Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human–wildlife conflict

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Reports of encounters between people and generalist urban-adapted carnivores are increasing around the world. In North America, coyotes *Canis latrans* are among the carnivores that appear to be especially capable of incorporating novel anthropogenic food types, including those found in cities. Consuming anthropogenic food may benefit coyotes by increasing their dietary diversity, but it may also lead to increased interactions and conflicts with humans. To test these hypotheses, we compared the diets of urban and rural coyotes from two urban and three rural sites spanning 32 200 km^2 in Alberta, Canada. We analyzed scat samples to calculate diet diversity at the level of both individuals (species per scat) and populations (Shannon index) and to determine the frequency of anthropogenic food consumption. We complemented this comparison with stable isotope analyses of hair samples taken from individual urban and rural coyotes that were or were not reported by the public for repeatedly visiting backyards and schoolyards during the day. Relative to rural coyotes, urban coyotes had more diverse diets at the level of both individuals and populations, consumed anthropogenic food more often, and animals less often, than rural coyotes. Although urban coyotes assimilated more anthropogenic food than the rural coyotes overall, the urban coyotes reported for conflict assimilated less protein and were more likely to be diseased. Our results suggest that processed anthropogenic food may contribute to the success of urban coyotes, but does not entirely correlate with conflict. Instead, some seemingly innocuous, but low-protein food sources such as bird feeders, compost, and cultivated fruit trees may contribute disproportionately to encounters with people for coyotes and other urban-adapted opportunistic carnivores.

Several generalist species have increased in distribution and abundance in urban areas (McKinney 2006), leading to changes in urban biodiversity (McKinney 2002) and rates of human–wildlife conflict (Curtis and Hadidian 2010). Many behavioural changes have been documented in urban-adapted wildlife, including changes in tolerance to human activity, habitat selection, the timing of activity, and changes in diet (reviewed by Gehrt and Riley 2010, Lowry et al. 2013). Generalist species with broad diets may be especially well-equipped at colonizing and adapting to new and highly variable habitats, such as urban areas, because they can exploit diverse food sources (Angert et al. 2011), enabling them to thrive even when natural foods are less available (Williams et al. 2006). Cities can provide many novel foods for wildlife because they contain more species of non-native flora and fauna (McKinney 2002, Grimm et al. 2008) and can contain anthropogenic food and waste year-round in the form of pet food, compost piles, bird seed, and refuse (Contesse et al. 2004, Williams et al. 2006). Species with sufficient dietary flexibility and tolerance of human activity

to exploit these foods may benefit from adding anthropogenic food to a natural diet, thereby increasing diet diversity. Combined with less mortality from predators and human hunters in cities, the diversity and abundance of food in cities may explain the higher survival and reproductive rates and population densities of urban-adapted carnivores (Gehrt and Riley 2010, Bateman and Fleming 2012).

Increasing rates of encounters with people have been documented for several urban-adapted species, including red foxes *Vulpes vulpes* (Contesse et al. 2004), raccoons *Procyon lotor* (Prange et al. 2004) and black bears *Ursus americanus* (Hopkins et al. 2012). It is widely understood that consumption of anthropogenic food, and resulting food conditioning, often contributes to human–wildlife conflict (Herrero 1985, Hopkins et al. 2012), but no single mechanism has been identified to predict why and which animals come into conflict with humans (Curtis and Hadidian 2010). Even when food is associated with conflict, specific links between apparent changes in diet and particular types of anthropogenic food must be identified to support specific attractant

management. By removing those attractants, lethal management of urban-adapted species might be prevented or reduced. Such approaches can promote positive experiences with urban wildlife and typically are more palatable to urban residents.

Reported rates of encounters between humans and coyotes have also increased in cities across North America (White and Gehrt 2009, Alexander and Quinn 2011, 2012, Poessel et al. 2013), which coincide with increases in coyote distribution and potentially changes in coyote behaviour (Gehrt and Riley 2010). Since the early 1800s, coyotes have expanded their range from the plains of the American Midwest to most regions in North America, including urban areas (Gompper 2002). This expansion in coyote distribution is likely supported by the tremendous flexibility coyotes express in both diet and foraging behaviour; coyotes can hunt in packs to prey on ungulates but can also forage individually for rodents, leporids, insects, fruit, and vegetation (Bekoff 2001). Urban coyotes also consume anthropogenic food, however the amount varies considerably between cities (Quinn 1997, Fedriani et al. 2001, Morey et al. 2007).

Because coyotes occur over such a wide range of habitats and have broad and flexible diets, they are an ideal study species for investigating relationships between diet, urbanization, and conflicts with people. We hypothesized that coyotes in urban areas would incorporate several types of anthropogenic food into their diets, thereby increasing both dietary breadth and the proportion of diets comprised by anthropogenic food. Because the consumption of anthropogenic food has been linked to conflict with people in other contexts, we also hypothesized that coyotes that consumed more anthropogenic food would be more likely to elicit nuisance reports by people. To test these hypotheses, we compared the diets of urban and rural coyotes and of coyotes that did or did not elicit repeated nuisance complaints from the public. If supported, these hypotheses suggest that urban coyotes may be better able to respond to changes in the availability of diet items than rural coyotes and that human–coyote conflict may be successfully mitigated with targeted attractant management.

