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Source: Journal of Mammalogy, 94(5):1141-1148. 2013.

Published By: American Society of Mammalogists

URL: <http://www.bioone.org/doi/full/10.1644/13-MAMM-A-109.1>

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Diets of sympatric red wolves and coyotes in northeastern North Carolina

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The recent co-occurrence of red wolves (*Canis rufus*) and coyotes (*Canis latrans*) in eastern North Carolina provides a unique opportunity to study prey partitioning by sympatric canids. We collected scats from this region and examined them for prey contents. We used fecal DNA analysis to identify which taxa deposited each scat and multinomial modeling designed for mark–recapture data to investigate diets of sympatric red wolves and coyotes. Diets of red wolves and coyotes did not differ, but the proportion of small rodents in the composite scats of both canids was greater in the spring than in the summer. White-tailed deer (*Odocoileus virginianus*), rabbits (*Sylvilagus* spp.), and small rodents were the most common diet items in canid scats. The similarity of diet between red wolves and coyotes suggests that these 2 species may be affecting prey populations similarly.

Key words: dietary overlap, DNA genotyping, *Canis latrans*, *Canis rufus*, coyote, food habits, red wolf, scat

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DOI: 10.1644/13-MAMM-A-109.1

Before European settlement, the ranges of the coyote (*Canis latrans*) and red wolf (*Canis rufus*) were largely allopatric; coyotes were limited primarily to the prairie regions of North America (Bekoff 1977), whereas red wolves occurred exclusively in eastern North America (Nowak 2002). The reintroduction and sustained management of red wolves in northeastern North Carolina following the recent expansion of coyotes into the eastern United States has created the unique circumstance of sympatric red wolf and coyote populations on the Albemarle Peninsula. Because the 2 species historically had mostly nonoverlapping ranges, little is known about their interspecific interactions or their combined effects on ecological communities.

In particular, the effects of predation on prey species by sympatric red wolves and coyotes are unknown. Clearly, in some situations canids have the ability to reduce prey populations (Seip 1995). A population of black-tailed deer (*Odocoileus hemionus*) in Alaska was brought to near

extinction by gray wolf (*Canis lupus*) predation (Klein 1995), and reintroduced gray wolves reduced ungulate abundance in Yellowstone National Park (Barber-Meyer et al. 2008). Canids also can have indirect effects on prey populations. For example, Crooks and Soulé (1999) suggested that the disappearance of coyotes in California resulted in increased numbers of mesopredators and a subsequent increase in predation upon native prey species by mesopredators.

Red wolves and coyotes are considered opportunistic carnivores, even though red wolf diets are relatively undocumented in the wild. In their historic range throughout the southeastern United States, the last remaining red wolves preyed upon raccoons (*Procyon lotor*), rabbits (*Sylvilagus* spp.), and hispid cotton rats (*Sigmodon hispidus*—Riley and



McBride 1972; Shaw 1975; Weller 1996) in coastal habitats of Texas and Louisiana. In the few diet studies of red wolves reintroduced to North Carolina, white-tailed deer (*Odocoileus virginianus*) also contributed significantly to the diet (Dellinger et al. 2011a; Kelly 1994).

Following extirpation of wolves in the eastern United States, coyotes expanded their range eastward (Hill et al. 1987; Gompper 2002; Laliberte and Ripple 2004). Coyotes are smaller and are thought to eat fewer large prey items (e.g., white-tailed deer and raccoons) than red wolves. Coyotes have a diverse diet that includes small and medium-sized mammals, vegetation, dump refuse, white-tailed deer, and domestic livestock (Hilton 1978; Gompper 2002; Schrecengost et al. 2008). Except in Florida and South Carolina, where vegetation was most abundant in scats, mammalian prey (e.g., rabbits and small rodents) have occurred most frequently in analyses of coyote diets in the southeastern United States (Gipson 1974; Hall 1979; Wooding 1984; Lee 1986; Blanton and Hill 1989; Schrecengost et al. 2008). In addition, Schrecengost et al. (2008) reported white-tailed deer fawns to be the most common component of coyote diets during the period of deer parturition and fawn rearing in South Carolina, and coyotes have apparently replaced gray wolves as an important predator of white-tailed deer in the northeastern United States (Gompper 2002; Kays et al. 2010). Thus, empirical evidence suggests that the diets of coyotes and red wolves may overlap and that coyotes may have filled a niche similar to that historically occupied by red wolves across the eastern and southern United States.

