MAIZE, FISH, AND DEER: INVESTIGATING DIETARY STAPLES AMONG ANCESTRAL HURON-WENDAT VILLAGES, AS DOCUMENTED FROM TOOTH SAMPLES

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Following the entry of Zea mays to northeast North America, Northern Iroquoian populations expanded their numbers and range. Isotopic values from bone collagen have shown fluctuations in reliance on this dietary staple. With permission of the Huron-Wendat Nation of Wendake, Quebec, we measured $\delta^{13}C_{\text{enamel}}$, $\delta^{13}C_{\text{dentine}}$, and $\delta^{15}N_{\text{dentine}}$ from 167 permanent teeth, retained before reburial of their ancestral skeletons, and $\delta^{13}C_{\text{collagen}}$, and $\delta^{15}N_{\text{collagen}}$ from adhering bone ($n = 53$). Enamel values encapsulate diet from ca. 1.5 to 4 years of age; dentine values reflect later childhood. Teeth are from 16 ancestral Huron-Wendat sites in southern Ontario. Isotopic values show consistent reliance on maize from early fourteenth to sixteenth centuries, with higher reliance in the seventeenth century—the time of contact with Europeans and disruptive changes. We show a difference between the diets of children and adults; children consumed more maize and less animal protein. White-tailed deer (Odocoileus virginianus) did not exploit maize fields, reflecting hunters’ exploitation of distant regions. New values from fish species ($n = 21$) are pooled with prior data, demonstrating diverse C and N stable isotope patterns. American eel (Anguilla rostrata) is particularly variable. Dietary protein sources were variable compared to the stability of maize: a reliable source of carbohydrate food energy across four centuries.
The focus of this study is the Huron-Wendat Nation, known by early French visitors to North America as the Huron. Primary (Biggar 1922–1936; Thwaites 1896–1901; Wrong 1939) and secondary ethnographic literature (Trigger 1976) as well as archaeological reconstructions (Birch and Williamson 2013) show their unique culture included palisaded villages of longhouses, well-defined political structures, maize production, fishing, hunting, trade, and warfare. While scholars debate the roles that migration events(s) and/or cultural diffusion played in the full realization of Northern Iroquoian lifeways, it is clear that the adoption of maize by lower Great Lakes region populations about 2,000 years ago set them on a course toward settled village life (Birch 2015; Williamson 2014). In this paper, we refer to those populations who lived along the north-central shore of Lake Ontario and eventually migrated north to join other groups in Simcoe County (Wendake) as ancestral Huron-Wendat (see Williamson 2014).

Relevant dietary features of ancestral Huron-Wendat culture include village relocations every 10 to 30 years (Warrick 2008) and shifting strategies of fisheries exploitation and deer hunting, and a lengthy period of breastfeeding of infants. Early villages (ca. A.D. 1300) were situated mainly on the Iroquois Sand Plain, a narrow band of sandy soils along the north shore of Lake Ontario. Within a century, populations had moved northward to the South Slope Till Plain, known for fertile, drought-resistant, loam-based soils (Birch and Williamson 2013; MacDonald 2002). Throughout the region, however, there were fewer heat units and frost-free days than those found in Zea mays production regions to the south. Major changes in settlement locales would also have led to adjustments in hunting territories and fisheries.

The quantity and types of fish remains that are recovered from village sites vary (Gates St-Pierre 2014), but all sites show yields from a variety of fish, reflecting different human behaviors as well as seasonal availability. Some fish from streams and rivers were likely obtained during spring spawning runs; exclusively lacustrine fish were mostly caught during fall spawning, and others would have been more consistently available throughout the warmer months of the year (Hawkins and Caley 2012; Needs-Howarth and Thomas 1998; van der Merwe et al. 2003). The animal bones at a site may not reflect what humans actually consumed there because of behavioral and taphonomic factors. Some fish, such as the lake-dwelling Salmonidae, may have been processed at the catch site, so that predominantly vertebrae were left at the consumption site (Williamson et al. 2003:56). Eel (Anguilla rostrata) may have been preserved and then used as travelling food or as goods, thereby dispersing their bones away from the processing site (Junker-Andersen 1988). The Recollect missionary Sagard describes how the fish were preserved whole, by suspending them from the rafters of longhouses (Wrong 1939:230). If, as Samuel de Champlain describes, the preserved fish were crushed into prepared combinations of food before consumption (Biggar 1922–1936:127), the bones and scales would be unrecognizable. There is evidence from historic accounts of trade in burbot (Lota lota) livers (oil) (Fox 2000), which may not have left much material evidence on archaeological sites. The faunal evidence for a broad range of fish species from both village and processing sites, combined with the diverse life histories of Great Lakes fish species, adds further complexity to the picture (Needs-Howarth 1999; van der Merwe et al. 2003).

Both large and small mammals were hunted and trapped. Deer meat was consumed when available and dogs (Canis lupus familiaris) were raised as hunting companions, ceremonial sacrifice, and food (Tooker 1964:66–67; Wright 2004:315). Woodchuck (Marmota monax) and other small animals were also trapped and consumed (Williamson et al. 2003:77–78), although since their body size is small, they probably did not contribute much to the isotopic signatures of human bone.

Although the proportion of white-tailed deer (Odocoileus virginianus) bones at ancestral Huron-Wendat sites is variable and deer remains are rare at most sites in historic Wendake (Robertson et al. 1995:77–80), we know hides would have been crucial for clothing and bedding. Both hunting and trade would have been necessary to meet these needs (Birch and Williamson 2013:111–117). By the turn of the sixteenth century, villages on the north shore of Lake Ontario required hunting territories the size of entire watersheds to help meet their needs (Needs-Howarth and Williamson 2010). Maize would most likely
have been traded to their northern Algonquian neighbors in exchange for additional hides.

