

Short Paper

Reconstructing the migration patterns of late Pleistocene mammals from northern Florida, USA

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Abstract

We used analyses of the strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) ratios of tooth enamel to reconstruct the migration patterns of fossil mammals collected along the Aucilla River in northern Florida. Specimens date to the late-glacial period and before the last glacial maximum (pre-LGM). Deer and tapir displayed low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that were similar to the ratios of Florida environments, which suggest that these taxa did not migrate long distance outside of the Florida region. Mastodons, mammoths, and equids all displayed a wide range of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. Some individuals in each taxon displayed low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that suggest they ranged locally, while other animals had high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that suggest they migrated long distances (>150 km) outside of the Florida region. Mastodons were the only taxa from this region that provided enough well-dated specimens to compare changes in migration patterns over time. Pre-LGM mastodons displayed significantly lower $^{87}\text{Sr}/^{86}\text{Sr}$ ratios than late-glacial mastodons, which suggests that late-glacial mastodons from Florida migrated longer distances than their earlier counterparts. This change in movement patterns reflects temporal changes in regional vegetation patterns.

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Introduction

Reconstructions of the migration patterns of extinct taxa are critical for studies of paleobiology, rates of evolution and extinction, and paleoclimatic reconstructions based on fossil animals. However, reconstructing the migration patterns of ancient animals is complicated by the fact that modern animals change their movement patterns in response to changing environmental conditions. For example, large herbivores often decrease their range size during drought conditions in order to remain near water supplies (Owen-Smith, 1988), and the average range size of a given species can change by a factor of five or more in response to changes in forage quality and/or local climatic conditions (Marchinton and Hirth, 1984). It is likely that ancient herbivores also altered their movement

patterns in response to geographic and temporal environmental changes.

Determining the degree to which the migratory behavior of extinct species varied could help determine whether or not extinct taxa were affected by environmental changes. For example, biological factors linked to migration may have contributed to the causes of the late Pleistocene megafauna extinction. Haynes (1991) suggested that drying climatic conditions in the late Pleistocene forced large herbivores, such as proboscideans, to decrease their range size (e.g., cluster around water holes), which caused overcrowding, increased nutritional stress, and increased vulnerability to Paleoindian hunters. Churcher (1980) proposed that mammoths seasonally migrated long distances (>1000 km one-way) and that Paleoindian hunters exploited this behavior by using natural traps along migration routes to increase their hunting success. Alternatively, it has also been suggested that climate-driven ecological changes disrupted proboscidean migration routes and thus caused nutritional stress that led to extinction (Martin and Klein, 1984; Holman et al., 1988). Such debates about the link

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between migration patterns and extinction have focused on proboscideans, but proboscideans are not the only prehistoric animals that might have migrated. For example, comparisons with modern zebra, which can migrate up to 120 km one-way, suggest that Pleistocene equids may also have migrated long distance (Berger, 2004).

Recent studies have demonstrated that analyses of the strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) ratios of an animal's tissues can be used to reconstruct the migration patterns of modern and fossil animals (e.g., Price et al., 1994; Chamberlain et al., 1996; Hoppe et al., 1999; Hoppe, 2004). This method works because the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of herbivores equal the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of ingested plants (Price et al., 1985), which equal the soluble Sr in soils. Soil Sr in turn varies with bedrock type and atmospheric input (Gosz and Moore, 1989; Miller et al., 1993). Thus, when soil $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are locally homogenous and regionally heterogeneous, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of migrants differ from those of resident animals. Florida environmental samples (i.e., plants, waters, and soils) have low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that range from 0.7080 to 0.7097 (Hoppe et al., 1999). In contrast, environments to the north that have sediments derived from the metamorphic and igneous rocks of the Appalachian Mountain have high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios ≥ 0.7110 (Fig. 1). Comparison of modern and fossil bivalves demonstrates that the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of Florida soils and waters have remained essentially constant since the last glacial age (Hoppe et al., 1999).

