Testing for Mississippian Period Turkey Management in the Archaeological Record of the Southeastern United States

Erin Kennedy Thornton, Tanya Peres, Kelly Ledford Chase, Brian M. Kemp, Ryan Frome, Aurelie Manin, Lauren Basnett, Krista McGrath, Camilla Speller, and Elizabeth J. Reitz

*People living in Mesoamerica and what is now the eastern and southwestern United States used turkeys (*Meleagris gallopavo*) as sources of meat, eggs, bones, and feathers. Turkey husbandry and domestication are confirmed in two of these regions (Mesoamerica and the American Southwest), but human-turkey interactions in Eastern North American (eastern United States and Canada) are not fully explored. We apply stable isotope ($\delta^{13}C$, $\delta^{15}N$) and ancient mitochondrial DNA analyses to archaeofaunal samples from seven sites in the southeastern United States to test whether turkeys were managed or captively reared. These combined data do not support prolonged or intensive captive rearing of turkeys, and evidence for less intensive management is ambiguous. More research is warranted to determine whether people managed turkeys in these areas, and whether this is generalizable. Determining whether turkeys were managed or reared in the southeastern United States helps define cultural and environmental factors related to turkey management or husbandry throughout North America. This inquiry contributes to discussion of the roles of intensified human-animal interactions in animal domestication.*

Keywords: turkey (*Meleagris gallopavo*), animal management, southeastern United States, Mississippian period, stable isotope analysis, ancient DNA

*Las personas que vivían en Mesoamérica y lo que ahora es el este y suroeste de los Estados Unidos usaban pavos (*Meleagris gallopavo*) como fuente de carne, huevos, huesos y plumas. La cría y la domesticación de pavos están confirmadas en dos de estas regiones (Mesoamérica y el suroeste de los Estados Unidos), pero las interacciones entre humanos y pavos en el parte este de Norteamérica (el este de los Estados Unidos y Canadá) no se exploran completamente. Aplicamos análisis de isótopos estables ($\delta^{13}C$, $\delta^{15}N$) y de ADN mitocondrial antiguo a muestras de arqueofauna de siete sitios en el sureste de los Estados*

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Unidos para determinar si los pavos fueron manejados o criados en cautiverio. Estos datos combinados no apoyan la cría en cautividad prolongada o intensiva de pavos, y la evidencia de un manejo menos intensivo es ambigua. Se necesita más investigación para determinar si la gente manejó pavos en estas áreas y si esto es generalizable. Determinar si los pavos fueron manejados o criados en el sureste de los Estados Unidos ayuda a definir los factores culturales y ambientales relacionados con el manejo o la cría de pavos en toda Norteamérica. Esta investigación contribuye a la discusión de los roles de las interacciones intensificadas entre humanos y animales en la domesticación animal.

Palabras clave: pavo (*Meleagris gallopavo*), manejo de animales, sureste de Estados Unidos, período del Misisipio, análisis de isótopos estables, ADN antiguo

In many parts of the southeastern United States,[1] wild turkeys (*Meleagris gallopavo*) were sources of meat, eggs, bones, and feathers for Indigenous Americans. At Mississippian period (AD 1000–1450) sites in the Southeast, they were a common food (Peres 2017) and often associated with contexts related to prestige, ritual, and feasting (Jackson and Scott 2003; Ledford and Peres 2018; Reitz et al. 2020). Given their importance as both utilitarian and ritual resources, and the successful domestication of the species in both the American Southwest and Mesoamerica (Manin et al. 2018; Speller et al. 2010), Indigenous peoples in Eastern North America (eastern United States and Canada) may have practiced flock management or small-scale captive rearing to promote turkey abundance.

Previous suggestions for turkey management or rearing in the Southeast are based primarily on sex ratios observed in zooarchaeological assemblages. Peres and Ledford (2016) argue that an overabundance of large-bodied male turkeys in Mississippian deposits at the Fewkes site (40WM1) demonstrates potential flock management. Wild-kill assemblages typically contain more females and subadults than large adult males. Similar evidence suggests that wild poults (juvenile turkeys) were reared at Moundville (1TU500; Jackson and Scott 2003:566). Selective hunting or elite provisioning, however, could also explain the observed overrepresentation of adult male turkeys in these assemblages. Other lines of archaeological evidence for turkey management or rearing are lacking.

Ethnographic and ethnohistoric accounts provide additional evidence for potential turkey management and rearing in the Southeast. The De Soto chronicles (AD 1539–1543) report that large quantities of turkeys, or "hens," were given to Spaniards by Indigenous peoples (Rangel 1993:280–281; Robertson 1993:83, 86, 165). Although these could be wild hunted turkeys, these large gifts raise the possibility that turkeys were penned or reared to ensure sufficient numbers were available for ceremonial or political events. Cherokee and other southeastern ethnohistoric accounts describe using scattered maize (*Zea mays*) to lure wild turkeys during hunting and rearing turkey poults from eggs to ensure reliable access to meat and feathers or to lure other wild turkeys (Lawson 1966 [1709]:149; White 1980; Whitthoft 1946:377). Similar ethnohistoric accounts of the provisioning or taming of wild animals exist for other parts of Eastern North America (e.g., Galton 1865; Sagard 1939), and a stable isotope study by Morris and colleagues (2016) suggests maize provisioning of wild turkeys in Late Woodland (AD 900–1600) southwestern Ontario.

Neither turkey domestication, defined as long-term controlled breeding, nor management, have been explored extensively in Eastern North America. Throughout this article we use the term "management" to broadly refer to human behaviors that intentionally promote increased turkey abundance and availability (Zeder 2015). These could include selective hunting, seasonal provisioning of wild flocks with maize, or captive rearing. We specifically use the term "rearing" to acknowledge the potential for nonintensive feeding and tending of turkeys without controlled breeding (Vigne 2011; Zeder 2015).

Turkeys are highly tolerant of anthropogenic environments. In both the American Southwest and Mesoamerica, turkey management led to domestication, but it is currently unknown whether turkey management was practiced in other parts of the species' natural range, such as the Southeast. Small-scale, nonintensive rearing could be largely invisible in the zooarchaeological record because it may not significantly increase the number of turkeys in archaeological assemblages. We therefore used stable isotope (δ^{13}C, δ^{15}N) and ancient DNA (aDNA) analyses to investigate whether turkeys were managed or captively reared at seven Mississippian period sites in the southeastern states of Tennessee and Georgia. Stable isotopes test for extensive maize consumption, a trait that distinguishes domestic and captive turkeys in both the American Southwest and Mesoamerica from their wild counterparts (Conrad et al. 2016; Lipe et al. 2016; Manin et al. 2018; McCaffery et al. 2014; Rawlings and Driver 2010; Thornton et al. 2016). Our genetic analyses assess the degree and nature of mitochondrial DNA (mtDNA) variation among the birds, which might indicate the degree of selective breeding (if any), the introduction of domestic turkeys from either Mesoamerica or the American Southwest, or both.

Turkey management would be consistent with other examples of complex human-environment interactions in the Southeast, such as plant domestication (Smith 2006) and fire and forest management (Abrams and Nowacki 2008; Delcourt et al. 1998). The Mississippian period is characterized by widespread maize agriculture, population growth, construction of large earthen mounds, and some degree of social inequality. Within this context, feasting and differential access to resources were important in negotiating and displaying status (Blitz 1993; Jackson and Scott 2003). In other parts of North America, turkey management and eventual domestication seem to have been motivated initially by controlling access to their feathers (Lipe et al. 2016; McKusick 2001) or by their use as status or ceremonial items (Thornton and Emery 2017). Increased demand for political or ceremonial events also could have motivated turkey management in the Southeast. Alternately, Mississippian peoples in Eastern North America may not have experimented with turkey management or rearing, despite adopting other Mesoamerican domesticates (e.g., maize, beans [*Phaseolus* spp.], and squash [*Cucurbita* spp.]) and the contemporary rearing of turkeys in both Mesoamerica and the American Southwest. Determining whether turkeys were managed or reared in the Southeast is thus relevant to a broader understanding of the cultural and environmental factors associated with the decision to invest in animal management or domestication. This line of inquiry also contributes to broader discussions of human-animal interactions beyond wild or domestic dichotomies (e.g., Zeder 2012, 2015).

North American Turkeys: Genetic and Dietary Diversity

Six subspecies of wild turkey are found in central and northern Mexico and the eastern and southwestern United States (Figure 1). The subspecies native to the eastern United States and Canada (*M. g. silvestris*) has the broadest geographic distribution but is not thought to have been domesticated. In contrast, subspecies native to the American Southwester and Mesoamerica were domesticated by approximately 300–100 BC (Badenhorst and Driver 2009; Lipe et al. 2016; Thornton and Emery 2017).