In the historic period, deer and fish were reserved mainly for feasts and were distributed according to status, with the prize pieces going to headmen (Tooker 1964:72–73). Maize, prepared in several different fashions, was eaten twice a day (Tooker 1964:67–68). Food availability depended on the seasons; for example, while fish and meat were scarce most of the year, during or immediately after a spawning run or deer hunt, meat was consumed regularly (Tooker 1964:65, 70).

Finally, although observations by early visitors to the Huron-Wendat do not include substantial commentary about nursing and weaning of infants, some visitors noted that the Huron-Wendat abstained from sex for two to three years while women were nursing (Thwaites 1896–1901: 8:127). We know of no special food practices directed toward children (Forrest 2010; Saunders and Melbye 1990); we assume that weaning occurred by three years of age and that children in these early years had access to the same foods as adults.

Analysis of the stable isotope composition of human bone can provide more precise estimates of prehistoric diet. We undertake such an analysis here to help clarify the roles of maize, fish, and deer in the diet of the ancestral Huron-Wendat through time and space.

**Context for Isotope-based Study of Huron-Wendat Diet**

The discovery that diet affects carbon isotope values as measured in body tissues, including bone collagen, allowed researchers to answer questions about the role of maize in the diets of some North American indigenous societies (van der Merwe and Vogel 1978). Metabolically speaking, the plant life of the Northeast is predominantly C₃ (Calvin cycle), and the tropical grass *Zea mays* is C₄ (Hatch-Slack cycle). These two types of photosynthesis produce plant tissues with different ¹³C/¹²C ratios. Animal tissues incorporate these distinctive isotopic ratios in predictable ways, with collagen enriched in ¹³C by about 5‰, and carbonate in bone apatite enriched by about 12–14‰ compared with the food consumed. Since collagen is a protein, its carbon derives preferentially from dietary protein, while carbonate in bone and enamel apatite comes from the whole diet: carbohydrates, proteins, and lipids (Howland et al. 2003; Kellner and Schoeninger 2007). Bone or enamel carbonate is therefore a sensitive indicator of changes in the importance of maize, which contributes primarily carbohydrates to the diet.

A second isotopic framework, that of δ¹⁵N, can be measured in target tissues and interpreted relative to trophic effects within the local ecosystem to provide information about protein sources (DeNiro and Epstein 1981). Nitrogen isotopic composition of tissues is used in paleodiet studies mainly to differentiate consumption of terrestrial versus aquatic foods (Schoeninger and DeNiro 1984). With each shift from diet to consumer tissue, δ¹⁵N values are enriched by +2 to +6‰. The δ¹⁵N_collagen value of an organism’s tissue will reflect the trophic level of the diet (Chisholm et al. 1982; Hedges and Reynard 2007; O’Connell et al. 2012). Because aquatic systems tend to be enriched in ¹⁵N, δ¹⁵N_collagen values can distinguish marine and in some cases freshwater resource consumers from terrestrial resource consumers.

Adoption of maize in northeast North America was an early focus of stable isotope analyses of bone. Thanks to the agreement of Huron-Wendat descendants to allow retention of one tooth per reburied ancestral skeleton (Pfeiffer and Lesage 2014), we are able to refine the story of aboriginal reliance on maize at its northernmost North American extent.

Prior studies of stable isotopes, chiefly from bone collagen, documented the beginning and subsequent intensification of maize agriculture in the region (Katzenberg et al. 1995; Schwarcz et al. 1985). These studies show considerable intersite and even intrasite variability (van der Merwe et al. 2003) that does not correlate with other dietary evidence (Hart and Lovis 2013). Schwarcz and colleagues postulated a peak in maize consumption ca. A.D. 1350. A large study of human teeth from the Moatfield ossuary (ca. fourteenth century) shows enriched δ¹³C. Did maize reliance subsequently decline? Others have recognized that exploration of dietary trends was hindered by the absence of isotope information from structural carbonate, which is a better tool for assessing whole diet (Harrison and Katzenberg 2003; Katzenberg 2006; Katzenberg and Harrison 1997), but human tissue samples for such studies have
not been readily available. With respect to protein as assessed from nitrogen isotopes, fish intake appears to have been important, but ingestion may have diminished as reliance on maize intensified (Katzenberg et al. 1995). Maize is about eight percent protein (Ellwood et al. 2013), but is deficient in the essential amino acids tryptophan and lysine. Consequently, maize ingestion might have tapered off, to avoid ill health effects (Schwarcz et al. 1985; van der Merwe et al. 2003).

Since the sampling of dental tissue was introduced in association with the 1997 excavation of the Moatfield ossuary (Williamson and Pfeiffer 2003), some Northern Iroquoian descendant communities have allowed controlled research on ancestors’ teeth. Analysis of carbon and nitrogen isotopes from Moatfield tooth samples demonstrated substantial intrasite variability in maize intake and reliance on high trophic level fish for protein (van der Merwe et al. 2003). Subsequent work on retained teeth from seven recently excavated Iroquoian sites demonstrated consistent reliance on maize, and variable patterns of fish exploitation (Pfeiffer et al. 2014). Most of the sites available for study are from the fourteenth and fifteenth centuries, and most sample sizes are modest (Moatfield excepted). For example, the basic pattern of maize introduction to the region was ascertained from 45 $\delta^{13}$C bone collagen values representing 14 archaeological sites, each of which was represented by one to five bone samples (Schwarcz et al. 1985). We need to augment this sample to explore temporal and spatial patterns in diet throughout Huron-Wendat culture history. This study adds new results from teeth and small fragments of adhering bone representing eight additional archaeological collections that were repatriated in 2013 (Pfeiffer and Lesage 2014). This brings the Northern Iroquoian study sample to 167 permanent teeth and 53 bone tissue samples from 16 archaeological sites (ca. A.D. 1300–1650). While this study does not address the initial adoption of maize, it allows exploration of the extent to which ancestral Huron-Wendat living along the north-central shore of Lake Ontario relied on this dietary staple, regardless of relocations and disruptions, such as internal and external interpersonal conflict. This study also allows an examination of reliance on maize in historic Wendake.

