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Isotope analysis reveals dietary overlap among sympatric canids

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When colonizing new regions, invading species might compete strongly with phylogenetically related species native to the regions they are colonizing, eventually leading to coexistence or displacement. In the southeast of the United States, recently established coyotes (*Canis latrans*) compete with red fox (*Vulpes vulpes)* and gray fox (*Urocyon cinereoargenteus*), although it remains unclear if competition is leading to resource partitioning or displacement by species. Using nitrogen and carbon stable isotopes, we tested the hypothesis that coyotes compete with foxes for food resources, with canids partitioning those resources to mitigate competition. We compared diets of canids in the southeast to those in the Plains region of the United States, a region where all three species historically have coexisted. We analyzed 217 hair samples from both regions pre-1960, prior to coyote colonization of the southeast, and post-2000, after coyotes were ubiquitous there, to assess differences in diet among species for both regions (southeast versus Plains and time periods, pre- versus postcolonization by coyotes). Modeling revealed significant dietary overlap among historical and contemporary populations in the southeast. Historically, all species partitioned resources in the Plains. Contemporarily, red fox and coyotes co-occurring in the Plains overlapped in diet; however, gray fox diet did not overlap with those of red fox and coyotes. Absence of partitioning in diet among co-occurring canids in the southeast indicates that interspecific competition could be strong in the region. Competition among canid populations in the southeast could lead to further resource partitioning among species that promotes coexistence or competitive exclusion of smaller fox species where coyote populations are abundant.

Key words: canid ecology, diet composition, interspecific competition, resource partitioning, stable isotopes

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

Interspecific competition often occurs after introduction of new, sometimes non-native or invasive, species to an area where they compete with already established populations for finite resources (Fritts and Rodda 1998; Stewart et al. 2002; Vilà and Weiner 2004). Species can become established in a new ecosystem by means of introduction (either directly or indirectly by humans) or natural shifts in range (Sakai et al. 2001; Angert et al. 2011). As new species become established, they compete with native populations, eventually leading to resource partitioning or competitive displacement among co-occurring species (Stewart et al. 2002; Gurnell et al. 2004; Mangla et al. 2011). Although some examples of resource partitioning are well described (Schoener 1974; Diamond 1978; Grace and

Wetzel 1981), due to the relatively slow-moving nature of ecological processes, researchers rarely quantify the influence of the processes that cause partitioning as it occurs. Rather, researchers typically are limited to observing species differences, character displacements, and postcompetitive niche overlap of established sympatric populations (Schoener 1974; Diamond 1978; Grace and Wetzel 1981). As large-scale patterns of change (e.g., globalization, climate change, and habitat loss) influence ecosystem form and function on ever broadening scales, scientists are observing greater frequency of natural and anthropogenic introductions and distributional changes of species (Hellmann et al. 2008; Hulme 2009). Evidence of interspecific competition and potential resource partitioning might be most pronounced at the frontiers of these changing distributional limits, where species are attempting to, or have recently established populations (reviewed in Sexton et al. 2009). These processes provide unique opportunities to quantify how introduced competition drives resource partitioning as it occurs.

The southeastern United States (hereafter southeast) has been colonized recently by coyotes (*Canis latrans*), which were considered established throughout the region by 2000 (Hinton et al. 2019). Several species of smaller carnivores, including red fox (*Vulpes vulpes*) and gray fox (*Urocyon cinereoargenteus*), already were established throughout the region prior to the coyote's arrival. Despite coexistence of these canids in other regions of North America (Harrison et al. 1989; Cypher 1993; Neale and Sacks 2001), fox populations in the southeast are newly sympatric with coyotes and are known to use similar habitats (Chamberlain and Leopold 2005). This recent sympatry among canids in the southeast provides a unique opportunity to investigate and describe ecological processes of interspecific competition that drive resource partitioning as it occurs. Coyotes are a highly adaptable generalist and consume prey items such as small mammals, lagomorphs, and even ungulates such as white tailed deer (*Odocoileus virginianus*); their diet overlaps with fox but ultimately is broader in scope relative to fox and other native carnivore species (Major and Sherburne 1987; Cypher 1993; Hinton et al. 2017; Cherry et al. 2016; Ward et al. 2018). Coyotes also use a variety of habitats and are known to exhibit overlapping space use with red and gray foxes (Gosselink et al. 2003; Chamberlain and Leopold 2005), increasing potential for depletion of prey resources in areas where these species co-occur. Although potential impacts of coyotes on prey populations have been well studied (Rollins and Carroll 2001; Lingle 2002; Kilgo et al. 2010), there is sparse information regarding long-term impacts of dietary overlap with other canid populations in the southeast.

Determining dietary breadth for a population of interest can be challenging, especially if diet composition changes seasonally as it does for coyotes (Bekoff 2001; Schrecengost et al. 2008; Ward et al. 2018; Webster 2020). Species with generalist diets typically are thought to be able to adapt to a wider array of environments throughout their range and are able to use a broad variety of food resources (Gehrig and Swihart 2002; Shipley et al. 2009). Analysis of stable isotopes of δ^{15}N and δ^{13}C in hair or other tissues is a well-established method to infer dietary composition and potential niche width of carnivore species such as coyotes (Bearhop et al. 2004; Caut et al. 2006; Layman et al. 2012; Murray et al. 2015). When quantified for individuals or species within the same trophic level, δ^{15}N generally is interpreted as assimilation of protein into body tissues, whereas δ^{13}C is generally inferred as assimilation of C4 vegetation into body tissues (either native or anthropogenic in nature—DeNiro and Epstein 1978, 1981). By comparing isotope levels among individuals and species, researchers can effectively determine differences in dietary composition and overlap (Bearhop et al. 2004; Caut et al. 2006). Isotope values also can be used to estimate niche width and structure and allow researchers to directly assess isotopic niche overlap among species (Bearhop et al. 2004; Jackson et al. 2011).

