FISEVIER

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo



Oxygen isotope analyses of ungulate tooth enamel confirm low seasonality of rainfall contributed to the African Humid Period in Somalia



Rachel E.B. Reid^{a,*}, Mica Jones^a, Steven Brandt^b, Henry Bunn^c, Fiona Marshall^a

- ^a Department of Anthropology, Washington University, St. Louis, MO 63117, United States of America
- ^b Department of Anthropology, University of Florida, Gainesville, FL 32611, United States of America
- ^c Department of Anthropology, University of Wisconsin, Madison, WI 53706, United States of America

ARTICLE INFO

Keywords: Carbon isotopes Serial-sampling Terrestrial paleoclimate Eastern Africa Dik-dik Warthog

ABSTRACT

During the African Humid Period (AHP), between ~14 and 5 ka, north and eastern Africa were much wetter and greener than they are today. Although the AHP has long been attributed to an increase in rainfall driven by orbital forcing, many details regarding the timing, pacing, and contributing moisture sources remain to be determined, especially for eastern Africa. Recent research suggests that both Atlantic and Indian Ocean moisture contributed to the AHP in eastern Africa. Large mammalian faunas from two Late Pleistocene/Holocene rockshelter sites in southern Somalia, Gogoshiis Qabe and Guli Waabayo, provide an unusual opportunity to investigate the AHP in an area of eastern Africa that is orographically isolated from Atlantic Ocean moisture. To track changes in aridity at these sites, we used the oxygen isotope aridity index, which exploits the difference in tooth enamel oxygen isotope (δ^{18} O) values between evaporation insensitive obligate drinkers and evaporation sensitive non-obligate drinkers to calculate a water deficit value. Water deficit values calculated from dik-dik (Madoqua spp.; non-obligate drinkers) and warthog (Phacochoerus spp.; obligate drinkers) tooth enamel δ^{18} O values at Gogoshiis Oabe and Guli Waabayo are in agreement and progressively increase toward the present. Additionally, two of three direct dated serially-sampled warthog teeth (ID 4032 and 4033) from Guli Waabayo demonstrate low seasonality of rainfall during much of the AHP (range in δ^{18} O $\leq 1.8\%$). One tooth (ID 4035) with high amplitude variability in δ^{18} O values (3.1‰) dates to 8470 \pm 66 cal yr B.P., a period identified as a lowstand in several lake level records. Our results suggest that regions isolated from Atlantic Ocean moisture likely experienced a less-pronounced AHP than those receiving moisture from multiple sources but indicate less seasonal variability than present. Our findings also support the presence of climate variability within the AHP.

1. Introduction

The climatic and vegetation shifts in northern and eastern Africa associated with the African Humid Period (deMenocal et al., 2000) were some of the most extensive documented on the African continent in the past 20,000 years. At the height of the African Humid Period, which lasted from about 14 to 5 thousand years ago, lush savannah grasslands and woodlands flourished in areas like the Sahara and parts of eastern Africa that are arid today (e.g., deMenocal et al., 2000; Gasse, 2000; Ivory and Russell, 2018). Subsequent aridity resulted in human migrations, however in the Horn of Africa (which today includes the nations of Djibouti, Eritrea, Ethiopia and Somalia) hunter-gatherers persisted throughout the Holocene (Jones et al., 2018; Lesur et al., 2014). The ultimate driver of the African Humid Period—increased rainfall induced by orbital forcing (Kutzbach and Otto-Bliesner,

1982)—is well-accepted. Regional variability in the timing and contributions of different moisture sources has yet to be worked out, however. This is especially true for eastern Africa, which is known for its high-altitude topography, low lying semi-arid regions and other diverse environments. The emerging consensus is that there were two moisture sources responsible for the African Humid Period in eastern Africa, as is the case today: Indian Ocean moisture and Atlantic Ocean moisture (Costa et al., 2014; Tierney et al., 2011a). Liu et al. (2017) recently argued that the African Humid Period in eastern Africa can be divided into two phases; the first (~12–8 ka) caused primarily by delivery of Atlantic Ocean moisture and the second (8–5.5 ka) driven by moisture from the Indian Ocean. The available data concerning this time period in eastern Africa mainly come from lakes along the Rift zone (e.g., Berke et al., 2014; Costa et al., 2014; Foerster et al., 2012; Junginger et al., 2014; Lyons et al., 2015; Morrissey and Scholz, 2014;

^{*} Corresponding author at: Campus Box 1114, One Brookings Dr., Washington University, St. Louis, MO 63130-4899, United States of America. E-mail address: rebreid@vt.edu (R.E.B. Reid).

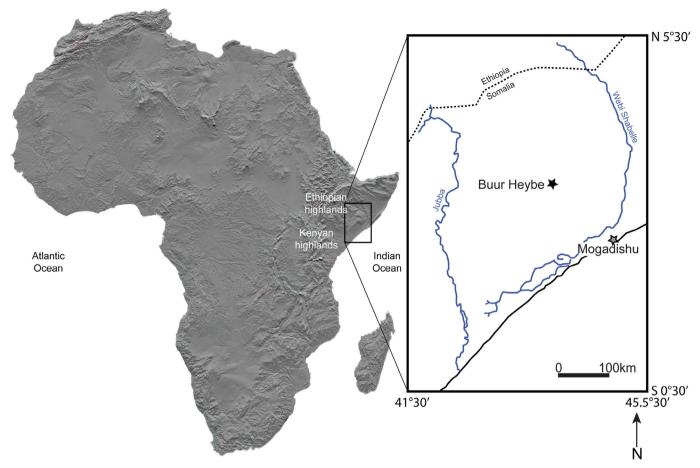


Fig. 1. Map of the Buur Heybe Inselberg in Somalia, modified from Brandt (1988). Topographic map of Africa sourced from NASA/JPL/NIMA.

Tierney et al., 2011b), mountains (Barker, 2001; Thompson, 2002), or from ocean cores off the coast of eastern Africa that receive sediment from rivers sourced in the highlands (Liu et al., 2017; Tierney and deMenocal, 2013). Two archaeological sites located outside the Rift Valley in Somalia provide an opportunity to examine changes in climate across this period in a previously unsampled region orographically isolated from Atlantic Ocean moisture (Fig. 1). The goal of our research was to determine the magnitude of the African Humid Period in the inter-riverine region of Somalia and to test the hypothesis that humid conditions during the African Humid Period in eastern Africa can be explained by low rainfall seasonality (Tierney et al., 2011a). To infer past climate and environment, we considered oxygen and carbon isotope values in ungulate tooth enamel sourced from two archaeological sites (Guli Waabayo and Gogoshiis Qabe) at Buur Heybe Inselberg in the inter-riverine region of Somalia (Fig. 1). We anchored these specimens in time by radiocarbon dating a subset of teeth from Guli Waabayo and rely on previously published dates for Gogoshiis Qabe (Brandt, 1988). Our research focused on three species—warthog (Phacochoerus spp.), dik-dik (Madoqua spp.), and bushpig (Potamochoerus spp.)—which are relatively abundant in the sites and obtain their water by different means. To estimate past aridity (as water deficit, WD) at the sites we generated a taxon-specific version of the recently updated oxygen isotope aridity index (Blumenthal et al., 2017; Levin et al., 2006) using data from Blumenthal et al. (2017). We also evaluated changes in rainfall seasonality by serial sampling oxygen isotope values in three directly dated warthog molars sourced from a range of depths within the Guli Waabayo assemblage. Because rainfall amount and seasonality control the distribution of vegetation throughout most of lowland tropical Africa, pollen records have been previously used to infer past changes in rainfall seasonality (Ivory et al., 2012), but the ability to resolve seasonal-scale rainfall patterns is limited. Serially-sampled teeth, therefore, provide a unique opportunity to investigate past seasonality. To contextualize the data acquired from archaeological warthog teeth, we also serially-sampled five modern warthog molars from Kenya.

2. Regional setting and approach

2.1. Setting

The adjacent rockshelters of Gogoshiis Qabe and Guli Waabayo (2.993 N, 44.304 E), are located at the base of Buur Heybe, a large granitic inselberg ~180 km northwest of the capital city, Mogadishu, in the inter-riverine area of Somalia (Fig. 1). The sites were first excavated in the late 1930s and early 1940s (Clark, 1954; Graziosi, 1940). Between 1983 and 1989 Steven Brandt and the Buur Ecological and Archaeological Project re-excavated the shelters, revealing a Late Pleistocene-Holocene sequence at Guli Waabayo and an early to late Holocene sequence at Gogoshiis Qabe (Brandt, 1986, 1988). Gogoshiis Qabe and Guli Waabayo are two of > 100 rockshelter sites found at Buur Heybe, the majority of which are thought to date to the early- to mid-Holocene based on pottery and stone tools (Brandt, 1988). These sites represent a rare archive-two of three Holocene Somali archaeological sites currently curated in the United States-which survived the destruction of the National Museum in Mogadishu. The climate of the surrounding area today is semi-arid with a mean annual rainfall of ~560 mm (Baker et al., 1995). Rainfall is distributed bimodally during two rainy seasons, from March-May and from October-November (Nicholson, 1996, 2017). Today, rainfall collects in artificial and natural pools below the inselberg, creating one of the few perennial water sources for the area. A few spring-fed water pools are also available. Vegetation around Buur Heybe is comprised of plants common to both wetter and drier precipitation regimes and includes deciduous and evergreen forests as well as bush and herbaceous ground cover (Brandt, 1988).

For some time, meteorologists and climatologists have considered two major convergence zones to define the present precipitation regimes in eastern Africa: the Intertropical Convergence Zone (ITCZ) and the Congo Air Boundary (CAB), which divides the air flows from the Atlantic and Indian Oceans (e.g., Nicholson, 1996; Tierney et al., 2011a). Nicholson (2018, 2017) has argued recently that the concept of the ITCZ is inappropriate for equatorial Africa. She suggests the seasonal cycle of rainfall in eastern Africa is better attributed to the lowlevel Turkana jet and changes in moisture flux associated with sea surface temperature changes in the western Indian Ocean (Yang et al., 2015). Moisture sourced from the Atlantic Ocean also plays a role in seasonal rainfall in the northern and northwestern parts of eastern Africa, such as northern Ethiopia, Eritrea, and Djibouti (Nicholson, 2017), as does moisture advection from the Congo Basin (Levin et al., 2009). Somalia, however, is orographically isolated from this Atlantic-Ocean-derived moisture by the Ethiopian and Kenyan Highlands, making it much more arid (Nicholson, 1996; Sepulchre et al., 2006). Precipitation in Somalia is instead derived from the Indian Ocean (Williams et al., 2012). Significant interannual variability in precipitation in easternmost Africa is caused by changes in Walker circulation—zonal atmospheric overturning cells driven by a basin-wide sea surface temperature (SST) differential—over the Indian Ocean (Tierney et al., 2011a; Konecky et al., 2014; Nicholson, 2017). Both proxy and model evidence suggest that, on multidecadal timescales, variations in the SST gradient across the Indian Ocean (and associated changes to Walker circulation) serve as a significant control on eastern African hydroclimate (Nicholson, 2017, 1996; Tierney and deMenocal, 2013).