Mitochondrial DNA analysis confirms that the southern Mexican subspecies (*M. g. gallopavo*) gave rise to the domestic turkeys bred and reared throughout the world today (Canales et al. 2019; Monteagudo et al. 2013; Speller et al. 2010). Genetic evidence also supports the independent domestication in the American Southwest of at least one other subspecies of wild turkey (Speller et al. 2010). Turkeys domesticated in the Southwest, however, do not appear to have contributed mtDNA to the genetic stock of modern domestic turkeys (Speller et al. 2010).

Within populations of Southwest archaeological turkeys, Speller and colleagues (2010) identified two major mitochondrial DNA haplogroups. The most common haplogroup (referred to as H1) has low genetic diversity and is genetically distinct from wild and domestic Mesoamerican turkeys and from the Merriam's subspecies (*M. g. merriami*), which is native to the Southwest. Speller and colleagues (2010) conclude that the H1 haplogroup represents a population of managed/domesticated turkeys introduced to the Southwest from outside the region, whereas the other major haplogroup (H2) corresponds to local/wild turkeys. Lipe and colleagues (2016), however, indicate that turkeys from both haplogroups were heavily maize-fed and kept within

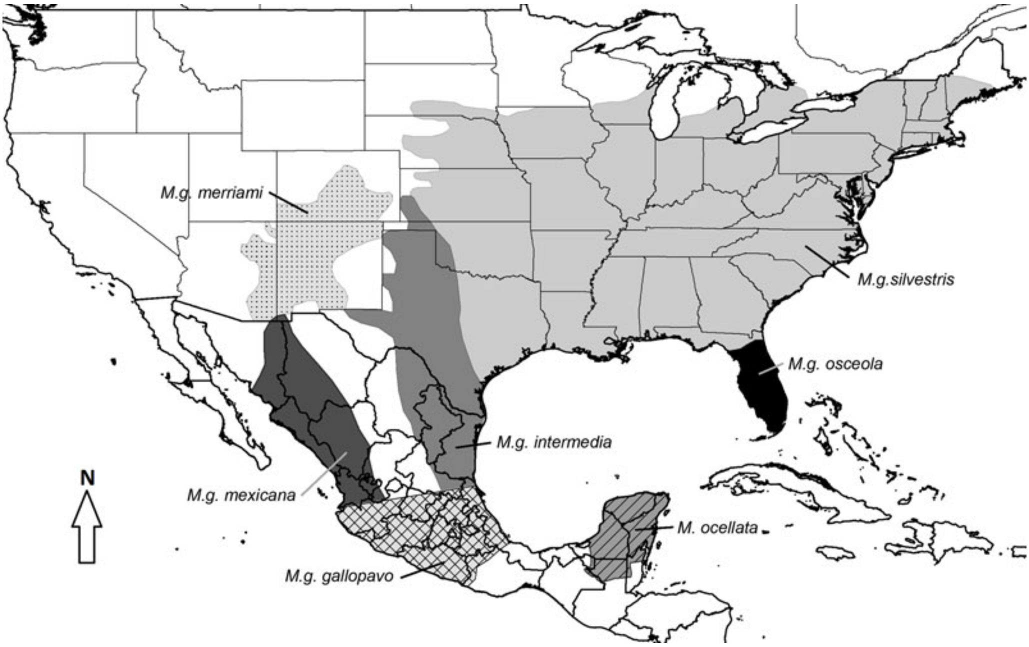

Figure 1. Map of North America showing the geographic ranges of the six subspecies of *Meleagris gallopavo* (*M. g. silvestris, M. g. osceola, M. g. merriami, M. g. intermedia, M. g. mexicana, M. g. gallopavo*) and the Central American ocellated turkey (*Meleagris ocellata*).

human settlements, clarifying that both haplogroups contributed to precolumbian domestic flocks. Domestic turkeys from Mesoamerica belong to haplogroup H3 (Speller et al. 2010). The genetics of archaeological eastern wild turkeys (*M. g. silvestris*) have not been documented but are expected to be similar to those previously reported for their modern counterparts (Mock et al. 2002; Speller et al. 2010).

Dietary Shifts Associated with Management or Captive Rearing

When animals are brought under human control, their diets often change due to range restrictions or consumption of human-provided fodder, food waste, or both. Stable carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope ratios serve as proxies for dietary shifts. Stable isotope analysis identifies management or captive rearing because dietary shifts may not be accompanied by morphological or genetic changes if breeding is not controlled, if the captive rearing and breeding process is in its early stages, or if there is extensive introgression between wild and captive-reared populations. Isotopic shifts associated with turkey husbandry and domestication have been identified in Mesoamerica and the American Southwest (Conrad et al. 2016; Lipe et al. 2016; Manin et al. 2018; McCaffery et al. 2014; Rawlings and Driver 2010; Thornton et al. 2016, 2012). Dietary shifts also indicate management or captive rearing of nondomesticated white-tailed deer (*Odocoileus virginianus*), rabbits/hares (Leporidae), golden eagles (*Aquila chrysaetos*), and large felids (*Panthera onca*, *Puma concolor*) in Mesoamerica (Somerville et al. 2016; Sugiyama et al. 2018, 2015; White et al. 2004), scarlet macaws (*Ara macao*) in the American Southwest (Somerville et al. 2010), and hutias (*Geocapromys ingrahami*) in the Caribbean (LeFebvre et al. 2019).

Wild turkeys have an omnivorous diet including fruits, flowers, seeds, nuts, insects, terrestrial gastropods, small lizards, and the leaves of shrubs, forbs, and grasses (Hurst 1992). Most foods consumed by wild turkeys are C_3 plants (e.g., fruits, shrubs, nuts, and flowers), but native C_4 grasses (e.g., *Panicum virgatum, Andropogon* *gerardii*) are also available in the Southeast. Although turkeys often are considered crop pests, turkeys in maize fields primarily consume insects and waste grain (i.e., grain left over from the previous harvest) instead of seedlings or ripening maize grains (Groepper et al. 2013). Turkeys will consume maize when it is made available by people or when crop pests such as deer, squirrels (Sciuridae), blackbirds (Corvidae), and raccoons (*Procyon lotor*) knock down stalks or pull off cobs to obtain grain (MacGowan et al. 2006; Otieno and Frenette 2017). Turkeys, therefore, had access to maize, but large quantities were not likely consumed unless it was provided to them as bait or fodder (Morris et al. 2016). Wild southeastern turkeys are expected to have largely C_3-based diets ($\delta^{13}C_{co} < -18‰$), whereas captive-reared turkeys would have C_4-based diets ($\delta^{13}C_{co} \geq -12‰$) reflecting heavy maize consumption. Mixed C_3/C_4 diets would indicate that wild turkeys consumed maize-eating insects, foraged in maize fields or middens, or consumed maize used as a hunting lure. Captive-reared turkeys fed C_3 plants, such as acorns (oak nuts), would be isotopically indistinguishable from wild birds. However, the strong maize signature observed in domestic turkeys elsewhere in North and Central America (Conrad et al. 2016; Jones et al. 2016; Lipe et al. 2016; Manin et al. 2018; Rawlings and Driver 2010; Thornton et al. 2016) suggests that similar patterns could be expected in the Southeast where maize was a staple resource.

Slightly higher $\delta^{15}N$ in domestic turkeys is reported for both the American Southwest and Mesoamerica (Lipe et al. 2016; Manin et al. 2018; McCaffery et al. 2014; Thornton et al. 2016). Higher $\delta^{15}N$ in captive-reared turkeys could reflect increased carnivory of animal pests associated with human settlements (DeNiro and Epstein 1981; Schoeninger and DeNiro 1984), rearing conditions that promote protein or water stress (Hobson et al. 1993), consumption of human or animal waste, or consumption of crops enriched in ^{15}N due to fertilization or nitrogen-cycle processes associated with crop or land management practices (Bogaard et al. 2007; Fraser et al. 2011; Guiry et al. 2018, 2020; Hart and Feranec 2020; Hwang et al. 2007; Szpak 2014). These possibilities may increase captive/domestic turkey $\delta^{15}N$ by ~1 to 4‰ over wild turkeys.

Materials and Methods

Stable Isotope Analysis

We analyzed bone collagen $\delta^{13}C_{co}$ and $\delta^{15}N$ in 83 archaeological turkeys from seven Mississippian sites: three mound centers containing multiple flat-topped earthen mounds arranged around a central plaza, two towns containing one or more platform mounds, one small village site, and one site interpreted as a chiefly compound (Figure 2; Table 1). Twenty-two white-tailed deer and four canids (*Canis* sp.) were included for comparison. Deer are primarily browsers and are expected to have a C_3-based diet, but their potential to feed in maize fields makes them a good comparison as a wild and potentially garden-hunted species. Canids presumed to be domestic dogs are used as a proxy for animals feeding largely within human settlement areas. Bone apatite $\delta^{13}C_{ap}$ was analyzed in a subsample of remains (61 turkeys, 5 deer, and 4 canids), but the results are not emphasized due to the greater potential for diagenesis in bone apatite compared to collagen (King et al. 2011). Contextual information is lacking for many samples (see Supplemental Text 1; Supplemental Table 3), but turkey remains primarily came from middens or trash pits with smaller quantities from structure floors ($n = 2$), and burial fill layers ($n = 6$).

