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Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*)

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The unprecedented rate of urbanization over the past several decades is a major concern for conservation globally and has given rise to the multidisciplinary field of urban ecology. This field explores the direct and indirect effects of human activities on food-web dynamics, community structure, and animal behavior in highly modified urban ecosystems. Urban ecosystems are typically characterized by reduced species diversity but increased abundance of a few species able to exploit anthropogenic food sources. For many urban mammalian and avian species direct resource subsidization is difficult to assess using traditional means such as scat analysis. Here we show how stable isotope analysis can be used to assess the exploitation of anthropogenic foods in an endangered carnivore, the San Joaquin kit fox (*Vulpes macrotis mutica*) inhabiting the southern San Joaquin Valley in California. Examination of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope data shows that kit foxes living in urban Bakersfield, California, extensively exploit anthropogenic foods, which sharply contrasts with dietary data derived from scat analysis. Urban kit foxes had significantly higher $\delta^{13}C$ and lower $\delta^{15}N$ values than foxes from adjacent nonurban areas and had similar isotope values as Bakersfield human residents, which suggests a shared food source. In contrast, examination of isotopic data for nonurban kit foxes shows that they largely consume the most abundant natural prey species found in their scats. Stable isotope analysis offers a rapid and cost-effective means of evaluating the degree to which urban wildlife populations exploit anthropogenic foods in areas where native C_4 vegetation is relatively uncommon or absent, important in assessing the direct impacts of human activities on food-web dynamics in urban ecosystems. We anticipate that the isotopic gradients used here will be useful in assessing the exploitation of anthropogenic foods in other urban wildlife populations. DOI: 10.1644/09-MAMM-A-362.1.

Key words: anthropogenic subsidies, diet, stable isotopes, urban ecology, *Vulpes macrotis*

Urban and suburban sprawl has resulted in increasing interactions among humans and wildlife populations globally. The study of such interactions has led recently to the creation of the multidisciplinary field urban ecology, in which ecologists often collaborate with anthropologists, geographers, and conservation biologists to develop a greater understanding of ecological and evolutionary processes in highly dynamic urban ecosystems (Alberti et al. 2003; Faeth et al. 2005; Grimm et al. 2008; Shochat et al. 2006). Certain animal species have adapted to human-dominated habitats well and benefit directly or indirectly from human activities for a variety of reasons, including food, shelter, escape from natural predation, or a combination of these factors (Adams et al. 2006; Faeth et al. 2005; Shochat et al. 2004). Scavengers (e.g., raccoons [*Procyon lotor*], opossums [*Didelphis virginiana*], crows [*Corvus* spp.], and gulls [*Larus* spp.]) and some opportunistic generalist carnivores (e.g., foxes [*Vulpes* spp.] and coyotes [*Canis latrans*]) are increasingly common in urban habitats, suggesting that the relatively high abundance of food and the ease with which it is acquired attract some

wildlife to urban areas (Adams et al. 2006; Sauter et al. 2006). It is difficult to identify the exploitation of anthropogenic food sources using traditional dietary proxies (e.g., scat analysis), however, because commercially processed foods typically do not contain identifiable, indigestible material (e.g., bone, hair, or chitinous exoskeletons) associated with the consumption of most natural prey.

Despite their endangered status, San Joaquin kit foxes (*Vulpes macrotis mutica*) commonly occur in suburban and urban areas in the southern San Joaquin Valley, including the large urban center of Bakersfield, California (Cypher 2010; Cypher and Frost 1999; Frost 2005), where little natural habitat remains. Kit foxes living within Bakersfield appear to prefer open habitats provided by golf courses, drainage sumps, vacant lots, and even school campuses.

Previous studies of the foraging ecology of the San Joaquin kit fox have focused on populations living in natural habitats (Moehrenschlager et al. 2004). In the Lokern Natural Area (Lokern) and Kern National Wildlife Refuge (Kern NWR), which are located to the west and northwest of Bakersfield, respectively (Fig. 1), kit foxes consume a wide variety of prey types, but rodents, especially kangaroo rats (*Dipodomys* spp.), appear to be preferred prey (Cypher 2003; McGrew 1979; Nelson et al. 2007). Urban kit foxes in Bakersfield consume some anthropogenic food, but it is thought that natural prey—rodents, insects, and birds—forms the majority of their diet (Cypher 2010; Cypher and Warrick 1993). Prey remains are commonly observed in urban kit fox scats, and although pieces of anthropogenic food packaging material (e.g., paper and plastic food wrappers) have been found in scats, the proportion of such food sources is difficult to quantify because their consumption typically does not produce identifiable traces in scats (Cypher 2010). Thus, the relative exploitation of anthropogenic food sources by the urban Bakersfield kit fox population remains unknown.

Recent studies have shown that processed foods commonly consumed by people living in North America typically have conspicuously high $\delta^{13}C$ values in comparison to food grown in many European and some South American countries (Bol and Pflieger 2002; Jahren and Kraft 2008; Nakamura et al. 1982; but see Nardoto et al. 2006). The principal reason for this trend is that many foods consumed by North Americans contain corn (*Zea mays*) or its common industrial derivative, corn syrup. Moreover, most domesticated animals (cattle, pigs, or poultry) reared for meat in North America are fed corn during the later stages of maturation prior to slaughter. Corn is a C_4 plant with distinctively high $\delta^{13}C$ values ranging from $-12‰$ to $-14‰$ in comparison to plants that use the C_3 photosynthetic pathway and have values ranging from $-22‰$ to $-29‰$ (Craig 1953; Farquhar et al. 1989). C_3 plants dominate primary production in terrestrial ecosystems in the western United States, although C_4 grasses are common seasonal components of native grassland ecosystems in central and southeastern North America (Suits et al. 2005).

