GROWTH RATE AND DURATION OF GROWTH IN THE ADULT CANINE OF *SMILODON GRACILIS*, AND INFERENCES ON DIET THROUGH STABLE ISOTOPE ANALYSIS

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Trophic structure and interconnectedness have important implications for diversity and stability in ecosystems. While it is generally difficult to determine trophic structure and the specific prey of predators in ancient ecosystems, analysis of stable isotope ratios in tooth enamel can be used to exclude taxa from a predator's diet. This study analyzes $\delta^{13}C_{v\text{-}pdb}$ and $\delta^{18}O_{v\text{-}pdb}$ values in a canine of *Smilodon gracilis* to understand tooth growth and the preferred prey of this species. Oxygen isotope results show a 5 mm/month growth rate and a duration of growth estimated to be 16 months long. The carbon isotope results suggest consumption of animals that depended only on C_3 plants. Due to overlap in $\delta^{13}C_{v\text{-}pdb}$ values, it appears that *Hemiauchenia* and *Platygonus* may have been included in the diet of this individual of *S. gracilis*, while *Equus* and *Mammuthus* were probably excluded. Also, the mean $\delta^{13}C_{v\text{-}pdb}$ values of *S. gracilis* were more negative than the prey, which may indicate prey captured in a closed environment, or consumption of species present at Leisey 1A but not yet analyzed isotopically. This study shows that determining trophic relationships and interconnectedness within ancient ecosystems is possible.

Key Words: *Smilodon*; tooth development; diet; stable isotopes; enamel

INTRODUCTION

Trophic interconnectedness has important implications for diversity and stability in ecosystems (De Angelis 1975; Williams & Martinez 2000). For ancient ecosystems, this interconnectedness generally can only be inferred based on taxonomy and comparison to modern analogs. It is uncommon to be able to determine the specific prey of a particular predator. However, variation in the stable carbon isotope ratio in tooth enamel typically reflects differences in diet, and can be used to determine if a carnivore preferred prey that predominantly ate C_3 or C_4 plants, if both C_3 and C_4 plants are available (Lee-Thorp et al. 1989a, b). Using this technique it is possible to determine what taxa, or at least exclude particular taxa, on which a predator fed.

The Leisey Shell Pit 1A (LSP 1A) fauna from Hillsborough County, Florida provides a unique opportunity to study trophic interconnectedness in an ancient ecosystem. This fauna contains numerous herbivores that can be categorized as either C_3 or C_4 feeders (Feranec & MacFadden 2000), as well as abundant carnivores that consumed them (Berta 1995). The most common carnivore found at the LSP 1A locality was the saber-toothed felid *Smilodon gracilis* (Berta 1995). The evolution of a saber-toothed morphology in the upper canines of mammalian carnivores has evolved convergently at least four times, within the marsupials, creodonts, nimravids, and felids (Simpson 1941; Emerson & Radinsky 1980). Much of the research that has been conducted on the saber-toothed morphology in *Smilodon* has focused on determining the function of the upper canine and its use during prey capture (Simpson 1941; Gonyea 1976; Emerson & Radinsky 1980; Akersten 1985). Another line of study concentrates on determining the timing and eruption sequence for the canine in *Smilodon* and other saber-toothed carnivores (Rawn-Schatzinger 1983; Tejada-Flores & Shaw 1984; Bryant 1988, 1990). These studies have yielded information about behavior and social dynamics within the particular taxa analyzed. Stable isotope analyses provide another means for determining the growth rate and duration of tooth growth in *S. gracilis*, as well as for determining diet.

In this study, I investigate the growth rate and duration of growth in the adult canine of *Smilodon gracilis*, and determine whether it shows a preference for preying upon C_3- or C_4-feeders in the hope of determining its preferred prey by analyzing stable carbon and oxygen isotope ratios found in tooth enamel.

