

Individual variation in anthropogenic resource use in an urban carnivore

Seth D. Newsome · Heidi M. Garbe · Evan C. Wilson ·
Stanley D. Gehrt

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Abstract With increasing urbanization, some animals are adapting to human-dominated systems, offering unique opportunities to study individual adaptation to novel environments. One hypothesis for why some wildlife succeed in urban areas is that they are subsidized with anthropogenic food. Here, we combine individual-level movement patterns with diet composition based on stable isotope analysis to assess the degree to which a rapidly growing population of coyotes (*Canis latrans*) in Chicago consumes anthropogenic resources. We used telemetry to classify coyotes into three groups based on social class and home range composition: (1) residents with home ranges in urban nature preserves; (2) residents with home ranges that had a high proportion of urban land; and (3) transients that had relatively large home ranges and variable use of urban land. We found that natural and anthropogenic resources in this system can be reliably partitioned with carbon isotopes. Mixing models revealed that resident coyotes associated with most urban nature preserves consumed trace to minimal amounts of anthropogenic resources, while coyotes that live in the urban matrix consume moderate (30–50 %) to high (>50 %) proportions of anthropogenic resources. Lastly, we found evidence of prey switching between

natural and anthropogenic resources and a high degree of inter-individual variation in diet among coyotes. In contrast to the expectation that urban adaptation may dampen ecological variation, our results suggest individuality in movement and diet exemplifies the successful establishment of coyotes in urban Chicago. Our study also suggests that direct anthropogenic food subsidization is not a prerequisite for successful adaptation to urban environments.

Keywords Urban ecology · Anthropogenic subsidies · Coyotes · Stable isotopes

Introduction

The rapidly expanding field of urban ecology examines interactions between humans and the organisms that occur in urban landscapes. Such interactions are increasing across the globe since the majority of the planet's human population now live in urban centers, a situation that has no historic precedence (Shochat et al. 2006; Grimm et al. 2008). The urbanization of relatively pristine rural or natural environments may lead to the decline and local extinction of species; however, there are some notable exceptions of species that can quickly adapt to and thrive in urban landscapes. These species offer ecologists and evolutionary biologists a unique opportunity to study how ecology and behavior influences the successful colonization of and adaptation (i.e., synanthropy) to novel anthropomorphic environments (Partecke et al. 2006; Partecke and Gwinner 2007; Moller 2008; Scales et al. 2011; Sih et al. 2012). Identifying which contexts, traits, and mechanisms that determine how successful wildlife populations are (or are not) in urban environments is also important from a conservation and management perspective and could potentially

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S. D. Newsome (✉)
Department of Biology, University of New Mexico, Albuquerque,
NM, USA
e-mail: newsome@unm.edu

H. M. Garbe · S. D. Gehrt
Max McGraw Wildlife Foundation, Dundee, IL, USA

E. C. Wilson · S. D. Gehrt
School of Environment and Natural Resources, The Ohio State
University, Columbus, OH, USA

provide predictions about which species may succeed in human-dominated landscapes and which may be locally extirpated (Moller 2008; Sih et al. 2011).

Wildlife survival and prosperity in urban environments is likely context dependent, even for populations of the same species. Commonalities among species that thrive in urban settings are their highly plastic behavior(s), large geographical ranges, and broad ecological niches (McKinney 2002; Fischer et al. 2012). Urban environments can offer direct biotic and abiotic benefits for animals, including shelter, refuge from predation, water, and food. Biotic benefits such as water and food are often termed anthropogenic subsidies. Previous work has revealed that anthropogenic subsidies may positively or negatively impact urban ecosystems through both direct and indirect pathways. From a population perspective, for example, the direct resource subsidization of urban consumers can lead to a numerical response in their abundance, driven by enhanced fecundity and survival (Prange et al. 2003; Nelson et al. 2007). Other studies have found that anthropogenic food resources may have negative impacts on animal nutrition and health. For example, Heiss et al. (2009) found that crow (*Corvus brachyrhynchos*) nestlings reared in suburban habitats and assumed to consume a higher proportion of anthropogenic foods had lower blood protein and calcium concentrations, indicating a nutritional limitation in comparison to their rural counterparts.

The enhanced availability of resources (food and water) is an often cited but poorly understood mechanism for attracting and sustaining wildlife populations in urban environments (McKinney 2002; Fischer et al. 2012). The degree to which urban mammal populations are directly or indirectly subsidized by human activities has typically been quantified via scat and gut content analysis for species that often serve as model study organisms because of their apparent success in urban environments such as coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and foxes (*Vulpes vulpes*) (Harris 1981; Doncaster et al. 1990; Fedriani et al. 2001; Contesse et al. 2004; Morey et al. 2007). For example, our own diet study of Chicago coyotes (Morey et al. 2007) quantified the frequency of occurrence of food packaging (e.g., plastic and paper) in scats. These traditional approaches are somewhat limited in urban settings, however, because most anthropogenic resources do not produce indigestible fragments that can be easily identified in scats and therefore the proportion of anthropogenic food is likely underestimated. For example, a comparison of scat and stable isotope analysis used to quantify the diets of urban San Joaquin kit foxes showed that anthropogenic food packaging was present in ~12.5 % of the 720 scats analyzed (Newsome et al. 2010), a similar proportion as birds (14.0 %), Coleoptera (13.1 %), and ground squirrels (10.7 %, *Spermophilus beecheyi*). In contrast, stable isotope analysis revealed that none of these

prey types made a large contribution to the diet of urban kit foxes, which had similar isotope values as humans from Bakersfield, suggesting that kit foxes and people consumed the same resources. This study showed that scat analysis is not a robust proxy for studying the diet of mammals living in urban environments, and suggested that isotopic analysis could be utilized in many urban environments because of the low degree of C₄ plant biomass found in many urban areas in North America.

Additionally, it is likely that population diet profiles are heavily influenced by a subset of individuals that are repeatedly sampled to an unknown degree; but see Fedriani and Kohn (2001) that genetically identified scats to individual coyotes. In particular, scats are more likely to come from alpha pairs, whereas other members of the population, such as transients that do not have well-established home ranges, are rarely sampled, if at all. To our knowledge, no study of urban coyotes has discriminated diets between residents and transients, and only one (Fedriani and Kohn 2001) has examined individual diets. Finally, diet studies of urban coyotes have largely examined scats collected from open spaces or natural fragments within the larger urban matrix, but scats are rarely collected from coyotes residing in the urban matrix proper, and thus the diet of these coyotes is unknown.

Coyotes have recently colonized many North American metropolitan areas following a remarkable range expansion (Laliberte and Ripple 2004). In urban environments, coyotes are an intriguing species within the carnivore guild because they often function as an apex predator (Crooks and Soulé 1999) and are capable of killing pets and people (Howell 1982; White and Gehrt 2009), interactions that often elicit strong reactions from the public (Miller et al. 2001). Thus, coyotes are a particularly important species on multiple levels to determine the extent to which anthropogenic resources alter their foraging ecology in urban systems. Using scat analysis, multiple studies of coyotes in various urban areas have consistently reported low prevalence of anthropogenic foods in their diets (Gehrt 2007; Gehrt and Riley 2010). Instead, typical food items like small mammals, lagomorphs, and ungulates are frequently the most common components of the urban coyote diet. This pattern across studies has contributed to a portrait of the coyote as an urban predator that largely avoids human foods (Gehrt and Riley 2010) in contrast to omnivorous mesopredators such as raccoons (Hadidian et al. 2010); however, the methods (scat analysis) commonly used to quantify diet composition likely underestimates anthropogenic resource use.

