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Article *in* Journal of Mammalogy · February 2017

DOI: 10.1093/jmammal/gyw233

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Journal of Mammalogy, xx(x):1–14, 2017
DOI:10.1093/jmammal/gyw233

Using diets of *Canis* breeding pairs to assess resource partitioning between sympatric red wolves and coyotes

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Foraging behaviors of red wolves (*Canis rufus*) and coyotes (*Canis latrans*) are complex and their ability to form congeneric breeding pairs and hybridize further complicates our understanding of factors influencing their diets. Through scat analysis, we assessed prey selection of red wolf, coyote, and congeneric breeding pairs formed by red wolves and coyotes, and found that all 3 had similar diets. However, red wolf and congeneric pairs consumed more white-tailed deer (*Odocoileus virginianus*) than coyote pairs. Coyotes forming breeding pairs with red wolves had 12% more white-tailed deer in their diet than conspecifics paired with coyotes. Contrary to many studies on coyotes in the southeastern United States, we found coyotes in eastern North Carolina to be primarily carnivorous with increased consumption of deer during winter. Although prey selection was generally similar among the 3 groups, differences in diet among different breeding pairs were strongly associated with body mass. Larger breeding pairs consumed more white-tailed deer, and fewer rabbits (*Sylvilagus* spp.) and other small mammals. Partitioning of food resources by sympatric red wolves and coyotes is likely via differences in the proportions of similar prey consumed, rather than differences in types of prey exploited. Consequently, our results suggest coexistence of red wolves and coyotes in the southeastern United States may not be possible because there are limited opportunities for niche partitioning to reduce competitive interactions.

Key words: body mass, *Canis latrans*, *Canis rufus*, coyote, diet, hybridization, red wolf, reproductive barriers, resource partitioning

Ecologists have consistently been interested in diets of carnivores because predation is an essential ecological process structuring communities and influences ecosystem productivity (Hairston et al. 1960; Paine 1969; Mills et al. 1993; Schmitz et al. 2000). Understanding relationships between carnivores and their food resources, and describing mechanisms influencing foraging behavior, is a central goal of carnivore management and conservation. In particular, body mass is a fundamental organism-level variable known to profoundly influence carnivore diets and interactions (Rosenzweig 1966; Gittleman 1985; Carbone et al. 1999; Donadio and Buskirk 2006). Indeed, carnivores weighing above a range of 15–20 kg subsist on larger vertebrate prey approaching their own body mass, primarily because of higher energetic demands and foraging constraints related to their body size (Carbone et al. 1999, 2007). Therefore, a thorough understanding of carnivore diets requires identifying primary factors influencing variation in resource use among competing carnivore species.

Although carnivores exhibit a wide range of morphologies, sympatric species within the same genus may exhibit significant dietary overlaps when their morphologies and body sizes are similar (Polis et al. 1989; Palomares and Caro 1999; Donadio and Buskirk 2006). Additionally, antagonistic encounters increase among co-occurring carnivores because similar use of prey requires use of similar habitats (Polis et al. 1989). For example, gray wolves (*Canis lupus*) and coyotes (*Canis latrans*) are well-known predators of ungulate species, in which coyotes prey proportionally more on neonates because coyotes are smaller than wolves (Patterson and Messier 2000; Smith et al. 2003; Berger et al. 2008). Most interspecific interactions documented between gray wolves and coyotes occur when coyotes attempt to scavenge wolf-killed ungulate carcasses, resulting in the displacement or death of individual coyotes by wolves (Smith et al. 2003; Switalski 2003; Merkle et al. 2009). Despite little spatial segregation from gray wolves, coyotes coexist with gray wolves in western North America because coyotes are capable of partitioning food resources (e.g., use of smaller mammalian prey) and modifying space use and scavenging behaviors to reduce antagonistic interactions with wolves (Switalski 2003; Atwood and Gese 2010).

Since the late Rancholabrean (130,000–10,000 ybp) through the early 20th century, red wolves (*Canis rufus*) were the only *Canis* taxon to occupy the southeastern United States (Nowak 1979, 2002, 2003). However, coyotes began colonizing the red wolf's historic range after eradication campaigns extirpated all but a few remnant wolf populations in the southeastern United States (McCarley 1962; Paradiso and Nowak 1972; USFWS 1989; Nowak 2002). Currently, red wolves and coyotes are sympatric in eastern North Carolina and it is the only region in the southeastern United States where *Canis* taxa co-occur in the wild (Hinton and Chamberlain 2014). Because sympatric red wolves and coyotes approach each other in body size and behavior, they forage on similar prey. Indeed, a recent study reported no difference between red wolves and coyotes in their consumption of small mammals, rabbits, and white-tailed deer (*Odocoileus virginianus*—McVey et al. 2013). Although coyotes use invertebrates and fruit as seasonal food resources, red wolves are not known to be omnivorous (Shaw 1975; Dellinger et al. 2011a; McVey et al. 2013). Individual red wolves are 7–18 kg heavier than the largest sympatric coyotes in eastern North Carolina (Hinton and Chamberlain 2014). Body size can be used to predict interactions of carnivores with prey (Gittleman 1985; LaBarbera 1989; Donadio and Buskirk 2006; Carbone et al. 2007) and, accordingly, red wolves should rely more on larger prey than coyotes. Therefore, partitioning of food resources between red wolves and coyotes is likely, with red wolves capable of subduing larger mammalian prey species.

Currently, eastern North Carolina supports 3 *Canis* taxa: red wolves, coyotes, and red wolf × coyote hybrids (hereafter, hybrids). Hybrids are produced when red wolves and coyotes form congeneric breeding pairs that defend territories and maintain pack dynamics typical of *Canis* taxa and are more likely to occur when mating opportunities for individuals are limiting (Hinton et al. 2013, 2017; Bohling and Waits 2015; Bohling et al. 2016). The ability of red wolves and coyotes to form congeneric breeding pairs may provide valuable insights into how resources are partitioned between both species, particularly when red wolves and coyotes in congeneric pairs are capable of sharing food and space simultaneously. Understanding prey selection of red wolves and coyotes, and how food resources are partitioned by *Canis* breeding pairs, are important steps to improving our knowledge of wolf and coyote interactions. Therefore, our primary purpose was to identify *Canis* breeding pairs and contrast their diets to examine factors associated with partitioning food resources among sympatric *Canis* taxa and how this may serve as a possible barrier to congeneric pairings and consequently hybridization. We hypothesized that body mass would influence the occurrence of prey types in diets of red wolves and coyotes, and that congeneric breeding pairs would have diets intermediate to red wolf and coyote breeding pairs.

