Stable isotope paleoecology of Late Pleistocene Middle Stone Age humans from the Lake Victoria basin, Kenya

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Abstract
Paleoanthropologists have long argued that environmental pressures played a key role in human evolution. However, our understanding of how these pressures mediated the behavioral and biological diversity of early modern humans and their migration patterns within and out of Africa is limited by a lack of archaeological evidence associated with detailed paleoenvironmental data. Here, we present the first stable isotopic data from paleosols and fauna associated with Middle Stone Age (MSA) sites in East Africa. Late Pleistocene (~100–45 ka, thousands of years ago) sediments on Rusinga and Mfangano Islands in eastern Lake Victoria (Kenya) preserve a taxonomically diverse, non-analog faunal community associated with MSA artifacts. We analyzed the stable carbon and oxygen isotope composition of paleosol carbonate and organic matter and fossil mammalian tooth enamel, including the first analyses for several extinct bovids such as Rusingoryx atopocranion, Damaliscus hypsodon, and an unnamed impala species. Both paleosol carbonate and organic matter data suggest that local habitats associated with human activities were primarily riverine woodland ecosystems. However, mammalian tooth enamel data indicate that most large-bodied mammals consumed a predominantly C4 diet, suggesting an extensive C4 grassland surrounding these riverine woodlands in the region at the time. These data are consistent with other lines of paleoenvironmental evidence that imply a substantially reduced Lake Victoria at this time, and demonstrate that C4 grasslands were significantly expanded into equatorial Africa compared with their present distribution, which could have facilitated dispersal of human populations and other biotic communities. Our results indicate that early populations of Homo sapiens from the Lake Victoria region exploited locally wooded and well-watered habitats within a larger grassland ecosystem.

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Introduction
Environmental change has been associated with a number of key events in human evolutionary history, including the dispersal of modern humans within and out of Africa (e.g., Scholz et al., 2007; Cowling et al., 2008; Carto et al., 2009; Compton, 2011; deMenocal, 2011; Blome et al., 2012; Potts, 2012; Faith et al., in press). Fossil and genetic data point to an East African origin of Homo sapiens between 200,000 and 100,000 years ago (McDougall et al., 2005; Gonder et al., 2007), with Middle Stone Age (MSA) archaeological sites providing the behavioral context for these early populations (McBrearty and Brooks, 2000; Tryon and Faith, 2013). Recent genetic evidence indicates that an East African population, ancestral to many sub-Saharan African lineages and to all non-African lineages, began to disperse within and out of Africa between 70 and 60 ka (thousands of years ago) (Soares et al., 2012). Several recent studies have focused on the role of Late Pleistocene (126–12 ka) environmental change in driving these modern human dispersal events (Carto et al., 2009; Blome et al., 2012), including population retreat to well-watered refugia during periods of increased aridity (Basell, 2008; Brandt et al., 2012). However, the impact of these studies is limited because the relevant data archives—particularly proxies for temperature, moisture availability, and vegetation—are poorly resolved spatially and temporally (reviewed in Blome et al., 2012).
Available faunal evidence indicates that early modern human populations in East Africa were part of extinct non-analog animal communities that were distinct in terms of taxonomic composition compared with regional modern mammal communities (Marean and Gifford-Gonzalez, 1991; Marean, 1992, 1997; Tryon et al., 2010; Faith et al., 2011; Faith et al., 2012, 2013, 2014; Tryon et al., 2012), and, as such, the paleoecology of these ancient populations remains poorly understood. Previous paleoenvironmental reconstructions of East African MSA sites using isotopic data have been restricted to the analysis of paleosols from site A5 (dated to ~100–80 ka) at Aduma, Ethiopia (Yellen et al., 2005), and no published studies to date have examined the stable isotope compositions of fossil mammals from this interval. Thus far, the rarity of detailed paleoenvironmental reconstructions from MSA archaeological and hominin fossil sites has obscured the ecological contexts that shaped the biology and behavior of East African modern humans.

Here we describe the first isotopic reconstruction of the paleoenvironmental context of early H. sapiens from the MSA of East Africa, using data from MSA archaeological sites on Rusinga and Mfangano Islands. These sites are dated to ca. 100–45 ka, overlapping with major dispersals of human populations out of East Africa. We combine the carbon (δ^{13}C) and oxygen (δ^{18}O) isotopic compositions of sediments (pedogenic carbonates, bulk sedimentary organic matter) and fossil mammalian tooth enamel to reconstruct local vegetation composition, assess habitats in the broader landscape sampled by mobile large-bodied ungulates, and estimate regional moisture availability. Taken together, these analyses inform our knowledge of the paleoecological context of early modern humans during this critical time period.

**Pleistocene records from Rusinga and Mfangano Islands**

Rusinga (0°24′S, 34°0′E) and Mfangano (0°27′S, 34°0′E) are near-shore islands in Lake Victoria (Fig. 1) that today receive approximately 1400 mm rainfall per year (Crul, 1995; Fillinger et al., 2004). Prior to substantial human habitation, the islands were likely covered by variably dense woodlands (Andrews, 1973), with the surrounding area on mainland Kenya including woodlands, bushlands, thickets, and forested habitats (White, 1983). Rusinga and Mfangano are remnants of the eruption and deposition of lavas and sediments of the Kisingiri volcano, inactive since the middle Miocene. Both islands share a similar bedrock lithology of Miocene lavas and volcanioclastics, unconformably overlain by poorly consolidated Pleistocene sediments (e.g., Peppe et al., 2009; Tryon et al., 2010). The Pleistocene Wasiiriya Beds of Rusinga and the Waware Beds of Mfangano are primarily made up of tuffaceous alluvial and fluvial sediments and weakly developed paleosols suggestive of a relatively unstable landscape dominated by episodic depositional events (Figs. 1–2; Tryon et al., 2012, 2013, 2014). Rare tufa deposits at the Nyamita locality (Rusinga) are indicative of small, local springs (Figs. 1–2; Tryon et al., 2014). The Wasiiriya and Waware Beds comprise identical sedimentary facies and show remarkable similarities in the fauna, the chemical composition of tephra deposits, and age estimates from fossil gastropods, suggesting that the Wasiiriya Beds on Rusinga and Waware Beds on Mfangano likely sample the same general interval of time during the Late Pleistocene (Tryon et al., 2012, 2014). This is confirmed by tephra correlations made between all fossil-bearing Pleistocene sites on Rusinga, Mfangano, and other nearby sites in the region (Blegen et al., 2014). We estimate that the artifact and fossil bearing strata on both islands range in age from ca. 100–45 ka. The minimum age for the deposits is constrained by calibrated radiocarbon dates on fossil gastropods (Limicolaria cf. L. martensiana) that have burrowed into the deposits, and the maximum age is defined by the eruption time of the inferred source volcanoes that produced distal tephra deposits found near the base of the sedimentary sequence (Tryon et al., 2010, 2012).

