Contents lists available at ScienceDirect



Journal of Archaeological Science: Reports

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

A Holocene paleoenvironmental record based on ungulate stable isotopes from Lukenya Hill, Kenya



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ARTICLE INFO ABSTRACT Keywords: Investigating the development of Holocene behavioral adaptations requires knowing how and why different Stable isotopes human groups are distributed on the landscape. An expanded dataset of site-specific environmental and habitat Lukenya Hill reconstructions from eastern Africa are crucial contextual components necessary for pushing this line of inquiry Athi-Kapiti Plains forward. This paper provides localized paleoenvironmental data from Holocene deposits at the multi-site African Humid Period Lukenya Hill archaeological complex on the Athi-Kapiti Plains of Kenya. Lukenya Hill preserves two temporal Eastern Africa units, an early-mid Holocene (~9.0-4.6 ka) and a late Holocene (~2.3-1.2 ka), which span the end of the African Humid Period and the onset of late Holocene aridification. Carbon isotope analysis of herbivore tooth enamel (n = 22) indicates an increase in open grasslands over time with the early-mid Holocene having a woodier signal than the late Holocene and Recent populations in the Athi ecosystem. This pattern deviates from local environmental sequences in the Lake Victoria and Lake Turkana basins, providing additional evidence of heterogeneous habitat conditions during the Holocene of eastern Africa. The expansion of locally specific paleoecological datasets in eastern Africa allows for an examination of the role climate and ecology played in human economic and behavioral development during the Holocene.

1. Introduction

Holocene climatic oscillations associated with the African Humid Period (AHP), a pluvial period in eastern Africa roughly spanning the timeframe \sim 15–5 ka, and the subsequent late Holocene aridification trend are thought to have had a strong effect on human dietary behavior and migration patterns. The drier climate and more open environments of the Holocene made it increasingly difficult to find large, wild mammals to hunt. As a result, early herders took advantage of open habitats and tsetse fly free corridors to move from the Nile valley to the east and south (Chritz et al., 2015; Ashley et al., 2017). The AHP in eastern Africa has been extensively studied from a regional perspective through lake-core and offshore climate proxies and is known to include drier intervals similar to the 'Younger Dryas' and the 8.2 ka event in the northern hemisphere (deMenocal et al., 2000; Tierney et al., 2011; Shanahan et al., 2015; Liu et al., 2017). A full assessment of the AHP's role in the development of human social and exchange networks during the Holocene, however, is hampered by a lack of environmental and habitat evidence directly associated with records of human behavior.

Studies of biogeochemical markers and water levels from modern and paleo-lakes in eastern Africa have demonstrated that the timing of humid-arid oscillations within the AHP, and the termination of the

AHP, were asynchronous across the region (Costa et al., 2014; Forman et al., 2014; Junginger et al., 2014; Bloszies et al., 2015; although see Tierney and deMenocal, 2013). Until recently, local paleoenvironment proxies during the Holocene for linking regional climatic events to human behavioral responses were restricted to the site of Enkapune Ya Muto on the Mau Escarpment west of Lake Naivasha in the Kenyan Rift Valley (Ambrose, 1984, 1998; Marean, 1992a; Marean et al., 1994). Enkapune Ya Muto, however, does not preserve the entire Holocene with an archaeological sequence primarily post-dating the AHP (\sim 7–1 ka). In an effort to contextualize the origins of herding in eastern Africa, Chritz et al. (2019) have provided an extensive paleoecological study of the Lake Turkana and Lake Victoria Basins, including tooth enamel stable isotopes, pollen, and leaf-wax biomarkers. This study indicated that the ecology of each basin responded differently to climatic changes during the Holocene with the Lake Victoria Basin characterized by grazing species feeding in open habitats throughout the Holocene while the Turkana Basin saw a shift from grazing species to mixed-feeding taxa at the end of the AHP \sim 5 ka (Chritz et al., 2015, 2019). Paleoecological conditions during the AHP, and the Holocene more broadly, are poorly known for areas outside of the lake regions in Kenya due to a lack of well-dated sites on the Kenyan plains. This study expands the record of Holocene paleoenvironments in Kenya to the site of Lukenya Hill which may have been a source of behavioral and socio-

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https://doi.org/10.1016/j.jasrep.2019.102016

Received 9 July 2019; Received in revised form 22 August 2019; Accepted 25 September 2019 2352-409X/ © 2019 Elsevier Ltd. All rights reserved.



Fig. 1. Map of the vegetation of eastern Africa showing the location of Lukenya Hill (1; star) on the Athi-Kapiti Plains and other Kenyan sites mentioned in the text: 2 – Enkapune Ya Muto; 3 – Wadh Lang'o; 4 – Luanda; 5 – Gogo Falls. Vegetation data and categories following White (1983).

economic changes.