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BACKGROUND

Isotopes in mammals

Variation in the oxygen isotope ratio during the ontogeny of a particular tooth has been noted in many ancient animals (Koch et al. 1989; Cerling & Sharp, 1996; Fricke & O'Neil 1996; Feranec 2004). Higher oxygen isotope ratios ($^{18}O/^{16}O$) within the tooth enamel of a particular organism suggest the ingestion of water during a warmer period (summer), while lower isotope ratios suggest ingestion when the water was colder (winter). The variation in oxygen isotope ratios may also be due to differences in source for the meteoric waters, but source variation may also be temperature dependant as in the seasonal rains of the central United States arising from the Gulf of Mexico or the Pacific Ocean (Amundson et al. 1996). If the duration of tooth and enamel growth extends over many warm and cold periods (seasons), one would expect cyclic variation within the oxygen isotope ratio of enamel apatite.

The carbon isotope ratio of mammalian apatite (e.g., bone or tooth enamel) reflects the isotopic ratio in the food of the particular animal (DeNiro & Epstein 1978; Lee-Thorp et al. 1989a, b; Koch 1998). Much related research has concentrated on determining whether herbivores fed on plants that used either the C_3 or C_4 photosynthetic pathway, but carbon isotope studies also have been applied to determining the diets of carnivores (Lee-Thorp et al. 1989a, b; Bocherens et al. 1994). Because herbivore species at LSP 1A can be classified as having preference for either C_3 or C_4 plants (Feranec & MacFadden 2000), and tooth enamel reflects the isotope value of the forage (Koch 1998), it is possible to use carbon isotopes to indicate if a carnivore preferred prey that were either C_3-feeders or C_4-feeders. In herbivores, isotopic values more negative than -8.0‰ are indicative of a pure C_3 diet, values more positive than -2.0‰ indicate a pure C_4 diet, and values between -8.0‰ and -2.0‰ suggest an intermediate, or mixed, C_3-C_4 diet (MacFadden & Cerling 1996). Due to differences in fractionation of isotopes between the food and tooth enamel (Lee Thorp et al. 1989a, b), carnivores will reflect the same isotopic values as do prey. For instance, a *Smilodon* that consumes only animals having foraged on C_3 plants would display $\delta^{13}C$ values more negative than -8.0‰. Although post-depositonal diagenesis can overprint isotopic values in bone (Schoeninger & DeNiro, 1982), tooth enamel reliably reflects isotopic values derived from feeding, and very rarely undergoes diagenetic alteration (Quade et al. 1992; Wang & Cerling 1994; Koch et al. 1997).

Leisey Shell Pit 1A

The Leisey Shell Pit 1A fauna has been biochronologically and paleomagnetically dated to about 1.5 million years ago (Ma; Morgan & Hulbert 1995; MacFadden 1995). The LSP 1A fauna are ideal for this study. Specimens of both carnivore and herbivore species are abundant at this locality making trophic comparisons possible. Further, the flora remove many of the problems that can occur when interpreting plant forage type based on isotopic values. The interpretations of isotopic values for individuals within LSP 1A are such that browsing animals will have $\delta^{13}C$ values in the C_3 range (< -8.0‰), while grass-feeding animals will have $\delta^{13}C$ values in the C_4 range (> -2.0‰). These interpretations are based on previous analysis (Feranec & MacFadden 2000), what is known about the present day flora, as well as the predicted effects of climate on the isotopic values in plants during the Pleistocene.

In Florida today, nearly all present-day browse is C_3 (> 97%; Stowe & Teeri 1978), while most of the grasses and sedges are C_4 (> 63% for Poaceae, and up to 43% for Cyperaceae; Teeri & Stowe 1976; Teeri et al. 1980; Sage et al. 1999). A study of modern floral composition on a site near the LSP 1A fossil locality shows that C_3 grasses and sedges may be present, but they are generally confined to wetter areas and generally are not widespread on the landscape (Huffman & Judd 1998). Pollen studies from LSP 1A show a similar pollen record to that found today (Rich & Newsome 1995). Also, vegetation models during glacial stages suggest the spread of grasslands and an increase in dominance of grasses and sedges using C_4 photosynthesis due to decreasing CO_2 levels (Webb 1991; Ehleringer et al. 1997; Cowling 1999). This would suggest that percentages of C_3 grasses in Florida are unlikely to have been significantly greater during the past. Further, C_4 browse is rare, so it is unlikely that percentages of these type of plants have significantly changed.

