

The isotopic ecology of late Pleistocene mammals in North America

Part 1. Florida

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Abstract

Mammoths and mastodons are common in Pleistocene deposits, yet these proboscideans and many other animals disappeared suddenly $\approx 10,000$ years ago. In this study, we reconstruct the diets of proboscideans and associated mammals through isotopic analysis of carbonate in tooth enamel apatite in order to test nutritional hypotheses for late Pleistocene extinction. We analyzed specimens from six sites in Florida, ranging from full glacial ($> 21,000$ BP) to late glacial (14,750 to 10,000 BP) age. The oxygen isotope composition of mammalian apatite covaries with meteoric water composition, which in turn varies with climate. Consequently, oxygen isotope analysis can be used to assess the potential for time-averaging or mixing of specimens from different geographic regions within fossil assemblages. The carbon isotope composition of an herbivore is controlled by the isotopic composition of the plants that it ingests. Carbon isotope analysis reveals that mastodons ate chiefly C_3 plants, presumably trees, shrubs and herbs, whereas mammoths consumed chiefly C_4 grass. Several nutritional hypotheses for late Pleistocene extinction entail the assumption that extinct taxa had specialized diets. The resource partitioning and focused feeding preferences of Florida's proboscideans corroborate this assumption, but they do not, in themselves, prove that nutritional stress was the cause of the late Pleistocene extinction. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The deglaciation following the last glacial maximum coincided with global ecological changes, including the extinction of many large animals (Martin

and Wright, 1967; Martin and Klein, 1984; Webb and Barnosky, 1989). For example, there are only two living proboscidean species, the African elephant (*Loxodonta africana*) and the Asian elephant (*Elephas maximus*), yet in the late Pleistocene, three different families of proboscideans roamed North America (Kurtén and Anderson, 1980). Mammutids, represented by the mastodon, *Mammuth americanum*, ranged across North America in the Pleistocene, but were most common in the eastern United States (Kurtén and Anderson, 1980; King and Saunders, 1984; Webb, 1992). Elephantids were represented by

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two species of mammoth: *Mammuthus columbi*, which ranged from southern Canada to Mexico, and *M. primigenius*, which ranged from Alaska to the northern United States. The Gomphotheriidae were common in the Miocene and Pliocene, but by the late Pleistocene only *Cuvieronius obliobunus* occurred in North America, though it and other gomphotheres occurred in Central and South America (Kurtén and Anderson, 1980; Webb, 1992).

Despite their abundance and wide range in North America, by 10,000 years ago proboscideans had disappeared, along with many other large animals (Meltzer and Mead, 1985; Beck, 1996). Two types of theories have been offered for this extinction. Some scholars attribute the extinction to a new predator, humans hunters (Martin, 1984). The overkill hypothesis is supported by the synchrony of extinctions with the arrival of large numbers of humans in North America, by the presence of tools capable of killing and rendering large mammals, and by the presence of butcher sites for some species (Martin, 1984; Webb and Barnosky, 1989). Yet, the lack of butcher sites for other species, the overall scarcity of butcher sites, and doubts about the role of large game hunting in human ecology have led some to conclude “that Paleoindian hunting was not the prime cause of, and perhaps did not even contribute to, the terminal Pleistocene extinctions” (Meltzer, 1993).

Researchers who doubt the role of hunting often attribute the extinctions to climatic and ecological change, particularly to nutritional stress induced by rapid changes in plant communities. If megafauna had coevolved with unique, high-diversity floras during the glacial and interstadial intervals, then the rapid floral change at the start of the interglacial may have created a nutritional ‘bottleneck’ for animals that could not adapt quickly to new floras (Guthrie, 1984; Graham and Lundelius, 1984; King and Saunders, 1984). Graham and Lundelius (1984) posit that the high diversity of herbivores in the Pleistocene of North America could only coexist in a tightly co-evolved system of resource partitioning, analogous to the grazing succession of African savannas. They argue that floral change would disrupt resource partitioning, leading to decreased diet quality and increased competition among herbivores, both of which would contribute to extinction. Guthrie (1984) offers a different dietary hypothesis, based on the assertion

that floral diversity was higher and growing season was longer in glacial and interstadial intervals than in the Holocene. He argues that to avoid large doses of plant toxins and to obtain an adequate supply of nutrients, animals that ferment food in their hind-gut (such as proboscideans, equids and tapirs) had to consume a wide array of plants. With shorter growing seasons and lower diversity floras in the Holocene, these organisms could not obtain the diverse mixture of plants they needed to survive.

Nutritional hypotheses entail assumptions about the diets of extinct fauna. The models of King and Saunders (1984) and Graham and Lundelius (1984) imply that extinct taxa were dietary specialists, adapted to a limited set of plant assemblages that could not be found in the Holocene. Graham and Lundelius’ (1984) model requires strong resource partitioning, which should be conspicuous between closely related, sympatric taxa of similar size. Guthrie (1984) hypothesis implies a different type of specificity, namely that extinct megafauna were obligate mixed-feeders.

Living elephants match neither pattern. African and Asian elephants live in a diverse array of ecosystems, where they subsist on floras that differ widely in composition and diversity (Owen-Smith, 1988; Sukumar, 1989). Some savanna elephants eat almost exclusively grass throughout the year, tropical forest elephants consume chiefly trees and shrubs, whereas other populations eat seasonally variable mixtures of grasses, trees and herbs. All the individuals in a population may have similar diets, or different groups within the population may have different diets. Modern elephant do not have diets as specialized as those implied by Graham and Lundelius’ (1984) model for extinct herbivores. Also, while some modern elephants are mixed-feeders, as Guthrie’s (1984) model entails for extinct herbivores, they are not obligate mixed-feeders. Modern elephants are opportunists, capable of living on nearly any dietary mixture. If Pleistocene proboscideans showed a similar level of opportunism, they seem unlikely victims of nutritional stress due to floral change.

Mammoths and mastodons have been interpreted as dietary specialists. Mastodons had relatively low-crowned molars with cusps arrayed in widely spaced lophs and high relief on the occlusal surface prior to heavy wear. This dental morphology and rare finds

of digesta led to the classification of mastodons as browsers (i.e., animals that fed primarily on leaves, twigs, bark and herbs) (Haynes, 1991; Webb et al., 1992). Mammoths had high-crowned molars with closely spaced enamel lophs coated with cementum, producing a ‘washboard’ occlusal surface. This tooth morphology and rare finds of mammoth digesta led to the classification of mammoths as grazers (i.e., animals that fed primarily on grass) (Maglio, 1973; Davis et al., 1985; Ukraitseva, 1993). Yet mammoth teeth are similar to the teeth of the opportunistic African and Asian elephants. Haynes (1991) notes that the high-crowned, ‘washboard’ teeth of elephants and mammoths “may permit a herbivore to eat an abrasive diet such as grasses, but clearly do not require such a diet.” In this study, the diets of Pleistocene mammals from Florida are assessed using carbon isotope analysis to test nutritional hypotheses for extinction.

1.1. Paleocology and paleoclimatology of Florida

The carbon isotope composition of herbivores is chiefly controlled by the photosynthetic pathway (C_3 , C_4 , CAM) of food plants, and the distribution of plants using these pathways is influenced by climate. Florida has a humid, subtropical climate, with ≈ 1400 mm of rain/year and mean annual temperatures ranging from $\approx 25^\circ\text{C}$ in the south to $\approx 20^\circ\text{C}$ in the north (Chen and Gerber, 1990). Temperate hardwood forests, pine forests and dry prairies occur in northern and central Florida. Scrub vegetation (scrub oak, rosemary, sand pine) occurs in dry, sandy, upland sites in central Florida. Southern Florida has tropical vegetation with a mixture of marsh, woodland and coastal ecosystems (Myers and Ewel, 1990). Today, $\approx 80\%$ of the grass species in southern Florida are C_4 plants; the remaining 20% are C_3 . The percentage C_4 grasses declines to the north such that only 55% of the grasses in Alabama are C_4 (Teeri and Stowe, 1976). Among sedges, 41% are C_4 in southern Florida in contrast to 18% in Alabama (Teeri et al., 1980). C_4 dicots are rare in Florida, as are plants using CAM photosynthesis, which occurs in cactuses, some upland herbs and epiphytes (Szarek and Ting, 1977; Stowe and Teeri, 1978; Teeri et al., 1978).

Lower sea level during the last glacial maximum ($\approx 25,000$ to 21,000 BP³) doubled the area of Florida (Fig. 1) and lowered water tables across the state (Watts and Hansen, 1988). Pollen analysis indicates that northern Florida supported pine forest mixed with broad-leafed trees and upland herbs, whereas pine forest and oak-herb scrub alternated in southern Florida. Pine and herbs may have dominated drier upland habitats, and broad-leafed trees may have dominated wetter habitats, but this interpretation cannot be tested through pollen analysis (Watts and Hansen, 1988). The importance of dune and upland herbs and the lack of mesic trees implies that Florida’s climate was more arid during the last glacial maximum (Watts and Stuiver, 1980; Watts and Hansen, 1988, 1994).