Within each site, we ensured the sampling of discrete individuals by restricting our sample to single skeletal elements from the same side of the body. When skeletal elements were nonredundant, we relied on element age and size comparisons to prevent redundant sampling of individuals. Isotopic sampling was limited to adult individuals because very young turkeys consume large quantities of arthropods and shift to eating more plants as they mature (Hurst and Stringer 1975). By only including adult turkeys, we controlled for age-based dietary variations.

Most samples ($n = 97$) were processed at Washington State University (WSU), with a subset ($n = 12$) processed at the Center for Applied Isotope Studies (CAIS) at the University of

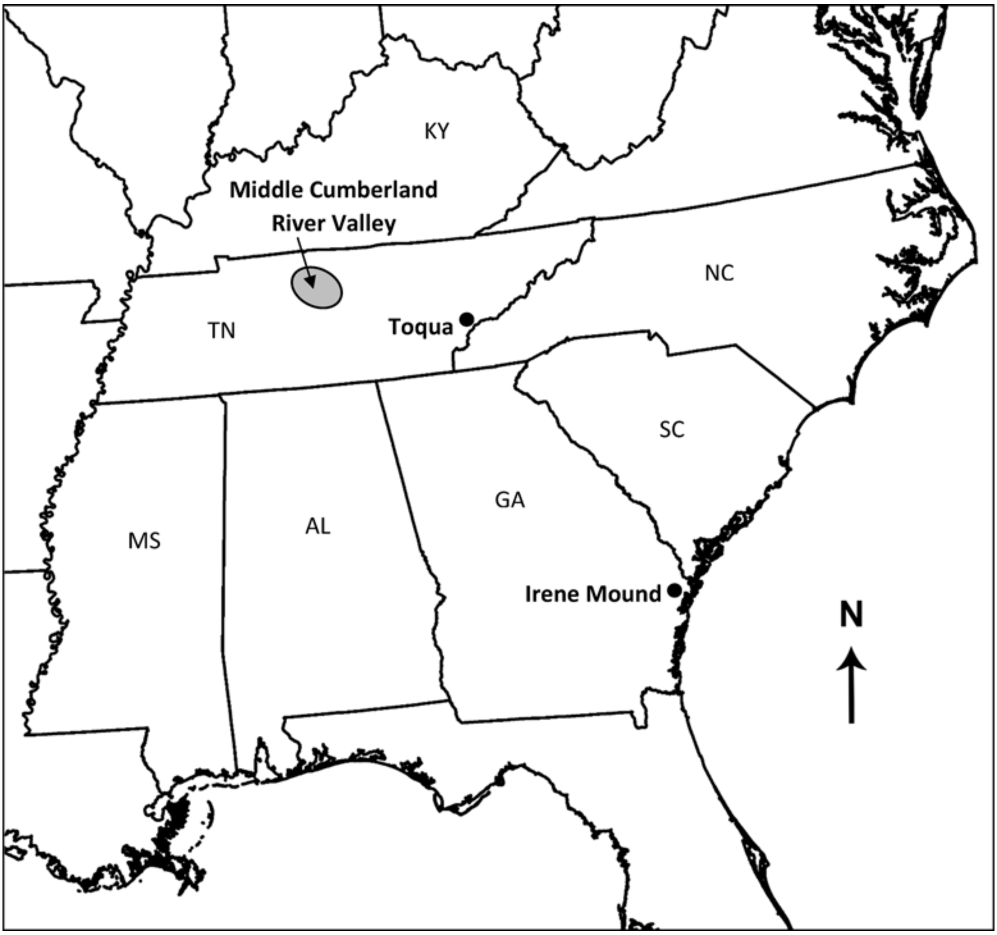

Figure 2. Map showing study sites. Middle Cumberland River Valley sites include Fewkes, Mound Bottom, Sandbar Village, Gordontown, and Inglehame Farm. Key: AL, Alabama; GA, Georgia; KY, Kentucky; MS, Mississippi; NC, North Carolina; SC, South Carolina; TN, Tennessee.

Georgia. Nearly identical procedures and equipment were used at both locations using a modified Longin (1971) method (see Supplemental Text 2 for a full description of the methods).

Bone collagen δ^{13}C and δ^{15}N values were accepted when atomic C:N ratios were 2.9–3.6 and when collagen yield was >1% of dry weight (Ambrose 1990). Data from samples not meeting

Table 1. Study Sites According to Chronology and Number of Individuals per Taxa Sampled for Isotopic Analysis.

Site (Site Number)	Chronology	Site Type	Turkey	Deer	Canid
Fewkes (40WM1)	AD 1150–1450	Mound center	37	12	4
Mound Bottom (40CH8)	AD 1100–1300	Mound center	22	—	—
Toqua (40MF6)	AD 1100–1500	Mound center	10	5	—
Inglehame Farm (40WM342)	AD 1350–1450	Village	6	—	—
Gordontown (40DV6)	AD 1250–1450	Town	3	—	—
Sandbar Village (40DV36)	AD 1000–1450	Town[a]	1	—	—
Irene Mound (9CH1)	AD 1150–1450	Chiefly compound	4	5	—
		Totals	**83**	**22**	**4**

[a]Sandbar village (40DV36) lacks an earthen mound but is currently interpreted as a peripheral section of the larger Mississippian town known as the Widemeier site (40DV9) (Smith and Moore 2012).

these criteria are reported but not included in data plots and statistical analyses. We assessed differences in mean $\delta^{13}C$ and $\delta^{15}N$ across categories via independent sample two-tailed *t*-tests assuming unequal variance.

Ancient DNA Extraction and Analysis

Ancient DNA was extracted from 31 turkey skeletal elements in two laboratories: WSU and the University of York (BioArCh). At WSU, DNA extraction followed methods described by Kemp and colleagues (2014) and Moss and colleagues (2014). At BioArCh, extraction methods followed those established by Yang and colleagues (1998) and modified as described in Speller and colleagues (2010; see Supplemental Text 3 for full description of the laboratory methods).

At both laboratories, overlapping amplicons were sequenced to cover a maximum of 506 bp of the turkey mtDNA D-loop spanning nucleotide positions 15507–16013 (based on a complete mtDNA genome of GenBank specimen EF153719; Guan et al. 2009). DNA extracts were PCR amplified using primers described in Kemp and colleagues (2017) and Speller and colleagues (2010). Successfully amplified PCR products were sequenced using forward or reverse primers or both at Eurofins Genomics (Ebersberg, Germany), Elim Biopharm (Hayward, California) or MC Lab (South San Francisco, California). Canid samples were amplified for various stretches of the D-loop using primers and conditions described by Kemp and colleagues (2017).

Turkey sequences were visually edited, and multiple sequences from the same bone were compiled into consensus sequences using ChromasPro software (www.technelysium.com.au) or Sequencher (version 4.8). The 25 turkey consensus sequences were submitted to GenBank under Accessions: MN587233-MN587257. The obtained ancient DNA sequences were BLAST-compared through GenBank to evaluate their identification as *M. gallopavo*. Multiple replicates of amplification and sequencing were used to confirm novel mutations and haplotypes and to resolve postmortem nucleotide damage. The obtained sequences were authenticated based on multiple criteria, including (a) the use of dedicated aDNA facilities, (b) no amplifications of expected length within the blank extracts and PCR negative controls, (c) multiple haplotypes observed within the dataset, and (d) amplification and sequencing conducted in independent laboratories yielding consistent results.

Initially, sequences were truncated to 435 bp (position 15567–16002) to remove primer sequences and make them comparable to published sequences. The obtained D-loop sequences were compared with 502 *M. gallopavo* sequences, including archaeological turkeys from the American Southwest (Kemp et al. 2017; Speller et al. 2010) and Mesoamerica (Manin et al. 2018), modern commercial breeds (Monteagudo et al. 2013), and North American wild turkeys (Mock et al. 2002; Szalanski et al. 2000). Multiple alignments of the haplotype sequences and published *Meleagris* mtDNA reference sequences were conducted using ClustalW (Thompson et al. 1994) through BioEdit (Hall 1999). Median-joining networks were created using Network (v. 5.0) and Network Publisher (Bandelt et al. 1999). Haplotype (*h*) and nucleotide (π) diversity were assessed based on a 309-bp fragment (positions 15651–15960) for which the majority of individuals contained sequence data and for which no polymorphisms could be observed within the larger 435-bp fragment. Diversity values were calculated for the Fewkes samples, contemporaneous archaeological turkey populations from the American Southwest (Kemp et al. 2017), and modern eastern wild turkey populations (Mock et al. 2002) using DnaSP v 5.10 (Librado and Rozas 2009). To ensure consistency with the Fewkes assemblage, diversity values for the comparative populations were assessed based on the same 309-bp fragment.