Comparative Rates and Durations of Growth

The crown height of the saber-tooth in *Smilodon gracilis* is similar to modern lions and tigers. Understanding the rate and duration of growth in the canines of the modern species may also aid in the determination of those parameters in *S. gracilis*. Lions and tigers appear to utilize slightly different strategies to grow their canines. Lions (*Panthera leo*) appear to grow their canines with a slow growth rate, but have a long duration of growth. Smuts et al. (1978) showed that the

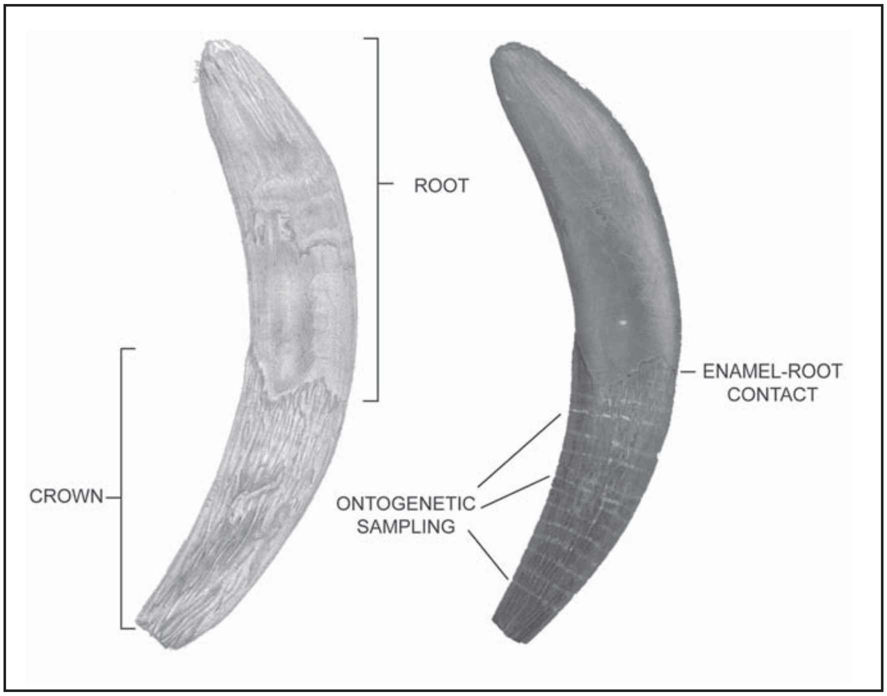

Figure 1. The upper canine of *Smilodon gracilis* (UF 87259) before and after isotopic sampling. Thirteen isotope samples were taken over 60 mm of the 80 mm length of canine enamel.

upper canine in *P. leo*, a social cat, appears in the alveoli between 9 and 11 months of age and finishes growing between 28 and 36 months. For modern lions, growth of the canines takes place between 17 and 27 months. Smuts et al. (1978) also show crown heights for individuals in Kruger National Park (KNP) to be between 37 mm and 56 mm. The fastest growth rate in the lion canines at KNP is therefore 3.3 mm/month, while the slowest growth rate is 1.3 mm/month.

In contrast to lions, tigers (*Panthera tigris*) appear to growth their canines with a quick growth rate, but have a shorter duration of growth. Mazak (1981) suggested that canines of *P. tigris*, with crown heights of up to 75 mm, are the longest in living felids. *P. tigris* canines begin to erupt between 8.5 and 9.5 months of age and finish erupting between 12 and 14 months of age (Mazak 1981). The maximal rate of growth in the canines would be between 13.6 and 30.0 mm/month if the canines began to form as the first permanent tooth (upper incisor 1) started to erupt. The minimum growth rate of the tiger canine would be 5.3 mm/month if the adult canine began to grow upon the birth of the individual.