To better understand the urban ecology of coyotes, we have been continuously monitoring them in the Chicago metropolitan area since 2000 using standard live capture, marking, and radiotelemetry. The Chicago metropolitan area is the third largest in the United States and

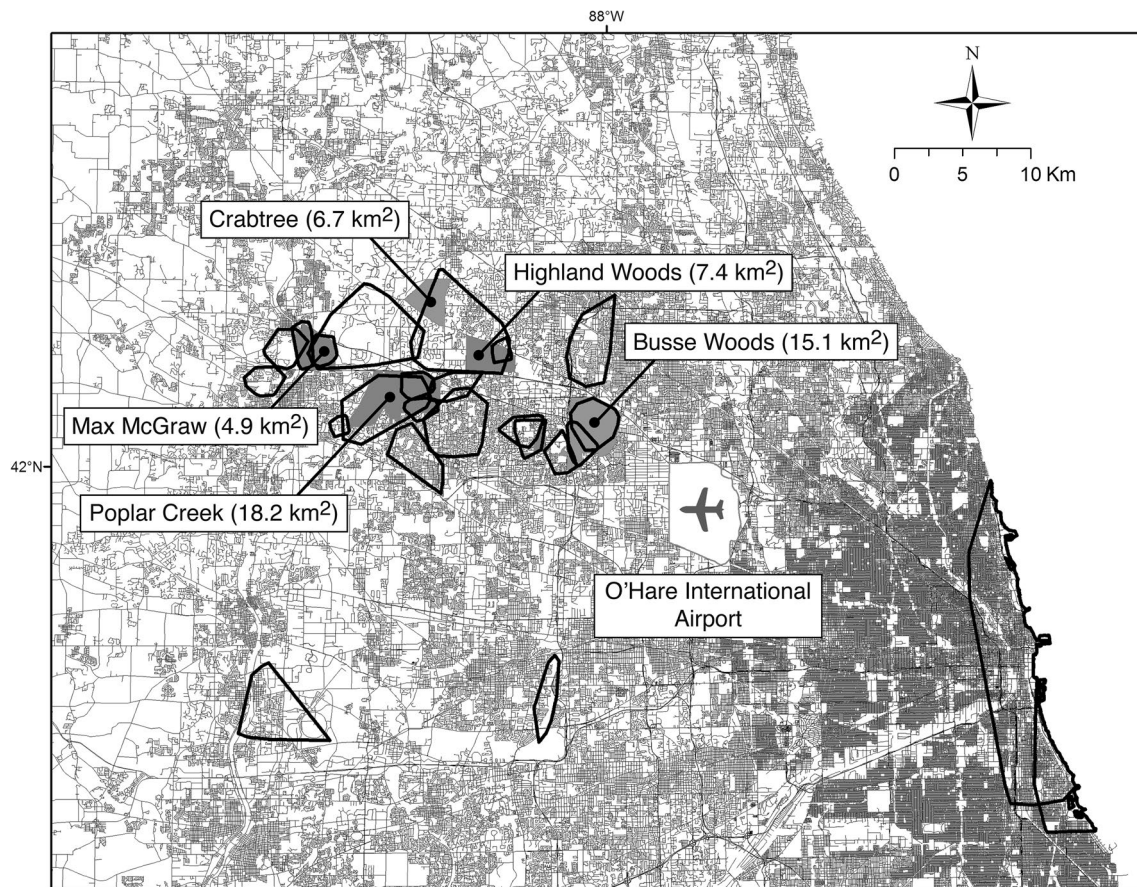


Fig. 1 The study area showing sites where coyotes (*Canis latrans*) and potential prey samples were collected during 2010–2012 from Busse Woods, Crabtree, Max McGraw, Highland Woods, and Pop-

lar Creek urban nature preserves shown as *solid gray polygons*. Area (km^2) of each nature preserve is noted in *parentheses*. *Black polygons* provide examples of individual coyote home ranges

includes >250 cities and >9 million people. The landscape is highly heterogeneous with a patchwork of natural habitat fragments (urban nature preserves; Fig. 1) and varying levels of residential and/or commercial urbanization. Chicago coyotes appear to be very successful in this system, and occur at higher densities, have higher juvenile and adult survival rates, and higher fecundity than reported for rural coyote populations (Gehrt and Riley 2010; Gehrt et al. 2011). However, we know little about how coyote diets vary as a function of habitat type, coyote density, and resource availability in this urban environment.

The recent appearance and apparent success of coyotes in Chicago and other metropolitan areas begs the question: can a large mammalian predator exist in an urban setting without direct subsidization in the form of anthropogenic food? More specifically, does anthropogenic resource use vary predictably between coyotes that largely occupy natural habitat fragments (urban nature preserves) versus the urban matrix typified by dense residential and/or commercial infrastructure? Coyotes are an excellent model organism with which to examine these questions because

they are generalist consumers capable of rapidly switching between prey. Here, we examined dietary variation among individual coyotes across an urbanization gradient from urban nature preserves to the surrounding urban matrix. We predicted that resident coyotes that occur in urban nature preserves largely consume natural prey (e.g., rodents and deer), while matrix coyotes whose home ranges encompass a high percentage of the urban matrix would consume a higher proportion of anthropogenic resources. We predicted that dietary variation would be highest among resident coyotes in urban nature preserves where they have access to a variety of natural prey sources (rodents, lagomorphs, deer) relative to matrix areas where natural prey sources are less abundant, but anthropogenic resources are likely more accessible. We also examined relationships between anthropogenic resource use and (1) coyote home range size, which varies from <1 to >100 km^2 in Chicago, and (2) the percentage of urban land in an individual's home range.

In addition to examining residents, we also examined transient coyotes that were solitary and had larger, more fluid home ranges that overlapped each other or other

residents. Transient individuals are an important but often overlooked component of urban wildlife populations because their behavior and movement patterns are less predictable than residents, and thus are more difficult to study. To our knowledge, no study has presented diet information for transients in urban landscapes. We expected that individual-level dietary variation would be highest in transients that did not have established home ranges, however, we made no predictions as to the degree of anthropogenic resource use by transient coyotes.

Materials and methods

Coyote capture

As part of a long-term research program, coyotes were captured from 2010 to 2013 at various study sites within the Chicago metropolitan area (Fig. 1) using relaxing cable neck restraints and padded MB-650 foothold traps (Minnesota Trapline; Pennock, MN, USA). Trapping was conducted opportunistically during the year except during summer months. Traps were typically checked at 12- to 24-h intervals, depending on location. Captured coyotes were removed from traps, transported to a laboratory, sedated with an intramuscular injection of Telazol (Fort Dodge Animal Health, Fort Dodge, IA, USA), and fitted with a VHF radiocollar (Advanced Telemetry Systems, Isanti, MN, USA) or GPS collar (Lotek, Newmarket, Ontario, Canada). Ear tags were inserted for further means of identification (NASCO Farm & Ranch, Fort Atkinson, WI, USA) and morphometric measurements were taken. A blood sample was collected for genetic and disease analysis and two vibrissa were plucked and stored at room temperature in paper envelopes for stable isotope analysis. Once recovered from immobilization, coyotes were released at the study site where captured. The Ohio State University Institutional Animal Care and Use Committee approved our animal-handling protocol (OSU IACUC #2010A00000113) and we followed trapping guidelines of the American Society of Mammalogists (Sikes et al. 2011). Additional vibrissa samples were collected from marked and unmarked coyotes found dead during the study.

