



**A SYNTHESIS OF THE CURRENT STATE OF KNOWLEDGE
REGARDING ECOLOGY AND MANAGEMENT OF COYOTES IN THE
SOUTHEASTERN UNITED STATES**

February 26, 2020

Prepared By:

SEAFWA Furbearer Working Group

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ACKNOWLEDGEMENTS

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Purpose of Document

There is a wealth of information regarding coyotes (*Canis latrans*) in North America, including past and ongoing studies, making it difficult for biologists and managers to keep current and accurately disseminate information to the public and identify research needs. The purpose of this document is to outline topics of investigation regarding coyote populations in the southeastern United States and provide an objective synthesis of the current knowledge of these topic areas based on available literature. This document will provide managers with an overview of each topic to assist in effective management decision-making and determination of future research needs.

Literature Review Methods

In a previous effort, Mastro et al. (2012) compiled >360 abstracts related to eastern coyote ecology, in which approximately 25% of those studies were conducted in the southeastern United States. Early coyote research in the southeastern U.S. was conducted in states first colonized by coyotes (Alabama, Florida, Mississippi, and Tennessee; see Figure 2 of Mastro et al. 2012) and are available as either peer-reviewed publications or unrefereed literature (e.g. theses, dissertations, and conference proceedings). As range expansion continued and interest in eastern coyote ecology and potential impacts increased, there have been increasing numbers of studies published in peer-reviewed journals on coyote populations in Georgia (Gates et al. 2014, Gulsby et al. 2015, 2017; Cherry et al. 2016*a, b, c*), North Carolina (McVey et al. 2013; Chitwood et al. 2014; Hinton and Chamberlain 2014; Hinton et al. 2015, 2017*a*; Swingen et al. 2016), South Carolina (Kilgo et al. 2012, 2014, 2017; Etheredge et al. 2015), Virginia (Bozarth

et al. 2015; Morin et al. 2016*a, b*; Bohling et al. 2017; Morin and Kelly 2017), and West Virginia (Albers et al. 2016, Bohling et al. 2017).

For the purpose of this review, topics of investigation were identified by contributors and the SEAFWA FWG, and a literature search was performed for each identified topic. For some topics, literature searches were performed in Google Scholar or other web-based tools. Additional pertinent manuscripts were identified in the literature cited sections of published and unpublished documents. Identified literature was then used to summarize current knowledge and uncertainty related to coyote ecology and management in the southeastern United States.

Topics of Investigation

Range Expansion

Paleontological records suggest that coyotes first appeared in their current morphological form by the early Pleistocene (1 Mya) and likely occupied much of North America including the eastern United States until the end of the Rancholabrean era (11,000 BP; Nowak 1979, 2002; Tedford et al. 2009). The presence of coyotes in eastern North America during the Pleistocene is consistent with a history of repeated range expansions and contractions across the North American continent (Nowak 1979, 2002). Coyotes are a medium-sized generalist predator which theory suggests presents a competitive disadvantage in colder climates when conditions favor larger-bodied competitors adapted for hypercarnivory of available megafauna associated with glacial periods (Van Valkenburgh et al. 2004, Koblmuller et al. 2012). However, the same traits likely allowed coyotes to adapt and thrive in warmer climatic conditions, in human-altered landscapes, and with reduction in interspecific interference competition when large *Canis sp.*

competitors were in decline or extirpated (Nowak 2002, Meachen and Samuels 2012, Van Valkenburgh 1999, Koblmuller et al. 2012).

Early literature restricted the proposed pre-Columbian coyote range to the Great Plains region of North America (Moore and Parker 1992, Parker 1995, Gompper 2002, Kyle et al. 2006). However, a review performed by Hody and Kays (2018) extended the coyote's pre-Columbian range to encompass most of the central and western regions of North America based on studies utilizing paleontological and historic data (Young and Jackson 1951; Nowak 1979, 2002, 2009; Figure 1) and this is the best knowledge to date.

Our understanding of the most recent coyote range expansion has evolved over time, including continued debates about specific colonization routes, the potential contribution of human-caused releases or escapes from hound hunting pen operations, the degree and importance of hybridization with other canid populations, and the genetic and morphological structure of resulting populations. Current general consensus is that coyotes remained largely restricted to the western and central regions of North America from the time of European colonization until the early 1900s but became ubiquitous throughout the United States by the early 2000s (Young and Jackson 1951, Nowak 2002, Hody and Kays 2018). Research incorporating paleontological and historic records suggests that the current range of coyotes resulted from 3 independent expansion events after European colonization of North America (Young and Jackson 1951; Nowak 1979, 2002; Tedford et al. 2009; Figure 2). The first event occurred during the 16th century when coyotes expanded their southern range from central Mexico into Central America with increasing land use conversion and human population densities in the region by the Spanish (Young and Jackson 1951; but see Hidalgo-Mihart et al. 2004). The second event was a northward expansion by coyotes from western and central

Canada into the Yukon and Alaska that coincided with human settlement and land conversion during the gold rushes of the late 19th century (Young and Jackson 1951, Nowak 1979). The final and last expansion event occurred in eastern North America during the 20th century in 2 spatially isolated fronts that began simultaneously during the 1920s (Young and Jackson 1951; Nowak 1979, 2002; Figure 2).

The eastern most range of the coyote from the Holocene until 1900 followed the Prairie Peninsula east of the Mississippi River through Illinois, southern Wisconsin, and northern Indiana (Cory 1912, Young and Jackson 1951, Jackson 1961, Mumford 1969, Nowak 1979, Hody and Kays 2018). After 1900, coyotes from that region moved eastward across the Great Lakes Region into New England (Nowak 1979). Bailey (1905) stated that coyotes were rare east of the semiarid mesquite region but that the range extended eastward as far as Cooke County, Texas, which is on the Oklahoma border and about 250 km west of the border with Arkansas, and as far as Fort Bend County, which is just southwest of modern-day Houston and 200 km west of Louisiana. After 1900, it is thought coyotes from the western and central regions of Oklahoma and Texas, and others from northern Missouri, moved into the eastern regions of Oklahoma and Texas and into Alabama, Arkansas, Louisiana, Mississippi, and Tennessee before colonizing the Gulf and Atlantic regions of the Southeast. Both eastern fronts later converged in the region encompassing Virginia, Kentucky, North Carolina, and Tennessee during the later 20th century (Bozarth et al. 2011; Heppenheimer et al. 2018*a, b*; Hody and Kays 2018).

This recent range expansion stimulated interest in the possible effects of early localized releases of coyotes by hunters, as well as the effects of hybridization with domestic dogs and wolves in facilitating range expansion into the southeastern United States (Hill et al. 1987, DeBow et al. 1998, Kays et al. 2010, Thornton and Murray 2014, Ellington and Murray 2015,

vonHoldt et al. 2016). Speculation about the role of introduction events by humans (intentional releases into or unintentional escapes from foxhound training enclosures) in coyote colonization of the Southeast has been fueled by reports of releases and records of coyotes prior to known establishment (Gipson 1978, Hill et al. 1987, Kilgo et al. 2010), and also evidence of admixture with domestic dogs in the southeastern U.S. population (Adams et al. 2003). Fener et al. (2005) examined the chronology of coyote records in New York state and found support for natural colonization routes compared to hypotheses that local releases contributed to range expansion. However, publications in the Southeast cite deliberate or accidental releases as possible contributors (Hill et al. 1987, DeBow et al. 1998). For example, DeBow et al. (1998) examined the spatial distribution of reports of coyotes over time in North Carolina and suggested that the erratic distribution of reports may have resulted from occasional releases prior to population establishment. Similarly, Hill et al. (1987) reported 20 documented cases of escapes or releases from foxhound training enclosures in areas where populations were not yet believed to be established (e.g. peninsular Florida and North Carolina).

While these introductions may have facilitated local populations on small spatial and temporal scales, it is unlikely these events played a significant role in the recolonization of coyotes across the Southeast (McCown and Scheick 2007) or that natural range expansion would not have culminated in coyotes becoming ubiquitous across the Southeast in the absence of any human assisted translocations. As in other regions of North America, coyote colonization in the Southeast likely occurred via range expansion from outside the region, rather than from introductions ahead of the colonization front.

The role and degree of hybridization with other *Canis* species during range expansion is also still being discovered. There is strong evidence of hybridization with wolf populations along

the northeastern front of range expansion and coyotes in the northeastern part of their range demonstrate relatively high levels of admixture with other *Canis sp.* (Monzon et al. 2014). Research in recent decades concerning discontinuities among regional coyote populations has focused on comparing morphological and genetic structure of northeastern coyotes to other populations (Thurber and Peterson 1991; Way 2007a, 2013; Kays et al. 2010; and Stronen et al. 2012). These studies present a case for morphological and genetic divergence of northeastern coyotes and suggest differences resulted from limited hybridization with wolf populations early in the initial range expansion through the Great Lakes region (Kays et al. 2010, Stronen et al. 2014). However, the degree of hybridization and exact colonization route has been hotly debated, due in part, to inferences that impacted the endangered status of local wolf populations (Wheeldon et al. 2010).

There have been fewer comprehensive studies of southeastern coyote morphology (McCarley 1962, Kennedy et al. 1986, Hinton and Chamberlain 2014) and population genetics (Damm et al. 2015, Bohling et al. 2017, Heppenheimer et al. 2018a) than in the Northeast. This is changing quickly with the publication of some recent studies in the Southeast. Degree of admixture with Great Lakes Region wolves appears to decrease with distance from the hybridization zone to the north and was low even in the northernmost southeastern states (6-16% in Virginia and West Virginia, Bohling et al. 2017). Current studies suggest some genetic and morphological distinction among western, northeastern, and southeastern coyote populations (Monzon et al. 2014, Hinton et al. 2019, Heppenheimer et al. 2018a, Heppenheimer et al. 2018b). However, there is still debate about the geographic extent and degree of genetic differentiation among the three regional populations and it is unknown if regional structure will persist or diminish as populations occur continuously across the landscape and sub-regional

populations have generally been found to be panmictic (no evidence of genetically isolating mechanisms, Bohling et al. 2017).

Genetic Structure

Early molecular studies on coyote populations in the Southeast were largely absent prior to the 1990s, but the few that did exist focused on differentiating coyotes from the experimental red wolf and hybrid individuals in and surrounding the designated red wolf recovery area (Ferrell et al. 1980, USFWS 1990). Following widespread colonization of coyotes in the eastern U.S., recent research has focused on identifying the colonization routes and suggest that the North Carolina, Kentucky, Tennessee, and Virginia region of the Southeast may be a contact zone for the northeastern and southeastern coyote expansion fronts (Bozarth et al. 2011; Heppenheimer et al. 2018*a, b*; Hinton et al. 2019). Haplotypes of gray wolves or Great Lakes Region wolves occur in coyotes in the northeastern part of this zone (Bozarth et al. 2011) but are absent to the south.

Initially, the mid-Atlantic was suggested to be the contact zone, as Bozarth et al. (2011) found mitochondrial DNA (mtDNA) haplotypes representative of regions to the south (South Carolina and Texas) and the north (Massachusetts, New York, and Pennsylvania Great Lakes wolf haplotypes) in a coyote population in northern Virginia. However, using nuclear DNA (nDNA; typically demonstrating more recent admixture) microsatellites from a larger sample of individuals from western Virginia and West Virginia, Bohling et al. (2017) found lower levels of admixture (6–16%) and no evidence of genetic structure within the region. It is important to note that nDNA and mtDNA change at rates which affects the temporal scale of inference of admixture. mtDNA is maternally inherited and slower to change, as only mutations will produce new microsatellite alleles in a population. Therefore we would expect analyses using mtDNA to

retain evidence of admixture from further in the past (a broader temporal extent), whereas nDNA changes at a faster rate because it is subject to recombination (changes are introduced with each generation with combinations of both parents' nDNA) and differences are considered to be more representative of recent or contemporary admixture. Heppenheimer et al. (2018a) conducted a larger study (in sample size and extent) by amplifying nDNA microsatellites from approximately 480 coyotes from 129 counties in 11 states along the Atlantic Coast and found that population structure corresponded to a north-south divide with an emerging contact zone between the 2 expansion fronts occurring proximate to the North Carolina and Virginia border. The proposed contact zone is approximately 240 km south of the samples collected by Bozarth et al. (2011) and southeast of the region evaluated by Bohling et al. (2017).