Both the Wasiiriya and Waware Beds contain multiple archaeological sites with MSA artifacts, such as bifacial points and Levallois flakes and cores (Tryon et al., 2010, 2012, 2014). Controlled excavations in 2009–2011 from three locations on Rusinga Island (one at Nyamita and two at Wakondo, including the Bovid Hill sub-locality and a second unnamed sub-locality) totaling 28 m² produced artifact densities of 1.20–6.50 lithic artifacts/m² (Tryon et al., 2010; Jenkins et al., 2012). These in situ artifact densities are within the range expected from the ‘scatter between the patches’ (Isaac, 1981) or the ‘veil of stones’ (Roebroeks et al., 1995), typical of open-air Paleolithic artifact (scatters across ancient landscapes

![Figure 1. Map of Rusinga and Mfangano Islands, Kenya, showing the Pleistocene sediments and the positions of localities mentioned in the text.](image-url)
Figure 2. Detailed stratigraphic sections measured at the Wakondo (12.07.09.01) and Nyamita (AV1001, AV1002, AV1003, AV1004, AV1005, AV1006, AV1008, 11.07.09.01, 11.07.09.02) localities from the Wasiriya Beds on Rusinga Island in 2009 and 2010, and stratigraphic section measured at the Kakrigu locality (DP1011) from the Waware Beds on Mfangano Island in 2010. Correlation between stratigraphic sections (indicated by solid line) is based on field observations and geochemical correlations of tephra deposits (Van Plantinga, 2011). Solid stars are those paleosol samples that fall within the expected enrichment range (+14–17‰ offset in δ13C values of carbonate and organic matter), and open stars are those that fall outside of the expected enrichment range.
Lithic artifacts have been found together in surface collections and in excavations with a diverse fossil fauna, including some specimens with cut-marks (Tryon et al., 2010). The Pleistocene faunas from Rusinga and Mfangano (Table 1) contain the largest number of extinct species of any Pleistocene site in East Africa during the last ~400 kyr (cf. Marean, 1992; Assefa et al., 2008; Dominguez-Rodrigo et al., 2008; Faith et al., 2011, 2012, 2013, 2014), with the extinct species Rusingoryx atopocranion (Pickford and Thomas, 1984; Faith et al., 2011) and Damaliscus hypsodon (Faith et al., 2012) being the most abundant. Relevant to paleoenvironmental reconstruction, the faunas include several taxa indicating locally wet conditions, such as Hippopotamus and two species of reduncine bovids.

The fluvial, alluvial, and tufa deposits that comprise the Wasiriya and Waware Beds are suggestive of riparian depositional environments (Tryon et al., 2010, 2014); however, these deposits are likely not representative of the broader, regional landscape. The abundance of bovids belonging to the tribes Alcelaphini (wildebeest and allies) and Antilopini (gazelles and allies; 85% of bovid specimens at Rusinga and 70% at Mfangano), which, together with extinct specialized grazers (Syncerus antiquus, Megalotragus sp., Rusingoryx atopocranion, D. hypsodon), suggest the prevalence of open grassland vegetation (Tryon et al., 2010, 2012, 2014; Faith et al., 2011). Oryx (Oryx beisa) and Grevy’s zebra (Equus grevyi) are both found here well outside their modern ranges where they inhabit arid to semi-arid grasslands and shrublands, suggesting drier conditions compared with the present (Faith et al., 2013).

Carbon isotopes and paleoecological reconstruction

The primary basis for using the stable carbon isotope compositions of pedogenic carbonate, sedimentary organic matter, and mammalian herbivore tooth enamel as paleoecological proxies is the well-established differences in fractionation of carbon isotopes during fixation of atmospheric CO₂ by plants using different photosynthetic pathways. Plants using the C₃ pathway (trees,
shrubs, cool growing season grasses) strongly discriminate against \(^{13}C\) during fixation of CO\(_2\) and so have low \(^{13}C\) values relative to atmospheric CO\(_2\) (modern C\(_3\) mean: \(-27.4 \pm 1.6\%\); O'Leary, 1981; Passey et al., 2002; Cerling et al., 2003; Diefendorf et al., 2010; Kohn, 2010); C\(_4\) plants (warm growing season grasses, most sedges) discriminate less against \(^{13}C\) and have \(^{13}C\) values closer to atmospheric CO\(_2\) (modern C\(_4\): \(-12.7 \pm 1.1\%\); O'Leary, 1981; Passey et al., 2002; Cerling et al., 2003; Diefendorf et al., 2010; Kohn, 2010). Plants using the CAM (Crassulacean acid metabolism) pathway (cacti, other succulents) typically have intermediate \(^{13}C\) values but do not comprise a substantial fraction of the diet of modern large bodied herbivores in East Africa and we do not consider them further (Kingdon, 1988a, b). Variation in C\(_3\) plants is primarily driven by environmental factors that must be considered in interpretations of proxy data. Photosynthetic recycling of respiring CO\(_2\) in closed forests imparts lower than average \(^{13}C\) values to plant tissues (the canopy effect; van der Merwe and Medina, 1991). In contrast, light and water stress in open habitats decrease fractionation during fixation of CO\(_2\), causing higher than average \(^{13}C\) values in plants (Ehleringer and Cooper, 1988). C\(_4\) plants are uncommon in closed forests today (Edwards and Smith, 2010), and fractionation by C\(_4\) plants does not vary in relation to habitat and rainfall in arid and semi-arid regions of southern Africa (Schulze et al., 1996; van der Merwe, 2004; but see; Buchmann et al., 1996; Cerling et al., 2003).