Using analyses of nitrogen and carbon stable isotopes, we compared dietary overlap among coyotes, red fox, and gray fox in the southeast, where coyotes have recently established, with populations in the Plains region where all three species have been sympatric since the Pleistocene (Meachen and Samuels 2012). To account for natural or anthropogenic shifts in food availability in both regions, we analyzed samples from each population from the time period prior to coyote colonization of the southeast (mid-19th century – 1960) and the period after coyotes were ubiquitous (2000 – 2018). We tested the predictions that: 1) newly established coyote populations in the southeast overlap in dietary breadth with both fox species; 2) prior to coyote colonization, gray and red fox partitioned resources in the southeast; 3) in the Plains region, long-term coexistence has resulted in dietary resource partitioning among all three species; and 4) coyotes, having relatively broader dietary breadth than foxes, have greater amounts of δ^{13}C and δ^{15}N in both regions sampled.

Materials and Methods

Sample areas and collection.—We collected hair samples from red fox, gray fox, and coyotes, from two regions of the United States: southeast and Plains (Fig. 1). We focused our sampling of established populations on red and gray foxes because they are canid species with broad, omnivorous diets that overlap substantially with coyotes in parts of their distributions (Lavin et al. 2003; Warsen et al. 2014), making them likely to compete for food resources with newly established coyote populations. For both regions, we focused our collection efforts over as narrow a spatial extent as practically possible, given availability of historical specimens, to mitigate expected natural variation in diets due to differences in environmental characteristics. We then delineated two time periods of interest: samples prior to coyote colonization of the southeast and contemporary samples from post-coyote colonization. We limited our historical time period to samples collected prior to, or in, 1960. Although delineating exactly when coyotes began to colonize the southeast is difficult, previous research suggests that colonization into areas where our sampling efforts were focused occurred after 1960 (Hinton et al. 2019). Coyotes were considered ubiquitous across the southeast by 2000 (Hinton et al. 2019), therefore all contemporary samples were collected

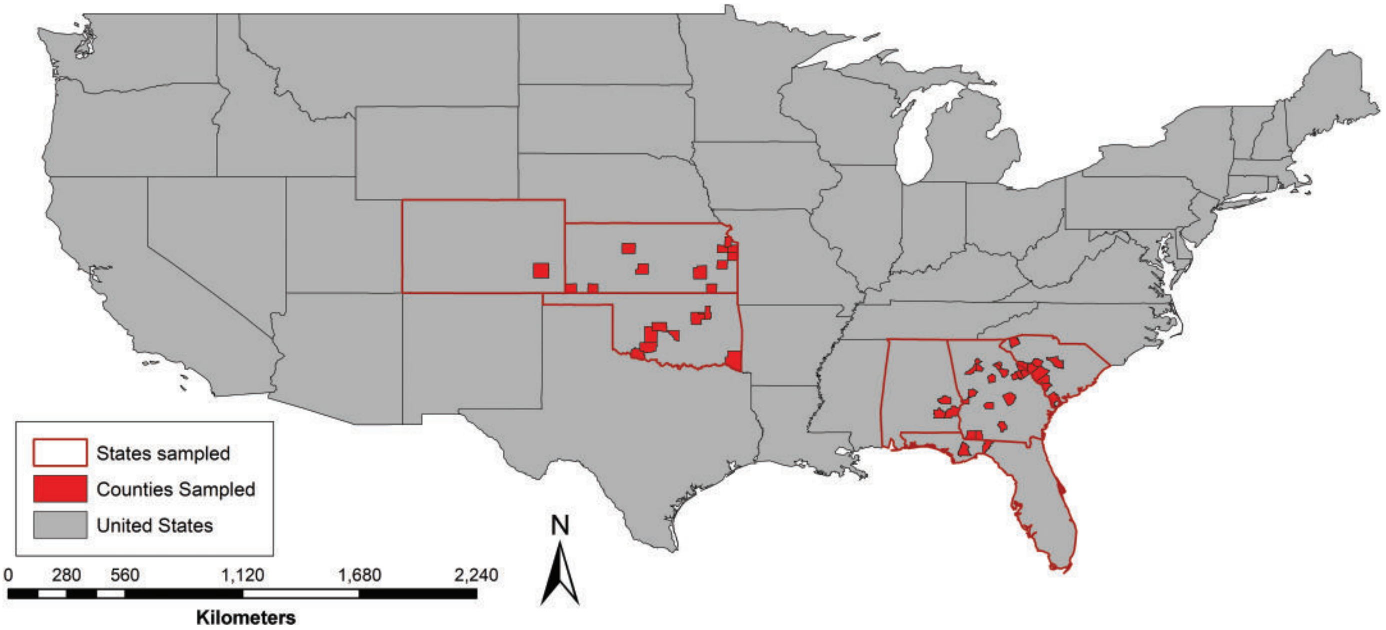

Fig. 1.—States where historical and contemporary hair samples were collected from coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes vulpes*) in the southeast and the Plains regions. For some samples, county information was not available.

after 2000. We collected all historical samples from museum preserved specimens of individuals collected from our desired regions pre-1960 (see Appendix 1).