While studies have found evidence of admixture with domestic dogs in eastern coyote populations, Adams et al. (2003) suggested this was attributable to occasional hybridization events with free-roaming dogs during naturally occurring range expansion when coyote populations were at very low densities. Coyote-dog hybridization has been a subject of interest to scientists since coyotes were first studied (Coues 1873) and was a common area of research throughout the mid- to late-20th century (Dice 1942, Hall 1943, Howard 1949, Bee and Hall 1951, Mengel 1971, Gipson et al. 1974, Fox 1975, Mahan et al. 1978). However, broad assessments of *Canis* morphology (Nowak 1979) and captive behavioral studies (Dice 1942, Mengel 1971) suggested that coyote-dog hybridization was rare throughout the coyote's range. Adams et al. (2003) sampled 112 coyotes from North Carolina, Virginia, and West Virginia and, although they found no evidence of ongoing hybridization, they observed the same mtDNA dog haplotype in 12 coyotes. The authors suggested dog ancestry resulted from a single hybridization

event that occurred during the early 19th century in which a hybrid female backcrossed into the coyote population.

A large scale study assessing genetic differences in regional (northeastern, southeastern, and western) populations of coyotes using nDNA microsatellites observed low levels of dog ancestry in the Northeast and Southeast, and admixed coyotes did not appear to be substantially more common in the Southeast (Hinton et al. 2019). This suggests that most coyote-dog hybridization likely occurred at low levels in recently expanded populations, but was nearly absent in populations from the coyote's historic range (Heppenhimer et al. 2018*b*, Hinton et al. 2019). However, Hinton et al. (2019) and two other studies also using nDNA microsatellites (reflecting more recent admixture) reported rare individual coyotes with evidence of high levels of contemporary admixture with domestic dogs in samples from western Virginia and West Virginia (Bohling et al. 2017), Florida (Hinton et al. 2019), and North Carolina (Bohling and Waits 2011, Hinton et al. 2019), suggesting occasional hybridization events may still occur in areas of the southeast. The geographical extent and context (facilitated through intentional human actions such as crossbreeding coyotes and dogs in captivity, or accidental and opportunistic hybridization with free-roaming dogs), is unknown.

Most studies concur that there are three clusters of genetic structure across the United States, although degree of separation among clusters is still debated, and inference is partially dependent on the type of molecular analysis used. Most recently, Heppenhimer et al. (2018*b*) used restriction site-associated DNA sequencing (RADseq) to genotype 394 coyotes from 28 states using 22,935 single-nucleotide polymorphisms (SNPs; a higher resolution genomics analysis compared to analyses using microsatellites) and found that overall population structure corresponded to the coyote's historic range and the two eastern expansion fronts. They also

observed comparable high levels of genomic diversity in all coyote populations and found evidence of selection (outlier loci occurrence out of expected equilibrium) for several genes in the expanded eastern populations associated with phenotypic traits thought to increase dispersal success.

The nuanced differences in the findings of Hinton et al. (2019) and Heppenheimer et al. (2018b) demonstrate the continued difficulties in identifying the historic sources of contemporary population structure depending on the sample sizes and localities of samples, and the molecular markers and analyses performed. For example, using nDNA microsatellite markers, the results of Hinton et al. (2019) suggested that northeastern coyotes were more genetically similar to western coyotes and that southeastern coyotes were more genetically distinct from the other two populations. Estimating expected heterozygosity with RADseq SNPs, Heppenheimer et al. (2018b) found evidence of “slightly elevated” heterozygosity in the southeastern population compared to the western and northeastern population which appears to support the finding of greater genetic distinction of southeastern coyotes compared to western and northern coyotes and challenges the conclusions of previous studies that suggested coyotes in the Southeast were genetically more similar to western populations than those in the Northeast (Adams et al. 2003, Kays et al. 2010, Way et al. 2010).

Hinton et al. (2019) hypothesized that although northeastern coyotes experienced hybridization with wolf populations during range expansion, colonization of the Northeast maintained continuous genetic migration (exchange of genes) with the established western coyote populations in the Prairie Peninsula, which extends into the southern region of the Great Lakes. Conversely, they argue, genetic migration during colonization of the Southeast may have been hindered by the extirpation of coyotes in parts of central and eastern Texas via massive

poisoning programs from 1900–1950 to protect sheep (Bailey 1905, Gabrielson 1936, Russell and Shaw 1971, Nowak 1979). They suggested a large “canid free” zone adjacent to the Southeast could have reduced immigration of western coyotes through Oklahoma, Missouri, and Arkansas to the Southeast.

However, Heppenheimer et al. (2018b) also used a Bayesian assignment test (STRUCTURE) to compare similarity and dissimilarity among populations using the same data set of RADseq SNPs (Figure 3). While they found support for three genetically distinct clusters (northeastern, southeastern, and western), the analysis also suggested northeastern and southeastern coyotes were more similar to each other compared to western coyotes, as initially proposed by previous studies (see upper panel of Figure 3 where $K = 2$, and samples from northeastern states cluster with samples from southeastern states, and not with samples from western states). Both interpretations indicate that southeastern coyote populations are more distinct than previously thought compared to western coyotes, but the exact mechanism and degree of difference among the three populations is still debateable. Further analyses using high resolution analyses with SNPs and including historical samples would likely improve our understanding of genetic structure in populations resulting from past dispersal routes and introgression, although continued genetic migration (exchange of alleles) is ongoing among all three regions along contact zones and could result in reduced structure overtime.

Morphological Structure

Similar to molecular research, early studies on coyote morphology in the southeast focused on differentiating coyotes and hybrids from the reintroduced experimental red wolf population (McCarley 1962, Elder and Hayden 1977, Nowak 1979) and from coyote-dog hybrids (Gipson et al. 1974). By the mid-1980s, studies focused on describing the morphological

structure of coyotes in the western regions of the Southeast (Lydeard et al. 1986, Lydeard and Kennedy 1988), as coyotes had not established populations along the Atlantic Coast. Although Gipson et al. (1974) reported that 13% of 284 canids caught in Arkansas were believed to be coyote-dog hybrids based on craniodental measurements, most early studies found little evidence of dog introgression in coyote populations (Nowak 1979, Lydeard et al. 1988) which was later confirmed by molecular studies (Adams et al. 2003, Bohling et al. 2017, Heppenhimer et al. 2018b, Hinton et al. 2019). By the 2000s, molecular approaches replaced morphometry as the primary tool for assessing questions related to coyote hybridization and demographic history of coyote populations. However, Hinton and Chamberlain (2014) tested the hypothesis that individuals from the reintroduced experimental red wolf population, coyotes, and their hybrids in eastern North Carolina could be reliably identified without molecular markers and reported that all three groups were distinguishable with moderately high (80–90%) accuracy using only body-size measurements. They also reported that F₁ and F₂ hybrids were incapable of reaching body sizes of adult red wolves and suggested that the individuals from the reintroduced experimental red wolf population represented a unique *Canis* phenotype in the Southeast.

Although there is a growing body of literature arguing that the morphological divergence observed in coyote populations of the Northeast is strongly associated with hybridization with wolves (Way 2007a, Kays et al. 2010, Thornton and Murray 2014), only a few studies of coyote morphological divergence have been conducted in the Southeast (Giordano and Pace 2000, Hinton and Chamberlain 2014, Hinton et al. 2019). Giordano and Pace (2000) assessed the morphometrics of coyote-like canids at Sabine National Wildlife Refuge, Louisiana and found that coyotes on the refuge were larger than other Louisiana coyotes, but smaller than red wolves captured in Louisiana by the Red Wolf Recovery Team from 1974-1980a). Mean body mass of

male (20.2 kg) and female (17.6 kg) coyotes reported in Giordano and Pace (2000) were similar to those reported by Hinton and Chamberlain (2014) for genetically identified hybrids in the North Carolina experimental population recovery area [male (17.8 kg) and female (16.3 kg)]. The area around Sabine National Wildlife Refuge was trapped by the United States Fish and Wildlife Service (USFWS) Red Wolf Recovery Program to remove red wolves to captivity from 1974–1980 (USFWS 1990, Giordano and Pace 2000, Hinton et al. 2013), and it has been suggested that the larger sizes of coyotes on the refuge may reflect a legacy of past hybridization with red wolves.

Information regarding morphological structure of coyote populations in the Southeast is limited, and where data exist, is rarely compared to those in other regions. In Virginia, Houben and Mason (2004) reported mean body mass of adult male and female coyotes to be 16.2 and 13.4 kg, respectively, and that observed mean body mass was similar to that reported in other studies throughout the eastern United States and Atlantic region of Canada. Hinton et al. (2019) compiled morphometric data from their own field studies and the scientific literature to compare morphology of southeastern coyotes to western and northeastern coyotes. They observed mean body mass increased across a west-to-east gradient, a trend reported in other studies (Gipson 1978, Moore and Miller 1986, Larivière and Crête 1993, Way 2007a, Kays et al. 2010). Northeastern coyotes were larger than western and southeastern coyotes, but maximum body mass achieved by coyotes was similar between western and southeastern populations (Figure 4; Hinton et al. 2019). A principal component analysis of linear body measurements and body mass indicated that southeastern coyotes were intermediate in body size to western and northeastern coyotes, exhibited shorter ear and tail lengths, and did not have narrower or shorter heads. Of 62 studies, Hinton et al. (2019) found that mean body mass for 100% and 90% of female and male

coyotes, respectively, did not exceed 18 kg, but maximum body mass ranged between 20.2–25.9 kg for 50% of the studies.

Focusing on body mass of coyotes can obscure other morphological variation not related to size, such as craniodental characters commonly used to delineate taxonomic boundaries (Nowak 1979 & 2002, Tedford et al. 2009). For example, ear, tail, and skull morphologies do not exhibit the same allometric relationship observed for the axial and appendicular skeleton that are more influenced by bearing of weight (Carter 1987, Reynolds 2002, Wang and Tedford 2010). Differences in appendage morphology among coyote populations may be an adaptation to change in habitat structure and other environmental factors, as ear length is commonly associated with thermoregulation and enhanced low-frequency hearing (Maloiy et al. 1982, Geffen and Girard 2003, Wang and Tedford 2010) and tail morphology is known to influence locomotion qualities (e.g., bursting, running, jumping, balance; Hickman 1979). However, skull morphology is strongly associated with feeding adaptations and craniodental characters (e.g., shape, dentition, biting force) and similarity in head dimensions among regions likely reflects a general similarity in diet among coyote populations in all 3 regions, as changes in shape (i.e., short vs. long) would indicate adaptation to differing stresses related to feeding ecology (Van Valkenburgh 1991, Wang and Tedford 2010, Curtis et al. 2018).

When species expand their ranges, populations in the expanding edges experience new selection pressures on reproduction and dispersal traits that stable populations do not (Gaston 2009, Sexton et al. 2009, Burton et al. 2010, Bell and Gonzalez 2011). Research shows that peripheral populations on the edges of ranges typically exist as lower densities and show selection for traits associated with greater dispersal ability (Travis and Dytham 2002, Phillips et al. 2008, Burton et al. 2010). Hinton et al. (2019) suggested that increased body size observed in

eastern coyote populations was likely induced by hybridization (Nowak 1979, 2002; Kays et al. 2010; Power et al. 2015) and then maintained by selection pressures for greater dispersal distances that improved immigration among peripheral populations on the expansion range. Similar conclusions were reached by Heppenheimer et al. (2018b) when they observed greater frequencies (out of equilibrium) of genes related to dispersal in southeastern and northeastern coyotes than in western coyotes. One hypothesis is larger body size is associated with greater fasting endurance compared to smaller individuals (Lindstedt and Boyce 1985, Millar and Hickling 1990, McCue 2010) which may have improved the probability of surviving dispersal into eastern forested habitats found to have lower resource availability for coyotes (Crête et al. 2001, Richer et al. 2002, Thibault and Oullett 2005).

