SPACE USE AND RESOURCE SELECTION BY COYOTES IN THE SOUTHEASTERN UNITED STATES

by

JENNIFER NICOLE WARD

(Under the Direction of Michael J. Chamberlain)

ABSTRACT

Coyotes (*Canis latrans*) are now widespread across North America. In the southeastern United States, managers of game and non-game species have expressed concern over coyote impacts. During 2015–2017, I monitored 147 coyotes with GPS transmitters in Alabama, Georgia, and South Carolina to document space use and habitat selection. I collected scat (n=1100) from 25 resident coyote territories to assess prey use. Transient coyotes exhibited broader space use than residents, as transient ranges averaged 132.7 ± 105.2 km^2, whereas resident home ranges averaged 17.6 ± 14.7 km^2. Residents and transients maintained ranges with similar habitat composition, but used habitats differently. Residents selected agriculture and forests, but avoided urban and roads. Transients selected agriculture, urban, and roads, but avoided shrub. White-tailed deer (*Odocoileus virginianus*) was the most important food source for residents. Differential use of prey by residents was influenced by habitat heterogeneity within home ranges. Landowners interested in managing coyotes should also consider that 80% of transients traversed ≤ 200 km^2.

INDEX WORDS: *Canis latrans*, home range, transient range, territory, habitat use, diet, space use

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TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS iv

LIST OF TABLES vii

LIST OF FIGURES ix

CHAPTER

1 INTRODUCTION AND LITERATURE REVIEW 1

OBJECTIVES 6

THESIS FORMAT 6

LITERATURE CITED 7

2 RESIDENT AND TRANSIENT COYOTE SPACE USE IN THE SOUTHEASTERN UNITED STATES 13

ABSTRACT 14

INTRODUCTION 16

STUDY AREA 19

METHODS 21

RESULTS 25

DISCUSSION 27

ACKNOWLEDGEMENTS 31

LITERATURE CITED 33

3 SIZE AND HABITAT COMPOSITION OF HOME RANGES INFLUENCE PREY USE BY COYOTES IN THE SOUTHEASTERN UNITED STATES 52

ABSTRACT 53

INTRODUCTION 54

STUDY AREA 57

METHODS 60

RESULTS 64

DISCUSSION 67

ACKNOWLEDGEMENTS 74

LITERATURE CITED 76

4 CONCLUSIONS AND MANAGEMENT IMPLICATIONS 99

LIST OF TABLES

Page

Table 2.1: Mean (±SD) space use (km^2) by resident and transient coyotes in Alabama, Georgia, and South Carolina during 2015-2017. 41

Table 2.2: Mean (±SD) space use (km^2) by season by resident and transient coyotes in Alabama, Georgia, and South Carolina during 2015-2017. 42

Table 2.3: Comparison of model fit among models with or without interactions used to test hypotheses about coyote resource selection at the 3rd order in Alabama, Georgia, and South Carolina, 2015-2016. Shown are Akaike's Information Criteria for small sample sizes (AIC$_c$), differences among AIC$_c$ (ΔAIC), and the conclusion regarding whether there was strong support for the interaction. 43

Table 2.4: Summary of results from generalized linear mixed models for predicting 3rd-order coyote habitat selection by transient and resident coyotes in Alabama, Georgia, and South Carolina, 2015-2017. Shown are β coefficients, standard error (SE), *z*-scores, *P*-values, odds ratios and their associated confidence intervals. 44

Table 2.5: Summary of generalized linear mixed models for predicting coyote habitat use corresponding to different landscape features potentially affecting 3rd-order habitat selection by transient and resident coyotes in Alabama, Georgia, and South Carolina, 2015-2017. Shown are Akaike's Information Criteria for small sample sizes (AIC$_c$) and differences among AIC$_c$ (ΔAIC). 45

Table 2.6: Parameter estimates for the best 3rd-order resource selection function for radio-collared coyotes in Alabama, Georgia, and South Carolina during 2015-2016. Shown are β coefficients, standard error (SE), *z*-scores, *P*-values, odds ratios and their associated confidence intervals. 46

Table 3.1: Frequency of occurrence of primary diet items identified in coyote (*Canis latrans*) scats collected from territories in Alabama and the Savannah River area of Georgia and South Carolina, January 2016–January 2017..89

Table 3.2: Summary of the 8 generalized linear mixed models used to predict frequency of occurrence of each prey category corresponding to different hypotheses of factors affecting use by coyotes in Alabama, Georgia, and South Carolina during 2016-2017. Shown are differences among Akaike's Information Criteria for small sample sizes (ΔAIC_c). 90

Table 3.3: Results from generalized linear mixed models for the top models for predicting frequency of occurrence of 5 prey items corresponding to different hypotheses of factors affecting use by coyote packs in AL, GA, and SC, 2016. Shown are β coefficients, standard error (SE), 95% confidence intervals (CI), *z*-scores, and *P*-values. 93

LIST OF FIGURES

Page

Figure 2.1: Map of counties (noted as shaded area) in Alabama, Georgia, and South Carolina, USA, where coyotes were trapped during 2015–2016. 47

Figure 2.2: Proportion of habitats within the 95% and 50% contour interval of resident and transient coyotes in Alabama, Georgia, and South Carolina during 2015-2017. Error bars represent 95% confidence intervals. 48

Figure 2.3: Relative probability of 3rd-order habitat selection by resident coyotes in the Piedmont and Upper Coastal Plains ecoregions of Alabama, Georgia, and South Carolina during 2015-2017. Selection indicated by red and avoidance indicated by blue..............49

Figure 2.4: Relative probability of 3rd-order habitat selection by transient coyotes in the Piedmont and Upper Coastal Plains ecoregions of Alabama, Georgia, and South Carolina during 2015-2017. Selection indicated by red and avoidance indicated by blue..............50

Figure 2.5: Map showing the variability in transient space use, ranging from almost linear movements (SC30M) to movements within a more localized but still broad area (GA38M) to space use that is a combination of those movements (GA15M). In comparison, resident space use (SC21F and GA13F) is more constrained within territories. Points of the same color are relocations from the same coyote. 51

Figure 3.1: Map of counties (noted as shaded area) in Alabama, Georgia, and South Carolina, USA, where coyotes were trapped during 2015–2016. 95

Figure 3.2: Map showing habitats within 95% kernel density estimated home ranges of 3 GPS-collared coyotes in Alabama, Georgia, and South Carolina 2015–2016. AL08F had 2,674 GPS fixes (home-range size of 20.0 km^2), GA41M had 1,797 GPS fixes (home-range size of 12.8 km^2), and SC31F had 1,781 GPS fixes (home-range size of 12.1 km^2). 96

Figure 3.3: Frequency of occurrence by month of 4 primary food categories in coyote scats collected from Alabama, Georgia, and South Carolina, USA during 2016. Error bars represent 95% confidence intervals. 97

Figure 3.4: Frequency of occurrence by month of adult and fawn white-tailed deer in coyote scats collected from Alabama, Georgia, and South Carolina, USA during 2016–2017. Shown above is the range of parturition dates for our study area......................................98

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The coyote (*Canis latrans*) is an adaptive generalist carnivore ubiquitous across most of North America. Historically ranging throughout the western and central regions of North America, coyotes expanded their range into eastern North America within the last century (Gompper 2002*a*, *b*, Nowak 2002). Extirpation of gray wolves (*C. lupus*), eastern wolves (*C. lycaon*), and red wolves (*C. rufus*) in the late 19th century eliminated interspecific competition responsible for limiting coyote distribution (Soulé et al. 1988, Thurber et al. 1992, Gompper 2002*b*, Berger and Gese 2007). Additionally, anthropogenic alteration to habitat, such as clear-cutting forests and conversion to agricultural land, has been linked to coyote range expansion by increasing food availability and accessibility (Gompper 2002*b*, Boisjoly et al. 2010). Coyotes readily adapted to anthropogenic landscapes (Morey et al. 2007, Grigione et al. 2011) perhaps aided by variable space use patterns that permit them to find and exploit resources.

Similar to wolves, coyotes form packs that defend territories centered on limited habitat resources often clumped in distribution such as food, cover, and denning sites (Bekoff et al. 1981, Gese et al. 1996, Gese and Ruff 1997, Hinton et al. 2015). Resident coyote packs consist of a mated pair, their pups, and non-dispersing juveniles (Bekoff and Wells 1980, Bekoff and Gese 2003). While associated with packs, juveniles assist in pup rearing, but eventually leave in search of mates and territories (Gese et al. 1996, Harrison 1992). Transient animals, including dispersing juveniles along with other coyotes lacking territories, typically use undefended areas between territories of resident pairs. They also move greater distances and use space less consistently than residents since they are not confined to movement solely within a territory (Bekoff and Wells 1980, Gese et al. 1988*a*, Kamler and Gipson 2000, Hinton et al. 2015).

Although coyote populations are ubiquitous at the landscape scale, local distributions of territories are more variable with coyotes typically favoring open or early successional habitats more than forested ones (Kamler and Gipson 2000, Schrecengost et al. 2009, Hickman et al. 2015, Hinton et al. 2015). For example, Hickman et al. (2014) found female coyotes in Georgia selected for pastures, food plots, and agricultural fields, and Schrecengost et al. (2009) observed coyotes in South Carolina selected for early successional areas including grass, brush, young hardwood (<10 years old), and young pine (<5 years old) stands. Some of these studies did not differentiate between residents and transients, but in general, the selection for open and early successional habitats was consistent with findings from other areas of North America. In western Mexico, coyotes selected for open habitats with low vegetation cover in an area dominated by tropical deciduous forest (Hidalgo-Mihart et al. 2006), whereas in Kansas resident coyotes selected for grassland over woodland and riparian habitats more than expected (Kamler and Gipson 2000). However, the status (i.e., resident and transient) of coyotes should be considered when assessing space use, habitat selection, and diet. Kamler and Gipson (2000) noted differences in habitat use between residents and transient coyotes, with transients using woodlands and agricultural fields more than expected. Likewise, Hinton et al. (2015) found differences in habitat selection between resident and transient coyotes in North Carolina, with both selecting agriculture, but residents selected for coastal bottomlands and edges, and transients selected more for roads (Hinton et al. 2015). Therefore, habitat selection may occur under different contexts for transients than residents because transients are actively searching for mates and quality habitats to establish territories whereas residents already have territories.

Coyote densities depend on the density of territories that can be established across the landscape. Territory size is often measured and reported as a home range (Laundre and Keller 1984, Wilson and Shivik 2011). Home range sizes of resident coyotes vary and reflect potential differences in habitat quality across landscapes (Gese et al. 1988*a*, Kamler and Gipson 2000, Way et al. 2002, Kamler et al. 2005) or possibly different methodologies used to estimate space use (Laundre and Keller 1984). For example, studies throughout North America have reported average home range size between 10 and 90 km^2 (Litvaitis and Shaw 1980, Springer 1982, Chamberlain et al. 2000, Schrecengost et al. 2009, Bekoff and Gese 2003, Hinton et al. 2015), but most studies did not account for whether coyotes were residents or transients. Hinton et al. (2015) suggested that energetic constraints associated with body size should set lower and upper limits to sizes of coyote home ranges, and variation within that range is influenced by habitat productivity and diet. Coyote populations are known to differ in body mass (Bekoff and Gese 2003, Way 2007) and regional differences in coyote body mass may influence variation observed in coyote home range sizes (Hinton et al. 2015).

Transient coyotes exhibit broader movements and revisit areas less often than residents (Gese et al. 1988*a*, Kamler and Gipson 2000, Hickman et al. 2015, Hinton et al. 2015). Unlike residents, transient coyotes do not have home ranges *per se* and traverse the landscape as solitary individuals in search of mates and territories. Movements of transients are intermittent, and localized movements similar to resident movements within territories are termed biding areas (Hinton et al. 2012, 2015). Indeed, space use in biding areas is consistent with maintenance of a temporary home range before the area is abandoned (Hinton et al. 2012, 2015). Hinton et al. (2015) noted that transiency is an important life history strategy for coyote populations because it facilitates population persistence through metapopulation dynamics and compensatory immigration.

Prey selection can also be influenced by space use and habitat selection. Coyotes are omnivores feeding primarily on mammalian prey, ranging from small mammals to ungulates, but also opportunistically on fruits, insects, and carrion (Bekoff 1977, Andelt 1987, Toweill and Anthony 1988, Bekoff and Gese 2003). Not surprisingly, coyote prey selection varies widely, with lagomorphs and rodents selected as primary prey in most landscapes (Hoerath and Causey 1991, Mills and Knowlton 1991, Kamler 1998, Hinton et al. 2017) whereas plant material is used when fruit and hard mast are abundant (Schrecengost et al. 2008). Regional differences in prey use by coyotes are known to be influenced by prey diversity and abundance, season, and age of coyotes (Bekoff and Gese 2003). Hinton et al. (2017) suggested that studies on coyote diets should avoid pseudoreplication by using coyote packs as sampling units and sampling within known territories. Furthermore, they noted that small scale studies have generally lacked the ability to account for social status and results may be disproportionately influenced by a few resident individuals. For example, Andelt (1985) conducted their diet study on a wildlife refuge 32 km^2 in size, Cherry et al. (2016) studied coyote diets in a 117 km^2 area of longleaf pine (*Pinus palustris*) habitat, Grigione et al. (2011) compared differences between the diets of wildland and suburban coyotes in a 38 km^2 area, and Hoerath and Causey (1991) studied coyote diets in a 6 km^2 area. Therefore, Hinton et al. (2017) suggested that coyote diet studies should occur at broader spatial scales to link prey selection to space use patterns and habitat selection, particularly for resident coyotes.

Because of the recent expansion of the coyote into the southeastern United States, it is important to understand their ecological role as an apex predator and their potential impacts on other wildlife species. Specifically, as a fairly recent predator to the region, coyote impacts on populations of game species, such as white-tailed deer (*Odocoileus virginianus*) and wild turkey (*Meleagris gallopavo*), are a growing concern among biologists and landowners (Kilgo et al. 2010). Although coyotes have replaced red wolves as the dominant canid predator in the Southeast, they may lack similar predation effects because wolves rely more on ungulates as primary prey (McCarley 1962, Dellinger et al. 2011, Benson et al. 2017, Hinton et al. 2017). Still, coyotes in this region are important fawn predators in some areas and are known to prey upon adult deer (Kilgo et al. 2012, Chitwood et al. 2014, Conner et al. 2015, Gulsby et al. 2015, Hinton et al. 2017). Therefore, a proper and broad-scaled assessment of coyote ecology is essential for identifying general patterns of coyote space use, habitat selection, and diet. Because management policies for many populations of game species (e.g., white-tailed deer) attempt to account for the potential impacts by coyotes (e.g., predation), it is important to incorporate accurate generalizations of coyote ecology to develop effective management policies.

Coyote space use varies considerably over broad areas (Hinton et al. 2015), and to better understand the ecological role that coyotes play in the Southeast, I broadly assessed coyote space use and prey use in Alabama, Georgia, and South Carolina while accounting for social status (resident vs. transient). Extensive movements by animals can bias estimates of important population parameters, such as dispersal and survival, for studies within limited study areas because it is less likely that marked individuals remain within study area boundaries (Baker et al. 1995). Indeed, it is typical for researchers to note that some radio-marked coyotes permanently left their study areas (Andelt 1985, Chamberlain et al. 2000, Schrecengost et al. 2009, Hinton et al. 2012). However, radio-marking coyotes with satellite collars permitted me to study coyote space use and diet over extensive areas without the constraints of study area boundaries observed in previous studies. Consequently, this approach permitted me to assess both resident and transient space use and habitat selection, and to assess diets of resident coyotes by collecting scats from known territories of radio-marked coyotes.

OBJECTIVES

My objectives were to assess space use and resource selection by coyotes across a broad expanse of the southeastern United States, with an emphasis on evaluating differences between residents and transients. I quantified resource use through habitat selection and prey use.

THESIS FORMAT

This thesis is written in manuscript format. Chapter 1 is an introduction and literature review on range expansion of coyotes and patterns of space use, habitat selection, and prey selection. Chapter 2 focuses on differences in space use and habitat selection between resident and transient coyotes in Alabama, Georgia, and South Carolina. Chapter 3 assesses prey use of resident coyotes from these same 3 states. Chapter 4 details the conclusions and management implications resulting from findings detailed in Chapters 2 and 3, which will be submitted to a peer-reviewed journal for publication.

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CHAPTER 2

RESIDENT AND TRANSIENT COYOTE SPACE USE IN THE SOUTHEASTERN UNITED STATES[1]

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[1] Ward, J. N., J. W. Hinton, T. Johannsen, M. Karlin, K. V. Miller, and M. J. Chamberlain. To be submitted to the Journal of Mammalogy.