Archaeological Sites in This Study

The archaeological sites in this study represent a cross section of Huron-Wendat cultural development. Four sites from the late thirteenth through the fourteenth century are associated with a time when small, non-palisaded villages were organized in diverse ways along the north-central shore of Lake Ontario, and when ossuaries with features consistent with the Feast of the Dead first appear (Williamson and Steiss 2003). There is negligible evidence of interpersonal violence (Jenkins 2016; Williamson 2007). In terms of food waste, fish bone is often a substantial proportion of the animal bone identified to class (Birch and Williamson 2013:104). Five sites from the fifteenth century are associated with a period of coalescence and conflict, during which villages grew in extent and population through amalgamation. These villages often had substantial palisades and extensive evidence of violent conflict. Four of our villages, occupied in the sixteenth century, were larger, coalesced, and integrated communities with far less evidence of violence (Birch and Williamson 2013:15–24). The clan structure of the historic Huron-Wendat may have been established by this time (Trigger 1976:154). Finally, following direct contact with Europeans, three sites from the seventeenth century represent a time of dramatic disruption. There were substantial reductions in population numbers as a result of European-introduced diseases, warfare with non-Huron-Wendat Iroquoian speakers, and the dispersal of the Huron-Wendat Nation from historic Wendake (Trigger 1976). Christian Island, the most recent of the sites in our study, is where the final stand of the Huron-Wendat in historic Wendake occurred.

Materials and Methods

Human Samples

Samples consist of permanent teeth from 16 archaeological sites, located between the north shore of Lake Ontario and Georgian Bay, in what is now Ontario, Canada (Figure 1). Table 1 provides information about types of sites and their estimated dates. Huron-Wendat funerary practice focused on secondary ossuary interments constructed during major rituals known as Feasts of the Dead.
Most human remains come from those complex features. Occasionally, human remains are encountered on village sites, either as loose elements (including teeth) or as individual interments. Previous publications describe eight of the 16 sites (Pfeiffer et al. 2014; van der Merwe et al. 2003). These eight sites include ossuaries and a special purpose site from the late thirteenth or early fourteenth century (Moatfield, Staines Road, Hutchinson), village sites and an ossuary from the fifteenth century (Damiani, Hidden Spring, Teston), and two village sites from the sixteenth century (Mantle and McKenzie). The site of Wainfleet, reported previously, has been excluded because it represents a different Iroquoian-speaking group.

As Huron-Wendat communities grew in size, the ossuaries associated with their Feasts of the Dead became larger. Researchers from the University of Toronto excavated several of those ossuaries between 1946 and 1975, which were the subject of bioarchaeological studies (Pfeiffer and Fairgrieve 1994). Following a memorandum of understanding with the Huron-Wendat Nation of Wendake, Québec, the skeletal remains of an estimated 1,700 ancestors from 12 sites were reburied on September 14, 2013 (Pfeiffer and Lesage 2014). This article reports on the analysis of samples of retained teeth from the large ossuaries of Fairty, Uxbridge, Kleinburg, Maurice, and Warminster (thought to be the historic site of Cahiaqué, visited by Samuel de Champlain in 1615), as well as the smaller collections of Bosworth, McKenzie-Woodbridge, and Christian Island.

The use of teeth (enamel and dentine) for studying diet is informed by the biology of tooth development. The timing of first permanent molar formation from a complete outline of the crown to root apex is 1.5 to 8.5 years (AlQahtani and Liversidge 2010). The crown forms prior to the root. Unlike bone, enamel does not remodel subsequent to its formation, and dentine is capable of only minimal remodeling. Teeth chosen for this study are well-preserved, non-carious, lightly

Figure 1. Map of the study area with sites identified by time period. The earliest sites are near the shore of Lake Ontario and more recent sites are farther north.
Table 1. Sites from which Human Enamel, Dentine and Bone Were Derived in this Study.

<table>
<thead>
<tr>
<th>Site name</th>
<th>Context</th>
<th>Date (A.D.)</th>
<th>Date Lab #</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fourteenth century</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 Staines Rd</td>
<td>Disturbed Ossuary</td>
<td>1030–1270*</td>
<td>Beta-156359</td>
<td>Pfeiffer et al. 2014; Williamson and Steiss 2003</td>
</tr>
<tr>
<td>2 Moatfield AkGu-65</td>
<td>Ossuary</td>
<td>1160–1290*</td>
<td>GX-26251</td>
<td>Pfeiffer et al. 2014; Williamson et al. 2003</td>
</tr>
<tr>
<td>3 Hutchinson AkGt-34</td>
<td>Special Purpose</td>
<td>Early fourteenth</td>
<td></td>
<td>Pfeiffer et al. 2014; Robertson 2004</td>
</tr>
<tr>
<td>4 Fairty AlGt-3</td>
<td>Ossuary</td>
<td>1365–1385*</td>
<td>Beta-397304</td>
<td>Williamson 2014</td>
</tr>
<tr>
<td><strong>Fifteenth century</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 Uxbridge BbGs-3</td>
<td>Ossuary</td>
<td>1415–1455*</td>
<td>Beta-403922</td>
<td>This study</td>
</tr>
<tr>
<td>6 Teston Road AlGv-2</td>
<td>Ossuary</td>
<td>1450–1500</td>
<td></td>
<td>Pfeiffer et al. 2014</td>
</tr>
<tr>
<td>7 Bosomworth BaGv-1</td>
<td>Cemetery</td>
<td>1450–1640*</td>
<td>Beta-316502</td>
<td>This study</td>
</tr>
<tr>
<td>8 Hidden Spring AlGu-368</td>
<td>Occupation</td>
<td>Mid fifteenth</td>
<td></td>
<td>Pfeiffer et al. 2014</td>
</tr>
<tr>
<td>9 Damiani AlGv-231</td>
<td>Village</td>
<td>Late fifteenth</td>
<td></td>
<td>Pfeiffer et al. 2014</td>
</tr>
<tr>
<td><strong>Sixteenth century</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10 Mantle AlGt-334</td>
<td>Village &amp; Cemetery</td>
<td>1487–1527**; 1446–1530*</td>
<td>Beta-217158; 217159</td>
<td>Birch and Williamson 2013</td>
</tr>
<tr>
<td>11 McKenzie-Woodbridge AkGv-2</td>
<td>Village</td>
<td>Early sixteenth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 Milne BeHb-28</td>
<td>Cemetery</td>
<td>Mid sixteenth?</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13 Kleinburg AlGv-1</td>
<td>Ossuary</td>
<td>1580–1610</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Seventeenth century</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 Warminster BdBv-1</td>
<td>Ossuary</td>
<td>1610–1620</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 Maurice BeHa-1</td>
<td>Ossuary</td>
<td>1630–1650</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16 Christian Island BeHb-3</td>
<td>Ossuary</td>
<td>1649–1651</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Calibrated 2 sigma.
**Calibrated 1 sigma.
worn permanent teeth. Most are first mandibular molars. The choice of permanent teeth was more varied in the Moatfield study. Values from enamel and dentine provide information about the diets of children.