Pelage Coloration

Eastern coyotes can exhibit considerable variation in coat color including melanism (e.g., black pelage; Figure 5), whereas coloration is more consistent in western coyotes. Occurrence of melanism in *Canis* has been linked to habitat type (Jolicoeur 1959, Gipson et al. 2002, Anderson et al. 2009), possibly to improve concealment. Melanism in canids has been traced to the K^B mutation in the melanocortin pathway for canids that appeared nearly 12,000–120,000 years ago (Anderson et al. 2009). The mutation is sometimes believed to have appeared in domestic dogs and then spread via introgression among dogs, wolves, and coyotes. Because historic evidence suggests that wolf species of eastern North America commonly exhibited melanism, Rutledge et al. (2009) suggested that the K^B allele originated in those species rather than in dogs. This may explain why only eastern coyotes exhibit melanism whereas western coyotes rarely do, despite co-existing with dogs and gray wolves. Regardless, the frequency of melanism in southeastern coyote populations is currently unknown, but Gipson (1976) reported 5–9% occurrence of

melanism in coyote populations of Arkansas. Similarly, Mowry and Edge (2014) reported the presence of melanistic coyotes in Georgia, and Caudill and Caudill (2015) found 7.4% of coyotes collected throughout Florida were melanistic. Caudill and Caudill (2015) noted that melanism varied through space from locally abundant to absent. The causative agents perpetuating variation in the frequency of melanism are complex and currently unclear. Despite the absence of melanism in western coyotes, occurrence of melanism appears to be below 10% in southeastern coyotes, as evident by the low proportion of individuals ($n = 425$) exhibiting melanism in Alabama (1.9%), Georgia (3.6%), North Carolina (5.9%), and South Carolina (5.4%) (University of Georgia, unpublished data). In addition to melanism, pelage of eastern coyotes can be highly variable including combinations of reds, browns and grays, and can change with season and age (Whiteman 1940), although no formal assessment of coloration and genetics has been conducted and it is not possible to use pelage to infer recent hybridization or ancestry.

Social Structure

Social structure of coyotes has been studied extensively in western (Bekoff and Wells 1980, 1982; Bowen 1981; Gese et al. 1988*a*, 1996*a*; Gese and Ruff 1997; Gese 1998; Hennessy et al. 2012) and northeastern (Messier and Barrette 1982; Harrison et al. 1991; Patterson and Messier 2000, 2001; Way 2007*b*) populations. However, social structure is poorly understood in southeastern populations, partly because the region's dense vegetation prohibits traditional methods of observation (visible monitoring of coyote behavior, including breeding pair formation, breeding, pup-rearing, and use of rendezvous sites).

Social monogamy and group living are common in *Canis* species (Kleiman 1967, Bekoff et al. 1981, MacDonald 1983, Gittleman 1989, Moehlman 1989, Geffen et al. 1996). Social monogamy is a primary characteristic of Canidae and all *Canis* species are considered obligate

monogamists (adult female requires assistance from other individuals including, at minimum, the parental male to rear young; Kleiman 1967, 1977). Assistance in rearing young can also include cooperative breeding involving the aid of non-breeding individuals (Way 2007*b*). However, details of pair-bonding among coyotes is not well-studied or understood (Bekoff and Gese 2003).

Social monogamy in canids is maintained by defending territories as mated pairs (Kleiman 1967). Defense of coyote territories involves excluding unrelated conspecifics from their home ranges and can allow for delayed dispersal of offspring where juveniles remain in their natal territories beyond their first year (Bekoff and Wells 1982, Harrison et al. 1991) resulting in increased group size. For example, eastern coyote breeding pairs have been found to maintain packs with as many as four subadult individuals (Way and Timm 2011), but group size can be highly variable. Larger groups of 10–12 individuals have been observed in a western population (Gese et al. 1996*b*) However, the largest group size currently reported for eastern coyotes consisted of a family group of 4-7 individuals in a highly urbanized area in Massachusetts (Way and Timm 2011)..

Group size should be a function of availability of food resources and competition for such among group members (Messier and Barrette 1982). Hence, group size is expected to vary by region and depend on habitat quality (Bowen 1981, Gese et al. 1988*a*). Early thought on group size in canids was based on cooperative-foraging hypothesis (Kleiman and Eisenberg 1973, Fox 1975, Zimen 1976, Lamprecht 1978), and researchers suggested larger groups of coyotes would be maintained by consistently exploiting and defending larger prey such as deer and moose (Bowen 1981, Gese et al. 1988*a*). However, a study at two forested study sites in Maine found 86% of juveniles dispersed before the age of 1, and all dispersed by 1.5, limiting possible group size (Harrison 1992). Harrison (1992) suggested low resource availability in the forested habitat

resulted in high juvenile dispersal rates despite the presence of large prey. Additional studies also found support for overall resource availability and resource aggregation (including fragmentation or resources) influencing group size in various regions across their range (Messier and Barrette 1982, Hidalgo-Mihart et al. 2004, Atwood 2006).

Messier and Barrette (1982) specifically challenged the cooperative-foraging hypothesis as they reasoned that increased group size would not increase the per capita consumption of large prey. To test this, they followed several family groups of coyotes in the forested, Appalachian region of Quebec, Canada and found that while group stability could be influenced by seasonal availability of larger prey, there was no evidence that overall group size was related to prey size. Instead, Messier and Barrette (1982) suggested that delayed dispersal was tolerated as juveniles could assist with provisioning sedentary young. Additionally, they proposed that population density could manifest as local territory saturation providing additional advantages to delayed dispersal for a group of related individuals. The southeastern U.S. presents novel habitat types and landscape contexts compared to previous studies and the flexibility that is well-documented in coyote group size further indicates local or regional study would be required to determine how coyote group size is influenced by specific environments (Messier and Barrette 1982).

Reproduction

The exact timing of breeding by coyotes in the southeastern U.S. is relatively unknown, but studies in other regions report coyote breeding seasons occurring during January–February with a gestation period of approximately 63 days (Bekoff and Gese 2003). Pups are reported to be born between mid-March through mid-May in the eastern United States (Andelt 1985, Harrison and Gilbert 1985, Way et al. 2001). The percentage of coyotes that breed in each year varies with local conditions and may be tied to number of breeding territories and available

resources (Windberg and Knowlton 1988, Knowlton and Gese 1995, Knowlton et al. 1999). Courtship and mate selection can begin as early as 2–3 months before successful copulation (Bekoff and Diamond 1976), with October–February representing the dispersal and pair-bonding seasons. Both males and females disperse and the distance and timing of dispersal is suspected to be correlated with food availability and population density (Gese et al. 1989, 1996*b*; Harrison et al. 1991; Harrison 1992), although dispersal is typically difficult to observe and reports are limited in most studies. Once breeding pairs are formed, changes in behavior such as increased territorial aggression, scent marking, and howling beginning at the breeding season may occur (Bekoff and Diamond 1976; Bekoff and Wells 1980; Gese and Ruff 1997, 1998). After the breeding season, male coyotes undergo testis regression, in which males experience a regression in testosterone levels and testicle sizes (Minter and DeLiberto 2008). Mean litter size typically varies between 3–7 (Knowlton 1972, Andelt 1985, Gese et al., 1989, Kennedy et al. 1990). Litter size is typically inversely correlated with population density, and positively correlated with food availability, suggesting density-dependent reproduction (Knowlton 1972; Todd and Keith 1983; Knowlton and Gese 1995; Windberg 1995; Gese et al. 1996*a, b*; O’Donoghue et al. 1997). The sex ratio of litters is generally 1:1 (Bekoff and Gese 2003).

Coyotes generally use dens when whelping and raising their young, although there are exceptions to this rule (Young and Jackson 1951, Harrison and Gilbert 1985, Ryon 1986, Way et al. 2001). For example, in eastern North Carolina, coyotes in habitats prone to flooding were observed using daybeds concealed by vegetation for whelping pups (J. W. Hinton, unpublished data). Pups begin eating regurgitated food at 3 weeks and, until pups are weaned at 6–8 weeks, activity is still concentrated at dens and daybeds. After 8 weeks, pups are taken to rendezvous sites that have been documented proximate to open habitats (Andelt et al. 1979, Harrison and

Gilbert 1985, Bekoff and Wells 1986). Pups appear to spend less time at rendezvous sites as summer progresses and exhibit greater use of their natal territories by winter or disperse and attempt to establish new territories (Andelt et al. 1979, Harrison and Gilbert 1985, Bekoff and Wells 1986).

Dispersal can occur as early as September in the first year, and the proportion of individuals that disperse in the first year is suspected to be related to local food availability (Harrison 1992). Preliminary data on coyote space use in Alabama, Georgia, and South Carolina show increased monthly space use during November–April, suggesting that pre-dispersing pups and juveniles make periodic excursions from their natal territories for several weeks before abandoning those areas to become transients (University of Georgia, unpublished data). Morin and Kelly (2017) also documented extraterritorial excursions by subadults prior to dispersal attempts. Juveniles may increase movements and make extraterritorial excursions to seek breeding opportunities (Harrison et al. 1991, Harrison 1992, Gese et al. 1996*b*) and avoid parent-offspring conflict between adults, resulting in dispersal and abandonment of natal territories (Gese et al. 1996*b*).

Seasonal dispersal appears to be relatively consistent across the eastern range with dispersal movements occurring in late-fall through early-spring in studies in Maine (Harrison 1992) and the Southeast (Ward 2017). Dispersal could also be related to increased mortality of residents during hunting seasons for other species, particularly deer and turkey (Chamberlain and Leopold 2001, Van Deelen and Gosselink 2006), that could result in pack disbandment. Recent studies in high mortality areas in Virginia and South Carolina (Morin and Kelly 2017, Kierepka et al. 2017) demonstrated rapid territory turnover and dispersal of residents from adjacent territories following removals of resident individuals (compensatory immigration), but the fate of

specific family groups following the removal of an individual within a territory has not been specifically studied. Pack dynamics are poorly understood relative to other facets of coyote ecology, such as pre-dispersal behaviors (Harrison et al. 1991, Gese et al. 1996b) and dispersal habits (Harrison 1992, Gese et al. 1996b), particularly in the southeastern United States.

Space Use

Coyote breeding pairs exhibit constrained movements over the landscape, as site fidelity is expressed by their consistent use and territorial defense of specific localities via passive (i.e., scent marking) and aggressive (i.e., physical conflict) behaviors to exclude conspecifics (Bekoff and Wells 1980, Windberg and Knowlton 1988, Knowlton and Gese 1995, Benson and Patterson 2013, Hinton et al. 2015, Ward et al. 2018). Individuals (breeders, juveniles, and pups) belonging to a pack and in possession of a territory are classified as residents, whereas transients are solitary coyotes that do not hold territories and exhibit nomadic movements with no site fidelity (Bowen 1981, Windberg and Knowlton 1988, Hinton et al. 2015, Morin and Kelly 2017). These space use patterns comprise behaviors that reflect how coyotes use their environment in response to environmental pressures. Although more is known about coyote space use behaviors than perhaps any other aspect of their ecology, researchers have traditionally focused on resident animals when studying space use of coyotes because residents comprise the breeding portion of populations. Throughout North America, coyote home-range sizes typically vary between 2.5 and 70 km² and space use by southeastern populations are typical of those reported for other regions of North America (see summaries in Leopold and Chamberlain 2000, Bekoff and Gese 2003).

Until recently, residents have been easier to study because their site fidelity and predictable movement patterns favor traditional telemetry techniques (i.e., very high frequency

VHF) that require intensive field effort to locate study animals. Conversely, space use by transient coyotes has rarely been assessed because transients traverse expansive areas and are difficult to track without global positioning systems (GPS) and satellite technology (Andelt 1985, Chamberlain et al. 2000, Gehrt et al. 2009, Schrecengost et al. 2009). For example, Andelt (1985) reported that coyotes considered to be transients in his study were located <50% of the time within their study area and Chamberlain et al. (2000) reported 33% of coyotes with VHF radio collars had permanently left their study area. In North Carolina, 3 coyotes (1 subadult male, 1 subadult female and 1 juvenile female) dispersed from Fort Bragg Military Installation and travelled considerable distances (> 192 km) before establishing new home ranges (Sasmal et al. 2018).