The carbon isotope compositions of pedogenic carbonate and organic matter in a paleosol can be used to infer the relative proportions of C\(_3\) and C\(_4\) plants biomass present in the soil at the time of pedogenesis (Cerling and Quade, 1993). Soil organic matter generally preserves the isotopic composition of the overlying plant biomass (Balesdent et al., 1993; Tieszen et al., 1997). Variable contributions of leaves and roots to soil organic matter and decomposition of organic matter by soil biota can lead to enrichment of organic matter in \(^{13}C\) of several permil relative to standing biomass (Hobbie et al., 2004; Chen et al., 2005; Wynn, 2007). In addition to inputs from the plant component of soil biomass, soil organic matter can include carbon derived from microorganisms, which can shift the \(^{13}C\) values from that of the overlying vegetation (Koch, 1998).

Pedogenic carbonates that precipitate at depths greater than ca. 30 cm in soils with moderate to high respiration rates reflect the isotopic composition of plant-derived CO\(_2\) with no direct contribution from atmospheric CO\(_2\) (Cerling, 1991). Soil CO\(_2\) (and therefore soil carbonate) is enriched in \(^{13}C\) by 4.4\(\%\) relative to plant-derived CO\(_2\) due to kinetic fractionation during diffusion of CO\(_2\) from the soil to the atmosphere (Amundson, 1989; Cerling, 1991; Cerling and Quade, 1993). Additionally, equilibrium fractionation during the precipitation of calcite will result in the enrichment of soil carbonates in \(^{13}C\) by ca. +9.8 to +12.4\(\%\) relative to soil CO\(_2\) for the temperature range 25–0 \(^\circ\)C (Deines et al., 1974; Romanek et al., 1992). Thus, pedocalcic carbonates formed at depth in productive soils will have \(^{13}C\) values that are ca. +14–17\(\%\) higher than unaltered soil organic matter. Deviation from this offset can indicate that one or both phases have been altered and should not be used for paleoenvironmental reconstruction. For example, in habitats with extreme aridity and/or low soil productivity, paleocalcic carbonates will be even more enriched in \(^{13}C\) due to deeper penetration into the soil of isotopically heavy atmospheric CO\(_2\) (Cerling, 1992, 1997; Quade and Levin, 2013).

The \(^{13}C\) values of herbivore tissues record the \(^{13}C\) values of the plants consumed with tissue-specific enrichments relative to diet (DeNiro and Epstein, 1978). Various methods have been proposed to test for diagenesis in enamel (Morgan et al., 1994; Kohn et al., 1999; Sponheimer and Lee-Thorp, 1999a; Schoeninger et al., 2003); however, the consensus is that the isotopic composition of enamel apatite from large-bodied animals is generally resistant to diagenesis during the fossilization process due to its highly crystalline state and extremely low organic content (LeGeros, 1991). Therefore, enamel can be used as a proxy for diet during the time over which tooth enamel was mineralizing (DeNiro and Epstein, 1978; Sullivan and Krueger, 1981; Tieszen et al., 1983; Ambrose and DeNiro, 1986; Lee-Thorp et al., 1989; Wang and Cerling, 1994; Cerling and Harris, 1999; Kohn et al., 1999; Lee-Thorp, 2000; Lee-Thorp and Sponheimer, 2013).

For large-bodied ungulates, the generally accepted enrichment factor for tooth enamel relative to diet is +14.1 \(\pm\) 0.5\(\%\), which is the mean value for numerous ruminant and non-ruminant species of artiodactyls and perissodactyls (Cerling and Harris, 1999; Passey et al., 2002). The carbon isotopic composition of mammalian herbivore tooth enamel reflects the relative dietary proportion of C\(_3\) and C\(_4\) plants during enamel mineralization, which takes place early in an animal’s life (DeNiro and Epstein, 1978; Lee-Thorp and van der Merwe, 1987). The total time of enamel mineralization in a single tooth is short (months to years) relative to the time of formation of both paleosol carbonates and organic matter (averaged over hundreds or thousands of years). However, because mammals generally move around the landscape the spatial scale integrated in the tooth enamel isotopic signal can be quite large (Kingston, 2007). In the case of large migratory herbivores found in the Pleistocene deposits on Rusinga, Susan Island, and probably as wildebeest (Connochaetes taurinus), plains zebra (Equus quagga), and probably D. hysudon (Faith et al., 2012), the paleoenvironmental information extracted from tooth enamel would be on a scale commensurate with that used by mobile populations of human foragers (i.e., tens to hundreds of square kilometers).