Calculation of home range sizes and percent urban land

We obtained radiolocations for coyotes by visual observations, triangulation with program LOCATE III (Pacer, Truro, Nova Scotia, Canada), or by circling the animal's location with a truck-mounted antenna and recording their location directly with a Global Positioning System (GPS) unit. The latter was possible when coyotes moved into the

urban matrix and the road system allowed us to closely follow animals. We located coyotes weekly during the day and bi-weekly at night; night rounds typically yielded five locations per coyote in a single night, typically 1–2 h apart.

We used the *adehabitatHR* package (Calenge 2006) in the R environment (R Core Team 2014) to estimate annual home ranges using 95 % minimum convex polygons. Annual home ranges were calculated for all radiocollared coyotes with a minimum of 30 locations in a year. For recently radiocollared individuals, we calculated a home range from data collected in the same year as the vibrissa sample. Many radiocollared coyotes were monitored for multiple years, and a vibrissa was collected when these animals were recaptured. For these cases, only location data recorded in the same year as the vibrissa was collected were used to estimate an annual home range for animals captured and sampled after 15 March of that year. For those sampled prior to 15 March, we used data from the previous year to estimate home ranges.

To identify coyotes using different parts of the landscape, we used a land-use type coverage with 28.5-m resolution from 1997 Chicago Wilderness/NASA Landsat Thematic Mapper images for use in ArcView GIS software (Wang and Moskovits 2001). We followed the reclassification scheme in Gehrt et al. (2009) where the original 164 Landsat categories were reclassified into 8 broad land cover types: Residential, Urban Grass, Urban Land, Open, Undeveloped, Water, Natural, and Agriculture; see Gehrt et al. (2009) for detailed descriptions of land use types. However, our interest was specifically focused on contrasting the use of natural habitat fragments and the larger urban matrix. Therefore, following Gehrt et al. (2009), we determined the composite proportion of Residential, Urban Grass, and Urban Land categories within the home range to characterize the extent to which each coyote used the urban matrix as the percentage of home range composed of urban land use.

We classified each coyote with sufficient radiotelemetry data as resident or transient following Gese et al. (1988) and Gehrt et al. (2009). Residents maintained an exclusive territory for >1 season and were associated with other coyotes (visually or via telemetry). Transients were solitary and occupied home ranges that overlapped multiple (>2) resident territories. Territories of residents were exclusive, whereas home ranges of transients overlapped each other and those of residents (Gese et al. 1988). We further partitioned residents into those that (1) resided primarily within contiguous urban nature preserves where home range composed of <50 % urban land use and (2) those that resided primarily in the urban matrix where home range composed of >50 % urban land use. We refer to the latter group as matrix coyotes. Lastly, we separated transients associated with Poplar Creek nature preserve from other transients

because they generally had smaller home ranges that largely remained within the preserve and consequently had a smaller proportion of urban land in their home range in comparison to transients from other areas.

Prey and coyote vibrissae collection

To assess coyote diets, hair tissue from common coyote prey items in the study area were identified and opportunistically collected during 2010–2013. As identified during a previous analysis of scats (Morey et al. 2007), common prey included deer mice (*Peromyscus* spp.), voles (*Microtus* spp.), squirrels (*Sciurus* spp.), rabbits (*Sylvilagus floridanus*), white-tailed deer (*Odocoileus virginiana*), and domestic cats (*Felis catus*). Samples were taken during unrelated mammal surveys or from roadkill animals within or surrounding each study site. Local human residents donated hair samples, which we analyzed for direct comparison to coyote vibrissae isotope values and to estimate the isotopic composition of human foods.

Stable isotope analysis

Prey and human hair samples were rinsed in a 2:1 chloroform:methanol solution to remove surface contaminants and homogenized with surgical scissors. Coyote vibrissae were also cleaned with a 2:1 chloroform:methanol solvent solution to remove surface contaminants and then sub-sampled into 0.2- to 0.3-mg segments using nail clippers; the length of each vibrissa was measured after every third segment was removed. Each vibrissae segment or homogenized hair sample was placed in a 3 × 5 mm tin capsule and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined using a Costech 4010 or CarloErba NC2500 elemental analyzer interfaced with a Finnegan Delta Plus XL mass spectrometer at the University of Wyoming Stable Isotope Facility (Laramie, WY, USA). Isotopic results are expressed as δ values, $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1,000 \times [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}} - 1]$, where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and standard, respectively; the units are expressed as parts per thousand, or per mil (‰). Analytical precision was determined through repeated analysis of internal reference materials calibrated to international standards; within-run standard deviations of these reference materials were ≤ 0.2 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Stable isotope mixing models

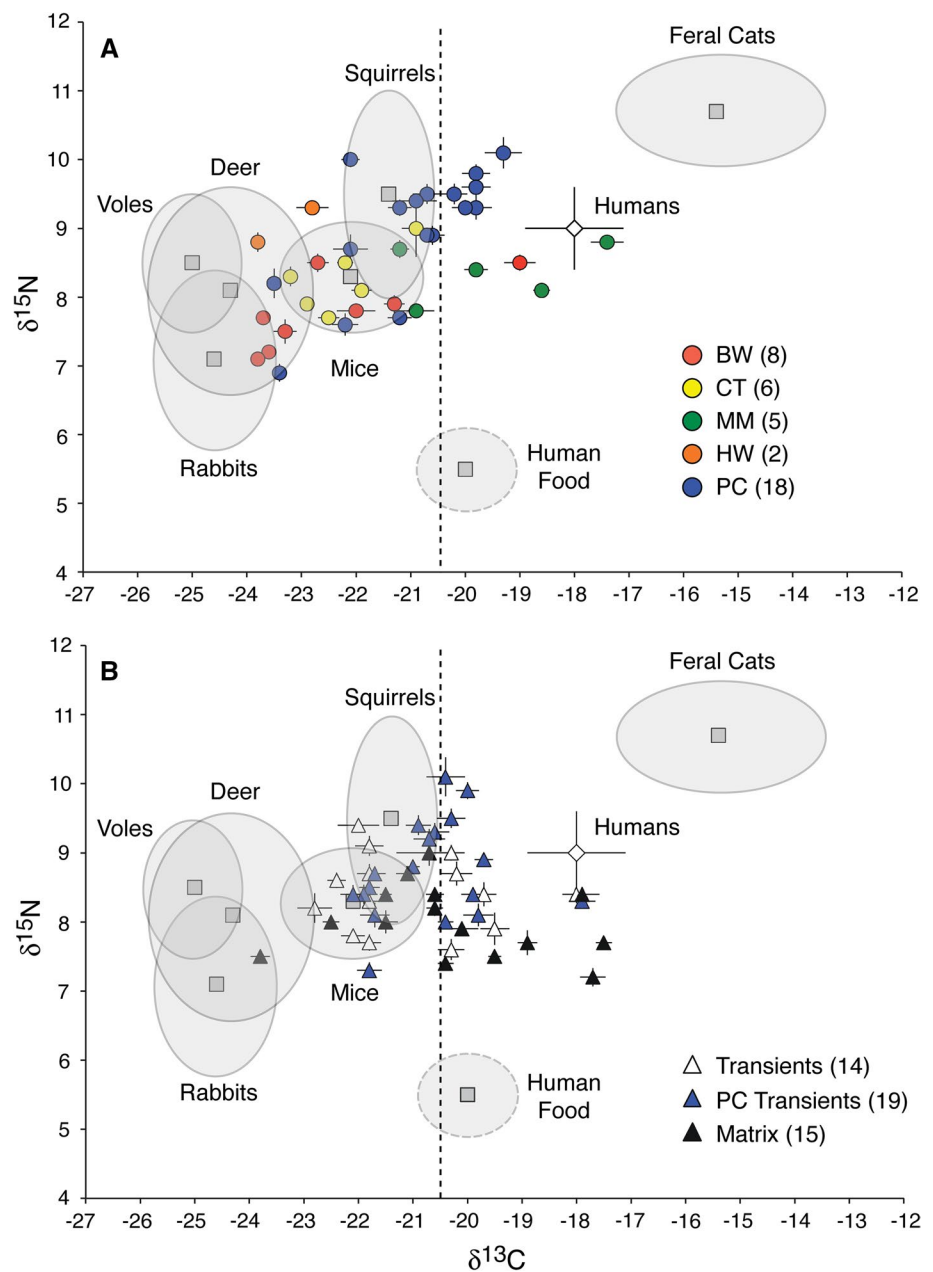
We used the Bayesian-based Stable Isotopes in R (SIAR) mixing model to quantify coyote diet composition (Parnell et al. 2010). Since deer, rabbits and voles had statistically indistinguishable isotope values (see below), we combined

