Food Habits and Anthropogenic Supplementation in the Diet of Coyotes (Canis latrans) Along an Urban-Rural Gradient

by

Erica M. Santana

A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama December 13, 2010

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

Copyright 2010 by Erica M. Santana

Approved by

James B. Armstrong, Chair, Professor of Wildlife Sciences Troy L. Best, Professor of Biology Suzanne C. Peurach, Museum Specialist

Abstract

Coyotes are recent colonists of the Southeast and have broadened their niche to include exploitation of urban areas. The aim of my study was to examine diet of coyotes inhabiting areas of differential development by humans and assess prevalence of anthropogenic feeding to detect a possible shift in dietary trends. In urban, exurban, and rural areas of east-central Alabama, 159 fecal samples were collected and examined to reconstruct the diet. Consumption of anthropogenic food did not vary significantly along an urban-rural gradient. Foods consumed were similar among habitats; coyotes consumed food items that were available. There was greater consumption of white-tailed deer (Odocoileus virginianus) in urban and rural areas than exurban areas, more feeding on insects in exurban areas than either urban or rural areas, and more consumption of vegetative matter in urban areas than in exurban or rural areas. While results of this study can provide insight to guide decisions about managing populations of urbanexurban coyotes in the Southeast, 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.

Acknowledgments

I sincerely thank James B. Armstrong, Troy L. Best, and Suzanne C. Peurach for valuable guidance and support throughout this project. Gratitude is extended to those who helped facilitate various facets of this project. I thank C. Hansen of the Auburn University Herbarium for assistance with identification of plants, E. Snoddy of the Auburn University Department of Entomology for help with identification of insects, S. Sammons and B. Trimble of the Auburn University Department of Fisheries and Allied Aquacultures for assistance with identifying fish scales and information about the study site, C. Guyer of the Auburn University Department of Biological Sciences for help with identification of herpetofauna, R. Thorington and C. Dove of the Smithsonian Institution for help with identification of osteological material and feathers, L. Crandall of the Southeastern Raptor Center for use of facilities and equipment, M. Smith and S. Ditchkoff of Auburn University Department of Forestry and Wildlife Sciences for help with building the GIS model and advice and guidance via discussion, undergraduates B. Rubeck, C. Irons, and M. Alcorn for assistance in processing samples, G. Gaston for help collecting scats, and P. Staudenmaier for wise council and constant willingness to provide support. I also extend a special thanks to P. Getsgow of Seale, Alabama, for contributing valuable insight and experience to the project. I am indebted to my family for their support throughout my academic journey, for their empathy, encouragement, and relentless love. I extend a most special thanks to Donna Hesterman, my mentor and friend, whose advice and counsel have been instrumental in my professional and personal

development. Funding was provided by the Auburn University School of Forestry and Wildlife Sciences and the Center for Forest Sustainability, and I thank them for their support.

Table of Contents

Abstract	ii
Acknowledgments	
List of Tables	
List of Figures	vii
Introduction	
Materials and Methods	7
Results	12
Discussion	16
Conclusion	30
Literature Cited	33

List of Tables

Table 1.	Number of occurrences, frequency of occurrence (expressed as a percentage), mean, standard error, minimum, and maximum values of volumetric proportions of food items of coyotes, September 2007-February 2009
Table 2.	Average estimates of volumetric proportions (expressed as a percentage) of food items of coyotes in differing areas of development by humans, September 2007-February 2009
Table 3.	Volumetric variation in means of food items along an urban-rural gradient for coyotes, September 2007-February 2009. Statistically homogenous subsets derived from least-squared means analysis are shown by lines below habitat numbers and ranked means. Sample size for each dietary category, degrees of freedom, <i>F</i> -ratios, and <i>P</i> -values are given
Table 4.	Comparison of studies of diets of coyotes in developed areas, including frequencies of occurrence (expressed as a percentage) for specific food items (modified from Gehrt 2007)

List of Figures

Figure 1.	Number of occurrences of anthropogenic foods consumed by	
	coyotes, September 2007-February 2009.	.53

INTRODUCTION

Research on diet is a cornerstone in wildlife management. As early as 1935, Errington noted the importance of studying diets of wildlife to understand life-history and nutritional requirements, and to lay groundwork for further, more specialized research. Knowing specific prey that an organism consumes can help explain foraging behavior and answer broader questions about feeding ecology, including availability, preference, seasonality, and abundance of foods (Windberg and Mitchell 1990, Rose and Polis 1998). Additionally, information on diet can assist wildlife managers in deciding which sources of food are important to preserve, enhance, or eliminate, or how diets of predators affect other species.

Research on diet of the coyote (*Canis latrans*) has spanned decades, e.g. Sperry (1934), Korschgen (1957), Gipson (1974), Bowyer et al. (1983), Quinn (1997), Cepek (2004); however, most literature about diet of coyotes reflects studies conducted in the western part of the range in North America. A geographic expansion of the range of coyotes into the eastern United States began in the early 20th century following extirpation of wolves (Young and Jackson 1951). This expansion occurred later in the Southeast than the Northeast, and it is likely that the dynamics (e.g., increasing densities) from this expansion are still changing across much of the southeastern region of the United States. While diet of coyotes in other regions and habitats has been studied extensively (desert, Hernandez and Delibes 1994; boreal forest, Samson and Crête 1997; Great Plains, Huebschman et al. 1997; coastal, Rose and Polis 1998),

and some studies have been conducted in the Southeast region (Lee and Kennedy 1986, Wooding et al. 1984, Hoerath and Causey 1991), none have focused specifically on anthropogenic sources of food or differences in diet where coyotes live in proximity to humans in the Southeast. There is a need for continued research on diet of coyotes, as there has been a dearth of studies conducted in the past 25 years, and the dynamic ecology of these adaptable animals likely has changed in areas where it has a close association with humans.

As the geographic range of coyotes expanded eastward, coyotes evolved physical adaptations to exploit new habitats (Bekoff and Wells 1982). Hilton (1978) emphasized differences in eastern coyotes compared to western populations, suggesting that changes in life-history traits could be attributed to hybridization with wolves. There are 19 extant subspecies of the coyote Wilson and Reeder (2005); Canis latrans frustor, the Southeastern coyote, is the largest and, based on the paucity of literature, appears to be the least known of these. Hybridization with wolves has allowed for an increase in size, as well as changes in cranial and dental morphology (Hilton 1978). These changes, paired with a wider diversity of prey, could cause dietary patterns of southeastern coyotes to vary considerably from coyotes in other regions. Hybridization with domestic dogs has been documented in southeastern coyotes (Adams et al. 2003); however, it is not clear whether this genetic influence is accountable for modifications in eastern populations (Nowak 2001). Eastern populations have a later eruption of teeth and a different order of emergence as opposed to western populations, a feature that could be the result of a mixed ancestry with domestic dogs (Beckoff and Jamison 1975). Hilton (1978) suggested that the

feeding strategy of eastern populations has expanded from the traditional role of an opportunistic scavenger and predator of small mammals to include larger prey when available.

Diets of coyotes at the urban-rural interface (the landscape interface between developed and undeveloped areas) have yet to be examined 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 2007), and human-coyote interactions in these areas (F. Boyd, per. comm.), it is critical that we understand dynamics of their diet in areas occupied by humans.