Stable isotope analysis is a useful dietary tool for animal ecologists, especially for those who work on elusive species difficult to observe in their natural habitats. The carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope compositions of animal tissues have been used to investigate trophic relationships and quantify diet composition of myriad terrestrial and marine species (Kelly 2000; Newsome et al. 2010; Schoeninger and DeNiro 1984). Through application of trophic discrimination factors to consumer isotope values, the isotopic composition of animal tissues can be compared directly to those of its diet. Typically, consumers are enriched in the rarer heavy isotope—^{13}C or ^{15}N—relative to their diets, and for examination of similar tissues among consumers and their prey this enrichment is ~1–2‰ for $\delta^{13}C$ and ~3–5‰ for $\delta^{15}N$ for each increase in trophic level (Kelly 2000; Vanderklift and Ponsard 2003).

In this study we used stable isotope analysis to determine the extent to which an urban wildlife population relies on anthropogenic food sources. We presented isotope values for hair and vibrissae (i.e., keratin) from 2 kit fox populations living in natural environments—Lokern and Kern NWR—together with values from kit foxes living within the city of Bakersfield. Kit fox values then were compared to isotope values of common natural prey species collected in Lokern and Bakersfield. Instead of directly comparing urban kit fox hair isotope values to those from anthropogenic food sources, we compared them to isotope values of human hair samples randomly collected from Bakersfield residents. Kit fox vibrissae samples from urban and nonurban populations also were subsampled to produce a continuous isotopic record to determine if individuals exhibit temporal (i.e., seasonal) shifts in dietary composition.

Materials and Methods

Study sites.—Kit fox tissues (hair and vibrissae), rodent hair, kit fox scats, or a combination of these, were collected from 3 principal locations in California near the southern terminus of the San Joaquin Valley. We studied nonurban kit fox populations from Lokern (~35°18′18.0N, 119°37′21.0W) and Kern NWR (~35°44′38.0N, 119°37′02.0W) and an urban population inhabiting the city of Bakersfield (~35°22′23.0N, 119°01′07.0W; Fig. 1). The southern San Joaquin Valley is characterized by hot, dry summers and cool, wet winters with average daily temperatures ranging from 4°C to 14°C in December and 21°C to 37°C in July. Precipitation in the southern San Joaquin Valley primarily falls in the winter and early spring when daytime temperatures favor the C_3 photosynthetic pathway (Ehleringer 1978; Paruelo and Lauenroth 1996; Tieszen et al. 1997), resulting in a mixed shrubland–grassland system dominated by C_3 plants ($\delta^{13}C \approx -27‰$). Lokern is located on the eastern flank of the Temblor Range near the small town of McKittrick, ~40 km west of Bakersfield. Kern NWR is located ~65 km northwest of Bakersfield. The Bakersfield study area was located primarily in the southwestern quadrant of the Bakersfield Metropolitan Area, which covers >580 km^2 and contained a rapidly growing human population of ~400,000 residents as of winter 2003 (Bakersfield Chamber of Commerce 2006). Hair samples from kit foxes of known sex were collected from Lokern in 2002, 2006, 2007, and 2008, and from Bakersfield in 2002,

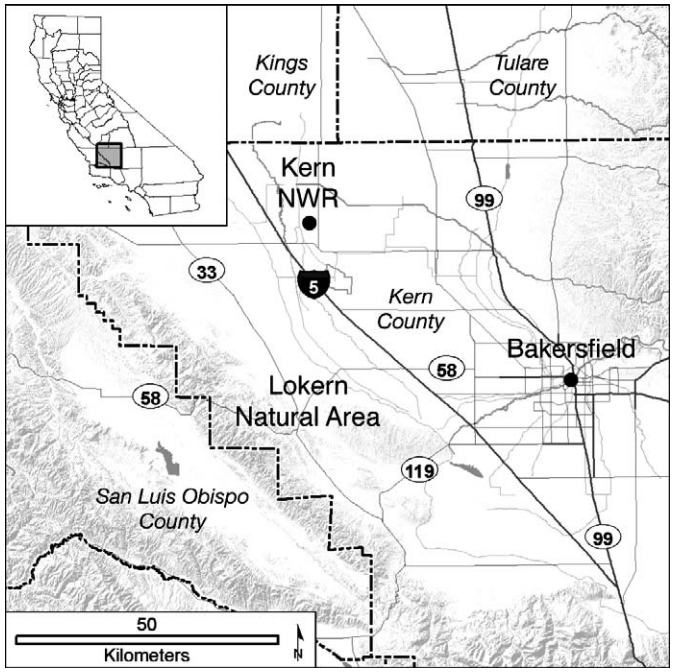

FIG. 1.—Map of the southern San Joaquin Valley showing the locations of the 3 populations examined in this study.

2006, and 2008. Hair samples from humans of known sex and age were collected from Bakersfield in 2008. Similar to many other canids, kit foxes undergo a single molt per year that occurs during the spring and early summer months. Because hair is metabolically inert, its isotopic composition reflects an average of diet consumed during those months.