these prey into a single prey source (Phillips et al. 2005). Thus, the seven distinct prey types shown in Fig. 2 were reduced to five prey sources for use in the mixing model, which included three sources of natural prey (squirrels, mice, and deer/rabbits/voles) and two sources of anthropogenic resources (human food and domestic cats).

We found no difference between mean and median source contribution for any prey source that contributed >10 % to an individual's diet. Thus, we report source contributions as means rather than medians. We classified a threshold of ~ 15 % or less as representing trace amounts of anthropogenic resource use because for any prey type input into the mixing model as a potential prey source, the model will always calculate a small contribution (<10 %) of this prey to a consumer's diet. The source distributions of prey that contribute small proportions are always right skewed; i.e., the median of the distribution is typically lower than the mean. Also note that the mean variance ($\pm\text{SD}$) of estimated source contributions for any prey type (anthropogenic or natural) was ± 10 %. Since we combined the mean contribution for human food and domestic cats post hoc to calculate the total anthropogenic resources consumed by each coyote, we conservatively chose 15 % as a threshold for trace amounts of anthropogenic resource use. Using this same logic, we defined minimal and moderate anthropogenic resource use as an estimated contribution of 15–30 and 30–50 %, respectively; >50 % consumption was categorized as high anthropogenic resource use.

We had to account for tissue-specific isotopic discrimination when choosing appropriate trophic discrimination factors (TDFs) for the SIAR mixing model. Typically, trophic discrimination factors (TDFs) represent the isotopic difference between a consumer's tissue (e.g., vibrissae) and that of its diet, which for carbon isotopes is commonly denoted by $\Delta^{13}\text{C}_{\text{tissue-diet}}$. Since coyotes consume but do not assimilate their prey's keratin (hair), we adjusted the $\delta^{13}\text{C}$ TDFs we used in the model. Keratinaceous tissues (hair or vibrissae) typically have higher $\delta^{13}\text{C}$ TDFs than muscle, blood, or liver, because keratins contain a somewhat unique amino acid composition rich in serine and glycine, two non-essential amino acids that have relatively high $\delta^{13}\text{C}$ values relative to other amino acids that are common constituents of animal tissue protein (Hare et al. 1991; Howland et al. 2003; Newsome et al. 2011). For example, $\delta^{13}\text{C}$ TDFs ($\Delta^{13}\text{C}_{\text{tissue-diet}}$) for carnivore keratins are 2–3 ‰ (Hobson et al. 1996; Roth and Hobson 2000; Newsome et al. 2010), but typically range from only 1–2 ‰ for blood, muscle, or liver (Hobson et al. 1996; Caut et al. 2009). Thus, we assumed that the $\delta^{13}\text{C}$ TDF when comparing keratin (vibrissae) of consumer (coyotes) to keratin (hair) of potential prey would be 1 ‰ lower than the TDF for prey tissues (e.g., muscle or liver) that would be assimilated by

Fig. 2 Keratin (vibrissa and hair) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data for coyotes (colored symbols) and potential prey (gray squares); error bars for coyotes represent standard error, ellipses for potential prey represent standard deviation, and sample sizes for coyote groups are shown in parentheses. **a** Includes resident coyotes from Busse Woods (BW), Crabtree (CT), Max McGraw (MM), Highland Woods (HW), and Poplar Creek (PC) urban nature preserves. **b** Includes data for transients and resident matrix coyotes; transients from Poplar Creek (PC) are separated from other transients (see text). Resident matrix coyotes are individuals whose home ranges contained >50 % urban land. Hair isotope values of potential prey have been corrected for trophic discrimination by adding 1.5 and 3.5 ‰ from measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively. Dashed vertical line denotes approximate $\delta^{13}\text{C}$ threshold between consumption of natural versus anthropogenic resources. Measured human hair mean isotope values (white diamond) are shown for comparison; error bars represent standard deviation. Mean isotope values for human food were estimated by subtracting 2.0 and 3.5 ‰ from measured human hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively (color figure online)



coyotes. This logic produced a $\delta^{13}\text{C}$ TDFs of 1.5 ‰ for use in the mixing models. Tissue-specific TDFs have not been reported for $\delta^{15}\text{N}$, thus we used the typical value of 3.5 ‰ for all prey types (Vanderklift and Ponsard 2003; Caut et al. 2009). Lastly, for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDFs, we used an error estimate (SD) of 0.5 ‰ in the mixing models.

The isotopic composition of human food was estimated from human hair using TDFs of 2.0 and 3.5 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Fig. 2). We then applied a $\delta^{13}\text{C}$ TDF ($\Delta^{13}\text{C}_{\text{tissue-diet}}$) of 2.5 ‰ for this prey source in the mixing model, which is typical of mammalian carnivore keratins (Roth and Hobson 2000; Newsome et al. 2010; Tyrrell et al. 2013).

Statistical analysis

All statistical analyses were performed with the program JMP (v.7.0; SAS Institute). We used a one-way analysis of variance (ANOVA) with a post hoc Tukey–Kramer HSD test to assess differences in isotope values among prey sources; for post hoc pairwise comparisons significance was assigned at a P value of <0.01. We used variance components analysis performed in JMP (v.10.0.2; SAS Institute) to quantify the within- and between-individual components of dietary variation for resident and transient coyotes from Poplar Creek, where we had large sample sizes.

Results

Coyote capture

Our study included data from 88 individual coyotes, including 41 females and 47 males. Coyotes ranged in age from 1 to 11 years of age. We analyzed vibrissae from all 88 individuals and estimated home range size and percent of urban land in home range (see below) for 70 (80 %) of these coyotes. Of the 88 individuals, 54 were categorized as residents and 34 were transients. Of the 54 residents, 15 coyotes were considered matrix animals whose home ranges contained a relatively high percentage (mean \pm SD = 75 ± 21 %) of urban land relative to coyotes from urban nature preserves.