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

Isotopes accumulate at different rates in all tissue types in mammalian vertebrates, thus multiple tissue types (e.g., hair, muscle, blood, and bone) can be used for stable isotope analysis. Because we compared historical and contemporary populations, we were limited for all samples to tissues typically preserved in museum collections (i.e., study skins or skulls). Furthermore, because our contemporary samples were collected from live-trapped individuals, it was important to minimize the negative impacts of sample collection. We therefore used guard hairs for all analyses. While hair is an effective indicator of stable isotope values for terrestrial mammals, it is important to note that hairs only indicate stable isotope accumulation during the time period the hair is metabolically active (i.e., growing—Newsome et al. 2010). Diets for all three species are known to shift seasonally (Hockman and Chapman 1983; Schrecengost et al. 2008; Ward et al. 2018), meaning values cannot reflect winter diets of our focal species. For canid species, hair provides data on diets of individuals since their last molt period, typically the spring/summer months of April–September for North America species (Castelló 2018). Thus, stable isotope values from canid hair samples can be thought to represent summer dietary breadth. For all contemporary samples and whenever possible for historical samples, we collected samples from individuals or specimens trapped during winter (Ward et al. 2018), when hair was metabolically inactive, so that hairs would provide dietary information for the previous summer. For all samples, we collected a minimum of 3 mg of guard hair from the withers (the ridge between the shoulder blades) of each individual. For each sample, we recorded date collected, state, and county of collection when possible, and sex of individual if known. All hair samples then were stored in opaque envelopes at room temperature until analysis.

Data analysis.—We prepared all hair samples for stable isotope analysis by first removing any debris or skin from the hair with soap and water, then rinsing with distilled water, drying with a sterile surface wipe, and allowing samples to sit at 22°C until dry. Following recommendations of Post et al. (2007), we did not extract lipids from hair samples because a preliminary analysis revealed that C:N ratios of all samples were < 4. After cleaning, we used scissors to homogenize the hair, then measured 2 mg of the sample and packed it into precombusted 5- × 9-mm tin capsules (Costech Analytical Technologies Inc., Valencia, California). For every 96 samples, we prepared three duplicate samples as a quality control measure. Packed capsules then were sent to the University of Georgia Stable Isotope Ecology Laboratory (SIEL) in Athens, Georgia for isotope ratio analysis of $\delta^{13}C$ and $\delta^{15}N$. The SIEL used standards in each analysis for Quality Assurance/Quality Control as well as calculating $\delta^{13}C$ and $\delta^{15}N$ (difference between a sample and natural abundance standard for which delta = zero; reported in parts per thousand) with atmospheric air being the standard for nitrogen analyses and the Chicago Pee Dee Belemnite Marine Carbonate Standard (United States National Institute of Standards and Technology, Gaithersburg, Maryland) for carbon. Measurement accuracy was within 0.2‰ for carbon and 0.3‰ for nitrogen.

Prior to analysis, we corrected for changes in atmospheric CO_2 over the last ~150 years (i.e., Suess effect—Keeling 1979). Based on core records, we applied a time-dependent correction of −0.005‰ per year between 1860 and 1960 and −0.022‰ per year since 1960 (Francey et al. 1999; Chamberlain et al. 2005). All samples were corrected to reflect 2018 values.

We used linear mixed-effects models to determine if differences in mean $\delta^{13}C$ and $\delta^{15}N$ existed within and among species between time periods for both regions. We also assessed intraspecific differences for each species from each region temporally to assess potential shifts in dietary composition. We modeled differences in $\delta^{13}C$ and $\delta^{15}N$ separately for all samples, and for each separate model, we subset data to only include data applicable to that model comparison (i.e., a model comparing isotopic levels among and contemporary gray fox in the Plains region would only include sample data for gray fox from the Plains). For all models, time period (historical and contemporary) and species (gray fox, red fox, and coyote) were included as fixed effects, as appropriate. To account for variation in the size of each region and variation of sampling location within each region, we included county of collection as a random effect when possible. This allowed us to account for potential limitations in sampling design that arose from not being able to sample the same individuals or exact locations between time periods. For some samples, location data were limited to state only. In all models, we used an alpha level of 0.05 to determine significance. We could not identify sex for a substantive proportion of the samples, so we did not include sex as a variable in our models. We undertook all modeling analyses using package "nlme" (Pinheiro et al. 2012).

To compare niche structure and overlap among species over time, we estimated isotopic niche space for each species in both regions and time periods by calculating size-corrected standard Bayesian ellipses using package "SIBER" (Jackson et al. 2011). This approach used Bayesian inference to estimate covariance matrices (a measurement of uncertainty around sample mean values), which were used to construct an ellipse and derive metrics such as area (Jackson et al. 2011). It was less sensitive to variation resulting from small sample sizes ($n < 30$), and thus we were able to accurately estimate each group's niche space regardless of sample size and make comparisons. To do this, we computed size-corrected standard ellipse area (SEA_c) and the proportion of overlap of SEA_c among species within each region and time period as a metric of how niche space and isotope ratios change within and among species over time. We carried out all statistical analyses in Program R (R Core Team 2013).