As the ice sheets retreated, the climate and vegetation of Florida changed as well. In southern Florida, pine dominated from 16,750 to 15,000 BP, with less abundant oak, hickory, elm and juniper/cypress. Oak forest/scrub and prairie developed by $\approx 14,000$ BP and persisted until ≈ 5750 BP, when pine forests and swamps expanded (Watts and Hansen, 1988, 1994). In northern Florida, broad-leafed mesic trees dominated from 17,500 to 14,500 BP, followed by pine and upland herbs from 14,500 to 11,500 BP. Finally, the oak forest/scrub and prairie vegetation of the early Holocene was replaced by pine forests and swamps in the late Holocene (Watts and Hansen, 1988). These patterns have been viewed as evidence that the late glacial and Holocene were wetter than the last glacial maximum, with maximum moisture in late Holocene (Watts and Hansen, 1988).

1.2. Carbon isotopes and vertebrate paleoecology

The carbon isotope value ($\delta^{13}\text{C}$)⁴ of carbonate apatite ($\text{Ca}_5[\text{PO}_4\text{CO}_3]_3[\text{OH},\text{CO}_3]$), the mineral in tooth enamel, reflects the isotopic composition of food, offset by a diet-tissue fractionation (DeNiro

³ BP refers to years before AD 1950. Radiocarbon years were converted to years BP using CALIB 3.0 (Stuiver and Reimer, 1993).

⁴ $\delta^{13}\text{C} = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}} \div ({}^{13}\text{C}/{}^{12}\text{C})_{\text{standard}} - 1] \times 1000$, where the standard is PDB. $\delta^{18}\text{O}$ follows the same conventions, where the ratios are ${}^{18}\text{O}/{}^{16}\text{O}$ and the standard is SMOW. Units are reported in parts per thousand (‰).

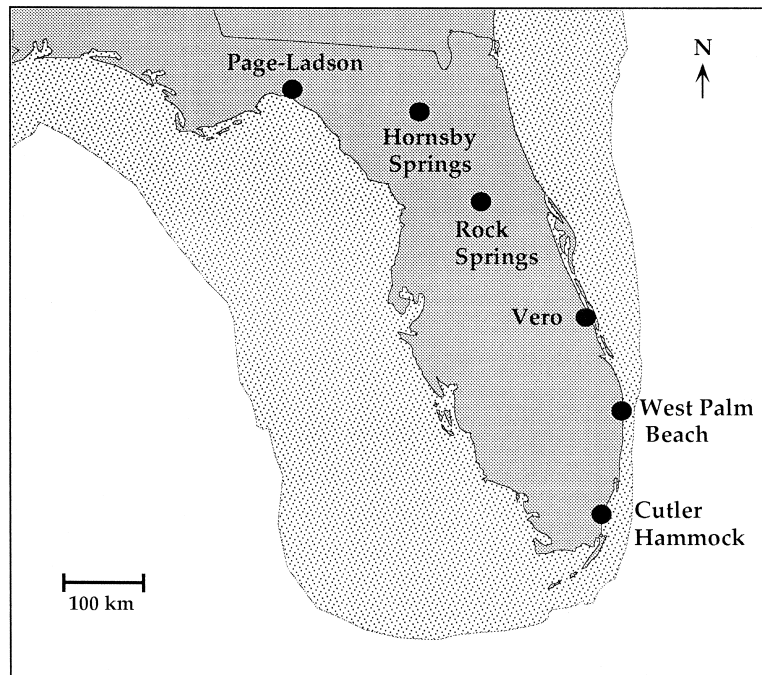


Fig. 1. Location of fossil sites. Stippled area shows the land area exposed during the last glacial maximum (from Webb, 1990).

and Epstein, 1978b; Vogel, 1978; Tieszen et al., 1979). The fractionation between diet and carbonate apatite in feeding experiments is +9 to +10‰, and the stable carbon isotope composition of apatite correlates with bulk diet (DeNiro and Epstein, 1978a; Ambrose and Norr, 1993; Tieszen and Fagre, 1993). The fractionation for wild herbivores is greater, $\approx +12$ to 13‰ (Lee-Thorp et al., 1989). This discrepancy between laboratory and field observations may relate to differences in diet quality and the extent of fermentation during digestion. To reconstruct the diets of extinct mammals, we use a diet-apatite fractionation of +13.5‰, determined between grass and grazers in Amboseli Park, Kenya (Koch et al., 1991; Bocherens et al., 1996).

The $\delta^{13}\text{C}$ of a plant depends primarily on the photosynthetic pathway used (Bender, 1968; Smith and Epstein, 1971; O'Leary, 1988). C_3 plants, which include all trees, most shrubs and herbs and grasses in cool regions and closed-canopy, tropical forests, have low $\delta^{13}\text{C}$ values ($-27 \pm 3\text{‰}$), whereas C_4 plants, which include warm/dry climate grasses, sedges and some herbs, have higher values ($-13 \pm$

2‰) (O'Leary, 1988; Tieszen and Boutton, 1989). In warm regions, grazers (C_4 -feeders) have carbonate apatite $\delta^{13}\text{C}$ values of $\approx 0.5\text{‰}$, whereas browsers (C_3 -feeders) average $\approx -13.5\text{‰}$ (Lee-Thorp et al., 1989; Bocherens et al., 1996).

Following early controversy regarding alteration of isotopic records from fossil apatite, it was demonstrated that while bone and dentin apatite were easily altered, tooth enamel apatite retains isotopic signatures with high fidelity, particularly on late Pleistocene to Holocene time scales (Schoeninger and DeNiro, 1982; Sullivan and Krueger, 1983; Lee-Thorp and van der Merwe, 1987, 1991; Koch et al., 1997). The $\delta^{13}\text{C}$ of fossil tooth enamel has become a powerful tool in paleodietary analysis, often used to distinguish among browsers, grazers and mixed-feeders (Quade et al., 1992; Lee-Thorp et al., 1994; Morgan et al., 1994).

Isotopic reconstruction of paleodiet is complicated by several factors. First, many succulent plants use CAM photosynthesis, which yields $\delta^{13}\text{C}$ values that vary between typical C_3 and C_4 values (Ehleringer, 1989). Succulent plants are rarely a significant pro-

portion of the biomass in non-desert regions, and their current contribution to the flora of Florida is small, even in dry upland regions. Second, because C_3 grasses and sedges may be locally abundant, $\delta^{13}C$ values from animals record the *minimum* amount of grass or sedge in the diet. Non-isotopic data or isotopic information on the diets of co-occurring taxa are required to conclude that an animal with a pure C_3 diet is a browser. Third, forest-floor plants in dense woodlands have low $\delta^{13}C$ values due to mixing of atmospheric CO_2 with ^{13}C -depleted CO_2 produced by soil respiration (Medina and Minchin, 1980). For example, in a subtropical forest in China, ferns, grasses, shrubs and trees average $\approx -31\text{‰}$, and C_4 plants are absent. In open habitats from this area, ferns, trees, shrubs, herbs and C_3 grasses average $\approx -27\text{‰}$, and C_4 grasses, sedges, and herbs average $\approx -12\text{‰}$ (Ehleringer et al., 1987). As a consequence of this 'canopy effect', forest-floor browsers in dense forests have low $\delta^{13}C$ values when compared to open-country browsers (Ambrose and DeNiro, 1986; van der Merwe and Medina, 1991).

A final complication arises from changes in the $\delta^{13}C$ of atmospheric CO_2 , which is fixed by plants during photosynthesis. Addition of carbon by fossil fuel burning has decreased the $\delta^{13}C$ of atmospheric CO_2 , though this trend is offset by increases in the $\delta^{13}C$ of atmospheric CO_2 with decreasing ice volume (Friedli et al., 1986; Marino and McElroy, 1991; Marino et al., 1992). Full glacial herbivores could have apatite $\delta^{13}C$ values $\approx 0.5\text{‰}$ higher than their modern counterparts, whereas late glacial herbivores could have values as much as 1.3‰ higher. These offsets due to change in the $\delta^{13}C$ of atmospheric CO_2 are significantly smaller than differences due to dietary variation.

MacFadden and Cerling (1996) studied the isotopic ecology of Neogene herbivores from Florida. They detected the arrival of C_4 plants in Florida between 9.5 and 4.5 million years ago and explored the correlation between morphology and diet as monitored by carbon isotopes. Our studies overlap at one site (Cutler Hammock), though they did not analyze proboscideans at this locality. We will determine the generality and time depth of the patterns in resource use for late Pleistocene mammals by comparison to MacFadden and Cerling's (1996) record.