The sympatry of red wolves and coyotes in eastern North Carolina provides a unique opportunity to compare food habits of these 2 canids directly. In allopatry, diet studies do not include the potential influence of interspecific competition and can be confounded by seasonal or habitat differences in prey availability (Andelt et al. 1987). Conversely, analysis of the diets of sympatric red wolves and coyotes within the same time frame and across the same landscapes reduces spatial and temporal variability and provides initial data on the potential combined effects of these predators on prey populations. We compared food habits of red wolves and coyotes using 2 recently developed methods: fecal DNA identification of canid taxa and multinomial analysis of food habits. We used a capture–mark–recapture model to test our hypothesis that diet would differ between red wolves and coyotes and diet, in general, would differ by biological seasons and calendar periods.

MATERIALS AND METHODS

Study area.—The study area was the 5-county Albemarle Peninsula (referred to as the Red Wolf Experimental Population Area in documents of the United States Fish and Wildlife Service [USFWS]). The study area included about 6,700 km² of federal, state, and private lands in Beaufort, Dare, Hyde, Tyrrell, and Washington counties, North Carolina. Public lands included Alligator River National Wildlife

Refuge, Pocosin Lakes National Wildlife Refuge, a bombing range shared by the United States Navy and Air Force, and numerous state-owned game management areas. Major land-cover types included agricultural fields (approximately 30%), pine (*Pinus* spp.) plantations (approximately 15%), pocosin (approximately 15%; including *Pinus serotina* and *Persea palustris*), nonriverine swamp forests (approximately 10%; including *Nyssa* spp., *Liquidambar styraciflua*, *Acer rubrum*, and *Chamaecyparis thyoides*), and saltwater marshes or open water (approximately 10%). Annual precipitation averaged 127 cm and seasonal average temperatures ranged from 5°C in winter to 27°C in summer (Beck et al. 2009). Elevation ranged from sea level to 50 m (Beck et al. 2009).

Potential prey species occurring in the study area included white-tailed deer, rabbits (*Sylvilagus floridanus*, *Sylvilagus palustris*), raccoon, feral hog (*Sus scrofa*), nutria (*Myocastor coypus*), muskrats (*Ondatra zibethicus*), hispid cotton rat, house mouse (*Mus musculus*), marsh rice rat (*Oryzomys palustris*), eastern harvest mouse (*Reithrodontomys humulis*), northern bobwhite (*Colinus virginianus*), and wild turkey (*Meleagris gallopavo*—Phillips et al. 2003). Additional sympatric predators were gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), raccoon, house cat (*Felis catus*), red wolf, coyote, red wolf–coyote hybrids (*C. rufus* x *C. latrans*), feral dog (*Canis familiaris*), bobcat (*Lynx rufus*), and black bear (*Ursus americanus*).

Sample collection.—We collected scats monthly from January 2009 through February 2010 by comprehensively surveying 190 km of nonpaved roads in areas known to be inhabited by red wolves or coyotes. Scats were placed in sealable plastic bags (Ziploc, SC Johnson, Racine, Wisconsin) and labeled. We exposed tweezers to an open flame to sterilize and collected a 0.4-ml portion of each scat for DNA analysis and then immersed it in 1.2 ml of DETS (DMSO, EDTA, TRIS, SALT) buffer contained in a 2-ml screw-top tube (Frantzen et al. 1998; Stenglein et al. 2010). We attempted to collect a scat subsample devoid of prey hair, bone, or vegetation, thus increasing the likelihood of obtaining the highest amount of usable canid DNA. The remainder of each scat sample was frozen to be sorted for food items at a later date.

