Environmental change and seasonal behavior of mastodons in the Great Lakes region inferred from stable isotope analysis

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ABSTRACT

We investigate seasonal variations in the diet and drinking water of four Great Lakes mastodon (*Mammut americanum*) specimens using stable isotope analysis of serially sampled inner-enamel bioapatite structural carbonate ($\delta^{13}C_{sc}$, $\delta^{18}O_{sc}$), and previously published bulk analyses. Isotopic analyses and thin section measurements showed that mastodon tooth enamel extension rates (~12–4 mm/yr, decreasing toward the cervix) were lower than those of mammoths or modern elephants. Mastodons had distinct and highly regular seasonal variations in $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$, which we interpret in the context of local glacial history and vegetation changes. Seasonal variations in $\delta^{18}O$ were large but variations in $\delta^{13}C$ were small, and may have been obscured if coarser sampling methods than our inner-enamel sampling approach were used. Thus, our approach may be particularly useful for understanding relatively small seasonal changes in $\delta^{13}C$ within C_3 environments. The seasonal patterns, though not entirely conclusive, suggest that the Ontario mastodons did not migrate over very long distances. Rather, the climate and seasonal dietary patterns of mastodons within the region changed over time, from ~12,400 to 10,400 ^{14}C yr BP (~15,000 – 12,000 cal yr BP). Insights gained using these methods can contribute to a better understanding of megafaunal extinctions and Paleoamerican lifeways.

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Introduction

One of the longest-standing and most heated debates in North American archeology revolves around the causes of the late Pleistocene megafaunal extinctions. Grayson (2007) suggests that this debate is no closer to resolution than it was over a century ago, and convincingly argues that the best way forward is to construct detailed biogeographies for the individual species involved. We suggest that in addition to understanding the distributions of species through time and space, it is also important to understand the temporal and spatial variability in the *behavior* of individual species. Proboscideans have figured largely in North American extinction debates, since there is evidence for human hunting/scavenging of mammoths (*Mammuthus* spp.) and mastodons (*Mammut americanum*) and these taxa went extinct during a period of rapid climate change (e.g., Haynes, 1991, 2008; Koch and Barnosky, 2006; Fisher, 2009; Haynes, 2013; Lima-Ribeiro and Diniz-Filho, 2013). The nature of Clovis lifeways (e.g., generalist or large-game specialist) is another topic of considerable debate (e.g., Cannon and Meltzer, 2004;

Surovell and Waguespack, 2009) in which mammoths and mastodons are integrally involved. Understanding proboscidean behavior can potentially provide insight into Clovis hunting strategies as well as direct information about the environments inhabited by Clovis people.

American mastodons were abundant in eastern North American during the late Pleistocene (McAndrews and Jackson, 1988; Yansa and Adams, 2012). Fisher and colleagues have shed considerable light on mastodon behavior using analysis of tusk growth increments, including isotopic compositions (e.g., Fisher, 2009). Tusk dentin has the advantage of containing both bioapatite and collagen, but the disadvantage of poorer bioapatite preservation relative to enamel (Ayliffe et al., 1994). Only a few studies have used tooth enamel to examine the seasonal behavior of American mastodons, and despite the animals being from mixed C_3–C_4 environments these studies found little or no seasonal variability in $\delta^{13}C$ values (Koch et al., 1998; Hoppe and Koch, 2006). The use of mastodon tooth enamel to reconstruct environmental conditions and seasonal diet in the Great Lakes region remains underexplored.

In a previous publication (Metcalfe et al., 2013), we reviewed the timing of mammoth and mastodon presence in the Great Lakes region (Ontario and western New York), the local glacial history (glacial retreat, formation of glacial lakes, and fluctuations in lake levels), and the pattern of regional vegetation changes. Further, we used bulk sampling (for $\delta^{13}C_{col}$, $\delta^{15}N_{col}$, $\delta^{13}C_{sc}$, $\delta^{18}O_{sc}$) to contrast mammoth and mastodon

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ecological niches. Here, we use the inner enamel serial-sampling approach (Metcalfe et al., 2011; Metcalfe and Longstaffe, 2012) to examine mastodon seasonal behavior in Ontario and western New York during distinct time periods from about 12,400 to 10,400 ^{14}C yr BP (between 15,000 and 12,000 cal yr BP). We combine these data with relevant bulk analyses from our previous publication to make inferences about general and seasonal environmental change and mastodon behavior in the region over time.

Materials and methods

Four Ontario mastodon tooth enamel specimens were obtained from the University of Western Ontario (ON5, ON7), London Museum of Archaeology (ON9), and Royal Ontario Museum (ON14) collections, and one New York mastodon tooth enamel specimen was obtained from the Hiscock site (NY4). All teeth were adult third molars (M6 after Laws, 1966). Further sample information and bulk isotopic data for these specimens have been published previously (Metcalfe et al., 2013), and are provided in Supplementary Table 1.

Enamel was chosen for analysis because it is less susceptible to diagenetic alteration than other biogenic tissues (Ayliffe et al., 1994). Spacing of drill lines was based on studies that found growth rates in the occlusal–cervical direction of about 1–2 mm/month for *Mammuthus columbi* and *Loxodonta africana* (Dirks et al., 2012; Metcalfe and Longstaffe, 2012; Uno et al., 2013) and about 0.4 to 1 mm/month for *Palaeoloxodon cypriotes* (Dirks et al., 2012). The inner enamel surfaces (IES) of four of the specimens were serially sampled, and the structural carbonate (sc) fraction ($\delta^{13}C_{sc}$, $\delta^{18}O_{sc}$) was analyzed as described in detail by Metcalfe et al. (2011) and Metcalfe and Longstaffe (2012). To summarize, a wedge of enamel encompassing the height of the crown was removed using a Dremel circular saw blade, and placed on a stage with the IES facing up. After removing any adhering dentin with a diamond burr, a Merchantek Micromill was used to drill very shallow lines (maximum 150 μm deep) into the IES. Drill lines were perpendicular to the height of the tooth, 100 μm wide (occlusal–basal direction) and 1 mm apart. Powder from each drill line was collected and analyzed separately. This serial sampling technique provides information about seasonal variations, in contrast to the bulk sampling strategy we employed previously in studying Great Lakes proboscidean enamel (Metcalfe et al., 2013), which provides an average over multiple seasons of diet and drinking water.

Proboscidean teeth develop over a period of some years (e.g., Saunders, 1977; Metcalfe et al., 2010; Dirks et al., 2012). Enamel formation begins at the crown and mineralization progresses outwards towards the enamel surface and downwards towards the cervix (Hillson, 2005). The innermost layer of enamel is strongly mineralized during or just after its formation, while the rest of the enamel undergoes a more gradual maturation process (Allan, 1967; Suga, 1979, 1989; Tafforeau et al., 2007). Thus, the inner-enamel serial-sampling strategy employed here results in less isotopic damping of the original environmental signal (i.e., drinking water and diet isotopic compositions) than traditional strategies that sample through the entire enamel thickness (Balasse, 2003; Zazzo et al., 2005; Metcalfe and Longstaffe, 2012). Since growth/extension rates and maturation times have not been previously determined for mastodon tooth enamel, it is difficult to estimate the precise degree of damping that might occur. However, assuming a growth rate similar to other proboscideans (Dirks et al., 2012; Metcalfe and Longstaffe, 2012; Uno et al., 2013) and rapid mineralization of the inner enamel (Allan, 1967; Suga, 1979, 1989; Tafforeau et al., 2007), damping should be minimal (Passey and Cerling, 2002; Kohn, 2004).

Enamel samples in this study were not pretreated, since previous work demonstrated that there was no significant effect of pretreatment on δ-values for these samples (Metcalfe, 2011; Metcalfe et al., 2011, 2013). Enamel (~0.5 to 0.8 mg) was transferred to vials and reacted with ortho-phosphoric acid at 90°C for 25 min, using a MultiPrep automated sampling device configured so that gas was transferred only after the reaction was complete (Metcalfe et al., 2009). Isotopic measurements were obtained using an Optima isotope-ratio mass-spectrometer in dual-inlet mode, as described in Metcalfe and Longstaffe (2012).