Scat analysis.—We determined the diet of kit foxes through analysis of scat samples by opportunistically collecting 484 kit fox scats from Lokern and 720 scats from Bakersfield in 2003 and 2004. Fresh scats were collected year-round on both study sites. Scats were air-dried in paper bags and then oven-dried at 60°C for ≥24 h to kill any parasite eggs and cysts. They then were placed in individual nylon bags, washed to remove soluble materials, and dried prior to separating and identifying contents of the remaining undigested material. Mammalian remains (e.g., hair, teeth, and bones) were identified using macroscopic (e.g., length, texture, color, and banding patterns) and microscopic (e.g., cuticular scale patterns) characteristics of hairs (Moore et al. 1974) and by comparing teeth and bones to reference guides (Glass 1981; Roest 1986) and specimens. Other vertebrates were identified to class and invertebrates to order, based on exoskeleton characteristics and comparison to reference specimens.

Isotopic and statistical methods.—Kit fox hair and vibrissae samples were collected from animals captured alive or recovered dead as part of several ongoing ecological investigations; samples were collected under United States Fish and Wildlife Service permit TE-825573 and a Memorandum of Understanding from the California Department of Fish and Game. All procedures involving live animals met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Samples from each individual fox were stored in labeled coin envelopes pending analysis. Hair samples of the most common rodent species were collected from scats found in urban and nonurban environments. Kangaroo rats are the primary prey for Lokern foxes, and pocket gophers (*Thomomys bottae*) and California ground squirrels (*Spermophilus beecheyi*) are the primary mammalian prey for urban foxes. Samples of rodent hair were collected only from scats in which remains of only 1 rodent species were present. We also collected chitinous exoskeletons of Orthoptera and Coleoptera from Lokern and Bakersfield scats, respectively. Bird feathers also were collected from Bakersfield scats, and we randomly collected hair samples from Bakersfield human residents of known sex and age at salons and barbershops in the city.

For carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) analysis, vibrissae, hair, feathers, and insect exoskeletons were rinsed once with a 2:1 chloroform : methanol solution to remove surface contaminants. Cleaned vibrissae were then subsampled into ~0.2- to 0.3-mg segments using nail clippers, and the length of the whisker was recorded from every 3rd sample. The number of vibrissae segments analyzed from each individual varied from 7 to 14 ($\bar{X} = 10$) depending on the length of each vibrissa. Kit fox hair, human hair, and bird feather samples were homogenized by cutting bulk samples into small pieces using surgical scissors and sealed in tin boats for isotopic analysis. Insect exoskeletons were homogenized with a small mortar and pestle and then sealed in tin boats for isotopic analysis. $\delta^{13}C$ and $\delta^{15}N$ isotope values were determined using an elemental analyzer (Carlo Erba, Milan, Italy) interfaced with either a Delta Plus XL or Delta V isotope ratio mass spectrometer (Thermo Scientific, West Palm Beach, Florida) at the Carnegie Institution of Washington (Washington, D.C.). Isotopic results are expressed as δ values, $\delta^{13}C$ or $\delta^{15}N = 1{,}000 \times [(R_{sample} - R_{standard})/R_{standard}]$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand, or per mil (‰). The within-run standard deviation of an acetalinide standard was ≤0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. As a control for sample quality we measured the [C]/[N] ratios of each sample. Atomic [C]/[N] ratios of all keratin samples (i.e., hair, vibrissae, and feathers) were 3.3–3.5, encompassing the theoretical atomic [C]/[N] ratio of keratin (3.4). Isotopic differences among urban and nonurban groups or individual kit fox vibrissae values were assessed using analysis of variance and a post hoc Tukey honestly significant difference test; a Levene's test was used to test for homoscedasticity. Last, we used a linear regression to characterize the negative relationship between kit fox vibrissae $\delta^{13}C$ and $\delta^{15}N$ values. All statistical tests were performed in JMP version 7.0.1 (SAS Institute Inc., Cary, North Carolina).

RESULTS

Kit fox scat analysis.—Identification of food remains in scats suggested that both the Lokern and Bakersfield fox

TABLE 1.—Occurrence and percent occurrence of prey types in Lokern Natural Area ($n = 484$) and Bakersfield, California ($n = 720$) kit fox scats. Kangaroo rats include 3 species: *Dipodomys heermanni*, *Dipodomys nitratoides brevinasus*, and *Dipodomys ingens*. Anthropogenic foods include paper and plastic food wrappers.

Common name	Scientific name	Lokern occurrences (%)	Bakersfield occurrences (%)
Kangaroo rat	*Dipodomys* spp.	329 (68.0)	0 (0.0)
Pocket mice	*Perognathus inornatus* and *Chaetodipus californicus*	30 (6.2)	0 (0.0)
Botta's pocket gopher	*Thomomys bottae*	0 (0.0)	53 (7.4)
California ground squirrel	*Spermophilus beecheyi*	0 (0.0)	77 (10.7)
Rabbits	*Lepus californicus* and *Sylvilagus audubonii*	17 (3.5)	16 (2.2)
Birds		16 (3.3)	101 (14.0)
Herpetofauna		26 (5.4)	12 (1.7)
Orthopterans		112 (23.1)	19 (2.6)
Coleopterans		27 (5.6)	94 (13.1)
Anthropogenic foods		0 (0.0)	90 (12.5)

populations depended primarily on small vertebrates and insects (Table 1), but differences existed in the species consumed by foxes in the 2 populations. Foxes in the Lokern population ate primarily kangaroo rats, with kangaroo rat remains found in 68.0% of the scats, but the Bakersfield foxes ate ground squirrels, pocket gophers, and a greater proportion of birds than those in the Lokern population. The most common insects consumed at Lokern were Orthoptera (grasshoppers, 23.1%), and the most common insects eaten in Bakersfield were Coleoptera (beetles, 13.1%). We found no evidence that the Lokern foxes ate foods of anthropogenic origin, but Bakersfield scats contained evidence of anthropogenic food consumption, as evidenced by the occurrence of food packaging material in 12.5% of urban kit fox scats (Table 1).

