ISOTOPIC RECORDS OF ECOLOGICAL VARIABILITY IN MODERN AND ANCIENT ENVIRONMENTS IN KENYA

by

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ABSTRACT

Stable isotope analysis of biological and geological materials has provided important information on environmental change over many timescales. Such records rely on an interpretive framework of large isotopic datasets of recent (i.e., modern and/or Holocene-aged) material in order to define paleoecological interpretations. This dissertation will contribute to a better understanding of ancient and historical ecological change in East Africa by (1) providing a modern interpretive framework for a megaherbivore, *Hippopotamus amphibius*, in East Africa and (2) investigating the relationship between climate and ecology in Kenya during the Holocene using multiproxy records, including stable isotopes of large mammalian herbivores and leaf wax biomarker isotopes.

Although *H. amphibius* (hippo) tooth enamel isotopes are widely used to understand paleoenvironment, little is known about their dietary variability across time and space. In this dissertation, I present an extensive study on stable isotope serial samples ($\delta^{13}C$ and $\delta^{18}O$) of modern hippos in order to understand the breadth of their dietary and behavioral flexibility in Kenya. This large dataset (10 mm interval samples of canine tooth enamel for 30 hippo canines; 1,410 samples in total) reveals the remarkable dietary diversity of hippos: they are indiscriminate feeders and can consume both C3 and C4 herbaceous forage. Furthermore, certain profiles with known death dates have captured isotopic indicators of ecological perturbations, such as drought and C3 plant encroachment following elephant extirpation.

Multiproxy records of ecology can provide even more paleoecological information than single-mammal records. Assumptions about environmental change in the fossil record are often based on inference from known global climate and presumed changes in ecology. Using a multiproxy approach (tooth enamel isotopes and leaf wax biomarkers), I present Holocene (11.8 Kya – present) paleoecological data from two basins: the arid Turkana Basin in northern Kenya and the more mesic Victoria Basin in southwestern Kenya. These data indicate that as the monsoon was weakening due to global climatic change (i.e, Milankovitch forcing), there was an increase in C_3 resources (bush, shrub, trees, and herbs) in Turkana, whereas Lake Victoria remained predominately C_4 (tropical lowland grasses). This interbasinal record reveals that we cannot make assumptions about changes in ecology in an entire region based on climatological forcing mechanisms alone.

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INTRODUCTION

1.1 Background

Stable isotope records of ecology from biological and geological materials have provided otherwise inaccessible knowledge of the ways in which mammals, ecosystems, and ancient people respond to perturbations in climate and ecology (Cerling et al. 2004; Cerling et al. 2005; Magill et al. 2013a; Magill et al. 2013b). Some isotopic records, such as those from certain biological tissues (e.g., hair and ever-growing teeth), can provide near-continuous records of how animals responded to disturbances in the natural world. In a paleoecological context, isotope records from fossil and archaeological mammalian tooth enamel have provided snapshots of their ecology, relating to changes in vegetation (Ambrose and Sikes 1991; Passey et al. 2002; Uno et al. 2011). These data, in concert with other isotope records from geological samples, particularly leaf wax biomarkers, can provide further context for paleoenvironment that is unbiased by mammalian behavioral characteristics, such as selective diets and migration.

These records are of special interest to researchers working in eastern Africa, where direct application of stable isotope techniques can address wide-ranging questions in climate-environment-human interactions over millions of years. Such questions involve the particular landscapes in which humans evolved, and the sorts of challenges and opportunities those landscapes may have presented to them. In a more recent context (<10,000 years), paleoecological records from stable isotopes can help clarify the environments that shaped modern human behavior, such as early food production. These two issues, though working on different temporal scales, go hand-in-hand, as recent sedimentological records can provide a model for understanding deep time climate-environment interactions in Eastern Africa.

Isotope records from biological material can also be used to address complicated questions of environmental change in historical ecology. Such data have assisted ecologists and paleoecologists in assessing dietary, behavioral, and environmental changes (Koch et al. 1995; Hirons et al. 2001; Ayliffe et al. 2004; Dalerum and Angerbjörn 2005; West et al. 2006; Zazzo et al. 2010). These data not only have utility in modern environments, but also in ancient environments, where they can provide a framework for how to interpret the past. Isotopic data from *Hippopotamus amphibius* canines can provide decadal-scale records due to their length and their recently understood ecological flexibility (Boisserie et al. 2005; Passey et al. 2005; Cerling et al. 2008). Questions still remain, however, as to exactly how variable these records are and what hippo dietary isotopes tell us about their immediate environment.

Over longer timescales, many researchers relate environmental changes in East Africa to climate changes. The climate of eastern African is driven primarily by Milankovitch cycles, periodic changes in the geometry of Earth's orbit that dictate the amount of solar insolation on Earth (Claussen et al. 1999; deMenocal et al. 2000; Stager et al. 2003; Laskar et al. 2004). Currently, precession of the equinoxes (Figure 1.1) is the driving orbital parameter that influences tropical climate (Kutzbach 1981; Berger and Loutre 1997; Clement et al. 2001; deMenocal 2004; Battisti and Naylor 2009; Clark et al. 2009). Insolation dictates the location and convective strength of the intertropical convergence zone (ITCZ), an area where Northern and Southern Hemisphere winds meet. The ITCZ moves seasonally, following peak solar insolation about equatorial Earth. Seasonal rainfall occurs in the ITCZ due to warming sea surface temperatures (SSTs) and differential heating between land and sea, which pulls moisture-rich air over the continents. When Northern Hemisphere peak solar insolation occurs as the earth is closest to the sun (the perihelion, Figure 1.1), the ITCZ strengthens, forming a low-pressure zone over northern Africa that drags moist air over the continent and intensifies the monsoon system (Nicholson 1996). During the early Holocene, precessionally driven high Northern Hemisphere insolation created mesic conditions known as the African Humid Period (AHP) (Kutzbach 1981; Braconnot et al. 2000; Gasse 2000; Russell et al. 2003; Mayewski et al. 2004; Garcin et al. 2007; Verschuren et al. 2009; Tierney et al. 2011b).

Lake level water budget models suggest that mean annual rainfall in the watersheds of Lakes Turkana, Victoria, Naivasha, and Nakuru-Elmenteita increased to 15–35% greater than 1980s levels during the AHP, filling the lakes to their highest extents and, in some cases, reaching overflow points (Hastenrath and Kutzbach 1983). As northern hemisphere insolation strength waned *c.* 5.5–5.0 Kya, a conspicuous arid period began in eastern Africa (Kutzbach 1981; deMenocal et al. 2000; Gasse 2000). In Lake Turkana, decreasing rainfall is demonstrated by falling lake levels observable via paleo-lake terraces, whereas in Lake Victoria, this trend is reflected in hydrogen isotopes from leaf waxes, albeit more gradually than in Turkana (Berke et al. 2012; Garcin et al. 2012).

Inferences of paleo- and/or historical ecology based on climatological data rely on the concept that rainfall is a major driver of the proportion of C_3 (woody plants, trees, and shrubs) vs. C_4 (tropical lowland grasses) biomass in African ecosystems, and particularly in savanna ecosystems. Woody cover can increase or decrease in response to climatological factors, such as changes in overall precipitation or seasonal distribution of rainfall (Marshall et al. 2007; Tierney et al. 2011a). However, the assumption that rainfall is the only driver of woody cover in savannas is problematic for many reasons, the first of which is that the term "savanna" is a broad ecological designation. A savanna is defined as a "mixed tree-grass system characterized by a discontinuous tree canopy in a conspicuous grass layer" (Ratnam et al. 2011). Savannas have 5–80% fractional woody cover; they include the structural categories grassland, wooded grassland, and woodland/ bushland/shrubland (Sankaran et al. 2005; Cerling et al. 2011; Good and Caylor 2011; Lehmann et al. 2011; Murphy 2012). However, many other ecological factors also influence the relative proportions of grass and woody cover (C_4 vs. C_3 plants): soil nutrients, grass and shrub competition with trees, underground biomass, fire frequency, and herbivory. Given all this, inferring ecological changes solely based on rainfall changes is tenuous (Sankaran et al. 2005).

Stable isotope analysis of mammalian tooth enamel is a useful indicator of modern and ancient environments in that dietary isotopes can differentiate between C_3 browsers and C_4 grazers (Lee-Thorp and Van der Merwe 1987; Ambrose and DeNiro 1989; Cerling et al. 1997). Tooth enamel resists diagenetic alteration and preserves well in the archaeological record, and is therefore preferred for paleoecological reconstructions (Lee-Thorp et al. 1989; Kohn and Cerling 2002; Uno et al. 2011). Isotopic measurements of enamel carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) can be used to understand diet, habitat, and climate (Levin et al. 2006; Lee-Thorp et al. 2007). In many instances, fauna provide the best estimates of environmental change over time, because many mammals adapt to changes in vegetation structure, and their isotopic signal is less temporally attenuated than other proxies (Kingston 2007).

Modern and ancient sediments also provide important information about past environments. Bulk isotopic measurements of soil organic matter can indicate overall terrestrial ecosystem structure via representation of C_3 vs. C_4 plants, which correspond roughly to woody plants versus tropical lowland grasses in Africa (Cerling et al. 1989; Ambrose and Sikes 1991; Cerling et al. 2011). The isotopic signature of bulk plant material recovered at molecular level in the form of leaf wax biomarkers can convey more specific information about floral composition of paleoenvironments than bulk organic material or tooth enamel (Eglinton and Hamilton 1967; Brincat et al. 2000; Freeman and Colarusso 2009). Terrestrial leaf wax lipids preserved in sediments (medium-high molecular weight *n*-alkanes and *n*-alkanoic acids) derive from aquatic organisms and plant leaf waxes, respectively. Thus, compound specific isotopic analyses ($\delta^{13}C$ and δD, deuterium) can convey highly specific information about paleoclimate, hydrology, and ecosystem structure (Xu and Jaffé 2008; Choudhary et al. 2009; Tierney et al. 2011b; Garcin et al. 2012). Thus, terrestrial biomarkers in lacustrine sediments represent a spatially integrated signal on a basinal scale (Talbot and Livingstone 1989).

This dissertation will provide new isotopic records defining environmental variability in both modern and ancient ecosystems in Kenya and Uganda. Understanding the drivers for East African environmental change requires empirical data connecting ecology with known climatic and biological perturbations. In recent environments, changes in savanna structure in national parks have been attributed to changes in herbivore biomass (especially elephants) and fire frequency (Dublin et al. 1990; Dublin 1995; Roques et al. 2001; Bradshaw et al. 2003; Western 2007; Valeix et al. 2011; Asner and Levick 2012). In Holocene paleoecological research, with the exception of a few studies (Ambrose and DeNiro 1989; Ambrose and Sikes 1991; Balasse and Ambrose 2005), most reconstructions of terrestrial paleoenvironments in Kenya in relation to archaeology have employed inferences from indirect paleoclimate records (Bower 1991; Gifford-Gonzalez 1998; Wright 2007; Prendergast and Lane 2010; Ashley et al. 2011).

1.2 Chapter Summaries

1.2.1. Chapter 2: Isotopic composition of wild *H. amphibius* canines reveals nonselective feeding behavior in Kenya

Chapter 2 explores the relationship between individual hippo dietary histories and their local environment. Isotopic work in the last 20 years has revealed that hippos are not strict selective C_4 grazers, as has been the long-standing assumption by ecologists. Hippos feed close to their aquatic environment, and thus likely reflect the proportion of C_3/C_4 herbaceous vegetation near their aquatic habitats, which can vary over the course of their lifetime due to changes in environmental conditions. To test this idea, we serially sampled (10 mm intervals) enamel from ever-growing hippo canines from wild hippos living in diverse environments across Kenya for $\delta^{13}C$ and $\delta^{18}O$. Enamel $\delta^{13}C$ values from these isotope profiles group significantly based on environmental classifications of the areas they come from, ranging from woodlands and forests to open grasslands. Similarly, radiocarbon dated profiles from hippos living in the same environment over the same time period and/or in the same geographic area reveal the variable nature of hippo diets among populations. These data show that enamel $\delta^{13}C$ values from hippos can be excellent recorders of local environment, though caution must be used when extrapolating hippo dietary isotope values to determine paleoecology of large areas.

1.2.2. Chapter 3: Decadal diet change in *Hippopotamus amphibius* in Queen Elizabeth National Park, Uganda.

Chapter 3 builds upon the data presented in Chapter 2 and applies the same techniques to capture a signal of C_3 succession in a savanna ecosystem in Uganda following a major ecological perturbation – the poaching and near extirpation of elephants from Queen Elizabeth Park (QEP), Uganda. Hippo canines from hippos living on the Mweya Peninsula in QEP that have either been radiocarbon dated or have known death dates were serially sampled for $\delta^{13}C$ and $\delta^{18}O$. These hippos exhibit a >80% C_4 diet throughout the 1960s, in agreement with vegetation transects from this time period that demonstrate an abundance of C_4 grasses on the peninsula. Following heavy poaching in QEP throughout the 70s and early 80s, informal vegetation assessments indicated succession of C_3 woody plants and forbs. Hippo dietary isotope values capture this increase in C_3 on the peninsula during the 80s and 90s, and reveal the extent to which C_3 herbaceous plants have encroached, decreasing grazing capacity on the peninsula. These results suggest that hippo canines can be excellent indicators of herbaceous vegetation change in savanna ecosystems and could be used in African parks to track C_3 encroachment, an ongoing issue in modern African ecology.

1.2.3. Chapter 4: Holocene paleoenvironments in Kenya, with perspectives on Holocene archaeology and Pleistocene environmental change

Changes in the strength of the East African monsoon due to orbital forcing have often been cited as drivers of terrestrial ecosystem change throughout the last 4 Ma. The nature of how terrestrial ecosystems respond to orbital forcing has only been empirically demonstrated in a few studies, and rarely with an interbasinal perspective. It is expected that regional changes in monsoon strength would be reflected in locally distinctive ways. To test this hypothesis, paleoecological records using faunal tooth enamel and sedimentary leaf wax biomarkers were generated and compiled for Holocene records, a time of well-constrained paleoclimatolgical change from orbital forcing, for two distinct lake basins in Kenya – the northern Turkana Basin and the southwestern Lake Victoria basin. Where possible, pollen was also included. The data indicate that abrupt aridification in Turkana did indeed coincide with dietary change in mammal herbivores, whereas the gradual ardification in Lake Victoria did not. Likewise, an inland archaeological site, Ele Bor (250 km from Lake Turkana) reveals no dietary change in herbivores. Furthermore, leaf wax and tooth enamel data tend to agree in Victoria, though not in Turkana (where samples overlap). These data show that orbital forcing has differential effects in climate and vegetation change, and paleoecology must be assessed basin by basin.

1.2.4. Chapter 5: Environments and trypanosomiasis risks for early herders in the later Holocene of the Lake Victoria Basin, Kenya

Herding was the earliest form of African food production, and transformed local populations of people and animals. Herders migrated from eastern to southern Africa around 2,000 years ago but only in small numbers. Zoonotic disease vectors, specifically the tsetse fly, which carries sleeping sickness, are thought to have impeded these movements. Archaeologists have argued that the presence of tsetse flies around Lake Victoria, Kenya, created a barrier preventing migration and forcing subsistence diversification. This study using stable isotope analysis of animal teeth reveals the existence of ancient grassy environments east of Lake Victoria, rather than tsetse-rich bushy environments. This overturns previous assumptions about environmental constraints on livestock management in a key area for southward movement of early herders.

1.3 References

Ambrose SH, DeNiro MJ (1989) Climate and habitat reconstruction using stable carbon and nitrogen isotope ratios of collagen in prehistoric herbivore teeth from Kenya. Quaternary Research 31:407–422.

Ambrose SH, Sikes NE (1991) Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. Science 253:1402–1405.

Ashley G, Ndiema EK, Spencer JQG, et al. (2011) Paleoenvironmental context of archaeological sites, implications for subsistence strategies under Holocene climate change, northern Kenya. Geoarchaeology 26:809–837.

Asner GP, Levick SR (2012) Landscape-scale effects of herbivores on treefall in African savannas. Ecology Letters 15:1211–1217.

Ayliffe LK, Cerling TE, Robinson T, et al. (2004) Turnover of carbon isotopes in tail hair and breath CO 2 of horses fed an isotopically varied diet. Oecologia 139:11–22.

Balasse M, Ambrose SH (2005) Mobilité altitudinale des pasteurs néolithiques dans la vallée du Rift (Kenya) : premiers indices de l'analyse du δ^{13}C de l'émail dentaire du cheptel domestique. Anthropozoologica 40:147–166.

Battisti DS, Naylor RL (2009) Historical warnings of future food insecurity with unprecedented seasonal heat. Science 323:240–244.

Berger A, Loutre MF (1997) Intertropical latitudes and precessional and half-precessional cycles. Science 278:1476–1478.

Berke MA, Johnson TC, Werne JP et al. (2012) Molecular records of climate variability and vegetation response since the Late Pleistocene in the Lake Victoria basin, East Africa. Quaternary Science Reviews 55:59–74.

Boisserie JR, Zazzo A, Merceron G, et al. (2005) Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. Palaeogeography, Palaeoclimatology, Palaeoecology 221:153–174.

Bower J (1991) The pastoral neolithic of East Africa. Journal of World Prehistory 5:49–82.

Braconnot P, Joussaume S, de Noblet N, Ramstein G (2000) Mid-Holocene and last glacial maximum African monsoon changes as simulated within the paleoclimate modelling intercomparison project. Global and Planetary Change 26:51–66.

Bradshaw R, Hannon G, Lister A (2003) A long-term perspective on ungulate-vegetation interactions. Forest Ecology and Management 181:267–280.

Brincat D, Yamada K, Ishiwatari R, et al. (2000) Molecular-isotopic stratigraphy of long-chain n-alkanes in Lake Baikal Holocene and glacial age sediments. Organic Geochemistry 31:287–294.

Cerling TE, Harris JM, Hart JA, et al. (2008) Stable isotope ecology of the common hippopotamus. Journal of Zoology 276:204–212.

Cerling TE, Harris JM, MacFadden BJ, Leakey MG (1997) Global vegetation change through the Miocene/Pliocene boundary. Nature 389:153–158.

Cerling TE, Harris JM, Passey BH, et al. (2004) Orphans' tales: seasonal dietary changes in elephants from Tsavo National Park, Kenya. Palaeogeography, Palaeoclimatology, Palaeoecology 206:367–376.

Cerling TE, Quade J, Wang Y, Bowman J (1989) Carbon isotopes in soils and palaeosols as ecology and palaeoecology indicators. Nature 341:138–139.

Cerling TE, Wittemyer G, Rasmussen HB, et al. (2005) Stable isotopes in elephant hair document migration patterns and diet changes. Proceedings of the National Academy of Sciences 103:371–373.

Cerling TE, Wynn JG, Andanje SA, et al. (2011) Woody cover and hominin environments in the past 6 million years. Nature 476:51–56.

Choudhary P, Routh J, Chakrapani G, Kumar B (2009) Biogeochemical records of paleoenvironmental changes in Nainital Lake, Kumaun Himalayas, India. Journal of Paleolimnology 42:571–586.

Clark P, Dyke A, Shakun J, et al. (2009) The last glacial maximum. Science 325:710–714.

Claussen M, Kubatzki C, Brovkin V, et al. (1999) Simulation of an abrupt change in Saharan vegetation in the mid-Holocene. Geophysical Research Letters 26:2037–2040.

Clement AC, Cane MA, Seager R (2001) An orbitally driven tropical source for abrupt climate change*. Journal of Climate 14:2369–2375.

Dalerum F, Angerbjörn A (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658.

deMenocal P (2004) African climate change and faunal evolution during the Pliocene-Pleistocene. Earth and Planetary Science Letters 220:3–24.

deMenocal P, Ortiz J, Guilderson T, et al. (2000) Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. Quaternary Science Reviews 19: 347–361.

Dublin HT (1995) Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire, and other factors. In: Sinclair A, Arcese P (eds) Serengeti II Dynamics, Management, and Conservation of an Ecosystem. pp 71–90.

Dublin HT, Sinclair A, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. Journal of Animal Ecology 59:1147–1164.

Eglinton G, Hamilton R (1967) Leaf epicuticular waxes. Science 156:1322.

