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Food habits and anthropogenic supplementation in coyote diets along an urban-rural gradient

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Abstract: Coyotes (*Canis latrans*) are recent colonists of the southeastern United States and have broadened their niche to include exploitation of urban areas. We examined the diet of coyotes inhabiting areas of differential development by humans and assessed prevalence of anthropogenic feeding, to detect a possible shift in dietary trends by collecting and examining 159 fecal samples from urban, exurban, and rural areas of east-central Alabama, USA. Consumption of anthropogenic food did not vary along the urban-rural gradient, and foods consumed were similar among habitats. While results of our study can provide insight to guide decisions about managing populations of urban-exurban coyotes in the region, further research should be conducted in a diversity of developed areas to assist wildlife managers in evaluating strategies for managing populations of urban-exurban coyotes.

Key words: anthropogenic feeding, *Canis latrans*, coyote, diet, food habits, scat analysis, urban carnivore

Research on the diet of coyotes (*Canis latrans*) has spanned decades (e.g., Sperry 1934, Young and Jackson 1951, Korschgen 1957, Gipson 1974, Bowyer et al. 1983, Quinn 1997, Cepek 2004) throughout much of North America. In the last 25 years, Alabama has experienced a gradual shift in reported human–coyote interactions from primarily agriculture to primarily exurban (Armstrong 2012, Damm et al. 2015). Exurban areas have approximately 6–25 homes/km^2 and include an interspersion of rural housing developments and agriculture along the edges of more developed urban areas (Hansen et al. 2005).

While studies of the diet of coyotes have been conducted in the southeast region of the United States (e.g., Wooding et al. 1984, Lee and Kennedy 1986, Blanton and Hill 1989, Hoerath and Causey 1991, Chamberlain and Leopold 1999, Etheredge et al. 2015, Kelly et al. 2015, Swingen et al. 2015, Cherry et al. 2016), none have focused specifically on anthropogenic sources of food or differences in diet where coyotes live in proximity to humans in the Southeast. With increasing populations in urban-exurban areas, as evidenced by increasing numbers of harvested coyotes (Alabama Division of Wildlife and Freshwater Fisheries 2013), and human–coyote interactions in these areas (F. Boyd, U.S. Department of Agriculture, personal communication), it is critical that we understand dynamics of their diet in areas occupied by humans.

White-tailed deer (*Odocoileus virginianus*) play a vital role in the diet of coyotes in some regions (Ozoga and Harger 1966, Todd 1985). In a study in west Alabama, Hoerath and Causey (1991) noted an increase in deer hair in coyote scat during fawning season and during hunting season (mid-October to mid-February). Outside of fawning season, presence of deer in the diet has been mostly attributed to non-predation sources (Hamilton 1974, Kleinman and Brady 1978, Cepek 2004, Schrecengost et al. 2008). However, other studies have verified predation on adult white-tailed deer by coyotes (Chitwood et al. 2014, Kilgo et al. 2016). It would appear that coyotes are behaving in a predatory fashion with regards to fawns (Holle 1978). Recently, there have been studies in the southeast region suggesting that survival of fawns has been significantly reduced by coyotes (e.g., VanGilder et al. 2009, Jackson and Ditchkoff 2013, Kilgo et al. 2014).

Anthropogenic feeding (i.e., feeding on foods associated with humans) in mammals often is linked to synurbanization—the adjustment animals make to specific conditions of the urban environment (Luniak 2004). Specific to coyotes, studies conducted in urbanized landscapes have reported diets dominated by natural foods, such as small mammals and seasonal fruits, with the presence of anthropogenic foods varying considerably (McClure et al. 1995, Fedriani et al. 2001, Morey et al. 2007). As noted by Van Vuren and Thompson (1982), coyotes will consume whatever foods are locally and seasonally available.

The urban-rural interface is the most resource-rich and fastest-growing habitat available to coyotes (Fedriani et al. 2001). Anthropogenic feeding indicates behavioral plasticity under anthropogenic pressure, and consumption of anthropogenic foods has been linked to certain behavioral changes (Timm et al. 2004). Absence of harassment allows animals to habituate to humans and a developed landscape (Orthmeyer et al. 2007), creating potential for negative coyote–human interactions including aggressive behavior and attacks on pets and humans.