Material and methods

Study areas

To measure changes in diet with urbanization, we compared the diets of coyotes from the two major urban centres in Alberta, Edmonton and Calgary, to those of coyotes in three more natural landscapes, Elk Island National Park, the region surrounding the town of Wabasca-Desmarais, and Ministik Lake (Fig. 1). Edmonton (53°32′N, 113°30′W) centres on the North Saskatchewan River valley and has a population of 870 000 people (population density = 1271 humans km⁻²). Calgary (51°03′N, 114°04′W) is situated on the Bow River valley and has 1.2 million inhabitants (population density = 1376 humans km⁻²). Located 50 km east of Edmonton, Elk Island National Park (53°37′N, 112°52′W) is a fenced 194 km² natural area containing high densities of ungulates and comprised by aspen parkland surrounded by agricultural development. Located 48 km southeast of

Figure 1. Map of study sites across Alberta, Canada. We collected coyote scats from two urban sites (Edmonton and Calgary, black circles) and two rural sites (Elk Island National Park (EINP) and Wabasca, gray circles). We also collected hair samples from coyotes in one urban site (Edmonton) and one rural site (Ministik).

Edmonton, Ministik Lake (53°21′N, 113°1′W) is a 109-km² bird sanctuary characterized mainly by aspen parkland and many small water bodies. Ministik is closed to the public and is 28 km away from the nearest town, thereby limiting the availability of anthropogenic food to coyotes. Our most remote site was an area of approximately 21 000 km² surrounding the town of Wabasca-Desmarais (approx. 1500 inhabitants; 55°57′N, 113°49′W) in northeastern Alberta. This area is characterized by boreal mixed-hardwood forest and scattered development resulting mainly from forestry and energy sectors (Latham et al. 2013). Although coyotes have occurred in Alberta for at least the last 100 yr (Bekoff 2001), reports of coyotes by the public have become prevalent in Edmonton and Calgary only since the 1980s (R. Cox pers. comm., Lukasik and Alexander 2011) and even more recently in Wabasca (Latham et al. 2013).

Scat collection

Coyote scats were collected on a variety of trails (i.e. game trails, gravel trails, and paved bike paths) following specified routes at least monthly. Trails were selected in areas with suspected coyote activity based on sightings, the presence of coyote tracks, and the presence of radio-collared coyotes. We collected 531 scats in Edmonton between 2009 and 2012 in parks, ravines, a zoo, and in fields at the Univ. of Alberta

South Campus agricultural research facility. In Calgary, we collected 484 coyote scats between 2006 and 2007 in parks and green spaces (Lukasik and Alexander 2012). We also collected 1221 scats in Elk Island National Park from 1994–2000 (Pruss 2002) and collected 120 coyote scats in Wabasca from 2005–2007. Scats in Wasbasca were collected opportunistically as part of an ongoing study on wolf diet (*Canis lupus*; Latham et al. 2013) but were not collected at Ministik Lake.

Coyote scats were distinguished from domestic dog *C. lupus familiaris* scat based on size, morphology, contents, and location. Coyote scats were distinguished by their diameter (18–25 mm; Arjo et al. 2002) and position in the middle of trails which coyotes likely use to demark territories (Bekoff 2001). Scats containing visible dog food (evident by flecks of grain) were rejected in the field (after Quinn 1997) to prevent overestimating the frequency of anthropogenic food consumption. Coyote scats were distinguished from wolves and foxes using tracks, the size of scats and the known locations of radio-collared coyotes. Scats collected in Edmonton, Elk Island, and Wabasca were stored at $-20°C$ and autoclaved prior to analysis (Pruss 2002) and scats collected in Calgary were frozen at $-80°C$ for at least 72 h prior to analysis (Lukasik and Alexander 2012).

Scat analysis

We categorized the diet items found in coyote scats into 22 groups of species (Table 1) and considered anthropogenic food sources to include domestic dogs and cats *Felis catus*, traces of garbage (e.g. plastic or paper), bird seed (i.e. sunflower seeds *Helianthus annuus* and millet *Panicum miliaceum*), and cultivated fruit (i.e. crab apples; *Malus* spp.). All other diet items were considered to be from natural sources. Mammalian hair was identified to species group by selecting hairs at random and inspecting them microscopically for medulla and scale patterns using keys (Moore et al. 1974). Coyote hair, distinguished from domestic dog hair using colour and size, was assumed to be from self-grooming. Other identified diet components included exoskeletons (insects), feather (birds), fruit skins and seeds (fruit, but not including crab apples and bird seed), and leaves and stems (vegetation).

We measured the prevalence and relative abundance of diet items in urban and rural coyote diet by calculating the frequency of occurrence and percent occurrence for each species group. Frequency of occurrence (scats containing item/total scats $\times 100$; Mattioli et al. 2004) calculates how often an item is consumed while percent occurrence (occurrence of item/occurrences of all items $\times 100$; Morehouse and Boyce 2011) calculates how often each diet item is found relative to all other diet items and sums to 100. We used these metrics because they both use the presence, rather than the volume, of diet items to support comparisons across items of varying volumes and levels of digestibility (e.g. bones vs soft anthropogenic food).