2.2. Isotopic background

The carbon and oxygen isotope compositions of mammalian tooth enamel are well-established tools for paleoenvironmental and paleoclimatic reconstructions of terrestrial environments (Bocherens et al., 1996; Koch, 1998; Kohn, 1996). Hydroxyapatite, the inorganic mineral phase of tooth enamel, is relatively stable in surface weathering environments and therefore less-susceptible to diagenesis than bone or dentine (Bocherens et al., 1996; Wang and Cerling, 1994). The carbon isotope (δ^{13} C) values of mammalian tooth enamel provide information about past diet, permitting reconstruction of habitat preferences as well as ecological niche dimensions (e.g., Ascari et al., 2018; Cerling et al., 2015; Chritz et al., 2019; Koch, 2007; Uno et al., 2018). Tooth enamel oxygen isotope values (δ^{18} O) can be measured in either phosphate or structural carbonate, which precipitate in equilibrium with one another but have different fractionations from body water (Bryant et al., 1996). In medium to large mammalian herbivores the δ^{18} O value of bioapatite is in equilibrium with body water and reflects the δ^{18} O value of meteoric (precipitation-derived) water via ingested drinking water, food, and inspired air (Kohn, 1996). Both animal physiology and drinking behavior also mediate the relationship between body and meteoric water δ^{18} O values (Kohn, 1996). In the African tropics, the δ^{18} O value of meteoric water is primarily dictated by rainfall amount, elevation, and moisture source (Levin et al., 2009) and is positively correlated with mean annual temperature. Temporal variations in enamel δ^{18} O values within a given taxon therefore document changes in climate and environment, such as aridity, precipitation seasonality, and precipitation source (Blumenthal et al., 2017; Bryant et al., 1996; Bryant and Froelich, 1995; Fricke and O'Neil, 1996; Kohn, 1996; Levin et al., 2006;

Drinking behavior is a particularly powerful predictor of oxygen isotope values in tooth enamel. Evaporation can enrich the δ^{18} O value of continental water bodies and this effect is even more pronounced in

leaves due to evapotranspiration (Barbour, 2007). Animals that are non-obligate drinkers, obtaining sufficient water from the leaves they eat, will have significantly higher tooth enamel δ^{18} O values, therefore, than obligate drinkers that require water from open water sources. The oxygen isotope aridity index capitalizes on the isotopic differences among taxa with different strategies for obtaining water; evaporation insensitive (EI) taxa (obligate drinkers) provide a record of meteoric water δ^{18} O values while evaporation sensitive (ES) taxa (non-obligate drinkers) have evaporatively enriched δ^{18} O values. By tracking changes in the difference between the δ^{18} O values of EI and ES taxa, changes in past aridity can be estimated using modern calibrations (Blumenthal et al., 2017; Levin et al., 2006).

Intra-tooth oxygen and carbon isotope values acquired through serial sampling provide a record of seasonal climate variability because mammalian tooth enamel forms incrementally as it erupts and, once mineralized, is not remodeled (Fricke and O'Neil, 1996; Koch et al., 1989). Samples taken in sequence perpendicular to the growth axis from the crown apex to the enamel-root junction provide a chronological isotopic record over the period of tooth growth. This sequential sampling approach has been used successfully in teeth from a range of species to investigate paleoclimate and paleoecology (Higgins and MacFadden, 2009; Nelson, 2005; Uno et al., 2018), past animal diet (Chritz et al., 2016; Zazzo et al., 2010), seasonal mobility patterns of domestic and wild animals (Balasse et al., 2002; Britton et al., 2009; Julien et al., 2012), and seasonality of birth (Balasse et al., 2012; Frémondeau et al., 2012). As obligate drinkers, warthogs (Phacochoerus spp.) fit with taxa with enamel carbonate δ^{18} O values that are correlated with surface water δ^{18} O values and that have an inter-annual range of values related to seasonal rainfall amount (Nelson, 2005; Yang et al., 2019). Warthogs also have high-crowned (hypsodont) molars that allow for a significant number of samples to be collected from a single tooth.

2.3. Faunal description

The faunal assemblages from Guli Waabayo and Gogoshiis Qabe at Buur Heybe Inselberg are large, generally well preserved, and taxonomically very similar to each other and to the Rifle Range Site from the nearby Buur Hakaba Inselberg (Jones et al., 2018) but unusual for Holocene eastern Africa. These sites contain diverse assemblages dominated by animals weighing < 20 kg (Brandt, 1988; Jones and Brandt, in prep). A total of 81,733 animal bones were recovered from the Guli Waabayo rockshelter between 1983 and 1989. Of those, 7087 (8.7%) specimens were identifiable to class or higher. Mammal specimens identified beyond class (Mammalia) comprise 70.6% (2861/ 4052) of the mammalian assemblage from the site. Bird, amphibian, and fish bones also occur in low frequencies. Small mammals (< 20 kg), especially dwarf antelope or dik-dik (Madoqua spp.) predominate, making up 76.4% (3096/4052) of the mammalian assemblage and only 23.6% (956/4052) is comprised of large mammals (> 20 kg), e.g. lesser kudu (Tragelaphus imberbis), hartebeest (Alcelaphus buselaphus), oryx (Oryx spp.), warthog (Phacochoerus spp.) and bushpig (Potamochoerus spp.). The Gogoshiis Qabe assemblage is broadly similar to Guli Waabayo, though has not yet been analyzed in detail. The faunal assemblages are presently housed at Washington University in St. Louis (Guli Waabayo) and the University of Wisconsin-Madison (Gogoshiis Qabe).

We conducted isotopic analyses on three taxa that were relatively abundant within the sites, obtain their water in different ways, and occupy slightly different ecological niches. Dik-dik (*Madoqua* spp.) are folivorous dwarf antelope in the tribe Neotragini. They inhabit dry regions of shrubby bush in eastern and southern Africa and they generally form monogamous pairs (Kranz, 1991) that maintain territories of ~5–30 ha (Kingdon, 2015). Dik-dik obtain the water they need from the leaves they eat and are not dependent on surface drinking water (Maloiy, 1973). Warthogs are also nonmigratory and are distributed throughout sub-Saharan Africa. The desert warthog (*Phacochoerus*

aethiopicus) is the species found in Somalia today (d'Huart and Grubb, 2001). Warthogs are primarily grazers, but also consume rhizomes, fruits and berries (Kingdon, 2015). Unlike dik-dik, warthogs are largely dependent on surface water resources, though not as much as bushpigs (*Potamochoerus larvatus*) (Harris and Cerling, 2006). Bushpigs are found in forested areas of east, central and southern Africa (Leus and Macdonald, 1997). They are omnivorous, foraging for roots, seeds, fruits and insects alone and in groups of up to 11 individuals (Venter et al., 2016).

3. Materials and methods

3.1. Excavation methods

Over the course of three field seasons between 1983 and 1989, Steven Brandt and his team dug thirty-two adjoining one-meter-square units at Gogoshiis Qabe and eleven adjoining one-meter-square units at Guli Waabayo (Supplementary Figs. S1 and S2). Excavations at Gogoshiis Qabe reached an average depth of 1.2 m below surface. At Guli Waabayo, nine of the eleven units reached ~1.5 m below surface and two went deeper to ~2.5 m below surface. At the time of excavation, profiles were drawn for at least one wall of each excavation square and the stratigraphy was described using grain size and the Munsell soil color chart. Both sites were excavated in 5 cm arbitrary levels unless natural stratigraphy was observed. All excavated sediments were dry screened using 5 mm mesh to ensure artifact recovery.

3.2. Bulk and serial sampling of teeth

We targeted teeth from dik-dik (n=28), warthog (n=19), and bushpig (n=7) for bulk analyses (Supplementary Table S1). We intentionally selected dental specimens from diverse proveniences to maximize coverage of the faunal sample through time and across the sites. Our sampling strategy reduced the likelihood that any of the specimens came from the same individual. In cases where we sampled multiple teeth from the same context (unit and level), we took into account tooth rows, side and age and avoided possible matches. It is, however, possible that some specimens travelled through the sequence due to mixing. We included some teeth that were not whole—though still identifiable—to maximize coverage of the site. Warthog teeth in particular were identifiable when fragmented as a result of their columnar structure and provided well preserved samples. When multiple teeth from the same individual were available (preserved in a mandible, for example), we sampled molars preferentially.

Because milk tends to be enriched in $^{18}{\rm O}$ and depleted in $^{13}{\rm C}$ in comparison to adult diets, teeth that form before an animal weans might have higher $\delta^{18}{\rm O}$ and lower $\delta^{13}{\rm C}$ values than those that form post-weaning (Fricke and O'Neil, 1996). Nonetheless, a recent study comparing variation in enamel $\delta^{13}{\rm C}$ and $\delta^{18}{\rm O}$ values along the tooth row in seven species of wild African mammals found no systematic offsets among teeth (Luyt and Sealy, 2018). The authors argued that any weaning signal may be swamped by large seasonal shifts and/or variation in birth seasonality, suggesting that sampling teeth that mineralize early is not a significant confounding effect for climatic interpretation.

For serial sampling, we targeted high crowned warthog molars (M_3s) . To our knowledge, wild and domestic Corsican pigs (Frémondeau et al., 2012) are the only suids to have thus far been the subject of a published modern calibration study of tooth formation processes and isotopic signatures. Warthogs—which are also suids—make excellent candidates for serial sampling because they have a characteristic third molar that is quite large and composed of columns of enamel-encased-dentine packed together by cementum. The third mandibular molar (M_3) erupts beyond the alveolar margin when the warthog is between ~ 17 and 20 months of age and increases in length into the 3–4 year age class (Mason, 1984). Eruption of the M_3 further

progresses sequentially from the anterior of the tooth to the posterior, such that with age and wear the anterior columns may be entirely worn away (Mason, 1984). Serial sampling perpendicular to the growth axis of the posterior third molar columns, then, should provide a record of about 1.5–2 years, depending on the degree of wear. Previous work on serially-sampled teeth has demonstrated that both tooth enamel formation and the methods used in serially-sampling lead to some blurring and attenuation of the original source water isotope signal (Green et al., 2018; Passey and Cerling, 2002; Zazzo et al., 2005).