While there is considerable geographic and seasonal variation, coyotes are mostly crepuscular (Beckoff 1977). In areas with much activity by humans, such as urban areas, coyotes alter diel patterns to avoid humans (Gehrt et al. 2009). Animals living in developed areas largely are nocturnal and tend to remain under cover during the day (Kitchen et al. 2000), in contrast to animals that vary activity according to season and energetic requirements (Shivik and Barrett 1997). This resultant shift to nocturnal foraging likely has precipitated changes in diet because nocturnal foraging limits prey to species that are active at night. In addition, activity by humans causes coyotes to avoid developed areas when possible (Gehrt et al. 2009); thus affecting foraging and hunting behaviors.

One potential area of dietary shift is predation on ungulates. Ungulates, particularly deer (*Odocoileus virginianus*, *O. hemionus*), play a vital role in diet in some regions (Todd 1985, Ozoga and Harger 1966); however, deer often have been presumed to be consumed as carrion (Kleinman and Brady 1978, Cepek 2004).

Although coyotes are capable of killing a healthy, adult deer, it is uncommon. Outside of fawning season, presence of deer in the diet has been mostly attributed to non-predation sources (Hamilton 1974, Schrecengost et al. 2008). Coyotes capitalize on fawns as food during the fawning season (Holle 1978). Recently, there have been studies in the Southeast suggesting that survival of fawns has been reduced significantly by coyotes (e.g., Kilgo 2009, VanGilder et al. 2009).

Anthropogenic feeding (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). With increasing movement of wild mammals into urban-exurban areas (areas on the outskirts of cities), populations will continue to adapt to human-generated conditions. In most instances, this includes exploitation of anthropogenic foods and sources of water and cover.

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). Coyotes will consume whatever foods are locally and seasonally available (Van Vuren and Thompson 1982).

The urban-rural interface is the most resource-rich and fastest growing habitat available to coyotes (Fedriani et al. 2001). Coyotes have inhabited urban areas for >40 years, but only recently have they caused conflicts with humans and domestic animals (Orthmeyer et al. 2007). Attacks on humans are rare, but seem to be increasing (Timm et al. 2004). When they occur, they often are linked to (or correlated with) attempts to obtain anthropogenic foods (Bounds and Shaw 1994). Anthropogenic feeding

indicates behavioral plasticity under anthropogenic pressure, and consumption of anthropogenic foods has been linked to certain behavioral changes (Timm et al. 2004). In some urban areas where coyotes are abundant and conspicuous, people actually feed them. This causes coyotes to lose their natural fear of humans and become less wary. Absence of harassment allows animals to habituate to humans and a developed landscape (Orthmeyer et al. 2007), creating potential for negative coyote-human encounters including aggressive behavior and attacks on pets and humans.

While the body of literature examining diet of coyotes is expansive, many are outdated. The urban coyote is a recent phenomenon, and the need for studies of urban populations of animals was not substantiated until animals began co-habitating with humans. An examination of diet is necessary to explore possible causes of a shift in diet in urban-exurban animals. The primary focus of this study was to examine diet of coyotes in areas of differing levels of development by humans in a region of the southeastern coastal plain, and to examine extent of anthropogenic feeding to determine if exurban habitats influence 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.

MATERIALS AND METHODS

Study area

This study was conducted in Lee County and the surrounding area in east-central Alabama; i.e., Chambers, Lee, Macon, Montgomery, Russell, and Tallapoosa counties. Alabama has a humid-subtropical climate characterized by high humidity (particularly in summer) and mild winters (Bailey 1980). The study area is temperate and rainy with hot summers and no dry season, and is characterized by ≥ 8 months of $10+^{\circ}C$ weather; the coldest month is January (mean temperature is $<18^{\circ}C$). Rainfall is greatest during

summer when thunderstorms are frequent. Typical vegetation is deciduous and mixed forest with second-growth pine forest (Bailey 1980).

The cities of Auburn and Opelika, Lee County, have undergone dramatic changes in recent decades and have doubled in size since the late 1980s (American Planning Association 2010). This growth has occurred in a serpentine fashion as a result of the Performance Zoning Regime, which allows for multiple land-uses within a district instead of the traditional Euclidean system (pertaining to geometric principles) of designating parcels of land for specific uses. The nature of this schematic has produced dynamic growth and development, highly influencing the juxtaposition of developed and natural areas, and thus, making classifying entire parcels of land inaccurate. To account for this variation, I created a multi-parameter, land-classification scheme within a geographic information system (GIS) based on type of landcover, population of humans, and density and type of roads.

Methods in the Field

Fecal samples (scats) were collected on public and private lands bimonthly and opportunistically by walking trails, roads, and footpaths, and by driving unpaved roads. Upon collection, scats were placed into plastic bags and labeled with date of collection, locality (description and GPS coordinates), and any special notes about the sample or locality, similar to methods described by Korschgen (1971). Samples were frozen at -20°C until analyzed.

Road-killed animals were collected opportunistically. Dissections were conducted and contents of the large intestine were collected; these samples were pooled with samples of scats.

Laboratory Methods

Frozen scats were thawed, individually placed into nylon mesh bags, washed in a commercial washing machine on a gentle cycle without soap, and manually separated in preparation for analysis. After washing, the fecal matrix was discarded and the residue conserved. Samples were placed into polystyrene jars and labeled. After washing, samples were dried at 80°C for 48 hours. At time of processing, scats were manually separated; food items were identified via macroscopic and microscopic techniques, comparing samples to reference collections of specimens (Auburn University Collection of Mammals, Auburn University Herbarium, United States National Museum of Natural History), and by using manuals or Internet resources to identify hair (Moore et al. 1974, Teerink 1991), seeds (Martin and Barkley 1961), and other food items. Items were quantified based on ocular estimates of volume (Andelt et al. 1987, Whitaker 1988, Atkinson and Shackleton 1991, Quinn 1997, Stratman and Pelton 1997). The number of samples that included a particular food item was determined using frequency of occurrence, which was calculated by dividing frequency of each item by total number of items and expressing it as a percentage.

Items were classified as taxonomically specific as possible and were later condensed into categories for statistical analysis. Anthropogenic items included synthetic materials such as plastic, paper products, rubber, tin foil, food wrappers, and human hair. In addition, other natural items made available by humans were included in this category and included remains of fish and crustaceans that were in scats collected from the Auburn University North Fisheries Unit, where fish and crustaceans are propagated for research and commercial sale, deer that occurred during the hunting season that were believed to

be consumed as carrion, and a cantaloupe rind. The category for fruit was all native fruits excluding persimmons, the other plant category included vegetation excluding persimmons, native fruits, and grasses, and the other mammals category included soricomorphs (Soricidae), feral hogs (*Sus scrofa*), and nine-banded armadillos (*Dasypus novemcinctus*).

Methods of Analysis

ArcMap in ArcGIS (ESRI) was used to classify sampling localities as urban, exurban, or rural. Samples were marked with individual GPS locations and made into a shape file in ArcMap. Three parameters were used to calculate classifications of use: density of populations of humans, type of landcover, and density and type of roads. Data on populations of humans were from the United States Census Bureau (2000 Census) and were measured as humans/km²/census block. Data for roads were from the Census Bureau (TIGER/Line files, http://www.census.gov/geo/www/tiger) and classified based on density and type of roads. Information on landcover was acquired from the Alabama GAP (Auburn University Alabama Cooperative Fish and Wildlife Research Unit). Each parameter was further classified 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/1.61km²; areas containing 1,000+ humans/1.61km² were classified as urban, and values between these (501-1,000 humans/1.61km²) were intermediate (exurban). Landcover 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. Roads were classified according to type (primary, secondary, and rural) and density (weighted by length of each type of road that persisted in each measurement unit). These ratings were averaged together to create an overall rating.

