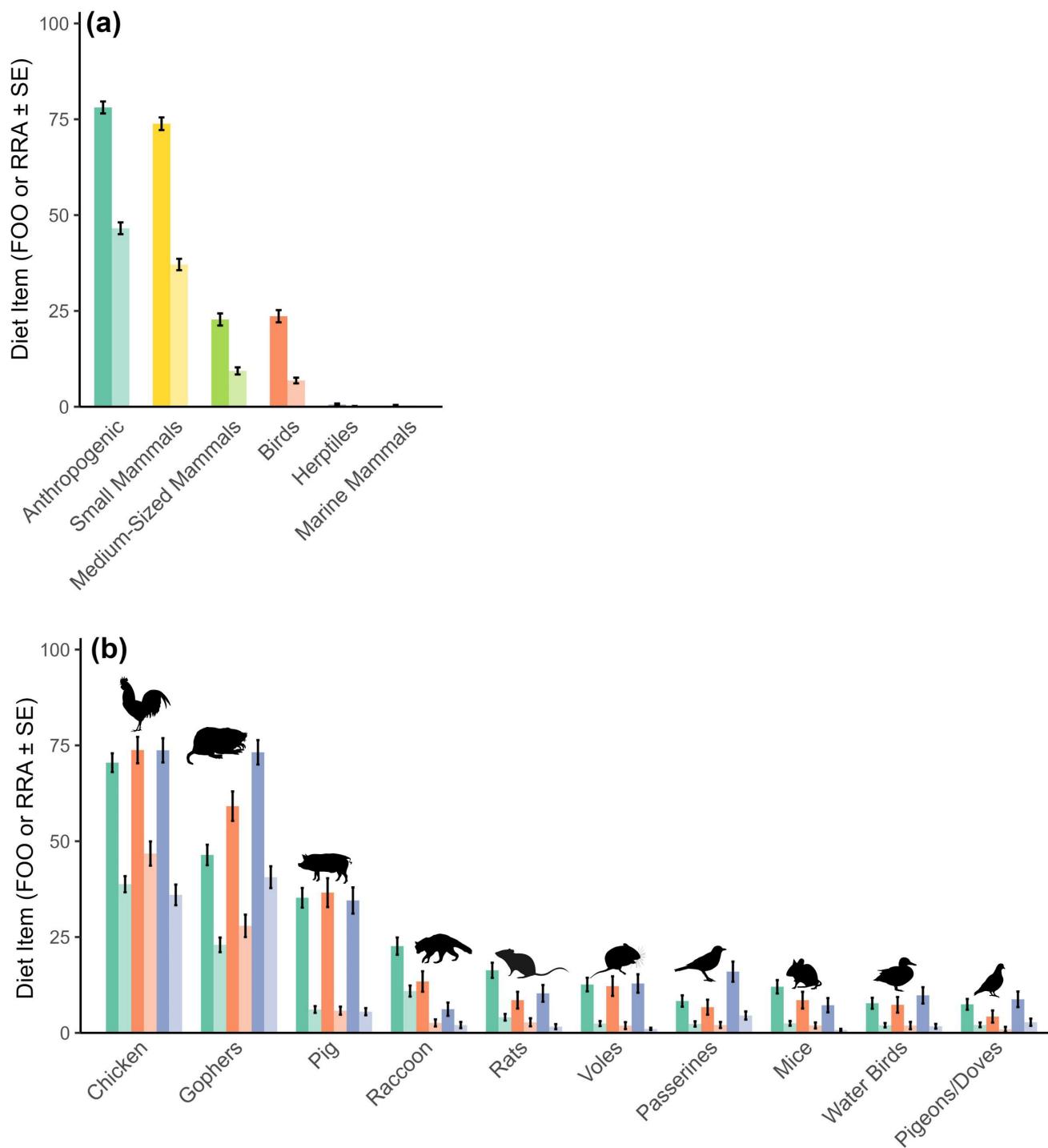
( $\phi = 2.86$ ,  $\beta = 0.03$ ,  $t = 3.94$ ,  $p = 0.003$ ). The RRA and FOO of nuisance rodents in territories were positively correlated with the number of food services in the territory (Figure 3; RRA:  $\phi = 36.7$ ,  $\beta = 0.008$ ,  $z = 4.565$ ,  $p < 0.001$ ; FOO:  $\phi = 2.95$ ,  $\beta = 0.007$ ,  $t = 4.68$ ,  $p = 0.001$ ). Population BIC/TNW was 0.52 ( $p = 0.001$ ), suggesting that 52% of the population niche width could be explained by between-individual variation. All but two coyote family groups had BIC/TNW values lower than the population's (range: 0.25–0.58), and group BIC/TNW values were negatively correlated with impervious surface cover (Figure 4;  $\phi = 21.6$ ,  $\beta = -0.01$ ,  $z = -2.06$ ,  $p = 0.04$ ).