To contextualize the results from serially-sampled archaeological warthog teeth from areas with bimodal rainfall regimes, we also serially-sampled five modern warthog teeth obtained from two sites near Lake Naivasha, Kenya . Like Somalia, this area experiences bimodal rainfall seasonality today, though the climate is generally less arid than in Somalia (WD = $153 \, \text{mm/yr}$; Blumenthal et al., 2017).

We initially cleaned all teeth by sonicating them in MilliQ water. Once dry, we used a toothbrush to scrub off any adhering soil. We used a hand-held drill (Kupa Inc., Anaheim, CA; Dremel, Robert Bosch Tool Corporation, Mount Prospect, IL) fitted with a tungsten drill bit to clean the teeth of remaining dirt and cementum. For bulk, whole tooth samples, we used a diamond drill bit to powder a ~ 2 mm wide section of enamel from the enamel-root junction up to the tooth crown. For serial samples, we used a diamond drill bit to powder ~ 2 mm wide grooves perpendicular to the growth axis; samples are spaced $\sim 1-2$ mm apart and we started at the tooth crown and worked down to the enamel-root junction. To remove organic contaminants and secondary exogenous carbonates, we pretreated the enamel powders with 30% hydrogen peroxide (24 h) and 1 M buffered acetic acid (also 24 h), respectively (Crowley and Wheatley, 2014).

3.3. Isotopic analyses

We conducted isotopic analyses at two institutions: Washington University in St. Louis (WUSTL) and the University of California, Santa Cruz (UCSC) and analyzed eight samples and standards at both institutions to ensure comparability. At WUSTL, we weighed ~1 mg of pretreated sample into individual glass exetainer vials, flushed the vials with He gas, and converted the samples to CO2 through reaction with anhydrous phosphoric acid (Epstein and Mayeda, 1953). Once acidified, samples were heated for 1 to 23 h at 70 °C on a Gas Bench II (Thermo Fisher Scientific, Waltham, MA, USA) and the evolved CO2 was analyzed on a Thermo Fisher Delta V Plus isotope ratio mass spectrometer. We used both internal and international standards (NBS-18, NBS-19, and LSVEC) to calibrate isotopic measurements; analytical errors are < 0.1‰ (1 σ) for $\delta^{13}C_{carb}$ and < 0.2‰ (1 σ) for $\delta^{18}O_{carb}$. At UCSC, pretreated samples were weighed to between 0.5 and 1 mg and analyzed on a Thermo Finnigan MAT253 isotope ratio mass spectrometer interfaced with a Kiel device. As at WUSTL, samples were converted to CO₂ with 100% phosphoric acid. Analytical precision (1σ) is based on repeated analyses of an in-house Carrara marble standard (CM05: $\delta^{13}C = 1.97\%$ VPDB, $\delta^{18}O = -1.61\%$ VPDB) calibrated to international standards NBS-18 and NBS-19: < 0.05% for $\delta^{13}C_{carb}$ and < 0.08% for $\delta^{18}O_{carb}$. We note the location of analysis in our results table (Supplementary Table S1). The average sample differences for a subset of eight samples and standards analyzed in both labs was $0.44\% \delta^{13}$ C and 0.16% for δ^{18} O (Supplementary Table S1). All isotopic values are expressed in per mil (%) notation on the VPDB scale. To convert oxygen isotope ratios in tooth enamel carbonate from the VPDB to the VSMOW scale for water deficit calculations, we used the following equation (Sharp, 2017):

$$\delta^{18}O_{VPDB} = (\delta^{18}O_{VSMOW} - 30.91)/1.03091 \tag{1}$$

We conducted all data analysis in R (R Core Team, 2017). To tie fossil δ^{18} O values measured in bulk tooth enamel carbonate to surface water sources, we also combined published calibration equations to convert the carbonate oxygen isotope values (δ^{18} O_{carb}) to values for

ingested water ($\delta^{18}O_{water}$). We first converted $\delta^{18}O_{carb}$ to phosphate values ($\delta^{18}O_{phosphate}$) using the apparent fractionation factor between these two substrates previously determined for horse tooth enamel ($\alpha = 1.0086$). This transformation is possible because the carbonate and phosphate portions of tooth enamel are in isotopic equilibrium (Bryant et al., 1996; Hoppe et al., 2004). Then, to estimate δ^{18} O_{water}, we averaged the $\delta^{18} {\rm O}_{\rm water}$ values calculated using five different published equations relating $\delta^{18} O_{phosphate}$ with ingested water (Delgado Huertas et al., 1995; Hoppe et al., 2004; Levinson et al., 1987; Longinelli, 1984; Luz et al., 1984). Given the considerable uncertainty associated with each of these equations, Jacumin and Venturelli (2015) argued that a difference of about 3–4‰ is required for calculated δ^{18} O_{water} values to be considered significantly different. We would have liked to also sample the spring water at Buur Heybe for isotopic analysis, but sample collection is not possible in this area of Somalia at present. Data for modern precipitation are also lacking from Somalia, though modelled estimates are available (Bowen and Revenaugh, 2003).

For considering past ungulate diets, we divided animals into three dietary groups based on their tooth enamel $\delta^{13}C$ values following Cerling et al. (2015): C_3 browsers (<-8%), mixed C_3 - C_4 diets (-8 to -1%), and C_4 grazers (>-1%). We did not estimate the percent contribution of C_4 resources to diet.

3.4. The oxygen isotope aridity index

To evaluate changes in aridity at the Somali rockshelter sites, we generated a taxon-specific oxygen isotope aridity index for dik-dik and warthog based on modern calibration data presented by Levin et al. (2006) and Blumenthal et al. (2017). In their 2017 update to the oxygen isotope aridity index, Blumenthal et al. (2017) argued that, despite the original assertion that Neotragini (dwarf antelope) belong in the ES category, the addition of new data suggests that Neotragini δ^{18} O values no longer significantly increase with water deficit (WD). Blumenthal et al. (2017) analyzed their data with a simple linear regression. When analyzed using a weighted linear regression, which is more appropriate given the distribution of data, Neotragini $\delta^{18}{\rm O}$ values are strongly and nearly significantly correlated with WD ($F_{1,4} = 7.109$, $R^2 = 0.64$, p = 0.05602; Fig. 2a). We additionally see a weak (statistically insignificant) correlation between warthog δ^{18} O values and WD $(F_{1,15} = 2.895, R^2 = 0.17, p = 0.1095; Fig. 2b)$ in the data presented by Blumenthal et al. (2017). The standard error of all the modern warthog epsilon values is also 0.46, which is below the threshold of 1.3 quoted by Blumenthal et al. (2017), suggesting that warthogs are, in fact, good candidates as an EI taxon. We proceeded, therefore, to evaluate the relationship between dik-dik and warthog epsilon values and WD, and found that they are positively correlated, though not significantly $(R^2 = 0.54, p = 0.1557, Fig. 2c)$. We calculated water deficits using the following equation derived for isotopic enrichment values of evaporatively sensitive dik-dik relative to warthogs:

WD =
$$(\varepsilon_{dikdik-warthog} + 4.1876)/0.002876$$

where $\epsilon_{dikdik\text{-warthog}}$ is the difference in oxygen isotope values between dik-dik and warthog tooth enamel and WD is the water deficit in mm/yr. Because water deficit estimates are more robust with larger sample sizes, we grouped samples into several broad temporal units at each site based on both site stratigraphy and radiocarbon dates. We additionally calculated a WD value for the African Humid Period as a whole based on values obtained only from directly dated teeth, which were obtained from Guli Waabayo. We recognize that water deficit estimates from this taxon-specific equation provide only general indications of changes in aridity, given the uncertainty in the equation and our relatively small sample sizes. Nonetheless, this equation provides the most accurate estimates possible for these rare sites from southern Somalia, which provide useful insights into the African Humid Period from a region of eastern Africa orographically isolated from Atlantic Ocean moisture.

3.5. Radiocarbon dating

Seven warthog and dik-dik tooth samples from Guli Waabayo were selected for radiocarbon dating. We did not date samples from Gogoshiis Oabe, as published dates already exist for this site (Brandt, 1988). We dated teeth for two reasons: first, we wanted direct dates from samples selected for isotopic analysis and second, collagen was not preserved. Particularly in arid regions such as Somalia, enamel provides a reliable material for radiocarbon dating at least as far back as 40,000 years (Zazzo and Saliège, 2011; Zazzo, 2014). Enamel apatite samples were prepared at the Environmental Isotope Paleogeochemsitry Laboratory, Department of Anthropology, University of Illinois, Urbana-Champaign following methods established by S. Ambrose (Marshall et al., 2018). Briefly, ground enamel samples were treated with 2.63% sodium hypochlorite, rinsed with deionized water (8×), reacted with 0.1 M acetic acid alternatingly under vacuum and N2 gas at atmospheric pressure (\sim 3–4 h), rinsed again (5 \times), and finally frozen and freeze dried. Prepared samples were processed at either the Radiocarbon Laboratory of the Illinois State Geological Survey at the University of Illinois or the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine. We calibrated dates using the Oxcal 4.3 program (Bronk Ramsey, 2009) using the IntCal13 curve (Reimer et al., 2013). Dates are reported in cal yr B.P. (calibrated years before 1950) as mean \pm 1 sigma.

4. Results

4.1. Radiocarbon dating and site chronology

We obtained AMS radiocarbon dates from seven faunal samples from Guli Waabayo, including six ungulate tooth enamel samples and one ungulate dentine sample. These calibrated dates (Table 1) span from the Late Pleistocene through the early Holocene, ranging from

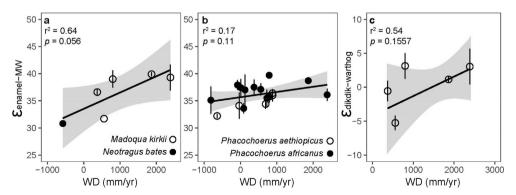


Fig. 2. Relationships between water deficit (WD) and $\varepsilon_{enamel-MW}$ for (a) modern dik-dik and (b) modern warthogs, and (c) the relationship between $\varepsilon_{dikdik-warthog}$ with WD. Data are sourced from Blumenthal et al. (2017).

Table 1
Radiocarbon dates for Guli Waabayo (GW) and Gogoshiis Qabe (GQ), Buur Heybe, Somalia.