Recent studies, particularly those in the Southeast, have attempted to account for transiency in studies of space use and habitat selection (Hinton et al. 2015, Hickman et al. 2016, Morin and Kelly 2017, Ward 2017). Regardless of VHF and GPS technology, research indicated that approximately 70% of studied coyotes were likely residents whereas the remaining 30% were transients (Windberg and Knowlton 1988; Gese et al. 1988*b*, 1990; Chamberlain et al. 2000). Hinton et al. (2015) and Ward (2017) were able to compare space use by resident and transient coyotes in the Southeast using GPS technology. Hinton et al. (2015) reported that coyote home ranges in eastern North Carolina ranged between 13–47 km² and suggested that coyote body size constrained the area that they could effectively exploit and defend as territories. Ward (2017) assessed space use of approximately 150 coyotes radio-marked with Iridium satellite collars in Alabama, Georgia, and South Carolina and reported that 80% of monitored coyotes had home ranges ≤ 20 km². Similar to previous assessments (Windberg and Knowlton 1988, Knowlton and Gese 1995, Knowlton et al. 1999), both studies reported that coyote

territories were spaced contiguously across the landscape like pieces of a puzzle, with coyotes using physical features such as rivers and roads to demarcate boundaries and reduce territory overlap. Both studies also reported that transients consisted of younger individuals than residents, which indicated that most transients were dispersing juveniles or displaced pups. However, as breeding pairs and packs were disrupted via natural or anthropogenic sources, older individuals who previously were residents became transient as well (Hinton et al. 2015, Ward 2017).

Although it is widely accepted by researchers that transient coyotes exhibit broader movements and revisit areas less often than do residents (Kamler and Gipson 2000, Gehrt et al. 2009, Hinton et al. 2015, Morin and Kelly 2017), researchers use different criteria for categorizing coyotes as residents or transient individuals. Accordingly, this can influence interpretations on the nature of transiency, with some authors considering transiency as a unique life stage of coyotes (Morin and Kelly 2017), while others consider the transient portion of coyote populations to be made up of individuals of every age class (Hinton et al. 2015). Regardless, home ranges of resident coyotes are considered stable, whereas spatial instability (i.e., shifting patterns) is viewed as characteristic of transient coyotes (Hinton et al. 2015, Morin and Kelly 2017). For example, transient coyotes in eastern North Carolina exhibited wide-ranging space-use patterns (64.5 km² to 633.4 km²). Many transients exhibited localized movements (i.e., clusters of locations) for several weeks that averaged about 21 km², and those areas appeared analogous to home ranges in both size and habitat composition (Hinton et al. 2015). Those areas were referred to as biding areas by several authors (Hinton et al. 2015; Morin and Kelly 2017; Ward 2017), as they suggested biding behavior may provide benefits to coyote populations by increasing survivorship of transients via familiarity of areas they roam, allow

transients to assess potential areas prior to establishing home ranges, and, when opportunities arise, replace residents upon death.

Forested habitats of eastern North America vary in their suitability for coyotes, and coyotes benefit most from forests with heterogenic landscapes. In coniferous forests of eastern Canada, researchers found that coyote habitat selection was influenced by areas with well-developed understories, as moderately dense understories were selected over dense understory because vegetative openings allowed coyotes to capture snowshoe hares with greater success (Dumond et al. 2001, Thibault and Ouellet 2005). Mixed and boreal forests of eastern Canada were shown to have limited suitability for coyotes because snowshoe hares and ungulates were more difficult to acquire during winter months in forested habitats (Crête et al. 2001, Richer et al. 2002). Similarly, Kays et al. (2008) suggested that coyotes in the Adirondacks area of New York preferred areas of reforestation or human disturbance over mature forests. They predicted that coyote densities would decline as forests matured because prey would become less available, but coyotes were able to exploit disturbed forests and thrive in rural landscapes.

Habitat Selection and Use

Studies in the Southeast have noted similar preference for moderately dense vegetative cover and open habitats when coyotes were hunting prey (Kamler and Gipson 2000, Schrecengost et al. 2009, Crimmins et al. 2012, Chitwood et al. 2014). By eliciting howling responses from coyotes, Cherry et al. (2016a) reported that coyotes were positively associated with open habitats and suggested these habitats were preferred by coyotes because they were structurally similar to the plains of central North America, a core region of the coyote's historic range. When accounting for residency and transiency in coyotes, Hinton et al. (2015) found that resident coyotes in eastern North Carolina tended to establish territories in predominantly

agricultural areas, whereas transient coyotes centered their movements and biding areas proximate to those same habitats via road networks. They also suggested that the use of roads by transients improved foraging opportunities and reduced energetic costs related to shifting and expansive space use.

Similarly, Ward (2017) monitored approximately 150 coyotes fitted with GPS radio-collars in Alabama, Georgia, and South Carolina and found that resident coyotes exhibited strong selection for agriculture, shrub habitats, and some forested areas such as riparian woodlands. Ward (2017) also reported that transients selected open habitats such as agriculture and pastures, but exhibited strong selection for roads, which residents avoided. Furthermore, predictive maps of habitat use in the Southeast suggest that coyote territories are unevenly distributed, as predicted use of areas by coyotes was patchy and residents favored agricultural landscapes over forested ones (Hinton et al. 2015, Ward 2017). Together, these studies suggest that coyotes likely are subject to lower carrying capacities in forested habitats than open ones.

Coyote populations exist along rural-to-urban gradients, and throughout North America they persist in metropolitan cities with dense human populations, such as Chicago, Los Angeles, and New York (Gehrt 2007, Gese et al. 2012). Studies indicate that coyote home ranges are smaller in urbanized landscapes than rural ones. For example, Gehrt (2007) noted that mean size of home ranges published for urban coyotes ($\bar{x} = 7.3 \text{ km}^2$) were smaller than the mean home-range size for rural coyotes ($\bar{x} = 17.5 \text{ km}^2$). Similarly, Gehrt (2007) reported smaller space use patterns for transient coyotes in urban landscapes than those in rural ones. In suburban areas, forest preserves, city parks, golf courses, and wooded residential areas provide coyotes cover and food resources (Morey et al. 2007, Gehrt et al. 2009). However, habitat fragmentation was observed to increase coyote space use patterns in urban landscapes, as larger home ranges may

be necessary to acquire enough small and disjointed natural areas to fulfill energetic demands (Riley et al. 2003; Gehrt et al. 2009, 2011; Bogan 2012; Gese et al. 2012).

Despite occupying landscapes dominated by human development, coyotes in metropolitan areas typically avoided land-use types associated with human activity (e.g., residential) or used them in proportion to availability within their home ranges (Quinn 1997, Grinder and Krausman 2001, Riley et al. 2003, Morey et al. 2007, Way et al. 2004). However, coyotes have been observed maintaining territories in metropolitan areas with minimum or no natural areas and elevated human activity (Gehrt et al. 2009). Nevertheless, coyotes adapt to urban areas by restricting activity to less-developed areas. During crepuscular and nocturnal periods, when human activity is lowest, coyotes will use urban habitats as travel paths to move among more suitable natural areas within their home ranges (Quinn 1997, Grinder and Krausman 2001, Gehrt et al. 2009, Gese et al. 2012). Notably, few coyotes monitored in urban studies were considered nuisance animals, as conflicts were associated with sick individuals or those exposed to wildlife feeding by humans (Gehrt et al. 2009). Unlike healthy coyotes in urban areas, diseased coyotes were observed using more developed areas, had larger monthly home ranges, and were more active during the day. As reported by Murray et al. (2015, 2017), anthropogenic food provides a low-quality but easily accessible food source for diseased coyotes.

Coyotes on the Albemarle Peninsula of eastern North Carolina are the only coyote population in the Southeast known to co-occur with a larger *Canis* species, the red wolf (Hinton et al. 2013, 2019). Both species are known to hybridize, and coyotes are more abundant than red wolves on the Albemarle Peninsula (Hinton et al. 2017b). Hybridization occurs because some red wolves can establish territories with smaller-sized coyote mates to form functional breeding pairs capable of defending territories and producing hybrid litters (Hinton et al. 2019). The

ability to form congeneric breeding pairs demonstrates that coyotes and red wolves have similar habitat preferences.

Space use of both species was positively associated with agricultural habitats (Dellinger et al. 2013; Hinton et al. 2015, 2016; Karlin et al. 2016). Although coyotes and red wolves both established home ranges primarily on the edges of agricultural fields, coyotes maintained smaller home ranges than red wolves ($\bar{x} = 27.2 \text{ km}^2$ vs. $\bar{x} = 68.4 \text{ km}^2$; Hinton et al. 2015, 2016). Some authors have suggested that coyotes would continue to be a persistent threat to red wolf recovery because they could occupy marginal habitat that red wolves could not (Gese et al. 2015, Murray et al. 2015). However, these studies did not consider the potential benefits of transient red wolves on the persistence and maintenance of wolf populations. Hinton et al. (2016) stressed that red wolves and coyotes use the same habitats and, because transient wolves often bide in lower quality habitats proximate to wolf territories, they could destabilize coyote packs and displace coyotes from areas not occupied by resident wolves. However, local red wolf densities are now too low to support enough transients to effectively recover lost territories and disrupt coyote encroachment. Because red wolves on the Albemarle Peninsula are so few (possibly less than 15 individuals), coyotes can exploit and defend areas of the peninsula and increase in numbers (Hinton et al. 2017b).

Feeding Habits

The presence of coyotes facilitates complex ecological interactions by exerting cascading effects on prey populations. Understanding prey selection by coyotes is fundamental to understanding their role in southeastern ecosystems. The coyote is an opportunistic, generalist carnivore that has a broad diet and is known to exhibit frequency-dependent switching strategies (Patterson et al. 1998, Bartel and Knowlton 2005) under which its moderate body size permits

broad use of mammalian prey that varies from small mammals and lagomorphs to ungulates (Gese et al. 1996a, O'Donoghue et al. 1998a, Lingle 2000, Cherry et al. 2016b, Benson et al. 2017). In a study of captive coyotes, the minimum energy demand of a 12.9 kg coyote could be met by consuming 8 white-tailed deer, 105 snowshoe hares (*Lepus americanus*), or 4,700 mice in a year (Litvaitis and Mautz 1980). Although coyotes can exploit a diversity of mammalian prey, they often shift their diets seasonally based on food availability. During summer and fall, they consume a variety of invertebrates and soft mast, such as wild plum (*Prunus* sp.), blackberries (*Rubus* sp.), wild grape (*Vitis* sp.), American beautyberry (*Callicarpa americana*), blueberry (*Vaccinium* sp.), prickly pear (*Opuntia littoralis*) and persimmon (*Diospyros* sp.) (Kelly et al. 2015, Swingen et al. 2016, Cherry et al. 2016b). Cherry et al. (2016b) also noted that when soft mast was not available in the winter months, coyotes in southwest Georgia heavily utilized agricultural crops, particularly peanuts, and suggested that human-introduced supplemental food sources may provide an increased carrying capacity. Several studies of coyotes in urban areas concluded that coyotes relied on small mammals (e.g., rodents and lagomorphs) and fruit as their dominant food source versus anthropogenic diet items (Quinn 1997, Fedriani et al. 2001, Morey et al. 2007, Gerht 2007). In a comparison of diet studies, Gerht (2007) noted use of anthropogenic food by coyotes ranged between 2–35%, with most occurring below 20%. It is believed that coyote's adaptable nature and ability to exploit novel habitats allows them to persist in urban landscapes and may facilitate human-coyote conflicts (Gehrt et al. 2009, Gese et al. 2012, Hennessy et al. 2012).