Stable isotope results are presented in standard delta (δ) notation, in units of per mil (‰). The $\delta^{13}C_{sc}$ values were calibrated to VPDB using NBS-19 ($+1.95‰$) and Suprapur ($-35.28‰$), and $\delta^{18}O_{sc}$ values were calibrated to VSMOW using NBS-19 ($+28.6‰$) and NBS-18 ($+7.2‰$) (Coplen, 1994; Coplen et al., 2006). Accuracy was assessed for carbon using NBS-18 ($\delta^{13}C$ measured $= -4.95 \pm 0.10‰$, n = 17; accepted $= -5.0‰$) and WS-1 calcite ($\delta^{13}C$ measured $= +0.70 \pm 0.14‰$, n = 4, accepted $= +0.76‰$), and for oxygen using Suprapur ($\delta^{18}O$ measured $= +13.10 \pm 0.18‰$, n = 17, accepted $= +13.25‰$) and WS-1 calcite ($\delta^{18}O$ measured $= +26.31 \pm 0.16‰$, n = 4, accepted $= +26.23‰$) (throughout this paper, values after $\pm$ are 1 standard deviation). The average difference from the mean of duplicate analyses of enamel samples was 0.05‰ for $\delta^{13}C_{sc}$ and 0.14‰ for $\delta^{18}O_{sc}$ (n = 10).

To directly compare the serially sampled isotopic results for different mastodon individuals (which have different growth rates), the distance axis was converted to time using a simple anchor-point method, as described by Metcalfe et al. (2011). In brief, it is assumed that one period (distance between two major peaks or valleys) in the $\delta^{18}O$ curve represents one year, and that there is a constant growth rate between adjacent peaks and valleys (i.e., within each half year). The former assumption is justified in the Growth rates and sampling resolution section; the latter is an oversimplification, but allows normalization of the x-axis so that patterns in different individuals can be directly compared.

Diet $\delta^{13}C$ values are calculated from enamel using an enamel-diet fractionation factor (α) of 1.0141, where $\alpha = (\delta^{13}C_{sc} + 1000) / (\delta^{13}C_{diet} + 1000)$ (Cerling and Harris, 1999). This value of α appears to be quite consistent for large mammalian herbivores (Cerling and Harris, 1999). Drinking water $\delta^{18}O_w$ values are determined using a two-step calculation, first by converting the oxygen isotope composition of structural carbonate to its equivalent as phosphate, $\delta^{18}O_p = 0.98$ $\delta^{18}O_{sc} - 8.32$ (Bryant et al., 1996; Iacumin et al., 1996), and second by converting the $\delta^{18}O$ of phosphate to that of drinking water, $\delta^{18}O_w = (\delta^{18}O_p - 23.3) / 0.94$ (Ayliffe et al., 1992). The former equation is robust for a variety of mammalian species, and the latter is specific to elephants.

A thin section was prepared for one specimen (ON5), a mastodon third molar (M6 after Laws, 1966). A wedge of enamel approximately 30 mm long (in the occlusal–basal direction) was cut from the cervical portion of the third loph, and a thin section ~150 μm thick, oriented in the occlusal–basal direction, was prepared using the method of Metcalfe and Longstaffe (2012). Crown extension rates (growth parallel to the height of the tooth) and enamel thickness (ET) growth rates (growth perpendicular to the height of the tooth) were estimated using incremental growth features visible in thin section, as described by Metcalfe and Longstaffe (2012), after Shellis (1984). In brief, measurements are made of the angle between the enamel–dentin junction and the Striae of Retzius (D), the angle between the enamel–dentin junction and the enamel prisms (I), and the distance between cross-striations along an enamel prism (d) (Fig. 1). The daily extension rate is calculated as c = d[(sin I/tan D) − cos I] (Shellis, 1984) and the daily enamel thickness growth rate as x = d(sin I) (Metcalfe and Longstaffe, 2012).

Radiocarbon dates are from cited references, reported as ^{14}C years before present (AD 1950), $\pm 1\sigma$. Calibrated dates were obtained using OxCal version 4.2 (Bronk Ramsey, 2009) with IntCal13 (Reimer et al., 2013), and are expressed as a range calculated from the 95% probability distribution function. The midpoint of the calibrated age range is used when a single calibrated age is needed.

Comparison of strategies for assessing multi-season/annual averages

As isotopic studies become more common, investigators increasingly make comparisons among studies conducted using different methodologies. Here, we briefly compare the results of bulk enamel sampling
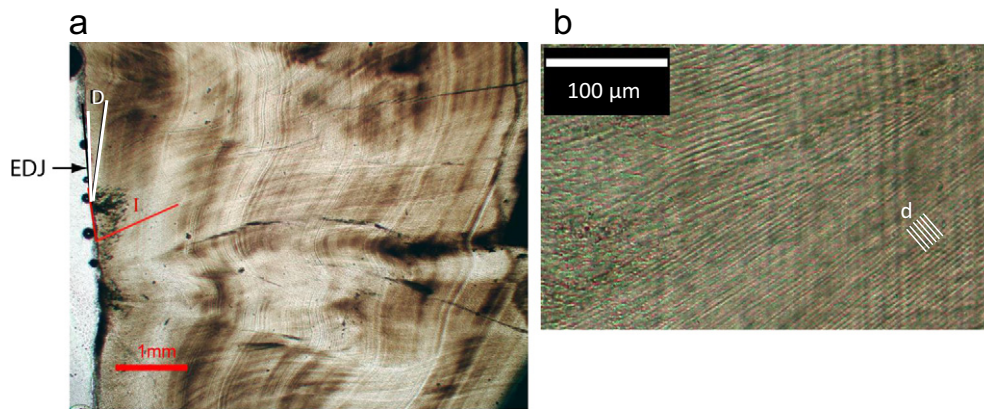
Figure 1. Photomicrographs of enamel from ON5, taken in plane-polarized light, illustrating features used for histological growth rate estimates. In these images, the enamel–dentin junction (EDJ) is towards the left, the outer enamel surface (OES) is towards the right, the occlusal surface is up and the cervix of the tooth is down. (a) Low-magnification photomicrograph of ON5 showing the angle between the enamel–dentin junction (EDJ) and Striae of Retzius (D) and between the EDJ and enamel prisms (I). (b) Higher-magnification photomicrograph illustrating cross-striation intervals, d (spaces between white lines).

employed by Metcalfe et al. (2013) with the inner-enamel serial-sampling approach employed in the present study. Our bulk sampling approach averaged several seasons of enamel growth by sampling the entire enamel thickness and >1 cm in the occlusal–basal direction (Metcalfe et al., 2013). The average over multiple seasons and years of growth can also potentially be estimated by taking the mean $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ values of all serial samples from a given specimen (i.e., data obtained in this study). For the mastodons included in this study, bulk and mean $\delta^{13}C_{sc}$ values for serial samples were positively correlated ($r = 0.9$, $n = 4$), with little or no offset between the values (on average, serial samples were 0.4‰ higher than bulk, with a range of offsets between 0.1 to 0.7‰). Bulk and mean $\delta^{18}O_{sc}$ values for serial samples were also positively correlated ($r = 0.8$, $n = 4$), but serial samples were on average 1.3‰ lower than bulk enamel $\delta^{18}O_{sc}$ values (range of offsets = 0.9 to 2.1‰). Lower mean $\delta^{18}O_{sc}$ values for serial samples were also observed in Columbian mammoths from Arizona (Metcalfe, 2011; Metcalfe et al., 2011). The reason for the offset is not clear, but may in part be related to the different mineralization rates for inner and outer enamel (Allan, 1967; Suga, 1979, 1989; Tafforeau et al., 2007). Regardless of the cause, these data highlight the importance of considering sampling methodologies when making data comparisons. In this paper, we use the serially sampled results to reconstruct seasonal changes. When discussing seasonally averaged/annual conditions, we use values obtained for bulk enamel (Metcalfe et al., 2013), since a larger number of individuals were analyzed using this method.

Results and discussion

Preservation

We previously reported multiple lines of evidence (carbonate contents, lack of correlation between carbonate contents and $\delta^{18}O$ or $\delta^{13}C$, powder X-ray diffraction and Fourier Transform Infrared Spectroscopy analysis of selected specimens) indicating excellent preservation of the enamel specimens included in this study (Metcalfe et al., 2013). In addition to those measures, thin section examination of a specimen (ON5) with similar macroscopic appearance to those used for serial sampling revealed clearly visible incremental growth features (e.g., Striae of Retzius, cross-striations) (Fig. 1). Furthermore, sinusoidal variations in the δ-values of serially sampled enamel such as we have shown here (see below) are unlikely to be produced by post-mortem alteration (Koch et al., 1989).

