Late Pleistocene Mammoth Herd Structure, Migration Patterns, and Clovis Hunting Strategies Inferred from Isotopic Analyses of Multiple Death Assemblages

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Late Pleistocene mammoth herd structure, migration patterns, and Clovis hunting strategies inferred from isotopic analyses of multiple death assemblages

Kathryn A. Hoppe

Abstract.—Many late Pleistocene fossil localities contain the remains of multiple mammoths. Some of these sites have been interpreted as representing the mass death of an entire herd, or family group, of mammoths. These assemblages have been cited as evidence of intense human predation and used to reconstruct mammoth population dynamics. However, these interpretations remain controversial because the taphonomic settings of many sites are still debated. To reconstruct the taphonomic setting of each site and the movement patterns of mammoths among sites, I used analyses of carbon, oxygen, and strontium isotope ratios in mammoth tooth enamel. The carbon isotopes of fossils vary with diet and local vegetation, oxygen isotopes vary with local climate, and strontium isotopes vary with local soil chemistry. If Pleistocene mammoths traveled together in small family groups, then mammoths from sites that represent family groups should have lower isotopic variability than mammoths from sites containing unrelated individuals. I tested this conjecture by comparing the isotopic variability among mammoths from two sites—one that represents the mass death of a single herd (Waco, Texas) and one representing a time-averaged accumulation (Friesenhahn Cave, Texas)—and then used these analyses to examine mammoths from three Clovis sites: Blackwater Draw, New Mexico; Dent, Colorado; and Miami, Texas. Low levels of carbon isotope variability were found to be the most diagnostic signal of herd/family group association. Although the variability of oxygen and strontium isotope ratios proved less useful for identifying family group assemblages, these signals did provide information about the movement patterns of individuals among different sites. High levels of variability in each of the isotope systems at Clovis sites suggest that all of the sites examined represent time-averaged accumulations of unrelated individuals, rather than the mass deaths of family groups.

In addition, analyses of the mean isotope values of Clovis mammoths show that although most mammoths from Blackwater and Miami had similar values, the values of Dent mammoths were significantly different. This demonstrates that the Dent mammoths belonged to a separate population and suggests that Clovis mammoths did not routinely undertake long distance (≥600 km) migrations.

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Introduction

Clovis artifacts were first discovered in association with mammoth remains in the 1930s (Sellards 1952), and it is generally accepted that at least some mammoths were butchered (e.g., Holliday et al. 1994; Haynes 1995). However, researchers continue to debate whether Clovis hunters routinely slaughtered groups of mammoths en masse, pursued individual mammoths, or merely scavenged already dead individuals (Sellards 1952; Saunders 1980, 1992; Martin and Klein 1984; Holliday et al. 1994; Haynes 1995). Resolving these questions will help evaluate the contribution of human hunting to the late Pleistocene extinction of proboscideans and other large terrestrial

mammals (Martin and Klein 1984; Soffer 1985; Fisher 1987; Frison 1998; Alroy 2001; Grayson et al. 2001; Johnson 2002).

Researchers who argue that human hunting caused (or strongly contributed to) the late Pleistocene extinction cite the timing of the extinction (Martin 1984; Alroy 2001); the presence of mammoth butcher sites (Haynes 1966; Haynes 1991); and mortality patterns suggestive of selectivity by human hunters (Saunders 1980, 1992; Fisher 1987). For example, analyses of the sex ratio and age profiles of mammoths at Clovis sites led Saunders (1980, 1992) to propose that several sites, including Miami and Dent, each represented the slaughter of a family group, which would suggest that Pa-

TABLE 1.   Characteristics of fossil sites examined in this study.

Locality	MNI*	Age (yr B.P.)	Taphonomy	Reference
Blackwater Draw	6+	ca. 11,000–13,000	Butcher Site	Sellards 1952; Haynes 1991; Haynes 1995
Dent	13	10,980 ± 90–11,200 ± 500	Butcher Site/Family Group?	Sellards 1952; Saunders 1980, 1992; Haynes et al. 1998
Friesenhahn Cave	100+	ca. 17,000–20,000	Natural Accumulation/ Carnivore Den	Haynes 1991; Graham 1976; Marean and Ehrhardt 1995
Miami	5	ca. 10,500–11,400	Butcher Site/Family Group?	Sellards 1952; Saunders 1980, 1992; Holliday et al. 1994
Waco	23	ca. 28,000	Natural Accumulation/ Family Group	Haynes 1997; Fox et al. 1992a

* Minimum number of individuals.

leo-Indian hunters exerted a high level of predation pressure (see Table 1, Fig. 1). However, other researchers argue that these sites represent time-averaged accumulations (Agenbroad 1980; Haynes 1987, 1991; Holliday et. al. 1994). In addition, Haynes (1987, 1991) used analyses of the age profile of mammoths from these same sites to argue that late Pleistocene mammoths displayed the poor general health
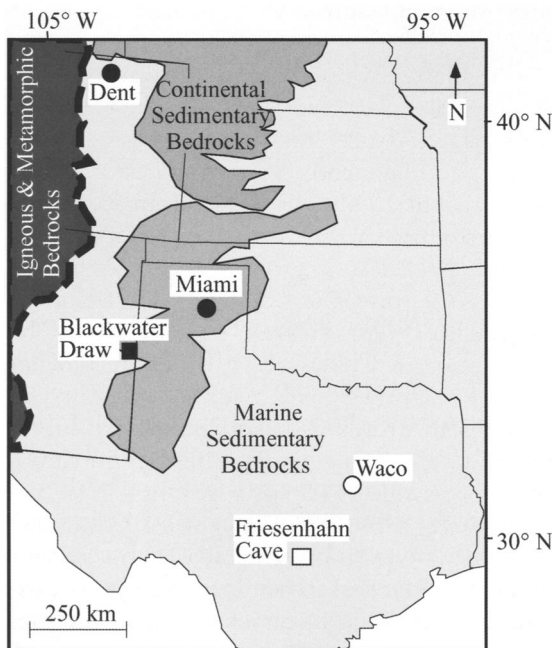

FIGURE 1.   Location of fossil sites. Known or proposed family group accumulations (circles), accumulations of unrelated individuals (squares), natural accumulations (white symbols), and Clovis butcher sites (black symbols). Dashed line represents the approximate edge of the igneous and metamorphic bedrocks of the Rocky Mountains. Bedrock geology mapped after Bayer 1983.

and low reproductive rates of a drought-stressed population, which support the view that climatic changes contributed to their extinction.

Traditional taphonomic methods have been unable to provide definitive discrimination between conflicting interpretations for many of these sites. Analyses of isotopic systems exhibiting natural variations may aid in distinguishing assemblages that contain a single family group from those that contain unrelated individuals. Observations of modern elephants, which are closely related to mammoths, provide a framework for predicting isotopic patterns in mammoth populations. Modern elephants typically associate in family groups of 5–30 animals that consist of related adult females and their immature offspring (Moss 1988; Sukumar 1989; Haynes 1991). Male offspring leave the family group upon reaching sexual maturity and may either travel independently or associate in temporary bachelor herds. Mature males can also associate with a matriarchal family group when a female is in estrous; observations of Asian elephants suggest that bulls may spend about 20% of their time associated with different family groups (Sukumar 1989). Because adult males are significantly larger than adult females, theoretical calculations suggest that males will travel farther than females to find food (Pennycuick 1979; Haynes 1991). The range size of females may be further reduced when a family group member is caring for a young calf. Because the members of a matriarchal family group move and feed together,

they encounter similar environmental conditions and similar isotopic signals. Thus, the members of a family group should display less isotopic variability than unrelated animals within a population. Likewise, we would expect that adult males in a population, whether they are independent or form a bachelor herd, would display greater isotopic variability than the members of a family group.