The Athi-Kapiti Plains, just to the southeast of Nairobi, Kenya, support an annual faunal migration of blue wildebeest (Connochaetes taurinus), plains zebra (Equus quagga), and hartebeest (Alcelaphus buselaphus), and has been utilized by humans and their ancestors for thousands, if not hundreds of thousands, of years as evidenced by the archaeological sites at Lukenya Hill (Fig. 1; Foster and Kearney, 1967; Foster and Coe, 1968; Gramly, 1976; Marean, 1990, 1992b, 1997). Composed of multiple open air and rockshelter sites, Lukenya Hill provides one of the most complete semi-continuous sequences of habitation in eastern Africa during the Holocene (Gramly, 1975, 1976; Marean, 1990, 1992b; Barut, 1994, 1997; Kusimba, 1999). Utilizing carbon (δ^{13} C) and oxygen (δ^{18} O) stable isotope analysis of herbivore tooth enamel, this study presents the first local Holocene paleoenvironmental record spanning the AHP, and tests whether the AHP was followed by increasing aridification on the plains of Kenya as it was elsewhere in eastern Africa. Two temporal aggregates consisting of an early-mid Holocene (~9.0-4.6 ka) and late Holocene (~2.3-1.2 ka) sequence allow for an assessment of local environments and habitats through much of the Holocene and if and how they responded to the global and regional climatic oscillations of this period. The local environments at Lukenya Hill which accompanied the AHP and its aftermath offer context for understanding the development of human behaviors on the Athi-Kapiti Plains, and reconstructing paleoenvironmental conditions at the time of the onset of herding in the broader eastern Africa region (Foster and Kearney, 1967; Ogutu et al., 2013).

1.1. Lukenya Hill context

Comprised of nearly 300 separate archaeological sites dating from the Acheulian through the Iron Age, Lukenya Hill is a gneissic inselberg rising above the Athi-Kapiti Plains about 40 km southeast of Nairobi, Kenya (Fig. 1). Today, this region is characterized by a semi-arid acacia bushland environment with two irregular rainy seasons in which it receives ~500 mm of precipitation per year. While unpredictable, the long rains tend to occur from March to May while the short rains come October to December (White, 1983; Marean, 1990, 1992b; Barut, 1994, 1997; Kusimba, 1999). Two of the Lukenya Hill sites – GvJm-19 and GvJm-22 – contain Holocene sequences which, together, span the AHP and the following onset of aridification (see Robinson, 2017 for a

Table 1

Lukenya Hill radiometric dates calibrated with the IntCal 13 curve in OxCal 4.3 (Bronk Ramsey, 2009; Reimer et	al., 201	3)
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Site	Material	Level	Original Age (in yr BP)	IntCal13 (cal yr BP) ^a	Lab Number
GvJm-19 [†]	Bone apatite	D.S. 25–30	4145 ± 240	4679 ± 337	GX-6754
GvJm-19 [†]	Bone collagen	D.S. 85–90	4200 ± 155	4744 ± 224	GX-7416
GvJm-19 [†]	Bone apatite	D.S. 50–55	6040 ± 225	6908 ± 254	GX-6755
GvJm-19 [†]	Bone apatite	D.S. 70–75	6770 ± 225	7652 ± 206	GX-6756
GvJm-19 [†]	Bone apatite	D.S. 90–95	8010 ± 340	8943 ± 397	GX-6757
GvJm-22 [‡]	Charcoal	A 45–50	1330 ± 100	1234 ± 104	N-1076
GvJm-22 [‡]	Bone collagen	A 45–50	1510 ± 50	1413 ± 61	UCLA-1709D
GvJm-22 [‡]	Bone collagen	C 70–75	2250 ± 50	$2245~\pm~62$	UCLA-1709C

* Non-calibrated age source: Nelson and Kimengich, 1984.

* Non-calibrated age source: Gramly, 1975.

 $^{\rm a}$ Calibrated ages as reported by OxCal 4.3. Given in text as 2σ ranges.

detailed review of the Pleistocene archaeology, chronology, and paleoenvironments of both GvJm-19 and GvJm-22).

GvJm-19, a rock overhang composed of one terminal Pleistocene and two early-mid Holocene archaeological components, was excavated from 1978 to 1980 as part of the University of Massachusetts Later Stone Age/Pastoral Neolithic project led by John Bower and Charles Nelson (Bower et al., 1977; Bower and Nelson, 1978). The two earlymid Holocene components are found between the surface and 110 cm below the surface. These levels were dated by conventional radiocarbon methods on five bone apatite and collagen samples (Nelson and Kimengich, 1984; Table 1) and have been calibrated at 95.4% confidence with the IntCal13 curve in OxCal 4.3 (Bronk Ramsey, 2009; Reimer et al., 2013). It is recognized here that these dates may be slight under-estimates of the true age of the deposits due to the possibility of contamination and recrystallization of bone with inclusions of modern carbon (Higham et al., 2006). That being said, all dates are within two half-lives of ¹⁴C, minimizing the risk of erroneous determinations (Higham et al., 2006), and are confidently placed within the Holocene on account of the recovered archaeology, particularly ceramics. The Holocene component of GvJm-19 is constrained by two dates: 9737–8149 cal yr BP (8010 \pm 340 ¹⁴C yr BP [GX-6757]; 90–95 cm below the surface) and 5353–4005 cal yr BP (4145 \pm 240 ¹⁴C yr BP [GX-6754]; 25–30 cm below the surface; Nelson and Kimengich, 1984; Marean, 1990; Kusimba, 1999). The earlier part of the Holocene assemblage at GvJm-19, from 80 to 110 cm below the surface, is aceramic while the later component contains ceramics, however, the lithic assemblage is similar between the two units. The small faunal assemblage (45 identified ungulate individuals based on dental and postcranial remains) is dominated by grazers (Table 2), particularly those which prefer a mix of moist and dry grass, such as hartebeest, plains zebra, oribi (Ourebia ourebi), and mountain reedbuck (Redunca fulvorufula)