Genetic distances between populations of wild North American turkeys (Mock et al. 2002), American Southwest archaeological turkeys (Kemp et al. 2017; Speller et al. 2010), and the Fewkes archaeological turkeys were calculated on this same 309-bp fragment, using Arlequin 3.5 software (Excoffier and Lischer, 2010). F_{ST} pairwise comparisons were obtained with the Reynold's coancestry coefficient calculation, and associated *p* values were calculated on 1,023 repetitions. Negative indices and distances that were not significantly different at a 0.05 threshold were considered as null. A neighbor

Table 2. Summary Statistics for Southeast Archaeological Turkeys, Deer, and Canids.

Site (# Samples[a])	Mean $\delta^{13}C_{co}$	STDEV [b] $\delta^{13}C_{co}$	Range $\delta^{13}C_{co}$	Mean $\delta^{15}N$	STDEV[b] $\delta^{15}N$	Range $\delta^{15}N$	Mean $\delta^{13}C_{ap}$
Turkeys							
Fewkes ($n = 37$)	−19.87	1.74	−22.20 to −15.42	4.46	0.42	3.77 to 5.88	−10.76
Toqua ($n = 10$)	−21.01	0.54	−21.88 to −20.24	4.66	0.42	4.09 to 5.30	—
Mound Bottom ($n = 22$)	−20.25	0.98	−22.11 to −18.69	4.54	0.51	3.54 to 5.78	−12.60
Sandbar Village ($n = 1$)	−22.08	—	—	4.13	—	—	−10.47
Inglehame Farm ($n = 6$)	−20.01	2.40	−22.15 to −15.47	4.61	0.44	4.05 to 5.21	−12.36
Gordontown ($n = 3$)	−19.74	0.58	−20.29 to −19.13	4.37	0.13	4.23 to 4.45	−11.86
Irene Mound ($n = 4$)	−19.71	0.59	−20.44 to −19.13	5.02	0.35	4.59 to 5.33	−8.83
Deer							
Fewkes ($n = 12$)	−21.88	0.64	−25.60 to −20.72	4.20	0.87	2.21 to 5.90	—
Toqua ($n = 5$)	−22.22	0.39	−22.56 to −21.62	4.73	0.93	3.45 to 6.03	—
Irene Mound ($n = 5$)	−22.29	0.49	−23.04 to −21.74	4.91	0.52	4.40 to 5.49	−11.13
Canids							
Fewkes ($n = 4$)	−9.73	1.32	−11.55 to −8.46	6.81	0.68	5.98 to 7.44	−6.27

[a] Number of collagen samples per site. 61 samples also were run for $\delta^{13}C_{ap}$ including turkeys from Fewkes ($n = 37$), Mound Bottom ($n = 14$), Sandbar Village ($n = 1$), Inglehame Farm ($n = 4$), Gordontown ($n = 1$), and Irene Mound ($n = 4$), deer from Irene Mound ($n = 5$), and canids from Fewkes ($n = 4$).

[b] STDEV = standard deviation.

joining tree of the distances matrix was created using the "ape" library (Paradis et al. 2004) implemented in R 3.3.3 (R Core Team 2017).

The canid samples yielded no amplicons, so we could not confirm species/subspecies (i.e., domestic dog [*Canis lupus familiaris*], wolf [*Canis lupus*], or coyote [*Canis latrans*]). Given that coyotes expanded into the Southeast in recent times (Hody and Kays 2018), the canids are likely dogs or wolves. Regardless of subspecies, $\delta^{13}C$ can be used as a proxy for human interaction or management with C_3-based diets expected in wild canids and more C_4-based diets in tame or domesticated canids (Monagle et al. 2018).

Results

Isotopic Evidence of Paleodiet

With the exception of one deer, all archaeological samples were well preserved, yielding acceptable atomic C:N ratios (2.9–3.6) and collagen yield weights (>1%). Accuracy of measured $\delta^{13}C$ and $\delta^{15}N$ was better than ± 0.2‰ based on replicate analysis ($n > 10$) of laboratory standards. Precision of $\delta^{13}C$ and $\delta^{15}N$ measured from repeated chemical isolation of collagen from archaeological samples ($n = 8$) was ± 0.15 and ± 0.10‰ for $\delta^{13}C_{co}$ and $\delta^{15}N$, respectively. Full isotopic results appear in Supplemental Table 1.

All southeastern turkeys had relatively low $\delta^{13}C_{co}$ (mean = −20.1‰; range = −15.4 to −22.2‰; Table 2), which distinguishes them from archaeological domestic turkeys from the American Southwest and Mesoamerica that consumed a maize-based diet ($\delta^{13}C_{co} \geq -12$‰; Lipe et al. 2016; Manin et al. 2018; Rawlings and Driver 2010; Thornton et al. 2016; Figure 3). Instead, turkeys from the Southeast resemble archaeological turkeys reported from southern Ontario (mean $\delta^{13}C_{co} = -20.6$‰; Figure 3; Guiry et al. 2021; Morris et al. 2016). Turkey $\delta^{13}C_{co}$ did not vary significantly between sites in Tennessee and Georgia (t-test $p = 0.24$) nor between sites with earlier (e.g., Mound Bottom) and later (e.g., Fewkes) Mississippian occupations (t-test $p = 0.29$). Eight turkeys had slightly higher $\delta^{13}C_{co}$ (−15.4 to −18.0‰) representing some consumption of C_4 resources. Except for a turkey from Inglehame Farm ($\delta^{13}C_{co} = -15.47$‰), all turkeys with higher $\delta^{13}C_{co}$ (≥−18‰) were from Fewkes ($\delta^{13}C_{co} = -16.6$ to −18.0; Figure 4). Available contextual information is limited, but the turkeys with mixed C_3/C_4 diets do not appear to be restricted to any particular context; instead they came from various site areas and deposit types including middens, structures, and burial fill deposits (see Supplemental Text 1; Supplemental Table 3).

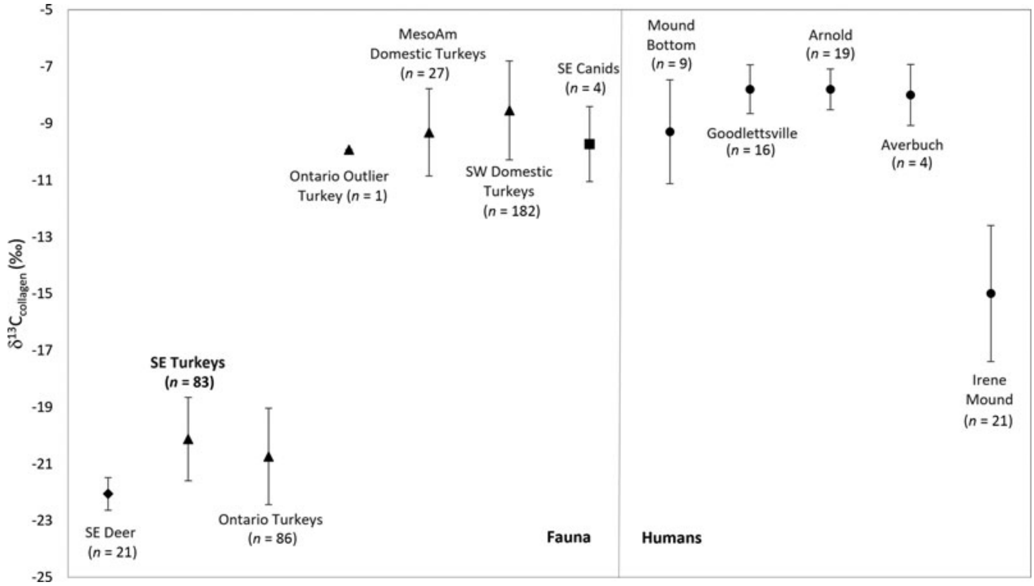

Figure 3. Comparison of mean (± 1 standard deviation) $\delta^{13}C_{co}$ of archaeological fauna from the Southeast (SE) including turkeys (triangles), deer (diamond), and canids (square) compared to published values of archaeological turkeys from southern Ontario, Canada (Guiry et al. 2021; Morris et al. 2016), domestic turkeys from Mesoamerica (MesoAM) (Thornton et al. 2016) and the American Southwest (SW) (Conrad et al. 2016; Lipe et al. 2016; Kellner et al. 2010; McCaffery et al. 2014; Rawlings and Driver 2010), and Mississippian period (AD 1150–1550) humans (circles) from Irene Mound (Hutchinson et al. 1992), and four sites in Tennessee's Cumberland River Valley (Mound Bottom, Goodlettsville, Arnold, and Averbuch; Buikstra et al. 1988).