ABSTRACT

Although space use and habitat selection are reflective of individual needs, such as reproduction, maintenance, and survival, they are also shaped by longer-term fitness implications, such as metapopulation dynamics that prevent population extinctions. In particular, species within the genus *Canis* exhibit strong fidelity to areas in which breeding pairs establish and defend territories from unrelated conspecifics via direct and indirect interactions. Although coyotes are well studied, their population structure is not well understood because previous researchers using very high frequency (VHF) collars were limited in their ability to document behaviors of wide-ranging individuals lacking a territory. Coyotes exhibiting territorial behavior are typically referred to as residents, whereas solitary, dispersing individuals are referred to as transients. We captured and monitored 147 coyotes across Alabama, Georgia, and South Carolina with GPS radio collars during 2015-2016 and focused on evaluating differences in space use and habitat selection between residents and transients. We identified 60 coyotes (40.8%) as residents and 48 (32.7%) as transients for the entire time they were monitored. Thirty-nine (26.5%) coyotes exhibited both residency and transiency during portions of their monitoring period. Transient ranges were larger ($t_{193} = 11.196, P < 0.001$) than home ranges of residents, and core areas of residents were smaller than biding areas used by transients ($t_{193} = 10.444, P < 0.001$). We assessed selection using resource selection functions, and we inferred selection occurred when known locations were closer to resource features than were random locations. Residents selected agriculture, forests, shrub, and wetland habitat, but avoided urban, pasture, water, and roads. Transients selected agriculture, urban areas, pastures, and roads while avoiding shrub habitats. To our knowledge, our study is the first to account for both resident and transient space use behaviors over a large geographic region. Although coyote territories appear

ubiquitous, their territories are unevenly distributed. Transients appear to move between resident territories and readily replace residents that expire or leave a territory vacant. We suspect that transients facilitate metapopulation dynamics and likely represent an important stage in the life cycle of every coyote.

INTRODUCTION

Space use and habitat selection are basic aspects of ecology central to understanding animal behavior. The home range concept is the fundamental measure of space use by animals and is used to determine habitat preferences (Burt 1943, Johnson 1980, Benson 2013). Space use, and therefore home range size, are influenced by internal and external factors such as allometric scaling correlations (McNab 1963, Schoener 1971), food availability (Jones 1990; Tufto et al. 1996, Powell et al. 1997), risk of predation (Desy et al. 1990, Tufto et al. 1996), and landscape characteristics (e.g, fragmentation and habitat productivity; Kittle et al. 2015). Although space use and habitat selection are reflective of individual needs, such as reproduction, maintenance, and survival (Verner 1977, Losin et al. 2016), they are also shaped by longer-term fitness implications, such as metapopulation dynamics that prevent population extinctions (Hanski and Gilpin 1991, Hanski 1998). In particular, species within the genus *Canis* exhibit strong fidelity to areas in which breeding pairs establish and defend territories from unrelated conspecifics via direct (e.g., aggressive interactions) and indirect (e.g., scent marking) interactions (Bekoff and Wells 1980, Gese 2001). Consequently, variable distribution in quality and locations of limiting resources influences the distribution and density of *Canis* territories on the landscape. Coyotes, one of the smaller species in the genus *Canis*, form breeding pairs that defend territories, which allows them to protect important resources vital to reproduction. Therefore, by positioning territories on limiting resources, such as productive habitats and cover, territorial behavior increases coyote survival and fitness (Knowlton et al. 1999, Kamler and Gipson 2000, Gese 2001, Hinton et al. 2015).

Although coyotes are well studied, their population structure is not well understood because previous researchers using very high frequency (VHF) collars were limited in their ability to document behaviors of wide-ranging individuals lacking a territory (Hinton et al. 2015, Morin and Kelly 2017). Previous studies focused on territorial coyotes and their offspring because most study areas were not extensive (e.g., ≤ 500 km^2) and monitoring relied on VHF technology, so transients often moved out of study areas and could no longer be tracked or were located too infrequently to estimate space use (Mills and Knowlton 1991, Chamberlain et al. 2000, Kamler et al. 2005). This approach is problematic because coyote populations are comprised of several observable social statuses, such as dependent offspring, dispersing subadults, breeding adults, and displaced and compromised individuals (Knowlton et al. 1999, Gese 2001, Gifford et al. 2017), and VHF often fails to capture the ephemeral nature of space use exhibited by coyotes as they transition into different social statuses. Consequently, varying spatiotemporal dynamics exhibited by coyote social statuses are important life history characteristics that permit populations to persist in anthropogenic landscapes (Hinton et al. 2015, Morin and Kelly 2017). Coyotes exhibiting territorial behavior (e.g., site fidelity) are typically referred to as residents, whereas solitary, dispersing individuals are referred to as transients (Gese et al. 1988, Kamler and Gipson 2000, Berger and Gese 2007, Morin and Kelly 2017). Different interpretations on the nature of transiency in coyote ecology have arisen, with some authors considering transiency as a unique life stage (Morin and Kelly 2017), while others do not (Hinton et al. 2015, 2016) because the transient portion of canid populations consists of individuals in every age class. Regardless, authors generally agree that transiency facilitates population persistence through compensatory immigration (Knowlton et al. 1999, Hinton et al. 2015, Morin and Kelly 2017).

Transients exhibit broader movements than residents and revisit areas less often (Gese et al. 1988, Kamler and Gipson 2000; Hickman et al. 2014, Hinton et al. 2015). While transients do not represent the breeding portion of coyote populations, they still facilitate population maintenance by connecting metapopulations via emigration and many eventually become breeders (Kamler and Gipson 2000, Hinton et al. 2015, Morin and Kelly 2017). Indeed, coyotes may appear ubiquitous on the landscape because transients can comprise 20–50% of populations and traverse many types of habitats. However, the distribution of territories is patchy and uneven, as coyotes are not equally adapted for all habitat types (Richer et al. 2002, Hinton et al. 2015, Morin and Kelly 2017). Consequently, extensive space use by transients allows them to emigrate in and out of subpopulations and contributes to metapopulation dynamics through 2 mechanisms. First, territorial vacancies are continuously available on the landscape through deaths of resident coyotes, and transients often acquire residency by replacing dead residents via immigration. In general, transients are thought to occupy the less suitable areas between resident territories (Kamler and Gipson 2000, Hinton et al. 2015, Mitchell et al. 2015), and this proximity to territories allows them to enter defended areas when residents die and compete for breeding opportunities. Second, because transients can disperse long distances to replace residents, they facilitate connectivity and gene flow among metapopulations. Transients are mostly younger coyotes (e.g., pups and juveniles) that disperse from source populations with high coyote densities. Compensatory immigration by transients may support sink populations where coyote densities are lower and mortality is greater (Morin and Kelly 2017). Therefore, extensive space use by transients facilitates connectivity among metapopulations, in which their ability to replace resident breeders lost to mortality may have profound effects on metapopulation structure, genetic health, and local persistence of populations.

Studies on space use and habitat selection have yielded important insights into coyote ecology. For example, studies on coyote space use and habitat selection throughout North

America have reported average home-range sizes between 2.5–70 km^2 with coyotes selecting for open and early successional habitats over forested habitats (Litvaitis and Shaw 1980, Springer 1982, Chamberlain et al. 2000, Gehrt et al. 2009, Schrecengost et al. 2009, Bekoff and Gese 2003, Hinton et al. 2015). However, coyotes are a wide-ranging species and their populations likely operate at larger spatial scales than at what previous studies were conducted. In fact, few published studies on coyote ecology occurred in study areas >1,000 km^2 (Prugh 2005, Reed et al. 2006, McVey et al. 2013, Hinton et al. 2015). Use of advanced technology (e.g., global positioning systems) allows the study of coyotes at broader scales, which offers better opportunities to monitor extensive space use by coyotes. Consequently, information from broad-scaled studies can strengthen our current knowledge of coyote ecology and improve understanding as to how coyotes persist in human-dominant landscapes. Our objectives were to quantify space use and habitat selection by coyotes and assess differences between residents and transients. We developed resource selection functions (RSFs) to map relative probability of habitat use by coyotes across our study areas. By assessing space use and habitat selection over a broad area, we sought to identify habitat characteristics where coyotes were most likely to occur, which could better inform wildlife managers in the southeastern United States.

STUDY AREA

The study area encompassed a broad region on private and public lands in southeastern Alabama (Macon, Barbour, and Pike counties), east central Georgia (Columbia, Jefferson, Lincoln, McDuffie, and Warren counties), and western South Carolina (Aiken, Edgefield, McCormick, and Saluda counties) totaling approximately 16,200 km^2 (Fig 2.1). These sites were situated at the interface of the Piedmont and Upper coastal plains ecoregions, and contained a mix of early successional, agricultural, forested, and urban habitats. The Piedmont was dominated by loblolly (*Pinus taeda*) pine plantations, and successional pine and hardwood forests containing white oak (*Quercus alba*), southern red oak (*Q. falcata*), hickory (*Carya* spp.), loblolly pine, and shortleaf pine. Pastures and agricultural fields were also intermittent on the landscape (Griffith 2010). The Upper coastal plain shared similar characteristics to the Piedmont, consisting of pastures and agricultural fields, pine plantations, and oak-hickory-pine woodlands. Furthermore, the Upper coastal plain contained Southern mixed forests with various pines, beech (*Fagus* spp.), sweetgum (*Liquidambar styraciflua*), southern magnolia (*Magnolia grandiflora*), laurel (*Q. laurifolia*) and live oak (*Q. virginiana*), and floodplains were characterized by oaks, red maple (*Acer rubrum*), sweetgum, American elm (*Ulmus americana*), and areas of cypress (*Taxodium* spp.; Griffith 2010). Agriculture in these regions included cotton, corn, tobacco, soybeans, and peanuts.

The study areas were in a mild sub-tropical climate and experienced all 4 seasons. Summers were generally hot and humid with an average high temperature of 28.9°C, and winters were generally mild with an average low temperature of 0.94°C (Griffith 2010, Southeast Regional Climate Center: Monthly and seasonal climate information 2017). The Piedmont received an average yearly rainfall of 123 cm, whereas the Upper coastal plain received an average of 136 cm (Griffith 2010).

The study area in Alabama (AL) was comprised of 60.9% forest, 12.5% woody wetlands and riparian areas, 9.0% pasture and hay, 7.7% agriculture, and 4.2% developed land and roads (Southeast Gap Analysis Project 2008). The remaining areas were open water, upland grassland and herbaceous vegetation, deciduous tree plantations, and sparsely vegetated areas. Nearby state and federal public lands included Barbour County Wildlife Management Area (WMA) and Tuskegee National Forest. The nearest major cities were Montgomery and Troy, AL. Coyotes captured in GA and SC surrounding the Savannah River commonly dispersed into each respective trapping area, likely representing 1 population [hereafter the Savannah River Area (SRA) population]. Forest (63.1%), pasture and hay (9.5%), upland grassland and herbaceous vegetation (7.2%), developed land and roads (6.9%), and agriculture (5.8%) composed most of the SRA study area (Southeast Gap Analysis Project 2008). The remaining percentage of habitat contained areas of open water, savanna and shrub-steppe, woody wetlands and riparian, mixed upland and wetland, deciduous tree plantation, and sparsely vegetated areas. Nearby GA state lands included Clarks Hill, Fishing Creek, Germany Creek, Keg Creek, and Soap Creek WMAs, and nearby SC state lands included James L. Mason and Stevens Creek WMAs. Federal lands included Sumter National Forest in SC and numerous tracts along Lake J. Strom Thurmond owned by the US Army Corps of Engineers (USACE). The closest major cities were Augusta, GA, Aiken, SC, and Greenwood, SC.

METHODS

Coyotes were trapped by professional trappers using foothold traps with offset jaws (provide trap type) during January–February 2015–2016, and were restrained using a catchpole, muzzle, and hobbles. Coyotes were sexed and weighed, and ages were estimated by tooth wear (Gipson et al. 2000). We categorized coyotes ≥2 years old as adults, 1–2 years old as juveniles, and <1-year-old as pups. Prior to release at capture sites, we fit coyotes with mortality-sensitive G2110E satellite collars (Iridium; Advanced Telemetry Systems, Isanti, Minnesota, USA) programmed to record a location every 4 hours beginning at midnight (0000, 0400, 0800, etc.). All animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (A2014 08-025-R2) and adhered to guidelines published by the American Society of Mammalogists (Sikes et al. 2011).

Because fidelity and defense of an area are key characteristics of home range behavior in coyotes (Gese 2001), we determined stability of space use by constructing rarefaction curves for each animal using their monthly home ranges (Vaughan et al. 2011). We classified individuals that had space use plateau ≥4 months after release as residents. In other words, to be classified as a resident, a coyote needed to occupy a stable territory for at least 4 months. Furthermore, we excluded from our analyses coyotes with <120 days of locations because they were not monitored long enough to deduce if they were residents or transients. We also excluded multiple coyotes from the same territory, instead using only the coyote present within that territory the longest, to avoid pseudoreplication. We then estimated space use of resident and transient coyotes using dynamic Brownian bridge movement models (dBBMMs). For coyotes who exhibited both transiency and residency during the time they were monitored, we ran dBBMMs separately on each period. This approach uses time-specific location data to estimate probability of use along the full movement track of each animal that generates a utilization distribution (Kranstauber and Smolla 2013). We used the R package ‘move’ in program R to produce dBBMMs. We used a GPS telemetry error estimate of 20m (Frair et al. 2010) for all locations and a moving window size of 21 with a margin of 7 locations for full movement tracks of each animal. We considered the 95% and 50% contour intervals for residents as home ranges and core areas, respectively, and the 95% and 50% contour intervals for transients as transient ranges and biding areas, respectively (Hinton et al. 2015, 2016). Along with developing composite home ranges and transient ranges for residents and transients, respectively, we also developed seasonal ranges for resident and transient coyotes. Our seasons were winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov). We then compared composite space use by residents and transients using *t*-tests and compared space use among seasons using analysis of variance (ANOVA).

We estimated predominant types of vegetative cover using a 30-m resolution digital landscape map of vegetative communities developed by the Southeast Gap Analysis Project (Southeast Gap Analysis Project 2008). For the habitat selection analysis, we reduced vegetation communities to the following 9 habitat classes with a 30m resolution: agriculture, developed (urban), forest, pasture, roads, early successional (shrub), water, and wetland. We developed a road layer because previous studies reported use of roads by coyotes for travel and foraging opportunities (Hinton et al. 2015). We created distance raster maps for all habitat classes using the Euclidean Distance tool in the Spatial Analyst toolbox in ArcMap 10.3 (Environmental Systems Research Institute 2014) to calculate the distance from every pixel to the closest landscape feature (Benson 2013, Benson et al. 2015, Hinton et al. 2015). We used analysis of variance (ANOVA) and Tukey tests for multiple comparisons to determine if habitat composition of home ranges, core areas, transient ranges, and biding areas differed.

As suggested by Manly et al. (2002), we followed the Design III (3^{rd}-order selection) to assess the relationship between habitats and coyote space use within their home ranges and transient ranges. We used individual coyotes as our sampling units and measured resource availability for each animal. To estimate resource selection functions (RSFs), we used a binomial approach by comparing characteristics of known locations to 3-times the number of random locations within home ranges and transient ranges of coyotes (Manly et al. 2002, Little et al. 2016). Because we used distance-based variables to assess habitat selection, we inferred selection occurred when known locations were closer to resource features than were random locations. Likewise, we inferred avoidance when known locations were farther from resource features than were random locations. We used generalized linear mixed models with a logit link in program R to compare habitat selection between resident and transient coyotes (R Development Core Team 2013). We included random intercepts for individual coyotes in each model to account for correlation of habitat use within individuals and the unbalanced telemetry data since individual coyotes differed in their number of GPS locations. We modeled resource selection using the R package lme4 (Bates et al. 2014) with a binary (0 = random, 1 = known) response variable. Before modeling, we rescaled all distanced-based maps for habitat variables by dividing by 200m to reduce model convergence issues (Little et al. 2016).

To develop RSFs for resident and transient coyotes, we used 4 general hypotheses to design 5 a priori candidate models to test factors associated with coyote use of landscape variables. First, we assumed forested habitat provided cover and shelter for coyotes. Second, we assumed roads provided movement corridors for coyotes. Third, we assumed treeless habitats (e.g., agriculture, pasture, shrub habitats) were preferred hunting areas for coyotes. Lastly, we assumed that habitats that periodically experienced inundation, such as wetlands, were avoided by coyotes. We removed each variable (i.e. habitat class) from a global model containing all 8 variables to determine the effect of each variable on the goodness of fit for the model. This enabled us to determine which habitat class influenced coyote occurrence the most and therefore had the greatest effect on model performance and indicated selection. We ranked the resulting models using the change in Akaike's Information Criterion (ΔAIC_c) to select which models best explained the trends seen in habitat selection (Burnham and Anderson 2002, Hinton et al. 2015). To examine any potential differences in habitat selection between resident and transient coyotes, we used all telemetry locations for residents and transients, included all habitat classes as main effects, and considered interactions between coyote status (resident = 1; transient = 0) and each habitat class variable. Next, we separated the data into resident and transient locations to form separate models for deriving 3rd-order habitat selection coefficients for each habitat class without interactions. We then used these coefficients from the best model for residents and transients respectively, in conjunction with the associated rescaled distance-based variables, to generate maps showing probability of habitat use by residents and transients in the Piedmont and Upper coastal plains ecoregions. As another method of interpreting the habitat selection results, we calculated scaled odds ratios and associated 95% confidence intervals for selection coefficients. We validated our best model using *k*-fold cross-validation. We used 10 folds ($k = 10$) to estimate performance of RSF models.