We measured the diet breadth of individual coyotes using the average number of species groups found per scat and, of coyote populations, by estimating the relative abundance (i.e. percent occurrence) for each species group and then calculating Shannon diversity index (*H'*) values as an index of diet trophic diversity (Fedriani et al. 2001, Morey et al. 2007). We calculated both values separately for the urban and rural sites and compared Shannon *H'* values using a modified *t*-test (Hutcheson 1970). We also took the

Table 1. Frequency of occurrence (scats containing item $\times 100$/total scats) and percent occurrence (scats containing item/occurrences of all items $\times 100$; in parentheses) of food items and diet diversity found in scats collected in two urban and two rural study sites in Alberta, Canada. P values refer to replicated G tests.

		Urban			Rural			
	Item	Edmonton	Calgary	Mean	Elk Island	Wasbasca	Mean	p
Natural	Cricetidae	55.9 (22.7)	75.4 (33.1)	65.65 (27.9)	46.1 (26.5)	51.5 (35.0)	48.8 (30.8)	0.04
	Sciuridae	14.7 (6.0)	16.3 (7.2)	15.5 (6.6)	1.8 (1.0)	2.6 (1.4)	2.2 (1.2)	<0.01
	Leporidae	34.8 (14.1)	7.6 (3.4)	21.2 (17.5)	2.1 (1.2)	4.1 (2.8)	3.1 (2.0)	<0.01
	Muskrat (*Ondatra*)	15.6 (6.3)	0	7.8 (3.2)	23.3 (13.4)	37.1 (25.2)	30.2 (19.3)	<0.01
	Mustelidae	22.2 (9.0)	0.62 (0.3)	11.41 (4.7)	0	0	0	<0.01
	Ungulate	12.4 (5.0)	8.1 (3.5)	10.25 (4.3)	46.1 (26.5)	33.0 (22.4)	39.6 (24.5)	<0.01
	Beaver (*Castor*)	2.4 (1.0)	0.21 (0.09)	1.3 (0.5)	11.1 (6.4)	1.0 (0.70)	6.1 (3.6)	0.58
	Porcupine (*Erethizon*)	1.5 (0.6)	0	0.75 (0.3)	0.45 (0.26)	0	0.23 (0.13)	0.90
	Birds (*Aves*)	3.8 (1.5)	13.2 (5.8)	8.5 (3.7)	7.9 (4.5)	7.2 (4.9)	7.6 (4.7)	0.78
	Insects (*Hexapoda*)	1.7 (0.7)	4.1 (1.8)	2.9 (1.3)	8.2 (4.7)	0	4.1 (2.4)	0.66
	Woodchuck (*Marmota*)	0	0	0	0	7.2 (4.9)	3.6 (2.45)	–
	Bovidae (domestic)	0	0	0	2.7 (1.6)	2.1 (1.4)	2.4 (1.5)	<0.01
	Bovidae (wild)	0	0	0	4.4 (2.5)	0	2.2 (1.3)	–
	Natural fruit	7.9 (3.2)	12.4 (5.4)	10.2 (4.3)	14.9 (8.6)	1.0 (0.70)	8.0 (4.7)	<0.01
	Vegetation	23.9 (9.7)	44.6 (19.6)	34.3 (14.7)	4.2 (2.4)	0	2.1 (1.2)	<0.01
Anthropogenic	Garbage	18.5 (7.5)	12.2 (5.4)	15.4 (6.5)	0	1.0 (0.70)	0.5 (0.35)	<0.01
	Cats *Felis catus*	6.0 (2.4)	0.62 (0.27)	3.31 (1.3)	0.53 (0.30)	0	0.27 (0.15)	0.03
	Dogs *Canis lupus fam*.	0.94 (0.4)	0.62 (0.27)	0.78 (0.3)	0.15 (0.086)	0	0.08 (0.043)	0.04
	Crab apples *Malus* sp.	2.8 (1.1)	29.1 (12.8)	16.0 (6.95)	0	0	0	<0.01
	Birdseed	21.7 (8.8)	2.5 (1.1)	12.1 (5.0)	0	0	0	<0.01
	Species per scat	2.60	2.45	2.54	–	1.46	1.46	0.03
	Shannon's H	2.41	2.2	2.3	1.83	1.74	1.74	<0.01
	Diet species richness	11.2	9.23	9.97	6.20	5.73	5.73	–

exponent of the Shannon index *H'* values to estimate the effective number of species groups in urban and rural coyote diets (Jost 2006).

We measured differences in composition of urban and rural coyote diets by comparing the frequency of occurrence of species groups using replicated G tests. We also compared the frequency of occurrence of species groups in the three seasons that are most ecologically relevant to coyotes: breeding (January–April), pup-rearing (May–August), and dispersal (September–December; Morey et al. 2007).