Teeth with some alveolar bone adhering to the roots were chosen for study whenever possible. After surface cleaning, enamel was ground from a broad surface on the side of the crown, using a variable speed, hand-held burr. The resulting powder was pre-treated and analyzed to yield a value for $\delta^{13}C_{\text{enamel}}$ that reflects childhood diet over the period of the crown’s formation. One root of each molar was sliced parallel to the long axis, producing a chunk that was processed to obtain collagen-based values for $\delta^{13}C_{\text{dentine}}$ and $\delta^{15}N_{\text{dentine}}$. These values reflect childhood dietary intake subsequent to weaning, and are biased toward the protein component of the diet. A subset of teeth was identified to be sectioned horizontally for a future study of age at weaning. For those teeth, values for three horizontal sub-samples from mid-root to apex were averaged to provide per-tooth values for $\delta^{13}C_{\text{dentine}}$ and $\delta^{15}N_{\text{dentine}}$. This reflects adult dietary intake, with a bias toward the protein component. No bone apatite values were generated.

The laboratory protocols were the same for all samples, including past analyses (Pfeiffer et al. 2014). In order to extract collagen from bone and dentin, small chunks (a few millimeters in diameter) were surface-cleaned by sanding lightly with fine sandpaper, then weighed and placed in about 0.2M HCl until they had decalcified. After rinsing in distilled water, they were soaked in 1M NaOH overnight to remove humic acids. The samples were left in distilled water (changed daily) for several days until the water remained neutral, then freeze-dried. Collagen weight was divided by starting weight and multiplied by 100 to give percentage collagen yield. Approximately half a milligram of collagen was weighed into a tin cup, combusted at 1020°C in an automated elemental analyzer, then swept in a stream of helium carrier gas through a Conflo inlet into a Delta V Plus light isotope mass spectrometer. Results are reported in parts per million (‰) relative to international standards Vienna PeeDee Belemnite (PDB, for carbon) and AIR (for nitrogen). Isotope ratios are expressed in the delta notation, where $\delta = (R_{\text{sample}} / R_{\text{standard}} - 1) * 1000$. $R$ is the ratio of the heavy to the light isotope. Repeated measurements of homogeneous in-house standard materials yielded standard deviations of less than 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

For tooth enamel, ca. 5–10 mg of enamel powder was removed as described above and placed in a 1.5 ml microcentrifuge tube. Each powder was treated with 1mL of 1.75 percent sodium hypochlorite for 45 minutes to remove organics, centrifuged, rinsed three times in distilled water, treated with 1mL of 1M acetic acid for 15 minutes, rinsed three times with distilled water, and freeze-dried. Mass spectrometer analysis was performed at University of Cape Town Archaeometry Laboratory, using a Finngan Gas Bench II coupled to a Delta Plus XP (Thermo-Finnigan) gas source mass spectrometer. The sample was reacted with 100 percent phosphoric acid at 72°C to generate carbon dioxide. $\delta^{13}C$ measurements are expressed relative to the Vienna PDB standard, as above.

Samples of Candidate Foods: Fish and Deer

Previously published isotopic values for samples of archaeologically derived fish bone representing diverse species were supplemented by values for $\delta^{13}C_{\text{bone}}$ and $\delta^{15}N_{\text{bone}}$ from 21 archaeological fish bone samples identified to at least the genus level, all recovered from Huron-Wendat sites. The new samples were chosen to expand our knowledge of less well-known food species, including American eel and burbot. The dynamic ecology of the region’s lakes and streams yields many fish species with diverse isotopic profiles. Fish species are grouped according to trophic level and other attributes of their lifecycle or biology: (a) several members of the family Salmonidae, which are piscivorous and have oily flesh amenable to smoking or drying and thus to off-site processing and delayed consumption; (b) catadromous fish, namely, American eel (Anguilla rostrata), a partly piscivorous fish that also has oily flesh and may have been consumed sometime after capture in altered form; (c) piscivorous fish with an oily liver, namely burbot, which shares habitat and food preferences with Salmonidae and spawns in winter (Scott 1967);
(d) various fish that are piscivorous as adults, considered desirable “game fish” in modern times; and (e) various benthic/pelagic prey species that are non-piscivorous. American eel spawn in the Atlantic Ocean. The young then migrate to freshwater, where they remain until sexual maturity approaches. At that point they return to the ocean to spawn and die.