Molecular methods.—Distinguishing the feces of sympatric carnivores of similar size is difficult (Davison et al. 2002). A concurrent study revealed that scats of red wolves and coyotes with a diameter between 14 mm and 28 mm cannot be differentiated by size alone (Dellinger et al. 2011b). Therefore, we used fecal DNA analysis to identify species, which also reduced error from the inclusion of nontarget taxa (Farrell et al. 2000). We extracted DNA from each scat using the Qiagen Stool Kit in a laboratory dedicated to extracting low-quality DNA. To differentiate scats deposited by canids from other carnivores, we performed a species identification test by amplifying a portion of the mitochondrial DNA control region following methods used by Onorato et al. (2006). When scat samples tested positive for *Canis*, we identified individuals to species using 17 microsatellite loci following methods outlined

by Bohling and Waits (2011). Loci were amplified in 2 separate multiplexes and alleles were accepted only if they were observed in ≥ 2 independent polymerase chain reactions (PCRs); homozygous genotypes were accepted if they were observed in ≥ 3 independent PCRs. The probability of identity for siblings was previously calculated by Bohling and Waits (2011) at 6 loci and was sufficiently low (0.003–0.006) to differentiate individuals. We regrouped duplicate genotypes using GenAlEx to identify unique individuals (Peakall and Smouse 2006). Genotypes obtained from scats also were compared with genotypes of known red wolves and coyotes captured by the USFWS biologists.

Evaluating genetic ancestry.—Known individuals previously captured by the USFWS had been evaluated for genetic ancestry using the red wolf pedigree and a maximum likelihood-based assignment test (Miller et al. 2003; Stoskopf et al. 2005; Adams 2006). We assessed genetic ancestry (q -value) of unknown individuals using the Bayesian clustering programs STRUCTURE 2.2 (Pritchard et al. 2000) and BAPS 5.1 (Corander et al. 2003, 2006) with representatives of 4 species as training sets following the methods and parameters outlined by Bohling and Waits (2011). The 4 species used for this analysis were coyotes from North Carolina and Virginia (82), gray wolves from Idaho and Alaska (37), domestic dogs (27), and pure red wolves composing the current wild population (151). Pure red wolves were defined as individuals with 100% red wolf ancestry as determined by the pedigree (Bohling et al. 2013).

A challenge with using the Bayesian programs is interpreting the output and determining criteria for assessing purity and the proportion of gene flow from an outside population (admixture). Typically, studies evaluating hybridization using Bayesian clustering programs (primarily STRUCTURE) rely solely on setting arbitrary thresholds for q -values when determining admixture (Vaha and Primmer 2006). We analyzed individuals of known ancestry using these programs to develop standardized thresholds for assessing admixture (Bohling et al. 2013). First, an individual was automatically considered a hybrid if there was statistical evidence for admixture with BAPS or STRUCTURE. For STRUCTURE, ancestry was considered statistically significant if the credibility interval surrounding a q -value did not overlap 0. Thus, an individual with q -values for 2 or more species with credibility intervals that did not overlap 0 was considered a hybrid. BAPS uses simulations to assess the statistical significance of ancestry coefficients and considers an individual admixed if the values are significant at $P < 0.1$ (Corander et al. 2006; Corander and Marttinen 2006), which we used as a threshold of admixture.

In addition, we developed a criterion on the basis of STRUCTURE q -values: any individual with a q -value < 0.75 for all 4 putative taxonomic groups was classified as a hybrid. Also, our experience suggests that a maximum q -value for any 1 group between 0.75 and 0.8 typically indicates hybrid ancestry (Bohling et al. 2013). To be conservative, we classified those individuals as hybrids; individuals with a q -value > 0.8 were classified as a member of the corresponding

taxonomic group. Although the 0.9 q -value threshold has been frequently used in the literature, our experience and other studies strongly suggest that the 0.8 q -value is adequate (Beaumont et al. 2001; Vaha and Primmer 2006; Barilani et al. 2007; Oliveira et al. 2008; Trigo et al. 2008; Sanz et al. 2009; Yokoyama et al. 2009).

Diet analysis.—We placed any scat identified as red wolf or coyote in nylon hosiery and laundered it in a washing machine using the gentle cycle, hot water, and detergent; contents that remained in the hosiery after washing were dried in a 65°C oven for 4 h. We identified prey species by microscopically and macroscopically comparing hair, bone, tooth, claw, and hoof fragments found in a scat to reference collections and identification manuals (Moore et al. 1997; Debelica and Theis 2009). Food items visually estimated to comprise $< 1\%$ by volume of the scat were excluded to minimize bias associated with overestimation (Knowlton 1964; Kelly 1991).