(Marean, 1990, 1992b; Cerling et al., 2015; Kingdon, 2015). For the purposes of this study, and due to the similarity in lithic technology throughout the sequence, the Holocene GvJm-19 material will be considered as one unit roughly corresponding to the end of the AHP.

GvJm-22, discovered and excavated by Richard Gramly in 1970-1971 (Gramly, 1975, 1976), contains both Pleistocene and Holocene components. Calibration of Gramly's (1975) conventional radiocarbon dates on charcoal and bone collagen (Table 1), indicate that the Holocene component, which includes all of the sediments from the surface to 110 cm below the surface, dates to between approximately 2369–2121 cal yr BP (2250 \pm 50 ¹⁴C yr BP [UCLA-1709C]; 70–75 cm below the surface) and 1442–1026 cal yr BP (1330 \pm 100 ¹⁴C yr BP [N-1076]; 45–50 cm below the surface). This Pastoral Neolithic assemblage contains microlithic stone tools along with Akira and Narosura ceramics (Marean, 1990, 1992b; Barut, 1997; Kusimba, 1999; Tryon et al., 2015). Again, the conventional radiocarbon dates may be slight under-estimates due to sample contamination with modern carbon, but the presence of Akira and Narosura ceramics confirm an age younger than ~3000 BP (Lane, 2013). The small faunal assemblage from the Holocene component of GvJm-22 (41 identified ungulate individuals based on dental and postcranial remains; Table 2) is dominated by grazers which prefer short green and fresh grasses, such as blue wildebeest and hartebeest (Marean, 1990, 1992b; Kingdon, 2015). Mixed-feeding taxa are rare at GvJm-22 (Marean, 1990, 1992b).

1.2. Stable carbon and oxygen isotopes

The carbonate fraction of tooth enamel is minimally affected by diagenesis and has been shown to preserve *in vivo* biological signals which can be used as proxy data for diet and drinking behavior, and, in turn, paleoenvironments (DeNiro and Epstein, 1978; Lee-Thorp, 1989;

Table 2

Faunal list from GvJm-19 and GvJm-22 based on dental and postcranial remains; numbers represent minimum number of individuals (MNI) (adapted and complied from Marean, 1990, 1992).

Order	Family	Tribe	Species	GvJm-19	GvJm-22
Artiodactyla	Bovidae	Aepycerotini	Aepyceros melampus	0	2
Artiodactyla	Bovidae	Alcelaphini	Alcelaphus buselaphus	8	10
Artiodactyla	Bovidae	Alcelaphini	Connochaetes taurinus	3	6
Artiodactyla	Bovidae	Antilopini	Eudorcas thomsonii	4	2
Artiodactyla	Bovidae	Bovini	Bos taurus	1	3
Artiodactyla	Bovidae	Caprini	Caprini sp.	2	4
Artiodactyla	Bovidae	Cephalophini	Sylvicapra grimmia	3	0
Artiodactyla	Bovidae	Neotragini	Oreotragus oreotragus	2	1
Artiodactyla	Bovidae	Neotragini	Ourebia ourebi	5	1
Artiodactyla	Bovidae	Neotragini	Madoqua kirkii	2	1
Artiodactyla	Bovidae	Neotragini	Raphicerus campestris	2	3
Artiodactyla	Bovidae	Reduncini	Redunca fulvorufula	4	1
Artiodactyla	Giraffidae		Giraffa camelopardalis	1	1
Artiodactyla	Suidae		Phacochoerus sp.	2	1
Artiodactyla	Suidae		Potamochoerus sp.	1	1
Perissodactyla	Equidae		Equus quagga	5	4