The primary focus of our study was to examine the diet of coyotes in areas of differing levels of development by humans in a region of the southeastern coastal plain of the United States, and to examine the extent of anthropogenic feeding to determine if exurban habitats influence the diet of coyotes. By measuring the extent of anthropogenic foods in the diet, managers can gain a better understanding of how coyotes are using the urban-exurban matrix. This information would provide a basis for management decisions regarding urban coyotes and reduce the risk of negative coyote–human interactions.

Methods

We conducted the study in east-central Alabama, centering on the cities of Auburn and Opelika (Lee County). These cities have doubled in size since the late 1980s (American Planning Association 2010), with this growth occurring in a meandering fashion as a result of the Performance Zoning Regime, which allows for multiple land uses within a district instead of the traditional Euclidean system (i.e., pertaining to geometric principles) of designating parcels of land for specific uses.

We collected fecal samples (scats) from September 2007 through February 2009 on public and private lands bimonthly and opportunistically by walking trails, roads, and footpaths, and by driving unpaved roads. In addition to scats, we collected road-killed animals on an opportunistic basis, and contents of the large intestine were taken for analysis. We processed scats in methods similar to those described by Korschgen (1971). We used frequency of occurrence (FOC) as an indicator of how often a diet item occurred and determined it by quantifying the number of samples that included a particular food item. This was a separate measurement from volumetric proportion, which we calculated by dividing the frequency of each item by the total number of items (and expressing it as a percentage). We classified items as taxonomically-specific as possible and later condensed items into categories for statistical analysis. Anthropogenic items included synthetic materials such as plastic, paper products, rubber, tin foil, food wrappers, and human hair.

To examine diets, we analyzed foods by volumetric intake (using estimates of volumetric proportions of items consumed), and frequency of consumption, (using frequency of occurrence for each item encountered; (Korschgen 1971). We used Statistical Analysis Software (SAS Institute, Inc. 2001) to perform a non-parametric chi-square test to determine the frequency at which items occurred in the diet across the urban-rural gradient. In instances where values in cells of the contingency table were <5, we used Fisher's exact test. We used a parametric, 1-way multivariate analysis of variance (MANOVA) on estimates of volumetric proportions to assess significance of categories of items across the gradient. Due to inherent non-normal distribution of proportional measures, we transformed volumetric measurements using an arcsine transformation to make the data more normal. Where relationships were detected, we conducted 1-way analysis of variance (ANOVA) and an *a posteriori* test (least-squares means) for multiple comparisons among means to assess differences among habitats.

We used ArcMap in ArcGIS (ESRI) to classify sampling localities as urban, exurban, or rural and 3 parameters to calculate classifications of use: density of populations of humans, type of land cover, and density and type of roads. We obtained data on populations of humans from the U.S. Census Bureau (2000) and categorized them as humans/km²/census block. We classified roads using data from the U.S. Census Bureau (Topologically Integrated Geographic Encoding and Referencing [TIGER]/Line files, <http://www.census.gov/geo/www/tiger>, accessed September 1, 2011) and based categories on density and type of roads. We acquired information on land cover from the Alabama GAP database (Auburn University Alabama Cooperative Fish and Wildlife Research Unit) with land cover types including individual ground cover types at 30 m resolution (e.g., mixed hardwood forest, agricultural land, impervious surfaces, etc.). We arranged cover types into a rating system on a scale of 1–3, with 1 being the most natural and 3 being the most developed. As defined by the United States Census Bureau, rural areas were census blocks that had a population of 0–500 humans/1.61 km²; areas containing 1,000+ humans/1.61 km² were classified as urban, and values between these (501–1,000 humans/1.61 km²) were intermediate (exurban). Land cover also was reclassified on a 1–3 scale with natural areas classified as 1, low-intensity development 2, and medium- and high-intensity development as 3. We classified roads according to type (primary for high-traffic highways and major roads, secondary for medium-traffic local highways and main roads, and rural for lower-traffic local roads) and density (weighted by length of each type of road that persisted in each measurement unit). We averaged these ratings together to create an overall rating of density, which we then paired with class of land cover to determine if each sampling locality was urban, exurban, or rural.