A 1.377-km² buffer, which is the average size of the core area of coyotes inhabiting the study area (H. Jantz, unpublished data), was placed around each sampling locality and area inside the buffer was used to determine classifications of habitats. Rankings of density of populations of humans and types of roads were paired with class of landcover to determine if each sampling locality was urban, exurban, or rural.

To examine diets thoroughly, I 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). Statistical Analysis Software (SAS Institute, Inc. 2001) was used to perform a non-parametric chisquare 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, Fisher's exact test was used. A parametric, one-way multivariate analysis of variance (MANOVA) was used on estimates of volumetric proportions to assess significance of categories of items across the gradient. Due to inherent non-normal distribution of proportional measures, volumetric measurements were transformed using an arcsine transformation to make the data more normal. Where relationships were detected, one-way analysis of variance (ANOVA) was conducted and an a posteriori test (least-squares means) for multiple comparisons among means was conducted to assess differences among habitats.

RESULTS

From Lee County and the surrounding counties, 159 scats were collected; 91 in rural areas, 46 in exurban areas, and 22 in urban areas. Data were analyzed prior to performing the arcsine transformation and results of the MANOVA were nonsignificant for all foods across the urban-rural gradient. After the transformation was applied, relationships became apparent; thus, illustrating the appropriateness and importance of the transformation.

Overall Diet

Frequencies of occurrence (FOC) for each item in the diet and means of volumetric proportions are in Table 1; volume of a food item consumed and frequency of consumption did not always coincide. The category including other plants was the most commonly encountered (FOC 54.09%). Amphibians were not detected and reptiles were the least-encountered item (FOC 1.26%). White-tailed deer (*Odocoileus virginiana*) was the most common mammalian prey (FOC 37.74%). FOC-values and means of volumetric proportions for each food item are listed in Table 1, and means of volumetric proportions by habitat for condensed food categories are in Table 2.

In terms of volumetric proportion, persimmons (*Diospyros virginiana*) and deer were the most important food items, with average proportions at 18.35% and 18.29%, respectively (Table 2). Overall, anthropogenic sources of food comprised 14.95% of the diet, occurring at a frequency of 13.84%.

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; Figure 1). Only one each of wild turkey (*Meleagris gallopavo*) and mourning dove (*Zenaida macroura*) was detected.

Diet Across the Urban-Rural Gradient

In rural areas, grass (Poaceae) was the most common food item (FOC 54.55%), but only comprised 4.21% of the diet of rural animals. While statistically nonnsignificant, there was an increasing trend in frequency of grass from urban to rural areas. Deer were in 39.56% of rural samples and were consumed in the greatest volume compared to other foods (21.26%) and differed significantly from exurban samples (P = 0.007; Table 3); however, persimmons were similar, occurring 31.87% of the time at a volume of 20.23%. The most common prey was insects (FOC 28.57%), while the most common mammalian prey were rodents at 24.18%.

In exurban areas, insects were the most common food item (FOC 45.65%), but only comprised 4.68% of the diet in exurban habitats. Proportions of insects in exurban areas were significantly greater than urban and rural areas (P = 0.025). Neither reptiles nor other mammals were in exurban samples and other invertebrates were the least-encountered items (FOC 4.35%). Deer, the most common mammalian prey overall, were in 26.09% of exurban samples.

Persimmons were the most prevalent item in terms of volume (20.26%) followed by rabbits (*Sylvilagus*; 13.91%).

In urban areas, other plants and deer were the most common items, both with a frequency of occurrence of 54.55%. Proportions of other plants were marginally significant 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 item at 50%. Consumption of deer in urban areas varied significantly from that in exurban areas (P = 0.007). Aside from deer, rodents were the most-encountered prey (FOC 27.27%). Deer were the most important item volumetrically (30.91%) followed by rodents (16.36%).

Persimmons were encountered most often in exurban (FOC 32.61%) and rural (FOC 31.87%) areas, but occurred in urban areas less frequently (FOC 18.18%). Other fruits (*Vaccinium*, *Vitis*, *Prunus*, *Pyrus*, *Malus*, *Rubus*, Rosaceae, and Moraceae), however, had an FOC of 50% in urban areas decreasing along a gradient toward rural areas. FOC was 37.78% in exurban areas and 26.37% in rural areas. Grass occurred most frequently in rural areas (FOC 54.55%) and <50% as much in urban areas (FOC 13.19%). Reptiles did not occur in exurban areas and were most often in urban areas (FOC 4.5%). Occurrence of birds was similar across the gradient, but frequency of consumption increased along the gradient with the FOC in rural areas at 5.49%, exurban 8.70%, and urban 9.09%. Rodents also were in similar frequencies in all habitats, but were most often in urban areas (FOC 27.27%) followed by rural areas (FOC 24.18%). Rabbits occurred most frequently in exurban habitats (FOC 19.57%) and <50% as

frequently in rural areas (FOC 8.79%). Deer were important across the gradient: exurban (FOC 26.09%), rural (FOC 39.56%), and urban (FOC 54.45%). Proportions of remains of deer were significantly greater in urban and rural areas than in exurban areas (P = 0.007). Other mammals (Soricidae, *Dasypus novemcinctus*, *Sus scrofa*) occurred only in rural areas. Abiotic material (bark, twigs, gravel) was common and occurred most frequently in rural areas (FOC 25.28%). Anthropogenic items were most prevalent in urban areas (FOC 22.73%) and occurred with similar frequency in both exurban (FOC 10.87%) and rural (FOC 10.99%) areas.

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 items were encountered 67 times (Figure 1). Synthetic materials were the most common anthropogenic items (20 occurrences), followed by hunter-killed deer (18 occurrences). It is important to mention that the inclusion of natural anthropogenic items with synthetic material increases prevalence of anthropogenic items nearly two-fold.

DISCUSSION

Overall Diet

The two most commonly consumed items in diets of coyotes were deer and persimmons. They are abundant in this region. Of particular interest to this study was consumption of anthropogenic foods. Urban and exurban areas generally are believed to be resource-rich areas for exploitation; however, prevalence of anthropogenic feeding did not vary significantly 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. Rural areas, while much less so than urban and exurban areas, are inhabited by humans and 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; thus, making trash a readily available, allochthonous (found in a place other than where it originated) resource for coyotes.

Deer comprised a large proportion of diet in frequency (FOC 37.74%) and volume (18.29%). Deer was the second-most important food item volumetrically after persimmons, which was almost identical (18.35%). 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).

The detection of game animals in scats of coyotes was diminutive. Contrary to beliefs of many local hunters, coyotes do not consume vast quantities of game animals. Wild turkeys and mourning doves were only consumed on one occasion each and no quail 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. Deer and raccoons (*Procyon lotor*) were detected, but believed to be consumed almost exclusively as carrion.