RESULTS

We captured and monitored 164 coyotes across AL, GA, and SC with GPS radio collars during 2015-2016. We excluded 17 coyotes from analyses due to an insufficient number of relocations, leaving 147 coyotes. We identified 60 coyotes (40.8%) as residents and 48 (32.7%) as transients for the entire time they were monitored. Thirty-nine (26.5%) coyotes exhibited both residency and transiency. Of these, 11 (7.5%) resident coyotes left their home ranges and became transients, 21 transient coyotes eventually established residency (14.3%), and 6 (4.1%) resident coyotes became transients for time periods ranging between 2 and 9 months before establishing a new territory. There was also 1 (0.7%) transient coyote that established a territory for 5 months and then returned to transiency. Resident home ranges ranged from 2.8 to 72.9 km^2 in size and averaged 17.6 ± 14.7 km^2 (mean ± SD). Transient ranges were larger ($t_{193} = 11.196, P < 0.001$), ranging from 11.7 to 586.6 km^2 and averaged 132.7 ± 105.2 km^2. Resident core areas averaged 2.6 ± 1.6 km^2 and were smaller than transient biding areas (14.5 ± 11.6 km^2; $t_{193} = 10.444, P < 0.001$). Resident home range and core area size did not differ between the AL and

SRA populations ($t_{105} = 0.146, P = 0.884$ and $t_{105} = 0.050, P = 0.960$, respectively; Table 2.1). Similarly, transient ranges and biding areas did not differ between populations ($t_{86} = 0.160, P = 0.873$ and $t_{86} = 0.339, P = 0.735$, respectively; Table 2.1). We detected no seasonal differences among the 95% and 50% contour intervals for residents ($F_{3,325} = 1.815, P = 0.144$ and $F_{3,325} = 1.590, P = 0.192$, respectively) or transients ($F_{3,215} = 1.631, P = 0.183$ and $F_{3,215} = 2.456, P = 0.064$, respectively; Table 2.2).

Resident and transient ranges were comprised of mainly forest, pine, shrub, agriculture, and wetland habitat with minor amounts of water and urban area (Fig. 2.2). We detected no difference in the proportions of habitat within resident home ranges, core areas, transient ranges, or biding areas for urban ($F_{3,386} = 1.930, P = 0.203$), forest ($F_{3,386} = 1.225, P = 0.300$), shrub ($F_{3,386} = 0.268, P = 0.849$), pasture ($F_{3,386} = 2.497, P = 0.059$), agriculture ($F_{3,386} = 0.273, P = 0.845$), and wetland ($F_{3,386} = 0.712, P = 0.545$). Core areas and biding areas had proportionally less water than home ranges ($F_{3,386} = 2.799, P = 0.040$), but water was a minor habitat type regardless.

When we developed our RSFs, model fit improved when accounting for coyote status (resident or transient), and fitting interactions between resource variables and status to explicitly test for differences in habitat selection between residents and transients provided support that coyote status affects resource selection (Tables 2.3 and 2.4). Thus, we mapped relative probability of habitat use by transient and resident coyotes separately (Figures 2.3 and 2.4). We found that all landscape features were important predictors for resident home ranges. Residents selected agriculture, forests, shrub, and wetland habitat, but avoided urban, pasture, water, and roads. For transients, water, forests, and wetlands were not important predictors of habitat use. Like residents, transients selected agriculture, but they also selected urban areas, pastures, and roads while avoiding shrub habitats. Our *k*-fold cross-validation correctly classified 82% and 87% of locations for transients and residents, respectively.

DISCUSSION

Hinton et al. (2015) noted that mean home-range for coyotes was commonly reported to be < 70 km^2 throughout North America, and suggested that coyote body size provided a ceiling to the amount of space that coyotes could effectively defend as territories. Similarly, our findings indicate that space use and habitat selection by coyotes across a broad region of the southeastern United States were consistent when accounting for coyote social status (residents vs. transients). We observed similar patterns of space use by resident coyotes in Alabama and along the Savannah River Area of Georgia and South Carolina, as home ranges ranged from 2.8 – 72.9 km^2 with nearly 76% ≤ 20 km^2 and only 4 home ranges ≥ 50 km^2. Similarly, we observed no difference in transient space use between populations, as nearly 81% of transients traversed areas $\leq$200 km^2 before dying, establishing a territory, or collar malfunction. Because most transient coyotes are likely dispersers (Camenzind 1978, Hinton et al. 2015), areas traversed by transients are important aspects of coyote population dynamics that are currently poorly understood. Indeed, previous studies suggested that dispersal distances in mammals are influenced by body size (Wolff 1999, Sutherland et al. 2000) and home range size (Bowman et al. 2002). Therefore, it is not surprising that we observed constraints on coyote space use, regardless of status, and most transients traversed areas 5–10x the size of the average resident home range.

Overall, coyotes showed strong selection for agriculture, but residents and transients exhibited markedly different use of habitats. Residents exhibited strong selection for agriculture and forested areas including riparian woodlands, and shrub habitats. Selection for forests differs from findings in many previous studies, whereas coyotes have been shown to prefer for more open and early successional type habitats (Kamler and Gipson 2000, Schrecengost et al. 2009, Hickman et al. 2015, Hinton et al. 2015). However, some forest types (i.e. pine plantations) in our study area were quite open, particularly in early seral stages. Forests may also represent lower risk habitat to residents that reduces mortality by anthropogenic means. Conversely, transients showed selection for open habitats such as agriculture and pastures, but exhibited selection for roads and areas of human development, which residents strongly avoided. Unlike residents, transients avoided shrub habitats. Because transients traverse areas more extensively than residents, they likely favor habitats, such as roads, that improve the efficiency of the movements by reducing energetic costs related to shifting and wide-ranging space use (Hinton et al. 2012, Hinton et al. 2015)

Previous studies reported that resident coyotes comprised most (approximately 70%) individuals monitored in coyote populations (Camenzind 1978, Gese et al. 1988, Kamler and Gipson 2000, Young et al. 2006, Hinton et al. 2015). Similarly, we found that residents comprised approximately 65% of radio-marked coyotes and home ranges averaged 17.6 km^2, did not differ between populations, and remained stable among seasons. Our results suggest considerable temporal and spatial stability of home ranges in coyote populations over a broad geographic area. This was unsurprising, as other studies have reported stable space use across seasons by resident coyotes across their geographic range (Camenzind 1978, Kitchen et al. 2000, Young et al. 2006, Hinton et al. 2015, Gifford et al. 2017). Similar to Hinton et al. (2015), we observed coyotes centering their territories on edges of open habitats (e.g., agriculture and shrub) and forests with higher percentages of open habitats in the interior (i.e., core areas) as forest habitat increased in the outer fringes. Coyote home ranges rarely exceeded 40 km^2, suggesting an important limitation in the size of coyote breeding territories. Indeed, home ranges contain a finite potential of food resources and, for territorial species, home ranges reflect a balance between energetic demand and quality and spatial distribution of food resources needed for survival and reproduction (Swihart et a. 1988, Bassett 1995, Tucker et al. 2014). Because body size restricts the upper limit of areas that coyotes can effectively exploit and defend as territories, it likely has a profound effect on abundance and distribution of territories and hence, coyote density.

Although some studies have suggested increased space use by eastern coyotes is advantageous (Ellington and Murray 2015), our experience suggests that there may be strong selection pressure on coyote populations to maintain smaller home ranges in anthropogenic landscapes. Nearly 75% of coyote deaths observed in our study were attributed to gunshot mortality with the remaining mortalities largely anthropogenic in source (e.g., trapping and vehicle collisions; J. W. Hinton, University of Georgia, unpublished data). Consequently, maintaining smaller home ranges reduces exposure to mortality risks (e.g., roads, hunted properties, ranches) and promotes densities capable of compensating for local mortality rates. This is evident by the fact that urban coyotes maintain smaller home ranges than rural coyotes, despite little to no difference in body size (Gehrt et al. 2009, Gehrt et al. 2011, Gese et al. 2012). Furthermore, resident coyotes in our study exhibited strong avoidance of high risk habitats associated with human activity, such as roads and developed residential areas, which may negatively influence home range size.

Although researchers commonly suggest that transients have large home ranges (Kamler and Gipson 2000, Morin and Kelly 2017), we offer that transients do not maintain home ranges because they are typically displaced individuals, dispersing pups and juveniles, or compromised (e.g., sick or injured) individuals not constrained by mates, offspring, and territories. Instead, we refer to the large area used by transients as their transient range. Similar to other studies (Hinton et al. 2012, 2015, Morin and Kelly 2017), transients commonly exhibited localized movements (i.e., clusters of locations) for several weeks that averaged 14.5 km^2. These biding areas likely represented attempts by coyotes to assess areas for opportunities to establish territories, as most transients eventually established home ranges in biding areas. Indeed, biding areas were similar in size and habitat composition of resident home ranges, and anecdotally, we noted movement patterns responsible for them appeared comparable to area restricted search behaviors (Fauchald and Tveraa 2003, Weimerskirch et al. 2007). Although space use by transients was unstable, wide-ranging (11.7–586.6 km^2), and exhibited shifting patterns (Fig. 2.5), mean size for transient ranges was 132 km^2 and, similar to residents, we detected no differences in transient ranges between populations and observed no effect of season on size of transient ranges. Given that we observed transient movements of approximately 90 coyotes (including those coyotes who displayed both residency and transiency), we suggest that most transients traverse areas under 200 km^2 during transiency with similar habitat composition of ranges, but used those habitats differently than residents.

Predictive maps suggest that coyote territories are unevenly distributed, as predicted use of areas by resident coyotes was patchy and residents favored agricultural landscapes. However, predicted use by transients exhibited a linear and veiny distribution of use that reflects their selection for roads and other linear corridors that facilitated movements. These results suggest the existence of coyote subpopulations comprised of areas with varying densities of territories that are maintained by emigration via broad-scale movements made by transients. From a population perspective, transiency permits coyotes to fill vacuums on the landscape that become available due to mortality of residents, and facilitates rapid restructuring of populations that experience severe perturbations, as well as promoting strong gene flow among subpopulations. Consequently, we agree with others (Hinton et al. 2015, Morin and Kelly 2017) that transiency is likely an important life history strategy for coyotes that facilities population persistence.

Transient coyotes are commonly perceived as subordinate individuals who are excluded to suboptimal space unoccupied by residents, and it is likely that most resident coyotes were transients prior to establishing territories. As a result, coyote social status is fluid by nature, in which individuals enter the transient portion of populations to seek out mates and territories and transition into residents. When released from their territories as either dispersing juvenile or displaced adults, coyotes are capable of traversing large areas because of their relatively large body size, physiology, and overall need to move in response to ecological demands (Harrison 1992, Gese et al. 1996). Behaviors associated with transiency permit coyotes to seek out new territories and breeding opportunities that facilitate metapopulation dynamics through dispersal and replacement of resident breeders (Hinton et al. 2015, Morin and Kelly 2017). This trait likely promotes a relative ubiquity of coyotes across the landscape that frustrates management control efforts, as individuals will traverse areas not capable of supporting resident territories and attempts at reducing local coyote densities may have limited impact due to transient movements. Consequently, transiency is likely vital to coyote persistence as these individuals connect subpopulations via emigration, and serve as an important surplus of individuals that can rapidly repopulate areas to prevent local extinctions. To our knowledge, our study is the first to account for both resident and transient space use behaviors over a large geographic region, and we believe these findings can be useful with formulating hypotheses or building models to predict coyote population dynamics.

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Table 2.1. Mean (±SD) space use (km^2) by resident and transient coyotes in Alabama, Georgia, and South Carolina during 2015-2017.

	Size of Area Used (km^2)			
	Alabama		Savannah River Area	
Coyote Status	95%	50%	95%	50%
Resident	17.3 ± 15.4	2.6 ± 1.7	17.7 ± 14.3	2.6 ± 1.6
Transient	130.2 ± 98.1	13.9 ± 10.2	134.0 ± 109.5	14.8 ± 12.4

Table 2.2. Mean (±SD) space use (km^2) by season by resident and transient coyotes in Alabama, Georgia, and South Carolina during 2015-2017.

	Size of Area Used (km^2)							
	Spring[a]		Summer[b]		Fall[c]		Winter[d]	
Status	95%	50%	95%	50%	95%	50%	95%	50%
Resident	17.9 ± 20.7	2.2 ± 1.9	13.2 ± 8.8	2.3 ± 1.4	15.0 ± 11.5	2.6 ± 1.5	18.0 ± 17.7	2.7 ± 1.9
Transient	98.3 ± 82.4	9.9 ± 9.3	84.6 ± 69.0	8.9 ± 7.1	64.4 ± 43.3	7.3 ± 6.5	85.6 ± 93.5	6.7 ± 6.2

[a]Mar–May; [b]Jun–Aug; [c]Sep–Nov; [d]Dec–Feb

Table 2.3. Comparison of model fit among models with or without interactions used to test hypotheses about coyote resource selection at the 3rd order in Alabama, Georgia, and South Carolina, 2015-2016. Shown are Akaike's Information Criteria for small sample sizes (AIC_c), differences among AIC_c (ΔAIC), and the conclusion regarding whether there was strong support for the interaction.

Models	k	AIC_c	Deviance	ΔAIC	Conclusions
Interactions	19	726,294.8	726,256.8	0	Interactions strongly supported
No interactions	9	727,510.5	727,490.5	1,215.7	
Null	2	728,174.5	728,170.5	1,879.7	

Table 2.4. Summary of results from generalized linear mixed models for predicting 3rd-order coyote habitat selection by transient and resident coyotes in Alabama, Georgia, and South Carolina, 2015-2017. Shown are β coefficients, standard error (SE), *z*-scores, *P*-values, odds ratios and their associated confidence intervals.

Model variables	β	SE	*z*	*P*	Odds ratio	Lower 95%	Upper 95%
Intercept	-3.298	0.308	-10.707	<0.001	0.427	0.377	0.484
Agriculture	-0.105	0.011	-9.851	<0.001	0.974	0.971	0.977
Status	-0.127	0.121	-1.052	0.293	0.949	0.932	0.966
Urban	-0.070	0.006	-11.510	<0.001	0.789	0.714	0.873
Forest	0.008	0.004	1.897	0.058	0.721	0.691	0.752
Pasture	-0.069	0.006	-11.785	<0.001	1.428	1.317	1.547
Roads	-0.045	0.006	-8.030	<0.001	1.391	1.296	1.494
Shrub	0.026	0.005	4.945	<0.001	0.919	0.901	0.937
Water	-0.005	0.005	-0.931	0.352	1.178	1.137	1.221
Wetlands	-0.008	0.005	-1.589	0.112	0.969	0.965	0.972
Agriculture x Status	-0.078	0.019	-4.062	<0.001	1.167	1.134	1.200
Urban x Status	0.111	0.009	12.669	<0.001	1.203	1.034	1.401
Forest x Status	-0.097	0.006	-15.171	<0.001	1.333	1.260	1.410
Pasture x Status	0.099	0.009	11.045	<0.001	0.299	0.257	0.347
Roads x Status	0.064	0.008	8.085	<0.001	0.695	0.626	0.770
Shrub x Status	-0.080	0.007	-11.408	<0.001	1.224	1.188	1.262
Water x Status	0.083	0.007	12.482	<0.001	0.861	0.817	0.907
Wetlands x Status	-0.027	0.007	-4.019	<0.001	0.919	0.901	0.937

Table 2.5. Summary of generalized linear mixed models for predicting coyote habitat use corresponding to different landscape features potentially affecting 3rd-order habitat selection by transient and resident coyotes in Alabama, Georgia, and South Carolina, 2015-2017. Shown are Akaike's Information Criteria for small sample sizes (AIC_c) and differences among AIC_c (ΔAIC).

Status	Models	k	AIC_c	Deviance	ΔAIC
Resident	Full model	9	413,471	413,451	0
	No roads- Ag+Ur+For+Past+Shr+Wa+Wet	8	413,480	413,462	9
	No pasture- Ag+Ur+For+Rd+Shr+Wa+Wet	8	413,488	413,470	17
	No urban- Ag+For+Past+Rd+Shr+Wa+Wet	8	413,511	413,493	40
	No wetland- Ag+Ur+For+Past+Rd+Shr+Wa	8	413,529	413,511	58
	No agriculture- Ur+For+Past+Rd+Shr+Wa+Wet	8	413,598	413,580	127
	No shrub- Ag+Ur+For+Past+Rd+Wa+Wet	8	413,606	413,588	135
	No water- Ag+Ur+For+Past+Rd+Shr+Wet	8	413,764	413746	293
	No forests- Ag+Ur+Past+Rd+Shr+Wa+Wet	8	413,860	413,842	389
Transient	No water- Ag+Ur+For+Past+Rd+Shr+Wet	8	312,969	312,951	0
	Full model	9	312,970	312,950	1
	No wetland- Ag+Ur+For+Past+Rd+Shr+Wa	8	312,971	312,953	2
	No forests- Ag+Ur+Past+Rd+Shr+Wa+Wet	8	312,972	312,954	3
	No shrub- Ag+Ur+For+Past+Rd+Wa+Wet	8	312,992	312,974	23
	No roads- Ag+Ur+For+Past+Shr+Wa+Wet	8	313,032	313,014	63
	No agriculture- Ur+For+Past+Rd+Shr+Wa+Wet	8	313,065	313047	96
	No urban- Ag+For+Past+Rd+Shr+Wa+Wet	8	313,103	313,085	134
	No pasture- Ag+Ur+For+Rd+Shr+Wa+Wet	8	313,111	313,093	142

Table 2.6. Parameter estimates for the best 3^{rd}-order resource selection function for radio-collared coyotes in Alabama, Georgia, and South Carolina during 2015-2016. Shown are β coefficients, standard error (SE), *z*-scores, *P*-values, odds ratios and their associated confidence intervals.