Previous analyses of fossils from the Page-Ladson site along the Aucilla River in northern Florida (Fig. 1) have provided

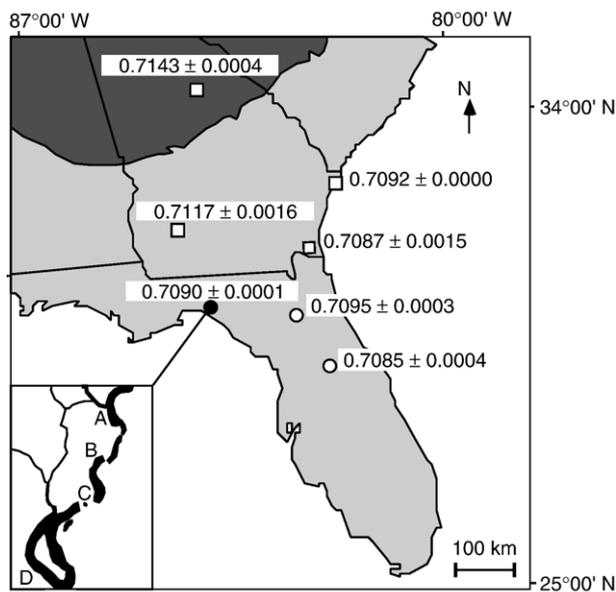


Figure 1. Map of the modern bedrock geology and environmental $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of Florida and Georgia. Light gray shading represents areas with sedimentary bedrock. Dark gray shading represents areas with igneous and metamorphic bedrocks. Circles mark the locations of modern plant and water samples. Squares mark the locations of modern rodent samples. Numbers represent the mean $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of modern samples $\pm 1\sigma$ (data from Hoppe et al., 1999). The location of Aucilla River fossil quarries is represented by the black circle. The inset map shows the locations of each site (drawn after Hemmings, 2000): A=Page-Ladson, B=Little River Rapids, C=Latvis/Simpson, D=Sloth Hole.

Table 1

Ages in radiocarbon years before present (^{14}C yr BP) of fossil locations along the Aucilla River, Florida

Locality	Radiocarbon date (^{14}C yr BP)	Calibrated age 1σ (calendar yr BP)*	Reference
Page-Ladson (8JE591)	12,350±50	14,180–14,810	Webb et al., 1998
Little River Rapids (8JE603)	11,450±90	13,210–13,500	Muniz, 1998, Webb et al., 1998
Little River Rapids (8JE603)	11,730±70	13,470–13,750	Muniz, 1998
Little River Rapids (8JE603)	12,130±70	13,920–14,420	Muniz, 1998, Webb et al., 1998
Latvis/Simpson (8JE1500)	31,610±240	36,280–36,880	Mihlbachler, 1998
Latvis/Simpson (8JE1500)	32,740±800	37,100–39,080	Mihlbachler, 1998
Sloth Hole (8JE121)	12,300±50	14,100–14,670	Webb et al., 1998
Sloth Hole (8JE121)	>41,980	–	Hemmings, 1998

*Calibration was done with CalPal online (<http://www.calpal-online.de>).

insight into the migration patterns of late-glacial taxa (Table 1). Bulk tooth enamel samples from deer and tapir displayed low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that suggest that they ranged primarily within Florida environments (Table 2). However, bulk enamel samples from coeval mastodons have high ratios that suggest that these animals migrated long distances (≥ 150 km) to the north (Hoppe et al., 1999). The one coeval mammoth analyzed displayed low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that suggest that it did not migrate long distance to the north, although it may have migrated long distance to the south within the isotopically homogenous environments of Florida.

Isotopic analyses of serial microsamples collected parallel to enamel growth lines or samples produced by laser ablation can provide additional information about subannual (e.g., seasonal) changes in the biology of large mammals (Hoppe et al., 2004; Hoppe and Koch, 2006; Tafforeau et al., 2007). Previous analyses of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of serial microsamples from one Aucilla River mammoth and one mastodon provide additional insight into the migration patterns of these animals. Samples from a late-glacial Page-Ladson mastodon show large variations in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (from 0.7078–0.7121) over a time period representing approximately 2 yr of growth (Hoppe et al., 1999; Hoppe and Koch, 2006). These microsamples demonstrate that this mastodon moved repeatedly back and forth between regions with high and low strontium, and are consistent with the interpretation that it migrated on a seasonal basis. In contrast, enamel microsamples representing 1 yr of growth from an Aucilla River mammoth display uniformly low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.7094–0.7096) and confirm that this mammoth did not migrate long distances to the north during the time period sampled (Hoppe and Koch, 2006).