This study also assessed enamel and dentine from 55 deer teeth recovered from archaeological sites located in a broad geographic region that includes the Huron-Wendat sites. These data are part of an ongoing study of population movements (Pfeiffer et al. 2013). The laboratory methods used for sample preparation and measurement of isotope values from fish and deer were the same as those described for the human samples.

Results

Enamel apatite is considered a reliable sample material due to its highly crystalline form and density (Lee-Thorp 2008; Lee-Thorp et al. 1997). The human teeth analyzed here all showed excellent macroscopic enamel preservation; the enamel was hard and white, with minimal discoloration or evidence of cracks or fissures. Any such areas were avoided during enamel sampling. Nearly all collagen extracts from dentine, human bone, and fish bone consisted of well-preserved collagen. Those with C:N ratios outside the 2.9 to 3.6 range (Ambrose 1990; Szpak 2011; Van Klinken 1999) were removed from further analysis. Indicators of collagen quality (percent C, percent N, and C:N ratios) for the samples from the eight sites not previously reported appear in the supplemental information (Supplemental Table 1). The reported isotopic results can be regarded with confidence, given the absence of evidence for diagenesis. Isotopic values from the 167 teeth and 53 samples of bone are summarized by each of the 16 sites, organized by century (Table 2).

Analyses of the human isotope values are based on the premise that $\delta^{13}C_{\text{enamel}}$ will reflect the whole diet, while $\delta^{13}C_{\text{dentine}}$ and $\delta^{13}C_{\text{bone collagen}}$ will be oriented toward dietary protein (Warinner and Tuross 2009). Nitrogen in dentine and bone collagen derives from protein foods. In the context of dietary reconstruction, offsets of 5‰ in $\delta^{13}C$ and 6‰ in $\delta^{15}N$ (O’Connell et al. 2012) are assumed between the ingested protein and human collagen, derived from either dentine or bone.

Isotope Values from Human Enamel and Dentine

The mean value for $\delta^{13}C_{\text{enamel}}$ for all 167 teeth in this study is $-3.57 \pm 1.45‰$ (Table 2, Figure 2). There are no significant differences among values from the fourteenth, fifteenth, and sixteenth centuries, but these results are significantly different from the group dating to the seventeenth century (Kruskal-Wallis post-hoc multiple comparison test, $p = .05$). This most recent group shows more enriched values, indicating greater consumption of maize. The coefficient of variation is greatest for the fourteenth century, where the standard deviation is 38.5 percent of the mean, compared to 35 percent, 33 percent, and 35 percent in the subsequent centuries. Each of the four sites from the fourteenth century shows more variation than is typical of the subsequent centuries.

The mean value for $\delta^{13}C_{\text{dentine}}$ is $-10.86 \pm 1.18‰$ ($n = 164$). Comparison of results for different time periods shows no significant chronological differences (Kruskal-Wallis post-hoc multiple comparison test, $p = .05$). Here, too, the variability is highest among the earliest sites. Figure 2 shows the two $\delta^{13}C$ measures from teeth. The difference between $\delta^{13}C_{\text{enamel}}$ and $\delta^{13}C_{\text{dentine}}$, or the carbonate-collagen spacing, is 7.28 ± 1.59‰ ($n = 164$). The centuries show mean values of 7.1 to 8.1‰. Within each site there is considerable variability of ranges when individuals are compared, with personal values of 0.6 to 11.4‰. Values for $\delta^{13}C_{\text{enamel}}$ are shown for sites arranged in approximate chronological order in Figure 3.

The mean value for $\delta^{15}N_{\text{dentine}}$ is 11.91 ± 0.98‰. Values from the fifteenth century are significantly different from the fourteenth (Figure 4; Mann-Whitney Z value = 4.44, $p < .01$). The fifteenth and sixteenth centuries are not different (Mann-Whitney Z value = 0.99, $p = .32$), but the seventeenth century is different from the sixteenth (Mann-Whitney Z value = 3.63, $p < .01$). More positive $\delta^{15}N$ values occur in the fourteenth and seventeenth centuries, when sites were located near Lake Ontario and Georgian Bay, respectively. The isotope values may reflect greater access to fish at those times. There is substantial variability from site to site (Table 2, Figure 5). The variation in human $\delta^{15}N_{\text{dentine}}$ is assumed to derive from dif-
Table 2. Summary Statistics for $\delta^{13}C$ and $\delta^{15}N$ Values for Human Enamel, Dentine, and Bone.

<table>
<thead>
<tr>
<th>Century</th>
<th>Site Name</th>
<th>Tooth N</th>
<th>Bone N</th>
<th>Enamel</th>
<th>Dentine</th>
<th>Bone</th>
<th>Dentin</th>
<th>Bone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\delta^{13}C$</td>
<td></td>
<td>$\delta^{15}N$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fourteenth</td>
<td>Moatfield$^b$</td>
<td>43</td>
<td>10</td>
<td>-4.19</td>
<td>-11.31</td>
<td>-12.16</td>
<td>12.69</td>
<td>12.18</td>
</tr>
<tr>
<td></td>
<td>Fairty</td>
<td>15</td>
<td>6</td>
<td>-3.76</td>
<td>-10.75</td>
<td>-10.58</td>
<td>11.68</td>
<td>11.63</td>
</tr>
<tr>
<td></td>
<td>Hutchinson$^c$</td>
<td>5</td>
<td>1</td>
<td>-3.74</td>
<td>-11.48</td>
<td>-12.2</td>
<td>13.0</td>
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$^a$Rows are means and standard deviations (‰).

$^b$van der Merwe; Williamson et al. 2003.