Diet Along the Urban-Rural Gradient

Diet of Urban Coyotes

Vegetation was an important part of the diet overall (the most commonly encountered food), but particularly in diets of urban coyotes in terms of volume and frequency of consumption. Vegetation in this category did not include fruit or grass and consisted of items such as leaves, pine needles, mosses, and a variety of seeds (e.g., catkins, samaras). Many have postulated that coyotes exploit urban areas for their abundant sources of anthropogenic food (MacCracken 1982, Quinn 1997, Timm et al. 2004, Fox 2006, Orthmeyer et al. 2007); however, results of my research do not support that claim. 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, needs to be consumed in greater volume. Coyotes are opportunists; they eat what is available. In urban areas, vegetation is widespread and abundant, and likely occurs at a greater diversity than in natural areas because it is supplemented by native and domestic cultivars. Likewise,

the long growing season and mild winters of the subtropical southeastern climate sustain a plethora of vegetation year round. 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 reside and is consistent with what others have observed (MacCracken 1982, McClure et al. 1995), providing additional evidence of the highly omnivorous diet of coyotes.

Deer was the most widely consumed item by urban coyotes (30.91%), 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. While deer are native to this area, it is unlikely that they are a common source of prey for coyotes, as a healthy, adult deer would pose a great challenge for even a pair of coyotes. Winters in the Southeast generally are mild and deer are not as highly stressed or malnourished as they are at northern latitudes; thus, deer in this region should not be easy targets for coyotes. Road-killed deer, however, are abundant and widespread, as deer-vehicle collisions are common and frequent.

Densities of deer in urban areas often surpass carrying capacity (Kilpatrick and Walter 1997), and unlike in rural areas, hunting is not permitted to regulate populations; thus, increasing the likelihood of such collisions. 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 persimmons as being the most heavily consumed item at 20.26% (Table 2). This is almost identical to what was observed in rural areas, where persimmons were consumed at 20.23% (second only to deer at 21.26%). Persimmon trees are common in natural areas of the Southeast, but not commonly encountered in urbanized landscapes. Volume of consumption reflects that persimmons are consumed in great amounts where they are available and less than half as much in areas where they are not (6.59% in urban areas). Proportions of foods in exurban areas are not greatly different from rural and urban areas. The only food that differed significantly in exurban areas was insects, which occurred in greater volume than urban and rural areas. This is likely due to the life-history traits of insects that were consumed. The majority of insects consumed were orthopterans (grasshoppers and crickets); these insects are most-often encountered in areas where grass is abundant. Exurban areas are laden with empty parcels, powerline corridors, and early successional areas that would support such insect life.

Deer occurred significantly 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 6.40% compared to 30.91% and 21.26% in urban and rural areas, respectively (Table 2). This is surprising because exurban areas should have relatively equal proportions of deer. Deer are 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.

Rabbits were the second most important food with respect to volume and occurred in greater volume in exurban areas than both urban and rural areas, although not significantly so. This is likely due to the nature of suburbia, with manicured lawns and yards providing a plethora of grasses and forbs that are attractive to lagomorphs. The nature of the suburban landscape also provides sources of cover and supplemental water, all of which attract rabbits to exurban areas (Craven 1993).

Diets of Rural Coyotes

In rural areas, grass was the most commonly encountered item, but only comprised 4.21% of the diet. Coyotes might be using grasses as a digestive agent similar to behavior observed in domestic dogs (Thorne 1995). The frequency at which it is consumed, paired with the low volume at which it occurs, supports this explanation. Others, however, pose alternate hypotheses as to the role of grass in the canid diet. Emmons (per. comm.) suggests that ingestion of grass serves a mechanical function, forming a bolus of indigestible fibers that serve to scrub the intestines, helping to eliminate intestinal parasites. Best et al. (1981) proposed that grasses may be a deliberate choice and suggested further investigation of the nutritive properties of grass and its importance in the diet of coyotes. In my study of urban and exurban areas, proportions of grass composed 5.82% and 6.04% of the diet, respectively.

While these do not comprise significant portions of the diet, they occur in more than trace amounts and their presence may be important, especially when other sources of food are unavailable. Volumetrically, deer was the most important food item in rural areas, followed closely by persimmons; this is similar to what was observed overall. Persimmons were common in natural areas and are nutritious, containing high amounts of glucose and proteins. When fruits ripen, they swell and fall from the tree, littering the ground with sweet, fermenting fruit. Coyotes gorge themselves under persimmon trees (P. Getsgow, per. comm.); it is not surprising that they are capitalizing on this abundant, high-energy fruit.

Trends along the Gradient

It was hypothesized that exurban areas would serve as a transitional zone from urban to rural habitats and that consumption of items would follow a trend along the gradient, either increasing or decreasing from more natural to more developed areas. With few exceptions, exurban areas commonly did not have intermediate levels of particular items in the diet. Increasing trends from urban to rural areas occurred in volumes of carnivores and non-insect invertebrates consumed; however, these relationships were not statistically significant, and could be the results of the nature of the Performance Zoning Regime. Frequency of fruits was greatest in urban areas and decreased along the gradient toward rural areas. As previously mentioned, this could be due to gardens and cultivated fruits in urban areas. Fruits consumed include species that are native, but also are cultivated commercially and residentially (i.e., *Pyrus, Rubus, Vitis*). The source of such fruits could be from naturally occurring plants, but in urban areas, they could have come from gardens, compost piles, or trash

cans. If their origins were known and confirmed, one could substantiate this resource as anthropogenic.

Anthropogenic Feeding

Anthropogenic items in the diet did not vary significantly along the urban-rural gradient in terms of frequency or proportion, even when non-traditional items were considered. Along the gradient, frequency of consumption of anthropogenic foods was greatest in urban areas (FOC 22.73%), while exurban and rural areas were similar, with FOC values of 10.87% and 10.99%, respectively. In terms of volume, however, anthropogenic foods were consumed mostly in rural areas (16.27%), followed by urban areas (15.73%), and least in exurban areas (11.96%). Although there was no significant difference along the gradient, anthropogenic items comprised a fair amount of the diet, occurring in 13.84% of samples, and being consumed at 14.95% 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 blindly, 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. Animals may not forage solely in the area around the sampling locality. The design of my study attempted to account for possible variation by using a buffer of the average size of core areas of animals instead of the specific point of collection to determine classifications of habitats in the GIS analysis. It is

possible that animals were traveling across the gradient (especially transient animals) and that home ranges may overlap both natural and developed areas.

Anthropogenic feeding often is associated with ingestion of trash, debris, and other synthetic 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. When such items were considered in this study, prevalence of anthropogenic items increased nearly two-fold. As evidenced by previous research, anthropogenic supplementation is as much a function of availability as is consumption of natural foods. Gier (1968) observed an increase in consumption of domestic poultry in areas of increased influence by humans. J. Fedriani (unpublished data) observed animals in a suburban area routinely foraging at a landfill, and Schrecengost et al. (2008) observed significantly increased consumption of feral hogs when carcasses were dumped at their study site following a period of extensive control efforts.

Deer was an important component of diet across the urban-rural gradient. While some researchers have documented depredation on white-tailed deer (Cook et al. 1971, Moore and Millar 1986, Kilgo 2009), this feeding behavior is most commonly observed at northern latitudes where animals coalesce into packs and prey upon winter-weakened deer. Predation on fawns, however, has been observed in the Southeast, and likely is increasing (Kilgo 2009, Saalfeld and Ditchkoff 2007). In my study, deer were consumed 60 times by coyotes; 18 during the period when fawns were most susceptible to predation (mid July through late September). I believe that most consumption of deer is a function of coyotes scavenging carrion. While

anthropogenic foods, such as road-killed deer, were underestimated, and the extent of anthropogenic supplementation in the diet is greater than actually observed.