Analyses of various combinations of carbon, nitrogen, lead, and strontium isotope ratios have been used to distinguish among separate populations of modern African elephants (van der Merwe et al. 1990; Vogel et al. 1990) and to track temporal changes in range use (Koch et al. 1995). Geographically and temporally segregated mammoth populations have likewise been shown to display distinct isotopic values (Bombin and Muehlenbachs 1985; Connin et al. 1998; Koch et al. 1998; Hoppe et al. 1999). Thus, we would expect mammoth family groups or subpopulations to exhibit distinct signatures as well. To test this hypothesis, I examined the scale of variations displayed by three isotopic systems preserved in mammoth teeth: carbon isotope values ($\delta^{13}C$), which track variations in diet and local vegetation; oxygen isotope values ($\delta^{18}O$), which track local climatic conditions; and strontium isotope ratios ($^{87}Sr/^{86}Sr$), which track geographic changes in local soils. The sources of variations in these systems are discussed in greater detail below.

As an initial test, I compared the variability found in mammoths from two sites in central Texas. One site (Waco) represents the mass death of 22 mammoths, the majority of which appear to have belonged to a single family group. The other site (Friesenhahn Cave) represents a time-averaged accumulation of several hundred unrelated individual (Table 1, Fig. 1). First I tested which isotopic system provides the best discrimination of family associations by comparing the isotopic patterns at these two sites, and then I compared the signatures of Clovis mammoths with those of mammoths from the central Texas sites (Fig. 1).

Environmental Controls on Carbon, Oxygen, and Strontium Isotopes

Tooth enamel bioapatite is often used for isotopic analysis because of its resistance to postmortem alteration (Lee-Thorp and van der Merwe 1991; Koch et al. 1997). The factors that control the isotope ratios of enamel in animals vary among the three isotope systems studied. The $\delta^{13}C$ value of carbonate in the apatite of herbivores directly reflects the average $\delta^{13}C$ of food plants, with a diet-apatite offset of 14.1‰ (Ambrose and Norr 1993; Cerling and Harris 1999). The $\delta^{13}C$ values of plants vary, in turn, with photosynthetic pathway (O'Leary 1988). Most trees, herbs, and cool-climate grasses use C_3 photosynthesis, which produces tissues with $\delta^{13}C$ values averaging $-27‰ \pm 3‰$. Grasses adapted to grow in warm, dry climates use C_4 photosynthesis and have $\delta^{13}C$ values averaging $-13‰ \pm 2‰$. A third group of plants, composed primarily of succulents, use CAM photosynthesis and display $\delta^{13}C$ values that vary between these two extremes (Ehleringer 1989). However, CAM plants did not form a major component of the Great Plains biomass during the late Pleistocene (Bryant 1977; Elias and Van Devender 1990; Hall and Valastro 1995), and thus it seems unlikely that Great Plains mammoths consumed a significant amount of CAM plants.

The relative abundance of modern C_4 grasses correlates with growing-season temperature and moisture (Teeri and Stowe 1976; Parulelo and Lauenroth 1996; Epstein et al. 1997; Tieszen et al. 1997). The localities in this study are currently surrounded by grasslands that contain 70–100% C_4 grasses in the south and 40–90% C_4 grasses in the north (Parulelo and Lauenroth 1996; Tieszen et al. 1997). The abundance of C_4 grasses during the Pleistocene would have been affected not only by changes in growing-season temperature and precipitation, but also by changes in atmospheric CO_2 levels (Teeri and Stowe 1976; Ehleringer et al. 1997; Collatz et al. 1998). However, the changes in these factors would have had different effects on C_4 abundance. For example, decreases in growing-season temperatures during the glacial (e.g., Toomey et al. 1993) would have favored the growth of C_3 grasses (Teeri and Stowe 1976; Ehleringer et al. 1997), whereas lower levels of atmospheric CO_2 levels (Neftel et al. 1988; Marino et al. 1992) would have favored the growth of C_4

grasses (Ehleringer et al. 1997; Collatz et al. 1998). The degree to which each factor affected the abundance of C_4 grasses in the Great Plains region during the last glacial is still debated. Climate-based vegetation models predict that C_4 grasses should have increased slightly during full glacial times in the southern Great Plains (Collatz et al. 1998), whereas reconstructions of the vegetation based on the $\delta^{13}C$ values of herbivore teeth suggest that the abundance of C_4 plants in the Southwest was similar to modern abundances (Connin et al. 1998).

Analyses of dental morphology and rare instances of preserved gut and fecal contents suggest that Pleistocene mammoths fed primarily on grass, although some individuals consumed a small amount (<20%) of trees, herbs, and shrubs (Davis et al. 1985; Mead et al. 1986). These observations have been confirmed by more extensive isotopic analysis of mammoths in North America and Eurasia (Bocherens et al. 1994, 1996; Connin et al. 1998; Koch et al. 1998). In extant browsers (i.e., animals that consume primarily C_3 trees, shrubs, and/or herbs) enamel $\delta^{13}C$ values average $-12.9‰$, whereas animals that feed on C_4 grass have enamel that averages about $1.1‰$ (Lee-Thorp and van der Merwe 1991; Bocherens et al. 1996; Cerling and Harris 1999). When calculating the expected $\delta^{13}C$ values for glacial animals, we need to account for the small shifts in plant $\delta^{13}C$ values due to the effects of anthropogenic carbon and glacial-interglacial changes in atmospheric $\delta^{13}C$ values (Marino et al. 1992). These shifts would have resulted in full glacial herbivores having enamel $\delta^{13}C$ values approximately $0.5‰$ higher than modern values; late glacial herbivores would have had enamel $\delta^{13}C$ values that averaged about $1.1‰$ higher than modern values (Koch et al. 1998).

The $\delta^{13}C$ value of mammoth enamel correlates closely with values from co-occurring grazers (e.g., bison), and with inferred variations in the local abundance of C_4 plants (Connin et al. 1998; Koch et al. 1998). Because the members of a mammoth family group would have fed in the same areas, they should all display similar $\delta^{13}C$ values. In contrast, unrelated animals that foraged in disparate regions should display more variable $\delta^{13}C$ values. Furthermore, mammoths that lived in the same region during different time periods might have different $\delta^{13}C$ values because of changes in the local abundance of C_4 grass.