In this study, we analyzed the $^{87}\text{Sr}/^{86}\text{Sr}$ of tooth enamel from additional Aucilla River mammoths, mastodons, deer, and tapir, in order to determine if the migration patterns reconstructed for late-glacial specimens are similar to those of individuals that lived before the last glacial maximum (pre-LGM). We also

Table 2
 $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of tooth enamel

	Sample #	Taxon	Tooth analyzed ^a	$^{87}\text{Sr}/^{86}\text{Sr}$
Latvis-Simpson	200674	<i>Equus</i>	Chk	0.71035
Latvis-Simpson	200675	<i>Equus</i>	Chk	0.71021
Latvis-Simpson	180220	<i>Mammut</i>	m3	0.70965
Latvis-Simpson	200666	<i>Mammut</i>	M	0.70951
Latvis-Simpson	200667	<i>Mammut</i>	M	0.70954
Latvis-Simpson	200654	<i>Odocoileus</i>	l m3	0.70867
Latvis-Simpson	200668	<i>Tapirus</i>	Chk	0.70826
Latvis-Simpson	200669	<i>Tapirus</i>	Chk	0.70881
Latvis-Simpson	200670	<i>Tapirus</i>	r M3	0.70898
Little River Rapids	200679	<i>Mammut</i>	M, partial	0.70995
Little River Rapids	200655	<i>Mammuthus</i>	Molar	0.70932
Little River Rapids	200689	<i>Tapirus</i>	l p3	0.70826
Sloth Hole	200549	<i>Mammut</i>	M	0.70883
Sloth Hole	200660	<i>Mammut</i>	M	0.71030
Sloth Hole	200665	<i>Mammut</i>	M	0.70905
Sloth Hole	47995a	<i>Mammuthus</i>	M	0.70970
Sloth Hole	47995b	<i>Mammuthus</i>	M	0.70965
Sloth Hole	200663	<i>Mammuthus</i>	M, partial	0.70991
Ohmes Collection	135730	<i>Mammuthus</i>	l m3	0.70957
Ohmes Collection	135731	<i>Mammuthus</i>	r m2	0.71039
Ohmes Collection	135733	<i>Mammuthus</i>	r m3	0.70872
Ohmes Collection	135734	<i>Mammuthus</i>	l m3	0.70917
Ohmes Collection	135737	<i>Mammuthus</i>	r M2	0.70874
Ohmes Collection	135738	<i>Mammuthus</i>	r M2	0.70994
Page-Ladson	148670	<i>Equus</i>	Chk	0.70968
Page-Ladson	148669 ^b	<i>Mammut</i>	M	0.71011
Page-Ladson	103505 ^b	<i>Mammut</i>	M1	0.70992
Page-Ladson	130570 ^b	<i>Mammut</i>	M	0.71007
Page-Ladson	148668 ^b	<i>Mammut</i>	m1	0.71144
Page-Ladson	150775 ^b	<i>Mammut</i>	M, partial	0.71010
Page-Ladson	192224	<i>Mammut</i>	l M3	0.70968
Page-Ladson	192226	<i>Mammut</i>	r M1	0.71113
Page-Ladson	92513 ^b	<i>Tapirus</i>	l M	0.70865
Page-Ladson	92568 ^b	<i>Tapirus</i>	m3	0.70872
Page-Ladson	92522 ^b	<i>Odocoileus</i>	Chk	0.70966
Page-Ladson	92563 ^b	<i>Odocoileus</i>	Chk	0.70857
Page-Ladson	147359 ^b	<i>Odocoileus</i>	l m3	0.70922
Page-Ladson	147362 ^b	<i>Odocoileus</i>	l m3	0.70921
Page-Ladson	147364 ^b	<i>Odocoileus</i>	l m3	0.70941
Page-Ladson	147365 ^b	<i>Odocoileus</i>	l m2	0.70873
Page-Ladson	150249 ^b	<i>Odocoileus</i>	l m1	0.70870
Page-Ladson	150470 ^b	<i>Odocoileus</i>	l m3	0.71075
Page-Ladson	151916 ^b	<i>Odocoileus</i>	Chk	0.70872
Page-Ladson	151917 ^b	<i>Odocoileus</i>	Chk	0.70912
Page-Ladson	151941 ^b	<i>Odocoileus</i>	Chk	0.70930
Page-Ladson	151942 ^b	<i>Odocoileus</i>	Chk	0.70893
Page-Ladson	14780 ^b	<i>Mammuthus</i>	m3	0.70893