Hair collection and stable isotope analysis

To overcome potential bias in diet estimated from scat samples, in which there may be few remnants of anthropogenic food, we compared the assimilated diets of individual urban and rural coyotes with known histories of conflicts with people using ^{13}C and ^{13}N stable isotope analysis. Stable isotope analysis can give a more accurate and long-term estimate of anthropogenic food consumption for several reasons. First, corn, as a C4 plant, has a distinctively high δ^{13}C signature (ratio of ^{13}C/^{12}C) and is present in virtually all processed food and as livestock feed (Jahren and Kraft 2008). Second, stable isotope analysis relates the diets of individual animals since their last molt to identify the cumulative effects of diet. Third, protein consumption can be estimated through δ^{15}N signatures (ratio of ^{15}N/^{14}N) because ^{15}N is preferentially retained in consumers and higher trophic levels (DeNiro and Epstein 1981).

We collected hair samples from coyotes that were live-trapped as part of an independent study on coyote movement (Murray et al. unpubl.) and dead coyotes provided by others. Urban hair samples included coyotes in the live-capture study plus coyotes that had been killed by vehicles or were euthanized by provincial government wildlife officers in response to repeated complaints from people within Edmonton city limits. Rural hair samples were collected from coyotes that were killed by a private wildlife pest management company following complaints by rural residents or were harvested on a licensed trap-line in Ministik.

We considered a coyote to have exhibited conflict-prone behaviour if it had generated complaints from the public that described behaviour consistent with habituation to people (threatening behaviour or repeated, diurnal visits to backyards and schoolyards). Coyotes that were reported by the public were identified based on the reports associated with animals that were euthanized or on ear tag numbers. Thus, all coyotes could be categorized in two ways: as urban or rural, and within those categories, as whether or not they were reported for conflict by the public. When coyotes were sampled, their body condition was scored on a scale from 1 to 5 based on coat quality and body fat (Windberg et al. 1991). We also noted whether the coyote exhibited signs of sarcoptic mange infestation, caused by the mite *Sarcoptes scabiei*, that results in hair loss, lesions, and skin thickening (Samuel et al. 2001).

For both live and dead coyotes, roughly a dozen guard hairs from the back of the neck were collected and prepared for stable isotope analysis following Hilderbrand et al. (1996). During preparation, hair was sectioned where

possible into two halves to estimate seasonal diet; the base of the hair contains the diet signature from the most recent months preceding collection and the tip contains diet signatures from the earliest months since the spring molt. For example, hair sampled in the fall is approximately six months old (since spring molt) and each half would contain three months of diet data. Sample δ^{15}N and δ^{13}C values (‰) were measured using a EuroEA Elemental Analyzer (EuroVector) and Isoprime Mass Spectrometer (GV Instruments) with a measurement standard deviation of ± 0.1 and ± 0.3‰ respectively, at the Biogeochemical Analytical Service Laboratory (Dept of Biological Sciences, Univ. of Alberta).

To quantify changes in coyote assimilation of protein and anthropogenic food with urbanization and conflict behaviour, variation in individual coyote δ^{13}C and δ^{15}N values was examined using linear mixed-effects (LME) models using package nlme in R (Pinheiro et al. 2012). We included coyote sex, age, body condition, presence of mange, season, site type (urban, rural), and conflict (yes, no) as well as interactions between season, site type, and conflict as covariates. We used forward selection to build our models based on the purposeful model-selection methods of Hosmer and Lemeshow (2000) using a p value of 0.05.

Results

Diet diversity and urbanization

Urban coyotes had more diverse diets than rural coyotes at both the population and individual levels (Fig. 2). Urban coyotes had higher average numbers of species groups per scat than rural coyotes ($t = 10.39$, DF = 1, p = 0.03; Table 1, Fig. 2). The number of species groups for rural coyote scats could only be calculated for Wabasca because these data were not available from Elk Island National Park. Urban coyote scats were also 47% more likely to contain
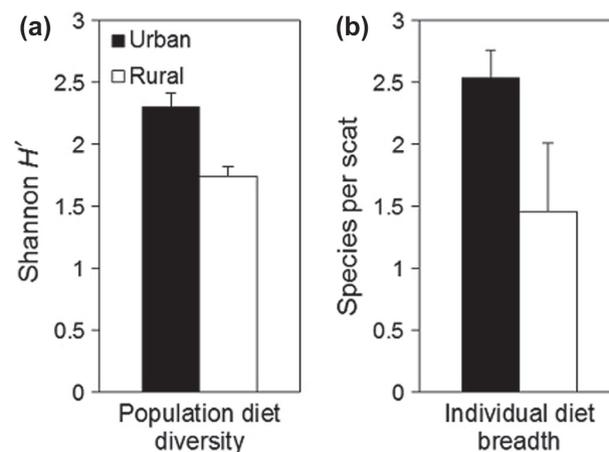

Figure 2. Diet diversity of urban coyote scats from two urban (black bars) and two rural sites (white bars). We measured population diet diversity by calculating Shannon's *H'* index from pooled scats (a) and measured individual diet breadth using the number of species per scat (b). Bars show mean values and error bars indicate standard error.

more than one species group than rural coyote scats (78% of urban scats, 41% of rural scats). Urban coyote scats also had significantly higher Shannon H' index values than rural coyote scats ($t \geq 2.35$, DF = 1, p < 0.01; Table 1, Fig. 2).