Wang and Cerling, 1994; Sponheimer and Lee-Thorp, 1999a,b; Cerling et al., 2003; Cerling et al., 2015). Stable carbon isotope analysis allows for differentiating between C₃ (trees, shrubs, and high-altitude grasses above \sim 2000 m) and C₄ (most low elevation tropical grasses in Africa) photosynthetic sources of herbivore diet. Plants which utilize the C₃ photosynthetic pathway have a modern δ^{13} C range of -22% to -36%and mean of $-27.4 \pm 2.0\%$. ¹³C increases in C₃ plants from wet to mesic and xeric habitats with $\delta^{13}C$ being most enriched in open, arid environments (Tieszen et al., 1979, 1983; O'Leary, 1981; Ambrose and DeNiro, 1986; Heaton, 1999; Passey et al., 2005). Isotopic variability of C₃ plants is related to the 'canopy effect' – photosynthetic recycling of respired CO₂ in closed canopy forests – and water, light, and temperature availability (van der Merwe and Medina, 1991; Diefendorf et al., 2010; Kohn, 2010). C₄ plants have δ^{13} C values ranging from about -14% to -10% with a mean of $-12.7 \pm 1.2\%$ (Hattersley, 1992; Heaton, 1999; Passey and Cerling, 2002; Cerling et al., 2003). Succulents utilize the CAM (Crassulacian acid metabolism) pathway and have δ^{13} C values between those of C₃ and C₄ plants (O'Leary, 1981, 1988; Heaton, 1999), however, they are not considered further in this study as it is unlikely that succulents comprised a significant portion of herbivore diets in eastern Africa during the Holocene (Cerling et al., 2003; Garrett et al., 2015). While individual C₃ and C₄ plants in certain habitats, such as marshes, may have isotopic values outside of the ranges quoted above, the generally non-overlapping δ^{13} C isotopic ranges for the two photosynthetic pathways in Africa are ideal for differentiating between browsers, grazers, and mixed-feeders based on broad dietary strategies. Considering a $\sim +14.1\%$ enrichment factor between ¹³C of diet and tooth enamel for large mammals (Cerling and Harris, 1999; Passey et al., 2005), these dietary categories are isotopically defined as follows: C_3 browsers ($\delta^{13}C < -9.0\%$); C_3 - C_4 $(-9.0\%) < \delta^{13}C < -2.0\%);$ mixed-feeders C₄ grazers $(\delta^{13}C > -2.0\%)$. All comparisons with modern animals are made with δ^{13} C values corrected to pre-industrial δ^{13} C of atmospheric CO₂ $(\delta^{13}C_{1750})$ as described and reported in Cerling et al. (2015).

Stable oxygen isotope composition has been used as a proxy for aridity where the lighter oxygen isotope, ¹⁶O, will be preferentially lost in evaporation of leaf and surface water relative to the heavier, ¹⁸O, isotope. The result of this scenario is heavier, or ¹⁸O enriched, signals recorded in faunal tooth enamel (Kohn, 1996; Levin et al., 2006). C₃ plants tend to have enriched values compared to surface water sources related to the rate of evapotranspiration of leaf water. As such, browsing taxa which rely primarily on leaf water typically have higher δ^{18} O values, as they track evaporative water deficit, than grazing taxa which drink primarily from surface sources. This difference is most evident in the dry season when evapotranspiration of leaf water is at its highest. During the rainy season grazers consume fresh green grass and have lower δ^{18} O values, but in the dry season they include more C₃ browse and water derived from plant leaves in their diet leading to higher δ^{18} O values. Therefore, higher δ^{18} O is associated with lower δ^{13} C in herbivores, especially mixed-feeders, in open environmental settings (Sponheimer and Lee-Thorp, 1999a,b, 2001, 2003, 2007; Cerling et al., 2008). While the difference between evaporation-sensitive and evaporation-insensitive taxa has been used to calculate an aridity index (Levin et al., 2006; Blumenthal et al., 2017), it is not done so here due to the small sample size of evaporation-sensitive browsing taxa in the Lukenya Hill dataset. Furthermore, drawing direct inferences from herbivore enamel δ^{18} O values is confounded by our current knowledge of the relationship of enamel δ^{18} O values to those of meteoric water, diet, and atmospheric oxygen and how these factors controlled δ^{18} O values of herbivore body water in the past (Levin et al., 2006; Levin, Zipser and Cerling, 2009; Faith, 2018). As such, the δ^{18} O data are interpreted cautiously.

2. Materials and methods

A total of 22 fossil herbivore teeth (GvJm-19 n = 17; GvJm-22

n = 5) from the Lukenya Hill archaeological collections curated at the National Museums of Kenya were sampled for stable carbon and oxygen isotope analysis (Supplementary Data Table 1). Sampling focused on molars, preferably third molars, to limit the potential for interference in the dietary signal from weaning (Kingston and Harrison, 2007). All taxa for which securely identified molars were available were sampled. Only a single tooth from partial or complete tooth rows was sampled to avoid sampling multiple teeth from the same individual. Each tooth was carefully cleaned of adhering sediment with a high-speed Brasseler dental drill (Forza L50k) interfaced with tapered tungsten-carbide bits. Approximately 2 mg of enamel powder was collected from each tooth by drilling a vertical line from the cement-enamel junction to the occlusal surface along broken edges. Samples were reacted with commercially available bleach (NaOCl) diluted 50% for 24 h in 1.5 mL microcentrifuge tubes to digest organic contaminants, followed by rinsing and centrifuging to a neutral pH with double distilled water. Samples were then treated with 0.1 M acetic acid for 4 h to remove secondary carbonates and again rinsed to neutrality with double distilled water and freeze-dried. Enamel samples were reacted with 100% phosphoric acid at 70 °C in a Kiel III carbonate extraction device interfaced with a Finnigan-MAT 252 isotope ratio mass spectrometer at the Light Stable Isotope Laboratory, Department of Geosciences, University of Florida, Gainesville. Precision was measured via repeated measures of the international calcium carbonate standard NBS-19 during sample analysis. Replicate measurements of the standard during analysis had errors of $\sim 0.05\%$ for carbon and $\sim 0.1\%$ for oxygen. Carbon and oxygen isotopic composition is reported in δ -notation where $\delta^{13}C$ or $\delta^{18}O = [(R_{sample}/R_{standard}) - 1]$, where $R = {}^{13}C/{}^{12}C$ or $^{18}\text{O}/^{16}\text{O}$, and δ is expressed in per mil, ‰, i.e., x1000‰. Carbon and oxygen values are reported relative to VPDB (Vienna Pee Dee Belemnite).