Freeman KH, Colarusso L (2009) Molecular and isotopic records of C4 grassland expansion in the late Miocene. Geochimica et Cosmochimica Acta 65:1439–1454.

Garcin Y, Melnick D, Strecker M, Olago D (2012) East African mid-Holocene wet–dry transition recorded in palaeo-shorelines of Lake Turkana, northern Kenya Rift. Earth and Plantary Science Letters 331-332: 322–334.

Garcin Y, Vincens A, Williamson D, et al. (2007) Abrupt resumption of the African Monsoon at the Younger Dryas-Holocene climatic transition. Quaternary Science Reviews 26:690–704.

Gasse F (2000) Hydrological changes in the African tropics since the Last Glacial Maximum. Quaternary Science Reviews 19:189–211.

Gifford-Gonzalez DP (1998) Early pastoralists in East Africa: ecological and social dimensions. Journal of Anthropological Archaeology 17:166–200.

Good SP, Caylor KK (2011) Climatological determinants of woody cover in Africa. Proceedings of the National Academy of Sciences 108:4902-4907.

Hastenrath S, Kutzbach J (1983) Paleoclimatic estimates from water and energy budgets of East African lakes. Quaternary Research 19:141–153.

Hirons AC, Schell DM, Finney BP (2001) Temporal records of $\delta^{13}C$ and $\delta^{15}N$ in North Pacific pinnipeds: inferences regarding environmental change and diet. Oecologia 129:591–601.

Kingston JD (2007) Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. American Journal of Physical Anthropology 45:20–58.

Koch PL, Heisinger J, Moss C, et al. (1995) Isotopic tracking of change in diet and habitat use in African elephants. Science 267: 1340–1343.

Kohn MJ, Cerling TE (2002) Stable isotope compositions of biological apatite. Reviews in Mineralogy and Geochemistry 48:455–488.

Kutzbach JE (1981) Monsoon climate of the early Holocene: climate experiment with the earth's orbital parameters for 9000 years ago. Science 214: 59–61.

Laskar J, Robutel P, Joutel F, et al. (2004) A long-term numerical solution for the insolation quantities of the Earth. Astronomy and Astrophysics 428:261–285.

Lee-Thorp JA, Sponheimer M, Luyt J (2007) Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. Journal of Human Evolution 53:595–601.

Lee-Thorp JA, Van der Merwe NJ (1987) Carbon isotope analysis of fossil bone apatite. South African Journal of Science 83:712–715.

Lee-Thorp JA, Van Der Merwe NJ, Sealy JC (1989) Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. Journal of Archaeological Science 16:585–599.

Lehmann CER, Archibald S, Hoffmann WA, Bond WJ (2011) Deciphering the distribution of the savanna biome. New Phytologist 191: 197–209.

Levin NE, Cerling TE, Passey BH, et al. (2006) A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Sciences 103:11201–11205.

Magill CR, Ashley G, Freeman KH (2013a) Ecosystem variability and early human habitats in eastern Africa. Proceedings of the National Academy of Sciences 110:1167–1174.

Magill CR, Ashley G, Freeman KH (2013b) Water, plants, and early human habitats in eastern Africa. Proceedings of the National Academy of Sciences 110:1175–1180.

Marshall JD, Hopley PJ, Weedon GP, et al. (2007) High-and low-latitude orbital forcing of early hominin habitats in South Africa. Earth and Planetary Science Letters 256:419–432.

Mayewski P, Rohling E, Curt Stager J, et al. (2004) Holocene climate variability. Quaternary Research 62:243–255.

Murphy B, Bowman DMJS (2012) What controls the distribution of tropical forest and savanna? Ecology Letters 15: 748–758.

Nicholson S (1996) A review of climate dynamics and climate variability in eastern Africa. In: Johnson TC, Odada EO (eds) The limnology, climatology and paleoclimatology of the East African Lakes. CRC Press, Boca Raton pp 25–56.

Passey BH, Cerling TE, Perkins ME, et al. (2002) Environmental change in the Great Plains: an isotopic record from fossil horses. The Journal of Geology 110:123–140.

Passey BH, Cerling TE, Schuster GT, et al. (2005) Inverse methods for estimating primary input signals from time-averaged isotope profiles. Geochimica et Cosmochimica Acta 69: 4101–4116.

Prendergast ME, Lane P (2010) Middle Holocene fishing strategies in East Africa: zooarchaeological analysis of Pundo, a Kansyore shell midden in northern Nyanza (Kenya). International Journal of Osteoarchaeology 20:88–112.

Ratnam J, Bond WJ, Fensham RJ, et al. (2011) When is a “forest” a savanna, and why does it matter? Global Ecology and Biogeography 20:653–660.

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268–280.

Russell J, Talbot M, Haskell B (2003) Mid-holocene climate change in Lake Bosumtwi, Ghana. Quaternary Research 60:133–141.

Sankaran M, Hanan NP, Scholes R, et al. (2005) Determinants of woody cover in African savannas. Nature 438:846–849.

Stager J, Cumming B, Meeker L (2003) A 10,000-year high-resolution diatom record from Pilkington Bay, Lake Victoria, East Africa. Quaternary Research 59:172–181.

Talbot M, Livingstone D (1989) Hydrogen index and carbon isotopes of lacustrine organic matter as lake level indicators. Palaeogeography, Palaeoclimatology, Palaeoecology 70:121–137.

Tierney JE, Lewis SC, Cook BI, et al. (2011a) Model, proxy and isotopic perspectives on the East African Humid Period. Earth and Planetary Science Letters 307:103–112.

Tierney JE, Russell JM, Damsté JSS, et al. (2011b) Late Quaternary behavior of the East African monsoon and the importance of the Congo Air Boundary. Quaternary Science Reviews 30:798–807.

Uno KT, Cerling TE, Harris JM, et al. (2011) Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. Proceedings of the National Academy of Sciences 108:6509–6514.

Valeix M, Fritz H, Sabatier R, et al. (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. Biological Conservation 144: 902–912.

Verschuren D, Damsté J, Moernaut J, et al. (2009) Half-precessional dynamics of monsoon rainfall near the East African Equator. Nature 462:637–641.

West JB, Bowen GJ, Cerling TE, Ehleringer JR (2006) Stable isotopes as one of nature's ecological recorders. Trends in Ecology & Evolution 21:408–414.

Western D (2007) A half a century of habitat change in Amboseli National Park, Kenya. African Journal of Ecology 45: 302–310.

Wright DK (2007) Tethered mobility and riparian resource exploitation among Neolithic hunters and herders in the Galana River basin, Kenyan coastal lowlands. Environmental Archaeology 12:25–47.

Xu Y, Jaffé R (2008) Biomarker-based paleo-record of environmental change for an eutrophic, tropical freshwater lake, Lake Valencia, Venezuela. Journal of Paleolimnology 40:179–194.

Zachos J, Pagani M, Sloan L, et al. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.

Zazzo A, Balasse M, Passey BH, et al. (2010) The isotope record of short- and long-term dietary changes in sheep tooth enamel: implications for quantitative reconstruction of paleodiets. Geochimica et Cosmochimica Acta 74:3571–3586.

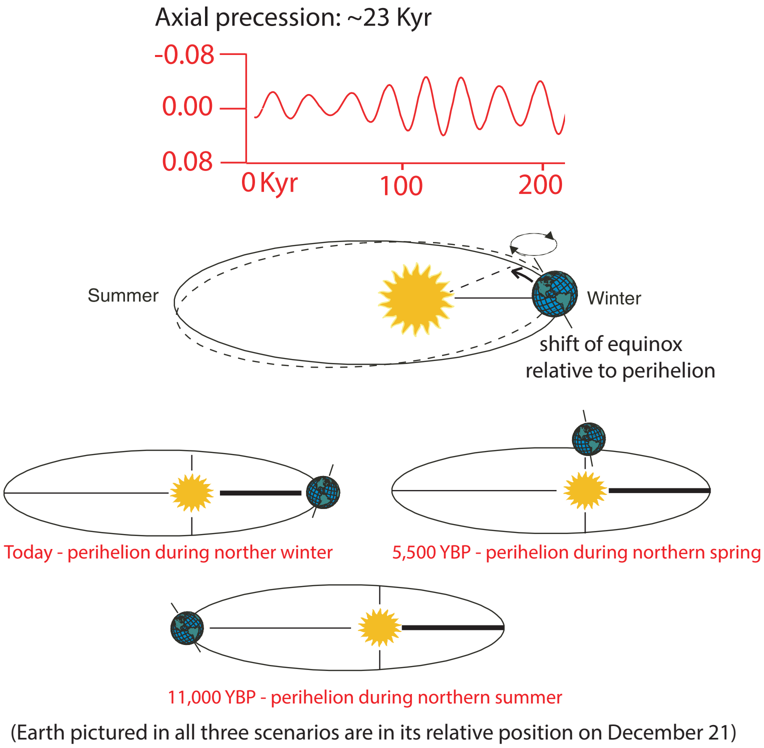

Figure 1.1: Axial precession and location of the perihelion throughout the Holocene. Modified from Zachos et al. (2001).

CHAPTER 2

ISOTOPIC COMPOSITION OF WILD *H. AMPHIBIUS* CANINES REVEALS NONSELECTIVE FEEDING BEHAVIOR IN KENYA

2.1. Abstract

The common hippopotamus (*Hippopotamus amphibius*) is a semi-aquatic megaherbivore that plays a crucial role as an ecosystem engineer in the environment that it inhabits. Dietary isotopes in hippo canines have long been of interest to the paleoecological community, as their canines are ever-growing and can potentially record up to 10 continuous years of their ecology. Bulk stable isotope data from hippo cheek teeth has revealed that hippos are not strict C_4 grazers, as previously thought. This necessitated further investigation into the ecological and dietary variability of hippos from different environments. To that end, hippo canine enamel was sampled serially (~10 mm) for $\delta^{13}C$ along the length of the canine from 30 wild hippos. These isotope profiles have revealed the remarkable variability in hippo diets that relate, broadly, to the structure of the ecosystems they inhabit and major environmental changes, such as drought. Though C_4 grasses and grassland exist in each of these localities, hippo dietary isotopes indicate that their C_4 intake can be as low as 40% in more C_3 environments, making them excellent indicators of C_3 herbaceous groundcover. These dietary records only record environment on a very local scale, given that they forage less than 6 km away from their aquatic habitat.

2.2. Introduction

Hippopotamus amphibius is a common megaherbivore (>1000 kg) found across Africa, living in a wide range of environments from arid savannas to forest (Eltringham 1999; Klingel 2008; Klingel 2013). They are semi-aquatic, spending the day in pools, rivers, and lakes, coming out of water at night to feed on herbaceous vegetation. Their feeding behavior is difficult to observe, as they feed nocturnally and tend to crop foods close to the ground, such that they create lawns of very short vegetation, deterring herbivores that prefer tall forage, such as elephants and buffalo (Field 1970; Arsenault and Owen Smith 2002; 2006; Kanga et al. 2011). They often stay close to their aquatic habitats to feed (1–6 km away) based on habitat structure and access to nutritious food (Eltringham 1974; Eltringham 1999; Lewison and Carter 2004). When necessary, they can wander quite far (up to 20 km) during rainy seasons due to lower trans-cutaneous water loss when moving on land (Vesey-FitzGerald 1960).

Hippos occupy unique roles in their ecosystems and serve as ecosystem engineers in the habitats where they live. Their manner of walking along the same paths towards food sources causes narrow water channels to form, contributing to swamp development and irrigation (Owen-Smith 1992; Chansa et al. 2011). Hippos require as much as ~20 kgs of food per day; these high dietary requirements and repeated journeys on land can lead to trampled and compacted soil, killing vegetation and transforming soil properties, especially when populations are high (Lock 1972). An intermediate number of hippos, however, can increase herbivore diversity and environmental mosaics (Bourlière and Hadley 1970; Lock 1972; Owen-Smith 1992; Fritz et al. 2002; Verweij et al. 2006; Kanga et al. 2011). Hippos also facilitate nutrient cycling between lakes and terrestrial environments (McCauley et al. 2015; Subalusky et al. 2015).

Despite the important roles hippos occupy in their environment, basic aspects of their ecology are still uncertain. Understanding hippo diets is of particular interest, as they have been and are still classified as strict selective grazers by ecologists (Field 1970; Olivier and Laurie 1974; Kanga et al. 2011; McCauley et al. 2015), though recent isotopic samples on modern and fossil hippos has revealed the broad nature of their feeding behavior (Boisserie et al. 2005; Cerling et al. 2008; Harris et al. 2008). These data have raised intriguing questions about the extent of hippo dietary flexiblity, both among environments and within individuals themselves. Understanding how dietary isotopes of hippos relate to their environment will help us better interpret isotopic data of hippos from the geologic past, since their canines are ever-growing and can record up to a decade of their recent life (Passey et al. 2005; Uno et al. 2013). This study aims to understand ecological and dietary variability within individuals across different environments through sequential isotope sampling of modern wild hippo canine enamel in order to quantify the degree of dietary flexibility within the species.

2.3 Materials and Methods

2.3.1. Sample collection

Hippo canines were collected from Kenya Wildlife Service (KWS) stockpiles; some of these had been shot by rangers for either herd management or had been identified as nuisance animals (i.e., crop raiding)(Figure 2.1). Tusk enamel powder was drilled at intervals, usually every 10 mm, using a diamond-tipped Dremel tool; these were sampled by Dr. Samuel Andanje (KWS) and trained students from Moi University, Kenya. To remove surface contaminants, the surface of the enamel was abraded off prior to drilling. Because samples were obtained from recently modern hippos, enamel powders were not treated because various treatment procedures are not distinguishable for modern tooth enamel (Passey et al., 2002; Cerling 2014).

In total, 1,410 samples were analyzed from 30 tusk profiles from national parks and protected areas across Kenya. Sample powders were weighed into silver capsules and stored in a drying cabinet until analysis. Samples were analyzed for $\delta^{13}C$ and $\delta^{18}O$ on a Finnigan MAT 252 coupled to a Carboflo dual-inlet carbonate device, which involves digestion in a common phosphoric acid bath at 90°C for 10 minutes. Stable isotope ratios are reported as δ values relative to the international carbon isotope standard, Vienna Pee Dee Belemnite (VPDB), using the standard permil (‰) notation, where $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000$, and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the sample and standard, respectively. Standard deviation of an internal carbonate standard (Carrara marble) was between +/- 0.1 and 0.2‰. Samples were corrected to 25ºC using modern tooth enamel samples analyzed at both 25º and 90ºC (Passey et al. 2007).

2.3.2. Environmental characterization

Characterization of eastern African environments was done using the Potential Natural Vegetation map for Eastern Africa (also called the "Vegetation and Climate Change in East Africa" map; VECEA) (Lillesø et al. 2011). This map in an updated, interactive version of the classic vegetation map for East Africa developed by White (White 1983). This map is a higher spatial resolution than the White map, and both ecoregions and physiognomic vegetation groups include environmental data, such as rainfall, altitude, and temperature. The VECEA also includes a Google Earth overlay, which was used to define vegetation characteristics for hippo localities. The VECEA map defines floristic vegetation types based on the degree of woody cover in an area, dominant woody species, and edaphic characteristics that may influence floral distribution within the vegetation type.

Environmental characterizations used in this and subsequent chapters follow the UNESCO classification scheme, developed and defined by White (1983) (Table 2.1). Unfortunately, hippo localities are coarsely defined – typically only to the national park or reserve in which the animal was shot or the carcass was found. Thus, defining habitat localities for many hippos is challenging, and generalized to the most prevalent ecosystem types, which in some cases are compound. Further classification for forest types, accounting for climatic and edaphic characteristics, are explained in the detailed descriptions given here.

The code "Bd" refers to the physiognomic vegetation type as "Somalia-Masai Acacia-Commiphora deciduous bushland and thicket". This vegetation type is most commonly characterized as a woodland, with thickets that can often be impenetrable (Kindt et al. 2011c). Rainfall within this vegetation type ranges between 250 and 500mm/year (White 1983), and grasses are more abundant in places where the soil is sandy and otherwise well-drained. The most typical example of this vegetation type is found within Tsavo National Park (White 1983).

The code "Wcd" refers to the physiognomic vegetation type "dry *Combretum* wooded grassland". This vegetation type is a variant of a more major, widespread East African ecosystem type "*Combretum* wooded grassland" (White 1983; Kindt et al. 2011c). *Wcd* areas occur in places that receive between 600 and 1800 mm of rainfall per year. As the name implies, most of the herbaceous layer is composed of grasses and herbs/forbs, with few thickets or bush present (Kindt et al. 2011b).

The code “wd” refers to the physiognomic vegetation type “Edaphic wooded grassland on drainage-impeded or seasonally flooded soils”. This vegetation type is similar to riverine wooded grasslands, though *wd* typically contains primarily *Acacia* species (White 1983). These environments typically are comprised of tall grasses that are frequently subject to burning and conspicuous stands of trees (White 1983; Kindt et al. 2011b).

The code “Fp” refers to the Zanzibar-Inhambane undifferentiated forest. This coastal forest variation is highly heterogeneous, with drier forest types covering a larger area on the coast (White 1983). This is the habitat type within the Boni National Reserve, from which the Adhi Dam hippo specimen came. This coastal forest is floristically diverse, though with a more closed canopy than Zanzibar-Inhambane woodland and scrub forest (Burgess et al. 1998; Tabor et al. 2010).

The code “Fq” refers to the physiognomic vegetation type as “Zanzibar-Inhambane scrub forest”. This coastal forest delineates the coastal region forests and inland bushlands and occupies areas where rainfall is between 500 and 750 mm/yr (White 1983). This is a highly diverse forest type without dominance of a single tree species, and occurs at low elevations, below 250m above sea level. This vegetation type has abundant woody vegetation with a high degree of floral and faunal endemism, especially within Arabuko-Sokoke National Park (Burgess and Muir 1994). The coastal floristic region within which this vegetation type occurs can be generalized as an undifferentiated forest, meaning changes in the structure and composition of vegetation types occur over short distances (White 1983).

The code “g” refers to the physiognomic vegetation type “edaphic grassland on drainage-impeded or seasonally flooded soils”. This vegetation type is distinct from type *wd* in that it is a true grassland, with <10% woody cover (White 1983; Kindt et al. 2011a). These grasslands are associated with seasonally or permanently waterlogged soils at altitudes below 1,500m and a large range in rainfall (between 200 and 1,400mm/yr) (Kindt et al. 2011a).

The code “R” refers to the physiognomic vegetation type “riverine wooded vegetation”. This is a compound vegetation designation encompassing several different physiognomic variants, including forest, woodland, and thicket. Unfortunately, finer resolution descriptions for hippos from these localities (Naivasha and Nakuru) were not available. This vegetation type is widely distributed across East Africa, and given that climate is not the primary driver of water availability, all variants of this vegetation type are edaphic.

This code is a mosaic vegetation classification comprised of *Acacia-Commiphora* deciduous wooded grassland (*Wd*) and *Combretum* wooded grassland (*Wc*). *Combretum* wooded grassland is a major vegetation type in East Africa (White 1983), though more abundant outside of Kenya (Kindt et al. 2011b). *Wd* environments are typical of the greater Serengeti ecosystem, and what distinguishes them from deciduous bushland and thicket (*Bd*) is the relative lower abundance of bushy plants and higher representation of perennial grasses, which may be the influence of biotic factors, such as herbivory, rather than climate (White 1983). This compound vegetation type is prevalent in Amboseli National Park.

The code *We/Wd* is a mosaic vegetation classification comprised of edaphic wooded grassland on drainage-impeded or seasonally flooded soils (*wd*) and biotic *Acacia* wooded grassland (*We*). *We* is a floristic type that is closely related to evergreen bushland (*Be*), though *We* environments typically experience higher grazing pressure, and thus support fewer evergreen thickets (White 1983; Kindt et al. 2011b). *We* environments can have discontinuous groundcover in more arid areas and occur largely above 1,250 m above sea level (White 1983). This compound vegetation type is commonly found in the Mara and Laikipia district.

The code "S" is a mosaic vegetation classification comprised of Somalia-Masai semi-desert grassland and shrubland (*S*). This distinctive vegetation type occurs in very arid regions and on sandy soils, particularly those with 100–250 mm/yr rainfall. In certain areas where this vegetation type exists, woody plants provide 2–20% of the ground cover, as either shrubs or bushy trees (White 1983). This vegetation type is present in the arid Turkana region and is most abundant along the lake margin.