Status	Model variables	β	SE	*z*	*P*	Odds ratio	Lower 95%	Upper 95%
Resident	Intercept	-1.438	0.531	-2.71	0.007	0.234	0.099	0.551
	Agriculture	-0.182	0.016	-11.32	<0.001	0.815	0.789	0.841
	Urban	0.041	0.006	6.51	<0.001	1.069	1.056	1.082
	Forest	-0.088	0.005	-19.41	<0.001	1.072	1.062	1.082
	Pasture	0.030	0.007	4.37	<0.001	1.028	1.014	1.042
	Roads	0.018	0.006	3.35	0.001	1.044	1.033	1.055
	Shrub	-0.054	0.005	-11.62	<0.001	0.946	0.937	0.955
	Water	0.079	0.005	17.19	<0.001	1.097	1.087	1.107
	Wetlands	-0.035	0.005	-7.72	<0.001	0.961	0.953	0.970
Transient	Intercept	-0.499	0.698	-0.72	0.475	0.608	0.191	1.939
	Agriculture	-0.104	0.011	-9.84	<0.001	0.905	0.887	0.925
	Urban	-0.071	0.006	-11.65	<0.001	0.933	0.922	0.944
	Forest	0.009	0.004	1.93	0.054	0.968	0.959	0.978
	Pasture	-0.069	0.006	-11.76	<0.001	0.939	0.929	0.950
	Roads	-0.045	0.006	-7.98	<0.001	0.953	0.943	0.963
	Shrub	0.026	0.005	4.87	<0.001	1.030	1.019	1.041
	Wetlands	-0.008	0.005	-1.75	0.081	0.995	0.985	1.005

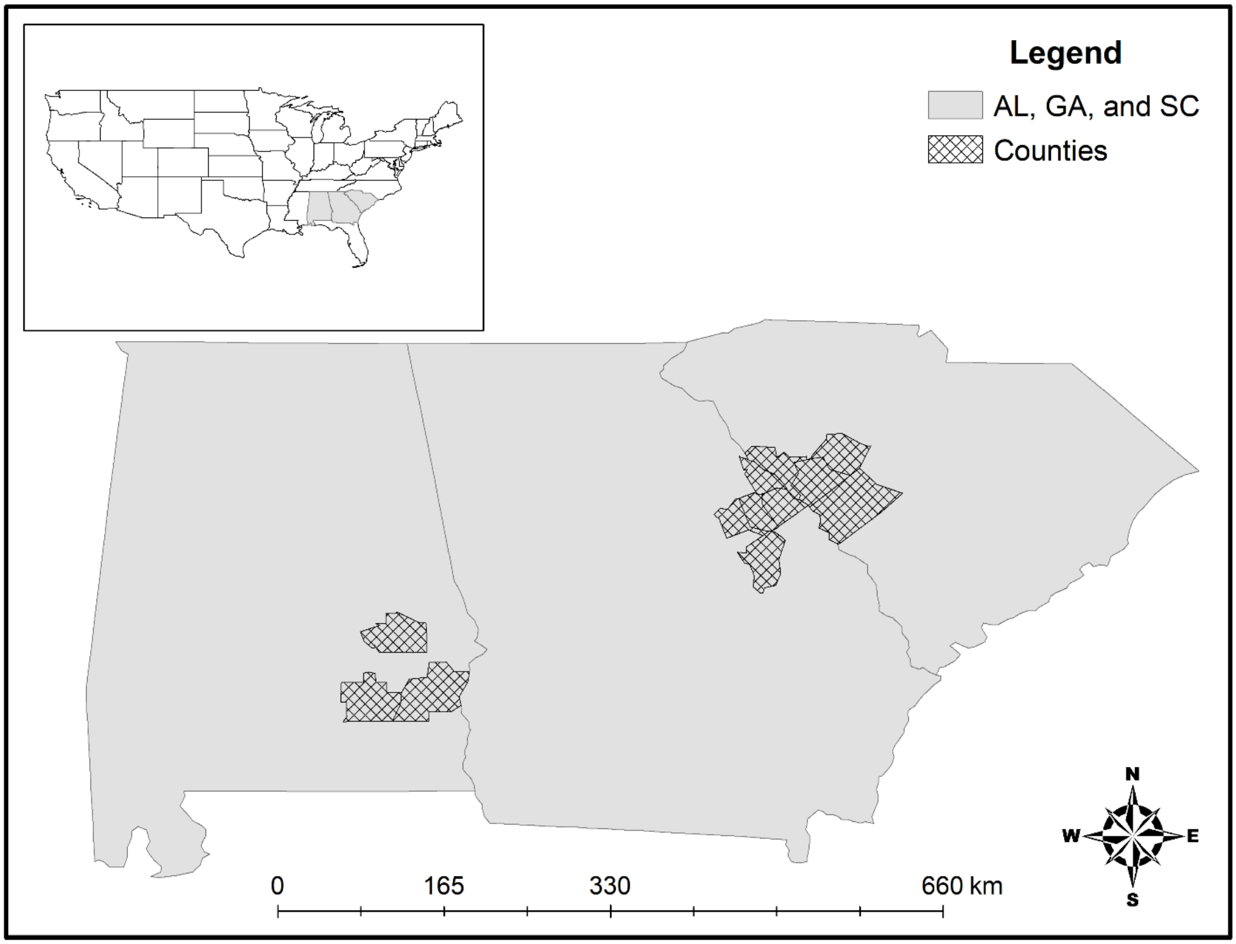

Fig. 2.1. Map of counties (noted as shaded area) in Alabama, Georgia, and South Carolina, USA, where coyotes were trapped during 2015–2016.

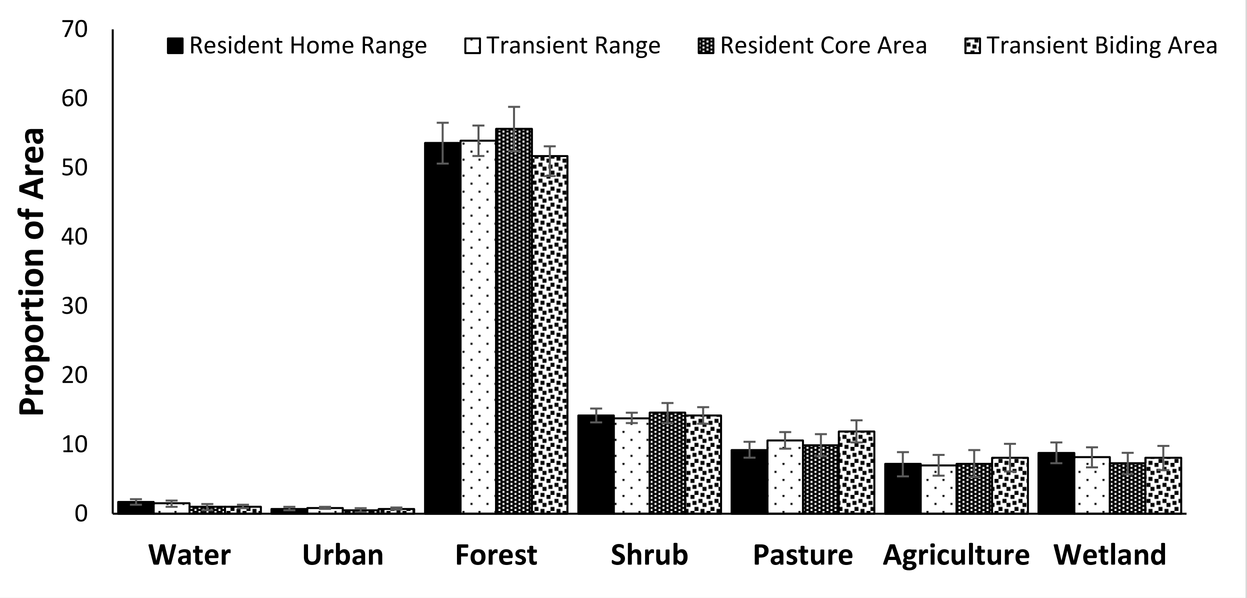

Fig. 2.2. Proportion of habitats within the 95% and 50% contour interval of resident and transient coyotes in Alabama, Georgia, and South Carolina during 2015-2017. Error bars represent 95% confidence intervals.

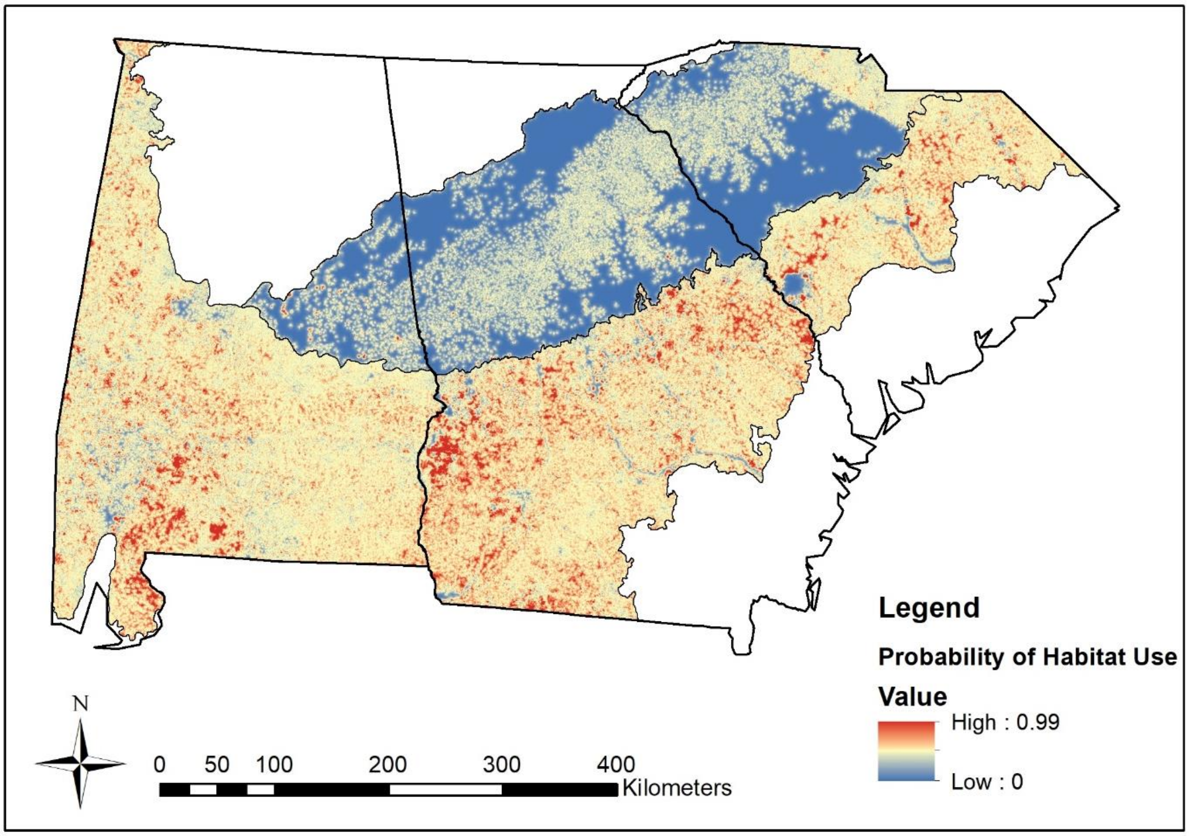

Fig. 2.3. Relative probability of 3rd-order habitat selection by resident coyotes in the Piedmont and Upper Coastal Plains ecoregions of Alabama, Georgia, and South Carolina during 2015-2017. Selection indicated by red and avoidance indicated by blue.

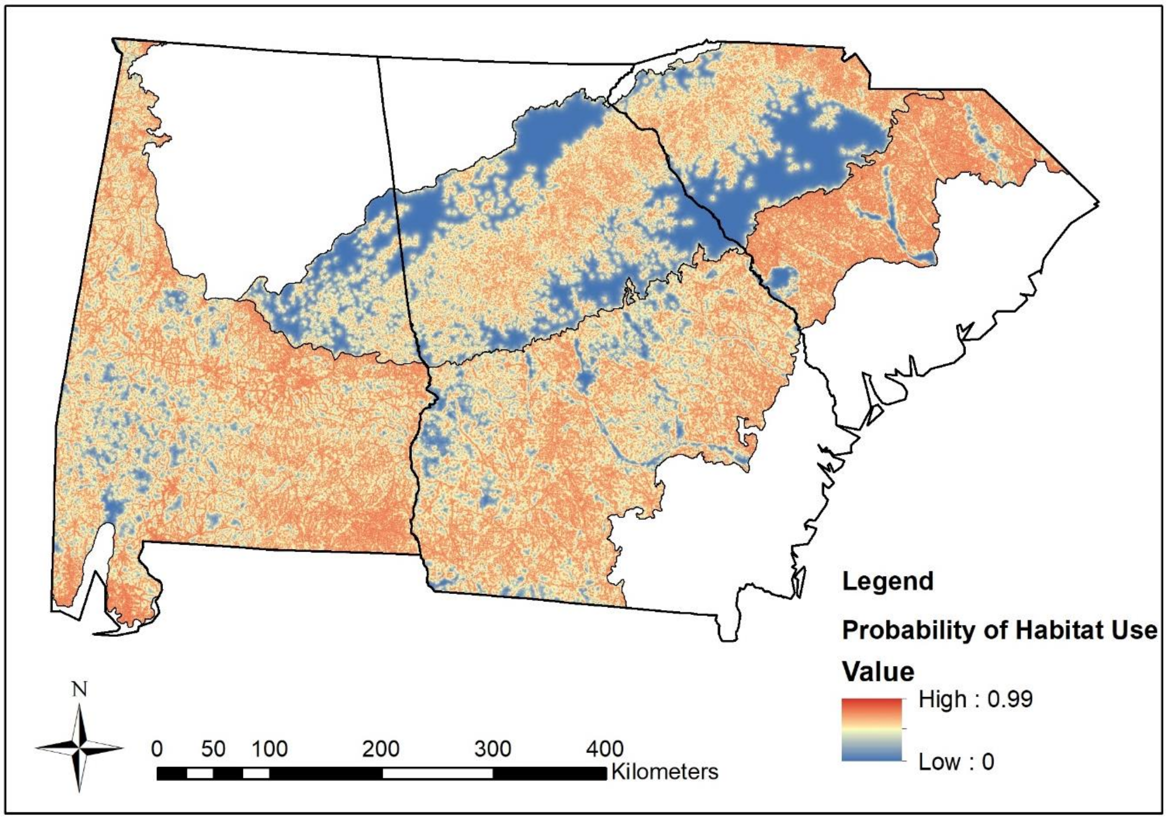

Fig. 2.4. Relative probability of 3rd-order habitat selection by transient coyotes in the Piedmont and Upper Coastal Plains ecoregions of Alabama, Georgia, and South Carolina during 2015-2017. Selection indicated by red and avoidance indicated by blue.