2.1. Statistical analysis

In addition to descriptive analyses, non-parametric Mann-Whitney U tests are employed to test for differences in δ^{13} C and δ^{18} O values between GvJm-19 and GvJm-22 at Lukenya Hill, between the late Pleistocene, represented by GvJm-19 (Robinson, 2017), and the Holocene at the site, and in comparing δ^{13} C values of alcelaphins at Lukenya Hill with those from Lake Victoria and Lake Turkana (Chritz et al., 2019). Non-parametric Kruskal-Wallis tests are used to investigate differences and trends in δ^{13} C values across the two Lukenya Hill time periods and the Recent Athi ecosystem (Cerling et al., 2015). All statistical analyses are conducted with the R Statistical Package (2014) and an a priori significance level of $\alpha = 0.05$.

The relative contribution of C_3 and C_4 biomass to herbivore diet is estimated from the $\delta^{13}C$ enamel values using a mixing model based on end-member $\delta^{13}C$ isotope values for C_3 and C_4 plants and the above described enrichment factor (Phillips, 2012; Cerling et al., 2015; Garrett et al., 2015):

$$\delta^{13}C_{\text{measured}} = \delta^{13}C_{C3} * f_{C3} + \delta^{13}C_{C4} * f_{C4},$$

where $\delta^{13}C_{C3}$ and $\delta^{13}C_{C4}$ are the assumed end-member values. While a variety of end-member estimates can be derived by considering temperature, humidity, water stress, CO₂ concentration, and vegetative functional type (Kohn, 2010; Diefendorf et al., 2010; Katoh et al., 2016), the values used here are -26.0% for C₃ plants and $-12.7 \pm 1.2\%$ for C₄ plants. The C₃ end-member represents an average of non-water stressed ($-27.4 \pm 2.0\%$) and water-stressed conditions (24.6 \pm 1.1‰). Both end-member values are commonly utilized in mixing models (Cerling et al., 2015; Passey et al., 2005; Chritz et al., 2015; Garrett et al., 2015). As the resulting percentages of C₃ and C₄ biomass consumption are only intended to be estimates, they are rounded to the nearest 5% following Chritz et al. (2015).



Fig. 2. Scatter bi-plots of enamel δ^{18} O values (y-axis) by enamel δ^{13} C values (x-axis) for all samples at the genus level for both GvJm-19 (top) and GvJm-22 (bottom). VPDB stands for Vienna Pee-Dee Belemnite.

3. Results

Combining the GvJm-19 and GvJm-22 datasets shows that Lukenya Hill was characterized by fauna feeding primarily on grasses during the Holocene (Fig. 2). Blue wildebeest (n = 5; 2.4 \pm 1.2‰) and hartebeest $(n = 5; 1.5 \pm 1.7\%)$ have high δ^{13} C values exceeding or approaching hyper-grazer classification ($\geq 2\%$; Cerling et al., 2015). All individual wildebeest and hartebeest are estimated to have consumed ~95% or greater C₄ vegetation, except one hartebeest from GvJm-19 which is estimated at ~80% (Supplemental Dataset 1). Low variability in δ^{13} C values suggests that there are likely no differences between GvJm-19 and GvJm-22 for these two species. Other grazers from GvJm-19, however, have lower estimated consumption of C₄ resources (Fig. 2). For instance, both reedbucks are estimated to have consumed ~90% C₄ vegetation, the oribi is estimated to have consumed \sim 85%, and the two plains zebras are estimated at ~95% and ~80%. While these values reflect dedicated grazing, they are lower than the estimated C₄ consumption of modern counterparts in the Athi ecosystem (Table 3; Cerling et al., 2015).

To investigate any changes over time between GvJm-19 and GvJm-22, and to see if there are any differences between these Holocene occupations and modern data, the small sample sizes of individual taxa requires grouping into dietary categories. Dietary categories are defined based on observational (Kingdon, 1982, 2015) and isotope data (Sponheimer et al., 2003, Cerling et al., 2003, 2015) and are as follows: grazers – hartebeest, blue wildebeest, mountain reedbuck, oribi, and plains zebra; mixed-feeders – Thomson's gazelle (*Eudorcas thomsonii*); browsers – common duiker (*Sylvicapra grimmia*), dik-dik (*Madoqua kirkii*), klipspringer (*Oreotragus oreotragus*) and steenbok (*Raphicerus campestris*); omnivores – bushpig (*Potamochoerus* sp.). Only the grazer dietary category, which contains 15 of the 22 total samples and all of the late Holocene sample, has a large enough size to justify further

Table 3

Estimated	mean	percent	: C4	vegetation	const	umed	by	individual	l taxa	for	the
early-mid	Holoce	ene, the	late	Holocene,	and t	he Re	cent	t rounded	to the	nea	rest
5%.											