$\delta^{13}C$ and $\delta^{15}N$ isotope values.—Kit fox hair samples collected from Lokern had significantly lower $\delta^{13}C$ and higher $\delta^{15}N$ values than kit fox or human hair samples collected within Bakersfield ($\delta^{13}C$: $F_{2,138} = 122.18$, $P < 0.0001$, $\delta^{15}N$: $F_{2,138} = 106.46$, $P < 0.0001$; Table 2; Fig. 2). Despite highly significant differences between mean hair isotope values for the urban and nonurban kit foxes, a small degree of overlap was evident in both $\delta^{13}C$ and $\delta^{15}N$ values for a relatively small percentage (7/88 or ~8%) of the individuals analyzed. Lokern and Bakersfield kit fox hair collected in the same year (e.g., 2008) was significantly different in both $\delta^{13}C$ and $\delta^{15}N$ (2008, $\delta^{13}C$: $F_{1,42} = 67.54$, $P < 0.0001$, $\delta^{15}N$: $F_{1,42} = 68.31$, $P < 0.0001$). Lokern kit foxes also showed significantly higher variance in $\delta^{15}N$ values in comparison to hair from kit foxes or humans collected in the city ($F_{2,138} = 22.75$, $P < 0.0001$). The mean $\delta^{15}N$ value of human hair was slightly (~1‰) but significantly higher than the mean $\delta^{15}N$ value of urban kit foxes ($F_{1,92} = 65.70$, $P < 0.0001$); no differences were found in mean $\delta^{13}C$ values between humans and kit foxes from Bakersfield ($F_{1,92} = 0.16$, $P < 0.67$). No sex-related differences occurred in $\delta^{13}C$ or $\delta^{15}N$ values within the urban kit foxes ($\delta^{13}C$: $F_{1,38} = 0.53$, $P > 0.10$, $\delta^{15}N$: $F_{1,38} = 0.07$, $P > 0.10$) or nonurban kit foxes ($\delta^{13}C$: $F_{1,45} = 2.41$, $P > 0.10$, $\delta^{15}N$: $F_{1,45} = 0.11$, $P > 0.10$).

Lokern kangaroo rats had significantly higher $\delta^{15}N$ ($F_{1,43} = 30.90$, $P < 0.0001$) but similar $\delta^{13}C$ values ($F_{1,43} = 0.59$, $P > 0.10$) as ground squirrels in Bakersfield (Table 2; Fig. 2C). Bakersfield pocket gophers had significantly lower mean $\delta^{13}C$ values than Lokern kangaroo rats or Bakersfield ground squirrels ($F_{2,54} = 35.79$, $P < 0.0001$). Bakersfield pocket gophers had mean $\delta^{15}N$ values that were significantly lower than Lokern kangaroo rats ($F_{1,34} = 22.32$, $P < 0.0001$) but similar to Bakersfield ground squirrels ($F_{1,31} = 1.67$, $P > 0.10$). Coleoptera and pocket gophers collected from Bakersfield had similar $\delta^{13}C$ and $\delta^{15}N$ values as Orthoptera collected from Lokern ($\delta^{13}C$: $F_{2,62} = 0.86$, $P > 0.10$, $\delta^{15}N$: $F_{2,62} = 0.33$, $P > 0.10$). Bird feathers collected from Bakersfield had significantly higher $\delta^{15}N$ values ($F_{1,57} = 14.13$, $P < 0.001$) than Coleoptera collected in the city. Birds also had significantly higher $\delta^{13}C$ values than pocket gophers or Coleoptera from Bakersfield ($F_{2,68} = 13.42$, $P < 0.0001$).

Temporal analysis of hair isotope values collected from Lokern revealed significant differences among years for mean $\delta^{13}C$ and $\delta^{15}N$ values. For $\delta^{15}N$, kit fox hair samples collected in 2008 ($n = 20$) were significantly lower by ~2‰ ($F_{3,43} =$

TABLE 2.—Mean $\delta^{13}C$ and $\delta^{15}N$ values and associated variation (*SD*) of kit fox and human hair samples collected from Lokern Natural Area (LOK) and Bakersfield (BAK) metropolitan area, California (Fig. 1). An asterisk (*) denotes data from Jahren and Kraft (2008). See Table 1 for scientific names of prey species.

Population and group or species	*n*	$\delta^{13}C$	*SD*	$\delta^{15}N$	*SD*	[C]/[N]
LOK kit foxes	47	−19.8	0.7	10.6	1.3	3.0 (0.1)
BAK kit foxes	43	−17.4	1.0	7.9	0.5	3.0 (0.1)
BAK humans	51	−17.5	0.8	8.8	0.5	3.1 (0.1)
LOK kangaroo rats	24	−20.4	1.1	8.5	1.5	3.1 (0.2)
LOK Orthoptera	23	−22.8	1.1	5.4	2.5	4.9 (0.5)
BAK ground squirrels	21	−20.1	1.6	6.5	0.7	3.0 (0.2)
BAK gophers	12	−23.8	1.1	6.1	1.3	3.2 (0.3)
BAK birds	29	−19.2	2.5	7.8	1.9	3.4 (0.2)
BAK Coleoptera	30	−22.6	3.9	5.8	2.2	4.8 (0.5)
Fast-food beef*	162	−18.0	2.9	6.1	0.4	—
Fast-food chicken*	161	−17.5	0.5	2.7	0.3	—