^a Abbreviations as follows: l=left, r=right, M=molar, Chk=cheek tooth; numbers represent position in tooth row.

^b Data from Hoppe et al., 1999.

analyzed teeth from several equids, as the migration patterns of fossil equids have not been assessed previously (Tables 1 and 2).

Studies of fossil pollen have been used to reconstruct paleoclimatic patterns and changes in vegetation across the southeastern United States. From 50,000 to 28,000 radiocarbon years before present (^{14}C yr BP), climates in Georgia and northern Florida were dryer than modern and the vegetation consisted of xeric woodlands mixed with open prairie habitats (Watts, 1973; Watts, 1980). Climates became wetter, and oak-dominated mesic forests grew from 31,000 to 29,000 ^{14}C yr BP.

Vegetation changed to open pine-dominated woodlands after 29,000 ^{14}C yr BP (Watts and Stuiver, 1980; Watts and Hansen, 1988; Watts et al., 1992). Climates became wetter again between 14,600 and 12,800 ^{14}C yr BP, and oak and mesic trees replaced the pines (Watts and Hansen, 1988; Watts and Hansen, 1994). From 12,800 to 11,200 ^{14}C yr BP, climatic conditions became drier and pine briefly increased before oak became dormant again in the Holocene (Watts and Hansen, 1994). Vegetation changes in southern Florida paralleled those in the north, but habitats were more open and include a higher percentage of shrublands and prairie vegetation (Watts, 1980; Watts and Hansen, 1988). If Pleistocene herbivores routinely migrated long distances, then their migration patterns may have shifted in response to these vegetation changes.

Material and methods

We sampled tooth enamel from equids (*Equus* sp.), mammoths (*Mammuthus columbi*), mastodons (*Mammut americanum*), tapirs (*Tapirus veroensis*), and white-tailed deer (*Odocoileus virginianus*) from fossil quarries located along a 10-km section of the Aucilla River (Fig. 1) in northern Florida (Hemmings, 2000). Specimens from the Latvis/Simpson site are pre-LGM in age, while specimens from the Little River Rapids and Page-Ladson sites are late-glacial in age (Table 1). Because only a limited number of proboscidean teeth with precise dates were available from this region, we also analyzed proboscideans from Aucilla River localities with less well-constrained dates that ranged from pre-LGM to the late-glacial in age (Sloth Hole and the Ohmes Collection). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of all specimens were compared to previously published analyses of environmental samples (i.e., soils, plants, rodents, clams, and surface waters) from Florida and Georgia (Hoppe et al., 1999).

Bulk samples of enamel were collected to determine the average isotopic composition of each tooth; each sample represents approximately 1 to 2 yr of growth (Koch et al., 1998). The outer surface of each tooth was removed before sampling. Powdered enamel samples were collected with a dental drill and pretreated with 0.1 N acetic acid to remove possible diagenetic contamination (Hoppe et al., 2003). Samples were next dissolved in 2.5 N hydrochloric acid and Sr was extracted by standard ion exchange chromatography (Walker et al., 1989). $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were measured on a VG354-S thermal ionization mass spectrometer. All measurements are referenced to a value of $^{87}\text{Sr}/^{86}\text{Sr}=0.71025$ for the NBS 987 Sr standard and are precise to within ± 0.00003 . The variance of late-glacial and pre-LGM specimens from each taxon was compared using an *F*-test. Mean $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were compared using Student's *t*-test (Norman and Streiner, 1992). Statistics were calculated using Microsoft Excel 2004 (Version 11.1.1).