RESULTS

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

Within the southeast, species-specific analysis revealed that $\delta^{13}C$ and $\delta^{15}N$ for gray foxes did not vary between historical and contemporary samples ($\beta = 0.17$, $t_{31} = 0.32$, $P = 0.75$ for $\delta^{13}C$; $\beta = 0.35$, $t_{31} = 0.69$, $P = 0.49$ for $\delta^{15}N$). Gray foxes from the Plains region historically had more enriched amounts of $\delta^{13}C$ and $\delta^{15}N$ than did contemporary individuals ($\beta = 3.25$, $t_{49} = 5.44$, $P < 0.001$ for $\delta^{13}C$; $\beta = 1.44$, $t_{49} = 3.39$, $P < 0.001$ for $\delta^{15}N$). Red foxes from the Plains region showed no difference between historical and contemporary samples ($\beta = -0.11$, $t_{11} = 0.11$, $P = 0.91$ for $\delta^{13}C$; $\beta = 0.20$, $t_{11} = 0.15$, $P = 0.88$ for $\delta^{15}N$). Similarly, red foxes in the southeast showed no temporal shifts in isotope values ($\beta = 0.62$, $t_{10} = 0.61$, $P = 0.55$ for $\delta^{13}C$; $\beta = -0.22$, $t_{10} = -0.74$, $P = 0.48$ for $\delta^{15}N$). Coyotes in the Plains historically had more enriched amounts of $\delta^{13}C$ than did contemporary individuals ($\beta = 2.46$, $t_{44} = 4.08$, $P < 0.001$), but no differences in $\delta^{15}N$ were observed ($\beta = 0.11$, $t_{44} = 0.33$, $P = 0.74$; Fig. 2).

Historically, neither $\delta^{13}C$ nor $\delta^{15}N$ isotope values differed between red and gray foxes in the southeast ($\beta = 0.85$, $t_{30} = 1.53$, $P = 0.13$ for $\delta^{13}C$; $\beta = 0.15$, $t_{30} = 0.40$, $P = 0.69$

Table 1.—Average $\delta^{13}C$ and $\delta^{15}N$ values and size-corrected standard ellipse area (SEA_c) for coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes vulpes*) from the Plains and southeast regions of the United States. Historical samples are those from animals harvested prior to 1 January 1960; contemporary samples were collected after 1 January 2000.

Region	Time period	Species	Number samples	Average $\delta^{15}N$	*SD* $\delta^{15}N$	Average $\delta^{13}C$	*SD* $\delta^{13}C$	SEA_c
Plains	Historic	Coyote	25	9.14	1.18	−16.54	2.31	9.81
		Gray fox	33	7.33	1.59	−18.37	2.19	10.37
		Red fox	8	9.31	1.97	−18.76	1.96	13.47
	Contemporary	Coyote	21	9.03	1.08	−19.00	1.65	5.02
		Gray fox	18	5.89	1.13	−21.62	1.73	5.59
		Red fox	5	9.11	2.69	−18.87	0.71	7.64
Southeast	Historic	Gray fox	24	6.67	1.02	−19.78	1.32	4.50
		Red fox	8	6.82	0.5	−19.55	1.47	2.51
	Contemporary	Coyote	61	7.03	1.26	−20.85	1.58	5.23
		Gray fox	10	6.31	1.96	−19.96	1.59	8.09
		Red fox	4	7.04	0.45	−18.93	1.99	2.77