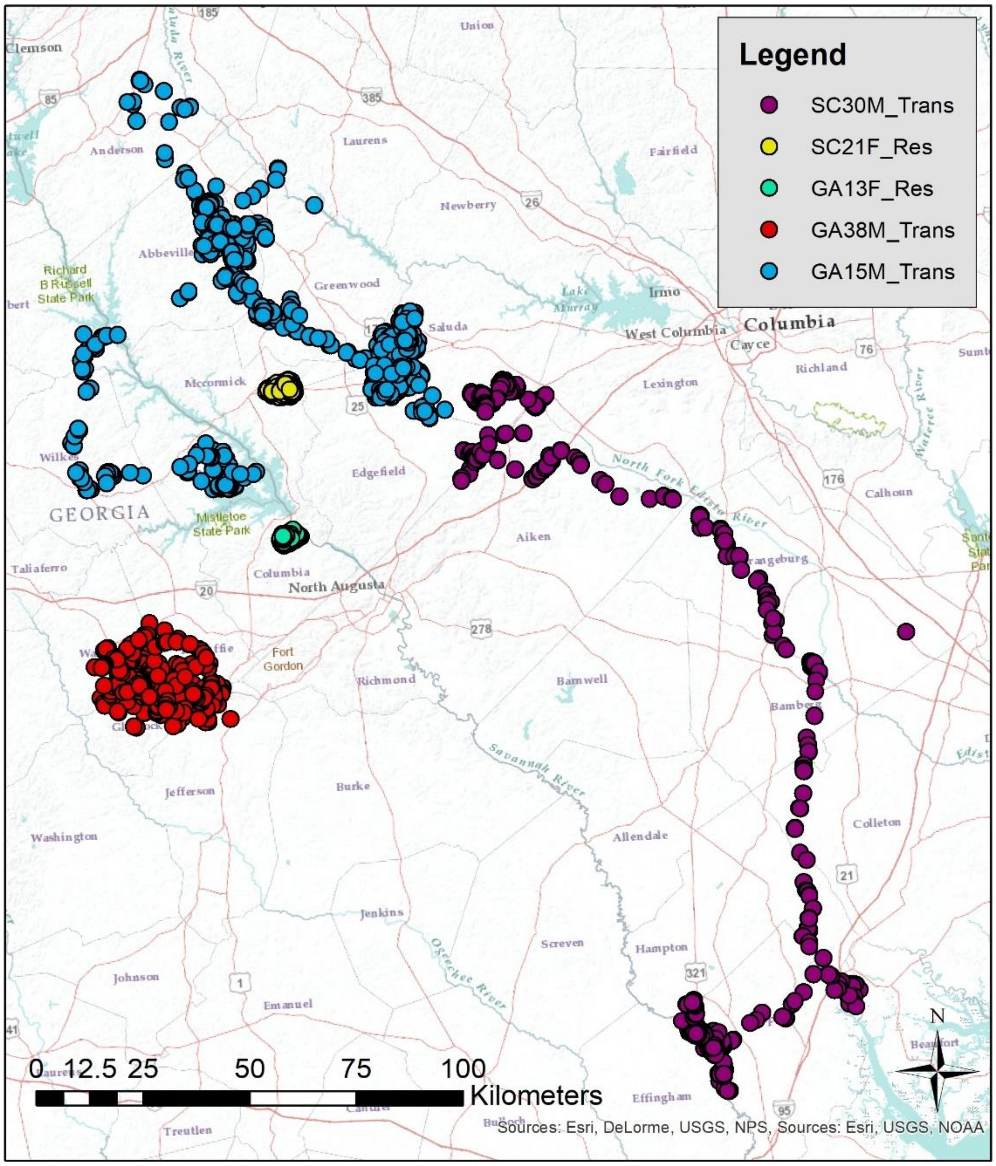

Fig. 2.5. Map showing the variability in transient space use, ranging from almost linear movements (SC30M) to movements within a more localized but still broad area (GA38M) to space use that is a combination of those movements (GA15M). In comparison, resident space use (SC21F and GA13F) is more constrained within territories. Points of the same color are relocations from the same coyote.

CHAPTER 3

SIZE AND HABITAT COMPOSITION OF HOME RANGES INFLUENCES PREY USE BY COYOTES IN THE SOUTHEASTERN UNITED STATES[1]

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[1] Ward, J. N., J. W. Hinton, T. Johannsen, M. Karlin, K. V. Miller, and M. J. Chamberlain. To be submitted to the Journal of Mammalogy.

ABSTRACT

To ensure reproductive success, coyotes establish and hold territories as family units. Coyotes exclude neighboring packs and solitary individuals (transients) from their territories so that transients traverse peripheral areas of territories and in areas of unoccupied by residents. We assessed prey use by coyotes by sampling scats from within known territories in southeastern Alabama and the Savannah River area of Georgia and South Carolina. By accounting for territories over a broad area, we incorporated the influence of space use and vegetative cover on coyote diets. Use of prey items was influenced by a combination of home-range size, habitat composition of home ranges, and mean monthly temperature. Use of white-tailed deer, rabbits (*Sylvilagus* spp), small mammals, and fruit was influenced by season, and the size and habitat composition of home ranges, indicating that resident coyotes can exploit a fluctuating prey base, despite their constrained space use. For example, use of adult deer was associated with cooler months, smaller coyote home ranges, and woody wetlands, whereas use of rabbits was associated with cooler months and open habitats, such as agriculture and grasslands. It appears that differential use of prey by coyotes is influenced by habitat heterogeneity within their home ranges and prey-switching behaviors may stabilize local interactions between coyotes and their food resources to permit stable year-round territories. Given that habitat composition affects coyote prey use, future studies should also incorporate effects of habitat composition on coyote distribution and abundance in efforts to further identify coyote influence on prey communities.

INTRODUCTION

Understanding prey selection by predators is a fundamental goal in ecology because it represents an essential ecological process influencing behavior, community structure, and ecosystem productivity. Coyotes (*Canis latrans*), the most widely distributed *Canis* species in North America, are generalist carnivores that have broad diets (Knowlton et al. 1999, Bekoff and Gese 2003). Although coyote prey use is influenced by relative prey densities, habitat, and seasonal prey availability, most studies across North America indicate that coyote prey extensively on mammals (e.g. lagomorphs, small mammals, ungulates) and use fruit during summer (Patterson et al. 1998, Knowlton et al. 1999, Patterson and Messier 2000, Bartel and Knowlton 2005, Cherry et al. 2016). Consequently, coyotes exhibit frequency-dependent switching strategies, in which their moderate body size (9–23 kg; Way 2007) permits them to use a broad range of mammalian prey that vary from small mammals (Gese et al. 1996*a*, O’Donoghue et al. 1998, Prugh and Oksanen 2005) to large ungulates (Gese and Grothe 1995, Lingle and Pellis 2002, Benson et al. 2017, Hinton et al. 2017).

Prior to the 20th century, coyotes were restricted to the central and western regions of North America (Young and Jackson 1951, Nowak 2002). Within their historic range, coyotes coexisted with larger gray wolves (*C. lupus*) that are a primary predator of large ungulate species, such as bison (*Bison bison*), elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Coyotes, like gray wolves, form packs via delayed dispersal of offspring (Gese et al. 1996*b*, Knowlton et al. 1999), indicating that a significant proportion of their populations reside and restrict foraging within territories. Although interspecific territoriality and spatial segregation occurs among *Canis* species when competing for limiting resources (Benson and Patterson 2013), coyotes and gray wolves routinely exhibit weak spatial segregation by which coyotes are able to exploit wolf-killed ungulates for scavenging (Paquet 1992, Berger and Gese 2007, Atwood and Gese 2010). Apart from central Ontario, Canada and northeastern North Carolina, USA, coyotes in eastern North America do not coexist with larger canids and, where they do co-occur with eastern wolves (*C. lycaon*) and red wolves (*C. rufus*), coyotes exhibit strong spatial segregation from the 2 eastern wolf species (Benson and Patterson 2013, Hinton et al. 2017). In nearly all of the eastern United States, coyotes do not compete with larger canids for use of white-tailed deer, the predominant native ungulate species of the region. Consequently, eastern coyotes may experience fewer opportunities for scavenging large ungulates than their western counterparts because of the absence of larger carnivores and fewer ungulate species in most of the eastern United States.

Coyote use of white-tailed deer has generated considerable concern by wildlife managers in the southeastern United States (Kilgo et al. 2010, Robinson et al. 2014) and studies of eastern coyotes provide notable contradictions on coyote use of deer. For example, early studies conducted on coyote diets in the eastern United States, likely relying on literature from western studies of coyote diets to interpret their results, assumed the occurrence of deer in coyote diet was a result of scavenging (Wooding et al. 1984, Lee and Kennedy 1986, Stratman and Pelton 1997). Recent studies have demonstrated widespread predation on fawns by coyotes during spring and summer (Saalfield and Ditchkoff 2007, Kilgo et al. 2012, Chitwood et al. 2015), but the ability of coyotes to kill adult deer throughout the year in the southeastern United States is unknown. Hence, many researchers still assume the occurrence of deer in coyote scats during fall and winter is a result of scavenging road- or hunter-killed deer, and the opportunistic take of deer wounded by hunters. Conversely, some authors have suggested scavenging by coyotes does not fully explain their use of white-tailed deer and that coyotes are likely capable of preying upon deer year-round. For example, Cherry et al. (2016) observed greater use of adult deer by coyotes after rather than during the firearm hunting season, which could not be accounted for by scavenging alone. Additionally, Hinton et al. (2017) observed a positive correlation between coyote body mass and occurrence of white-tailed deer in coyote diets and suggested that body size likely influenced coyote predation of deer. Furthermore, Hinton et al. (2017) reported that low occurrence of species commonly found as roadkill in coyote diets suggested that coyotes did not exploit roadways for scavenging opportunities. Regardless, interactions between coyotes and white-tailed deer in the southeastern United States remain poorly understood.

Because coyotes are cooperative breeders and social units spatially segregate on the landscape (Benson and Patterson 2013, Hinton et al. 2015, 2017), effects of coyote predation are likely greatest in areas where prey populations and coyote territories overlap, as observed in wolves (Mech 1977, Mech et al. 1980). Accordingly, studies that analyze scats to assess coyote diets should account for residency because coyote occurrence can vary greatly on the landscape (Hinton et al. 2015) and studies conducted across small study sites may artificially inflate sample sizes and incorporate pseudo-replication in their analyses by treating scats, rather than territories, as sampling units (Dellinger et al. 2011, Hinton et al. 2017). Therefore, we conducted a broad-scaled assessment of prey use by resident coyotes in 2 separate populations in southeastern Alabama and the Savannah River area of Georgia and South Carolina. By accounting for territories over a broad area, we were able to assess the influence of space use and vegetative cover on prey use by coyotes. Coyote food habits are diverse and we hypothesized that size and habitat composition of home ranges would influence the frequency of prey observed in coyote diets. By assessing coyote prey use over broad geographic regions, we sought to better understand how residency and habitat composition of territories influenced coyote predation on local prey species, such as white-tailed deer.

STUDY AREA

The study area encompassed a broad region on private and public lands in southeastern Alabama (Barbour, Macon, and Pike Counties), east-central Georgia (Columbia, Jefferson, Lincoln, McDuffie, and Warren Counties), and western South Carolina (Aiken, Edgefield, McCormick, and Saluda Counties) totaling approximately 16,200 km^2 (Figure 3.1). These sites were situated at the interface of the Piedmont and Southeastern Plains ecoregions, and contained a mix of early successional, agricultural, forested, and urban habitats. The Piedmont was dominated by loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine plantations, and successional pine and hardwood forests containing white oak (*Quercus alba*), southern red oak (*Q. falcata*), hickory (*Carya* spp.), loblolly pine, and shortleaf pine, and pastures and agricultural fields were also intermittent on the landscape (Griffith 2010). The Southeastern Plains shared similar characteristics to the Piedmont, consisting of pastures and agricultural fields, pine plantations, and oak-hickory-pine woodlands; however, longleaf pine (*P. palustris*) dominated in this region. Furthermore, the Southeastern Plains contained southern mixed forests with various pines, beech (*Fagus* spp.), sweetgum (*Liquidambar styraciflua*), southern magnolia (*Magnolia grandiflora*), laurel oak (*Q. laurifolia*) and live oak (*Q. virginiana*), and floodplains were characterized by oaks, red maple (*Acer rubrum*), sweetgum, American elm (*Ulmus americana*), and areas of cypress (*Taxodium* spp.; Griffith 2010). Agriculture in these regions included cotton, corn, tobacco, soybeans, and peanuts.

The study areas were in a mild sub-tropical climate and experienced all 4 seasons, as summers were generally hot and humid with an average high temperature of 20°C, and winters were generally mild with an average low temperature of 1°C (Griffith 2010, Southeast Regional Climate Center 2017). The Piedmont received an average yearly rainfall of 123 cm, whereas the Southeastern Plains received an average of 136 cm (Griffith 2010).

Potential food items for coyotes included rabbits (*Sylvilagus* spp.), wild turkeys (*Meleagris gallopavo*), white-tailed deer, wild hog (*Sus scrofa*), eastern woodrats (*Neotoma floridana*), hispid cotton rats (*Sigmodon hispidus*), mice (*Peromyscus* spp.), shrews (*Blarina* spp., *Sorex* spp.), voles (*Microtus* spp.), armadillos (*Dasypus novemcinctus*), oppossums (*Didelphis virginiana*), squirrels (*Sciurus* spp.), insects, persimmons (*Diospyros virginiana*), blackberry (*Rubus* spp.), wild plums (*Prunus* spp.), pokeweed (*Phytolacca americana*), wild grape (*Vitis* spp.), and black cherry (*Prunus serotina*; Schrecengost et al. 2008, Kelly et al. 2015, Cherry et al. 2016). Other carnivores in competition for these food items included raccoons (*Procyon lotor*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), and bobcat (*Lynx rufus*; Griffith 2010).

The study area in Alabama was comprised of 56.5% forest and woodland, 12.5% woody wetlands and riparian areas, 9.0% pasture and hay, 7.7% agriculture, 4.4 % evergreen plantation, and 4.2% developed land and roads. The remaining areas were open water, upland grassland and herbaceous vegetation, deciduous tree plantations, and sparsely vegetated areas. Nearby state and federal public lands included Barbour County Wildlife Management Area (WMA) and Tuskegee National Forest. Coyotes captured in Georgia and South Carolina commonly dispersed into each respective trapping area, and likely represented 1 population [hereafter the Savannah River Area (SRA) population]. Forest and woodland (40.0%), evergreen plantation (23.1%), pasture and hay (9.5%), upland grassland and herbaceous vegetation (7.2%), developed land and roads (6.9%), and agriculture (5.8%) composed most of the SRA study area. The remaining percentage of habitat contained areas of open water, savanna and shrub-steppe, woody wetlands and riparian, mixed upland and wetland, deciduous tree plantation, and sparsely vegetated areas. Nearby Georgia state lands included Clarks Hill, Fishing Creek, Germany Creek, Keg Creek, and Soap Creek WMAs, and nearby South Carolina state lands included James L. Mason and Stevens Creek WMAs. Federal lands included Sumter National Forest in South Carolina and numerous tracts along Lake J. Strom Thurmond owned by the United States Army Corps of Engineers.

We recognized that coyotes could directly prey on white-tailed deer via take of fawns and adults, or through opportunistic take of animals wounded by hunters and carcasses. Availability of deer in these 2 populations differed somewhat due to different hunting season dates and timing of deer reproduction (e.g., breeding and parturition dates). In the Alabama population, peak breeding occurred from early January through mid-February (C. Cook, Alabama Department of Conservation and Natural Resources, unpublished data; Cook and Gray 2003), hence parturition in Alabama peaked during July and August, with neonates available from July through October. In the SRA, peak breeding occurred from early October through mid-November (Stickles et al. 2015, Ruth and Cantrell 2017), so peak parturition occurred during May and June. However, breeding dates were highly variable in the SRA, hence fawns were available to some degree from March through August. Therefore, across our study areas, neonate fawns were available to coyotes for 8 months of the year. Deer hunting occurred throughout both study sites. In our Alabama study areas, hunting began on 15 October and ended on 10 February. In our Georgia study areas, hunting began on 10 September and ended on 8 January. Finally, in our South Carolina study areas, hunting began 15 September and ended 1 January. Consequently, human hunting provided a seasonally available source of deer to coyotes across 6 months during fall and winter.

METHODS

We used professional trappers to capture coyotes using foothold traps with offset jaws during January–February 2015–2016. Animals were restrained using a catchpole, muzzle, and hobbles. We determined animal sex and weight, and estimated age by tooth wear (Gipson et al. 2000). We categorized coyotes ≥2 years old as adults, 1–2 years old as juveniles, and <1-year-old as pups. Prior to release at capture sites, we fit coyotes with mortality-sensitive G2110E satellite collars (Iridium; Advanced Telemetry Systems, Isanti, Minnesota, USA) programmed to record a location every 4 hours beginning at midnight (0000, 0400, 0800, etc.). All animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (A2014 08-025-R2) and adhered to guidelines published by the American Society of Mammalogists (Sikes et al 2011).

Because our goal was to evaluate prey use by resident coyotes, we determined stability of space use using a rarefaction curve for each animal by calculating monthly home ranges (Dellinger et al. 2013). We identified resident coyotes as animals that resided in an area and showed stable space use for ≥4 months. We then calculated annual home ranges and core use areas using 95% and 50% fixed kernel density estimates from utilization distributions performed in Geospatial Modelling Environment using the h-plugin smoothing parameter (GME; Beyer 2014) and ArcMap 10.3 (Environmental Systems Research Institute 2014). We used *t*-tests to compare mean home range sizes between the AL and SRA populations.

Once we identified resident coyotes after 4 months of monitoring, we estimated home ranges and began collecting scats along roads, trails, and other areas within and proximate to core areas within known territories at least once a month during January 2016–January 2017 (Fig. 3.2). This approach minimized the chance of collecting scats from transient coyotes, as resident coyotes typically exclude unrelated conspecifics from their territories (Benson and Patterson 2013, Hinton et al. 2017). For example, Dellinger et al. (2011) matched 96% of 196 scats to the genotypes of individual red wolves in territories they sampled, showing inclusion of non-pack member scats was low. Nevertheless, we recognize that our sample likely included scats not belonging to resident coyotes maintaining each territory, but we offer that this occurred infrequently.