To make quantitative interpretations of our carbon isotope data, we must consider long-term and historical changes in the \(^{13}C\) of atmospheric CO\(_2\). The \(^{13}C\) of atmospheric CO\(_2\) has varied by several permil over geologic time due to natural changes in the global carbon cycle (Leuenberger et al., 1992; Zachos et al., 2001; Gröcke, 2002; Tippette et al., 2010) and has been decreasing over the last 200 years due to the addition of CO\(_2\) from fossil fuel combustion with lower \(^{13}C\) values (Friedli et al., 1986; Marino and McElroy, 1991). Many previous paleoenvironmental studies using carbon isotope ratios have not addressed long-term changes in the \(^{13}C\) of atmospheric CO\(_2\) so here we lay out a detailed methodology. To compare measured \(^{13}C\) values of paleosol and fossil mammal tooth enamel with comparable data from modern ecosystems, we first estimated the \(^{13}C\) of atmospheric CO\(_2\) during the Late Pleistocene using \(^{13}C\) and \(^{18}O\) values of the benthic foraminifera genus Cibicidoides from Deep Sea Drilling Project (DSDP) site 607 (Zachos et al., 2001, 2008) and the atmospheric CO\(_2\) \(^{13}C\) reconstruction method of Tippette et al. (2010) with one modification. Tippette et al. (2010) used a long-term average \(^{18}O\) value for seawater of 0.0\(\%\) for 5–0 Ma in their calculations, but to account for the impact of global ice volume during the Pleistocene, we use a \(^{18}O\) value for seawater of 1.0\(\%\) in our calculation (Zachos et al., 2001; Miller et al., 2005). Using these calculations, our estimated \(^{13}C\) value for atmospheric CO\(_2\) from 45 to 100 ka is \(-6.6 \pm 0.4\%\). Our fossil samples are compared with a modern comparative dataset collected from published datasets with publication dates ranging from the 1980s through the 2010s; as most of these publications do not provide collection dates, we chose an approximate average value for modern atmospheric CO\(_2\) value of \(-8.0\%\) based on these sample/publication dates (Keeling et al., 2001). We use the difference between our estimated Late Pleistocene \(^{13}C\) value and the modern value (1.4\(\%\)) to correct our measured values from Rusinga and Mfangano Islands to the equivalent value under the modern atmosphere.

The relative contribution of C\(_3\) biomass to soil organic matter and paleosol carbonates or mammalian diets can be estimated from measured \(^{13}C\) values using a simple linear mixing model between
end members $\delta^{13}C$ values for C3 and C4 plants and enrichments for paleosol carbonates or tooth enamel:

$$\delta^{13}C_{\text{measured}} = \delta^{13}C_{\text{C1}} \cdot f_{\text{C1}} + \delta^{13}C_{\text{C4}} \cdot (1 - f_{\text{C3}}).$$

where $\delta^{13}C_{\text{C3}}$ and $\delta^{13}C_{\text{C4}}$ are the assumed end member $\delta^{13}C$ values (and can be modified by adding enrichments appropriate to the measured substrate) and $f_{\text{C3}}$ is the fraction of C3 biomass contributing the measured $\delta^{13}C$ value.

Because fractionation of carbon isotopes during precipitation of pedogenic carbonate is temperature-dependent (Deines et al., 1974; Romanek et al., 1992), enrichments for paleosol carbonate in the mixing model are partially temperature-dependent and the mixing model also requires information on soil temperature, which we cannot constrain with our data. Thus, we only use the mixing model to interpret our tooth enamel data as large bodied mammals precipitate tooth enamel at an approximately constant body temperature of 37 °C (Longinelli, 1984; Luz et al., 1984).

For tooth enamel data, the critical step is the assumption of end member $\delta^{13}C$ values. One approach is to use the mean values for both C3 and C4 plants based on large datasets from analyses of modern plants (~27.4 ± 1.6% and ~12.7 ± 1.1%, respectively; Cerling and Harris, 1999; Passey et al., 2002; Cerling et al., 2003; Diefendorf et al., 2010; Kohn, 2010). However, modern C3 and C4 plants both exhibit considerable variation in $\delta^{13}C$ values, and, as discussed above, the greater variability of C3 plants is due to environmental effects. Of particular concern here is that drought-stressed C3 plants can have mean $\delta^{13}C$ values as high as ~24.6 ± 1.1% (Cerling and Harris, 1999; Passey et al., 2002), and, given that paleoecological evidence from the Rusinga and Mfangano faunas suggests a predominantly open and semi-arid grassland, mean C3 and C4 end member values are likely to overestimate the proportion of C3 plants and underestimate the proportion of C4 plants in the diets of herbivores. Given the importance of aridity as a climatic factor in the Late Pleistocene East African paleoenvironmental record, we want to be cautious about our assumptions to avoid circularity in our interpretations. Rather than use a single set of assumptions about end member values, we present five different versions of the mixing model that are increasingly conservative in their assumptions about aridity and the abundance of C4 biomass and cover the plausible range of quantitative reconstructions of diet. This approach allows us to interpret the paleoenvironmental implication of the diet reconstructions from tooth enamel $\delta^{13}C$ values under all end-member assumptions. In these versions, the end member values used are: (A) mean C3 and C4 modern plant $\delta^{13}C$ values, (B) mean C3 end member shifted positively by one standard deviation (1.6%) and unaltered mean C4 end member, (C) arid climate C3 end member and unaltered mean C4 end member, (D) arid climate C3 end member and mean C4 end member shifted positively by one standard deviation (1.1%), and (E) arid climate C3 end member shifted positively by one standard deviation (1.1%) and mean C4 end member shifted positively by one standard deviation (1.1%).

**Aridity index based on mammalian tooth enamel oxygen isotope values**

The oxygen isotope composition of tooth enamel reflects the $\delta^{18}O$ value of body water/fluids and body temperature. Bioapatite and body fluids are assumed to form in oxygen isotope equilibrium as oxygen exchange between body water, blood phosphate, and blood carbonate occurs rapidly (Nagy, 1989; Ambrose and Norr, 1993; Tieszen and Fagre, 1993; Koch, 1998, 2007). Because leaf water is enriched in $^{18}O$ relative to meteoric water due to evaporation, animals that obtain a large proportion of their water from leaves (i.e., evaporation sensitive or ES taxa) will have enriched enamel bioapatite $\delta^{18}O$ values relative to contemporaneous and sympatric animals that must drink from a surface water source (i.e., evaporation insensitive or EI taxa). Local relative humidity and surface temperatures will influence the total amount of enrichment for leaf water; these variables ultimately affect the total amount of evaporation (Luz et al., 1990; Flanagan et al., 1991; Fricke et al., 1998; Sponheimer and Lee-Thorp, 1999b; Levin et al., 2006).