Moreover, Fewkes turkeys recovered within the same feature, including refuse pits and burial fill deposits, show variable $\delta^{13}C_{co}$, indicating that turkeys with varying diets were disposed of in the same location.

Among the archaeological turkeys, there is a weak positive correlation between $\delta^{13}C_{co}$ and $\delta^{15}N$ ($r = 0.264$; Figure 5). Elevated $\delta^{15}N$ has also been observed in archaeological domestic turkeys and other taxa consuming crops (e.g., Barton et al. 2009; Guiry et al. 2018, 2020; Lipe et al. 2016; Manin et al. 2018; Thornton et al. 2016). This association lends some support to the contribution of maize to diets of southeastern archaeological turkeys with elevated $\delta^{13}C_{co}$, but other explanations including the consumption of maize-consuming insects, and protein or water stress cannot be ruled out.

Southeastern archaeological turkeys have slightly higher $\delta^{13}C_{co}$ than archaeological deer from the same site (deer mean $\delta^{13}C_{co} = -22.1‰$; t-test $p < 0.01$), which could be due to turkeys' greater omnivory (i.e., trophic level increases in $\delta^{13}C$; Caut et al. 2009) or their greater consumption of mast and seeds that have slightly higher $\delta^{13}C$ in comparison to leaves that deer consume in greater quantities (Cernusak et al. 2009). The diets of archaeological turkeys and deer contrast with those of southeastern archaeological canids tested in this study (mean $\delta^{13}C_{co} = -9.7‰$; mean $\delta^{15}N = 6.8‰$) and humans reported from published sources ($n = 69$, mean $\delta^{13}C_{co} = -9.9‰$; $n = 21$, mean $\delta^{15}N = 10.2‰$), which consumed more maize and fed at higher trophic levels (Figure 3; Table 2). High $\delta^{13}C_{co}$ in the archaeological canids suggests that they were tame or domesticated animals feeding within human settlements. The isotopic similarity of southeastern archaeological turkeys to deer and their pronounced isotopic separation from southeastern canids and humans contrast with isotopic patterns observed at sites in the American Southwest and Mesoamerica where domestic turkeys were reared on maize (Conrad et al. 2016; Lipe et al. 2016; Manin et al. 2018; McCaffery et al. 2014; Rawlings and Driver 2010; Thornton et al. 2016).

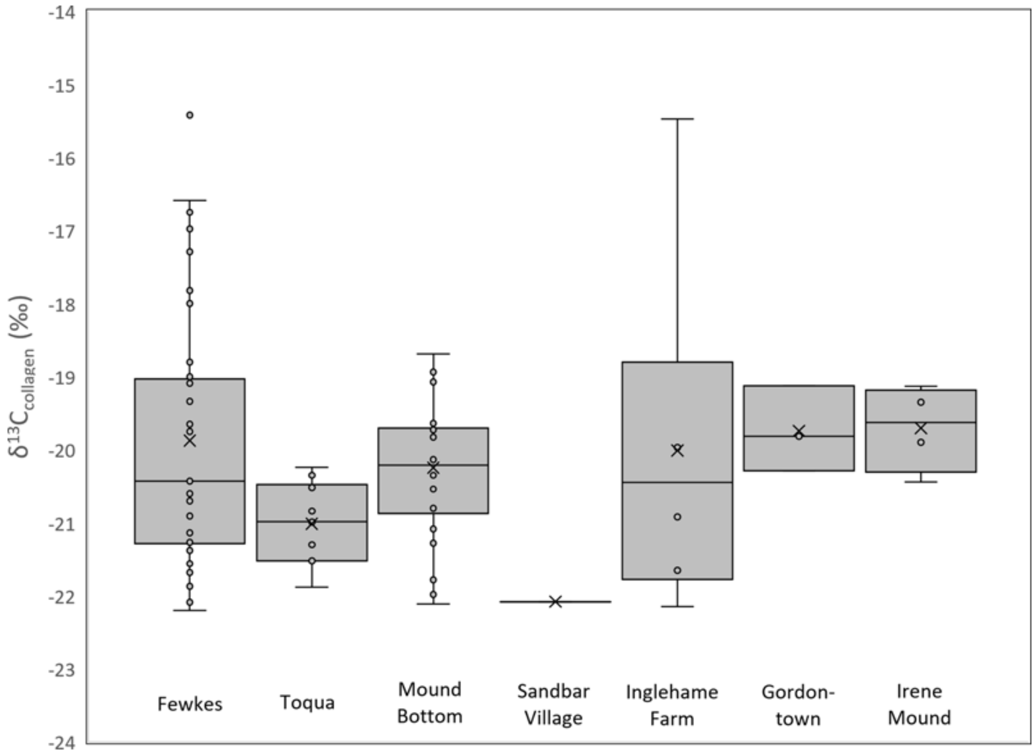

Figure 4. Median (horizontal line), mean (X) and interquartile range (box) of Southeast turkey $\delta^{13}C_{co}$.

The preferential routing of carbon from dietary protein to bone collagen (Ambrose and Norr 1993) allows for the potential underestimation of maize consumption in $\delta^{13}C_{co}$ if the protein component of the diet is largely C_3 (Froehle et al. 2010, 2012; Harrison and Katzenberg 2003). This could be expected in turkeys eating maize and invertebrates that fed on C_3 resources. The contribution of C_4 resources to southeastern turkey diets is somewhat more evident in bone apatite ($\delta^{13}C_{ap} = -8.00$ to -15.66‰), but the amount is less than that consumed by southeastern canids ($\delta^{13}C_{ap} = -5$ to -6.9‰, this study; see also Emerson et al. 2020; Guiry et al. 2021; Hogue 2003) and Mesoamerican domestic turkeys ($\delta^{13}C_{ap} = -0.6$ to -7.8‰; Thornton et al. 2016; Figure 6). Although some southeastern turkeys consumed a mixed C_3/C_4 diet, $\delta^{13}C_{ap}$ does not indicate extensive consumption of maize or other C_4 plants. The isotopic results thus do not support extensive maize provisioning or captive rearing of turkeys at the sampled Mississippian sites.

Ancient mtDNA Results

We recovered mitochondrial DNA from 25 of the 31 turkey bones (81%), which yielded DNA sequences consistent with *M. gallopavo*. Five of the samples yielded the entire 435-bp sequence, and an additional 10 samples yielded partial mtDNA profiles (309 bp) sufficient for haplotype identification (Table 3). From these observations, four distinct haplotypes were recovered from the remains: eHap1 (seven individuals), eHap2 (six individuals), eHap3 (one individual), and eHap4 (one individual). The remaining 10 samples produced sequences too short in length to be used to confidently assign membership in one mitochondrial lineage or another (these are indicated as "partial" in Table 3).

The two more common haplotypes identified in the archaeological remains, eHap1 and eHap2, are observed in modern eastern wild turkeys (*M. g. silvestris*), whereas eHap3 and eHap4 are unique, differing by a single mutation from haplotypes observed in eastern wild turkey and

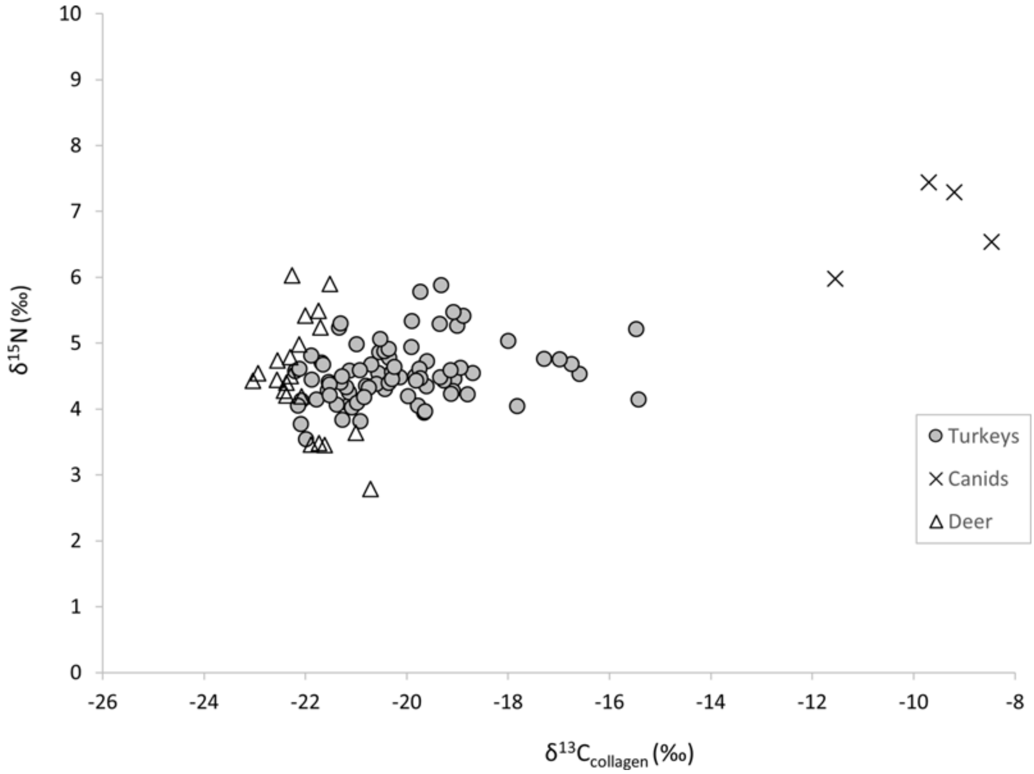

Figure 5. $\delta^{13}C_{co}$ and $\delta^{15}N$ for archaeological turkeys, deer, and canids.