Potential prey and human stable isotope values

Isotope values of particular prey (e.g., deer or squirrels) collected from different nature preserves were similar so we used samples collected from all sites when calculating mean isotope values and associated variance (SD) of potential prey types. We found significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among potential prey sources available to coyotes (Fig. 2). For $\delta^{13}\text{C}$ ($F_{6,162} = 240.0$, $P < 0.0001$), domestic cats (-16.9 ± 1.9 ‰, $n = 22$) had higher mean (\pm SD) values than all other prey sources. Squirrels (-22.9 ± 0.8 ‰, $n = 25$) and deer mice (-23.6 ± 1.4 ‰, $n = 17$) had similar $\delta^{13}\text{C}$ values, but these two prey sources had higher mean values than other natural prey. Deer (-25.8 ± 1.4 ‰, $n = 31$), voles (-26.5 ± 0.9 ‰, $n = 19$), and rabbits (-26.1 ± 1.1 ‰, $n = 11$) had similar mean $\delta^{13}\text{C}$ values. Lastly, humans (-22.9 ± 0.8 ‰, $n = 37$) had higher mean $\delta^{13}\text{C}$ values than natural prey sources but significantly lower values than domestic cats. For $\delta^{15}\text{N}$ ($F_{6,162} = 70.4$, $P < 0.0001$), domestic cats (7.2 ± 0.8 ‰, $n = 22$) had higher mean (\pm SD) values than all other prey sources. Squirrels (6.0 ± 1.5 ‰, $n = 25$) had higher mean $\delta^{15}\text{N}$ values than other natural prey except voles (5.0 ± 1.0 ‰, $n = 19$). Voles had similar mean $\delta^{15}\text{N}$ values as deer mice (4.8 ± 0.8 ‰, $n = 17$) and deer (4.6 ± 1.5 ‰, $n = 31$), but significantly higher mean values than rabbits (3.6 ± 1.3 ‰, $n = 11$). Deer mice, deer, and rabbits had similar mean $\delta^{15}\text{N}$ values. Lastly, humans (8.9 ± 0.6 ‰, $n = 37$) had higher mean $\delta^{15}\text{N}$ values than potential prey available to coyotes.

Coyote stable isotope values, home range size, and percent urban land in home range

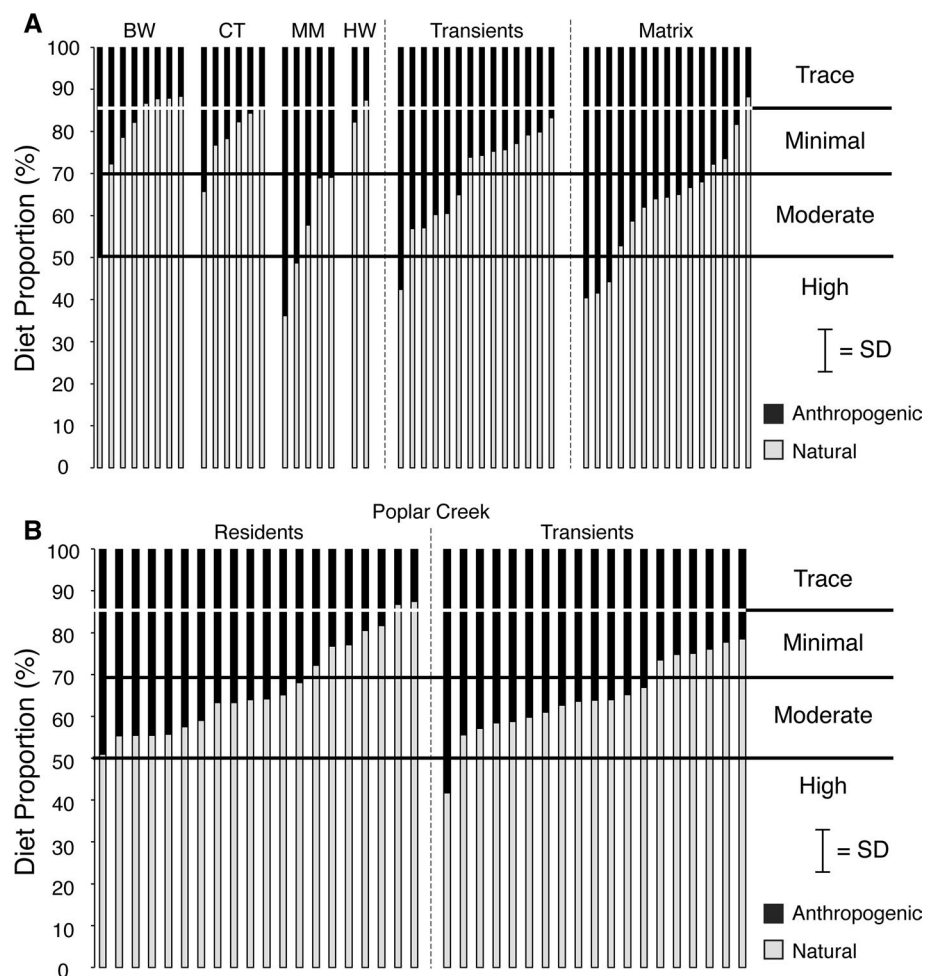
Individual coyotes occupied a large proportion of the $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ isotopic prey space defined by the isotope values of potential prey (Fig. 2). We chose a threshold $\delta^{13}\text{C}$ value of -20.5 ‰ to differentiate natural from

anthropogenic resources (dashed vertical line in Fig. 2) defined by the standard deviation of the natural prey source with the highest mean $\delta^{13}\text{C}$ value (squirrels). We estimated the isotope values of human food by subtracting 2.0 and 3.5 ‰ from measured human hair isotope values, which yielded mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of -20 ± 0.9 and 5.5 ± 0.6 ‰ for this potential food source (Fig. 2). The mean $\delta^{13}\text{C}$ value and associated variance (\pm SD) of human food overlapped slightly with our anthropogenic-natural threshold $\delta^{13}\text{C}$ value (-20.5 ‰), but the estimated mean $\delta^{15}\text{N}$ value for human food was lower than nearly all other natural or anthropogenic sources of prey, except rabbits that had significantly lower $\delta^{13}\text{C}$ values (see above). Thus, human foods have a unique isotope value relative to other sources of prey available to coyotes in Chicago.

The degree of variation in mean $\delta^{13}\text{C}$ values was similar but large among nature preserve resident and transient coyotes; mean $\delta^{13}\text{C}$ values ranged from -24 to -17 ‰ among individuals (Fig. 2). The degree of variation in mean $\delta^{15}\text{N}$ values was also similar among nature preserve residents and transients, and ranged from 7 to 10 ‰. Most resident coyotes (~ 75 %) from urban nature preserves had relatively low $\delta^{13}\text{C}$ values indicating they primarily consumed natural prey; however, there were several residents from Poplar Creek ($n = 6$), Max McGraw ($n = 3$), and Busse Woods ($n = 1$) that had mean $\delta^{13}\text{C}$ values higher than the anthropogenic threshold of -20.5 ‰ (Fig. 2a). In contrast, approximately half of the transient coyotes we analyzed had mean $\delta^{13}\text{C}$ values that were higher than the -20.5 ‰ threshold (Fig. 2b). Matrix coyotes also had a high degree of variation in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among individuals, and a large proportion (>50 %) of the individuals we analyzed had high mean $\delta^{13}\text{C}$ values greater than -20.5 ‰ indicative of anthropogenic resource use. Variance component analysis of (resident and transient) coyotes from Poplar Creek, where we had adequate sample sizes ($n = 39$, 563 vibrissae segments), shows that the within-individual component (WIC) of variance accounts for 41 % (0.85/2.09) and 33 % (0.29/0.88) of the total isotopic variance (or total isotopic niche width, TINW) in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively. Further, the ratio of WIC to TINW was lower among residents ($\delta^{13}\text{C}$: 36 % or 0.82/2.29; $\delta^{15}\text{N}$: 29 % or 0.30/1.03) in comparison to transients ($\delta^{13}\text{C}$: 47 % or 0.89/1.89; $\delta^{15}\text{N}$: 38 % or 0.28/0.73) at Poplar Creek.