Site	Sample ID	Lab ID	Taxon	Material	Unit	Depth below datum	14 C age \pm 1 σ yr B.P.	Calibrated date yr B.P. (95.4% confidence)	Mean $\pm 1\sigma$ calibrated date yr B.P.	Reference
GW	4033	UCI A4686	Warthog	Enamel apatite	S6W18	170–180	6435 ± 20	8405–8536	7370 ± 52	This study
GW	4035	UCI A4684	Warthog	Enamel apatite	S8W18	140-145	7665 ± 20	8536-8405	8448 ± 31	This study
GW	4041	ISGS A3819	Warthog	Enamel apatite	S8W18	180-185	7840 ± 20	8559-8648	8604 ± 45	This study
GW	9204	ISGS A3355	Dik-dik	Dentine collagen	S8W18	210-215	8120 ± 35	8993-9233	9113 ± 120	This study
GW	4029	ISGS A3820	Warthog	Enamel apatite	S9W17	200-205	9780 ± 25	11,185-11,239	$11,212 \pm 27$	This study
GW	9256	ISGS A3821	Dik-dik	Enamel apatite	S9W17	200-205	$10,715 \pm 30$	12,620-12,730	$12,675 \pm 55$	This study
GW	4032	UCI A4685	Warthog	Enamel apatite	S9W17	265-270	$11,910 \pm 25$	13,575-13,791	$13,683 \pm 108$	This study
GQ	1	GX-12436	Human	Bone apatite	S12W33, S13W32, S13W33, S14W33	80–87	8120 ± 440	8071–10,220	9104 ± 530	Brandt, 1988
GQ	2	GX-12127	Human	Bone apatite	S12W33, S12W34, S13W33, S13W34	84–92	6720 ± 430	6671–8445	7600 ± 443	Brandt, 1988
GQ	4	Beta-7473	Human	Bone apatite	S12W32, S12W33, S13W32, S13W33	83–88	5430 ± 90	5996–6400	6201 ± 108	Brandt, 1988
GQ	5	GX-12138	Human	Bone apatite	S15W31, S15W32, S16W31, S16W32	90–104	7060 ± 350	7263–8630	7942 ± 341	Brandt, 1988
GQ	6	GX-12438	Human	Bone apatite	S16W30, S16W31, S17W30	80-97	7400 ± 850	6566-10,685	8550 ± 1025	Brandt, 1988
GQ	9	GX-12129	Human	Bone apatite	\$16W34, \$16W35, \$17W34, \$17W35	79–90	7120 ± 735	6494–9895	8156 ± 846	Brandt, 1988
GQ	10	GX-12437	Human	Bone apatite	S16W34, S17W34, S17W35	73-80	7730 ± 420	7725–9550	8677 ± 476	Brandt, 1988
GQ	11	GX-12130	Human	Bone apatite	S15W34, S15W35, S16W34	79–97	7500 ± 445	7573-9448	8442 ± 492	Brandt, 1988
GQ	13	GX-12131	Human	Bone apatite	S17W33, S17W34	77-105	7275 ± 445	7325-9250	8201 ± 475	Brandt, 1988

Note Lab ID symbols: UCI = University of California, Irvine; ISGS = Illinois State Geological Survey; GX = Geochron Laboratories of Kruger Enterprise, Boston, MA. All GW samples are AMS dates.

Table 2
Summary of tooth enamel isotope data for dik-dik, warthog, and bushpig tooth enamel from Guli Waabayo and Gogoshiis Qabe.

Site	Taxon	n	Min δ ¹³ C (VPDB)	Max δ ¹³ C (VPDB)	Mean δ ¹³ C (VPDB)	SD δ^{13} C (VPDB)	Min δ ¹⁸ O (VSMOW)	Max δ ¹⁸ O (VSMOW)	Mean δ ¹⁸ O (VSMOW)	SD δ ¹⁸ O (VSMOW)
Guli Waabayo	Dik-dik	14	-14.7	-10.1	-12.5	1.3	30.4	35.5	32.3	1.2
Guli Waabayo	Warthog	11	-2.4	1.8	0.3	1.1	25.6	34.1	30.7	2.7
Guli Waabayo	Bushpig	4	-10.9	-6.6	-8.1	1.9	27.4	30.5	29.2	1.4
Gogoshiis Qabe	Dik-dik	14	-15.7	-12.4	-13.8	0.9	28.9	33.4	30.8	1.5
Gogoshiis Qabe	Warthog	8	-0.4	1.2	0.2	0.5	28.5	32.6	30.5	1.3
Gogoshiis Qabe	Bushpig	3	-15.2	-7.7	-10.9	3.9	22.5	30.5	27.5	4.4

13,683 \pm 108 cal yr B.P. to 6252 \pm 43 cal yr B.P. There is considerable mixing of individual faunal samples within the site due to bioturbation common in rockshelters, as was observed during excavation. For this reason, we rely heavily on directly dated tooth enamel samples in our analysis. Certain excavation units, however, appear to be less mixed than others, judging from the three dates from S8W18, for example, which are in stratigraphic order. Radiocarbon dates from Guli Waabayo suggest the site was occupied from at least \sim 14,000 cal yr B.P. until \sim 6000 cal yr B.P. Previously published bone apatite dates from human skeletal remains (n=9) from Gogoshiis Qabe, range from 8677 \pm 476 cal yr B.P. to 6201 \pm 108 cal yr B.P. and indicate that occupation at Gogoshiis Qabe overlapped in time at least partially with occupation at Guli Waabayo (Brandt, 1988).

4.2. Bulk isotopes and aridity index

We analyzed 11 warthog, 14 dik-dik, and four bushpig teeth from Guli Waabayo, which were sourced from throughout the sequence at the site (Table 2, Supplementary Table S1, Fig. 3). At Guli Waabayo, dik-dik have the highest mean tooth enamel $\delta^{18} O_{carb}$ values followed by warthogs and then bushpigs (Table 2). Warthogs have the highest mean tooth enamel δ^{13} C values at Guli Waabayo, followed by bushpigs and then dik-dik (Table 2). Dik-dik δ^{18} O values increase from deep in the record toward the surface (R² = 0.26, p = 0.136) while warthog δ^{18} O values display the opposite trend ($R^2 = 0.57$, p = 0.02; Fig. 3). In contrast to δ^{18} O values, there are no trends with depth for δ^{13} C values in either dik-dik or warthogs at Guli Waabayo. Using only dated teeth (n = 7) that squarely align with the African Humid Period, we calculated a water deficit value of 1474 ± 397 mm/yr for the African Humid Period at Guli Waabayo (dates from 13,683 ± 108 cal yr B.P. to 6252 ± 43 cal yr B.P.). To explore temporal variability at the site, we split samples into two components based on site stratigraphy. Water deficit values increase from 1053 ± 595 mm/yr between 275 and 220 centimeters below datum (cmbd; depth below an arbitrary reference point at the surface) to 1912 ± 452 mm/yr from 215 to 140 cmbd (with sample 4037 excluded from the calculation).

We analyzed eight warthog, 14 dik-dik, and three bushpig teeth from Gogoshiis Qabe (Table 2, Supplementary Table S1, Fig. 4). As at Guli Waabayo, dik-dik have the highest mean tooth enamel δ^{18} O values at Gogoshiis Qabe followed by warthogs and then bushpigs (Table 2). Gogoshiis Qabe warthogs also have the highest mean δ^{13} C values while dik-dik have the lowest (Table 2). Unlike Guli Waabayo, Gogoshiis Oabe dik-dik and warthog δ^{18} O values do not have clear linear relationships with depth (Fig. 4). Instead, both dik-dik and warthog values increase from deep in the record to a depth of 100-105 cmbd, suddenly drop at depths of 85-100 cmbd, and then increase again toward the surface (Fig. 4). Dik-dik and warthog δ^{13} C values remain relatively constant throughout the record, however, displaying values consistent with C3-dominated browsers and C4-dominated grazers, respectively (Cerling et al., 2015; Uno et al., 2018). Based on previous radiocarbon results (Brandt, 1988; see Table 1, Fig. 4), we assume the teeth from Gogoshiis Qabe span the African Humid Period and therefore combined them to calculate a single water deficit value of $1607 \pm 755 \,\text{mm/y}$ for the site. To explore temporal variability further at Gogoshiis Qabe, we split samples into three components based on site stratigraphy. This reveals an increasing trend in water deficit values from deep in the record toward the surface, though errors overlap. We see values increasing from 1159 \pm 277 mm/yr between 165 and 145 cmbd to 1636 \pm 892 mm/yr from 65 to 105 cmbd and finally to 1804 \pm 586 mm/yr from 55 to 45 cmbd.

4.3. Serial samples

We serially-sampled three warthog teeth from Guli Waabayo (samples 4035, 4033, and 4032) sourced from a range of depths below datum (Fig. 5, Supplementary Table S3). The serially-sampled warthog teeth are not in perfect stratigraphic order but this does not affect our analysis because each tooth was directly dated. The oldest sample (4032) was recovered from 265 to 270 cmbd and dates to $13,683 \pm 108$ cal yr B.P., the second oldest sample (4035) was recovered from 140 to 145 cmbd and dates to 8470 \pm 66 cal yr B.P., and the youngest (4033) dates to 7370 \pm 52 cal yr B.P. and was recovered from 170 to 180 cmbd. We obtained fifteen samples from tooth 4032, which has δ^{13} C values ranging from 0.1 to 1.9% VPDB and δ^{18} O values that range from 31.0 to 32.8% VSMOW. Tooth 4035, from which we obtained thirteen samples, has δ^{18} O values that fall between 30.2 and 33.4% VSMOW and δ^{13} C values ranging from 0.1 to 1.0% VPDB. Finally, we obtained thirteen samples from tooth 4033, which has δ^{18} O values of 30.0 to 31.1% VSMOW and δ^{13} C values that range between -0.1 to 1.1% VPDB. Most notably, there is significant variability in the amplitude of oxygen isotope variation among the serially-sampled teeth (from 1.8% for 4032, to 3.2% for 4035, back to 1.1% for 4033; Fig. 5). Minor shifts in the average oxygen isotope values are also evident, with teeth 4035, 4032, and 4033 displaying average δ^{18} O values of $31.7 \pm 1.0\%$, $32.1 \pm 0.6\%$, and $30.5 \pm 0.4\%$, respectively.