Taxon/Dietary Class	Early-Mid Holocene %C4 (n)	Late Holocene %C4 (n)	Recent Athi [†] %C ₄ (<i>n</i>)
Grazers			
Alcelaphus buselaphus	90 (2)	100 (3)	100 (16)
Connochaetes taurinus	100 (3)	100 (2)	100 (22)
Ourebia ourebi	85 (1)	-	-
Redunca fulvorufula	90 (2)	-	100 (2)
Equus quagga	85 (2)	-	100 (3)
Mixed Feeders			
Eurdorcus thomsoni	85 (2)	-	75 (10)
Browsers			
Oreotragus oreotragus	30 (1)	-	5 (2)
Sylvicapra grimmia	0(1)	-	10 (1)
Madoqua kirki	25 (1)	-	-
Raphicerus campestris	5 (1)	-	0 (4)
Omnivores			
Potamochoerus sp.	20 (1)	-	-

[†] Recent Athi ecosystem data compiled from Cerling et al. (2015).

statistical analysis. Overall, a Mann-Whitney *U* test finds a significant difference (p = 0.003) between the δ^{13} C values for grazers from Lukenya Hill and the Recent Athi ecosystem. δ^{13} C values for the archaeological (n = 15; $1.2 \pm 1.6\%$) and Recent (n = 43; $3.1 \pm 1.2\%$) datasets indicate greater C₄ consumption in the present. Dividing the Lukenya Hill grazers into early-mid Holocene and late Holocene temporal units, the mean δ^{13} C values (early-mid Holocene n = 10: $0.6 \pm 1.3\%$; late Holocene n = 5: $2.6 \pm 1.1\%$) suggests a trend towards higher δ^{13} C values over time within the Lukenya Hill



Fig. 3. Box-and-whisker plots of enamel δ^{13} C values overlaid by individual data points for the three most common grazing taxa at Lukeyna Hill. In addition to individual taxa, one set of boxplots combines δ^{13} C data from all alcelaphins – the most common bovid tribe in the sample – and one set of boxplots combines δ^{13} C data from all grazers. Asterisks in the 'All Grazers' category indicate significant differences based on Mann-Whitney *U* tests. Boxes represent the upper and lower quartiles for each taxon and whiskers indicate the full range for each taxon; hashes within boxes represent the median value. Colored circles indicate a taxon represented by only one sample. Open (white) circles represent outliers. VPDB stands for Vienna Pee-Dee Belemnite. Recent Athi ecosystem δ^{13} C isotope data from Cerling et al. (2015).

assemblage. This trend is supported by a Kruskal-Wallis test which finds a significant change over these three temporal intervals (p < 0.001; χ^2 : 17.318). Post-hoc pairwise Mann-Whitney U tests reveal that the trend is driven by the early-mid Holocene which is significantly different from both the late Holocene (p = 0.016) and the Recent (p < 0.001). No difference is found between the late Holocene and the Recent (p = 0.401). The early-mid Holocene has lower δ^{13} C values than the late Holocene or the Recent Athi ecosystem (Fig. 3). While these results are tantalizing, caution should be exercised in interpreting them as indicating a shift in habitat over time at Lukenya Hill. It is possible that inter-taxonomic variation within the grazers may be driving this trend as the late Holocene GvJm-22 assemblage does not contain reedbuck, oribi, or plains zebra like the early-mid Holocene GvJm-19 dataset. A Mann-Whitney U indicates that the reedbuck-oribi-plains zebra grazing component from GvJm-19 (n = 5; $-0.1 \pm 0.7\%$) has significantly lower δ^{13} C values (p = 0.012) than the alcelaphins from GvJm-22 while the alcelaphins from GvJm-19 (n = 5; 1.3 \pm 1.5‰) are not different (p = 0.144) from the GvJm-22 alcelaphins.

 δ^{18} O values for both wildebeest (n = 5; $-1.8 \pm 2.1\%$) and hartebeest (n = 5; $-1.9 \pm 0.8\%$) are low and similar to the modern annual δ^{18} O value (-3.2‰) of the Athi river system (Marwick et al., 2014). These results complement the high δ^{13} C values and suggest extensive feeding on fresh green grasses which are well-watered. The greater variability in wildebeest δ^{18} O values may indicate a difference over time between GvJm-19 and GvJm-22. A Mann-Whitney U test on all samples failed to find a significant difference in δ^{18} O values between the two sites (p = 0.529). Recognizing that grazers and browsers have different water consumption and retention physiologies, a second Mann-Whitney U was conducted on just the grazing taxa from the two sites. This test also failed to find any significant difference (p = 0.757) between GvJm-19 (n = 10; $-1.4 \pm 2.0\%$) and GvJm-22 (n = 5; $-2.2 \pm 0.6\%$). Interpretations of δ^{18} O data are confounded by several factors (Levin et al., 2006, 2009; Faith, 2018), but it does not appear as if there is any evidence for a change in aridity over time at Lukenya Hill.