Growth rates and sampling resolution

The serially sampled enamel $\delta^{13}C_{sc}$ and/or $\delta^{18}O_{sc}$ values for all four mastodons exhibit regular periodicity (Fig. 2). Periods for $\delta^{18}O_{sc}$ (based on the distance between peaks or valleys) are quite consistent among individuals (11–12 mm/yr in the enamel closest to the occlusal surface and 4–6 mm/yr in the enamel nearest the cervix). In high-latitude locations, the $\delta^{18}O$ values of precipitation typically follow a sinusoidal pattern over time, with a period of one year (Rozanski et al., 1993). When such a pattern is observed in tooth enamel, it typically reflects a seasonal pattern in the $\delta^{18}O$ of drinking water (e.g., Koch et al., 1989; Kohn et al., 2002; Zazzo et al, 2005), though it is possible for non-sinusoidal input signals to produce sinusoidal patterns in enamel (Passey and Cerling, 2004). Here, we use enamel histology to test the hypothesis that one period in the $\delta^{18}O$ curve represents one year of growth.

Histology-based crown extension rate estimates (i.e., rates of growth in the occlusal-basal direction, or tooth height) made for one mastodon tooth (Fig. 1) ranged from about 5–8 mm/yr for enamel near the top of the section (i.e., about 30 mm above the cervix) to 2–6 mm/yr for enamel near the cervix (Table 1). These histological estimates are generally congruous with the estimates from isotopic analysis (above). Histological estimates that are lower than the isotopic estimates are consistent with the former including material closer to the cervix than the latter. The periods for $\delta^{18}O_{sc}$ and the histological growth rate estimates decrease towards the cervix, consistent with the general mammalian reduction in enamel growth rates near the cervix (Hillson, 2005; Smith et al., 2006) and specific observations for other proboscideans (Dirks et al., 2012). Given that the periodicity in the $\delta^{18}O_{sc}$ curve is highly regular, consistent among individuals, and generally in agreement with histological extension rate estimates, the assumption that one period in the $\delta^{18}O_{sc}$ curve represents one year of growth is supported.

The extension rates of these mastodon teeth are lower than those of African elephants (14–16 mm/yr) (Uno et al., 2013) or Columbian mammoths (estimated at 13 to 23 mm/yr by Metcalfe (2011), Metcalfe et al. (2011), and Metcalfe and Longstaffe (2012)), and at 32.3 - 62.5 µm/day (or 12–23 mm/yr) by Dirks et al. (2012). Slower growth for mastodons than mammoths or elephants supports the hypothesis of Dirks et al. (2012) that lower crowned teeth tend to have lower extension rates, both among species and within individuals. One implication of this growth rate difference is that serial samples for mastodons need to be more closely spaced than those for mammoths to obtain a similar temporal resolution.
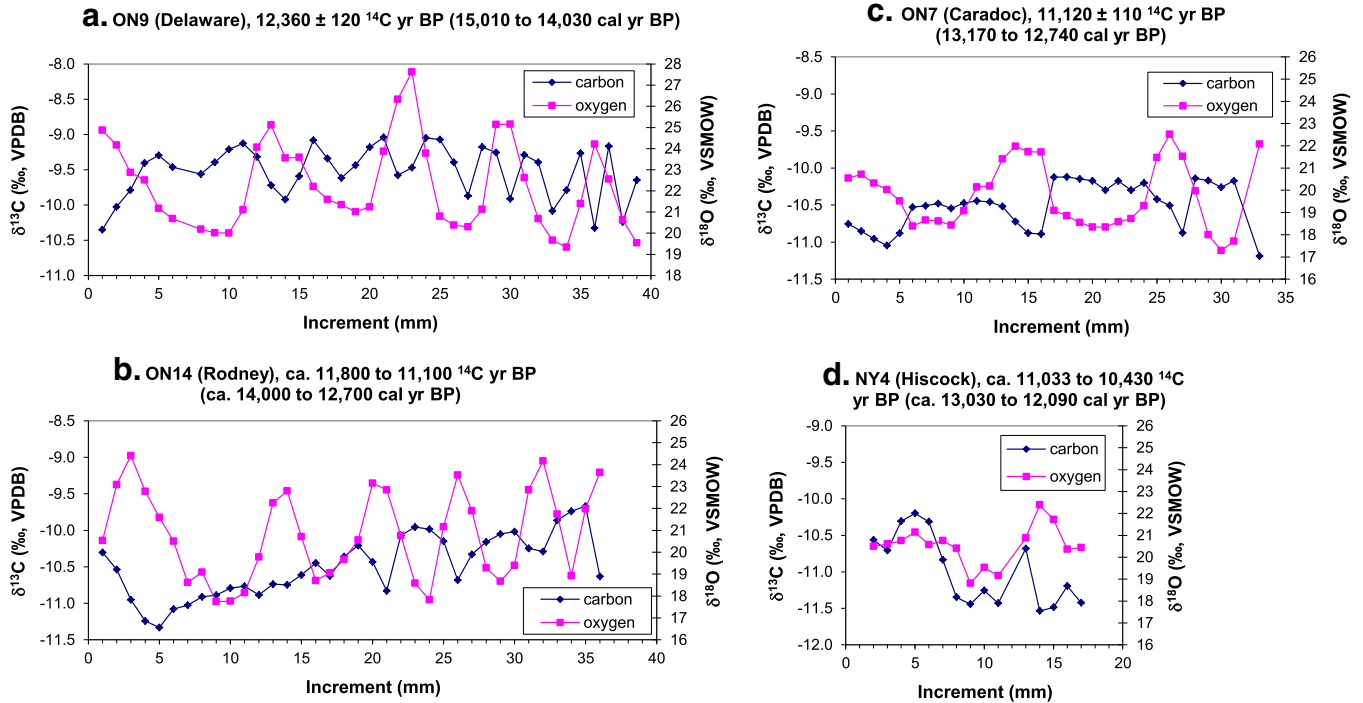
Figure 2. Carbon and oxygen isotope results for serial sampling of inner enamel from Great Lakes mastodons. Higher increment numbers are closer to the cervix.

Histological estimates of the mastodon tooth enamel growth rate through the enamel thickness (i.e., perpendicular to the height of the tooth) were 1.4 – 1.7 mm/yr (3.7 – 4.6 μm/day) in the portion of the section closer to the occlusal surface and 0.7 – 1.1 mm/yr (1.8 – 3.0 μm/day) closer to the cervix. We note that unlike extension rates, ET growth rates for this mastodon are similar to those calculated previously for a Columbian mammoth (0.8 – 1.5 mm/yr) (Metcalfe and Longstaffe, 2012). The reason for the similarity is that although mastodons can have shorter cross-striation intervals (daily secretion rates along enamel prisms, "d" in Table 1), they also have much larger angles between the enamel prisms and enamel–dentin junction ("I" in Table 1) than do mammoths (Metcalfe and Longstaffe, 2012).

Neither the enamel thickness nor the extension rate estimates presented here represent the full range of variation over the height of the tooth (since the section did not cover the entire tooth height). However, like the extension rate, the ET growth rate was lower near the cervix. From a sampling point of view, this indicates that samples drilled to identical depths could result in differential time averaging

depending on distance from the cervix. Samples drilled near the cervix would represent a longer period of time (potentially resulting in more isotopic damping), because of slowed growth in both the tooth height and enamel thickness.

Our inner enamel sampling strategy resulted in 4 to 12 analyses per year of growth in the occlusal–cervical direction. Based on a growth rate of 4 to 12 mm/yr (or 11 – 33 μm/day) in the occlusal–cervical direction, our line width of 100 μm would average about 3 to 9 days of growth. Based on our enamel thickness growth rate estimates, our drilling depth of 150 μm would integrate at most 1 to 3 months of growth (since the drill bit was V-shaped, most of the enamel was obtained from the shallowest depths, meaning the true estimate of integration is likely closer to 1 month). As argued by Kohn et al. (2002), averaging this amount of growth is not a serious problem for seasonal isotopic analysis because animals do not respond instantly to changes in environmental $\delta^{18}O$ values. Rather, oxygen residence time within the body is typically several weeks, meaning that even if we were able to sample daily growth increments, the isotopic signal would represent an integration of variations that occurred over the preceding several weeks (Kohn et al., 2002). These calculations suggest that our sampling strategy does not cause significant isotopic averaging (or, consequently, damping) above that already present because of oxygen residence time.