## Individual-level diet

Diet composition was significantly different among family groups (PERMANOVA: RRA  $F = 3.99$ ,  $R^2 = 0.15$ ,  $p < 0.001$ ; FOO  $F = 2.68$ ,  $R^2 = 0.12$ ,  $p < 0.001$ ; Appendix S1: Table S2) and individuals (PERMANOVA: RRA  $F = 1.68$ ,  $R^2 = 0.06$ ,  $p < 0.001$ ; FOO  $F = 1.90$ ,  $R^2 = 0.07$ ,  $p < 0.001$ ; Appendix S1: Table S2). The greatest component of variation was attributed to family group, but individual identity also explained a significant amount of the variation. Together, individual identity nested in family group explained 21% and 19% of the variation in the diet data for RRA and FOO, respectively. Many pairs of individuals had significantly different diet

composition, but only a few pairs of individuals had significantly different dispersion (Appendix S1: Table S2).

Individual-based rarefaction curves indicated high sample coverage (>80%) for 20 of 22 frequently sampled individuals ( $\geq 8$  scats) (Appendix S1: Figure S6, Table S5). PS<sub>i</sub> values for these individuals ranged from 0.38 to 0.83, indicating that individuals differed in their overlap with the population niche (Figure 2b; Appendix S1: Table S5). The representation of food types differed among individuals (data tabs. 5 and 6: <https://doi.org/10.5061/dryad.9s4mw6mqr>); some coyotes had nearly three times the RRA of anthropogenic food as others (Figure 2b). Scats from one coyote, SFCoy17 in Glen Canyon, had only trace amounts of anthropogenic food (RRA = 3.64%  $\pm$  3.3); rather, this individual's scats included a large percentage of reads from striped skunks (*Mephitis mephitis*) (RRA = 41.0%  $\pm$  14.3). Other individuals also consumed unique diet items. For example, pigeons and doves were represented in nearly half of the scats from SFCoy95 at Coit Tower (FOO = 46.2%  $\pm$  13.8; RRA = 15.2%  $\pm$  9.4). Similarly, high read frequencies and proportion of passerines were detected in scats from SFCoy31 at Corona Heights Park (FOO = 36.4%  $\pm$  14.5; RRA = 22.5%  $\pm$  12.1). However, within family groups, species representation was relatively consistent, with individuals from the same family groups overlapping more in ordination space (nMDS) than unrelated individuals (Appendix S1: Figure S4c).