We use the index of Levin et al. (2006) to estimate aridity from measured $\delta^{18}O$ values of mammalian tooth enamel. This aridity index relies on the relationship between water deficit and the $\delta^{18}O$ enrichment ($\epsilon^*$) between ES and EI taxa based on measured $\delta^{18}O$ enamel values. Water deficit (WD) is the difference between potential evapotranspiration (PET) and mean annual precipitation (MAP). The $\delta^{18}O$ value of the body water of ES taxa (hence tooth enamel) will track $\delta^{18}O$ enrichment in leaf water due to evaporation, and, conversely, the $\delta^{18}O$ value of body water (and tooth enamel) of EI will track the $\delta^{18}O$ value of meteoric water. As many of the same species Levin et al. (2006) used in their calibration study have been recovered from Rusinga and Mfangano Islands, we can apply the aridity index to these species and do not need to rely on assumptions of taxonomic uniformitarianism. For comparison, we calculated modern WD values for Rusinga Island and nearby Kisumu (75 km east-northeast; WD = 774 and 562 mm, respectively) using PET and MAP values from the WORLDCLIM model (Hijmans et al., 2005).

**Materials and methods**

**Stratigraphic context**

Isotopic analyses focused on paleosol carbonate and bulk organic samples collected from stratigraphic sections measured through the Nyamita and Wakondo localities on Rusinga Island and the Kakiru locality on Mfangano Island. Weakly developed paleosols found within the Wasiriya and Waware beds include pedogenic features such as small carbonate nodules (<1 cm), granular texture, pressure faces, Mn-staining, and calcified root traces. The majority of our samples derive from Nyamita, where an approximately 14 m thick succession of Wasiriya Beds sediments is exposed for ~1 km along a single north-south trending valley (Van Plantinga, 2011). Correlative tephra deposits (as determined by electron probe microanalyses of the volcanic glass phase; termed Nyamita Tuff and Wakondo Tuff, respectively) link the Nyamita and Wakondo localities (Fig. 4) and have facilitated the study of lateral variation among sedimentary facies, which is described in detail by Tryon et al. (2010), Van Plantinga (2011). Sampled fossil teeth derive largely from surface contexts where original stratigraphic position within the Late Pleistocene deposits could be determined.
Laboratory analytical techniques

Paleosol samples were collected from ten stratigraphic sections at the Wakondo and Nyamita localities in the Wasiriya beds of Rusinga Island, and one section at the Kakrigu locality in the Waware Beds on Mfangano Island during the 2009–2011 field seasons (Fig. 2).

Paleosol samples for carbonate analysis were roasted in vacuo for one hour at 400 °C to eliminate water and organic matter and then reacted with 100% phosphoric acid in a Kiel automatic carbonate extraction device. The carbon and oxygen isotopic composition of the resulting carbon dioxide gas was measured using a Finnigan MAT 252 isotope ratio mass spectrometer and normalized by repeated analysis of both a commonly used (but uncertified) laboratory standard (Carrara marble) and a certified international carbonate standard (NBS-19). Paleosol samples for bulk soil organic matter analysis were reacted with 0.5 M hydrochloric acid for 24 h to eliminate any carbonates and then rinsed with deionized water five times. Samples were then dried in a 60 °C oven for 48 + hours to remove any remaining water. Following combustion in a Costech ECS 4010 elemental analyzer, the carbon isotopic composition of the resulting CO2 was measured using Thermo Delta V isotope ratio mass spectrometer (and normalized by in sequence analyses of a laboratory standard (UCSC Pugel) and NIST 2711a (Montana soil)). Analytical precision for all measured values is better than 0.1‰ based on repeated analyses of the standards.

Fifty-nine teeth identifiable to tribe, genus, or species were sampled from eight Rusinga Island localities and two Mfangano Island localities. Approximately 7 mg of tooth enamel were drilled from each specimen using a diamond bur. Care was taken to avoid any cracks in the enamel or specimens with evidence of alteration (such as discoloration). Following one of several established and commonly used protocols (Koch et al., 1997; e.g., Bibi, 2007; Clementz et al., 2009; Feranc et al., 2009; Gehler et al., 2012; McLean and Emslie, 2012; Domingo et al., 2013; Feranc and Pagnac, 2013; Clementz et al., 2014), sample powders were reacted with 30% hydrogen peroxide at 8 °C for 48 h to remove any organic contaminants. The enamel samples were then rinsed five times with water and reacted with 1 M acetic acid with a 1 M calcium acetate buffer (pH: 5) at 8 °C for 24 h to remove any exogenous carbonate. Samples were again rinsed five times and then freeze dried for 24 h. The cleaned enamel samples and approximately 2 cm of silver thread (to react with any SO2 generated during acidification) were reacted with 100% phosphoric acid in a Kiel automatic carbonate extraction device. A Finnigan MAT 252 isotope ratio mass spectrometer was used to measure the carbon and oxygen isotopic composition of the resulting CO2. Values were normalized by repeated analysis of carbonate standards (Carrara marble, NBS-19) and analytical precision for all values is better than 0.1‰. All isotope analyses of paleosols and teeth were completed at the University of Minnesota Stable Isotope Lab.

