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The stable isotope ecology of mammals in the southern Kenyan Rift Valley

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ABSTRACT

Global climate change is often invoked to explain major events in human evolution; however, in eastern Africa, basin-scale biotic and abiotic processes may exert greater evolutionary pressure on mammalian communities than global climate does. The southern Kenyan Rift Valley preserves a record of evolutionary trends over the last one million years, including evidence for the earliest known Middle Stone Age (MSA) technology and the emergence of the taxonomically modern large herbivore communities in eastern Africa by ~300 ka. Evidence of these evolutionary events coincided with a time when wet-dry climate variability was likely heightened in eastern Africa; however, we need more data to establish the links between climate change and evolutionary pressures on early humans and mammalian herbivores. Here we report carbon and oxygen isotope data from fossil teeth of large herbivores living in the Olorgesailie Basin and nearby at Lainyamok between 1.0 to 0.3 Ma. Herbivore diets were largely invariant through time, even after a significant faunal turnover that marks the appearance of species that are characteristic of the region today. Over 85% of individuals sampled were committed C₄-grazers with $\delta^{13}\text{C}_{\text{enamel}}$ values > 0 ‰, including notably, every elephant in our sample population. This is in contrast to dietary behaviors of these same species today, many of which include considerable amounts of C₃ browse in their diets, such as the elephants. These observations mean that the reorganization of mammalian communities by 300 ka cannot be used to infer a shift in resource availability in the southern Kenya Rift during the periods of fossil accumulation. The continued usage of C₄ grasses as a food resource in this region across this transition may indicate that the fossil assemblages represent environments that were buffered from the effects of regional climate events, emphasizing the importance of local tectonics and hydrology in controlling the environments of these records. The dominance of grazers and near-absence of browsing herbivores also means that functional modernity of the herbivore community did not arise in the southern Kenya Rift Valley until after ~300 ka. This result adds to the growing understanding that present-day and historical conditions may not be appropriate analogues for understanding environments and ecosystems of even the very recent past.

1. INTRODUCTION

Environmental change has long been considered as a driver of human evolution (e.g. Potts 1998, Grove 2012 and references therein) and there is an increasing number of studies that link orbitally-driven changes in global climate to human evolution (e.g. Behrensmeyer 2006, Kingston et al. 2007, Trauth 2007, deMenocal 2011, Grove 2011, Tierney et al. 2017). Among these links, it has been proposed that periods of high variability in global climate fostered the development of adaptability as a trait within lineages of hominins (Potts and Faith 2015). Specifically, it has been suggested that enhanced wet-dry variability in the southern Kenyan Rift Valley was a source of environmental change during the time of the first appearance of Middle Stone Age (MSA) technology in eastern Africa at ~320 ka (Potts et al. 2018). Additionally, between ~499-320 ka there was an 85% turnover in the large mammals of the southern Kenyan Rift, resulting in the emergence of the taxonomically modern community of large mammal species characteristic of eastern Africa today (Potts et al. 2018). It has been proposed that an increasingly variable climate produced more variability in vegetation resources, which favored smaller bodied generalist species who were better able to cope with frequent changes in their environment than the larger-bodied specialists they replaced (Potts et al. 2018).

However, the specific role of global climate in this faunal turnover is unclear. Environmental change in terrestrial contexts is driven not only by changes in climate, but also by tectonics, and by the biotic interactions of organisms in an ecosystem (e.g. Asner et al. 2015, Lupien et al. 2018). In many places, the behavior of large herbivores plays a major role in ecosystem function (e.g. Falk et al. 2015, Asner et al. 2015, Schmitz et al. 2018, Berzaghi et al. 2019). Faith et al. (2019) identify significant changes in the traits of large herbivores (e.g. body size, diet, digestive physiology) within eastern African faunal communities between the late Pleistocene and the present day, and suggest that large herbivore communities in eastern Africa did not functionally resemble modern communities until after 700 ka. The lack of information about herbivore dietary behavior from the last million years limits our understanding of how the beginning of functional modernity relates to the appearance of taxonomically modern species at the time of the faunal turnover. Likewise, we do not know how the changing ecology of large herbivores influenced the hominins of the region. Therefore, a record of climate alone is not sufficient to determine how climate affected the evolution of organisms; we need to understand ecology in order to explore the role of climate variability in producing evolutionary pressure on mammalian herbivores and early humans. Here, we use carbon and oxygen isotope distributions in tooth enamel from fossil mammals to investigate ecological changes in the southern Kenyan Rift during the last 1 Ma.

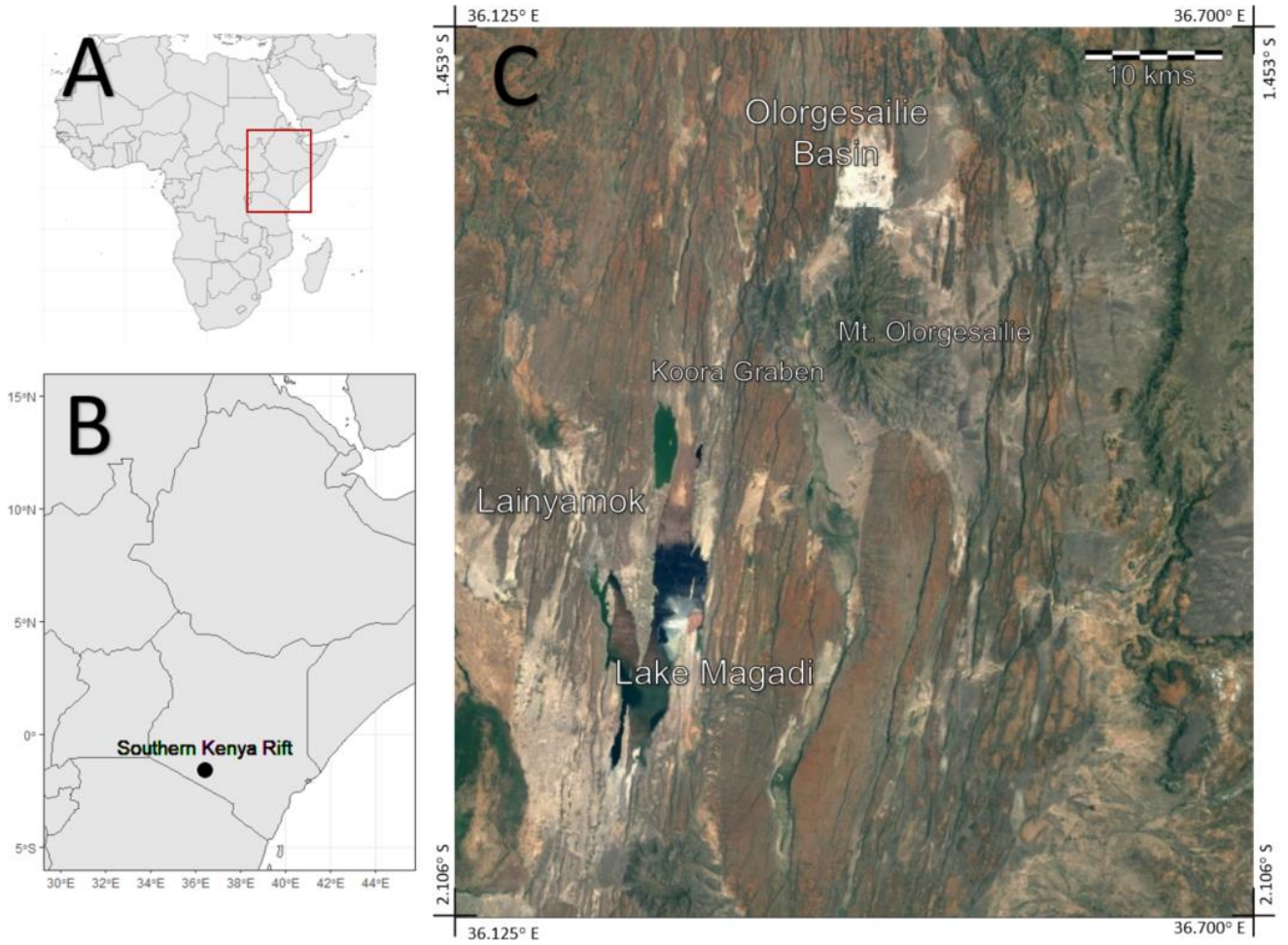


Figure 1. **A)** Location of the East Africa Rift Valley within Africa **B)** The location of the southern Kenyan Rift Valley, **C)** Notable localities within southern Kenyan Rift Valley including the Ologesailie Basin, Lainyamok, and Lake Magadi (imagery from Google Earth).