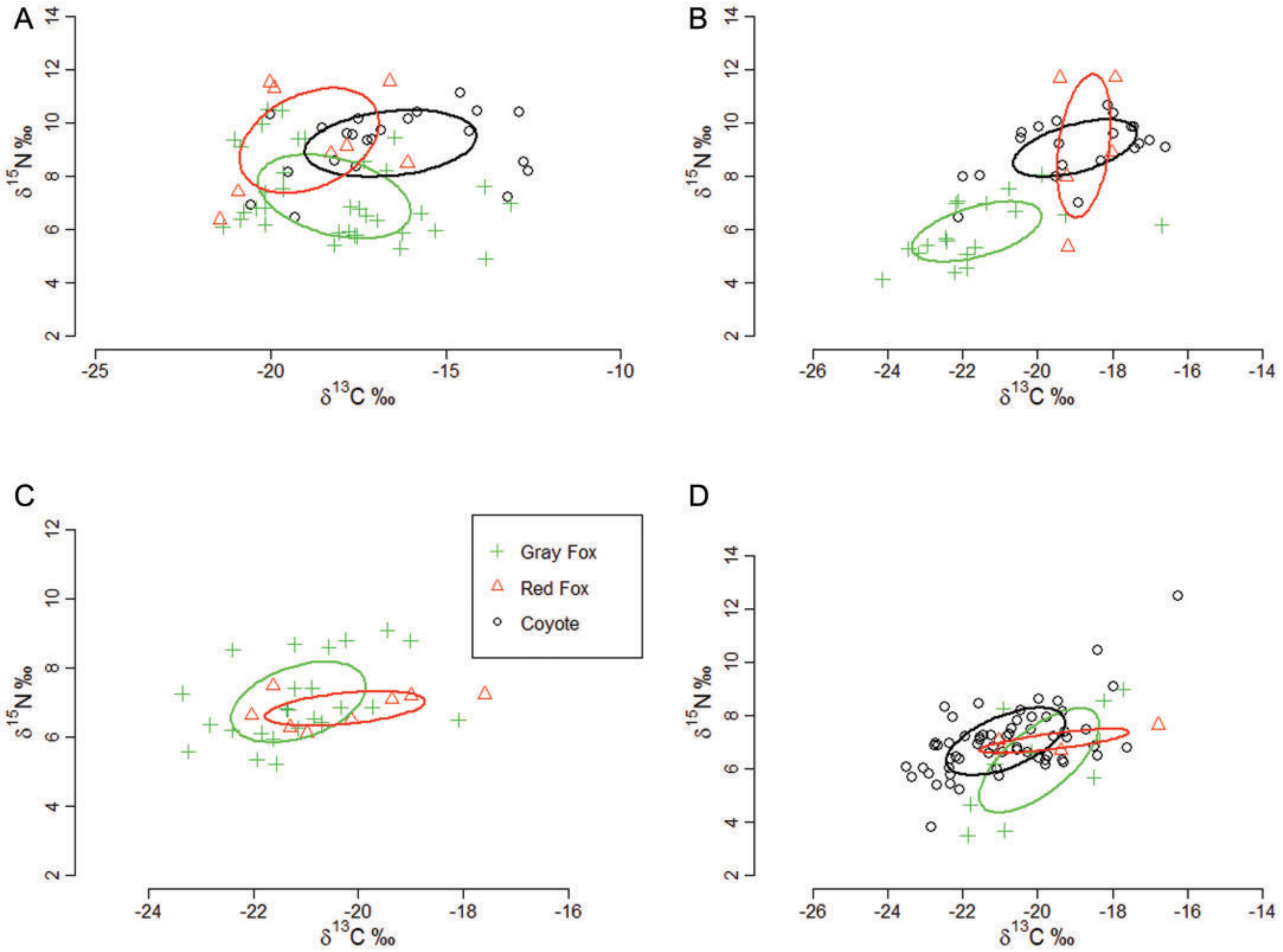

Fig. 2.—Stable isotope Bayesian standard ellipses adjusted for sample size (size-corrected standard ellipse area [SEA_c]) drawn using $\delta^{13}C$ and $\delta^{15}N$ values for canid species sampled from A) plains, B) contemporary plains, C) southeast, and D) contemporary southeast. The proportion of ellipse overlap among species is in Tables 2.

for $\delta^{15}N$). Similarly, analysis of contemporary samples of red foxes, gray foxes, and coyotes in the southeast revealed no differences between foxes and coyotes for either $\delta^{13}C$ or $\delta^{15}N$ ($\beta = 0.89$, $t_{71} = 1.63$, $P = 0.11$ for gray fox $\delta^{13}C$; $\beta = -0.72$, $t_{71} = -1.56$, $P = 0.12$ for gray fox $\delta^{15}N$; $\beta = 0.008$, $t_{71} = 0.011$, $P = 0.99$ for red fox $\delta^{15}N$; $\beta = 1.30$, $t_{71} = 1.57$, $P = 0.12$ for red fox $\delta^{13}C$). In the Plains region, $\delta^{15}N$ did not differ between coyotes and red foxes ($\beta = 0.18$, $t_{63} = 0.29$, $P = 0.77$), but gray foxes had depleted $\delta^{15}N$ ($\beta = -1.81$, $t_{63} = -4.54$, $P < 0.001$) relative to coyotes. Gray foxes and red foxes had depleted $\delta^{13}C$ compared to coyotes ($\beta = -1.82$, $t_{11} = -3.11$, $P = 0.002$ for gray fox; $\beta = -2.33$, $t_{63} = -2.59$, $P = 0.01$ for red fox). Contemporary samples from the Plains showed that gray foxes still had more depleted $\delta^{13}C$ and $\delta^{15}N$ than did red foxes and coyotes ($\beta = -2.62$, $t_{41} = -5.04$, $P < 0.001$ for $\delta^{13}C$; $\beta = -3.13$, $t_{41} = -7.27$, $P < 0.001$ for $\delta^{15}N$). Red foxes and coyotes in the Plains did not differ in $\delta^{13}C$ or $\delta^{15}N$ ($\beta = 0.24$, $t_{41} = 0.30$, $P = 0.77$ for $\delta^{13}C$; $\beta = 0.08$, $t_{41} = 0.13$, $P = 0.90$ for $\delta^{15}N$).

Standard ellipse estimates supported the trends seen in modeling, with Plains populations generally having lower overlap in isotopic niche space than did southeast populations (Table 2). Historical overlap of standard ellipses among red and gray fox samples from the southeast was 25.9%, while contemporary overlap was 18.2%. For contemporary canid populations in the southeast, overlap was greatest among coyotes and red foxes (20.8%). Ellipse overlap of historical and contemporary gray fox populations was relatively low (10.7%) and gray foxes experienced an increase in niche space from 4.50 to 8.09 (Table 1). For historical Plains populations, overlap of standard ellipses was greatest among coyotes and red foxes (19.0%), whereas coyotes and gray foxes had relatively little overlap (5.7%). Contemporarily, gray foxes had almost no overlap with either red foxes (0%) or coyotes (< 0.001%). Furthermore, contemporary gray foxes in the Plains had almost no overlap (< 0.001%) with historical gray fox populations in the same region, and estimated SEA_c for gray foxes in the Plains shrank from 10.37 historically to 5.59 contemporarily. Red fox and

Table 2.—Proportion of overlap in size-corrected standard ellipse area between species sampled from both time periods from the Plains (values shown below the diagonal) and the southeast (values shown above the diagonal) regions of the United States. Historical samples are those from animals harvested in 1872–1960; contemporary samples were collected in 2000–2018.

Species–time period	Coyote–historic	Red fox–historic	Gray fox–historic	Coyote–contemporary	Red fox–contemporary	Gray fox– contemporary
Coyote–historical						
Red fox–historical	19.0		25.9		54.0	
Gray fox–historical	5.7	16.9				10.7
Coyote–contemporary	16.6				20.8	18.2
Red fox–contemporary		37.9		29.0		19.1
Gray fox–contemporary			< 0.001	< 0.001	0	

coyote populations had increased overlap (29.0%) relative to historical populations, and both populations' estimated niche space shrank over time (Table 1; Appendix II).