Results vary among studies where anthropogenic supplementation of urban and exurban coyotes have been observed (Table 4). Gehrt (2007) compared aspects of the ecology of urban coyotes and summarizes studies with regard to consumption of small mammals (which he claimed dominated the diet of coyotes in urbanized areas). Prevalence of native small mammals and anthropogenic items varied among studies. The only consistent result among studies was low occurrence of cats (Felis catus; greatest FOC was 2%), which is consistent with my study. It is important to note that Gehrt (2007) compared studies in terms of frequency of occurrence of items, a measure of how often a particular item is consumed; this does not take into account the volume at which the item was consumed, meaning that an item ingested at 5% volume and an item ingested at 100% volume both account for one detection. This method may grossly over or underestimate importance of items in the diet as no measure of quantity is used to assess use of items. This may be particularly misleading when making projections of importance of foods in the diet, and how diet varies.

In my study, statistical analyses indicated a significant relationship between volume and frequency of other plants consumed along the urban-rural gradient.

Volumetric analyses indicated a relationship between amount of insects consumed in exurban areas and amount of deer consumed in urban and rural areas. These results however, are not reflected in comparisons of frequency of occurrence. This supports

the idea that frequency of occurrence alone is not a sufficient indicator of the diet of coyotes and does not adequately capture variation in consumption of foods, particularly when diets are being assessed in different habitats.

Another obstacle in comparisons of studies and, thus, resulting ambiguity in reconstruction of diet, is the lack of specificity applied to identification of foods. Here, I make a strong recommendation for specific identification of taxa when possible. Broadly identifying foods and lumping foods into categories simplifies analyses, but limits insight that specific identification provides. For instance, lumping vegetative items into the same category can be misleading, as consumption of different types of vegetation is of paramount importance; especially, when they vary in availability by season. If vegetative items are not identified specifically, there is no distinction between fruit or grass, or among other types of vegetation. This is critical when examining diet of an omnivore with catholic food habits.

Because assemblages of species of prey vary widely in different regions of the United States, studies must be conducted across a variety of geographically specific areas to accurately understand the diet of coyotes. While diet will vary according to geographic ranges of various species of prey, specific identification of taxa allows for comparison of the consumption of prey that occupy similar niches, which may be important.

Considerations

While analysis of scats is a valid and widely used method of assessing diet in coyotes (Bowyer et al. 1983, Andelt et al. 1987, Fedriani et al. 2001, Cepek 2004) and other canids (Arjo et al. 2002, Green and Flinders 1981), there are shortcomings

to this method. Post-digestive investigation does not account for differential digestibility of foods; thus, certain foods may be under-estimated or not detected. Items such as soft-bodied insects and fleshy fruits are nearly impossible to detect in scats unless other parts of the food are consumed and retained. This is of particular concern when assessing degree of anthropogenic feeding because one is dependent upon persistence of synthetic materials to indicate consumption of human-related foods. Given the time and monetary constraints associated with this type of research, analysis of scats is the most efficient method. An analysis of stomach contents may be able to reconstruct the diet more precisely, because items in the stomach are largely intact and easier to identify. More advanced techniques may be used to further enhance precision; e.g., analysis of fatty acids has been used to assess anthropogenic feeding in American black bears (Ursus americanus; Thiemann et al. 2008). It is likely that this technique will be successful when used for other carnivores and its application to studies of diet of coyotes may reveal that anthropogenic feeding is more common than recorded previously.

Statistical analyses produced few significant results with regard to foods consumed along the urban-rural gradient. It is important to note, however, that statistical significance may not equate to biological significance. While certain trends did not have statistical significance, their presence (or absence) is vital in assessing overall diet. More important than significant *P*-values are the biological implications of observed feeding patterns. The observation of statistical significance (or a lack thereof) is specific to a particular research objective in which the attempt is to explain variation in a system; *P*-values (the indicators of statistical significance) are

dependent on the design of the experiment, primarily size of the sample and, thus, results of statistical analyses are somewhat limited in their application. Explaining the biological significance of observed variation has more merit in applying results of studies to global, rather than local, systems (Johnson 1999), especially when the purpose of conducting research is to gain information from which to base management decisions.

While considerable effort was made to acquire even samples across habitats, samples decreased from rural to urban habitats, because scats in urban areas were not as prevalent or conspicuous as in rural areas. Since sample numbers were not equal in all habitats, the proc GLM statement was used in SAS (as opposed to the proc ANOVA command) when conducting the MANOVA, which is designed to process unbalanced data. A test of effect of size of sample was conducted within the MANOVA to estimate how important habitat was when accounting for differences in foods. Low η^2 -values for most dependent variables (food categories) indicated that habitat type is not a strong influence on the variation of food item consumption by coyotes, and an increase in number of samples would not necessarily mean that more samples would yield additional significant differences. However, a greater sampling effort spread over a longer time may increase size of sample and aid in acquisition of a more even distribution of samples along the gradient, potentially rendering more precise results.

Previous studies of diet of coyotes in developed areas have been conducted in highly urbanized cities (Chicago, Morey et al. 2007; San Diego, MacCracken 1982; Los Angeles, Fedriani et al. 2001). 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 I expected to observe intermediate levels of natural 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 my study site may or may not be influenced by this landscape. Future research in landscapes of varying levels of development and juxtaposition may help to further elucidate diet of coyotes in diverse urban areas.

As evidenced by my study, prevalence of anthropogenic food does not vary significantly in the diet of coyotes in areas of differential urbanization.

Anthropogenic supplementation occurs in a similar frequency across the urban-rural gradient. If anthropogenic sources of food are not significant in the diet, then it is likely that there are other resources that coyotes are exploiting in urban and exurban areas. This could be in the form of supplemental sources of water, cover, den sites, etc. It also is possible that other animals (e.g., rodents, rabbits) are drawn to these areas and, thus, coyotes follow those prey.

A key difference between my research and previous studies is the high occurrence of deer in the diet. Previous studies have noted that rodents and lagomorphs serve as the main mammalian prey in urban areas. I believe that this difference in feeding pattern is not a reflection of a shift to larger prey, but exhibition of the opportunistic feeding behavior of coyotes on carrion. Another difference is increased consumption of vegetation compared to studies in other regions. While taking of seasonal fruits in

urban areas has been documented (Atkinson and Shackleton 1991, Quinn 1997), diets of coyotes in my study and those of others had a heavy reliance on soft mast and other plant matter (Schrecengost et al. 2008, Stratman and Pelton 1997). This is likely due to mild winters, a diverse assemblage of plants, and a longer growing season. While diet in urban areas may differ in composition from that of coyotes in other urban areas, opportunistic feeding behaviors is preserved in these animals.

While anthropogenic supplementation did not vary significantly across habitats, it did comprise 14.95% of overall diet. If these animals are regularly incorporating anthropogenic resources into their diet, this could indicate a shift in natural-history traits. A shift in diet could lead to greater densities, higher survival, and better fitness; thus, altering population dynamics of southeastern animals. In contrast, however, consumption of anthropogenic foods may impair health of individuals and negatively impact their natural foraging and predatory behavior (Grace 1976). Some animals dependent on supplemental sources of food may cause damage to property as they search for anthropogenic resources (Peine 2001). Animals consuming anthropogenic foods are likely to be animals that cause conflict, as anthropogenic feeding has been observed as a precursor to aggressive behavior (Timm et al. 2004).