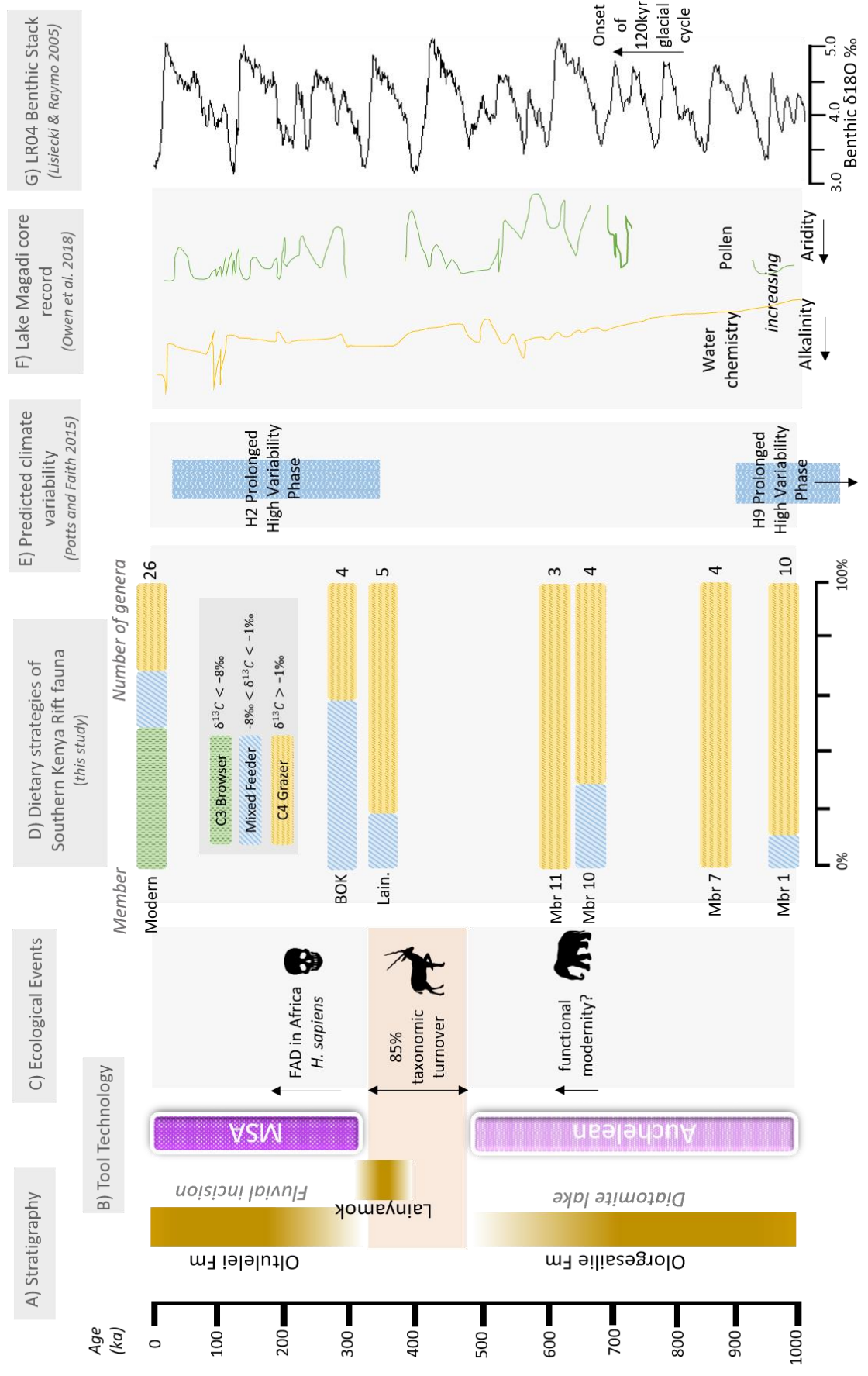


Figure 2. **A)** Stratigraphy of southern Kenyan Rift sediments showing the erosional unconformity between ~499-320 ka (Deino et al. 2018) **B)** Technology present in the southern Kenyan Rift, showing the appearance of Middle Stone Age (MSA) technology post-unconformity (Brooks et al. 2018) **C)** Significant ecological and evolutionary events including first appearance of *H. sapiens*, major faunal turnover and hypothesized earliest appearance of functionally modern herbivore communities in eastern Africa (Richter et al. 2017, Potts et al. 2018, Faith et al. 2019, respectively) **D)** For each member, the proportions of total genera in each fossil assemblage which fall within the dietary categories of browser, grazer, or mixed feeder based on the average tooth enamel $\delta^{13}\text{C}$ value for individuals in the genus (definitions and modern data from Cerling et al. 2015; fossil data from this study). We view these results as tentative pending further refinement of taxonomic identities. **E)** Predicted periods of prolonged (>192 ka) high climate variability in the last 1 Ma, potentially a cause of variability in resource availability (Potts and Faith 2015) **F)** Regional environmental indicators from the Lake Magadi Core (Owen et al. 2018). Left/yellow: Na/Ca ratio showing increasing lake alkalinity through the sequence. Right/green: Poaceae/aquatic pollen ratios indicating variable wet/dry periods with trend toward increasing aridity. Display of data is approximate. **G)** Benthic foraminiferal $\delta^{18}\text{O}$ record showing glacial (high $\delta^{18}\text{O}$) and interglacial (low $\delta^{18}\text{O}$) periods over the last 1 Ma, including the transition to the dominance of 120 kyr orbital cycle at ~700 ka (Lisiecki and Raymo 2005).

2. BACKGROUND

2.1 Study area and records

The Kenyan Rift Valley is a region of active tectonics and contains a rich record of human evolution. Rifting has created successive basins, and frequent volcanism provides datable material that allows for precise chronologies of fossil assemblages (e.g. Deino et al. 2018). The rifting has also created a fractured landscape with complex topography, supporting high biological diversity (Badgley et al. 2017), and the potential for different environments and ecological dynamics occurring within adjacent basins (Levin 2015). In these fractured landscapes, it is especially important to use environmental proxies which capture information on spatial scales which are relevant to the faunal communities being studied (Reed 2008).

The Olorgesailie Basin, in the southern Kenyan Rift Valley, contains a sediment record from the last 1.2 Ma (see Figure 1). The fourteen members of the Olorgesailie Formation compose the lower stratigraphy of the basin and are primarily diatomite lake deposits with volcanic tuffs (Isaac 1978). The Olorgesailie Formation is overlain by the Oltulelei Formation, which is dominated by fluvial deposition (Table 1; Behrensmeyer et al. 2018). Strata of the Olorgesailie and Oltulelei Formations contain abundant mammalian fossils and stone artifacts (Isaac 1978, Brooks et al. 2018, Potts et al. 2018, Deino et al. 2018). The two formations are separated by an erosional unconformity, from 499-320 ka, possibly driven by a change of base level at nearby Lake Magadi, although the role of orbital cycles in controlling erosion and aggradation in the basin has also not been ruled out (Behrensmeyer et al. 2018, Deino et al. 2018, Owen et al. 2018).

The Oltulelei Formation contains the earliest known transition from the Acheulean tool technology, characterized by handaxes and large stone tools, to the Middle Stone Age (MSA) tool technology characterized by smaller and more intricate stone tools, evidence of long distance transport of higher quality materials like obsidian, and the use of pigments possibly associated with increased symbolic behavior and increased cognitive ability in the hominins of the basin after ~320 ka compared to the Acheulean tool-users which preceded them (Brooks et al. 2018, Potts et al. 2018). Although the transition to the MSA in the Olorgesailie Basin is not associated with hominin fossils, it occurs around the time of the emergence of *Homo sapiens* elsewhere, estimated to be 350-260 ka (Schlebusch et al. 2017). The oldest known *H. sapiens* fossils have been found in Morocco and are dated to ~300 ka (Richter et al. 2017). There are very few other sites in eastern Africa which can be used to document this period, making Olorgesailie critically important for understanding this stage of human evolution.

A major change in mammalian fauna of the southern Kenyan Rift occurs during the erosional unconformity between the Olorgesailie and Oltulelei Formations. Between 499 – 320 ka, there is disappearance of species and appearance of new species which results 85% in a turnover in the large mammals (Potts et al. 2018). At Lainyamok, ~35km to the southwest, sediments and fossils dated to 390-330 ka provide a record during the critical time missing at Olorgesailie (Potts et al. 1988, Potts and Deino 1995). Together, the sediments of the Olorgesailie Basin and Lainyamok contain a record of hominin activity and faunal evolution in southern Kenya spanning from 990 ka to 305 ka (Table 1).

The fossil mammal communities from the BOK sites of the Oltulelei Formation and at Lainyamok are some of the earliest assemblages of taxonomically modern mammals in eastern Africa. They contain only representatives of extant species with the exception of one species of antelope, *Damaliscus hypsodon*, a relative of the modern topi (Potts and Deino 1995, Faith et al. 2012), which is not present in extant mammal populations. This turnover is characterized by the replacement of larger species with smaller-bodied relatives (Potts et al. 2018). The new species that appeared during the turnover at Lainyamok and in the Oltulelei Formation (< 390 Ka) include many of the animals that are iconic of eastern Africa today, such as *Loxodonta africana* (the modern African elephant), *Hippopotamus amphibius*, *Phacochoerus* warthogs, and others (Potts et al. 2018).

Increasing aridity and variability in climate may have been a source of evolutionary pressure in southern Kenya, driving both the change in hominin behavior and the faunal turnover by decreasing resource predictability (Potts and Faith 2015, Potts et al. 2018). Increased aridity in the region during the last 1 Ma is evident from the core record at Lake Magadi (~40 km SW of the Olorgesailie Basin), where Na/Ca ratios track the development of an alkaline lake, and pollen ratios are interpreted as a sign of

increasing aridity (Owen et al. 2018). Potts and Faith (2015) model orbital cycles and identify a period of sustained high climate variability in eastern Africa from 358-50 ka (stage H2). However, it is not clear how these identified features in eastern African paleoclimate manifested on the landscape and in the ecosystems where early hominins and mammals lived.

2.2 Tooth Enamel Stable Isotopes

Here, we use an isotopic record of herbivore dietary change during a faunal turnover to test the influence of climate on the interaction of these animals with their environment. The stable isotope composition of tooth enamel preserves information about past environments, as experienced by the organisms that lived within those environments (Du et al. 2019). Isotope values are reported in a standard permil (‰) notation shown in equation (1), where R is the ratio between isotopes A and B (e.g. $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$):

$$\delta_{A-B} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 \quad (\text{equation 1})$$

The carbon isotope values ($\delta^{13}\text{C}$) and oxygen isotope values ($\delta^{18}\text{O}$) of an animal's tissues depend primarily on the animal's diet and water source (Cerling and Harris 1999, Blumenthal et al. 2017). Tooth enamel is the preferred tissue for isotope analysis in fossil mammals because it preserves $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals with low susceptibility to diagenesis compared to other tissues like bone (Cerling and Harris 1999). Teeth preserve well in the fossil record, and even isolated or fragmentary teeth can provide useful taxonomic information which informs interpretation of isotope results. For most mammals, tooth enamel forms only during the first few years of the animal's life; once formed, no chemical exchange occurs between the enamel and the rest of the animal's tissues (Du et al. 2019).

