ASSESSMENT OF COYOTE (*CANIS LATRANS*) MOVEMENT ECOLOGY, PREY SELECTION, AND RESOURCE PARTITIONING IN THE SOUTHEASTERN UNITED STATES

by

SARAH C. WEBSTER

(Under the Direction of James C. Beasley and Michael J. Chamberlain)

ABSTRACT

Although historically absent from the eastern United States, coyotes (*Canis latrans*) have expanded their range across the continent and are now established throughout most of North America. Range expansion of coyotes has had notable impacts on newly colonized ecosystems, including altering prey population dynamics and increasing interference competition for resources among established predator populations. The success of coyotes can be attributed to their behavioral plasticity in diet, habitat selection, and space use. In particular, territoriality and both intra- and inter-specific competition can influence coyote resource use and partitioning, but these relationships have not been well studied in the Southeast. As a result, managers and researchers recognize the need for a more comprehensive understanding of coyote ecology, particularly space use strategies (i.e., territoriality), habitat selection, and prey selection in recently colonized regions to elucidate how coyotes move through landscapes and impact established predator and prey populations. To address this, I assessed fine scale movement ecology, resource selection, and prey selection of coyotes in the

Southeastern U.S., and investigated habitat and prey resource partitioning among coyotes and established native canid populations. I found that both territoriality and interspecific competition influence coyote movement and prey selection. Importantly, individual variation among coyotes was noteworthy throughout all datasets used in this work, emphasizing the substantive behavioral variation among individuals. I believe that both territoriality and potential competition should be considered to effectively elucidate behavioral patterns in future coyote ecology research.

INDEX WORDS: Coyote; Movement Ecology; Space Use; Resource Partitioning; Prey Selection; Interspecific Competition

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DEDICATION

For everyone who loves and supports me but won’t ever read this.

(It’s okay Nana, I’ll tell you about it over waffles)

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Although historically absent from the eastern United States (U.S.), coyotes (*Canis latrans*) have expanded their range across the continent and are now established throughout most of North America (Parker 1995). The first reports of coyotes in the eastern U.S. date as far back as 1927, but these reports were often isolated, unsubstantiated, or otherwise attributed to captive releases (Young and Jackson 1951). By 1987, coyotes were thought to have established isolated populations in parts of the Southeast, and by the mid-1990s were present in all southeastern states (Gipson 1978; Hill et al. 1987; Ruth 2010). Range expansion of coyotes has had notable impacts on newly colonized ecosystems, including altering prey population dynamics (Kilgo et al. 2010; Crimmins et al. 2012; Swingen et al. 2015) and increasing interference competition for resources among established predator populations (Harrison et al. 1989; Johnson et al. 1996; Berger and Gese 2007). Many of these observed trends are thought to be density dependent, with impacts becoming more pronounced as coyote populations increase and animals saturate the landscape (Gompper 2002). As a result, managers and researchers recognize the need for a more comprehensive understanding of coyote ecology, particularly space use strategies (i.e., territoriality), habitat selection, and prey selection in recently colonized regions to elucidate how coyotes move through landscapes and impact established predator and prey populations.

Coyotes are generalists, adapting to urban, agricultural, forested, and industrial landscapes (Gompper 2002). A mid-size canid typically weighing between 8-20 kg, coyotes currently maintain the largest geographic range of any wild canid species in the continental U.S. (Gese et al. 2008). The success of coyotes can be attributed to their behavioral plasticity in diet, habitat selection, and space use strategies (Gompper 2002). Behavioral plasticity in coyotes is dynamic and complex, with multiple environmental and biological factors influencing individual behavior at any given time (Bekoff 1978; Gese et al. 1996; Atwood 2006). For example, coyotes can vary their habitat use and prey selection based on availability, season, and competition (Bekoff and Wells 1980; Andelt 1985; Cypher et al. 1994; Ward et al. 2018). This adaptability allows coyotes to change their patterns of resource selection, and often partition resources with both conspecifics and other predators to increase fitness and survival (Gese et al. 1996; Kitchen et al. 1999; Neale and Sacks 2001*a*). In particular, territoriality and both intra- and inter-specific competition can influence coyote resource partitioning (Kamler and Gipson 2000; Gehrt et al. 2009; Hinton et al. 2015; Newsome et al. 2015; Morin and Kelly 2017). However, the implications of resource partitioning within coyote populations, as well as among recently sympatric populations of coyotes and native predator populations, have not been well explored in the Southeast.

Partitioning of prey resources among coyotes and other predator populations has been documented in portions of the coyote's range (Theberge and Wedeles 1989; Kitchen et al. 1999; Neale and Sacks 2001*a*). Coyotes are opportunistic foragers, with a diverse and broad diet that fluctuates depending on prey availability and season (Bekoff 1978; Litvaitis and Mautz 1980; Cypher et al. 1994; Newsome et al. 2015; Ward et al. 2018). In the Southeast, primary prey items include white-tailed deer (*Odocoileus virginianus*), rabbits (*Sylvilagus floridanus*), small mammals, soft mast, and anthropogenic food waste (Schrecengost et al. 2008; Cherry et al. 2016; Ward et al. 2018). Coyotes also commonly scavenge available carrion, especially during winter (Bekoff and Wells 1980; Paquet 1992). In some cases, coyote predation has been found to negatively affect prey populations; however, such impacts typically are limited to prey populations with lower initial densities (Kilgo et al. 2012; Robinson et al. 2014; Chitwood et al. 2015; Kilgo et al. 2016). Although dietary consumption of native species has been a key management concern, relatively little is known about the influence of territorial status or interspecific competition on coyote prey selection and diet breadth in the Southeast. This is in part due to the logistical barriers of simultaneously collecting diet and movement data from free-roaming individuals over long temporal periods. However, understanding how territoriality and interspecific competition impacts prey selection and partitioning is critical to developing effective management strategies.

Habitat selection also varies greatly in coyotes depending on territoriality, habitat availability, and competition (Hinton et al. 2015; Morin and Kelly 2017; Sasmal et al. 2019). Previous studies have investigated coyote space use and habitat selection, but relatively few have accounted for territoriality when conducting their analyses. Within a population, coyotes exhibit two disparate strategies of territoriality: defending a mutually exclusive home range (referred to as residents) or moving nomadically across a landscape as a transient (Bekoff and Wells 1986; Kamler and Gipson 2000). Of previous studies that differentiated between resident and transients, all noted that resident coyotes were found to select for open grassland, pasture, and agricultural habitats while avoiding developed habitats (Kamler and Gipson 2000; Hinton et al. 2015). However, patterns of habitat selection for transient coyotes are more ambiguous. Kamler and Gipson (2000) found transients avoided grasslands and selected for woodlands, whereas Hinton et al. (2015) found transient coyotes exhibited similar selection trends to residents by selecting for open habitats, although transients were more likely to use roads. Thus, patterns of selection for transient coyotes, and the implications of habitat partitioning on coyote populations, remain ambiguous.

Interspecific competition also influences habitat selection by coyotes, and previous works have shown evidence of competition and habitat partitioning among coyotes and other predator populations throughout their range (Harrison et al. 1989; Neale and Sacks 2001*b*; Berger and Gese 2007). In the Southeast, where coyote colonization is relatively recent, potential competition and habitat partitioning among newly sympatric predator species has not been well studied. One exception is the red wolf (*Canis rufus*), an endangered species that has been extensively studied in relation to potential competition with coyotes throughout its remnant range (Roth et al. 2008; Hinton et al. 2016; Hinton et al. 2017). Previous work noted that coyotes and red wolves both selected for agricultural habitats and likely competed for resources (Hinton and Chamberlain 2010; Hinton et al. 2015; Hinton et al. 2016). However, these studies typically categorized habitats broadly and did not differentiate among agricultural crops when assessing selection, nor did they investigate the potential for temporal partitioning of habitats to mitigate competition. It remains unclear if coyotes and red wolves are partitioning habitat and what implications partitioning may have on future red wolf recovery.

In this dissertation, I aim to fill these knowledge gaps regarding fine scale movement ecology, resource selection, and prey selection of coyotes in the Southeast, and investigate habitat and prey resource partitioning among coyotes and established canid populations. In Chapter 2, I investigate fine-scale habitat partitioning between red wolves and coyotes in eastern North Carolina. To accomplish this, I used data from global positioning system (GPS) transmitters deployed on 23 red wolves and 13 coyotes in eastern North Carolina. This allowed me to quantify spatial and temporal patterns of habitat partitioning between both species and explore the implications of habitat partitioning on movement ecology.

Chapter 3 examines differences in movement ecology and fine-scale habitat selection between resident and transient coyotes using First Passage Time (FPT) analyses. To accomplish this, I deployed GPS transmitters on 171 coyotes across Alabama, Georgia, and South Carolina, which allowed me to assess how both residents and transients move and use primary landcover types across the Southeast. I also quantified step length and movement rates, which allowed me to assess differences in movement patterns between resident and transient coyotes. This study represented one of the first broad-scale studies (>16,000 km^2) of coyote space use and habitat selection in the Southeast.

Chapter 4 assesses dietary partitioning among resident and transient coyotes in the Southeast. To accomplish this, I collected guard hair samples from 63 coyotes monitored with GPS transmitters in Chapter 3. GPS data for sampled coyotes allowed me to determine the territorial status (i.e., resident or transient) of sampled individuals, and I then analyzed hair samples for nitrogen and carbon stable isotopes to quantify diet composition and niche overlap. I quantified resident and transient coyote diet composition by comparing coyote isotopic data with isotopic data for common prey species to estimate the proportional contributions of each potential food source to coyote diets.

To identify potential impacts of coyotes on native southeastern canids, in Chapter 5 I investigate temporal shifts in diet of gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), and coyotes in response to coyote colonization of the Southeast. To accomplish this, I used nitrogen and carbon stable isotopes to quantify contemporary diet overlap among the 3 species and historic diet overlap among red and gray fox in the Southeast. I compared these data to similar data I collected in the Plains region of the U.S., where all 3 species have been sympatric for centuries. I analyzed 217 hair samples from gray fox (n = 85), red fox (n = 25), and coyote (n = 107) from both regions pre-1960 (prior to coyote colonization of the Southeast) and post-2000 (after coyotes were ubiquitous). I then assessed differences among species, regions, and time periods. This study was the first to investigate temporal patterns in dietary partitioning of sympatric canids in the Southeast and the Plains regions. Finally, Chapter 6 integrates observed patterns of resource selection and partitioning from previous chapters and draws conclusions about coyote ecology in the Southeast.

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CHAPTER 2

SELECTION OF AGRICULTURAL COVER BY SYMPATRIC RED WOLVES (*CANIS RUFUS*) AND COYOTES (*CANIS LATRANS*) DURING PUP-REARING

Webster, S.C., Chamberlain, M.J., Hinton, J.W., and Beasley, J.C. To be submitted to *Journal of Mammalogy*.

Abstract

Widespread decline in native vegetation communities caused by anthropogenic land use has contributed to declines in native predators globally. For the endangered red wolf (*Canis rufus*), population declines due to agricultural development eventually led to their extirpation from the Southeastern United States. Currently only one red wolf population in eastern North Carolina exists, where they are sympatric with coyotes (*Canis latrans*), a generalist species with similar patterns of habitat use and selection, which increases interspecific competition and hinders red wolf recovery. To sustain red wolf recovery, it's vital to thoroughly understand both species' fine-scale habitat selection and space use, particularly during time periods of important ecological activity like pup-rearing. We measured fine-scale habitat selection of both red wolves and coyotes during pup-rearing season to assess spatial and temporal habitat partitioning between species. We used spatial data for red wolves and coyotes within an area of sympatry to quantify space use and individual habitat selection within home ranges for both species. We delineated selection among different habitat types, including among crop types (corn, cotton, soybean) and between diel periods (diurnal, nocturnal). We found that selection patterns differed between diel periods for both species, indicating temporal variation in habitat selection. Both species selected for corn diurnally and nocturnally, but coyotes also selected other crop types nocturnally. We found evidence for temporal partitioning of wetland habitats, with coyotes selecting wetlands diurnally whereas wolves selected wetlands nocturnally. Our findings indicate that previously documented selection for agricultural habitat by both species was likely driven by selection for corn crops specifically, although coyotes also use other crop types

nocturnally. Further, both species appear to temporally partition wetland habitats, which may mitigate competition for prey resources. Although we found evidence for temporal partitioning of habitats, strong selection for corn by both species indicated that potential interspecific competition remains high, which could negatively impact red wolf recovery.

Introduction

Human land use has transformed many terrestrial ecosystems into mosaics of natural (e.g., forests) and anthropogenic habitats (e.g., agriculture; Saunders et al. 1991; DeFries et al. 2004; Foley et al. 2005). Such anthropogenic modifications to the landscape have resulted in extensive loss of native vegetation communities (Noss et al. 2014; Martinuzzi et al. 2015), ultimately reducing biodiversity and altering the behavioral ecology of wildlife that inhabit agricultural ecosystems. Within the southeastern United States, grassland and pine savannah habitats once encompassed ~37 million ha across the landscape, but 20th-century agricultural land-use and fire suppression that allowed forest encroachment caused widespread loss (~97%) of these habitats (Brewer 2008; Frost 1993; Ware et al. 1993; Noss et al. 1995). This extensive land use change has contributed to the decline in biodiversity of ecosystems in the southeastern United States, including the extirpation of large, native predators such as the Florida panther (*Puma concolor coryi*) and red wolf (*Canis rufus*) from much of the region (Onorato et al. 2010; Hinton et al. 2013).

For red wolves, agricultural land-use led to habitat loss and increased their contact with livestock and homesteads, which increased interactions with humans (Hinton et al. 2013; 2017*a*). Human intolerance of red wolves led to government-sponsored control programs that resulted in wolf declines and eventual extirpation from the region by the mid-20th century (Hinton et al. 2013). To facilitate recovery of the species, during the late-20th century red wolves were reintroduced into the Albemarle Peninsula of northeastern North Carolina because the region predominantly consisted of coastal bottomland forests with an abundant white-tailed deer (*Odocoileus virginianus*) population, low human density, and no established coyote population. However, due to a range expansion during the late-20th century, coyotes have also colonized the Albemarle Peninsula, so red wolves and coyotes are currently sympatric in this region (Hinton et al. 2013, 2015*a*; Gese et al. 2015). Coyotes are a generalist species with considerable habitat and dietary plasticity, allowing them to exploit natural and human-modified landscapes for food and cover (Bekoff and Wells 1980; Schrecengost et al. 2009). Conversely, red wolves are more specialized than coyotes in their diet and habitat needs, relying on white-tailed deer and forest habitats for food and cover (Hinton et al. 2013; Hinton et al. 2016, Ward et al. 2018).

Contrary to previous assumptions that wolves favor forest cover and wetlands, red wolves on the Albemarle Peninsula exhibit strong selection for agricultural cover, a behavior also exhibited by coyotes on the peninsula (Dellinger et al. 2013; Hinton et al. 2015*b*, 2016; Karlin et al. 2016). Agricultural cover is known to offer quality foraging areas for canids (Brinkman et al. 2004; Dellinger et al. 2011, Hinton et al. 2017*b*), despite exposing them to greater mortality rates because of increased contact with humans (Van Deelen and Gosselink 2006; Hinton et al. 2017*a*). Previous studies noted that red wolves and coyotes used similar types of vegetation cover and prey, but that red wolves required larger territories and relied on white-tailed deer more than coyotes (Hinton et al. 2015, 2016, 2017*b*). Hinton et al. (2017*b*) suggested the substantial overlap in resource use of both red wolves and coyotes may hinder coexistence of these species because opportunities for niche partitioning were limited.

However, previous research has shown canids exhibit disparate patterns of habitat selection during different diel periods, and these differences may mitigate competition or human conflict (Nelson et al. 2007; Mitchell et al. 2015; Murray et al. 2015). Despite the potential for interspecific competition between red wolves and coyotes, it remains unclear if either species exhibits fine scale spatial or temporal (i.e., nocturnal vs. diurnal) partitioning of cover that may mitigate competition between the species and reduce interactions with humans. For example, individuals may exhibit differential use of different crop types in agricultural areas between diel periods that may affect coyote and red wolf interactions and their exposure to humans. Notably, crop cover only occurs during the warmer parts of the year (April–September), coinciding with pup-rearing activities. Patterns of selection for specific crops by red wolves and coyotes may play an important role in pup survival, as these areas provide cover and access to potential prey during a time of the year when mortality is lowest for both species in agricultural landscapes (Van Deelen and Gooselink 2006; Hinton et al. 2017). Red wolf pup survival is a critical component of the designated United States Fish and Wildlife Service (USFWS) Red Wolf Recovery Program (Recovery Program), which aims to restore and manage wild red wolf populations in eastern North Carolina (Bartel and Rabon 2013; Hinton et al. 2013). Understanding both red wolf and coyote habitat selection during pup rearing is vital to understanding and ultimately increasing red wolf pup survival. Therefore, investigating selection for different crop types by red wolves and coyotes, as well as the effect of diel period on their use of crop fields, will assist in understanding how agricultural habitats influence canid population dynamics.

Our objective was to investigate red wolf and coyote habitat selection during the pup rearing season, with particular focus on effects of crop type and diel period (diurnal vs. nocturnal) on habitat selection. We predicted both species would select crop types that provide suitable cover/refugia, but that coyotes would select a greater variety of crop types given their behavioral plasticity. Additionally, we predicted that use of agricultural habitats would be greater at night, and during the day both species would be more likely to select canopied forest habitats that may provide improved refugia from humans and weather.

Methods

Study Area

The Albemarle-Pamlico Peninsula in eastern North Carolina served as the Red Wolf Recovery Area (hereafter the Recovery Area) during our study. The Recovery Area was approximately 6,000 km^2 of rural landscape comprised of coastal bottomland forests/pocosin (~35%), pine plantations (*Pinus* spp.; ~15%), herbaceous wetlands (~5%), row-crop agriculture (i.e., corn [Zea *mays*], cotton [*Gossypium* spp.], soybean [*Glycine max*], winter wheat [*Triticum aestivum*]; ~30%), and other minor vegetative communities (~10%; see Fig 1). Approximately 5% of the Recovery Area was comprised of open water such as lakes, rivers, and streams. Variability in elevation on the Albemarle Peninsula was minor and ranged from 0–50 m, and annual average precipitation ranged from 122–132 cm. Summers were hot and humid with daily maximum temperatures ranging from 27°C–38°C, whereas winters were cool with daily maximum temperatures ranging from -4°C–7°C.

Capture and monitoring

From October through May 2007–2011, we coordinated with the USFWS Recovery Program to assist in their annual trapping of red wolves and coyotes. The Recovery Program used padded foot-hold traps (Victor no. 3 Softcatch, Lititz, USA) to capture and radio-mark red wolves and coyotes for long-term monitoring and management. Because the red wolf is listed as critically endangered under the United States Endangered Species Act (ESA) and by the International Union for Conservation of Nature (IUCN), our trapping efforts operated under a cooperative agreement with the USFWS Recovery Program. Coyotes were not a listed or protected species and the North Carolina Wildlife Resources Commission (NCWRC) was the permitting authority for their capture and release. Our methods to capture, handle, and process both species were in cooperation with the USFWS and NCWRC, were approved by the Louisiana State University Agricultural Center 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 restrained using a catchpole, muzzle, and hobbles. Most animals were not anesthetized, but some were chemically immobilized with an intramuscular injection of 1.9 mg/kg ketamine HCl and 0.4 mg/kg xylazine HCl for processing. All animals were sexed, measured, and weighed. Age of captured red wolves was known if individuals were carrying a subcutaneous passive integrated transponder (PIT) tag inserted into the animal during the Recovery Program's annual surveys of suspected red wolf dens. Ages of individuals (both coyotes and wolves) without PIT tags were estimated by tooth wear (Gier 1968; Gipson et al. 2000). We categorized individuals ≥2 years old as adults, <2 but ≥1-year-old as juveniles, and <1-year-old as pups. Notably, the Recovery Program sterilized coyotes so they would not hybridize with red wolves (Gese and Terletzky 2015). We fitted all individuals with a mortality-sensitive GPS radio-collar (Lotek 4400S, Newmarket, Ontario, Canada) that recorded a location every 5-hours. All individuals were released at the capture site and subsequently monitored to identify the distribution of territories of resident individuals in the Recovery Area. We identified residents as individuals of breeding age (≥2 years old) that maintained a territory for ≥4 months (Bekoff and Wells 1980; Hinton et al. 2015, 2016). We also classified non-dispersing juveniles as residents. We classified individuals as transients when they displayed nomadic, wandering movements throughout the peninsula (Hinton et al. 2015, 2016).

Because we were interested in fine scale habitat selection by red wolves and coyotes during pup rearing, we only included movement data collected during the annual crop growing season of April–September, which coincided with pup-rearing by both species (Hinton and Chamberlain 2010). In months between growing seasons, crop fields were typically left barren or planted with winter wheat. By limiting our analyses of movement data to the growing season, we were able to quantify use of crop cover during months when the crops were available for use.

Habitat Data

We obtained annual land cover data from the United States Geological Survey (USGS) National Gap Analysis Project (GAP) Land Cover Data Set (US Geological Survey 2011; 90 m^2 pixel size). Because modern farming practices involve rotating crops among fields or changing plantings annually, we obtained annual land cover data for 2008–2011 when red wolves and coyotes were radio-collared. This allowed us to account for annual changes in availability of crops throughout the study period. For each year, we reclassified the corresponding land cover layer into 5 landcover types: forest, wetlands, corn, cotton, and soybeans. Additionally, we obtained a 2009 layer of all roads on the peninsula from Weyerhaeuser Inc. We created distance raster maps for each landcover type and road features using the Euclidean distance tool in the Spatial Analyst toolbox in ArcGIS 10.3 (ESRI, Redlands, California, U.S.A.) to quantify the distance from each pixel to each landcover type.

Home Range Analysis

We used fixed point local convex hull methods (k-LocoH; Getz and Wilmers 2004; Getz et al. 2007) using the adehabitatHR package (Calenge 2006) in Program R (R Core Team 2016) to construct 99% isopleth home ranges for red wolves and coyotes during the pup-rearing season (April–August). We only included residents during the growing season of the respective year they were monitored, as residents are more likely to form breeding pairs and rear offspring (Andelt 1985; Hinton et al. 2015, 2016, 2017b). The *k*-LocoH method constructs convex hulls associated with each point and its *k*-1 nearest neighbors. The union of these hulls is finite and can be used to represent the home range of the individual. We used *k*-LocoH methods to estimate home ranges because territories consisted of hard edges between agriculture and natural habitats, or abutted bodies of water. LocoH methods account for these hard boundaries when constructing home range polygons (Getz and Wilmers 2004). We used *t*-tests to examine differences in home range size between red wolves and coyotes. To determine if the proportion of landcover types within home ranges differed between red wolf and coyote home ranges, we used analysis of variance (ANOVA) and Tukey tests for multiple comparisons. We used an alpha value of 0.05 for all tests of significance.

Resource Selection Modeling

We used third-order resource selection functions (RSFs) to quantify relationships between landcover type and space use within red wolf and coyote home ranges using a used vs. available approach (Manly et al. 2002). This approach reveals habitat selection patterns by comparing known used locations (GPS locations) to random available locations taken across the individual's estimated home range. We modeled each species independently and individual red wolves or coyotes were replicates. We quantified availability of landcover types for each individual using random locations within home ranges at a ratio of 1:1 with GPS locations. From each used and available location, we then measured Euclidean distance to each landcover type of interest. We then used a binomial generalized linear mixed model (GLMM) with a logit link to quantify differences in selection of each landcover type within home ranges. Prior to modeling, we rescaled values for distance-based variables by dividing by one standard deviation. To avoid multicollinearity, we examined correlations among landcover variables by deriving a matrix of all possible Spearman correlation coefficient values. Any variables with a significant correlation ($r^2 > 0.4$; $P < 0.05$) were not simultaneously included in the same model in subsequent analysis. We inferred selection when used locations were significantly more likely to be closer to a particular landcover type (i.e., shorter distance) compared to random available locations (Manly et al. 2002).

Because we were interested in potential differences in selection between diurnal and nocturnal time periods, we first created models using all location data and allowed interactions between a binary variable (0 = nocturnal, 1 = diurnal) and each habitat type. Diel periods were designated based on average sunrise/sunset periods for April – September. We defined diurnal as 06:00 – 20:00 hrs and nocturnal as 20:01 – 5:59 hrs. Additionally, we allowed interactions between year and each landcover type to test for an effect of year on habitat selection. After determining whether diel period affected habitat selection for each species, we partitioned location data into diurnal and nocturnal time periods, and developed separate habitat selection models that included all landcover types without interactions. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to select the best model from a set of models that included the global model and all possible subsets (Burnham and Anderson 2002). We used all models within 2 AICc units of the top model to derive model-averaged parameter estimates as appropriate. We then used parameter estimates for each landcover type from the top model(s) to derive relative predicted habitat selection across the Recovery Area for each species. To evaluate model fit of the top models, we used a *k*-fold approach to perform a cross-validation as this method has been shown to be the most appropriate for use-availability RSF models (Johnson et al. 2006).