Results of Bayesian mixing models indicated, with a few exceptions, resident coyotes from Busse Woods, Crabtree, and Highland Woods urban nature preserves consumed trace to minimal amounts of anthropogenic resources and instead focused on natural prey (Fig. 3). The mean (\pm SD) proportion of anthropogenic resources in the diets of residents ($n = 16$) from these urban nature preserves was 20 ± 10 ‰. Resident coyotes from Max McGraw (Fig. 3a) and Poplar Creek (Fig. 3b) consumed a higher proportion of

Fig. 3 Stable isotope mixing model results for individual coyotes *gray bars* represent mean proportion of natural prey, *black bars* represent mean proportion of anthropogenic resources. **a** Includes results for residents from Busse Woods (BW), Crabtree (CT), Max McGraw (MM), and Highland Woods (HW) urban nature preserves, as well as transient and matrix coyotes. **b** Shows data for residents and transients associated with Poplar Creek nature preserve. *Horizontal bars* represent index of anthropogenic resource use; see text for an explanation of how thresholds were determined. Magnitude of mean error (SD) of (natural or anthropogenic) resource proportions is shown and is equivalent to $\pm 10\%$



anthropogenic resources than their counterparts from Busse Woods, Crabtree, and Highland Woods. The mean (\pm SD) proportion of anthropogenic resources in the diets of residents from Max McGraw ($n = 5$) and Poplar Creek ($n = 18$) was $36 \pm 12\%$. The mean (\pm SD) proportion of anthropogenic resources in the diets of transients ($n = 33$) was $33 \pm 10\%$. Lastly, the mean (\pm SD) proportion of anthropogenic resources in the diets of matrix coyotes ($n = 15$) was $37 \pm 14\%$. More interesting than mean proportions is the degree of variation observed among individuals that live in similar habitats and have similar movement patterns. For example, anthropogenic resource use varied from 18 to 60 % among matrix coyotes that had a high mean (\pm SD) proportion ($75 \pm 21\%$) of urban land in their home range.

In general, resident coyotes had small home ranges ($<10 \text{ km}^2$) in comparison to transients; resident coyotes from Crabtree are the only exception to this pattern (Fig. 4a). Despite having small home ranges, some residents had a high percentage of urban land in their home range. In contrast, the percentage of urban land in home range significantly increased with home range size in transient coyotes ($y = 0.63x + 10.3$, $R^2 = 0.43$ ($F_{1,22} = 14.9$, $P = 0.001$);

this pattern was more robust when only examining Poplar Creek transients ($y = 0.65x + 8.8$, $R^2 = 0.85$ ($F_{1,16} = 79.1$, $P < 0.0001$). Lastly, there was no clear pattern between home range size and the percentage of urban land in home range for matrix coyotes, which had a high mean percentage ($>75\%$, range 35–100 %) of urban land in their home range.

When pooling across all (matrix and nature preserve) resident and transient coyotes we found no relationship between mean vibrissa $\delta^{13}\text{C}$ value and home range size (Fig. 4b), or the percentage of urban land in home range (Fig. 4c). Most matrix coyotes had a high proportion of urban land in their home range (Fig. 4c), but had a wide range of home range sizes from <1 to $\sim 140 \text{ km}^2$ (Fig. 4b). While residents generally had smaller home ranges than transients (Fig. 4a, b), we found that mean vibrissae $\delta^{13}\text{C}$ values varied widely by as much as 5–6 ‰ in both groups.

Discussion

Our use of stable isotopes, combined with radiotelemetry, allowed us to elucidate patterns of diet across the

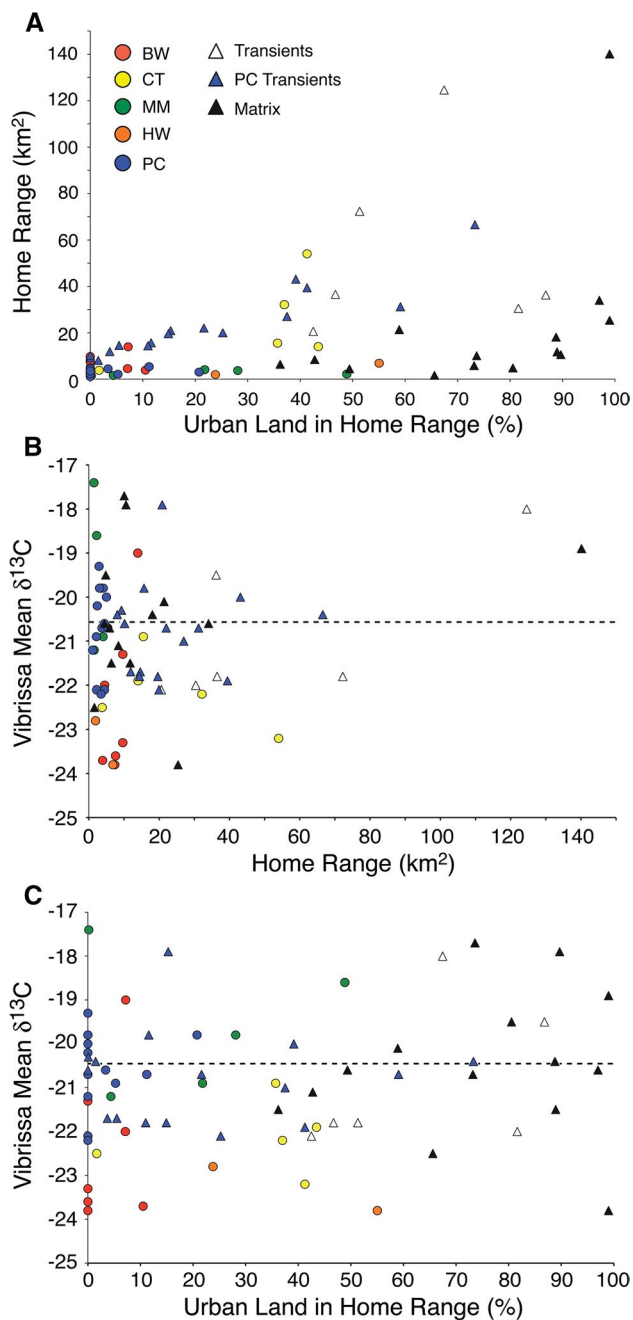


Fig. 4 **a** Relationship between coyote home range size (km²) and percent of urban land in each home range; see Fig. 1 for sample sizes of coyote groups. Resident coyotes from Busse Woods (BW), Crabtree (CT), Max McGraw (MM), Highland Woods (HW), and Poplar Creek (PC) are represented as circles; transient and matrix coyotes are represented as triangles. Home range sizes of coyotes that occur in highly urbanized areas are typically larger than those that use natural habitat fragments, but note high degree of individual variation. Relationship between vibrissa mean $\delta^{13}\text{C}$ (\pm SD) value and home range size (**b**) and percent urban land (**c**) in each home range; legend in (**a**) applies to other panels. Dashed horizontal lines in (**b**) and (**c**) denotes approximate threshold between consumption of natural versus anthropogenic resources; see Fig. 2 (color figure online)

metropolitan coyote population with a greater resolution than has previously been described for this species. Although natural prey items dominated most diets, considerable individual variation in diet, particularly use of anthropogenic foods, occurred across the landscape and within nature preserves. In general, our results suggest a higher prevalence of anthropogenic foods in the diet of urban coyotes than reported by previous studies using scat analysis, particularly for those coyotes living within the urban matrix. Overall, our results reveal a complex pattern of resource use among coyotes in the Chicago metropolitan area, manifested through individual variation, that may partially explain the apparent success of this species in heavily developed landscapes.