The carbon isotope value in tooth enamel is derived from diet, which for herbivores means that tooth enamel $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{\text{enamel}}$) are controlled by the $\delta^{13}\text{C}$ values of the vegetation they eat. In eastern African during the Pleistocene, the first order control on $\delta^{13}\text{C}_{\text{enamel}}$ is the proportion of C_3 vegetation (trees, shrubs, some grasses) vs. C_4 vegetation (arid grasses) in herbivore diet (Cerling et al. 2003). These food resources are isotopically distinct due to the greater degree of discrimination against ^{13}C by plants using the C_3 photosynthetic pathway, compared with plants using the C_4 photosynthetic pathway (Cerling et al. 2003). Oxygen isotopes in tooth enamel ($\delta^{18}\text{O}_{\text{enamel}}$) preserve information about the $\delta^{18}\text{O}$ values of an animal body water, which reflects physiology, diet, water-use strategy and the environment of the sampled animal (Blumenthal et al. 2017).

2.3 Interpretive Framework for $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$

Before using tooth $\delta^{13}\text{C}_{\text{enamel}}$ values to infer diet, it is important to understand the biotic and abiotic factors that can influence the $\delta^{13}\text{C}$ signal on its way from the atmosphere, into plants, and ultimately into animal tissues. $\delta^{13}\text{C}$ values of plants are dependent on environmental factors including humidity and light conditions (Kohn 2010, Farquhar et al. 1989, Madhavan et al. 1991). The reasonable range for $\delta^{13}\text{C}$ values in C_3 plants in open canopy environments in dry regions (but excluding extreme environments like the Atacama Desert) is -20 to -30‰ (Kohn 2010). The $\delta^{13}\text{C}$ of C_4 plants is typically -14‰ to -10‰ (Cerling et al. 1997). Changes in $\delta^{13}\text{C}$ of atmospheric CO_2 during the Cenozoic produced a commensurate variance in the $\delta^{13}\text{C}$ of terrestrial plants, a range of 2‰ (Tippie et al. 2010). During the last 1 Ma, the $\delta^{13}\text{C}$ of atmospheric CO_2 has ranged from \sim -7.25‰ to -6.5‰, with an average value of \sim -6.75‰, which is slightly lower than the conventional “pre-industrial” value of -6.5‰, and thus needs to be accounted for when comparing data from this study to other tooth enamel datasets (Tippie et al. 2010). Although diet-tissue fractionation of carbon isotopes occurs during digestion, and the degree of fractionation is determined by digestive physiology and body mass (Tejada-Lara 2018), we do not consider body mass in this study and instead assume the conventional fractionation factor of \sim 14‰ across all taxa (e.g. Cerling et al. 2015). Using a mixing model built on these considerations (where C_3 plants have a $\delta^{13}\text{C}$ value of -25‰, C_4 plants have a $\delta^{13}\text{C}$ value of -12‰, atmospheric $\delta^{13}\text{C}$ is 0.25‰ lower than standard preindustrial value, and the large herbivore dietary fractionation factor is +14‰) we can determine that tooth enamel isotope values above \sim 0‰ $\delta^{13}\text{C}$ come from individuals with less <10% C_3 resources in their diets. For the sake of easy comparison between datasets, we define three categories: browsers ($\delta^{13}\text{C}_{\text{enamel}} < -8\text{‰}$), grazers ($\delta^{13}\text{C}_{\text{enamel}} > -2\text{‰}$), and mixed feeders (intermediate $\delta^{13}\text{C}_{\text{enamel}}$ values) following Cerling et al. (2015).

To a first order, $\delta^{18}\text{O}$ in large herbivores is dependent on the local hydrology. Surface waters can undergo evaporation causing their $\delta^{18}\text{O}$ increase, and a water with a $\delta^{18}\text{O}$ value greater than 0‰ has almost certainly evaporated to some extent (Gat 1996). The amount of evaporation is correlated with residence time at the surface, and residence time maybe be controlled by local topography and tectonics. The diet-tissue fractionation factor of oxygen isotopes diminishes for animals with greater body mass, and therefore the $\delta^{18}\text{O}_{\text{enamel}}$ values of largest taxa most closely resemble the original composition of ingested water $\delta^{18}\text{O}$ (Bryant and Froelich 1995). Herbivore $\delta^{18}\text{O}_{\text{enamel}}$ is also affected by the proportion of their body water that comes from ingested water vs. water derived from diet (Blumenthal et al. 2017). Leaf waters tend to have higher $\delta^{18}\text{O}$ values than surface water bodies because of the intense evaporation that occurs in plant leaves as they respire, and therefore herbivores that are

less reliant on drinking surface water may have higher $\delta^{18}\text{O}_{\text{enamel}}$ values (Blumenthal et al. 2017). Modern waters in Kenya (stream, river, springs, well, rain and tap water) have an average $\delta^{18}\text{O}$ value of $-2.5 \pm 2.4\text{‰}$ (Levin et al. 2009). Changes in $\delta^{18}\text{O}_{\text{enamel}}$ values of the herbivores in this study may be indicative changes in the source of the herbivore's body water or changes in $\delta^{18}\text{O}$ of the water source. $\delta^{18}\text{O}_{\text{enamel}}$ values can also be used to construct an aridity index (Blumenthal et al. 2017).

3. METHODS

3.1 Sampling Fossil Teeth

Fossil teeth were sampled for isotopic analysis from the collections of the National Museums of Kenya. Sampled teeth came primarily from fossiliferous horizons in five members of the Olorgesailie Formation (Members 1, 7, 10, 11 and 13), two sites in the Olkesiteti Member of the Oltulelei Formation (BOK1-E and BOK2; approximately age equivalent, see Deino et al. 2018), the Oltepesi Member of the Oltulelei Formation, and from Lainyamok (Table 1, Supplementary Table 1).

Taxonomic identifications are based on information available from the museum collections: on tags included with specimens or via the working specimen lists maintained by Dr. Richard Potts. Where a sample had multiple proposed identifications from different researchers, the most recent identification was used. For the purpose of this thesis, all taxonomic identifications are considered provisional, pending further review. All sampled teeth were photographed to aid in further identification in the future. Because fragmentary teeth were targeted for sampling, it may not be possible to identify some teeth beyond the family level. However, these teeth are still useful because in some instances lower level taxonomic designations can be inferred from knowledge of which species were extant at the time. For example, Equids in the upper Members of the Olorgesailie formation are likely *Equus*, given the last appearance date (LAD) or other Equid genera, and all Proboscideans are likely *Elephantidae*, given the LAD of other Proboscidean families in eastern Africa.

We prioritized sampling teeth that could be sampled with minimal disruption to the tooth's morphology, such as teeth with existing broken edges. We did not sample from teeth that appeared poorly preserved, which were typically distinguished by being light colored and friable. We targeted isolated 2nd and 3rd molars wherever possible. To remove samples of enamel, we used a Forza LMK50 dental drill with carbide and diamond drill bits operated between 6000-9000 RPM. Carbide drill bits were used to remove surface debris and clean enamel surface. Tooth enamel powder was collected on weighing paper and transferred to 5mL centrifuge tubes. Friable samples were swaddled in Kimwipes to prevent the vibrations from the drill knocking off dirt and other debris onto the weighing paper. Enamel

samples were taken from along broken edges where possible. On teeth without broken edges, small patches were drilled from the surface of the enamel in minimally disruptive locations.

Location	Formation	Member or site	Age (ka)	Lithology	Depositional Environment	Technology	#Teeth sampled
Ologesailie Basin	Oltulelei Fm.	Oltepesi		Alternating fine and coarse siliciclastic sediments	Incision and infill	MSA	1
		Olkesiteti - BOK sites	320-295	Primarily fine siliciclastic sediments, some coarse volcanic materials	Fluvial, wet conditions, wetland indicators	MSA	20
Lainyamok		Khaki 2 layer	397 - 334	Massive silts with cobble sized pieces of trachyte and inclusions of lower-lying materials	Subaerial mudflow	Possible MSA	18
<i>Erosional unconformity in the Ologesailie Basin, 499 ka - 320 ka</i>							
Ologesailie Basin	Ologesailie Fm.	Member 13	609-499	Primarily diatomite with paleosol in upper section of the member	Lake and subaerial exposure	<i>no sites</i>	1
		Member 11	671-609	Mainly paleosol with bedded diatomite, and some sands and gravels and tuffs	Oscillating subaerial exposure and lake	Acheulean, with greater degree of material selectivity	31
		Member 10	671	Sands and gravels with pumice	Subaerial exposure	Acheulean	12
		Member 7	974-780	Subaerial exposure	Subaerial exposure and wetlands	Acheulean	36
		Member 1	992-974	Mixture of bedded diatomite, paleosols, and reworked paleosols	Osculating lake, subaerial exposure and wetlands	Acheulean	60

Table 1. Description of fossil localities and Ologesailie Basin stratigraphy. #Teeth sampled indicates the number of teeth from that locality which were sampled for isotope analysis in this study. Member and site ages from Deino and Potts (1990) and Deino et al. (2018). Lithology and depositional environment from Potts et al. (1988), Potts et al. (1999), Behrensmeyer et al. (2002), and Behrensmeyer et al. (2018). Technology descriptions from Potts et al. (1999), Brooks et al. (2018) and Deino et al. (2018).