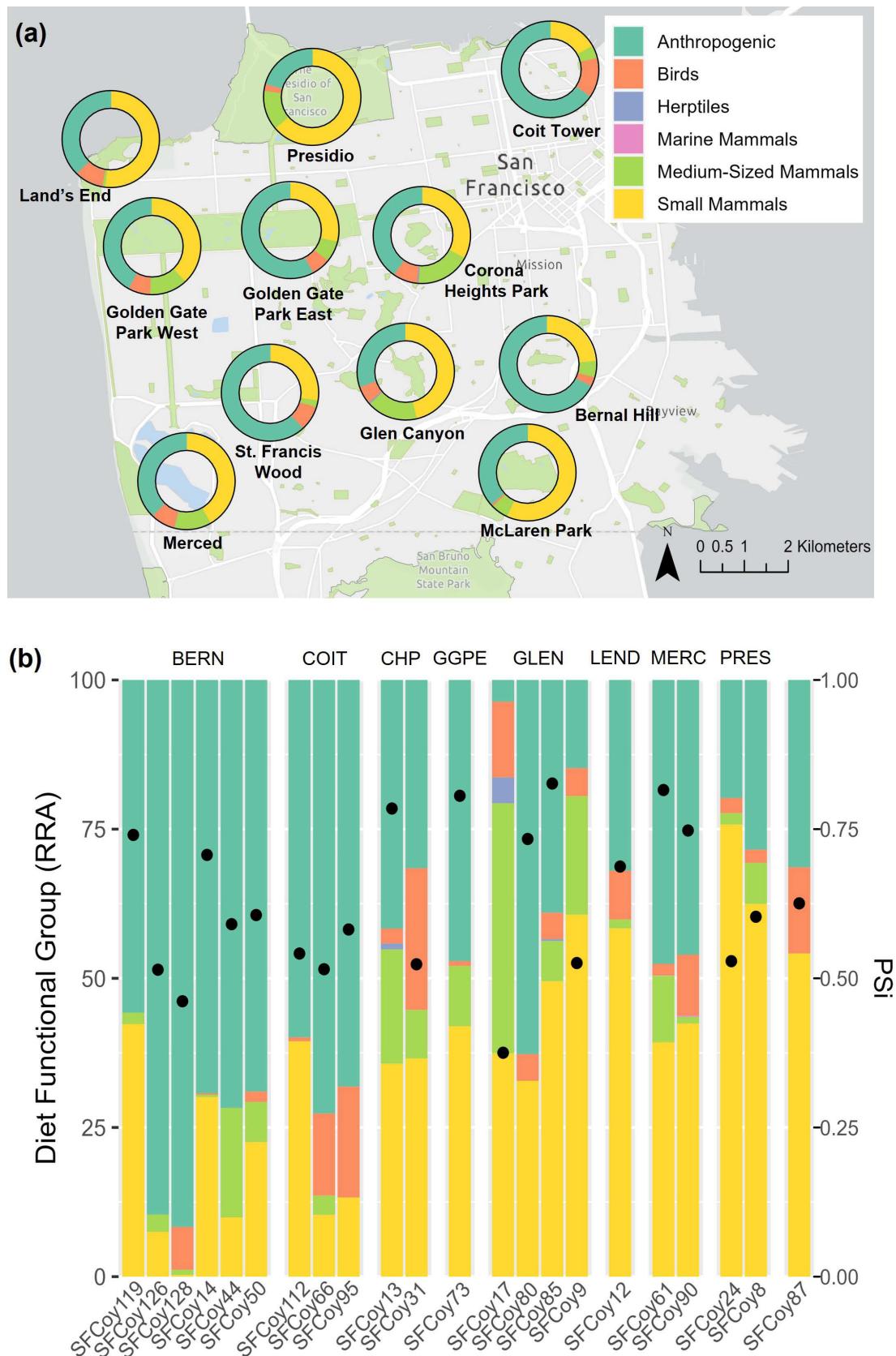


**FIGURE 1** Frequency of occurrence (FOO; darker colors) and relative read abundance (RRA; lighter colors) with SE of diet items across 707 coyote scats collected in San Francisco, California, USA, summarized as (a) dietary functional groups and (b) the 10 prey species most frequently detected by season: Dispersal (July–October), turquoise; mating (November–February), red; and pupping (March–June), purple. Rats (*Rattus rattus*, *R. norvegicus*), all bird species in the order Passeriformes, mice (*Mus musculus* and *Peromyscus sonoriensis*), and water birds (all waterfowl species and *Fulica americana*) represent multiple pooled diet items. All silhouettes were taken from PHYLOPIC and reused under a Creative Commons license.

## DISCUSSION

By leveraging molecular techniques, we revealed variability in coyote diets at family and individual levels. We

demonstrated that individual coyotes in San Francisco had diverse diets corresponding to territories with different environmental conditions. Specifically, anthropogenic food and nuisance rodents in coyote diet varied as a