Additional isotopic averaging occurs because of the gradual mineralization (maturation) that occurs after initial enamel deposition (Allan, 1967; Suga, 1979, 1989; Tafforeau et al., 2007). Estimations of the degree of damping can be made if growth rates and timing/geometry of maturation (i.e., length of enamel undergoing maturation at a given time) are known (Passey and Cerling, 2002; Kohn, 2004). We have determined the former but not the latter, which are extremely difficult or impossible to measure for extinct animals (Tafforeau et al., 2007). However, if the IES is almost fully mineralized very soon after deposition, the length of maturation becomes largely irrelevant, and isotopic damping is relatively insignificant. If so, the amplitudes of seasonal signals observed in the mastodon teeth are reasonably close to (i.e., only slightly lower than) those that occurred in the diet and drinking water. Be that as it may, our interpretations below would not

Table 1
Histological measurements and growth rate estimates from photomicrographs of ON5 mastodon enamel, after Shellis (1984) and Metcalfe and Longstaffe (2012).

	Enamel region	
	Occlusal	Cervical
d (μm)	4.0–4.8	1.9–3.1
I (°)	68.7–71.6	70.3–73.4
D (°)	10.5–13.7	10.0–15.3
c (μm/day)	13.7–23.1	5.9–16.1
c (mm/yr)	5.0–8.4	2.2–5.9
x (μm/day)	3.7–4.6	1.8–3.0
x (mm/yr)	1.4–1.7	0.7–1.1

d = distance between cross-striations, measured 100–600 μm from the enamel–dentin junction (EDJ).
I = angle between enamel prisms and the EDJ, in the occlusal direction.
D = angle between Striae of Retzius and the EDJ, in the occlusal direction.
c = extension rate (occlusal–basal direction). c = d[(sin I / tan D) − cos I].
x = enamel thickness growth rate (perpendicular to tooth height). x = d(sin I).

be altered if it were shown that significant damping occurred, since they rely on comparisons among teeth from the same species sampled in the same way, and since damping can only decrease amplitudes (i.e., the large observed variations must be the result of environmental variations that were at least that large).

Migration

If mastodons migrated long distances (i.e., 1000s of km) over a period of several years, we would expect upward or downward trends in the overall pattern of δ-values, assuming that they migrated into areas with higher or lower meteoric water $\delta^{18}O$ values. For example, areas south of southwestern Ontario would likely have had higher water $\delta^{18}O$ values because of their lower latitude locations (Rozanski et al., 1993). Ingesting water with progressively higher $\delta^{18}O$ values would have caused an upward trend in the running average of enamel $\delta^{18}O$ values. In the absence of such trends in our data (Figs. 2, 3), this type of migration (or dispersal) is unlikely. Instead, annual average enamel $\delta^{18}O$ values and the large seasonal amplitudes for each Ontario individual are relatively consistent over a period of several years. This suggests that mastodons remained within a local home range where the isotopic compositions of drinking water varied seasonally in a similar fashion from year to year. In theory, this pattern could also be produced by migration between two locations with different drinking water isotopic compositions. However, the very strong similarity in both seasonal amplitudes and the actual $\delta^{18}O$ values of two presumably unrelated mastodons (ON14 and ON7) support our interpretation that these patterns reflect local variations in drinking water $\delta^{18}O$. A study of modern migratory caribou found small intra-individual differences in enamel $\delta^{18}O$ (≤ 3‰) and large variations among individuals (>5‰), even though the animals were from the same herd and lived and died within 10 yr of one another (Britton et al., 2009). Britton et al. (2009) proposed that rapid seasonal migration between areas with diverse isotopic

compositions contributed to damping the intra-individual seasonal signal, and that the extreme environmental conditions and large geographic range resulted in inconsistent $\delta^{18}O$ values among individuals. Although caribou and mastodons had very different diets, physiologies, and tooth formation/mineralization rates, the processes described by Britton et al. (2009) would have had similar effects on isotopic patterning for both species. In contrast to the results for migratory caribou, the mastodons in the present study had very large variations in $\delta^{18}O$ within individuals and strong similarities among individuals. We argue that the most likely explanation for this data pattern is that the mastodons studied here did not migrate long distances. This is not to say that they did not engage in seasonal or annual movements, but rather, that they did so within a fixed local region.

Seasonal drinking-water and enamel $\delta^{18}O$ values

The high-amplitude seasonal variations (differences between maximum and minimum $\delta^{18}O$ values within individuals, ranging from 5.5 to 8.6‰) suggest that these mastodons drank water primarily from precipitation-fed puddles, streams, or ponds rather than the much larger lakes of the Ontario, Erie, and Huron basins (see Fig. 2 in Metcalfe et al., 2013). For comparison, modern Lake Erie has monthly seasonal variations in $\delta^{18}O$ of less than 2‰, whereas monthly precipitation in the region varies by 8‰ (Huddart et al., 1999).

The drinking-water $\delta^{18}O_{water}$ values calculated from enamel $\delta^{18}O_{sc}$ range from −15.6 to −4.8‰ (Table 2, Supplementary Table 2). For comparison, the mean monthly $\delta^{18}O$ values of modern precipitation on the north shores of Lakes Erie and Ontario range from about −12 to −4‰ (Huddart et al., 1999; F. Longstaffe, unpublished data). There is considerable overlap between these ranges, with lower winter $\delta^{18}O$ values for mastodon drinking water suggesting cooler-than-modern temperatures.
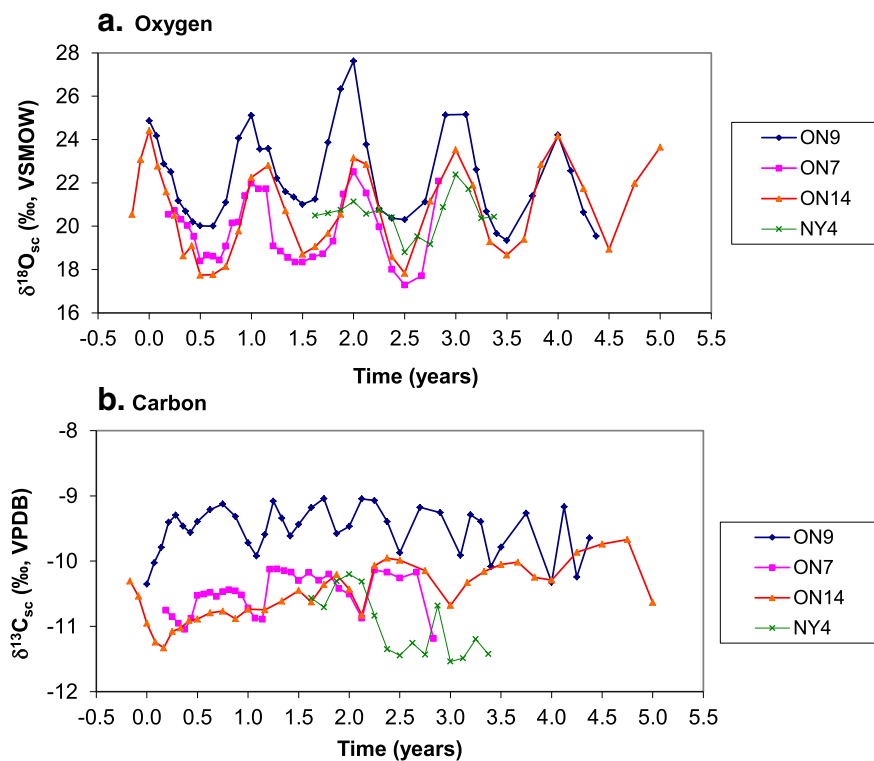

Figure 3. Comparison of carbon and oxygen isotope results for serial sampling of inner enamel from Great Lakes mastodons. To facilitate comparison, the distance axis has been transformed to time assuming one period for $\delta^{18}O_{sc}$ represents one year, as described in the text. The reference point for time is arbitrary, so although the data are stacked for comparison of seasonal trends, the true "calendar" years of formation for each sample differed.

Table 2
Summary of isotopic results for serially sampled Great Lakes mastodons.