Results

During 2007–2011, we monitored 35 red wolves and 19 coyotes fitted with GPS radio-collars. All collared animals were adults. Monitoring periods for each individual varied from 5 to 16 months depending on collar life and individual survival/mortality. We included 23 red wolves (14M: 9F) and 13 coyotes (6M: 7F) in our analyses that were considered residents during the growing season of the respective year they were monitored.

Mean (± SD) home-size for red wolves and coyotes was 65.6 km^2 ± 16.2 and 27.4 km^2 ± 19.62, respectively, with wolves maintaining larger home-ranges than coyotes ($t_{36} = -2.67$, $P = 0.019$). We detected no differences in home-range size between sexes for red wolves ($t_{36} = 0.91$, $P = 0.192$) or coyotes ($t_{36} = 0.07$, $P = 0.917$). Home ranges for both species mostly consisted of corn, soybeans, and wetland cover types (Figure 2). Proportion of each landcover type within home ranges did not differ between red wolves and coyotes (Table 1).

We detected differences in habitat selection during diurnal and nocturnal time periods for both species, with the top ranked model for both species allowing for interactions between diel period and each landcover type (Table 2). The global model best explained both diurnal and nocturnal selection for coyotes and nocturnal selection for red wolves, whereas 2 models best explained diurnal selection for red wolves (Tables 3, 4). Diurnally, red wolves were more likely to select corn and forests, and avoided soybeans, cotton, and roads. Nocturnally, wolves were more likely to select wetlands and corn, and were more likely to avoid soybean, cotton, and forests (Table 5; Figure 3). Coyotes were more likely to avoid forests, soybean, and roads and were more likely to select corn, cotton, and wetlands during diurnal periods. Coyotes were more likely to select roads, soybean, cotton, and corn, and were more likely to avoid forests during nocturnal periods (See Table 6; Figure 4). The model validation tests correctly binned 76% of diurnal locations and 77% of nocturnal locations for coyotes. For red wolves, model validation tests correctly binned 76% of diurnal locations and 75% of nocturnal locations.

Discussion

We observed substantial differences in home range sizes between red wolves and coyotes, which were comparable to previously reported estimates for both species in the southeastern U.S. (red wolves: 7.8 – 272.8 km^2; Chadwick et al. 2010; Dellinger et al. 2013; Hinton et al. 2016; coyotes: 10.1-47.4 km^2; Holzman et al. 1992; Schrecengost et al. 2009; Hinton et al. 2016). These differences likely reflect morphological differences in body mass and energetic requirements between the two species, which can impact patterns of space use, especially during pup-rearing when reproductively active adults have added energetic demands created by offspring (Gompper and Gittleman 1991; Roth et al. 2008; Hinton et al. 2015; Hinton et al. 2018). Although space use differed between red wolves and coyotes, the average proportion of landcover types within home ranges did not. Similar to previous studies, we found that red wolf and coyote home ranges were comprised of all crop types in greater proportions than were available across the

Recovery Area (Dellinger et al. 2013; Hinton et al. 2015*b*, 2016; Karlin et al. 2016). However, in our study substantive proportions of a landcover type in an individual's home range did not necessarily translate to positive selection in the RSF model. Instead, modeling revealed that selection and avoidance of crops differed among crop types for both species, revealing more nuanced patterns of selection that were previously undescribed. Additionally, we found differences in selection between diel periods, indicating that both species alter selection patterns depending on time of day. By delineating among landcover types and examining trends between diel periods, we were able to effectively describe fine scale patterns of selection, particularly of different crop types in the Recovery Area.

Red wolves selected corn both diurnally and nocturnally, indicating its potential importance during pup-rearing consistent with previous research noting that red wolves used agricultural areas as rendezvous sites (Hinton and Chamberlain 2010). Our findings that corn was the only agricultural cover type that wolves selected, and that selection of corn fields was strong both day and night, indicates that corn likely provides a favorable environment for both adults and pups. The linear planting, narrow structure, and height of corn at maturity may provide easily traversable, effective refugia for both adults and pups and provide foraging opportunities (Brinkerhoff et al. 2005; Salek et al. 2009; Fogarty et al. 2018). Thus, the physical structure of corn fields likely facilitates their use as refugia and foraging habitat, driving selection of this habitat during both diel periods.

In addition to strong selection for corn fields, we found that wolves also exhibited selection of forested areas during diurnal periods and wetlands during nocturnal periods.

Diurnal selection of forests supported our hypothesis that canopied habitats may be important sources of refugia during the pup-rearing season. Forests with substantial canopies are more likely to provide shade and favorable ambient temperatures during daylight hours, potentially making them suitable refugia and rendezvous sites during high summer temperatures (Demarchi and Bunnell 1993; Keppel et al. 2017). However, in the Recovery Area canopied forests were predominantly pocosin or coastal bottomland forest, which have dense understory and are prone to flooding (Weakley and Schafale 1991), potentially reducing the ability of animals to traverse these areas. So, while forest habitats likely provide favorable conditions diurnally when ambient temperatures are high, foraging and movement are likely more difficult. Conversely, nocturnal selection of wetlands may be driven by increased foraging opportunities in these areas. Although the primary prey species of red wolves is white-tailed deer (*Odocoileus virginianus*), wolves are known to prey on other mammals found in the Recovery Area, including semi-aquatic rodent species such as beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), and nutria (*Myocastor coypus*), which are found in wetlands (Lee et al. 1982; Townsend and Butler 1996; Dellinger et al. 2011). Red wolf nocturnal selection of wetlands, when many semi-aquatic prey species are active, may reflect foraging efforts of wolves in these areas.

Coyote selection of landcover types was more varied than wolves, which is unsurprising given their generalist nature (Bekoff and Wells 1986; Hinton et al. 2016). Additionally, coyotes in our study system were sterile (Gese and Terletzky 2015) and thus their selection was not constrained or influenced by pup-rearing activities. Previous work has shown that sterilized coyotes exhibit different foraging patterns than fertile individuals (Bromley and Gese 2001; Seidler et al. 2014). It’s possible that if coyotes in our study had been able to reproduce, their selection behaviors may also have been constrained by pup-rearing activities. Despite this, coyotes were similar to wolves in that they were more likely to select corn fields both diurnally and nocturnally, indicating these areas were likely favorable refugia for both species. However, unlike wolves, coyotes were more likely to exhibit nocturnal selection for all crop types (corn, soybean, and cotton). Due to the tall height of corn compared to other crop types, it is likely the only crop type that provided total cover (i.e., is taller than both wolves and coyotes, obscuring them entirely from view) during the day. Nocturnally, coyotes were more likely to select other crops that likely provide many of the same benefits (easy to traverse, improved olfaction for foraging) as corn. Additionally, coyotes are more likely than wolves to consume small mammals or lagomorphs (Dellinger et al. 2011; Ward et al. 2018), prey species that are known to use agricultural fields during summer (Mills et al. 1991; Cavia et al. 2005). By using multiple crop types nocturnally rather than concentrating in corn, coyotes also likely mitigate competition with the larger red wolf (Hinton et al. 2015*b*). Additionally, coyotes were also more likely to select roads nocturnally. Linear features such as roads are known to be used by coyotes as travel corridors, especially nocturnally when human activities are less (thus decreasing mortality risk; Benson et al. 2015). Thus, coyote selection for agricultural fields is likely driven by a combination of refugia, foraging opportunities, and avoidance of red wolves.

Successfully rearing offspring in the wild is a critical component to red wolf population viability in the Recovery Area (Hinton et al. 2013). For red wolves, habitat selection by male and female residents is likely constrained by their ability to find suitable refugia for pups (i.e., provides effective cover while also avoiding contact with humans, heat stress conditions, or difficult terrain pups can’t traverse safely) while maintaining proximity to foraging resources. For coyotes, selection is likely driven by their ability to find suitable refugia while minimizing contact with humans and/or red wolves which may be using similar habitats. Overall, despite some differences in habitat selection patterns, both coyotes and red wolves exhibited strong selection for corn fields with almost no evidence of temporal partitioning. Thus, the potential for competition between these species remains high and has the potential to hinder red wolf recovery in the wild.

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Tables and Figures

Table 2.1: Test statistics from ANOVAs comparing proportions of landcover types in estimated home ranges of coyotes and red wolves within the Albemarle Peninsula in eastern North Carolina, USA during 2007-2011.

Cover Type	*t* statistic	P Value
Corn	0.225822	0.411327
Soybean	-1.39504	0.085776
Cotton	-0.91141	0.184072
Wetland	0.863396	0.196818
Forest	-0.15997	0.436901

Table 2.2: AIC_c model rankings for models of both red wolf and coyote 3^{rd} – order resource selection within the Albemarle Peninsula in eastern North Carolina, USA during 2007-2011. Shown are Akaike's Information Criteria for small sample sizes (AIC_c), differences among AIC_c (ΔAIC), parameter counts (K), AICc weights (AIC_w), and log likelihood values (LL).

Species	Model	AICc	ΔAICc	K	AIC_w	LL
Red Wolf	Diel Interactions (time period x each variable)	44854.28	0.00	15	1	-22412.13
	No Interactions	44896.52	42.24	8	0	-22440.26
	Year Interactions (yr x each variable)	45479.17	624.89	33	0	-22628.54
	Null Model	45510.48	656.20	2	0	-22753.24
Coyote	Diel Interactions	52276.70	0.00	15	1	-26831.54
	No Interactions	52520.58	243.87	8	0	-26896.54
	Year Interactions	53473.98	1197.28	33	0	-26913.27
	Null Model	53721.50	1444.79	2	0	-27014.20

Table 2.3: $\mathrm{AIC_c}$ model rankings for models of red wolf diurnal and nocturnal resource selection within the Albemarle Peninsula in eastern North Carolina, USA during 2007-2011. Shown are Akaike's Information Criteria for small sample sizes ($\mathrm{AIC_c}$), differences among $\mathrm{AIC_c}$ (ΔAIC), parameter counts (K), AICc weights ($\mathrm{AIC_w}$), and log likelihood values (LL).

Diel Period	Model	AICc	ΔAICc	K	$\mathrm{AIC_w}$	LL
Diurnal	Roads+Soy+Cotton+Corn	25573.63	0.00	6	0.63	-12780.81
	Global	25574.69	1.06	8	0.37	-12779.34
	Corn+Cotton+Soy	35640.79	67.16	5	0	-12815.40
	Soy+Cotton	25805.51	231.45	4	0	-12898.54
	Corn	25905.51	331.88	3	0	-12949.75
Nocturnal	Global	19285.22	0.00	8	0.97	-9634.61
	Corn+Cotton+Soy	19292.60	7.38	5	0.02	-9641.30
	Roads+Corn+Cotton+Soy	19294.41	9.18	6	0.01	-9641.20
	Soy+Cotton	19428.01	142.78	4	0	-9710.00
	Corn	19492.39	207.17	3	0	-9743.20

Table 2.4: AIC_c model rankings for models of coyote diurnal and nocturnal resource selection within the Albemarle Peninsula in eastern North Carolina, USA during 2007-2011. Shown are Akaike's Information Criteria for small sample sizes (AIC_c), differences among AIC_c (ΔAIC), parameter counts (K), AICc weights (AIC_w), and log likelihood values (LL).

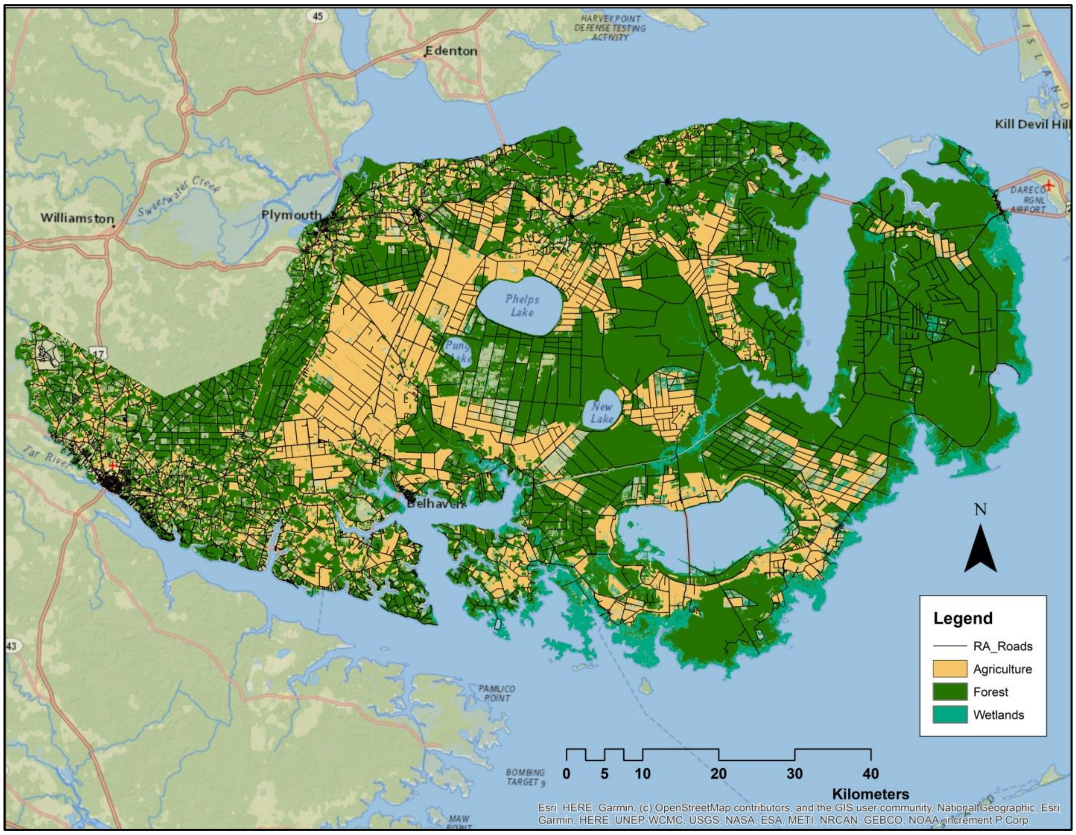
Diel Period	Model	AICc	ΔAICc	K	AIC_w	LL
Diurnal	Global	31698.32	0.00	8	1	-15841.16
	Roads+Corn+Cotton+Soy	31771.02	72.69	6	0	-15879.51
	Corn+Cotton+Soy	31916.54	218.21	5	0	-15953.27
	Wetlands	31975.41	277.09	3	0	-15984.70
	Corn	32152.46	454.14	4	0	-16072.23
Nocturnal	Global	20606.63	0.00	8	1	-10295.3
	Roads+Corn+Cotton+Soy	20628.93	22.30	6	0	-10308.46
	Corn+Cotton+Coy	20665.05	58.42	5	0	-10327.52
	Soy+Cotton	20734.19	127.56	4	0	-10363.09
	Corn	20863.60	256.97	3	0	-10428.80

Table 2.5: Beta coefficient estimates for the top model for red wolf resource selection in the Albemarle Peninsula in northeastern North Carolina from 2007-2011. Shown are beta estimates (β), standard error (SE), and *P*-value (P). *Denotes model averaged estimate.

Diel Period	Covariate	β	SE	***P***
Diurnal	Corn*	-1.12	0.09	<0.001
	Cotton*	0.23	0.03	<0.001
	Soybeans*	0.73	0.07	<0.001
	Roads*	0.51	0.06	<0.001
	Forest	-0.11	0.06	0.086
	Wetlands	0.03	0.05	0.596
Nocturnal	Corn	-1.10	0.10	<0.001
	Cotton	0.40	0.03	<0.001
	Soybeans	0.29	0.09	<0.001
	Roads	-0.05	0.07	0.496
	Forest	0.25	0.07	<0.001
	Wetlands	-0.12	0.06	0.035

Table 2.6: Beta coefficient (β), standard error (SE), and P-value (*P*) estimates for the top model for coyote resource selection in the Albemarle Peninsula in northeastern North Carolina from 2007-2011. *Denotes model averaged estimate.

Diel Period	Covariate	β	SE	P
Diurnal	Corn	-0.77	0.06	<0.001
	Cotton	0.17	0.02	<0.001
	Soybeans	0.17	0.05	0.002
	Roads	0.58	0.05	<0.001
	Forest	0.51	0.06	<0.001
	Wetlands	-0.14	0.04	<0.001
Nocturnal	Corn	-0.59	0.07	<0.001
	Cotton	-0.09	0.03	<0.001
	Soybeans	-0.67	0.07	<0.001
	Roads	-0.47	0.07	<0.001
	Forest	0.28	0.07	<0.001
	Wetlands	0.07	0.04	0.111



Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community, National Geographic, Esri, Garmin, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, increment P Corp.

Figure 2.1: Map of Albemarle Peninsula of northeastern North Carolina with primary landcover types during 2011.

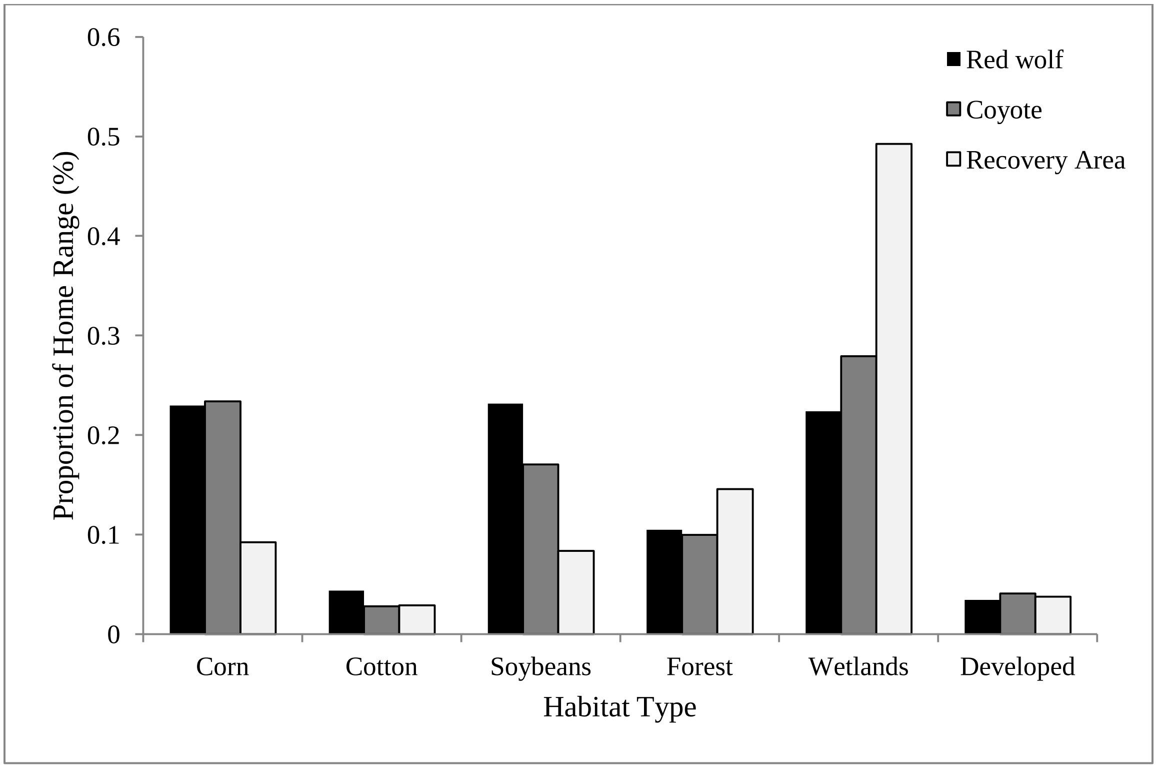


Figure 2.2: Proportion of landcover types within red wolf and coyote 99% isopleth k-LocoH home ranges, and average proportion of landcover types within the Recovery Area during 2007 – 2011 in the Albemarle Peninsula in northeastern North Carolina. No significant differences were found between species.

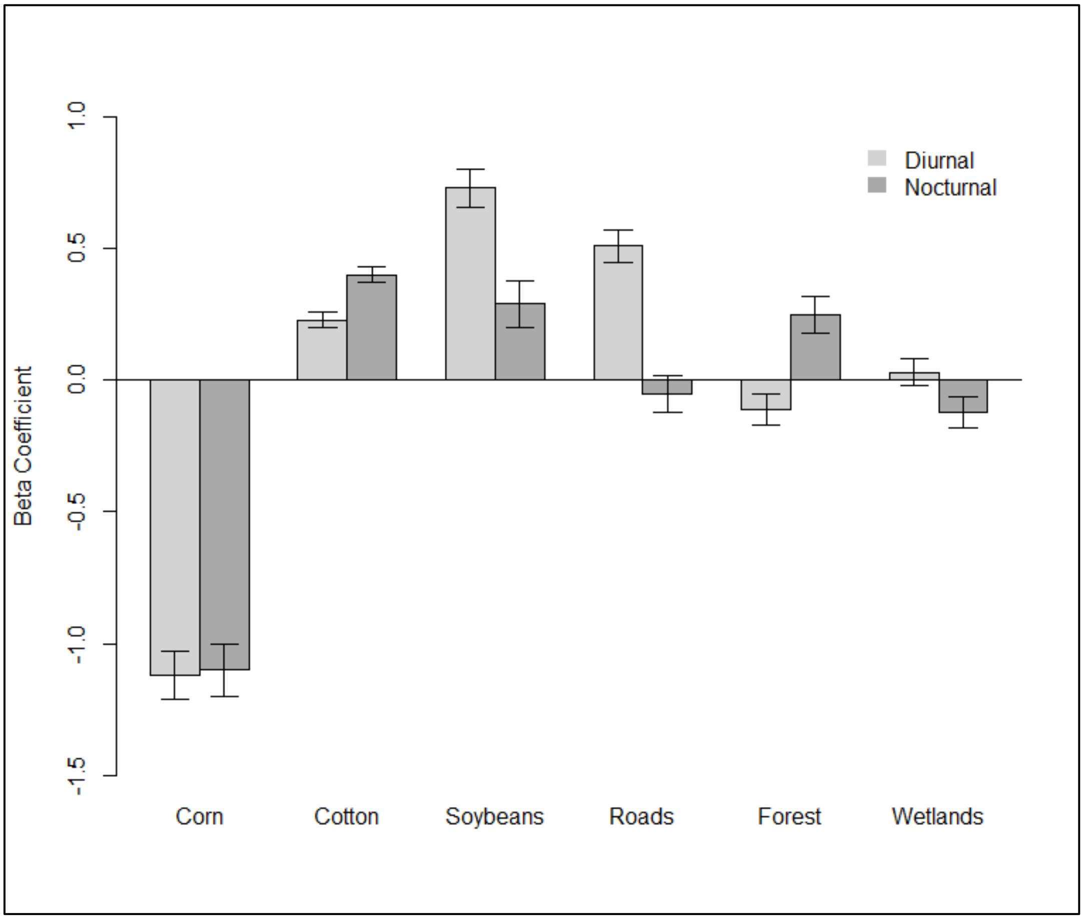


Figure 2.3: Beta coefficient estimates for red wolf resource selection during diurnal and nocturnal periods in the Albemarle Peninsula in northeastern North Carolina during 2007-2011.

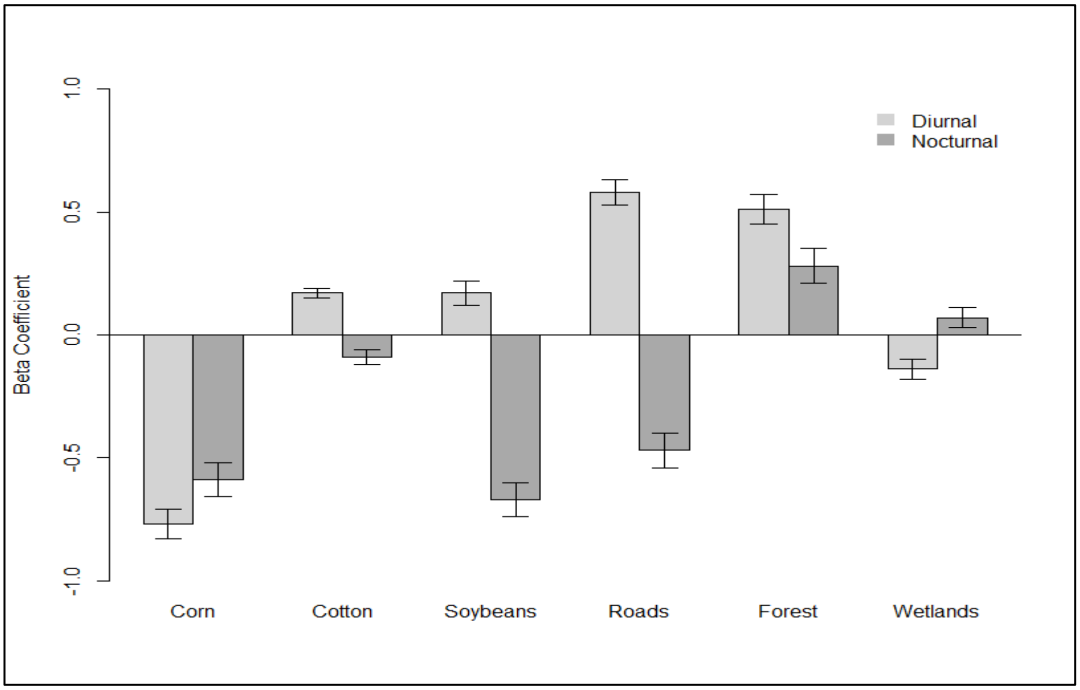


Figure 2.4: Beta coefficient estimates for coyote resource selection during diurnal and nocturnal periods in the Albemarle Peninsula in northeastern North Carolina during 2007-2011.