Discriminating between natural and anthropogenic resources with stable isotope analysis

An important aspect of our study is the reliable discrimination of anthropogenic and natural resources consumed by coyotes, and analyses of isotope data for potential food sources in the Chicago area showed that anthropogenic resources could be distinguished from natural prey items with stable isotopes (Fig. 2). Even after application of suitable trophic discrimination factors to estimate the isotopic composition of human foods from that of human hair, the distribution of natural versus anthropogenic resources in $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ bivariate space suggests that isotope analysis is a reliable proxy for assessing the relative consumption of anthropogenic versus natural prey by Chicago coyotes. Specifically, the low $\delta^{13}\text{C}$ values for natural prey relative to domestic cats and human foods shows that primary productivity at urban nature preserves is dominated by plants that use the C₃ photosynthetic pathway, characterized by $\delta^{13}\text{C}$ values that range from -28 to -22 ‰ (Farquhar et al. 1989). In contrast, many commercially produced foods consumed by humans and their pets in North America have conspicuously high $\delta^{13}\text{C}$ values because they contain corn (*Zea mays*) or its industrial derivative corn syrup (Jahren and Kraft 2008); livestock reared for human consumption in North America are also commonly fed corn during the later stages of maturation prior to slaughter. Corn utilizes the C₄ photosynthetic pathway that produces $\delta^{13}\text{C}$ values ranging from -12 to -14 ‰ (Farquhar et al. 1989). Our results are similar to those reported for resources available to San Joaquin kit foxes in California (Newsome et al. 2010), despite regional differences in the abundance of C₄ plants between the Midwest and California (Teeri and Stowe 1976). Thus, we anticipate that isotope analysis can be used to examine anthropogenic resource use in wildlife from other metropolitan areas throughout North America (Lavin et al. 2003; Newsome et al. 2010).

The estimated mean nitrogen isotope ($\delta^{15}\text{N}$) value of human food is lower than nearly all of the natural prey items available to coyotes in Chicago, with the exception of rabbits (*Sylvilagus floridanus*). This pattern is also similar to that found in Bakersfield, California, where the estimated $\delta^{15}\text{N}$ value of human food was lower than natural prey available to San Joaquin kit foxes (Newsome et al. 2010). Lastly, humans from Chicago and Bakersfield have statistically indistinguishable hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and the isotopic variation (SD) among humans from both areas was lower than that observed in most natural prey items. The similarity in mean isotope values between humans in California and the Midwest, coupled with the low degree of isotopic variance among them in comparison to natural consumers in both locations, is likely a product of the commercial corn-based diet consumed by people in the United States (Jahren and Kraft 2008).

Anthropogenic resource use in Chicago coyotes

To what extent does use of anthropogenic foods relate to population density and space use by a mammalian carnivore in an urban landscape? It has been hypothesized that one of the primary reasons why some wildlife species increase in abundance and reduce their space use in urban environments is because they benefit from (direct) biotic subsidies in the form of anthropogenic resources (food and/or water) that are predictable and easy to procure relative to natural prey (McKinney 2002). Unfortunately, few studies have directly addressed this hypothesis for mammalian carnivores, likely because of the focus on sampling only near edges of urban landscapes (e.g., Fedriani and Kohn 2001) or limitations of traditional methods used to quantify animal diet composition, especially in quantifying anthropogenic resource use at the individual level; an exception is Fedriani and Kohn (2001) who used genetic analysis to assess the individual identity of scat samples.

For mammalian carnivores, especially canids, an indirect proxy for resource availability is home range size (Gittleman and Harvey 1982), and previous work has found that urban canids often have smaller home ranges than their rural counterparts (Cavillini 1996; Goszczynski 2002; Riley et al. 2003; Atwood et al. 2004). Our previous work in Chicago (Gehrt et al. 2011) and data for the coyotes examined here supports this pattern, as home ranges for resident coyotes in Chicago are generally much smaller than rural populations. Within the Chicago landscape, however, there is a reverse trend in which the home range size of resident coyotes in nature preserves is smaller than those of coyotes that reside within more heavily developed urban areas (Gehrt et al. 2009, 2011). We also found that, for transient coyotes, home range size was positively correlated with the proportion of urban land in home ranges

(Fig. 4a; Gehrt et al. 2009). Likewise, apparent densities followed this trend, with the highest coyote densities occurring in the nature preserves with the smallest home range sizes (Gehrt et al. 2011), which is similar to observations of coyotes from another urban system (Fedriani et al. 2001). In contrast to theory, our results revealed use of anthropogenic foods by coyotes was not related to a reduction in home range size, and increase in local density, for residents or transients. Within the urban nature preserves, where coyote home ranges were smallest and densities highest, use of anthropogenic foods was highly variable, but overall lower than diets of coyotes elsewhere. The relatively low levels of anthropogenic foods in the diets of residents of these natural areas does not appear to be related to availability, but rather to the availability of natural foods and a resistance to the use of human foods. Nearly all the urban nature preserves in our study area are open to the public, and annual human visitation in some popular preserves is high. For example, human visitation at Poplar Creek and Busse Woods each exceeds 1 million people per year (Gehrt et al. 2009) and contain large numbers of open garbage cans easily accessible by coyotes and other mammalian carnivores (Gehrt 2004; Prange et al. 2003). Thus, human activities in urban nature preserves produce an abundant and predictable source of anthropogenic resources, yet most resident coyotes largely avoid these resources. Small home range sizes within urban nature preserves are likely the result of a combination of the presence of abundant natural resources and coyote avoidance of human development outside of nature preserves (Gehrt et al. 2009).

Interestingly, we found differences in the degree of natural versus anthropogenic resource use among resident coyotes sourced from different preserves. Use of anthropogenic foods was most pronounced at Poplar Creek and Max McGraw, where approximately half the residents at each site consumed moderate proportions (30–50 %) of anthropogenic resources (Fig. 3), but had small home ranges (<10 km²) containing a small percentage (<20 %) of urban land. These individuals also had higher intra-individual (i.e., within-vibrissa) $\delta^{13}\text{C}$ variance (Newsome et al., unpublished), suggesting that they were switching between natural and anthropogenic prey. Most residents from Busse Woods, Crabtree, and Highland Woods consumed trace to minimal amounts of anthropogenic resources and instead relied heavily on natural prey (Figs. 2a, 3a). Many of these residents also had small home ranges (<15 km²), but the proportion of urban land in some individual's home ranges ranged from 25 to 55 % (Fig. 4a). For example, three of the five resident coyotes from Crabtree for which we had telemetry data had a high proportion of urban land in their home range (36–44 %), but had mean $\delta^{13}\text{C}$ values less than −22 ‰ indicating they primarily consumed natural prey

(Fig. 4b, c). Despite the high proportion of urban land in their home range and access to anthropogenic resources, the coyotes from these urban nature preserves appear to be selecting for natural prey that is likely more abundant in preserves relative to urban matrix habitat.