$^c$Pfeiffer et al. 2014; values for two deciduous teeth from Damiani (UCT 13706) and Hidden Spring (UCT 13702) included in previously published data set have been omitted here.
Figure 2. Boxplots of human $\delta^{13}C_{\text{enamel}}$ (dotted white) and $\delta^{13}C_{\text{dentine}}$ (white) (‰) for groups, organized by century. Each box represents median and quartiles; box length = interquartile range, whiskers indicate min and max values. Outliers are represented by circles. Outliers are outside the interquartile range by 1.5 times or more.

Figure 3. Boxplots of human $\delta^{13}C_{\text{enamel}}$ values (‰) for each of the 16 sites in this study, organized in approximate chronological order. Each box represents median and quartiles; box length = interquartile range, whiskers indicate min and max values. Outliers are represented by circles and stars. Outliers are outside the interquartile range by 1.5 times or more, with starred values more extreme than circled values.
Figure 4. Boxplots of human $\delta^{15}N_{\text{dentine}}$ (‰) organized by century. Each box represents median and quartiles; box length = interquartile range, whiskers indicate min and max values. Outliers are represented by circles.

Figure 5. Boxplots of human $\delta^{15}N_{\text{dentine}}$ (‰) for each of the 16 sites in this study, organized in approximate chronological order. Each box represents median and quartiles; box length = interquartile range, whiskers indicate min and max values. Outliers are represented by circles and stars.
ferences in the quantities and types of protein foods consumed. Values for $d^{15}N_{\text{dentine}}$ are shown for sites arranged in approximate chronological order in Figure 5.

**Isotope Values from Human Bone**

Bone samples were available from 13 of the 16 sites, always in smaller numbers than tooth samples. The mean value for $d^{13}C_{\text{bone}}$ is $-11.9 \pm 1.1\%$; for $d^{15}N_{\text{bone}}$ it is $12.2 \pm 1.1\%$.

Values of $d^{13}C_{\text{bone}}$ and $d^{15}N_{\text{bone}}$ from two of the sites in this study, Fairyly and Kleinburg, have been reported previously (Schwarz et al. 1985), although with smaller samples. There is generally good agreement, with mean values within $0.2\%$.

**Isotope Values from Fish Bone**

The isotope values from 21 samples of archaeological fish bone chosen to expand our knowledge of candidate fish species are incorporated into a larger table of fish isotope values (Supplemental Table 2). The values include seven American eel, eight burbot, five largemouth bass, and one walleye. Together with values from the literature, the resulting 92 data points are plotted in Figure 6 in terms of the five fish categories described above.

The isotopic values for American eel are distinctive in two ways. The $d^{13}C$ values are heavier than the typical fresh water benthic-pelagic feeders, and both $d^{13}C$ and $d^{15}N$ are highly variable ($n = 11$; $d^{13}C = -18.5 \pm 3.69\%$; $d^{15}N = 8.9 \pm 1.32\%$).
This variability may reflect diversity in the ages of the fish. Those that are older would retain less of the marine signal from their time in the ocean than would the elvers. The fish with the oily liver, burbot, \(n = 9; \delta^{13}C = -19.8 \pm 1.26\%_\text{o}; \delta^{15}N = 12.0 \pm 1.19\%_\text{o}\) has a mean \(\delta^{13}C\) value very similar to that of the Salmonidae \(n = 17; \delta^{13}C = -20.1 \pm 0.84\%_\text{o}; \delta^{15}N = 9.91 \pm 1.23\%_\text{o}\). Each of these groups clusters tightly, with burbot having higher \(\delta^{15}N\) values than the Salmonidae. The \(\delta^{15}N\) values for the piscivorous fish (northern pike, yellow perch, and others) are about one trophic level above the values of their prey. The most positive \(\delta^{13}C\) values among the fishes (with values that could mimic maize in target human tissues) are some of the American eel, the pumpkinseed \(Lepomis gibbosus\), and the freshwater drum \(Aplodinotus grunniens\). Most of the fishes, particularly the fishes that can be caught en masse during their spawning period (e.g., Salmonidae and non-Salmonidae piscivorous fish), have \(\delta^{15}N\) values reflecting a \(C_3\) ecosystem, but with highly variable \(\delta^{15}N\) values.

Isotope Values from Deer Tissues

Isotopic values from deer bone taken from the literature show \(C_4\) diets and low variability (Katzenberg 1989; 2006; Morris 2015; Table 3). Fifty-five deer teeth from sites in the study region generated a mean \(\delta^{13}C_{\text{enamel}}\) of \(-15.0 \pm 1.2\%_\text{o}\) (range \(-18.3\) to \(-11.9\)) and \(\delta^{13}C_{\text{dentine}}\) of \(-22.3 \pm 0.9\%_\text{o}\) (range \(-25.9\) to \(-20.5\)). These values are also consistent with \(C_4\) diets, showing no evidence of foraging from maize fields. The markedly negative \(\delta^{13}C\) values and the consistent absence of a \(C_4\) signal from samples of this species may reflect an historic preference for forest plant species compared with contemporary behavior; the species is known to be an agricultural pest in modern times. The results may indicate that the deer were hunted from deeply forested regions, at a distance from maize fields (also noted by Morris 2015). \(\delta^{15}N_{\text{dentine}}\) for the deer in this study is \(6.2 \pm 1.0\%_\text{o}\) (range \(3.5\) to \(9.0\)).