Discussion

Resource partitioning occurs commonly across multiple phyla, including plants, invertebrates, vertebrates, and fungi, and serves as an ecological process to minimize resource depletion and competition, thereby allowing some species to remain sympatric through time (Roughgarden 1976; Chase and Leibold 2003; Finke and Snyder 2008). Our findings supported our hypotheses that dietary breadth and isotopic niche space of recently established coyote populations in the southeast overlapped with those of red and gray foxes, indicating a lack of resource partitioning among newly sympatric populations. When drawing conclusions about dietary breadth of a population, it is important to remember that population dietary niche space estimates do not necessarily provide information on individual specialization or differentiation within the population but rather the niche breadth of the population has a whole (Layman et al. 2007). Nevertheless, when sample sizes are robust, the potential influence of individual outliers is minimized, and conclusions can confidently be drawn about population dietary niche breadth and overlap. Given the extent of overlap between coyotes and foxes in the southeast, our data suggest coyotes are competing with foxes for food resources, increasing interspecific competition among these species.

Congruent with historical accounts of red and gray fox diet composition in the southeast (Nelson 1933; Scott 1955), our findings also suggest that gray and red foxes in the southeast historically have competed for food resources. Nevertheless, now that coyotes have become established throughout the southeast, we would expect increased exploitative competition among the canids, leading to stronger interspecific competition between foxes and coyotes for food resources. Previous research has noted dietary overlap between coyotes and various species of foxes (Kitchen et al. 1999; Neale and Sacks 2001; Azevedo et al. 2005), and all three species in our study are considered opportunistic foragers with diets consisting of animal (e.g., small mammals, reptiles/amphibians, and ground-nesting birds) and plant material (e.g., fruits, grasses, and agricultural crops), with composition varying seasonally (Hockman and Chapman 1983; Schrecengost et al. 2008; Ward et al. 2018). When competition occurs, morphological differences in body size among competitors determine which species is favored in competition (Alatalo and Moreno 1987; Richards et al. 2006). Relatively larger body sizes can allow coyotes to be resistant to interference competition (i.e., interspecific killing) with foxes, increase their mobility on the landscape, and increase their diet breadth (Palomares and Caro 1999; Nupp and Swihart 2000; Scharf et al. 2000; Caro and Stoner 2003). Indeed, coyotes are likely to be the dominant canid when in direct competition with foxes because their moderately large body size and increased resilience to structural shifts in ecosystems allow them to switch among a broader variety of food resources compared to smaller fox species with relatively narrower dietary breadths. For example, coyotes commonly hunt and kill ungulate prey (Gese and Grothe 1995; Lingle 2002; Keller and Millspaugh 2013; Benson et al. 2017; Hinton et al. 2017), as well as exploit food items commonly used by gray and red foxes, such as lagomorphs, small mammals, insects, and fruit (Major and Sherburne 1987; Cypher 1993; Ward et al. 2018).

In the continued absence of food partitioning in the southeast, we expect coyotes to dominate over gray and red fox when competition, as observed in other coyote–fox interactions throughout North America (Levi and Wilmers 2012; Newsome and Ripple 2015). Indeed, annual harvest records for the state of South Carolina show a decrease in gray and red fox harvests over the past decade, while coyote harvests have increased (J. Butfiloski, Furbearer and Alligator Program Coordinator, South Carolina Department of Natural Resources [SCDNR], pers. comm., 2016). Similarly, documented captures of gray and red fox on the Savannah River Site of ~800 km^2 in southwestern South Carolina, with scientifically rigorous survey records of mammal populations, severely declined between the early 1960s and mid 2010s (Wood and Odum 1964; Webster and Beasley 2019). In the future, we would expect to see evidence of resource partitioning among canids in the southeast as foxes acclimate to the presence of coyotes. Resource partitioning might take the form of food resource partitioning, where fox shift their dietary breadth to minimize overlap with coyotes or might occur by means of spatial or temporal segregation of habitats among species, as is seen in other regions where coyote and fox species overlap (Harrison et al. 1989; Neale and Sacks 2001; Gosselink et al. 2003; Kelly et al. 2020). If observed declines in fox abundance continue, however, coyotes might suppress fox populations in areas of the southeast before resource partitioning effectively mitigates interspecific competition.

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

In the Plains populations where coyotes have historically been sympatric with red and gray foxes, stable isotope values indicated that these populations historically partitioned food resources, and coyotes and gray foxes in particular had little overlap in estimated isotopic niche space (5.7%). Contemporarily, gray foxes continue to partition resources with both species (Fig. 2). Gray foxes are thought to have the narrowest dietary breadth of the three species, with a diet consisting of large amounts of soft mast, insects, vegetation, and agricultural crops (Hockman and Chapman 1983; Neale and Sacks 2001). This relatively narrow dietary breadth is thought to be the result of allometric differences among these species, with the gray fox's relatively small body size limiting the size and type of prey it is capable of using while simultaneously lowering energetic requirements, allowing it to more readily subsist on lower quality food items (i.e., native vegetation—Persson 1985; Carbone et al. 2007). Indeed, both historical and contemporary samples suggest gray foxes have consistently maintained a δ^{13}C- and δ^{15}N-depleted diet relative to coyotes. In addition, gray fox historically had a δ^{15}N-depleted diet and contemporarily have a δ^{13}C- and δ^{15}N-depleted diet relative to red fox in the Plains. Due to their ability to readily climb trees (Jeselnik 1981; Fritzell 1987), gray foxes generally prefer forested habitats, a relatively sparse habitat type occurring mainly along forested areas immersed in surrounding grassland throughout the Plains region (Fuller and Cypher 2004; Cooper et al. 2012). Combined, these spatial limitations on where gray fox occur on the landscape and allometric limitations on prey use are likely driving both historical and contemporary resource partitioning among gray fox and other carnivores. Likely, food resource partitioning with the other species became more pronounced as suitable habitat diminished, and competition for prey resources remained strong among these larger canids such as coyotes and red foxes.