We placed scats in plastic bags labeled with the date and a unique identification number, and stored them at -20.0°C for future analysis. We dried scats in an oven at 85°C for 48 h and then bagged individual scats in nylon stockings with waterproof labels and soaked them in water for 24 h prior to washing. We washed scats in a washing machine twice on the regular cycle with detergent. This separated hair, bone, and other undigested food items from fecal material. We subsequently dried scats in a drying oven at 50°C for 48 h prior to examining scat contents. To identify prey remains in scat, we visually analyzed each scat for food items, which we assigned to 1 of 5 categories: white-tailed deer, rabbits, small mammals (mice, rats, shrews, and voles), plants, and other food items (birds, insects, opossum, raccoon, armadillo, cattle, reptiles and anthropogenic material). As needed, we examined food items microscopically or compared them to reference collections for identification. To further assess the use of deer, we differentiated adult deer hair in scats from fawns. We measured hair widths using an eyepiece reticule with a microscope and categorized hairs $\leq$ 80 micrometers as fawns and hairs >80 micrometers as adults (Adorjan and Kolenosky 1969). We recorded frequency of occurrence (FO) of each food category for each scat. When an item constituted $\leq$ 1% of a scat it was treated as a trace item and excluded from analyses (Ciucci et al. 1996, Dellinger et al. 2011, Hinton et al. 2017). We chose to use FO because it is the most commonly used method in diet studies and is readily interpretable (Klare et al. 2011, Larson et al. 2015). Although FO is known to overestimate the importance of small prey and underestimate importance of large prey, it is highly concordant for ranking food items in diets of carnivores and can provide valuable insight into resource use (van Dijk et al. 2007, Klare et al. 2011, Larson et al. 2015). We analyzed the effects of population (Alabama vs SRA) and month on the FO prey categories using univariate statistical methods, such as *t*-tests, analysis of variances (ANOVAs), and Tukey tests for multiple comparisons.

By identifying territories, we accounted for other factors, such as home range size, population (Alabama or SRA), and habitat composition within home ranges. We estimated predominant types of vegetative cover using a 30-m resolution digital landscape map of vegetative communities developed by the Southeast Gap Analysis Project (GAP; Southeast Gap Analysis Project 2008). We reduced these predominant vegetative communities to 4 primary vegetative communities (agriculture and pastureland, grasslands, forested areas, and woody wetlands) and calculated the proportion of home ranges consisting of these communities. Forested communities included both deciduous and evergreen habitats, and woody wetlands contained forest or shrub vegetation that accounted for at least 20% of cover and soils periodically inundated with water (Southeast GAP Analysis Project 2008). We used *t*-tests to determine if the proportion of habitat types that made up coyote home ranges differed between the Alabama and SRA populations.

Biological seasons are influenced by phenology, which is known to vary over large geographic areas. Therefore, we incorporated mean monthly temperatures to create a continuous variable that better captured seasonal variation than calendar months, as phenology is largely driven by temperature. We also used FO of each prey item as a binary response variable (1 = present in scat, 0 = absent from scat) in generalized linear mixed models with a logit link using

Program R (R Development Core Team 2013) to determine which factors influenced FO of each prey item observed in scats. These factors included mean monthly temperature, population, home-range size, agriculture and pastures, woodlands, grasslands, and woody wetlands. We included random intercepts for coyote packs to account for pack variation. Prior to modeling, we rescaled values for all continuous variables by subtracting their mean and dividing by 2 standard deviations (Gelman 2008) and conducted correlation analysis to ensure that independent variables were not highly correlated ($r < 0.7$).

We developed 7 biologically relevant *a priori* models using 7 general hypotheses to test factors that may influence coyote use of each prey item. First, we used a binary variable for population (1 = SRA, 0 = Alabama) because we hypothesized that prey use differed between populations because diets can fluctuate over wide geographic areas. Second, we hypothesized that prey use by coyotes would be influenced by mean monthly temperature. Increased temperatures during summer can discourage attempts to pursue large prey because physically demanding activities during peak summer temperatures may expose coyotes to heat stress (Speakman and Krol 2010, Terrien et al. 2011), and availability of certain prey (e.g., fawns and fruits) are associated with warmer temperatures. Third, we hypothesized that coyotes with larger home-ranges occupied lower quality habitat and would have relatively less white-tailed deer in their diet when compared to coyotes with small home ranges, because coyotes are assumed to be optimal foragers and large prey, such as white-tailed deer, should provide greater return per unit foraging effort (Pyke et al. 1977, MacCracken and Hansen 1987, Sacks and Neale 2002). Fourth, we hypothesized agriculture and pastures would influence prey use because coyotes are known to associate with agricultural habitats (Richer et al. 2002, Gosselink et al. 2003, Hinton et al. 2015, Cherry et al. 2017). Fifth and sixth, because coyotes are known to be cursorial predators and are associated with open habitats, we hypothesized that grasslands would increase their ability to hunt mammalian prey, whereas woodlands would decrease this ability (Van Valkenburgh 1985, Pierce et al. 2000, Richer et al. 2002). Finally, because coyotes are known to avoid wetlands in the southeastern United States (Hinton et al. 2015, Cherry et al. 2017), we hypothesized that woody wetlands would decrease their ability to hunt mammalian prey.

Generally, the number of models (*R*) should be less than sample sizes and model sets should range between 8–20 (Burnham et al. 2011). Therefore, we did not consider all possible model combinations because *R* would exceed our sample size and because it commonly leads to overfitting (Anderson and Burnham 1999, Burnham and Anderson 2002, Anderson 2008). To create a balanced model set (each variable represented in equal number of models), we removed each of the 7 variables from the global model for each prey item to compare performances of varying model sets to the global models. We also included the intercept-only model for each prey item as a baseline for comparison (Burnham et al. 2011). Removing each variable from the global model enabled us to determine which variable most influenced prey use and therefore had the greatest effect on model performance. We ranked the resulting models using the change in Akaike's Information Criterion (ΔAIC_c) to select which models best explained trends in prey use (Burnham and Anderson 2002).

RESULTS

We collected 1,100 scats from 25 territories during January–December 2016. The mean and standard deviation of scats collected per pack was 44±25. Overall, 92±33 scats were collected per month. Home range size varied from 5.8 km^2 to 29.6 km^2, and average home range size and standard deviation across populations was 16.5±6.5 km^2. We detected a weak difference between populations (t_{23}=1.74, P=0.095), which coyotes in Alabama had larger home ranges than those in the SRA (19.6±5.2 km^2 vs 15.0±6.7 km^2). Core area size varied from 1.0 km^2 to 6.1 km^2, and average home range size and standard deviation across populations was 3.2±1.3 km^2, and did not differ between populations (t_{23}=0.80, P=0.435). Average percentage of forested habitat across populations was 65.5±15.0, and home ranges of coyotes in the SRA were comprised of lower proportions of forested habitat than in Alabama (61.0% vs. 75.1%; t_{23}=-2.39, P=0.026). Grasslands averaged 9.2±5.6% across populations, but home ranges of coyotes in the SRA were comprised of greater proportions of grasslands than in Alabama (12.2% vs. 3.0%; t_{23}=5.42, P<0.001). Average percentage of woody wetlands within coyote home ranges was 8.1±7.3, but home ranges in Alabama were comprised of greater proportions of woody wetlands than in the SRA (16.7% vs. 4.1%; t_{23}=-6.79, P<0.001). However, the proportions of agriculture and pastureland within coyote home ranges did not differ between populations (t_{23}=-0.71, P=0.484) and averaged 14.8±9.4%.

We detected no difference in FO of deer $(t_{23} = 0.52, P = 0.652)$, adult deer $(t_{23} = -1.25, P = 0.224)$, fruits $(t_{23} = -0.31, P = 0.759)$, or other food items $(t_{23} = 0.55, P = 0.587)$ between the Alabama and SRA populations (Table 3.1). However, we detected a difference in FO of fawns $(t_{23} = 2.59, P = 0.016)$ and small mammals $(t_{23} = -2.16, P = 0.041)$, and a marginal difference in rabbits $(t_{23} = 1.90, P = 0.071)$ between populations (Table 3.1). Small mammals were consumed more in Alabama, whereas fawns and rabbits were consumed more in the SRA (Table 3.1). Deer, rabbits, small mammals, and fruits comprised most prey items identified in scats, and since the occurrence of other prey items was negligible, we report the percentages but did not further evaluate them.

We found that FO differed across months for small mammals $\left(F_{11,145} = 2.24, P = 0.015\right)$ and fruit $\left(F_{11,145} = 10.06, P \leq 0.001\right)$, but not for rabbits $\left(F_{11,145} = 1.25, P = 0.259\right)$

or deer $\left(F_{11,145} = 1.47, P = 0.150\right)$ (Fig. 2.3). However, we observed differences in monthly FO of adult deer $\left(F_{11,145} = 5.03, P \leq 0.001\right)$ and fawns $\left(F_{11,145} = 5.88, P \leq 0.001\right)$ (Fig. 3.4). Tukey tests for multiple comparisons of monthly means indicated small mammal consumption was greatest during early spring (Feb-Apr) and late summer (Aug and Sep). Additionally, Tukey tests revealed FO of fruits peaked during June–December and was lowest during January–May. Consumption of adult deer peaked during November and January and was lowest during May–October. Unsurprisingly, FO of fawns was greater in May and June compared to September–April.

For FO of deer, population, home-range size, and woody wetlands had the strongest effect on the model performance (Tables 3.2 and 3.3). Use of deer was greater in the SRA than Alabama, increased during cooler temperatures, and coyotes with smaller home ranges comprised of more woody wetlands and less grassland habitats consumed more deer than those with larger home-ranges comprised of less woody wetlands (Tables 3.2 and 3.3). For FO of adult deer, mean monthly temperature and home-range size had the strongest effect on model performance, in which coyotes consumed more adult deer during cooler months (late fall–early spring) and coyotes with smaller home-ranges consumed more adult deer than those with larger home-ranges (Tables 3.2 and 3.3). For FO of fawns, population and mean monthly temperatures had the strongest effect on model performance, as fawns were consumed more during warmer months (spring–summer) and used more by coyotes in the SRA than Alabama (Tables 3.2 and 3.3). For FO of rabbits, all variables except home-range size had strong effects on model performance. Consumption of rabbits occurred more frequently in Alabama and during cooler months, was positively correlated with agriculture and pastures, grasslands, and woodlands within coyote home ranges, and was negatively correlated with woody wetlands (Tables 3.2 and

3.3). Coyote population and home-range size were correlated with small mammal use by coyotes, in which coyotes in Alabama consumed more small mammals than in the SRA and greater home-range size was positively correlated with use of small mammals (Tables 3.2 and 3.3). For fruit, mean monthly temperature had the greatest effect on model performance (Table 3.2). Use of fruit by coyotes was greatest during warmer months (late Spring–early Fall) and was negatively correlated with home ranges with more agriculture and pastures and woodlands (Table 3.3).

DISCUSSION

Prey use by coyotes in Alabama and the SRA of Georgia and South Carolina was dominated by white-tailed deer, rabbits, small mammals, and fruit (e.g., persimmon, blackberry, plums, and muscadine (*Vitis rotundifolia*). Although these results are consistent with many previous studies of prey use in the southeastern United States (Andelt et al. 1987, Hoerath and Causey 1991, Kelly et al. 2015, Cherry et al. 2016), our findings provide novel insights because assigning scats to coyote territories permitted us to correlate consumption of prey with the size and habitat composition of home ranges, as well as seasonal changes. For instance, Schrecengost et al. (2008) studied coyote diets proximate to our study areas in the SRA and reported similar use and seasonal changes in mammalian prey and fruit by coyotes. However, they reported that rabbits were not an important food item for coyotes because FO of rabbits only peaked at 31% during February and was <17% during other months. Conversely, our results indicated that rabbits were important prey for coyotes, as monthly FOs for rabbits ranged between 11.3–39.1% and peaked during March, which coincides with the coyote whelping season. Our findings differ from Schrecengost et al. (2008) because our study area was considerably larger in size (10,530 km^2 vs. 800 km^2) and we correlated consumption of rabbits to habitat composition of coyote home ranges, and found a negative correlation with woody wetlands and use of rabbits. Specifically, coyote use of rabbits was positively correlated with cooler temperatures, less dense woodlands, and open habitats, such as agriculture and grasslands. This indicates that rabbit predation by coyotes was greatest in territories with more open habitats and during cooler months of the year. This is an important distinction because 97% of Schrecengost et al.'s (2008) study area consisted of forested habitats, whereas forested habitats comprised 63% of our study area. Therefore, we believe our findings demonstrate the importance of assessing coyote diets broadly on the landscape and accounting for local variation in diets by assigning scats to territories.

Home ranges contain a finite potential of food resources and, for territorial species, home ranges reflect a balance between energetic demand and quality and spatial distribution of food resources needed for survival and reproduction (Swihart et al. 1988, Bassett 1995, Tucker et al. 2014). In other words, once costs of basic survival have been met, resources acquired from territories can be subsequently transferred to reproductive activities. Space use by resident coyotes is constrained by their territorial behavior, as they rarely venture outside their territories unless they are dispersing offspring (Windberg and Knowlton 1988, Kamler and Gipson 2000, Hinton et al. 2015). For example, we recorded 2,674, 1,781, and 1,797 GPS fixes respectively from coyotes AL08F, SC31F, and GA41M (Fig. 3.2). During those 8–13 months, we observed no excursions from their home ranges and this likely indicates that resident coyotes acquire large enough territories to cope with local temporal and spatial variability in food resources. Furthermore, space use patterns are largely driven by foraging movements and home-range size reflects the extent of foraging movements of resident coyotes. Therefore, prey we observed in scats of resident coyotes was likely acquired and consumed within their home ranges.

Although consumption of deer varied considerably among packs, mean monthly FO of deer in coyote scats varied between 28–53.4% and deer appeared to be an important food resource year-round. Our findings suggest that size and habitat composition of home ranges also influenced coyote use of white-tailed deer. Coyotes in the SRA consumed more deer than coyotes in Alabama, but this difference was largely driven by the greater consumption of fawns in the SRA compared to Alabama. Overall, coyote use of deer was weakly associated with cooler mean monthly temperatures, but strongly associated with smaller home ranges and home ranges with greater proportions of woody wetland habitats and less amounts of grasslands. Although coyotes are associated with open habitats (Van Valkenburg 1985, 1999, Kamler and Gipson 2000, Hinton et al. 2015, Cherry et al. 2017), open habitats may also reduce coyote predation on deer, as the ability of deer to detect and outrun coyotes is an important factor affecting their susceptibility to predation (Gese and Grothe 1995, Patterson et al. 1998, Lingle and Pellis 2002). Indeed, coyote home ranges exhibited a mixture of open and forested habitats and heterogeneity of habitat types within home ranges may provide alternative prey for coyotes, as well as impede the ability of white-tailed deer to detect and escape coyotes due to increased plant structure associated with transitional areas among habitats.

Searching for prey involves important costs per unit of time (MacArthur and Pianka 1966, Werner and Hall 1974, Griffiths 1980, Petroelje et al. 2014), and the observed negative correlations between home-range size and use of white-tailed deer suggests an important energetic balance resident coyotes likely weigh. That is, preying on deer may provide coyotes with greater net energy per unit of search time than smaller prey, such as rabbits and small mammals. For example, coyote use of small mammals was positively correlated with home-range size. We observed a lack of correlation between use of small mammals and habitat correlates, suggesting that microhabitat conditions are likely more influential for predicting coyote use of small mammals relative to the coarse habitat types we used. Nevertheless, to maximize net energy gains from diets consisting mostly of small particle-sized food, such as invertebrates and small mammals, coyotes may require larger home ranges to satisfy mass-related energetic requirements, as smaller prey have lower absolute energy than larger prey and are respectively patchy and temporally limited in distribution and availability (Carbone et al. 1999). Indeed, it is well established that home-range size is inversely correlated with habitat quality (Rosenzweig 1981, 1991) and the combination of large home ranges and greater use of small prey may indicate that resident coyotes are inhabiting lower quality habitat than those with smaller home ranges and greater use of larger prey.

Previous studies indicated that coyote predation of white-tailed deer in the southeastern United States occurred primarily on fawns during summer, and that consumption of deer during winter was a result of scavenging of carcasses discarded by deer hunters (Chamberlain et al. 1999, Thornton et al. 2004, Schrecengost et al. 2008). However, we observed consistent use of white-tailed deer throughout the year; adult deer were consumed during all months, and factors influencing deer use differed among adults and fawns. Specifically, use of adult deer was strongly associated with cooler months and smaller home ranges, whereas use of fawns was strongly associated with warmer months, weakly associated with woody wetlands and grasslands, and fawns were used more by coyotes in the SRA. This was not surprising, as the greatest use of fawns occurred at the height of the fawning season in the SRA (May–June; Fig. 3.4), and although to a lesser extent, throughout the fawning season in Alabama (July–August; Fig. 3.4). Although fawns were an available prey source during nearly 8 months of the year, fawns only accounted for most occurrence of deer in scats during May and June, because fawns are most susceptible to coyote predation during their first few weeks of life (Kilgo et al. 2012, Chitwood et al. 2015, Shuman et al. 2017).