3.2 Isotopic Analysis

The tooth enamel powders were pretreated to remove inorganic carbonate and other impurities using a conventional pretreatment method (e.g. Cerling et al. 2015). Tooth enamel powders were treated with a 3% hydrogen peroxide solution for fifteen minutes, then rinsed three times with deionized water, followed by another treatment of buffered 0.1 M acetic acid solution for fifteen minutes and three more rinses with water. The powders were dried overnight in a 60°C oven. Samples were reacted with phosphoric acid at 76°C and analyzed on a Thermo Finnigan MAT 253 with Kiel IV preparation device at the Stable Isotope Laboratory at the University of Michigan. Isotope values are reported relative to Vienna-Pee Dee Belemnite (VPDB). The raw $\delta^{18}\text{O}$ values for CO_2 were converted to the equivalent $\delta^{18}\text{O}$ values for carbonate using an acid digestion fractionation factor for $\text{CO}_3\text{-CO}_2$ of 1.008528, which was derived using a formula developed for fossil tooth enamel and a reaction temperature of 76°C (Passey et al. 2007).

Analyses were standardized to NBS-19 carbonate standards and all analyses averaged within 0.2‰ of the IAEA accepted value for $\delta^{13}\text{C}$, and indistinguishable for $\delta^{18}\text{O}$. The standard deviation of NBS-19 within each run was better than 0.05‰ for $\delta^{13}\text{C}$ and 0.09‰ for $\delta^{18}\text{O}$ for all runs. Two fossil tooth enamel working standards (NFE and NHP) were run as external standards to assess the precision of the runs, and performed with standard deviations of 0.03‰ ($\delta^{13}\text{C}$) and 0.11‰ ($\delta^{18}\text{O}$) and 0.15‰ ($\delta^{13}\text{C}$) and 0.12‰ ($\delta^{18}\text{O}$), respectively (inter-run performance). When examining groups of results, means are presented accompanied by standard deviations indicated by the \pm symbol. When comparing between two means, a t-test is used where $t()$ indicates the degrees of freedom and p-values indicate the likelihood that the difference between two means occurred by chance (the difference between two means is considered significant at $p < 0.05$). For modern animals described in this in this study, $\delta^{13}\text{C}$ values have been corrected to reflect pre-industrial isotope values for atmospheric carbon ($\delta^{13}\text{C}_{1750}$) making them comparable to the fossil individuals (Cerling et al. 2015). Statistical analysis was performed in the programming language R.

Member	Bovid					Elephantid				
	N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$		N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
OLT	1	-8.6	-	4.3	-	-	-	-	-	-
BOK	7	-0.4	3.5	4.2	2.2	3	0.9	0.3	-0.3	0.3
Lain	13	0.8	3.1	4.3	2.1	1	2.4	-	-1.0	-
13	-	-	-	-	-	1	2.2	-	0.5	-
11	7	1.3	4.0	2.7	0.8	9	2.8	1.6	0.5	1.2
10	1	3.2	-	5.8	-	-	-	-	-	-
7	2	1.5	1.7	3.9	0.2	7	1.1	0.8	0.0	1.2
1	15	1.7	3.3	3.2	1.5	6	1.9	1.0	1.6	3.5
unknown	1	4.4	-	3.0	-	-	-	-	-	-
Total	49	0.8	3.6	3.7	1.8	27	1.9	1.3	0.5	1.9

Member	Equid					Hippopotamid				
	N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$		N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
OLT	-	-	-	-	-	-	-	-	-	-
BOK	4	1.0	0.4	1.9	1.6	3	-2.4	5.1	0.1	3.9
Lain	1	1.5	-	2.8	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-
11	4	0.8	0.5	2.8	1.2	6	1.4	1.3	-1.8	2.2
10	5	1.8	0.8	4.4	1.2	2	-1.1	0.2	-1.0	1.9
7	7	1.5	0.8	2.5	1.4	4	-1.3	1.4	-1.0	1.6
1	8	1.6	0.9	2.0	1.4	11	1.5	0.9	1.3	1.0
unknown	-	-	-	-	-	4	1.2	1.1	-0.2	0.5
Total	29	1.4	0.8	2.7	1.5	30	0.5	2.2	-0.1	2.0

Member	Rhinocerotids					Suid				
	N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$		N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
OLT	-	-	-	-	-	-	-	-	-	-
BOK	1	-5.0	-	2.7	-	2	0.8	0.4	1.8	2.0
Lain	-	-	-	-	-	3	1.0	0.6	3.1	0.9
13	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	4	0.7	1.0	2.3	1.9
10	1	-5.3	-	2.9	-	3	1.4	1.0	0.7	1.2
7	2	2.3	0.2	1.4	0.8	3	1.3	1.1	0.2	2.5
1	11	1.2	1.6	1.8	0.8	4	1.5	0.5	2.7	0.6
unknown	-	-	-	-	-	2	0.9	0.8	2.7	1.0
Total	15	0.5	2.7	1.8	0.8	22	1.1	0.8	2.0	1.6

Member	<i>Theropithecus oswaldi</i>					Unknown taxon				
	N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$		N teeth	$\delta^{13}\text{C}$		$\delta^{18}\text{O}$	
		Mean	SD	Mean	SD		Mean	SD	Mean	SD
OLT	-	-	-	-	-	-	-	-	-	-
BOK	-	-	-	-	-	-	-	-	-	-
Lain	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-
11	1	0.6	-	3.4	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-	-
7	11	0.7	0.4	3.1	0.6	-	-	-	-	-
1	2	1.0	0.3	2.3	1.1	3	2.1	1.9	2.5	2.5
unknown	12	1.0	0.5	2.7	0.6	-	-	-	-	-
Total	26	0.9	0.4	2.9	0.7	3	2.1	1.9	2.5	2.5

Table 2. Tooth enamel stable isotope results reported relative to VPDB and in ‰ units. Results are binned by gross taxa group (bovids, elephantids, equids, hippopotamids, rhinocerotids, suids, and *Theropithecus oswaldi*) and by Member. SD is the standard deviation of the sample. Cell colors show the range of $\delta^{13}\text{C}$ (-8.6‰ as darkest green to +4.4‰ as brightest yellow) and the range of $\delta^{18}\text{O}$ (-1.8‰ as deepest blue to +5.8‰ as deepest red).

4. RESULTS

In all, 161 fossil teeth were analyzed from the Olorgesailie and Oltulelei Formations (Table 1). 19 teeth sampled from the Olorgesailie Basin could not be confidently assigned to a member. Teeth that were not assigned to a member are included in Table 2 and Supplementary Table 1 but they are not included in the analyses below. An additional 18 teeth were analyzed from Lainyamok. The sampled teeth come from eight mammalian families (bovids, elephantids, equids, hippopotamids, rhinocerotids, suids, and cercopithecids). Since all of the cercopithecids that we sampled are attributed to genus *Theropithecus* and presumed to be *T. oswaldi*, we use this species level taxonomy in presenting the results. Summaries of carbon and oxygen isotope results by unit and taxon are provided in Table 2.

Bovids sampled in this study come from the tribes Alcelaphini, Hippotragini, Tragelaphini, Antilopini, Bovini and Aepycerotini and are rarely identified to genus. The range of $\delta^{13}\text{C}_{\text{enamel}}$ values for all bovids is -8.6‰ to 4.7‰, reflecting the broad range of dietary strategies among bovid tribes. The lowest $\delta^{13}\text{C}_{\text{enamel}}$ values ($-3.5 \pm 3.2\%$) are found within the Tragelaphini, who are C_3 -browsers in the present day based on a sample from a variety of eastern African environments (Cerling et al. 2015; Figure 4).

Equids in this sample are mostly assigned to the genus *Equus*, although our sample includes one *Eurygnathohippus* sp. from Olorgesailie Member 1 and two *Hipparion* sp. from Olorgesailie Member 7 (see Supplemental Table 1). The $\delta^{13}\text{C}_{\text{enamel}}$ values for all equids range from 0.1 to 2.8‰, with a mean of $1.4 \pm 0.7\%$. In general, the equids show little variation in $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ values within members, and through time within our sample. There is also no significant difference between the $\delta^{13}\text{C}$ values of individuals from the genera *Hipparion*, *Eurygnathohippus* and *Equus* that co-occurred in Members 1 and 7 ($t(10) = -0.64$, $p = 0.54$).