Stable isotope results and interpretations

Pedogenic carbonates and bulk soil organic matter

Twenty of the 75 sediment samples exhibit the expected +14–17‰ offset in δ13C values of pedogenic carbonate and organic matter (ΔCO3-OM), indicating that these are appropriate for use in paleoenvironmental reconstructions (Fig. 5, Supplementary Online Material [SOM] Table 1). This subset of paleosols comes from several stratigraphic sections along a ~1 km transect at the Nyamita locality on Rusinga (Fig. 1, SOM Table 1). The stratigraphic sections at Nyamita and Wakondo were correlated using the chemical composition of volcanic glass in the Nyamita and Wakondo Tuffs, allowing us to demonstrate that the paleosol carbonates discussed here are from roughly contemporaneous strata that sample different parts of the landscape (Tryon et al., 2010; Van Plantinga, 2011). Although we do not have unambiguously reliable isotopic data from paleosols in other Wasiriya or Waware Bed localities (Fig. 1), tephra correlations indicate that all of the Wasiriya and Waware Bed deposits are contemporaneous (Blegen et al., 2014). Furthermore, the similarities in large mammal taxonomic composition and in the sedimentary facies at all localities on both islands (e.g., Tryon et al., 2012, 2014) indicate that the deposits at Nyamita are representative of local environments on Rusinga and Mfangano Islands during the Late Pleistocene.

For those samples with ΔCO3-OM = +14–17‰, percent carbon and δ13C value of organic matter are not correlated (r = 0.07, p = 0.78), but for the samples that have ΔCO3-OM values outside of the range of 14–17‰, percent carbon and δ13C value of organic matter have a weak but statistically significant positive correlation (r = 0.54, p < 0.001). Additionally, for most of those samples, ΔCO3-OM is less than 14‰. One interpretation is that the carbonate δ13C values are reliable and that degradation of organic matter by soil microbiota shifted organic matter systematically to lower δ13C values. This requires preferential consumption of isotopically heavy compounds by soil microbiota during degradation, leaving a residue of organic matter with low δ13C values. Degradation would have to have been completed after the bulk of carbonate precipitated. Under this interpretation, samples with higher carbon content and higher δ13C values (i.e., greater C4 biomass) would be closer to pristine than those with lower carbon content and lower δ13C values. However, early organic matter diagenesis in modern soils enriches residual organic matter in δ13C (Wynn et al., 2005; Wynn, 2007), which would lead to a negative correlation between percent carbon and organic matter δ13C value. Thus, it is possible that all organic matter δ13C values are within a couple permil of original soil organic matter values and most carbonate δ13C do not reflect only soil derived CO2.

All but three carbonate samples were a mix of very small, distributed nodules and disseminated carbonate within the matrix

Figure 5. Paleosol carbonate and organic matter δ13C values. Diamonds are those samples from the Nyamita locality, squares represent samples from the Wakondo locality, and circles represent samples from the Kakrigu locality. Solid symbols are those samples that fall within the expected enrichment range (+14–17‰ offset in δ13C values of carbonate and organic matter), and open symbols are those that fall outside of the expected enrichment range. The shaded area indicates the expected enrichment range. Samples that fall outside this shaded area most likely represent sediments with a significant soil microbiota contribution, carbonates formed under low soil respiration rates, or non-pedogenic carbonates.
that could reflect later, non-pedogenic precipitation of cements that could be influenced by the sub-surface hydrology related to the nearby tufa deposits. In addition, equilibrium fractionation of carbon isotopes during precipitation of carbonate is temperature-dependent, and the enrichment of pedogenic carbonate in $^{13}$C relative to source CO$_2$ is inversely proportional to soil temperature (Deines et al., 1974; Romanek et al., 1992). Thus, for the range of soil temperatures (40–25 °C) measured in modern Kenyan soils (Passey et al., 2010), we would expect less enrichment of soil carbonates in $^{13}$C than for the temperature range of 25–0 °C that is commonly assumed (ca. +7.2 to +9.8‰ versus +9.8 to +12.4‰, respectively). We do not have independent estimates of soil temperatures for our samples, but many of the samples with $\Delta_{CO3-OM}$ less than 14‰ may reflect higher than expected soil temperature and actually be reliable for paleoenvironmental interpretation. It is notable in this regard that the samples with high soil organic matter $\delta^{13}$C values and relatively low carbonate $\delta^{13}$C values indicate higher proportions of C$_4$ biomass and therefore less woody cover and shade, which would result in higher soil temperatures.

As there is no simple means to determine whether the pedogenic carbonate or organic matter preserves original isotopic composition, and given that we do not have constraints on soil temperature at the time of carbonate precipitation, the conservative approach taken here is to consider only those samples from Nyamita ($n = 20$) for which carbonate and organic matter $\delta^{13}$C values reflect the expected offset range (14–17‰) for modern soils (Fig. 5). To interpret the paleosol carbonate and organic matter carbon isotopic values within the context of modern biomes, we use published $\delta^{13}$C values from modern tropical soils and the UNESCO classification of African vegetation based on woody cover as well as more commonly used ecosystem classifications (Fig. 6a and b; White, 1983; White et al., 2009; Cerling et al., 2010, 2011). Of 11 modern tropical ecosystems with soil organic matter $\delta^{13}$C values within one standard deviation of the mean $\delta^{13}$C for our samples (after correction to the equivalent modern value), five are statistically indistinguishable based on Student’s $t$-tests (Table 2): dry deciduous forest, woodland, Ethiopian riparian woodland, (riparian) woodland, and shrubland/bushland. From this list, and based on the fluvial character of the Wasiriya and Waware Beds and presence of spring deposits, the most consistent interpretation is that the Rusinga and Mfangano habitats sampled were riparian woodlands. This implies 40–80% woody cover with an open stand of trees and a field layer of grasses (White, 1983).