2.3.3. Relationships between hippos from different environments

To explore environmental constraints on $\delta^{13}C$ dietary enamel values, carbon isotope values were grouped and tested for similarities between enamel $\delta^{13}C$ and environment using a Kruskal-Wallis test (non-normality confirmed using a Shipro-Wilk test). This test was followed by a Tukey-Kramer (Nemenyi) post-hoc test using the Pairwise Multiple Comparison of Mean Ranks (PMCMR) package in R (Ihaka and Gentleman 1996). The Nemenyi post-hoc test uses mean rank sums on groups of unequal size (Tukey-Kramer method) and also applies a family-wise error method to control for false positives (Sokal and Rohlf 1994). These tests are necessary for this dataset, as the carbon isotopes values within these environmental groups come from profiles of individuals, though still independent samples of diet. Certain profiles were excluded from the analysis, denoted by asterisks, with explanations given under Figure 2.2.

2.4. Results

Isotope profiles are depicted graphically as boxplots in Figure 2.2 and grouped by environment in Figure 2.3, highlighting the remarkable range in $\delta^{13}C$ values across all hippo profiles from different localities in Kenya. Overall, $\delta^{13}C$ values from all hippo profiles exhibit a remarkable range of ~12‰. These values place hippo dietary isotopes within the dietary designation of mixed feeders (Figure 2.4; Table 2.2). Hippo enamel $\delta^{13}C$ profile plots for individuals are presented in Appendix A, revealing the range and dietary breadth of this single species of megaherbivore across an entire country. Mean $\delta^{13}C$ values range from 0.8‰ (the most enriched values) near Lake Turkana to -6.6‰ in Mwea Reserve (the most depleted). These results indicate that, at most, ~95% of the resources consumed by hippos in Kenya come from C_4 plants, whereas at least ~40% of the resources are C_4. Such a range in dietary flexibility in large African herbivores has only been observed in those with known mixed-feeding or seasonal diets, such as elephants or impala (Wronski 2002; Cerling et al. 2004; Owen Smith and Chafota 2012).

This dataset reveals the diversity of hippo diets across environments in Kenya, and moreover that this dietary diversity is constrained within environments. The greatest ranges in carbon isotope values are from those that were from nuisance animals (Figure 2.2, denoted with an asterisk). Carbon isotope values from hippos separate statistically into four distinct groups, based on the broad physiognomic vegetation characterizations of the parks and reserves they came from: *Bd*, *Wcd*, *wd, Fp* (Tsavo, Mwea, Meru, Buffalo Springs, Chyulu, Olbolosat, Adhi Dam, and Kisumu); *Fq, g, R, Wd/Wc* (Mokowe, Arabuko Sokoke, Mpeketoni, Minjila, Naivasha, Nakuru, Amboseli); *We/wd* (Laikipia, Maasai Mara); *S* (Turkana) (Figure 2.3; Table 2.3).

In addition to exhibiting large ranges in δ^{13}C values across profiles, certain hippo profiles also show large ranges in δ^{18}O values across profiles. Such isotopic profiles include Chyulu (δ^{18}O range: 4.7‰), Kisumu (δ^{18}O range: 4.4‰), Mwea #2 (δ^{18}O range: 4.8‰), Mwea – Gitaru Dam (δ^{18}O range: 5.2‰), Meru (δ^{18}O range: 4.2‰), K08-201 (δ^{18}O range: 5.2‰), K01-TSW-291 (δ^{18}O range: 4.8‰), Nakuru (δ^{18}O range: 4.7‰) (see Appendix A). Oxygen isotopes in hippos reflect the isotopic value of their aquatic habitat due to their permeable skin that allows for high rates of cutaneous water loss (on land) and exchange (in water) (Luck and Wright 1964; Levin et al. 2006; Cerling et al. 2008). These ranges in δ^{18}O values may represent changing habitat or changing values of the source water themselves, either from meteoric changes or other climatic forcing.

2.5 Discussion

2.5.1. Hippo dietary variability across Kenya

Bulk hippo dietary flexibility, in both modern *H. amphibius* and throughout recent hippopotamus evolution, has been demonstrated through stable isotope analysis (Boisserie et al. 2005; Cerling et al. 2008; Harris et al. 2008). This dataset reveals the extent of hippo dietary variability within individuals, which was not previously known. Large ranges in isotope values are evident from nuisance animals, such as in Tsavo (K08-201; δ^{13}C range: 8.3‰), Naivasha - Crater Lake (NaivashaCL; δ^{13}C range: 7.6‰), two Arabuko-Sokoke hippos (AS-168; δ^{13}C range: 6.2‰ and AS-166; δ^{13}C range: 4.4‰), but also in non-nuisance animals, such as Mwea #2 (δ^{13}C range: 5.8‰), Ol Bolossat (δ^{13}C range: 6.2‰), Meru (δ^{13}C range: 6.9‰), and Tsavo #1 (δ^{13}C range: 7.2‰) (Table 2.2).

Hippos are known crop raiders in many parts of Africa, and can cause expensive damages and loss of income for local famers (Weladji and Tchamba 2003; Naughton-Treves and Treves 2005; Kendall 2011; Kanga et al. 2012). This crop-raiding behavior is exacerbated by human impact and land-use change on their natural habitat, primarily for agriculture and livestock grazing (Lewison 2007; Kanga et al. 2011).

Of the non-crop raiding individuals in this dataset, $\delta^{13}C$ ranges across profiles can still be quite large. Of particular note are the four hippos from Mwea National Reserve, which all exhibit average $\delta^{13}C$ enamel values between -5.7 and -6.6‰, with relatively large ranges in $\delta^{13}C$ across the profiles (between 3-5.8‰) (Table 2.2). Mwea is categorized as *Bd* – "Somalia-Masai Acacia-Commiphora deciduous bushland and thicket", and has dense bushy riparian corridors and woody vegetation (Chira and Kinyamario 2009). The depleted values for the four hippos from this reserve may indicate an abundance of C_3 in the herbaceous understory, facilitated by abundant bush and woody vegetation (see Chapter 3). It is also important to consider dietary input from agricultural sources in this region. Mwea has been extensively developed in a large rice-production scheme in Kenya (Kabutha and Mutero 2002), and though there have been reports of hippos raiding rice paddies in this area, the four hippos from Mwea were not known to have been killed for animal management purposes (S. Andanje, *pers. comm.*). Other profiles reveal divergences in ecology from populations in the same geographic area. For example, two tusks from the Lake Naivasha area (Crayfish Camp and Crater Lake) show how hippos record distinct environmental differences and disturbance in different parts of the lake basin (Figure 2.5). The profile from Crayfish Camp, a protected area with an abundance of grasses and herbaceous vegetation, has a mean $\delta^{13}C$ value of -

1.7‰ +/- 1.3, a diet consisting of roughly 75% C_4 resources. The hippo profile from the Crater Lake area, however, was shot for crop raiding, and lived in an area wherein much of the natural environment had been converted to agricultural land (S. Andanje, *pers. comm.*). This hippo profile exhibits a steady increase in $\delta^{13}C$ over the course of its life until it was shot by KWS for crop raiding. Differences in $\delta^{18}O$ between these two hippos reflect the difference in isotopic source waters in separate parts of the Naivasha lake basin (Ojiambo et al. 2001). These hippos reveal the ways in which these profiles capture heterogeneity within the same area, and how two hippos from the same geographic area can appear as though they come from two distinct ecological localities, though only 15 km apart.

2.5.2. Hippo canine isotopes as a record for environmental change

Another way in which these isotope values can be used in modern environments is as a record of change within a given area using precisely dated canine enamel (Uno et al. 2013). Two profiles from Tsavo National Park reveal the utility of using canine enamel as a marker of environmental change (Figure 2.6). One radiocarbon-dated profile (K00-291) indicates that a hippo died in 1996, during a drought. Stable carbon isotopes from this profile indicate that the C_3 component of this hippo's diet increased over the last 3 years of its life, in addition to an enrichment in $\delta^{18}O$ values. The radiocarbon-dated specimen K08-201 overlaps the end of the K00-291 profile and shows the same carbon isotope trend, followed by an increase in C_4 resources to its diet as the drought improved. Both of these hippos came from a locality near a river in the northern part of Tsavo National Park – Mtito Andei. A third hippo profile (sample ages approximated using the average hippo growth rate of ~40 mm/yr) (Uno et al. 2013) complicates this environmental record – K09-TSV, a hippo that lived in Mzima Springs, a naturally flowing spring that was unaffected by the drought. These hippos not only reveal dietary change forced by drought conditions in the national park, but variability across the park during a single ecological event. Serially sampled and dated hippo canines can be used as excellent records of environmental change, if from the same population.

On a more local scale, it has been suggested that hippo tusk isotope profiles might record seasonal-scale variability (Passey et al. 2005; Souron et al. 2012). To addresses this question, one tusk (Turkana – Koobi Fora 1) was sampled at high resolution (2–3mm) and radiocarbon dated in order to calculate its growth rate (~27 mm/yr). Even this resolution, however, fails to consistently capture the ~2‰ annual variability in $\delta^{18}O$ recorded in Lake Turkana surface waters (Cerling 1996), except in a few instances, such as between 1978 and 1979 (Figure 2.7). Even at such high sampling resolution, hippos do not perfectly record local water conditions, pointing to the need to understand other factors that may determine $\delta^{18}O_{enamel}$, such as physiology.

2.5.3. Changing environments at the end of life

Certain trends in both $\delta^{13}C$ and $\delta^{18}O$ are reflected across many isotope profiles in this dataset. Specifically, in the final 1–2 years of life (assuming a static growth rate of ~4 cm/yr, with a maximum growth rate of ~8cm/yr), many hippo profiles show a significant enrichment in $\delta^{18}O$ in the last year of life relative to the rest of their life (Wilcoxan rank sum test with Bonferroni correction, $P<0.05$; Appendix A). Specific profiles which exhibit this trend include: ($\delta^{13}C$, $\delta^{18}O$), Nakuru ($\delta^{18}O$), Mwea #1 ($\delta^{13}C$, $\delta^{18}O$), Mwea #2 ($\delta^{13}C$), Chyulu ($\delta^{18}O$), Kisumu ($\delta^{13}C$), Meru ($\delta^{13}C$, $\delta^{18}O$), Mpeketoni ($\delta^{18}O$), Witu ($\delta^{18}O$), ($\delta^{13}C$), Buffalo Springs ($\delta^{18}O$), and Aberdares ($\delta^{13}C$, $\delta^{18}O$) (see Appendix A). Of these individuals, the death circumstances are only known for Tsavo #1, Arabuko Sokoke #1, and the Aberdares tusks. All three of these hippos died in unusual environmental conditions – both Tsavo #1 and Arabuko Sokoke #1, died during a drought year, and the hippo from the Aberdares NP locality may have walked from somewhere else – possibly Lake Naivasha – as hippos are uncommon in the park and this individual was previously unkown in the park (*S. Andanje, pers. comm.*).

These data indicate that, for some individuals, there may have been an environmental circumstance or change in behavior (such as migration or crop raiding) that may have contributed to their death. The onset of drought in the last year of life in the Tsavo #1 and Arabuko Sokoke #1 tusks resulted in steadily increasing $\delta^{18}O$ values in tooth enamel recording their last year of life (Appendix A, Figure 2.6), and similarly, these conditions resulted in vegetation change, recorded in $\delta^{13}C$ values in their final year of life, though the Arabuko Sokoke #1 hippo was shot for crop raiding (Appendix A). Without knowing the specific life histories of other hippo individuals in which these isotopic changes occurred in their final year of life, it is difficult to tell which scenarios are likely. In any case, these data highlight a uniform trend in enamel stable isotopes that may reflect larger environmental changes in the last year of life, and may provide evidence for local environmental change or drought in the fossil record.

2.5.4. Hippo dietary variability across environments

Bd, Wcd, wd, Fp (Bushland/Wooded Grassland environments)

The hippos that exhibit the most depleted isotope values throughout their dietary isotope profiles all come from distinctly bushy/wooded environments in Kenya. These areas include: Adhi Dam (within the Boni National Preserve), Tsavo National Park, Mwea National Reserve, Meru National Park, Buffalo Springs National Reserve, Chyulu Hills National Park, Lake Olbolossat, and the Kisumu area (Lake Victoria). The ecological characterizations of these localities based on the potential natural vegetation map corresponds to on-the-ground ecological research in these areas. Generally, these localities have many C_3 plants and woody vegetation. Chyulu and Tsavo West are ecologically similar to each other with similar representation of C_4 grasses, flowering dicots, and shrubs in both parks (Jensen and Belsky 1989). Woody vegetation has increased in Tsavo since 1970 as the elephant population has decreased, similar to woody increases seen in Queen Elizabeth Park (Corfield 1973; Lock 1993; Leuthold 1996; Plumptre et al. 2010). Mwea National Reserve is similarly a wooded environment, comprised of bushland, woodland, and wooded grassland (Chira and Kinyamario 2009). Likewise, Buffalo Springs National Reserve is also a dry savanna woodland and wooded grassland ecosystem with riverine woodland along the Ewaso Ngiro River, where many hippos live (Wittemyer 2001; Ihwagi et al. 2010). Meru is likewise described as a dry wooded grassland/bushland environment (Neal 1984). The natural area around Lake Olbolossat is a forest, though hippos use only the 2–3 km near the lake itself (Njeri 2003; Kinyili 2014). Likewise, the environment in the Boni National Preserve is a dry coastal forest/woodland, diverse in both flora and fauna (Burgess et al. 1998; Tabor et al. 2010). The modern ecology of Lake Victoria Basin in the unaltered areas — Ruma National Park — is a wooded grassland/bushland, within which woody plants have encroached over the last 50 years with the loss of large browsers (Muriuki et al. 2003).

Trees and other woody vegetation impart a strong influence on the floral composition of the herbaceous layer in Africa savanna environments. It is common for C_3

herbs and dicots to flourish under isolated tree canopies in savannas, and increasing tree density in such savannas negatively influence grass density in those same localities through soil modification and competition for water (Scholes and Archer 1997; Hudak et al. 2003; Bond 2008; February and Higgins 2010). Some, though not all, of these localities have experienced increasing woody vegetation over the last 50 years as a result of large browser removal (Leuthold 1996; Muriuki et al. 2003), while other environments became more woody due to edaphic and/or climatological factors (Chira and Kinyamario 2009). The hippos from these environments all similarly record diets consisting of predominately C_3 resources and are likely recording C_3 herbaceous vegetation in these parks, which may have been facilitated by an abundance of woody plants.

Fq, g, R, Wd/Wc (grassy woodland/grassland/riparian environments)

Hippo dietary isotope values within this grouping largely reflect the more open, grassy nature of these environments. The most depleted average profile value within this group is the hippo from Arabuko Sokoke (-3.6‰), the most forested environment within these hippo habitats. The ecology of the Kenyan a coastal area is diverse, and now consists of grassland, scrub forest, and the biologically diverse Arabuko-Sokoke forest (*Fq*), which once covered much of the Kenyan coast (Moomaw 1960). Through logging and transformation of the coastal ecosystems to agricultural and rangeland purposes, much of the forest has been converted to grasslands, which are abundant on the coast (type *g*) (Oyugi et al. 2008). The basins of lakes Naivasha (*Wd/Wc*) and Nakuru (*R*), in the valley of the central rift, are both characterized as open to densely wooded *Acacia* woodland/more open savanna grasslands, transitioning to bushland/forests along the rift escarpment, with an abundant representation of Poaceae, Asteraceae, and Leguminosae in areas where herbivores graze (Kutilek 1974; Ambrose and Sikes 1991; Maitima 1991; Mutangah 1994; Mutangah and Agnew 1996). The dominance of wooded grasslands in these immediate lake basins, though still a rich representation of woody vegetation, explains the more enriched $\delta^{13}C$ values of hippos from these lakes (Naivasha: -1.93‰, Nakuru: -0.8‰). Amboseli National Park, unlike many other Kenyan parks, has undergone a woodland/bushland reduction and a grassland expansion in recent years (Altmann et al. 2002; Western 2007). A more C_4 inclusive diet is evident from the Amboseli hippo (-1.4‰)

We/wd (edaphic/biotic wooded grassland)

Hippo dietary isotopes from the Laikipia Plateau and Maasai Mara are statistically distinctive from other similar ecosystems in that isotope values from these profiles are more depleted than values from other similar savanna parks, the *Fq, g, R, Wd/Wc* hippos. Isotopic values from the Laikpia hippo tusk (-2.7‰) are difficult to explain, as the Laikipia Plateau is a large, diverse region with natural *Acacia* and *Commiphora* wooded grassland, xeric scrub bushland vegetation (Young et al. 1995; Kahindi et al. 2010). Though C_4 grasses are dominant in wooded grasslands on the plateau, forbs are common, especially in well-drained soils or recently burnt grasslands (Taylor et al. 2005). These more depleted values could represent increased intake of C_3 plants on the plateau, or this hippo could have been raiding crops or consuming resources from an overgrazed area, as land-use change for agricultural purposes is common in Laikipia (Young et al. 1998; Gadd 2005). Hippo habitats within the Mara River in Maasai Mara National Park are comprised of trees along the riparian corridor, grading into bushland and thicket, then into grassland (Olivier and Laurie 1974). This area – 1.5 km away from the water – is the environment used by hippos for feeding. Hippos were noted to have consumed grass in 1974, though such dietary behavior may be out of date (see Chapter 3), as the Mara ecosystem was open and grassy due to high elephant browsing activity. Recently, woodlands have recovered due to over-grazing by livestock (Dublin 1986; Dublin et al. 1990; Reid and Ellis 1995; Lamprey et al. 2004). The more depleted carbon isotope values from the Mara hippo may reflect increasing C_3 facilitated by woodland development.

S (Somalia-Maasai semi-desert grassland/shrubland)

The arid grasslands around the margins of Lake Turkana are distinctive and occur specifically in very arid environments (<200mm rainfall/yr) in northern Kenya and Somalia (White 1983). This distinctive halophytic C_4 grassland around the lake margin consisting primarily of *Sporobolus spp.* is where lake-dwelling hippos feed. These dietary isotope values reflect this area and give a local signal of lake-side ecology (Cerling et al. 2003; Levin et al. 2011).

2.5.5. Hippo diets as a reflection of local environment

Hippo dietary isotope values group into four distinct categories, which relate broadly to these physiognomic ecosystem types. It is important to note that hippos forage close to their aquatic habitats unless under ecological duress, such as overcrowded watering holes or insufficient herbaceous grazing lawns (Eltringham 1999; Klingel 2008). These hippo dietary profiles have revealed the flexible nature of their dietary strategies in greater detail than previously explored (Boisserie et al. 2005; Cerling et al. 2008), though dietary isotope profiles are still restricted and defined by food availability within their environment. This result suggests that hippos are not selective feeders and do not seek out specific species of herbaceous plants, specifically C_4 grasses as previously thought, as nearly all of these parks, reserves, and ecosystems have open grassy vegetation and grasslands within them. Likewise, these dietary profiles reveal distinctive differences even within the same ecosystem, such as the two hippos from Lake Naivasha (Figure 2.4). These data provide strong evidence that hippo dietary isotope values can serve as excellent markers of herbaceous C_3/C_4, but on a hyper-local scale.

On an individual scale, these profiles record distinctive, specific records of local environmental change and stability. Though many profiles record isotope variability on the order of several permil across an individual's lifetime, some isotope records showcase remarkable environmental stability in both $\delta^{13}C$ and $\delta^{18}O$. These records come from a variety of environments, including lakes (the two Turkana hippos, Figures 2.7 and Appendix A), natural springs (Mzima Springs, K09-TSV; Figure 2.5), and rivers (Amboseli and Laikipia, Appendix A). These data are critical for informing paleoecologists on how to interpret isotopic data from fossil hippo enamel, especially from samples taken from hippo canine or molar enamel. Though it appears that, broadly, hippo $\delta^{13}C$ values reflect those of local environment, there is still potential for bias by extreme ecological events, such as drought. Likewise, only in a few individuals is $\delta^{18}O$ relatively stable over the entire course of hippo enamel growth period, meaning that fossil hippo enamel used for paleoaridity proxies may also be biased by extreme environmental events. With these caveats taken into consideration, hippo canine enamel in both modern and fossil environments are remarkable archives of environmental change, stability, and life history in these animals, and can serve as excellent records of local ecology, up to a decade.