Hippopotamids are represented at Olorgesailie by two species: *Hippopotamus gorgops* and the smaller *Hippopotamus amphibius* in the younger units (Potts et al. 2018). The majority of hippopotamids from the Olorgesailie Basin are not identified to species; however, we assume that the hippopotamid teeth from the Oltulelei Formation are *H. amphibius*, while the hippopotamid teeth from the Olorgesailie Formation are *H. gorgops* (there are no hippopotamids from Lainyamok in this sample). The one individual identified as *H. amphibius* is from the BOK sites and it has a $\delta^{13}\text{C}_{\text{enamel}}$ value of -8.0‰. This

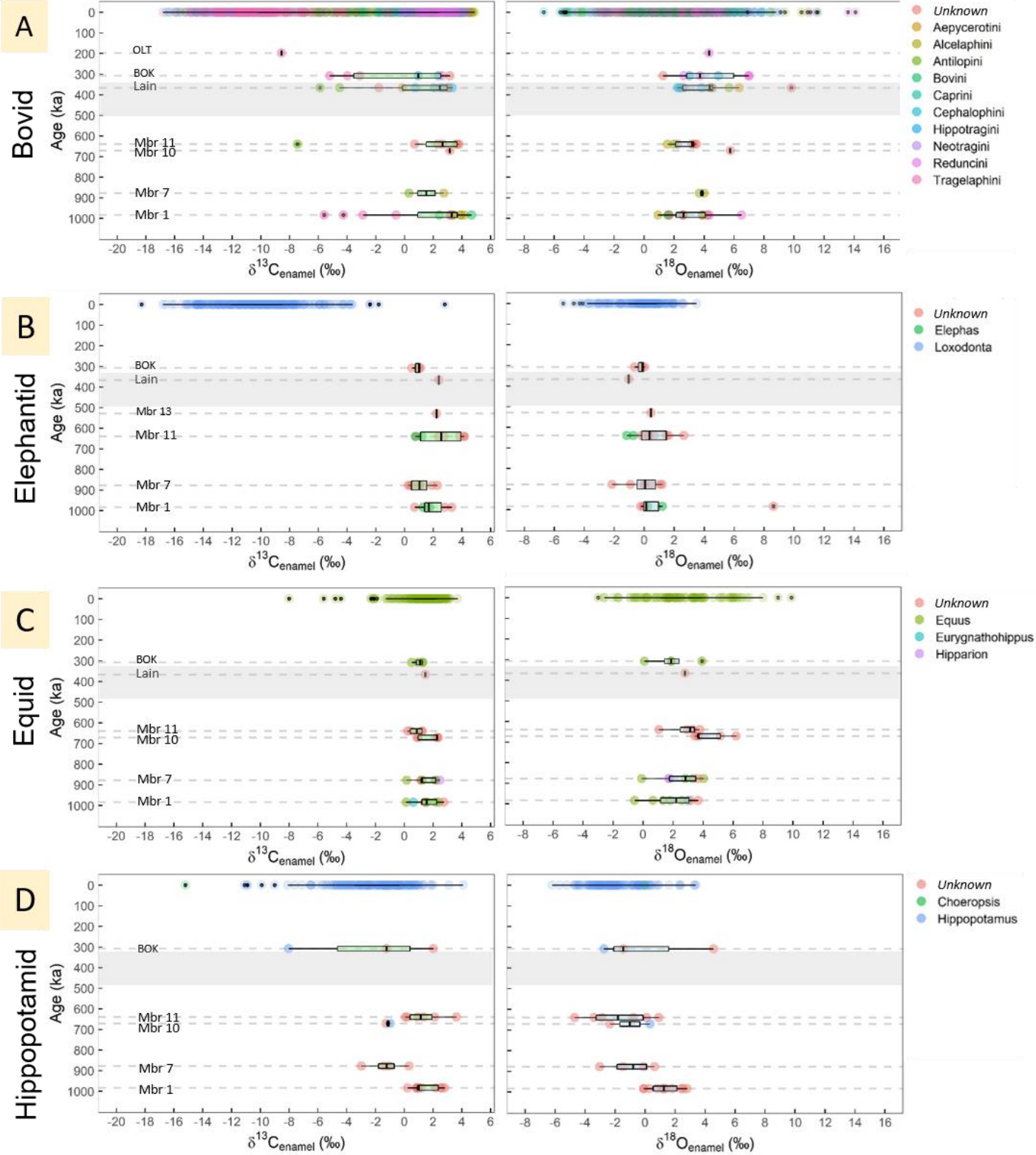
is notably lower than the average $\delta^{13}\text{C}_{\text{enamel}}$ value of all other hippopotamid teeth was $0.5 \pm 2.2\text{‰}$ (Table 2). The average $\delta^{18}\text{O}_{\text{enamel}}$ value for all hippopotamids in this study is $-0.9 \pm 2.0\text{‰}$. Although there is large variation in $\delta^{18}\text{O}_{\text{enamel}}$ values, the hippopotamids generally have lower $\delta^{18}\text{O}_{\text{enamel}}$ values than other groups.

Rhinocerotids from both *Ceratotherium simum* and *Diceros bicornis* are present in our sample but only five of the 15 rhinocerotids at Olorgesailie are identified beyond the family level (there are no rhinocerotids from Lainyamok in our sample). However, unidentified rhinocerotid teeth can be assigned to a genus with reasonable confidence because modern *C. simum* (grazing white rhinos) have significantly higher $\delta^{13}\text{C}$ values than *D. bicornis* (browsing black rhinos) ($t(32.4)$, $p < 0.001$) due to dietary differences between the two genera (modern data from Cerling et al. 2015).

Suids include individuals identified as *Metridiochoerus* sp., *Kolpochoerus majus*, and *Phacochoerus* sp. All suids in this study have carbon isotope values $> -0.4\text{‰}$. There is little variation in $\delta^{13}\text{C}_{\text{enamel}}$ values through time or between different genera of suids in this sample (Table 2).

All cercopithecids in the sample are identified to genus *Theropithecus*, with some further identified as *T. oswaldi*. The majority of *Theropithecus* teeth sampled are from Member 7 (12 sampled teeth await member identification). The $\delta^{13}\text{C}_{\text{enamel}}$ values for all *Theropithecus* show remarkably tight grouping: an average value of $0.9 \pm 0.4\text{‰}$ ($n = 25$).

The proboscidean teeth sampled for isotopic analysis were often highly fragmentary (i.e. isolated tooth plate fragments) and in many cases could not be identified beyond Order Proboscidea; however, given the known last appearance date of other proboscidean families, the individuals at Olorgesailie and Lainyamok are all almost certainly Elephantidae (Harris 1976, Werdelin and Sanders 2010). The samples for this study includes teeth identified as *Elephas* sp. (Members 1 and 11) and one that was further identified as *E. recki* (Member 1). We note that *Loxodonta africana*, the modern African elephant, is present in the Olkesiteti Member, while *E. recki* is not (Potts et al. 2018). Therefore, the two elephantids from the BOK sites in this study are presumed *Loxodonta* rather than *Elephas*. The $\delta^{13}\text{C}_{\text{enamel}}$ values for all of the sampled elephantids range from $+0.3$ to $+5.2\text{‰}$, with a mean of $+1.9 \pm 1.3\text{‰}$ (Table 2). There are no clear trends in $\delta^{13}\text{C}_{\text{enamel}}$ values among the sampled elephantids through time, although the small sample sizes from younger members limits identification of trends (Figure 2B). The $\delta^{18}\text{O}_{\text{enamel}}$ values for all elephantids range from -2.2 to $+8.6\text{‰}$, with a mean of $+0.5 \pm 1.9\text{‰}$. One individual elephantid from Member 1 has a $\delta^{18}\text{O}_{\text{enamel}}$ value of $+8.6\text{‰}$, which is nearly 6‰ higher than the next highest value for an individual.