Urban coyotes consumed much more anthropogenic food, which were present in 26% (n = 267) of all urban coyote scats and < 1% (n = 11) of rural scats ($G = 25.31$, DF = 1, p < 0.01; Fig. 3a). Urban coyotes also consumed animals 29% less often, relative to other items, than rural coyotes ($G = 18.62$, DF = 1, p < 0.01; Fig. 3b). Urban coyotes consumed more domestic cats and dogs than did rural coyotes, but both groups consumed domestic animals less often than other mammal species (Table 1). Urban coyotes also consumed small mammals (i.e. cricetid rodents, leporids, sciurids) 24% more often and consumed ungulates and muskrats *Ondatra zibethicus* 74% less often than rural coyotes ($G \geq 4.72$, DF = 1, p < 0.01; Fig. 3a). Prey use varied seasonally but the patterns were similar across urban and rural sites. Coyotes did not exhibit significant seasonal changes in consumption of anthropogenic food ($G = 1.93$, DF = 2, p = 0.39).

Figure 4. Average δ^{15}N and δ^{13}C stable isotope values of coyote hair samples. Sampled coyotes were from urban (circles, n = 49) or rural areas (triangles, n = 23) and were either reported for conflict by the public (black; n_{Urban} = 15, n_{Rural} = 8) or were not (white; n_{Urban} = 34, n_{Rural} = 15). Bars show standard deviation.

Assimilated diet and urbanization

We analyzed hair samples from 49 urban and 23 rural coyotes for stable isotopes. Of these, 15 urban (three adult males, five adult females, four subadult males, three subadult females) and eight rural (four adult males, one subadult female, three subadult males) coyotes were reported by the public (15/49 (urban) vs 8/23 (rural); test for independence $G = 0.12$, DF = 1, p = 0.72). Urban coyotes were more likely than rural coyotes to exhibit poor body condition or mange infestation (19/49 (urban) vs 0/23 (rural); $G = 12.68$, DF = 1, p < 0.01). Urban coyotes that exhibited conflict-prone behaviour were also more likely to have poor body condition or exhibit mange infestation (12/15), whereas coyotes that did not elicit complaints were more likely to be in good or very good condition (28/34; $G = 17.41$, DF = 1, p < 0.01). None of the rural coyotes that exhibited conflict-prone behaviour had poor body condition or apparent mange infestation.

As predicted, urban coyotes assimilated more processed anthropogenic food, as measured by δ^{13}C stable isotope signatures, than did rural coyotes (urban: –22.6 ± 1.3‰; rural: –23.7 ± 0.6‰; LME β_{Urban} = 1.04 ± 0.35, $t = 3.00$, DF = 72, p < 0.01; Fig. 4). Urban coyotes assimilated similar amounts of ^{15}N as rural coyotes, suggesting they consumed similar amounts of protein (urban: 7.55 ± 2.35‰; rural: 7.84 ± 1.03‰; LME β_{Urban} = 0.33 ± 0.61, $t = 0.53$, DF = 72, p = 0.60; Fig. 4). In contrast to our prediction, urban coyotes that exhibited conflict-prone behaviour did not assimilate significantly more ^{13}C, suggesting they did not consume significantly more processed anthropogenic food than other coyotes (urban conflict: –22.4 ± 1.56‰; all other coyotes: –22.9 ± 1.06‰; LME $\beta_{Urban \times Conflict}$ = –0.54 ± 0.66, $t = –0.82$, DF = 72, p = 0.41; Fig. 4). Rather, urban coyotes that exhibited conflict-prone behaviour assimilated significantly less protein than all other coyotes (urban conflict: 6.3 ± 0.79‰; all other coyotes: 8.0 ± 0.22‰; $\beta_{Urban \times Conflict}$ = –2.68 ± 1.30, $t = –2.05$, DF = 72, p = 0.04; Fig. 4).
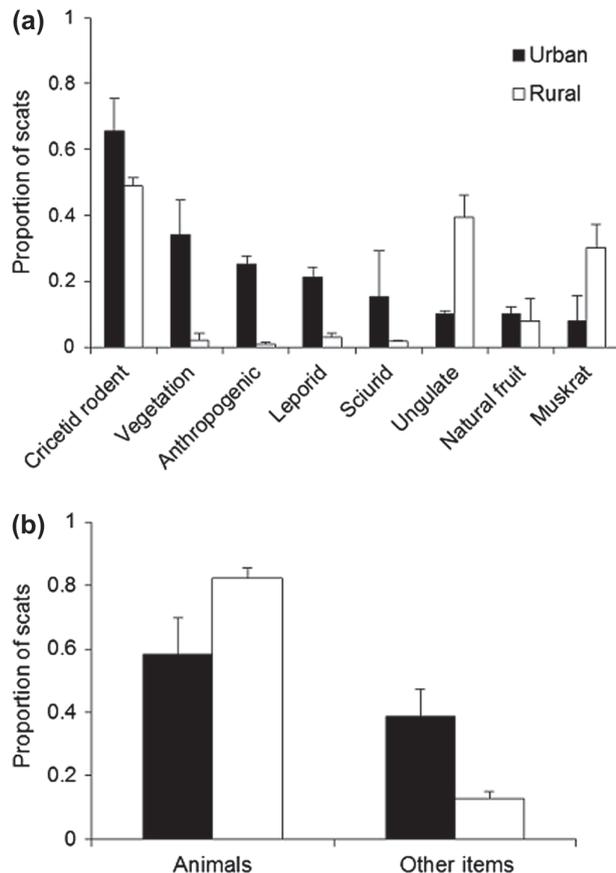