Rio Grande wild turkey (*M. g. intermedia*) populations, respectively (Supplemental Figure 1). Fewkes turkeys group closely with most of the eastern wild turkeys, and the population is not significantly different from neighboring wild modern eastern populations from the Black Warrior and Scotch wildlife management areas in Alabama and the Ozark Mountains in Missouri (Figure 7). The recovered haplotypes, however, are distinct from turkeys recovered from archaeological sites in the American Southwest (Kemp et al. 2017; Speller et al. 2010) and Mexico (Manin et al. 2018; Supplemental Figure 1).

Genetic diversity indices for Fewkes turkeys indicate they are more similar to modern wild turkey populations than to managed or domestic archaeological turkey stocks. The haplotype diversity of the Fewkes assemblage is 0.657, within the range (0.556–0822) of modern eastern wild turkey populations from surrounding states (Figure 8; Supplemental Table 2). In contrast, haplotype diversity for contemporaneous archaeological turkey stocks in the American Southwest (Kemp et al. 2017) is much lower, ranging from 0 to 0.222. The turkeys from southwestern sites such as Shields Pueblo, Sand Canyon, Arroyo Hondo, and Albert Porter Pueblo display reduced genetic diversity associated with captive rearing (Figure 8) and, in the case of Shields Pueblo, evidence for enriched $\delta^{13}C$ associated with maize provisioning (Rawlings and Driver 2010).

Discussion and Conclusions

Isotopic and genetic analyses of Mississippian turkeys show no evidence of prolonged or intensive captive rearing at the southeastern sites tested. Unlike archaeological turkeys from the American Southwest and Mesoamerica, southeastern turkeys show no evidence of extensive maize consumption or evidence of genetic management. Moreover, genetic analysis does not indicate domestic turkeys were introduced from other regions.

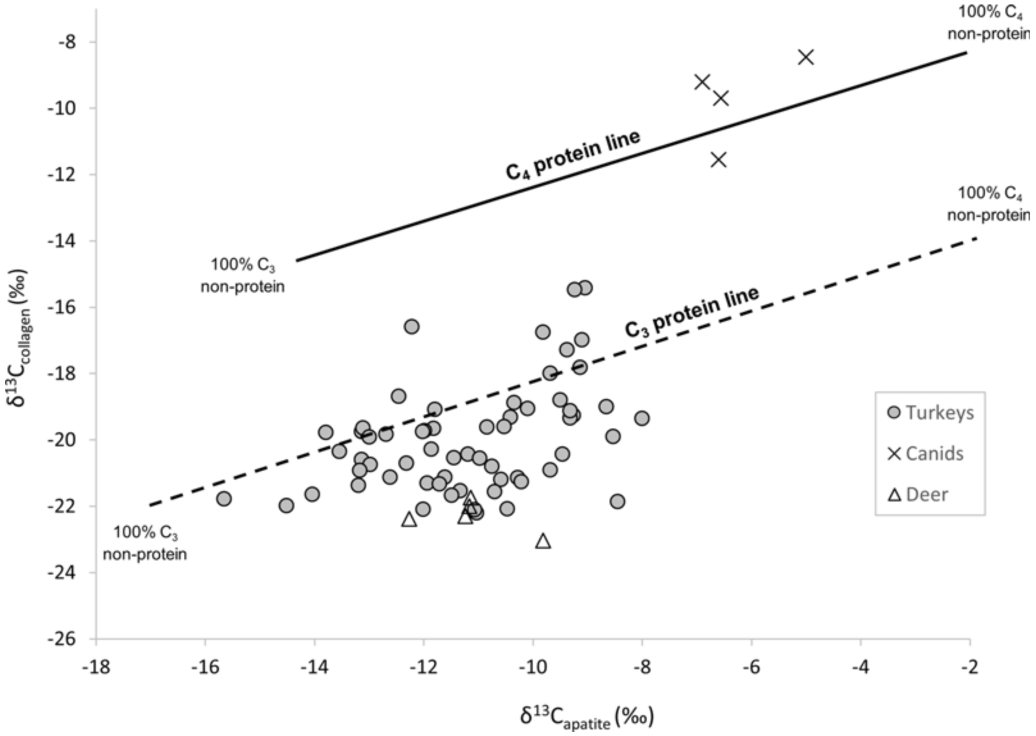

Figure 6. Collagen and apatite $\delta^{13}C$ for archaeological turkeys, deer, and canids plotted with reference to C_3-based (dashed line) and C_4-based (solid line) protein models by Kellner and Schoeninger (2007).

Isotopic Indicators of Rearing, Provisioning, and Garden-Hunting

C_4/maize-based diets of archaeological canids in this and other studies (e.g., Emerson et al. 2020; Guiry et al. 2021; Hogue 2003) indicate that maize was an abundant food resource available to animals in Mississippian communities. If southeastern turkeys were reared in pens or were free-range village animals, they should have had higher $\delta^{13}C$ and $\delta^{15}N$ similar to archaeological domestic turkeys in Mesoamerica and the American Southwest (Conrad et al. 2016; Lipe et al. 2016; McCaffery et al. 2014; Rawlings and Driver 2010; Thornton et al. 2016), as well as the isotopic outlier from southern Ontario (Morris et al. 2016). Higher turkey $\delta^{13}C_{co}$ ($> -12‰$) in these other regions is attributed to heavy maize consumption, whereas higher $\delta^{15}N$ in captive turkeys is ascribed to the consumption of fertilized maize, greater ingestion of insects, consumption of human or animal feces, or some combination of these factors (McCaffery et al. 2014; Rawlings and Driver 2010; Thornton et al. 2016). Substantially higher $\delta^{13}C_{co}$ and $\delta^{15}N$ was not observed in our southeastern turkeys nor in archaeological turkeys from other southeastern sites (Manzano et al. 2019; Price 2009; Rogers 2011).

Although no southeastern turkeys fell within the range of domestic turkeys from other regions, slightly higher $\delta^{13}C_{co}$ (-18 to $-15.42‰$) indicates a mixed C_3/C_4 diet in eight southeastern archaeological turkeys. Similar levels of $\delta^{13}C_{co}$ (-18.3 to $-14.7‰$) were observed in 10% of the archaeological turkeys from southern Ontario (Guiry et al. 2021; Morris et al. 2016). Morris and colleagues (2016) interpret such intermediate values as evidence of turkey management through intentional maize provisioning. However, the amount of maize available to wild-foraging turkeys in the absence of intentional human provisioning remains difficult to quantify, and some wild, nonprovisioned taxa have been shown to consume large quantities of maize (Guiry et al. 2021, 2020).

Table 3. Summary of Turkey mtDNA Results.