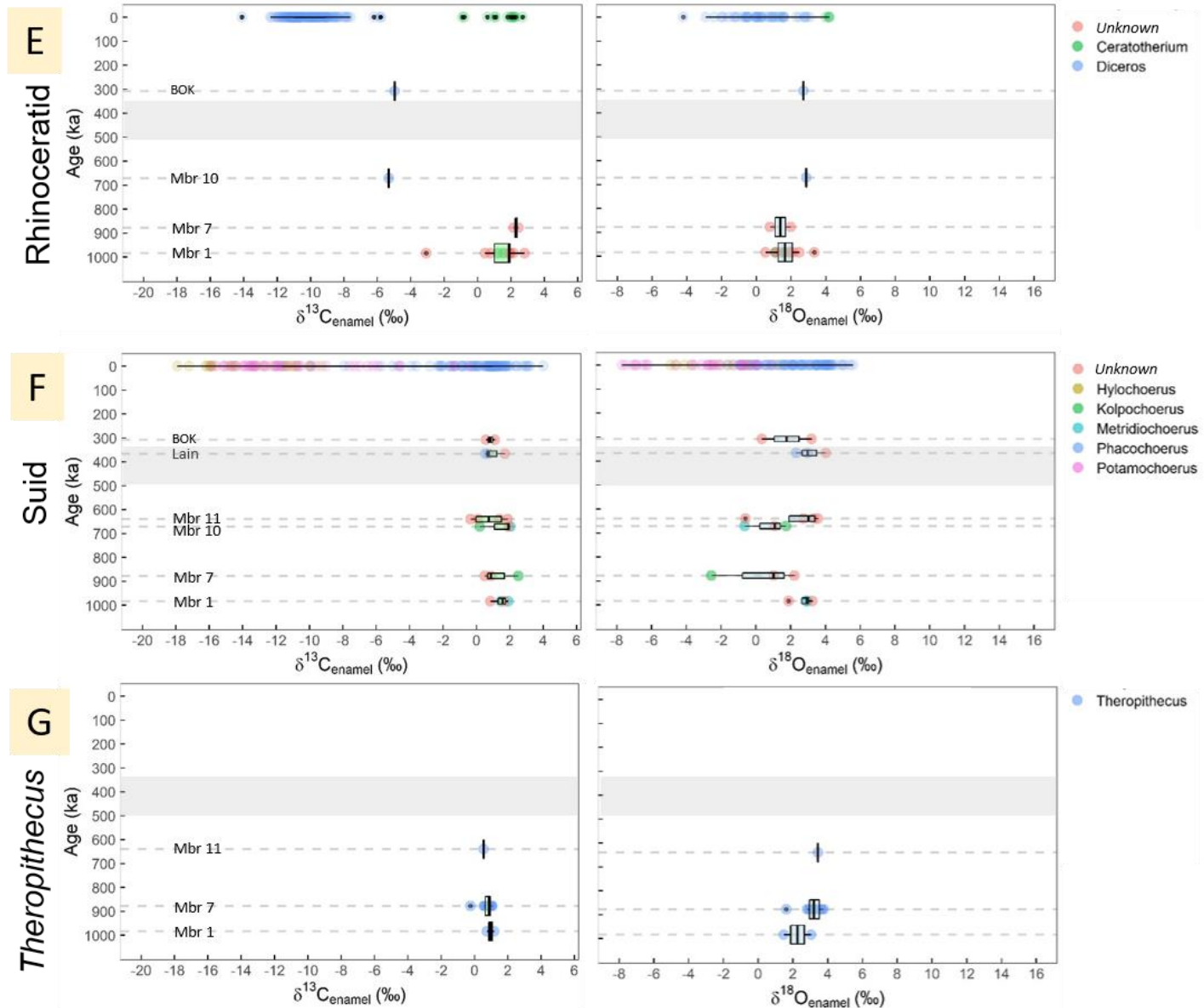


Figure 3. Isotopic composition of mammalian herbivores of the southern Kenyan Rift Valley. Boxplots by member show $\delta^{13}\text{C}_{\text{enamel}}$ (left) and $\delta^{18}\text{O}_{\text{enamel}}$ (right) results for each major taxon group: (A) bovids, (B) elephantids, (C) equids, (D) hippopotamids, (E) rhinocerotids, (F) suids, and (G) *Theropithecus oswaldi*. The middle bar shows the mean, boxes show 1st and 3rd quartiles, whiskers are 1.5 times the interquartile range (the variation between the 1st and 3rd quartiles of the data), and outliers outside the 1.5 times interquartile range are indicated by solid points. Colored points show individual analyses, and are grouped by genus (or tribe for bovids in panel A). The $\delta^{13}\text{C}_{\text{enamel}}$ values from modern herbivores in eastern Africa are from Cerling et al. (2015) that include individuals sampled from a range of eastern African habitats and have been corrected to reflect pre-industrial isotope values for atmospheric carbon ($\delta^{13}\text{C}_{1750}$) making them comparable to the fossil data. Note, this dataset of modern teeth includes individuals sampled from forested and high elevation sites, which are not good analogs for Ologresailie; we plan to use a subset of this dataset in future analysis, which may affect the results. The $\delta^{18}\text{O}_{\text{enamel}}$ values of modern animals come from Blumenthal et al. 2017. The grey box represents the interval of time where sediment is missing from the Ologresailie Basin, during which the faunal turnover occurred.

5. DISCUSSION

5.1 Interpretation of Dietary Behaviors through Time from Tooth Enamel $\delta^{13}\text{C}$

High $\delta^{13}\text{C}_{\text{enamel}}$ values indicate a greater degree of C_4 -grazing among mammalian herbivores, while intermediate and low $\delta^{13}\text{C}_{\text{enamel}}$ values indicate mixed feeding and C_3 -browsing, respectively. From $\delta^{13}\text{C}_{\text{enamel}}$ values of fossils in our sample, the proportion of C_4 food resources in the diets of the herbivores in the southern Kenyan Rift appear to have been largely invariant for the last 1 million years, even after the appearance of modern species after 499 ka. Over 85% of the individuals sampled from Olorgesailie and Lainyamok yield $\delta^{13}\text{C}_{\text{enamel}}$ values greater than 0‰, indicating that the overwhelming majority of individuals were grazers, consuming almost exclusively C_4 food resources. When the data from individuals are averaged within a genus, 90% of genera sampled from the southern Kenyan Rift classify as C_4 grazers ($\delta^{13}\text{C}_{\text{enamel}} > -2\text{‰}$) and the other 10% are mixed-feeders ($-8\text{‰} < \delta^{13}\text{C}_{\text{enamel}} < -2\text{‰}$) (classifications following Cerling et al. 2015). These results indicate that all of the taxonomic groups of large herbivores from the southern Kenyan Rift Valley included in our sample used C_4 food resources to a significant extent, including the groups known for browsing in the present day, such as the Elephantids. It is, however, important to note that some modern-day browsing taxa groups are not well represented in our sample (e.g. *D. bicornis*, the browsing rhinoceros), or not represented at all (e.g. Giraffids), so we may not be capturing the entire breadth of dietary behavior with our sample.

A change in resource availability has been suggested as a cause of evolutionary pressure during the time of the faunal turnover in the southern Kenyan Rift 499 – 320 ka (Potts et al. 2018). If that was the case, we would expect the diets of herbivores from the Olorgesailie Formation to be different from the diets of the herbivores which replaced them at Lainyamok and in the Oltulelei Formation. However, we see no isotopic evidence of significant dietary change associated with the appearance of new species between 499 – 320 ka in the southern Kenyan Rift.

For example, there are two lineages of suids in the southern Kenyan Rift, neither of which show evidence of dietary change within the sequence (Figure 4A and B). Although the *Kolpochoerus* is viewed as the ancestor of the *Hylochoerus* “forest hog” (Bishop et al. 2010), there is no evidence from this study that *Kolpochoerus* sp. adopted any C_3 -browsing or mixed-feeding behavior before 600 ka at Olorgesailie (N = 2, mean $\delta^{13}\text{C} = 1.4\text{‰}$; see Figure 4A). The *Metridiochoerus* sp. sampled from the Olorgesailie Formation (N = 4, mean $\delta^{13}\text{C}_{\text{enamel}} = 1.7\text{‰}$), have a similar isotope value to the two descendant *Phacochoerus* sp. sampled from Lainyamok (N = 2, mean $\delta^{13}\text{C}_{\text{enamel}} = 0.7\text{‰}$), indicating that this lineage did not significantly change its diet during the faunal turnover (Figure 4B). Although modern eastern African suids have a wide range of dietary strategies (Cerling et al. 2015), the suids present at

Ologesailie were all grazers and do not show evidence of dietary change associated with the evolution of new genera in their lineages. All suids in this study have carbon isotope values $> -0.4\text{‰}$, indicative of diets dominated by C_4 grasses. There is no evidence of C_3 vegetation being an important part of the diet of any suid sampled from the Ologesailie Basin or Lainyamok.

Another notable change during the faunal turnover is the replacement of *Hippopotamus gorgops* with the smaller-bodied *Hippopotamus amphibius* (Potts 2018). Apart from one anomalous $\delta^{13}C_{\text{enamel}}$ value for an individual in the BOK sites, the $\delta^{13}C_{\text{enamel}}$ values of hippopotamids sampled in the Ologesailie Basin do not show change in diet through time. The mean $\delta^{13}C_{\text{enamel}}$ value for hippopotamids at Lainyamok and the Oltulelei Formation (presumed *H. amphibius*) is -2.4‰ ($N = 3$) while the mean $\delta^{13}C_{\text{enamel}}$ value for hippopotamids in the Ologesailie Formation (presumed *H. gorgops*) are -0.1‰ ($N = 23$). Curiously, a single individual identified as *H. amphibius* (from BOK) has a $\delta^{13}C_{\text{enamel}}$ value of -8.0‰ , notably lower than that of the other two hippopotamids from BOK (mean = 0.4‰) (Figure 4C). We plan to confirm the ID of this sample. Otherwise, $\delta^{13}C_{\text{enamel}}$ values of all hippopotamids in this sample indicate that they are dedicated C_4 -grazers or mixed-feeders.

The carbon isotope data from other taxonomic groups likewise show little dietary change through time (Table 2; Figure 3). The equids of the southern Kenyan Rift remain committed C_4 -grazers throughout the entirety of the last 1 Ma. Where the genus *Equus* is coincident with the genera *Hipparion* and *Eurygnathohippus* in Ologesailie Members 1 and 7, there is no distinguishable difference in the diets of these three groups. The *T. oswaldi* at Ologesailie are consistently C_4 -grazers, which is consistent with other $\delta^{13}C_{\text{enamel}}$ values from older members of the *Theropithecus* genus that indicate the increased proportion of C_4 graze in their diets from 4 to 1 Ma (Cerling et al. 2013). The bovid family has the greatest variation of $\delta^{13}C_{\text{enamel}}$ values within the record, reflecting the variety of dietary strategies among bovid tribes. However, there is only one individual bovid (a tragelaphine from the OLT locality) that can be classified as a C_3 -browsers from its $\delta^{13}C_{\text{enamel}}$ value of -8.6‰ . All other Bovids in the sample are C_4 -grazing or mixed-feeders. Apart from this one individual, there is no resolvable variation in either mean or standard deviation of $\delta^{13}C_{\text{enamel}}$ values of bovids between members. The current level of taxonomic identification of bovids in this study does not provide enough resolution for recognizing trends at the genus level, although we hope that this may change with subsequent work on taxonomic identification.

The notable difference between our sample of the Pleistocene fossil communities in the southern Kenyan Rift and the modern herbivore communities in present-day eastern Africa is the lack of indications of browsing behavior. For example, it is noteworthy that at Ologesailie the “browsing”

rhinocerotids yield $\delta^{13}\text{C}_{\text{enamel}}$ values that indicate a substantial portion of graze in their diets. Rhinocerotids in the sample for this study include individuals identified as *C. simum* and *D. bicornis*, which are grazers and browsing in the present day, respectively. This bifurcation in the behavior of rhinocerotids taxa groups has been documented isotopically since at least 3 Ma (Cerling et al. 2015). We also identify a bimodal distribution of $\delta^{13}\text{C}_{\text{enamel}}$ values for the rhinocerotids in our sample with a significantly different $\delta^{13}\text{C}_{\text{enamel}}$ values: there are 12 individuals including three identified as genus *Ceratotherium* with a mean $\delta^{13}\text{C}_{\text{enamel}}$ value of $+1.8 \pm 0.6\text{‰}$, and three rhinocerotids including two identified as *D. bicornis* with a mean $\delta^{13}\text{C}_{\text{enamel}}$ value of $-4.4 \pm 1.0\text{‰}$ ($t(-12.3)$, $p < 0.001$). However, the $\delta^{13}\text{C}_{\text{enamel}}$ values of the group of low- $\delta^{13}\text{C}_{\text{enamel}}$ rhinocerotids in this sample is significantly higher than modern browsing *D. bicornis* and in the range of mixed feeding ($t(7.9)$, $p < 0.001$) (modern data from Cerling et al. 2015). Although we have identified two isotopically distinct groups of rhinocerotids in our sample, neither occupies the browsing niche of modern browsing rhinocerotids.