MATERIALS AND METHODS

This study was conducted in the Red Wolf Recovery Area (hereafter, Recovery Area) on the Albemarle Peninsula of eastern North Carolina (Beaufort, Dare, Tyrrell, and Washington counties; Fig. 1). The Recovery Area consisted of approximately 6,000 km^2 of federal, state, and private lands. The Albemarle Peninsula is an intensively farmed agricultural-hardwood bottomland forest matrix in which approximately 45% of the landscape was characterized by agricultural and commercial timber activities (McKerrow et al. 2006). Corn, cotton, soybeans, and winter wheat were the primary agricultural crops and comprised approximately 30% of the land cover, whereas commercial pine (*Pinus* spp.) plantations comprised approximately 15%. The remaining 55% of land cover types were pocosin (peatlands with a low and dense evergreen shrub layer and pond pine [*Pinus serotina*]; 15%), coastal bottomland hardwood forests (15%), saltwater marsh (5%), open water (10%), and other land cover types (10%). Climate was typical of the mid-Atlantic: 4 distinct seasons, nearly all equal in length, with annual precipitation averaging between 122 and 132 cm. Summer climate was typically hot and humid with daily temperatures ranging from 27°C to over 38°C and winters were relatively cool with daily temperatures ranging between −4°C and 7°C. Potential mammalian prey of red wolves and coyotes included white-tailed deer, raccoons (*Procyon lotor*), rabbits (*Sylvilagus* spp.), wild pigs (*Sus scrofa*), nutria (*Myocastor coypus*), muskrats (*Ondatra zibethicus*), hispid cotton rats (*Sigmodon hispidus*), mice (*Peromyscus* spp.), voles (*Microtus* spp.), and shrews (*Blarina* spp., *Sorex* spp.—McVey et al. 2013).

Methods to capture, handle, and process red wolves and coyotes were approved by the Louisiana State University Agricultural Institutional Animal Care and Use Committee (Protocol Number AE2009-19) and met guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011). Red wolves and coyotes were captured within the Recovery Area during annual trapping efforts conducted by the USFWS Red Wolf Recovery Program (hereafter, Recovery Program). Red wolves and coyotes were measured and weighed, and sex was determined. Ages and genetic confirmation of captured red wolves were known if individuals were carrying a subcutaneous passive integrated transponder (PIT) tags inserted during annual surveys of red wolf dens (Beck et al. 2009; Rabon et al. 2013; Hinton et al. 2016a). Ages of captured red wolves without PIT tags and coyotes were estimated by tooth wear (Gier 1968; Gipson et al. 2000), and a blood sample was taken for genetic confirmation. The Recovery Program categorized red wolves and coyotes ≥ 2 years old as adults, 1- to 2-year-old as juveniles, and < 1-year-old as pups. Coyotes

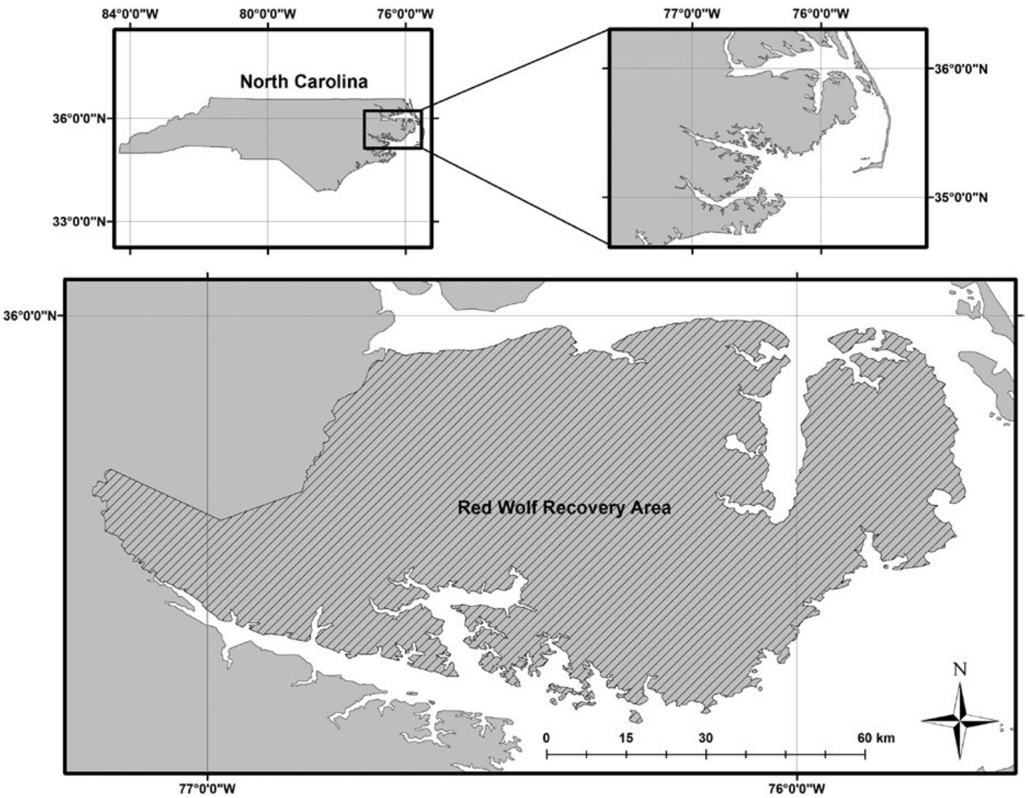

Fig. 1.—Map of North Carolina showing the location of the Red Wolf Recovery Area (hatched area) in the northeastern portion of the state.

captured within the Recovery Area by USFWS personnel were sterilized and released where captured to act as space holders until those coyotes were displaced by red wolves or were removed for management reasons (Gese and Terletzky 2015; Hinton et al. 2017). Coyotes used in this study were taken to a local veterinary clinic for surgical sterilization where males and females were sterilized by vasectomy and tubal ligation, respectively (Gese and Terletzky 2015). This process kept hormonal systems intact and avoided disrupting breeding and territorial behavior (Bromley and Gese 2001; Gese and Terletzky 2015). Once red wolves and coyotes were fully processed, individuals were fitted with either mortality-sensitive VHF radiocollars (Telonics, Mesa, Arizona) or mortality-sensitive GPS radiocollars (Lotek Engineering, Newmarket, Ontario, Canada), released, and then monitored by the Recovery Program during weekly telemetry flights. Weekly monitoring efforts via aircraft allowed the Recovery Program to identify territories of radiomarked red wolves, coyotes, and congeneric pairs on the landscape.

Resident breeding pairs were identified as radiocollared individuals of breeding age (≥ 2 years old) that were temporally and spatially associated with one another and had been defending a territory for ≥ 6 months (Hinton et al. 2017). Biologists confirmed breeding pair status during spring den visits (March–May) by locating dens and daybeds of females to verify presence of litters of known radiocollared breeding pairs. Red wolves paired with a sterilized coyote (congeneric pairs) and coyote pairs were confirmed through field monitoring and occasionally by den visits if coyotes had not been sterilized.

We defined 3 types of *Canis* breeding pairs: red wolf (2 red wolves), coyote (2 coyotes), and congeneric (red wolf with a coyote). Some red wolf pairs consisted of older individuals that mated for several years and functioned as packs because they included juveniles and pups, whereas newly formed breeding pairs did not have juveniles or pups. Coyote pairs did not have juveniles and pups because at least 1 breeder was sterilized to suppress coyote presence and reproduction adjacent to red wolf territories. Congeneric pairs were comprised of a red wolf and a coyote and did not have juveniles and pups because the coyote in the pair was sterilized to prevent hybridization (Gese and Terletzky 2015).