CHAPTER 3

RESIDENT AND TRANSIENT COYOTES EXHIBIT DIFFERENTIAL MOVEMENT PATTERNS AND HABITAT SELECTION IN THE SOUTHEASTERN UNITED STATES

Webster, S.C., Chamberlain, M.J., Hinton, J.W., and Beasley, J.C. To be submitted to *Journal of Mammalogy*.

Abstract

Coyotes (*Canis latrans*) are a highly adaptable canid species whose behavioral plasticity has allowed them to persist in a wide array of habitats and climates throughout North America. As generalists, coyotes are able to alter movement patterns and change territorial strategies between residency and transiency to maximize fitness. Several studies have investigated coyote space use and habitat selection, but the relatively few studies that have differentiated between resident and transient individuals have reported conflicting patterns of selection for both groups. Thus, ambiguity remains about resident and transient coyote movement patterns and habitat selection. We aimed to quantify habitat selection for resident and transient coyotes using first passage time (FPT) analysis, which quantifies habitat selection by delineating where along an individual's movement path they exhibit area-restricted search (ARS) behaviors. We quantified monthly movement rates for 171 coyotes (76 resident, 53 transient) and then used estimated FPT values and generalized linear mixed models to quantify monthly habitat selection for resident and transient coyotes. Transients had greater movement rates than residents across all months except January. Resident coyotes selected agricultural landcover during fall and winter, but avoided agriculture during spring. Residents avoided developed habitats May – August, avoided deciduous landcover June – August, and avoided wetlands from September – January except November. Edge density was generally positively correlated with resident ARS behaviors. Transient coyotes were more likely to engage in ARS behavior near developed areas throughout much of the year. Transients selected for wetlands during July – September and avoided agriculture during all months except June and July. Both residents and transients generally selected

for areas with greater densities of edge habitat. Although we observed high individual variation in space use and habitat selection, our study found substantive differences in habitat selection between resident and transient coyotes, providing further evidence of the complexity and plasticity of coyote habitat selection temporally.

Introduction

Coyotes (*Canis latrans*) are a highly adaptable canid species whose behavioral plasticity has allowed them to persist in a wide array of habitats and climates, ranging from relatively undisturbed natural areas to highly developed urban environments (Bekoff 1978; Bekoff and Wells 1986; Gompper 2002). As opportunistic generalists, coyotes are able to switch among various food resources (Patterson et al. 1998; Randa et al. 2009), alter movement patterns to minimize conflicts with conspecifics, other predators, and humans (Fedriani et al. 2000; Berger and Gese 2007), and change individual social strategies to maximize survival and reproduction (Macdonald 1983). These characteristics have facilitated an extensive range expansion and growth of coyote populations over the past century, while other canid populations have declined (Hody and Kays 2018; Hinton et al. 2019).

Range expansion of coyotes has had several impacts on newly colonized ecosystems, including altering prey population dynamics (Kilgo et al. 2010, Crimmins et al. 2012; Swingen et al. 2015) and increasing interference competition for resources among established predator populations (Harrison et al. 1989; Johnson et al. 1996; Berger and Gese 2007). Many of these observed trends are thought to be density dependent, with impacts becoming more pronounced as coyote populations increase and animals saturate the landscape (Gompper 2002). As a result, managers and researchers recognize the need for a more comprehensive understanding of coyote spatial ecology, particularly territoriality and habitat selection, in recently colonized regions.

Adult coyotes typically exhibit one of two patterns of territorial space use: residency or transiency. Residents maintain small, mutually exclusive home ranges as breeding pairs whereas transients typically move across landscapes without a social group and often overlap with other individuals’ home ranges (Kamler and Gipson 2000; Bekoff and Gese 2003; Gese 2004). Territorial status has substantive implications for how coyotes interact with their surrounding environments, including habitat use and prey selection (Mills and Knowlton 1991; Ward et al. 2018). Transient coyotes typically move alone, exhibit low site fidelity, and do not breed (Kamler and Gipson 2000) whereas resident animals exhibit high site fidelity to their territory and can maintain territories for several years (Kitchen et al. 2000; Gese 2004). Resident animals that maintain territories are thought to have greater foraging success (Gese 1996) and are less vulnerable to human persecution (Knowlton et al. 1999). Transient animals typically move nomadically across the landscape in what are often referred to as biding areas until they can establish residency when habitat becomes available (Carmenzind 1978; Hinton et al. 2015; Morin and Kelly 2017).

Several studies have investigated coyote space use and habitat selection, but relatively few have differentiated selection between resident and transient behaviors when conducting their analyses. Of those that made this differentiation, all noted that resident coyotes were found to select for open grassland, pasture, and agricultural habitats while avoiding developed habitats (Kamler and Gipson 2003; Hinton et al. 2015). However, patterns of habitat selection for transient coyotes are more ambiguous. Kamler and Gipson (2003) found transients avoided grasslands and selected woodlands, whereas Hinton et al. (2015) found transient coyotes exhibited similar selection trends to residents by selecting open habitats, although transients were more likely to use roads than residents. Transient coyotes have also been documented using habitats associated with human development (Gerht et al. 2009; Mitchell et al. 2015). Notably, previous studies faced logistical and practical limitations in sample sizes or data resolution that may have impacted observed trends. Additionally, most previous research has quantified habitat selection by both residents and transients based on an individual's estimated home range (e.g., 3rd-order resource selection functions [RSF]), an approach that may not be appropriate for transient coyotes who do not have stable home ranges over time (Morin and Kelly 2017). For species who do not maintain stable home ranges, characterization of movement behaviors along an individual's movement path and association of those behaviors with the habitats in which they occur may be a more appropriate approach to determine habitat selection.

One such approach, first passage time (FPT) analyses (Fauchald and Tveraa 2003), allows for fine-scale delineation of where an animal is spending time by estimating when an individual is exhibiting area-restricted search behavior (ARS; i.e., slow travel speed and high tortuosity) along its movement path. By using FPT analyses, researchers can infer habitat selection based on where an animal is engaging in ARS behaviors (e.g., foraging) vs. non-ARS behavior (e.g., traveling), and these methodologies have successfully been used previously to investigate fine-scale habitat selection of other mesocarnivores such as raccoons (*Procyon lotor*; Fauchald and Tveraa 2003; Byrne and Chamberlain 2012). Additionally, FPT analyses do not rely on estimated home ranges required by traditional resource selection methodologies, ultimately reducing uncertainty in inferred patterns of selection, especially for individuals which do not maintain home ranges. Thus, our goal was to quantify fine-scale habitat selection of resident and transient coyotes across the southeastern United States using FPT analyses to distinguish patterns of resource selection between resident and transient individuals. We hypothesized that both resident and transient coyote habitat selection and movement rates would vary throughout the year, but predicted that residents would exhibit stronger temporal patterns in selection than transients (i.e., transient habitat selection would vary more than would resident). We also predicted that ARS behaviors in transient coyotes would be positively correlated to human development throughout the year. Lastly, we predicted that ARS behaviors in resident coyotes would be positively correlated with open habitats such as grassland/agriculture/pastureland, whereas transient ARS behaviors would occur in a greater variety of habitats.

Methods

Study Area

Our study area included regions of Alabama (Barbour, Macon, and Pike Counties), Georgia (Columbia, Jefferson, Lincoln, McDuffie, and Warren Counties), and South Carolina (Aiken, Barnwell, Edgefield, McCormick, and Saluda Counties) in the southeastern United States, totaling approximately 16,200 km^2 (Figure 1). Coyotes captured in Georgia and South Carolina commonly moved between the respective study areas, and likely represented one population, leaving two distinct study areas: the Alabama study area (ASA) and the Savannah River study area (SRA). Both study areas were comprised predominantly of privately-owned land, but approximately 20% of the

SRA was comprised of the Savannah River Site (SRS), an 803 km^2 federal facility operated by the U.S. Department of Energy (DOE). Both study areas had mild sub-tropical climate throughout the year. Summers were generally hot and humid with an average high temperature of approximately 30°C, whereas winters were mild with an average low temperature of approximately 1°C (NOAA 2018). Habitats in both the ASA and the SRA were a mix of successional forest, agriculture, pastureland, pine plantations, and urban habitats. Agriculture in these regions included cotton (*Gossypium spp.*), corn (*Zea mays*), tobacco (*Nicotiana tabacum*), soybeans (*Glycine max*), and peanuts (*Arachis hypogaea*).

Data Collection

We deployed GPS collars on coyotes over three fall/winter seasons in 2015, 2016, and 2017. We captured animals with foothold traps (Victor #3 Softcatch, Woodstream Corporation, Lititz, Pennsylvania, USA; MB 550 or MB 450, Minnesota Trapline Products, Pennock, Minnesota, USA) with offset or padded jaws. During 2015-2016, animals were restrained with a catchpole, muzzle, and hobbles for processing. During 2017, animals were anesthetized prior to processing using a Ketamine/Xylazine mixture administered at 0.8 ml/kg for Ketamine and 0.1 ml/kg for Xylazine. We then determined sex, weight, and age using tooth wear (Gipson et al. 2000). Coyotes >2 years old were considered adults, whereas 1-2 year olds were considered juveniles, and animals <1 year old were classified as pups. We fitted each animal with a mortality-sensitive satellite collar (either G2110E Iridium collar, Advanced Telemetry Systems, Isanti, Minnesota, USA or Litetrack Iridium collar, Lotek Wireless Inc., New Market, Ontario, Canada). Collars recorded locations at a 4-hour interval. Prior to release, we administered anesthetized animals Yohimbine at 1.0 ml/kg. All animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (protocols A2014 08-025-R2 and A2015 05-004-A5). To access lands to trap, state agencies and the DOE granted permission for publicly owned property while we obtained permission from landowners to access privately owned lands.

Movement Data Analysis

To determine territorial status of collared animals, we used a combination of estimated seasonal home range size (Kamler and Gipson 2000) and a rarefaction curve for each animal created by calculating monthly home ranges (Dellinger et al. 2013). We classified resident coyotes as animals that showed stable space use for $\geq$ 3 months and had home ranges smaller than 45 km^2. Transients were animals with ranges larger than 45 km^2 and variable space use over time. Using both methods for identifying territorial status allowed for confident classification of residents and transients, but also meant that we were unable to determine territorial status of animals with <3 months of movement data due to mortality or collar failure. If we were unable to determine territorial status for an individual, it was excluded from further analysis. For transient animals, we refer to space use patterns were referred to as biding areas because transients do not maintain territories (Hinton et al. 2012; Morin and Kelly 2017).

Previous research has shown that coyote space use varies seasonally due to a variety of biological and ecological attributes (Kamler and Gipson 2000; Hinton et al. 2015; Sasmal et al. 2019). However, the criteria researchers use to define ecologically or biologically relevant seasons typically varies among studies (e.g., seasons defined by environmental conditions vs. organism behaviors) depending upon the research question, data resolution, and study duration. Variation in season delineation can potentially bias results or mask important trends in spatial data (Thompson and McGarigal 2002; Basille et al. 2013). To mitigate this issue, we decided to conduct all spatial analyses by month. Quantifying movement on a monthly basis allowed us to minimize potential bias due to mis-classification of relevant seasons. We also quantified average step length and movement rates for both resident and transient coyotes by month to determine if movement behaviors between the two classes differed temporally. We defined step length as the distance in meters between two consecutive locations along the animal's movement path, and quantified movement rate by dividing step length between two locations by the time interval between those locations. Most time intervals were approximately 4 hrs, and we excluded locations that had time intervals >24 hrs. To determine if movement rates differed between residents and transients, we conducted two-tailed unequal variance *t*-tests for each month. An alpha value of 0.05 was used to determine significance in all statistical tests.

We used FPT analyses following Fauchald and Tveraa (2003) to quantify relationships between landscape features and monthly coyote space use and movement behaviors. FPT is the time required for an animal to cross a circle of a given radius (Johnson et al. 1992), and can be used to infer movement behaviors when FPT values are estimated along an individual's movement path. Low FPT values are associated with faster linear movements whereas higher FPT values indicate an animal's movements are slower and more sinuous. More sinuous movements are inferred as ARS behavior, often associated with foraging or loafing behaviors. Thus, researchers are able to differentiate between different behavioral states (i.e., travelling vs. foraging/loafing) and quantify which habitats these behaviors occur within. We analyzed movement paths from resident and transient coyotes on a monthly basis by subsetting movement data by month and requiring an individual to have a minimum of 90 relocations within a month to be included in each monthly analysis. To determine the appropriate scale at which to estimate FPT values, we first interpolated locations every 20m along movement paths and calculated FPT values at these locations for circles with radii ranging from 10 – 4000 m in 10-m increments. We then calculated the variance of log-transformed FPT values for each trajectory and circle radius to determine at which radius the variance peaked, indicating the scale at which individuals were concentrating ARS behaviors (Fauchald and Tverra 2003). This scale varied across individual movement paths, so we calculated an average scale across all individuals for each month for comparisons (Frietas et al. 2008, Byrne and Chamberlain 2012). We then re-calculated FPT values for all individuals using the averaged radius size for each month. By estimating FPT values at differing scales monthly and only including individuals which met robust data thresholds, we minimized bias introduced by seasonal and individual variation in movement patterns.

Habitat Analyses

We assessed habitat composition of the study areas using a 30 m resolution National Land Cover Database (NLCD) 2016 land cover raster layer. Using Spatial Analyst in ArcMap 10.3, we reclassified the NLCD raster layer into six primary landcover types: mixed deciduous forest, pine forest, wetland, open (e.g., pastureland, grassland, early successional habitat, barren land), agriculture, and developed. Because coyotes are known to use edge habitats (i.e., the boundary between two landcover types; Heske et al. 1999; Tigas et al. 2002; Hinton et al. 2015), we also calculated edge density throughout both study areas using package “landscapemetrics” in Program R (Hesselbarth et al. 2019; R Core Team 2018).

To determine which landcover characteristics were associated with ARS behaviors, we measured the distance of each location along an individual’s movement path to each landcover type, and quantified average edge density within a 100m radius around each location. We then used a generalized linear mixed model (GLMM) to determine if areas with high FPT values (i.e., areas where individuals were engaging in ARS behaviors) were associated with particular habitat characteristics. We included FPT values as a continuous, fixed effect in all models. Traditionally, FPT values are reduced into two binary, categorical variables of ARS and non-ARS values (Fauchald and Tverra 2003). However, given the high level of individual variation we observed in sampled individuals, particularly among transient coyotes, creating a discrete threshold between FPT values in order to create a binary variable would likely introduce bias into our model interpretations. By quantifying FPT values as a continuous variable we mitigated this potential bias and ultimately allowed for more nuanced interpretation of model outputs. We modeled resident and transient animals separately for each month so the scale of FPT estimated values was consistent for all data included in a model. For both classes of coyote in each month, we ran a suite of GLMMs with all landcover variables and all relevant subsets. In all models, we included individual coyote as a random effect to account for spatial and temporal autocorrelation between each individual’s movement data. To avoid multicollinearity, we examined correlations among model variables by deriving a matrix of all possible Spearman correlation coefficient values. Any variables with a significant correlation ($r^2 > 0.6$; $P < 0.05$) were not simultaneously included in the same model in subsequent analysis. We inferred selection when locations with high FPT values were significantly closer in distance (meters) to certain landcover types than locations with low FPT values. We then used Akaike's Information Criterion (AIC) to assess model performance, and used the top performing model to estimate model parameters, including beta coefficients (β), of selection for each habitat characteristic within the model. In the event that >1 model was within 2 AIC units of the top model, we model averaged to derive parameter estimates (Burnham and Anderson 2002). We conducted all statistical analyses in Program R (R Core Team 2018).

Results

We deployed collars on 193 coyotes, 54 in the ASA and 139 in the SRA. We excluded 22 coyotes from analysis due to an insufficient number of relocations. Of the remaining 171 coyotes, 76 (44.4%) were residents and 53 (30.1%) were transients for the entire time they were monitored, whereas 42 (24.6%) exhibited both residency and transiency. We included individuals who were both residents and transients at different time periods during monitoring in analyses, but separated their movement paths into different paths during residency and transiency. Movement rates varied between residents and transients across all months except January and December, with transients generally having longer step lengths and greater movement rates than residents (Table 1; Figure 2).

We evaluated 1,501 monthly movement paths (900 resident and 601 transient), with the number of movement paths included in each month ranging from 52 – 74 individuals. We observed ARS behaviors in all monthly movement datasets analyzed, and the average radius at which ARS behaviors occurred varied considerably across months (Figure 3). Modeling analyses revealed that all landcover variables affected ARS behaviors throughout the year; however, which variables were important and the direction of correlation (i.e., positive or negative) varied among months (Tables 2 & 3; Figures 4 & 5). Resident coyotes were more likely to engage in ARS behavior near agriculture during fall and winter months, but avoided agriculture during spring months. Residents avoided developed habitats during May – August, avoided deciduous landcover during June – August, and avoided wetlands from September – January except during November (Figure 4). Edge density was positively correlated with resident ARS behaviors in all months except April, June, July, and October (see Figure 4). Transient coyotes were more likely to engage in ARS behavior near developed areas throughout much of the year (Table 5; Figure 5). Transient ARS behavior was also more likely to occur near wetlands during July – September. Transients were more likely to avoid agriculture across most months except June and July. Edge density was positively correlated with transient ARS behaviors in all months except March, August, and November (Table 5; Figure 5).

Discussion

We found that ARS behaviors of coyotes correlated to specific landcover types across the Southeast, suggesting both resident and transient coyotes use particular habitats to engage in ARS behaviors such as foraging or loafing. Our results partially supported our first hypothesis that habitats correlated with ARS behaviors would vary throughout the year. However, we found substantive variation in the direction and magnitude of correlations for both residents and transients, implying considerable temporal variation in individual and group behavior. This finding is not entirely surprising, as habitat selection by coyotes has previously been shown to be highly variable and context dependent, even for resident individuals (Harrison et al. 1991; Patterson and Messier 2001; Gosselink et al. 2003). Additionally, contrary to traditional RSF approaches that rely solely on an animal's physical location to infer selection of particular habitats, FPT analysis accounts for the animal's movement path and associates physical locations with biological activities such as foraging or denning (Fauchald and Tverra 2003). Thus, although coyotes may be more likely to be located in particular habitats throughout time, our findings suggest they are likely engaging in ARS behaviors in a diversity of habitats, reflecting their behavioral plasticity and opportunistic foraging strategy (Gosselink e al. 2003; Ward et al. 2018).

We observed that movement rates varied across months for both residents and transients, although transient movement rates were greater than those of residents in all months except January. Previous work has found that transients typically have larger ranges (Kamler and Gipson 2000; Hinton et al. 2015) and greater movement rates than residents (Sasmal et al. 2019). Our estimated monthly movement rates of coyotes were generally less than those previously reported in other studies for both residents (165.5 – 202.1 m/hr vs. 295.3-449.8 m/hr; Sasmal et al. 2019) and transients (183.4 – 229.7 m/hr vs. 283.0 – 488.5 m/hr; Sasmal et al. 2019). These differences likely arise from differences in the temporal scale at which movement rates were calculated between studies (monthly vs. seasonal) and our increased sample size, which would minimize the effect of outlier movement steps (i.e., long-distance dispersal). Residents had lower movement rates during breeding and pup-rearing season (March – August), with the lowest movement rates in June, a time when pups are likely emerging from the den yet still have limited mobility, thus indirectly limiting mobility of adults caring for pups

(Andelt 1985). Residents had the greatest movement rates during September, likely coinciding with dispersal of pups from their natal range (Andelt 1985; Bekoff and Wells 1986). Transients also had greatest movement rates during September, but exhibited relatively high movement rates throughout much of the year, with the lowest movement rates occurring in January (183.4 m/hr; Figure 2b).

Previous research has found clear patterns of habitat selection in both resident and transient coyotes (Holzman et al. 1992; Kamler and Gipson 2000; Hinton et al. 2015). Transient coyotes were previously found to be more likely to select for human-disturbed habitats such as roads and urban development (Kamler and Gipson 2000; Hinton et al. 2015). Similarly, we found that transient ARS behaviors were more likely to occur near developed areas during February and June – October, supporting our hypothesis that transient ARS behaviors would be correlated with human developments. Conversely, residents were less likely to exhibit ARS behaviors near developed areas during January and May – September. Importantly, this time period overlaps with when individuals may be rearing pups (April – Sept; Bekoff and Wells 1986; Kilgo et al. 2017), an activity only resident coyotes engage in (Mills and Knowlton 1991; Geese 2004). High FPT values associated with resident ARS behaviors during these months are likely a combination of denning (April – May), pup-rearing (May – Sept), and foraging (year-round) behaviors. Due to our large sample size and study extent, we did not attempt to quantify if resident animals successfully reproduced each year of monitoring, and thus we cannot differentiate between these behaviors. However, resident avoidance of developed areas, and by proxy human activities known to increase mortality risk (Kitchen et al. 2000), during pup-rearing may be a strategy to increase survival of both parents and pups during pup-rearing.

We found resident ARS behaviors were generally more likely to occur near wetlands from February – August (excluding June), which encompasses breeding (Jan – March) and pup-rearing season (April – Sept) for resident coyotes. Residents with offspring are limited in their movements by the relatively reduced mobility of young pups (Andelt 1985; Gese 2004). Focusing foraging and pup rearing activities closer to wetlands and free water sources may decrease energetic costs associated with accessing water sources for both themselves and their offspring. Additionally, transient ARS behaviors were more likely to occur near wetlands from July – September. Resident and transient selection for wetlands overlaps with the warm summer months when the risk of heat stress for both are higher, and access to water for hydration and thermoregulation can mitigate this risk for both adults and (for residents) pups (Afik and Pinshow 1993). Likewise, edge density was generally an important variable for both residents and transients, and the correlation between ARS behaviors and edge density was always positive when it is was significant. This finding supports previous work indicating edge habitats provide important foraging opportunities for coyotes (Heske et al. 1999; Hinton et al. 2015).

Importantly, FPT analysis is known to be dependent on scale (Frair et al. 2005; Byrne and Chamberlain 2012), with periods of ARS behavior potentially nested within larger periods of restricted movement behavior along an animal’s movement path. The scale of ARS behaviors can be influenced by several different factors including habitat configuration and territoriality (Fauchald and Tveraa 2003; Friar et al. 2005; Byrne and

Chamberlain 2012). In particular, territoriality can influence the ability to delineate ARS behaviors because an individual may restrict its movements to within its home range due to territorial boundaries, and not necessarily because of ARS behaviors (e.g., foraging). All resident coyotes in our study could easily traverse their estimated home range during the month period at which we estimated FPT, allowing for the possibility that an animal may turn back on its path as it moves among portions of its home range in addition to foraging or resting behaviors. However, our research objectives were not to infer specific behaviors (i.e., foraging vs. denning vs. resting) within periods of ARS behavior, but rather to associate general ARS behavior with landcover characteristics for both resident and transient animals. Furthermore, the substantive variation in space use and movement rates among resident and transient animals and the temporal scale of our movement data (i.e., relocations every 4 hrs) likely indicate that patterns associated with inferred behavioral states may also vary widely among individuals. Regardless, we believe that the resolution of our analysis and spatial scale at which we inferred ARS behaviors were sufficient and appropriate to elucidate landcover characteristics associated with these behaviors.

The complex, variable patterns in space use and habitat selection of both residents and transients make effective, continued management of coyotes difficult, especially at a landscape scale. Although we found clear evidence of habitat selection in both resident and transient animals, the substantive variation among individual coyotes indicates that broad, generalized management actions may not be appropriate for targeting coyotes at a population level. Indeed, previous research has found that large-scale management efforts in the Southeast are rarely successful at long term management of coyote populations

(Kilgo et al. 2014; Kierepka et al. 2017). Rather, management actions are likely to be more effective at small scales when individual patterns of movement behavior are known.

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Figures and Tables

Table 3.1: Averaged estimates of monthly 95% ranges and 50% core areas for 171 resident and transient coyotes monitored from January 2015 – Jun 2017 in the tri-state region of Alabama, Georgia, and South Carolina, USA.