Likewise, the Tragelaphini bovids at Olorgesailie have significantly higher $\delta^{13}\text{C}_{\text{enamel}}$ values than their modern counterparts in eastern Africa ($t(5.85)$, $p < 0.001$; see Figure 4D). The average modern Tragelaphini is a browser (mean $\delta^{13}\text{C}_{\text{enamel}}$ of -8.5‰ , $N = 35$), while specimens identified as Tragelaphini at Olorgesailie are mixed feeders (mean $\delta^{13}\text{C} = -2.5\text{‰}$, $N = 5$). Like the rhinocerotids, this is an instance of where a taxonomic group known for browsing in the present day instead engaged in mixed feeding during the time period preserved in the southern Kenyan Rift sediments. The result is that our sample does not contain any taxa group with $\delta^{13}\text{C}_{\text{enamel}}$ values indicative of true browsing, and every individual in the sample made use of C_4 food resources to some extent.

There is enduring interest in the timing of the extirpation of the grazing elephant, *Elephas recki*, from Africa and appearance of the modern African browsing elephant, *Loxodonta africana*, which occurred during the Pleistocene (e.g. Sanders et al. 2010, Manthi et al. 2019). The lower Olorgesailie beds contain *E. recki* while the upper beds contain *L. africana* (Potts et al. 2018). The $\delta^{13}\text{C}_{\text{enamel}}$ values of the elephantids in our sample ($N = 27$) indicate that they were all grazers, consuming almost exclusively C_4 food resources, with little change through time (Figure 3B). There are no individuals in our sample with $\delta^{13}\text{C}_{\text{enamel}}$ values indicative of browsing or mixed feeding behavior. This is significant because it suggests that, at least in the southern Kenyan Rift, the transition to browsing behaviors among elephantids occurred very recently, post-300 ka and not as a function of the faunal turnover or at the first appearance of *L. africana*. This is important because it shows that elephantids persisted in their grazing niche through 300 ka, which has significant implications for the organization of the southern

Kenyan Rift ecosystem, given the importance of *L. africana* as an ecosystem engineer in the region today.

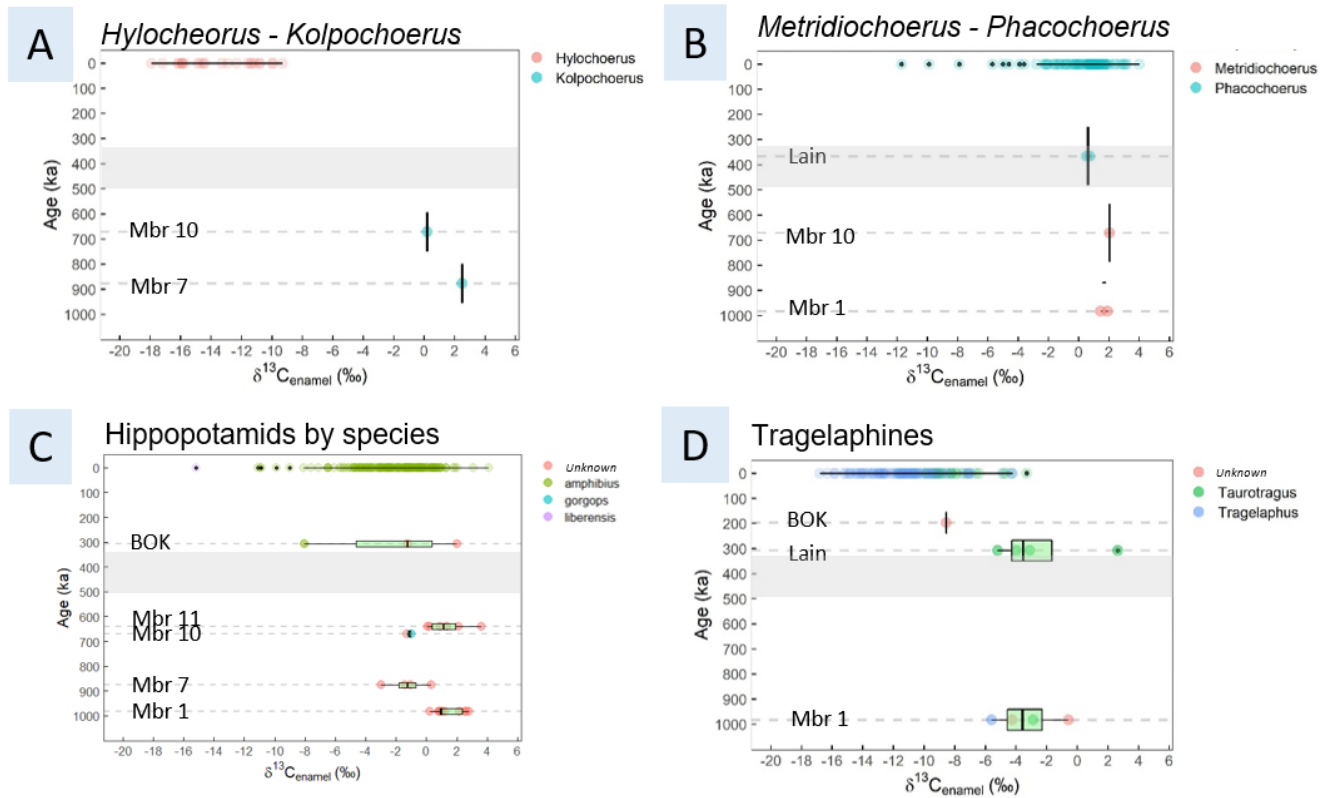


Figure 4. Box plots illustrating dietary behavior at finer taxonomic resolution than in Figure 3: **A)** the *Kolpochoerus-Hylochoerus* lineage, **B)** the *Metridiochoerus-Phacochoerus* lineage, **C)** hippopotamids differentiated to the species level, and **D)** Tragelaphini bovds.

5.2 Implications for the Emergence of Functional Modernity

Megaherbivores have an outsized impact on the functioning of their ecosystems (Smith et al. 2016). By selectively removing and consuming plant tissues, they limit above ground biomass (McInnes et al. 1992, Berzaghi et al. 2019), reduce the frequency and intensity of fires (Holdo et al. 2009, Schmitz et al. 2018), control the movement of energy and nutrients through an ecosystem (Schmitz et al. 2018), and can impact the carbon cycle and the release of methane from soils through trampling and altering the distribution of vegetation (e.g. Schmitz et al. 2018, Smith et al. 2015, Falk et al. 2015). In particular, modern elephants have been described as “ecosystem engineers” for their role in altering the distribution of woody vegetation (e.g. Davis et al. 2018, Morrison et al. 2016, Asner et al. 2015, Hayes 2012). Modern elephants are C₃ browsers who are known to topple and kill small trees (diameter <30 cm) in pursuit of their preferred vegetation (Berzaghi et al. 2019). This promotes patchy, open canopy

forests with increased variety in vegetation height and reduced above ground biomass, but enhances net primary productivity and nutrient retention as trees are kept in a state of constant early succession (Berzaghi et al. 2019, Davis et al. 2018). Forest modification by elephants also affects a wide range of other landscape conditions important for other taxa, such as the amount of habitat available for birds and other tree dwellers, the sight lines for predators, the dynamics of fires, and the availability of food resources for other herbivores (Valeix et al. 2019). Therefore, understanding the dietary behavior of fossil elephantids key to understanding the functioning of past ecosystems.

Carbon isotope results show that the communities of herbivores in the southern Kenyan Rift had distinctly different dietary behavior in the past than communities of herbivores in eastern Africa in the present day. Specifically, there was a much greater proportion of C₄ graze being consumed by the community as a whole, little evidence of browsing, and several notable taxa groups with dietary behavior different from their modern counterparts, such as the elephantids. Because of the myriad effects of elephantid on their ecosystems, it is unreasonable to expect that an ecosystem in which elephantid are behaving radically differently from their modern behavior would be functioning the same way as a modern ecosystem.

Faith et al. (2019) consider dietary behavior to be one of the traits that determine “functional modernity” of herbivore communities, which is a trait separate from a community's taxonomic modernity. By comparing physiological traits such as size, dietary physiology and diet categories, they argue that herbivore communities in eastern Africa over the last 4 Ma have almost never been analogous in function to modern eastern African communities, and that the rise of functional modernity in this region did not occur until after 700 ka. Our results, with dietary information for the large herbivores from the southern Kenyan Rift, show that functional modernity did not occur in this region until after 300 ka, and that functional modernity lagged behind the appearance of taxonomically modern communities at Lainyamok and in the Oltepesi Formation. Although this finding applies only locally to the southern Kenyan Rift, these results indicate more generally that modern behaviors cannot be inferred from the presence of modern fauna.

5.3 Implications for Role of Climate in the Faunal Turnover

The faunal turnover in the southern Kenyan Rift has been linked to climate-driven environmental change (Potts et al. 2018). However, our results show stability in herbivore diet throughout the history of the southern Kenyan Rift, meaning that the appearance of taxonomically modern herbivore communities by 300 ka cannot be used to infer a change in vegetation or resource

availability in the southern Kenyan Rift. Despite a period of high climate variability beginning at ~350 ka (Potts and Faith 2015), it appears that C₄ grasses were an abundantly available food resource for mammalian communities of the southern Kenyan Rift during the time intervals that preserve fossils and evidence for early human activity.