The $\delta^{18}O$ values of mammalian apatite are correlated with the $\delta^{18}O$ of ingested water (i.e., drinking water and dietary water) (Longinelli 1984; Luz et al. 1985; Bryant and Froelich 1995). The $\delta^{18}O$ values of ingested waters correlate, in turn, with those of meteoric water. In temperate and high-latitude regions, the $\delta^{18}O$ value of precipitation and surface water varies with temperature, with low values in cold regions and high values in warmer regions (Dansgaard 1964; Rozanski et al. 1993; Coplen and Kendall 2000). For example, the $\delta^{18}O$ value of precipitation in Waco, Texas, averages $-3.8‰$, and precipitation in Chicago, Illinois, averages $-7.0‰$ (Rozanski et al. 1993). Geographic differences in the $\delta^{18}O$ of local water are especially pronounced in mountainous areas, because climate varies sharply with altitude (Siegenthaler and Oeschger 1980). The value of meteoric water also changes with seasonal differences in temperature. In Waco, for example, summer precipitation averages $7‰$ higher than winter precipitation (IAEA/WMO 2001). Animals sample these environmental variations by directly drinking surface waters and by ingesting the water in plants, which is derived from surface waters (Förstel 1978; DeNiro and Epstein 1979; Saurer et al. 1997). However, plant waters may be enriched in ^{18}O relative to surface waters due to evapotranspiration, with the degree of enrichment varying from almost none when relative humidity is high, to $>20‰$ when relative humidity is low (Förstel 1978).

The water ingested by Pleistocene mammoths on the Great Plains may have differed in $\delta^{18}O$ from the water ingested by modern grazers for several reasons. First, mean values may have shifted with changes in temperature or the source of moisture (i.e., the Pacific Ocean versus the Gulf of Mexico) (Humphrey and Ferring 1994; Connin et al. 1998). Second, seasonal climatic variations may have been less extreme under glacial conditions (Bryant 1977; Elias and Devender 1990; Toomey et al. 1993; Blum et al. 1994; Hall and Valastro 1995),

thus reducing the amplitude of seasonal isotopic variations. Third, changes in humidity would alter the effect of evapotranspiration on leaf water. Still, analyses of the $\delta^{18}O$ values of Pleistocene mammals from the southwestern United States indicates that surface waters under full glacial and late glacial conditions exhibited $\delta^{18}O$ patterns similar to those found today (Connin et al. 1998).

All members of a mammoth family group experience the same climatic conditions, so they should display similar enamel $\delta^{18}O$ values. If the mammoths at a site are time-averaged, or if they represent a mixture of migrant and resident individuals, then they should display high $\delta^{18}O$ variability (Stuart-Williams et al. 1996; Koch et al. 1998). Additionally, because climatic gradients also control the abundance of C_4 grass, climatically induced changes in the $\delta^{18}O$ values of mammoths should correlate with changes in their $\delta^{13}C$ values.

Unlike carbon or oxygen isotopes, Sr isotopes are not measurably fractionated by chemical or biological processes. Consequently, the Sr isotope composition of an herbivore equals that of ingested Sr, which is taken in largely via food plants (Lenihan et al. 1967; Price et al. 1985). The Sr isotope composition of plants tracks the composition of Sr dissolved in soil solutions, which is derived from bedrock weathering and atmospheric deposition (Gosz and Moore 1989; Miller et al. 1993; Chadwick et al. 1999). In general, the Sr isotope composition of plants, soils, and surface waters varies geographically in response to differences in the age and composition of bedrock and variations in dust input. Analyses of $^{87}Sr/^{86}Sr$ ratios have been used to track the movements of modern mammals, birds, and fish (van der Merwe et al. 1990; Vogel et al. 1990; Koch et al. 1995; Chamberlain et al. 1996), as well as fossil animals (Koch et al. 1992; Hoppe et al. 1999) and prehistoric humans (Sealy et al. 1995; Ezzo et al. 1997).

Bedrock in the Great Plains and central Texas exhibits variations in age and lithology that should generate geographic differences in $^{87}Sr/^{86}Sr$ ratios (Bayer 1983). For example, the bedrock in central Texas, near Waco and Friesenhahn Cave, consists primarily of Mesozoic and Cenozoic marine sediments that have rel-

atively low $^{87}Sr/^{86}Sr$ ratios ranging from 0.7070 to 0.7092 (Hess et al. 1986; Faure 1986; Denison et al. 1994). Thus, soils and plants in the area should also have relatively low $^{87}Sr/^{86}Sr$ ratios. In contrast, the Dent site is surrounded by sediments derived primarily from the Precambrian igneous and metamorphic rocks of the Rocky Mountains, which display relatively high $^{87}Sr/^{86}Sr$ ratios of >0.7110 (Bayer 1983; Faure 1986; Blum and Erel 1995). The Blackwater Draw and Miami sites are surrounded by a mixture of continental and marine sediments (Bayer 1983), and thus their local environments are likely to display variable $^{87}Sr/^{86}Sr$ ratios.

The members of a mammoth family group will display similar $^{87}Sr/^{86}Sr$ ratios if each family group had a consistent, well-defined home range and if animals ranged on a scale comparable to the scale of geographic variation in $^{87}Sr/^{86}Sr$ ratios. Furthermore, analysis of $^{87}Sr/^{86}Sr$ ratios may help identify factors that cause carbon and oxygen isotope ratios to vary among populations. For example, if shifts in $^{87}Sr/^{86}Sr$ ratio coincide with shifts in $\delta^{18}O$ and/or $\delta^{13}C$ values, then all three may reflect, in part, the effects of spatial mixing of the faunal assemblage. In contrast, if the $^{87}Sr/^{86}Sr$ ratios of an assemblage are uniform while the $\delta^{18}O$ and/or $\delta^{13}C$ values are not, then the site may represent a time-averaged assemblage of individuals from the same region.

Materials

Localities

Friesenhahn Cave (Bexar County, Texas).—Friesenhahn Cave is a one-room cave located in the Edwards Limestone near the edge of the Edwards Plateau in south-central Texas. Over 300 whole and 200 broken teeth of Columbian mammoths (*Mammuthus columbi*) have been recovered as well the remains of bison, canids, deer, horses, mastodons, peccary, tapir, and several large felids (Graham 1976). Radiocarbon dates reveal that Pleistocene deposition continued from ca. 17,000 to ca. 20,000 years before present (yr B.P.) (Graham 1976). Taphonomic analysis and the abundance of sabertoothed cat (*Homotherium serum*) remains suggest that this site was a saber-toothed cat den (Graham 1976; Marean and Ehrhardt 1995).

Waco (McLennan County, Texas).—The Waco mammoth site is located on a river terrace near the Bosque River, in central Texas. This site represents the rare occurrence of a mass death where most remains consist of articulated skeletons preserved in the positions in which they died (Fox et al. 1992a). A total of 23 Columbian mammoths have been recovered from this site, along with the skeleton of a camel and a single horse tooth. All mammoths were recovered from a single stratigraphic layer representing one depositional event, with the exception of one individual recovered from a higher stratigraphic level, which likely represents a separate event. Only mammoths from the lower stratigraphic level were analyzed for this study. This level consists of a thin lens (<36 cm) of fine-grained silty clay, which was derived from the calcareous rock of the Edwards Plateau of central Texas (Fox et al. 1992a). All of the animals in the lower level appear to have perished catastrophically in the near-shore waters of the Bosque River and have been radiocarbon dated to about 28,000 yr B.P. (Fox et al. 1992a; Haynes 1992). The bones lack weathering, abrasion, polishing, or fragmentations indicative of postmortem trampling, suggesting that the carcasses were rapidly buried after death (Fox et al. 1992a). The mammoths consist primarily of mature females and juveniles; only one adult male (SM-19) was recovered. The age profiles, sex ratio, and death positions of the mammoths suggest that the adult females and juveniles were members of a family group (Haynes 1987, 1992; Fox et al. 1992a). The adult male would have belonged to the same population of mammoths, but would not have been a member of the family group; it is likely that he was temporarily associating with the females either because a cow was in estrus or simply because of the proximity of water (Sukumar 1989).