Red foxes in the Plains historically had depleted δ^{13}C relative to sympatric coyotes, an indicator that coyotes were consuming greater amounts of C4 plants (e.g., crops and anthropogenic foods—Jahren and Kraft 2008) or prey that use C4 plants (e.g., small mammals in a grassland ecosystem). This partitioning may have mitigated competition, with fox relying more heavily on nonanthropogenic resources than coyotes to meet energetic requirements, a tradeoff more easily achieved by red fox due to allometric differences in body size and energy requirements (Persson 1985). Contemporarily, red fox and coyotes do not appear to be partitioning food resources and have substantial overlap in isotopic niche space (29.0%), a finding congruent with previous studies of dietary breadth of these two species in the Plains (Azevedo et al. 2005). The contemporary diminishment of food partitioning among red fox and coyotes relative to historic populations perhaps indicates that food partitioning has been replaced with another mechanism to mitigate interspecific competition. Previous research has shown coyotes will spatially exclude red fox from certain habitats where coyotes are present by means of interspecific strife (e.g., prairie habitat—Voigt and Earle 1983; Sargeant et al. 1987; Harrison et al. 1989). Spatial partitioning of habitat allows both species to remain sympatric at a landscape scale without necessarily limiting or shifting red fox dietary composition to lower quality diet items, a trend supported by the contemporary overlap in diet we observed.

Our research shows that dietary overlap between coyotes and other canids in the southeast, a region coyotes recently colonized, appears to be substantial, and resource partitioning might not be occurring or yet be apparent. The latter would not be surprising given that ecological processes typically play out slowly over time. In the Plains, where the species have historically been sympatric, clear partitioning of food resources is evident, particularly between coyotes and gray fox. It remains unclear whether similar partitioning will occur in southeast populations, especially because abundance of gray foxes appears to be declining in parts of the southeast (J. Butfiloski, Furbearer and Alligator Program Coordinator, SCDNR, pers. comm., 2016). While we are confident in our data and conclusions, it is important to acknowledge that because we did not directly assess dietary composition of contemporary predator populations (i.e., compare isotopic values among predator species and potential prey resources), it is possible that some fine-scale food resource partitioning might be occurring. It also is unclear to what extent interference competition might initiate partitioning of food resources among sympatric canid populations. Thus, future research and monitoring of fox and coyote populations throughout the southeast is necessary to ultimately elucidate how dietary overlap and other mechanisms of interspecific competition will affect fox populations. If dietary overlap remains substantial among these sympatric canid species we can expect the observed declines in southeast fox populations to continue.

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Appendix I

Museum specimens examined: GMNH = Georgia Museum of Natural History; KUBI = Kansas University Biological Institute; USNM = Smithsonian United States National's Museum of Natural History.

Catalog ID	Museum of origin	Date	Species	Sex
16203	KUBI	14 January 1946	Coyote	Female
16526	KUBI	14 April 1946	Coyote	Male
81873	KUBI	28 November 1959	Coyote	Male
16212	KUBI	3 March 1946	Coyote	Female
16213	KUBI	3 March 1946	Coyote	Male
16214	KUBI	3 March 1946	Coyote	Female
14676	KUBI	26 January 1945	Coyote	Male
16215	KUBI	3 March 1946	Coyote	Male
16216	KUBI	3 March 1946	Coyote	Female
16217	KUBI	10 March 1946	Coyote	Male
16219	KUBI	10 March 1946	Coyote	Male
16220	KUBI	10 March 1946	Coyote	Female
5283	KUBI	29 June 1927	Coyote	Male
72389	KUBI	11 January 1957	Coyote	Female
69616	KUBI	19 June 1956	Coyote	Female
14675	KUBI	28 January 1945	Coyote	Male
266392	USNM	3 February 1941	Coyote	Male
266391	USNM	3 February 1941	Coyote	Female
266390	USNM	29 January 1941	Coyote	Unknown
266389	USNM	22 January 1941	Coyote	Male
266388	USNM	21 January 1941	Coyote	Unknown
266387	USNM	9 December 1940	Coyote	Female
266386	USNM	1940	Coyote	Female
266383	USNM	9 February 1940	Coyote	Male
266384	USNM	5 March 1940	Coyote	Unknown
266382	USNM	9 February 1940	Coyote	Unknown
266144	USNM	9 October 1940	Coyote	Unknown
265570	USNM	13 February 1940	Coyote	Female
261642	USNM	12 November 1932	Coyote	Female
251068	USNM	18 November 1932	Coyote	Male
251067	USNM	12 November 1932	Coyote	Male
251066	USNM	12 November 1932	Coyote	Female
251065	USNM	12 November 1932	Coyote	Male
235605	USNM	17 February 1921	Coyote	Female
235604	USNM	16 February 1921	Coyote	Male
235603	USNM	24 January 1921	Coyote	Male
235602	USNM	20 January 1921	Coyote	Male
136631	USNM	18 February 1905	Coyote	Unknown
235606	USNM	17 February 1921	Coyote	Female
135747	USNM	Unknown	Coyote	Female
135750	USNM	Unknown	Coyote	Male
135749	USNM	Unknown	Coyote	Female
135447	USNM	4 June 1904	Coyote	Male
135746	USNM	28 January 1904	Coyote	Male
135076	USNM	30 October 1904	Coyote	Male