Results

The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of deer and tapir remain constant with time. All tapir specimens and the one pre-LGM deer analyzed

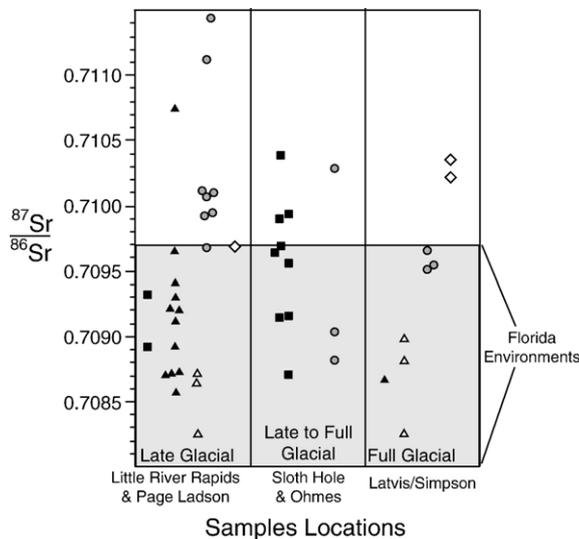


Figure 2. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of tooth enamel from the Aucilla River fossil quarries. Black squares = mammoths; gray circles = mastodons; black triangles = deer; white triangles = tapir; white diamonds = equids. Shaded gray area represents the range of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios expressed by Florida environmental samples.

have low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (<0.7090) (Table 2, Fig. 2) similar to the ratios from Florida environmental samples (Hoppe et al., 1999). There is no significant difference between the variability or mean values of pre-LGM and late-glacial tapirs (F -test, $p=0.42$; t -test, $p=0.31$), and the ratio of the pre-LGM deer falls within the range of values for late-glacial deer (Fig. 2).

In contrast, the ratios of mastodons show significant changes. The late-glacial mastodons analyzed in this study have high ratios (mean = 0.71025 ± 0.00077) that are similar to those previously found in late-glacial mastodons from Page-Ladson (0.71033 ± 0.00063) and are higher than Florida environmental samples (Hoppe et al., 1999). However, all pre-LGM mastodons have low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (mean = 0.70957 ± 0.00007), similar to those of Florida environments and significantly lower than the ratios of late-glacial mastodons (t -test, $p < 0.03$). The three mastodons of indeterminate age display a range of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.70905 to 0.71030). The highest ratio is similar to the ratios of late-glacial mastodons. The lowest ratios are somewhat lower than those found in pre-LGM mastodons, but they are consistent with the ratios of Florida environmental samples.

The new late-glacial mammoth analyzed has a low $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of 0.70932, which is similar to previously measured ratios for late-glacial mammoths and Florida environmental samples. The mammoths of indeterminate age display a mixture of high and low ratios; six have ratios similar to those of the Florida environmental samples, while three display ratios that are higher than any environments in Florida (Table 2, Fig. 2).

The two pre-LGM equids analyzed have high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (mean = 0.71028), which indicate that they migrated long distances outside of the Florida region. The one late-glacial equid measured had a ratio of 0.70968, which is similar to the highest $^{87}\text{Sr}/^{86}\text{Sr}$ ratios found in Florida environments and suggests that it did not migrate to the north (Fig. 2).

Discussion

Before the biological significance of the Sr isotope composition of any fossil can be interpreted, we must first establish that diagenetic Sr has not altered biogenic $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. We argue that the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of our samples are biogenic because: (1) diagenetic alteration should most strongly affect the oldest teeth with the thinnest enamel, yet the pre-LGM equid teeth (which have relatively thin enamel ≤ 2 mm thick) preserve $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that are distinct from those of the Aucilla River environments, and (2) it has been shown that the pretreatment effectively removes $\geq 95\%$ of any diagenetic strontium from enamel samples ≤ 15 myr old (Budd et al., 2000; Hoppe et al., 2003; Lee-Thorp and Sponheimer, 2003).