Information about coyote diets in the southeastern United States is typically provided by studies assessing prey items found in stomachs and scats of coyotes (Gipson 1974, Wooding et al. 1984, Crossett and Elliott 1991, Chamberlain and Leopold 1999, Morin et al. 2016, Swingen

et al. 2016). Along with studies of space use, coyote food habits have been commonly studied in the Southeast since they began colonizing the region (Gipson 1974, Wooding et al. 1984, Lee and Kennedy 1986, Hoerath and Causey 1991). There is considerable variation in results reported among coyote diet studies published during different decades that may reflect differences in coyote and prey densities during those decades. For example, current coyote and game populations (e.g., white-tailed deer, wild turkey [*Meleagris gallopavo*]) are more abundant in the Southeast than those of the mid- to late-20th century. Therefore, it is not surprising that studies of coyote diets conducted during the coyote colonization phase or game restoration period reported low use of deer and other game species, and greater use of livestock (e. g. Crossett and Elliot 1991), than did studies conducted after 2000 when game populations were better established throughout the Southeast.

Coyote depredation on game species, as well as threatened and endangered species, has generated considerable interest by wildlife managers in the Southeast (Kilgo et al. 2010). Studies suggest that coyote depredation has a minimal impact on game birds (e.g., wild turkey and bobwhite quail [*Colinus virginianus*]; Wagner and Hill 1994, Spears et al. 2003, Staller et al. 2005, Melville et al. 2015, Byrne and Chamberlain 2018) and waterfowl (Sargeant et al. 1984, 1993; Johnson et al. 1989; Greenwood et al. 1995; Messmer 1995; Sovada et al. 1995) and may be beneficial to gamebird populations by directly or indirectly reducing other mammalian nest predators (Gompper 2002, Prugh et al. 2009, Levi and Wilmers 2012, Lesmeister et al. 2015).

In a review of coyote removal studies, Guthrey (1995) found coyote mortality of bobwhite to be almost completely compensatory, with negligible effects on population dynamics and suggested that coyotes may benefit other upland game birds. However, there is growing concern that coyote depredation of shorebird and sea turtle nests could be detrimental to

threatened and endangered populations. For example, coyotes were reported to be responsible for approximately one-third of South Carolina's documented egg losses for loggerhead sea turtles (*Caretta caretta*) during the 2009 nesting season (Eskew 2012). Similarly, coyotes accounted for approximately 74% of known cases of mammalian predation of sea turtle nests on Cape Lookout National Seashore during the 2017 nesting season (NCWRC 2018).

Although coyotes can depredate shorebird and sea turtle nests (Krogh et al. 1999, Engeman et al. 2003, Ivan and Murphy 2005, Méndez-Rodríguez and Álvarez-Castañeda 2016, Swaisgood et al. 2018), other research suggests that coyotes can increase nest success of shorebirds and sea turtles by killing or displacing foxes, raccoons (*Procyon lotor*), and feral cats or by causing behavioral shifts in these nest predators that limits their impact on shorebird and sea turtle populations (Sovada et al. 1995, Gehrt and Clark 2003, Levi and Wilmers 2012). Regardless, the positive and negative effects of coyotes on gamebird, shorebird, and sea turtle populations appear to be context-dependent, and the extent and drivers of this variation have not been well characterized.

In the eastern United States, white-tailed deer are thought to be an important food resource for coyotes and there is considerable concern among wildlife managers and the public that coyote depredation on deer neonates (i.e., ≤ 3 mo. old) may be significant enough to effect deer populations (Kilgo et al. 2010; Kilgo et al. 2012; Robinson et al. 2014). Several studies have shown that coyotes are a major predator of neonate white-tailed deer in the Southeast (Saalfeld and Ditchkoff 2007, Jackson and Ditchkoff 2013, Chitwood et al. 2015, Kelly et al. 2015, Nelson et al. 2015, Watine and Giuliano 2016) and that mortality from coyotes may be additive (Kilgo et al. 2014). Coyote predation of adult deer is believed to be low (Kilgo et al. 2016) with most use of adults resulting from scavenging of carcasses made available by human

hunters and road kill (Wooding et al. 1984, Stratman et al. 1997, Schrecengost et al. 2008, Swingen et al. 2016).

Recent research suggested scavenging by coyotes may not fully explain their use of white-tailed deer and that some coyotes may prey on adult deer throughout the year (Cherry et al. 2016b, Hinton et al. 2017a, Ward et al. 2018). For example, Cherry et al. (2016b) observed greater use of adult deer by coyotes after rather than during the firearm hunting season, which could not be accounted for by scavenging of hunting-related deer carcasses alone. However, no information was provided on the possible availability of deer carcasses resulting from other causes (vehicle collisions, starvation, disease, illegal shooting, crop damage, kill permits, etc.). Ward et al. (2018) reported a negative correlation between coyote home-range size and use of adult deer in Alabama, Georgia, and South Carolina. Because coyotes should theoretically require large foraging radii to track temporal and spatial variation in carrion availability, they suggested coyotes may have acquired adult deer through depredation. However, an abundance of carcasses in a small area could also account for the observed result. Also, increased viability of carcasses during winter months would likely result in repeat visits to the same carcass (and shorter movement distances). Almost no information exists regarding the availability of deer carcasses in areas where coyote food habits were studied and most conclusions regarding the frequency that coyotes prey upon adult deer are purely speculative.

Ward (2017) monitored 164 coyotes fitted with GPS collars and assessed the diets of 25 packs in Alabama, Georgia, and South Carolina and reported that coyote diets were comprised mostly of white-tailed deer, rabbits, small mammals, and fruit. Ward (2017) reported that mean monthly frequency of occurrence of deer in coyote scats varied between 28-53.4% and deer appeared to be an important food resource year-round, with greatest use of fawns occurring at the

height of the fawning season in Georgia and South Carolina (May-June), and although to a lesser extent, throughout the fawning season in Alabama (July-August). However, Ward (2017) observed consistent use of white-tailed deer throughout the year, as adult deer were consumed during all months. Although coyotes will opportunistically consume deer killed or wounded by hunters, Ward (2017) noted that the spatial distribution of hunted lands varied across the landscape, as did hunting pressure and hunting activity, and opportunities for coyotes to consistently exploit carcasses were likely limited due to constrained space use by residents.

Despite the widespread distribution of feral pigs and the availability of pig carcasses, Ward (2017) rarely observed pig remains in coyote scats, nor did she commonly detect animals frequently found as roadkill, suggesting that scavenging may not be an important foraging strategy for resident coyotes in the Southeast, as previously suggested by Hinton et al. (2017a). It is plausible that juvenile white-tailed deer, particularly those that are not part 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). Therefore, Ward (2017) suggested that some adult hair (based on diameter) she recovered from scats belonged to juvenile white-tailed deer and speculated that coyote predation on juvenile deer may be more common than previously thought.

Although not in the southeastern region of the U.S., fawn mortality studies conducted in both Delaware and Pennsylvania have applicability in southeastern states with similar habitats such as Virginia and West Virginia. Dion (2018) found that in a study area in Delaware where predators (i.e. black bear, bobcat, and coyotes) were functionally absent, 90-day survival estimate for fawns was 0.54. This was lower than fawn survival in in Pennsylvania where 63-day

survival was estimated at 0.72 in agricultural landscape and 0.57 in forested landscape with the aforementioned predators present (Vreeland et al. 2004). In 2015-16 Gingery et al. (2018) determined fawn survival at 182-days to be 0.51 in a forested study area and 0.71 in a study area with more of an agricultural habitat component in Pennsylvania. Both Pennsylvania studies cited predation as a major cause of fawn mortality. Vreeland et al. (2004) noted that there was no indication that fawn survival rates were preventing deer population growth in a study where causes of mortality were similarly attributed to both bears and coyotes. From these studies, it would appear that predation mortality in good habitats may be compensatory in the northern part of the southeast region.

Scat analysis is the most commonly used method to determine carnivore diets because it is a noninvasive method with low financial costs that provides a broad picture of food habits (Bacon et al. 2011, Klare et al. 2011, Steenweg et al. 2015). However, there are 2 biases to consider when determining the reliability of diet studies using scat analysis to characterize coyote food habits.

First, several studies have reported variable success in the ability of researchers to correctly differentiate scats of sympatric carnivores of similar size when using morphological attributes and measurements (Davison et al. 2002, Reed et al. 2004, Harrington et al. 2010, Dellinger et al. 2011, Lonsinger et al. 2015, Morin et al. 2016a). Misidentification could result in overestimation of coyote dietary niche breadth, overestimation of niche overlap between coyotes and other carnivores, and erroneously suggest more interspecific competition (Morin et al. 2016a). To overcome this problem, researchers can use scat DNA to positively identify scats from target taxa and increase the accuracy of their findings (Reed et al. 2004, Prugh et al. 2008, McVey et al. 2013, Morin et al. 2016a). However, low target DNA concentration, DNA

degradation, and co-purification of inhibitors that demand extra laboratory procedures to improve success and reliability of using scat DNA can make genotyping methods unaffordable for many research projects (Ramón-Laca et al. 2015).

Second, despite advances in genotyping to discriminate coyote scats from those of other species and to identify unique individuals in populations, pooling scats continues to be a pervasive practice when studying coyote diets (Reed et al. 2004, Prugh et al. 2008, McVey et al. 2013, Morin et al. 2016a). Because coyotes are cooperative breeders with packs spatially segregated on the landscape (Windberg and Knowlton 1988, Knowlton et al. 1999, Benson and Patterson 2013), studies using scat analysis to assess coyote diets should account for packs and defended territories because studies conducted across small study sites (e.g., $\leq 500 \text{ km}^2$) may artificially inflate sample sizes and incorporate pseudo-replication in their analyses by treating scats, rather than packs, as sampling units (Hinton et al. 2017a, Gable et al. 2017, Ward et al. 2018). Consequently, studies that pooled scats over meaningful sampling units could be biased due to variability in intrinsic, social, and environmental factors that are difficult to account for even when using noninvasive molecular methods. For instance, by using coyote packs as sampling units, Ward et al. (2018) provided more accurate inferences of coyote prey use than previous studies by accounting for inter-pack variability and correlating prey consumption with size and habitat composition of coyote home ranges. Schrecengost et al. (2008) studied coyote diets proximate to Ward et al.'s (2018) study area and both studies reported similar use and seasonal changes in mammalian prey and fruit by coyotes. Schrecengost et al. (2008) reported that rabbits were not an important food item for coyotes because frequency of occurrence of rabbits only peaked at 31% during February and was $<17\%$ during other months. Conversely, Ward et al. (2018) reported that rabbits were important prey for coyotes, as monthly frequency of

occurrence for rabbits ranged between 13.8–34.3% and was greatest during January–April (28.7–34.3%), which coincides with coyote breeding and whelping seasons. Findings of Ward et al. (2018) differ from Schrecengost et al. (2008) because their study area was considerably larger in size (10,530 km² vs. 800 km²) than Schrecengost et al. (2008) and they correlated consumption of rabbits to size and habitat composition of coyote home ranges, finding a correlation with increasing home range sizes and decreasing vegetation density with use of rabbits. This indicates that rabbit consumption was greatest in larger territories and open habitats, and occurred more during colder than warmer months.

Recently, diets of coyotes co-occurring with red wolves on the Albemarle Peninsula of eastern North Carolina were assessed (McVey et al. 2013, Hinton et al. 2017a). Both studies reported that coyotes and red wolves were largely carnivorous and consumed primarily mammalian prey, such as white-tailed deer, rabbits, and small mammals. McVey et al. (2013) observed no difference in diets of coyotes and red wolves, suggested that there may be relatively little ecological pressure for resource partitioning, and speculated coyotes may be fulfilling the historic niche that red wolves once had in the Southeast. Using a spatially targeted sampling method and packs as their sampling unit, Hinton et al. (2017a) observed differences in proportional use of prey by coyotes and red wolves and suggested that there were limited opportunities for resource partitioning between the 2 species. For example, Hinton et al. (2017a) reported that white-tailed deer were the dominant prey in diets of red wolves, followed by rabbits and small mammals, and use of deer by wolves was consistent among seasons. Conversely, rabbits were observed as the dominant prey of coyotes and followed equally by deer and small mammals, and seasonal differences in use of rabbits and deer by coyotes were observed. Use of deer was positively correlated with combined body mass of coyote and red wolf breeding pairs

and use of deer was 12% greater for coyotes in breeding pairs with wolves than for those paired with conspecifics.