Fossil data on the growth rate and duration of growth of canines for *Smilodon fatalis*, a closely related species from Rancho La Brea, California suggest that this particular species utilized both a quick growth rate and a long duration of growth. It appears that individuals of *S. fatalis* grew the crown of the saber-tooth at a rate up to 7mm/month and had a duration of growth of about 18 months (Feranec 2004).

METHODS

Sample Collection and Analysis

One upper canine of *Smilodon gracilis* (UF 87259) from the Leisey Shell Pit 1A locality in Hillsborough County, Florida was obtained from the Vertebrate Paleontology Collections at the Florida Museum of Natural History and was sampled for both carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope values. Mammal teeth grow and develop disto-proximally such that the distal portion of the tooth crown forms when the individual is younger, while the proximal portion of the crown forms when the individual is older. The canine was ontogenetically sampled perpendicular to the growth axis of the tooth from the enamel-root junction toward the tip of the canine. Sampling involved drilling ~5 mg of pristine enamel along visible growth increments using a 0.3 mm round tip carbide drill bit and a variable speed Dremel ™ rotary tool (Fig. 1). The pristine enamel powder was then prepared similar to the procedures described by MacFadden and Cerling (1996) and Koch et al. (1997). The powder was first treated with 30% hydrogen peroxide for 24 hours to remove organics, then decanted

Table 1. $\delta^{13}C$ values and predicted diets for the large herbivores in Leisey Shell Pit 1A. Data obtained from MacFadden and Cerling (1996), Feranec and MacFadden (2000), and Feranec (2003).

Genus	Mean $\delta^{13}C$ Value (Range)	Diet
Equus	-3.0‰ (-5.1‰ to -1.5‰)	C_4 grazer
Hemiauchenia	-6.4‰ (-8.7‰ to -3.2‰)	Intermediate Feeder
Mammuthus	-2.5‰ (-4.6‰ to -0.6‰)	C_4 grazer
Platygonus	-7.0‰ (-9.2‰ to -3.9‰)	Intermediate Feeder

and washed with distilled water, soaked in 0.1 N acetic acid for 24 hours to remove any diagenetic carbonate, decanted and washed again with distilled water, rinsed with 100% ethyl alcohol, and dried overnight. A total of 13 samples were collected and prepared from the canine.

After treatment, the samples were analyzed using an ISOCARB automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer within the Department of Earth and Ocean Sciences at the University of California, Santa Cruz. The ~1 mg samples were dissolved in 100% phosphoric acid at 90ºC to create CO_2. The results were compared using the following equation $X = [(R_{sample}/R_{standard})-1] * 1000$. Where X is the $\delta^{13}C$ or $\delta^{18}O$ value, and R = $^{13}C/^{12}C$ or $^{18}O/^{16}O$, and all isotope values are reported relative to V-PDB (Coplen, 1994). The precision for the analysis was 0.1‰ for carbon and 0.1‰ for oxygen.

Herbivores of the Leisey Shell Pit

Stable carbon isotope data for *Equus* (horse), *Hemiauchenia* (camelid), *Mammuthus* (mammoth), and *Platygonus* (peccary) from the LSP 1A locality were gathered from the literature (MacFadden & Cerling 1996; Feranec & MacFadden 2000; Feranec 2003). There were 28 total prey specimens included in this study, 7 *Equus* specimens, 10 specimens of *Hemiauchenia*, 6 specimens of *Mammuthus*, and 5 specimens of *Platygonus* (Appendix 1). Mean differences among the herbivores and between *Smilodon gracilis* and the herbivores were compared by using ANOVA and LSD tests. LSD tests are similar to t-tests but take into account multiple comparisons. Statistical analyses were run on Microsoft Excel 2000 and SPSS Student Version 8.0 for Windows, with significance set at $p<0.05$.