2.6 Conclusions

This extensive dataset of serial enamel samples from hippo canines reveals the remarkable dietary variability within and among hippo individuals across environments in Kenya, ranging over 12‰ across all individuals. These data refine our thinking about modern hippo ecology and diets and their indiscriminate feeding nature within the confines of their environment. These data provide an important benchmark for natural ecology and dietary variability for hippos in modern environments that can help identify nuisance animals isotopically, as hippos can cause significant crop damage and income loss for agriculturalists (Naughton-Treves and Treves 2005; Kendall 2011; Nyirenda and Chansa 2011). Similarly, these hippo dietary isotope values provide a modern comparison for fossil and archaeological hippo isotope values. Previous studies on modern isotope values are derived from bulk enamel samples from molars (Cerling et al. 2008). These canine serial samples reveal the range of values within individuals. Though hippo dietary isotopes appear to reflect, to some degree, their environment of origin, isotopic indicators of diet still only reflect the environment immediately around their aquatic habitat, and thus reflect a local snapshot of their environment. Care must be taken when interpreting isotopic values of hippo enamel from the fossil record, and the extensive range and variability in their ecology and behavior must be considered.

2.7 Acknowledgements

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2.8 References

Altmann J, Alberts SC, Altmann SA, Roy SB (2002) Dramatic change in local climate patterns in the Amboseli basin, Kenya. African Journal of Ecology 40:248–251.

Ambrose SH, Sikes NE (1991) Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. Science 253:1402–1405.

Arsenault R, Owen Smith N (2002) Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313–318.

Boisserie JR, Zazzo A, Merceron G, et al. (2005) Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. Palaeogeography, Palaeoclimatology, Palaeoecology 221:153–174.

Bond WJ (2008) What limits trees in C_4 grasslands and savannas? Annual Review of Ecology, Evolution, and Systematics 39:641–659.

Bourliére F, Hadley M (1970) The ecology of tropical savannas. Annual Review of Ecology and Systematics 1:125–152.

Burgess ND, Clarke GP, Rodgers WA (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. Biological Journal of the Linnean Society 64:337–367.

Burgess ND, Muir CE (1994) Coastal forests of Eastern Africa: biodiversity and conservation. Society for Environmental Exploration/Royal Society for the Protection of Birds: UK.

Cerling TE (2014) 14.12: Stable isotope evidence for hominin environments in Africa. In: Cerling TE (eds) Treatise on Geochemistry Second Edition. Elsevier, Amsterdam, pp 157–167.

Cerling TE (1996) Pore water chemistry of an alkaline lake: Lake Turkana, Kenya. In: Johnson TC, Odada EO (eds) The Limnology, Climatology and Paleoclimatology of the East African Lakes. CRC Press, Boca Raton, pp 225–240.

Cerling TE, Harris JM, Leakey M, Mudida N (2003) Stable isotope ecology of northern Kenya with emphasis on the Turkana Basin. In: Leakey MG, Harris JM (eds), Lothagam: The dawn of humanity in eastern Africa. Columbia University Press, New York, pp 583–603.

Cerling TE, Harris JM, Hart JA, et al. (2008) Stable isotope ecology of the common hippopotamus. Journal of Zoology 276:204–212.

Cerling TE, Harris JM, Passey B, et al. (2004) Orphans' tales: seasonal dietary changes in elephants from Tsavo National Park, Kenya. Palaeogeography, Palaeoclimatology, Palaeoecology 206:367–376.

Chansa W, Milanzi J, Sichone P (2011) Influence of river geomorphologic features on hippopotamus density distribution along the Luangwa River, Zambia. African Journal of Ecology 49:221–226.

Chira RM, Kinyamario JI (2009) Growth response of woody species to elephant foraging in Mwea National Reserve, Kenya. African Journal of Ecology 47:598–605.

Corfield T (1973) Elephant mortality in Tsavo National Park, Kenya. African Journal of Ecology 11:339–368.

Dublin HT (1986) Decline of the Mara woodlands: the role of fire and elephants. PhD Thesis, University of British Columbia.

Dublin HT, Sinclair A, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. Journal of Animal Ecology 59:1147–1164.

Eltringham SK (1999) The hippos: natural history and conservation. Academic Press, London.

Eltringham SK (1974) Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus. Journal of Applied Ecology 11:855–865.

February EC, Higgins SI (2010) The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. South African Journal of Botany 76: 517–523.

Field CR (1970) A study of the feeding habits of the hippopotamus (*Hippopotamus amphibius* Linn.) in the Queen Elizabeth National Park, Uganda, with some management implications. Zoologica Africana 5:71–86.

Fritz H, Duncan P, Gordon IJ, Illius AW (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. Oecologia 131:620–625.

Gadd ME (2005) Conservation outside of parks: attitudes of local people in Laikipia, Kenya. Environmental Conservation 32:50–63.

Harris JM, Cerling TE, Leakey MG, Passey B (2008) Stable isotope ecology of fossil hippopotamids from the Lake Turkana Basin of East Africa. Journal of Zoology 275:323–331.

Hudak AT, Wessman CA, Seastedt TR (2003) Woody overstorey effects on soil carbon and nitrogen pools in South African savanna. Austral Ecology 28:173–181.

Ihaka R, Gentleman R (1996) R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299–314.

Ihwagi FW, Vollrath F, Chira RM, et al. (2010) The impact of elephants, *Loxodonta africana*, on woody vegetation through selective debarking in Samburu and Buffalo Springs National Reserves, Kenya. African Journal of Ecology 48:87–95.

Jensen CL, Belsky AJ (1989) Grassland homogeneity in Tsavo National Park (West), Kenya. African Journal of Ecology 27:35–44.

Kabutha C, Mutero CM (2002) From government to farmer-managed smallholder rice schemes: the unresolved case of the Mwea irrigation scheme. In: Blank HG, Mutero CM, Murray-Rust H (eds) The Changing Face of Irrigation in Kenya Opportunities for Anticipating Change in Eastern and Southern Africa. Colombo, Sri Lanka, pp 191–210.

Kahindi O, Wittemyer G, King J, Ihwagi F (2010) Employing participatory surveys to monitor the illegal killing of elephants across diverse land uses in Laikipia–Samburu, Kenya. African Journal of Ecology 48: 972–983.

Kanga EM, Ogutu JO, Piepho H-P, Olff H (2011) Hippopotamus and livestock grazing: influences on riparian vegetation and facilitation of other herbivores in the Mara Region of Kenya. Landscape Ecol Eng 9:47–58.

Kanga EM, Ogutu JO, Piepho H-P, Olff H (2012) Human–hippo conflicts in Kenya during 1997–2008: vulnerability of a megaherbivore to anthropogenic land use changes. Journal of Land Use Science 7:395–406.

Kendall CJ (2011) The spatial and agricultural basis of crop raiding by the vulnerable common hippopotamus (*Hippopotamus amphibius*) around Ruaha National Park, Tanzania. Oryx 45:28–34.

Kindt R, Lillesø J, van Breugel P, et al. (2011a) Potential natural vegetation map of eastern Africa, Volume 5: Description and tree species composition for other potential natural vegetation types. Forest and Landscape, Denmark.

Kindt R, van Breugel P, Lillesø J, et al. (2011b) Potential natural vegetation of eastern Africa, Volume 3: Description and tree species composition for woodland and wooded grassland potential natural vegetation types. Forest and Landscape, Denmark.

Kindt R, van Breugel P, Lillesø J, et al. (2011c) Potential natural vegetation of eastern Africa, Volume 4: Description and tree species composition for bushland and thicket potential natural vegetation types. Forest and Landscape Denmark.

Kinyili BM (2014) Impacts of participatory forest management approach in Ol Bolossat forest, Nyandarua Country, Kenya. Master's Thesis, Kenyatta University.

Klingel H (2008) Das Flusspfred. In: Macdonald AA, Gansloßer U (eds) Wilde Schweine und Flusspferde. pp 353–370.

Klingel H (2013) Hippopotamus. In: Kingdon J, Hoffmann M (eds) Mammals of Africa. London, pp 68–78.

Kutilek MJ (1974) The density and biomass of large mammals in Lake Nakuru National Park. African Journal of Ecology 12: 201–212.

Lamprey RH, Reid RS, Reid RS (2004) Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? Journal of Biogeography 31: 997-1032.

Leuthold W (1996) Recovery of woody vegetation in Tsavo National Park, Kenya, 1970‐94. African Journal of Ecology 34: 101–112.

Levin NE, Cerling TE, Passey B (2011) Stable isotope ecology in the Omo‐Turkana Basin. Evolutionary Anthropology: Issues, News, and Reviews 20:228–237.

Levin NE, Cerling TE, Passey B, et al. (2006) A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Sciences 103:11201–11205.

Lewison R (2007) Population responses to natural and human‐mediated disturbances: assessing the vulnerability of the common hippopotamus (*Hippopotamus amphibius*). African Journal of Ecology 45:407–415.

Lewison RL, Carter J (2004) Exploring behavior of an unusual megaherbivore: a spatially explicit foraging model of the hippopotamus. Ecological Modelling 171: 127–138.

Lillesø J, van Breugel P, Kindt R, et al. (2011) Potential natural vegetation of eastern Africa, Volume 1. The Atlas. Forest & Landscape Denmark, Copenhagen.

Lock J (1993) Vegetation change in Queen Elizabeth National Park, Uganda: 1970–1988. African Journal of Ecology 31: 106-117.

Lock JM (1972) The effects of hippopotamus grazing on grasslands. The Journal of Ecology 60:445-467.

Luck CP, Wright PG (1964) Aspects of the anatomy and physiology of the skin of the hippopotamus (*H. amphibius*). Experimental Physiology 49:1–14.

Maitima JM (1991) Vegetation response to climatic change in central Rift Valley, Kenya. 35: 234–245.

McCauley DJ, Dawson TE, Power ME, Finlay JC (2015) Carbon stable isotopes suggest that hippopotamus-vectored nutrients subsidize aquatic consumers in an East African river. Ecosphere 6:art52.

Moomaw JC (1960) A study of the plant ecology of the coast region of Kenya. Government Printer, Nairobi.

Muriuki GW, Njoka TJ, Reid RS (2003) Tsetse, wildlife and land-cover change in Ruma National Park, South-western Kenya. Journal of Human Ecology 14: 229–235.

Mutangah JG (1994) The vegetation of Lake Nakuru National Park, Kenya: a synopsis of the vegetation types with annotated species list. Journal of East African Natural History. Journal of East African Natural History 83: 71–96.

Mutangah JG, Agnew A (1996) Structure and diversity comparison of three dry forests at Nakuru National Park, Kenya. 34:146–157.

Naughton-Treves L, Treves A (2005) Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People and Wildlife Conflict or Coexistence, pp 252–277.

Neal BR (1984) Relationship between feeding habits, climate and reproduction of small mammals in Meru National Park, Kenya. African Journal of Ecology 22:195–205.

Njeri T (2003) Habitat utilization by birds, hippopotamus (*Hippopotamus amphibius*) and livestock in Lake Ol'Bolossat, Kenya. Master's Thesis, Kenyatta University.

Nyirenda VR, Chansa WC (2011) Wildlife crop depredation in the Luangwa Valley, eastern Zambia. Journal of Ecology and the Natural Environment 3: 481-491.

Ojiambo BS, Poreda RJ, Lyons WB (2001) Ground water/surface water interactions in Lake Naivasha, Kenya, using $\delta^{18}O$, δD, and $^{3}H/^{3}He$ Age-Dating. Ground Water 39:526–533.

Olivier RCD, Laurie WA (1974) Habitat utilization by hippopotamus in the Mara River*. African Journal of Ecology 12:249–271.

Owen Smith N, Chafota J (2012) Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). Journal of Mammalogy 93:698–705.

Owen-Smith RN (1992) Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge.

Oyugi JO, Brown JS, Whelan CJ (2008) Effects of human disturbance on composition and structure of *Brachystegia* woodland in Arabuko-Sokoke Forest, Kenya. African Journal of Ecology 46: 374–383.

Passey B, Cerling TE (2002). Tooth enamel mineralization in ugulates: implications for recovering a primary isotope time-series. Geochimica et Cosmochimica Acta 66: 3225-3234.

Passey B, Cerling TE, Schuster GT, et al. (2005) Inverse methods for estimating primary input signals from time-averaged isotope profiles. Geochimica et Cosmochimica Acta 69: 4101–4116.

Passey BH, Cerling TE, Levin NE (2007) Temperature dependence of oxygen isotope acid fractionation for modern and fossil tooth enamels. Rapid Communications in Mass Spectrometry 21:2853–2859.

Plumptre AJ, Kirunda B, Mugabe H, et al. (2010) The impact of fire and large mammals on the ecology of Queen Elizabeth National Park. Wildlife Conservation Society and Woods Hole Research Centre, 57 p.

Reid RS, Ellis JE (1995) Impacts of pastoralists on woodlands in south Turkana, Kenya: livestock-mediated tree recruitment. Ecological Applications 5: 978–992.

Scholes R, Archer S (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 517–544.

Souron A, Balasse, Boisserie JR (2012) Intra-tooth isotopic profiles of canine from extant *Hippopotamus amphibius* and the late Pliocene hippopotamids (Shungura Formation, Ethiopia): insights into the seasonality of diet and climate. Palaeogeography, Palaeoclimatology, Palaeoecology 342-343: 97–110.

Sokal RR, Rohlf FJ (1994) Biometry, 3rd edn. W. H. Freeman, New York City.

Subalusky AL, Dutton CL, Marshall ER (2015) The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. Freshwater Biology 60: 512–525.

Tabor K, Burgess ND, Mbilinyi BP, et al. (2010) Forest and woodland cover and change in coastal Tanzania and Kenya, 1990 to 2000. Journal of East African Natural History 99:16–45.

Taylor D, Lane PJ, Muiruri V, et al. (2005) Mid- to late-Holocene vegetation dynamics on the Laikipia Plateau, Kenya. The Holocene 15:837–846.

Uno KT, Quade J, Fisher DC, et al. (2013) Bomb-curve radiocarbon measurement of recent biologic tissues and applications to wildlife forensics and stable isotope (paleo)ecology. Proceedings of the National Academy of Sciences 110: 11736–11741.

Vesey-FitzGerald DF (1960) Grazing succession among East African game animals. Journal of Mammalogy 41:161–172.

Weladji RB, Tchamba MN (2003) Conflict between people and protected areas within the Bénoué Wildlife Conservation Area, North Cameroon. Oryx 37: 72–79.

Western D (2007) A half a century of habitat change in Amboseli National Park, Kenya. African Journal of Ecology 45: 302–310.

White F (1983) The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. United Nations Educational, Scientific and Cultural Organization, La Chaux-de-Fonds, 356 p.

Wittemyer G (2001) The elephant population of Samburu and Buffalo Springs National Reserves, Kenya. African Journal of Ecology 39:357–365.

Wronski T (2002) Feeding ecology and foraging behaviour of impala *Aepyceros melampus* in Lake Mburo National Park, Uganda. African Journal of Ecology 40:205–211.

Young TP, Okello BD, Kinyua D (1998) KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. African Journal of Range and Forage Science 14: 92–104.

Young TP, Patridge N, Macrae A (1995) Long-term glades in acacia bushland and their edge effects in Laikipia, Kenya. Ecological Applications 5:97–108.

Verweij RJT, Verrelst J, Loth PE, et al. (2006) Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. Oikos 114:108–116.

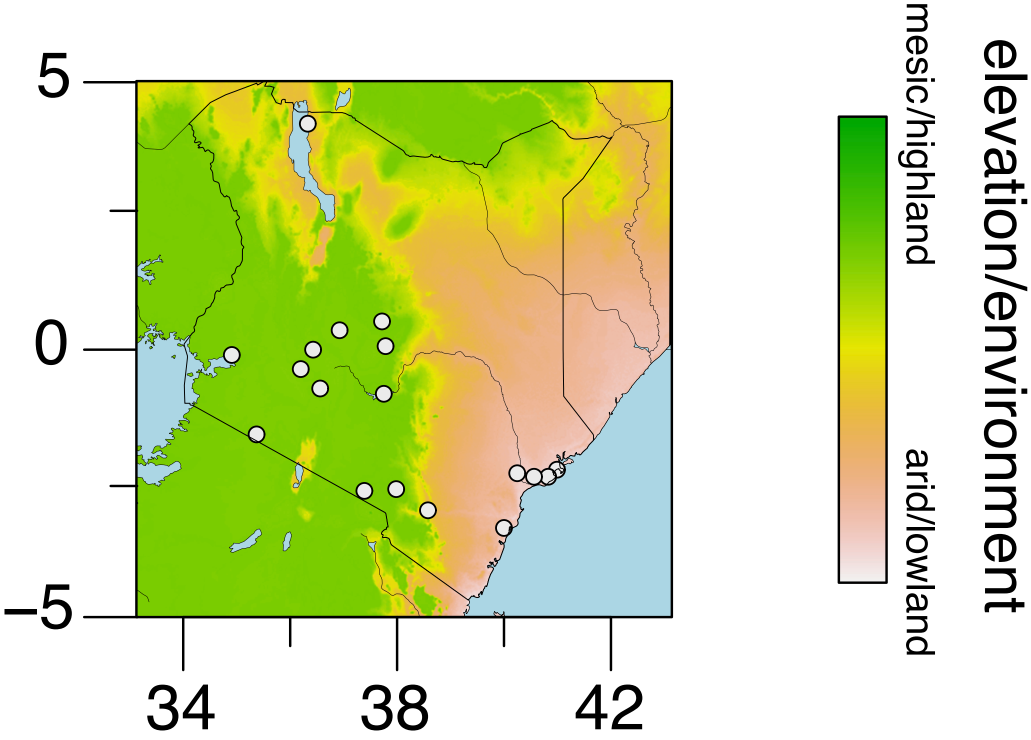

Figure 2.1: Map of localities where hippos were collected.

Table 2.1: UNESCO vegetation classification scheme (from White, 1983).

Forest	continuous stand of trees at least 10m tall, with interlocking crowns.
Woodland	open stand of trees at least 8m tall, with canopy cover of >40% and a grass-dominated herbaceous layer.
Bushland	open stand of bushes 3–7m tall, with canopy cover of >40%.
Thicket	closed stand of bushes 3–7m tall.
Shrubland	open or closed stand of shrubs up to 2m tall.
Grassland	dominated by grasses and other herbs and forbs, either with or without woody plants exceeding no more than 10% canopy cover.
Wooded grassland	dominated by grasses and other herbs and forbs, with woody canopy cover between 10 and 40%.