Specimen	Lab[a]	Coordinates	Mutations	Haplotype
FEW-0151	WSU; BioArCh	15651–15800; 15875–16013		Partial
FEW-0152	BioArCh	Fail		
FEW-0154	BioArCh	15651–15960	15808C, 15886T, 15953C	eHap2
FEW-0155	WSU; BioArCh	15554–15800; 15875–16013	(15886T, 15953C)	Partial
FEW-0158	WSU; BioArCh	15875–16013	(15953C)	Partial
FEW-0159	BioArCh	Fail		
FEW-0160	WSU	Fail		
FEW-0161	BioArCh	15651–15960	15677C, 15749G, 15796T, 15808C, 15864C, 15953C	eHap3
FEW-0162	WSU; BioArCh	15554–16013	15808C, 15953C	eHap1
FEW-0163	WSU	15730–16013	(15808C, 15953C)	Partial
FEW-0164	WSU; BioArCh	15651–16013	15808C, 15886T, 15953C	eHap2
FEW-0165	WSU; BioArCh	15651–16013	15808C, 15953C	eHap1
FEW-0166	WSU; BioArCh	15554–16013	15808C, 15953C	eHap1
FEW-0167	WSU; BioArCh	15651–16013	15808C, 15953C	eHap1
FEW-0168	WSU; BioArCh	15651–16013	15808C, 15886T, 15953C	eHap2
FEW-0169	WSU; BioArCh	15651–15800		Partial
FEW-0170	WSU; BioArCh	15651–16013	15808C, 15953C	eHap1
FEW-0171	WSU	15730–15967	(15886T, 15953C)	Partial
FEW-0172	WSU	Fail		
FEW-0173	WSU; BioArCh	15651–15800		Partial
FEW-0174	WSU; BioArCh	15651–15960	15808C, 15886T, 15953C	eHap2
FEW-0175	WSU	15730–15874	(15808C)	Partial
FEW-0176	WSU; BioArCh	15651–15931	(15808C, 15886T)	Partial
FEW-0177	WSU; BioArCh	15651–16013	15808C, 15953C	eHap1
FEW-0178	WSU; BioArCh	15554–16013	15686T, 15808C, 15953C	eHap4
FEW-0179	WSU	Fail		
FEW-0181	WSU; BioArCh	15651–15996	15808C, 15886T, 15953C	eHap2
FEW-0183	WSU; BioArCh	15554–15960	15808C, 15886T, 15953C	eHap2
FEW-0184	WSU; BioArCh	15730–16013	(15953C)	Partial
FEW-0185	BioArCh	Fail		
FEW-0186	WSU; BioArCh	15554–16013	15808C, 15953C	eHap1

Note: Sequences and mutational positions are relative to the turkey mtDNA reference sequence (EF153719; Guan et al. 2009).
[a]WSU = Washington State University Ancient DNA Lab; BioArCh = University of York Ancient DNA Lab.

In the American Southwest, small subsets of archaeological turkeys also yield $\delta^{13}C_{co}$, indicating a mixed C_3/C_4 diet. These individuals are either free-range domestic turkeys eating a mix of human-provided maize and wild foods (Jones et al. 2016) or wild turkeys that occasionally raided maize fields or consumed wild C_4/CAM resources (Conrad et al. 2016; McCaffery et al. 2014). Similar uncertainty exists for interpreting archaeological Mesoamerican ocellated turkeys (*Meleagris ocellata*) with intermediate $\delta^{13}C_{co}$ (−18 to −13‰). These could be wild garden-hunted birds or intentionally provisioned animals (Manin et al. 2018; Thornton et al. 2016).

Accurately reconstructing where precolumbian turkeys fall on the wild to domestic continuum is crucial for understanding how people influenced and interacted with animal populations through direct (e.g., provisioning) and indirect means (e.g., landscape or land cover modification). Unfortunately, determining the human agency or intentionality in managing and promoting turkey populations is not as simple as observing the degree to which isotopic ratios deviate from an expected wild, C_3-based diet. Although stable isotope analysis can readily identify domestic or captive-reared birds consuming almost exclusively human-provided maize ($\delta^{13}C_{co} > -12‰$), isotopic analyses less readily document lower levels of human provisioning because wild turkey diets can vary greatly and regions differ in the availability of wild C_4 resources. The method

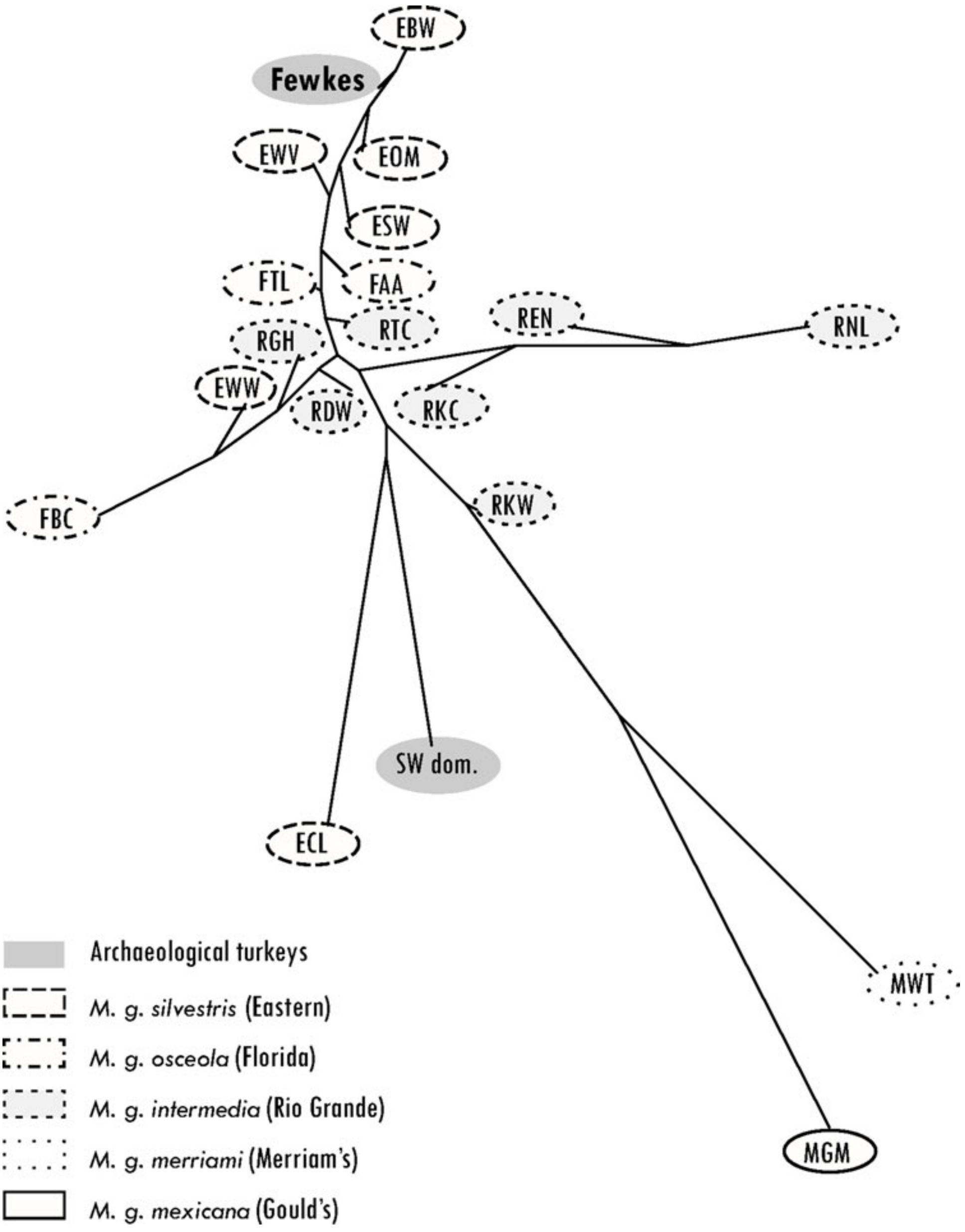

Figure 7. Unrooted neighbor-joining tree displaying the relationship between the Fewkes turkeys and North American modern (Mock et al. 2002) and archaeological (Speller et al. 2010) turkey populations. Comparative sequences were obtained from GenBank. Fewkes turkeys are compared with archaeological samples from the American Southwest and modern North American wild subspecies. The first letter of each population abbreviation refers to the subspecies designation (E = *M.g. silvestris* (Eastern); F = *M.g. osceola* (Florida); R = *M.g. intermedia* (Rio Grande). Additionally, MWT = *M.g. merriami* (Merriam's), MGM = *M.g. mexicana* (Gould's), *and* SW dom. = archaeological Southwest domestic turkeys.

also cannot detect captive or managed turkeys provisioned with C_3 resources such as acorns because their $\delta^{13}C$ would be identical to wild turkeys.