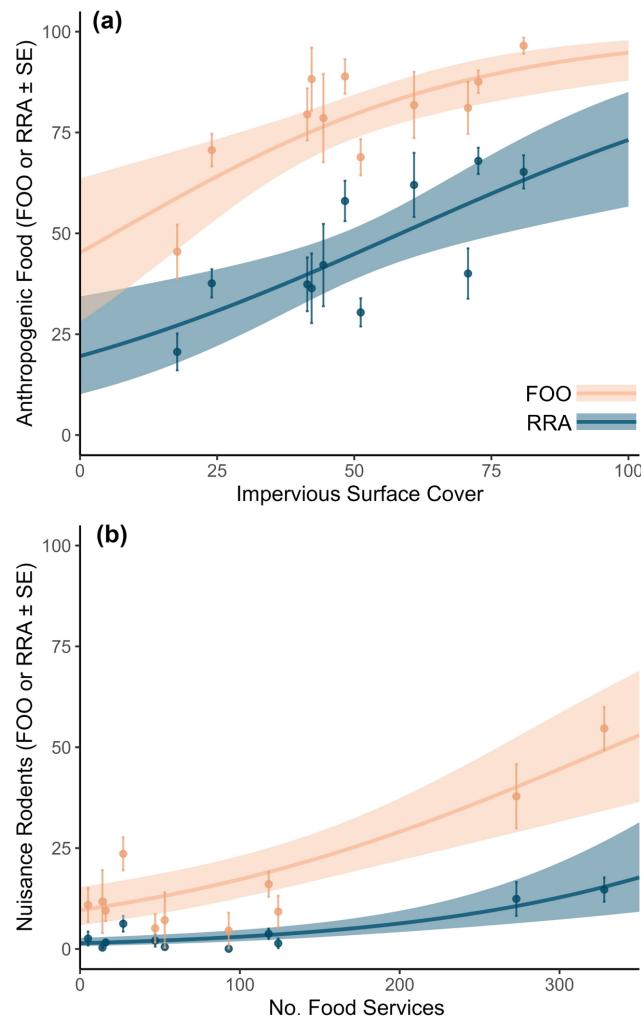


**FIGURE 2** Legend on next page.

function of the impervious surface cover and number of food services in territories, respectively. The greatest dietary differences were between Presidio and Coit Tower, even though a coyote can easily traverse the 3-km distance between them. The Presidio is the largest green space in San Francisco ( $6 \text{ km}^2$ ) and has many native plant communities, sprawling grasslands, and a low percent cover of impervious surfaces. Conversely, Coit Tower is a tourist attraction in the densely populated Telegraph Hill neighborhood and, in part as a result of historical redlining, has less plant cover and lower species richness than formerly greenlined neighborhoods such as the Presidio (Estien, Fidino, et al., 2024; Estien, Wilkinson, et al., 2024). Additionally, the extent to which individual coyotes in the same family groups differed in their diets varied with urbanization, with greater evidence for individual diet specialization among group members living in less urbanized territories and weaker niche differentiation among group members living in more urbanized territories. Accordingly, our results suggest that microgeographic differences in the spatial distribution of resources can have large effects on diet composition and niche partitioning, even in a highly mobile and generalist species.

### Individual variation in resource use is linked to urban landscape heterogeneity

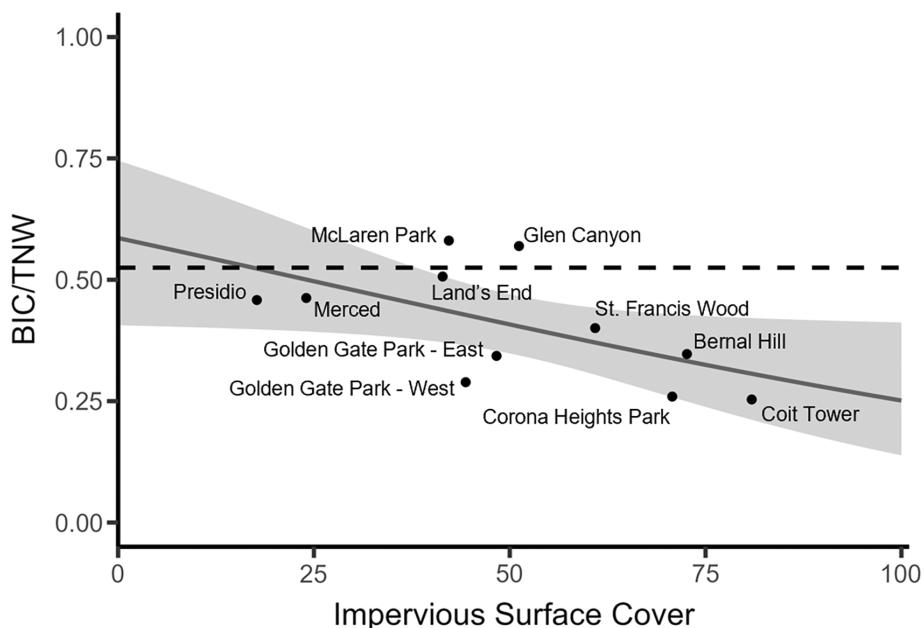
Although intraspecific dietary variation was extensive in the population ( $\text{BIC} > \text{WIC}$ ), coyotes in the same family group had relatively similar diets ( $\text{BIC} < \text{WIC}$ ), particularly in family groups living in the territories with the most impervious surface cover. In these heavily urbanized areas, green spaces are small, fragmented, and landscaped, and novel food resources (i.e., anthropogenic foods and nuisance rodents) are abundant due to litter, restaurants, and intentional feeding of coyotes. Coyote exploitation of human-associated diet items may ameliorate competition for food resources, thereby reducing individual niche differences among group members occupying the same territory. Conversely, in the most naturally vegetated and expansive territories, we found evidence for greater between-individual diet differentiation.