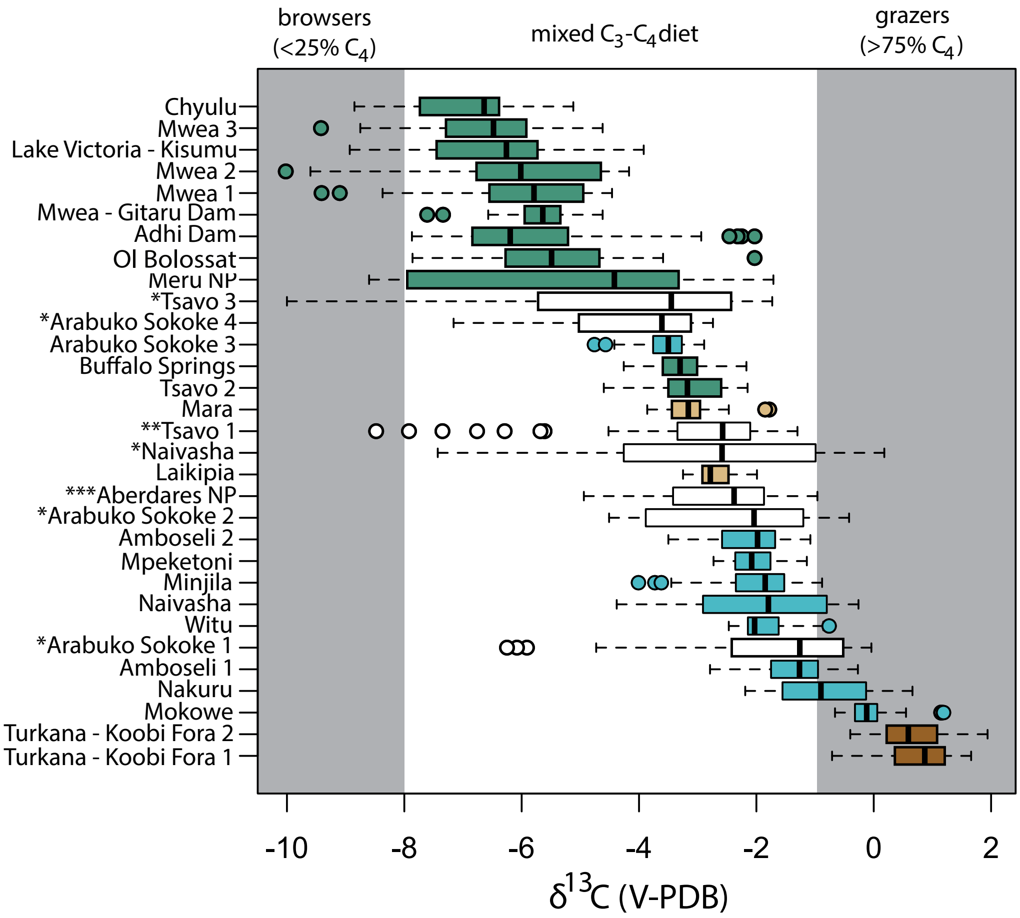

Figure 2.2: Mean boxplots of δ^{13}C values from hippo canine enamel profiles. Boxplot colors correspond to environmental groupings given in Figure 2.3. *denotes nuisance animals not included in statistical analysis. **died in drought. ***denotes animals with unknown provenance.

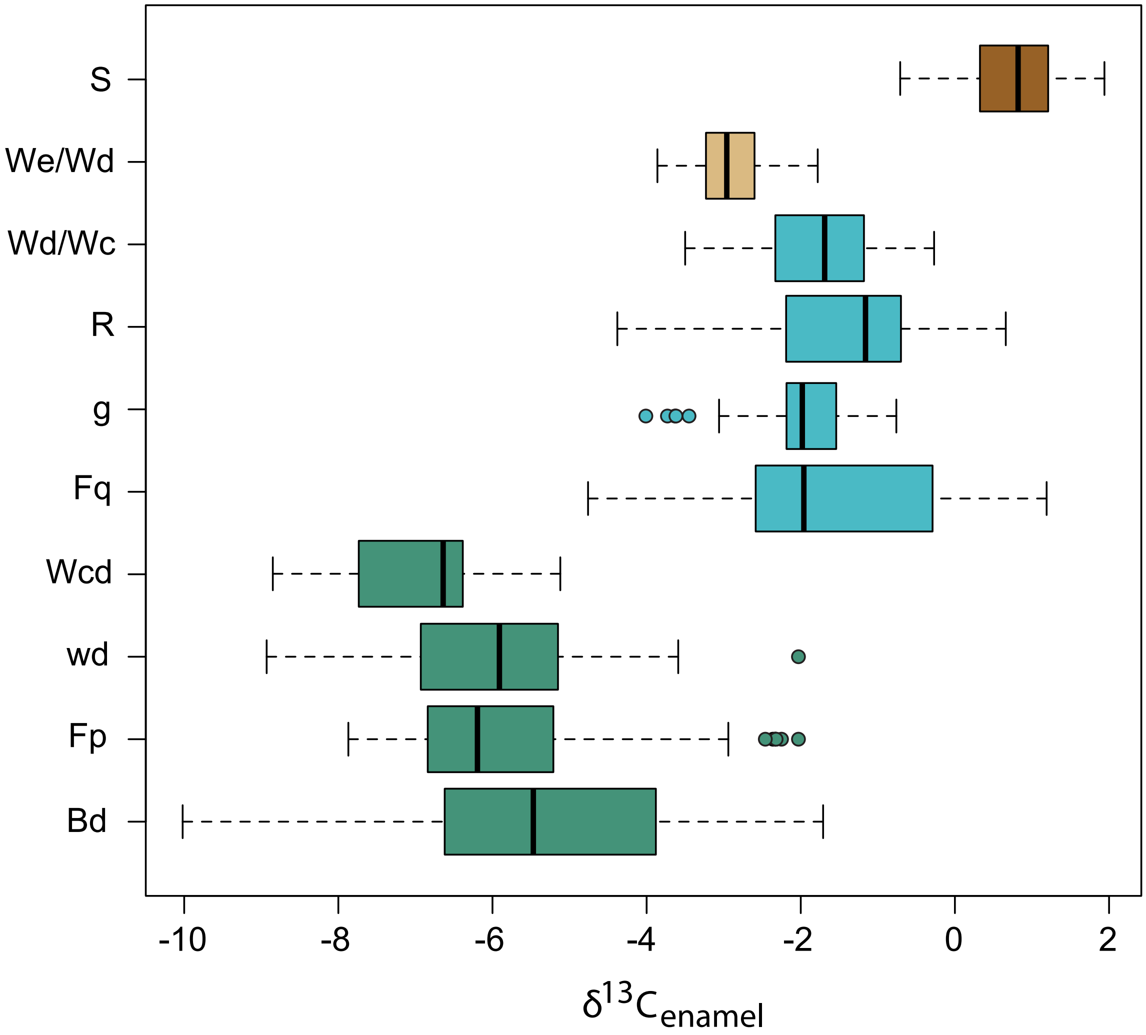

Figure 2.3: Mean boxplots of enamel isotope values grouped by environment. Boxplot colors correspond to statistically significant ecological groupings (*P* values presented in Table 2.3).

Table 2.2: Hippo tusks sampled by locality. Starred hippos were excluded from analysis for reasons given below this table.

Sample ID	Locality	Year of death	Method	Length (mm)	$\delta^{13}C$ avg.	SD
***Aberdares	Aberdares NP			325	-2.7	1.0
KWS-Adhidam	Adhi Dam	ca. 2008	known	495	-5.6	1.7
Amboseli H1/H2	Amboseli #1			465	-1.4	0.6
KWS-AMB-0401	Amboseli #2	ca. 2008	known	425	-2.1	0.7
*AS168	Arabuko Sokoke #1	1996		340	-1.7	1.6
*K00-AS-167	Arabuko Sokoke #2	1996		432	-2.3	1.3
Arabuko - Sokoke 2008	Arabuko Sokoke #3	2002		295	-3.6	0.5
*AS166	Arabuko Sokoke #4	1996		272	-4.2	1.3
Buffalo Springs	Buffalo Springs	2010	known	465	-3.2	0.5
Chyulu	Chyulu			315	-7	0.9
Kisumu	Kisumu			405	-6.4	1
K01-LAI-191	Laikipia	ca. 2000	known	470	-2.7	0.3
Mara	Maasai Mara			345	-3.1	0.5
Meru	Meru NP			275	-5.1	2.4
KWS Minjila (Tana River)	Minjila			525	-2.1	0.7
Mokowe	Mokowe			485	-0.1	0.4
Mpeketoni	Mpeketoni			535	-2.1	0.4
Mwea, Gitaru Dam	Mwea - Gitaru Dam			405	-5.7	0.6
Mwea 2009	Mwea #1	2008	known	595	-5.9	1.2
Mwea NR MAR	Mwea #2	2005	known	595	-6.1	1.4
Mwea NP 2007	Mwea #3	2007	known	605	-6.6	1.0

*crop raider
**died in drought
***unknown origin locality

Table 2.2 (continued)

Sample ID	Locality	Year of death	Method	Length (mm)	$\delta^{13}C$ avg.	SD
*KWS-Naivasha	Naivasha - CL			525	-2.8	2.2
KWS-NAIV-CF-1108	Naivasha - CF	ca. 2008	known	585	-1.9	1.3
KWS-LNakuru-Kabutini-5	Nakuru			315	-0.8	0.8
Olbolossat	Ol Bolossat			345	-5.5	1.4
**K01-TSW-291	Tsavo #1	1996	^{14}C/ known	605	-3.1	1.6
Tsavo - 2009 (Mzima Springs)	Tsavo #2		known	595	-3.2	0.6
K08-201	Tsavo #3	Oct. 2007	known	535	-4.8	2.5
Koobi Fora 2011	Turkana - Koobi Fora 1	1980	^{14}C	485	0.8	0.5
KEN-09-115	Turkana - Koobi Fora 2	ca. 2005	known	425	0.6	0.6
Witu	Witu			575	-1.9	0.4

*crop raider
**died in drought
***unknown origin locality

Table 2.2 (continued)

Sample ID	**$\delta^{18}O$ avg.**	**SD**	**Env.**	**Lat.**	**Long.**
***Aberdares	-2.6	0.7	?	-0.4158	36.6667
KWS-Adhidam	-1.7	0.8	Fp	-1.5397	41.4496
Amboseli H1/H2	-5.7	0.3	wd/Wc	-2.7207	37.297
KWS-AMB-0401	-5.2	0.4	wd/Wc	-2.7207	37.297
*AS168	-4.5	0.6	Fq	-3.3298	39.8772
*K00-AS-167	-3.4	0.7	Fq	-3.3298	39.8772
Arabuko - Sokoke 2008	-3.2	0.5	Fq	-3.3298	39.8772
*AS166	-3	0.6	Fq	-3.3298	39.8772
Buffalo Springs	-3.9	0.3	Bd	0.4936	37.6111
Chyulu	-3.7	1.5	Wcd	-2.549	37.876
Kisumu	-3.9	0.4	wd	-0.2209	34.6387
K01-LAI-191	-2.4	1	We/Wd	0.3726	36.7869
Mara	-4.1	0.4	We/Wd	-1.5987	35.2782
Meru	-4.7	1	Bd	0.088	38.1899
KWS Minjila (Tana River)	-2.3	0.8	g	-2.2843	40.1392
Mokowe	-3.5	0.3	Fq	-2.232	40.8406
Mpeketoni	-1.4	1.1	Fq	-2.3904	40.6968
Mwea, Gitaru Dam	-3.5	0.8	Bd	-0.8259	37.6846
Mwea 2009	-4.1	0.8	Bd	-0.8259	37.6846
Mwea NR MAR	-4.3	1.2	Bd	-0.8259	37.6846
Mwea NP 2007	-3.5	0.6	Bd	-0.8259	37.6846
*KWS-Naivasha	-3.7	1	R	-0.7729	36.3375
KWS-NAIV-CF-1108	0.5	0.7	R	-0.7876	36.4107
KWS-LNakuru-Kabutini-5	-1.3	1.3	R	-0.3834	36.1359
Olbolossat	-2.3	1.1	wd	-0.1556	36.4405
**K01-TSW-291	-4.3	0.8	Bd	-2.9642	37.9104
Tsavo - 2009 (Mzima Springs)	-4.4	0.5	Bd	-2.9835	38.0217
K08-201	-2.2	1.5	Bd	-2.1833	38.4166
Koobi Fora 2011	1.4	0.7	S	3.9472	36.1858
KEN-09-115	1.2	0.4	S	3.9472	36.1858
Witu	-2.5	0.8	g	-2.3728	40.3984

*crop raider
**died in drought
***unknown origin locality

Table 2.3: *P* values of relationships between environmental groupings of $\delta^{13}C$ enamel values from pairwise comparisons using a Tukey-Kramer (Nemenyi) test.

	Bd	**Fp**	**Fq**	**g**	**R**
Fp	1				
Fq	*<0.0001*	*<0.0001*			
g	*<0.0001*	*<0.0001*	1		
R	*<0.0001*	*<0.0001*	0.99	0.99	
S	*<0.0001*	*<0.0001*	*<0.0001*	*<0.0001*	*<0.0001*
Wcd	0.23	0.73	*<0.0001*	*<0.0001*	*<0.0001*
wd	0.93	0.99	*<0.0001*	*<0.0001*	*<0.0001*
Wd/Wc	*<0.0001*	*<0.0001*	1	1	1
We/Wd	*<0.0001*	*<0.01*	0.05	*<0.01*	*<0.01*

Table 2.3 (continued)

	S	**Wcd**	**wd**	**Wd/Wc**
Fp				
Fq				
g				
R				
S				
Wcd	*<0.0001*			
wd	*<0.0001*	0.94		
Wd/Wc	*<0.0001*	*<0.0001*	*<0.0001*	
We/Wd	*<0.0001*	*<0.0001*	*<0.0001*	0.02

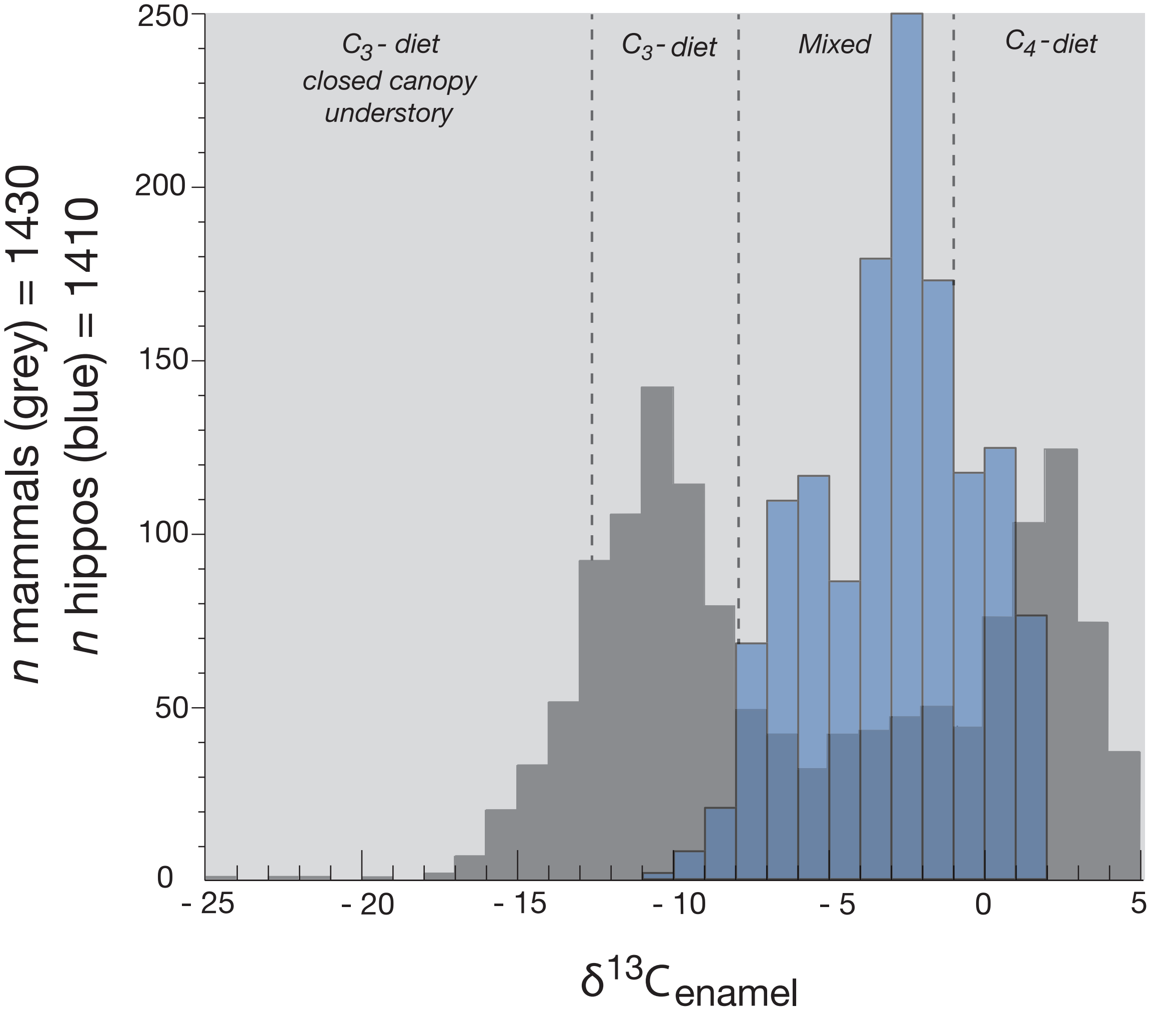

Figure 2.4: Comparison of hippo profile isotope values (blue) vs. other mammal enamel isotope values (data from Cerling 2014).

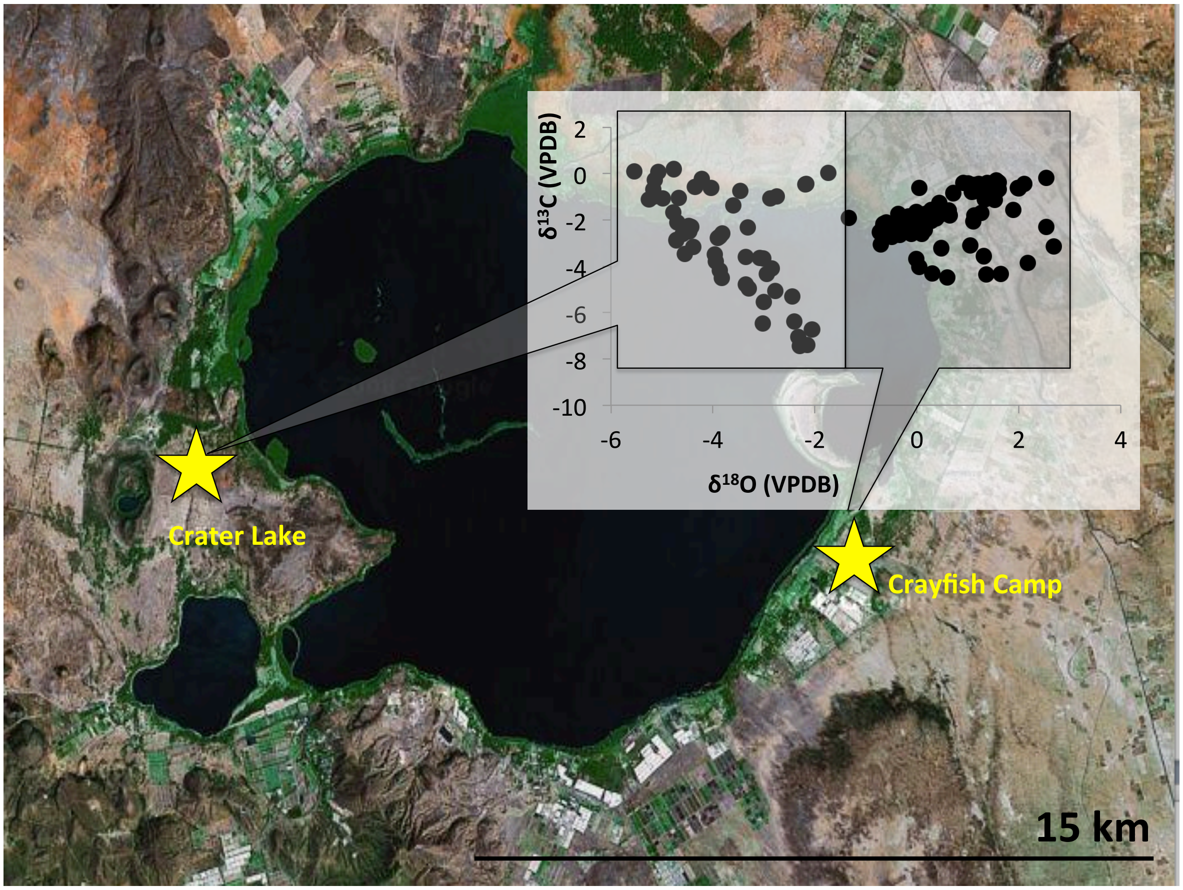

Figure 2.5: Comparison of two hippos from Lake Naivasha – Crayfish Camp vs. Crater Lake.