Miami (Roberts County, Texas).—The Miami locality is situated near the eastern edge of the Southern High Plains. It has yielded the partial remains of at least five Columbian mammoths, which were recovered from a single bed of silty clay sediments that were deposited in a shallow (<2 m deep) seasonal pond between ca. 10,000 and ca. 11,400 yr B.P. (Sellards 1952; Holliday et al. 1994). The association of Clovis projectile points and scrapers with the mammoth remains suggests that at least some of these animals were butchered (Sellards 1952). However, researchers still argue about whether these animals were killed by Paleo-Indians or were butchered after they had died of natural causes (see review by Holliday et al. 1994). Analyses of the age profiles of mammoths from this site led Saunders (1980, 1992) to suggest that the Miami mammoths represent a family group that was slaughtered in a single event. Other researchers argue that this assemblage represents unrelated animals that had already died, or were weakened by drought, when the Paleo-Indians encountered them (Sellards 1952; Haynes 1987, 1991).

Blackwater Draw (Roosevelt County, New Mexico).—Blackwater Draw, also referred to as Clovis or Blackwater Locality No. 1, is the type locality for the Clovis Paleoindian Culture. The site is situated in a dry drainage channel on the Southern High Plains in eastern New Mexico. At least six Columbian mammoths have been recovered, as well as extinct bison, horses, camels, and several small mammals (Sellards 1952; Lundelius 1972; Saunders 1980, 1992; Haynes 1991; Saunders and Daeschler 1994). The mammoth remains occur in two separate unconsolidated sand units. The older unit, referred to as the "Gray Sand," the "Speckled Sand," or "Unit B," has yielded radiocarbon dates that range between 11,380 ± 150 and 12,790 ± 160 yr B.P. The lower part of this unit was deposited in a pond fed by a vigorous spring, but water levels dropped as deposition progressed (Haynes 1995). The other unit, referred to as the "Brown Sand Wedge," or "Unit C," is a discontinuous lens of material that has yielded radiocarbon dates averaging 11,290 ± 240 yr B.P.; this unit was formed by debris flows and may have been deposited during a period of regional drought (Haynes 1995). Most of the mammoths examined in this study were excavated from the Gray Sand, although one (E6) was recovered from the Brown Sand Wedge. Associated Clovis artifacts and cut marks on bones provide evidence that at least some of the mammoths were butchered. However, a detailed study of

the occurrence of cut marks on two mammoths recovered from the upper portion of Unit B suggest that these mammoths were butchered significantly after death when the carcasses had stiffened (Saunders and Daeschler 1994). In addition, the age profile, sex ratio, and stratigraphic separation of the mammoths at this site demonstrate that these animals were not a family assemblage; most individuals appear to have died in separate events (Saunders 1980, 1992; Saunders and Daeschler 1994; Johnson and Holliday 1997).

Dent (Weld County, Colorado).—The Dent site is located in a tributary gully of the South Platte River in northern Colorado. It has yielded abundant bones and teeth from the remains of at least 13 individual Columbian mammoths, which were recovered from a layer of silt and fine sand deposited in a localized mudflow on an alluvial fan (Sellards 1952; Saunders 1980, 1992; Haynes 1991; Haynes et al. 1998). Faunal material may have been redeposited, but the lack of weathering or wear on bone surfaces suggests that these remains were not transported far. Radiocarbon dates from bones and bone collagen range from 10,980 ± 90 to 11,200 ± 500 yr B.P. Associated Clovis stone tools suggest that these animals were butchered by human hunters. The age profile of the animals led Saunders (1980, 1992) to suggest that Dent mammoths represented a single family group that was killed and butchered simultaneously, but Haynes (1987) argued that the age profile suggests a drought-killed assemblage of unrelated individuals.

Methods

I analyzed samples of bulk tooth enamel from 46 mammoths (Table 2). Each sample was collected from an area of the tooth that represented at least a year of growth; although seasonal variations in the isotopic value of enamel were thus averaged, potential annual variations in isotopic ratios may still exist (Koch et al. 1998). Unlike most mammals, mammoths continued forming teeth, and tooth enamel, throughout most of their adult lives (Haynes 1991). Because each cheek tooth of an adult mammoth continued to mineralize for over a decade, samples collected from dif-

TABLE 2. Sample numbers, isotopic values, and summary statistics for mammoth tooth enamel.

Sample no.*	$^{87}Sr/^{86}Sr$	$\delta^{13}C$	$\delta^{18}O$
Dent			
DMNH-1636-a	0.7116	−3.7	23.2
DMNH-1636-b	0.7112	−4.1	22.5
DMNH-1893	0.7111	−7.9	23.4
DMNH-1895	0.7114	−5.1	23.0
DMNH-1896	0.7112	−1.6	25.2
DMNH-1897		−4.3	25.5
DMNH-1898	0.7120	−6.2	25.1
DMNH-1899	0.7117	−4.4	22.6
DMNH-1900	0.7112	−4.4	22.4
DMNH-3801	0.7114	−4.2	21.3
DMNH-3802	0.7113	−4.0	22.8
DMNH-3809	0.7111	−3.9	24.9
mean	0.7114	−4.5	23.6
1σ	0.0003	1.6	1.4
Miami			
TMM 30721-3	0.7092	−3.2	28.7
TMM 30721-4		−0.9	29.2
TMM 30721-5	0.7086	−4.0	31.2
mean	0.7089	−2.7	29.7
1σ		1.6	1.3
Friesenhahn Cave			
TMM 933-133	0.7095	−5.1	29.9
TMM 933-296	0.7090	−1.5	30.0
TMM 933-358		−1.4	29.1
TMM 933-1013	0.7091	−1.2	30.4
TMM 933-1006	0.7094	−0.1	29.9
TMM 933-1309	0.7089	−1.7	28.1
TMM 933-1505	0.7093	−0.1	30.1
TMM 933-1506	0.7095	−1.2	29.2
TMM 933-2014		0.0	30.0
TMM 933-2015	0.7092	−1.4	28.9
TMM 933-2243		−1.0	29.2
TMM 933-2676	0.7097	−1.9	30.1
TMM 933-3407	0.7095	−3.5	31.5
mean	0.7093	−1.5	29.7
1σ	0.0003	1.4	
Waco**			
SM-1	0.7098		
SM-3	0.7086	−2.6	30.0
SM-4	0.7101	−2.0	30.4
SM-5-a	0.7093	−3.3	31.0
SM-5-b		−2.6	28.1
SM-5-c		−3.8	27.3
SM-6	0.7095	−3.3	29.1
SM-9	0.7098	−2.3	30.4
SM-11		−2.7	28.5
SM-12-a	0.7102	−2.7	31.1
SM-12-b		−2.5	30.2
SM-12-c		−3.0	30.4
SM-12-d		−2.8	30.6
SM-13	0.7097	−3.5	30.0
SM-14	0.7093	−2.0	30.7
SM-21	0.7083	−2.2	30.6
mean	0.7095	−2.7	29.9
1σ	0.0006	0.5	0.8
SM-19**	0.7107	−2.7	30.3

TABLE 2. Continued.