Data analysis.—Food habits often are compared using contingency tables, analysis of variance, or similar techniques (Dumond et al. 2001; Morey et al. 2007). These approaches can lead to pseudoreplication as each sampling unit (scat) usually contains more than 1 food item, all of which are assumed to be independent of one another (Lemons et al. 2010). Recording each food item as present or absent in a single scat yields a structure similar to capture histories for closed-capture, capture–mark–recapture data and thus allows the use of Program MARK to analyze diets and estimate diet selection accurately (Lemons et al. 2010). We placed food items into 6 categories: white-tailed deer, rabbits, small rodents (house mice, marsh rice rats, white-footed mice, eastern harvest mice, hispid cotton rats), other mammals (muskrats, raccoons, domestic and feral hogs), vegetation (corn [*Zea mays*], blackberry [*Rubus* spp.], persimmon [*Diospyros virginiana*], Poaceae), and other (e.g., insects, human refuse). Each category was recorded as present or absent with a 0 or 1 in a multinomial sequence for each scat. We analyzed diet data using Huggins' (1989) models for closed populations in Program MARK and calculated the overdispersion parameter \hat{c} using a goodness-of-fit statistic (Anderson et al. 1994; Burnham and Anderson 2002; Williams et al. 2002; Lemons et al. 2010). Because \hat{c} was determined to be 1.23, we used quasi-corrected Akaike information criterion (QAIC_c) values for our analysis (Anderson et al. 1994).

We built 6 models to examine the best predictor of canid diets; the variables in these models included canid taxon, time divided into biological periods, and time divided into calendar periods (Table 1). Biological periods were pair bonding (December–February), pup rearing (March–May), and dispersal (June–November—Morey et al. 2007). Calendar periods were spring (March–May), summer (June–August), fall (September–November), and winter (December–February). The first 3 models used calendar period, biological period, or canid taxon individually as the predictor. Models 4 and 5 included interaction between canid taxon and biological period and interaction between canid taxon and calendar period. The

TABLE 1.—Number of occurrences and percent occurrence of food items in *Canis rufus* ($n = 179$) and *Canis latrans* ($n = 64$) scats from January 2009 to February 2010 in eastern North Carolina.

Taxa	<i>Canis rufus</i> No. (%)	<i>Canis latrans</i> No. (%)
White-tailed deer	77 (31.2)	25 (24.8)
Rabbits (<i>Sylvilagus</i> spp.)	88 (35.6)	30 (29.7)
Small rodents	38 (15.4)	33 (32.7)
Other mammals	15 (6.1)	8 (7.9)
Vegetation	22 (8.9)	3 (3.0)
Other	7 (2.8)	2 (2.0)

last model was a fully parameterized model and included all 3 variables.

To develop results comparable with previous studies, we also calculated percent occurrence for diet categories. We defined percent occurrence for each canid as the number of times a food item occurred divided by the total number of occurrences of all food items (Schrecengost et al. 2008).

RESULTS

From 1,163 scats, we identified an individual genotype for 228 scats. The remaining scats were either those of unclassified canids or nontarget taxa or were unable to be identified using fecal DNA genotyping due to low-quality DNA of the scats. Of those 228 scats, 179 were identified as red wolf (49 individuals) and 64 as coyote (34 individuals). No identifiable

coyote scats were collected in February or October–December 2009.

Rabbits, white-tailed deer, and rodents were the prey most frequently eaten by red wolves and coyotes (Fig. 1). The scats of red wolves contained white-tailed deer in every month. Rodents appeared in 15% of red wolf scats and 33% of coyote scats (Table 1). Raccoons appeared only in 4 red wolf scats and 2 of these occurrences were from scats from the same individual that were collected in proximity. Other mesopredators were not detected in any scats. A single item made up greater than 95% of the scat volume in 55% of the coyote and 71% of the red wolf scats.

The only competitive mark–recapture model ($\Delta\text{QAIC}_c \leq 2$) included only calendar period as a predictor for canid diet (Table 2), and models including taxon comparisons all had $\Delta\text{QAIC}_c > 12$ and had extremely low weights. Parameter estimates from this model indicated that more rodents were consumed during the spring than during the summer (Fig. 2). Diets did not differ over time when the sampling period was divided into biological periods, nor did diet differ between red wolves and coyotes (Table 1).