1.3. Oxygen isotopes: physiological controls and paleoclimatology

We analyzed the oxygen isotope composition of carbonate in apatite to assess the extent of geographic and time averaging in fossil assemblages. This analysis is possible because the $\delta^{18}O$ of apatite is related to the $\delta^{18}O$ of meteoric water (Longinelli, 1984; Luz and Kolodny, 1985; D'Angela and Longinelli, 1990). This relationship holds because: (1) mammals ingest meteoric water as drinking water and water in plants, (2) ingested water plays a dominant role in determining the $\delta^{18}O$ of body water, and (3) mammals form their teeth and bones at a constant temperature ($\approx 37^\circ C$) in presumed equilibrium with body water (Luz et al., 1984; Nagy, 1989). Small variations in metabolism that affect oxygen balance have little impact on the body water of large mammals (e.g., > 100 kg), thus these animals track the composition of ingested water most closely (Ayliffe et al., 1992; Bryant and Froelich, 1995).

The $\delta^{18}O$ of meteoric water varies geographically and temporally. At first order, the $\delta^{18}O$ of meteoric water is correlated with temperature, with low values in cold regions and higher values in warmer regions (Dansgaard, 1964). The $\delta^{18}O$ of meteoric water also varies seasonally, with low values in cold months and higher values in warm months. If animals drink from rivers and lakes that have not experienced significant evaporation, they will ingest a representative sample of meteoric water for the basin. These sources may vary seasonally if fed by runoff; if fed by groundwater, they are should be largely invariant (Fritz, 1981; Gat, 1981a,b). The water in plants, the other important source of ingested water, is similar in composition to surface water, except for the water in leaves. Leaf water may be ^{18}O -enriched due to preferential loss of ^{16}O via evapotranspiration (Gonfiantini et al., 1965). The effect is substantial in arid regions, but its impact decreases with increasing humidity (Dongmann et al., 1974).

Because of the link between climate, meteoric water $\delta^{18}O$ and apatite $\delta^{18}O$, if a locality yields fossils that display high isotopic variability, the site may contain animals that formed their teeth under different climatic regimes. The most obvious explanations would be either that the site is time-averaged, containing a mixture of glacial and interglacial mam-

mals, or that some of the animals at the site are nonresident. In this study, we will look for high variability and patterns of covariation between carbon and oxygen isotopes that might be taken as evidence of either geographic or temporal mixing of faunas.

2. Materials and methods

2.1. Sample selection

We analyzed 72 specimens from six localities (Fig. 1) ranging in age from full glacial ($> 21,000$ BP) to late glacial (15,000 to 10,000 BP). At each site enamel was obtained from as many mammoths (*M. columbi*) and mastodons (*M. americanum*) as possible. A single gomphothere (*C. obligobunus*) was analyzed. At each locality, we sampled taxa with better known dietary preferences. For known browsers, we analyzed white-tailed deer (*Odocoileus virginianus*), extinct long-nosed peccary (*Mylohyus nasutus*) and extinct tapir (*Tapirus veroensis*). Extinct flat-headed peccary (*Platygonus compressus*) occurred at several sites, but this species had behavioral and skeletal adaptations suggesting a more open habitat and, perhaps, a more grass-rich diet (Kurtén and Anderson, 1980). It was not included in our analysis of browsers. For known grazers, we examined locally extinct horses (*Equus* sp.) and bison (*Bison* sp.). Samples were obtained from the collections of the Florida Museum of Natural History. Because enamel grows by accretion, we tried to sample material that formed over several years to ensure that samples reflected an average composition for the individual.

We also collected enamel representing a time-series from a mammoth tooth plate. To obtain enamel deposited during a short time in the animal's life, microsamples were drilled from shallow (< 0.5 -mm deep), thin (< 1 -mm thick) furrows parallel to growth increments on the tooth plate. From incremental banding, the microsamples are inferred to represent ≈ 2 years of growth.

2.2. Localities

2.2.1. Page-Ladson, Jefferson County

Human-modified bones and lithic artifacts in association with a variety of extinct vertebrates have

made this site the focus of much attention (Dunbar et al., 1989). Although submerged in the bed of the Aucilla River, stratigraphic analysis indicates that the site contains undisturbed deposits laid down within a small sinkhole pond. In addition to many well-preserved vertebrate fossils, this site has yielded an abundance of plant remains, some of which are thought to represent material ingested by mastodons (Webb et al., 1992). All samples analyzed in this study come from a well-constrained stratigraphic level bracketed by radiocarbon dates ranging from $12,330 \pm 120$ to $12,570 \pm 200$ ($14,410 \pm 210$ to $14,750 \pm 330$ BP). Vertebrates from this site include *Mammut*, *Mammuthus*, *Equus*, *Tapirus*, *Bison*, *Mylohyus* and *Odocoileus*, and all except *Bison* yielded tooth enamel. In addition, a *Mammuthus* molar plate was microsampled to examine subannual variation.

2.2.2. Hornsby Springs, Alachua County

This site has yielded abundant lithic artifacts mixed with fossil vertebrates (Dolan and Allen, 1961). It is located in a sinkhole in which several springheads have been active since the Pleistocene. A radiocarbon date on a freshwater shell marl provides a minimum age for the site of 9880 ± 270 ($\approx 12,300$ to $10,750$ BP). No other material suitable for dating has been recovered. The large uncertainty is due to redundancy in radiocarbon calibration in this age range. Enamel was obtained from *Mammut*, *Mammuthus*, *Equus*, *Tapirus* and *Odocoileus*.

2.2.3. Rock Springs, Orange County

Vertebrates from this inland site were recovered from the bed of a spring run, about 100 m downstream of the current springhead. Faunal analysis confirms a Rancholabrean age for the site, but no radiocarbon dates are available (Webb, 1974; Kurtén and Anderson, 1980; Wilkens, 1983). The excellent state of preservation of the fossils and their depositional setting suggest that the site may be late glacial, though mixing with older faunas cannot be excluded. As a springhead, the deposit probably accumulated during a period when water tables were high in response to deglaciation and sea level rise. We analyzed samples of *Mammut*, *Mammuthus*, *Equus* and *Tapirus*. *Mylohyus*, *Bison* and *Odocoileus* also occur at the site.

2.2.4. Vero, Indian River County

The discovery in 1915 of human remains and artifacts in association with extinct vertebrates drew early attention to this site (Weigel, 1962). Samples for this study were recovered from Vero bed 2, which has been identified as a pond or marsh deposit. Radiocarbon dates on charcoal associated with fossils range from $> 30,000$ to 8200 ± 960 ($> 30,000$ to 9000 BP). However, a stream runs through the site at present, raising the possibility that fossil material may be mixed with more recent remains. A wide variety of vertebrates have been recovered from this site; we sampled *Mammut*, *Mammuthus*, *Equus*, *Bison*, *Odocoileus* and *Mylohyus*.

2.2.5. West Palm Beach, Palm County

Converse (1973) described the fauna of this site. Radiocarbon analysis of a mastodon rib yielded a full glacial age of $21,700 \pm 900$ ($\approx 25,000$ BP; Buckley and Willis, 1972). The vertebrate fauna represents a coastal marsh community with both fresh water and terrestrial taxa. Proboscideans are the most abundant taxa in the fauna, with *Mammut*, being the most common, followed by *Mammuthus*. While *Mammut* and *Mammuthus* ranged throughout Florida, this is the only site of Wisconsinan age where *Cuvieronius* has been identified. We sampled the three proboscidean species and *Bison* for isotopic analysis.

2.2.6. Cutler Hammock, Dade County

This coastal site accumulated in a sinkhole on a small ridge of Pleistocene limestone (Emslie and Morgan, 1995). Taphonomic evidence suggests that much of the collection was accumulated in a carnivore den. The mixture of cultural artifacts and human remains with extinct fauna suggests a latest Pleistocene age of $\approx 11,000$ to 9500 BP (Carr, 1986). Although no material associated with extinct fauna was sufficiently well preserved for radiocarbon analysis, charcoal recovered from a level less than 0.5 m above strata bearing extinct fauna yields a minimum date for human presence of 9670 ± 120 (10,990 to 10,550 BP). We sampled enamel from *Odocoileus*, *Mammuthus*, *Mylohyus* and *Bison* and include data from MacFadden and Cerling (1996) in our statistical analysis and discussion.