We also serially-sampled five modern warthog teeth acquired from Lake Naivasha, Kenya (Table 3, Supplementary Table S4). Between 19 and 30 samples were taken per tooth. Both $\delta^{13}\mathrm{C}$ and $\delta^{18}\mathrm{O}$ values in the warthog teeth show some degree of sigmoidal fluctuation (Supplementary Fig. S3). Average $\delta^{13}\mathrm{C}$ values for the teeth range from $-3.6 \pm 1.8\%$ to $0.33 \pm 0.8\%$ (VPDB; Table 3). Average $\delta^{18}\mathrm{O}$ values range from $30.4 \pm 1.0\%$ to $32.2 \pm 0.7\%$ (VSMOW) and all teeth have relatively high amplitudes of variation in $\delta^{18}\mathrm{O}$ values ($\geq 3\%$), reflecting the high seasonality of rainfall in the region today (Table 3, Supplementary Fig. S3).

5. Discussion

5.1. Site chronology

The seven dates we obtained for Guli Waabayo suggest that the samples studied span a period of at least ~8000 years of occupation at the site from ~14,000 to 6000 cal yr B.P. Stone artefacts and some faunal specimens were recovered from depths well below the dated teeth reported on here (Jones and Brandt, in prep), therefore it is reasonable to believe that occupation at Guli Waabayo extended deeper into the Pleistocene. The same is likely true of Gogoshiis Qabe (Brandt, 1988). Although certain one-meter square excavation units at Guli

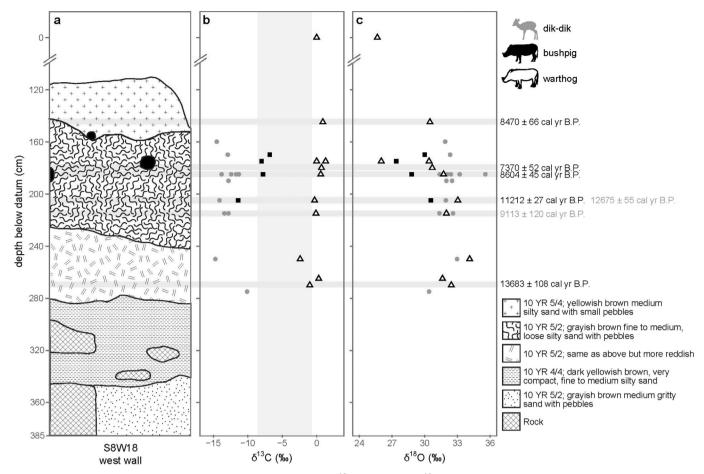


Fig. 3. Representative stratigraphy for Guli Waabayo (a) plotted next to (b) δ^{13} C values and (c) δ^{18} O values (VSMOW) measured in dik-dik (gray circles), bushpig (black squares), and warthog (open triangles) tooth enamel carbonate. Black circles in (a) illustrate holes or depressions caused by termites and/or rodents. Vertical gray band in (b) delineates C_3 browsers (left of band) from C_4 grazers (right of band) (Cerling et al., 2015). Dates listed to the right of (c) that are written in black are from warthog teeth and those written in gray are from dik-dik. Stratigraphy was described in the field using both grain size and Munsell soil colors (e.g., 10 YR 5/4).

Waabayo appear to be sequential and less mixed than others, it is difficult to say with confidence that all the tooth enamel samples we collected are in stratigraphic order. The only way to confirm the stratigraphic placement of each specimen studied would be to date the entire sample, which is impossible for many of the very small dik-dik teeth.

5.2. Enamel isotope values

The low standard deviations for both dik-dik and warthog tooth enamel δ^{13} C values at Guli Waabayo and Gogoshiis Qabe suggest that these taxa maintained similar diets over many thousands of years. Dikdik δ^{13} C values fall consistently into the range expected for C₃ browsers while warthog δ^{13} C values fall consistently in the range expected for C₄ grazers (Cerling et al., 2015). Bushpigs at both sites have δ^{13} C values that suggest they are mixed feeders, browsing combined with consumption of some C4 foods. This is consistent with expectations for bushpigs, which today consume browse in addition to fruits and insects (Venter et al., 2016). Unlike enamel δ^{13} C values, dik-dik, warthog and bushpig enamel δ^{18} O values vary with depth (and therefore broadly with time) at both sites. Changes in oxygen isotope values in dik-dik tooth enamel are not surprising, given that we expect oxygen isotope values to increase or decrease in dik-dik with increasing or decreasing aridity, respectively. Warthog and bushpig tooth enamel should serve as a faithful recorder of surface water δ^{18} O values, which also change seasonally, depending on temperature and rainfall amount. Given that the nearly modern warthog sample from Guli Waabayo has the lowest

 δ^{18} O value (25.7‰, ID 4034), opposite expectations for arid conditions, we suspect that the low δ^{18} O values exhibited by several of the warthogs and bushpigs at Guli Waabayo reflect spring water values, rather than meteoric water. Tooth enamel samples with extremely low δ^{18} O values (\leq 28‰ VSMOW, n=3) come from drinking water sources with a mean calculated $\delta^{18}O_{water}$ value of $-6.2 \pm 1.3\%$ VSMOW, which falls below expected values for first rains from Indian Ocean moisture $(\sim -3\%)$; Levin et al., 2009; Rozanski et al., 1993). These samples also fall outside the range of values for modern warthogs (29.3-36.7%) VSMOW, n = 82; Blumenthal et al., 2017) and modern bushpigs (28.1-31.1% VSMOW, n = 11; Blumenthal et al., 2017) in Africa. Furthermore, other than the near modern sample, the samples with low values come from a narrow depth range in the sequence (\sim 170–185 cmbd) dating to about 7000–9000 cal yr B.P., which corresponds with a dry event evidenced by lake low stands elsewhere in eastern Africa (Bloszies et al., 2015; Junginger et al., 2014; Marshall et al., 2011). It may be that, during dry periods within the decline of the African Human Period, bushpigs and warthogs switched to consuming spring water because it was a more reliable drinking water source than rainfed pools. It is also quite possible that bushpigs and warthogs were partitioning water resources at Buur Heybe, with bushpigs preferentially consuming spring water, and that this partitioning broke down during dry spells when warthogs were unable to find alternative water sources. Alternatively, the bulk isotope samples from bushpigs and warthogs may just be capturing the full range of expected variability in precipitation δ^{18} O values for this region (which today varies by as much as 3.4-4.2%); (Bowen, 2008).

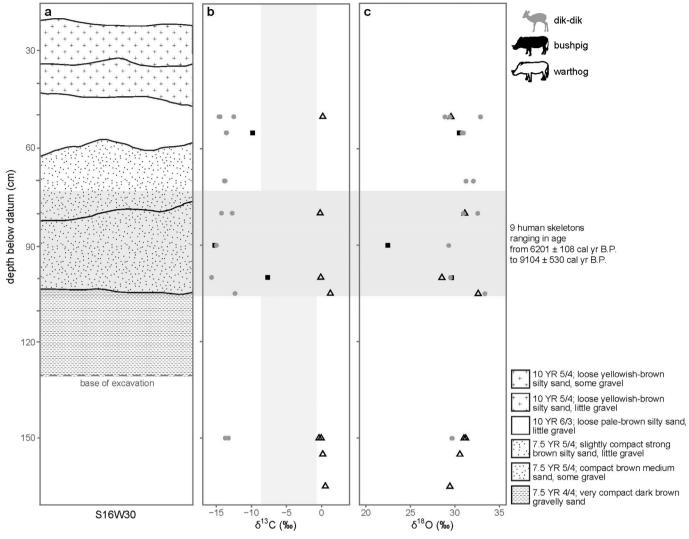


Fig. 4. Representative stratigraphy for Gogoshiis Qabe (a) plotted next to (b) δ^{13} C values and (c) δ^{18} O values (VSMOW) measured in dik-dik (gray circles), bushpig (black squares), and warthog (open triangles) tooth enamel carbonate. Vertical gray band in (b) delineates C_3 browsers (left of band) from C_4 grazers (right of band) (Cerling et al., 2015). Some squares were excavated to greater depths than illustrated for S16W30. Stratigraphy was described in the field using both grain size and Munsell soil colors (e.g., 10 YR 5/4).

5.3. Holocene climate and the aridity index

The climate in eastern Africa has changed dramatically since the Late Pleistocene. Prior to the Humid Period, Somalia, like much of the rest of the region, is thought to have experienced arid conditions during the Last Glacial Maximum (\sim 26–19 ka). Further drying is associated with the North Atlantic cooling event Heinrich 1 (H1; Stager 2011; \sim 19–15 ka), wet conditions with the Bølling-Allerød period (\sim 15–13 ka), and a return to dry conditions during another North Atlantic cold event, the Younger Dryas (YD, \sim 13–12 ka) (Tierney and deMenocal, 2013). The timing of the onset and the termination of the Humid Period itself remains unresolved, however, in part because researchers disagree on whether the African Humid Period began before or after the Younger Dryas. For the purposes of our analysis, we assume that the African Humid Period began \sim 14 ka with the onset of generally wetter conditions in eastern Africa at the conclusion of H1.

Given that Somalia is orographically isolated from Atlantic Ocean moisture, we expected that water deficit values for the African Humid Period in Somalia would be lower than today, but not exceptionally low. However, the water deficit value calculated for the African Humid Period at Guli Waabayo based on directly dated teeth $(1474 \pm 397 \, \mathrm{mm/yr})$ and those calculated for Gogoshiis Qabe

(between 1159 \pm 277 mm/yr and 1804 \pm 586 mm/yr) are very similar to—if not a little higher—than WD values for Somalia today. Following the methods outlined by Blumenthal et al. (2017), we calculated a present day WD value of 1057 mm/yr for Baidoa, Somalia, located ~70 km northwest of Buur Heybe, based on temperature and precipitation data collected from 1961 to 1970 (Baker et al., 1995). With a mean annual temperature of 26.4 °C and mean annual precipitation of 575 mm/yr, present day Baidoa is considered semi-arid (Baker et al., 1995). We are encouraged by the fact that the water deficit records from Guli Waabayo and Gogoshiis Qabe are in broad agreement and that they show a progressive increase toward the conclusion of the African Humid Period, which fits with expectations based on records from other eastern African archives (e.g., Bloszies et al., 2015; Costa et al., 2014). The similarity of the African Humid Period water deficit values to the modern value suggests that the African Humid Period was much less pronounced in regions of eastern Africa isolated from Atlantic Ocean moisture. This result also complements our current understanding of significant local climatological and ecological variability in eastern Africa through the African Humid Period (Chritz et al., 2019). Nonetheless, given the aforementioned uncertainty in our WD estimates, these WD values for Somalia in the Holocene are better considered as broad estimates that provide a benchmark to which

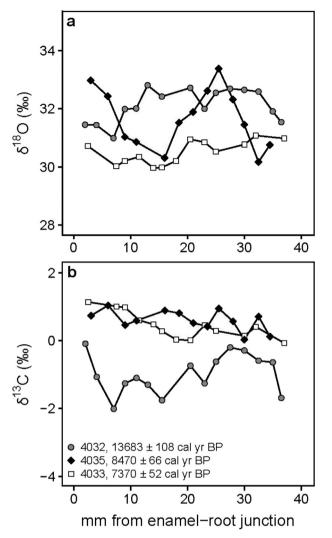


Fig. 5. (a) $\delta^{18}{\rm O}$ values (VSMOW) and (b) $\delta^{13}{\rm C}$ values (VPDB) measured in three directly dated serially-sampled warthog teeth from Guli Waabayo.

to compare to in future research. Future work at these sites could also focus on the abundant ostrich eggshells found in the site assemblages, in which the isotope values of both shell carbonate and protein can be used to reconstruct past climate (Niespolo et al., 2018).