Table 2. Isotopic results of *Smilodon gracilis* from the Leisey Shell Pit 1A locality, Hillsborough County, Florida. Distance is given from the enamel-root contact on the anterior of the canine. All isotopic values are given relative to the V-PDB.

Sample Name	Distance (in mm)	$\delta^{13}C$	$\delta^{18}O$
RSF 0109A	6.2	-8.3	-0.4
RSF 0109B	10.9	-8.3	-0.6
RSF 0109C	17.3	-8.3	-0.7
RSF 0109D	21.9	-8.9	-0.6
RSF 0109E	27.7	-9.0	-0.4
RSF 0109F	30.6	-9.0	-0.1
RSF 0109G	33.0	-9.1	0.6
RSF 0109H	36.5	-8.9	0.2
RSF 0109I	40.8	-8.8	0.8
RSF 0109J	44.5	-8.9	0.7
RSF 0109K	48.5	-8.8	1.0
RSF 0109L	53.1	-8.8	1.3
RSF 0109M	57.3	-8.9	1.0

RESULTS

Carbon Isotope Analysis of Leisey Shell Pit 1A Herbivores

The mean $d^{13}C_{v\text{-}pdb}$ value for *Equus* was -3.0‰ with a standard deviation of 1.3‰, and a range from -5.1‰ to -1.5‰ (Table 1, Appendix 1). The mean $d^{13}C_{v\text{-}pdb}$ value for *Hemiauchenia* was -6.4‰ with a standard deviation of 2.2‰, and a range from -8.7‰ to -3.2‰. The mean $d^{13}C_{v\text{-}pdb}$ value for *Mammuthus* was -2.5‰ with a standard deviation of 1.3‰, and a range from -4.6‰ to -0.6‰. *Platygonus* had a mean $d^{13}C_{v\text{-}pdb}$ value of -7.0‰ with a standard deviation of 2.0‰, and a range from -9.2‰ to -3.9‰. *Equus* was significantly different in carbon isotope value from both *Hemiauchenia* ($p<0.001$) and *Platygonus* ($p<0.001$). *Equus* did not differ from *Mammuthus*. Stable carbon isotope values for *Mammuthus* were significantly dif-

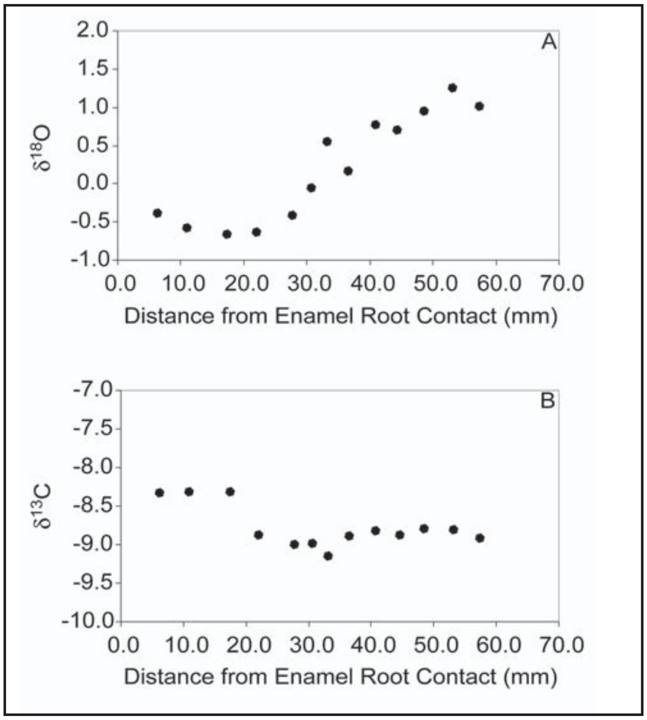

Figure 2. Oxygen (A) and Carbon (B) isotope results for *Smilodon gracilis* (UF 87259). Results suggest that nearly one year was sampled and this individual had a growth rate of about 5 mm/month. This individual also showed a preference for feeding on animals that had a strict C_3 diet.

ferent from both *Hemiauchenia* (p<0.001) and *Platygonus* (p<0.001). Stable carbon isotope values did not differ between *Hemiauchenia* and *Platygonus*.