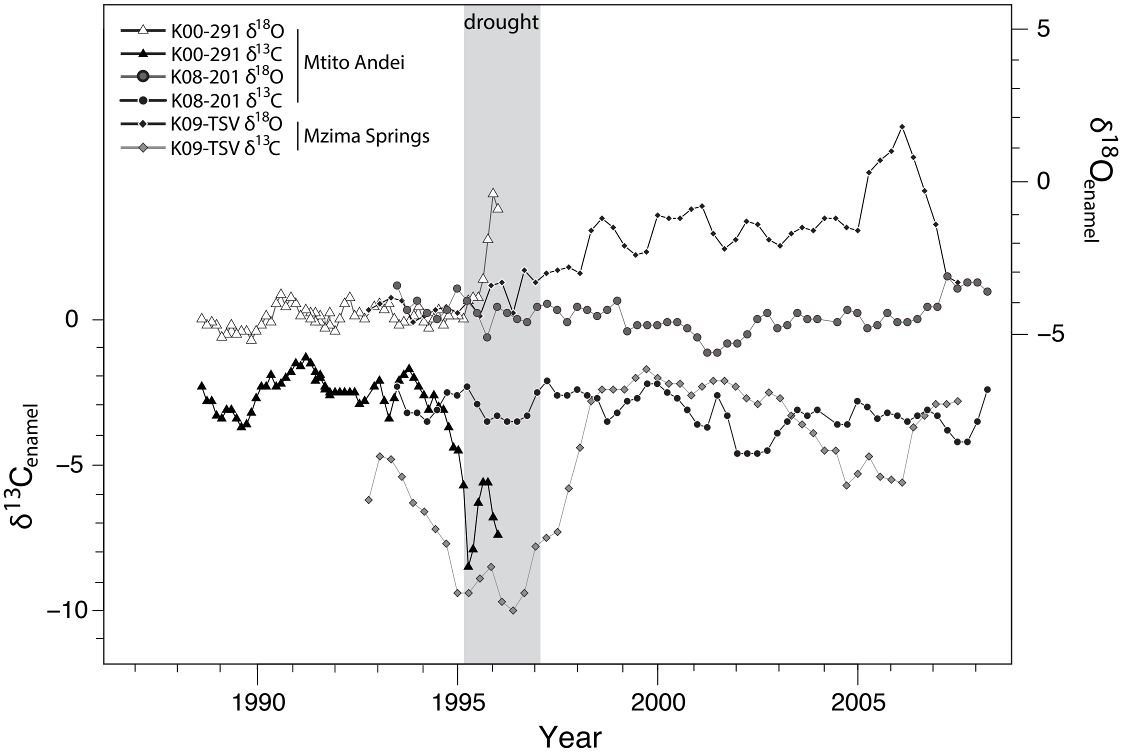

Figure 2.6: Isotope profiles of three Tsavo hippo canines showing differential responses to drought in the park based on locality.

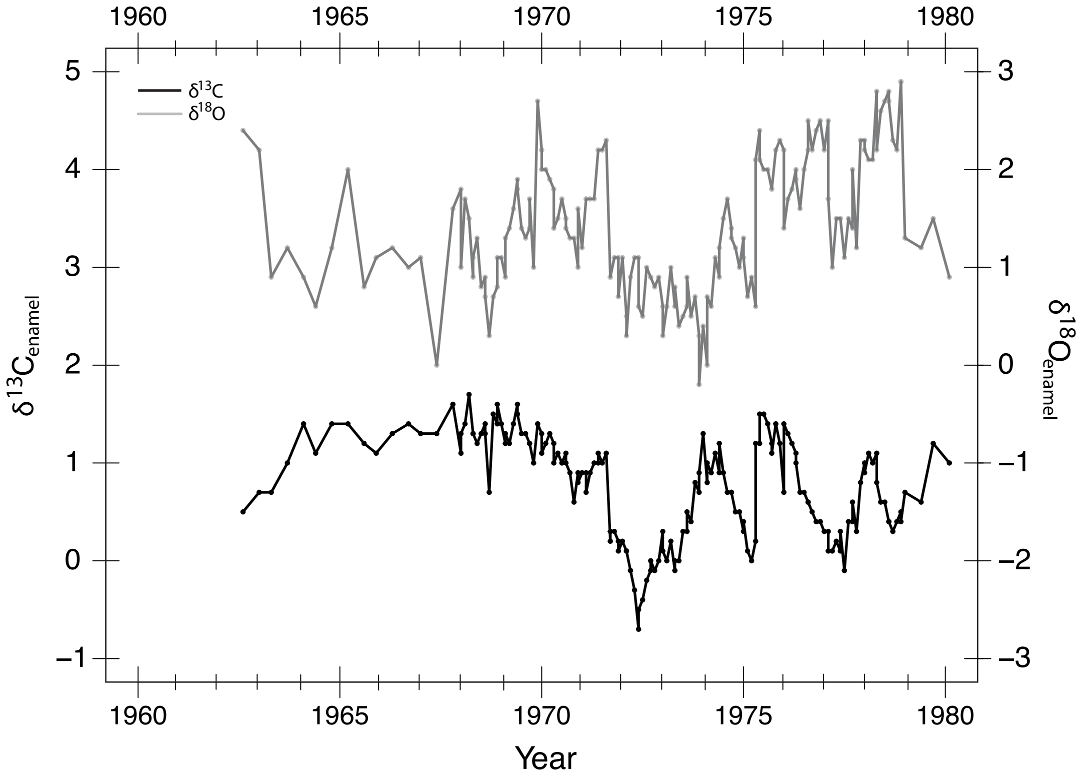

Figure 2.7: High resolution δ^{13}C and δ^{18}O enamel data from KF-

CHAPTER 3

DECADAL DIET CHANGE IN *HIPPOPOTAMUS AMPHIBIUS* IN QUEEN ELIZABETH NATIONAL PARK, UGANDA

3.1 Abstract

Megaherbivores (>1000kg) occupy important roles in African environments as ecosystem engineers, and changes to their ecology can result in major - and sometimes devastating - effects on their ecosystems. Despite their ecological importance, some basic aspects of their ecology (such as diet) remain poorly understood. Previous behavioral and gut/fecal content studies have categorized the common hippopotamus (*Hippopotamus amphibius*) as selective grazers, although isotopic analyses in East and Central African hippopotamus have suggested otherwise. Potential ecological drivers for dietary change remain poorly understood. We examine dietary flexibility in hippos over time within a single population using serial carbon isotope ratios ($\delta^{13}C$) in canine enamel from individuals that lived in Queen Elizabeth National Park, Uganda (QEP) near the Mweya Peninsula from 1960–1990s, a period characterized by significant expansion of bushy/woody vegetation following heavy poaching of elephants and other large mammals. Three hippo canines record a dietary switch within the Mweya hippo population from grazing (>80% C_4) to a mixed C_3/C_4 diet (between 55–70% C_4), likely driven by changes in the floral composition of the herbaceous vegetation layer. These data highlight the ability of hippos to cope with large-scale ecosystem change, and that

encroachment of C_3 plants has occurred in both woody and herbaceous layers, as recorded in hippo canine enamel isotopes, further decreasing grazing capacity in the park.

3.2 Introduction

3.2.1 *Hippopotamus* ecology

The common hippopotamus (*Hippopotamus amphibius*) is a large bodied herbivore found across Africa that lives in varied environments, ranging from arid savanna (see Chapter 2 for description) to forest (Eltringham 1999; Klingel 2008; 2013). They are semi-aquatic, spending the day resting in pools, rivers, and lakes, and feeding nocturnally on terrestrial vegetation (Vesey-FitzGerald 1960). Hippos generally feed less than 6 km away from their aquatic habitats and require as much as 20 kgs of foliage per day; these high feeding requirements and repeated journeys on land can lead to trampled and compacted ground, which can deter vegetation growth and transform soil properties (Lock 1972). Hippos can significantly restructure grazing areas, mowing tall grasses into short, closely-cropped lawns, which deters feeding by herbivores that prefer tall grasses, such as elephants and buffalo (Arsenault & Owen Smith 2002).

Early studies of hippo ecology suggested that hippos selectively feed on C_4 grasses (Field 1970; 1972). However, stable isotope ratios of carbon $^{13}C/^{12}C$ in hippo biological tissues reveal considerable variability in the consumption of C_3 plants (herbs, forbs and shrubs) and C_4 plants (tropical grasses <3000 m), indicating a range in diets from purely C_3-based to purely C_4-based (Boisserie *et al.* 2005; Cerling *et al.* 2008; see Chapter 2). Hippos have an unusual digestive anatomy, as they tend to masticate food to large particles that are inefficiently digested, relative to other ungulates, via non-ruminating foregut fermentation, with long digesta retention times and low metabolic rates (Clauss *et al.* 2004; Schwarm *et al.* 2006). Hippos are sometimes regarded as nuisance animals, as they frequently raid crops of maize, rice, and groundnut (Weladji & Tchamba 2003; Naughton-Treves & Treves 2005; Nyirenda & Chansa 2011); this nuisance status can impede conservation efforts.

3.2.2 Megaherbivores as ecosystem engineers

Megaherbivores, such as hippos and elephants (*Loxodonta africana*), play critical roles in African ecosystems, including the maintenance of open grasslands, the modification of trophic guild structure (Owen-Smith 1992; Fritz *et al.* 2002; Duffy 2003; Asner & Levick 2012). Though hippos impact vegetation relatively near their aquatic habitats, elephants are important influencers of overall savanna habitat structure and function, and exert a higher level of influence (Beuchner & Dawkins 1961; Field 1971; Dublin *et al.* 1990; Barnes 2001). Elephants achieve this through selective browsing, predominantly on trees and thickets, which contributes to the persistence of open grasslands; high elephant populations can lead to woodland decline and can result in the extirpation of woody plants in areas of high elephant browsing (Dublin 1986). Elephants also facilitate other herbivore communities present by reducing predator cover in savannas (Laundré *et al.* 2001; Valeix *et al.* 2011).

Elephant populations are declining across Africa due to poaching, and loss of these important megaherbivores will undoubtedly alter the stability and function of savanna ecosystems, and woody plant representation in savannas will increase (Wittemyer *et al.* 2014). In addition to this issue, climatological forcing and increasing global CO_2 is facilitating bush encroachment (increasing numbers of unpalatable woody plants) across Africa (Ward 2005; Wiegand *et al.* 2005). We also have a poor understanding of how elephant extirpation will affect other large-bodied keystone species, such as hippos, especially given the possibility for increasing C_3 plants in areas where these animals live.

We use ecological records and stable isotope proxy data from Queen Elizabeth National Park, Uganda (QEP) to understand the extent of ecological and behavioral change in a large population of hippos associated with a well-documented collapse in elephant populations. Our aims are to understand (1) the flexibility of hippo diets over time following a population collapse in elephants, (2) the ecological consequences of hippos feeding in disturbed environments, and (3) the extent of C_3 herbaceous/bush encroachment that occurred following the elephant population collapse. We use stable isotope analysis of hippo canines to estimate the diet contributions of C_3 and C_4 plants to hippos inhabiting the Mweya Peninsula in QEP following an environmental disturbance (poaching and elephant culling in the 1970s) and associated large-scale environmental change (transformation of C_4 grasslands to mixed C_3/C_4 herbaceous ground cover and wooded areas).

3.2.3 Stable isotope ecology in African mammals

Stable isotope analysis is a powerful tool for understanding aspects of mammalian herbivore ecology in Africa, and is particularly useful for generating ecological records on time and space scales that are difficult or impossible to observe (Boutton *et al.* 1983; Ambrose & DeNiro 1986; Lee-Thorp & Van der Merwe 1987; Koch *et al.* 1990; Harris & Cerling 2002; Cerling *et al.* 2003; Cerling *et al.* 2004; 2005; 2008; Harris *et al.* 2008; Blumenthal *et al.* 2012; Cerling *et al.* 2013; Van Der Merwe 2013; Oelze *et al.* 2014). Stable carbon isotope analysis ($\delta^{13}C$) of herbivore tooth enamel can reveal the relative proportions of C_3 vs. C_4 in the diets of African herbivores, and the relationship between $\delta^{13}C_{diet}$ and $\delta^{13}C_{enamel}$ values is well-understood in African ungulates (Cerling & Harris 1999; Passey *et al.* 2005). Hippo canines represent excellent long-term archives of their ecology, since they are ever-growing and include isotopic input spanning 10 or more years of enamel growth (Laws 1968; Passey *et al.* 2005; Uno *et al.* 2013; see Chapter 2). Therefore, stable isotope analysis of tusks is ideal for quantifying primarily nocturnal feeding behavior of hippos, which is difficult to observe, particularly for generating multiyear to decadal-scale ecological records from deceased animals.

3.2.4 History of ecological research in Queen Elizabeth Park, Uganda

Queen Elizabeth Park (Figure 3.1) is located in western Uganda in the Albertine Rift Valley, along the border of the Democratic Republic of Congo (DRC). The park is 1,979 km^2, surrounding Lakes Edward and George, which are connected via the Kazinga Channel. Rainfall varies between 600 and 1400 mm/yr during March-May and in September- November, and is highest along the rift escarpment and along the Rwenzori Mountains, (Plumptre *et al.* 2010b). The soils in the park are rich in volcanic ash, leading to rich vegetation growth and high net primary production, with a high number of globally threatened and endemic plant and animal species (Field 1970; Plumptre *et al.* 2007a; 2010a).

Detailed ecological research has been ongoing in QEP since the early 1950s due to the presence of the Nuffield Unit of Tropical Animal Ecology, which operated until the early 90s, focusing on issues of large herbivore and vegetation interactions with a wildlife management perspective (Plumptre *et al.* 2010b). This research has provided the foundation for our understanding of megaherbivore ecology in Africa (Eltringham 1999;

Klingel 2008), and also has documented two critical natural experiments, (1) a controlled hippo cull between the 1950- 60s and (2) extensive elephant poaching in the 70s, which can be used to understand long-term ecological change in African savannas (Petrides & Swank 1965).

Throughout the park's history, the effects of three major ecosystem drivers have been identified: elephant browsing, hippo grazing, and fire (Plumptre *et al.* 2010a). The hippo population was particularly abundant in the 1960s, leading to overexploitation of grasslands and competitive exclusion of other grazing ungulates. Considering the high dietary needs of wild hippos, the effects of significant overgrazing on the grass community by hippos at their peak population of about 14,000 individuals in the park was considerable, leaving bare-ground in areas where they fed (Field 1970; Plumptre *et al.* 2010b). The controlled hippo population culls began in 1958, stimulating new grass growth in areas around Lake Edward, particularly the Mweya Peninsula, that had been decimated by intense overgrazing and trampling by hippos (Thornton 1971). Subsequently, grasslands flourished and herbivore community diversity recovered (Eltringham 1974).

In the 1960s and 70s, hippos were observed to feed predominately in grasslands on or near Mweya (i.e., within a few kilometers of Lake Edward) (Lock 1972) that were maintained by elephant browsing and fire (Field 1971; Dublin *et al.* 1990). Dominant grasses included *Sporobolus pyramidalis*, *Bothriochloa inscultpa, Chloris gayana*, *Themeda triandra* and *Hyparrhenia filipendula,* all C_4 grasses that grow in heavily grazed areas (Lock 1972; Strugnell & Pigott 1978). Trees and shrubs in small thickets occasionally clustered around emergent *Euphorbia candelabrum* (Strugnell & Pigott

1978), and elephants preferred to feed in unburnt areas with *Capparis tomentosa* (thicket) and tall-grass *S. pyramidalis* (Field & Laws 1970).

At the time of census in the mid-1970s, QEP had the highest large herbivore biomass (~20,000 kg/km^{-2}) on Earth (Field & Laws 1970; Coe *et al.* 1976). From 1972 to 1980, during the reign of Idi Amin, management of all national parks essentially ceased, and widespread poaching decimated herbivore populations (Muwanika *et al.* 2003; Aleper & Moe 2006). Herbivore and vegetation surveys conducted in the mid-1970s on the Mweya peninsula revealed that, at the time, herbivore biomass was still relatively high and *Hyparrhenia filipendula, Heteropogon contortus*, and *Bothriochloa insculpta* grasslands were still present. Intensification of poaching activities, resulting in collapsing herbivore populations and a genetic bottleneck event (Eltringham & Malpas 1980; Muwanika *et al.* 2003) and C_3 succession, occurred in the late 1970s (Yoaciel 1981). The population of elephants within the park fell from 4,139 to 150 individuals, and although hippo populations also contracted, they maintained genetic diversity during this poaching event, possibly due to influx of individuals from the DRC side of Lake Edward (Muwanika *et al.* 2003).

Heavy wildlife poaching continued into the mid-1980s (Muwanika *et al.* 2003), by which time there was a significant expansion in the size and number of thickets and trees (predominantly *Euphorbia candelabrum* and *Turraea robusta*) due to the declining elephant population (Field 1971; Wyatt & Eltringham 1974; Dublin *et al.* 1990; Lock 1993). Hippo feeding intensified around the Mweya Peninsula, as low-level poaching kept hippos away from inland wallows and close to Lake Edward (Lock 1993; Plumptre *et al.* 2010a). Hippo range restriction resulted in a positive-feedback for thicket encroachment: repeated trips onto land led to soil compaction, shunting rainwater into thickets and reducing fire fuel, further suppressing grass regrowth (Thornton 1971; Lock 1972; Eltringham 1974; Van Langevelde *et al.* 2003). The end result of these environmental changes was an increase in shrubs, trees, and thickets throughout much of the park, though most intensely around the Mweya Peninsula.

3.3. Materials and Methods

3.3.1 Sample collection and analysis

Lower hippo canines were sampled from individuals who died on the Mweya Peninsula within Queen Elizabeth National Park. Date of death was assigned using recorded death dates (if known) or through radiocarbon dating of tusk enamel (Uno *et al.* 2013). Calendar years for hippos tusk samples were assigned using two methods. The 1960-1970 tusk was dated using bomb-curve radiocarbon dating (Uno *et al.* 2013). The death years for the other two tusks were known – 1991 and 2000. Using an average hippo lower canine growth rate of 4.4 cm/yr from five wild hippo tusks measured with bomb radiocarbon by Uno (2013), the calendar years were estimated for each sample in the profile assuming a constant growth rate.

Samples of enamel were drilled at intervals along the length of the tusk using a diamond-tipped drill bit and Dremel tool. Enamel powders were treated with 2% H_2O_2 for 30 minutes to remove organics, then washed 3 times with distilled water. Enamel samples were reacted with 100% phosphoric acid in a common acid bath in a dual-inlet Carboflo carbonate device. Stable isotope ratios $^{13}C/^{12}C$ and $^{18}O/^{16}O$ of resulting CO_2 were analyzed on an MAT 252, and stable isotope ratios are reported as delta (δ) values relative to the international carbon isotope standard, Vienna Pee Dee Belemnite (VPDB), following the standard permil (‰) notation, where $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000$, and R_{sample} and $R_{standard}$. Enamel isotope values were corrected relative to an internal carbonate standard (Carrara marble) calibrated to VPBD and two in-house enamel standards. Dietary designations for hippos are given based on estimated dietary intake of C_4 plants (lowland tropical grasses) and C_3 plants (trees, shrubs, herbs). This is calculated using the isotope enrichment factor (ε*) between diet and herbivore tooth enamel of 14.1‰ (Cerling & Harris 1999), using the average isotopic value of modern C_3 and C_4 plants in eastern and central Africa (Cerling 2014; Cerling *et al.* 2015).

3.4. Results

Stable isotope analysis revealed significant differences (Kruskal-Wallis and Nemenyi *post-hoc* test, $P<0.05$) in the isotopic composition of tusk enamel among the three Mweya hippos (Table 3.1). The 1970 tusk reveals a diet of greater than 80% C_4 grass intake from *ca*. 1960 to 1970 (Figure 3.2 and Appendix B). The 1991 hippo profile is significantly more depleted in $\delta^{13}C$ than the 1970 profile, indicating a mixed C_3/C_4 diet (*ca*. 65% C_4) from 1982 to 1991, following collapse of the elephant population in Queen (Figure 3.2, Appendix B). The third tusk includes the time interval from 1985 to 2000 with an estimated diet ranging from *ca*. 55 to 70% C_4. Both the 1991 and 2000 individuals show local minima in $\delta^{13}C$ values for the *ca*. 1988–1989 interval. Previously published hippo molar enamel isotope values from the DRC side of Lake Edward during the 2000s and 1990s are similar those from serial samples in QEP, with 1990s DRC values ranging from -7 to -2‰, 2000s DRC values -7 to -1‰, though slightly more depleted than QEP values (Cerling *et al.* 2008).