APPENDIX I Continued

Catalog ID	Museum of origin	Date	Species	Sex
134503	USNM	24 November 1904	Coyote	Female
134502	USNM	24 November 1904	Coyote	Male
26980	GMNH	2 November 2000	Grey fox	Male
116196	USNM	3 December 1901	Grey fox	Male
181199	USNM	11 January 1890	Grey fox	Male
18198	USNM	9 January 1890	Grey fox	Female
52060	USNM	1893	Grey fox	Unknown
274483	USNM	15 December 1943	Grey fox	Unknown
282677	USNM	14 December 1938	Grey fox	Male
287676	USNM	28 December 1937	Grey fox	Female
273308	USNM	23 December 1942	Grey fox	Unknown
272249	USNM	19 Dec1941	Grey fox	male
234425	USNM	6 November 1919	Grey fox	Male
234422	USNM	27 October 1919	Grey fox	Female
232414	USNM	16 April 1919	Grey fox	Female
81936	KUBI	28 January 1960	Grey fox	Female
83578	KUBI	October 1952	Grey fox	Unknown
1614	KUBI	December 1889	Grey fox	Unknown
1639	KUBI	8 December 1872	Grey fox	Unknown
43870	KUBI	6 December 1951	Grey fox	Female
56741	KUBI	3 January 1954	Grey fox	Female
72411	KUBI	9 February 1957	Grey fox	Female
63759	KUBI	August 1954	Grey fox	Female
71972	KUBI	29 January 1953	Grey fox	Male
1162	GMNH	17 October 1953	Grey fox	Male
906	GMNH	4 November 1951	Grey fox	Male
905	GMNH	20 October 1951	Grey fox	Male
239	GMNH	28 December 1947	Grey fox	Female
911	GMNH	14 July 1951	Grey fox	Female
1161	GMNH	11 November 1952	Grey fox	Male
1577	GMNH	19 November 1955	Grey fox	Female
1635	GMNH	20 October 1953	Grey fox	Female
1272	GMNH	11 November 1954	Grey fox	Male
2409	GMNH	13 January 1962	Grey fox	Male
1464	GMNH	27 November 1954	Grey fox	Unknown
99	GMNH	3 December 1958	Grey fox	Female
507406	USNM	13 December 1955	Grey fox	Female
79125	USNM	24 February 1896	Grey fox	Male
254665	USNM	20 August 1929	Grey fox	Unknown
189016	USNM	27 December 1915	Grey fox	Unknown
265663	USNM	13 March 1940	Grey fox	Female
251183	USNM	Winter 1933–34	Grey fox	Female
251182	USNM	Winter 1933–34	Grey fox	Male
256058	USNM	15 December 1930	Grey fox	Male
175595	USNM	11 January 1912	Grey fox	Unknown
175594	USNM	1 November 1912	Grey fox	Unknown
14610	KUBI	10 January 1945	Grey fox	male
14611	KUBI	20 January 1945	Grey fox	Female
155349	KUBI	Unknown	Grey fox	Male
154169	KUBI	December 1947	Grey fox	male
154170	KUBI	3 November 1947	Grey fox	Male
154171	KUBI	22 May 1949	Grey fox	Male
154172	KUBI	11 May 1949	Grey fox	Male
27337	KUBI	28 April 1948	Grey fox	Female
27338	KUBI	5 May 1948	Grey fox	Male
27340	KUBI	5 May 1948	Grey fox	Male
27341	KUBI	5 May 1948	Grey fox	Male
35114	KUBI	22 January 1950	Red fox	Male
35115	KUBI	27 January 1950	Red fox	Male
56539	KUBI	25 October 1953	Red fox	Male
81874	KUBI	14 October 1959	Red fox	Female
39177	KUBI	19 November 1950	Red fox	Male
107623	USNM	1900	Red fox	Male
507405	USNM	18 May 1960	Red fox	Male
507404	USNM	1960	Red fox	Female
14608	KUBI	8 January 1945	Red fox	Male
14609	KUBI	28 January 1945	Red fox	Female
2531	GMNH	27 January 1963	Red fox	Male
2304	GMNH	10 December 1960	Red fox	Female
612	GMNH	15 March 1950	Red fox	Unknown
1267	GMNH	12 November 1954	Red fox	Unknown
599	GMNH	22 April 1950	Red fox	Male

Appendix II

Community-level metrics associated with each population community (i.e., historical Plains populations, contemporary southeast populations, etc.) examined in this study: variation of $\delta^{13}C$ and $\delta^{15}N$ values, total area of a convex hull around each community (TA), mean distance to centroid (CD), mean nearest neighbor distance (MNND), and standard deviation of the nearest neighbor distance (SDNND). Note that TA and SDNND values are not included for the southeast–historical community because a minimum of three groups was needed to calculate those metrics. NA = Not Applicable.

Metric	Southeast–historical	Southeast–contemporary	Plains–historical	Plains–contemporary
$\delta^{13}C$ variation	0.19	0.724	2.10	3.22
$\delta^{15}N$ variation	0.88	1.297	2.32	2.86
TA	NA	0.47	2.40	0.27
CD	0.45	0.63	1.37	1.86
MNND	0.90	0.93	2.25	1.53
SDNND	NA	0.18	0.06	2.21