While patterns of anthropogenic resource use do not explain coyote use of urban nature preserves, diet switching from natural prey to human foods may be important for coyotes to reside within developed landscapes with minimal natural habitat. Few, if any, studies have reported on diets of coyotes that reside in heavily developed landscapes or the core of urban areas, therefore it was unknown whether coyotes from these areas maintain the same resistance to anthropogenic foods that is evident in most individuals sourced from nature preserves. The relatively larger home ranges of matrix coyotes suggests that resources are more limited or widely dispersed in the matrix compared to nature preserves, but matrix coyotes exhibit the same pattern of habitat selection as coyotes that reside in preserves (Gehrt et al. 2009, 2011), with strong selection for whatever natural habitat patches are available within their home ranges, which suggests that they are also exhibiting the same food habits. However, our result that anthropogenic resource use in transient and matrix coyotes was generally higher than observed in residents from urban nature preserves (Fig. 3) suggests that use of anthropogenic foods may allow coyotes to occupy landscapes with reduced availability of natural foods.

Although we documented a general trend for higher anthropogenic resource use for matrix residents than for coyotes residing in nature preserves, there was individual variation among matrix coyotes, indicating that not all coyotes were using the same pathways to exploit developed areas. A few matrix coyotes had a high percentage (30–90 %) of urban land in their home range, but had mean $\delta^{13}\text{C}$ values less than -21‰ indicative of minimal consumption of anthropogenic resources, and diets similar to coyotes in nature preserves. Thus, these matrix coyotes specialized on natural prey even though they likely have easy access to anthropogenic resources.

As with coyotes residing exclusively within the urban matrix, diets of transient coyotes within urban areas are virtually unknown. Although there was a trend for larger home ranges containing a higher percentage of urban land (Fig. 4a), anthropogenic resource use varied widely among transient coyotes. For example, four of six transient coyotes that had between 40 and 90 % of urban land in their home range consumed minimal proportions of anthropogenic resources (Figs. 3, 4c). These individuals appear to be selecting for natural prey even though they likely have ample access to anthropogenic resources. In contrast, most of the Poplar Creek transient coyotes that moved outside the nature preserve had mean $\delta^{13}\text{C}$ values indicating moderate use of anthropogenic resources. Transients

likely move between urban nature preserves and the urban matrix to consume a mixture of natural and anthropogenic resources. Similar to their resident counterparts, most of the Poplar Creek transients that plot near the $\delta^{13}\text{C}$ threshold (-20.5‰) separating natural from anthropogenic resources also had high intra-vibrissae $\delta^{13}\text{C}$ variation (Newsome et al., unpublished) suggesting that they switch between these two general types of resources.

Evidence of individual diet specialization in Chicago coyotes

Individual diet specialization has been observed in a wide range of consumers; see reviews by Bolnick et al. (2003) and Araújo et al. (2011). Intraspecific competition for resources is a principal mechanism for promoting and maintaining individuality in diet (Svanbäck and Persson 2004; Svanbäck and Bolnick 2007; Tinker et al. 2008; Bolnick et al. 2010; Newsome et al. 2015). In Chicago nature preserves, coyote densities are exceptionally high (5–10 coyotes/km²) relative to densities of other rural and urban coyote populations (Gehrt et al. 2011), a condition that could possibly lead to greater intraspecific competition and individual diet specialization. Coyote population size in urban nature preserves has steadily increased over the past decade, and telemetry data show that the home range size of resident coyotes in some urban nature preserves such as Poplar Creek has decreased (Gehrt et al., unpublished). Given that home range sizes for many resident coyotes in urban nature preserves are exceptionally small ($<3\text{ km}^2$), but fecundity, survival, and densities are high, it seems that preserves are exceptionally productive habitat for coyotes. Unfortunately, we have little information on how resource availability varies in Chicago's nature preserves, so we cannot assess at this time if coyote densities are approaching carrying capacity when intraspecific competition promotes individual diet specialization.

Although there is little evidence that coyote populations in urban nature preserves are approaching carrying capacity, we did find some evidence for individual diet specialization. We were surprised to find that mean vibrissa isotope values of resident coyotes within a single urban nature preserve were highly variable ($\delta^{13}\text{C}$ range: 6–7 ‰; $\delta^{15}\text{N}$ range: 3–4 ‰; Fig. 2a), but intra-individual variation was generally low ($\text{SD} \leq 1\text{‰}$), suggesting that individual coyotes maintain different diets for multiple months. For example, the degree of isotopic variation among individual coyotes from Poplar Creek is similar to that observed among coyotes from all other urban nature preserves (Fig. 2a). Variance component analysis of (resident and transient) coyotes from Poplar Creek shows that the WIC of variance accounts for 41 % and 33 % of the total variance in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively. Further, the ratio of the WIC to total isotopic variance (total isotopic niche width

or TINW) was lower among Poplar Creek residents ($\delta^{13}\text{C}$: 36 ‰; $\delta^{15}\text{N}$: 29 ‰) in comparison to transients ($\delta^{13}\text{C}$: 47 ‰; $\delta^{15}\text{N}$: 38 ‰). The WIC/TINW ratio of ~33 ‰ for Poplar Creek residents is similar to those observed in sea otter populations known to exhibit a high degree of individual diet specialization (Newsome et al. 2009, Newsome et al. 2015). At this time, we can only hypothesize that the evidence of individuality is driven by intraspecific competition at Poplar Creek, where coyote densities are extremely high and individual home range sizes have steadily decreased over time. Ongoing work at this and other urban nature preserves to quantify resource availability will further explore individual diet specialization in Chicago coyotes.

A current limitation to our approach that we will address with future research is the estimation of coyote vibrissae growth rates and whether they grow continuously (i.e. linearly) or are seasonally shed during molt. Experiments on captive mammalian carnivores show that (1) vibrissae exhibit linear growth to provide a multi-month record of ecological information, and (2) vibrissae growth rates likely scale with body mass (Hirons et al. 2001; Tyrrell et al. 2013; Robertson et al. 2013, Newsome et al., unpublished). We predict that coyotes (15–20 kg) will have mean vibrissae growth rates in the range of ~8–12 cm/year, but are currently quantifying vibrissae growth rates in captive coyotes. Since the mean length of vibrissae collected from wild coyotes in Chicago is ~6 cm, the vibrissae isotope profiles produced by our approach likely represent ~6–8 months of dietary information.

Conclusions

First, our results show that direct anthropogenic food subsidization is not a prerequisite for successful adaptation to urban environments. Urban nature preserves may act as refugia for urban coyotes and appear to contain enough natural prey to support high coyote densities relative to that observed in rural or natural settings. Second, contrary to the expectation that (1) habitat homogenization in urban environments dampens ecological opportunity, and (2) urban wildlife populations are highly subsidized with anthropogenic resources resulting in decreased dietary diversity, our results suggest that individual coyotes in urban Chicago use a variety of foraging and movement strategies. For example, coyotes that live in the same contexts (urban nature preserves or urban matrix) with similar sized home ranges and urbanization in their home range have different diets. This scenario, coupled with the heterogeneous and dynamic nature of urban landscapes, provides an ideal study system to explore the costs and benefits of divergent strategies for successful adaptation to urban environments. Lastly, our study is an example of how stable isotope analysis, and

carbon isotope ($\delta^{13}\text{C}$) data in particular, can be used as reliable proxy for quantifying anthropogenic resource use by wildlife in urban environments.

Author contribution statement SDN and SDG originally formulated the idea; SDN, HMG, ECW, and SDG developed methodology; all authors conducted fieldwork; SDN, ECW, and SDG analyzed the data and performed statistical analyses; and SDN wrote the manuscript; other authors provided editorial advice.

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