Territorial Status	Month	95% Ranges (km^2)	SD	50% Core Areas (km^2)	SD
Resident	January	21.281	36.067	4.512	7.535
	February	30.514	111.698	4.986	15.203
	March	13.550	11.066	2.665	2.3404
	April	14.981	21.680	2.666	2.670
	May	11.188	9.028	1.986	2.119
	June	13.552	17.242	2.637	4.007
	July	12.023	8.961	2.165	1.806
	August	11.969	9.414	2.506	1.924
	September	12.083	6.480	2.833	1.781
	October	12.586	8.869	2.971	2.310
	November	13.557	9.966	3.043	1.902
	December	14.662	12.031	3.418	2.675
Transient	January	202.135	319.233	41.221	68.050
	February	561.444	1209.618	128.206	296.284
	March	480.156	994.499	121.707	283.034
	April	355.873	827.615	83.521	226.819
	May	321.155	498.468	72.075	112.362
	June	377.043	1033.125	95.773	278.459
	July	349.524	678.559	82.899	219.060
	August	297.166	904.558	67.256	188.364
	September	449.668	1412.657	116.945	306.678
	October	387.233	924.212	95.882	279.923
	November	367.444	412.386	86.333	106.229
	December	276.899	382.687	57.248	89.601

Table 3.2: Sample estimates for two-tailed unequal variance t-tests comparing monthly movement rates between resident and transient coyotes monitored from January 2015 – June 2017 in the tri-state region of Alabama, Georgia, and South Carolina, USA.

Month	*t* statistic	Degrees of freedom	P Value
Jan	-0.086	7973.7	0.9314
Feb	-9.4502	17174	<0.001
Mar	-11.464	19507	<0.001
Apr	-14.939	16973	<0.001
May	-11.417	12346	<0.001
Jun	-12.213	9318.5	<0.001
Jul	-7.468	8546.1	<0.001
Aug	-4.732	10478	<0.001
Sep	-5.6754	8116.2	<0.001
Oct	-4.702	8803.5	<0.001
Nov	-2.442	8084.8	0.015
Dec	-1.127	5994.1	0.259

Table 3.3: Beta coefficient, standard error, t value, and *P* value estimates of the top-ranked generalized linear mixed model (GLMM) estimating habitat selection for resident coyotes monitored from January 2015 – June 2017 in Alabama, Georgia, and South Carolina.

Month	Habitat Type	Beta Estimate	Standard Error	t Value	P Value
January	Deciduous	-63.69	23.82	-2.67	<0.001
	Wetland	28.47	10.94	2.60	<0.001
	Cropland	-19.35	7.79	-2.48	<0.001
	Develop	60.12	10.73	5.60	<0.001
	Pine Forest	98.00	10.73	4.19	<0.001
	Edge Density	68.24	23.38	2.88	<0.001
February	Deciduous	58.10	23.77	2.45	0.014
	Wetland	-28.47	11.39	-2.49	0.014
	Cropland	-20.92	7.25	-2.89	0.003
	Develop	-7.99	10.31	-0.78	0.04
	Pine Forest	-129.94	24.10	-5.39	<0.001
	Edge Density	12.94	1.65	9.33	<0.001
March	Deciduous	-63.15	17.87	-3.53	<0.001
	Wetland	-19.05	8.32	-2.28	0.02
	Cropland	-26.01	4.48	-5.80	<0.001
	Develop	1.42	7.98	0.18	0.88
	Pine Forest	26.19	18.54	1.40	0.17
	Edge Density	14.26	6.25	2.34	0.02
April	Deciduous	37.54	27.86	1.35	0.1
	Wetland	-39.42	11.68	-3.38	<0.001
	Cropland	75.06	4.72	15.89	<0.001
	Develop	10.88	12.44	0.87	0.34
	Pine Forest	-26.36	27.98	-0.94	0.38
	Edge Density	24.25	18.77	1.01	0.27
May	Deciduous	13.78	19.95	0.69	0.49
	Wetland	-17.23	8.37	-2.06	0.04
	Cropland	11.18	3.25	3.44	<0.001
	Develop	32.69	9.41	3.47	<0.001
	Pine Forest	-35.92	20.65	-1.74	0.08
	Edge Density	19.16	2.12	1.24	<0.001
June	Deciduous	72.92	21.56	3.38	<0.001
	Wetland	15.33	9.30	1.65	0.09
	Cropland	70.38	3.51	20.07	<0.001
	Develop	31.91	10.28	3.10	0.001
	Pine Forest	-1.16	23.77	-0.05	0.9

	Edge Density	4.44	0.74	0.72	0.06
July	Deciduous	42.52	21.69	1.96	0.04
	Wetland	-56.07	9.30	-6.03	<0.001
	Cropland	-2.39	3.41	-0.70	0.48
	Develop	95.29	9.54	9.99	<0.001
	Pine Forest	-26.90	23.06	-1.17	0.24
	Edge Density	15.89	11.19	1.02	0.35
August	Deciduous	38.17	26.92	1.42	0.04
	Wetland	-17.59	10.87	-1.62	<0.001
	Cropland	3.74	3.42	1.09	0.48
	Develop	81.31	12.60	6.45	<0.001
	Pine Forest	49.00	29.28	1.67	0.24
	Edge Density	22.28	1.89	9.79	<0.001
September	Deciduous	32.08	25.02	1.28	0.19
	Wetland	50.70	10.23	4.95	<0.001
	Cropland	12.49	3.61	3.46	<0.001
	Develop	-17.29	13.74	-1.26	0.2
	Pine Forest	-93.09	27.41	-3.40	<0.001
	Edge Density	68.62	14.61	4.41	<0.001
October	Deciduous	-6.52	26.18	-0.25	0.80
	Wetland	30.49	11.35	2.69	0.007
	Cropland	-12.89	4.04	-3.19	0.001
	Develop	8.18	13.20	0.62	0.54
	Pine Forest	-46.80	27.93	-1.68	0.09
	Edge Density	-1.24	6.77	0.23	0.66
November	Deciduous	60.39	21.78	2.77	0.005
	Wetland	-3.27	9.29	-0.35	0.73
	Cropland	-33.12	5.17	-6.40	<0.001
	Develop	-45.65	10.34	-4.10	<0.001
	Pine Forest	38.05	21.42	1.77	<0.001
	Edge Density	12.28	2.38	8.21	<0.001
December	Deciduous	3.08	30.18	0.10	0.92
	Wetland	44.39	12.53	3.54	<0.001
	Cropland	-49.03	8.03	-6.11	<0.001
	Develop	26.29	13.68	1.92	0.05
	Pine Forest	30.75	29.22	1.05	0.29
	Edge Density	52.97	6.05	5.78	<0.001

Table 3.4: Beta coefficient, standard error, t value, and *P* value estimates of the top-ranked generalized linear mixed model (GLMM) estimating habitat selection for transient coyotes monitored from January 2015 – June 2017 in Alabama, Georgia, and South Carolina

Month	Habitat Type	Beta Estimate	Standard Error	t Value	P Value
January	Deciduous	-147.84	13.52	-10.94	<0.001
	Wetland	31.99	10.90	2.94	0.003
	Cropland	37.99	4.79	7.92	<0.001
	Develop	10.29	11.12	0.93	0.35
	Pine Forest	54.46	18.27	2.98	0.002
	Edge Density	21.28	5.68	4.67	<0.001
February	Deciduous	-78.59	12.97	-6.06	<0.001
	Wetland	15.16	5.67	2.67	0.007
	Cropland	42.24	2.25	18.79	<0.001
	Develop	-20.49	6.80	-3.01	0.002
	Pine Forest	22.53	10.36	2.18	0.02
	Edge Density	33.84	3.71	15.45	<0.001
March	Deciduous	-95.95	14.47	-6.63	<0.001
	Wetland	19.06	6.18	3.08	0.002
	Cropland	7.66	2.10	3.64	<0.001
	Develop	-3.93	6.55	-0.59	0.55
	Pine Forest	-8.49	10.50	0.81	0.42
	Edge Density	5.58	2.72	1.72	0.06
April	Deciduous	-31.82	11.13	-3.55	10.44
	Wetland	-6.96	5.73	-1.41	0.16
	Cropland	10.33	2.14	6.31	<0.001
	Develop	15.48	6.06	2.87	0.004
	Pine Forest	96.24	12.36	10.44	<0.001
	Edge Density	19.51	2.63	16.35	<0.001
May	Deciduous	-5.53	8.39	-1.66	0.62
	Wetland	1.54	6.26	-0.71	0.79
	Cropland	7.96	2.07	-2.09	<0.001
	Develop	24.11	6.62	-2.55	<0.001

	Pine Forest	-8.70	13.38	-6.22	0.48
	Edge Density	16.94	4.34	3.12	<0.001
June	Deciduous	-13.94	8.39	-1.66	0.09
	Wetland	-4.45	6.26	-1.71	0.48
	Cropland	-4.32	2.07	-2.09	0.04
	Develop	-16.85	6.62	-2.55	0.01
	Pine Forest	-83.18	13.38	-6.22	<0.001
	Edge Density	3.16	1.89	1.22	0.04
July	Deciduous	13.84	6.25	2.22	0.02
	Wetland	-25.03	6.09	-4.11	<0.001
	Cropland	-5.38	2.14	-2.52	0.012
	Develop	-55.88	6.58	-8.49	<0.001
	Pine Forest	49.43	10.71	4.61	<0.001
	Edge Density	24.37	8.81	2.69	<0.001
August	Deciduous	-15.30	10.35	-1.48	0.14
	Wetland	-28.19	6.02	-4.69	<0.001
	Cropland	4.82	2.01	2.40	0.01
	Develop	-21.81	7.04	-3.05	0.002
	Pine Forest	-5.46	13.05	-0.42	0.68
	Edge Density	-0.23	6.92	-0.02	0.95
September	Deciduous	-20.80	16.49	-1.26	0.21
	Wetland	-15.09	7.88	-1.91	0.05
	Cropland	44.99	2.85	15.76	<0.001
	Develop	-69.98	9.48	-7.38	<0.001
	Pine Forest	75.71	15.30	4.95	<0.001
	Edge Density	20.61	3.19	8.64	<0.001
October	Deciduous	-13.05	8.52	-1.53	0.13
	Wetland	2.18	4.56	0.48	0.63
	Cropland	2.79	1.64	1.69	0.09
	Develop	-18.86	6.15	-3.06	0.002
	Pine Forest	15.71	10.13	1.56	0.12
	Edge Density	9.48	1.83	6.34	<0.001
November	Deciduous	5.27	12.83	4.11	<0.001
	Wetland	-4.22	7.68	-0.05	0.96
	Cropland	3.51	3.23	10.72	<0.001
	Develop	-2.10	9.83	-2.13	0.033
	Pine Forest	2.53	15.43	1.64	0.11
	Edge Density	1.71	0.94	1.27	0.34
December	Deciduous	148.06	21.68	6.83	<0.001

Wetland	-94.08	11.21	-8.39	<0.001
Cropland	7.46	4.77	1.56	0.12
Develop	-19.25	13.15	-1.46	0.14
Pine Forest	57.99	18.77	3.09	0.002
Edge Density	48.26	25.33	2.28	0.002

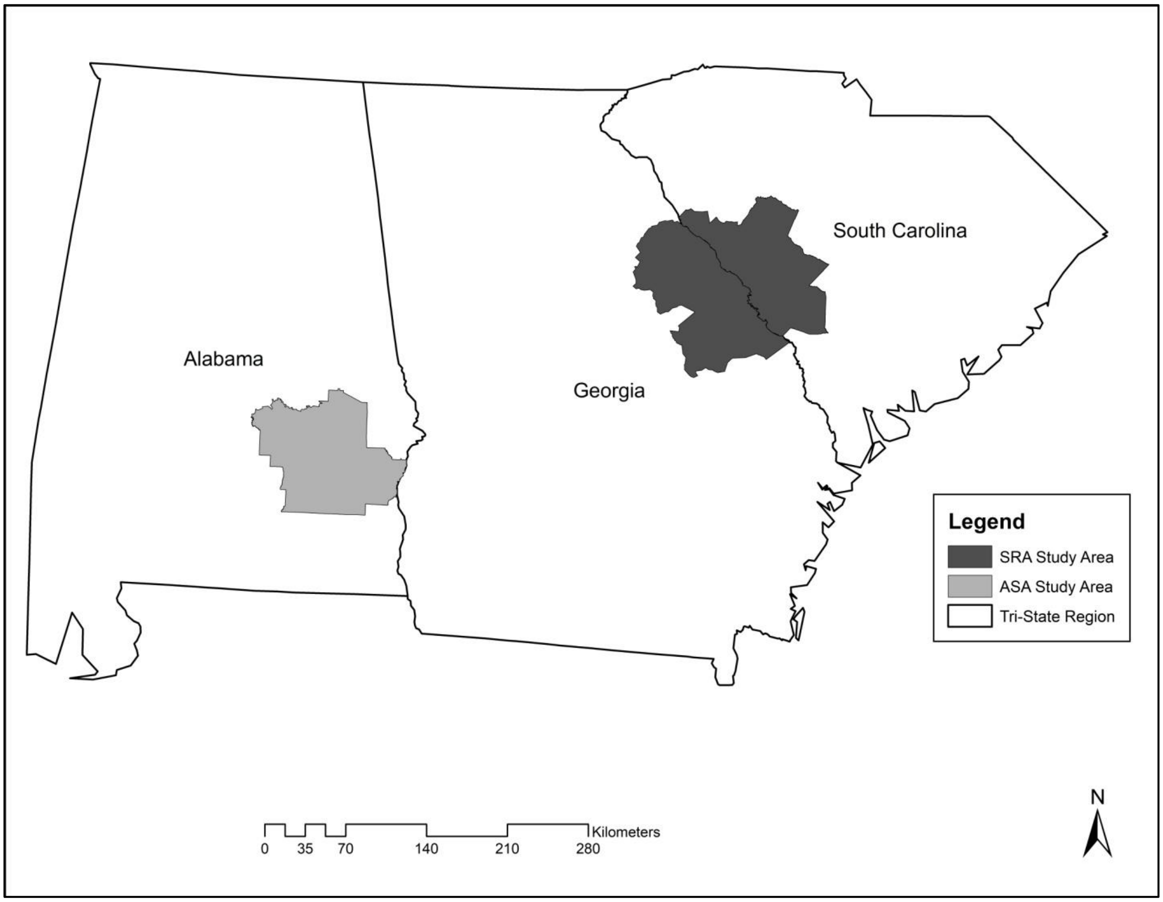
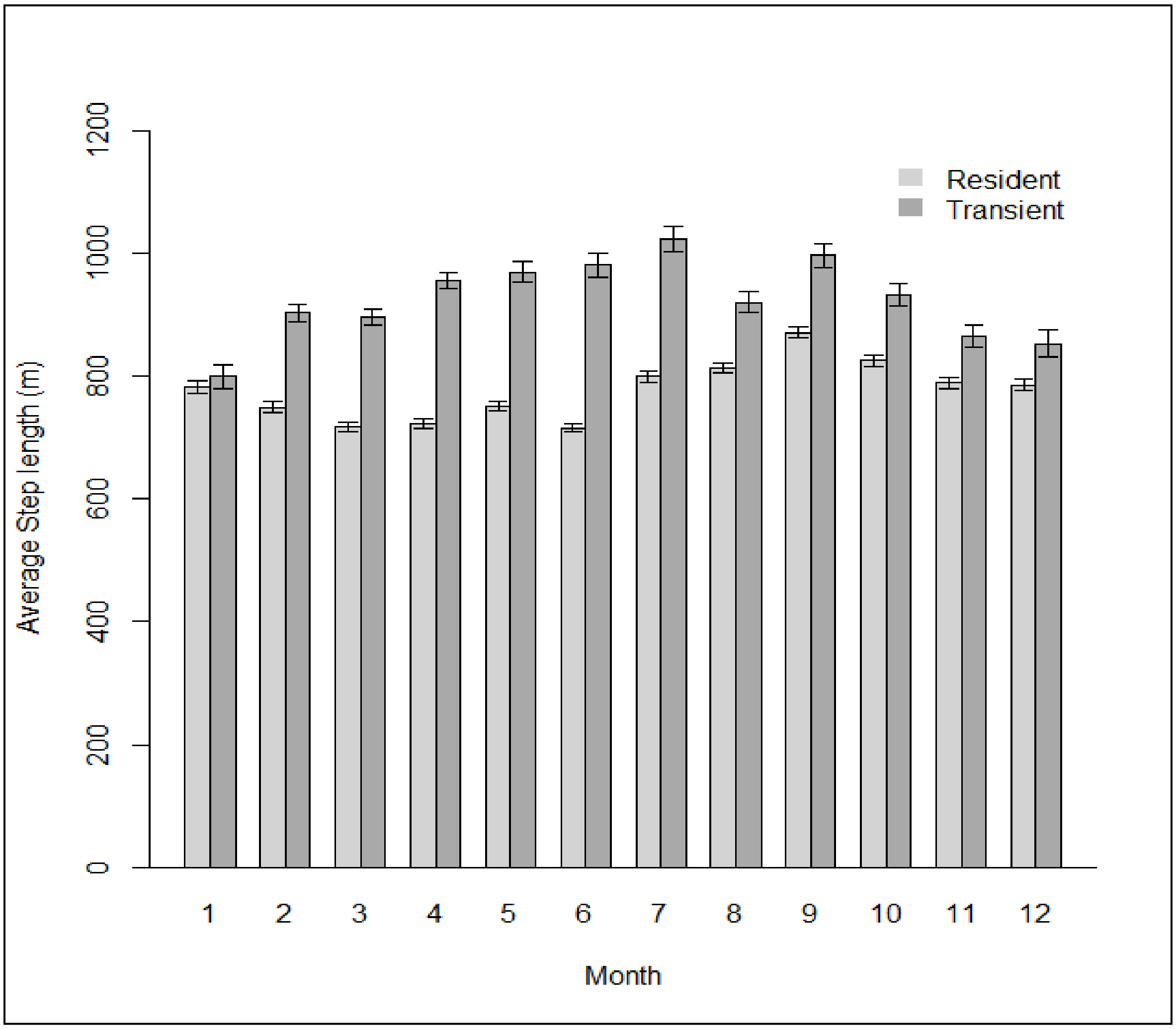


Figure 3.1: The Alabama study area (ASA) and the Savannah River study area (SRA), located in Alabama, Georgia, and South Carolina, USA where coyotes were captured and monitored with GPS collars during 2015 – 2017.

a)


Average Step length (m)
0
200
400
600
800
1000
1200
Resident
Transient
1
2
3
4
5
6
7
8
9
10
11
12
Month

b)

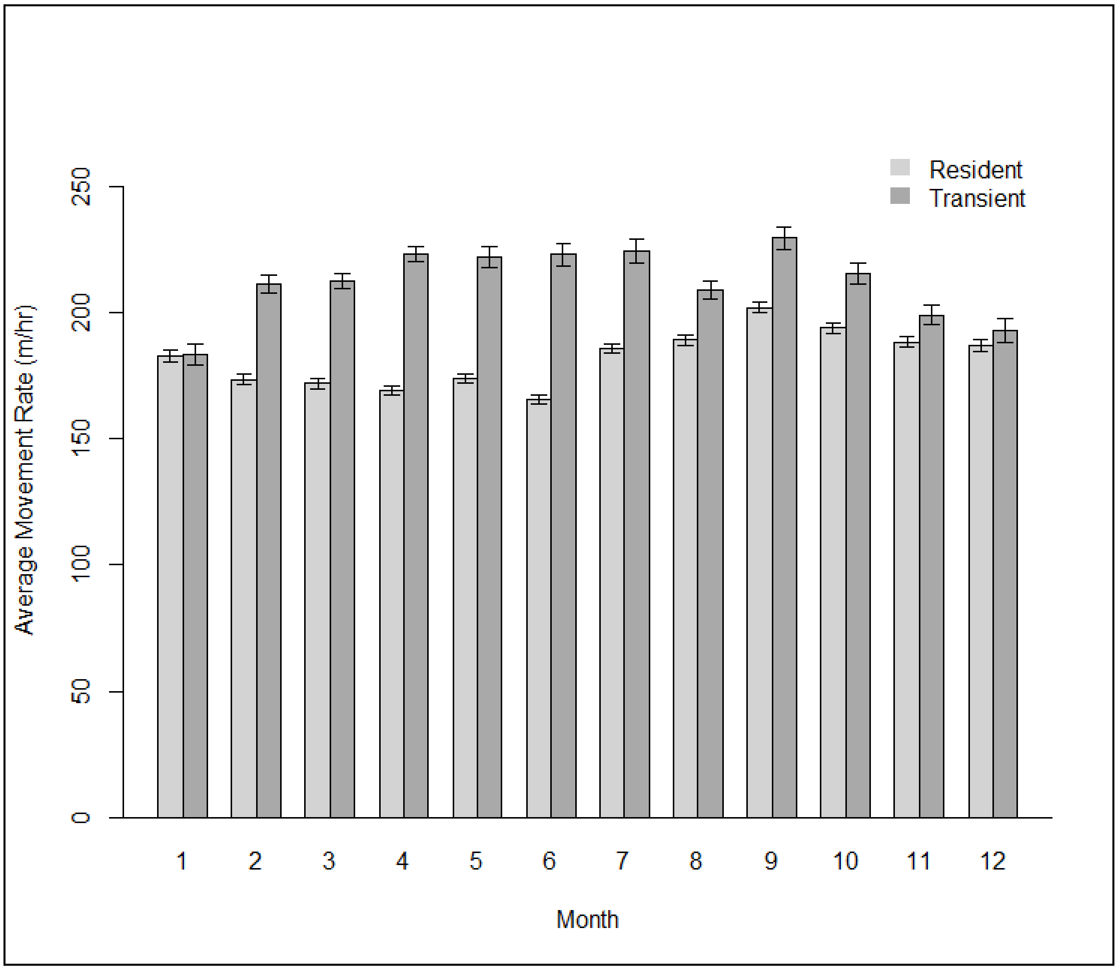


Figure 3.2: Average monthly step length (*a*) and average monthly movement rate (*b*) for resident and transient coyotes monitored from January 2015 – June 2017 in the tri-state region of Alabama, Georgia, and South Carolina. Error bars shown represent standard error.

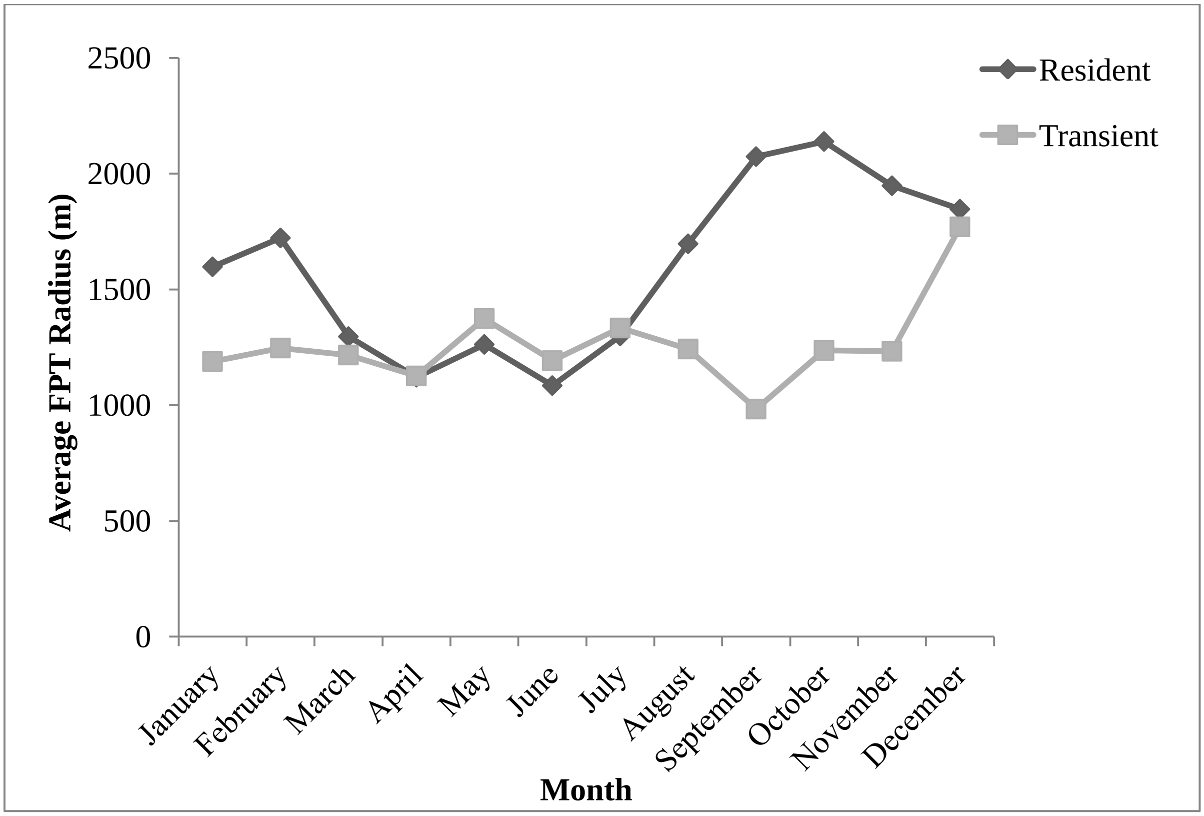


Figure 3.3: Average estimated radius at which First Passage Time (FPT) values were calculated each month for resident and transient coyotes in the tri-state region of Alabama, Georgia, and South Carolina.