To delineate territories of red wolf, coyote, and congeneric pairs, we calculated home ranges of each breeding pair using Geospatial Modeling Environment (GME—Beyer 2014) and ArcMap 10.3 (Environmental Systems Research Institute 2014). Utilization distributions were generated using the h-plugin smoothing parameter within GME. We created home ranges for red wolf, coyote, and congeneric pairs by calculating 95% fixed kernel density estimates (Worton 1989; Seaman and Powell 1996) and then surveyed home ranges of breeding pairs at least once per month for scat collection from January 2009 through December 2011. We surveyed paved, gravel, and dirt roads by foot, all-terrain vehicles, and trucks, and opportunistically collected scat from known resident red wolves and coyotes captured during annual trapping. Scats were bagged, dated, marked with a unique identification number, and stored in a freezer for later dissection and analysis. We identified scat as belonging to red wolves and coyotes by physical appearance, including size (Dellinger et al. 2011b), and the presence of tracks or other *Canis* sign in the immediate area of the scat. Using scats as the sampling unit can artificially inflate sample sizes and lead to pseudo-replication when scats repeatedly collected from territories of breeding pairs are treated independently. By using *Canis* breeding pairs as our sampling unit, we provided a study design to address these concerns (Hulbert 1984; Millar and Anderson 2004).

By sampling only in known territories of radiomarked red wolves and coyotes, we attempted to minimize the influence of transient individuals in our analysis and account for effects of body mass of resident breeders, habitat composition and density of deer of home ranges, and season on diets of resident red wolves and coyotes. This is a biologically reasonable approach because red wolves and coyotes exclude *Canis* transients from their territories so that transients bide in peripheral areas of territories and in areas unoccupied by residents (Hinton et al. 2015a, 2016b). Furthermore, Benson and Patterson (2013a) documented strong spatial segregation between eastern wolves (*Canis lycaon*), coyotes, and their hybrids in and around Algonquin Provincial Park, Ontario, Canada. Similarly, red wolves, coyotes, and their hybrids exhibit strong spatial segregation in eastern North Carolina (J. Hinton, University of Georgia, pers. comm.; see Fig. 2). Therefore, among *Canis* taxa in eastern North Carolina, red wolves and coyotes maintain exclusive territories, except when wolves and coyotes form congeneric breeding pairs that share and defend space. Our sampling approach allowed us to collect data from territories of red wolves and coyotes that formed congeneric pairs to document food habits of *Canis* breeding pairs responsible for hybridization. We assigned scats within known territories to red wolf, coyote, or congeneric pairs but excluded those that could not be associated with known breeding pairs. Dellinger et al. (2011a) reported that 96% of 196 scats collected from red wolf territories matched the genotypes of individuals from packs of interest. Like Dellinger et al. (2011a), our sample units were *Canis* breeding pairs so we assumed that scats collected within known territories belonged to pairs of interest. We acknowledge that this approach allowed some inclusion of scats from other canids; however, this occurrence was likely rare.

We examined scats assigned to red wolf, coyote, and congeneric pairs for prey remains. Individual scats were placed in nylon stockings and secured in small, nylon mesh bags with waterproof labels for washing. Scats were soaked in water for 24 h before being transferred to a washing machine and washed on the regular cycle with detergent 3 times to separate hair and bone fragments from fecal matter. We allowed scats to air dry for 72 h prior to examining scat contents. Once dried, we identified undigested food items microscopically and macroscopically by comparing them to reference collections and identification manuals (Debelica and Theis 2009). We assigned prey remains to 1 of 6 categories: white-tailed deer (hereafter, deer), rabbits, small mammals (mice, rats, shrews, and voles), furbearers (defined here as muskrats, nutria, and raccoons), pigs (feral and domestic), and other food items (birds, insects, vegetative material, and anthropogenic material). Items that

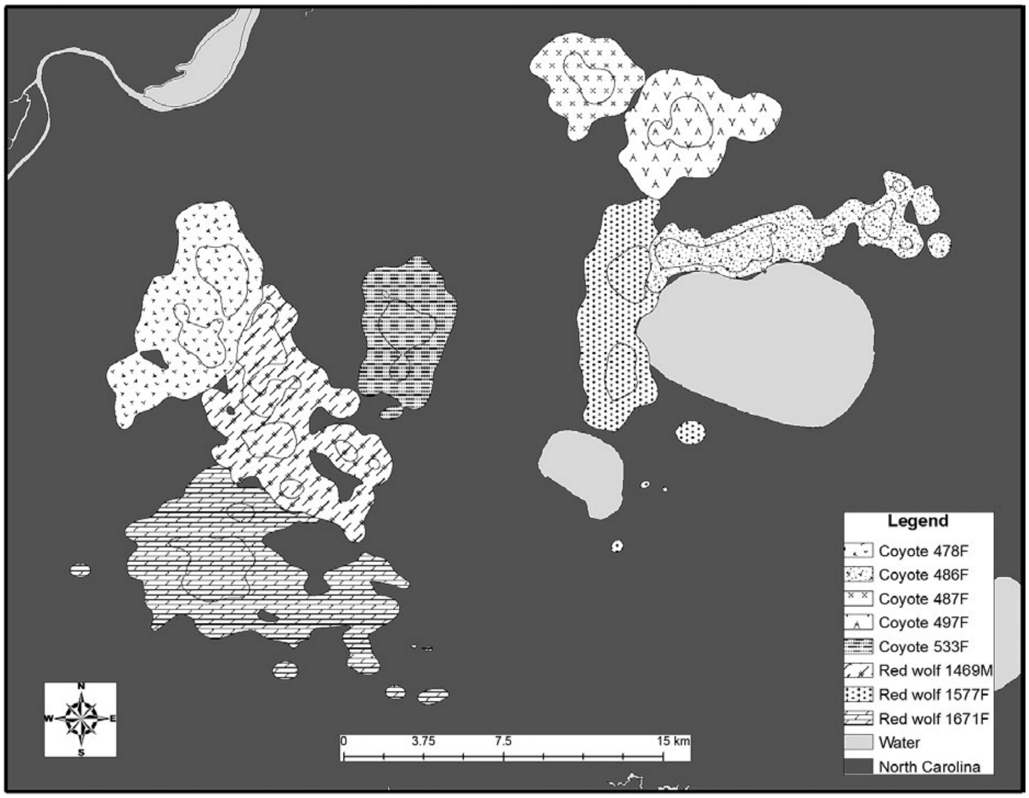

Fig. 2.—Spatial distribution of home ranges and core areas for several coyotes (*Canis latrans*) and red wolves (*Canis rufus*) in the Red Wolf Recovery Area located in northeastern North Carolina, 2009–2011.

comprised ≤ 1% of prey found in scat were treated as trace items and excluded from analyses to reduce bias (Ciucci et al. 1996; Kamler et al. 2007; Dellinger et al. 2011a). As recommended by Ciucci et al. (1996) and Mattioli et al. (2004), observers were trained in identifying scat contents by practicing with reference material prior to analyses.

Following identification of prey remains in scat, we quantified diet as the proportion based on the frequency of occurrence of scats (FO; proportion of total scats in which each item was found) for each prey category detected in scats (Arjo et al. 2002; Dellinger et al. 2011a; McVey et al. 2013). We chose to focus our analyses on FO because it is the most commonly used method in diet studies and is readily interpretable (Zabala and Zuberogoitia 2003; Klare et al. 2011; Larson et al. 2015). We recognize that FO does not approximate the volumetric importance of items in the diet, but it can provide valuable insight into resource use by carnivores (Klare et al. 2011; Larson et al. 2015). Furthermore, FO is highly concordant for ranking of food items in diets of carnivores (Zabala and Zuberogoitia 2003; van Dijk et al. 2007; Klare et al. 2011).