Highly diverse and variable wild turkey diets are a complicating factor. As opportunistic omnivores, turkeys may show great intra- and

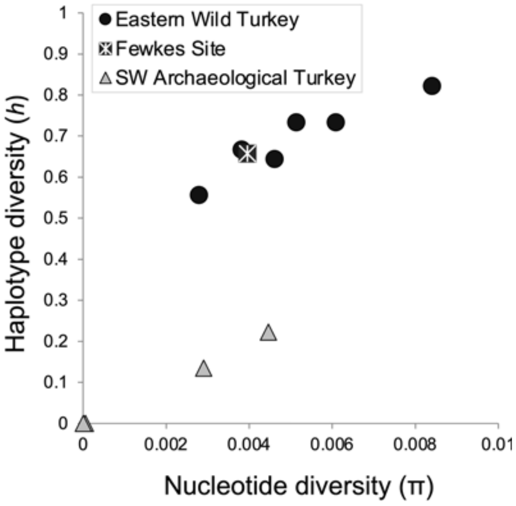

Figure 8. Haplotype and nucleotide diversity of the Fewkes turkey assemblage compared to modern eastern wild turkey (*M.g. silvestris*) populations and archaeological turkeys from sites in the American Southwest (SW) listed in Supplementary Material Table 2.

interannual dietary variation sensitive to local environmental factors, such as the amount and configuration of forest cover and proximity to water (Otieno and Frenette 2017). Wild turkeys could display a broad range of isotopic values reflecting this dietary diversity. Across their broad geographic range, modern North American turkeys exhibit $\delta^{13}C_{co}$ indicative of pure C_3 to highly mixed C_3/C_4 diets, which argues in favor of wild turkey isotopic diversity ($\delta^{13}C_{co}$: −21.5 to −14.7‰, reflecting 1.5‰ correction for modern burning of fossil fuels to make modern $\delta^{13}C_{co}$ comparable to archaeological $\delta^{13}C_{co}$; Jones et al. 2016; Lipe et al. 2016; Morris et al. 2016). Significant changes in land cover and configuration, wildlife management practices, hunting pressure, and the shift to mechanized agriculture further complicate the comparison of modern and archaeological turkey diets because they alter the balance of C_3 and C_4 resources in turkey habitats and diets.

Seasonal maize provisioning of turkeys is one of several possible explanations for slightly higher $\delta^{13}C$ observed in southeastern archaeological turkeys. Other explanations include turkey consumption of insects or other invertebrates, native C_4 grasses, or maize damaged by other crop pests. Slightly higher turkey $\delta^{13}C$ should be interpreted cautiously until we have a better idea of the full range of nonprovisioned turkey diets, as these values could reflect a diversity of human-animal interactions from wild hunting to active provisioning.

Implications for Human-Turkey Interactions in Eastern North America

Increasing data indicate past human-animal interactions in North America that defy simple classifications of species as either wild or domestic (e.g., Jones et al. 2016; LeFebvre and deFrance 2018; LeFebvre et al. 2019; Morris et al. 2016; Somerville et al. 2016; Sugiyama et al. 2015, 2017; Thornton and Emery 2017; Valadez Azúa 2003). It is likely that Mississippian populations occasionally provisioned turkeys with dried maize and tolerated or even promoted their presence in fields or middens as a means of pest control, thereby increasing local wild game populations. Higher $\delta^{13}C$ in archaeological turkeys broadly indicates turkeys' tendency to tolerate anthropogenic habitats, which inevitably brought them into greater and more complex interactions with human populations. This mirrors recent observations of domesticated millet (*Panicum miliaceum*, *Setaria italica*) consumption by wild pheasants (*Phasianus colchicus*) at the Dadiwan site in China 5,900–7,900 years ago (Barton et al. 2020). In the case of turkeys, provisioning them with maize would promote higher winter survival rates, larger brood sizes, and smaller home ranges while decreasing fear of humans, all of which would increase local access to turkeys and promote further human-turkey interactions.

Regardless of whether Mississippian populations intentionally provisioned turkeys to improve hunting or to manage wild populations, our sample does not indicate long-term captive rearing or controlled breeding. Our sample, however, is limited in size and geographic scope and may not be representative of all Mississippian sites in the Southeast. Current research on North American plant and animal domestication reveals that the domestication process was characterized by prolonged periods of low-intensity cultivation or rearing and that regions varied greatly in the timing and intensity of food production (Smith 2011, 2017). For example, turkey domestication in the American Southwest originally focused on low-level rearing primarily for feathers, with more intensive rearing for subsistence purposes emerging centuries later and only in areas of highest population pressure (Kohler et al. 2012; Lipe et al. 2016). In the Maya region, domestic turkeys were first adopted from northern Mesoamerica in the Late Preclassic (~350 BC) but were reared in very small numbers at select sites for use in elite ceremonial display until more widespread adoption after AD 1000 (Thornton and Emery 2017; Thornton et al. 2012). In both cases, turkey rearing was not initially accompanied by substantial increases in the numbers of turkeys in zooarchaeological assemblages, nor was turkey rearing necessarily present at all contemporary sites.

Wild turkey provisioning or captive rearing of poults hatched from wild-collected eggs may have occurred in Eastern North America on a limited basis at a few sites or in specific regions. Future research may reveal evidence for small-scale and patchily distributed turkey rearing in Eastern North America. The single maize-fed turkey identified by Morris and colleagues (2016) from southern Ontario supports the need for expanded isotopic testing to document the existence and extent of this practice. Additional lines of evidence, such as demographic profiles and paleopathology, should also be explored in more depth because of the potential for managed or captive turkeys to be provisioned with foods other than maize.

The wild turkey's tameness and tolerance for anthropogenic environments predispose it to greater and more complex interactions with humans and their built environments. The well-established history of plant cultivation in Eastern North America also provides a cultural context for the emergence of other complex human-environment interactions including animal management or rearing beyond domestic dogs. Finally, it remains possible that the idea for turkey rearing diffused to Eastern North America from the American Southwest or Mesoamerica. Our study found no evidence of turkeys being introduced from these confirmed centers of turkey domestication, but the regions share some cultural foundations and subsistence practices, and there is limited evidence of economic interaction (Blitz 2010; Carpenter 2020; Washburn et al. 2014).

Although the potential for turkey rearing and domestication existed in the Southeast, there are many types of intensified human-animal interactions that would not lead to either outcome (Vigne 2011; Zeder 2015). The decision to engage in more controlled use of animal resources is highly complex and is influenced by many factors, including the local diversity, abundance, seasonality, and sustainability of wild faunal resources; the amount of surplus crops available for use as animal fodder; and the social demand for particular animal resources. Eastern North America differs from other regions where turkey domestication emerged (i.e., American Southwest and Central Mexico) in terms of the overall diversity and abundance of faunal resources used by past societies. In particular, the greater availability of aquatic taxa and overall ecological productivity of the Eastern Woodlands offered more options for protein acquisition. Within this ecological context, specialization or greater reliance on turkeys may have been less likely. The wetter and mixed landscape mosaic of forest and agricultural fields in Eastern North America also could sustain higher populations of turkeys near human settlements. Maize provisioning, or fallow field and forest management could be an effective means of promoting local turkey populations without investing resources in animal rearing.

Reconstructing the nature of human-turkey interactions in Eastern North America is critical to understanding the overall process of turkey domestication throughout the Americas. Through comparative assessment of spatial and temporal variation in the types and intensity of turkey use, management, or domestication practiced, it will be possible to assess the social and environmental contexts that influenced region-specific interaction with this potential animal domesticate. The current study, by expanding research on turkey domestication in the American Southeast, moves us toward this goal, but additional detailed studies throughout the turkey's natural range are needed before we can advance more formal theories.

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Data Availability Statement. Ancient DNA sequences were submitted to GenBank under Accessions MN587233–MN587257. Stable isotope data are reported in the supplementary material and are available from the WSU Department of Anthropology Stable Isotope Lab. Archaeological faunal materials analyzed as part of this research are curated at Florida State University, the Tennessee Division of Archaeology, the Tennessee Department of Transportation, the University of Georgia, and the McClung Museum of Natural History and Culture in Knoxville, Tennessee.

Supplemental Material. For supplemental material accompanying this article, visit https://doi.org/10.1017/aaq.2021.58.

Supplemental Text 1. Archaeological site and sample descriptions.

Supplemental Text 2. Stable isotope analysis laboratory methods.

Supplemental Text 3. Ancient DNA extraction and analysis laboratory methods.

Supplemental Table 1. $\delta^{13}C$ and $\delta^{15}N$ of Archaeological Turkeys, Deer, and Canids.

Supplemental Table 2. Haplotype and Nucleotide Diversity for the Fewkes Assemblage, Other Archaeological Turkeys, and Modern Turkeys.

Supplemental Table 3. Context Descriptions for Archaeological Turkeys.

Supplemental Figure 1. Median-joining network displaying the relationships between the Fewkes turkeys and existing archaeological (Manin et al. 2018; Speller et al. 2010) and modern (Mock et al. 2002; Monteagudo et al. 2013; Szalanski et al. 2000) turkey sequences obtained from GenBank. Fewkes turkeys (purple) are compared with archaeological samples from the American Southwestern (gray), Mexico (black), modern breeds (white), and wild subspecies (various colors).

Note

1. Modern geopolitical boundaries are used throughout to refer to our study area. For the purposes of this article, the Southeast refers to the southeastern portion of the United States and includes the modern states of Alabama, Florida, Georgia, Mississippi, North Carolina, South Carolina, and Tennessee.

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