LSIS #	Site	n	$\delta^{13}C_{sc}$ (‰, VPDB)				$\delta^{13}C_{diet}$ (‰, VPDB)				$\delta^{18}O_{sc}$ (‰, VSMOW)				$\delta^{18}O_{water}$ (‰, VSMOW)			
			Mean ± SD	Min	Max	Range	Mean ± SD	Min	Max	Range	Mean ± SD	Min	Max	Range	Mean ± SD	Min	Max	Range
ON9	Delaware	38	−9.5 ± 0.4	−10.4	−9.0	1.3	−23.3 ± 0.4	−24.1	−22.8	1.3	22.3 ± 2.1	19.3	27.6	8.3	−10.4 ± 2.2	−13.5	−4.8	8.6
ON7	Caradoc	32	−10.5 ± 0.3	−11.2	−10.1	1.1	−24.3 ± 0.3	−24.9	−23.9	1.1	19.7 ± 1.5	17.3	22.5	5.2	−13.1 ± 1.5	−15.6	−10.2	5.5
ON14	Rodney	36	−10.5 ± 0.4	−11.3	−9.7	1.7	−24.2 ± 0.4	−25.1	−23.4	1.6	20.8 ± 2.0	17.7	24.4	6.7	−12.0 ± 2.1	−15.1	−8.2	7.0
NY4	Hiscock	15	−11.0 ± 0.5	−11.5	−10.2	1.3	−24.7 ± 0.5	−25.3	−24.0	1.3	20.5 ± 0.9	18.8	22.4	3.6	−12.2 ± 0.9	−14.0	−10.3	3.7

LSIS #: Sample ID used for Laboratory for Stable Isotope Science analyses, and referred to in this study.

In high-latitude locations, the $\delta^{18}O$ values of precipitation are typically highest in summer and lowest in winter (Dansgaard, 1964; Rozanski et al., 1993). Regions close to glaciers could potentially have the reverse pattern, with the lowest $\delta^{18}O_{sc}$ values occurring because of summer influxes of glacial meltwater into the local watershed. We reject the latter possibility because the lakes of the Erie basin did not receive glacial meltwater input during most of the time that mastodons occupied Ontario (see Fig. 2 in Metcalfe et al., 2013). Furthermore, our comparison of proboscidean drinking-water $\delta^{18}O$ values to those of ancient Great Lake bottom water, modern precipitation, and modern Great Lake seasonal variations suggests that mastodon drinking water was primarily derived from precipitation, not meltwater (Metcalfe et al., 2013). Therefore, we base the interpretations that follow on the assumption that peaks in the $\delta^{18}O_{sc}$ curves represent summer and valleys represent winter. This approach is supported by analyses of mammoth and mastodon tusk dentin from southern Michigan and western New York, for which slow-growth zones (inferred winters) corresponded to minima in their serially sampled $\delta^{18}O_{sc}$ curves (Koch et al., 1989).

General and seasonal environmental changes over time

Here, we make inferences about mastodon diet and behavior at discrete moments in time, based on serial samples of inner tooth enamel (this study) and on bulk analyses for radiocarbon-dated specimens (Metcalfe et al., 2013). Plants that employ the C_3 photosynthetic pathway (i.e., almost all plants in cold-climate regions such as the Pleistocene Great Lakes) typically have $\delta^{13}C$ values less than −21.5‰ (O'Leary, 1988; Cerling et al., 1999). All four serially sampled mastodons consumed 100% C_3 diets throughout the year (calculated $\delta^{13}C_{diet}$ range = −25.3 to −22.8‰) (Table 2, Supplementary Table 2). Nevertheless, they had highly regular (albeit small) variations in $\delta^{13}C$ values. These, along with climatic inferences from other isotopic proxies, are discussed below.

Circa 12,400 ^{14}C yr BP (ca.15,000 – 14,000 cal yr BP) (ON9)

The date obtained for ON9 (12,360 ± 120 ^{14}C yr BP, AA84998, dentin collagen) (15,010 – 14,030 cal yr BP) is to our knowledge the oldest recorded for a mastodon from southern Ontario (Metcalfe et al., 2013). The date corresponds to the transition between Lake Warren and Early Lake Erie, when the land in southern Ontario was permanently exposed for the first time and virtually treeless dense tundra vegetation covered the landscape, in contrast to the open forest environment typically associated with mastodons (see Metcalfe et al., 2013 for review). Humans had probably not yet entered the region (Ellis et al., 2011).

The data for this individual are unique. The range of serially sampled $\delta^{18}O_{sc}$ values (8.3‰) is larger than those of the other Ontario mastodons (5.2 and 6.7‰), indicating greater seasonal variation in drinking water and (possibly) temperature (Table 2). Furthermore, both the $\delta^{18}O_{sc}$ maxima and minima for ON9 tend to be higher than those of the other mastodons (Fig. 3), corresponding to warmer summer and winter temperatures, greater aridity (including increased evaporation of surface and leaf waters), and/or a lower proportion of glacial meltwater input into drinking water. This fits our understanding of the environment at the time: temperatures were higher than they would be 1000 yr later (Yu, 2000), and water levels in the Erie Basin were declining as it was cut off from glacial meltwater inputs (Metcalfe et al., 2013). We note that deep ocean water was on average 1.0 ± 0.1‰ higher during the Last Glacial Maximum than it is currently, because a greater volume of low-^{18}O water was tied up in glacial ice (Schrag et al., 2002). Although deep ocean water isotopic composition cannot be related directly to surface water compositions because of differing evaporation/precipitation regimes, in theory higher $\delta^{18}O$ in oceanic source waters ultimately transported to the Great Lakes region via precipitation could also have contributed slightly to the higher $\delta^{18}O$ values of this older mastodon.

The $\delta^{13}C$ values for this individual are also generally higher than those of the other (later) mastodons (Fig. 3). This is consistent with the more open tundra vegetation that existed prior to the establishment of spruce woodlands. The landscape was dense with shrubs (including *Alnus, Dryas, Juniperus,* and *Salix*) and herbs (*Cyperaceae* and others), but there were very few trees (McAndrews and Jackson, 1988; Yu, 2000, 2003). Higher $\delta^{13}C$ values are consistent with a lack of forest canopy (van der Merwe and Medina, 1991), lower water availability (Murphy and Bowman, 2009), and higher temperatures (Tieszen, 1991). In contrast to the wetter environments occupied by later mastodons, this earlier environment may have been relatively dry, as manifested by lowered lake levels in the Erie Basin (Lewis et al., 2012). Lower atmospheric CO_2 contents during this time period may also have contributed to higher dietary plant $\delta^{13}C$ values, as in the case of European megaherbivores (Richards and Hedges, 2003; Hedges et al., 2004; Stevens and Hedges, 2004). We also note that the $\delta^{13}C$ of atmospheric CO_2 was about 0.2‰ lower between 17,000 and 12,000 cal yr BP than during the early Holocene (Leuenberger et al., 1992; Schmitt et al., 2012). This change was too small to have a significant effect on plant $\delta^{13}C$ values (Toolin and Eastoe, 1993) or on mastodons (even if they dated within this range of maximum decrease), and is not considered further.

The $\delta^{15}N_{col}$ values of ON9 (Metcalfe et al., 2013) are lower than those for individuals dating to later periods (Table 3), consistent with the greater abundance of nitrogen-fixing pioneer vegetation such as *Alnus* and *Dryas* (Hobbie et al., 2000; Yu, 2003; Makarov, 2009). Previous studies have found that European megaherbivores have low $\delta^{15}N$ values around the time of the Last Glacial Maximum, but these gradually increase during the Holocene (Richards and Hedges, 2003; Hedges et al., 2004; Stevens and Hedges, 2004). The low $\delta^{15}N$ values could predominantly reflect less developed soil conditions soon after glacial retreat (Richards and Hedges, 2003; Stevens and Hedges, 2004).

The patterns in both $\delta^{18}O$ and $\delta^{13}C$ for this individual are highly regular. We note that the variations in $\delta^{13}C$ are small (range = 1.3‰), so they would likely not be observed using sampling strategies that average longer periods of time (i.e., by drilling deeper or from the outer enamel surface). The relationship between the $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ curves is striking (Fig. 2): both the maxima and minima for $\delta^{18}O_{sc}$ (inferred summers and winters, respectively) are associated with minima for $\delta^{13}C$. In other words, the period of the $\delta^{13}C_{sc}$ curve is half that of the $\delta^{18}O_{sc}$ curve, with $\delta^{13}C_{sc}$ minima occurring twice per inferred year. To our knowledge this pattern has not been previously reported for any taxon.