3.5. Discussion

3.5.1 Hippos dietary change on the Mweya Peninsula, 1970–2000

Hippos have been characterized as selective C_4-grazers that feed on short grasses and sedges (which comprises 95-99% of their diet), supplemented by forbs (Owen-Smith 1992). This dietary classification was established by stomach content analysis done by Field (1970), conducted on hippos in QEP during the 1960s, when grasses were abundant. Bulk stable isotope analysis of hippo tooth enamel values from individuals across East Africa have already revealed the diversity of hippo diets from different localities (Boisserie *et al.* 2005; Cerling *et al.* 2008).

Changes in hippo diet within the Mweya Peninsula hippo population track changes in herbaceous groundcover on the peninsula. Environments where hippos are now abundant look strikingly different from those of the 1960s, where herbaceous groundcover on the Mweya Peninsula consisted predominately of grazing-tolerant C_4 grasses (Lock 1972; Strugnell & Pigott 1978). In surveys conducted in 1992 and 2009, Plumptre and others (2010) found that *Cynodon dactylon* (a C_4 grass), *Commelina diffusa*, *C. africana* (C_3 herbs), *Asystasia gangetica* (C_3 forb), *Cyanotis foecunda* (a C_3 flowering herb), *Achyranthes aspera* (C_3 herb), *Ocimum suaveolens* (C_3 herb), *Oplismenus hirtellus* (C_4 grass), and two *Cyperus* species have become dominant. Thus, hippos feeding areas from the 1960s have changed almost completely from C_4 grasses to predominantly C_3 herbaceous groundcover (Lenzi Grillini *et al.* 1996), which is reflected in hippo dietary isotopes. Hippo canine carbon isotopes record this herbaceous vegetation change within the Mweya Peninsula, and reveal the extent of encroaching C_3 herbaceous plants in the area. The expansion of nongrassy ground vegetation further restricts grazing capacity of the peninsula and decreases herbivore biodiversity and biomass.

3.5.2 Long-term effects of elephant poaching

The effects of elephant poaching in the park have caused a restructuring of QEP's ecology. Aerial photographs and photomosaic analysis of vegetation types within the park between 1950 and 2006 indicate an increase in woody cover of ~30% across QEP (Plumptre *et al.* 2010b). Civil war in the DRC in 1998 led to heavy poaching in Virunga National Park and other areas near QEP, resulting in herbivore migration to QEP and contributed to the partial recovery of herbivore communities, which may explain the delayed later succession of woody plants (Plumptre *et al.* 2007b). Although there is some lag time between early succession of woodlands and wooded grasslands in savannas, the effects of decreased vegetation maintenance by megaherbivores and fires have already resulted in bare-ground, scrubby/bushy environments where hippo feeding areas once were significant (Plumptre *et al.* 2010b). Elephant populations have been increasing in the park since 1990 (from ~500 to almost 3000 in 2005; Plumptre *et al.* 2010a) inhibiting only very recent woody cover encroachment in the park in some areas, but not in the Mweya peninsula (Plumptre *et al.* 2010a).

Our findings also reveal that hippos are not such selective feeders that they will only feed upon short grass, but can shift their diets to accommodate increased C_3 herbaceous groundcover when preferred grasses are no longer present. Therefore, hippos track herbaceous vegetation change, and carbon isotopic records from serially sampled hippos tusks may provide a much needed resource for investigating historical ecological change across tropical grassy biomes in Africa. This approach may also be useful for augmenting wildlife monitoring and management efforts of populations that are not being regularly studied due to conflict or cannot easily be observed.

3.5.3 Elephant poaching and the future of African savannas

Although the deleterious effects of human conflict and wildlife poaching as a mechanism for ecosystem destabilization are known, little has been studied on the long-term ecological effects of overharvesting on ground vegetation in savanna ecosystems (Dudley *et al.* 2002). Our findings demonstrate that in addition to bush encroachment (Prins & van der Jeugd 1993), elephant poaching results in C_3 encroachment in the herbaceous ground layer of savannas as well. Therefore, the long-term and wide-reaching effects of bush encroachment, such as changes in nutrient composition of soil, depleting %C, and %N in heavily encroached areas (Hudak *et al.* 2003), are further compounded by suppression of C_4 grass growth, a critical resource for numerous mesoherbivores in savanna ecosystems. The combined effects of bush and herbaceous encroachment forces certain herbivores outside of protected areas, compromising management and conservation efforts. The combined effects of bush encroachment, which has already occurred in many places in Africa (Scholes & Archer 1997; Roques *et al.* 2001; Ward 2005; Wiegand *et al.* 2005), and elephant poaching, which is occurring at unprecedented rates (Wittemyer *et al.* 2014), are likely to further exacerbate habitat degradation and suppress populations of grazing herbivores. Further characterization of herbaceous vegetation change in protected areas may be useful for understanding the rate of C_3 encroachment and to devise management strategies for African savanna parks in a changing global environment.

3.6. Conclusions

These isotopic data highlight the flexible nature of hippopotamus diets within populations over time, and show that hippos are able to adjust their diets after a major ecological shift. Decreasing elephant populations around Africa should not negatively inhibit hippo populations because hippos can adapt to the widespread changes in herbaceous vegetation. Hippos are key ecological engineers, consuming and spreading nutrients on land and transforming soil properties and landscapes that increase environmental heterogeneity. Hippo canine profiles can preserve a 10-year, or longer, record of diet history. As such, serial samples in hippo canines are long-term records of African ecology. In Queen Elizabeth Park, Uganda, these isotope records of hippo enamel indicate changes in C_3-vegetation, not only in woody vegetation as a result of elephant culling, but also in herbaceous vegetation layers. These data are critical for wildlife management within African savanna parks, as increasing C_3 vegetation in both woody and herbaceous layers of savanna parks decreases grazing capacity for grass-feeding herbivores. This outcome may result in pushing grazers outside of protected areas, posing serious threats for conservation in Africa.

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3.8. References

1. Aleper, D. & Moe, S.R. (2006). The African savannah elephant population in Kidepo Valley National Park, Uganda: changes in size and structure from 1967 to 2000. *African Journal of Ecology*, 44, 157–164.

2. Ambrose, S.H. & DeNiro, M.J. (1986). The isotopic ecology of East African mammals. *Oecologia*, 69, 395–406.

3. Arsenault, R. & Owen Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. *Oikos*, 97, 313–318.

4. Asner, G.P. & Levick, S.R. (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters*, 15, 1211–1217.

5. Barnes, M. (2001). Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. *African Journal of Ecology*.

6. Beuchner, H. & Dawkins, H. (1961). Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology*, 42, 752–766.

7. Blumenthal, S.A., Chritz, K.L., Rothberg, J. & Cerling, T.E. (2012). Detecting intraannual dietary variability in wild mountain gorillas by stable isotope analysis of feces. *Proceedings of the National Academy of Science*, 109, 21277–21282.

8. Boisserie, J.R., Zazzo, A., Merceron, G., Blondel, C., Vignaud, P., Likius, A., *et al.* (2005). Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 221, 153–174.

9. Boutton, T., Arshad, M.A. & Tieszen, L.L. (1983). Stable isotope analysis of termite food habits in East African grasslands. *Oecologia*, 59, 1–6.

10. Cerling, T.E. (2014). 14.12 Stable Isotope Evidence for Hominin Environments in Africa. *Treatise on Geochemistry*. 2nd edn. Elsevier Ltd.

11. Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., *et al.* (2015). Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proceedings of the National Academy of Sciences*, 112, 11467-11472.

12. Cerling, T.E. & Harris, J.M. (1999). Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia*, 120, 347–363.

13. Cerling, T.E., Chritz, K.L., Jablonski, N.G., Leakey, M.G. & Manthi, F.K. (2013). Diet of *Theropithecus* from 4 to 1 Ma in Kenya. *Proceedings of the National Academy of Sciences*, 110, 10507–10512.

14. Cerling, T.E., Harris, J.M. & Passey, B.H. (2003). Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy*, 84, 456–470.

15. Cerling, T.E., Harris, J.M., Hart, J.A., Kaleme, P., Klingel, H., Leakey, M.G., *et al.* (2008). Stable isotope ecology of the common hippopotamus. *Journal of Zoology*, 276, 204–212.

16. Cerling, T.E., Harris, J.M., Leakey, M. & Mudida, N. (2003). Stable isotope ecology of northern Kenya with emphasis on the Turkana Basin. *Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York*, 583–603.

17. Cerling, T.E., Harris, J.M., Passey, B.H., Ayliffe, L., Cook, C., Ehleringer, J., *et al.* (2004). Orphans' tales: seasonal dietary changes in elephants from Tsavo National Park, Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 206, 367–376.

18. Cerling, T.E., Wittemyer, G., Rasmussen, H.B., Vollrath, F., Cerling, C.E., Robinson, T.J., *et al.* (2005). Stable isotopes in elephant hair document migration patterns and diet changes. *Proceedings of the National Academy of Sciences*, 103, 371–373.

19. Clauss, M., Schwarm, A., Ortmann, S., Alber, D., Flach, E.J., Kühne, R., *et al.* (2004). Intake, ingesta retention, particle size distribution and digestibility in the hippopotamidae. *Comparative Biochemistry and Physiology-Part A: Molecular & Integrative Physiology*, 139, 449–459.

20. Coe, M.J., Cumming, D.H. & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, 22, 341–354.

21. Dublin, H.T. (1986). Decline of the Mara woodlands: The role of fire and elephants. PhD Dissertation, University of British Columbia.

22. Dublin, H.T., Sinclair, A. & McGlade, J. (1990). Elephants and Fire as Causes of Multiple Stable States in the Serengeti-Mara Woodlands. *Journal of Animal Ecology*, 59, 1147–1164.

23. Dudley, J.P., Ginsberg, J.R., Plumptre, A.J., Hart, J.A. & Campos, L.C. (2002). Effects of War and Civil Strife on Wildlife and Wildlife Habitats. *Conservation Biology*, 16, 319–329.

24. Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, 6, 680–687.

25. Eltringham, S.K. (1974). Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus. *Journal of Applied Ecology*, 11, 855.

26. Eltringham, S.K. (1999). *The Hippos: Natural History and Conservation*. Academic Press, London.

27. Eltringham, S.K. & Malpas, R.C. (1980). The decline in elephant numbers in Rwenzori and Kabalega Falls National Parks, Uganda. *African Journal of Ecology*, 18, 73–86.

28. Field, C.R. (1970). A study of the feeding habits of the hippopotamus (*Hippopotamus amphibius* Linn.) in the Queen Elizabeth National Park, Uganda, with some management implications, *Zoologica Africana*, 5, 71–86.

29. Field, C.R. (1971). Elephant ecology in the Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, 9, 99–123.

30. Field, C.R. (1972). The food habits of wild ungulates in Uganda by analyses of stomach contents. *African Journal of Ecology*, 10, 17–42.

31. Field, C.R. & Laws, R.M. (1970). The distribution of the larger herbivores in the Queen Elizabeth National Park, Uganda. *Journal of Applied Ecology*, 7, 273–294.

32. Fritz, H., Duncan, P., Gordon, I.J. & Illius, A.W. (2002). Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620–625.

33. Harris, J.M. & Cerling, T.E. (2002). Dietary adaptations of extant and Neogene African suids. *Journal of Zoology*, 256, 45–54.

34. Harris, J.M., Cerling, T.E., Leakey, M.G. & Passey, B.H. (2008). Stable isotope ecology of fossil hippopotamids from the Lake Turkana Basin of East Africa. *Journal of Zoology*, 275, 323–331.

35. Hudak, A.T., Wessman, C.A. & Seastedt, T.R. (2003). Woody overstorey effects on soil carbon and nitrogen pools in South African savanna. *Austral Ecology*, 28, 173–181.

36. Klingel, H. (2008). Das Flusspferd. In: *Wilde Schweine und Flusspferde* (eds. Macdonald, A.A. & Gansloßer, U.). pp. 353–370.

37. Klingel, H. (2013). *Hippopotamus*. In: *Mammals of Africa* (eds. Kingdon, J. & Hoffmann, M.). London, pp. 68–78.

38. Koch, P.L., Cruz-Uribe, K. & Fogel, M.L. (1990). The isotopic ecology of plants and animals in Amboseli National Park, Kenya. *Annual Report to the Director*.

39. Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, 79, 1401–1409.

40. Laws, R. (1968). Dentition and ageing of the hippopotamus. *African Journal of Ecology*, 6, 19–52.

41. Lee-Thorp, J.A. & Van der Merwe, N.J. (1987). Carbon isotope analysis of fossil bone apatite. *South African Journal of Science*, 83, 712–715.

42. Lenzi Grillini, C.R., Viskanic, P. & Mapesa, M. (1996). Effects of 20 years of grazing exclusion in an area of the Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, 34, 333–341.

43. Lock, J. (1993). Vegetation change in Queen Elizabeth National Park, Uganda: 1970–1988. *African Journal of Ecology*, 31, 106–117.

44. Lock, J.M. (1972). The effects of hippopotamus grazing on grasslands. *The Journal of Ecology*, 60, 445–467.

45. Muwanika, V.B., Siegismund, H.R., Okello, J.B.A., Masembe, C., Arctander, P. & Nyakaana, S. (2003). A recent bottleneck in the warthog and elephant populations of Queen Elizabeth National Park, revealed by a comparative study of four mammalian species in Uganda national parks. *Animal Conservation*, 6, 237–245.

46. Naughton-Treves, L. & Treves, A. (2005). Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. In: People and Wildlife: Conflict or Coexistence? (eds) Woodroffem R., Thirgood, S. & Rabinowitz, A. pp. 252–277.

47. Nyirenda, V.R. & Chansa, W.C. (2011). Wildlife crop depredation in the Luangwa Valley, eastern Zambia. *Journal of Ecology and the Natural Environment*, 3, 481–491.

49. Oelze, V.M., Head, J.S., Robbins, M.M., Richards, M. & Boesch, C. (2014). Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis. *Journal of Human Evolution*, 66, 95–106.

50. Olivier, R. (1991). *Elephant Conservation Plan for Uganda*. Uganda National Parks.

51. Owen-Smith, R.N. (1992). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press.

52. Passey, B.H., Cerling, T.E., Schuster, G.T., Robinson, T.F., Roeder, B.L., Krueger, S.K. (2005). Inverse methods for estimating primary input signals from time-averaged isotope profiles. *Geochimica et Cosmochimica Acta*, 69, 4101–4116.

53. Petrides, G.A. & Swank, W.G. (1965). Population densities and the range-carrying capacity for large mammals in Queen Elizabeth National Park, Uganda, 1, 209–225.

54. Plumptre, A.J., Davenport, T., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., *et al.* (2007a). The biodiversity of the Albertine Rift. *Biological Conservation*, 134, 178–194.

55. Plumptre, A.J., Kirunda, B., Mugabe, H., Stabach, J., Driciru, M., Picton-Phillipps, G., *et al.* (2010a). *The Impact of Fire and Large Mammals on the Ecology of Queen Elizabeth National Park*. Wildlife Conservation Society and Woods Hole Research Centre.

56. Plumptre, A.J., Kujirakwinja, D., Treves, A., Owiunji, I. & Rainer, H. (2007b). Transboundary conservation in the greater Virunga landscape: its importance for landscape species. *Biological Conservation* 134, 279–287.

57. Plumptre, A.J., Pomeroy, D., Stabach, J., Laporte, N., Driciru, M., Nangendo, G., *et al.* (2010b). The effects of environmental and anthropogenic changes on the Savannas of the Queen Elizabeth and Virunga National parks. In: The Ecological Impact of Long-Term Changes in Africa's Rift Valley (ed. Plumptre, A.J.). Nova Publishers, pp. 88–105.

58. Prins, H. & van der Jeugd, H.P. (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*, 81, 305–314.

59. Roques, K.G., O'connor, T.G. & Watkinson, A.R. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38, 268–280.

60. Scholes, R. & Archer, S. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 517–544.

61. Schwarm, A., Ortmann, S., Hofer, H., Streich, W., Flach, E., Kühne, R., *et al.* (2006). Digestion studies in captive Hippopotamidae: a group of large ungulates with an unusually low metabolic rate. *Journal of Animal Physiology and Animal Nutrition*, 90, 300–308.

62. Strugnell, R.G. & Pigott, C.D. (1978). Biomass, shoot-production and grazing of two grasslands in the Rwenzori National Park, Uganda. *The Journal of Ecology*, 66, 73–96.

63. Thornton, D.D. (1971). The effect of the complete removal of *Hippopotamus* on grassland in the Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, 9, 47–55.

64. Uno, K.T., Quade, J., Fisher, D.C., Wittemyer, G., Douglas-Hamilton, I., Andanje, S. *et al.* (2013). Bomb-curve radiocarbon measurement of recent biologic tissues and applications to wildlife forensics and stable isotope (paleo) ecology. *Proceedings of the National Academy of Science*, 110, 11736–11741.

65. Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D., Duncan, P. (2011). Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation,* 144, 902–912.

66. Van Der Merwe, N.J. (2013). Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. *South African Journal of Science*, 109, 14 Pages.

67. Van Langevelde, F., Bond, W.J., Van De Vijver, C.A.D.M., Kumar, L., Van De Koppel, J., De Ridder, N., *et al.* (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84, 337–350.

68. Vesey-FitzGerald, D.F. (1960). Grazing succession among East African game animals. *Journal of Mammalogy*, 41, 161–172.

69. Ward, D. (2005). Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science*, 22, 101–105.

70. Weladji, R.B. & Tchamba, M.N. (2003). Conflict between people and protected areas within the Bénoué Wildlife Conservation Area, North Cameroon. *Oryx*, 37, 72–79.

71. Wiegand, K., Ward, D. & Saltz, D. (2005). Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. *Journal of Vegetation Science*, 16, 311–320.

72. Wittemyer, G., Northrup, J.M., Blanc, J., Douglas-Hamilton, I., Omondi, P. & Burnham, K.P. (2014). Illegal killing for ivory drives global decline in African elephants. *Proceedings of the National Academy of Sciences*, 111, 13117–13121.

73. Wyatt, J.R. & Eltringham, S.K. (1974). The daily activity of the elephant in the Rwenzori National Park, Uganda. *African Journal of Ecology*, 12, 273–289.

74. Yoaciel, S.M. (1981). Changes in the populations of large herbivores and in the vegetation community in Mweya Peninsula, Rwenzori National Park, Uganda. *African Journal of Ecology*, 19, 303–312.

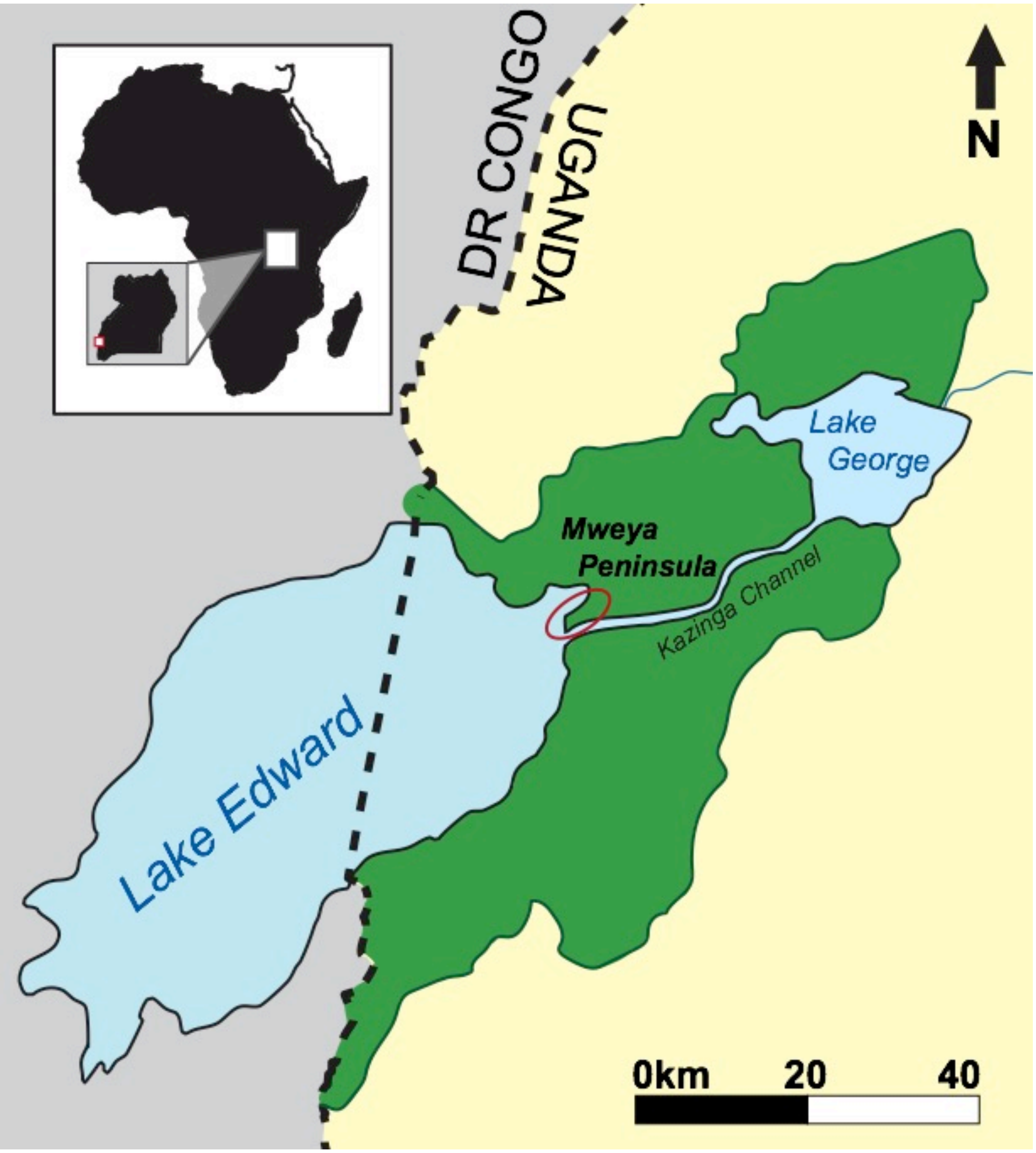

Figure 3.1: Map of Queen Elizabeth Park, Uganda. The red circle highlights the Mweya Peninsula.