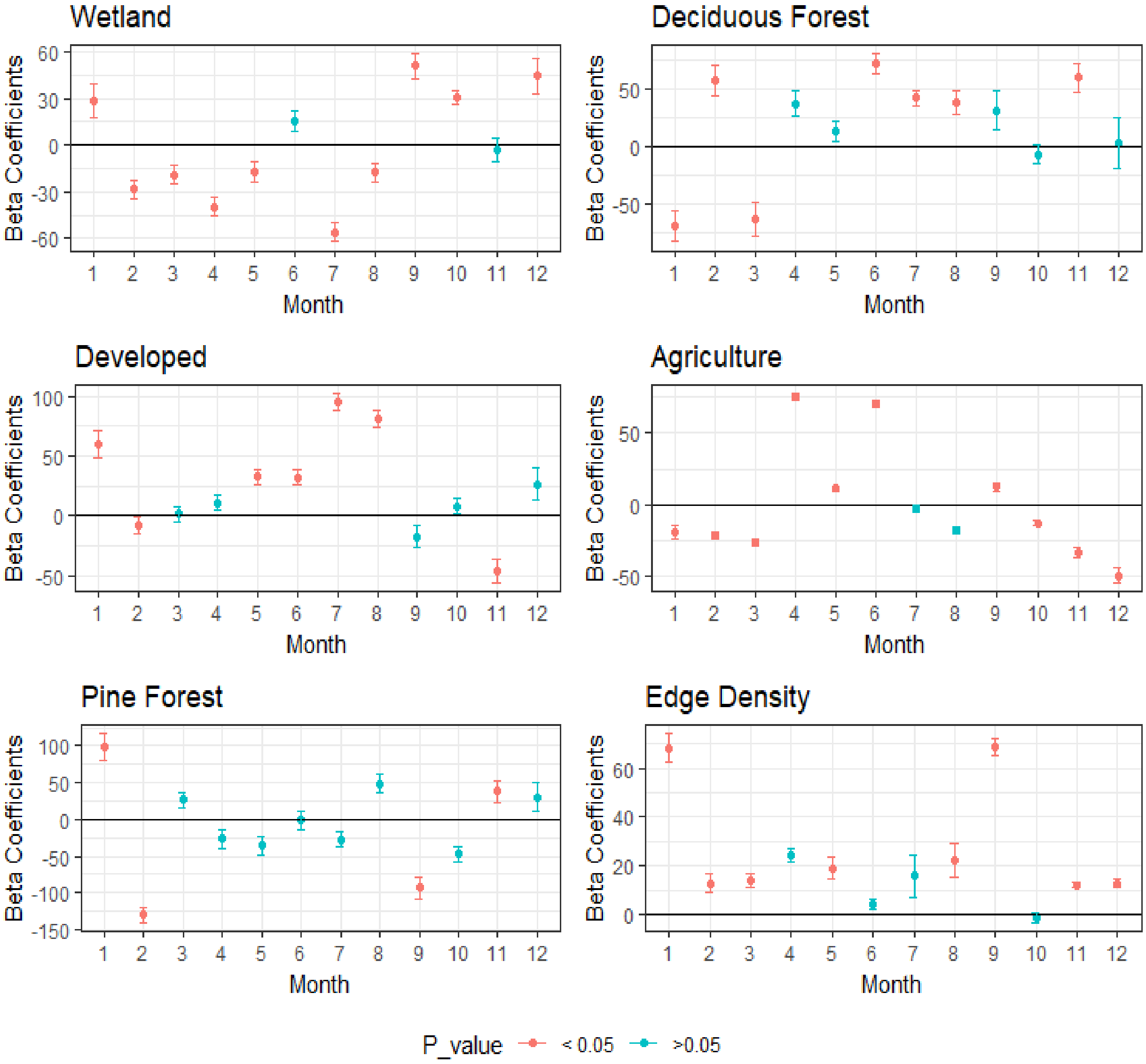


Figure 3.4: Beta coefficient estimates of habitat selection for resident coyotes monitored from January 2015 – June 2017 in the tri-state region of Alabama, Georgia, and South Carolina. Error bars shown represent standard error.

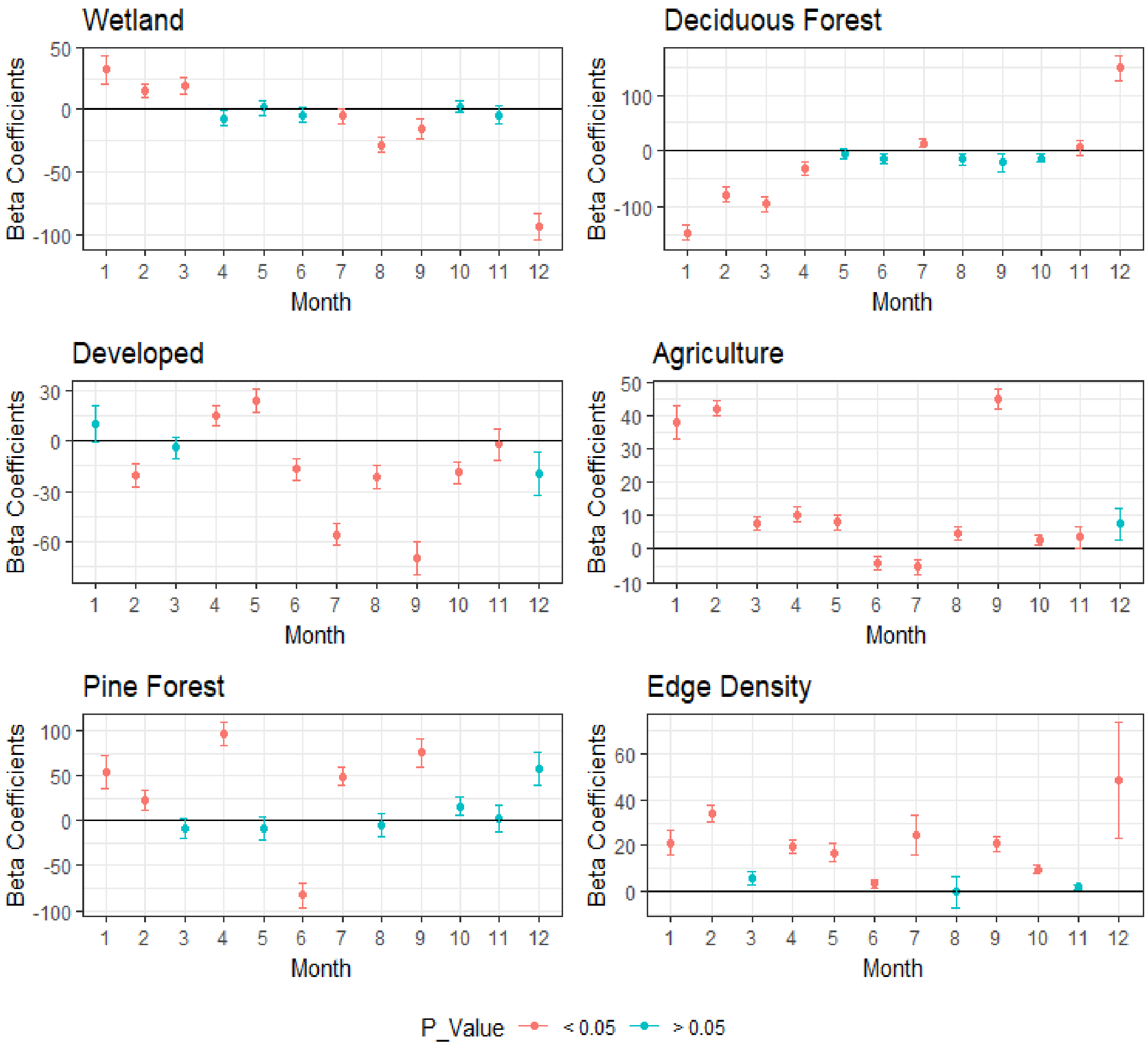


Figure 3.5: Beta coefficient estimates of habitat selection for transient coyotes monitored from January 2015 – June 2017 in the tri-state region of Alabama, Georgia, and South Carolina. Error bars shown represent standard error.

CHAPTER 4

DIETARY PARTITIONING OF RESIDENT AND TRANSIENT COYOTES (*CANIS LATRANS*) IN THE SOUTHEASTERN UNITED STATES

Webster, S.C., Chamberlain, M.J., Hinton, J.W., and Beasley, J.C. To be submitted to *Journal of Mammalogy*.

Abstract

For many species, the relationship between space use and diet composition is complex, with individuals adopting varying space use strategies such as territoriality to facilitate resource acquisition. Coyotes (*Canis latrans*) exhibit two disparate strategies of space use, either defending a mutually exclusive home range (resident) or moving nomadically across a landscape (transient). Resident coyotes have increased access to food resources, thus increasing foraging success while minimizing energetic costs of movement. Conversely, transients do not defend home ranges and are able to redirect energetic costs of home range defense into movement and/or foraging. These differences in space use attributed to different behavioral strategies likely influence foraging and ultimately diet composition, but these relationships have not been well studied. We investigated diet composition of resident and transient coyotes in the southeastern U.S. by pairing individual space use patterns with analysis of stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) to assess diet. During 2016-2017, we monitored 48 coyotes (22 residents, 26 transients) with GPS transmitters in the southeastern U.S. We also collected guard hair samples from all monitored coyotes, and quantified stable isotopes of ^{15}N and ^{13}C to assess diet breadth and composition. We found that transient coyotes consumed greater proportions of anthropogenic foods (39.0%) compared to residents (14.4%), and transient diet composition varied considerably among individuals. Resident diets were primarily comprised of white-tailed deer (30.6%) and rodents (43.0%). Our results suggest territorial status of coyotes influences niche space and diet composition. Although high levels of variation in diet composition are unsurprising given the generalist nature of

coyotes, our findings suggest that patterns of variation in diet are unique between resident and transient coyotes.

Introduction

Space use and diet composition are inextricably linked, with movement patterns influencing the diversity and abundance of food resources available for consumption (Mills and Knowlton 1990; Fedriani et al. 2001; Bracis et al. 2015). For example, physiological, morphological, and behavioral constraints on mobility can limit an individual’s access to food resources, especially in systems where density and distribution of resources vary temporally (Ydenberg and Krebs 1987; Breuner and Hahn 2003; Höner et al. 2004; Shipley 2007; Bracis et al. 2015; Brandt et al. 2015). In many species, behavioral adaptations to individual space use such as territoriality have evolved to facilitate resource acquisition, and territoriality can influence foraging success in varying ways (Kacelink et al. 1981; Waser 1981; Ydenberg and Krebs 1987). In some species, energetic trade-offs exist between territorial defense and foraging success, with individuals sacrificing food intake for territorial vigilance (Kacelink et al. 1981; Ydenberg and Krebs 1987). Conversely, territorial defense also can mitigate competition for food resources and lead to increased memory of resource distribution within a territory, thus increasing foraging success within territories (Gese et al. 1996; Gese 2001; Bracis et al. 2015). Such varied outcomes of the same behavioral strategy speak to the complexity of behavioral adaptations to optimize foraging, and show the need to further elucidate the relationship between space use strategies and diet.

Coyotes (*Canis latrans*) are a generalist carnivore with highly variable space use and a wide diet breadth (Holzman et al. 1992; Gompper 2002; Hinton et al. 2015; Ward et al. 2018). Within a population, coyotes exhibit two disparate strategies of space use, either defending a mutually exclusive home range (referred to as residents) or moving nomadically across a landscape as a transient (Bekoff and Wells 1986; Kamler and Gipson 2000). Residents typically use less space than transients but both groups exhibit seasonal differences in movement behaviors (Kamlet and Gipson 2000; Hinton et al. 2015; Webster Chapter 3). Because of their spatial fidelity, resident coyotes have increased access to food resources, thus increasing foraging success while minimizing energetic costs of movement (Bekoff and Wells 1981, 1986; Gese et al. 1996). Conversely, transients do not defend home ranges, and are thought to be able to redirect energetic costs of home range defense into movement and/or foraging (Bekoff and Wells 1981, 1986). These differences in space use attributed to different behavioral strategies likely influence foraging and diet composition, but the relationship between the two remains ambiguous.

Several studies have investigated prey selection of resident and transient coyotes by examining stomach or scat contents, which provide short term data of what an individual recently ingested (Gara 1986; Klare et al. 2011; Morin et al. 2016). Further, previous studies that quantified both diet composition and territorial status for the same individuals used methods that relied on collecting samples from within defined home ranges, limiting sample collection to only resident animals (Hinton et al. 2017; Ward et al. 2018). Thus, diet breadth of transient coyotes in the Southeast, and differences between resident and transient diet breadth, remain uncertain. One approach to quantify diet breadth and composition of both residents and transients is to couple space use patterns with analysis of stable isotopes of nitrogen (^{15}N) and carbon (^{13}C) for individual coyotes. Analysis of stable isotopes of ^{15}N and ^{13}C in animal tissues is a well established method to infer diet composition and breadth of carnivore species (Bearhop et al. 2004; Caut et al. 2006; Murray et al. 2015; Newsome et al. 2015). When paired with individual metrics of space use, stable isotope analysis allows researchers to effectively quantify diet composition for individuals exhibiting different space use strategies (i.e., resident vs. transient; Newsome et al. 2015).

Using stable isotope analyses of nitrogen and carbon coupled with space use of sampled individuals, we compared diet overlap and composition of resident and transient coyotes in the Southeast United States. We predicted 1) resident and transient coyote diet breadth would overlap substantially, but that transient coyotes would have enriched nitrogen and carbon isotopes relative to residents, indicating increased consumption of anthropogenic foods and 2) resident coyotes would have higher proportions of white-tailed deer in their diets than transients.

Methods

Study Area

Our study area was comprised of approximately 16,200 km^2 of private and public lands across Alabama (Barbour, Bullock, Macon, Montgome and Pike Counties), Georgia (Columbia, Jefferson, Lincoln, McDuffie, and Warren Counties), and South Carolina (Aiken, Barnwell, Edgefield, McCormick, and Saluda Counties) in the southeastern United States (Figure 1). Coyotes captured in Georgia and South Carolina commonly moved between the respective study areas, and likely represented one population, leaving two distinct study areas: the Alabama study area (ASA) and the Savannah River study area (SRA). Both study areas had mild sub-tropical climate throughout the year. Summers were generally hot and humid with an average high temperature of 20°C, while winters were mild with an average low temperature of 1°C (NOAA 2018). Habitats in both the ASA and the SRA were a mix of successional forest, agricultural, pastureland, managed pine forests, and urban habitats. Agriculture in these regions primarily included cotton (*Gossypium spp.*), corn (*Zea mays*), tobacco (*Nicotiana tabacum*), soybeans (*Glycine max*), and peanuts (*Arachis hypogaea*).

Data Collection

To assess coyote space use, we deployed GPS collars on coyotes during 2016 and 2017. We captured animals with foothold traps (Victor #3 Softcatch, Woodstream Corporation, Lititz, Pennsylvania, USA; MB 550 or MB 450, Minnesota Trapline Products, Pennock, Minnesota, USA) with offset or padded jaws. During 2016, animals were restrained with a catchpole, muzzle, and hobbles for processing. During 2017, animals were anesthetized prior to processing using a Ketamine/Xylazine mixture administered intramuscularly at 0.8 mg/kg for Ketamine and 0.1 mg/kg for Xylazine. Each animal was fitted with a mortality-sensitive satellite collar (either G2110E Iridium collar, Advanced Telemetry Systems, Isanti, Minnesota, USA or Litetrack Iridium collar, Lotek Wireless Inc., New Market, Ontario, Canada) set to record locations at a 4-hour interval. We also collected hair samples to determine diet breadth by clipping 10-20 guard hairs from the withers (i.e., area in between the shoulder blades) of each individual. We stored hair samples in paper envelopes in a climate controlled facility until the time of analysis. Prior to release, anesthetized animals were administered Yohimbine at 1.0

mg/kg. All animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (protocols A2014 08-025-R2 and A2015 05-004-A5).

We used samples from coyotes and potential food sources to determine diet breadth of resident and transient coyotes with stable isotope analysis of Nitrogen ($\delta^{15}N$) and Carbon ($\delta^{13}C$). Nitrogen is generally interpreted as an indicator of trophic level, whereas carbon is generally inferred as assimilation of C4 vegetation (either native or anthropogenic in nature; DeNiro and Epstein 1978; DeNiro and Epstein 1981). Comparing isotope enrichment among individual consumers allows researchers to understand diet breadth and, when incorporating isotope data from potential food sources, allows for estimation of diet composition (Bearhop et al. 2004; Caut et al. 2006).

Determining diet breadth for a population of interest can be challenging, especially if diet composition changes seasonally like it does for coyotes (Schrecengost et al. 2008; Swingen et al. 2015; Ward et al. 2018). While hair is an effective indicator of stable isotope values for terrestrial mammals, it is important to note that hairs only indicate stable isotope accumulation during the time period the hair is metabolically active (i.e., growing; Newsome et al. 2010). For canid species, hair provides data on diets of individuals since their last molt period, typically the spring/summer months of April – September in North America (Castelló 2018). Thus, stable isotope values from canid hair samples can be thought to represent summer diet breadth.

To estimate proportional contributions of food items to coyote diets, we identified potential food items commonly consumed by coyotes in our study region from the literature (Schrecengost et al. 2008; Murray et al. 2015; Ward et al. 2018), from which we collected samples to derive stable isotope estimates. We targeted items typically consumed during summer to correspond to the time period relevant to our coyote hair samples. Potential food source groups included: white-tailed deer (*Odocoileus virginianus*), rodents (cotton rat [*Sigmodon hispidus*], Southern flying squirrel [*Glaucomys volans*]), native fruit (persimmon [*Diospyros virginiana*], blackberry [*Rubus* spp.]), and anthropogenic food (represented by human isotope values, see below). We collected deer and cotton rat hair samples from legally harvested or road killed individuals in Aiken County, South Carolina, and Oglethorpe and Athens-Clarke Counties, Georgia. Flying squirrels were opportunistically live trapped using Sherman traps (H.B. Sherman Traps, Inc. Tallahassee, Florida, USA) in Athens-Clarke County, Georgia. Hair samples from all prey species were collected by clipping hairs from the withers (i.e., area between the shoulder blades) of each animal. All animal handling procedures for rodents were approved by the University of Georgia Institutional Animal Care and Use Committee (protocol A2018 06-024). Blackberry and persimmon samples were collected on private farms in Oglethorpe County, GA. We stored samples in plastic storage bags, with hair samples stored at room temperature and fruit samples in a -20°C freezer until analysis.

To represent assimilation of anthropogenic food resources, we compared coyote hair isotopes to previously published isotope values for North American human hair samples (Nardoto et al. 2006; Newsome et al. 2010; Newsome et al. 2015). We averaged isotopic enrichment values from multiple studies, and thus included samples that were collected in different regions (California, Illinois, and Utah) than where we sampled coyotes. This could lead to increased variation or inaccuracy of modeled isotopic enrichment values relative to actual enrichment of anthropogenic foods in the Southeast U.S. (Hulsemann et al. 2015). However, all isotopic values for assimilated human diet fell within a narrow range (-17.5 – -18.8‰ δ^{13}C and 8.8 – 9.4‰ δ^{15}N). Similar isotopic enrichment of human samples, despite differences in collection locations, likely reflects how U.S. commercial food systems operate on a national and/or international scale (Harlan, J.R. 1975), with food products being transported throughout the country. Large-scale food production and industry have led to similar availabilities of different anthropogenic foods and ultimately a relatively homogenous food supply across different regions (Jahren and Kraft 2008; Khoury et al. 2014). Given the homogeneity of human diets across regions, we feel confident that anthropogenic food items likely have similar isotopic enrichment regardless of the region in which they were consumed by humans or wildlife.

Movement Data Analysis

To determine territorial status of collared animals, we used a combination of estimated monthly home range size (Kamler and Gipson 2000) and a rarefaction curve of space use for each animal created by calculating monthly home ranges (see Dellinger et al. 2013). We used fixed kernel density estimators to calculate monthly home ranges in R (R Core Team 2018) using the “href” smoothing parameter and ArcMap 10.3 (Environmental Systems Research Institute. ArcMap 10.3. ESRI, Redlands, California). Resident coyotes were animals that showed stable space use for $\geq$ 3 months and had home ranges < 45 km^2 (Kamler and Gipson 2000; Dellinger et al. 2013). We classified transients as animals with home ranges > 45 km^2 and unstable space use over time (i.e., low site fidelity). Using both methods for identifying territorial status allowed for unambiguous classification of residents and transients, but also meant that we were unable to determine territorial status of animals with <3 months of movement data due to mortality or collar failure. For transient animals, space use patterns were not considered home ranges because transients do not maintain territories, instead we referred to them as transient ranges (Hinton et al. 2012).

Diet Breadth Analysis

We prepared all hair samples for stable isotope analysis by first removing any debris or skin from the hair using a sterile surface wipe. Then, using scissors to macerate the hair, we measured 1-2 mg of the sample and packed it into pre-combusted 5×9mm tin capsules (Costech Analytical Technologies Inc., Valencia, California, U.S.A.). For fruit samples, we first freeze-dried and homogenized them using an electric blade grinder. Once homogenized, we measured a 1-2 mg sample and packed it into a tin capsule as above. In addition, we prepared duplicate samples for 10% of samples from each species as a quality control measure. We then sent prepared capsules to the University of Georgia Stable Isotope Ecology Laboratory (SIEL) in Athens, Georgia, USA for isotope ratio analysis of $\delta^{13}C$ and $\delta^{15}N$. Isotope ratio analysis involves transformation of solid-phase samples to gas phase by extremely rapid and complete flash combustion of the sample material. The ionized combustion product is then mass analyzed by means of differing mass/charge ratios among the various isotopic species of CO_2 and N_2. The SIEL used standards in each analysis for QAQC as well as calculating $\delta^{13}C$ and $\delta^{15}N$ (the difference between a sample and natural abundance standard for which delta = zero; reported in parts per thousand) with air being the standard for nitrogen analyses and the Chicago PDB Marine Carbonate Standard (U.S. National Institute of Standards and Technology, Gaithersburg, Maryland, U.S.A.) for carbon.

We used a multi-faceted approach to determine differences between resident and transient coyote diet breadth and estimate diet composition based on sampled food resources. First, we used linear mixed-effects models (LMM) to determine if differences in $\delta^{13}C$ and $\delta^{15}N$ existed between resident and transient coyotes using the package "nlme" (Pinheiro et al. 2012). In all models, we included territorial status and sex as fixed effects, and sampling location (i.e., study area) as a random effect. We used an alpha value of 0.05 to determine significance in all models. Second, to compare niche structure and overlap between resident and transient coyotes relative to potential food sources, we estimated isotopic niche space for both groups by plotting the isotope values for all coyote hair samples, calculating convex hulls around each group, and then calculating size-corrected standard Bayesian ellipses using package "SIBER" (Jackson et al. 2011). We then computed the total area of each convex hull (TA), sample size-corrected standard ellipse area (SEA_c), and the proportion of overlap of standard ellipses between resident and transient coyotes.

Finally, we estimated the proportional contributions of each food source to resident and transient coyote diet composition using stable isotope analysis in R (SIAR, package "simmr"; Parnell et al. 2010). The SIAR is a Bayesian stable isotope mixing model that uses Markov Chain Monte Carlo (MCMC) methods and accounts for error in estimates of fractionation factors and variation in elemental concentrations of carbon and nitrogen in food sources that could bias model output (Phillips and Koch 2002). Prior to analysis, we corrected for changes in atmospheric CO_2 over the last ~150 years (i.e., the Suess effect; Keeling 1979). Based on core records, we applied a time dependent correction of -0.022‰ per year (Francey et al. 1999). All samples were corrected to reflect 2019 values. Additionally, we applied diet-to-hair fractionation factors developed for red fox (*Vulpes vulpes*) to all food source isotope values (excluding anthropogenic isotope values, which already represented assimilated diet items) by adding 2.6‰ for ^{13}C and 3.2‰ for ^{15}N (Roth and Hobson 2000). Red fox are a generalist canid species with similar diet breadth to coyotes, and the fractionation factors developed for fox have been successfully applied in coyote diet studies previously (Cypher 1993; Reid and Koch 2017). We conducted all statistical analyses in Program R (R Core Team, 2018).

Results

We collected coyote guard hair samples from 63 captured individuals across both study areas, (n = 5 for ASA, n = 58 for SRA). Of those, samples from 61 individuals were successfully analyzed for nitrogen and carbon stable isotopes. We excluded 13 individuals because we could not adequately determine territorial status, leaving 48 individuals included in our analyses. We found that 26 coyotes were transients (52.6%; 10 female, 12 male) and 22 were residents (46.4%; 9 female, 17 male). Resident and transient coyotes occupied similar isotopic niche space (Figure 2), and overlap between standard ellipses of resident and transient coyotes was 64.2% (Figure 3). Linear modeling analysis revealed that transient coyotes had higher levels of $\delta^{15}N$ ($\beta = 1.04$, $t_{(56)} = 2.97$, $P=0.03$) than residents, but they did not differ in the amounts of $\delta^{13}C$ in their diet ($\beta = 0.42$, $t_{(56)} = 0.91$, $P = 0.37$; Figure 2). Isotope values did not differ between sexes ($\beta = 0.33$, $t_{(56)} = 0.79$, $P = 0.43$ for $\delta^{13}C$ and $\beta = 0.37$, $t_{(56)} = 1.18$, $P = 0.2$ for $\delta^{15}N$). When we estimated Bayesian standard ellipses for both groups, transients had greater estimated TA and SEA_c than did residents (TA = 17.83, $SEA_c = 5.96$ for transients and TA = 13.63, $SEA_c = 4.88$ for residents), indicating transients had a broader isotopic niche space.