Figure 3. Differences in prey use in urban (black bars) and rural (white bars) coyote scats from two urban and two rural studies in Alberta, Canada. (a) The frequency of occurrence (displayed as proportion of scats that contained item) for the diet items that differed significantly between urban and rural coyotes. (b) The proportion of analyzed scats from urban or rural coyotes that contained prey remains such as hair, bones, or teeth (animals) and all other items including anthropogenic food. Error bars show standard deviation.
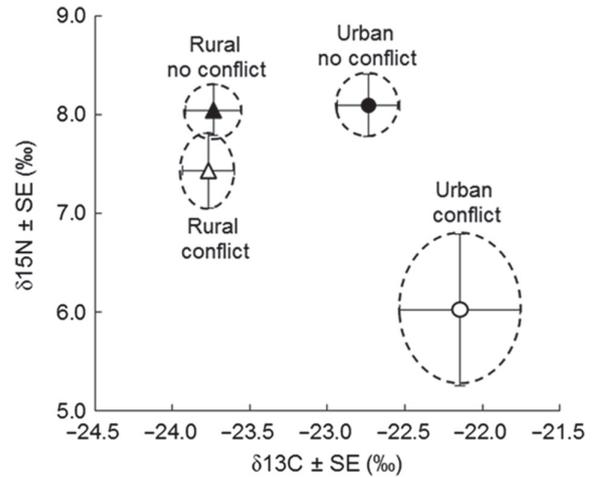
Discussion

We assessed whether the consumption of anthropogenic food was associated with increased diet breadth and conflict with people in urban coyotes. We found that urban coyotes had more diverse diets than rural coyotes at both the population and individual levels with the addition of anthropogenic food. We also found that urban coyotes reported for conflict assimilated less protein but similar levels of processed anthropogenic food relative to other urban coyotes.

Urban coyotes had more diverse diets than rural coyotes by consuming the full complement of prey types used by rural coyotes (e.g. sciurids, beavers *Castor canadensis*, mustelids, muskrats, and ungulates) in addition to anthropogenic food of several types. This result supports the hypothesis that coyotes, like other urban-adapted species, may succeed in cities in part because they can exploit novel food sources. In general, increased diet diversity is presumed to increase consumer survival and reproduction because consumers are less reliant on any particular diet item and can better accommodate changes in resource availability (Suryan et al. 2000, Lefcheck et al. 2013). In addition to these benefits, anthropogenic food in cities may be more abundant (Contesse et al. 2004), and exhibit longer growing seasons (Grimm et al. 2008). All of these factors may contribute to higher survival and reproductive rates, and could account for the smaller home ranges observed in urban relative to rural coyotes (Gehrt and Riley 2010).

Increased access to anthropogenic food might be one reason that urban coyotes in our study appeared to be less reliant on consuming animals than rural coyotes. This change makes the diet of urban coyotes more similar to those of more omnivorous urban adapters like raccoons, striped skunks *Mephitis mephitis*, stone marten *Martes foina*, and opossums *Didelphis virginiana* (Bateman and Fleming 2012). In general, urban adapters may even favour anthropogenic food over natural sources because it is more constantly available; sources of food like garbage cans, fruit trees, compost piles, and bird feeders are predictable in space and time, potentially lowering foraging costs (Votier et al. 2010, Weiser and Powell 2010). This predictability, in addition to high caloric content and similarity to natural food, might be one reason that cultivated fruit is the type of anthropogenic food most frequently consumed by coyotes in many cities (reviewed by Gehrt and Riley 2010, this study). Both urban and rural coyotes consumed small mammals as their primary prey source, supporting the suggestion that coyotes can control rodent populations and increase rodent diversity (Henke and Bryant 1999).