Results

Overall diet

From Lee County and the surrounding counties, we collected 159 scats—91 in rural areas, 46 in exurban areas, and 22 in urban areas. Frequencies of Consumption (FOC) for each item in the diet and means of Volumetric Proportions (VP; Table 1) did not always coincide. We encountered the "other plants" category most commonly (FOC 54.1%). We did not detect amphibians and found reptiles to be the least-encountered item (FOC 1.3%). We encountered white-tailed deer as the most common mammalian prey (FOC 37.7%).

In terms of VP, persimmons (*Diospyros virginiana*) and deer were the most important food items.

Overall, we found anthropogenic sources of food comprising 15.0% of the diet volumetrically, being consumed at a frequency of 13.8%. Anthropogenic supplementation was comparable across the gradient and did not significantly vary among habitats. It is noteworthy to mention that deer consumed during the hunting season were presumed to have been scavenged from hunter kills and comprised a large proportion of anthropogenic feedings (18 occurrences). Only 1 each of wild turkey (*Meleagris gallopavo*) and mourning dove (*Zenaida macroura*) were detected (Table 2, Aves).

Diet along the urban-rural gradient

We found grass (Poaceae) to be the most common food item (FOC 42.8%) but it only comprised 4.2% of the total volume of diet of rural animals; there was an increasing trend in frequency of grass from urban to rural areas. Deer were in 39.6% (FOC) of rural samples, were consumed in the greatest volume compared to other foods (21.3%), and differed from exurban samples ($P = 0.007$); however, persimmons were similar to deer, occurring 31.9% of the time at a volume of 20.2%. The most common prey based on FOC were insects (28.6%), while the most common mammalian prey were rodents at 24.2%.

In exurban areas, insects were the most common food item (FOC 45.7%), but were only 4.7% of the volume in exurban habitats. The proportion of insects in the diet in exurban areas was greater than in urban and rural areas ($P = 0.025$). Neither reptiles nor the category "Other Mammals" (Table 2) were in exurban samples, and "Other Invertebrates" were the least-encountered items (FOC 4.4%). Deer, the most common mammalian prey overall in exurban areas, were in 26.1% of exurban samples. Persimmon was the most prevalent item in terms of volume (20.3%), followed by rabbits (*Sylvilagus* spp.; 13.9%).

In urban areas, "Other Plants" and deer were the most common items, both with a frequency of consumption of 54.6%. Proportions of other plants used were slightly greater in urban areas compared to exurban areas ($P = 0.057$), as was their frequency of occurrence ($P = 0.056$). Other native fruit was the next most frequent

Table 1. Occurrences, frequency of occurrence (FOC, expressed as a percentage), mean, standard error, and maximum values of volumetric proportions of food items of coyotes (*Canis latrans*), September 2007 to February 2009.