The fact that pre-LGM deer and tapir have low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that are similar to those of their late-glacial counterparts suggests that the majority of these animals ranged only locally within the Florida environment, and that their movement patterns did not change significantly with time. This is consistent with observations that modern tapir and white-tailed deer have an average home range less than 20 km in diameter (Williams, 1979; Marchinton and Hirth, 1984). However, one late-glacial deer (with an $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of 0.71075) differs from this general pattern. This sample likely represents the dispersal, or permanent long-distance move, to a new home range of an isolated individual. Modern white-tailed deer have been observed to move distances of up to 200 km during one-way dispersal events, independent of environmental stress, but such events are rare (Marchinton and Hirth, 1984; Berger, 2004). The fact that the variability of deer and tapir does not change over time suggests that the average dispersal rate and migration distances were similar for pre-LGM and late-glacial individuals.

In contrast, the migration distances of mastodons appear to have increased with time; the low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of pre-LGM mastodons (range = 0.70951 to 0.70965) demonstrate that they spent less time in high $^{87}\text{Sr}/^{86}\text{Sr}$ ratio environments than their late-glacial counterparts (Hoppe et al., 1999) and may indicate that they only ranged locally within Florida environments. However, it is also possible that these animals moved long distance within Florida environments (e.g., they could have moved up to 400 km to the south). In addition, because the Florida environments display $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that range as low as 0.7080, we cannot rule out the possibility that the pre-LGM mastodons migrated into northern environments with higher $^{87}\text{Sr}/^{86}\text{Sr}$ ratios but spent a larger proportion of their time in Florida environments with low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. Two of the Sloth Hole mastodons of indeterminate age displayed very low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.70905 and 0.70883), which more strongly suggests that these animals did not migrate outside of the Florida region. It thus appears that some mastodons ranged only within Florida environments. Analyses of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of serial enamel microsamples would provide additional details about the movements of these animals and reveal whether or not their $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, and thus their movement patterns, changed on a seasonal basis.

Most mammoths analyzed and both of the late-glacial mammoths have relatively low ratios similar to those of Florida

environments (Fig. 2). Thus, they either moved only locally or they moved long distance only within Florida environments. Previous analyses of strontium and oxygen isotope ratios of enamel microsamples from an Aucilla River mammoth suggest the former (Hoppe and Koch, 2006). Because the only precisely dated mammoths from these localities are late-glacial in age, we cannot determine whether or not mammoth movement patterns changed with time. However, because 30% of the mammoths of indeterminate age have high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios demonstrating that they migrated long distances (≥ 150 km), mammoth migration patterns either altered with time or different individuals within populations displayed different migration behavior.

Although only three equid teeth were available for analyses, the high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the two pre-LGM equids demonstrate that at least some individuals within this taxon migrated long distance into Georgia environments (≥ 150 km one-way). This is the first record of long distance migration in fossil equids, but it is consistent with the observed migration distances of zebra and other large herbivores in modern Africa (Berger, 2004). In contrast, the low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the late-glacial equid suggest that it ranged primarily within Florida environments. These differences in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios could result from a temporal change in the migration patterns of Florida equids, but the current data set is too small to rule out the possibility that coeval equids displayed different migration patterns. Additional equids need to be analyzed in order to determine what the average migration distances of this taxon were and if this behavior changed over time. However, the fact that at least some equids migrated long distance is relevant to the interpretation of paleoclimatic reconstructions that are based on analyses of fossil equids (e.g., Passey et al., 2002), because it demonstrates that these fossils may include individuals that migrated from other geographic regions that had different climatic conditions.

The lack of a single consistent pattern of change in the migration patterns of the Florida taxa may result from the diversity of diets found among the animals analyzed. Analyses of carbon isotope ratios of fossils and digesta from the Aucilla River sites have demonstrated that each taxon in this study consumed different diets (i.e., mastodons consumed browse plants, mammoths consumed primarily grass, and equids consumed a mixture of grass and browse) and that dietary patterns did not significantly change with time (Koch et al., 1998, Webb et al., 1992; Hoppe and Koch, 2006). Thus, the different dietary requirements of each taxon may have caused them to respond differently to changing vegetation patterns. Specifically, the observed migration shifts may reflect changes in the distribution and abundance of grasslands. Analyses of pollen suggest that prairies and dune grasslands were important habitats on the Southern Coastal Plain, to the north of the Aucilla River, before 30,000 ^{14}C yr BP. However, the abundance of open grassland habitats in this region had declined by the late-glacial when pine and oak forests dominated the landscape (Watts, 1973, 1980; Watts and Stuiver, 1980; Watts and Hansen, 1988; Watts and Hansen, 1994). We would thus predict that pre-LGM equids and mammoths would spend more time in northern environments than their late-glacial counter-