The associations between the consuming anthropogenic food and being reported by the public differed for urban and rural coyotes. Both populations contained similar proportions of conflict animals, however all urban coyotes consumed more processed anthropogenic food than rural coyotes. By contrast, protein assimilation was similar for coyotes in urban and rural areas that were not reported for conflict, but it was much lower for reported coyotes in urban areas, the majority of which had signs of sarcoptic mange. The relatively low levels of assimilated protein in the diet of coyotes reported by the public suggest that these animals may be hunting less frequently, perhaps because these animals often exhibited poor health and body condition. Animals with poor body condition or ectoparasite infestations may be less able to hunt for prey owing to lost endurance (sensu Alzaga et al. 2008) or intolerance to colder temperatures at peak hunting times (crepuscular or nocturnal hours, sensu Bekoff 2001). These coyotes may have used anthropogenic food because it could be obtained passively and is often reliable in space and time. Alternatively, they may have sought out carbohydrate-rich foods because they increase the rate of fat accumulation (Brand-Miller et al. 2002). Via either starting point, the lesser protein consumption by sick coyotes would be expected to accelerate declines in body condition (Ezenwa 2004) and these animals may fail to obtain or defend a high-quality territory (Kamler and Gipson 2000) which may promote the use of human-dominated areas.

Our results have several implications for reducing human–coyote conflict in cities. The differences in scat composition between urban and rural coyotes, combined with the lower protein assimilation by coyotes reported for conflict-prone behaviour, suggest that some attractants are more problematic than others. This difference in protein assimilation equated to over one half of a full trophic level (DeNiro and Epstein 1981), which suggests that coyotes reported for conflict consumed fewer prey and more low-protein foods such as compost, cultivated fruit, and bird seed (Van Hemert et al. 2012). Our scat data supported this suggestion; cultivated fruit was the most prevalent form of anthropogenic food in Calgary and bird seed was the most common type in Edmonton. A suggestion that cultivated fruit, compost, and bird seed are highly attractive to wildlife is not new; they are already known to attract black bears in North America (Merkle et al. 2011), red foxes in Switzerland (Contesse et al. 2004), raccoon dogs *Nyctereutes procyonoides* in Finland (Kauhala and Kowalczyk 2011), and raccoons in both Japan (Ikeda et al. 2004) and North America (Prange et al. 2004). By contrast, cats and dogs combined were present in less than 5% of scats and that value was even lower in most other studies (Gehrt and Riley 2010). Although consumption of dogs by coyotes was quite rare, territorial attacks on dogs may remain another important source of conflict (Lukasik and Alexander 2011).

The contribution of food conditioning to conflict behaviour is well known (Herrero 1985, Hopkins et al. 2012); less well established is the link between conflict and specific types of food and our speculation that low-protein food sources may contribute disproportionately to conflict, potentially through poor nutrition. We recommend that future studies explore this association mechanistically by comparing the long-term diets and behaviours of individual animals to identify and secure the foods that are most likely to produce conflict. This work may reveal that some kinds of anthropogenic foods, such as backyard compost piles and unharvested crab apples, have been overlooked as important contributors to conflict involving urban coyotes. As urbanization expands and rates of conflict between humans and wildlife continue to rise, coexistence will be increasingly dependent on detailed knowledge of how urban-adapted species use anthropogenic resources.

References

Alexander, S. M. and Quinn, M. S. 2011. Coyote (*Canis latrans*) interactions with humans and pets reported in the Canadian print media (1995–2010). – Hum. Dimens. Wildl. 16: 345–359.

Alexander, S. M. and Quinn, M. S. 2012. Portrayal of interactions between humans and coyotes (*Canis latrans*): content analysis of Canadian print media (1998–2010). – Cities Environ. 4: Article 9.

Alzaga, V. et al. 2008. Body condition and parasite intensity correlates with escape capacity in Iberian hares (*Lepus granatensis*). – Behav. Ecol. Sociobiol. 62: 769–775.

Angert, A. L. et al. 2011. Do species' traits predict recent shifts at expanding range edges? – Ecol. Lett. 14: 677–689.

Arjo, W. M. et al. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. – J. Mammal. 83: 754–766.

Bateman, P. W. and Fleming, P. A. 2012. Big city life: carnivores in urban environments. – J. Zool. 287: 1–23.

Bekoff, M. 2001. Coyotes: biology, behavior, and management. – Blackburn Press.

Brand-Miller, J. C. et al. 2002. Glycemic index and obesity. – Am. J. Clin. Nutr. 76: 281S–5S.

Contesse, P. et al. 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. – Mamm. Biol. 69: 81–95.

Curtis, P. and Hadidian, J. 2010. Responding to human–carnivore conflicts in urban areas. – In: Gehrt, S. et al. (eds), Urban carnivores: ecology, conflict, and conservation. Johns Hopkins Univ. Press, pp. 201–211.

DeNiro, M. J. and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. – Geochemica Cosmochim. Acta 45: 341–351.

Ezenwa, V. O. 2004. Interactions among host diet, nutritional status and gastrointestinal parasite infection in wild bovids. – Int. J. Parasitol. 34: 535–542.

Fedriani, J. M. et al. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals ? An example with coyotes in southern California. – Ecography 24: 325–331.

Gehrt, S. D. and Riley, S. P. D. 2010. Coyotes (*Canis latrans*). – In: Gehrt, S. et al. (eds), Urban carnivores: ecology, conflict, and conservation. Johns Hopkins Univ. Press, pp. 79–95.

Gompper, M. E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of north-eastern North America by coyotes. – Bioscience 52: 185–190.