Food item	# Occurrences	% FOC	SE	Mean	Min	Max
Non-vascular land plants (Bryophyta)	5	3.14	0.002	0.001	0.000	0.100
Grass fam. (Poaceae)	68	42.77	0.050	0.010	0.000	1.000
Maple fam. (Aceraceae)	1	0.63	0.001	0.001	0.000	0.150
Buttercup fam. (Rannunculaceae)	6	3.77	0.006	0.003	0.000	0.500
Rose gen. (*Rubus*)	6	3.77	0.001	0.001	0.000	0.075
Apple gen. (*Malus*)	2	1.26	0.002	0.001	0.000	0.200
Pear gen. (*Pyrus*)	5	3.14	0.001	0.001	0.000	0.100
Drupe fruits (Prunus)	5	3.14	0.001	0.001	0.000	0.100
Birch fam. (Betulaceae)	11	6.92	0.006	0.003	0.000	0.300
Mulberry and fig fam. (Moraceae)	4	2.52	0.011	0.007	0.000	1.000
Legume fam. (Fabaceae)	2	1.26	<0.001	<0.001	0.000	0.050
Gourd fam. (Cucurbitaceae)	1	0.63	0.002	0.002	0.000	0.250
Walnut fam. (Juglandceae)	1	0.63	<0.001	<0.001	0.000	0.050
Coffee and madder fam. (Rubiaceae)	1	0.63	<0.001	<0.001	0.000	0.010
Nightshade fam. (Solanaceae)	2	1.26	<0.001	<0.001	0.000	0.010
Mustard gen. (*Brassica*)	2	1.26	<0.001	<0.001	0.000	0.050
Oak gen. (*Quercus*)	11	6.92	0.008	0.004	0.000	0.650
Elm gen. (*Ulmus*)	1	0.63	<0.001	<0.001	0.000	0.050
Alder gen. (*Alnus*)	2	1.26	0.002	0.001	0.000	0.150
Pine (*Pinus*)	14	8.81	0.007	0.003	0.000	0.400
Blueberry (*Vaccinium* spp.)	4	2.52	0.001	0.001	0.000	0.100
Grape gen. (*Vitis*)	13	8.18	0.25	0.010	0.000	0.900
Cranesbill gen. (*Geranium*)	2	1.26	<0.001	<0.001	0.000	0.010
Tulip poplar (*Liriodendron tulipifera*)	2	1.26	<0.001	<0.001	0.000	0.505
Persimmon (*Diospyros virginianus*)	53	33.33	0.184	0.027	0.000	1.000
Ragweed (*Ambrosia artemesifolia*)	1	0.63	0.001	0.001	0.000	0.100
Unknown plant matter	20	12.58	0.012	0.004	0.000	0.600
Arachnids (Arachnida)	2	1.26	<0.001	<0.001	0.000	0.050
Segmented worms (Annelida)	1	0.63	<0.001	<0.001	0.000	0.010
Beetle fam. (Coleoptera)	28	17.61	0.013	0.006	0.000	0.950
Grasshopper/cricket fam. (Orthoptera)	23	14.47	<0.001	<0.001	0.000	0.008
Butterfly/moth fam. (Lepidoptera)	5	3.14	0.005	0.003	0.000	0.500
Earwig fam. (Dermaptera)	1	0.63	<0.001	<0.001	0.000	0.100
True flies (Diptera)	3	1.89	0.001	0.001	0.000	0.050
Wasp/bee/ant fam. (Hymenoptera)	5	3.14	0.001	0.001	0.000	0.100
Unknown insect	2	1.26	<0.001	<0.001	0.000	0.050
Snails (Gastropoda)	3	1.89	<0.001	<0.001	0.000	0.050
Crustaceans (Crustacea)	1	0.63	0.006	0.006	0.000	0.950
Wood lice (Isopoda)	1	0.63	<0.001	<0.001	0.000	0.050