2.3. Sample preparation and isotopic analysis

The outer layer of enamel and adhering dentin or cementum were removed with a dental drill. Enamel powder was obtained by drilling under magnification or by crushing in an agate mortar and pestle. Powders were soaked for 24 h in 1 ml 2–3% sodium hypochlorite to remove organic contaminants, rinsed 5 times in deionized water, reacted with 1 ml 1.0 N acetic acid/calcium acetate buffered solution for another 24 h to remove diagenetic carbonate minerals, then rinsed a final 5 times in deionized water and freeze dried (Koch et al., 1997).

Carbon and oxygen isotope compositions of enamel powders were determined on a VG Optima gas source mass spectrometer using an ISOCARB automated carbonate system (Department of Geosciences, Princeton University). Samples were dissolved by reaction in constantly stirred 100% phosphoric acid at 90°C. Water and carbon dioxide generated during reaction were separated cryogenically. Reaction time for each sample was greater than 7 min. Precision (1σ) for analysis of calcite and enamel apatite standards was $\leq 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Replicate analysis of enamel samples ($n = 24$) differed by 0.2‰ for carbon and oxygen. Data for all samples are reported in Appendix A.

2.4. Statistical analysis

To determine whether differences in mean value between species or within species among sites are significant, we used ANOVA, accepting the null hypothesis of no difference among means unless $p < 0.05$. To identify the sources of significant differences in mean value in these multiple comparisons, we used Scheffé's test with $\alpha = 0.05$ (Norman and Streiner, 1992). For comparison of means between two populations, we used t -tests. Statistics were calculated using Excel 5.0.

3. Results

3.1. Carbon isotope analysis

The difference in mean $\delta^{13}\text{C}$ value between mastodons and mammoths is strongly significant (t -

Table 1
Mean isotopic values and percent C₄ plants consumed by Pleistocene herbivores in Florida

Taxon	Site	N	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	Percent C ₄
<i>Mammuthus</i>					
	Page-Ladson	2	0.1 ± 0.4	30.9 ± 0.4	90 ± 3
	Hornsby Springs	1	-5.6	30.9	49
	Rock Springs	4	-3.7 ± 2.7	29.7 ± 1.6	62 to 67 ± 19
	Vero Beach 2	4	-1.9 ± 0.3	30.1 ± 1.0	75 to 79 ± 2
	West Palm Beach	2	-0.6 ± 0.4	29.3 ± 1.1	89 ± 3
	Cutler Hammock	6	-0.9 ± 1.1	30.7 ± 1.3	82 ± 8
	<i>Average</i>	19	-1.8 ± 2.0	30.2 ± 1.2	
<i>Cuvieronius</i>					
	West Palm Beach	1	-6.1	27.6	49
<i>Mammut</i>					
	Page-Ladson	4	-10.9 ± 1.0	29.5 ± 0.6	11 ± 7
	Hornsby Springs	5	-11.9 ± 0.4	30.9 ± 0.9	4 ± 3
	Rock Springs	3	-11.6 ± 0.6	30.1 ± 0.3	6 to 10 ± 4
	Vero Beach 2	3	-11.8 ± 0.9	29.4 ± 0.6	5 to 9 ± 7
	West Palm Beach	9	-10.1 ± 0.4	29.0 ± 0.7	21 ± 3
	<i>Average</i>	24	-11.0 ± 1.0	29.7 ± 0.9	
<i>Equus</i>					
	Page-Ladson	1	-5.6	29.5	47
	Hornsby Springs	2	-7.1 ± 2.3	29.3 ± 1.2	38 ± 17
	Rock Springs	2	-6.5 ± 4.1	31.7 ± 0.1	43 to 47 ± 29
	Vero Beach 2	2	-3.2 ± 0.1	31.0 ± 0.8	66 to 70 ± 1
	Cutler Hammock	4/0	-0.3 ± 0.4		86 ± 3
	<i>Average</i>	11/7	-3.7 ± 3.7	30.5 ± 1.4	
<i>Bison</i>					
	Vero Beach 2	2	-2.1 ± 2.7	28.5 ± 1.0	73 to 78 ± 19
	West Palm Beach	2	0.0 ± 0.2	30.2 ± 0.7	93 ± 2
	Cutler Hammock	4/2	-0.4 ± 2.5	29.6 ± 1.2	86 ± 18
	<i>Average</i>	8/6	-0.7 ± 2.6	29.5 ± 1.3	
<i>Tapirus</i>					
	Page-Ladson	2	-11.7 ± 0.4	26.7 ± 0.5	5 ± 3
	Hornsby Springs	1	-12.3	29.8	5
	Rock Springs	2	-13.4 ± 0.5	27.8 ± 1.0	-7 to -3 ± 3
	<i>Average</i>	5	-12.5 ± 0.9	27.8 ± 1.5	
<i>Mylohyus</i>					
	Vero Beach 2	2	-10.9 ± 0.1	28.1 ± 0.5	11 to 15 ± 1
	Cutler Hammock	3	-9.8 ± 1.4	28.6 ± 1.1	18 ± 10
	<i>Average</i>	5/4	-10.3 ± 1.4	28.4 ± 1.0	
<i>Odocoileus</i>					
	Page-Ladson	2	-12.4 ± 0.9	27.4 ± 1.3	0 ± 6
	Vero Beach 2	2	-14.3 ± 1.1	31.0 ± 0.8	-13 to -9 ± 8
	Cutler Hammock	2	-12.6 ± 0.2	31.4 ± 1.2	-1.3 ± 1.2
	<i>Average</i>	6	-13.1 ± 1.3	30.0 ± 2.3	

N is number of specimens analyzed at each site. When two numbers are given, the first is N for carbon, the second is N for oxygen. Data are means ± 1σ for N > 2. For N = 2, deviation is half the difference between the values. A range of values for percent C₄ is presented at mixed sites, which may contain glacial and interglacial individuals. Means and deviations derived from data in Appendix A.