Seasonal decreases in proboscidean $\delta^{13}C_{sc}$ could have been caused by a number of factors, including (1) metabolism of stored fats, (2) changes in the dietary proportions or isotopic compositions of aquatic plants, (3) changes in plant macronutrient contents (i.e., increased proportions of plant proteins and lipids relative to cellulose or carbohydrates), (4) changes in terrestrial plant taxa consumed, (5) changes in plant parts consumed, (i.e., increases in leaves relative to non-photosynthetic plant parts such as bark, roots, seeds, and fruits) and/or (6) increased

water availability and decreased water use efficiency (WUE) of plants. Each possibility is discussed further below.

(1) Winter metabolism of fat stores, which are depleted in ^{13}C (DeNiro and Epstein, 1977), has been invoked to explain the low $\delta^{13}C$ values of bulk collagen from mammoths (Bocherens, 2003; Szpak et al., 2010) and serially sampled tusk collagen from mastodons (Fisher and Fox, 2003). However, to our knowledge the effects of seasonal fat metabolism on $\delta^{13}C$ values have not been directly demonstrated. More generally, the effects of nutritional stress on animal $\delta^{13}C$ values are difficult to evaluate because studies vary widely in experimental conditions, such as organism(s) used, health status and age, type of stressor, and tissue analyzed (see McCue and Pollock, 2008 for review). For ON9, the higher $\delta^{18}O$ values relative to those in later periods (Fig. 3) suggest that winters were comparatively mild, and that greater fat metabolism is an unlikely explanation for the low $\delta^{13}C$ values. Even if fat metabolism played a role in decreasing winter $\delta^{13}C_{sc}$ values, the summer decreases would remain unexplained. We consider that explanations (2), (3), (4), (5), and (6) are more likely contributors to the seasonal pattern for this individual.

(2) Aquatic plants were consumed by mastodons (Lepper et al., 1991; Teale and Miller, 2012). Drucker et al.'s (2010) review of modern vegetation in Alaska and Canada showed that aquatic plants tended to have higher $\delta^{13}C$ values than boreal forest plants. Similarly, Severud et al. (2013) found that "floating leaf" aquatic macrophyte vegetation in northern Minnesota has $\delta^{13}C$ values on average about 4‰ higher than woody terrestrial vegetation, and Milligan (2008) found that freshwater vegetation in both Old Crow (Yukon Territory) and James Bay (Quebec) had significantly higher $\delta^{13}C$ values than terrestrial vegetation, by about 2–10‰. On theoretical grounds, Saunders et al. (2010) suggested that submerged aquatic plants available to the Brewster Creek mastodon (Illinois) would have had higher $\delta^{13}C$ values than terrestrial plants because of dissolved limestone in local water bodies. If we assume that aquatic plants had higher $\delta^{13}C$ values than terrestrial plants in Ontario around 12,400 ^{14}C yr BP (ca. 14,500 cal yr BP), the seasonal variations in ON9 could have been caused by decreases in aquatic plant consumption during both summer and winter. However, the carbon isotope compositions of aquatic plants are highly variable, ranging from about −47 to −8‰ depending on a variety of biotic and abiotic processes (Finlay and Kendall, 2007). Moreover, high rates of carbonate dissolution do not necessarily result in high $\delta^{13}C$ values for aquatic plants, in part because aquatic plants commonly utilize CO_2 derived from respiration, which produces very low $\delta^{13}C$ values (Keeley and Sandquist, 1992). For example, Pazdur et al. (1999) found that aquatic plants and algae in a karst environment of southern Poland had $\delta^{13}C$ values ranging from about −49 to −25‰, as low or lower than those of terrestrial C_3 plants. Hyodo and Longstaffe (2011) found that the $\delta^{13}C$ value of organic matter in Lake Superior, which

Table 3
Summary of seasonal patterns (this study) and bulk stable isotope data and radiocarbon dates (Metcalfe et al., 2013).

	Radiocarbon date (^{14}C yr BP)	Calibrated date (cal yr BP)	(‰, VPDB) Bulk $\delta^{13}C_{col}$	(‰, AIR) Bulk $\delta^{15}N_{col}$	(‰, VPDB) Bulk $\delta^{13}C_{sc}$	(‰, VSMOW) Bulk $\delta^{18}O_{sc}$	Seasonal pattern for $\delta^{13}C_{sc}$, $\delta^{18}O_{sc}$
ON9	12,360 ± 120	15,010 – 14,030	−20.1 (−20.9)	2.2 (2.0)	−10.1	23.1	Low $\delta^{13}C$ in summer and winter
ON3	11,820 ± 120	13,970 – 13,430	−20.7	4.6	−10.9	23.3	No seasonal data
ON14	ca. 11,800 – 11,100 [a]	14,000 – 12,700 [a]	−20.2	3.1	−10.5	22.2	Low $\delta^{13}C$ in summer, high $\delta^{13}C$ in winter
ON7	11,120 ± 110	13,170 – 12,740	−19.9 (−20.1)	3.6 (2.6)	−11.2	20.6	Low $\delta^{13}C$ in summer, high $\delta^{13}C$ in winter
NY4	11,033 ± 40 to 10,430 ± 60 [b]	13,030 – 12,090 [b]	−20.9	3.5	−11.3	22.7	Erratic, generally high $\delta^{13}C$ in summer, low in winter

Bulk $\delta^{13}C_{col}$ and $\delta^{15}N_{col}$ were obtained from dentin collagen (except those in parentheses, which were obtained from bone collagen) (Metcalfe et al., 2013).
Bulk $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ were obtained from tooth enamel bioapatite by Metcalfe et al. (2013).
[a] Not directly dated. See text for explanation of inferred dates.
[b] Not directly dated. Range given is from direct radiocarbon dates on mastodon collagen from the same site (Laub, 2003, 2010).

may have been derived from both terrestrial and aquatic sources, was a relatively constant −27‰ over the last 10,600 yr. Thus, we currently have insufficient knowledge of aquatic plant abundances and isotopic compositions in the ancient Great Lakes region to evaluate their effects on mastodon $\delta^{13}C_{sc}$ values.

(3) Plant proteins and lipids tend to have lower $\delta^{13}C$ values than cellulose or carbohydrates (Tieszen and Boutton, 1989; Tieszen, 1991; Hobbie and Werner, 2004; Bowling et al., 2008; Cernusak et al., 2009). We would expect animal intake of proteins and lipids to be highest during the growing season because of increased fruit and seed availability and greater nutrient contents in newly grown plants, which would cause mastodon $\delta^{13}C_{sc}$ values to decrease during spring/summer (but not winter). However, the situation may be complicated by differing macronutrient contents of fruits and seeds that mature at different times of year (e.g., Herrera, 1982).

(4, 5) Seasonal changes in plant taxa or plant parts consumed could have occurred because of changes in shrub and herb availability and/or mastodon selectivity. Vegetation available ca. 12,400 ^{14}C yr BP (ca. 14,500 cal yr BP) included a variety of plants that were present year-round (e.g., *Juniperus*, *Dryas*), some that likely lost their leaves during winter (e.g., *Salix*), and others that were probably only above-ground during the growing season (e.g., *Artemisia*). Modern subarctic browsers tend to select winter forage that is low in harmful secondary chemicals, which vary seasonally (Bryant and Kuropat, 1980). Teale and Miller (2012) presented evidence that the Hyde Park mastodon consumed *Salix* and *Populus* in winter and *Alnus* in spring. *Alnus* and *Salix* were particularly abundant in Ontario ca. 12,400 ^{14}C yr BP (ca. 14,500 cal yr BP) (Yu, 2000, 2003). We lack the detailed knowledge of $\delta^{13}C$ variations in these specific plants needed to evaluate the effects that they would have on mastodon $\delta^{13}C$ values, but seasonal variations have been observed for other C_3 plants (e.g., Murphy and Bowman, 2009). Dietary increases in leaves, which are ^{13}C-depleted relative to non-photosynthetic plant parts like bark, roots, seeds, and fruits (Hobbie and Werner, 2004; Codron et al., 2005; Ometto et al., 2006), could have contributed to summer decreases in $\delta^{13}C$, but leaf-consumption increases seem unlikely in winter.

(6) Both summer and winter decreases in mastodon $\delta^{13}C$ values could be related to increased water availability and associated decreases in the water use efficiency of plants (Murphy and Bowman, 2009; Wooller et al., 2011) — either because those seasons were actually wetter, or because mastodons preferentially consumed plants from wetter environments during those seasons. Such effects would have been particularly pronounced in the relatively dry habitat of ON9.