CONCLUSION

Overall, few significant differences in diet of coyotes were observed along the urban-rural gradient. This was somewhat unexpected. The dynamic nature of the landscape was a likely explanation for the similar distribution of resources along the gradient. Coyotes in the three habitats likely were consuming what was available, which was similar among habitats. Results of my study largely are 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. Other than increased consumption of anthropogenic foods in developed areas, diet varies widely, with natural items comprising the bulk of the diet. Results of my research support previous conclusions that coyotes are highly adaptable, opportunistic omnivores, and supports the claim by Wade (1978) that availability is the rule that governs diet of coyotes. Thus, I 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.

Management Implications

The diversity of animal prey and vegetation consumed was greatest in rural areas. This supports the notion that rural areas provide a sufficient variety of natural foods for coyotes without them having to exploit urban and exurban areas for additional food resources; however, they continue to do so. This is disadvantageous to wildlife managers as coyotes pose a myriad of potential hazards to humans and domestic

animals. Attacks by coyotes on humans and pets have become an increasing problem (Timm et al. 2004). Coyotes are vectors for a multitude of zoonotic diseases including rabies, sarcoptic mange, canine parvovirus, and distemper. Wildlife managers and stakeholders alike would be wise to alter behaviors to promote exclusion of coyotes from urban and exurban areas. Perhaps, the greatest and most effective tool in achieving this goal is harassment. Many organizations responsible for controlling damage by wildlife (e.g., Internet Center for Wildlife Damage Management, various state agencies) encourage the use of repellants and frightening devices to exclude coyotes (it is important to note that these methods should be implemented only with proper training and education). Discouraging coyotes from entering urbanized areas and limiting or eliminating potential anthropogenic resources will likely drive them away. Repeated, aggressive harassment will allow coyotes to retain a natural fear of humans and make them less likely to move into developed areas. This is the most important action. Securing trash receptacles, bringing pet food in at night, keeping small pets indoors, and similar actions are only secondary to intense harassment measures. If non-lethal techniques are not an option for offending animals, persistent animals may need to be managed by aversive conditioning to curb, and hopefully eliminate, anthropogenic feeding.

To effectively manage populations of urban coyotes (and other urban carnivores), a comprehensive understanding of their complex niche must first be achieved.

Supplementation of anthropogenic resources, human-induced stress, and differences in availability of resources in developed areas largely influence the behavior of animals residing in such areas. Once managers can distinguish behavioral and

ecological differences between rural animals, and their adapted, exurban-dwelling counterparts, effective, long-term, population-management strategies can be implemented.

LITERATURE CITED

- Adams, J. R., J. A. Leonard, and L. P. Waits. 2003. Widespread occurrence of a domestic dog mitochondrial DNA haplotype in southeastern US coyotes. Molecular Ecology 12: 541-546.
- Andelt, W. F., F. F. Knowlton, and K. Cardwell. 1987. Variation in coyote diets associated with season and successional changes in vegetation. Journal of Wildlife Management 51:273-277.
- Arjo, W. M., D. H. Pletscher, and R. R. Ream. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. Journal of Mammalogy 83:754-766.
- Atkinson, K. T., and D. M. Shackleton. 1991. Coyote, *Canis latrans*, ecology in a rural-urban environment. Canadian Field-Naturalist 105:49-54.
- Bailey, R. G. 1980. Description of the ecoregions of the United States. United States

 Department of Agriculture Miscellaneous Publication 1391:1-77.
- Bekoff, M. 1977. Canis latrans. Mammalian Species 79:1-9.
- Bekoff, M., and R. Jamison. 1975. Physical development in coyotes (*Canis latrans*) with a comparison to other canids. Journal of Mammalogy 56:685-692.
- Bekoff, M., and M. C. Wells. 1982. Behavioral ecology of coyotes: social organization, rearing patterns, space use, and resource defense. Zeitschrift für Tierpsychologie 60:281-305.

- Best, T. L, B. Hoditschek, and H. H. Thomas. 1981. Foods of coyotes (*Canis latrans*) in Oklahoma. Southwestern Naturalist 26:67-69.
- Bounds, D. L., and W. W. Shaw. 1994. Managing coyotes in U.S. national parks: human-coyote interactions. Natural Areas Journal 14:280-284.
- Bowyer, R. T., S. A. McKenna, and M. E. Shea. 1983. Seasonal changes in coyote food habits as determined by fecal analysis. American Midland Naturalist 109: 266-273.
- Cepek, J. D. 2004. Diet composition of coyotes in the Cuyahoga Valley National Park, Ohio. Ohio Journal of Science 104:60-64.
- Cook, R. S., M. White, D. O. Trainer, and W. C. Glazener. 1971. Mortality of young white-tailed deer fawns in South Texas. Journal of Wildlife Management 35:47-56.
- Craven, S. R. 1993. Cottontail rabbits. Pp. D75-D80 in Prevention and control of wildlife damage (S. E. Hygnstrom, R. M. Timm, and G. E. Larson, eds.).

 University of Nebraska Cooperative Extension Service, Lincoln.
- Errington, P. L. 1935. The significance of food habits research in wildlife management. Science 81: 378-379.
- Fedriani, J. M., T. K. Fuller, and R. M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. Ecography 24:325-331.
- Fox, C. H. 2006. Coyotes and humans: can we coexist? Proceedings of the Annual Vertebrate Pest Conference 22:287-293.

- Gehrt, S. D. 2007. Ecology of coyotes in urban landscapes. Proceedings of the Wildlife Damage Management Conference 12:303-311.
- Gehrt, S. D., C. Anchor, and L. A. White. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045-1057.
- Gier, H. T. 1968. Coyotes in Kansas. Agricultural Experimental Station, Kansas State University, College of Agriculture and Applied Science, 118 pp.
- Gipson, P. S. 1974. Food habits of coyotes in Arkansas. Journal of Wildlife Management 38:848-853.
- Grace, E. 1976. Interactions between men and wolves at an Arctic outpost on Ellesmere Island. Canadian Field-Naturalist 90:149-156.
- Green, J. S., and J. T. Flinders. 1981. Diets of sympatric foxes and coyotes in southeastern Idaho. Great Basin Naturalist 41:251-254.
- Hamilton, W. J., Jr. 1974. Food habits of the coyote in the Adirondacks. New York Fish and Game Journal 21:177-181.
- Hernandez, L., and M. Delibes. 1994. Seasonal food habits of coyotes, *Canis latrans*, in the Bolsón de Mapimí, southern Chihuahuan Desert, Mexico. Zeitschrift für Säugetierkunde 59:82-86.
- Hilton, H. 1978. Systematics and ecology of the eastern coyote. Pp. 209-228 in Coyotes: biology, behavior, and management (M. Bekoff, ed.). Academic Press, New York, 384 pp.

- Hoerath, J. D., and M. K. Causey. 1991. Seasonal diets of coyotes in western central Alabama. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 45:91-96.
- Holle, D. M. 1978. Food habits of coyotes in an area of high fawn mortality.