**FIGURE 3** Regression lines and 95% confidence regions (shaded) relating the frequency of occurrence (FOO) and relative read abundance (RRA) with SE in each coyote territory of (a) anthropogenic food versus mean percent impervious surface cover and (b) nuisance rodents versus number of food services. Each dot represents a coyote territory.

With less access to human-provided food, individuals in these territories may experience increased competition for resources, leading to higher levels of specialization. Moreover, ecological opportunity may be greater in natural spaces if they host a greater diversity of natural prey species, thereby allowing individuals to differentiate.

**FIGURE 2** (a) Dietary variation across coyote territories in San Francisco, California, USA. Rings display the average relative read abundance of dietary functional groups in each territory. (b) Dietary variation across 22 frequently sampled coyotes (8–24 samples per individual) from 8 territories and including 1 transient coyote (far right bar) in San Francisco, California, USA. Color blocks represent the average relative read abundance (RRA) of dietary functional groups in each individual. Black dots correspond to the estimated individual proportional similarity index (PSI), a measure of individual dietary specialization that represents the average similarity between each individual's diet and the population's diet. Family groups were Bernal Hill (BERN), Coit Tower (COIT), Corona Heights Park (CHP), Glen Canyon (GLEN), Land's End (LEND), Merced (MERC), and Presidio (PRES).



**FIGURE 4** Regression line and 95% confidence region (shaded) relating the proportion of the total niche width (TNW) explained by between-individual variation (BIC), or BIC/TNW, in each coyote family group to the mean percent impervious surface cover in its territory. The dashed line represents the population-level BIC/TNW (0.52).

The overall effect of urbanization on diet specialization was contingent on the scale of analysis: within family groups, we found evidence that urbanization reduced individual niche differences, but at the city scale, we found strong evidence of individual niche differentiation in the population as a whole. Comparing the strength of group-level and population-level individual niche differences between urban and nonurban environments would be a useful next step to better understand the role of humans in mediating niche specialization.

The observed similarity in diet within family groups could also be reinforced by social learning, as coyotes can acquire novel behaviors learned from family members (Young et al., 2019). Gregariousness and social learning augment the acquisition of novel foods and have been suggested to play a role in the development of individual specialization in vertebrates (Araújo et al., 2011; Estes et al., 2003; Sacks & Neale, 2002). Quantification of the diets of coyotes from birth to breeding-territory establishment (e.g., post-natal dispersal) could help disentangle the relative influence of landscape-driven versus learned dietary preferences, particularly if individuals disperse to areas with environmental conditions divergent from those of their natal habitats.

Although most of the variation in diet was attributed to differences among territories, some individuals in the same family groups had markedly different diets, as evidenced by territories with BIC/TNW values higher than the population mean (e.g., Glen Canyon). For instance, as noted above, one coyote in Glen Canyon