Dietary Interpretations

Ethnographic and archaeological evidence indicates that the central components of the ancestral Huron-Wendat diet were maize, deer meat, and fish, with many plants and animals supplementing these core items (Hart and Lovis 2013). This study confirms prior observations that deer did not raid maize fields, but rather relied on a \(C_3\) diet. While deer may have been hunted in local watersheds on sites situated along the north shore of Lake Ontario, ethnographic descriptions of historic-period deer hunts indicate that there were collective efforts involving hundreds of men in the fall to late winter when deer gathered together in forest wintering areas. The hunters channeled deer into enclosures where they were slaughtered and processed, and the meat was brought back to villages (Biggar 1922–1936:60–61). This hunting method may explain the deer isotope signature observed for deer hunted in historic times in areas far from maize fields. We note that dogs may have contributed to the isotopic signatures reported here, especially among late northern villages like Maurice where considerable amounts of dog bone were recovered; however, the Maurice village is not associated with the later Maurice ossuary from which our samples are derived (Williamson 2014:37).

Complexity is introduced to this picture by the diversity of fish isotopic patterns, with \(\delta^{13}C\) values along a spectrum. Information from human \(\delta^{13}C_{\text{enamel}}\) and \(\delta^{13}C_{\text{dentine}}\) indicates that a substantial proportion of the foodstuffs consumed during childhood, from which teeth were built, followed the \(C_3\) metabolic pattern. Given the consistently \(C_3\) isotopic values from local deer, the primary source of \(C_4\) food was the direct consumption of
maize. However, some fish may also have contributed to enriched isotopic values. We recognize that there are significant problems with the application of mixing models in archaeological dietary reconstructions (Makarewicz and Sealy 2015). For heuristic purposes only, we consider a linear mixing model in which the C$_3$ and C$_4$ endpoints for enamel (i.e., 100-percent C$_3$ foods versus 100-percent C$_4$ foods) lie at -13 and +1, respectively (van der Merwe, Williamson et al. 2003). The mean $\delta^{13}$C$_{\text{enamel}}$ value of -3.57 ± 1.4‰ suggests that substantially more than 50 percent of total dietary carbon came from C$_4$ foods: predominantly maize, supplemented by some fishes. Based on archaeological and ethnohistoric data, Heidenreich (1971:163) estimated that maize made up 65 percent of the Huron-Wendat diet during the early historic period of A.D. 1600 to 1650. This appears to be a reasonable figure.

For the sake of comparison with a tradition of research that approaches the exercise from the perspective of $\delta^{13}$C$_{\text{bone collagen}}$, using endpoints of -20 and -5‰ (see Matson 2016), the mean value of -11.93‰ suggests that slightly less than half the diet as captured by this protein-biased signal came from C$_4$ foods. Contrary to studies that have suggested ill effects on health from overreliance on maize (Schwarcz et al. 1985; van der Merwe, Pfeiffer et al. 2003; van der Merwe, Williamson et al. 2003), this evidence suggests that intake of tryptophan and lysine would have been adequate.

**Insights into Behavior**

Some indications of community dynamics are evident in plots of the isotopic data for each site, organized in approximate chronological order (Figure 3). While different sample sizes must be kept in mind, the values for $\delta^{13}$C$_{\text{enamel}}$ illustrate features that are consistent with current understandings of the ancestral Huron-Wendat. In addition to an increased contribution of maize to diet in the seventeenth century, we note a trend of less internal site variation through time. This suggests a tendency toward more coordinated economic activity within villages. Initially, in the fourteenth century, lineages within villages may have been free to seek security through diversity in economic practice, resulting in substantial within-village variation with respect to dependence on maize. With the formation of larger villages resulting from both population growth and coalescence, communities required more agricultural surplus to address the risk of crop failure and to trade with northern Algonquians in exchange for hides (Birch and Williamson 2013:117). This heightened commitment to agriculture resulted in community-wide, coordinated field clearance and cultivation systems, which would have reduced the time available for harvesting other, naturally occurring resources. As a result, diet became more standardized among villagers. Ultimately, with the move to Wendake at the beginning of the seventeenth century, these same pressures, exacerbated later by the threat of interpersonal hostility, led to an actual proportional increase in the consumption of maize.

We note that a shift in the degree of reliance on maize over time is apparent from analyses of $\delta^{13}$C$_{\text{enamel}}$, but not from $\delta^{13}$C$_{\text{dentin collagen}}$. We suggest this is because the carbon in dentin and bone collagen is preferentially derived from protein foods. Values from enamel will be more sensitive to whole-diet shifts. In a situation where maize is already a major component of the diet, $\delta^{13}$C$_{\text{dentin collagen}}$ is therefore not very sensitive to modest increases in the amount of maize consumed. The carbon in tooth enamel carbonate is, however, derived from all components of the diet: proteins, carbohydrates, and lipids. It is therefore a better tracer of the importance of maize in high-maize diets.

Nitrogen is obtained from protein foods, so $\delta^{15}$N in consumers provides information about the protein component of the diet. In addition to deer and fish, the Huron-Wendat could access other sources of animal protein such as dogs, other small mammals, and birds. Those foods are not considered here. Detailed interpretation of consumer $\delta^{15}$N values is difficult because of uncertainty about the magnitude of the diet-to-tissue spacing in $\delta^{15}$N in humans and other consumers. This has been debated in the literature; estimates range from 3 to 4‰ up to 6‰ (Caut et al. 2009; Hedges and Reynard 2007; O’Connell et al. 2012). Figure 6 shows that, for this Iroquoian population, diet-to-tissue spacing of 3 to 4‰ means average $\delta^{15}$N$_{\text{diet}}$ of approximately 9‰, precluding the consumption of significant quantities of deer with its $\delta^{15}$N of approximately 6‰. Given that deer constitute the bulk of the mammalian meat weight
represented on some ancestral Huron-Wendat sites, this scenario seems unlikely. Diet-to-tissue spacing of $6\%e$ means an average $\delta^{15}N_{\text{diet}}$ of approximately $6\%e$, consistent with a diet in which almost all protein came from deer. The true value lies somewhere between the two, depending on the proportion of $15N$ enriched fish in the diet. The most plausible interpretation is based on spacing larger than 3 to 4‰. When values for $\delta^{15}N_{\text{dentine}}$ are considered among sites organized chronologically (Figure 5), the variations between sites appear to reflect local circumstances, both ecological and sociopolitical. Additional explorations on a site-by-site basis may help to elucidate the meaning of the results presented here.