Hinton et al. (2017a) suggested that food resources were partitioned by coyotes and red wolves via differences in the proportions of similar prey (e.g., deer and rabbits), rather than differences in types of prey exploited. Unlike western North America, where gray wolves (*Canis lupus*) and coyotes coexist through differential use of ungulates, the Southeast lacks diversity in ungulate communities. Currently, the only ungulates in much of the region are white-tailed deer and wild pigs (Laliberte and Ripple 2004) and the presence of few ungulate prey species increases dietary overlap and similar use of habitats by coyotes and red wolves, which increases interspecific competition. Consequently, significant overlap in resource use and limited opportunities for niche partitioning (i.e., few ungulate species) may prevent coexistence between the two species (Hinton et al. 2017a).

Demographics, Survival, and Mortality

Coyote demographics and population dynamics have been studied in many areas throughout North America. Coyotes are monestrous, with the dominant breeding pair producing a single litter per territory each spring. During the whelping season, coyote densities increase in areas as litters are born but the birthing pulse is followed by a gradual decline as pups die or disperse and associated pack members leave during winter. Stable coyote populations require on average that breeding adults only recruit enough surviving offspring into the breeding population to replace themselves. It has been estimated that less than 10% of the young of a given pair of coyotes need to survive to maintain local populations (Knowlton et al. 1999).

Including the Southeast, estimates of coyote density range from 0.2–2.3 coyotes/km² with generally increasing densities from northern to southern North America (Andelt 1985, Babb and

Kennedy 1989, Samson and Crête 1997, Patterson and Messier 2001, Richer et al. 2002, Bekoff and Gese 2003, Young et al. 2006, Kilgo et al. 2014, Morin et al. 2016*b*). The greatest densities reported for coyotes occur in southern Texas. Food availability is considered the major factor regulating coyote densities through survival and reproduction. Although it is argued that unexploited populations tend to fluctuate around carry capacity by having an older age structure, higher survival rates, lower reproductive rates, larger pack sizes, and lower recruitment rates (Windberg and Knowlton 1988, Knowlton et al. 1999, Bekoff and Gese 2003), the magnitude of these responses by coyote populations to anthropogenic mortality is relatively unknown for southeastern populations.

Annual mortality caused by humans varies between 0.38–1.00, as human activities, particularly shooting, trapping, and vehicle collisions, cause a greater proportion of coyote deaths than natural causes, including those in lightly exploited populations (Knowlton 1972, Andelt 1985, Gese et al. 1989, Windberg 1995, Chamberlain and Leopold 2001, Van Deelen and Gosselink 2006, Young et al. 2006). For example, most deaths reported by Chamberlain and Leopold (2001) were attributed to opportunistic take by deer and turkey hunters during the fall and spring hunting seasons, respectively. Van Deelen and Gosselink (2006) reported that 58% of coyote mortalities in their study were shooting deaths. Similarly, a broad-scale assessment of coyotes in Alabama, Georgia, and South Carolina attributed 52% and 26% of coyote deaths to shooting and trapping, respectively (University of Georgia, unpublished data).

Annual survival for adult coyotes is most often reported to range between 0.50–0.80 (Chamberlain and Leopold 2001, Windberg et al. 1985), but has also been reported to be lower in more intensively exploited populations (Morin et al. 2016*a*). Survival of pups and juveniles 0.5-1.5 years of age is lower than for adults (Windberg et al. 1985). Survival is also influenced

by social status. In a 4-year study in Colorado, annual survival rates of residents, transients, and dispersers were 0.87, 0.61, and 0.39 respectively (Gese et al. 1989). Notably, net survival only needs to be between 0.30 and 0.40 for population persistence (Knowlton 1972, Andelt 1985, Gese et al. 1989, Windberg 1995, Chamberlain and Leopold 2001, Van Deelen and Gosselink 2006, Young et al. 2006).

Survival for coyotes is typically greatest during summer with a sharp decline during winter. Because hunters and trappers are primarily responsible for coyote mortalities, increased survival during summer is reflective of the absence of shooting mortalities. Coyotes are more susceptible to opportunistic killing by hunters when vegetative cover declines and sportsmen take to the field during fall and winter. Despite evidence that anthropogenic mortality is the primary source of mortality for coyotes, spatial and temporal risks associated with mortality for coyotes are comparatively unknown in southeastern populations.

Attitudes and Opinions About Coyotes

Public perceptions and attitudes about coyotes are varied and influenced by numerous variables (Draheim et al. 2019). Some people fear coyotes and express concern for both human life and the lives of animals that are important to humans. These animals include pets, livestock, and other wildlife such as white-tailed deer, as well as agricultural crops. However, there is also a growing segment of society favoring coexistence with coyotes with reduced support for lethal control. Human dimensions survey data help to sort out public attitudes with the intent of providing managers with ways to educate people and message management programs.

Human attitudes and opinions about coyotes are dependent on the context in which people encounter or perceive encountering coyotes. Opinions of residents of rural areas may

vary, particularly if the person surveyed is a crop or livestock producer. Attitudes of both rural and non-rural residents may vary if a person has young children or pets. Hunters, especially white-tailed deer hunters, also have attitudes and opinions related to their perceived effects that coyotes may have on game species. Attitudes and opinions are central to how people respond to coyote management options, especially lethal methods of control.

Studies suggest that knowledge regarding coyote biology, behavior, and management is low (Drake et al. 2017, Bovard et al. 2011). Residence, gender, education level, occupation, and pet ownership are all variables that influence level of knowledge. An older survey (Arthur 1981) showed that the general public was most supportive of nonlethal methods for controlling coyotes that prey on sheep and cattle and when lethal methods are used, they prefer shooting from the ground. Fruit and vegetable growers in Alabama were neutral, though slightly in favor of coyote control (average score 3.6; Philipp and Armstrong 1995), whereas livestock producers were neutral but leaning more strongly toward control (average score 3.9; Philipp and Armstrong 1994) with average scores from a Likert scale where 1 = maximum protection and 5= maximum control.

A nation-wide survey conducted by George et al. (2016) compared attitudes toward coyotes between 1978 and 2014. In this survey, attitudes changed from a relatively neutral attitude toward a more positive attitude. This change, as well as positive changes in attitudes about other species in their study, was attributed to the shift in value orientation from domination toward mutualistic (Manfredo et al. 2009).

Coyotes are often subject to misinformation and conspiracy theory. In a survey of Pennsylvania hunters, Bovard et al. (2011) learned that hunters believed coyotes have been introduced in Pennsylvania by the Pennsylvania Game Commission or the auto insurance

industry. The degree that misinformation or conspiracy theory influences attitudes and opinions is not known.

Management of Coyotes

Coyote removal became a priority with the passage of the Animal Damage Control Act of 1931 and remains a primary objective of the U.S. Department of Agriculture (USDA) Animal and Plant Health Inspection Service Wildlife Services (Hawthorne 2004, Bacon 2013). Coyotes are often targeted during predator control programs because of the perceived threat to livestock (Knowlton et al. 1999), game species (Kilgo et al. 2010, Robinson et al. 2014), and public health and safety (Gompper 2002, Draheim et al. 2013). However, attempted reductions to coyote populations have historically yielded poor results, as evidenced by their range expansion and ubiquitous occurrence across most of North America. As coyotes continue to adapt to the diverse landscapes of the southeastern U.S., wildlife managers will be faced with novel human-coyote conflict issues. In addressing these conflicts, it is crucial to recognize the importance of the human perception of predators and consider these factors in integrated management approaches.

The following paragraph is summarized from the North Carolina Wildlife Resource Commission Coyote Management Plan (North Carolina Wildlife Resources Commission 2018). Historically, bounties have met with continued failure to control coyote populations across North America. Pitt et al. (2001) noted that a coyote population can recover within one year after a 60% reduction in numbers. Morin (2015) noted that higher densities of coyotes can result after high mortalities due to territory disruption and immigration by transient individuals. Kilgo et al. (2014) demonstrated that reducing coyote numbers on their study area in South Carolina by 78% in each of three years resulted in numbers rebounding within 9 months. Due to density dependent recruitment and rapid recolonization of vacant territories, attempts to reduce coyote populations

are not likely to be effective (Morin 2015). Additionally, bounty program case studies have repeatedly shown that such programs are ineffective at reducing predator numbers enough to have a long-term affect on reducing predation on livestock or species of concern (Bennitt 1948, Omand 1950, Switzenberg 1950, Nielson 1973, Theberge 1973, Parker 1995, Bartel and Brunson 2003, Sillero-Zubiri et al. 2004).

In 2017, Georgia and South Carolina instituted coyote harvest incentive programs to increase harvest and interest in hunting coyotes. Neither of these programs resulted in a substantial increase in numbers of coyotes harvested that would be significant enough to impact landscape level populations. In Georgia, the additional harvest equated to one additional coyote harvested per county plus one, or 160 animals (there are 159 counties in Georgia). Ninety-three percent of respondents of incentive hunt registrants in South Carolina indicated that they had shot a coyote while deer hunting prior to the program being created. So, very few additional hunters were created.

Throughout North America, coyotes exist along rural-to-urban gradients. Management of coyotes along this gradient is complex and controversial, as resource managers utilize a variety of lethal and non-lethal methods intended to mitigate coyote-human conflicts (Mitchell et al. 2004, Shivik 2004). In urban areas, increasing rates of encounters with people have been documented for coyotes with food conditioning and loss of fear to humans contributing to human-coyote conflicts (Timm et al. 2004, White and Gehrt 2009, Alexander and Quinn 2011, Poessel et al. 2013, Murray et al. 2015).

Coyotes adjust their activity patterns to avoid both spatial and temporal interactions with humans. Most human-coyote interactions are simply sightings, rather than physical interactions (Gehrt et al 2009). Coyotes involved in conflicts are often individuals exposed to intentional or

unintentional feeding (Gehrt et al. 2009; Murray et al. 2015, 2017). Problems with nuisance coyotes have gained the attention of many city officials, as coyotes occasionally prey on cats and small dogs (Grubbs and Krausman 2009, Gehrt et al. 2013, Kays et al. 2015) and, in extremely rare cases, coyotes have attacked people (Timm et al. 2004, Baker and Timm 2017).

Current approaches to address coyote-human conflicts in urban areas usually involves education of the public and municipal officials to modify human behaviors that are often the cause of the conflict. Lethal control is sometimes needed to address conflicts involving habituated coyotes in urban areas (Fox 2006, Huot and Bergman 2007). Human-dimension approaches are often used to identify perceptions of coyotes, conflict levels, and acceptable management goals related to coyotes. Outreach efforts generally focus on contradicting myths and misperceptions, increasing public appreciation of the ecological benefits that coyotes provide (Crooks and Soulè 1999, Prugh et al. 2009, Levi and Wilmers 2012), developing accurate perceptions by the public about the risks (or lack thereof) coyotes pose to people and pets (Gompper 2002, Timm et al. 2004, Baker and Timm 2017), and encouraging communities to prevent and mitigate interactions with coyotes (Fox 2006, Weckel et al. 2015). More specifically, management strategies for mitigating coyote-human conflict focuses on educating residents about the ecology of coyotes to reduce the potential for conflicts, notifying residents to expect when coyote activity may increase (e.g., dispersal and pup rearing seasons), implementing wildlife feeding ordinances (including restrictions on feeding free-roaming cats) to ensure that local coyotes do not become food conditioned, and altering human behaviors to decrease the likelihood of coyote habituation.