Circa 11,800 ^{14}C yr BP (ca. 14,000 – 13,400 cal yr BP) (ON3)

ON3 was radiocarbon-dated to 11,820 ± 120 ^{14}C yr BP (AA84989, dentin collagen) (13,970 – 13,430 cal yr BP), coincident with low-level Early Lake Erie and open spruce woodland vegetation, the typical Ontario mastodon habitat (Metcalfe et al., 2013). Unfortunately no seasonal data are available for this specimen. Its high $\delta^{18}O_{sc}$ value is almost identical to that of the earlier mastodon (ON9), but its high $\delta^{15}N_{col}$ and slightly lower $\delta^{13}C_{sc}$ values are closer to those of the later mastodon, ON7 (11,120 ± 110 ^{14}C yr BP; 13,170 – 12,740 cal yr BP) (Table 3). These compositions are consistent with the transitional date of the specimen and our understanding of temporal changes in Great Lakes hydrology ($\delta^{18}O$) and vegetation ($\delta^{15}N$, $\delta^{13}C$). At both ~12,400 ^{14}C yr BP (ca. 15,000 – 14,000 cal yr BP) and ~11,800 ^{14}C yr BP (ca. 14,000 – 13,400 cal yr BP), lake levels in the Erie basin were relatively low, glacial meltwater did not enter the Erie basin (Lewis et al., 2012), and evaporative enrichment may have further

increased water $\delta^{18}O$ values. However, by about 11,200 ^{14}C yr BP (ca. 13,100 cal yr BP) glacial meltwater had returned to the Erie basin, causing lake levels to rise dramatically (Lewis et al., 2012) and possibly decreasing local temperature (Lewis and Anderson, 1992). Thus, ON3 (11,820 ± 120 ^{14}C yr BP; 13,970 – 13,430 cal yr BP) lived under hydrological/climatic conditions more similar to those experienced by the earlier mastodon (ON9, 12,360 ± 120 ^{14}C yr BP, 15,010 – 14,030 cal yr BP) than the later mastodon (ON7, 11,120 ± 110 ^{14}C yr BP, 13,170 – 12,740 cal yr BP). In contrast to the timing of hydrological changes, the abrupt shift in vegetation from dense tundra to open woodland occurred earlier (~12,000 ^{14}C yr BP; ca. 14,000 – 13,800 cal yr BP), and spruce woodland persisted until sometime between 10,900 and 10,000 ^{14}C yr BP (12,800 – 11,500 cal yr BP) (Karrow and Warner, 1988; Yu, 2000; Ellis et al., 2011). Thus, ON3 lived among vegetation more similar to that available to the later mastodon (ON7) than the earlier mastodon (ON9). This discussion highlights the importance of understanding the timing of local changes in climate, hydrology, and vegetation when interpreting animal isotopic compositions.

Circa 11,100 ^{14}C yr BP (ON14, ON7) (ca. 13,200 – 12,700 cal yr BP)

The only available dates for ON14 (11,400 ± 450 ^{14}C yr BP and 12,000 ± 500 ^{14}C yr BP; 14,760 – 12,400 cal yr BP and 15,680 to 12,980 cal yr BP) were derived from associated muck (McAndrews and Jackson, 1988), which is a much less reliable substrate than collagen. The bulk $\delta^{15}N_{col}$ and $\delta^{18}O_{sc}$ values for ON14 are intermediate between those of ON3 (11,820 ± 120 ^{14}C yr BP; 13,970 to 13,430 cal yr BP) and ON7 (11,120 ± 110 ^{14}C yr BP, 13,170 to 12,740 cal yr BP) (Table 3), and its serially sampled results are remarkably similar to those of ON7 (Figs. 2, 3), which suggest that ON14 and ON7 experienced similar climatic conditions and engaged in similar seasonal behaviors. Therefore, we suggest that ON14 dates to between 11,800 and 11,100 ^{14}C yr BP (ca. 14,000 – 12,700 cal yr BP), and discuss its seasonal patterns along with ON7, below.

ON7 was radiocarbon-dated to 11,120 ± 110 ^{14}C yr BP (AA84980, bone collagen) (13,170 – 12,740 cal yr BP), a time when Erie basin lake levels had begun to rise and spruce woodlands dominated the terrestrial landscape (Metcalfe et al., 2013). It is generally thought that Paleoindians using Clovis-like (Gainey) tools entered Ontario by about 11,000 ^{14}C yr BP (Ellis et al., 2011), so data for ON7 (and ON14) should provide information on the environments first encountered by humans in the region.

The $\delta^{18}O_{sc}$ values for serial samples of ON7 and ON14 are lower than those of ON9 (Fig. 3), which suggests cooler and/or wetter conditions consistent with the gradual decrease in temperature between about 13,000 and 11,000 ^{14}C yr BP (ca. 15,700 – 12,700 cal yr BP), and/or the abrupt pre-Younger Dryas (Gerzensee/Killarney) cooling event that occurred shortly before 11,000 ^{14}C yr BP (ca. 12,900 – 12,700 cal yr BP) (Yu and Eicher, 1998; Yu, 2000). Decreased surface water evaporation could also have contributed to the lower $\delta^{18}O_{sc}$ values during this time period. Additionally, the lower $\delta^{18}O_{sc}$ values could reflect the return of meltwater inflow from the Huron basin into the Erie basin at this time, which may have decreased the $\delta^{18}O$ values of water bodies that were still predominantly precipitation-derived.

The lower $\delta^{13}C_{sc}$ values reflect the major differences in climate and vegetation during this time interval compared to the preceding one, particularly the establishment of spruce woodlands after 12,000 ^{14}C yr BP (14,000 – 13,800 cal yr BP). While these woodlands were relatively open, the establishment of some forest canopy might still have decreased plant $\delta^{13}C$ values (van der Merwe and Medina, 1991). In addition, trees themselves tend to have lower $\delta^{13}C$ values than other plant forms (e.g., shrubs or cushions) (Tieszen, 1991). Trees were a major component of mastodon diets when available (Teale and Miller, 2012). The lower $\delta^{13}C$ values may also be related to a higher atmospheric CO_2

content than during the earlier time period (Richards and Hedges, 2003; Hedges et al., 2004; Stevens and Hedges, 2004).

The pattern of seasonal variations in $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ for ON7 and ON14 is straightforward (Fig. 2). The $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ curves have equal periods and a negative relationship: $\delta^{13}C_{sc}$ values decrease in summer (similar to ON9) and increase in winter (unlike ON9). Of the six factors that could contribute to seasonal decreases in $\delta^{13}C_{sc}$ (see above), two can be eliminated or deemed unlikely. First, metabolism of stored fats does not fit the pattern, since $\delta^{13}C_{sc}$ values were high in winter. Second, major winter increases in water availability and decreased water use efficiency (WUE) seem unlikely in the spruce wetland environment these individuals inhabited.

It is likely that mastodons relied heavily on bark and twigs during this interval, as they tended to do when trees were available (Green et al., 2005; Teale and Miller, 2012). Year-round consumption of woody plants is supported by analysis of pollen and plant macrofossils (Teale and Miller, 2012) and growth layers in twigs browsed by mastodons (Ponomarenko and Telka, 2003). Plant taxa previously shown to vary seasonally in mastodon diets (*Salix, Populus, Alnus*) (Teale and Miller, 2012) were relatively uncommon during this time period (Yu, 2000). Nevertheless, seasonal selectivity of certain plant parts and taxa (i.e., during winter, a greater proportion of woody plant parts relative to leaves, along with aquatic plants and/or lichens) remains possible. Non-photosynthetic plant parts tend to have higher $\delta^{13}C$ values than leaves (Hobbie and Werner, 2004; Codron et al., 2005; Ometto et al., 2006), so winter increases in bark and twig consumption could have been largely responsible for the observed seasonal pattern. Lichens, which tend to have high $\delta^{13}C$ values (Barnett, 1994), may also have been consumed (along with tree parts) in greater quantities during winter than summer. A negative relationship between $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ in the tooth enamel of European Pleistocene steppe bison (*Bison priscus*) was previously attributed to winter consumption of lichens (Julien et al., 2012). As described above, the isotopic composition of aquatic plants in the Pleistocene Great Lakes region has not been determined, but if they had high $\delta^{13}C$ values and were consumed in greater quantities in winter they could have accentuated winter increases in $\delta^{13}C$. Finally, changes in plant macronutrient contents (winter decreases in plant lipid and protein contents) remain an additional possibility. In sum, the low-^{13}C summers and high-^{13}C winters could have been caused by a combination of seasonal changes in plant macronutrient contents and winter increases in the consumption of woody plant parts, lichens, and aquatic plants.