To reflect anthropogenic effects of agricultural practices on the landscape, we divided each year into two 6-month seasons based on agricultural practices: growing (1 March–31 August) and harvest (1 September–28 February). The growing season represented a time when agricultural fields provided cover and increased foraging opportunities for red wolves and coyotes, whereas the harvest season represented a time when those fields were barren and presumably offered no cover and fewer foraging opportunities. We used body mass of breeders (combined body mass of both breeders), density of deer (number of deer harvested by hunters/km^2), and percent agriculture (percent land cover within the 95% contour home range comprised of agriculture) as explanatory variables to account for changes in dietary composition of *Canis* breeding pairs. Because red wolf pairs were capable of breeding, we tested whether pack size (number of known individuals in a pack) was associated with wolf diets.

We included a measurement for deer abundance as a variable because deer are known to be an important food resource for red wolves (Dellinger et al. 2011a; McVey et al. 2013) and coyotes (Chamberlain et al. 1999; Schrecengost et al. 2008; Kilgo et al. 2012; Cherry et al. 2016) in the southeastern United States. We used county-level hunter harvest data collected by the North Carolina Wildlife Resources Commission as an index to deer abundance in the Recovery Area. Estimates of deer harvest ranged between 0.18 and 1.94 deer/km^2. Between 2009 and 2011, deer harvest remained relatively stable for each of the 5 counties (North Carolina Wildlife Resources Commission 2016). Although harvest reports do not reflect true deer densities or account for hunter effort, they provide a reliable index of relative deer abundance and serve as the basis for monitoring deer populations (Roseberry and Woolf 1991; Lukacs et al. 2011).

We used chi-square contingency table analysis to test if the frequency of prey items in scats differed among *Canis* breeding pairs and between seasons. We used generalized linear mixed models with a logit link in R (R Development Core Team 2013) to compare factors influencing occurrence of prey in scats for each breeding pair with a binary (0 = no occurrence, 1 = occurred) response variable. Those factors included combined body mass of breeders, percent of home ranges comprised of agricultural habitat, deer density, and season. We included random intercepts for breeding pairs in each model to account for variation and unequal number of scats collected per breeding pair. We conducted a second analysis for red wolf pairs that included pack size to account for potential influences of offspring on prey use by wolves. Prior to modeling, we rescaled values for all continuous variables by subtracting their mean and dividing by 2 *SD*s (Gelman 2008).

We used 4 general hypotheses to design 5 a priori candidate models to test factors associated with use of each prey category by *Canis*. First, we included a binomial variable for season (1 = growing, 0 = harvest) because prey selection may be influenced by time of year. Second, we included combined body mass of breeders because we hypothesized that prey selection was associated with body size. Third, we included the proportion of home ranges comprised of agriculture because we assumed prey selection was a function of habitat composition. Finally, we included the index of white-tailed deer abundance because we hypothesized that prey selection was influenced by deer density. We then removed each of these 4 variables from a global model to compare performances of varying model sets to the global model. This allowed us to deduce which variable (season, body mass, habitat, and deer density) had the strongest effect on improving model performance. For red wolf pairs, we also tested whether pack size was associated with prey selection by red wolf packs. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and used ΔAIC_c to select which models best supported factors influencing use of prey categories by *Canis* breeding pairs (Burnham and Anderson 2002).

RESULTS

From 2009 to 2011, we collected and analyzed 1,485 scats from 13 red wolf pairs, 17 coyote pairs, and 10 congeneric pairs. Mean combined body mass of breeders in congeneric pairs (43.5 kg ± 1.2) were intermediate to red wolf (57.2 kg ± 0.9) and coyote (29.5 kg ± 0.7) pairs ($F_{2,39} = 284.65$, $P < 0.001$). Mean age of breeders in red wolf pairs (4.6 years ± 0.4) was greater than breeders in coyote (2.8 years ± 0.3) and congeneric (3.0 years ± 0.3) pairs ($F_{2,39} = 7.32$, $P = 0.002$). Red wolf, coyote, and congeneric pairs accounted for 47.3%, 37.3%, and 15.4% of collected scats, respectively.

Red wolf, coyote, and congeneric pairs differentially used deer ($\chi^2_2 = 34.05$, $P \leq 0.001$), rabbits ($\chi^2_2 = 53.57$, $P \leq 0.001$), small mammals ($\chi^2_2 = 84.05$, $P \leq 0.001$), pigs ($\chi^2_2 = 14.40$, $P = 0.002$), and other prey items ($\chi^2_2 = 26.40$, $P \leq 0.001$); deer and rabbits comprised most prey items identified in scats (Table 1). We detected no difference in use of furbearers among *Canis* breeding pairs ($\chi^2_2 = 0.03$, $P = 0.987$). Red wolf pairs consumed more deer and pigs than coyote pairs, whereas coyote pairs consumed more rabbits, small mammals, and other prey items than red wolf pairs (Table 1). Congeneric pairs used deer and furbearers similar to red wolf pairs, but used small mammals and pigs similar to coyote pairs (Table 1). Congeneric use of rabbits was intermediate of red wolf and coyote pairs, whereas use of other prey items was greater (Table 1).

We detected no seasonal differences in consumption of deer (χ^2_1 = 2.82, P = 0.094) and pigs (χ^2_1 = 1.31, P = 0.252) by red wolf pairs (Table 2). Red wolves consumed more rabbits (χ^2_1 = 10.39, P = 0.002), small mammals (χ^2_1 = 17.99, $P \leq$ 0.001), and other prey items (χ^2_1 = 11.25, $P \leq$ 0.001) during the harvest season, whereas furbearers (χ^2_1 = 18.13, $P \leq$ 0.001) were consumed more during the growing season (Table 2). We detected no seasonal differences in consumption of small mammals (χ^2_1 = 1.58, P = 0.210), furbearers (χ^2_1 = 1.24, P = 0.267), pigs (χ^2_1 = 1.69, P = 0.194), and other prey items (χ^2_1 = 0.33, P = 0.568) by coyotes (Table 2). Coyotes consumed more deer (χ^2_1 = 13.73, $P \leq$ 0.001) during the harvest season, whereas rabbits (χ^2_1 = 12.482, $P \leq$ 0.001) were consumed more during the growing season (Table 2). We detected no seasonal differences in consumption of furbearers (χ^2_1 = 1.38, P = 0.241), pigs (χ^2_1 = 0.63, P = 0.429), and other prey items (χ^2_1 = 1.32, P = 0.250) by congeneric pairs (Table 2). Congeneric pairs consumed more rabbits (χ^2_1 = 9.39, P = 0.002) and small mammals (χ^2_1 = 6.50, P = 0.011) during the harvest season, whereas deer (χ^2_1 = 5.65, P = 0.017) were consumed more during the growing season (Table 2).

Combined body mass of *Canis* breeding pairs had the strongest effect on the performance of global models for FO of deer, rabbits, and small mammals whereas season had the strongest effect for furbearers and other prey items (Table 3). Deer density had the strongest effect on the performance of the global model for FO of pigs (Table 3). Combined body mass of *Canis* breeding pairs had a positive relationship with FO of deer (r^2 = 0.26, P = 0.002; Fig. 3A), whereas percent cover by agricultural fields showed a weak negative relationship (Table 4). The FO of rabbits was negatively associated with combined body mass of *Canis* breeding pairs (Table 4). For small mammals, combined breeder body mass and growing season was negatively associated with FO. Growing season was positively associated with FO for furbearers (Table 4). The FO of pigs was positively correlated with percent cover by agriculture and negatively correlated with deer density (Table 4). Lastly, FO of other prey items was negatively correlated with percent cover by agriculture and positively correlated with deer density (Table 4).