Sample no.*	$^{87}Sr/^{86}Sr$	$\delta^{13}C$	$\delta^{18}O$
Blackwater Draw			
Blackwater-A			
TMM-818	0.7081	−0.9	27.8
TMM-937	0.7086	0.3	29.3
mean	0.7084	−0.3	28.6
Blackwater-B			
TMM-M3	0.7095	−8.7	23.8
TMM-126	0.7100	−8.6	22.2
SMU-no catalog #	0.7092	−7.2	23.9
mean	0.7096	−8.2	23.3
1σ	0.0004	0.8	1.0

* Key to cataloged specimens: DMNH = Denver Museum of Natural History, paleontology collection number; TMM = Texas Memorial Museum, paleontology site-specimen number; SM = Strecker Museum, Waco mammoth site number; SMU = Southern Methodist University, paleontology collection number. Samples with a, b, c, or d represent multiple bulk samples from the same tooth.

** Because sample SM-19 represents an adult male, it could not have been a member of the proposed family group and is therefore excluded from calculated mean values.

ferent individuals, even those that died at the same time, likely represent material deposited in different years. If mammoth diets or movement patterns differed dramatically from year to year, then individuals would display large inter-annual isotopic variations, which could potentially mask any similarity produced by the association of animals in a family group. Thus, the scale of potential variation within an individual must be documented before we can fully evaluate the meaning of variations among different individuals. I therefore investigated the scale of intratooth variability by analyzing different bulk samples collected from multiple places on the same tooth in several individuals.

Carbon and oxygen samples were prepared according to the methods described by Koch et al. (1998), then analyzed on a VG Optima or a Prism gas source mass spectrometer with an ISOCARB automated carbonate system. Dissolution of samples was achieved by reaction in a constantly stirred bath of 100% phosphoric acid at 90°C. Results are reported in standard delta (δ) notation and units are reported in parts per thousand (‰), where $\delta^{13}C = [((^{13}C/^{12}C_{sample} \div {}^{13}C/^{12}C_{standard}) - 1) \times 1000]$ and the standard is PDB. $\delta^{18}O$ values follow the same convention, where the ratios are $^{18}O/^{16}O$ and the standard is SMOW. Precision for analyses of calcite standards was ≤0.2‰ for

$\delta^{13}C$ and $\delta^{18}O$. Replicate analyses of enamel samples ($n = 10$) differed by 0.1‰ ± 0.1‰ (mean ± 1σ) for carbon and by 0.3‰ ± 0.2‰ for oxygen.

Strontium samples were prepared for analysis according to methods described by Hoppe et al. (1999) and measured on a VG354-S thermal ionization mass spectrometer. All measurements are referenced to a value of $^{87}Sr/^{86}Sr = 0.71025$ for the NBS 987 Sr standard and are precise to within ± 0.00005.

Analytical results for multiple samples from the same tooth were averaged for the purposes of statistical analysis. Differences in variances of isotope values were examined by using an F-test. Significant differences among mean values at different sites were evaluated by using a t-test or one-way analysis of variance (ANOVA). Scheffé's tests were used to resolve significant differences among multiple pairwise comparisons of sites (Norman and Streiner 1992).

Results

In order to interpret isotopic differences among individuals, the range of values found within a single tooth must first be established. I therefore examined multiple samples of bulk tooth enamel taken from different sections of the same tooth. The degree of intratooth variability differed for each isotopic system. The $\delta^{13}C$ values of multiple samples from the same tooth differed by an average values of −0.7‰, with a standard deviation (1σ) of 0.4‰. The $\delta^{18}O$ values of bulk samples from the same tooth displayed greater variability, differing on average by 1.8‰ ± 1.7‰. The $^{87}Sr/^{86}Sr$ of multiple bulk samples differed by 0.0004.

Carbon Isotopes.—The isotopic variability found among individuals from the family group (adult females and juveniles) from Waco and the Friesenhahn Cave sites can be used to contrast the variability found among family group members versus the variability among unrelated individuals. This comparison shows that mammoths from the same family group had relatively homogeneous $\delta^{13}C$ values, compared with the values of unrelated mammoths preserved together. The $\delta^{13}C$ values of mammoths from the Waco family group were tightly clustered (Table 2, Fig.
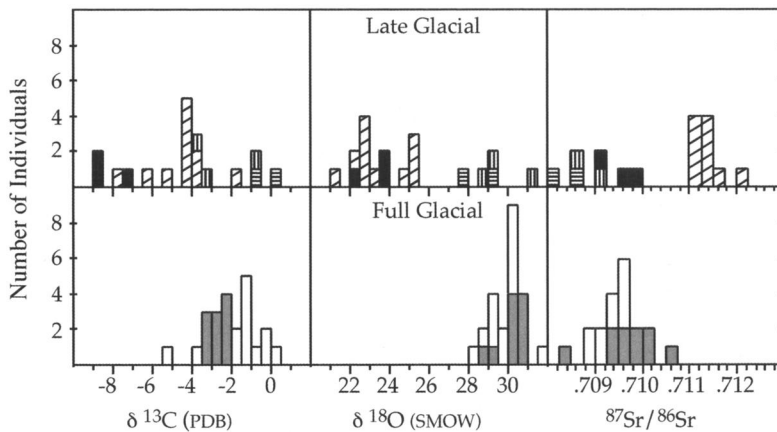
FIGURE 2. Distribution of the δ^{13}C values, δ^{18}O values, and ^{87}Sr/^{86}Sr ratios in Great Plains mammoths: Dent (diagonal cross-hatching), Blackwater-A (horizontal stripes), Blackwater-B (black), Miami (vertical stripes), Waco (gray), and Friesenhahn Cave (white).

2), with values that varied by a maximum of 1.5‰ (mean = −2.7‰ ± 0.5‰), whereas mammoths from Friesenhahn Cave displayed δ^{13}C values that varied 5.1‰ (mean = −1.5‰ ± 1.4‰). The difference in variance at these two sites was significant (F-test: $p \leq 0.01$).