We analyzed 8 fruit (5 blackberry and 3 persimmon) samples, 3 rodent samples (1 cotton rat and 2 flying squirrel), and 4 white-tailed deer samples (Table 1). The stable isotope mixing model revealed that rodents comprised the greatest proportion of resident coyote diets (43.0 ± 24.0%) followed by white-tailed deer (30.6 ± 22.0%; Table 2, Figure 4). Transient coyote diets were largely comprised of anthropogenic foods (39.0 ± 7.5%), with all other food source groups contributing similarly (18.6 – 23.3% mean contribution, Table 2, Figure 4). When we compared proportional contributions of each food source between resident and coyote diets, we found that residents had a relatively high probability of having greater proportions of deer (60.9%) and rodents (74.3%) in their diets, but had a relatively low probability of having proportionally more fruit (33.7%) or anthropogenic food (1.1%) in their diet compared to transient coyotes (Figure 5).

Discussion

We found that although resident and transient coyote diets during the spring/summer overlapped substantially, proportional contributions of food resources varied. Transients had enriched δ^{15}N relative to residents, likely from consuming greater proportions of anthropogenic foods. Previous work has found that transient coyotes are more likely to use habitats closer to human development (Kamler and Gipson 2000; Newsome et al. 2015; Webster Chapter 3), which can lead to increased encounters with humans and domesticated animals (i.e., livestock, pets; Mitchell et al. 2015). Increased time spent in proximity to humans likely leads to increased foraging opportunities for anthropogenic foods relative to resident coyotes.

It is important to note that we collected coyote hair samples at the time of capture, so these samples reflected diet of the previous summer months when the hairs were last metabolically active (Castello 2018). However, all movement data were collected after capture and hair sampling. Therefore, it's possible that a sampled individual moved from residency to transiency or vice versa between the time period represented by hair samples and the time period in which we monitored movements. We note that previous studies detailing aspects of residency and transiency in coyotes have reported relatively few individuals that changed territorial strategies during monitoring periods of 6-12 months (Bekoff and Wells 1986; Morin and Kelly 2017; Webster Chapter 3). Thus, it's unlikely that a substantial number of individuals were misclassified as either residents or transients in our analyses.

Our findings indicate that both resident and transient coyotes consumed white-tailed deer, although residents consumed a greater proportion of deer relative to transients, supporting our hypothesis that residents consume more deer. Extant literature has detailed use of deer by coyotes throughout the Southeast U.S., via both scavenging and predation, particularly during spring and summer when neonates are available (Schrecengost et al. 2008; Kilgo et al. 2012; Jackson and Ditchkoff 2013; Nelson et al. 2015; Ward et al. 2018). Although coyotes are known to consume adult deer during spring/summer as well (Chitwood et al. 2014; Ward et al. 2018), because fawn density and coyote consumption of fawns is highest during this period (Schrecengost et al. 2008; Ward et al. 2018) it is likely that estimated proportional contribution of deer in both resident and transient diets reflects fawn consumption (Kilgo et al. 2012; Nelson et al. 2015).

Transient coyotes exhibited substantive variation among individuals in the estimated contributions of all potential food sources, suggesting considerable variation in diet among individuals (Figure 4). Specifically, two transient individuals had nitrogen enrichment values that fell outside of two standard deviations from the sample mean. However, removing these two points from analysis did not alter our overall conclusions or the significance of any performed analyses. Given that these outliers were not driving observed trends, and that transients are known to have highly variable diet composition (Klare et al. 2011; Morin et al. 2016), we felt confident including these samples in analyses. The variation we observed in transient diet composition is likely due to nomadic movement patterns of transient coyotes, which leads to greater spatial and temporal variations in prey encounters (Mills and Knowlton 1991; Hinton et al. 2015; Mitchell et al. 2015; Morin and Kelly 2017). Variation in prey encounters thus influences prey availability temporally, and ultimately leads to greater variation in diet composition.

Resident coyotes exhibited high variation in the proportional contributions of rodent and deer to their diet, which corresponds with previous works that have noted considerable individual variation in diet composition among resident coyotes (Gompper 2002; Newsome et al. 2015; Ward et al. 2018), often driven by prey availability (Mills and Knowlton 1991; Hinton et al. 2017). Given the relatively broad spatial and temporal scale at which we sampled coyotes, it’s likely that prey availability of rodents and deer differed across the landscape and may have driven variation in proportional contributions of both food sources to resident coyote diets. However, further research is needed to explicitly quantify variations in prey availability in our study system to better elucidate the underlying factors driving diet variability among resident coyotes. Regardless, our results indicate that territorial status of coyotes influences niche space and diet composition. Although high levels of variation in diet composition are unsurprising given the generalist nature of coyotes (Bekoff and Wells 1986; Gompper 2002), our findings suggest that patterns of variation are unique among resident and transient coyotes.

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Tables and Figures

Table 4.1: Mean and standard deviation (SD) of $\delta^{13}C$ and $\delta^{15}N$ isotopes for common coyote food sources. Samples for all food sources except anthropogenic foods were collected in Georgia and South Carolina, U.S. during 2019. Anthropogenic food values were derived from averaging previously published isotopic values for assimilated human diet (see Nardoto 2006; Newsome et al. 2010; Newsome 2010).

Food Source	$\delta^{13}C$		$\delta^{15}N$	
	Mean	SD	Mean	SD
Fruit	-25.164	1.601	3.77	0.55
Deer	-21.805	0.598	6.418	0.555
Rodent	-21.563	1.312	6.463	1.141
Anthropogenic*	-18.272	0.7	9.03	0.6

Table 4.2: Estimates of mean and standard deviation (SD) of proportional contributions of potential food sources to diets of resident and transient coyotes from Alabama, Georgia, and South Carolina, U.S. during 2016-2017.

Food Source	Residents		Transients	
	Mean	SD	Mean	SD
Fruit	0.120	0.082	0.186	0.091
Deer	0.306	0.220	0.209	0.132
Rodent	0.430	0.240	0.233	0.145
Anthropogenic	0.144	0.065	0.390	0.075

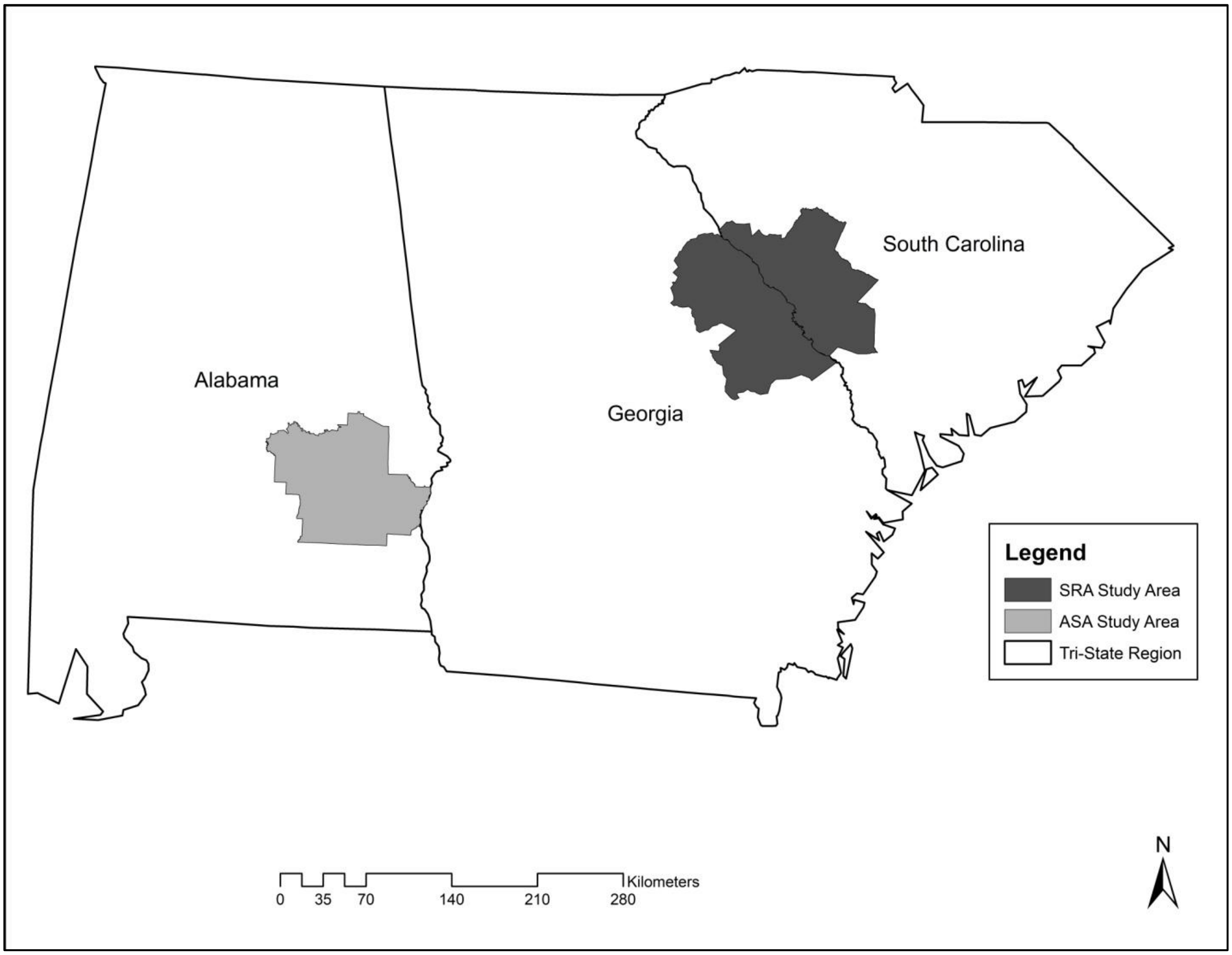


Figure 4.1: Alabama study area (ASA) and the Savannah River study area (SRA), located in Alabama, Georgia, and South Carolina, U.S. where we sampled coyotes for isotopic enrichment of carbon and nitrogen and estimated coyote space use during 2016-2017.

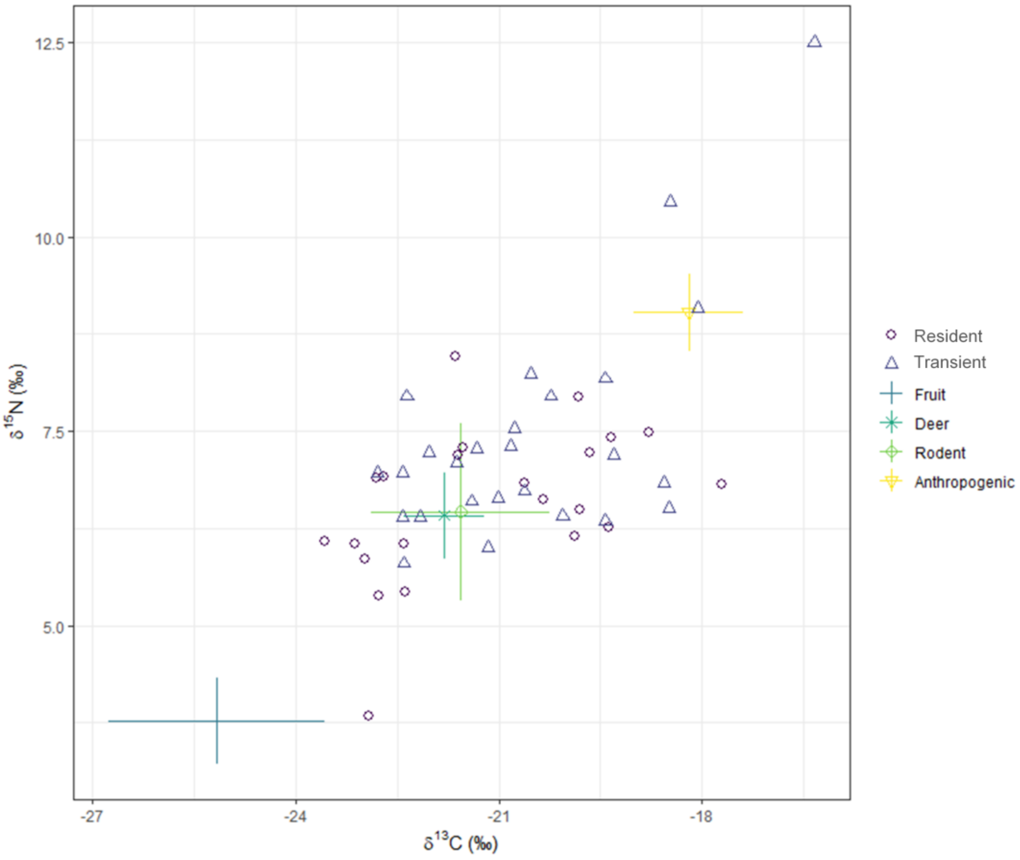


Figure 4.2: δ^{13}C and δ^{15}N values of resident and transient coyotes in Alabama, Georgia, and South Carolina, U.S. during 2016-2017. Also depicted is the estimated isospace (i.e., mean and standard deviations) of potential food items.

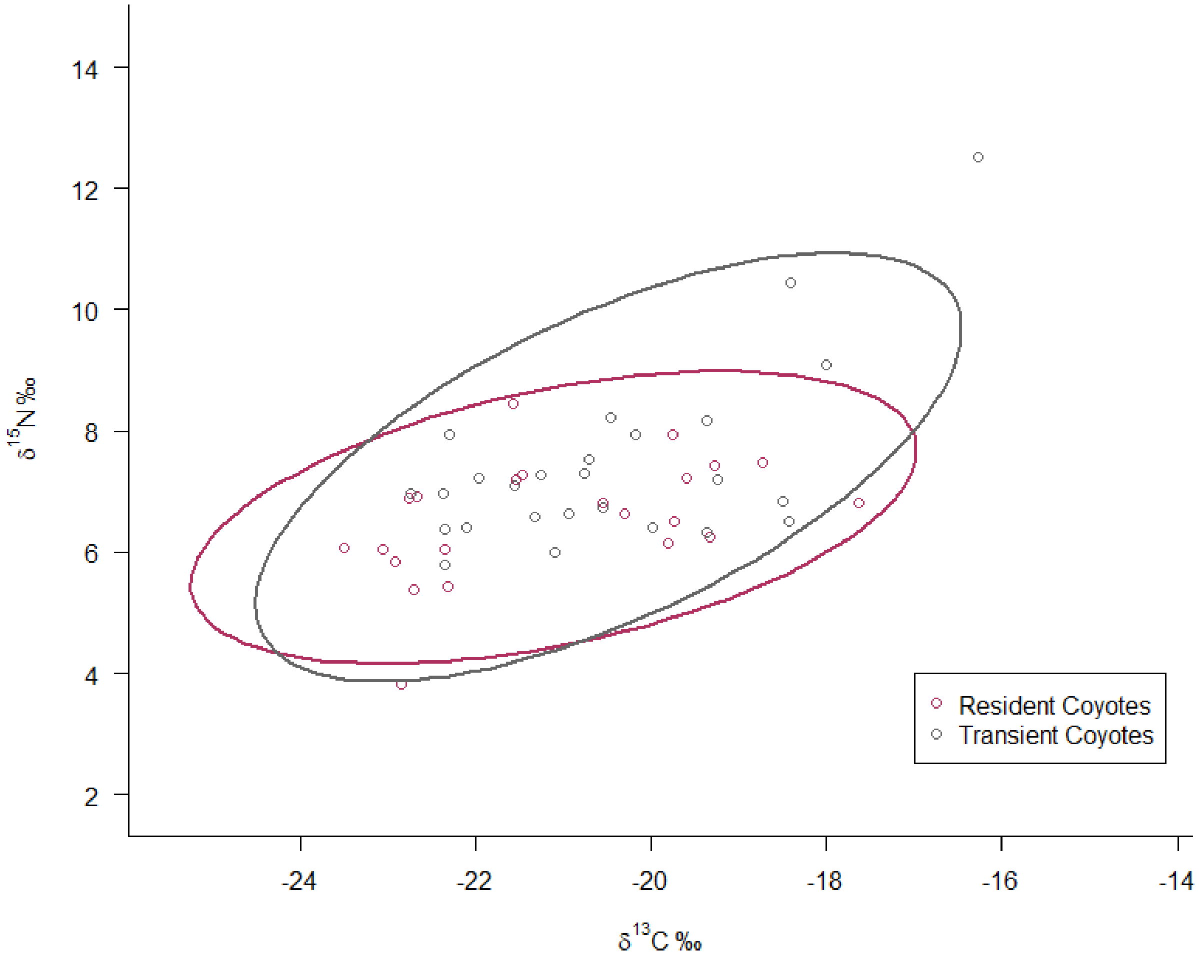


Figure 4.3: δ^{13}C and δ^{15}N values and estimated Bayesian standard area ellipses (SEA$_c$) of isotopic niche space for resident and transient coyotes in Alabama, Georgia, and South Carolina, U.S during 2016-2017.

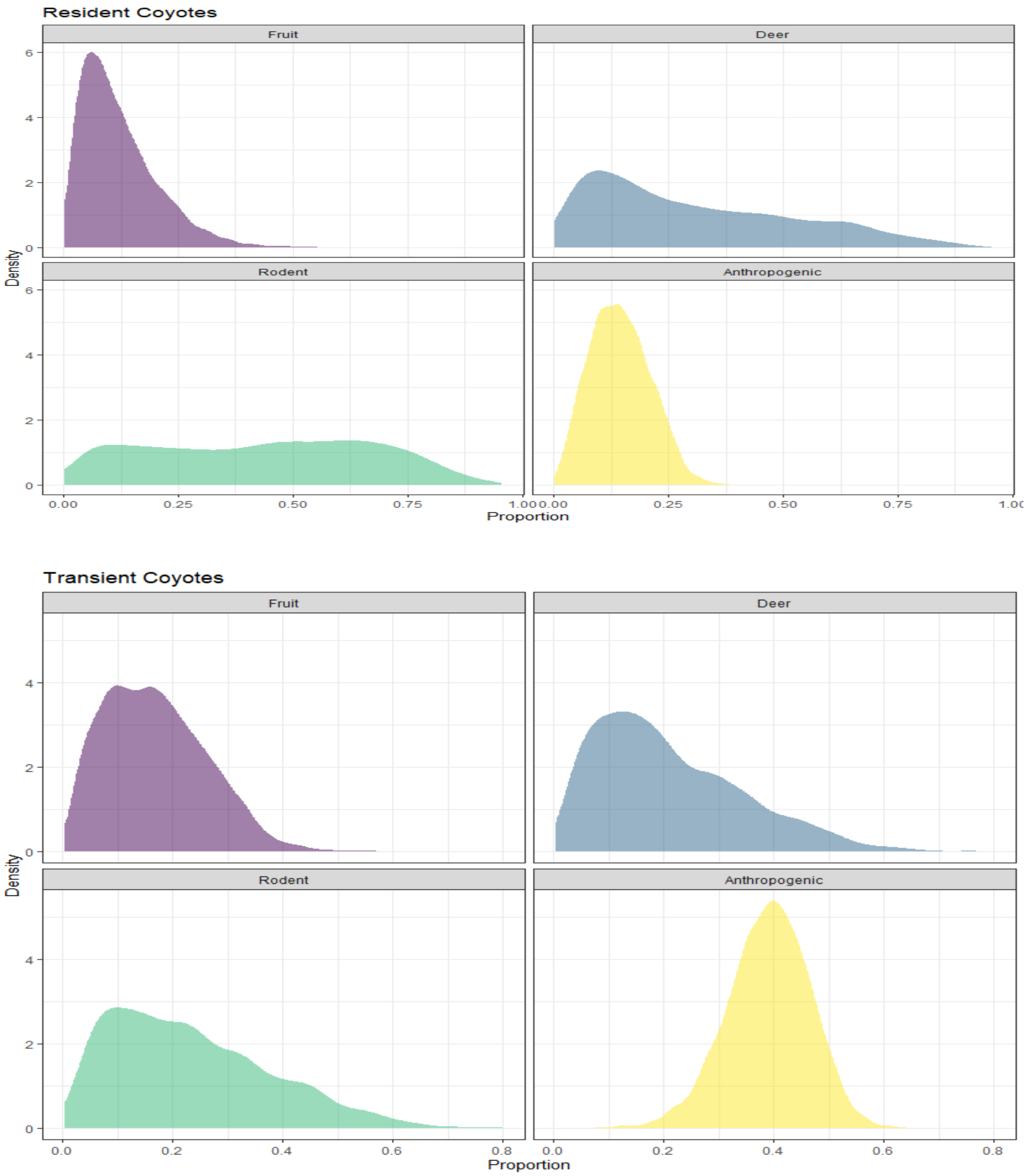
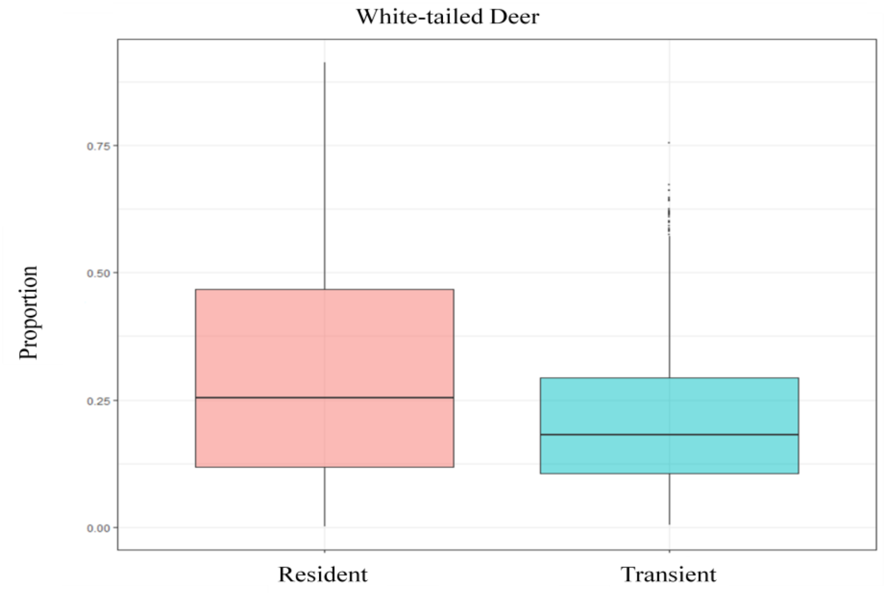
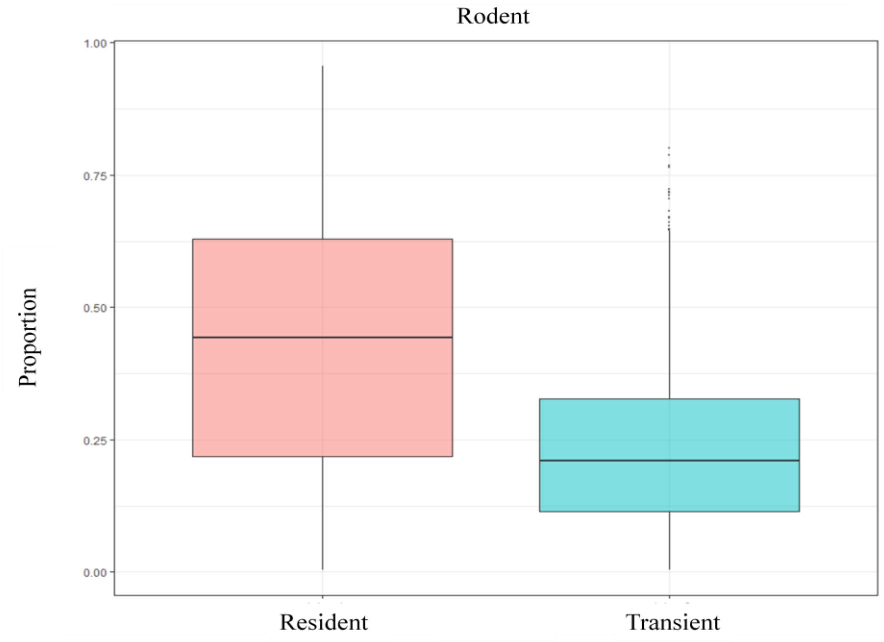


Figure 4.4: Estimated density distribution of proportions of food items in resident and transient coyote diets in Alabama, Georgia, and South Carolina, U.S. during 2016-2017.