Recent studies suggest coyote predation on adult deer in the southeastern United States is low (Ditchkoff et al. 2001, Chitwood et al. 2014, Kilgo et al. 2016); however, studies in other parts of the white-tailed deer's range have shown predation to be an important source of mortality across age classes (Long et al. 1998, Lingle 2000, Patterson and Messier 2000). We suggest that coyote use of deer is complex and that a combination of landscape characteristics, phenology, and human activity increases coyote predation on white-tailed deer. Our data clearly show that coyotes use deer during fall and winter hunting seasons, and clearly coyotes will opportunistically consume deer killed or wounded by hunters. However, the spatial distribution of hunted lands varies across the landscape, as does hunting pressure and hunting activity, and opportunities for coyote to consistently exploit carcasses are likely limited due to constrained space use by residents. Furthermore, despite the widespread distribution of feral pigs in our study areas and the availability of pig carcasses, we rarely observed pig remains in coyote scats, nor did we commonly detect animals frequently found as roadkill, suggesting that scavenging is not an important foraging strategy for resident coyotes.

Coyote use of white-tailed deer during the hunting season may relate to season changes in deer movements due to breeding activities, as evident by increased deer-vehicle collisions during fall and winter (Etter et al. 2002, Sudharsan et al. 2006, Steiner et al. 2014). White-tailed deer are known to increase movements to exploit mating opportunities and use riskier habitats to avoid human hunters (Sudharsan et al. 2006, Webb et al. 2010, Steiner et al. 2014, Foley et al. 2015, Simoneaux et al. 2016). Consequently, changes in deer space use patterns may increase deer presence in areas occupied by coyotes and exposes adults to greater risk of predation, likely explaining use of deer we observed during peak deer breeding seasons in both study areas. Likewise, coyote use of white-tailed deer during winter after hunting and breeding seasons could be influenced by decreased body condition and rut-related injuries of male deer, making them more susceptible to predation (Nelson and Mech 1986). We also suspect that predation of juvenile deer accounted for the observed use of deer well after hunting seasons ended. Lingle (2000) and Long et al. (1998) both noted that predation on juveniles was a relevant source of mortality. Notably, there is a dearth of information detailing mortality and predation rates of juvenile deer, as most studies focus on deer ≥1.5 years of age or fawns.

It is plausible that juvenile white-tailed deer, particularly those that are not members of matriarchal family groups (i.e., males, orphaned females) may suffer greater mortality to predation than adults, as they are solitary individuals encountering seasonal changes in human activity and resource availability for the first time and may be prone to riskier decision-making (Lima and Dill 1990). Indeed, Nelson and Mech (1981) noted substantive mortality in white-tailed deer between 6–10 months old, and coyote predation was an important source of mortality for deer ≥6 months old in Pennsylvania (Vreeland et al. 2004) and New Brunswick (Ballard et al. 1999). Though a small sample size, Campbell et al. (2005) noted that mortality of juvenile males in West Virginia was 0.27 during winter, which included predation loss to coyotes. Additionally, fawns lose spots on the pelage around 90–120 days (Sauer 1984, Smith 1991), but it is unknown when hair follicles on fawns mature to the diameter thickness of adult deer hair. Therefore, we suspect that some adult hair (based on diameter) we recovered from scats belonged to juvenile white-tailed deer, and speculate that perhaps coyote predation on juvenile deer is more common than previously thought.

We noted that differential use of white-tailed deer, rabbits, small mammals, and fruit was influenced by season, and the size and habitat composition of coyote home ranges, indicating that resident coyotes are capable of exploiting a fluctuating food base despite their constrained space use. For example, it is well known that coyotes consume fruit during summer and some studies suggest that fruit may buffer coyote predation of fawns (Andelt et al. 1987, Stratman and Pelton 1997, Cherry et al. 2016). Similarly, we observed seasonal use of fruits, as mean monthly temperature had a strong association with coyote use of fruit. However, we also observed a weak negative association of fruit consumption with agricultural habitats and woodlands. This is not surprising as coyotes exhibit broad use of fruits (i.e., persimmons, blackberry, pears, plums, muscadine, peaches, *Smilax* spp.) that become available during spring through fall and occur in a wide variety of habitats. Additionally, our findings suggest that use of fruit was opportunistic as use of mammalian prey did not appreciably decrease with increasing use of fruit. In particular, mean monthly FO of mammalian prey in coyote scats was 78.6% and varied between 60.0–95.8%, whereas mean monthly FO of fruit was 33.8% and ranged between 0.7–68.0%. This suggests that coyotes in the southeastern United States rely primarily on nutritionally superior mammalian prey and supplement their diet with fruit when available (McNab 1995).

The presence of coyotes facilitates complex ecological interactions by exerting cascading effects on prey populations, and their predation on white-tailed deer creates conflicts with sustained harvests of deer in regions of the southeastern United States (Kilgo et al. 2010, 2012). Furthermore, coyotes do not coexist with other large carnivores throughout most of the southeastern United States and they contend with lower medium-to-large prey diversity relative to western counterparts (Harrison 1992, Patterson et al. 1998, Hinton et al. 2017). Consequently, coyotes likely exert stronger top-down effects on southeastern ecosystems than expected and, although predation rates on ungulates by coyotes are significantly less than larger carnivores such as mountain lions and wolves (Pierce et al. 2000, Arjo et al. 2002, Benson et al. 2017, Hinton et al. 2017), recent studies in the Southeast suggest that the presence of coyotes may negatively influence white-tailed deer foraging behaviors and induce reproduction suppression (Cherry et al. 2015, 2016). Despite these top-down effects on local prey populations, strong site fidelity by resident coyotes, as exhibited by the relative spatial stability of their home ranges, indicates that they are defending a finite area while maintaining a foraging strategy commensurate with the distribution and availability of prey in their territories (Bassett 1995, Swihart et al. 1988). In conclusion, it appears that differential use of prey by coyotes is influenced by the habitat heterogeneity of their home ranges and prey-switching behaviors may stabilize local interactions between coyotes and their food resources to permit stable year-round territories. Indeed, heterogeneous landscapes and density-dependence are known to stabilize predator-prey interactions through frequency-dependent prey-switching (O'Donoghue et al. 1998, Patterson et al. 1998) and by providing refugia for prey (Hebblewhite et al. 2005, Kauffman et al. 2007). Future assessment of the effects of these factors on distribution and abundance of coyotes is essential for understanding the effects of coyote predation on mammalian communities in the southeastern United States.

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Table 3.1. Frequency of occurrence of primary prey items identified in coyote (*Canis latrans*) scats collected from resident territories in Alabama and the Savannah River Area of Georgia and South Carolina, January 2016 –January 2017.

	# of scats	% white-tailed deer			% rabbit	% sm[a]	% fruit	% other[b]
		total	adult	fawn				
Alabama (*n* = 8)	300	38.0	33.6	4.4	14.5	32.3	30.7	14.7
Savannah River Area (*n* = 17)	800	42.1	26.7	15.1	23.9	22.7	27.9	16.3

[a]Small mammal: rat, mouse, shrew, and vole species; [b]Insects (i.e., grasshoppers and beetles), opossum, raccoon, armadillo, cow, birds, reptiles and human trash

Table 3.2. Summary of the 8 generalized linear mixed models used to predict frequency of occurrence of each prey category corresponding to different hypotheses of factors affecting use by coyotes in Alabama, Georgia, and South Carolina during 2016-2017. Shown are differences among Akaike's Information Criteria for small sample sizes (ΔAIC_c).

Prey category	Model	*K*	Deviance	ΔAIC_c	ω
White-tailed deer	No AgPast- SRA[a]+Temp[b]+HR[c]+Woods[d]+WW[e]+Grass[f]	8	1421.0	0	0.34
	No Woods- SRA+Temp+HR+WW+AgPast[g]+Grass	8	1421.4	0.3	0.29
	Full Model- SRA+Temp+HR+Woods+WW+AgPast+Grass	9	1419.7	0.9	0.22
	No Temp- SRA+HR+Woods+WW+AgPast+Grass	8	1422.4	2.4	0.10
	No Grass- SRA+Temp+HR+Woods+WW+AgPast	8	1423.4	4.3	0.04
	No WW- SRA+Temp+HR+Woods+AgPast+Grass	8	1426.0	6.8	0.01
	No SRA- Temp+HR+Woods+WW+AgPast+Grass	8	1434.7	9.5	0.00
	No HR- SRA+Temp+Woods+WW+AgPast+Grass	8	1443.8	11.8	0.00
Adult deer	No SRA- Temp+HR+Woods+WW+AgPast+Grass	8	1230.7	0	0.24
	No Woods- SRA+Temp+HR+WW+AgPast+Grass	8	1230.8	0	0.24
	No Grass- SRA+Temp+HR+Woods+WW+AgPast	8	1231.1	0.4	0.19
	No AgPast- SRA+Temp+HR+Woods+WW+Grass	9	1230.2	1	0.14
	No WW- SRA+Temp+HR+Woods+AgPast+Grass	8	1233.5	1.6	0.11
	Full Model- SRA+Temp+HR+Woods+WW+AgPast+Grass	8	1233.5	2	0.09
	No HR- SRA+Temp+Woods+WW+AgPast+Grass	8	1245.3	13.4	0.00
	No Temp- SRA+HR+Woods+WW+AgPast+Grass	8	1279.1	57.4	0.00
Fawn	No Woods- SRA+Temp+HR+WW+AgPast+Grass	8	565.9	0	0.29
	No AgPast- SRA+Temp+HR+Woods+WW+Grass	8	567.0	0	0.29
	No HR- SRA+Temp+Woods+WW+AgPast+Grass	9	565.1	1.6	0.13
	No Grass- SRA+Temp+HR+Woods+WW+AgPast	8	567.5	1.8	0.12
	Full Model- SRA+Temp+HR+Woods+WW+AgPast+Grass	8	571.3	1.9	0.11
	No WW- SRA+Temp+HR+Woods+AgPast+Grass	8	573.9	3.3	0.06
	No SRA- Temp+HR+Woods+WW+AgPast+Grass	8	575.7	9.6	0.00
	No Temp- SRA+HR+Woods+WW+AgPast+Grass	8	648.5	80.8	0.00
Rabbit	No HR- SRA+Temp+Woods+WW+AgPast+Grass	8	1074.3	0	0.61
	Full Model- SRA+Temp+HR+Woods+WW+AgPast+Grass	9	1074.0	1.3	0.32

	No SRA- Temp+HR+Woods+WW+AgPast+Grass	8	1078.0	4.9	0.05
	No Temp- SRA+HR+Woods+WW+AgPast+Grass	8	1078.2	9	0.01
	No WW- SRA+Temp+HR+Woods+AgPast+Grass	8	1080.8	9.6	0.01
	No Woods- SRA+Temp+HR+WW+AgPast+Grass	8	1082.5	9.8	0.00
	No AgPast- SRA+Temp+HR+Woods+WW+Grass	8	1083.6	13.4	0.00
	No Grass- SRA+Temp+HR+Woods+WW+AgPast	8	1087.9	17.2	0.00
Small mammal	No Temp- SRA+HR+Woods+WW+AgPast+Grass	8	1253.1	0	0.22
	No AgPast- SRA+Temp+HR+Woods+WW+Grass	8	1269.2	0.1	0.21
	No Woods- SRA+Temp+HR+WW+AgPast+Grass	8	1269.3	0.2	0.20
	No Grass- SRA+Temp+HR+Woods+WW+AgPast	9	1269.4	0.3	0.19
	Full Model- SRA+Temp+HR+Woods+WW+AgPast+Grass	8	1271.1	2	0.08
	No WW- SRA+Temp+HR+Woods+AgPast+Grass	8	1271.4	2.3	0.07
	No SRA- Temp+HR+Woods+WW+AgPast+Grass	8	1273.5	4.4	0.02
	No HR- SRA+Temp+Woods+WW+AgPast+Grass	8	1274.5	5.4	0.01
Fruit	No SRA- Temp+HR+Woods+WW+AgPast+Grass	8	1241.6	0	0.26
	No HR- SRA+Temp+Woods+WW+AgPast+Grass	8	1241.6	0	0.26
	No WW- SRA+Temp+HR+Woods+AgPast+Grass	8	1258.2	0.6	0.19
	No Grass- SRA+Temp+HR+Woods+WW+AgPast	8	1243.0	1.4	0.13
	Full Model- SRA+Temp+HR+Woods+WW+AgPast+Grass	8	1241.5	1.9	0.10
	No AgPast- SRA+Temp+HR+Woods+WW+Grass	9	1245.3	3.7	0.04
	No Woods- SRA+Temp+HR+WW+AgPast+Grass	8	1246.3	4.7	0.02
	No Temp- SRA+HR+Woods+WW+AgPast+Grass	8	1275.0	33.4	0.00

[a]Population (AL or SRA); [b]Average temperature per month; [c]Home range size; [d]Proportion of home range comprised of forested habitat; [e]Proportion of home range comprised of woody riparian habitat; [f]Proportion of home range comprised of grassland; [g]Proportion of home range comprised of agriculture and pasture land

Table 3.3. Results from generalized linear mixed models for the top models for predicting frequency of occurrence of 5 prey items corresponding to different hypotheses of factors affecting use by coyote packs in AL, GA, and SC, 2016. Shown are β coefficients, standard error (SE), 95% confidence intervals (CI), *z*-scores, and *P*-values.

Prey Category	Model Variables	β	SE	95% CI	*z*	*P*
White-tailed Deer	Intercept	-1.239	0.235	-1.453, -0.517	-5.280	<0.001
	SRA[a]	1.064	0.306	0.115, 1.305	3.472	<0.001
	Temp[b]	-0.117	0.063	-0.232, 0.019	-1.873	0.061
	HR[c]	-0.299	0.071	-0.461, -0.124	-4.189	<0.001
	Woods[d]	0.181	0.074	0.000, 0.446	2.427	0.015
	WW[e]	0.311	0.106	0.066, 0.579	2.923	0.003
	Grass[f]	-0.253	0.113	-0.183, 0.226	-2.239	0.025
Adult deer	Intercept	-0.944	0.071	-1.101, -0.807	-13.359	<0.001
	Temp	-0.512	0.068	-0.647, -0.379	-7.488	<0.001
	HR	-0.326	0.079	-0.483, -0.172	-4.127	<0.001
	Woods	0.027	0.100	-0.184, 0.227	0.271	0.787
	WW	0.159	0.095	-0.028, 0.347	1.673	0.094
	AgPast[g]	-0.110	0.105	-0.324, 0.094	-1.053	0.292
	Grass	-0.106	0.111	-0.330, 0.111	-0.961	0.337
Fawn	Intercept	-4.920	0.620	-6.253, -3.703	-7.938	<0.001
	SRA	2.573	0.753	1.054, 4.173	3.420	<0.001
	Temp	1.304	0.183	0.965, 1.690	7.131	<0.001
	HR	-0.219	0.172	-0.599, 0.119	-1.275	0.202
	WW	0.579	0.297	-0.032, 1.191	1.951	0.051
	AgPast	-0.157	0.193	-0.580, 0.230	-0.814	0.415
	Grass	-0.494	0.259	-1.040, 0.050	-1.909	0.056
Rabbit	Intercept	-0.699	0.291	-1.287, -0.115	-2.399	0.016
	SRA	-0.950	0.401	-1.749, -0.161	-2.370	0.018
	Temp	-0.229	0.073	-0.374, -0.086	-3.130	0.002
	Woods	0.440	0.129	0.187, 0.715	3.411	<0.001
	WW	-0.507	0.138	-0.783, -0.224	-3.665	<0.001
	AgPast	0.545	0.124	0.294, 0.800	4.401	<0.001
	Grass	0.799	0.167	0.473, 1.150	4.775	<0.001
Small mammal	Intercept	-0.427	0.294	-1.040, 0.176	-1.451	0.147
	SRA	-0.862	0.393	-1.677, -0.062	-2.195	0.028
	HR	0.226	0.090	0.043, 0.413	2.518	0.012
	Woods	-0.064	0.129	-0.339, 0.204	-0.496	0.620
	WW	-0.227	0.138	-0.498, 0.064	-1.644	0.100
	AgPast	0.04	0.133	-0.235, 0.317	0.322	0.748
	Grass	0.100	0.168	-0.236, 0.459	0.596	0.551

Fruit	Intercept	-1.034	0.186	-1.444, -0.671	-5.551	<0.001
	Temp	0.466	0.082	0.307, 0.629	5.699	<0.001
	HR	0.033	0.187	-0.348, 0.431	0.177	0.859
	Woods	-0.691	0.297	-1.323, -0.077	-2.326	0.020
	WW	0.204	0.220	-0.251, 0.659	0.928	0.354
	AgPast	-0.567	0.273	-1.138, -0.002	-2.081	0.037
	Grass	-0.403	0.295	-1.011, 0.221	-1.367	0.172

[a]Population (AL or SRA); [b]Average temperature per month; [c]Home range size; [d]Proportion of home range comprised of forested habitat; [e]Proportion of home range comprised of woody riparian habitat; [f]Proportion of home range comprised of grassland; [g]Proportion of home range comprised of agriculture and pasture land