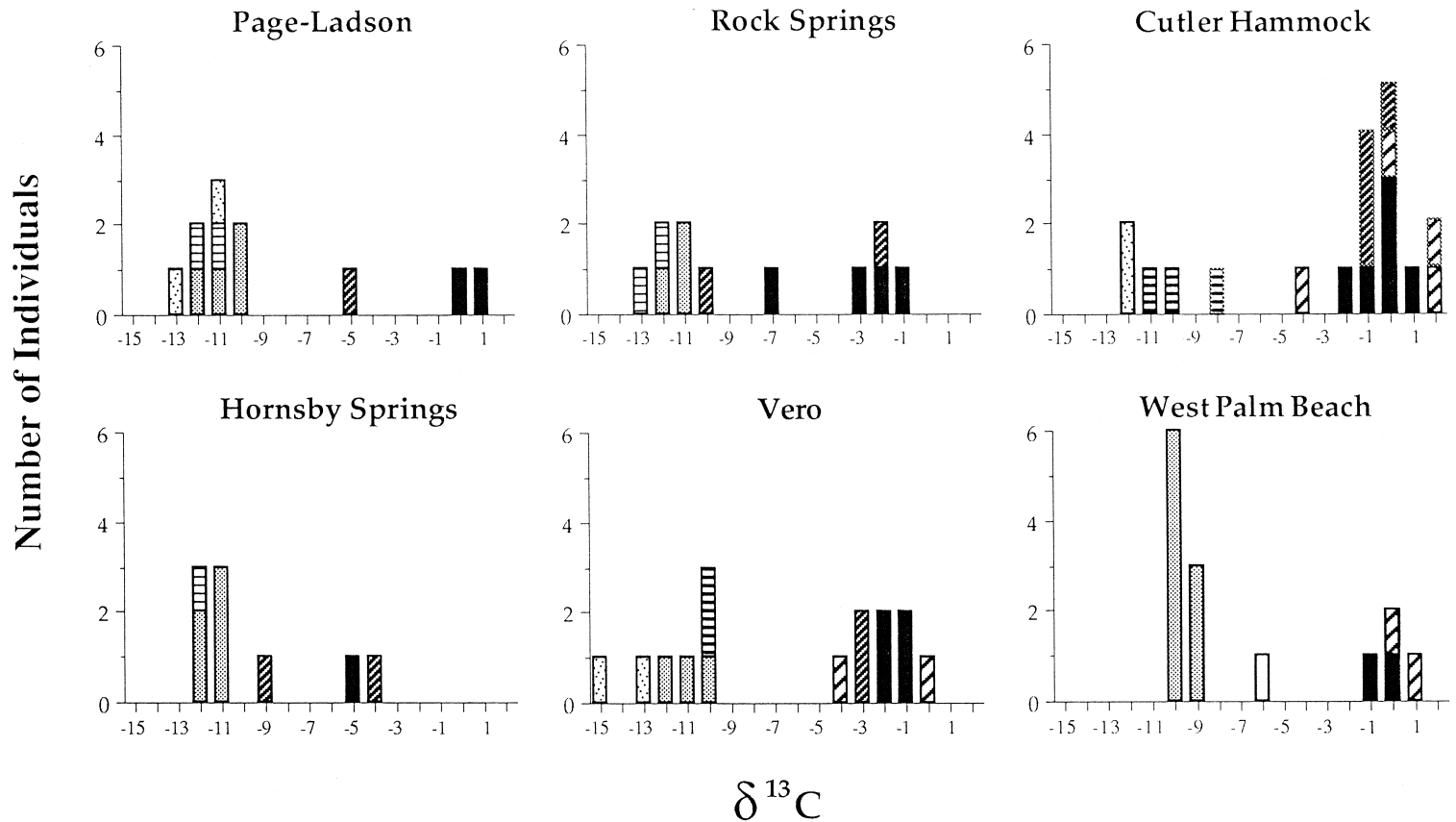


Fig. 2. Histograms of $\delta^{13}\text{C}$ values for mammalian species at each locality. ■, *Mammuthus*; ■, *Mammut*; □, *Cuvieronius*; (box with widely-spaced diagonal lines), *Bison*; (box with closely-spaced diagonal lines), *Equus*; (box with widely-spaced horizontal lines), *Mylohyus*; (box with closely-spaced horizontal lines), *Tapirus*; (box with dots), *Odocoileus*. Symbols in gray for Cutler Hammock indicate data from MacFadden and Cerling (1996).

Table 2
Isotope values of microsamples from the Page-Ladson mammoth

Distance from occlusal surface (mm)	Apatite $\delta^{13}\text{C}$	Apatite $\delta^{18}\text{O}$
1.0	-0.5	30.0
1.9	-0.6	29.5
3.0	-0.3	29.4
4.4	-0.6	30.2
5.2	-0.4	30.7
6.3	-0.7	30.6
8.7	-0.8	30.7
10.2	-0.7	30.4
12.5	-0.4	31.2
14.1	-0.3	31.8
15.7	-0.3	31.6
16.9	-0.7	31.5
Average	-0.5	30.6
+1 σ	± 0.2	± 0.8

test, $p < 0.001$). The gomphothere, *Cuvieronius*, from West Palm Beach has a value intermediate between mastodons and mammoths (Table 1, Fig. 2). When compared to presumed browsers, mastodons have a lower mean value than peccary and higher mean than deer or tapir (Table 1). The differences in mean value among all these species are significant ($F_{3,36} = 9.9$, $p < 0.001$). Differences between

mastodon and peccary and between deer and tapir are not significant (Scheffé's test, $p < 0.05$). In contrast, the differences in mean between mastodon or peccary and deer are significant, as is the difference between peccary and tapir. Tapir and mastodon are not significantly different. When compared to presumed grazers, mammoths have a lower mean than bison and a higher mean than horses (Table 1). The differences in mean value among mammoths, bison, and horses are not significant ($F_{2,35} = 3.1$, $p = 0.06$).

While different mastodon populations have generally similar $\delta^{13}\text{C}$ values (Table 1), the differences in mean value among populations are significant ($F_{4,19} = 9.4$, $p < 0.001$). The chief source of variability is the West Palm Beach mastodons, with a mean value significantly higher than all populations except Page-Ladson (Scheffé's test, $p < 0.05$). The differences in mean value among mammoth populations are marginally significant ($F_{4,13} = 3.2$, $p = 0.05$), but there are no significant differences between pairs of populations. Mammoth, horse and bison have higher within-species variability (average $1\sigma = 2.8\%$) than mastodon, tapir, deer and peccary (average $1\sigma = 1.2\%$). High within-species variability may result from higher within-site and higher among-site variation.

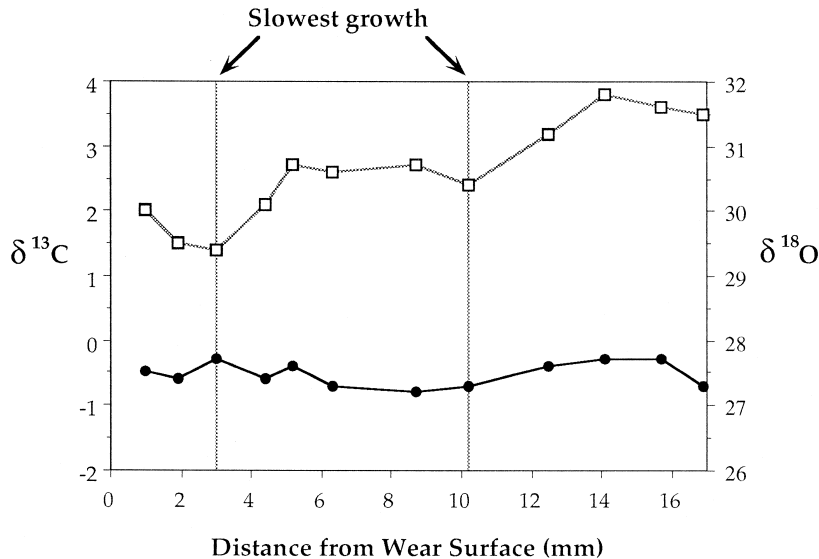


Fig. 3. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of microsamples from the Page-Ladson mammoth molar (UF 14779). ● carbon, □, oxygen.

The time series from the Page-Ladson mammoth is inferred to represent ≈ 2 years of growth (see below) (Table 2, Fig. 3). Carbon isotope values range only 0.5‰, and the mean for the samples is -0.5 ‰. If this low within-individual variability is typical, bulk samples should provide an excellent monitor of the average $\delta^{13}\text{C}$ value of an individual, especially if bulk values indicate nearly pure C_3 or C_4 diets.

3.2. Oxygen isotope analysis

Mastodons and mammoths have similar mean $\delta^{18}\text{O}$ values (Table 1). Only Vero and Rock Springs have sufficient numbers of mastodons and mammoths to test for within-site differences, and at these sites proboscideans are not significantly different (*t*-test, $p > 0.3$). The significance of the large difference in $\delta^{18}\text{O}$ between Page-Ladson mastodons and mammoths cannot be tested statistically, but a potential source for this difference is discussed below. When compared to browsers, mastodons have a higher mean value than peccary and tapir, and a lower mean than deer (Table 1). The mean values for mammoths, bison and horses range only 1.0‰. The differences in mean value among all species are significant ($F_{6,64} = 3.7$, $p < 0.005$). However, the only significant difference uncovered in multiple comparison was between tapir and mammoth (Scheffé's test, $p < 0.05$).

Since differences in $\delta^{18}\text{O}$ between mastodons and mammoths are not significant, we pooled data from these species to examine geographic and temporal patterns. Differences in $\delta^{18}\text{O}$ among late glacial proboscideans (Cutler Hammock, 30.7 ± 1.3 ‰; Hornsby Springs, 30.9 ± 0.8 ‰; Page-Ladson, 30 ± 0.9 ‰) are not significant ($F_{2,15} = 1.3$, $p > 0.3$). We lack sites to test for geographic variation during full glacial times. Temporal shifts in $\delta^{18}\text{O}$ are clear in southern Florida. The difference in mean between full glacial proboscideans of West Palm Beach (29.1 ± 0.7 ‰) and late glacial proboscideans of Cutler Hammock is significant (*t*-test, $p < 0.001$).

Microsamples from the Page-Ladson mammoth range from 29.4 to 31.8‰ (Table 2). The lowest values occur in zones of slowed accretion, which are inferred to represent winter growth (Fig. 3). In addition to oscillations in phase with growth, $\delta^{18}\text{O}$ val-

ues increase with distance from the occlusal surface (i.e., from earlier to later in the animal's life).

4. Controls on isotopic variation in Pleistocene mammals in Florida

4.1. Inferences regarding mixing in fossil assemblages

The percentage of C_4 plants in a flora is sensitive to climate (Teeri, 1979). Conclusions about the diets of Pleistocene herbivores will be affected if sites contain taxa that lived under different climatic regimes. Climatically mixed faunas could be produced if localities are time-averaged, containing both full glacial and interglacial animals. If animals in an assemblage had largely disjunct geographic ranges (i.e., some from the north and some from the south), they may have fed under different climatic regimes. Finally, specimens may be transported from distant sites to the depositional locality. We chose sites with minimal probability of post-mortem transport and attempted to choose sites with maximum temporal resolution. However, we can test for evidence of mixed-faunas through oxygen isotope analysis.