Season had the strongest effect on the performance of global models for FO of rabbits, small mammals, and furbearers observed in red wolf scats, whereas habitat and deer density had the strongest effect for pigs and other prey items, respectively (Table 5). Combined body mass of red wolf breeding pairs had the strongest effect on the performance of global models for FO of deer (Table 5). Growing season was negatively correlated with FO of rabbits in red wolf scats, whereas percent cover by agriculture was positively correlated (Table 6). The FO of small mammals in red wolf scats was negatively correlated with growing season (Table 6). Growing season, percent cover by agriculture, and pack size were positively correlated

Table 1.—Frequency of occurrence of primary diet items in the scat of red wolf (*Canis rufus*), coyote (*Canis latrans*), and mixed congeneric *Canis* breeding pairs in eastern North Carolina, 2009–2011.

	No. of scats	% Deer	% Rabbit	% Small mammal[a]	% Furbearer[b]	% Pig	% Other[c]
Red wolf (*n* = 13)	702	60.3	36.5	21.7	10.0	3.4	8.6
Coyote (*n* = 17)	554	44.1	57.1	44.4	9.9	0.9	15.0
Congeneric (*n* = 10)	229	57.2	48.0	42.4	9.6	0.4	21.0

[a] Rat, mouse, shrew, and vole species.
[b] Muskrats, nutrias, and raccoons.
[c] Insects (i.e., grasshoppers and beetles), vegetation, fruit, bird species, and human trash.

Table 2.—Frequency of occurrence (%) of foods in the scats of red wolf (*Canis rufus*) packs (*n* = 702 scats), coyote (*Canis latrans*) pairs (*n* = 554 scats), and congeneric pairs (*n* = 229 scats) by season in northeastern North Carolina, 2009–2011.

	Red wolf packs		Coyote pairs		Congeneric pairs	
	Harvest[a]	Growing[b]	Harvest	Growing	Harvest	Growing
Deer	56.1	63.0	52.0	36.4	51.1	67.1
Rabbits	44.3	32.1	49.5	64.3	56.0	35.2
Small mammals[c]	30.4	16.7	41.7	47.0	48.9	31.8
Furbearers[d]	3.5	13.6	8.5	11.3	7.8	12.5
Pigs	2.4	4.0	0.4	1.4	0.7	0.0
Other[e]	13.5	6.0	15.8	14.1	23.4	17.1

[a] September through February.
[b] March through August.
[c] Rat, mouse, shrew, and vole species.
[d] Muskrats, nutrias, and raccoons.
[e] Insects (i.e., grasshoppers and beetles), vegetation, fruit, bird species, and human trash.

Table 3.—Generalized linear mixed models for predicting frequency of occurrence of 6 prey categories corresponding to different hypotheses of factors affecting use by *Canis* breeding pairs in northeastern North Carolina, 2009–2011. Shown are differences in Akaike's Information Criteria for small sample sizes (AIC_c) between the model and lowest AIC_c in the model set (ΔAIC_c), number of estimable parameters (k), Akaike model weight (ω_i), and a measure of model fit (deviance).

Prey category	Model	k	Deviance	ΔAIC_c	ω_i
White-tailed deer	No deer density—Season[a] + BWt[b] + Ag[c]	5	1,976.3	0.0	0.40
	No season—BWt + Ag + DD[d]	5	1,976.8	0.5	0.31
	Full model—Season + BWt + Ag + DD	6	1,975.6	1.3	0.21
	No habitat—Season + BWt + DD	5	1,979.5	3.2	0.08
	No breeder body mass—Season + Ag + DD	5	1,991.3	15.0	0.0
Rabbits	No season—BWt + Ag + DD	5	1,971.1	0.0	0.32
	No deer density—Season + BWt + Ag	5	1,971.3	0.2	0.29
	No habitat—Season + BWt + DD	5	1,971.5	0.4	0.26
	Full model—Season + BWt + Ag + DD	6	1,971.0	1.9	0.13
	No breeder body mass—Season + Ag + DD	5	1,982.2	11.1	0.0
Small mammals	No deer density—Season + BWt + Ag	5	1,778.2	0.0	0.52
	Full model—Season + BWt + Ag + DD	6	1,778.2	2.0	0.20
	No habitat—Season + BWt + DD	5	1,780.8	2.6	0.15
	No season—BWt + Ag + DD	5	1,781.1	2.9	0.13
	No breeder body mass—Season + Ag + DD	5	1,790.5	12.3	0.0
Furbearers	No deer density—Season + BWt + Ag	5	929.6	0.0	0.40
	No breeder body mass—Season + Ag + DD	5	930.6	1.0	0.24
	No habitat—Season + BWt + DD	5	930.8	1.2	0.21
	Full model—Season + BWt + Ag + DD	6	929.6	2.0	0.15
	No season—BWt + Ag + DD	5	947.3	17.7	0.0
Pigs	No breeder body mass—Season + Ag + DD	5	262.4	0.0	0.41
	No season—BWt + Ag + DD	5	263.7	1.5	0.19
	Full model—Season + BWt + Ag + DD	6	262.2	1.8	0.17
	No habitat—Season + BWt + DD	5	264.7	2.3	0.13
	No deer density—Season + BWt + Ag	5	265.2	2.8	0.10
Other	No breeder body mass—Season + Ag + DD	5	1,106.7	0.0	0.45
	No habitat—Season + BWt + DD	5	1,107.9	1.2	0.25
	Full model—Season + BWt + Ag + DD	6	1,106.5	1.8	0.18
	No deer density—Season + BWt + Ag	5	1,110.0	3.3	0.09
	No season—BWt + Ag + DD	5	1,112.2	5.5	0.03

[a] Growing season.

[b] Combined body mass of breeders.

[c] Proportion of home range comprising agriculture.

[d] Deer density.

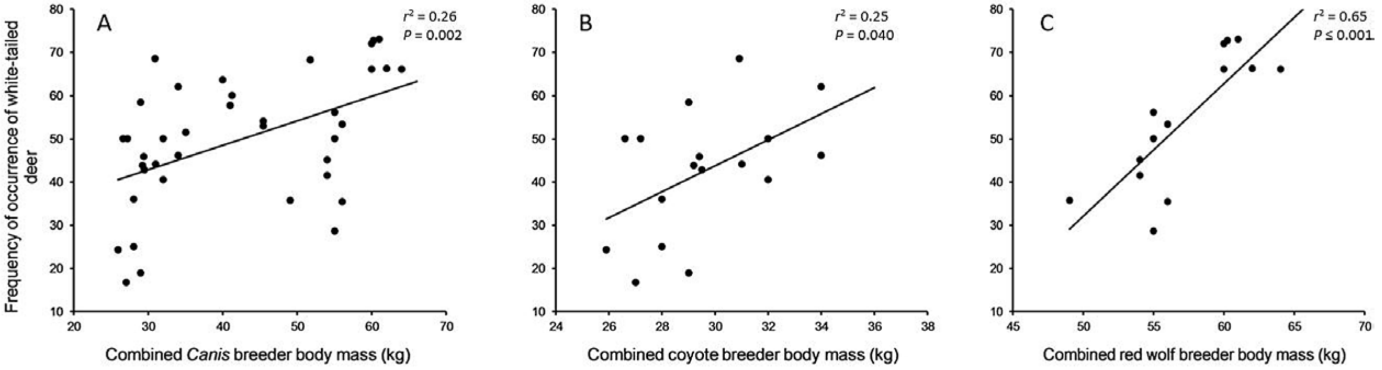

Fig. 3.—Correlation between frequency of occurrence of white-tailed deer (*Odocoileus virginianus*) in scats and combined body mass (kg) of A) congeneric *Canis* breeding pairs, B) coyote (*Canis latrans*) breeding pairs, and C) red wolf (*Canis rufus*) breeding pairs.

with FO of furbearers in red wolf scats (Table 6). The FO of pigs was positively correlated with percent cover by agriculture and negatively correlated with deer density (Table 6). The FO of other prey items was negatively correlated with growing season and positively associated with deer density (Table 6). Combined breeder body mass was positively correlated with FO of deer in coyote ($r^2 = 0.25$, $P = 0.040$; Fig. 3B) and red wolf scats ($r^2 = 0.65$, $P \leq 0.001$; Fig. 3C; Table 6), whereas no correlation was observed in congeneric pairs ($r^2 = 0.12$, $P = 0.234$).