4. Discussion

4.1. Lukenya Hill local environment in a regional context

The Holocene record at Lukenya Hill is a temporal extension of late Pleistocene environmental conditions, particularly at GvJm-19 where a terminal Pleistocene occupation is dated to ~14 ka (Nelson and Kimengich, 1984; Marean, 1990). Grazers in the Pleistocene at GvJm-19 were found to have low δ^{13} C values and high δ^{18} O values indicating generally arid conditions and increased dry grass or C₃ feeding in open habitats (Robinson, 2017). These Pleistocene grazers (n = 10; $-0.4 \pm 1.5\%$) have significantly lower (Mann-Whitney U: p = 0.043) δ^{13} C values than the Holocene grazers from both GvJm-19 and GvJm-22 at Lukenva Hill (Fig. 3; n = 15; 1.2 \pm 1.6%). This may reflect the amelioration of harsher and more arid conditions at the end of the Pleistocene, perhaps associated with the Last Glacial Maximum at northern latitudes, with the onset of the AHP (Robinson, 2017). This shift in grazer δ^{13} C values, however, is not associated with one in δ^{18} O values (Mann-Whitney U: p = 0.675; Pleistocene: $-2.1 \pm 1.4\%$; Holocene: $-1.7 \pm 1.7\%$).

While the Lukenya Hill isotope data support the general pattern of a warm and wet early-mid Holocene followed by a warm and dry late Holocene in eastern Africa (Kiage and Liu, 2006; Costa et al., 2014; Junginger et al., 2014; Bloszies et al., 2015), subtle local differences are evident. Early-mid Holocene pollen records from across eastern Africa indicate significant amounts of forest taxa (Mworia-Maitima, 1991; Olago, 2001; Kiage and Liu, 2006). This appears to be corroborated at Lukenya Hill where not only are browsers and mixed-feeders present and consuming C_3 resources, but mountain reedbuck and plains zebra are also interpreted to have consumed some C_3 plants. The shift from a more to less diverse faunal community over time at Lukenya Hill may reflect faunal turnover as a response to ecological changes. In the late Holocene lake level and diatom records in the Lake Turkana and Victoria basins indicate a rapid and abrupt shift to aridity at ~5–4 ka corresponding with the end of the AHP (Forman et al., 2014; Chritz

et al., 2019), but only in the pollen record from Lake Naivasha is there evidence for rapid phytogeographic change from grassy woodlands to open grasslands (Mworia-Maitima, 1991). The interpretation of the late Holocene environment at Enkapune Ya Muto as arid and open (Ambrose, 1984, 1998; Marean, 1992a) is supported by the combined environmental records from Lake Naivasha (Kiage and Liu, 2006).

High-resolution paleoenvironmental datasets from archaeological sites indicate that global and regional climate changes may be locally evident, but do not always result in dramatic changes to local habitats and environmental conditions (Chritz et al., 2019). At Lukenya Hill, both the taxon distributions and the δ^{13} C isotope data indicate more grassy environments. In the late Holocene, grazers are seen to be consuming significantly more C_4 biomass than in the early-mid Holocene. and all grazing taxa match their recent counterparts in estimated percent C4 consumption. In contrast to regional records from the Rift Valley lakes and Lake Victoria basin (Tierney et al., 2011; Chritz et al., 2019), there is no evidence for a major shift in aridity between the two periods present at Lukenya Hill based on the $\delta^{18}\text{O}$ values. The Lukenya Hill data agree more closely with the Mount Kenya diatom record (Barker et al., 2001) and the Mount Kilimanjaro ice core records (Thompson et al., 2002). These records do indicate a shift from warm and wet conditions in the early-mid Holocene to warm and dry conditions in the late Holocene, but without an abrupt and extended period of aridity at the termination of the AHP. It should be noted though that while the results indicate a gradual shift in environmental conditions at Lukenya Hill, it is possible that a more rapid change in aridity occurred in the period between the early-mid Holocene and late Holocene but has not been identified as that time interval is not represented archaeologically at the site.

The late Holocene aridification trend has been ascribed to cooling sea-surface temperatures resulting in a weakened Indian Ocean monsoon (Kuhnert et al., 2014; Weldeab et al., 2014; Liu et al., 2017), and a westward shift of the Congo Air Boundary (Costa et al., 2014; Junginger et al., 2014). The combination of these climatic events suggests a gradient of decreasing rainfall from east to west across eastern Africa. While Lukenya Hill would have also received weaker rains in the late Holocene than in the early-mid Holocene, it would have received greater rainfall than Enkapune Ya Muto near Lake Naivasha and the Lake Victoria and Turkana basin sites. Under this scenario, environments may become more open at Lukenya Hill, as evidenced in the $\delta^{13}C$ data, without corresponding isotopic evidence for a shift to aridity.