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Food item	# Occurrences	% FOC	SE	Mean	Min	Max
Unknown vertebrate	2	1.26	0.001	<0.001	<0.001	0.050
Bony fish (Osteicthyes)	9	5.66	0.019	0.009	0.000	0.950
Amphibians (Amphibia)	0	0.00	0.000	0.000	0.000	0.000
Reptiles (Reptilia)	2	1.26	0.003	0.002	0.000	0.300
Birds (Aves)	11	6.92	0.017	0.007	0.000	0.750
Eastern gray squirrel (*Sciurus carolinensis*)	6	3.77	0.080	0.004	0.000	0.600
Fox squirrel (*Sciurus niger*)	2	1.26	0.011	0.008	0.000	0.000
Eastern chipmunk (*Tamias striatus*)	1	0.63	0.003	0.003	0.000	0.400
North American beaver (*Castor canadensis*)	2	1.26	0.011	0.008	0.000	0.900
Hispid cotton rat (*Sigmodon hispidus*)	15	9.43	0.052	0.016	0.000	1.000
Vole gen. (*Microtus*)	8	5.03	0.017	0.008	0.000	0.700
Eastern harvest mouse (*Reithrodontomys humulis*)	2	1.26	0.001	0.001	0.000	0.010
Southeastern pocket gopher (*Geomys pinetis*)	1	0.63	<0.001	<0.001	0.000	0.050
True rat gen. (*Rattus*)	3	1.89	0.012	0.007	0.000	0.800
House mouse (*Mus musculus*)	1	0.63	0.001	0.001	0.000	0.100
Meadow jumping mouse (*Zapus husdonius*)	1	0.63	0.002	0.002	0.000	0.300
Cottontail gen. (*Sylvilagus*)	25	15.72	0.098	0.022	0.000	1.000
Nine-banded armadillo (*Dasypus novemcinctus*)	1	0.63	0.001	0.002	0.000	0.100
White-tailed deer (*Odocoileus virginanus*)	60	37.74	0.183	0.026	0.000	1.000
Coyote (*Canis latrans*)	4	2.52	0.002	0.001	0.000	0.150
Gray fox (*Urocyon cinereoargenteus*)	1	0.63	0.000	0.000	0.000	0.010
Raccoon (*Procyon lotor*)	4	2.52	0.012	0.007	0.000	0.650
Oppossum (*Didelphis virginiana*)	4	2.52	0.007	0.005	0.000	0.800
Bobcat (*Lynx rufus*)	1	0.63	0.000	0.000	0.000	0.001
Shrew (*Soricomorpha*)	2	1.26	0.000	0.000	0.000	0.003
Pig (*Sus scrofa*)	1	0.63	0.006	0.006	0.000	1.000
House cat (*Felis catus*)	12	7.55	0.028	0.011	0.000	0.900
Domestic dog (*Canis lupus familiaris*)	1	0.63	0.006	0.006	0.000	1.000
Human (*Homo sapiens*)	2	1.26	0.000	0.000	0.000	0.010
Unknown mammal	8	5.03	0.008	0.006	0.000	1.000
Soil	11	6.92	0.026	0.009	0.000	0.750
Bark/twigs	16	10.06	0.008	0.002	0.000	0.200
Gravel/rocks	15	9.43	0.007	0.002	0.000	0.150
Anthropogenic	20	12.58	0.042	0.012	0.000	0.900
Unknown material	3	1.89	0.010	0.007	0.000	0.850

Table 2. Average estimates of volumetric proportions (%) of food items of coyotes (*Canis latrans*) in differing areas of development by humans, Lee Co., Alabama, USA, September 2007 to February 2009.

Food item	Rural	Exurban	Urban
Persimmons	20.23	20.26	6.59
Other native fruits	4.34	11.29	9.33
Grasses	4.21	6.04	5.82
Other plants	5.07	2.07	7.50
Insects	1.13	4.68	0.30
Other invertebrates	1.18	0.04	0.00
Amphibians	0.00	0.00	0.00
Reptiles	0.33	0.00	0.68
Birds	1.44	2.72	0.68
Rodents	11.13	10.76	16.36
Rabbits	7.36	13.91	11.14
Deer	21.26	6.40	30.91
Carnivores	3.32	0.67	0.05
Other mammals	3.19	0.00	0.00
Unknown mammals	1.18	0.24	0.05
Abiotic materials	3.40	5.22	4.14
Anthropogenic	16.27	11.96	15.73

item at 50%. Consumption of deer in urban areas varied from that in exurban areas (P = 0.007). Aside from deer, rodents were the most-encountered prey (FOC 27.3%). Deer were the most important item volumetrically (30.9%), followed by rodents (16.4%).

Diversity of diet was greatest in rural areas with a total of 66 kinds of items, and least in urban areas with 32 items; diversity was intermediate in exurban areas with 37 items recorded. In terms of vegetation, 21 species of plants were in diets of rural coyotes, 10 in exurban, and 16 in urban. Diversity of prey was greatest in rural areas at 25 items and decreased along the gradient, with 14 items in exurban areas and 11 in urban areas.