consumed numerous striped skunks. This was unexpected given that several urban coyote diet studies either did not detect skunk (Duncan et al., 2020; Grigione et al., 2011; Morey et al., 2007; Murray et al., 2015; Poessel et al., 2017) or rarely detected skunk (Henger et al., 2022; Larson et al., 2020; Reed et al., 2023; Shedd et al., 2020), despite the abundant availability of skunk carcasses from road mortalities, and that the skunk's noxious spray is a deterrent for coyotes (Schiefelbein & Stankowich, 2016; Walton & Larivière, 1994). We cannot determine whether the skunks were hunted or scavenged. Regardless, the large contribution of specific diet items in individuals' diets, such as skunk in the diet of SFCoy17 ( $PS_i = 0.38$ ;  $n = 11$  scats) and anthropogenic food in the diets of SFCoy128 ( $PS_i = 0.46$ ;  $n = 8$  scats) and SFCoy126 ( $PS_i = 0.51$ ;  $n = 11$  scats), was suggestive of individual dietary specialization and reflected in the low  $PS_i$  values of these individuals relative to more generalized individuals with  $PS_i$  values of  $>0.70$ .

### Land cover and land use impact the consumption of human-associated foods

Much of the dietary variation among territories stemmed from differences in the consumption of chicken, an anthropogenic food obtained from garbage, pet food, and intentional feeding of coyotes. Although the overall detection of anthropogenic foods was high at the population level, we found strong correlations among family

groups between impervious surface cover and the representation of anthropogenic food in scats, consistent with our prediction that land cover is associated with coyote diet. Impervious surface cover was strongly correlated with urban cover and human population density, suggesting that coyote use of anthropogenic foods was, to some extent, promoted by the intensity of urbanization. Coyotes presumably consumed anthropogenic foods in these areas either because natural prey were less available, human food supplementation and wildlife feeding were more abundant, or both. Overall, our results suggest that where coyotes had access to less-developed habitat, their consumption of anthropogenic food decreased, echoing findings from studies on carnivore diets at the wildland-urban interface (Kirby et al., 2016; Manlick & Pauli, 2020; Smith et al., 2018).

Similarly, the number of food services in a territory was strongly correlated with the consumption of nuisance rodents, highlighting that human economic and cultural activities influenced urban coyote diet. Food services attract urban rodents and the number of rat complaints and rat sightings in other US cities are correlated with the number of restaurants (Parsons et al., 2021; Sánchez et al., 2021). Accordingly, as we observed at Coit Tower and Corona Heights Park, where restaurants and rat populations were more abundant, coyotes consumed them more. That variation in urban coyote diet was associated with within-city differences in land cover and land use highlights how foraging strategies and niche variation of urban animals may be linked to human behavior, built infrastructure, and the social systems that regulate resource distribution in cities (Wilkinson et al., 2023).

## Applications to management of human–wildlife interactions

Beyond providing insights on patterns of dietary variation in an urban coyote population, our results are also of wider interest for urban practitioners tasked with mitigating human–wildlife conflict in cities. We demonstrated that not all family groups and individual coyotes exploited human food subsidies to the same degree, with anthropogenic food detections varying from only trace signals to the dominant food group. Moreover, that individual diets were most similar within the family groups occupying the most intensely urbanized areas suggests that urban development might push more individuals toward specializing on human foods by limiting the diversity of individual foraging strategies available. The food conditioning, habituation, and boldness associated with coyote consumption of human foods facilitate conflict with people, which has been steadily rising in

cities over the last decade (Baker & Timm, 2017; Farr et al., 2023; White & Gehrt, 2009). Accordingly, there is a need to quantify the contribution of human food to the diet across cityscapes to locate hotspots of feeding and attractants for further intervention and to predict where conflict is most likely to emerge. Furthermore, given that only a small proportion of individuals in a population tend to come into conflict with people (Swan et al., 2017), individual-level studies are critical to developing a mechanistic understanding of how behaviors that produce conflict develop, particularly in generalist species with high behavioral plasticity. Such individual-level studies provide a strong foundation for coexistence-based management practices such as selective control (e.g., targeted aversive conditioning, translocation, or removal) rather than generalized removal (Swan et al., 2017). To our knowledge, our study is the first to combine metabarcoding and genotyping to study the diet of an urban animal population at the individual level. Molecular methods that permit forensic identification of individuals provide data that explore individuality, and, when coupled with other tools such as behavioral assessments and tracking technologies, provide a strong bedrock of evidence for developing selective management interventions.