First, if localities contain animals that lived under different climates, we would expect higher within-species oxygen isotope variability than is observed in nonmigratory populations of modern species. The only modern fauna for which sufficient data are available is from Amboseli Park, Kenya (Koch et al., 1991; Koch et al., 1995; Bocherens et al., 1996). In Amboseli, the average within-species $\delta^{18}\text{O}$ standard deviation for six species (buffalo, elephant, hippopotamus, rhinoceros, wildebeest, zebra) is 1.1‰ (Bocherens et al., 1996). Data from both bone and enamel apatite are included in this calculation. The average standard deviation for grazers (buffalo, wildebeest, zebra) is ± 0.9 ‰, slightly less than the average standard deviation of ± 1.3 ‰ for browsers and mixed-feeders (elephant, hippopotamus, rhinoceros). Within-species variability exceeding 1.1 to 1.3‰ should be considered significant.

Will temporal-mixing or disjunct geographic ranges induce variability beyond 1.3‰? For temporal-mixing, if we assume that the difference between late glacial and full glacial proboscideans in southern

Florida is due solely to climate change, a shift of 1.6‰ may be typical. Glacial/interglacial changes in the $\delta^{18}\text{O}$ of meteoric water of ≈ 1 to 2‰ have been reported in other continental regions (Rozanski, 1985; Claassen, 1986; Heaton et al., 1986; Plummer, 1993). The drinking water/apatite $\delta^{18}\text{O}$ relationship for elephants has a slope of ≈ 0.9 (Ayliffe et al., 1992), therefore a 2‰ shift in drinking water corresponds to a 1.8‰ shift in apatite. Glacial/interglacial $\delta^{18}\text{O}$ shifts exceed the average within-species standard deviation for Amboseli.

Determining potential variability due to inclusion of individuals from populations with disjunct ranges is more difficult. Geographic gradients in the $\delta^{18}\text{O}$ of meteoric water are poorly constrained in the southeastern US. Plummer (1993) reports a mean $\delta^{18}\text{O}$ value for meteoric water in central Georgia ($\approx 33^\circ\text{N}$) of $\approx -4.5\text{‰}$, whereas the calculated $\delta^{18}\text{O}$ of water falling over the Everglades ($\approx 26^\circ\text{N}$) is $\approx -2\text{‰}$, though surface waters can have higher values due to evaporation (Meyers et al., 1993). If the same gradient ($\approx 2.5\text{‰}/1000$ km) applied in the Pleistocene, a 1.1‰ difference between individuals could be produced if the animals deposited tooth enamel in regions that were separated by ≈ 450 km. If steeper gradients were present or if animals ranged more widely, greater differences could be expected.

Thus, either time-averaging or mixture of individuals with disjunct ranges in fossil assemblages could increase within-species $\delta^{18}\text{O}$ variability beyond the value for modern, nonmigratory populations. Among proboscideans, only Rock Springs mammoths exceed the average deviation for Amboseli browsers, and only one other group (Cutler Hammock mammoths) exceed the average deviation for all Amboseli herbivores. None of the sites have mastodons with higher variability than modern herbivores. Among the other species, Hornsby Springs horses, Cutler Hammock bison, and deer at Page-Ladson and Cutler Hammock exceed the average modern deviation, but none exceed the average for modern browsers. There is little support from within-species $\delta^{18}\text{O}$ variability for disjunct ranges or temporal mixing, except for Rock Springs mammoths.

Between-species variation provides another clue to mixing. For large animals of similar body size, metabolic effects on the $\delta^{18}\text{O}$ of body water should be similar (Bryant and Froelich, 1995). Differences

in $\delta^{18}\text{O}$ between mastodons and mammoths from the same site may, therefore, indicate temporal mixing or differences in geographic range. Page-Ladson is the only site where average $\delta^{18}\text{O}$ values for mastodons and mammoths differ by more than 1.1‰. At Page-Ladson, both taxa are recovered from low-energy pond sediments that are tightly bracketed by radiocarbon dates, reducing the potential for temporal mixing. The relatively low $\delta^{18}\text{O}$ values for Page-Ladson mastodons, relative to Page-Ladson mammoths and the late glacial mastodons and mammoths at Hornsby Springs, may indicate that these animals spent part of the year further north, where they could have consumed ^{18}O -depleted waters. Interestingly, there is preliminary evidence from Sr isotopes supporting the suggestion that Page-Ladson mastodons may have ranged further north (Hoppe et al., 1995).

4.2. Carbon isotopes and the diets of late Pleistocene herbivores

General expectations regarding proboscidean diets are confirmed by carbon isotope analysis. Mastodons have low $\delta^{13}\text{C}$ values that cluster with those for known browsers; mammoths have high values similar to those for bison. MacFadden and Cerling (1996) obtained similar results for several Rancholabrean and Irvingtonian (≈ 1.5 Ma) mammoths and mastodons. Can we conclude from these results that mastodons were browsers? Assuming that bison and mammoths ate grass in proportion to its availability, we would conclude that C_3 grasses and sedges were rare in the late Pleistocene of Florida. However, mammoths and bison may have lived in open habitats dominated by C_4 plants, whereas mastodons may have inhabited closed forests containing C_3 grasses and sedges. Thus, we cannot conclude that mastodons consumed only browse, but we can exclude the idea that they ate significant amounts of grass from open habitats. Furthermore, analysis of mastodon digesta from the Page-Ladson site supports the conclusion that these animals consumed only browse, not C_3 grass or sedges (Webb et al., 1992).

We estimated the percentage of C_3 vs. C_4 plants in the diets of late Pleistocene mammals (Table 1, Appendix A). At most sites, mastodon and peccary consumed diets with 0 to 15% C_4 plants. West Palm

Beach mastodons are an exception; their $\delta^{13}\text{C}$ values indicate diets with $\approx 20\%$ C_4 plants. On average, mammoths and bison consumed $> 75\%$ C_4 plants, but they had more variable diets. Except at Cutler Hammock, late Pleistocene horses consumed a higher percentage of C_3 plants ($\approx 50\%$) than co-occurring grazers. This is a high proportion for a presumed grazer in an area with abundant C_4 grass. Equids at Cutler Hammock ate as much C_4 grass as bison or mammoths (MacFadden and Cerling, 1996).

Among browsers, tapir and deer have lower $\delta^{13}\text{C}$ values than mastodon and long-nosed peccary, implying a lower percentage of C_4 plants in their diets. Many deer and tapir have C_4 proportions below zero (Table 1), indicating that an assumption of the calculation is wrong. The calculation is sensitive to the diet-apatite fractionation. If we assume a greater fractionation for all herbivores (from 14.5 to 16.5‰), browsers no longer yield negative percent C_4 , but grazers yielding greater than 100% C_4 appear. The discrepancy could be alleviated if we assume that tapir and deer have a greater fractionation, and that other herbivores have the lower fractionation calculated for Amboseli herbivores. However, there is no a priori reason to expect the fractionation to vary among these taxa. A more likely explanation is that deer and tapir fed in dense, closed forests, consuming plants with unusually low $\delta^{13}\text{C}$ values due to the canopy effect. In a study of the canopy effect on a modern Amazonian food web using bone collagen, tapir had $\delta^{13}\text{C}$ values lower than other forest floor feeders, and $\approx 4\%$ lower than typical open country browsers (van der Merwe and Medina, 1991). MacFadden and Cerling (1996) analyzed several tapirs from Miocene and Pliocene faunas as old as late Clarendonian (9.5 Ma). Tapirs had the lowest $\delta^{13}\text{C}$ values in Miocene faunas, and only camelids had lower values in Pliocene faunas. If our preliminary conclusion about the source of low $\delta^{13}\text{C}$ values in tapirs is correct, browsing in dense woodlands may be an ancient pattern in tapirs, which implies, in turn, that such woodlands have been a feature of the landscape of Florida for 10 million years. The size of these forest patches is an open question. Higher $\delta^{13}\text{C}$ values in mastodon and long-nosed peccary may indicate that they fed in more open habitats, where C_4 grasses and sedges were more abundant and/or where the canopy effect was reduced.

Mammoths have higher variability in $\delta^{13}\text{C}$ values than mastodons and browsers, indicating greater mixing of C_3 and C_4 food items in their diets. There are three possible sources of this variability. First, because the percentage of C_4 grass and sedge species varies from north-to-south, the increased C_3 consumption by mammoths at Rock Springs and Hornsby Springs may reflect a greater local abundance of C_3 grass. Recall, however, that Rock Springs mammoths exhibit high within-species variability in $\delta^{18}\text{O}$ values, which may be related to mixing of individuals that lived under different climates. This hypothesis is supported by the observation that $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values covary among Rock Springs mammoths (Appendix A), suggesting that more C_3 -rich diets (low $\delta^{13}\text{C}$) were consumed under cooler climatic regimes (low $\delta^{18}\text{O}$). Finally, greater variability in the consumption of C_3 vs. C_4 plants by mammoths may indicate that they were truly mixed-feeders. However, as only individuals from northern sites ate high proportions of C_3 plants, we favor the hypothesis that mammoths were tracking climate-related changes in grassland composition.