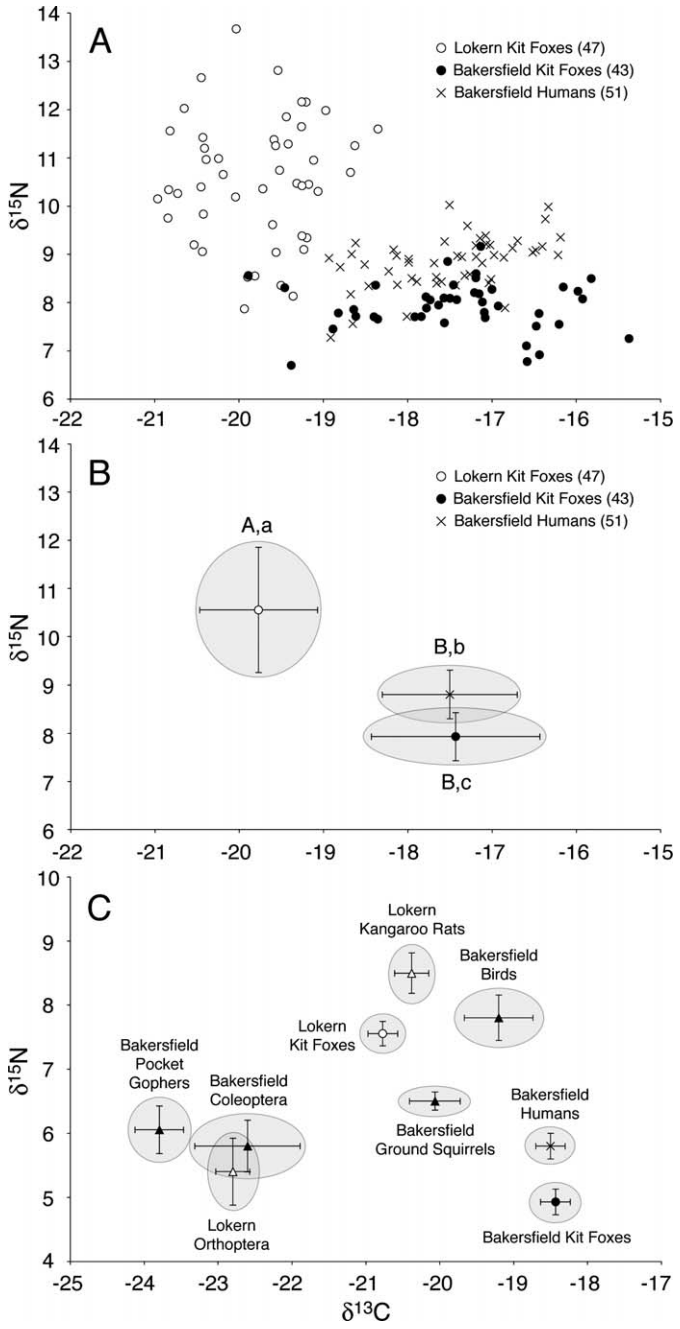

Fig. 2.—A) Individual kit fox and human hair $\delta^{13}C$ and $\delta^{15}N$ values from Lokern Natural Area (Lokern) and Bakersfield, California, and B) mean isotope values for each group. Different uppercase and lowercase letters in panel B denote significant differences in mean $\delta^{13}C$ and $\delta^{15}N$ values, respectively, among groups; errors bars represent *SD*. C) Trophic-corrected mean kit fox and human hair, and measured potential prey $\delta^{13}C$ and $\delta^{15}N$ values from Lokern and Bakersfield. Mean kit fox and human hair values have been corrected by subtracting 1‰ and 3‰, respectively, from measured $\delta^{13}C$ and $\delta^{15}N$ isotope values presented in Table 2 and Fig. 2B. Error bars represent *SE*.

7.71, $P < 0.001$) than hair collected in 2002 ($n = 11$) and 2006 ($n = 11$); we found no significant differences in $\delta^{15}N$ ($F_{2,24} = 1.05$, $P > 0.10$) between hair collected in 2002, 2006, and 2007 ($n = 5$). For $\delta^{13}C$, Lokern hair samples collected in 2006 and 2007 had slightly (~1‰) but significantly lower values ($F_{3,43} = 13.86$, $P < 0.0001$) than hair collected in 2002 and 2008. Bakersfield kit fox hair samples collected in 2008 had significantly lower $\delta^{15}N$ than hair collected in the city during 2002 and 2006 ($F_{2,37} = 7.38$, $P < 0.01$). No significant differences in $\delta^{13}C$ were found among Bakersfield kit fox hair collected in 2002, 2006, and 2008 ($F_{2,37} = 0.56$, $P > 0.10$).

Differences in $\delta^{13}C$ and $\delta^{15}N$ between hair and vibrissae collected at Bakersfield were not significant ($\delta^{13}C$: $F_{1,136} = 3.99$, $P > 0.05$, $\delta^{15}N$: $F_{1,136} = 0.01$, $P > 0.10$). At Lokern, vibrissae $\delta^{13}C$ values were slightly but significantly higher than those of hair ($F_{1,131} = 26.43$, $P < 0.0001$), but no differences were discovered in $\delta^{15}N$ between these tissues ($F_{1,131} = 0.88$, $P > 0.10$). Intraindividual isotopic variation in kit fox vibrissae in all populations was relatively low in comparison to interindividual variation (Table 3; Fig. 3). Kit fox vibrissae from Bakersfield, however, appear to have a smaller degree of interindividual variation in mean vibrissae isotope values (especially in $\delta^{15}N$) than those from wild kit foxes collected from Lokern or Kern NWR (Table 3; Fig. 3).