Smilodon gracilis Oxygen Isotope Analysis

The oxygen isotope values within the *Smilodon gracilis* canine had a mean $\delta^{18}O_{v\text{-}pdb}$ value of 0.2‰ with a standard deviation of 0.7‰, and ranged from -0.7‰ to 1.3‰ (Table 2, Fig. 2a). The oxygen isotope pattern suggests enamel growth during different seasons when the water ingested was warmer (summer) and colder (winter). The pattern indicates that nearly one year was sampled, showing about 60 mm of enamel growth over the year, resulting in a growth rate of about 5 mm/month. The total length of enamel in the *S. gracilis* canine was estimated to be 80 mm implying a 16-month growth period if enamel growth rate remained constant.

Smilodon gracilis Carbon Isotope Analysis

The mean $\delta^{13}C_{v\text{-}pdb}$ value for *Smilodon gracilis* was -8.8‰ with a standard deviation of 0.3‰, and a range from -9.1‰ to -8.3‰ (Table 2, Fig. 2b). The carbon isotope values from *S. gracilis* suggest consumption of animals that depended primarily on a diet of C_3 plants. These values generally concentrate near -8.9‰, except for the last three samples when the individual was older, which concentrate near -8.3‰. The carbon isotope values do not show the same type of seasonal fluctuation, as did the oxygen isotope values. Stable carbon isotope values in *S. gracilis* were significantly different from *Equus* (p<0.001), *Hemiauchenia* (p<0.001), *Mammuthus* (p<0.001), and *Platygonus* (p<0.032).

DISCUSSION

The results from the $\delta^{18}O$ analysis in *Smilodon gracilis* shows that the rate of growth for the canine is about 5 mm/month, and it had a duration of growth of about 16 months. These results are similar to the growth rate and duration of growth found in *S. fatalis* from Rancho La Brea, which had a growth rate of about 7 mm/month and a growth period of about 18 months (Feranec 2004). Similar to *S. fatalis*, the canine of *S. gracilis* appears to have achieved its large size by having a quick growth rate and a long duration of growth.

Knowing the $\delta^{13}C$ values of this individual of *Smilodon gracilis*, and the values of some of the major herbivores of the LSP 1A Local Fauna (Fig. 3), it is possible to determine what taxa, or at least exclude taxa, on which *S. gracilis* fed. The data suggest that *S. gracilis* did not commonly feed on either *Equus* or *Mammuthus*. This result is similar to that found for *S. fatalis* and the general exclusion of *Equus* from its diet (Coltrain et al. 2004; Feranec 2004; Kohn et al. 2005). The data also suggest that *S. gracilis* differed from *Hemiauchenia* and *Platygonus*. However, there is some overlap in $\delta^{13}C$ values between this individual of *Smilodon* and for individuals of both *Hemiauchenia* and *Platygonus* (Fig. 3), so that these genera cannot be excluded from the general diet. The mean $\delta^{13}C$ value for the *S. gracilis* specimen is more negative than the mean values of the other herbivore species studied. One reason for this negative value might be due to the hunting of prey, which lived in more closed habitat. The negative values observed in the saber-tooth may reflect a closed canopy effect (van der Merwe & Medina 1991). A second reason for the negative values in *S. gracilis* might be its having eaten individuals from species that have yet to be sampled isotopically, which themselves have more negative $\delta^{13}C$ values. Species such as *Tapirus haysii*, *Palaeolama mirifica*, and *Odocoileus*