Florida's horses are enigmatic. If mammoths and bison accurately record the proportions of C_3 vs. C_4 grass in floras, we must conclude either that most Pleistocene horses fed selectively on C_3 grasses, that they fed in microhabitats with abundant C_3 grasses and sedges, or that they fed on both grass and browse. C_3 -feeding by horses in Florida is ancient. The average $\delta^{13}\text{C}$ value for late Blancan horses in Florida is $-3.7 \pm 1.9\%$ ($n = 6$), whereas Irvingtonian horses average $-2.5 \pm 1.0\%$ ($n = 3$) (MacFadden and Cerling, 1996). Modern equids prefer grazing over browsing (Owaga, 1975; Duncan, 1992), but North American feral horses consume significant amounts of browse (Committee on Wild and Free-Roaming Horses and Burros, 1982). We view mixed-feeding as more likely, but grazing in a closed-canopy woodland cannot be ruled out as an explanation for the C_3 plants in horse diets.

If food resources were limited, it would be expected that large, sympatric, closely related herbivores would have different diets. Florida's proboscideans meet this expectation. On average, C_4 grass comprised 10 to 15% of the diet of mastodons, whereas at the sites in southern Florida, mammoths took $\approx 15\%$ C_3 vegetation. At West Palm Beach,

the gomphothere *Cuvieronius* had a value intermediate between browsers and grazers. We interpret these intermediate isotope values as evidence that this individual *Cuvieronius* was a mixed-feeder.

What can be concluded about nutritional hypotheses for late Pleistocene extinction from isotopic data? A rigorous treatment of this question can only be conducted when data from a greater geographic range of populations are in hand, but two points are clear. First, mastodon and mammoth populations exhibit more focused feeding, as measured by carbon isotopes, than modern elephant populations. These species focused on either grass or browse and different individuals in the same population had similar diets. The $\delta^{13}\text{C}$ standard deviation for Amboseli elephants is 2.1‰ for enamel apatite ($n = 6$) (Bocherens et al., 1996), similar to the value of 2.2‰ determined for a larger sample ($n = 40$) of elephant bone collagen (Koch et al., 1995). Among proboscideans, only the potentially mixed Rock Springs mammoths have a standard deviation of this size. All other Florida proboscideans have standard deviations half as large as Amboseli elephants.

Secondly, proboscideans partitioned resources and, perhaps, habitat. These observations match the predictions of Graham and Lundelius' (1984) model. Although the data do not support Guthrie (1984) hypothesis of committed mixed-feeding by extinct taxa, neither do they conclusively falsify the model. Mastodons and mammoths from Florida had focused diets, but each species did consume a small fraction (10 to 15%) of food from the alternate photosynthetic pathway. Further sampling may demonstrate that mammoths were pure grazers (i.e., that the C_3 food in their diet was grass, not browse). However, carbon isotopes cannot illuminate the diversity of browse plants consumed, yet browse is the food resource most heavily protected by toxins. Direct evidence from digesta at Page-Ladson indicates that these mastodons ate a wide diversity of plants including fruits represented by the seeds of grapes, gourds and poppies (Webb et al., 1992).

Increased geographic coverage may open both hypotheses to further attempts at falsification. If we discover that patterns of resource utilization vary greatly with geographic region, as is the case for modern elephants, we will have evidence that extinct proboscideans could subsist on different types of

plants. Such a pattern would suggest that, at the species level, extinct proboscideans were dietary opportunists, a feeding strategy consistent with neither nutritional model for extinction.

4.3. Seasonal changes in precipitation and diet

What can be concluded about seasonality of precipitation and seasonal changes in diet from molar microsamples? Minima in $\delta^{18}\text{O}$ occur in zones where growth bands are compressed due to slow growth (e.g., ≈ 3 and 10 mm) (Fig. 3, Table 2). Today, low $\delta^{18}\text{O}$ values in precipitation occur in winter (Dansgaard, 1964). Thus, oxygen isotopes suggest that tooth growth slowed in winter when food may have been scarce and energy costs for thermal maintenance were maximal. A similar pattern holds for late glacial proboscideans from the Great Lakes (Koch, 1989; Koch et al., 1989). Using oxygen isotopes and slow growth to demarcate annual increments, we estimate that this tooth was growing ≈ 7 mm/year in a dorso-ventral direction. Each sample contains enamel formed over at least 2 months.

The annual range of values for the Page-Ladson mammoth is $\approx 1.5\%$, and the total range across two-and-a-half years of growth is $\approx 2.4\%$ (Table 2). This low amplitude of seasonal variation in apatite $\delta^{18}\text{O}$ values would seem to imply little seasonal variation in meteoric water $\delta^{18}\text{O}$ values or temperature. At Hatteras, NC and Waco, TX, (the well-studied sites closest to Florida), the difference in $\delta^{18}\text{O}$ between warm and cold months is ≈ 4.5 and 7‰, respectively, corresponding to temperature differences of 17.5 and 22.5°C, respectively (Koch, 1989). However, insolation differences, climate models and other proxy data all indicate that seasonal temperature differences in the Northern Hemisphere were greater than modern at 12,000 and 9000 BP (Kutzbach et al., 1993). Thus the seasonal record of $\delta^{18}\text{O}$ from the mammoth molar must be an attenuated record of variations in precipitation $\delta^{18}\text{O}$. Attenuation could be due to hydrologic mixing prior to ingestion or by physical mixing during sample collection.

While molar microsamples, at least as sampled at present, do not record the full amplitude of seasonal variability in the $\delta^{18}\text{O}$ of ingested water, they do provide a record of season. The ability to recognize

enamel grown in different seasons is of interest for paleobiological and paleoecological questions. For example, carbon isotope data in the Page-Ladson mammoth do not differ between winter and summer, indicating the diet of this individual was relatively constant. Analysis of strontium isotope variations in concert with oxygen isotopes may indicate if proboscideans migrated seasonally between different habitats (Hoppe et al., 1995).

5. Conclusion

Oxygen isotope analysis of vertebrate apatite has been applied, with mixed success, as a potential paleoclimatic proxy. Our goals were much less ambitious. First, through analysis of within-species and between-species $\delta^{18}\text{O}$ variability, we demonstrated that most fossil assemblages show no evidence for mixing of animals that lived under different climatic regimes. In two cases (Rock Springs mammoths and Page-Ladson mastodons), oxygen isotope evidence for disjunct ranges or temporal mixing is supported by independent evidence (carbon and strontium isotopes), though the possibility of migration clearly needs further testing. Second, we used oxygen isotope variations across the molar of a mammoth to determine the season of deposition of enamel apatite, and then demonstrated that diet, as indicated by $\delta^{13}\text{C}$ values, did not change seasonally.

Carbon isotope analysis reveals that late Pleistocene proboscideans in Florida had distinct diets. Mastodons have low $\delta^{13}\text{C}$ values, indicating a diet rich in C_3 plants, presumably trees, shrubs and herbs. Mammoths have higher, more variable $\delta^{13}\text{C}$ values, indicating a diet variably enriched in C_4 grass. This might be viewed as evidence that mammoths had less specialized diets, but the fact that increased C_3 consumption only occurs in northern sites suggests that mammoths were merely tracking the proportions of C_3 vs. C_4 grass in paleofloras. Both extinct proboscidean species were more specialized feeders than modern elephants, matching the dietary predictions of Graham and Lundelius (1984) more closely than those of Guthrie (1984), but this conclusion must be viewed with caution due to the limited geographic scope of this study. Given dietary

specialization, the possibility exists that these species may have been vulnerable to dietary stress during periods of rapid floral change. Yet, even a firm demonstration that mammoths and mastodons had specialized diets would not prove that nutritional stress was responsible for their extinction, only that it was a possibility. Further study with new isotopic or paleopathologic proxies are necessary to determine whether or not extinct taxa actually suffered nutritional deprivation at the end of the Pleistocene.

Carbon isotopes also provide information about vegetation structure and habitat partitioning by mammals. Assuming bison and mammoths are nonselective grazers, the grass cover at the southern full glacial site, West Palm Beach, and the late glacial sites of Cutler Hammock and Page-Ladson was between 80 and 95% C_4 , whereas at Hornsby Springs and Vero Beach, the proportion of C_4 grass was between 50 and 80%. These differences are most likely responses to differences in climate across late glacial and full glacial Florida. Furthermore, low $\delta^{13}\text{C}$ values for tapir and deer may be interpreted as evidence of foraging in dense woodlands. This conclusion is preliminary; it must be tested by more extensive study of tapir and deer and by analysis of the extent of forest floor ^{13}C -depletion in modern woodlands. However if the preliminary result is supported, it implies that, at least in patches, trees and shrubs occurred in dense forests with closed canopies, and not just as widely scattered individuals in a more open, mixed woodland/grassland ecosystem. Isotopic analysis of herbivores has the potential to illuminate aspects of vegetation structure beyond the scope of palynologic methods (Watts and Hansen, 1988).