 Proceedings of the Oklahoma Academy of Science 58:11-15.
- Huebschman, J. J., S. E. Hygnstrom, and J. A. Gubanyi. 1997. Coyote food habits at DeSoto National Wildlife Refuge, Nebraska. Prairie Naturalist 29:99-110.
- Hussain, A., J. B. Armstrong, D. B. Brown, and J. Hogland. 2007. Land-use pattern, urbanization, and deer-vehicle collisions in Alabama. Human-Wildlife Conflicts 1:89-96.
- Johnson, D. H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763-772.
- Kilgo, J. C. 2009. Coyotes in the East: are they impacting deer? Forest Landowners March-April:5-8.
- Kilpatrick, H. J., and W. D. Walter. 1997. Urban deer management: a community vote. Wildlife Society Bulletin 25:388-391.
- Kitchen, A. M., E. M. Gese, and E. R. Schauster. 2000. Changes in coyote activity patterns to reduced exposure to human persecution. Canadian Journal of Zoology 78:853-857.
- Kleinman, D. G., and C. A. Brady. 1978. Coyote behavior in the context of recent canid Research. Pp. 163-188 in Coyotes: biology, behavior, and management (M. Bekoff, ed.). Academic Press, New York, 384 pp.

- Korschgen, L. J. 1971. Procedures for food habits analysis. Pp. 233-250 in Wildlife management techniques (R. H. Giles, Jr., ed.). The Wildlife Society,Washington DC, 623 pp.
- Korschgen, L. J. 1957. Food habits of the coyote in Missouri. Journal of Wildlife Management 21: 424-435.
- Lee, R. M., and M. L. Kennedy. 1986. Food habits of the coyote in Tennessee.

 Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 40:364-372.
- Luniak, M. 2004. Synurbanization---adaptation of animal wildlife to urban development. Proceedings of the International Urban Wildlife Symposium 4:50-55.
- MacCracken, J. G. 1982. Coyote foods in a southern California suburb. Wildlife Society Bulletin 10:280-281.
- Martin, A. C., and W. D. Barkley. 1961. Seed identification manual. University of California Press, Berkeley, 220 pp.
- McClure, M. F, N. S. Smith, and W. W. Shaw. 1995. Diets of coyotes near the boundary of Saguaro National Monument and Tucson, Arizona.

 Southwestern Naturalist 40:101-125.
- Moore, G. C., and J. S. Millar. 1986. Food habits and average weights of a fall-winter sample of eastern coyotes, *Canis latrans*. Canadian Field-Naturalist 100:105-106.

- Moore, T. D., L. E. Spence, C. E. Dugnolle, and W. G. Hepworth. 1974.

 Identification of the dorsal guard hairs of some mammals of Wyoming.

 Wyoming Game and Fish Department Bulletin 14:1-77.
- Morey, P. S., E. M. Gese, and S. Gehrt. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. American Midland Naturalist 158:147-161.
- Nowak, R. M. 2001. Evolution and taxonomy of coyotes and related *Canis*. Pp. 3-16 in Coyotes: biology, behavior, and management (M. Bekoff, ed.).

 Academic Press, New York, 384 pp.
- Orthmeyer, D. L., T. A. Cox, J. W. Turman, and J. R. Bennett. 2007. Operational challenges of solving urban coyote problems in southern California.

 Proceedings of the Wildlife Damage Management Conference 12: 344-357.
- Ozoga, J. J., and E. M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. Journal of Wildlife Management 30:809-819.
- Parker, T. S. 1999. Food habits of the coyote (*Canis latrans*) in urban and suburban areas of western Tennessee. M.S. thesis, University of Memphis, Memphis, Tennessee.
- Peine, J. D. 2001. Nuisance bears in communities: strategies to reduce conflict.

 Human Dimensions of Wildlife 6:223-237.
- Quinn, T. 1997. Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. Northwest Science 71:1-5.
- Rose, M. D., and G. A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998-1007.

- Saalfeld, S. T., and S. S. Ditchkoff. 2007. Survival of neonatal white-tailed deer in an exurban population. Journal of Wildlife Management 71:940-944.
- Samson, C., and M. Crête. 1997. Summer food habits and population density of coyotes, *Canis latrans*, in boreal forests of southeastern Québec. Canadian Field-Naturalist 111:227-233.
- Schrecengost, J. D., J. C. Kilgo, D. Mallard, H. Scott Ray, and K. V. Miller. 2008.

 Seasonal food habits of the coyote in the South Carolina Coastal Plain.

 Southeastern Naturalist 7:135-144.
- Shivik, J. A., and M. M. Barrett. 1997. Coyote activity patterns in the Sierra Nevada.

 Great Basin Naturalist 57:355-358.
- Sperry, C. C. 1934. Winter food habits of coyotes: a report of progress, 1933.

 Journal of Mammalogy 15:286-290.
- Stratman, M. R., and M. R. Pelton. 1997. Food habits of coyotes in northwestern Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 51:269-275.
- Teerink, B. J. 1991. Hair of West-European mammals: atlas and identification key.

 Cambridge University Press, Cambridge, United Kingdom, 223 pp.
- Thiemann, G. W., R. S. Stahl, S. Baruch-Mordo, and S. W. Breck. 2008. Trans fatty acids provide evidence of anthropogenic feeding by black bears. Human-Wildlife Conflicts 2:183-193.
- Thorne, C. 1995. Feeding behavior of domestic dogs and the role of experience. Pp. 103-113 in The domestic dog: its evolution, behaviour and interactions with

- people (J. Serpell, ed.). Cambridge University Press, Cambridge, United Kingdom, 268 pp.
- Timm, R. M., R. O. Baker, J. R. Bennett, and C. C. Coolahan. 2004. Coyote attacks: an increasing suburban problem. Transactions of the North American Wildlife and Natural Resources Conference 69:1-10.
- Todd, A. W. 1985. Demographic and dietary comparisons of forest and farmland coyote, *Canis latrans*, populations in Alberta. Canadian Field-Naturalist 99:163-171.
- VanGilder, C. L., G. R. Woods, and K. V. Miller. 2009. Effects of intensive predator removal of white-tailed deer recruitment in Northeast Alabama. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 63:11-16.
- Van Vuren, D., and S. E Thompson, Jr. 1982. Opportunistic feeding by coyotes.

 Northwest Science 56:131-135.
- Wade, D. A. 1978. Coyote damage: a survey of its nature and scope, control measures and their application. Pp. 209-228 in Coyotes: biology, behavior, and management (M. Bekoff, ed.). Academic Press, New York, 384 pp.
- Whitaker, J. O., Jr. 1988. Food habits analysis of insectivorous bats. Pp. 171-189 in Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.).

 Smithsonian Institution Press, Washington DC, 920 pp.
- Wilson, D. E., and D. M. Reeder. 2005. Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Johns Hopkins University Press, Baltimore, Maryland, 2,142 pp.

- Windberg, L. A., and C. D. Mitchell. 1990. Winter diets of coyotes in relation to prey abundance in southern Texas. Journal of Mammalogy 71:439-447.
- Wooding, J. B., E. P. Hill, and P. W. Sumner. 1984. Coyote food habits in Mississippi and Alabama. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 38:182-188.
- Young, S. P., and H. H. Jackson. 1951. The clever coyote. University of Nebraska Press, Lincoln, 411 pp.

Table 1. Number of occurrences, frequency of occurrence (expressed as a percentage), mean, standard error, and maximum values of volumetric proportions of food items of coyotes, September 2007-February 2009.