In rural areas, depredation of livestock and wildlife by coyotes is a principal cause of human-coyote conflict and has long been considered a serious problem for livestock producers

and wildlife managers (Beasom 1974, Knowlton and Gese 1995, Knowlton et al. 1999, Kilgo et al. 2010, Robinson et al. 2014). Although both lethal and non-lethal methods are used to attempt to resolve problems with nuisance coyotes, lethal control is often perceived to be the most inexpensive and effective method of reducing depredation in rural areas (Conover 2001, Mitchell et al. 2004). Lethal control methods have also been implemented to benefit economically valuable species, such as ungulates (Hurley et al. 2011, Kilgo et al. 2014) and livestock (Graham et al. 2005, Mabelle et al. 2015) and to mitigate declines in certain threatened and endangered species (Harding et al. 2001, Smith et al. 2010). Nonselective removal of coyotes assumes that fewer coyotes translates to lower rates of depredation on livestock and wildlife, whereas selective removal aims to target specific individuals responsible for the conflict while minimizing population impacts on non-problem coyotes. Although nonselective removal of coyotes has been the primary means of manipulating coyote populations in the Southeast, the inadequacies of indiscriminate lethal control have called attention to non-lethal approaches that are more ecologically, economically, or socially appropriate (Mitchell et al. 2004, Bergstrom et al. 2014, Way 2014, Newsome et al. 2015, Treves et al. 2016). Possible non-lethal intervention to reduce depredation on livestock include corralling livestock during periods of vulnerability (Schiess-Meier et al. 2007), installing predator-proof fencing around small vulnerable areas (Breitenmoser et al. 2005), using guardian animals (Linhart et al. 1979, Andelt and Hopper 2000, Shivik 2006, Gehring et al. 2010), and installing fladry (Davidson-Nelson and Gehring 2010).

Lethal control is often conducted to prevent establishment of coyotes in coastal habitats and minimize depredation on nests. In some cases, zero tolerance policies are implemented during the nesting season (spring and summer) to permit resource agency staff or contractors to shoot coyotes near nesting areas. A recent study reported that California least terns (*Sternula*

antillarum browni) and western snowy plover (*Charadrius nivosus nivosus*) experienced greater nest success in areas with more cover, a consequence of lower levels of predation on plovers (Swaigood et al. 2018). Because aspects of tern and plover nesting ecology are governed by the role of camouflage in reducing predation, Swaigood et al. (2018) suggested habitat management of vegetation cover, vegetation heterogeneity, and provision of woody debris would benefit shorebird reproductive success. For other wildlife populations, habitat management and better harvest regulations of game species may be better mechanisms through which managers can mitigate real or perceived coyote impacts on wildlife populations and may prove more effective than nonselective removal (Gaillard et al. 2000, Ballard et al. 2001, Forrester and Wittmer 2013, Gulsby et al. 2015).

While some studies reported an immediate increase in deer recruitment in the months following coyote removal (Howze et al. 2009, VanGilder et al. 2009), other studies have shown that increases in survival and recruitment may not be sustained over longer time scales or larger spatial scales. For example, Kilgo et al. (2014) and Gulsby et al. (2015) reported that intensive multi-year coyote removal had only a modest positive effect on fawn survival and recruitment and suggested that the rapid influx of transients limited the efficacy of repeated, intensive removal efforts. In areas with low-density deer populations and significant predation pressure on neonates, Chitwood et al. (2015) suggested that protecting adult females from harvest may not offset population declines, but reductions in adult female harvest is an important first step because coyote removal is likely an impractical management approach by itself. Given the uncertainty of coyote-removal efforts, reducing bag limits on antlerless deer to increase adult female survival and stabilize deer populations (Kilgo et al. 2010, 2014; Robinson et al. 2014) or encouraging non-lethal methods such as manipulating habitat conditions to provide fawns

refugia from coyote predation (Gulsby et al. 2015) are often suggested to be used in concert with lethal control.

Additionally, Bragina et al. (2019) evaluated deer populations from 1981 to 2014 (coincident with coyote colonization of the Southeast) across 384 counties in six southeastern states and found positive deer population growth in all states. Time since coyote arrival was not a significant predictor in any population models, indicating that the lack of an effect was consistent over the course of coyote colonization. They suggest that even though deer are prominent in southeastern coyote diets, their rate of predation may not be great enough (particularly the low rate of adult deer predation) to cause widespread declines in deer, and that despite low fawn survival in some populations, high adult female survival can sustain the population.

Habitat management can be used to reduce coyote predation on white-tailed deer by improving understory cover and providing refugia for fawns, as several studies have shown varying levels of predation related to changes in habitat type. Gulsby et al. 2017 found that a diversity of stand types and a landscape with abundant edge habitat was associated with a decrease in coyote predation risk of fawns in South Carolina. Saalfeld and Ditchkoff (2007) found that coyotes exhibit high predation rates on neonate white-tailed deer in exurban areas and suggested that habitat played a role in predation rates, as the majority of fawns found in the study were in areas of sparse cover in an open landscape. These habitat effects may be site specific, as other studies have reported only a weak or no increase in fawn survival relative to cover (Kilgo et al. 2014, Chitwood et al. 2015). Some have also hypothesized that availability of alternative prey items, such as small mammals, may lead to decreased fawn predation, but Kelly et al. (2015) observed minimal impact of the availability of alternative prey items on fawn depredation.

Management of coyotes is often conducted in anticipation of the effects of depredation rather than from a mechanistic understanding of coyote population dynamics (Sacks et al. 1999, Mahoney et al. 2018). Previous studies have noted that lethal strategies often fail because resident breeding pairs are the most resistant to nonselective removal techniques. These studies have investigated the efficacy of selective and non-lethal approaches which focus on small spatial areas and specific classes of animals (Till and Knowlton 1983, Sacks et al 1999, Conner et al. 2008, Seidler et al. 2012). More specifically, Sacks et al. (1999) found that coyotes responsible for sheep depredation were breeding, territorial animals, and recommended that control efforts focus on these individuals. Other studies showed the absence of pups reduced energetic needs of the pack, thus reducing depredation on domestic sheep and pronghorn fawns (Till and Knowlton 1983, Bromley and Gese 2001, Seidler et al. 2012).

Sterilization has been used as a tool to reduce depredation, under the assumption that provisioning offspring is energetically costly, and, in the absence of offspring, resident coyotes may be less likely to target larger prey if they do not need to provision for pups. Conner et al. (2008) simulated scenarios of lethal and non-lethal control techniques at varying spatial scales and reported that random sterilization could have the strongest impact on coyote population dynamics than any other scenario, especially during the post-control period. However, Conner et al. (2008) concluded that fertility control would not be an option until inexpensive and coyote-specific delivery methods become available. Instead, they concluded that lethal control at local scales that removed coyotes from a reduced area could be the most effective strategy that required fewer removals and produced a larger impact.

As a demonstration of the potential impact of sterilization on coyote densities, fertility control as a tool used in the USFWS Red Wolf Recovery Program in northeastern North

Carolina is herein presented. As part of the program, fertility control of coyotes as a unique approach to limit hybridization (Stoskopf et al. 2005, Gese et al. 2015) was studied. Following the implementation of the Red Wolf Adaptive Management Plan in 2000 (Kelly et al. 1999, Stoskopf et al. 2005, Hinton et al. 2013, Gese et al. 2015), 390 coyotes and hybrids on the Albemarle Peninsula were sterilized and used as placeholders to suppress coyote reproduction and prevent coyotes that consort with red wolves from producing hybrids (Gese and Terleztsky 2015; Bohling and Waits 2015; Bohling et al. 2016; Hinton et al. 2017*b*, 2018). By capturing, sterilizing, and then releasing coyotes and hybrids back in the wild, the USFWS Red Wolf Recovery Program manipulated canid breeding pairs of non-red wolves to suppress hybridization and introgression. Several studies suggested this strategy was effective at limiting hybridization $\leq 4\%$ in the wild red wolf population because sterile coyotes were able to hold territories and prevent fertile transient coyotes from acquiring territories and eventually reproducing (Gese and Terleztsky 2015, Bohling et al. 2016, Hinton et al. 2017*b*). However, it is unknown how the use of sterile coyotes inhibited the establishment of large coyote packs and may have affected coyote densities on the Albemarle Peninsula.

Of the 390 coyotes caught under the Recovery Program, approximately 60% were released back into the wild as sterilized placeholders (Hinton et al. 2017*b*). Using trap line data, Hinton et al. (2017*b*) reported that by 2013, the ratio of coyotes to red wolves on the Albemarle Peninsula was approximately 2:1. With the inclusion of hybrids, the ratio of coyotes and hybrids to red wolves was approximately 2.5:1. During 2013, the red wolf population annually fluctuated around 120 individuals and these ratios indicate that approximately 420 canids occupied the Albemarle Peninsula, of which 240 were coyotes. Once released, coyotes were monitored between 0–2936 days with approximately 79% of sterilized coyotes monitored for less than 2

years. The leading cause of death for sterilized coyotes were management actions (63%) followed by gunshot (11%), vehicle (8%), unknown (8%), natural (6%), and trap related (4%). The peninsula is approximately 6,000 km² and these estimates derived from Hinton et al. (2017c) suggest that coyote densities were approximately 0.04 coyotes/km². This estimate is considerably smaller than ranges of 0.2–2.3 coyotes/km² reported in studies throughout North America, and it is speculated that the combination of red wolf presence and aggressive fertility control has potential to reduce coyote density over broad areas.

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Figure 1: Geographic range expansion of the coyote (taken from Hody and Kays 2018).

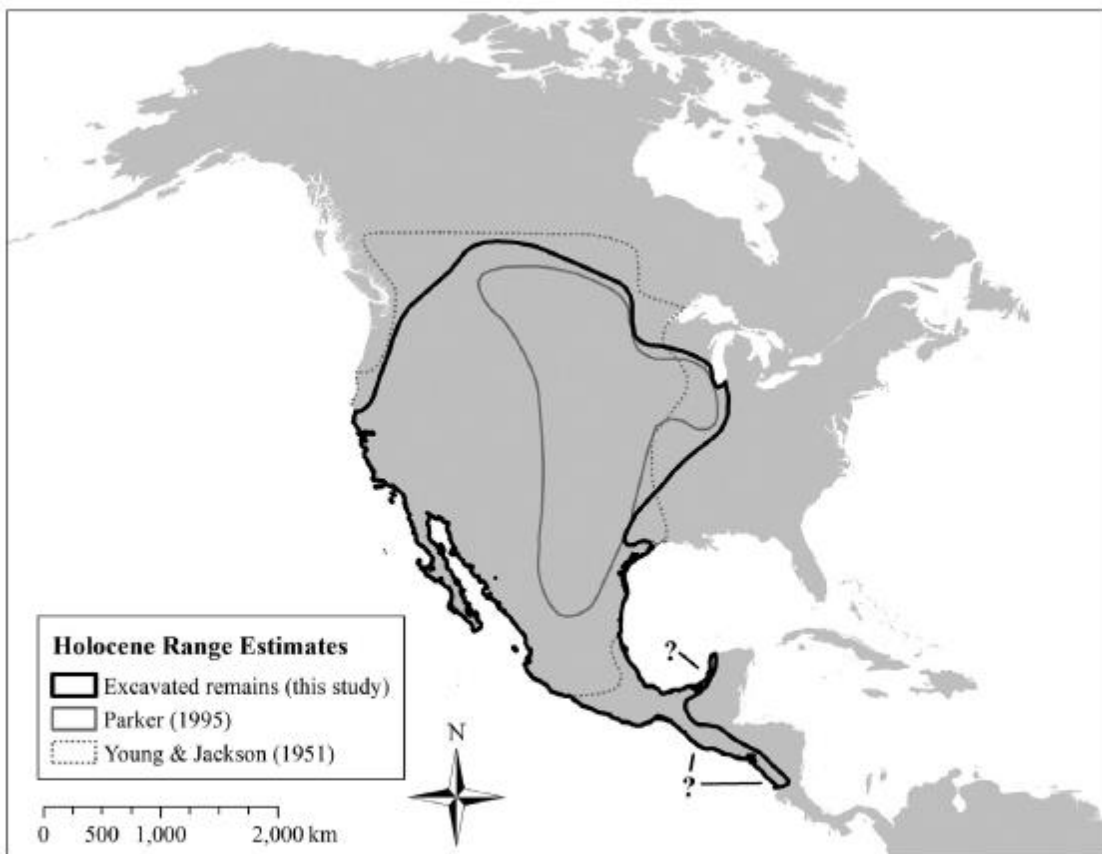


Figure 1. Comparison of Holocene coyote range maps, pre-expansion. Fossil and zooarchaeological remains suggest that coyotes were distributed throughout western North America prior to European colonization, contrary to widely-cited accounts (e.g., Parker 1995).