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Appendix A. Isotopic data and percent C₄ plants in diets for Pleistocene mammals from Florida

Taxon	UF no. ^a	Part ^b	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	Percent C ₄ ^c
Page-Ladson					
<i>Mammuthus</i>	14779 *	M?	-0.2	30.6	87
<i>Mammuthus</i>	14780 *	M ₃	0.5	31.3	92
<i>Mammut</i>	103505 *	M ¹	-10.0	29.2	17
<i>Mammut</i>	103570	M1?	-12.2	30.2	1
<i>Mammut</i>	148668	M1	-11.0	28.8	10
<i>Mammut</i>	148669 *	M1	-10.3	29.8	15
<i>Equus</i>	148670 *	M?	-5.9	29.5	47
<i>Tapirus</i>	92513	IM?	-12.0	27.2	3
<i>Tapirus</i>	92568	chk	-11.3	26.3	8
<i>Odocoileus</i>	92522	chk	-11.5	26.2	6
<i>Odocoileus</i>	92563	chk	-13.3	28.7	-6
Rock Springs					
<i>Mammuthus</i>	4383	frag	-3.9	27.9	60 to 65
<i>Mammuthus</i>	4473	frag	-7.4	28.8	36 to 40
<i>Mammuthus</i>	48987	frag	-1.1	31.0	81 to 85
<i>Mammuthus</i>	119828	frag	-2.4	31.2	72 to 76
<i>Mammut</i>	4385 *	P/M?	-11.2	30.5	9 to 13
<i>Mammut</i>	48986	P/M?	-12.3	29.8	1 to 5
<i>Mammut</i>	119827 *	IM ₃	-11.3	30.0	8 to 12
<i>Equus</i>	48974 *	M ₅	-10.5	31.8	13 to 18
<i>Equus</i>	48975 *	M?	-2.4	31.6	72 to 76
<i>Tapirus</i>	48970	M?	-13.8	28.8	-10 to -6
<i>Tapirus</i>	148673 *	chk	-12.9	26.8	-4 to 1
Hornsby Springs					
<i>Mammuthus</i>	987 *	dP4?	-5.6	30.9	49
<i>Mammut</i>	919	P4	-12.1	29.7	2
<i>Mammut</i>	985	M2	-11.9	30.3	4
<i>Mammut</i>	1005 *	M1	-12.3	31.8	1
<i>Mammut</i>	3356 *	M3	-11.3	31.7	8
<i>Mammut</i>	3886 *	M ₅	-11.9	30.9	3
<i>Equus</i>	4024 *	M ²	-4.5	30.5	55
<i>Equus</i>	27529 *	M ²	-9.4	28.2	21
<i>Tapirus</i>	2289	IP ¹	-12.3	29.8	1
Vero Beach Unit 2					
<i>Mammuthus</i>	8620	P/M?	-1.5	30.2	78 to 82
<i>Mammuthus</i>	8636 *	P/M?	-2.2	30.4	73 to 78
<i>Mammuthus</i>	8637	P/M?	-2.1	31.1	74 to 78
<i>Mammuthus</i>	8638	P/M?	-1.9	28.7	75 to 79
<i>Mammut</i>	2721	P/M?	-11.8	30.0	4 to 9
<i>Mammut</i>	8622	P/M?	-12.7	29.3	-2 to 2
<i>Mammut</i>	8640	P/M?	-10.8	28.8	11 to 15
<i>Equus</i>	8099	rM?	-3.3	30.1	65 to 69
<i>Equus</i>	8100	dP ³	-3.1	31.8	66 to 71
<i>Bison</i>	8633	rP ₄	-4.9	27.5	54 to 58
<i>Bison</i>	8635B	IM ₂	0.6	29.6	93 to 97
<i>Mylohyus</i>	8590	M?	-10.8	28.6	11 to 15
<i>Mylohyus</i>	8593	M?	-10.9	27.5	10 to 15
<i>Odocoileus</i>	1872	chk	-15.3	31.9	-21 to -17
<i>Odocoileus</i>	8611	rM ³	-13.2	30.2	-6 to -2

West Palm Beach

<i>Mammuthus</i>	51197	frag	-0.1	30.4	92
<i>Mammuthus</i>	148672 *	P/M?	-1.0	28.2	86
<i>Mammut</i>	18504	rM ₂	-10.2	28.8	20
<i>Mammut</i>	18505	rM ²	-9.7	28.5	24
<i>Mammut</i>	51191 *	M ³	-10.7	29.9	16
<i>Mammut</i>	51192	M ₃	-9.6	28.0	24
<i>Mammut</i>	51194	P/M?	-10.0	29.3	21
<i>Mammut</i>	51195	P/M?	-9.5	28.3	25
<i>Mammut</i>	51196A *	P/M?	-10.4	29.5	18
<i>Mammut</i>	51196B *	P/M?	-10.2	29.4	20
<i>Mammut</i>	148671	IM ²	-10.3	29.7	19
<i>Cuvieronius</i>	55108 *	dP ₄	-6.1	27.6	49
<i>Bison</i>	51151	M ³	-0.2	30.9	91
<i>Bison</i>	17063	M ¹	0.2	29.5	95

Cutler Hammock

<i>Mammuthus</i>	148679	P/M?	-2.9	31.7	68
<i>Mammuthus</i>	148680	P/M?	0.2	30.8	90
<i>Mammuthus</i>	148681	P/M?	0.0	31.1	89
<i>Mammuthus</i>	148682	P/M?	-0.9	28.1	82
<i>Mammuthus</i>	148683	P/M?	-0.3	31.3	87
<i>Mammuthus</i>	148684	P/M?	-1.4	31.0	79
<i>Equus</i>	MCF102a	I	0.2		90
<i>Equus</i>	MCF102b	rP ^{3/4}	-0.4		86
<i>Equus</i>	MCF103	rP ₂	-0.5		85
<i>Equus</i>	MCF104	P/M?	-0.6		84
<i>Bison</i>	14685	P/M?	-4.4	30.8	57
<i>Bison</i>	14686	IP ₄	1.9	28.5	102
<i>Bison</i>	MCF98	P/M?	1.5		99
<i>Bison</i>	MCF99	P/M?	-0.5		85
<i>Mylohyus</i>	148675	M ²⁻³	-10.0	27.6	17
<i>Mylohyus</i>	148677	M ²	-11.4	29.7	7
<i>Mylohyus</i>	MCF100	rM ^{2/3}	-8.0		31
<i>Odocoileus</i>	148687	IM ₃	-12.4	30.2	0
<i>Odocoileus</i>	148688	IM ₃	-12.8	32.6	0

^aAll samples from Vert. Paleo. Collection, Florida Mus. of Nat. Hist. UF No. refers to cataloged specimens, MCF refers to uncataloged specimens from MacFadden and Cerling (1996). *Marks samples analyzed in duplicate. MCF data are italicized. ^bPart of tooth analyzed. Abbreviations: l = left, r = right, d = deciduous, I = incisor, P = premolar, M = molar, chk is a cheek tooth (upper or lower), numbers or ? refer to position in tooth row, superscript vs. subscript indicate upper vs. lower teeth. ^cPercent C₄ consumption is calculated as follows. Apatite $\delta^{13}\text{C}$ for a pure C₄ feeder equals the value for modern C₄ plants (-13‰) + the diet-apatite fractionation (+13.5‰) - the shift in $\delta^{13}\text{C}$ of atmospheric CO₂ (Δ). For late glacial times (14,000 to 10,000 BP), Δ ranges from 1.3 to 0.9‰ so we use an average of 1.1‰, whereas for full glacial times, we use $\Delta = 0.5\text{‰}$ (Marino and McElroy, 1991, Marino et al., 1992). For mixed sites, we present the range generated using both values. To calculate Δ , we assume atmospheric CO₂ = -7.6‰ today (Friedli et al., 1986). For late glacial animals, a pure C₄ feeder would have an enamel carbonate $\delta^{13}\text{C}$ of $\approx 1.6\text{‰}$, whereas a pure C₃ feeder be $\approx -12.4\text{‰}$. Finally, assuming an isotopic mass balance, the percent of C₄ vegetation consumed can be calculated using the following equation: $\delta^{13}\text{C}_{\text{apatite}} = (\delta^{13}\text{C}_{\text{pure C}_4 \text{ feeder}})(X) + (\delta^{13}\text{C}_{\text{pure C}_3 \text{ feeder}})(1 - X)$, where X is percent C₄ vegetation consumed.

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