## Advantages and disadvantages of DNA metabarcoding in cities

At the population level, we observed a high frequency of anthropogenic food in scats (78%) comparable with another study that used a molecular approach to quantify coyote diet in New York City (64%) (Henger et al., 2022). Estimates from both studies are higher than reported by most previous studies of coyote diet in other cities, which did not use diet metabarcoding (Lukasik & Alexander, 2011; Morey et al., 2007; Peterson et al., 2021; Poessl et al., 2017). In particular, we demonstrated that human-provided foods originating from pet foods, garbage, or intentional feeding of wildlife foods (i.e., chicken, pork, beef, and fish) were a significant component of the coyote diet in San Francisco. Importantly, these diet items would likely have been missed via morphological approaches, suggesting that traditional methods may underestimate the importance of processed foods to the diet of urban animals.

Our molecular approach generated a noninvasively collected and high-resolution dataset, but it was challenging to longitudinally sample most individuals in the population and we did not capture anthropogenic diet items originating from plant-based foods (e.g., corn) or from arthropods (e.g., insects or marine invertebrates). Stable isotope analysis may better capture long-term individual

diets as coyote vibrissae grow over six to eight months and can be subsampled to reflect the dietary patterns of individuals over time (Newsome et al., 2015). Additionally, the tracer  $\delta^{13}\text{C}$  can estimate the contribution of corn-based anthropogenic foods to individual diets (Kirby et al., 2016; Newsome et al., 2015). However, obtaining samples for isotope analyses can be challenging as it requires collecting tissues from live or deceased animals. Furthermore, stable isotope analysis produces low-resolution data that cannot resolve complex food webs; mixing models can only include a few dietary sources, which must be isotopically distinct (Phillips et al., 2014). Isotope mixing models are also heavily influenced by the dietary sources included and the prior selection of their relative contributions (Stock et al., 2018). Diet data from DNA metabarcoding could help minimize uncertainty stemming from underdetermination (having many more sources than isotope tracers) by informing model prior distributions and better constraining dietary estimates (Stock et al., 2018). Overall, DNA metabarcoding and stable isotope analysis offer complementary approaches to diet analysis in urban environments, with each better suited to different research objectives dependent on the desired taxonomic resolution and temporal scale of the study.

Diet metabarcoding in cities also lends itself well to participatory science methods, which are more easily employed in urban areas than in remote ones. Participatory methods can improve data resolution, increase sample size and sampling extent, and validate results (Callaghan et al., 2020; Cooper et al., 2007). For example, although fin whales are rare in San Francisco, we confirmed this detection with iNaturalist ([www.inaturalist.org](http://www.inaturalist.org)), which documents species worldwide through participant reports. We collected the scat containing fin whale DNA in the Merced territory in May 2021. According to iNaturalist reports, a dead fin whale had recently washed ashore (Co, 2021). This observation validates the sensitivity and specificity of diet metabarcoding approaches for fecal DNA and highlights the utility of participatory science data for ground truthing results from studies using environmental DNA.

## CONCLUSIONS

Our study revealed extensive intraspecific variation in coyote diet that was associated predictably with urban landscape heterogeneity (i.e., impervious surface cover and number of restaurants). These results suggest that urbanization may contribute to the diversification of foraging strategies and dietary niches across populations and that patterns of individual variation in resource use

are shaped by human-driven environmental variation. Because intracity behavioral variation has received relatively little attention in urban–wildlife research, these findings warrant expanded urban–wildlife research on individual variation both among and within cities, its causes, and its potential consequences.

## AUTHOR CONTRIBUTIONS

Tal Caspi and Benjamin N. Sacks conceived the ideas. Tal Caspi, Benjamin N. Sacks, and Stevi L. Vanderzwan designed the laboratory methodology. Tal Caspi and Janet Kessler collected the data. Tal Caspi, Monica G. Serrano, and Stevi L. Vanderzwan performed the laboratory research, which was supervised by Benjamin N. Sacks. Tal Caspi led the data curation, analysis, and visualization, which were aided by Benjamin N. Sacks, Monica G. Serrano, and Christopher J. Schell. Tal Caspi led the writing, and all authors discussed, edited, and approved the final version. Tal Caspi, Benjamin N. Sacks, and Christopher J. Schell contributed to funding acquisition.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data, data tables, and code associated with this study (Caspi et al., 2024) are available from Dryad: <https://doi.org/10.5061/dryad.9s4mw6mqr>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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