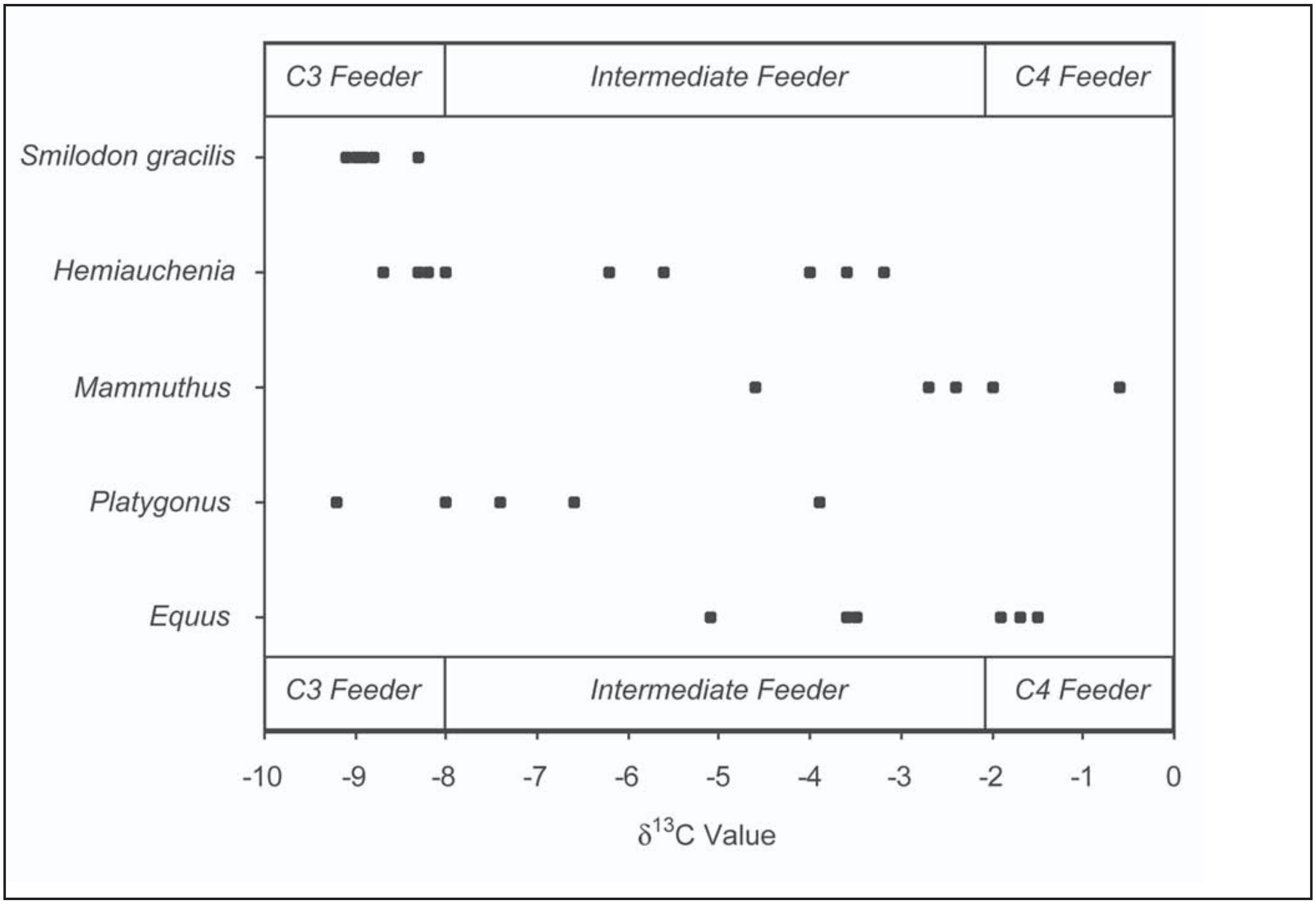

Figure 3. Comparison of the carbon isotope results of the herbivores and *Smilodon gracilis* from the Leisey Shell Pit 1A locality. These data suggest that *Equus* and *Mammuthus* were generally not included in the diet of *S. gracilis*, while *Hemiauchenia* and *Platygonus* could not be excluded from its diet due to overlap with some individual carbon isotope values.

virginianus are all known to occur at LSP 1A, are suspected to inhabit more closed canopy environments, and feed on C_3 plants (Morgan & Hulbert 1995; MacFadden & Cerling 1996; Kohn et al. 2005). To elucidate why *S. gracilis* has such negative $\delta^{13}C$ values, more isotopic analyses will need to be completed.