DISCUSSION

Diets of red wolves and coyotes were similar as indicated by significant year-round overlap. Although there are no previous comparisons of diets of red wolves and coyotes, comparisons between gray wolf and coyote diets have shown varying

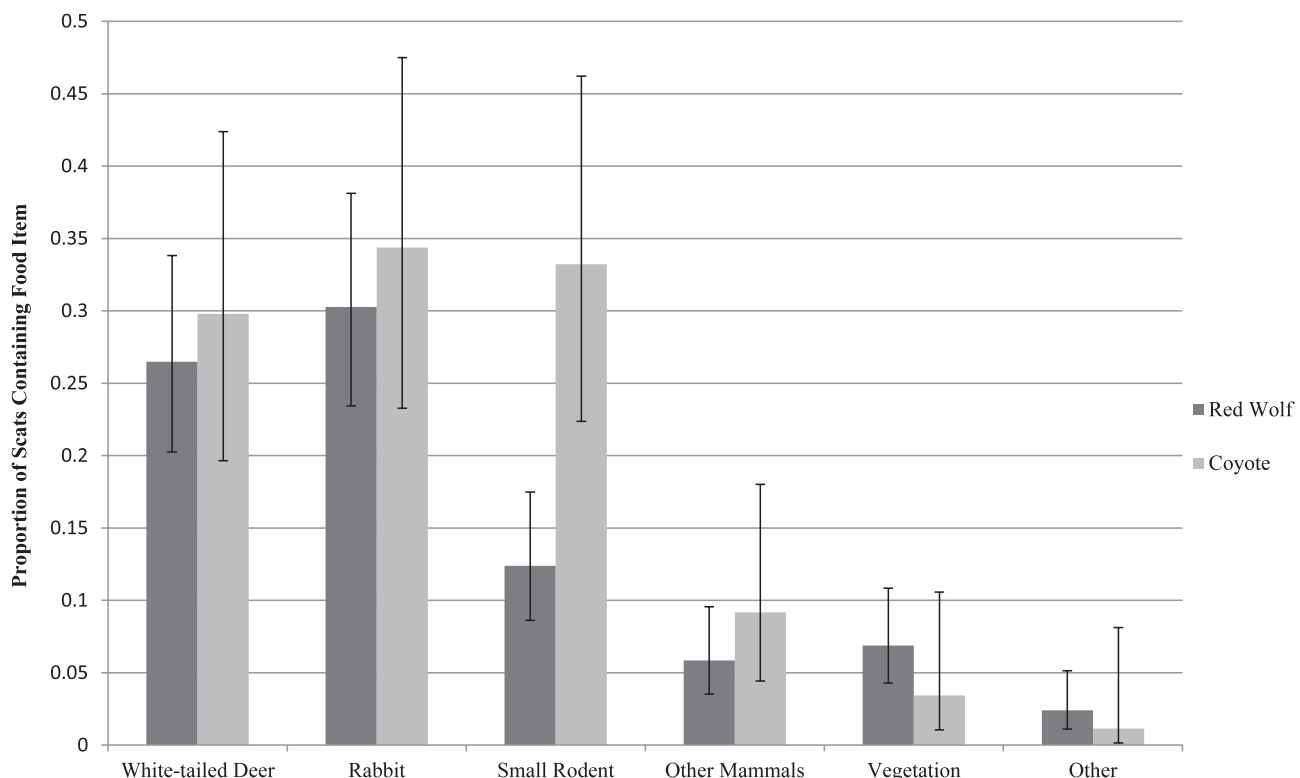


FIG. 1.—Diet estimates for red wolves and coyotes from Program MARK from January 2009 to February 2010 in eastern North Carolina. Error bars represent 95% confidence intervals.

Table 2.—Model sets and model results used to describe the diets of red wolves (*Canis rufus*) and coyotes (*Canis latrans*) from January 2009 to February 2010 in eastern North Carolina.