Anthropogenic feeding

Anthropogenic feeding is often associated with ingestion of trash, debris, and other synthetic (man-made) material; however, anthropogenic foods may go undetected if their origin is not carefully considered. Supplementation in the form of natural foods provided by humans may be overlooked (e.g., commensal rodents, livestock, and domestic pets). We detected anthropogenic items 67 times in our sample. Synthetic materials were the most common anthropogenic items (20 occurrences), followed by deer (18 occurrences). It is important to mention that the inclusion of natural anthropogenic items (naturally occurring items provided as supplemental items by humans) with synthetic material increased the prevalence of anthropogenic items nearly 2-fold.

Discussion

We found that coyotes were consuming similar items along the urban-rural gradient and that they were continuing to operate as opportunistic feeders, eating what was most readily available. With regards to anthropogenic supplementation, coyotes fed on a wide variety of items and appeared to be nonselective in what they consumed.

Overall diets

Urban and exurban areas generally are believed to be resource-rich areas for exploitation; however, prevalence of anthropogenic feeding did not differ across the urban-rural gradient and was relatively similar in each habitat. This is not surprising, as availability of anthropogenic foods seems to be consistent along the gradient. While rural areas by definition have a lower human population, they receive nominal amounts of vehicular traffic. Refuse along roadsides, in washes, and along property boundaries is common. Also, cities do not collect trash outside their limits, and residents of rural areas either take their waste to a community dump site or burn it on their own property, making trash a readily available resource for coyotes.

Deer (FOC 37.7%, VP 18.3%) was the second most important food item volumetrically after persimmon, which was almost identical in volume (18.4% VP). This is somewhat novel for animals in urban-exurban areas, as similar studies do not report such high occurrence of deer in diets of coyotes (MacCracken 1982, Atkinson and Shackleton 1991, McClure et al. 1995, Fedriani et al. 2001).

With the exception of white-tailed deer, the detection of Alabama-recognized game animals in scats of coyotes was diminutive. Wild turkey and mourning dove were only consumed on 1 occasion each, and no quail (*Coturnix coturnix*) or waterfowl were detected. While rabbits occurred commonly, they were in exurban areas where hunting was not permitted, thus eliminating potential competition between hunters and coyotes. These results should not be interpreted to rule out nest predation, for which evidence may not persist since the soft tissues of eggs and natal animals are often not evidenced in scat.

Diets along the urban-rural gradient

Diet of urban coyotes. Vegetation was an important part of the diet overall (the most commonly encountered food), particularly in diets of urban coyotes in terms of volume and frequency of consumption. A possible reason for frequent consumption of plant material in urban areas could be that other sources of nourishment are lacking. Increased consumption of vegetation could be because non-mast plants are not as nutritious as other foods (e.g., fruits, animal protein) and therefore need to be consumed in greater volume. Increased consumption of vegetation in urban areas could merely be a function of availability of such items, and a paucity of others, as was postulated by Stratman and Pelton (1997). In urban areas, many invertebrates and mammals were not encountered in the diet, most likely because these items usually are not associated with urban areas. This supports the hypothesis that coyotes are eating what is locally available in the habitat in which they are foraging, consistent with what others have observed (MacCracken 1982, McClure et al. 1995).

Deer was the most widely consumed item by urban coyotes (30.9% VP) and differed significantly from exurban areas, occurring twice as much by volume as any other item consumed; this is presumably in the form of carrion from road-killed animals. Road-killed deer in Alabama are abundant and widespread, as deer–vehicle collisions are common and frequent (Hussain et al. 2007). After deer and other plants, fruit followed closely in terms of frequency of consumption. This is not surprising because many suburban-dwellers cultivate gardens and berry patches that are easily exploited by coyotes.

Diet of exurban coyotes. Exurban areas, the presumed transition zone for dietary shifts, revealed persimmon as being the most heavily consumed item at 20.3% VP. This is almost identical to what was observed in rural areas, where persimmon was consumed at 20.2% VP. Persimmon trees are common in natural areas of the Southeast but are not commonly encountered in urbanized landscapes. The only food that differed significantly in exurban areas was insects, which occurred in greater volume than in urban and rural areas. This is likely due to the life-history traits of insects that were consumed. The majority of insects consumed consisted of orthopterans (grasshoppers and crickets); these insects are most often encountered in areas where grass is abundant. Exurban areas are laden with empty parcels, power line corridors, and early successional areas that would support such insect life.