Figure 2: Map of the progressive expansion of the coyote's present distribution since 1685 to today, as adopted and updated from Young and Jackson (1951) and Nowak (1979).

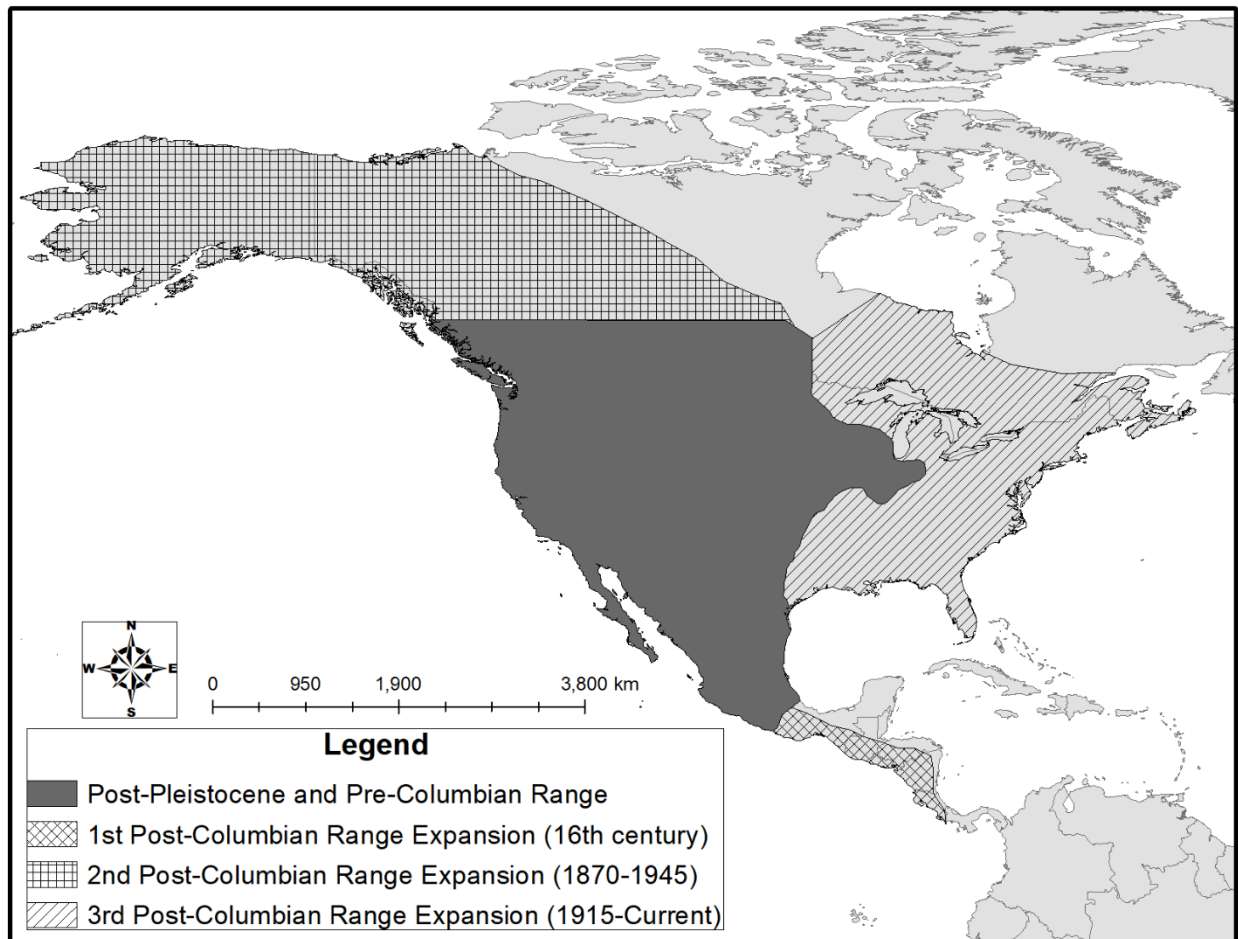


Figure 3: Genetic structure of coyotes across the United States and southern Canada inferred by Bayesian clustering in STRUCTURE at $K=2$ and $K=3$ with sampling locations indicated on the x-axis (taken from Heppenheimer et al. 2018b). This analysis consisted of 22,935 SNPs collected from 394 coyotes collected from 28 states. In the below figure, every individual is represented by a single vertical column, and columns from the same states are merged horizontally forming a single block. Each individual is assigned to a population or genetic cluster represented by a color, individual columns with more than one color occur when there is admixture (evidence of SNPs from more than one cluster), and the height of the color within a bar is the estimated proportion of admixture from each cluster or population. In the figure below, the assignment cluster analysis assignment is shown for two possible scenarios: 1) the whole sampled population consists of 2 genetically distinct populations (top panel, $K = 2$), and 2) the sampled population consists of 3 genetically distinct populations (bottom panel, $K = 3$). The comparison of the two provided greatest support for three ($K = 3$) distinct clusters or populations based on genetic similarity and dissimilarity, and samples within these clusters generally align with the geographic designations for western, northeastern, and southeastern states. The cluster assignments when the number of clusters is constrained to 2 ($K = 2$) suggests that there is more similarity among coyotes in northeastern and southeastern states (navy blue in the top panel) compared to coyotes from western states (green). The bars with multiple colors indicate an estimated proportion of admixture for individuals sampled within each state (for example, in the top panel, there is more evidence of admixture among western and eastern clusters in Missouri, Oklahoma, and Minnesota, than there is in samples from Idaho or Maine). In the bottom panel, individuals from Louisiana, Alabama, Florida, Georgia and South Carolina show no evidence of admixture with populations from the northeast and west, whereas individuals from North

Carolina, Kentucky, and Virginia show increasing amounts of admixture with populations from the north, and Pennsylvania shows the greatest amount of admixture from the southeastern population.

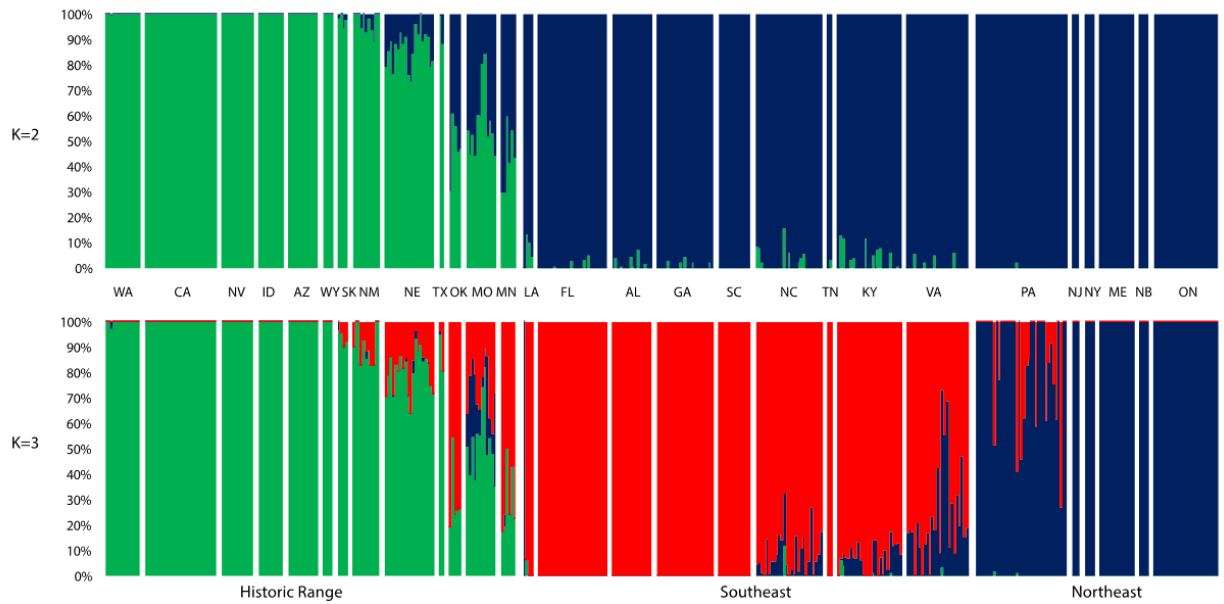


Figure 4: Mean body mass of coyote populations by major regions. Letters above the bars represent statistical differences among regions within male, female, and maximum weight categories ($P < 0.05$, Tukey's test; taken from Hinton et al. 2019).

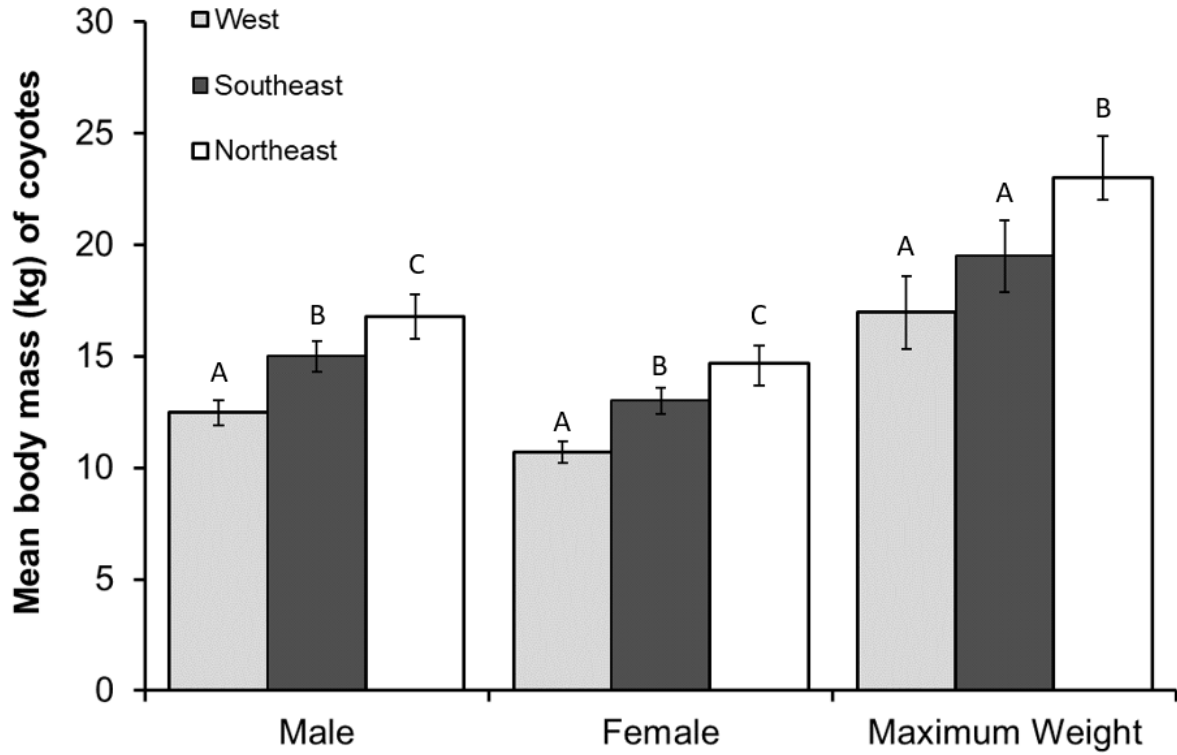


Figure 5: (A) A melanistic coyote collected from Edgefield County, South Carolina during 2015.

(B) A black and tan coyote compared to a typically colored coyote; both collected from Washington County, North Carolina during 2010.