For the 20 samples that have $\Delta_{CO3-OM} = 14–17$‰, the distribution of both organic matter and carbonate $\delta^{13}$C values indicate dominantly C$_3$ biomass at Nyamita with a few samples that suggest

![Figure 6](image-url)
the presence of a minor C₄ grass component (Fig. 6c). These samples include the three carbonate nodules that were larger (although still less than ca. 1 cm in diameter) and distinct enough to be analyzed separately from matrix. However, if we assume that all of the organic matter samples are unaltered, the distribution of the 75 organic matter δ¹³C values also indicates a broad, dominantly C₃ mode and a second, narrower C₄ mode consistent with a temporally or spatially variable woodland and tropical grassland ecosystem. Despite our uncertainty as to the reliability of the carbonate data, the distribution for all 75 paleosol carbonate δ¹³C values notably has a similar shape although with a secondary mode that suggests a lower percentage of C₄ grasses at these sites than the secondary mode for the organic matter δ¹³C values (Fig. 6d).

As the Rusinga and Mfangano faunal community does not have a clear modern analog either, Cerling et al. (2010, 2011) demonstrated that δ¹³C values of soil organic matter could be used to estimate percent woody cover for tropical soils (using average end member δ¹³C values for C₃ and C₄ biomass of ca. −26.2 and −12.5‰, respectively; see Cerling et al., 2010:Fig. 1). This method allows for a paleoenvironmental reconstruction that is not dependent on a modern ecosystem analog and indicates an average of 64% woody cover (±18%) for the 20 samples that have ΔCO₂-OM = 14−17‰—a woodland habitat that is consistent with our reconstruction from carbonate and organic matter δ¹³C values. Interestingly, we see local variability in paleosol δ¹³C values across the ~1 km Nyamita transect (see SOM Table 1), with samples collected above the Nyamita Tuff pointing to an increase in C₃ plant cover towards the spring deposit, suggestive of a moisture gradient influencing local biomass composition.

Mammalian tooth enamel: carbon isotopes

Tooth enamel δ¹³C values are presented in Figs. 7 and 8, and are given by specimen with summary statistics for each taxon in SOM Table 2. Regardless of which end members are assumed in the linear mixing model, most (>76%) of the individual mammal specimens sampled consumed >70% C₄ plants. The different mixing models result in only ~10% variation in the reconstructed amount of C₄ biomass in the diet of each specimen because most individuals consumed such a high proportion of C₄ biomass. For example, Rusingoryx atopocranion (mean δ¹³C = −0.6‰) is estimated to have consumed 74−86% C₄ plant biomass, depending on the mixing model assumed. The isotopic data confirm that the Late Pleistocene fauna is dominated by grazing species, with the only pure C₃ feeder represented by a single Hippopotamus specimen from Mfangano Island, which exhibited an uncommonly low δ¹³C value. taxa with a predominantly C₄ diet (δ¹³C > −1‰, cf. Kingston, 2007; Kingston and Harrison, 2007) account for 87% and 74% of the ungulate specimens sampled from Rusinga and Mfangano, respectively. The abundance of C₄ feeders relative to C₃ browsers or C₃-C₄ mixed feeders implies the existence of an expansive C₄ grassland in the region. Indeed, the relative abundance of C₄ feeders at Rusinga exceeds the proportions observed in modern open habitat areas in Africa, including Ngorongoro, Serengeti, and Lake Turkana (Spoinheimer and Lee-Thorp, 2003, Fig. 9).

The extinct boids analyzed from Rusinga and Mfangano show a strong preference for C₄ grasses. For the previously unsampled extinct alcelaphine boids, Rusingoryx atopocranion and D. hypsodon, the average enamel δ¹³C values (−0.6 ± 1.9‰ and −0.2 ± 2.7‰, respectively) demonstrate they were consuming a diet of almost exclusively C₄ grasses, consistent with inferences derived from their morphology (Faith et al., 2011, 2012). A single measurement for the extinct unnamed impala, distinguished from modern Aepyceros melampus by its large size and exceptional hypodonta (Faith et al., 2014), yields a δ¹³C value toward the C₄ end member value for tooth enamel (−2.7‰). This is likewise consistent with its dental morphology, although the δ¹³C value also falls within the range of observed values of modern impala—a species characterized by exceptional dietary flexibility ranging from C₄ to

![Figure 7. Enamel carbon and oxygen isotope values of fossil mammals from Rusinga and Mfangano Islands. Enamel δ¹³C values expressed as modern equivalents based on mean estimated δ¹³C value of late Pleistocene atmospheric CO₂ of −6.6 ± 1‰ (see text) and modern δ¹³C value of −8.0‰. Heavy dashed lines represent expected δ¹³C values of enamel for herbivores eating end member diets with mean C₃ and C₄ plant δ¹³C values of −27.4 and −12.7‰, respectively; grey boxes indicate one standard deviation around mean values for C₃ and C₄ plants (±1.6 and 1.1‰, respectively). Long dashed line represents the expected enamel δ¹³C value for end member C₁ diet under arid conditions (−24.5‰, all plant values from Passey et al., 2002)). Percent C₄ is calculated using a linear mixing model: δ¹³C(unknown) = xδC₄ + (1 − x)δC₃, where x is the percent C₄ and end member δ¹³C values are given by C₃ and C₄. We calculated mixing models for five pairs of end members using an apparent enamel enrichment relative to diet of ~14‰ (Cerling and Harris, 1999): (A) mean C₃ and C₄ plant δ¹³C values (i.e., heavy dashed lines), (B) mean C₃ end member shifted positively by one standard deviation (1.6‰) and mean C₄ end member, (C) arid climate C₃ end member (i.e., long dashed line) and mean C₄ end member, (D) arid climate C₃ end member and mean C₄ end member shifted positively by one standard deviation (1.1‰), which is the most conservative model with regards to estimated C₄ percent in diet, (E) arid climate C₃ end member shifted positively by one standard deviation (11‰) and mean C₄ end member shifted positively by one standard deviation (1.1‰).](https://example.com/figure7.png)
C₃ dominated diets (e.g., Sponheimer et al., 2003a; Codron et al., 2006, Fig. 8). Our data also include the first isotopic analyses for the extinct giant buffalo (*Syncerus antiquus*; average $\delta^{13}C = 0.5\%$) and giant wildebeest (*Megalotragus* sp.; average $\delta^{13}C = -2\%$) from the Late Pleistocene of East Africa, with results showing that both consumed at least 80% C₄ plant biomass, consistent with isotopic
evidence for these taxa in South Africa (Lee-Thorp and Beaumont, 1995; Codron et al., 2008). Although the δ13C values from most of the Late Pleistocene taxa sampled in this study fall within the range of their modern con specifics (Fig. 8), the suids in particular suggest a substantial departure from their modern representatives. The bushpig (Potamochoerus sp.) sampled from the Wasiiriya Beds was consuming an unusually high proportion of C4-derived foods (δ13C = 0.9‰; 77–87% C4), overlapping with the extant warthog (Phacochoerus). In contrast, extant Potamochoerus porcus from equatorial Africa has a mixed C3–C4 diet, although consisting primarily of C3 plants (mean δ13C = −9.4 ± 5.3‰), whereas extant Phacochoerus aethiopicus (δ13C = −0.5 ± 1.2‰) and Phacochoerus africanus (δ13C = −1.4 ± 1.0‰) are grazers and consume diets of pure C4 biomass (Harris and Cerling, 2002; Kingston and Harrison, 2007). Bushpigs are omnivorous, with preferred plant foods including roots, tubers, bulbs, rhizomes, grasses, berries, and fruits (Bishop, 2010). The δ13C signal found in these fossil bushpigs further attests to the dominance of C4 plant species in the environment and may reflect a greater reliance on C4 grasses or consumption of C4 underground storage organs (e.g., Yeakel et al., 2007).