We discovered a significant negative linear trend in the kit fox vibrissae data set, with mean $\delta^{15}N$ values decreasing as $\delta^{13}C$ increased ($F_{1,23} = 82.15$, $P < 0.0001$; Fig. 3). In general, vibrissae from wild areas had higher mean $\delta^{15}N$ and lower $\delta^{13}C$ values than vibrissae from Bakersfield, but some overlap was apparent. Kern NWR vibrissae clustered into 2 isotopically distinct groups, and 2 individuals collected in 2008 plotted close to the Bakersfield kit foxes (Fig. 3). Only 1 of these individuals (U122M; Table 3) was statistically indistinguishable ($\delta^{13}C$: $F_{1,22} = 2.50$, $P > 0.10$, $\delta^{15}N$: $F_{1,22} = 3.40$, $P > 0.05$) from 1 Bakersfield kit fox (6285M). The other Kern NWR kit fox (U123M) that plots near the Bakersfield individuals (Fig. 3) has significantly lower $\delta^{13}C$ ($F_{1,23} = 22.52$, $P < 0.0001$) values than Bakersfield individual 6285M and significantly higher $\delta^{15}N$ values than Bakersfield individual U113F ($F_{1,24} = 17.65$, $P < 0.001$). The other 3 Kern NWR individuals collected in 1994 had significantly higher $\delta^{15}N$ but lower $\delta^{13}C$ values than Bakersfield foxes ($\delta^{13}C$: $F_{14,136} = 89.26$, $P < 0.0001$, $\delta^{15}N$: $F_{14,136} = 257.63$, $P < 0.0001$). Lokern vibrissae clustered into 3 isotopically distinct groups (Fig. 3), but all of the Lokern kit foxes had significantly different $\delta^{13}C$ or $\delta^{15}N$ values, or both, than the Bakersfield kit foxes ($\delta^{13}C$: $F_{19,161} = 75.10$, $P < 0.05$, $\delta^{15}N$: $F_{19,161} = 158.13$, $P < 0.05$).

Discussion

Isotopic comparisons between tissues of urban and wild kit foxes (hair), 3 rodent species (hair), 2 types of insects (chitinous exoskeletons), birds (feathers), and humans (hair) suggest that kit foxes living in Bakersfield extensively exploit anthropogenic food sources. After correcting for tissue-specific trophic discrimination by subtracting 1‰ and 3‰, respectively, from mean kit fox hair $\delta^{13}C$ and $\delta^{15}N$ values, urban kit foxes do not overlap with those of the rodent species,

TABLE 3.—Mean $\delta^{13}C$ and $\delta^{15}N$ values and associated variation (*SD*) of kit fox vibrissae collected from Lokern Natural Area, Bakersfield, and the Kern National Wildlife Refuge, California. Year of collection, sex, overall length (cm), and number of subsamples obtained from each vibrissa are noted. M = male; F = female.

Site and individual	Year	Sex	Length (cm)	*n*	$\delta^{13}C$	*SD*	$\delta^{15}N$	*SD*
Lokern								
6375	2008	M	6.4	8	−18.4	0.2	10.6	0.6
6555	2008	M	7.5	10	−18.6	0.6	10.9	0.5
6239	2008	M	6.7	11	−20.0	0.2	12.0	0.5
6551	2008	M	6.8	10	−18.9	0.5	11.0	0.2
6538	2008	M	5.2	7	−18.5	0.2	9.5	0.1
6536	2008	F	6.5	8	−18.6	0.2	10.3	0.5
6512	2008	F	6.2	9	−20.2	0.2	12.0	0.3
6270	2008	F	6.7	8	−19.9	0.3	12.0	0.4
6471	2008	F	7.0	8	−18.9	0.2	9.0	0.4
6506	2008	F	6.3	7	−18.8	0.2	9.2	0.3
$\bar{X}$ (*SD*)			6.5 (0.6)	9	−19.1 (0.7)	0.3 (0.2)	10.7 (1.2)	0.4 (0.2)
Bakersfield								
6532	2008	M	8.1	13	−17.7	0.7	8.2	0.5
6535	2008	M	6.9	10	−17.1	0.8	8.2	0.3
6285	2007	M	7.2	11	−17.7	0.5	8.8	0.6
6534	2008	M	5.5	7	−17.0	0.7	8.4	0.5
6380	2007	M	5.8	9	−17.4	0.7	7.7	0.3
6531	2008	M	5.3	7	−14.7	0.3	6.9	0.1
6366	2008	F	7.7	9	−15.3	0.6	7.4	0.5
6292	2008	F	7.0	10	−17.1	0.5	7.0	0.3
6372	2008	F	6.2	7	−16.5	0.2	8.3	0.2
U113	2008	F	6.9	12	−18.2	0.4	8.1	0.3
$\bar{X}$ (*SD*)			6.7 (0.9)	10	−16.9 (1.1)	0.5 (0.2)	7.9 (0.6)	0.3 (0.1)
Kern NWR								
U123	2008	M	7.6	14	−18.7	0.5	8.8	0.4
U122	2008	M	8.0	13	−17.3	0.8	9.1	0.3
U118	1994	M	6.3	9	−21.5	0.6	11.8	0.2
U124	1994	F	7.0	11	−20.8	0.8	12.5	0.4
U119	2008	F	5.5	9	−20.6	0.1	13.0	0.2
$\bar{X}$ (*SD*)			6.9 (1.0)	11	−19.8 (1.7)	0.6 (0.3)	11.0 (2.0)	0.3 (0.1)

birds, or insects (Coleoptera) present in their scats. Instead, trophic-corrected urban kit foxes have statistically indistinguishable $\delta^{13}C$ but slightly lower $\delta^{15}N$ values than humans living in Bakersfield, suggesting that Bakersfield kit foxes and humans consume similar foods.