Increasing aridity has also been proposed as a potential driver of evolution in the southern Kenyan Rift (Owen et al. 2018). The Lake Magadi drill core, 40 km SW of Olorgesailie, shows increases in both alkalinity and the proportion of pollen from aridity-linked vegetation during the last 1 Ma (Owen et al. 2018). As an additional route toward assessing changes in the aridity between time periods in the southern Kenyan Rift, the $\delta^{18}\text{O}_{\text{enamel}}$ values in this study can be used to construct an aridity index using the approach outlined by Blumenthal et al. (2017). This method employs the fact that $\delta^{18}\text{O}_{\text{enamel}}$ of some taxa increase with a greater sensitivity to water deficit (evaporation sensitive; ES), than other taxa (evaporation insensitive; EI), due to difference in their sources of body water. We compared four combinations of ES-EI taxa pairs to derive an estimate of water deficit following Blumenthal et al. (2017). Of the four comparisons made (Tragelaphini-Hippo, Hippotragini-Hippo, Tragelaphini-Elephant, and Tragelaphini-Rhino), three show that the BOK sites had a greater water deficit (were more dry) than Olorgesailie Member 1 (see Supplementary Table 2). However, all comparisons show that the BOK sites had significantly lower water deficit (were less dry) than present-day Olorgesailie (~1900 mm/yr vs. ~1100 mm/yr today; Blumenthal et al. 2017). It is important to note that we view these results as tentative due to the small sample sizes of ES taxa, and the need to verify the taxonomic identification of some samples.

Although increasing aridity cannot be discounted as a factor in the evolution of organisms during this time, the persistence of grass throughout the Olorgesailie sequence itself cannot be taken as indicative of an environmental response to increasing aridity, as grasslands can arise without a link to aridification (Polisar et al. 2019). In eastern Africa today, lakeshore environments, such as in Lake Nakuru National Park, support the year-round growth of lush grasses that are suitable to sustain populations of grazing herbivores. In fact, for some taxa such as impala (*Aepyceros melampus*), $\delta^{13}\text{C}_{\text{enamel}}$ analyses indicate that the proportion of C₄ resources in their diets increase with increasing mean annual precipitation of their habitat (data from Cerling et al. 2015; see Figure 5). Once established, herbivores can perpetuate a grassland environment by suppressing growth of shrubs (Hempson et al. 2015).

The steady presence of grass in the Olorgesailie Basin during a period of high climate variability indicates that a force other than climate was responsible for mediating the environmental conditions of the southern Kenyan Rift. The tectonic history of the Olorgesailie Basin has created variable hydrological

conditions that may have had an important impact on type of vegetation in the Basin (see Table 1). Each fossil-producing horizon at Olorgesailie represents no more than a few thousand years and may be representative of short durations of exceptional conditions (Deino and Potts 1990). The presence of fossils may be more likely to occur during times of tectonic stability and sediment accumulation (conditions that also favor the presence of a lake in the basin), rather than periods of fluvial incision. Although grasses' shorter roots make them more sensitive to drought than trees and shrubs (Faith et al. 2018), the presence of a lake in the basin would raise the water table, insulating a grassland from effects of climate and allow the grassland to persist during periods of regional climate variability. Changing tectonics in the Basin may also have biased the Olorgesailie faunal record toward over-representing certain environmental conditions and phases in the Basin's history. Tectonics may also be partially responsible for the Lake Magadi core record by altering the catchment area of pollen and water entering the lake. Therefore, tectonics may exert a stronger control over the environmental records of the southern Kenyan Rift Valley than global or regional climate.

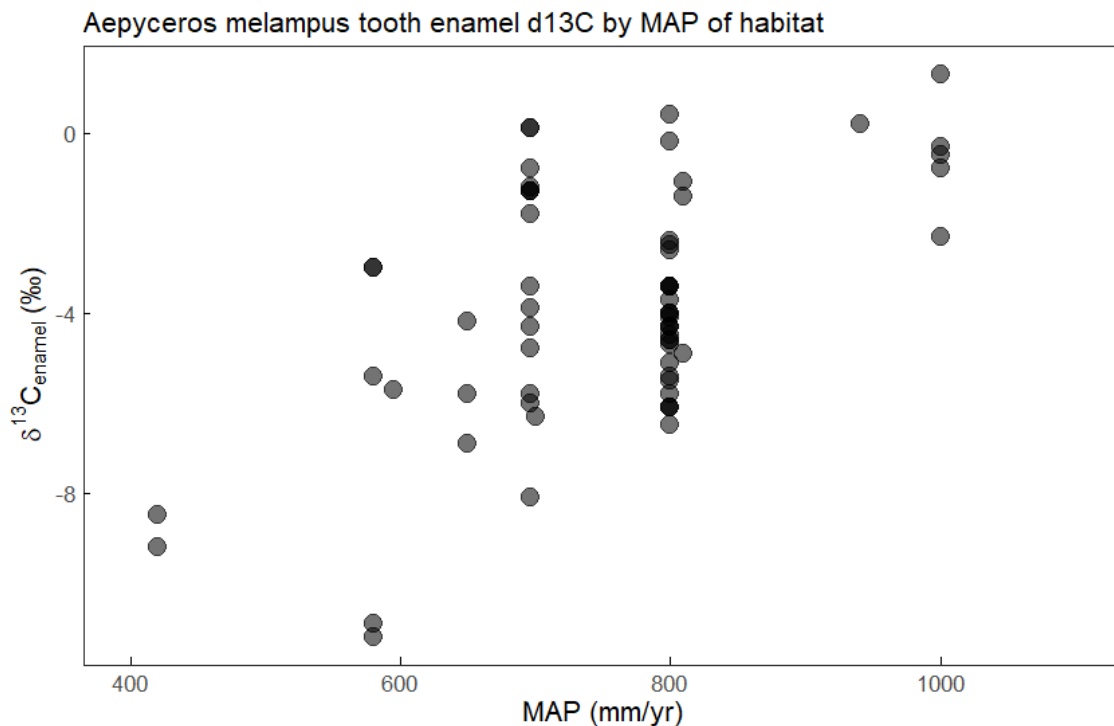


Figure 5. Tooth enamel (or enamel-equivalent) $\delta^{13}\text{C}$ for modern *Aepyceros melampus* collected from localities in Kenya, plotted against mean annual precipitation (MAP) of those localities ($\delta^{13}\text{C}$ data from Cerling et al. 2015; MAP data approximate from climate-data.org). Points are displayed at 50% transparency.

6. CONCLUSION

The sediments of the Olorgesailie Basin and nearby Lainyamok preserve environmental information from the last 1 million years of the southern Kenyan Rift Valley, an important setting in eastern African's paleohistory. This period of time is crucial for understanding the ecological dynamics that gave rise to modern communities of fauna and the development of more complex hominin behaviors.

The relationship between climate and the faunal turnover in the southern Kenyan Rift Valley remains unclear. In our investigation of the dietary behavior of the large herbivores of the Olorgesailie Basin, we do not find evidence that the faunal turnover in the southern Kenyan Rift was associated with changes in food resource availability. If vegetation resource variability was a contributing factor in the turnover, it was not a wholesale change in the availability of C₃ and C₄ resources, although this conclusion does not rule out other changes in vegetation, which may not be detectable in herbivore $\delta^{13}\text{C}_{\text{enamel}}$ values. Rather, we suggest that the tectonics of the region buffered the environment in the Basin from the effect of a variable climate: chiefly, that the presence of a lake in the basin created conditions favorable for sustaining a stable grassland. This grassland may have been further maintained by the grazing herbivores themselves (Hempson et al. 2015). This finding reemphasizes the importance of understanding environments as a product of the interaction between both abiotic and biotic factors.

Furthermore, the appearance of taxonomically modern organisms cannot be used to infer the beginning of a functionally modern ecosystem. The final reorganization of the southern Kenyan Rift ecosystem into its present state occurred after the appearance of taxonomically modern herbivore communities at ~300 ka. The faunal turnover was not an onset of the modern ecosystem; rather it was the opening to an additional chapter in the ecological history of the southern Kenyan Rift. Likewise, it appears that the more complex human behaviors of the MSA in the southern Kenyan Rift may predate the appearance of modern environments and ecosystems, and that modern ecosystems of the southern Kenyan Rift cannot be used as an analog for understanding hominin behavior during this time. The origins of MSA tool users and modern African mammals occurred within ecosystems that were dissimilar to the modern southern Kenyan Rift ecosystems.

This study does not explain how the functional modernity of herbivore communities arose after 300 ka. The appearance of a modern ecosystem may have occurred as a gradual change in the time after the faunal turnover, or alternatively, the present-day conditions of the southern Kenyan Rift may be fundamentally different than the past and not represented in the fossil record. For example, the grassy

abundance of the Ologesailie record may have only occurred during periods of aggradation in the basin, making it unfair to compare to today's tectonic configuration favoring erosion.

It may not be fair in the first place to expect that the past ecosystems of the southern Kenyan Rift should trend through time toward the present eastern African ecosystems. Our understanding of natural history is weighted toward the present, since that is the period of geological time that is the easiest to study. The present configuration of the eastern African ecosystems may not provide a good analog for understanding the functioning of the southern Kenyan Rift ecosystem in the past. There may be something about the present that is incongruous with the past in these environments, such as the millennia of human interactions with the landscape or changes in land use and agriculture associated with colonialism in Kenya beginning in the 19th century (Maathai 2006). Recognizing that current eastern African ecosystems function differently from the ecosystem in which many iconic eastern African species first appeared may have impacts on ecological restoration projects and aid conservation efforts for those species. Careful investigation of past ecosystems may also help distinguish what role humans have had on altering these systems, which can lead to a better sense of our species' past and future relationship with eastern African ecosystems.

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