Model	QAIC _c ^a	ΔQAIC _c	Model weight	K ^b
Calendar	1,135.87	0	0.94	24
Biological period	1,141.58	5.71	0.05	18
Taxon	1,148.00	12.13	0.00	12
Taxon × biological period	1,148.98	13.11	0.00	36
Taxon × calendar	1,150.28	14.41	0.00	48
Taxon × biological period × calendar	1,150.28	14.41	0.00	48

^a QAIC_c, quasi-corrected Akaike information criterion.

^b Number of parameters in each model.

degrees of overlap and resource partitioning (Meleshko 1986; Thurber et al. 1992). Similar diets between sympatric taxa may imply spatial or temporal separation between the 2 or a superabundance of prey (Johnson et al. 1996). Given the low human populations, large expanses of open space, and extensive cover of agricultural fields in our study area, high prey abundance was likely.

The change in diet of red wolves and coyotes between the spring and summer calendar periods likely was related to corresponding changes in prey availability. Seasonal variation in food items has been reported in canid food habit studies (Smith and Kennedy 1983; Gese et al. 1988). Litvaitis and Shaw (1980) noted that the highest trapping success of rodents

and greatest frequency of rodents in coyote scats occurred during winter, and Harrison and Harrison (1984) documented a correlation between availability and amount of berries found in coyote scats. Further study of prey abundance and diet items across replicated seasons is needed, however, to determine if changes in canid diets in our study area can be attributed to seasonal prey availability.

The diet of coyotes in eastern North Carolina appears generally similar to coyote diets in other areas in the southeastern United States. One possible difference was our finding that insects and vegetation were relatively unimportant for coyotes, which contrasts with results of other studies in the region (Smith and Kennedy 1983; Blanton 1988; Stratman and Pelton 1997; Schrecengost et al. 2008). However, we suspect that our results may have underestimated insects and vegetation. We commonly detected orthopterans, primarily grasshoppers, in scats but these items rarely contributed > 1% of the scat volume, and were thus excluded from our analysis. Additionally, we collected several scats composed entirely of orthopterans or persimmon and blackberry seeds, but lack of fecal material prevented collection of useable DNA samples and species identification was unsuccessful in these cases.

Several recent studies have suggested that coyotes may be suppressing white-tailed deer populations in the eastern United States through fawn, and possibly adult, mortality (Schrecengost et al. 2008; Kilgo et al. 2012). Our diet analyses showed