Mammalian tooth enamel: oxygen isotopes

Using the ES-warthog aridity index regression (from Levin et al., 2006), δ18O values for the Rusinga and Mfangano Island fauna predict a water deficit (WD) of 974 mm (Fig. 10), which is considerably more arid than present day Rusinga Island and nearby Kisumu (WD = 774 and 562 mm, respectively). Based on our current sample size of isotopic data for fossil mammals, we do not yet have sufficient statistical power to compare this estimate quantitatively with modern values for the region or with values for other Late Pleistocene fossil sites. However, the aridity implied by our estimated WD is consistent with previous paleoecological inferences based on the fauna, which also suggest that the surrounding region consisted of habitats that were more arid than present day environments (Tryon et al., 2010, 2012, 2014; Faith et al., in press). Assuming comparable evapotranspiration in the past, the WD of 974 mm implies a 200 mm (>20%) reduction in annual rainfall (to ~820 mm/yr). A drop in annual rainfall of this magnitude would initiate a series of feedback mechanisms leading to a reduction in lake level (Broecker et al., 1998; Milly, 1999). The estimated reduction in precipitation and lake levels would be even greater if evapotranspiration were lower, that is, between 100 and 45 ka, as is likely under cooler temperatures. A significantly reduced Lake Victoria is also consistent with bathymetric and ecological models suggesting a minimum ~25 m drop in lake level, connecting Rusinga and Mfangano to the mainland at the time of hominin occupation (Tryon et al., 2012, 2014).

Discussion and conclusion

Regional approaches to reconstructing paleoenvironments typically provide resolution at temporal or spatial scales that exceed those relevant to hominin populations (e.g., Blome et al., 2012). However, the combined evidence here from sediments, fauna, and isotopic analyses of paleosol carbonates and soil organic matter documents both the microhabitats where MSA artifacts and fauna accumulated as well as the broader landscape that would have been exploited by human foragers. Our analyses suggest that the Late Pleistocene deposits on Rusinga and Mfangano Islands sample stream- or spring-side woodland settings (64 ± 18% woody cover) within a larger C4 grassland environment that was drier than today. The dominance of ungulates with a diet of primarily C4 vegetation provides strong evidence for a substantially greater expansion of C4 grasslands into equatorial eastern Africa than was previously known. In comparison with ~2 Ma sediments from the nearby site of Kanjera (Plummer et al., 2009), it may be that C4 grasslands repeatedly expanded and contracted across the Lake Victoria region in relation to Pleistocene climate fluctuations. However, the association of stone tools with the paleosols and fossils sampled here suggest that, in some cases, humans persisted during intervals of drier conditions with expanded grassland cover rather than migrating into wetter habitats. They did this by exploiting locally closed and well-watered habitats within the larger grassland communities.

The aridity index, although based on limited data, suggests an increased water deficit and as much as a 20% reduction in annual precipitation compared with the region today. As the expanse of Lake Victoria is largely rainfall dependent (Kendall, 1969; Broecker et al., 1998; Milly, 1999), this and other lines of evidence imply a substantial reduction in water level, likely transforming Rusinga and Mfangano into topographic highpoints on a grassland landscape, which would have supported more wooded habitats in an otherwise rich open grassland ecosystem (Tryon et al., 2014). The association of lake level decline together with the expansion of grasslands across the Lake Victoria basin has also been documented during the Last Glacial Maximum (Kendall, 1969; Talbot and Livingstone, 1989; Talbot et al., 2006), suggesting a general pattern that may have occurred repeatedly during drier phases of the Pleistocene. These environmental changes would have facilitated hominin dispersal between equatorial East Africa and Central Africa by the removal of probable biogeographic barriers, including the lake itself and the equatorial forest belt (reviewed in Faith et al., in press). Genetic evidence for possibly environmentally mediated dispersals during the Late Pleistocene is provided by Soares et al. (2012), who document the dispersal of hominin populations from East Africa to Central Africa between 60 and 35 ka and their dispersal out of Africa between 70 and 60 ka. Thus, climatically driven changes in past environments may have played a central role in facilitating hominin dispersals during the Late Pleistocene.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2014.10.005