White-tailed Deer
Proportion
0.00
0.25
0.50
0.75
Resident
Transient


Rodent
Proportion
0.00
0.25
0.50
0.75
1.00
Resident
Transient

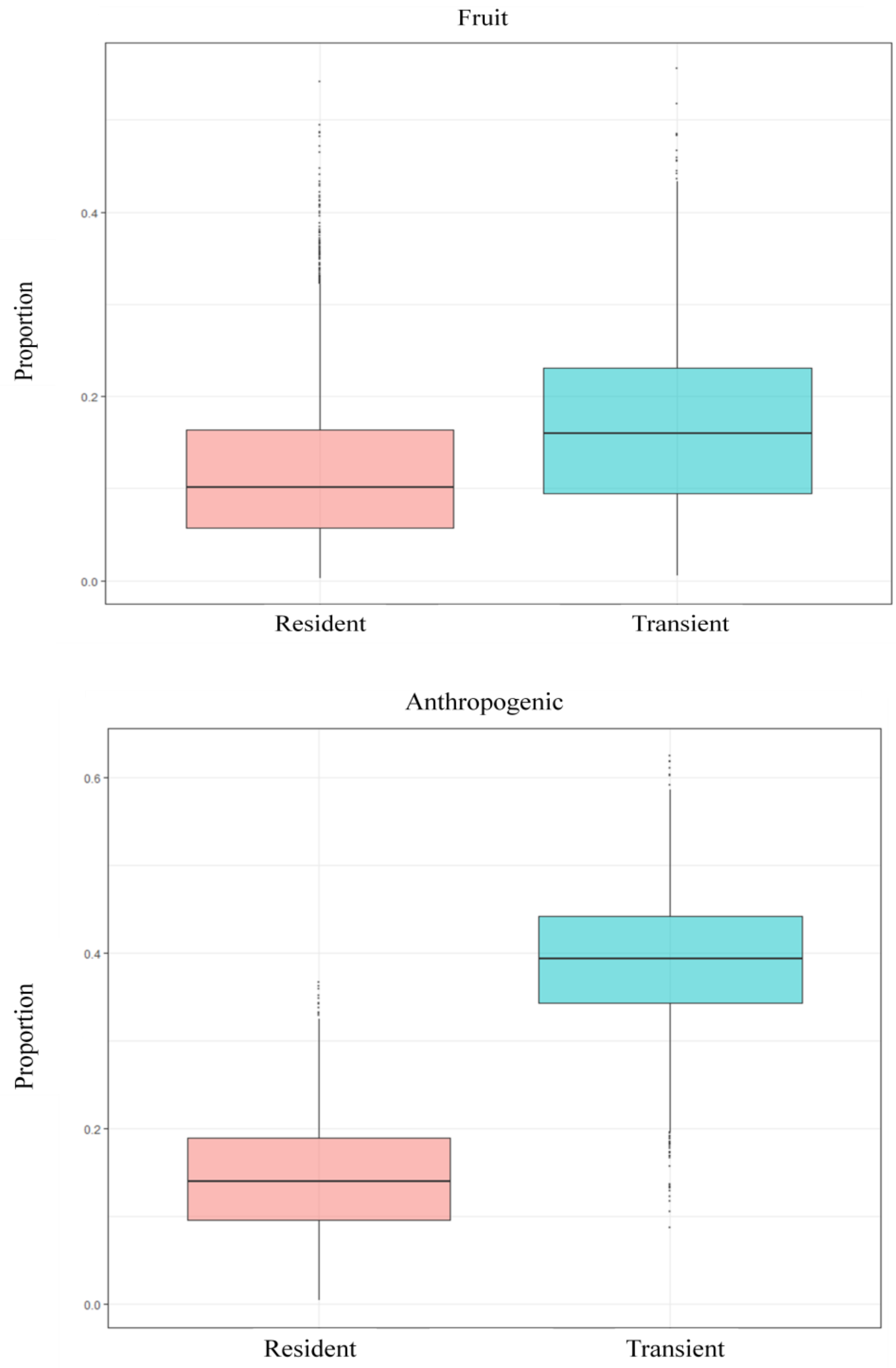


Figure 4.5: Comparisons of estimated proportional contributions of white-tailed deer, rodents, fruit, and anthropogenic foods to the diet of resident and transient coyotes in Alabama, Georgia, and South Carolina, U.S during 2016-2017.

CHAPTER 5

ISOTOPE ANALYSIS REVEALS DIETARY OVERLAP AMONG SYMPATRIC CANIDS

Webster, S.C., Chamberlain, M.J., Hinton, J.W., and Beasley, J.C. Submitted to *Journal of Mammalogy*, 3/15/20.

Abstract

When colonizing new regions, non-native species will interact and compete with native species, eventually leading to coexistence via resource partitioning or displacement via competitive exclusion. In the Southeast U.S., coyotes (*Canis latrans*) compete with red fox (*Vulpes vulpes)* and gray fox (*Urocyon cinereoargenteus*), although it remains unclear if competition is leading to partitioning or displacement among species. Using nitrogen and carbon stable isotopes, we tested the hypothesis that coyotes compete with foxes for food resources, but native canids partition food resources to mitigate this competition. We compared these data to data from the Plains region of the U.S., where all three species have been sympatric for centuries. We analyzed 217 hair samples from both regions pre-1960, prior to coyote colonization of the Southeast, and post-2000 after coyotes were ubiquitous and assessed differences among species, regions, and time periods. Modeling revealed significant diet overlap among historic and contemporary populations in the Southeast. In the Plains, all species historically partitioned resources. Contemporarily, Plains red fox and coyotes overlap in diet; however, gray fox have increased partitioning from the other species. Absence of food resource partitioning indicates interspecific competition between Southeast coyotes and fox. Further research is needed to determine if other mechanisms of partitioning may be occurring, and what long term consequences of interspecific competition may emerge for Southeast carnivore populations.

Introduction

Resource partitioning, particularly of food resources, is an important ecological phenomenon to mitigate resource depletion and possible competitive exclusion among species (Abrams 1986; Schluter 2000; Adams 2004; Northfield et al. 2010). Resource partitioning has the potential to increase fitness, promote coexistence, stabilize population sizes, and improve ecosystem function (Roughgarden 1976; Kahmen et al. 2006; Finke and Synder 2008). Mechanisms that drive resource partitioning, both intraspecific and interspecific, have been described in various fauna and flora and typically include morphological and genetic variations among species that differentiate the metabolic needs of competing populations (Brown 1981; Grace and Wetzel 1981; (Toft 1985; Winemiller 1989; Mangla et al. 2011). In particular, interspecific competition is thought to be a common driver of resource partitioning, and may ultimately determine niche breadth of populations (reviewed in Schluter 2000).

Interspecific competition often occurs after introduction of new, sometimes non-native or invasive, species to an area where they compete with already established populations for finite resources (Fritts and Rodda 1998; Stewart et al. 2002; Vila and Weiner 2004). Species can become established in a new ecosystem via introduction (either directly or indirectly by humans) or natural shifts in range (Sakai et al. 2001; Angert et al. 2011). As new species become established, they compete with native populations for finite resources, eventually leading to resource partitioning or competitive displacement among co-occurring species (Stewart et al. 2002; Gurnell et al. 2004; Mangla et al. 2011). Although some examples of resource partitioning have been well described (Schoener 1974; Diamond 1978; Grace and Wetzel 1981), due to the relatively slow moving nature of ecological processes, researchers rarely quantify the influence of ecological processes on creating partitioning as it occurs. Rather, researchers are typically limited to observing species differences, character displacements, and post-competitive niche overlap of established sympatric populations (Schoener 1974; Diamond 1978; Grace and Wetzel 1981). As large-scale patterns of change (e.g., globalization, climate change, habitat loss, etc.) influence ecosystem form and function on ever broadening scales, scientists are observing greater frequency of natural and anthropogenic introductions and range changes of species (Hellmann 2008; Hulme 2009). Evidence of interspecific competition and potential resource partitioning may be most pronounced at the frontiers of these changing range limits, where species are attempting to or have recently established populations (reviewed in Sexton et al. 2009), providing opportunities to quantify how introduced competition may drive resource partitioning as it occurs.

The Southeast United States has been recently colonized by coyotes (*Canis latrans*), with coyotes considered established throughout the region by 2000 (Hody and Kays 2018, Hinton et al. 2019). Several species of smaller mesocarnivores, including red fox (*Vulpes vulpes*) and gray fox (*Urocyon cinereoargenteus)*, were already established throughout the region prior to the coyote's arrival. Despite co-existence in other regions of North America (Harrison et al. 1989; Cypher 1993; Neale and Sacks 2001), fox populations in the southeastern United States (hereafter Southeast) are newly sympatric with coyotes and are known to use similar habitats (Chamberlain and Leopold 2005). This recent sympatry among canids in the Southeast provides a unique opportunity to investigate and describe ecological processes of interspecific competition that drive resource partitioning as it occurs. Coyotes, which are highly adaptable generalists, consume prey items such as small mammals, lagomorphs, and even ungulates like white tailed deer (*Odocoileus virginianus*), a diet that overlaps with fox and other native carnivore species (Major and Sherburne 1986; Cypher 1993; Cherry et al. 2016; Ward et al. 2019). Additionally, coyotes use a variety of habitats, and are known to exhibit overlapping space use with both red and gray fox (Gosselink et al. 2003; Chamberlain and Leopold 2005), increasing potential for depletion of prey resources in areas where these species co-occur. Although potential impacts of coyotes on prey populations have been well studied (Rollins and Carroll 2001; Kilgo et al. 2010; Cherry et al. 2016), there is a paucity of information regarding long term impacts of diet overlap with other canid populations in the Southeast.

Using analyses of nitrogen and carbon stable isotopes, we compared diet overlap of coyotes, red fox, and gray fox within the Southeast, where coyotes have recently established, to populations in the Plains region where all three species have been sympatric for well over a century (Sargeant et al. 1987; Cypher 1993). To account for naturally occurring shifts in diet over time, we analyzed samples from each population from the time period prior to coyote colonization of the Southeast (mid 19th century – 1960) and the period after coyotes were ubiquitous (2000–2018). We tested the hypotheses that 1) newly established coyote populations in the Southeast overlap in diet breadth with both fox species, 2) prior to coyote colonization, gray and red fox partitioned resources in the Southeast, 3) in the Plains region long-term coexistence has resulted in dietary resource partitioning among all three species, and 4) coyotes have greater amounts of $\delta^{13}C$ and $\delta^{15}N$ than fox in both regions sampled.

Methods

Sample Areas and Collection

We collected hair samples from red fox, gray fox, and coyotes from two regions of the U.S.: the Southeast and the Plains (Fig 1). For both regions, we focused our collection efforts over as narrow a spatial extent as practically possible, given the availability of historical specimens, to mitigate expected natural variation in diet due to differences in environmental characteristics. We then delineated two time periods of interest: historic samples prior to coyote colonization of the Southeast and contemporary samples from post-coyote colonization. We limited our historical time period to samples collected prior to or in 1960. Although delineating exactly when coyotes began to colonize the Southeast have proven difficult, previous research suggests that colonization into areas where our sampling efforts were focused occurred after 1960 (Hinton et al. 2019). Coyotes were considered ubiquitous across the Southeast by 2000 (Hody and Kays 2018), and thus all contemporary samples were collected after 2000. We collected all historic samples from museum preserved specimens of individuals collected from our desired regions pre-1960 (See Appendix 1).

In the Southeast, we collected contemporary samples via live trapping individuals as part of a larger project investigating coyote population ecology and opportunistically from road killed individuals. Descriptions of capture and handling methods used to obtain contemporary samples from the Southeast can be found in Ward et al. (2018), and all animal handling protocols and procedures were approved under the Institutional Animal Care and Use Committee at the University of Georgia (protocol number A2014 08-025-R2) and met guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011). We collected contemporary Plains samples from pelts collected by a private fur buyer in southwest Oklahoma.

Determining diet breadth for a population of interest can be challenging, especially if diet composition changes seasonally like it does for coyotes (Bekoff 2001; Schrecengost et al. 2008). Analysis of stable isotopes of δ^{15}N and δ^{13}C in hair or other tissues is a well established method to infer diet composition and potential niche width of carnivore species (Bearhop et al. 2004; Caut et al. 2006; Murray et al. 2015). When quantified for individuals or species within the same trophic level, δ^{15}N is generally interpreted as assimilation of protein into body tissues whereas δ^{13}C is generally inferred as assimilation of C4 vegetation into body tissues (either native or anthropogenic in nature; DeNiro and Epstein 1978; DeNiro and Epstein 1981). By comparing isotope levels among individuals and species researchers can effectively determine differences in diet composition and overlap (Bearhop et al. 2004; Caut et al. 2006). Additionally, isotope values can be used to estimate niche width and structure and allows researchers to directly assess isotopic niche overlap among species (Bearhop et al. 2004; Jackson et al. 2011).

Isotopes accumulate in all tissue types in mammalian vertebrates, and thus multiple tissue types (e.g., hair, muscle, blood, bone, etc.) may be used for stable isotope analysis. However, because we compared historic and contemporary populations, we were limited to tissues typically preserved in museum collections, study skins or skulls, for all historic samples. Further, because our contemporary samples were collected from live-trapped individuals, it was important to minimize the invasiveness of sample collection. Thus, we used guard hairs for all analyses. While hair is an effective indicator of stable isotope values for terrestrial mammals, it is important to note that hairs only indicate stable isotope accumulation during the time period the hair is metabolically active (i.e., growing; Newsome et al. 2010). However, diets for all three species are known to shift seasonally (Hockman and Chapman 1983; Schrecengost et al. 2008; Ward et al. 2018), meaning values cannot reflect winter diets of our focal species. For canid species, hair provides data on diets of individuals since their last molt period, typically the spring/summer months of April – September for North America species (Castelló 2018). Thus, stable isotope values from canid hair samples can be thought to represent summer diet breadth. We only collected samples from individuals/specimens trapped during winter (see Ward et al. 2018), when hair was metabolically inactive so that hairs would provide diet information for the previous summer.

For all samples, we collected a minimum of 3 mg of guard hair from the withers region (i.e., the ridge between the shoulder blades) of each individual. For each sample, we recorded 1) date collected, 2) state and county of collection, and 3) sex of individual if known. All hair samples were then stored in opaque envelopes at room temperature until analysis.

Data Analysis

We prepared all hair samples for stable isotope analysis by first removing any debris or skin from the hair with soap and water, then rinsing with distilled water and drying with a sterile surface wipe and allowing samples to sit at 22 ° **C** until dry. Then, using scissors to homogenize the hair, we measured 2 mg of the sample and packed it into pre-combusted 5x9mm tin capsules (Costech Analytical Technologies Inc., Valencia, California, U.S.A.). For every 96 samples, we prepared 3 duplicate samples as a quality control measure. Packed capsules were then sent to the University of Georgia Stable Isotope Ecology Laboratory (SIEL) in Athens, GA for isotope ratio analysis of $\delta^{13}C$ and $\delta^{15}N$. The SIEL used standards in each analysis for QAQC as well as calculating $\delta^{13}C$ and $\delta^{15}N$ (the difference between a sample and natural abundance standard for which delta = zero; reported in parts per thousand) with atmospheric air being the standard for nitrogen analyses and the Chicago PDB Marine Carbonate Standard (U.S. National Institute of Standards and Technology, Gaithersburg, Maryland, U.S.A.) for carbon.

Prior to analysis, we corrected for changes in atmospheric CO^2 over the last ~150 years (i.e., the Suess effect; Keeling 1979). Based on core records, we applied a time dependent correction of -0.005‰ per year between1860-1960 and -0.022‰ per year since 1960 (Francey et al. 1999; Chamberlain et al. 2005). All samples were corrected to reflect 2018 values.

We used linear mixed-effects models to determine if differences in mean $\delta^{13}C$ and $\delta^{15}N$ existed within and among species between time periods for both regions. We also assessed intraspecific differences for each species from each region temporally to assess potential shifts in diet composition. We modeled differences in $\delta^{13}C$ and $\delta^{15}N$ separately for all samples. For all models, time period (historic, contemporary) and species (gray fox, red fox, coyote) were included as fixed effects as appropriate. To account for variation in the size of each region sampled for each time period, we included county of collection as a random effect. In all models we used an alpha level of 0.05 to determine significance. We could not identify sex for a substantive proportion of the samples, so we did not include sex as a variable in our models. We conducted all modeling analyses using package “nlme” (Pinheiro et al. 2012)

Additionally, to compare niche structure and overlap among species over time we estimated isotopic niche space for each species in both regions and time periods by calculating size-corrected standard Bayesian ellipses using package "SIBER" (Jackson et al. 2011). We then computed standard ellipse area (SEA_c) and the proportion of overlap of standard ellipses among species within each region and time period as a metric of how niche space and isotope ratios change within and among species over time. We conducted all statistical analyses in Program R (R Core Team, 2013).

Results

We collected 220 hair samples, and 217 (107 coyote, 85 gray fox, 25 red fox) were successfully analyzed for $\delta^{13}C$ and $\delta^{15}N$ (Table 1). Historic sample collection dates ranged from 1872 – 1960 based on availability of specimens in museum collections (Appendix 1). Southeastern samples, both historic and contemporary, were collected from Alabama, Georgia, South Carolina, and the panhandle of Florida, whereas Plains samples were collected from Oklahoma, Kansas, and eastern Colorado (Fig 1). For 26 samples, location data was limited to state only, and 74 samples lacked sex information due to the nature of the collection (i.e., historic collection or collections for fur trade).

Within the Southeast, species-specific analysis revealed $\delta^{13}C$ and $\delta^{15}N$ for gray foxes did not vary between historic and contemporary samples ($\beta = 0.17$, $t_{(31)} = 0.32$, $P = 0.75$ for $\delta^{13}C$; $\beta = 0.35$, $t_{(31)} = 0.69$, $P = 0.49$ for $\delta^{15}N$). However, gray foxes from the Plains region historically had more enriched amounts of $\delta^{13}C$ and $\delta^{15}N$ than did contemporary individuals ($\beta = 3.25$, $t_{(49)} = 5.44$, $P = <0.001$ for $\delta^{13}C$; $\beta = 1.44$, $t_{(49)} = 3.39$, $P = 0.001$ for $\delta^{15}N$). Red foxes from the Plains region showed no difference between historical and contemporary samples ($\beta = -0.11$, $t_{(11)} = -0.11$, $P = 0.91$ for $\delta^{13}C$ and $\beta = 0.20$, $t_{(11)} = 0.15$,

$P = 0.88$ for $\delta^{15}N$). Similarly, red foxes in the Southeast also showed no temporal shifts in diet ($\beta = 0.62$, $t_{(10)} = 0.61$, $P = 0.55$ for $\delta^{13}C$ and $\beta = -0.22$, $t_{(10)} = -0.74$, $P = 0.48$ for $\delta^{15}N$). Coyotes in the Plains historically had more enriched amounts of $\delta^{13}C$ than did contemporary individuals ($\beta = 2.46$, $t_{(44)} = 4.08$, $P = <0.001$), but no differences in $\delta^{15}N$ were observed ($\beta = 0.11$, $t_{(44)} = 0.33$, $P = 0.74$; Fig 2).

Historically, neither $\delta^{13}C$ nor $\delta^{15}N$ isotope values differed between red and gray foxes in the Southeast ($\beta = 0.85$, $t_{(30)} = 1.53$, $P = 0.13$ for $\delta^{13}C$; $\beta = 0.15$, $t_{(30)} = 0.40$, $P = 0.69$ for $\delta^{15}N$). Similarly, analysis of contemporary samples of red foxes, gray foxes, and coyotes in the Southeast revealed no differences between foxes and coyotes for either $\delta^{13}C$ or $\delta^{15}N$ ($\beta = 0.89$, $t_{(71)} = 1.63$, $P = 0.11$ for gray fox $\delta^{13}C$; $\beta = -0.72$, $t_{(71)} = -1.56$, $P = 0.12$ for gray fox $\delta^{15}N$; $\beta = 0.008$, $t_{(71)} = 0.011$, $P = 0.99$ for red fox $\delta^{15}N$; $\beta = 1.30$, $t_{(71)} = 1.57$, $P = 0.12$ for red fox $\delta^{13}C$). In the Plains region, $\delta^{15}N$ did not differ between coyotes and red foxes ($\beta = 0.18$, $t_{(63)} = 0.29$, $P = 0.77$), but gray foxes had depleted $\delta^{15}N$ ($\beta = -1.81$, $t_{(63)} = -4.54$, $P = <0.001$). Both gray foxes and red foxes had depleted $\delta^{13}C$ compared to coyotes ($\beta = -1.82$, $t_{(11)} = -3.11$, $P = 0.002$ for gray fox; $\beta = -2.33$, $t_{(63)} = -2.59$, $P = 0.01$ for red fox). Contemporary samples from the Plains showed that gray foxes still had more depleted $\delta^{13}C$ and $\delta^{15}N$ than did red foxes and coyotes ($\beta = -2.62$, $t_{(41)} = -5.04$, $P = <0.001$ for $\delta^{13}C$; $\beta = -3.13$, $t_{(41)} = -7.27$, $P = <0.001$ for $\delta^{15}N$). Red foxes and coyotes in the Plains did not differ in $\delta^{13}C$ or $\delta^{15}N$ ($\beta = 0.24$, $t_{(41)} = 0.30$, $P = 0.77$ for $\delta^{13}C$; $\beta = 0.08$, $t_{(41)} = 0.13$, $P = 0.90$ for $\delta^{15}N$; Fig 3).

Standard ellipse estimates supported the trends seen in modeling; with plains populations generally having lower overlap in isotopic niche space than did Southeast populations (Table 2; Table 3). Historic overlap of standard ellipses among red and gray fox samples from the Southeast was 25.9%, while contemporary overlap was 18.2%. For contemporary canid populations in the Southeast, overlap was greatest among coyotes and red foxes (20.8%). Ellipse overlap of historic and contemporary gray fox populations was relatively low (10.7%) and gray foxes experienced an increase in niche space (from 4.50 to 8.09; Table 1). For historic plains populations, overlap of standard ellipses was greatest among coyotes and red foxes (19.0%), whereas coyotes and gray foxes had relatively little overlap (5.7%; see Table 3). Contemporarily, gray foxes had almost no overlap with either red foxes (0%) or coyotes (<0.001%). Further, contemporary gray foxes in the plains had almost no overlap (<0.001%) with historic gray fox populations in the same region, and estimated SEA$_c$ for gray foxes in the plains shrank from 10.37 historically to 5.59 contemporarily. Red fox and coyote populations had increased overlap (29.0%) relative to historic populations, and both populations' estimated niche space shrank over time (See Table 1).

Discussion

Resource partitioning commonly occurs across multiple phyla (e.g., plants, invertebrates, vertebrates, fungi) and partitioning serves as an ecological process to minimize resource depletion and competition, thus allowing some species to remain sympatric through time (Roughgarden 1976; Chase and Leibold 2003; Finke and Snyder 2008). Our findings supported our hypotheses that diet breadth and isotopic niche space of recently established coyote populations overlapped with those of red and gray foxes, indicating a lack of resource partitioning among newly sympatric populations. Given the extent of overlap between coyotes and foxes in the Southeast, our data suggest coyotes likely are competing with foxes for food resources, increasing potential interspecific competition among these species.

Although overlap in prey selection and the resulting interspecific competition may lead to resource partitioning, in our study system this process may be confounded by the potential for interference competition (i.e., coyote harassment and/or killing of foxes), which is common among canid species with overlapping ranges (Sargeant et al. 1987; Cypher and Spencer 1998; Kitchen et al. 1999; Gehring and Swihart 2003; Kamler et al. 2003). Interference competition has been known to drive spatial or temporal partitioning of habitat at varying scales (Berger and Gese 2007; Temple et al. 2010; Deuel et al. 2017), and among canids the selection pressure resulting from interference competition is typically greater on the physiologically smaller species (i.e., the species more vulnerable to interspecific killing; Schoener 1983, Palomares and Caro 1999). In addition, interspecific interactions, including competition, can be influenced by disease dynamics and transmission among species (Levin 1970; Holt and Pickering 1985). Coyotes have the potential to act as reservoirs of common canid diseases such as sarcoptic mange (Guo et al. 1986) and canine distemper (Almberg et al. 2010), diseases known to disproportionately affect red and gray fox, respectively (Trainer and Hale 1969; Davidson et al. 1992). Thus, habitat partitioning driven by interference competition or disease dynamics may influence food availability and selection by foxes in the Southeast in addition to food resource competition.

Congruent with historical accounts of red and gray fox diets composition in the Southeast (Nelson 1933; Scott 1955), our findings suggest Southeastern gray and red foxes historically competed for food resources. However, now that coyotes have become established throughout the Southeast we would expect additive exploitation of food resources foxes use, leading to interspecific competition between foxes and coyotes for food resources. Previous research has noted diet overlap between coyotes and various species of fox (Kitchen et al. 1999; Neale and Sacks 2001; Azevedo et al. 2005) and all three species in our study are considered opportunistic foragers with diets consisting of both animal (e.g., small mammals, reptiles/amphibians, and ground-nesting birds) and plant material (e.g., fruits, grasses, agricultural crops), with composition varying seasonally (Hockman and Chapman 1983; Schrecengost et al. 2008; Ward et al. 2018). When competition occurs, morphological differences among competitors determine which species is favored in competition (Alatalo and Moreno 1987; Richards et al. 2006). Relatively larger body sizes can allow coyotes to be resistant to interference competition (i.e., interspecific killing) with foxes, increase their mobility on the landscape, and increase their diet breadth (Palomares and Caro 1999; Nupp and Swihart 2000; Scharf et al. 2000; Caro and Stoner 2003). Indeed, coyotes are likely to be the dominate canid when in direct competition with foxes because of their increased resilience to structural shifts in ecosystems, such as switching among fluctuating food resources compared to smaller fox species with relatively narrower diet breadths (Gehring and Swihart 2003).