Grimm, N. B. et al. 2008. Global change and the ecology of cities. – Science 319: 756–760.

Henke, S. and Bryant, F. 1999. Effects of coyote removal on the faunal community in western Texas. – J. Wildl. Manage. 63: 1066–1081.

Herrero, S. 1985. Bear attacks: their causes and avoidance. – Winchester Press.

Hilderbrand, G. V. et al. 1996. Use of stable isotopes to determine diets of living and extinct bears. – Can. J. Zool. 74: 2080–2088.

Hopkins, J. B. et al. 2012. Stable isotopes to detect food-conditioned bears and to evaluate human–bear management. – J. Wildl. Manage. 76: 703–713.

Hosmer, D. W. and Lemeshow, S. 2000. Applied logistic regression. – Wiley-Interscience.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. – J. Theor. Biol. 29: 151–154.

Ikeda, T. et al. 2004. Present status of invasive alien raccoon and its impact in Japan. – Global Environ. Res. 8: 125–131.

Jahren, A. H. and Kraft, R. A. 2008. Carbon and nitrogen stable isotopes in fast food: signatures of corn and confinement. – Proc. Natl Acad. Sci. USA 105: 17855–17860.

Jost, L. 2006. Entropy and diversity. – Oikos 113: 363–375.

Kamler, J. F. and Gipson, P. S. 2000. Space and habitat use by resident and transient coyotes. – Can. J. Zool. 78: 2106–2111.

Kauhala, K. and Kowalczyk, R. 2011. Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: history of colonization, features behind its success, and threats to native fauna. – Curr. Zool. 57: 584–599.

Latham, A. D. M. et al. 2013. Spatial relationships of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) with woodland caribou (*Rangifer tarandus caribou*) during the calving season in a human-modified boreal landscape. – Wildl. Res. 40: 250–260.

Lefcheck, J. S. et al. 2013. Physiological effects of diet mixing on consumer fitness: a meta-analysis. – Ecology 94: 565–572.

Lowry, H. et al. 2013. Behavioural responses of wildlife to urban environments. – Biol. Rev. Camb. Phil. Soc. 88: 537–549.

Lukasik, V. and Alexander, S. 2011. Human–coyote interactions in Calgary, Alberta. – Hum. Dimens. Wildl. 16: 114–127.

Lukasik, V. M. and Alexander, S. M. 2012. Spatial and temporal variation of coyote (*Canis latrans*) diet in Calgary, Alberta. – Cities Environ. 4: Article 8.

Mattioli, L. et al. 2004. Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north-eastern Apennine, Italy. – J. Zool. 264: 249–258.

McKinney, M. L. 2002. Urbanization, biodiversity and conservation. – Bioscience 52: 883–890.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. – Biol. Conserv. 127: 247–260.

Merkle, J. A. et al. 2011. Using stable isotope analysis to quantify anthropogenic foraging in black bears. – Hum.-Wildl. Interact. 5: 159–167.

Moore, T. D. et al. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. – Wyoming Game and Fish Dept.

Morehouse, A. T. and Boyce, M. S. 2011. From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. – Front. Ecol. Environ. 9: 440–445.

Morey, P. S. et al. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan Area. – Am. Midl. Nat. 158: 147–161.

Pinheiro, J. et al. 2012. nlme: linear and nonlinear mixed effects models. R package version 3.1-118. – < http://CRAN.R-project. org/package = nlme>.

Poessel, S. A. et al. 2013. Patterns of human–coyote conflicts in the Denver Metropolitan Area. – J. Wildl. Manage. 77: 297–305.

Prange, S. et al. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movement and spatial distribution. – J. Mammal. 85: 483–490.

Pruss, S. D. 2002. Ecology of coyotes (*Canis latrans*) in Elk Island National Park, Alberta, Canada. – PhD thesis, Dept of Ren. Res., Univ. of Alberta, Edmonton, AB, Canada.

Quinn, T. 1997. Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. – Northwest Sci. 7: 1–5.

Samuel, W. et al. 2001. Parasitic diseases of wild mammals. – Iowa State Univ. Press.

Suryan, R. M. et al. 2000. Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. – Condor 102: 374–384.

Van Hemert, C. et al. 2012. Stable isotopes identify dietary changes associated with beak deformities in black-capped chickadees (*Poecile atricapillus*). – Auk 129: 460–466.

Votier, S. C. et al. 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. – J. Appl. Ecol. 47: 487–497.

Weiser, E. L. and Powell, A. N. 2010. Does garbage in the diet improve reproductive output of glaucous gulls? – Condor 112: 530–538.

White, L. A. and Gehrt, S. D. 2009. Coyote attacks on humans in the United States and Canada. – Hum. Dimens. Wildl. 14: 419–432.

Williams, N. S. G. et al. 2006. Range expansion due to urbanization: increased food resources attract grey-headed flying-foxes (*Pteropus poliocephalus*) to Melbourne. – Austral Ecol. 31: 190–198.

Windberg, L. A. et al. 1991. Body size and condition of coyotes in southern Texas. – J. Wildl. Dis. 27: 47–52.