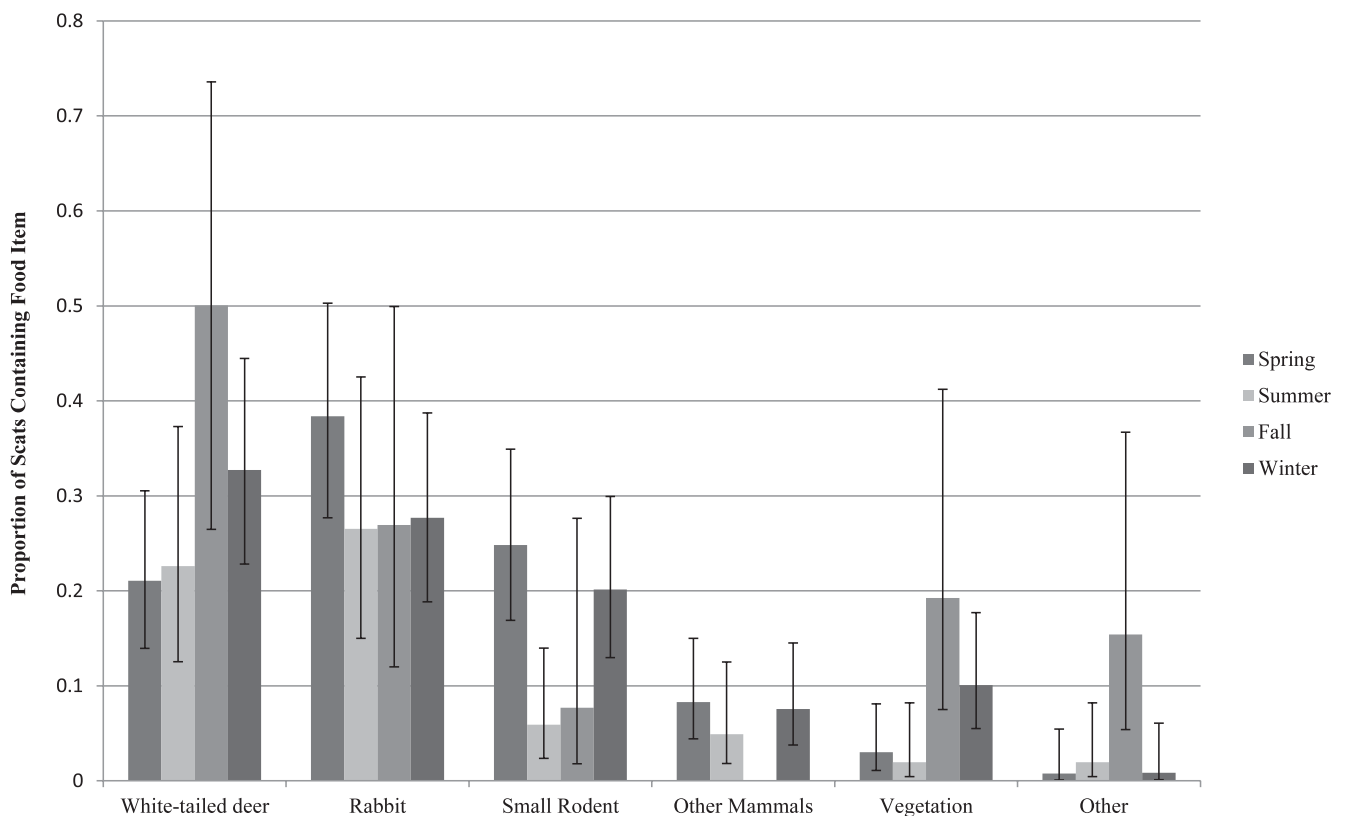


FIG. 2.—Diet estimates of large canids by calendar period from Program MARK from January 2009 to February 2010 in eastern North Carolina. Error bars represent 95% confidence intervals.

that white-tailed deer was an important component of both red wolf and coyote diets year round. Although we did not differentiate adult deer from fawns, several scats contained small hooves, bones, and teeth of fawns. Coyote diet studies in other states suggested that deer carrion may make up a large proportion of the diet (Arjo and Pletscher 1999; Switalski 2003), but we were unable to determine the amount of deer consumed as carrion, nor were we able to determine the proportion of the diet containing fawns.

Species identification using fecal DNA ensured that scats used in our analyses were of target taxa (Farrell et al. 2000; Bohling and Waits 2011). Previous food habit studies of gray wolves and coyotes used scat size as a determinant of animal origin, excluding extremely large or small scats to avoid inclusion of feral dogs, foxes, and bobcats (Arjo et al. 2002; Carrera et al. 2008; Schrecengost et al. 2008). Despite the poor success rate of species identification in our study (26.5%), excluding noncanid scats from our analysis and positively identifying scats from red wolves and coyotes increased the accuracy of our findings.

Our results show that the diets of red wolves and coyotes do not differ significantly in eastern North Carolina where their ranges overlap. Although food resources during our study may have been abundant (with relatively little ecological pressure for resource partitioning), we speculate that red wolves and coyotes coexist in eastern North Carolina through mechanisms other than prey partitioning. Additionally, the diet similarity between the 2 taxa suggests that red wolves and coyotes affect prey populations similarly and may, at least partially, be fulfilling the historic niche that canids once had in the southeastern United States.

ACKNOWLEDGMENTS

This project was funded by the North Carolina Wildlife Resource Commission and the North Carolina State University Fisheries, Wildlife, and Conservation Biology Program. A. Facka and P. Lemons provided help with data analysis. J. Hinton and J. Dellinger provided assistance with scat collection and diet analysis. C. Daystar, S. Lasher, and L. Green helped with diet analysis. Lab assistance was provided by E. Herrera, A. Knapp, and M. Sterling. We also thank the USFWS Red Wolf Recovery team for help in scat collection and facilitating access to USFWS properties. Weyerhaeuser Company, Matamuskeet Ventures, and other local landowners also allowed access to their properties.

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Submitted 3 May 2013. Accepted 8 May 2013.

Associate Editor was Winston P. Smith.