5.4. Serial samples and seasonality

When we look to other studies using serially-sampled teeth in the region, authors have made the case that changes in amplitude reflect changes in rainfall seasonality. Uno et al. (2018) serially-sampled three Pleistocene equid teeth from Olduvai Gorge in Tanzania and observed that the amplitude of variation in δ^{18} O increased from just 1.0% (ID L62-104, FC West) and 0.8% (ID L1-48, MNK Main) for two teeth from interval IIB to 2.3% (ID L10-523, HWK EE) for a tooth from interval IIA. They argued that these data suggest that rainfall seasonality was

reduced in interval IIB relative to interval IIA. Roberts et al. (2018) serially-sampled five fossil Oryx spp. (non-obligate drinkers) and Equus spp. (obligate drinkers) from a Pleistocene site in the Nefud Desert of Saudi Arabia, arguing that large ranges in both Oryx and Equus intratooth $\delta^{18}O$ values (3–6.1‰ and 3.7–6.8‰, respectively) suggest high seasonality of rainfall interspersed with arid conditions leading to significant evaporation.

The low degree of amplitude of oxygen isotope variation in two of the warthog teeth that we studied (Fig. 5; direct dated to $13,683 \pm 108$ cal yr B.P. and 7370 ± 52 cal yr B.P.) suggests that the African Humid Period in Somalia was marked at these times by low seasonality of rainfall amount relative to the present. Our sample sizes are small, but these data are nonetheless strikingly different from today. Modern serially-sampled warthog teeth from Lake Naivasha, Kenya, have much greater amplitudes of oxygen isotope variation (Table 3, Supplementary Fig. S3). Therefore, our findings support the predictions by some modeling efforts (Tierney et al., 2011a), that suggest that humid conditions during the eastern African Humid Period can be at least in part explained by increased dry season precipitation relative to the present. A wetter dry season—an increase in June through September precipitation relative to today-could have been caused by changes in the zonal moisture flux. It is suggested that warm SSTs in the western Indian Ocean could have weakened Walker circulation, resulting in greater rainfall over the western Indian Ocean and East Africa (Tierney et al., 2011a). Other modeling studies have suggested that the African Humid Period in eastern Africa was driven instead by increased wet season precipitation in December through February (Otto-Bliesner et al., 2014). The Holocene tooth enamel records presented here cannot rule out an increase in wet season rainfall amount, however they do suggest that rainfall was not confined to a particular season during some of the African Humid Period. Tooth 4035 (8470 \pm 66 cal yr B.P.), which displays a high amplitude of oxygen isotope variation, dates to a period identified in Rift Valley lake level records as a lowstand (Bloszies et al., 2015; Junginger et al., 2014; Marshall et al., 2011) and in hydrogen isotope records from both lake and ocean cores as D-enrichment corresponding to aridification (Costa et al., 2014; Konecky et al., 2011; Tierney et al., 2008). This suggests that rainfall seasonality was not uniform throughout the African Humid Period. It is likely that both rainfall seasonality and amount changed during these dry periods, such as the drought event at $\sim 8.5 \, \text{ka}$.

6. Conclusions

By combining bulk and serially-sampled carbon and oxygen isotope data measured in artiodactyl tooth enamel from Gogoshiis Qabe and Guli Waabayo, we have shown that the climate Somalia experienced during the African Humid Period was drier than that of highland regions of eastern Africa and similar to the present Somali region, however, rainfall was less seasonal than in the present. Water deficit calculations for Guli Waabayo and Gogoshiis Qabe agree, indicating that the climate became progressively more arid toward the conclusion of the African Humid Period. Water deficit values throughout overlap in error with present day Baidoa, Somalia (1057 mm/yr), located ca. 70 km to the northwest of the two Buur Heybe sites. Records from Rift Valley lakes (e.g., Bloszies et al., 2015; Costa et al., 2014; Junginger et al., 2014) suggest a largely wetter climate during the African Humid

Table 3
Summary of tooth enamel isotope data for serially-sampled modern warthog teeth from Lake Naivasha area, Kenya.

Site	Tooth ID	n	Mean δ^{13} C (VPDB)	SD δ^{13} C (VPDB)	Range δ^{13} C (VPDB)	Mean δ^{18} O (VSMOW)	SD δ^{18} O (VSMOW)	Range δ ¹⁸ O (VSMOW)
GsJi	B119	21	-1.1	1.3	3.9	31.5	1.2	4.1
GsJi	B384	19	0.3	0.8	2.7	30.6	1.3	5.5
GtJi	B33	26	-0.2	0.8	2.7	30.6	0.9	3.3
GtJi	B56.1	26	-2.3	0.7	2.5	32.2	0.7	3.0
GtJi	B58.2	30	-3.6	1.8	5.5	30.4	0.9	3.4

Period in eastern Africa. The lack of such a suggestion for the Buur Heybe sites implies that regions of eastern Africa, such as Buur Heybe, which are isolated from Atlantic Ocean moisture, did not experience as wet an African Humid Period as highland regions lying in the path of that additional moisture source. Climate during the African Humid Period in Somalia nonetheless differed from the present, as a lack of oxygen isotope variation in two of three serially-sampled archaeological warthog teeth (δ^{18} O amplitudes < 2‰) provides evidence for a reduction in the seasonality of rainfall relative to the present (modern tooth δ^{18} O amplitudes $\geq 3\%$). A high amplitude of oxygen isotope variation in one tooth (4035; 3.2%) dating to 8470 \pm 66 cal yr B.P. indicates that climatic variability was, however, still a feature of the African Humid Period, Although few in number, the serially-sampled warthog teeth provide a unique and previously unattained seasonalscale glimpse of the African Humid Period in this region. As other records have suggested, the African Humid Period was not simply an extended humid period, but rather a more complicated and variable time period that was on average more humid than today. Additional terrestrial climate studies from eastern Africa, particularly east of the Ethiopian and Kenyan Highlands, are warranted to further investigate seasonality during the African Humid Period as well as the importance of Atlantic Ocean moisture.

Data availability

All data generated in this study are available in the Supplementary material.

Acknowledgements

This study was funded in part by an American Association of University Women Postdoctoral Fellowship to REBR and a National Science Foundation Dissertation Fellowship to MJ and FM (BCS-1821996). We thank the Somali Academy of Arts and Sciences both for permission to conduct field work as well as for logistical support in the field. We also thank Stanley Ambrose for advice and assistance with dating samples as well as for providing the modern warthog teeth and undergraduate student Emily Rehmann for assistance with serially-sampling the modern warthog teeth. We also appreciate the thoughtful comments provided by three anonymous reviewers on a previous draft of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.109272.

References

- Ascari, S.H., Njau, J.K., Sauer, P.E., Polly, P.D., Peng, Y., 2018. Fossil herbivores and crocodiles as paleoclimatic indicators of environmental shifts from Bed I and Bed II times of the Olduvai Gorge, Tanzania. Palaeogeogr. Palaeoclimatol. Palaeoecol. 511, 550–557. https://doi.org/10.1016/j.palaeo.2018.09.021.
- Baker, C., Eischeid, J., Karl, T., Diaz, H., 1995. 1994: The quality control of long-term climatological data using objective data analysis. In: Preprints of AMS Ninth Conference on Applied Climatology. Dallas, TX.
- Balasse, M., Ambrose, S.H., Smith, A.B., Price, T.D., 2002. The seasonal mobility model for prehistoric herders in the south-western cape of South Africa assessed by isotopic analysis of sheep tooth enamel. J. Archaeol. Sci. 29, 917–932. https://doi.org/10. 1006/jasc.2001.0787.
- Balasse, M., Obein, G., Ughetto-Monfrin, J., Mainland, I., 2012. Investigating seasonality and season of birth in past herds: a reference set of sheep enamel stable oxygen isotope ratios. Archaeometry 54, 349–368. https://doi.org/10.1111/j.1475-4754. 2011.00624.x.
- Barbour, M.M., 2007. Stable oxygen isotope composition of plant tissue: a review. Funct. Plant Biol. 34, 83. https://doi.org/10.1071/FP06228.
- Barker, P.A., 2001. A 14,000-year oxygen isotope record from diatom silica in two alpine lakes on Mt. Kenya. Science 292, 2307–2310. https://doi.org/10.1126/science. 1059612.
- Berke, M.A., Johnson, T.C., Werne, J.P., Livingstone, D.A., Grice, K., Schouten, S., Sinninghe Damsté, J.S., 2014. Characterization of the last deglacial transition in