Analyses of the δ^{13}C values of mammoths from Clovis sites revealed that the individuals at each of the Clovis sites display highly variable values. In fact, the δ^{13}C values of mammoths at every Clovis site have greater variability than those of mammoths at Friesenhahn Cave (Table 2, Fig. 2). Additional information may be gained by examining patterns in the δ^{13}C values within and among Clovis site mammoths. The δ^{13}C values of mammoths at Dent and Miami displayed the same standard deviation (1.6‰), whereas mammoths from Blackwater Draw displayed a much higher standard deviation of 4.4‰. In fact, individuals from Blackwater Draw displayed both the highest and lowest values of any mammoth in this study. Inspection of the pattern of values among Blackwater Draw mammoths revealed that, in contrast to other populations, animals from Blackwater Draw displayed two distinct patterns of values (Fig. 2). One group of animals displayed values of −0.3‰ ± 0.8‰, and the other group had significantly different values with a mean of −8.2‰ ± 0.8‰ (t-test: $p < 0.01$). Thus, for additional statistical comparisons, the Blackwater Draw mammoths were separated into two

groups, referred to as Blackwater-A and Blackwater-B (see Table 2).

ANOVA comparison of mean values among the Clovis sites revealed highly significant differences ($p < 0.0001$). Post-hoc, pairwise comparisons revealed that mean values for mammoths from Blackwater-B were significantly different from all other population means (Scheffé's test: $p < 0.01$). In addition, the mean value for mammoths from Blackwater-A was significantly different from the mean for Dent (Scheffé's test: $p < 0.05$), but not from the mean for Miami (Scheffé's test: $p > 0.05$). No significant differences were found between the mean values of Miami and Dent mammoths (Scheffé's test: $p > 0.05$).

Oxygen Isotopes.—In contrast to the patterns observed in δ^{13}C values, the δ^{18}O values of mammoths from the Waco family group displayed no significant differences from those at Friesenhahn Cave (Table 2, Fig. 2). Each population had similar mean values and a standard deviation of approximately 0.8‰. Data from Clovis-associated mammoths revealed that mammoths from Dent and Blackwater-B had relatively low mean values of 23.5‰ ± 1.4‰ and 23.3‰ ± 1.0‰, respectively, whereas mammoths from Miami and Blackwater-A displayed relatively high mean values of 29.7‰ ± 1.3‰ and 28.6‰ ± 1.0‰, respectively.

ANOVA comparison of mean δ^{18}O values at Clovis sites revealed that differences among

sites were highly significant ($p < 0.0001$). Pairwise comparison demonstrated that the relatively low mean $\delta^{18}O$ values observed at Dent and Blackwater-B were not significantly different from one another (Scheffé's test: $p > 0.05$), but both means were significantly different from the relatively high mean $\delta^{18}O$ values found at Miami and Blackwater-A (Scheffé's test: $p < 0.001$). The mean $\delta^{18}O$ values of Miami and Blackwater-A mammoths were not significantly different from one another (Scheffé's test: $p > 0.05$).

Strontium Isotopes.—The $^{87}Sr/^{86}Sr$ ratios of mammoths from Waco and Friesenhahn Cave displayed no significant difference; the mammoths from Waco displayed somewhat greater variability (0.7096 ± 0.0007) than mammoths from Friesenhahn Cave (0.7093 ± 0.0003) (Table 2, Fig. 2), but the differences were not significant (*F*-test: $p > 0.05$).

Mammoths from the Clovis sites exhibited within-site $^{87}Sr/^{86}Sr$ variability that was intermediate between the variability found in Waco and Friesenhahn Cave mammoths. Mammoths from Blackwater-A and Miami displayed similar mean values of 0.7083 ± 0.0004 and 0.7089 ± 0.0004, respectively. Dent and Blackwater-B mammoths displayed higher values of 0.7096 ± 0.0004 and 0.7114 ± 0.0003, respectively. ANOVA comparison of mean $^{87}Sr/^{86}Sr$ values showed that differences among Clovis populations were significant ($p < 0.0001$). Pairwise comparison demonstrates that the mean $^{87}Sr/^{86}Sr$ ratio for Dent mammoths was significantly different from the mean values for all other populations (Scheffé's test: $p < 0.0001$). Furthermore, the mean for Blackwater-B mammoths was significantly different from the mean for Blackwater-A mammoths (Scheffé's test: $p < 0.01$). The mean value for Miami mammoths was not significantly different from that of either Blackwater population (Scheffé's test: $p > 0.05$).

Discussion

Isotopic Analyses as Tracers of Family Group Associations.—A biogeochemical signal is useful for identifying related animals only if it varies less within an individual and within a family group than among unrelated individuals. Of the three signals we examined, only

$\delta^{13}C$ values met these criteria. The relative uniformity of the $\delta^{13}C$ values within and among the individuals from Waco suggests that these individuals all consumed a similar diet that did not vary greatly from year to year. We can use enamel $\delta^{13}C$ values to calculate the percentage of C_4 grass in each animal's diet by using (1) the average fractionation between diet and enamel found in modern herbivores (Cerling and Harris 1999) and (2) estimated $\delta^{13}C$ values for dietary plants, based on average $\delta^{13}C$ values of modern C_3 and C_4 plants that have been adjusted for the changing atmospheric $\delta^{13}C$ values in the late Pleistocene (Marino et al. 1992; Koch et al. 1998). These calculations suggest that the Waco mammoths ate a diet consisting of approximately 70–80% C_4 grass (mean = 77% $\pm$ 4%). The range of $\delta^{13}C$ values of these mammoths may represent seasonal differences in the $\delta^{13}C$ values of plants (Farquhar et al. 1989) and/or seasonal variations in the amount of C_3 grasses or C_3 browse plants consumed by each individual (Tieszen 1994).

The greater range of $\delta^{13}C$ values displayed by mammoths at Friesenhahn Cave suggests that they consumed a more diverse diet, which we calculate ranged from approximately 60% to 95% C_4 grass (mean = 85% $\pm$ 10%). This variation may have resulted from differences in the amount of C_3 browse consumed by each animal, but independent evidence suggest that mammoths were primarily grazers (Connin et al. 1998; Koch 1998; Koch et al. 1998; Hoppe and Koch in press). Thus, the range of $\delta^{13}C$ values observed most likely resulted primarily from geographic and/or temporal changes in the local abundance of C_4 versus C_3 grass. This interpretation is supported by the observation that other grazing herbivores at Friesenhahn Cave, such as bison, displayed a similar range of $\delta^{13}C$ values (P. Koch personal communication 2002). A minor amount (ca. 0.5‰) of the $\delta^{13}C$ variation may also reflect long-term temporal changes in atmospheric $\delta^{13}C$ values (Marino et al. 1992), which would have produced corresponding changes in the average $\delta^{13}C$ of plants and herbivores.