Applying a 3‰ keratin–diet trophic discrimination factor (C. M. Kurle, pers. comm.) to mean urban and wild rodent hair $\delta^{13}C$ values yields an approximate mean $\delta^{13}C$ value of −23‰ to −27‰ for Bakersfield and Lokern plants, which shows that primary production in both urban and nonurban kit fox habitats in the southern San Joaquin Valley is dominated by plants using the C_3 photosynthetic pathway. In contrast, human diets in the United States are characterized by a high consumption of corn-based foods with relatively high $\delta^{13}C$ values (indicative of a C_4 photosynthetic pathway) in comparison to the wild ecosystems adjacent to most urban or suburban centers in western North America (Suits et al. 2005). For example, mean $\delta^{13}C$ values of beef and poultry products from 3 popular restaurant chains throughout the United States ranged from −15‰ to −20‰ (Jahren and Kraft 2008). Due to differences in tissue amino acid composition, keratin (rodents and birds) typically has higher $\delta^{13}C$ values by ~1–2‰ (Roth and Hobson 2000) than associated muscle assumed to be assimilated by kit foxes. Applying a 1.5‰ discrimination factor to prey keratin $\delta^{13}C$ values to account for tissue-specific differences in amino acid composition shows that natural prey have higher $\delta^{13}C$ values than anthropogenic foods (Jahren and Kraft 2008; Table 2). Several studies have used $\delta^{13}C$ values to infer the origin of commercial meat products, based on the assumption that most nonorganic North American domesticated animals are typically fed corn before slaughter (Morrison et al. 2000; Schmidt et al. 2005; Schoeller et al. 1980; Schwertl et al. 2005). The conspicuous carbon isotope signature of a North American diet also has been used to assess transient travel activities of humans through comparison of hair $\delta^{13}C$ values to that of domestic animals reared in countries worldwide (Bol and Pflieger 2002).

Strong support for extensive exploitation on anthropogenic foods is also evident in the $\delta^{15}N$ data. Kit foxes and kangaroo rats collected in Lokern had significantly higher and more variable $\delta^{15}N$ values than their urban counterparts. Plants and animals inhabiting semiarid environments typically have higher $\delta^{15}N$ values (Amundson et al. 2003; Austin and Vitousek 1998; Handley et al. 1999; Murphy and Bowman

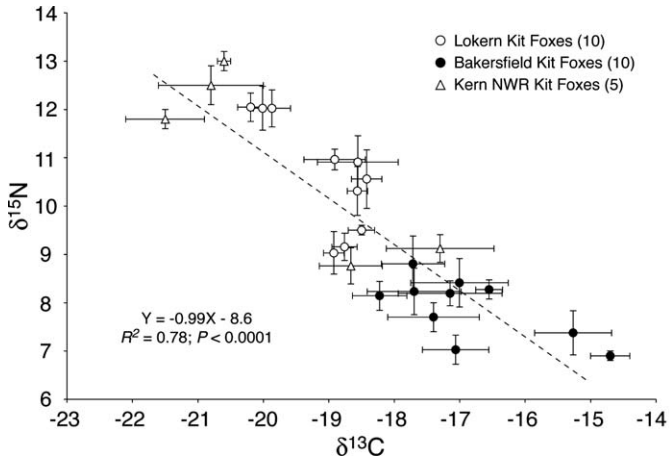

Fig. 3.—Mean $\delta^{13}C$ and $\delta^{15}N$ values of all segments sampled from each kit fox vibrissa collected from the Lokern Natural Area, Bakersfield, and Kern National Wildlife Refuge, California. Error bars represent *SD*. See Table 3 for the number of segments recovered from each vibrissa.

2006) than many commercially produced meat products consumed by humans in the United States, which are characterized by low and relatively invariant $\delta^{15}N$ values. Popular fast-food menu items collected from across the United States have mean $\delta^{15}N$ values that ranged only from 6.0‰ to 6.4‰ for beef and 2.2‰ to 2.5‰ for poultry (Jahren and Kraft 2008; Table 2), which is significantly lower and less variable than mean and variance of $\delta^{15}N$ values for Lokern kangaroo rats.

The higher degree of $\delta^{15}N$ variation in Lokern than in Bakersfield kit fox hair was primarily driven by interannual isotopic variation. Plant $\delta^{15}N$ values are negatively correlated with water availability (Amundson et al. 2003; Austin and Vitousek 1998), which varies widely from year to year in the southern San Joaquin Valley. Annual rainfall in Bakersfield ranged from ~75 mm (2007) to ~340 mm (1998) from the period 1980–2008 (National Oceanic and Atmospheric Administration; http://www.wrh.noaa.gov/hnx/bflmain.php); mean (±*SD*) rainfall over the same period was ~160 (±60) mm. Therefore, the large degree of interannual variation in Lokern kit fox hair $\delta^{15}N$ values is likely related to local variation in the base of the food web, with $\delta^{15}N$ of plants varying in response to rainfall.