Table 4.—Results from generalized linear mixed models for the top models for predicting frequency of occurrence of 6 prey categories corresponding to different hypotheses of factors affecting use by *Canis* breeding pairs in northeastern North Carolina, 2009–2011. Shown are β coefficients, *SE*, 95% *CI*s, *z*-scores, and *P*-values.

Prey category	Model variables	β	*SE*	95% *CI*	*z*	*P*
White-tailed deer	Intercept	−0.251	0.103	0.041, 0.458	2.450	0.014
	Growing season	−0.139	0.112	−0.377, 0.092	−1.173	0.241
	Combined breeder body mass	0.778	0.163	0.451, 1.141	4.772	< 0.001
	Agriculture	−0.277	0.152	−0.576, 0.066	−1.824	0.068
Rabbits	Intercept	−0.223	0.100	−0.422, −0.022	−2.227	0.026
	Combined breeder body mass	−0.785	0.215	−1.233, −0.362	−3.652	< 0.001
	Agriculture	0.136	0.194	−0.257, −0.528	0.702	0.483
	Deer density	0.135	0.255	−0.382, 0.638	0.529	0.597
Small mammals	Intercept	−0.654	0.121	−0.873, −0.397	−5.390	< 0.001
	Growing season	−0.225	0.130	−0.492, 0.019	−1.728	0.084
	Combined breeder body mass	−0.868	0.1982	−1.245, −0.438	−4.377	< 0.001
	Agriculture	0.225	0.1839	−0.145, 0.601	1.225	0.221
Furbearers	Intercept	−2.858	0.194	−3.275, −2.499	−14.705	< 0.001
	Growing season	0.838	0.207	0.438, 1.259	4.040	< 0.001
	Combined breeder body mass	−0.309	0.242	−0.806, 0.221	−1.276	0.202
	Agriculture	0.3023	0.2422	−0.206, 0.801	1.248	0.212
Pigs	Intercept	−5.149	0.606	−6.656, −4.156	−8.492	< 0.001
	Growing season	0.572	0.483	−0.329, 1.591	1.186	0.236
	Agriculture	1.688	0.898	0.090, 3.835	1.881	0.060
	Deer density	−2.056	0.854	−4.035, −0.448	−2.407	0.016
Other	Intercept	−1.736	0.141	−2.017, −1.461	−12.297	< 0.001
	Growing season	−0.420	0.173	−0.759, −0.080	−2.430	0.015
	Agriculture	−0.314	0.194	−0.697, 0.093	−1.614	0.107
	Deer density	0.669	0.280	0.107, 1.234	2.389	0.017

Discussion

Diets of red wolves and coyotes are central to their ecological role and our results provide new documentation of resource partitioning in a region where *Canis* hybridization occurs. Like Dellinger et al. (2011a) and McVey et al. (2013), our results demonstrate that red wolves and coyotes in eastern North Carolina are largely carnivorous and consume primarily mammalian prey, such as deer, rabbits, and small mammals. McVey et al. (2013) suggested that diets of red wolves and coyotes did not differ in eastern North Carolina. However, we observed differences in proportional use of prey by red wolves and coyotes. White-tailed deer were the dominant prey in diets of red wolves followed by rabbits and, to a lesser extent, small mammals. Red wolves consistently used deer regardless of season. However, use of secondary (rabbits) and tertiary (small mammals and furbearers) prey by red wolves differed seasonally. Conversely, rabbits were the dominant prey in diets of coyotes followed equally by deer and small mammals. Seasonal differences in use of prey by coyotes were only observed for rabbits and deer; coyotes consumed more deer and fewer rabbits during the harvest (September–February) than growing season (May–August). Increased use of deer during fall and winter by coyotes, and low use of insects and vegetation is contrary to many studies conducted on diets of coyotes in the southeastern United States (Chamberlain et al. 1999; Thornton et al. 2004; Schrecengost et al. 2008; Kilgo et al. 2012; Swingen et al. 2015). We speculate that differences between our results and previous studies stem from accounting for the effect of body mass of red wolves and coyotes on their food habits, and social status of our focal animals as resident breeders.

Canis species lack adaptations for physically controlling prey during the act of depredation (i.e., grappling abilities) and increased body mass improves their ability to subdue larger prey. MacNulty et al. (2009) observed the ability of gray wolves in Yellowstone National Park to kill ungulates improved with increased body size. Average body mass of coyotes in the northeastern regions of North America are larger than those reported elsewhere (Way 2007) and is thought to improve their ability to kill ungulates (Kays et al. 2010; Benson and Patterson 2013b). Indeed, carnivores weighing above the 15–20 kg range shift their diets to larger vertebrate prey that approach their own body mass, because exploiting small prey (i.e., small mammals, insects, vegetative material) requires higher intake rates that are energetically costly for large carnivores and limit their ability to meet absolute energy requirements (Carbone et al. 1999, 2007). Coyotes in eastern North Carolina approach the 15–20 kg threshold, whereas even the smallest red wolves are above it (Hinton and Chamberlain 2014). Consequently, it was not surprising to observe a moderate correlation between body mass of coyotes and frequency of deer in their diet, and a stronger correlation for red wolves (Fig. 3). These results suggest that variation in body sizes of red wolves and coyotes influences their diets because the costs (energy spent) and benefits (calories gained) to pursue, subdue, and consume similar prey differ between wolves and coyotes. Coyotes now occupy nearly all of North America, and considerable variation in body size could explain why diets vary regionally, in which some coyote populations are more carnivorous than others. However, body mass is routinely ignored in diet studies of coyotes and

Table 5.—Generalized linear mixed models for predicting frequency of occurrence of 6 prey categories corresponding to different hypotheses of factors affecting use by red wolf packs in northeastern North Carolina, 2009–2011. Shown are differences in Akaike's Information Criteria for small sample sizes (AIC_c) between the model and lowest AIC_c in the model set (ΔAIC_c), number of estimable parameters (k), Akaike model weight (ω_i), and a measure of model fit (deviance).