Although enamel $\delta^{13}C$ values provided information useful for identifying family group

assemblages, enamel $\delta^{18}O$ values presented a more complex pattern. Multiple bulk samples from the same individual exhibited a wide range of values (up to 3.7‰). As a result of this within-individual variation, the $\delta^{18}O$ values of mammoths from the same family group displayed the same range of variability as those from unrelated animals. Within- and among-individual variations most likely resulted from differences in the $\delta^{18}O$ of ingested waters, which may been due to several factors. First, mammoths may have consumed water from different sources. For example, Waco mammoths probably drank water from both the Brazos and the Bosque Rivers (Fox et al. 1992a). Because these rivers originate in different regions, they would have had $\delta^{18}O$ values that differed from each other, as well as from that of local precipitation (Coplen and Kendall 2000). Second, and perhaps more significantly, the $\delta^{18}O$ values of precipitation vary on an interannual and on a seasonal basis (Rozanski et al. 1993). Thus, even mammoths from the same family group may have teeth with different $\delta^{18}O$ values, because animals of different ages would have formed their teeth during different years. Indeed, recent work on modern terrestrial mammals (Bocherens et al. 1996; Clementz and Koch 2001) indicates that the $\delta^{18}O$ values of animals from a single population can have standard deviations ranging from 0.5‰ to 2.0‰. Despite the range of $\delta^{18}O$ expressed in mammoths from central Texas, individuals at both sites displayed almost identical mean $\delta^{18}O$ values. This suggests that the average $\delta^{18}O$ values of precipitation, and thus local climatic conditions, were similar during the deposition of each site.

In summary, the variability of mammoth $\delta^{18}O$ values in central Texas does not appear to provide useful information about taphonomy, but in locations where gradients in the $\delta^{18}O$ of local precipitation are greater (e.g., in mountainous regions), analyses of enamel $\delta^{18}O$ values may provide a more diagnostic signal of co-association. In addition, because mammoth tusks grew continually throughout life, analyses of tusk $\delta^{18}O$ values may prove a stronger test of family group association; an examination of material mineralized during the last few years of each individual's life

might reveal distinctive shared seasonal patterns in the $\delta^{18}O$ values of related animals.

Analyses of the variability of mammoth $^{87}Sr/^{86}Sr$ ratios does not appear to be useful for identifying related animals, at least not in central Texas; contrary to expectations, the mammoths from Waco displayed a greater range of values than mammoths from Friesenhahn Cave. It seems probable that soils, and thus plants, near Waco displayed a greater range of $^{87}Sr/^{86}Sr$ ratios than those found around Friesenhahn Cave. Although both sites are located on marine sedimentary rock, the $^{87}Sr/^{86}Sr$ ratios of some soils near Waco may be influenced by sediments carried by the Bosque River. This river originates in northwestern Texas where bedrock $^{87}Sr/^{86}Sr$ ratios are higher than those found in central Texas (Fig. 1). The mean $^{87}Sr/^{86}Sr$ ratios of mammoths from both Texas sites were higher than the values expected for local bedrocks, suggesting that both environments contain some Sr derived from external sources. Although the variability of local $^{87}Sr/^{86}Sr$ ratios in central Texas environments apparently overwhelms any behaviorally induced similarity in the ratios of family group members, the range of ratios observed in all central Texas mammoths was small when compared with expected regional gradients (e.g., between Texas versus Colorado). Thus, comparisons of the $^{87}Sr/^{86}Sr$ of animals from different regions should still yield information about migratory behavior. It is also interesting to note that the Waco bull displayed the highest $^{87}Sr/^{86}Sr$ ratio of any animal at that site, which is consistent with predictions that bulls should range farther than matriarchal family groups. However, additional characterization of the $^{87}Sr/^{86}Sr$ gradients in environments around the Waco site would be needed to confirm this hypothesis.

Taphonomy and Paleodiet of Clovis Mammoths.- The high variability of isotopic values, especially $\delta^{13}C$ values, displayed by mammoths from the Clovis sites examined in this study suggests that each site contains a mixture of unrelated individuals rather than a family group assemblage. This conclusion relates most directly to the controversy surrounding the taphonomy of the Dent and Miami sites,
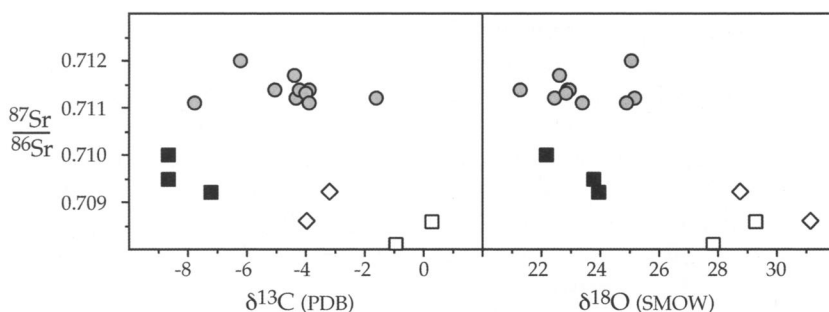
FIGURE 3.   The ^{87}Sr/^{86}Sr ratio of Clovis mammoths plotted against corresponding δ^{13}C values and δ^{18}O values: Dent (gray circles), Blackwater-A (open squares), Blackwater-B (black squares), and Miami (open diamonds).

because researchers agree that Blackwater Draw mammoths represent an attritional assemblage (Sellards 1952; Saunders 1980, 1992; Holliday et al. 1994; Haynes 1995). Our results support the interpretations of Haynes (1987, 1991), who concluded that all of these sites were attritional assemblages. It thus appears that Clovis hunters in this region did not slaughter entire family groups of mammoths en masse, but rather hunted, or at least scavenged, mammoths on an individual basis. However, further work is needed to resolve whether other mass accumulations of Clovis mammoth (i.e., Lehner, Arizona; Murry Springs, Arizona; and Colby, Wyoming) likewise represented the deaths of unrelated individuals.

The range of δ^{13}C values observed within mammoths at each site demonstrates that different individuals consumed varying percentages of C_4 versus C_3 plants. We calculate that mammoths from Blackwater-A consumed the most C_4 vegetation (mean = 82%), followed by those at Miami (65% ± 11%), Dent (52% ± 10%), and then Blackwater-B (26% ± 6%). Because mammoths were primarily grazers (Davis et al. 1985; Mead et al. 1986), their δ^{13}C values should reflect local variations in the abundance of C_4 versus C_3 grasses. This interpretation is supported by the observation that the differences in calculated percentages of C_4 plants consumed by each mammoth population, except Blackwater-B, are similar to the modern difference in the abundance of C_4 grass at each site (Parulelo and Lauenroth 1996; Epstein et al. 1997; Tieszen et al. 1997). However, the low percentage of C_4 grasses in the diet of Blackwater-B mammoth suggests

that these individuals lived in an environment where the abundance of C_4 grasses was significantly lower. This would have resulted if they lived either in a generally cooler region or during times when the local climate at Blackwater Draw was significantly cooler (i.e., if Blackwater-B mammoths represent animals redeposited from full glacial sediments).

Migration Patterns of Clovis Mammoths.—Researchers have theorized, largely by analogy with modern elephants, that Pleistocene mammoths migrated long distances on a seasonal basis (Churcher 1980; Olivier 1982; Holman et al. 1988). For example, Churcher (1980) proposed that North American mammoths migrated more than 2000 km on a biannual basis, and Olivier (1982) suggested that Siberian mammoths seasonally migrated distances of approximately 650 km.

If the Great Plains mammoths routinely undertook long-distance migrations, then mammoths at all of the Clovis sites in this study should display similar ^{87}Sr/^{86}Sr ratios. However, the Dent mammoths display ^{87}Sr/^{86}Sr ratios that are distinct from those of mammoths at Blackwater Draw and Miami (Figs. 2, 3), demonstrating that the Dent mammoths belonged to a distinct population. Thus, we conclude that Great Plains mammoths did not routinely migrate between northern Colorado and the southern High Plains, which are separated by about 600 km.