Circa 11,000–10,400 ^{14}C yr BP (NY4) (ca.13,000 – 12,100 cal yr BP)

Mastodon NY4 is from the Hiscock site in western New York, so differences from Ontario mastodons may be related to geographical locations and/or temporal differences. NY4 was not directly dated, but previous radiocarbon dates on Hiscock mastodon bone collagen roughly correspond to the Younger Dryas chronozone (Lewis et al., 1994; Yu, 2000), ranging from 11,033 ± 40 ^{14}C yr BP (13,030 – 12,770 cal yr BP) – 10,430 ± 60 ^{14}C yr BP (12,540 – 12,090 cal yr BP) (Laub, 2003, 2010). Humans were present in the region at this time (Ellis et al., 2011) and Clovis-like (Gainey) or post-Clovis artifacts and reworked mastodon bone tools (ca. 11,000 – 10,600 ^{14}C yr BP; 13,000 – 12,500 cal yr BP) were found in the same stratigraphic layer as the Hiscock mastodon remains (Ellis et al., 2003; Laub and Spiess, 2003; Storck and Holland, 2003; Tomenchuk, 2003). However, there is no direct evidence for predation of mastodons by humans at the Hiscock site (Ellis et al., 2003; Laub and Spiess, 2003). The vegetation around Hiscock at this time was transitioning from spruce woodland to pine forest (McAndrews, 2003). In addition to spruce, mastodons at the site also appear to have consumed an abundance of non-arboreal upland plants, including Gramineae, Cyperaceae, Compositae, and Rosaceae (Miller, 1988; McAndrews, 2003).

Some of the $\delta^{13}C_{sc}$ values for serial samples of NY4 are lower than those of the Ontario mastodons (Fig. 3b), consistent with the generally lower carbon isotope compositions of Hiscock mastodons (Metcalfe et al., 2013). Lower $\delta^{13}C$ values are consistent with a cooler climate, wetter environment, and/or increased canopy cover, which are all possible given the site's context. The $\delta^{18}O_{sc}$ values for serial samples of NY4 are well within the range obtained for ON7 and ON14 (ca. 11,100 ^{14}C yr BP; 13,200 – 12,700 cal yr BP) (Fig. 3a), and the bulk values are also similar (Table 3). However, the $\delta^{18}O_{sc}$ curve for NY4 has a lower amplitude and possibly less regular periodicity than observed for ON7 and ON14 (Figs. 2, 3). This suggests that Hiscock mastodons utilized multiple local water sources during the year, and perhaps ones whose oxygen isotope compositions did not seasonally vary by large amounts, such as groundwater and/or lake water. Fisher and Fox (2003) also suggested that Hiscock mastodons utilized multiple water sources, based on a lack of correspondence between slow winter growth periods in tusks with low $\delta^{18}O_{sc}$ values. A number of local water sources would have been available to Hiscock mastodons, including Lake Tonowanda, a long and shallow lake with input from the Erie basin located only a few kilometers northwest of the Hiscock site (Muller and Calkin, 1988), Lake Tcakowageh, a small lake to the east of the site (Muller and Calkin, 1988), and the local springs feeding the Hiscock site itself (Laub et al., 1988; Laub, 2003), though water at the site was saline and unlikely to be a major drinking source (Ponomarenko and Telka, 2003).

Another major contrast with the Ontario specimens is that NY4 had $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ curves with high and low values occurring at approximately the same time (i.e., an apparent positive relationship). Similar patterns were observed for some serially sampled mastodon tusks from the Hiscock, along with minimal seasonal changes in increment thicknesses (Fisher and Fox, 2003). The Younger Dryas climatic changes and/or increased Paleoindian presence may have disrupted previously established mastodon dietary habits, or these patterns may be representative of the environment surrounding the Hiscock site. Either way, it appears that seasonal changes in drinking water, plant availability and/or mastodon behavior (e.g., migration) were less regular at this time and location.

Conclusions

Methodological

We obtained detailed seasonal records for mastodon diet and drinking water in the latest Pleistocene C_3 environments of the Great Lakes region using inner enamel surface serial sampling and isotopic analysis. Our inner enamel sampling method recovered highly regular low-magnitude seasonal variations in $\delta^{13}C$ values that might have been obscured by drilling deeper into the enamel or through the outer enamel surface. Thus, our approach may be particularly useful for understanding seasonal changes in $\delta^{13}C$ within C_3 environments, where variations would generally be quite small.

Our growth rate analysis demonstrated that mastodon teeth have lower extension rates (but not lower enamel thickness growth rates) than mammoths or modern elephants. For mastodons, both extension rates and enamel thickness growth rates decreased towards the cervix. Knowledge of growth rates can be used to inform future sampling strategies. Comparison of bulk and serially sampled mean $\delta^{13}C_{sc}$ and $\delta^{18}O_{sc}$ values showed consistent offsets, which further suggests that consideration of sampling methodology, particularly the depth and location of drilling, is important when comparing data from different studies.

Environmental change and mastodon behavior in the Great Lakes region

Our interpretations were based on a very small number of specimens, but considered multiple isotopic proxies and detailed seasonal data for securely dated individuals. We argue that the mastodons

studied here did not undertake long-distance migrations. Rather, they relied on local water sources whose isotopic compositions changed seasonally (probably precipitation-fed ponds, streams, or puddles rather than the larger water bodies within the Great Lakes basins).

The earliest directly dated Ontario mastodon (12,360 ± 120 ^{14}C yr BP; 15,010 – 14,030 cal yr BP) had high drinking water δ^{18}O and dietary δ^{13}C values, consistent with a relatively warm and dry climate, low lake levels in the Erie basin, open tundra vegetation, and lower atmospheric CO_2. The low $\delta^{15}N_{col}$ values of this individual were likely a result of less-developed soil conditions and a diet based on shrubs and herbs, including pioneer nitrogen-fixing taxa such as *Alnus* and *Dryas*. The data for serial samples from this individual indicate large seasonal variations and a unique pattern of regular δ^{13}C lows in both summer and winter, which probably resulted from seasonal fluctuations in water availability, plant protein and lipid contents, and season-specific consumption of certain plant species (particularly *Alnus* and *Salix*, which were abundant at this time) and/or plant parts (i.e., leaves).

Between 11,800 and 11,100 ^{14}C yr BP (ca. 14,000 – 12,700 cal yrBP), tundra vegetation in Ontario was replaced by spruce woodlands (Karrow and Warner, 1988; Yu, 2000; Ellis et al., 2011). Increases in mastodon $\delta^{15}N_{col}$ values were likely related to a decreased reliance on nitrogen-fixing taxa and maturing soil conditions. Overall decreases in $\delta^{13}C_{sc}$ values reflected increased atmospheric CO_2, a wetter environment with greater canopy cover, and a much greater proportion of trees in the diet. Early on, hydrological conditions were similar to those during the previous ~600 ^{14}C yr, with relatively high drinking water δ^{18}O values reflecting low lake levels in the hydrologically closed Erie Basin and associated climatic conditions. Later (by 11,200 ^{14}C yr BP, or ca. 13,100 cal yr BP), drinking water δ^{18}O values decreased, corresponding to cooler temperatures, more ^{18}O-depleted precipitation, decreased surface water evaporation, and an influx of glacial meltwater. The seasonal pattern of low $\delta^{13}C_{sc}$ values in summer and high $\delta^{13}C_{sc}$ values in winter was likely a product of winter decreases in plant protein and lipid contents, and increased consumption of woody plant parts along with lichens and possibly aquatic plants.

Compared to Ontario mastodons, Hiscock mastodons from New York (ca. 11,000 – 10,400 ^{14}C yr BP, or 13,000 – 12,100 cal yr BP) had less regular seasonal variations and a completely different seasonal pattern. At this time and location, mastodons relied on multiple water sources with distinct isotopic compositions and possibly lower seasonal variability in isotopic composition (see also Fisher and Fox, 2003). These patterns could simply reflect different conditions at this location. If typical of the larger region, they suggest a major change in plant availability and/or mastodons diets, possibly as a result of Younger Dryas climate change.

This study used serially sampled and bulk isotopic results, along with independent chronologies of climatic, hydrological, and vegetational change, to infer changes in mastodon diet, behavior, and environmental conditions over time in the Great Lakes region. Although the number of individuals studied is small, the data suggest that distinct patterns of isotopic variations, as well as different isotopic compositions, may characterize different individuals and time periods.

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