4.2. Comparison to enamel stable isotope records from the Lake Victoria and Turkana basins

Few additional local paleoenvironmental records for the Holocene in eastern Africa have been published. While both Lake Victoria and Lake Turkana are between ~500 and 600 km to the north and west of Lukenya Hill, archaeological sites in these basins provide the only temporally relevant enamel stable isotope data for comparison. As mentioned earlier, Chritz et al. (2019) found that these two basins responded differently to the end of the AHP and the subsequent onset of Holocene aridity. Based on faunal enamel data, the Lake Victoria basin was characterized by an abundance of C₄ plants throughout the middle and late Holocene while the Turkana basin saw a shift in herbivore diets towards more C_3 biomass after ~5 ka. Results from Lukenya Hill are more similar to those from the Lake Victoria sites, including Luanda, Wadh Lang'o, and Gogo Falls (Fig. 1). Since much of the data provided by Chritz et al. (2019) come from teeth identified only to the level of bovid tribes the best direct comparison can be made with alcelaphins (wildebeest and hartebeest) which account for 10 of the 22 samples at Lukenya Hill (Fig. 4). Mean δ^{13} C values for Lake Victoria (n = 34; 1.8 \pm 1.2‰) and Lukenya Hill (1.9 \pm 1.5‰) alcelaphins are very similar (Mann-Whitney U: p = 0.667). Alcelaphins from Chritz and colleagues' (2019) Lake Turkana lakeside sites, however, have a much lower mean δ^{13} C (*n* = 15; -0.1 ± 2.2‰). These values are significantly lower than those from Lukenya Hill (Mann-Whitney *U*: p = 0.012), likely reflecting the shift to increased mixed-feeding identified in the Chritz et al. (2019) study. Chritz et al. (2019) do not report any alcelaphin data from the Turkana regional site of Ele Bor. Based on these comparisons, Lukenya Hill was similar to the Lake Victoria basin in being characterized by open and grassier environments throughout the Holocene. Although there may have been some change in phytogeography at Lukenya Hill as indicated by other grazers; it does not appear as if that habitat shift was as dramatic as the one in the Lake Turkana basin. Instead, the results from Lukenya Hill support an ecological response to the end of the AHP somewhere between that of the Lake Victoria and Turkana basins (Fig. 4).

5. Conclusion

Identifying the conditions and selective pressures of Holocene economic and social changes in eastern Africa has been hampered by a lack of local paleoenvironmental datasets. The multi-site complex of Lukenya Hill, which sits on a historic ungulate migratory route on the Athi-Kapiti Plains, offers a rare, nearly-continuous, glimpse into climatic conditions of the Holocene from ~9.0 to 1.2 ka. The evidence from the $\delta^{13}C$ record of faunal tooth enamel and the shift towards a grazer-dominated faunal community at this site indicates that the earlymid Holocene may have been more wooded than the late Holocene. These results fit with the overall eastern African pattern of moist and closed environments during the Holocene component of the AHP followed by a drying and opening of the environment. At Lukenya Hill, however, there is no evidence for a significant shift in aridity over time, perhaps revealing a local response to the end of the AHP which was characterized by a muted change in aridity compared with sites further to the west in the Rift Valley and the Lake Turkana Basin. To echo Chritz et al. (2019), additional local environmental records from inland and coastal sites across eastern Africa will help refine our understanding of any relationships between climate, ecology, and human economic behaviors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

I thank the curators and staff of the National Museums of Kenya, especially Purity Kiura, Emma Mbua, and Idle Farah, for research access to the Lukenya Hill archaeological collection. Research was conducted under a Kenyan National Council for Science and Technology research permit issued to J.R.R., and sample export was facilitated by Edward Opiyo with the NCST. I thank Richard Gramly for permission to study the Lukenya Hill collection and Curtis Marean for providing field notes and discussion regarding the faunal identifications. Mass spectrometry was performed with the help of John Krigbaum and Jason Curtis in the Departments of Anthropology and Geosciences and the Light Stable Isotope Laboratory at the University of Florida. I thank Andy Howard for handling this manuscript and the anonymous reviewers for taking the time to provide careful and thoughtful comments. All travel, research, and analyses for this project was supported by a National Science Foundation - Archaeology Doctoral Dissertation Improvement Grant (BCS-1245803) to J.R.R. and Dietrich W. Stout.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2019.102016.



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Fig. 4. Box-and-whisker plots of enamel δ^{13} C values for alcelaphins from the Holocene deposits of Lukenya Hill in comparison to Holocene data from Lake Victoria and Lake Turkana. The Lukenya Hill alcelaphins are presented as a combined unit as well as from GvJm-19 and GvJm-22 separately. Sample sizes are in parentheses on the y-axis below the name of the site/location. Boxes represent the upper and lower quartiles for each taxon and whiskers indicate the full range for each taxon; hashes within boxes represent the median value. Open circles represent outliers. VPDB stands for Vienna Pee-Dee Belemnite. Lake Victoria and Lake Turkana δ^{13} C isotope data from Chritz et al. (2019).

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