We attempted to assess seasonal shifts in kit fox resource use or baseline changes in primary producer isotope values, or both, by subsampling kit fox vibrissae collected from 2 natural areas (Lokern and Kern NWR) and Bakersfield. In combination with isotopic data of common prey, the small degree of intraindividual isotopic variation observed in vibrissae from Lokern and Kern NWR suggests that primary production in these areas are dominated by plants that use the C_3 photosynthetic pathway. Likewise, the low degree of intraindividual versus interindividual isotopic variation suggests that resource use at the individual level remains relatively constant through time but that different individuals might consume different types of resources. Patterns in inter- versus intraindividual isotopic variation in vibrissae have been used to examine individual dietary specialization in marine consumers (Lewis et al. 2006; Newsome et al. 2009) and might be useful in studies of terrestrial consumers.

Our finding that urban kit foxes extensively exploit anthropogenic foods highlights a major difference between dietary data derived from scat and isotopic analysis. Examination of kit fox scat data from Bakersfield shows a relatively even occurrence of prey types in comparison to scats from Lokern. With the exception of anthropogenic foods, the consumption of any of these natural prey types typically will produce indigestible material such as bone, hair, feather, and chitinous exoskeletons, which is why scat analysis is a useful ecological tool. In contrast, anthropogenic foods are less likely to produce identifiable fragments in consumer scats unless the consumer accidentally consumes the indigestible material often used to package human foods. Our results suggest that scat analysis of urban consumers therefore can provide a biased view of diet because prey types that typically do not contain indigestible remains (e.g., anthropogenic foods) are likely underrepresented.

Perhaps because of the availability of anthropogenic foods and intensive exploitation by Bakersfield kit foxes, this population is demographically more stable than wild populations in the southern San Joaquin Valley (Cypher 2010). Higher kit fox densities, smaller home ranges, and higher and less variable reproductive rates in the urban environment are likely due to the abundance and consistent availability of anthropogenic food. Kit foxes in natural areas are subject to dramatic annual variation in prey availability, which is related to annual variation in rainfall (Cypher et al. 2000; Ralls and Eberhardt 1997). Wild kit foxes in the Carrizo Plain (~25 km west of Lokern) maintained large home ranges of sufficient size to sustain their own body mass and condition during periods of prey scarcity (White and Ralls 1993). The primary effect of prey scarcity is to reduce female reproductive success (Cypher et al. 2000; White and Ralls 1993), so reproductive rates in nonurban fox populations vary more than those in Bakersfield. Higher survival rates in Bakersfield foxes also could relate to the scarcity of large predators (Cypher 2010), because interference competition with coyotes is a significant source of mortality for kit foxes in nonurban areas in the southern San Joaquin Valley (Cypher and Spencer 1998; Cypher et al. 2000; Nelson et al. 2007; Ralls and White 1995).

One might expect that the consistent consumption of anthropogenic foods would lead to a series of negative trade-offs for kit foxes and other members of the urban Bakersfield ecosystem, but little evidence for such effects exists. Anthropogenic foods can have nutritional deficiencies (e.g., calcium) in comparison to some natural prey (Pierotti and Annett 1990). Although Cypher and Frost (1999) found differences in hematological and serological values between urban and nonurban kit foxes, including higher cholesterol levels among urban foxes, urban foxes have higher survival rates than nonurban foxes. The consistent consumption of

''junk food'' potentially could affect reproductive rates and development in young animals (Heiss et al. 2009), but kit foxes in Bakersfield have higher fecundity than wild populations (Cypher 2010). Consistent use of urban habitats by endangered animals also could subject kit foxes to increased exposure to infectious disease agents carried by nonnative feral and domesticated species that are abundant in urban environments (Cypher 2010; Wobeser 2007), but no serious disease epidemics have been documented in urban kit foxes. Wild animals that live in close proximity to urban and suburban environments also can lose their fear of humans, leading to intimate interactions that often have detrimental consequences for animals. In addition, the increased presence of a small carnivore such as a kit fox in high densities relative to natural levels could result in increased top-down control of vulnerable native herbivores and omnivores that inhabit urban ecosystems (Crooks and Soulé 1999; Faeth et al. 2005). These trade-offs do not appear to be impacting the kit fox population or their natural prey within the metropolitan Bakersfield area (Cypher 2010; Cypher et al. 2003); however, the primary cause of mortality among urban kit foxes is collision with vehicles, and several individuals are suspected of having died of exposure to toxicants (e.g., rodenticide or antifreeze—Cypher 2010).

The significant negative trend between mean $\delta^{13}C$ and $\delta^{15}N$ values of kit fox vibrissae collected from 3 habitats in the southern San Joaquin Valley provides an informative summary of general isotopic patterns among food sources available to wild and urban kit fox populations in this region. Urban to nonurban isotopic gradients similar to the one we have documented likely could be used to assess anthropogenic food subsidies in other urban wildlife populations in regions where native C_4 vegetation is entirely absent or not abundant (e.g., western and northeastern North America, western South America, and northern Asia). Our results indicate that stable isotopes can provide a rapid and cost-effective means of evaluating the degree to which wild animal populations exploit anthropogenic subsidies in these regions, which is a crucial 1st step in assessing the impacts of human activities on wildlife populations and food-web dynamics in urban ecosystems.

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