- tropical East Africa: insights from Lake Albert. Palaeogeogr. Palaeoclimatol. Palaeoecol. 409, 1–8. https://doi.org/10.1016/j.palaeo.2014.04.014.
- Bloszies, C., Forman, S.L., Wright, D.K., 2015. Water level history for Lake Turkana, Kenya in the past 15,000 years and a variable transition from the African Humid Period to Holocene aridity. Glob. Planet. Change 132, 64–76. https://doi.org/10.1016/j.gloplacha.2015.06.006
- Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.-P., Chritz, K.L., Harris, J.M., Jehle, G.E., Cerling, T.E., 2017. Aridity and hominin environments. Proc. Natl. Acad. Sci. 114, 7331–7336. https://doi.org/10.1073/pnas.1700597114.
- Bocherens, H., Koch, P., Mariotti, A., Geraads, D., Jaeger, J.-J., 1996. Isotopic bio-geochemistry (¹³C, ¹⁸O) of mammalian enamel from African Pleistocene hominid sites. Palaios 11, 306–318.
- Bowen, G.J., 2008. Spatial analysis of the intra-annual variation of precipitation isotope ratios and its climatological corollaries: precipitation isotopic seasonality. J. Geophys. Res. Atmos. 113. https://doi.org/10.1029/2007JD009295.
- Bowen, G.J., Revenaugh, J., 2003. Interpolating the isotopic composition of modern meteoric precipitation: isotopic composition of modern precipitation. Water Resour. Res. 39. https://doi.org/10.1029/2003WR002086.
- Brandt, S.A., 1986. The Upper Pleistocene and early Holocene prehistory of the Horn of Africa. Afr. Archaeol. Rev. 4, 41–82. https://doi.org/10.1007/BF01117035.
- Brandt, S.A., 1988. Early Holocene mortuary practices and hunter-gatherer adaptations in southern Somalia. World Archaeol. 20, 40–56.
- Britton, K., Grimes, V., Dau, J., Richards, M.P., 2009. Reconstructing faunal migrations using intra-tooth sampling and strontium and oxygen isotope analyses: a case study of modern caribou (*Rangifer tarandus granti*). J. Archaeol. Sci. 36, 1163–1172. https://doi.org/10.1016/j.jas.2009.01.003.
- Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51 (1), 337–360.
- Bryant, D.J., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochim. Cosmochim. Acta 59, 4523–4537. https://doi.org/10.1016/0016-7037(95)00250-4.
- Bryant, D.J., Koch, P.L., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. Geochim. Cosmochim. Acta 60, 5145–5148. https://doi.org/10.1016/S0016-7037(96) 00308-0.
- Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris, J.M., Hart, J.A., Kirera, F.M., Kaleme, P., Leakey, L.N., Leakey, M.G., Levin, N.E., Manthi, F.K., Passey, B.H., Uno, K.T., 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. Proc. Natl. Acad. Sci. 112, 11467–11472. https://doi.org/10.1073/pnas.1513075112.
- Chritz, K.L., Blumenthal, S.A., Cerling, T.E., Klingel, H., 2016. Hippopotamus (*H. am-phibius*) diet change indicates herbaceous plant encroachment following megaherbivore population collapse. Sci. Rep. 6. https://doi.org/10.1038/srep32807.
- Chritz, K.L., Cerling, T.E., Freeman, K.H., Hildebrand, E.A., Janzen, A., Prendergast, M.E., 2019. Climate, ecology, and the spread of herding in eastern Africa. Quat. Sci. Rev. 204, 119–132. https://doi.org/10.1016/j.quascirev.2018.11.029.
- Clark, J.D., 1954. The Prehistoric Cultures of the Horn of Africa. Cambridge University Press. Cambridge. England.
- Costa, K., Russell, J., Konecky, B., Lamb, H., 2014. Isotopic reconstruction of the African Humid Period and Congo Air Boundary migration at Lake Tana, Ethiopia. Quat. Sci. Rev. 83, 58–67. https://doi.org/10.1016/j.quascirev.2013.10.031.
- Crowley, B.E., Wheatley, P.V., 2014. To bleach or not to bleach? Comparing treatment methods for isolating biogenic carbonate. Chem. Geol. 381, 234–242. https://doi. org/10.1016/j.chemgeo.2014.05.006.
- Delgado Huertas, A., Iacumin, P., Stenni, B., Sánchez Chillón, B., Longinelli, A., 1995. Oxygen isotope variations of phosphate in mammalian bone and tooth enamel. Geochim. Cosmochim. Acta 59, 4299–4305. https://doi.org/10.1016/0016-7037(95) 00286-9.
- deMenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., Yarusinsky, M., 2000. Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. Quat. Sci. Rev. 19, 347–361.
- d'Huart, J.-P., Grubb, P., 2001. Distribution of the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*) in the Horn of Africa. Afr. J. Ecol. 39, 156–169. https://doi.org/10.1046/j.0141-6707.2000.00298.x.
- Epstein, S., Mayeda, T., 1953. Variation of O-18 content of waters from natural sources. Geochim. Cosmochim. Acta 4, 213–224.
- Foerster, V., Junginger, A., Langkamp, O., Gebru, T., Asrat, A., Umer, M., Lamb, H.F., Wennrich, V., Rethemeyer, J., Nowaczyk, N., Trauth, M.H., Schaebitz, F., 2012. Climatic change recorded in the sediments of the Chew Bahir basin, southern Ethiopia, during the last 45,000 years. Quat. Int. 274, 25–37. https://doi.org/10.1016/j.quaint.2012.06.028.
- Frémondeau, D., Cucchi, T., Casabianca, F., Ughetto-Monfrin, J., Horard-Herbin, M.-P., Balasse, M., 2012. Seasonality of birth and diet of pigs from stable isotope analyses of tooth enamel (δ^{18} O, δ^{13} C): a modern reference data set from Corsica, France. J. Archaeol. Sci. 39, 2023–2035.
- Fricke, H.C., O'Neil, J.R., 1996. Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for palaeoclimatological and palaeobiological research. Palaeogeogr. Palaeoclimatol. Palaeoecol. 126, 91–99. https://doi.org/10.1016/S0031-0182(96)00072-7.
- Gasse, F., 2000. Hydrological changes in the African tropics since the Last Glacial Maximum. Quat. Sci. Rev. 19, 189–211. https://doi.org/10.1016/S0277-3791(99) 00061-X.
- Graziosi, P., 1940. L'Eta della Pietra in Somalia: risulti di una missione di ricerche paletnologiche nella Somalia italiana. G.C. Sansoni, Firenze, Italy.
- Green, D.R., Smith, T.M., Green, G.M., Bidlack, F.B., Tafforeau, P., Colman, A.S., 2018. Quantitative reconstruction of seasonality from stable isotopes in teeth. Geochim.

- Cosmochim. Acta 235, 483-504.
- Harris, J.M., Cerling, T.E., 2006. Dietary adaptations of extant and Neogene African suids. J. Zool. 256, 45–54. https://doi.org/10.1017/S0952836902000067.
- Higgins, P., MacFadden, B.J., 2009. Seasonal and geographic climate variabilities during the Last Glacial Maximum in North America: applying isotopic analysis and macrophysical climate models. Palaeogeogr. Palaeoclimatol. Palaeoecol. 283, 15–27. https://doi.org/10.1016/j.palaeo.2009.08.015.
- Hoppe, K.A., Amundson, R., Vavra, M., McClaran, M.P., Anderson, D.L., 2004. Isotopic analysis of tooth enamel carbonate from modern North American feral horses: implications for paleoenvironmental reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 203, 299–311. https://doi.org/10.1016/S0031-0182(03)00688-6.
- Iacumin, P., Venturelli, G., 2015. The 8¹⁸O of phosphate of ancient human biogenic apatite can really be used for quantitative palaeoclimate reconstruction? Eur. Sci. J. 11, 221–235.
- Ivory, S.J., Russell, J., 2018. Lowland forest collapse and early human impacts at the end of the African Humid Period at Lake Edward, equatorial East Africa. Quat. Res. 89, 7–20. https://doi.org/10.1017/qua.2017.48.
- Ivory, S.J., Lézine, A.-M., Vincens, A., Cohen, A.S., 2012. Effect of aridity and rainfall seasonality on vegetation in the southern tropics of East Africa during the Pleistocene/Holocene transition. Quat. Res. 77, 77–86. https://doi.org/10.1016/j. yqres.2011.11.005.
- Jones, M.B., Brandt, S.A., 2019. Long Term Small Game Hunting in Late Pleistocene and Holocene Somalia. (in prep.).
- Jones, M.B., Brandt, S.A., Marshall, F., 2018. Hunter-gatherer reliance on inselbergs, big game, and dwarf antelope at the Rifle Range Site, Buur Hakaba, southern Somalia ~20,000 5,000 BP. Quat. Int. 471, 55–65. https://doi.org/10.1016/j.quaint.2017.09.030.
- Julien, M.-A., Bocherens, H., Burke, A., Drucker, D.G., Patou-Mathis, M., Krotova, O., Péan, S., 2012. Were European steppe bison migratory? ¹⁸O, ¹³C and Sr intra-tooth isotopic variations applied to a palaeoethological reconstruction. Quat. Int. 271, 106–119. https://doi.org/10.1016/j.quaint.2012.06.011.
- Junginger, A., Roller, S., Olaka, L.A., Trauth, M.H., 2014. The effects of solar irradiation changes on the migration of the Congo Air Boundary and water levels of paleo-Lake Suguta, Northern Kenya Rift, during the African Humid Period (15–5 ka BP). Palaeogeogr. Palaeoclimatol. Palaeoecol. 396, 1–16. https://doi.org/10.1016/j. palaeo.2013.12.007.
- Kingdon, J., 2015. The Kingdon Field Guide to African Mammals, 2nd edition. Princeton University Press, Princeton, NJ.
- Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annu. Rev. Earth Planet. Sci. 26, 573–613. https://doi.org/10.1146/annurev.earth.26.1.573.
- Koch, P.L., 2007. Isotopic study of the biology of modern and fossil vertebrates. In: Michener, R.H., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing Ltd..
- Koch, P.L., Fisher, D.C., Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct proboscideans: a measure of season of death and seasonality. Geology 17, 515. https://doi.org/10.1130/0091-7613(1989)017 < 0515:OIVITT > 2.3.CO;2.
- Kohn, M.J., 1996. Predicting animal 8¹⁸O: Accounting for diet and physiological adaptation. Geochim. Cosmochim. Acta 60, 4811–4829.
- Konecky, B.L., Russell, J.M., Johnson, T.C., Brown, E.T., Berke, M.A., Werne, J.P., Huang, Y., 2011. Atmospheric circulation patterns during late Pleistocene climate changes at Lake Malawi, Africa. Earth Planet. Sci. Lett. 312, 318–326. https://doi.org/10.1016/j.epsl.2011.10.020.
- Konecky, B., Russell, J., Vuille, M., Rehfeld, K., 2014. The Indian Ocean Zonal Mode over the past millennium in observed and modeled precipitation isotopes. Quat. Sci. Rev. 103, 1–18
- Kranz, K.R., 1991. Monogamy in the dik-dik. Appl. Anim. Behav. Sci. 29, 87–105. https://doi.org/10.1016/0168-1591(91)90239-T.
- Kutzbach, J.E., Otto-Bliesner, B.L., 1982. The sensitivity of the African-Asian monsoonal climate to orbital parameter changes for 9000 years BP in a low-resolution general circulation model. J. Atmos. Sci. 39, 1177–1188.
- Lesur, J., Hildebrand, E.A., Abawa, G., Gutherz, X., 2014. The advent of herding in the Horn of Africa: new data from Ethiopia, Djibouti and Somaliland. Quat. Int. 343, 148–158. https://doi.org/10.1016/j.quaint.2013.11.024.
- Leus, K., Macdonald, A.A., 1997. From babirusa (Babyrousa babyrussa) to domestic pig: the nutrition of swine. Proc. Nutr. Soc. 56, 1001–1012. https://doi.org/10.1079/ PNS19970105.
- Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. Proc. Natl. Acad. Sci. 103, 11201–11205. https://doi.org/10.1073/pnas.0604719103.
- Levin, N.E., Zipser, E.J., Cerling, T.E., 2009. Isotopic composition of waters from Ethiopia and Kenya: insights into moisture sources for eastern Africa. J. Geophys. Res. 114. https://doi.org/10.1029/2009JD012166.
- Levinson, A.A., Luz, B., Kolodny, Y., 1987. Variations in oxygen isotopic compositions of human teeth and urinary stones. Appl. Geochem. 2, 367–371. https://doi.org/10. 1016/0883-2927(87)90021-7.
- Liu, X., Rendle-Bühring, R., Kuhlmann, H., Li, A., 2017. Two phases of the Holocene East African Humid Period: inferred from a high-resolution geochemical record off Tanzania. Earth Planet. Sci. Lett. 460, 123–134. https://doi.org/10.1016/j.epsl.2016. 12.016.
- Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochim. Cosmochim. Acta 48, 385–390. https://doi.org/10.1016/0016-7037(84)90259-X.
- Luyt, J., Sealy, J., 2018. Inter-tooth comparison of 8¹⁵C and δ¹⁸O in ungulate tooth enamel from south-western Africa. Quat. Int. 495, 144–152. https://doi.org/10.1016/j.quaint.2018.02.009.
- Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between