Prey category	Model	k	Deviance	ΔAIC_c	ω_i
White-tailed deer	No pack size—Season[a] + BWt[b] + Ag[c] + DD[d]	6	902.2	0.0	0.29
	No deer density—Season + BWt + Ag + Pack[e]	6	902.6	0.4	0.23
	No habitat—Season + BWt + DD + Pack	6	902.7	0.5	0.22
	No season—BWt + Ag + DD + Pack	6	903.4	1.2	0.16
	Full model—Season + BWt + Ag + DD + Pack	7	902.2	2.0	0.10
	No breeder body mass—Season + Ag + DD + Pack	6	913.2	9.0	0.0
Rabbits	No breeder body mass—Season + Ag + DD + Pack	6	901.2	0.0	0.32
	No pack size—Season + BWt + Ag + DD	6	901.6	0.4	0.27
	No deer density—Season + BWt + Ag + Pack	6	901.9	0.7	0.23
	Full model—Season + BWt + Ag + DD + Pack	7	900.9	1.7	0.14
	No habitat—Season + BWt + DD + Pack	6	906.9	5.7	0.02
	No season—BWt + Ag + DD + Pack	6	907.1	5.9	0.02
Small mammals	No breeder body mass—Season + Ag + DD + Pack	6	704.9	0.0	0.25
	No habitat—Season + BWt + DD + Pack	6	704.9	0.0	0.25
	No deer density—Season + BWt + Ag + Pack	6	704.9	0.0	0.25
	No pack size—Season + BWt + Ag + DD	6	706.3	1.4	0.13
	Full model—Season + BWt + Ag + DD + Pack	7	704.9	2.0	0.10
	No season—BWt + Ag + DD + Pack	6	710.0	5.1	0.02
Furbearers	No breeder body mass—Season + Ag + DD + Pack	6	409.1	0.0	0.43
	No deer density—Season + BWt + Ag + Pack	6	409.7	0.6	0.32
	Full model—Season + BWt + Ag + DD + Pack	7	408.9	1.8	0.17
	No pack size—Season + BWt + Ag + DD	6	412.5	3.4	0.07
	No habitat—Season + BWt + DD + Pack	6	416.9	7.8	0.01
	No season—BWt + Ag + DD + Pack	6	440.3	31.2	0.00
Pigs	No pack size—Season + BWt + Ag + DD	6	196.2	0.0	0.27
	No breeder body mass—Season + Ag + DD + Pack	6	196.2	0.0	0.27
	No season—BWt + Ag + DD + Pack	6	196.5	0.3	0.24
	Full model—Season + BWt + Ag + DD + Pack	7	196.0	1.8	0.11
	No deer density—Season + BWt + Ag + Pack	6	199.3	3.1	0.06
	No habitat—Season + BWt + DD + Pack	6	199.5	3.4	0.05
Other	No breeder body mass—Season + Ag + DD + Pack	6	394.6	0.0	0.31
	No pack size—Season + BWt + Ag + DD	6	394.8	0.2	0.28
	No habitat—Season + BWt + DD + Pack	6	395.3	0.7	0.22
	Full model—Season + BWt + Ag + DD + Pack	7	394.6	2.0	0.11
	No season—BWt + Ag + DD + Pack	6	398.1	3.5	0.05
	No deer density—Season + BWt + Ag + Pack	6	398.8	4.2	0.03

[a] Growing season.

[b] Combined body mass of breeders.

[c] Proportion of home range comprising agriculture.

[d] Deer density.

[e] Number of individuals in red wolf packs.

we suggest that future studies account for individual body mass and, at minimum, assign diets to social units.

Results from previous studies in the southeastern United States indicated coyote predation of deer occurs primarily on fawns during summer, and that consumption of deer during winter is a result of scavenging of carcasses resulting from deer hunting (Chamberlain et al. 1999; Thornton et al. 2004; Schrecengost et al. 2008). However, Cherry et al. (2016) observed greater use of adult deer by coyotes after rather than during the firearm hunting season and suggested use of adult deer by coyotes was not restricted to scavenging. Similarly, our data do not indicate scavenging explains increased use of deer during winter. First, the positive relationship between consumption of deer and body mass of *Canis* taxa implies that body size is an important trait for canids to acquire deer in their diet through predation, whereas scavenging is opportunistic and should be less affected by body mass. Indeed, coyotes in other regions of North America have been documented hunting and killing white-tailed deer (Patterson and Messier 2000; Lingle and Pellis 2002), mule deer (*Odocoileus hemionus*—Bowyer 1987; Lingle and Pellis 2002), elk (*Cervus elaphus*—Gese and Grothe 1995), bighorn sheep (*Ovis canadensis*—Bleich 1999), pronghorn (*Antilocapra americana*—Keller et al. 2013), moose (*Alces alces*—Benson and Patterson 2013b), and other large prey. Therefore, it is reasonable to assume that coyotes in the southeastern United States can kill adult deer throughout the year. Second, availability and accessibility of deer carcasses likely varies spatially and temporally across the landscape. The strict spatial segregation of *Canis* territories increases costs of scavenging considerably via aggressive encounters with other

Table 6.—Results from generalized linear mixed models for the top models for predicting frequency of occurrence of 6 prey categories corresponding to different hypotheses of factors affecting use by red wolf breeding pairs in northeastern North Carolina, 2009–2011. Shown are β coefficients, *SE*, 95% *CI*s, *z*-scores, and *P*-values.

Prey category	Model variables	β	*SE*	95% *CI*	*z*	*P*
White-tailed deer	Intercept	−1.611	0.382	−2.363, −0.700	−4.220	< 0.001
	Growing season	0.195	0.176	−0.152, 0.540	1.108	0.268
	Combined breeder body mass	4.114	0.739	2.368, 5.578	5.569	< 0.001
	Agriculture	0.172	0.247	−0.406, 0.657	0.695	0.487
	Deer density	−0.190	0.309	−0.795, 0.512	−0.615	0.539
Rabbits	Intercept	−0.383	0.156	−0.711, −0.083	−2.453	0.014
	Growing season	−0.469	0.182	−0.711, −0.112	−2.582	0.010
	Agriculture	0.612	0.249	0.134, 1.192	2.455	0.014
	Deer density	−0.286	0.316	−0.943, 0.349	−0.903	0.366
	Pack size	0.155	0.224	−0.295, 0.635	0.695	0.487
Small mammals	Intercept	−0.687	0.730	−2.217, 0.787	−0.941	0.347
	Growing season	−0.531	0.229	−0.973, −0.073	−2.324	0.020
	Combined breeder body mass	−0.265	1.607	−3.562, 3.055	−0.165	0.869
	Agriculture	−0.081	0.409	−0.918, 0.815	−0.197	0.844
	Pack size	0.496	0.410	−0.310, 1.315	1.209	0.227
Furbearers	Intercept	−3.729	0.4137	−4.621, −2.988	−9.015	< 0.001
	Growing season	1.968	0.411	1.212, 2.839	4.782	< 0.001
	Agriculture	1.405	0.521	0.453, 2.513	2.694	0.007
	Deer density	0.548	0.563	−0.569, 1.665	0.974	0.330
	Pack size	0.791	0.339	0.076, 1.453	2.331	0.020
Pigs	Intercept	−4.874	0.767	−6.639, −3.552	−6.352	< 0.001
	Growing season	0.350	0.560	−0.675, 1.573	0.624	0.533
	Agriculture	2.208	1.274	−0.194, 5.207	1.733	0.083
	Deer density	−2.211	1.243	−4.792, 0.314	−1.779	0.075
	Pack size	−0.849	0.906	−2.713, 0.982	−0.937	0.349
Other	Intercept	−1.733	0.226	−2.205, −1.254	−7.672	< 0.001
	Growing season	−0.596	0.315	−1.227, 0.022	−1.891	0.059
	Agriculture	−0.348	0.374	−1.114, 0.604	−0.930	0.353
	Deer density	1.394	0.546	0.096, 2.437	2.555	0.011
	Pack size	0.207	0.420	−0.584, 1.069	0.493	0.622