CONCLUSIONS

The isotopic data presented here suggests that the growth rate for the canine in *Smilodon gracilis* was about 5 mm/month, while the duration of growth was about 16 months. The data also showed that *S. gracilis* preyed upon individuals that had a strict C_3 diet, at least during the time while the adult canine of the analyzed individual was growing. Carbon isotope data from *Equus*, *Hemiauchenia*, *Mammuthus*, and *Platygonus* suggest that *Equus* and *Mammuthus* were not commonly included in the diet while the canine was forming. *Hemiauchenia* and *Platygonus* could not be excluded from the general diet of *S. gracilis*, due to overlap in carbon isotope values. Because the carbon isotope values of *S. gracilis* were more negative, in general, than many of the individual herbivores at the Leisey Shell Pit 1A locality, the data might be reflecting prey capture in a closed environment with the more negative numbers symptomatic of a canopy effect, or consumption of species that have yet to be sampled isotopically. More isotopic analyses will need to be completed to determine what is causing the negative $d^{13}C$ values in *S. gracilis*. Finally, this study shows that determining trophic relationships and interconnectedness between organisms within a particular ancient ecosystem is possible.

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Appendix 1. Sample number, Genus, UF Catalog Number, Element, and $\delta^{13}C$ value for the individual herbivores from the Leisey Shell Pit 1A locality included in this study. Abbreviations: L, Left; R, Right; M, upper molar; m, lower molar; P, upper premolar; p, lower premolar; # refers to tooth position. RSF-## refers to data from Feranec and MacFadden (2000), MCF&C ##-## refers to data from MacFadden and Cerling (1996), and RSF 00## refers to data from Feranec (2003).

Sample Number	Genus	UF Catalog Number	Element	$\delta^{13}C$ value
RSF-1	*Equus*	65461	Lm3	-1.9
RSF-2	*Equus*	65462	Lm3	-1.7
RSF-3	*Equus*	63880	Lm3	-3.6
RSF-4	*Equus*	86077	Lm3	-3.6
RSF-5	*Equus*	63876	Lm3	-5.1
RSF-7	*Platygonus*	87834	RM3	-6.6
RSF-8	*Platygonus*	63922	Lm3	-8.0
RSF-9	*Platygonus*	87830	Lm3	-9.2
RSF-10	*Platygonus*	81238	Rm3	-7.4
RSF-11	*Platygonus*	80117	Lm3	-3.9
RSF-13	*Mammuthus*	81707	Rm3	-2.7
RSF-14	*Mammuthus*	86975	Lm3	-2.4
RSF-15	*Mammuthus*	86137	Rm	-2.0
RSF-16	*Mammuthus*	86974	Rm3	-2.7
RSF-17	*Mammuthus*	67451	M3	-4.6
RSF-19	*Hemiauchenia*	64219	Lm3	-8.0
RSF-20	*Hemiauchenia*	80053	Rm3	-8.3
RSF-21	*Hemiauchenia*	142321	Lm3	-5.6
RSF-22	*Hemiauchenia*	64315	LP4	-8.3
RSF-23	*Hemiauchenia*	83964	RP4	-3.6
MCF&C 96-81	*Equus*	80047	M3	-1.5
MCF&C 96-83	*Equus*	None	Rp2	-3.5
MCF&C 96-85	*Mammuthus*	None	M plate	-0.6
RSF 0036	*Hemiauchenia*	132000	Rm3	-3.2
RSF 0037	*Hemiauchenia*	84239	LP3	-4.0
RSF 0038	*Hemiauchenia*	85085	RM	-8.7
RSF 0039	*Hemiauchenia*	80737	RP4	-8.2
RSF 0040	*Hemiauchenia*	83965	RM3	-6.2