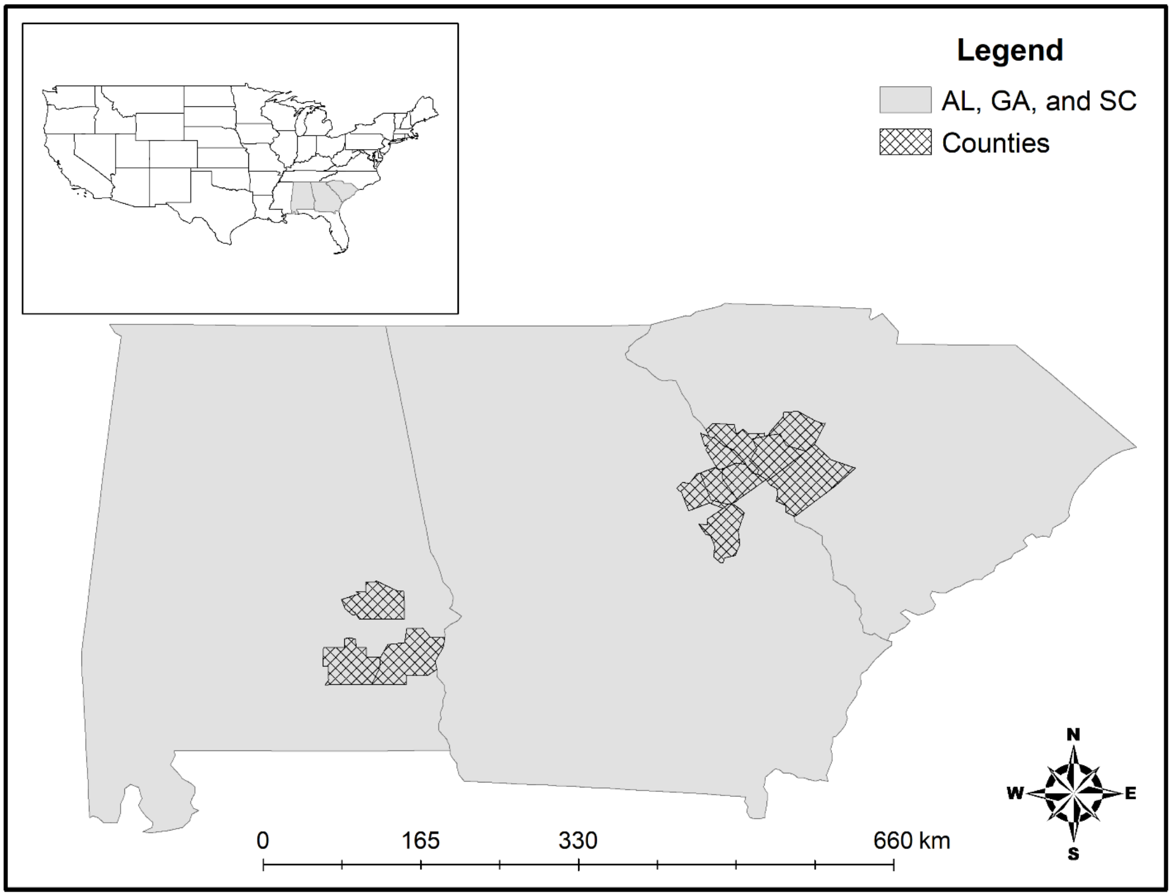

Fig. 3.1. Map of counties (noted as shaded area) in Alabama, Georgia, and South Carolina, USA, where coyotes were trapped during 2015–2016.

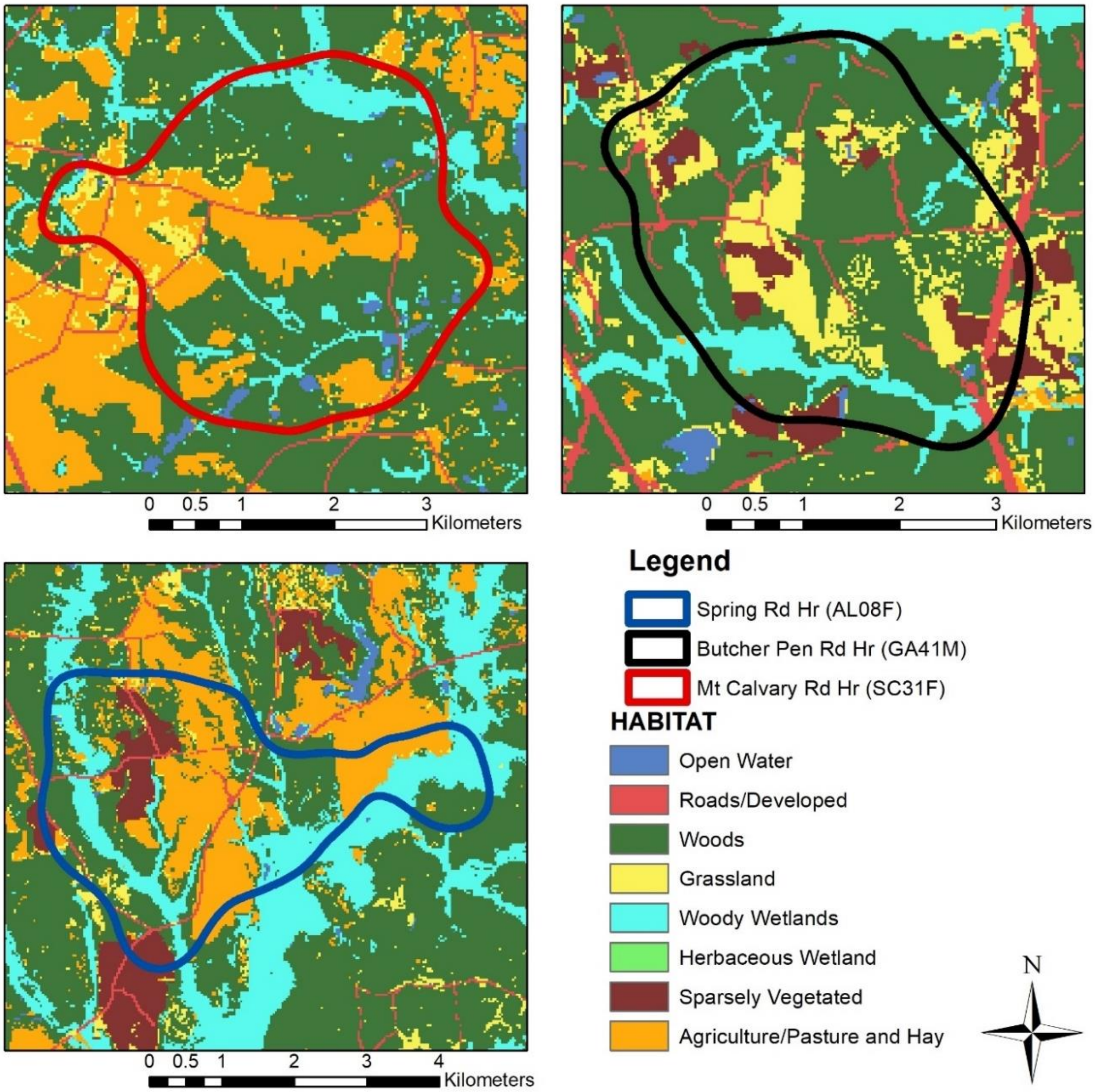

Fig. 3.2. Map showing habitats within 95% kernel density estimated home ranges of 3 GPS-collared coyotes in Alabama, Georgia, and South Carolina 2015–2016. AL08F had 2,674 GPS fixes (home-range size of 20.0 km^2), GA41M had 1,797 GPS fixes (home-range size of 12.8 km^2), and SC31F had 1,781 GPS fixes (home-range size of 12.1 km^2).

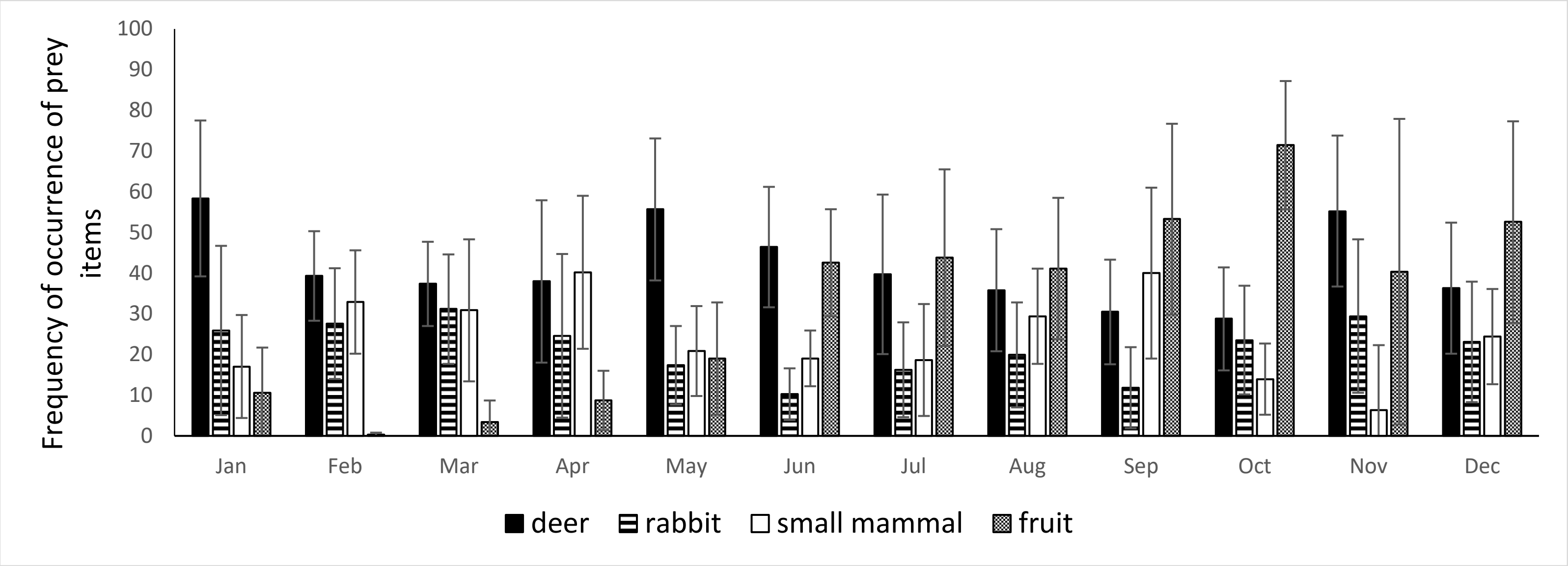

Fig. 3.3. Frequency of occurrence by month of 4 primary prey items for coyotes in Alabama, Georgia, and South Carolina, USA, 2016–2017. Error bars represent 95% confidence intervals.

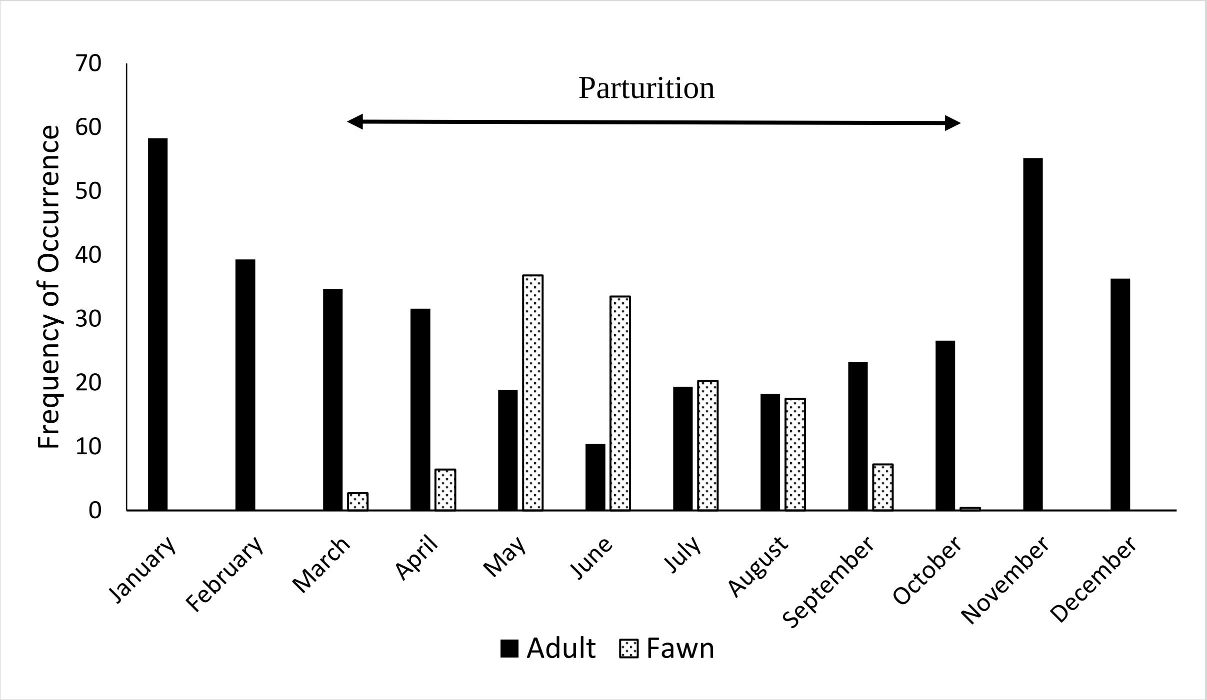

Fig 3.4. Frequency of occurrence by month of adult and fawn white-tailed deer in coyote scats collected from Alabama, Georgia, and South Carolina, USA, during 2016–2017. Shown above is the range of parturition dates for our study areas.

CHAPTER 4

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

During 2015-2016, 164 coyotes were captured and monitored across AL, GA, and SC with GPS radio collars. To assess prey use by resident coyotes, I sampled scat in 25 resident territories and collected 1,100 scats during January 2016–January 2017. Deer, rabbits, small mammals, and fruits comprised most prey items identified in scats. I detected no difference in use of deer, adult deer, fruits, or other food items between the AL and SRA populations. However, small mammals occurred more frequently in scats in AL, whereas fawns and rabbits occurred more frequently in the SRA. Furthermore, use of small mammals, fruit, adult deer, and fawns differed across months, whereas use of rabbits and deer in general did not. Consistent use of rabbits and deer throughout the year demonstrate the importance of these prey items to resident coyotes. Indeed, my results show deer to be an important prey item throughout the annual cycle of coyotes, a novel finding as coyote consumption of deer has primarily been thought to occur mainly on fawns during spring and summer and carcasses during hunting seasons. In fact, I found little support for scavenging as an important year-round means of obtaining food for resident coyotes.

By collecting scat from resident territories, I was able to attribute what residents were eating to habitats found within their home ranges. Coyotes with smaller home ranges comprised of more woody wetlands and less grassland habitats consumed more deer than those with larger home-ranges comprised of less woody wetlands. Consumption of rabbits was positively correlated with agriculture and pastures, grasslands, and woodlands within coyote home ranges, and was negatively correlated with woody wetlands. I failed to find a habitat correlate for use of small mammals, indicating a finer scale assessment may be needed. Use of fruit by coyotes was negatively correlated with home ranges with more agriculture and pastures and woodlands Therefore, I offer these findings demonstrate the importance of assessing coyote diets broadly on the landscape and accounting for local variation in diets by assigning scats to territories. My findings suggest that land management focused on habitat heterogeneity may be ideal to ensure diverse prey sources for coyotes, which may reduce predation on deer. Future studies perhaps can monitor resident animals while altering habitat conditions to evaluate the effects of habitat heterogeneity more directly.

I noted that 60 collared coyotes (40.8%) were residents and 48 (32.7%) were transients for the entire time they were monitored, and 39 (26.5%) exhibited both residency and transiency stages. Thus, the majority of the coyote population resides in territories, but transiency is still an important life stage that likely every coyote experiences. Resident home-ranges averaged 17.6 ± 14.7 km^2 (mean ± SD) and were significantly smaller than transient ranges, which averaged 132.7 ± 105.2 km^2. Resident core areas averaged 2.6 ± 1.6 km^2 and were significantly smaller than transient biding areas, which averaged 14.5 ± 11.6 km^2. However, biding areas, which we considered to be consistent with transients attempting to establish a territory, were similar in size to home ranges. I also noted that almost 81% of transients traversed ≤ 200 km^2, suggesting most land owners must consider a much larger area around their properties when interested in managing coyote abundance.

Habitat composition within resident and transient ranges was similar, and comprised of mainly forest, shrub, agriculture, and wetland habitat with minor amounts of water and urban area. However, residents and transients selected habitats differently. Residents selected agriculture, forests, shrub, and wetland habitat, but avoided urban, pasture, water, and roads.

Transients selected agriculture, urban areas, pastures, and roads while avoiding shrub habitats. Because resident and transient coyotes exhibit different space use patterns, it has been hard to manage their populations. Local control efforts may be feasible, but those efforts are often associated with roads and other habitats selected for by transients, which likely does not impact local prey populations like it would if residents were the ones most impacted. Furthermore, not only do the long-distance movements and dispersal by transient coyotes documented by our study prove that coyote management has to be undertaken at a broader scale than simply at the local level, but transients make up a substantial portion of the coyote population. Managers have to be aware that transients are traversing across the landscape in search of new areas and opportunities to breed, ready to quickly enter vacant territories when they become available.