red wolves and coyotes (Paquet 1992; Berger and Gese 2007; Benson and Patterson 2013a) and risks having transients usurp mates and territories when residents leave their territories undefended to scavenge. We suggest transient canids are more likely to take advantage of scavenging opportunities because their movements are not restricted to territories, and compromised (i.e., sick or injured) and inexperienced (i.e., young dispersers) individuals likely accept greater risks to acquire food. Finally, roadkill surveys in our study area reported low occurrence of deer carcasses on roadsides, whereas amphibians (i.e., frogs and salamanders), birds (i.e., passerine species), and reptiles (i.e., snakes and turtles) comprised most roadkill (McCollister and van Manen 2010; Smith 2011; Vaughan et al. 2011). Mammalian road kill largely consisted of Virginia opossums (*Didelphis virginiana*) and raccoons (McCollister and van Manen 2010; Smith 2011; Vaughan et al. 2011). We rarely detected amphibians, passerine birds, reptiles, Virginia opossums, and raccoons in red wolf and coyote scats. These findings suggest residents of both species do not exploit roadways for scavenging opportunities, likely because the low energetic returns from small carrion do not outweigh the risk of scavenging along roadways. Additionally, avian scavengers, such as American crows (*Corvus brachyrhynchos*), black vultures (*Coragyps atratus*), and turkey vultures (*Cathartes aura*), are more proficient and well suited to exploiting small carrion along roadways and likely reduce scavenging opportunities for coyotes and red wolves.

Body size is the most distinguishing feature between red wolves and coyotes (Hinton and Chamberlain 2014) and, like other canid communities, competition is strongly asymmetrical with larger wolves displacing smaller coyotes (Gese and Terletzky 2015). Coyotes differ from other carnivore competitors (i.e., bobcats, foxes, and black bears) because they are capable of consorting with red wolves to form congeneric breeding pairs. However, when conspecific mates are available, both species exhibit assortative mating and red wolves effectively displace coyotes (Gese and Terletzky 2015; Hinton et al. 2017; Bohling and Waits 2015; Bohling et al. 2016). Little to no information exists on the consorting behaviors of hybridizing *Canis* species but our results demonstrate individual red wolves and coyotes are capable of sharing space and food resources to overcome limited mating opportunities. This leads to several key observations. First, our results indicate the red wolf population in eastern North Carolina is likely limited more by the availability of mates than space and food resources because wolves will share those resources with coyotes to form congeneric breeding pairs. Second, resource partitioning and reproductive partitioning are likely intrinsically intertwined for red wolves and coyotes. In the same manner that body size influences resource partitioning between red wolves and coyotes through differential use of space and food resources, body size may influence reproductive partitioning through assortative mating (Pfennig and Pfennig 2010; Schemske 2010). Red wolves and coyotes consort because of weak reproductive barriers and mate fidelity likely results from behavioral mechanisms that result in similar use of space, habitat, and prey that permit consorting individuals to complement one another (Hinton 2014; Hinton et al. 2015b). However, benefits derived by choosing certain mates rather than others can be difficult to quantify because those benefits can be subtle.

Our study was not designed to document how red wolves and coyotes adjust energy budgets associated with differences in breeder body mass and hunting efficiency when forming congeneric pairs, but our results imply that the presence of the red wolf in congeneric pairs increases the ability to prey on deer. For example, coyotes that formed breeding pairs with red wolves had 12% more white-tailed deer in their diet than conspecifics paired with coyotes. However, negative effects of smaller coyotes on congeneric pairs likely manifest in their space use patterns. Red wolves maintain larger home ranges than coyotes, whereas no difference in home-range size was detected for congeneric and coyote pairs (Hinton 2014). Because coyotes in eastern North Carolina do not maintain home ranges above 47 km^2 (Hinton et al. 2015a) and their average body mass approaches the transitional range of 15–20 kg reported by Carbone et al. (2007), they can effectively switch between hunting small prey and deer when prey abundance changes within smaller territories. Most red wolves maintain home ranges over 47 km^2 to accommodate their greater energetic demands and reliance on deer as their primary prey (Hinton et al. 2016b). Given the disparity in body mass between mates, how congeneric pairs reconcile costs and benefits associated with differences in spatial and dietary needs remains unknown. Although 5 of 10 congeneric pairs in this study included female red wolves, nearly 70% of all congeneric pairs documented in the Recovery Area during 1991–2013 included small female wolves and male coyotes (Hinton et al. 2017). Therefore, we hypothesize that energetically demanding activities, such as foraging and defending territories, could create incompatibilities between red wolves and coyotes and prevent successful congeneric pair formations (Hinton 2014; Hinton et al. 2015b). Such incompatibilities may be reduced for smaller red wolves, such as females weighing < 27 kg, and permit formation of congeneric pairs.

Competitive exclusion theory implies that coexistence depends on the degree to which shared resources are limiting and partitioned by sympatric competitors (Gause 1934; Hardin 1960). Red wolves and coyotes display similar habitat selection (Hinton et al. 2015a, 2016b) and our results show they rely on similar prey, albeit in different proportions. Consequently, significant overlap in resource use indicates that competition between red wolves and coyotes is likely intense and may not promote coexistence. In western North America, multiple large ungulate species co-occur, but only white-tailed deer and wild pigs occur in much of the southeastern United States (Laliberte and Ripple 2004). Currently, the presence of few ungulate prey species in most of the red wolf's historic range increases dietary overlap and similar use of habitats, which increases competition between wolves and coyotes. Therefore, partitioning of food resources by sympatric red wolves and coyotes may occur via differences in proportions of similar prey consumed, rather than differences in types of prey exploited. Furthermore, red wolves and coyotes maintain exclusive territories in which displacement of canids is unidirectional, with red wolves displacing coyotes but not vice versa (Gese and Terletzky 2015). However, when mating opportunities are lacking, similar use of resources allows red wolves and coyotes to successfully form and maintain congeneric breeding pairs. Congeneric breeding pairs are problematic to red wolf recovery because they promote reproductive interference by coyotes and facilitate the genetic assimilation of small red wolf populations into the larger regional coyote population. Developing conservation strategies to strengthen reproductive isolation between red wolves and coyotes will result in fewer congeneric pairings and reduce hybridization but those strategies are unlikely to facilitate coexistence. Fredrickson and Hedrick (2006) and Hinton et al. (2013) suggested the extent to which reproductive barriers and positive assortative mating existed between red wolves and coyotes were the most important factors determining success of red wolf recovery. The findings of our study support those assertions and indicate coexistence of red wolves and coyotes in the southeastern United States may not be possible because there are limited opportunities for niche partitioning to reduce competitive interactions.

Acknowledgments

This research was funded by the North Carolina Wildlife Resources Commission, Warnell School of Forestry and Natural Resources at the University of Georgia, and the United States Fish and Wildlife Service Red Wolf Recovery Program. Thanks to J. McVey for contributing scat samples to our study and providing constructive comments on the manuscript. We appreciate support of the Red Wolf Recovery Program, specifically A. B. Beyer, R. B. Harrison, C. F. Lucash, H. F. Mauney, M. L. Morse, R. W. Nordsven, and D. R. Rabon, Jr. We thank J. D. Clark for review of this manuscript for the U.S. Geological Survey Fundamental Science Practices. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the North Carolina Wildlife Resources Commission and the U.S. Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Submitted 7 September 2016. Accepted 22 December 2016.

Associate Editor was Eric Gese.