parts, and that large browsers, such as mastodons, would respond in the opposite manner. Thus, the observed changes in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are consistent with the interpretation that Florida taxa changed their migration behavior over time in response to changing vegetation patterns. This raises the possibility that reconstructions of migration patterns of fossil taxa with known diets could be used to refine reconstructions of regional vegetation patterns. However, more precisely dated fossil individuals from Florida need to be analyzed in order to determine whether or not the migration patterns of these fossil taxa correlate with vegetation changes.

Conclusions

Our results demonstrate that fossil taxa from northern Florida had a wide range movement patterns, and that different individuals from the same taxon displayed different behaviors. Most samples analyzed (including pre-LGM mastodons, a late-glacial equid, most mammoths, deer, and tapir) have low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that suggest they moved only within Florida environments. However, the high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the late-glacial mastodons, the pre-LGM equids, and $\sim 30\%$ of the indeterminate-aged mammoths demonstrate that these individuals migrated long distance (≥ 150 km) into Georgian environments. This confirms that at least some individuals within these taxa were migratory, which has important implications for paleoenvironmental reconstructions based on these taxa. Our results suggest that mastodons altered their migration patterns over time, and they are consistent with the hypotheses that equids and mammoths likewise alter their movements in response to changing regional vegetation patterns.

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References

- Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18, 320–331.
- Budd, P., Montgomery, J., Barreiro, B., Thomas, R.G., 2000. Differential diagenesis of strontium in archaeological human dental tissues. *Applied Geochemistry* 15, 678–694.
- Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X., Sherry, T.W., Graves, G.R., 1996. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109, 132–141.
- Churcher, C.S., 1980. Did North American mammoths migrate? *Canadian Journal of Anthropology* 1, 103–105.
- Gosz, J.R., Moore, D.I., 1989. Strontium isotope studies of atmospheric inputs to forested watersheds in New Mexico. *Biogeochemistry* 8, 115–134.
- Haynes, G., 1991. *Mammoths, Mastodonts, and Elephants: Biology, Behavior, and the Fossil Record*. Cambridge University Press, Cambridge.
- Hemmings, C.A., 1998. Probable association of Paleoindian artifacts and mastodon remains from Sloth Hole, Aucilla River, North Florida. *Current Research in the Pleistocene* 15, 16–17.