- mammalian bone-phosphate and environmental drinking water. Geochim. Cosmochim. Acta 48, 1689–1693. https://doi.org/10.1016/0016-7037(84)90338-7.
- Lyons, R.P., Scholz, C.A., Cohen, A.S., King, J.W., Brown, E.T., Ivory, S.J., Johnson, T.C., Deino, A.L., Reinthal, P.N., McGlue, M.M., Blome, M.W., 2015. Continuous 1.3-million-year record of East African hydroclimate, and implications for patterns of evolution and biodiversity. Proc. Natl. Acad. Sci., 201512864. https://doi.org/10.1073/pnas.1512864112.
- Maloiy, G.M.O., 1973. The water metabolism of a small East African antelope: the dik-dik. Proc. R. Soc. Lond. B Biol. Sci. 184, 167–178. https://doi.org/10.1098/rspb.1973.
- Marshall, M.H., Lamb, H.F., Huws, D., Davies, S.J., Bates, R., Bloemendal, J., Boyle, J., Leng, M.J., Umer, M., Bryant, C., 2011. Late Pleistocene and Holocene drought events at Lake Tana, the source of the Blue Nile. Glob. Planet. Change 78, 147–161. https://doi.org/10.1016/j.gloplacha.2011.06.004.
- Marshall, F., Reid, R.E.B., Goldstein, S., Storozum, M., Wreschnig, A., Hu, L., Kiura, P., Shahack-Gross, R., Ambrose, S.H., 2018. Ancient herders enriched and restructured African grasslands. Nature 561, 387–390. https://doi.org/10.1038/s41586-018-0456-9
- Mason, D.R., 1984. Dentition and age determination of the warthog Phacochoerus aethiopicus in Zululand, South Africa. Koedoe 27, 79–119.
- Morrissey, A., Scholz, C.A., 2014. Paleohydrology of Lake Turkana and its influence on the Nile River system. Palaeogeogr. Palaeoclimatol. Palaeoecol. 403, 88–100. https:// doi.org/10.1016/j.palaeo.2014.03.029.
- Nelson, S.V., 2005. Paleoseasonality inferred from equid teeth and intra-tooth isotopic variability. Palaeogeogr. Palaeoclimatol. Palaeoecol. 222, 122–144. https://doi.org/ 10.1016/j.palaeo.2005.03.012.
- Nicholson, S.E., 1996. A review of climate dynamics and climate variability in Eastern Africa. In: Johnson, T., Odada, E.O. (Eds.), The Limnology, Climatology and Paleoclimatology of the East African Lakes. Gordon and Breach Publishers.
- Nicholson, S.E., 2017. Climate and climatic variability of rainfall over eastern Africa: climate over Eastern Africa. Rev. Geophys. 55, 590–635. https://doi.org/10.1002/2016RG000544.
- Nicholson, S.E., 2018. The ITCZ and the seasonal cycle over equatorial Africa. Bull. Am. Meteorol. Soc. 99, 337–348. https://doi.org/10.1175/BAMS-D-16-0287.1.
- Niespolo, E., Sharp, W.D., Tryon, C.A., Faith, J.T., Lewis, J., Ranhorn, K.L., Mambelli, S., Miller, M.J., Dawson, T.E., 2018. Light stable isotopes of ostrich eggshells provide site-specific paleoenvironmental records during the middle-to-later stone age transition in eastern Africa. In: Presented at the GSA Annual Meeting in Indianapolis, Indiana, USA 2018, https://doi.org/10.1130/abs/2018AM-319835.
- Otto-Bliesner, B.L., Russell, J.M., Clark, P.U., Liu, Z., Overpeck, J.T., Konecky, B., deMenocal, P., Nicholson, S.E., He, F., Lu, Z., 2014. Coherent changes of southeastern equatorial and northern African rainfall during the last deglaciation. Science 346, 1223–1227. https://doi.org/10.1126/science.1259531.
- Passey, B.H., Cerling, T.E., 2002. Tooth enamel mineralization in ungulates: implications for recovering a primary isotopic time-series. Geochim. Cosmochim. Acta 66 (18), 3225–3234.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. (Vienna, Austria)
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55 (4), 1869–1887.
- Roberts, P., Stewart, M., Alagaili, A.N., Breeze, P., Candy, I., Drake, N., Groucutt, H.S., Scerri, E.M., Lee-Thorp, J., Louys, J., Zalmout, I.S., 2018. Fossil herbivore stable isotopes reveal middle Pleistocene hominin palaeoenvironment in 'Green Arabia'. Nat. Ecol. & Evol. 2 (12), 1871.
- Rozanski, K., Araguas-Araguas, L., Gonfiantini, R., 1993. Isotopic patterns in modern global precipitation. In: Swart, P. (Ed.), Climate Change in Continental Isotopic Records. Geophysical Monograph Series AGU, Washington, D.C., pp. 1–36.
- Sepulchre, P., Ramstein, G., Fluteau, F., Schuster, M., Tiercelin, J.-J., Brunet, M., 2006. Tectonic uplift and eastern Africa aridification. Science 313, 1419–1423. https://doi.org/10.1126/science.1129158.
- Sharp, Z., 2017. Principles of Stable Isotope Geochemistry, 2nd edition. .
- Thompson, L.G., 2002. Kilimanjaro ice core records: evidence of Holocene climate change in tropical Africa. Science 298, 589–593. https://doi.org/10.1126/science.1073198.
- Tierney, J.E., deMenocal, P.B., 2013. Abrupt shifts in Horn of Africa hydroclimate since the Last Glacial Maximum. Science 342, 843–846. https://doi.org/10.1126/science. 1240411.
- Tierney, J.E., Russell, J.M., Huang, Y., Damste, J.S.S., Hopmans, E.C., Cohen, A.S., 2008. Northern Hemisphere controls on tropical southeast African climate during the past 60,000 years. Science 322, 252–255. https://doi.org/10.1126/science.1160485.
- Tierney, J.E., Lewis, S.C., Cook, B.I., LeGrande, A.N., Schmidt, G.A., 2011a. Model, proxy and isotopic perspectives on the East African Humid Period. Earth Planet. Sci. Lett. 307, 103–112. https://doi.org/10.1016/j.epsl.2011.04.038.
- Tierney, J.E., Russell, J.M., Sinninghe Damsté, J.S., Huang, Y., Verschuren, D., 2011b. Late Quaternary behavior of the East African monsoon and the importance of the Congo Air Boundary. Quat. Sci. Rev. 30, 798–807. https://doi.org/10.1016/j. quascirev.2011.01.017.
- Uno, K.T., Rivals, F., Bibi, F., Pante, M., Njau, J., de la Torre, I., 2018. Large mammal diets and paleoecology across the Oldowan–Acheulean transition at Olduvai Gorge, Tanzania from stable isotope and tooth wear analyses. J. Hum. Evol. 120, 76–91. https://doi.org/10.1016/j.jhevol.2018.01.002.
- Venter, J.A., Seydack, A., Smith, Y.E., 2016. A Conservation assessment of *Potamochoerus larvatus*. In: Child, M., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H. (Eds.), The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa,

pp. 5

- Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 107, 281–289. https://doi.org/10.1016/0031-0182(94)90100-7.
- Williams, A.P., Funk, C., Michaelsen, J., Rauscher, S.A., Robertson, I., Wils, T.H.G., Koprowski, M., Eshetu, Z., Loader, N.J., 2012. Recent summer precipitation trends in the Greater Horn of Africa and the emerging role of Indian Ocean sea surface temperature. Clim. Dyn. 39, 2307–2328. https://doi.org/10.1007/s00382-011-1222-y.
- Yang, W., Seager, R., Cane, M.A., Lyon, B., 2015. The annual cycle of East African precipitation. J. Clim. 28, 2385–2404. https://doi.org/10.1175/JCLI-D-14-00484.1.
- Yang, D., Uno, K.T., Cerling, T.E., 2019. Comparing intratooth isotope profiles of modern warthogs and fossil suids: a potential proxy for hydroclimate seasonality of hominin fossil sites. In: Presented at the 88th Annual Meeting of the American Association of
- Physical Anthropologists, Hoboken, NJ, USA.
- Zazzo, A., 2014. Bone and enamel carbonate diagenesis: a radiocarbon prospective. Palaeogeogr. Palaeoclimatol. Palaeoecol. 416, 168–178.
- Zazzo, A., Saliège, J.F., 2011. Radiocarbon dating of biological apatites: a review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 310 (1-2), 52-61.
- Zazzo, A., Balasse, M., Patterson, W.P., 2005. High-resolution δ13C intratooth profiles in bovine enamel: implications for mineralization pattern and isotopic attenuation. Geochim. Cosmochim. Acta 69 (14), 3631–3642.
- Zazzo, A., Balasse, M., Passey, B.H., Moloney, A.P., Monahan, F.J., Schmidt, O., 2010. The isotope record of short- and long-term dietary changes in sheep tooth enamel: implications for quantitative reconstruction of paleodiets. Geochim. Cosmochim. Acta 74, 3571–3586. https://doi.org/10.1016/j.gca.2010.03.017.