Deer occurred less frequently in diets and in lower volumes in exurban areas than in urban and rural areas. Volumetric proportion of deer in the diet was 6.4% compared to 30.9% and 21.3% in urban and rural areas, respectively. This is surprising, because exurban areas should have relatively equal proportions of deer compared to urban and rural areas. Deer were common in residential areas, and vehicular-traffic patterns are sufficient to produce road-killed animals in a similar proportion to their occurrence in urban areas; thus, deer–vehicle collisions might be nearly as common in exurban areas as they are in urban areas. Deer–vehicle collisions occur more often in fragmented landscapes of mixed use, such as exurban areas (Hussain et al. 2007). Low occurrence of deer in diets of exurban coyotes is puzzling.

Diets of rural coyotes. In rural areas, grass was the most commonly encountered item, but only comprised 4.2% VP of the diet. Possible theories for coyotes' use of grasses are: as a digestive agent similar to behavior observed in domestic dogs (Thorne 1995); a mechanical function, forming a bolus of indigestible fibers that serve to scrub the intestines, helping to eliminate intestinal parasites (L. Emmons, Smithsonian Institution, personal communication); and a deliberate choice, suggesting further investigation of the nutritive properties of grass and its importance in the diet of coyotes (Best et al. 1981). Volumetrically, deer was the most important food item in rural areas, followed closely by persimmon; this is similar to what was observed overall.

Anthropogenic feeding

Although there was no difference along the gradient, anthropogenic items comprised a fair amount of the diet, occurring in 13.8% of samples, and being consumed at 15% volume, the third most important food volumetrically. It is possible that anthropogenic foods are widely available and not concentrated in urban-exurban areas as was hypothesized. Another possible explanation could be that animals feeding in urban and exurban areas are not strictly foraging in those areas. As samples were collected without knowledge of sex, age, or social status of the individual from which it was collected, there was no information available regarding home range or other behaviors.

Deer was an important component of diet across the urban-rural gradient. Predation on fawns has been observed in the Southeast (Saalfeld and Ditchkoff 2007, Kilgo et al. 2014). In this study, deer were consumed 60 times by coyotes, 18 during the period when fawns were most susceptible to predation (mid-July through late September in this study area). We hypothesized that most consumption of deer is a function of coyotes scavenging carrion. While traditional evidence of anthropogenic feeding was detected, it is likely that natural anthropogenic foods, such as road-killed deer, were underestimated, and the extent of anthropogenic supplementation in the diet was greater than actually observed.

Previous studies of diet of coyotes in developed areas have been conducted in highly urbanized cities in the United States, such as San Diego, California (MacCracken 1982), Los Angeles, California (Fedriani et al. 2001), and Chicago, Illinois (Morey et al. 2007). Results of this study are largely consistent with studies in developed areas (MacCracken 1982, Atkinson and Shackleton 1991, McClure et al. 1995, Parker 1999, Fedriani 2001, Morey et al. 2007). Diet varied by locality and availability. While the Auburn-Opelika area meets the technical definition of an urban area, the degree of development and juxtaposition of the landscape differ considerably from more traditional urban areas. This could explain the lack of a clearly defined transition zone in exurban areas, where it was expected to observe intermediate levels of native and non-native foods. As prevalence of anthropogenic food has differed considerably among studies, the relatively low occurrence of anthropogenic foods in urban-exurban areas at this study site may or may not be influenced by this landscape.

Management implications

Overall, we observed few differences in diet of coyotes along the urban-rural gradient. The dynamic nature of the landscape was a likely explanation for the similar distribution of resources along the gradient. Coyotes in the 3 habitats likely were consuming what was available, which was similar among habitats. Results of this research support previous conclusions that coyotes are highly adaptable, opportunistic omnivores, and supports previous research that availability is the rule that governs diet of coyotes. Thus, we believe that the diet is not necessarily shifting; coyotes simply are continuing to operate as opportunists, taking advantage of anthropogenic supplementation when it is available. Future research in landscapes of varying levels of development and juxtaposition may help to further elucidate diet of coyotes in diverse urban areas.

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