	Number	Frequency				
	of	of	Standard			
Food item	occurrences	occurrence (%)	error	Mean	Min	Max
Bryophyta	5	3.14	0.002	0.001	0.000	0.100
Poaceae	68	42.77	0.050	0.010	0.000	1.000
Aceraceae	1	0.63	0.001	0.001	0.000	0.150
Rannunculaceae	6	3.77	0.006	0.003	0.000	0.500
Rubus	6	3.77	0.001	0.001	0.000	0.075
Malus	2	1.26	0.002	0.001	0.000	0.200
Pyrus	11	6.92	0.027	0.011	0.000	1.000
Prunus	5	3.14	0.001	0.001	0.000	0.100

Table 1 continued.

	Number	Frequency				
	of	of	Standard			
Food item	occurrences	occurrence (%)	error	Mean	Min	Max
Betulaceae	11	6.92	0.006	0.003	0.000	0.300
Moraceae	4	2.52	0.011	0.007	0.000	1.000
Fabaceae	2	1.26	< 0.001	< 0.001	0.000	0.050
Cucurbitaceae	1	0.63	0.002	0.002	0.000	0.250
Juglandaceae	1	0.63	< 0.001	< 0.001	0.000	0.050
Rubiaceae	1	0.63	< 0.001	< 0.001	0.000	0.010
Solanaceae	2	1.26	< 0.001	< 0.001	0.000	0.010
Brassica	2	1.26	< 0.001	< 0.001	0.000	0.050
Quercus	11	6.92	0.008	0.004	0.000	0.650
Ulmus	1	0.63	< 0.001	< 0.001	0.000	0.050

Table 1 continued.

	Number	Frequency				
	of	of	Standard			
Food item	occurrences	occurrence (%)	error	Mean	Min	Max
Alnus	2	1.26	0.002	0.001	0.000	0.150
Pinus	14	8.81	0.007	0.003	0.000	0.400
Vaccinium	4	2.52	0.001	0.001	0.000	0.100
Vitis	13	8.18	0.025	0.010	0.000	0.900
Geranium	2	1.26	< 0.001	< 0.001	0.000	0.010
Liriodendron tulipifera	2	1.26	< 0.001	< 0.001	0.000	0.050
Diosporos virginiana	53	33.33	0.184	0.027	0.000	1.000
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
Arachnida	2	1.26	< 0.001	< 0.001	0.000	0.050

Table 1 continued.

	Number	Frequency				
	of	of	Standard			
Food item	occurrences	occurrence (%)	error	Mean	Min	Max
Annelida	1	0.63	< 0.001	< 0.001	0.000	0.010
Coleoptera	28	17.61	0.013	0.006	0.000	0.950
Orthoptera	23	14.47	< 0.001	< 0.001	0.000	0.008
Lepidoptera	5	3.14	0.005	0.003	0.000	0.500
Dermaptera	1	0.63	< 0.001	< 0.001	0.000	0.010
Diptera	3	1.89	0.001	0.001	0.000	0.050
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
Gastropoda	3	1.89	< 0.001	< 0.001	0.000	0.010
Crusacea	1	0.63	0.006	0.006	0.000	0.950

Table 1 continued.

	Number	Frequency					
	of	of	Standard				
Food item	occurrences	occurrence (%)	error	Mean	Min	Max	
Isopoda	1	0.63	< 0.001	< 0.001	0.000	0.050	
Unknown vertebrate	2	1.26	0.001	< 0.001	0.000	0.050	
Osteichthyes	9	5.66	0.019	0.009	0.000	0.950	
Amphibia	0	0.00	0.000	0.000	0.000	0.000	
Reptilia	2	1.26	0.003	0.002	0.000	0.300	
Aves	11	6.92	0.017	0.007	0.000	0.750	
Sciurus carolinensis	6	3.77	0.080	0.004	0.000	0.600	
Sciurus niger	2	1.26	0.011	0.008	0.000	0.000	
Tamias striatus	1	0.63	0.003	0.003	0.000	0.400	
Castor canadensis	2	1.26	0.011	0.008	0.000	0.900	

Table 1 continued.

	Number	Frequency				
	of	of	Standard			
Food item	occurrences	occurrence (%)	error	Mean	Min	Max
Sigmodon hispidus	15	9.43	0.052	0.016	0.000	1.000
Microtus	8	5.03	0.017	0.008	0.000	0.700
Reithrodontomys humulis	2	1.26	0.001	0.001	0.000	0.010
Geomys pinetis	1	0.63	< 0.001	< 0.001	0.000	0.050
Rattus	3	1.89	0.012	0.007	0.000	0.800
Mus musculus	1	0.63	0.001	0.001	0.000	0.100
Zapus hudsonius	1	0.63	0.002	0.002	0.000	0.300
Sylvilagus	25	15.72	0.098	0.022	0.000	1.000
Dasypus novemcinctus	1	0.63	0.001	0.002	0.000	0.100
Odocoileus virginanus	60	37.74	0.183	0.026	0.000	1.000

Table 1 continued.

	Number	Frequency				
	of	of	Standard			
Food item	occurrences	occurrence (%)	error	Mean	Min	Max
Canis latrans	4	2.52	0.002	0.001	0.000	0.150
Urocyon cinereoargenteus	1	0.63	< 0.001	< 0.001	0.000	0.010
Procyon lotor	4	2.52	0.012	0.007	0.000	0.650
Didelphis virginiana	4	2.52	0.007	0.005	0.000	0.800
Lynx rufus	1	0.63	0.000	0.000	0.000	0.000
Soricomorpha	2	1.26	0.000	0.000	0.000	0.002
Sus scrofa	1	0.63	0.006	0.006	0.000	1.000
Felis catus	12	7.55	0.028	0.011	0.000	0.900
Canis lupus familiaris	1	0.63	0.006	0.006	0.000	1.000
Homo sapiens	2	1.26	< 0.001	< 0.001	0.000	0.010

Table 1 continued.

	Number	Frequency				
	of	of	Standard			
Food item	occurrences	occurrence (%)	error	Mean	Min	Max
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 (expressed as a percentage) of food items of coyotes in differing areas of development by humans, September 2007-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

Table 3. Volumetric variation in means of food items along an urban-rural gradient for coyotes, September 2007-February 2009. Statistically homogenous subsets derived from least-squared means analysis are shown by lines below habitats and ranked means.

Sample sizes for each category, degrees of freedom, *F*-ratios, and *P*-values are given.

			•	of variance			
Food item	n	df	F-ratio	<i>P</i> -value		sults of leans analy	east-squares ysis
Other plants	22	2,156	2.93	0.057	3 0.178	1 0.130	2 0.067
Insects	46	2,156	3.79	0.025	2 0.112	1 0.046	3 0.021
Deer	91	2,156	5.17	0.007	3 0.436	0.327	2 0.116

Table 4. Comparison of studies of diet of coyotes in developed areas, including frequencies of occurrence (expressed as a percentage) for specific food items (modified from Gehrt 2007).

Study				Domestic		
site	n	Leporids	Rodents	cats	Anthropogenic	Source
San Diego, CA	97	14	8	2	17	MacCracken 1982
Los Angeles, CA	250	15	40	1	16	Fedriani et al. 2001
Tucson, AZ	667	32	28	1	35	McClure et al. 1995
Chigaco, IL	1,429	18	42	1	2	Morey et al. 2007
Albany, NY	274	40	14	<1	<1	D. Bogan and R. Kays, unpublished da
Memphis, TN	675	10	32	2	7	Parker 1999
Auburn, AL	68	6	9	1	6	E. Santana, unpublished data

Figure 1. Number of occurrences of anthropogenic foods consumed by coyotes, September 2007-February 2009.