- Hemmings, C.A., 2000. Inventory of inundated Paleoindian sites in the lower Aucilla-Wacissa River Drainage, Jefferson County, North Florida. *Current Research in the Pleistocene* 17, 39–41.
- Holman, J.A., Abraczinskas, L.M., Westjohn, D.B., 1988. Pleistocene proboscideans and Michigan salt deposits. *National Geographic Research* 4, 4–5.
- Hoppe, K.A., 2004. Late Pleistocene mammoth herd structure, migration patterns, and Clovis hunting strategies inferred from isotopic analyses of multiple death assemblages. *Paleobiology* 30, 129–145.
- Hoppe, K.A., Koch, P.L., 2006. The biogeochemistry of the Aucilla River fauna. In: Webb, S.D. (Ed.), *The First Floridians and Last Mastodons: The Page-Ladson Site on the Aucilla River*, Topics in Geobiology. Plenum Press, New York, pp. 379–401.
- Hoppe, K.A., Koch, P.L., Carlson, R.W., Webb, S.D., 1999. Tracking mammoths and mastodons: reconstruction of migratory behavior using strontium isotope ratios. *Geology* 27, 439–442.
- Hoppe, K.A., Koch, P.L., Furutani, T.T., 2003. Assessing the preservation of biogenic strontium in fossil bones and tooth enamel. *International Journal of Osteoarchaeology* 13, 20–28.
- Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206, 355–365.
- Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotope ecology of late Pleistocene mammals in North America part 1: Florida. *Chemical Geology* 152, 119–138.
- Lee-Thorp, J., Sponheimer, M., 2003. Three case studies used to reassess the reliability of fossil bone and enamel isotope signals for paleodietary studies. *Journal of Anthropological Archaeology* 22, 208–216.
- Marchinton, R.L., Hirth, D.H., 1984. Behavior. In: Halls, L.K. (Ed.), *White-Tailed Deer: Ecology and Management*. Stackpole Books, Harrisburg, pp. 129–168.
- Martin, P.S., Klein, R.G. (Eds.), 1984. *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, Arizona.
- Mihlbachler, M.C., 1998. Late-Pleistocene mastodon and digesta from Little River, North Florida. *Current Research in the Pleistocene* 15, 116–118.
- Miller, E.K., Blum, J.D., Friedland, A.J., 1993. Determination of soil-exchangeable cation loss and weathering rates using Sr isotopes. *Nature* 362, 438–441.
- Muniz, M., 1998. Preliminary results of excavations and analysis of Little River Rapids: a prehistoric inundated site in North Florida. *Current Research in the Pleistocene* 15, 48–49.
- Norman, G.R., Streiner, D.L., 1992. *Biostatistics: The Bare Essentials*. Mosby, St. Louis.
- Owen-Smith, R.N., 1988. *Mega-Herbivores*. Cambridge University Press, New York.
- Passey, B.H., Cerling, T.E., Perkins, M.E., Voorhies, M.R., Harris, J.M., Tucker, S.T., 2002. Environmental change in the Great Plains: an isotopic record from fossil horses. *Journal of Geology* 110, 123–140.
- Price, T.D., Connor, M., Parsen, J.D., 1985. Bone chemistry and the reconstruction of diet: strontium discrimination in white-tailed deer. *Journal of Archaeological Science* 12, 419–442.
- Price, T.D., Johnson, C.M., Ezzo, J.A., Jonathan, E., Burton, J.H., 1994. Residential mobility in the prehistoric Southwest United States; a preliminary study using strontium isotope analysis. *Journal of Archaeological Science* 21, 315–330.
- Tafforeau, P., Bentaleb, I., Jaeger, J.-J., Martin, C., 2007. Nature of laminations and mineralization in rhinoceros enamel using histology and X-ray synchrotron microtomography: potential implications for palaeoenvironmental isotopic studies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 246, 206–227.
- Walker, R.J., Carlson, R.W., Shirey, S.B., Boyd, F.R., 1989. Os, Sr, Nd, and Pb isotope systematics of southern African peridotite xenoliths: implications for the chemical evolution of subcontinental mantle. *Geochimica et Cosmochimica Acta* 53, 1583–1595.
- Watts, W.A., 1973. The vegetation record of a Mid-Wisconsin interstadial in northwest Georgia. *Quaternary Research* 3, 257–268.
- Watts, W.A., 1980. The late Quaternary vegetation history of the southeastern United States. *Annual Review of Ecology and Systematics* 11, 387–409.
- Watts, W.A., Stuiver, M., 1980. Late Wisconsin climate of northern Florida and the origin of species-rich deciduous forest. *Science* 210, 326–327.
- Watts, W.A., Hansen, B.C.S., 1988. Environments of Florida in the late Wisconsin and Holocene. In: Purdy, B.A. (Ed.), *Wet Site Archaeology*. Telford Press, Caldwell, New Jersey, pp. 307–323.
- Watts, W.A., Hansen, B.C.S., 1994. Pre-Holocene and Holocene pollen records of vegetation history from the Florida peninsula and their climate implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 109, 167–176.
- Watts, W.A., Hansen, B.C.S., Grimm, E.C., 1992. Camel Lake: a 40,000-yr record of vegetational and forest history from northwest Florida. *Ecology* 73, 1056–1066.
- Webb, S.D., Dunbar, J., Newsom, L., 1992. Mastodon digesta from north Florida. *Current Research in the Pleistocene* 9, 114–116.
- Webb, D.D., Hemmings, C.A., Muniz, M.P., 1998. New radiocarbon dates for Vero tapir and stout-legged llama from Florida. *Current Research in the Pleistocene* 15, 127–128.
- Williams, K.D., 1979. Radio-tracking tapirs in the primary rain forest of west Malaysia. *Malayan Nature Journal* 32, 253–258.