For the population analyzed in this study, mean $\delta^{13}C_{\text{bone collagen}}$ (-11.91 ± 1.05; $n = 53$) is significantly more negative than $\delta^{13}C_{\text{dentine}}$ (-10.86 ± 1.18; $n = 164$) ($t = 5.8; d.f. = 215; p < .01$). Pairwise comparison of the two tissues based only on those individuals with both measures yields the same result ($t = 7.70; d.f. = 53; p < .01$). A pairwise comparison of $\delta^{13}N_{\text{bone collagen}}$ (mean = 12.24 ± 1.07; $n = 53$) with $\delta^{15}N_{\text{dentine}}$ of the same individuals indicates that these values do not differ significantly ($t = .13; d.f. = 52; p > .05$). One possibility is that there is a previously unrecognized difference in $13C$ enrichment from diet to dentine compared with diet to bone. The small number of studies in the literature that report both $\delta^{13}C_{\text{bone collagen}}$ and $\delta^{13}C_{\text{dentine}}$ for the same individuals do not, however, reveal a difference (France and Owsey 2015; Salazar-Garcia et al. 2014), making a metabolic explanation unlikely. We therefore infer that the diets of Iroquoian children (at the time of dentine formation) included a greater proportion of $C_4$ food (i.e., maize) than the diets of adults, as reflected in alveolar bone. Adults consumed more $C_3$ based foods, a category that includes venison and fish.

Conclusions

Our study shows that ancestral Huron-Wendat communities living along the north shore of Lake Ontario demonstrated consistency in the degree of reliance on maize as a staple food through the fourteenth, fifteenth, and sixteenth centuries A.D., then a shift to greater maize consumption in the seventeenth century. The results of this study correct earlier interpretations that postulated vacillations in ingestion of maize. That narrative should be replaced by one that shows consistent, pervasive reliance on maize, supplemented by dietary protein that varies by community in ways that are consistent with ecological, seasonal, and cultural constraints. Second, we demonstrate a previously undocumented difference between children’s and adults’ diets. Young children relied on maize to a greater extent than adults, and likely had less access to animal protein.

As archaeologists establish an era in which we work collaboratively with descendant communities, it is important that we examine past statements and correct them when needed. Based on incomplete information that best reflected protein sources, earlier narratives about maize farming practices attributed behaviors to past peoples that appear to have been capricious. Isotopic values from small numbers of samples taken from sometimes imprecisely dated sites showed dramatic temporal and spatial variation, suggesting that some groups ingested more maize than was healthy, while neighbors ingested much less. The information provided in this study illustrates that at least some of this variability in $\delta^{13}C_{\text{bone collagen}}$ values could reflect different exploitation of fish. For example, some local communities may have had access to the more $13C$ enriched eel and some of the nominally piscivorous taxa, while others may have focused on the less enriched Salmonidae and burbot.

Contrary to earlier studies of smaller samples from Iroquoian sites, the contribution of maize to the diet did not peak prior to the era of European contact; it increased during those disrupted times. In prior isotopic studies, maize seemed always to be present from the thirteenth century onward, but its trajectory made little sense. Indeed, there was no trajectory. The most positive $\delta^{13}C$ values were from the early fourteenth century (Moatfield, based on $\delta^{13}C_{\text{enamel}}$ and Fairty, based on $\delta^{13}C_{\text{bone collagen}}$). The current study corrects this perception. It provides a temporal and spatial perspective of over 400 years, during which the ancestral Huron-Wendat nation grew in numbers and went through some challenging times. Throughout the whole period, maize consumption was a stable factor, despite the challenges of generating yields in a northern, temperate climate. The proportion of
maize in the overall diet increased only during the tumultuous seventeenth century—a time during which food scarcity could have arisen from myriad disruptions that restricted access to traditional hunting and fishing locations and when maize may have been the only stable, accessible source of food. Rather than a story of fits and starts, we see reliance on maize as a dietary staple in a society that honed impressive horticultural knowledge and skill over the centuries.

**Acknowledgments.** This research was undertaken in collaboration with the Huron-Wendat Nation of Wendake, Québec. These research results have been shared with them. We thank the students and teaching assistants who participated in the University of Toronto Science Abroad program in 2011, 2013, and 2014: Arden Azini, Amy Beresheim, Michelle Cameron, Gina Carroll, Jenna Coutinho, L. Elizabeth Doyle, Anne Drury, Crystal Forrest, Heather Kristjanson, Alanna Leale, Natasha Leclerc, Nicole Legro, Stephanie Luik, Stephen Mclisaac, Zhiang (Danny) Pan, Magdalena Sobol. We received support from staff and post-graduate students at the University of Cape Town, including Vincent Hare, John Lanyon, Julie Luyt, and Ian Newton. We thank Madeline Zhu for help with the statistical evaluation of the results, Jonas Fernandez for preparation of Figure 1, and John Hart for his comments on an earlier draft of this paper. Sealy acknowledges support from the South African Research Chairs Initiative of the National Research Foundation and the Department of Science and Technology. Some components of this work were presented at the Society for American Archaeology meetings, San Francisco, April 2015.

**Supplemental Materials.** Supplemental materials are linked to the online version of this paper, which is accessible via the SAA member login at www.saa.org/member-login.

Supplemental Table 1. Isotope Values and Collagen Quality Indicators for Tooth Enamel, Dentin and Bone Samples New to This Study.

Supplemental Table 2. Carbon and Nitrogen Isotope Values from Bone Collagen of Likely Food Fish; Individual Values.

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