In the continued absence of food partitioning in the Southeast, we would expect coyotes to dominate over fox when competition exists because of their larger body size, relatively wider diet breath, and ability to predate a larger array of food resources while meeting energetic requirements (Gehring and Swihart 2003). Indeed, annual harvest records for the state of South Carolina show a decrease in gray and red fox harvests over the past decade, while coyote harvests have increased (J. Butfiloski, Furbearer and

Alligator Program Coordinator, SCDNR, unpublished data). Similarly, documented captures of gray and red fox on the Savannah River Site, an approximately 800 km^2 area with scientifically rigorous survey records of mammal populations in southwestern South Carolina, has severely declined between the early 1960s and mid 2010s (Wood and Odum 1964; Webster and Beasley 2019). In the future, we would expect to see evidence of resource partitioning among canids in the Southeast as foxes adapt to the presence of coyotes. However, if observed declines in fox abundance continue, coyotes may competitively exclude foxes from parts of the Southeast before resource partitioning effectively mitigates interspecific competition.

In the Plains populations, where coyotes have been sympatric with red and gray foxes for well over a century, stable isotope values indicated these populations historically partitioned food resources and coyotes and gray foxes in particular had little overlap in estimated isotopic niche space (5.7%). Contemporarily, gray foxes continue to partition resources with both species (Fig 2; Table 3). Gray foxes are thought to have the narrowest diet breadth of the three species, with a diet consisting of large amounts of soft mast, insects, vegetation, and agricultural crops (Hockman and Chapman 1983; Neale and Sacks 2001). This relatively narrow breadth is thought to be the result of allometric differences between these species, with the gray fox's relative small body size limiting the size and type of prey they are capable of using while simultaneously lowering their energetic requirements, allowing them to more readily subsist on lower quality food items (i.e., native vegetation; Persson 1985). Indeed, both historical and contemporary samples suggest gray foxes have consistently maintained a $\delta^{13}C$ and $\delta^{15}N$ depleted diet relative to red foxes and coyotes in the Plains. Due to their ability to use a semi-arboreal foraging strategy (Fritzell 1987; Jeselnik 1981), gray foxes generally prefer forested habitats, a relatively sparse habitat type occurring mainly along forested areas immersed in surrounding grassland throughout the Plains region (Fuller and Cypher 2004; Cooper et al. 2012). Combined, these spatial limitations on where gray fox occur on the landscape and allometric limitations on prey use are likely driving both historical and contemporary resource partitioning among gray foxes and other carnivores. Likely, food resource partitioning with the other species became more pronounced as suitable habitat diminished, and competition for prey resources remained strong among these larger canids such as coyotes and red foxes.

Red foxes in the Plains historically had depleted $\delta^{13}C$ relative to coyotes, an indicator coyotes were consuming greater amounts of C4 plants (e.g., crops, anthropogenic foods; Jahren and Kraft 2008) or prey which utilize C4 plants (e.g., small mammals in a grassland ecosystem). This partitioning may have mitigated competition, with fox relying more heavily on non-anthropogenic resources than coyotes to meet energetic requirements, a trade off more easily achieved by red fox due to allometric differences in body size and energy requirements (Persson 1985). Contemporarily, red fox and coyotes do not appear to be partitioning food resources and have substantial overlap in isotopic niche space (29.0%), a finding congruent with previous studies of diet breadth of these two species in the Plains (Azevedo et al. 2006). The contemporary diminishment of food partitioning among red fox and coyotes relative to historic populations (See Table 3) indicates that perhaps food partitioning has been replaced with another mechanism to mitigate interspecific competition. Previous research has shown coyotes will spatially exclude red fox from certain habitats where coyotes are present via interspecific strife (e.g., prairie habitat; Voigt and Earle 1983; Sargeant et al. 1987; Harrison et al. 1989). Spatial partitioning of habitat allows both species to remain sympatric at a landscape scale without necessarily limiting or shifting red fox diet composition to lower quality diet items, a trend supported by the contemporary overlap in diet we observed.

Our research shows that dietary overlap between coyotes and other canids in the Southeast, where coyotes have recently established populations, appears to be substantial and resource partitioning may not be occurring or may not yet be apparent. The latter would be unsurprising given that ecological processes typically play out slowly temporally. In the Plains, where the species have historically been sympatric, clear partitioning of food resources is evident, particularly between coyotes and gray fox. It remains unclear whether similar partitioning will occur in Southeast populations, especially because gray fox population abundance appears to be in decline in parts of the Southeast (J. Butfiloski, Furbearer and Alligator Program Coordinator, SCDNR, unpublished data). It also is unclear the extent to which interference competition may initiate partitioning of food resources among sympatric canid populations. Thus, future research and monitoring of fox and coyote populations throughout the Southeast is necessary to ultimately elucidate how diet overlap and other mechanisms of interspecific competition will affect fox populations.

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Tables and Figures

Table 5.1: Average $\delta^{13}C$ & $\delta^{15}N$ values and size-corrected Standard Ellipse Area (SEA_c) for Coyote, Gray Fox, and Red Fox from the Plains region and the Southeast region of the United States. Historic samples are those from animals harvested prior to 1/1/1960, while Contemporary samples were collected post 1/1/2000.

Region	Time Period	Species	Number Samples	Average **$\delta^{15}N$**	SD **$\delta^{15}N$**	Average **$\delta^{13}C$**	SD **$\delta^{13}C$**	SEA_c
Plains	Historic	Coyote	25	9.14	1.18	-16.54	2.31	9.81
		Gray Fox	33	7.33	1.59	-18.37	2.19	10.37
		Red Fox	8	9.31	1.97	-18.76	1.96	13.47
	Contemporary	Coyote	21	9.03	1.08	-19	1.65	5.02
		Gray Fox	18	5.89	1.13	-21.62	1.73	5.59
		Red Fox	5	9.11	2.69	-18.87	0.71	7.64
Southeast	Historic	Gray Fox	24	6.67	1.02	-19.78	1.32	4.50
		Red Fox	8	6.82	0.5	-19.55	1.47	2.51
	Contemporary	Coyote	61	7.03	1.26	-20.85	1.58	5.23
		Gray Fox	10	6.31	1.96	-19.96	1.59	8.09
		Red Fox	4	7.04	0.45	-18.93	1.99	2.77

Table 5.2: Proportion of overlap in size-corrected standard ellipse area between species sampled from both time periods from the Southeast region of the United States. Historic samples are those from animals harvested between 1872 – 1960, while Contemporary samples were collected between 2000 – 2018.

			Southeast		
Species – Time Period	Red Fox – Historic	Gray Fox – Historic	Coyote – Contemporary	Red Fox – Contemporary	Gray Fox – Contemporary
Red Fox – Historic	--	25.9	--	54.0	--
Gray Fox – Historic	25.9	--	--	--	10.7
Coyote – Contemporary	--	--	--	20.8	18.2
Red Fox – Contemporary	54.0	--	20.8	--	19.1
Gray Fox – Contemporary	--	10.7	18.2	19.1	--

Table 5.3: Proportion of overlap in size-corrected standard ellipse area between species sampled from both time periods from the Plains region of the United States. Historic samples are those from animals harvested between 1872 – 1960, while Contemporary samples were collected between 2000 – 2018.

			Plains			
Species – Time Period	Coyote – Historical	Red Fox – Historical	Gray Fox – Historical	Coyote – Contemporary	Red Fox – Contemporary	Gray Fox - Contemporary
Coyote – Historic	--	19.0	5.7	16.6	--	--
Red Fox – Historic	19.0	--	16.9	--	37.9	--
Gray Fox – Historic	5.7	16.9	--	--	--	<0.001
Coyote – Contemporary	16.6	--	--	--	29.0	<0.001
Red Fox – Contemporary	--	37.9	--	29.0	--	0
Gray Fox – Contemporary	--	--	<0.001	<0.001	0	--

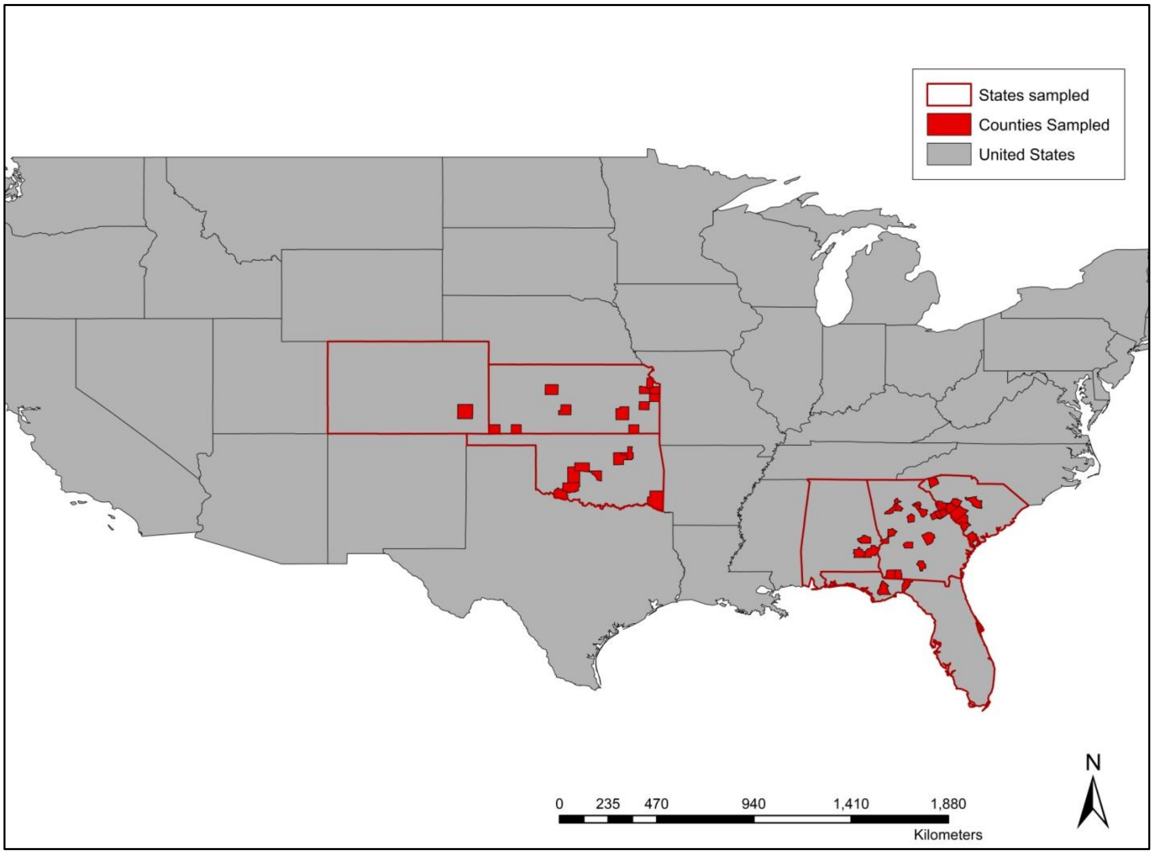

Figure 5.1: States where historical and contemporary hair samples were collected from coyotes, red fox, and gray fox in the southeast and the Plains regions. For some samples, county information was not available.

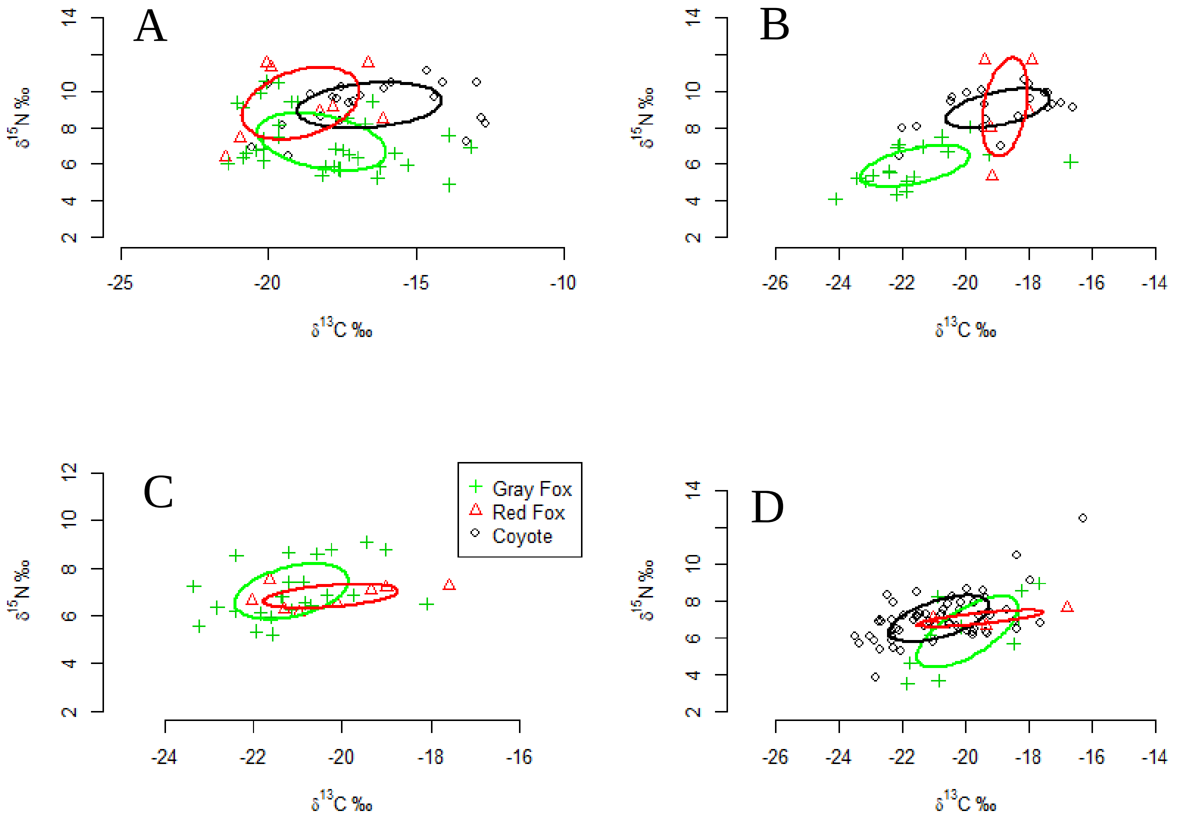

Figure 5.2: Stable isotope Bayesian standard ellipses adjusted for sample size (SEA$_c$) drawn using δ^{13}C & δ^{15}N values for canid species sampled from historic plains (A), contemporary plains (B), historic Southeast (C), and contemporary Southeast (D). The proportion of ellipse overlap between species appears in Tables 2 and 3

Appendices

Appendix I – Museum specimens examined as part of this research. KUBI = Kansas University Biological Institute; USNM = Smithsonian National Museum of Natural History; GMNH = Georgia Museum of Natural History.

Catalog ID	Museum of Origin	Date	Species	Sex
16203	KUBI	1/14/1946	Coyote	Female
16526	KUBI	4/14/1946	Coyote	Male
81873	KUBI	11/28/1959	Coyote	Male
16212	KUBI	3/3/1946	Coyote	Female
16213	KUBI	3/3/1946	Coyote	Male
16214	KUBI	3/3/1946	Coyote	Female
14676	KUBI	1/26/1945	Coyote	Male
16215	KUBI	3/3/1946	Coyote	Male
16216	KUBI	3/3/1946	Coyote	Female
16217	KUBI	3/10/1946	Coyote	Male
16219	KUBI	3/10/1946	Coyote	Male
16220	KUBI	3/10/1946	Coyote	Female
5283	KUBI	6/29/1927	Coyote	Male
72389	KUBI	1/11/1957	Coyote	Female
69616	KUBI	6/19/1956	Coyote	Female
14675	KUBI	1/28/1945	Coyote	Male
266392	USNM	2/3/1941	Coyote	Male
266391	USNM	2/3/1941	Coyote	Female
266390	USNM	1/29/1941	Coyote	Unknown
266389	USNM	1/22/1941	Coyote	Male
266388	USNM	1/21/1941	Coyote	Unknown
266387	USNM	12/9/1940	Coyote	Female
266386	USNM	1940	Coyote	Female
266383	USNM	2/9/1940	Coyote	Male
266384	USNM	3/5/1940	Coyote	Unknown
266382	USNM	2/9/1940	Coyote	Unknown
266144	USNM	10/9/1940	Coyote	Unknown
265570	USNM	2/13/1940	Coyote	Female
261642	USNM	11/12/1932	Coyote	Female
251068	USNM	11/18/1932	Coyote	Male
251067	USNM	11/12/1932	Coyote	Male
251066	USNM	11/12/1932	Coyote	Female
251065	USNM	11/12/1932	Coyote	Male
235605	USNM	2/17/1921	Coyote	Female

235604	USNM	2/16/1921	Coyote	Male
235603	USNM	1/24/1921	Coyote	Male
235602	USNM	1/20/1921	Coyote	Male
136631	USNM	2/18/1905	Coyote	Unknown
235606	USNM	2/17/1921	Coyote	Female
135747	USNM	Unknown	Coyote	Female
135750	USNM	Unknown	Coyote	Male
135749	USNM	Unknown	Coyote	Female
135447	USNM	6/4/1904	Coyote	Male
135746	USNM	1/28/1904	Coyote	Male
135076	USNM	10/30/1904	Coyote	Male
134503	USNM	11/24/1904	Coyote	Female
134502	USNM	11/24/1904	Coyote	Male
26980	GMNH	11/2/2000	Grey Fox	Male
116196	USNM	12/3/1901	Grey Fox	Male
181199	USNM	1-11-1890	Grey Fox	Male
18198	USNM	1-9-1890	Grey Fox	Female
52060	USNM	1893	Grey Fox	Unknown
274483	USNM	12/15/1943	Grey Fox	Unknown
282677	USNM	12/14/1938	Grey Fox	Male
287676	USNM	12/28/1937	Grey Fox	Female
273308	USNM	3/23/1942	Grey Fox	Unknown
272249	USNM	2/19/1941	Grey Fox	male
234425	USNM	11/6/1919	Grey Fox	Male
234422	USNM	10/27/1919	Grey Fox	Female
232414	USNM	4/16/1919	Grey Fox	Female
81936	KUBI	1/28/1960	Grey Fox	Female
83578	KUBI	Oct-52	Grey Fox	Unknown
1614	KUBI	Dec 1889	Grey Fox	Unknown
1639	KUBI	12-8-1872	Grey Fox	Unknown
43870	KUBI	12/6/1951	Grey Fox	Female
56741	KUBI	1/3/1954	Grey Fox	Female
72411	KUBI	2/9/1957	Grey Fox	Female
63759	KUBI	Aug-54	Grey Fox	Female
71972	KUBI	1/29/1953	Grey Fox	Male
1162	GMNH	10/17/1953	Grey Fox	Male
906	GMNH	11/4/1951	Grey Fox	Male
905	GMNH	10/20/1951	Grey Fox	Male
239	GMNH	12/28/1947	Grey Fox	Female
911	GMNH	7/14/1951	Grey Fox	Female
1161	GMNH	11/11/1952	Grey Fox	Male
1577	GMNH	11/19/1955	Grey Fox	Female
1635	GMNH	10/20/1953	Grey Fox	Female
1272	GMNH	11/11/1954	Grey Fox	Male

2409	GMNH	1/13/1962	Grey Fox	Male
1464	GMNH	11/27/1954	Grey Fox	Unknown
99	GMNH	12/3/1958	Grey Fox	Female
507406	USNM	12/13/1955	Grey Fox	Female
79125	USNM	2-24-1896	Grey Fox	Male
254665	USNM	8/20/1929	Grey Fox	Unknown
189016	USNM	12/27/1915	Grey Fox	Unknown
265663	USNM	3/13/1940	Grey Fox	Female
251183	USNM	Winter 1933-34	Grey Fox	Female
251182	USNM	Winter 1933-34	Grey Fox	Male
256058	USNM	12/15/1930	Grey Fox	Male
175595	USNM	1/11/1912	Grey Fox	Unknown
175594	USNM	11/1/1912	Grey Fox	Unknown
14610	KUBI	1/10/1945	Grey Fox	male
14611	KUBI	1/20/1945	Grey Fox	Female
155349	KUBI	Unknown	Grey Fox	Male
154169	KUBI	Dec-47	Grey Fox	male
154170	KUBI	11/3/1947	Grey Fox	Male
154171	KUBI	5/22/1949	Grey Fox	Male
154172	KUBI	5/11/1949	Grey Fox	Male
27337	KUBI	4/28/1948	Grey Fox	Female
27338	KUBI	5/5/1948	Grey Fox	Male
27340	KUBI	5/5/1948	Grey Fox	Male
27341	KUBI	5/5/1948	Grey Fox	Male
35114	KUBI	1/22/1950	Red Fox	Male
35115	KUBI	1/27/1950	Red Fox	Male
56539	KUBI	10/25/1953	Red Fox	Male
81874	KUBI	10/14/1959	Red Fox	Female
39177	KUBI	11/19/1950	Red Fox	Male
107623	USNM	1900	Red Fox	Male
507405	USNM	5/18/1960	Red Fox	Male
507404	USNM	1960	Red Fox	Female
14608	KUBI	1/8/1945	Red Fox	Male
14609	KUBI	1/28/1945	Red Fox	Female
2531	GMNH	1/27/1963	Red Fox	Male
2304	GMNH	12/10/1960	Red Fox	Female
612	GMNH	3/15/1950	Red Fox	Unknown
1267	GMNH	11/12/1954	Red Fox	Unknown
599	GMNH	4/22/1950	Red Fox	Male

CHAPTER 6

CONCLUSIONS

A thorough understanding of coyote spatial ecology, habitat selection, and prey selection is critical to developing successful coyote population management strategies for the Southeast. I studied 4 important components of coyote ecology that demonstrate how territoriality and interspecific resource partitioning can lead to shifts in movement behavior or diet. In Chapter 2, I demonstrated that where coyotes are sympatric with the larger red wolf, fine-scale temporal and spatial habitat partitioning occurs, likely as a mechanism to mitigate competition. Both species showed temporal variation in habitat selection patterns and appeared to temporally partition their use of wetland habitats. Further, coyotes selected for and used a broader diversity of habitats than red wolves. Despite this, both species also exhibited strong selection for agricultural fields planted in corn, which may lead to interspecific competition for suitable habitat. Greater plasticity in coyote habitat selection is unsurprising, but may present management challenges for long term red wolf population recovery.

Through analysis of GPS movement data for 171 coyotes in the Southeast, in Chapter 3 I found that territoriality influenced coyote habitat selection and space use, despite high individual variation. Transient coyotes had greater movement rates compared to residents, and transients were generally more likely to spend time near developed areas and away from agricultural habitats. Residents avoided developed areas, but selected for agricultural habitats during spring. Both residents and transients selected for wetland habitats during summer, and generally selected for areas with high edge density throughout the year. The high variation in movement patterns in both groups (residents and transients) suggests that other environmental or biological factors likely influence movement and habitat selection temporally, emphasizing the complexity of behavioral plasticity in coyote populations.

In Chapter 4 I further investigated intra-specific differences in behavior among coyotes relative to territoriality status, and found that diet composition differed between residents and transients. The diet of transients was primarily comprised of anthropogenic foods (39.0 ± 7.5%), whereas resident diets were comprised largely of rodents (43.0 ± 23.7%) and white-tailed deer (30.6 ± 21.9%). Despite differences in composition, overlap between niche breadth of residents and transients was relatively high (64.2%), suggesting that although territoriality influences diet composition, resident and transient coyotes still occupy similar niche space.

In Chapter 5 I investigated the potential impacts of coyotes on native canids in the Southeast by examining historic and contemporary diet of these species using stable isotopes. I found evidence for historic dietary overlap between red and gray fox, and contemporary dietary overlap among coyotes and fox, suggesting that food resource partitioning may not be occurring or may not yet be apparent. The latter would be unsurprising given that ecological processes typically play out slowly over time. In the continued absence of food partitioning in the Southeast, interspecific competition among coyote and fox may remain high. I speculate that coyotes will dominate over fox when competition exists because of their larger body size, relatively wider diet breath, and ability to predate a larger array of food resources while meeting energetic requirements.

In the Plains, where the three species have historically been sympatric for centuries, clear partitioning of food resources is evident, particularly between coyotes and gray fox.

In conclusion, I suggest that both territoriality and interspecific competition influence coyote movement and prey selection in the Southeast. Importantly, individual variation among coyotes was noteworthy throughout all datasets used in this work, emphasizing the substantive behavioral variation among individuals. I believe that both territoriality and potential competition should be considered to effectively elucidate behavioral patterns in future coyote ecology research.