At least some Clovis mammoths, however, appear to have migrated shorter distances. Both the Blackwater-B and Dent mammoths display low δ^{13}C and low δ^{18}O values, which suggest that these mammoths inhabited regions with relatively cool climates and drank

water that precipitated under relatively cold climatic regimes (Faure 1986; Rozanski et al. 1993) (Fig. 3). These findings are consistent with our interpretation that the Dent mammoths represented a separate population; a similar gradient exists today in the average $\delta^{13}C$ values of local grasses (Tieszen et al. 1997) and the $\delta^{18}O$ values of local streams (Kendall and Coplen 2001). However, it is somewhat surprising that the Blackwater-B mammoths display values that are distinct from the higher $\delta^{13}C$ and $\delta^{18}O$ values displayed by other mammoths at Blackwater Draw, as well as those at Miami. We would expect all mammoths at these sites to display a similar range of stable isotopic values since the abundance of C_4 grasses and the average $\delta^{18}O$ values of precipitation are similar at both sites (Tieszen et al. 1997; Kendall and Coplen 2001). The discrete values of Blackwater-B mammoths demonstrate that these animals, like the mammoths at Dent, inhabited cooler climates than the Blackwater-A and Miami mammoths.

Analysis of $\delta^{13}C$ and $\delta^{18}O$ values alone cannot distinguish whether the Blackwater-B mammoths inhabited a different geographic region or lived during a different, cooler, time period. However, the discrete $^{87}Sr/^{86}Sr$ ratios of Blackwater-B mammoths confirm that these individuals represent a population with a different geographic range; the $^{87}Sr/^{86}Sr$ ratios of mammoths from Blackwater-B suggest that they ranged into habitats in the Rocky Mountains (a distance of about 200 km). It is also possible that Blackwater-B mammoths would display high $^{87}Sr/^{86}Sr$ ratios and low $\delta^{18}O$ values if they ranged primarily along river valleys where sediments and water were derived from the Rocky Mountains. However, the low $\delta^{13}C$ values of this population suggest that they lived in cooler climatic conditions that supported primarily (ca. 70%) C_3 grasses, and the high-elevation regions in the Rocky Mountains are the closest such habitat to Blackwater Draw. In contrast, the relatively low $^{87}Sr/^{86}Sr$ ratios of mammoths from Miami and Blackwater-A (Fig. 3) suggest that these animals did not range into the Rocky Mountains, inhabiting instead the local environments of the southern High Plains. The similarity of the

isotopic values of mammoths from Blackwater-A population and Miami further suggests either that the local $^{87}Sr/^{86}Sr$ ratios were not significantly different at these sites or that mammoths regularly moved between the two sites (a distance of about 250 km).

In summary, isotopic analyses demonstrate that Clovis mammoths from the Great Plains region did not routinely undertake large-scale migrations (≥ 600 km) but may have migrated moderate distances of several hundred kilometers. The question remains as to whether this migratory behavior was typical of all mammoths; Clovis animals may have displayed atypical behavior due to the stress of human predation or environmental changes. For example, depositional evidence suggests that the Miami site and parts of the Blackwater site were deposited during a period of regional drought (Haynes 1987; Holliday et al. 1994; Haynes 1995). Thus, the Clovis mammoths may have been forced to alter their normal movement patterns to find water. However, several lines of evidence suggest that the migration patterns of Clovis mammoths were not atypical. For example, the full glacial mammoths at Waco and Friesenhahn Cave displayed low $^{87}Sr/^{86}Sr$ ratios that were different from the values of mammoths at Dent but similar to the values of Miami and Blackwater-A mammoths. This suggests that full glacial mammoths likewise ranged only locally within Texas. In addition, analyses of the $^{87}Sr/^{86}Sr$ ratios of late and full glacial mammoths from Florida demonstrate that Florida mammoths likewise did not undertake large-scale (>500 km) migrations (Hoppe et al. 1999).

Conclusions

All of the isotope systems examined here displayed variations among mammoths from different sites, but only the $\delta^{13}C$ values displayed a pattern useful for identifying family group associations. The tight clustering of $\delta^{13}C$ among individuals from the Waco family group demonstrates that all of these mammoths consumed very similar diets, which averaged 77% C_4 grasses. The broader range of values among the unrelated mammoths at Friesenhahn Cave shows that these individuals lived either in different areas or at different

times, and/or that they exploited a wider range of resources. Thus, in regions where C_4 grasses were abundant, analyses of the $\delta^{13}C$ values of associated mammoths can aid in identification of family group associations.

Analyses of the $\delta^{13}C$ variability among Clovis mammoths further suggest that none of the sites examined contain family group associations. It thus appears that Clovis hunters of the southern and central Great Plains did not slaughter entire family groups of mammoths, but rather hunted or scavenged mammoths on an individual basis. However, additional analyses of mammoths from other regions must be undertaken before we can determine whether this holds true for all Clovis sites containing multiple mammoths.

The isotopic patterns of Clovis mammoths also provide information about the paleoecology of these animals. The fact that Dent mammoths have $^{87}Sr/^{86}Sr$ ratios that are distinct from those of other Clovis mammoths demonstrates that the Dent animals belonged to a separate, distinct population. This suggests that Clovis mammoths did not routinely migrate between Dent and the other Clovis sites, a distance ≥ 600 km. Further information about mammoth movement patterns is provided by the Blackwater Draw mammoths, which appear to have belonged to two separate populations. One population (Blackwater-A) displays $\delta^{13}C$ values, $\delta^{18}O$ values, and $^{87}Sr/^{86}Sr$ ratios similar to those seen in mammoths from Miami, which is approximately 250 km away from Blackwater Draw. The other Blackwater mammoths (Blackwater-B) have isotope ratios that suggest they ranged into the Rocky Mountains, a distance of at least 200 km from the site. Taken together these patterns suggest that mammoths may have typically ranged over distances of a few hundred kilometers, but less than 600 km. These results are consistent with previous studies of the migration patterns of late Pleistocene mammoths (Hoppe et al. 1999), which demonstrated that Florida mammoths did not undertake long-distance (≥ 500 km) migrations. However, it remains possible that the seeming mobility of Clovis mammoths across distances of several hundred kilometers represented atypical behavior induced by local climatic stresses, such as drought, or growing human predation.

The fact that at least some mammoths appear to have migrated distances of several hundred kilometers has important ramifications for studies that seek to use isotopic signals in mammoths to reconstruct local climatic conditions. Although such analyses may provide useful information in regions where climates were spatially homogeneous, they may prove misleading in regions where climates differed greatly on a relatively small geographic scale (e.g., at sites in or near mountainous terrain). Additionally, analysis of the Waco family-group mammoths demonstrates that even closely related individuals can exhibit a wide range of $\delta^{18}O$ values. Thus, although $\delta^{18}O$ values from multiple mammoths at a single site probably provide a robust estimate of the population mean, the statistical (and climatic) significance of differences among the $\delta^{18}O$ values of a limited number of individuals per site is suspect.

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