Table 3.1: δ^{13}C values (mean and range) for the three hippo canines. *P*-values from Kruskal-Wallis with Tukey and Kramer (Nemenyi) post-hoc test (executed in R) verify that the three hippos have distinctive feeding niches.

ID	**Length (cm)**	**Death Year**	**Method**	**δ^{13}C mean**	**δ^{13}C range**	***P*-value (vs. 1970)**	***P*-value (vs. 1991)**	***P*-value (vs. 2000)**
KL	37	1970	^{14}C	-0.1	-2.0	-	<0.0001	<0.0001
Queen VIC	35.5	1991	known	-3.3	-2.5	<0.0001	-	<0.01
Q-09-KL	66.5	2000	known	-3.0	-2.5	<0.0001	<0.0001	-

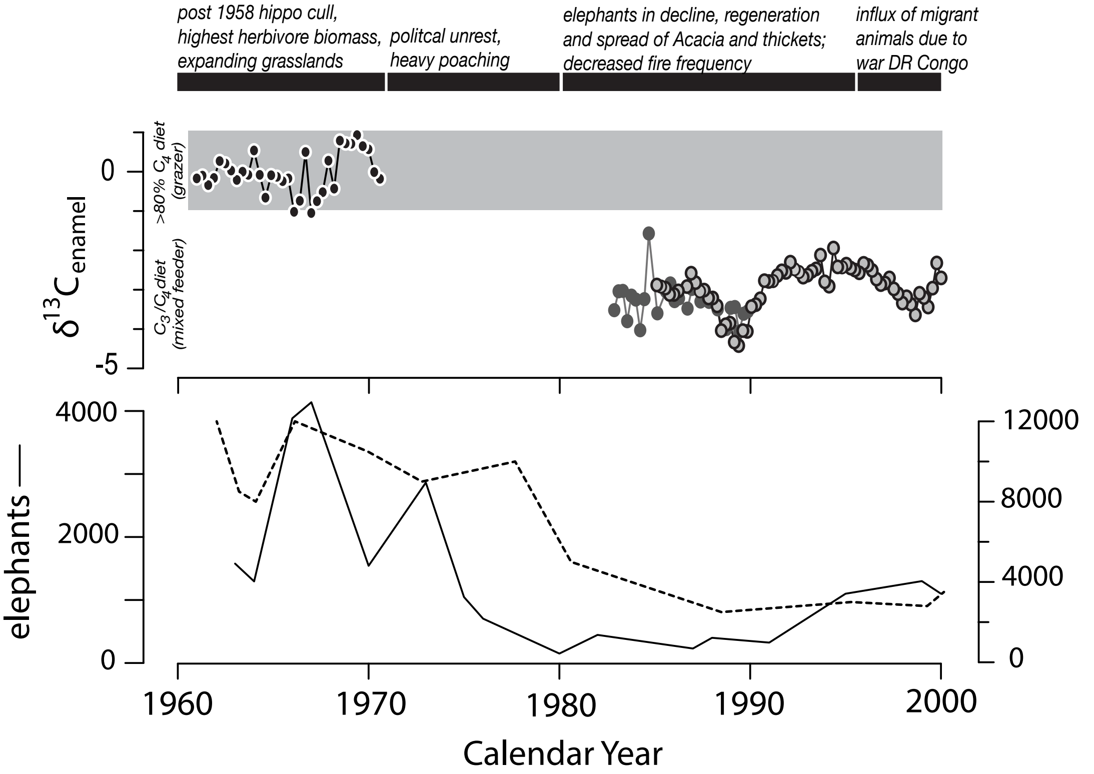

Figure 3.2: Carbon isotope profiles of the three Queen Elizabth hippo serial samples (1970 tusk in black, 1991 tusk in dark grey, 2000 tusk in light grey) and number of hippos (dotted line) and elephants (solid line) present in the park over time (Olivier 1991; Plumptre *et al.* 2010a). The chronolgy of major ecological and political events is listed above the graph.

CHAPTER 4

HOLOCENE PALEOENVIRONMENT IN KENYA, WITH PERSPECTIVES ON HOLOCENE ARCHAEOLOGY AND PLEISTOCENE ENVIRONMENTAL CHANGE

4.1 Abstract

Paleoenvironmental research in East Africa has long relied on the relationship between orbital forcing, regional climate, and vegetation response to reconstruct regional paleoecology, yet the connections between these three factors remains poorly understood. An interbasinal reconstruction (northern Lake Turkana and southwestern Lake Victoria) of Holocene paleoecology in Kenya may clarify these relationships. Previous climatological studies indicate that Lake Turkana responded abruptly to a weakening monsoon system at the end of the African Humid period (5.5 kya), forced by decreasing solar insolation (deMenocal et al., 2000; Garcin et al., 2012), whereas Lake Victoria responded more gradually to orbital forcing, as indicated by δD_{wax} values (Berke et al., 2012a). Tooth enamel stable isotope records from Turkana also indicate a change in the diet of herbivores in the Turkana Basin with increasing C_3 dietary components. Comparisons of early Holocene tooth enamel and leaf wax biomarker data reveal contrasting environments in Turkana, wherein herbivore diets include an abundance of C_4 resources, but leaf waxes indicate fluctuating C_3-C_4 input to the sedimentary record. In the Lake Victoria Basin, both $\delta^{13}C_{wax}$ values and tooth enamel dietary isotopes indicate

an abundance of C_4 resources in the basin throughout the Holocene. This is in contrast to the pollen record, which indicates high (~40%) Moraceae (mesic tree) presence in the early Holocene, which decreases until present, and low (~10%) Poaceae (grass) pollen, which increases until present. These contrasting paleoecological records highlight disagreements noted in other studies (Feakins et al., 2013; Levin, 2015), calling for re-evaluation of either pollen or leaf wax records, and how they may relate to carbonate proxies of paleoenvironment. Furthermore, these data do not support a uniform shift in ecology across Kenya, in accordance with insolation forcing, indicating that regional responses to orbital forcing must be assessed basin-by-basin. Finally, these data indicate that the same environmental factors which may have influenced the appearance of early herders in the Turkana Basin (i.e., abrupt climatological change and potentially ecological change) was not a factor in the Lake Victoria Basin, as gradual climate change did not result in abrupt, or even significant, ecological changes.

4.2 Introduction

4.2.1 Paleoecology and Holocene orbital forcing in East Africa

Much research has been dedicated to understanding the relationships between climate and ecology in East Africa; specifically, what controls the distribution of woody and non-woody vegetation in modern (Coughenour and Ellis, 1993; Good and Caylor, 2011; Mills et al., 2012; Ratnam et al., 2011; Sankaran et al., 2005; Scholes and Archer, 1997), future (Bond and Midgley, 2000; Buitenwerf et al., 2012; Cramer et al., 2001; Moncrieff et al., 2013; Murphy and Bowman, 2012), and past environments (Berke et al., 2012a; deMenocal, 2011; Sinninghe Damsté et al., 2011; Willis et al., 2013). Establishing the connection between orbital forcing, climate change, and ecological response in the geologic record has been central to this research (Ashley, 2007; Kingston, 2007; Kutzbach et al., 1996; Magill et al., 2013a; 2013b; J. D. Marshall et al., 2007; Maslin and Christensen, 2007; Verschuren et al., 2009). Many causal connections linking climate to ecology in African environments are missing and/or poorly understood (deMenocal, 2014; Kingston, 2007; Levin, 2015; Potts, 2013). Researchers have identified Holocene paleoenvironment as the key to understanding the connection between orbitally forced climate and ecology in East Africa (deMenocal et al., 2000; Gasse, 2000; Mayewski et al., 2004; Renssen et al., 2003; Tierney et al., 2011a). The early Holocene was a time of high insolation forcing, with evidence for high humidity and a stronger monsoon system across many parts of Africa, called the “African Humid Period” (“AHP”) (deMenocal et al., 2000; Tierney et al., 2011b). This event terminated sometime around 5.5 kya, forced by decreasing insolation and a weakening regional monsoon.

Despite the abundance of climate records and modeling studies that have illuminated the nature of Holocene orbital forcing and terrestrial climate, associated ecological records for this time period are lacking. This is especially true in Kenya, where the anthropological and archaeological record is one of the richest in Africa. Studies linking changes in Holocene climate and ecology have revealed interbasinal differences in lacustrine records and have illuminated the complex ways in which ecology and environmental forcing are linked (Berke et al., 2012a; 2012b; Castañeda et al., 2009; Costa et al., 2014; Vincens et al., 2010). Currently, though, less attention has been given to records of ecology from these basins, and whether vegetation proxies indicate changes associated with climate dynamics during this time period. Such data would allow researchers to better interpret records of ecology from deeper time periods, and gain insight into the ways in which vegetation dynamics in East Africa relate to orbital forcing on a regional scale.

4.2.2 Holocene archaeology and paleoenvironment

The Holocene archaeological record documents the transition from foraging to food production, a fundamental shift in subsistence economy that is among the most significant cultural adaptations in human history. African food production began and spread in unusual ways: herding (i.e., keeping domestic animals without sole reliance on livestock for subsistence) preceded plant cultivation in many parts of Africa, whereas farming was the first form of food production in most parts of the world (Marshall and Hildebrand, 2002). Herding originated in the eastern Sahara around ~9,000 BP and spread through varied environments, reaching the southern tip of Africa seven millennia later. Herding spread into NW Kenya's Turkana Basin around 4.5 ka (Barthelme, 1985), shortly after the termination of the AHP. The use of domestic livestock is not seen in the Central Rift, approximately 500 km south, until ~3 ka (Ambrose, 1998; Gifford-Gonzalez, 2000). Early herding in Kenya, particularly around Lake Turkana, coincides with social and cultural changes, such as construction of megalithic architecture and production of Nderit Ware, a distinctive and previously unknown pottery (Bower, 1991; Grillo and Hildebrand, 2013; Hildebrand et al., 2011).

People may have begun herding in response to shifting climatic conditions that made it advantageous to guide animals to optimal environments and water sources (Marshall, 1990; Owen and Renaut, 1986; Smith, 1992). Many authors have suggested that changing climatic conditions may have been responsible, directly or indirectly, for the spread of herding as insolation-induced mesic conditions during the early Holocene

(11.7-8.2 ka; following Holocene formal stratigraphic designations of Walker et al., 2012) gave way to changing climates during the middle Holocene (8.2-4.2 ka) and more arid climate regimes during the late Holocene (4.2 ka-present) in many parts of eastern Africa (deMenocal et al., 2000; Tierney et al., 2011b; Walker et al., 2012). For example, early herding around Lake Turkana (the lower portions of the Turkana Basin, Figure 4.1) coincides with a sharp decrease in regional humidity (Owen et al., 1982), as indicated by the position of paleo-lake terraces (Garcin et al., 2012). In contrast, the Victoria Basin (or more specifically, the Winam Gulf area, Figure 4.1) sees livestock slightly later, *c.* 3.5 ka, and leaf wax deuterium isotopes indicate a more gradual decrease in humidity, in contrast to abrupt climatological changes in the Turkana Basin (Berke et al., 2012a; Prendergast, 2010).

Although there is a general chronological association between the end of the AHP and the southward spread of herding, connections between changes in climate, terrestrial ecology, and human behavior are complex and often not synchronous between basins (Blome et al., 2012; Tierney et al., 2011a). Establishing causal links between regional climate change and the spread of herding is complicated due to issues of resolution and interpretation of archaeological and paleoenvironmental datasets, and also due to dilemmas over whether chronological correlations imply causal association. Empirical records for terrestrial paleoecological conditions directly associated with archaeological material are surprisingly limited. Paleoecological data from stable isotopes can shed light on changes in the distribution of woody cover, an important determinant of overall ecosystem structure in the tropics (see Chapter 2 for a thorough description of woody cover and African ecosystem classification). Woody cover distribution is influenced by mean annual precipitation and seasonal distribution of rainfall, which, in turn, affect plant and herbivore biomass (Bell, 1982; Good and Caylor, 2011; Murphy and Lugo, 1986; Scholes and Archer, 1997). Because of these complicated environmental relationships, inferring ecosystem change from regional climate data is insufficient and limits our understanding of the ecosystems in which early herders lived, either by choice or circumstance.

Three possible predictions for paleoecological changes through the Holocene include: 1) C_3 plant dominance during the later Holocene due to rainfall seasonality and anthropogenic influences, such as amplified prevalence of grazing animals after 5 Ka (Sankaran et al., 2005); 2) increased warm season rainfall in the early Holocene causing C_4 grasses to out-compete C_3 woody plants prior to 5 Ka; 3) the system may also oscillate between more C_3 and C_4 during high insolation periods, as there may be a destabilizing effect of rainfall excess on savanna ecosystem structure (Sankaran et al., 2005). Furthermore, floral change seen in northern localities may represent a local pattern distinct from the more southerly localities, and manifest sooner and more abruptly, because changes in insolation are dampened at lower latitudes (Laskar et al., 2004). Comparing paleoecological proxies for C_3 and C_4 cover from archaeological sites in NW Kenya (Turkana) and SW Kenya (Victoria) will evaluate these regional differences and provide insight into the distinctive archaeological records of early food producers from these basins.

This chapter will take a multiproxy approach to paleoecology by combining isotopic data from archaeological mammalian herbivore teeth, lacustrine leaf wax biomarkers, and pollen to understanding how basinal-scale vegetation dynamics relate to climate forcing. This approach will help account for differences in spatial and temporal integration between these two proxies, and will provide a deeper, more nuanced understanding of the relationship between climate and vegetation change in East Africa. Records will be explored in two lake basins with two distinctive archaeological histories for early herding in eastern Africa. These lake basins exhibited differing responses to Holocene climate forcing: the Lake Turkana Basin responded abruptly to termination of the AHP (deMenocal et al., 2000; Garcin et al., 2007) and the Lake Victoria Basin responded more gradually to the termination of the AHP (Berke et al., 2012a). Resulting data will indicate what environmental changes, if any, occurred at Holocene archaeological sites in Kenya within the context of solar forcing and changing climate dynamics (Claussen et al., 1999; deMenocal et al., 2000; Garcin et al., 2012; Murphy and Lugo, 1986; Stager et al., 2003).

4.3 Study Design and Location

4.3.1 Study design

Understanding how ecosystems changed over time is assisted by $\delta^{13}C$ analysis of herbivorous mammalian tooth enamel as a proxy for changes in local plant biomass and animal behavior. Tooth enamel samples taken via identical sampling strategies from similar taxa found at Holocene archaeological sites in Lake Turkana and Lake Victoria are analyzed for $\delta^{13}C$ and $\delta^{18}O$. Isotope data from archaeological specimens are compared to previously published modern values (Cerling et al., 2008; Kohn et al., 1996; 1998; Levin et al., 2006; Schoeninger et al., 2002; Cerling et al., 2015), leaf wax biomarkers for Lake Turkana (this study), and Lake Victoria (Berke et al., 2012b) in order to assess how site-specific ecology relates to basinal scale records. Three-hundred thirty-three tooth enamel samples were analyzed (93 from six Turkana sites, 49 from Ele Bor, and 189 from three Lake Victoria sites) to answer these questions (Figure 4.2), generating a dataset that substantially exceeds previous Holocene isotope studies in eastern Africa (Ambrose and DeNiro, 1989; Ambrose and Sikes, 1991; Balasse and Ambrose, 2005a). $\delta^{13}C$ data from enamel and leaf wax biomarkers provide direct isotopic information relating herbivore ecology and terrestrial ecosystem structure, respectively, to orbitally-mediated climate change. In particular, herbivore fossil enamel isotopes are useful for interpreting local, terrestrial ecological changes associated with calculated insolation and evaluating inferred changes in monsoon strength based on previously published records of lake levels, sedimentary biomarkers, and aridity. These data are key for understanding the local manifestations of changing monsoon strength across basins and provide quantitative data for ecological changes that occurred before, during, and after the spread of herding throughout Kenya.

4.4 Materials and Methods

4.4.1 Archaeological tooth enamel

Teeth from archaeological sites in Lake Turkana (including the site of Ele Bor, as somewhat higher elevation, ~800 m a.s.l.) and Lake Victoria (primarily from the Winam Gulf) were sampled for $\delta^{13}C$ and $\delta^{18}O$ from collections in National Museum of Kenya (NMK). A new Turkana site was found (“Equid Site”) and existing collections were supplemented by field collected specimens during survey with the Later Prehistory of West Turkana project led by Drs. Elisabeth Hildebrand and John Shea (Stony Brook University). Samples from Ele Bor (Site M), 200 km east of Lake Turkana, were drilled from collections stored in the NMK**.** Samples were photographed and drilled with a diamond tipped drill bit using a Dremel tool and stored in 1.7 ml centrifuge tubes following destructive sampling procedures outlined by the National Museums of Kenya.

Samples were prepared for isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) at the University of Utah. Archaeological enamel prep involves treatment of samples (1-0.5mg enamel) with a weak acid (0.1M buffered acetic acid) to for 30 minutes remove labile carbonates, weighed into silver capsules and dried under vacuum at 200 °C before digestion in a common phosphoric acid bath at 90 °C for 15 minutes. Samples were analyzed for $\delta^{13}C$ and $\delta^{18}O$ on a Finnigan MAT 252 coupled to a Carboflo dual-inlet carbonate device (common phosphoric acid bath at 90°C for 15 minutes reaction time). Stable isotope ratios are reported as delta (δ) values relative to the international carbon isotope standard, Vienna Pee Dee Belemnite (VPDB), using the standard permil (‰) notation, where $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000$, and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the sample and standard, respectively. Standard deviation of an internal standards (Carrara marble, MHS, FRS) was between +/- 0.1 to 0.2‰. Modern samples were corrected to MHS and fossil samples to FRS for the temperature effect for phosphoric acid digestion of tooth enamel (Passey et al., 2007).

Dietary designations for herbivores are based on estimated consumption of C_4 plants (tropical grasses) and C_3 plants (trees, shrubs, herbs), which is calculated using a hypothetical 100% C_4 diet and an isotope enrichment (ε*) between diet and herbivore tooth enamel of 14.1‰ (Cerling and Harris, 1999). Estimated carbon isotope composition of tooth enamel for a 100% C_4 diet is based on the average isotopic value of modern C_4 plants in eastern and central Africa (-12.9‰, n = 764) (Cerling, 2014). Changes in the isotopic composition of atmospheric CO_2 due to the combustion of fossil fuels between modern environments and pre-industrial Holocene (presented here as $\delta^{13}C_{1750}$) were accounted for by adding 1.6‰ to the modern average $\delta^{13}C$ of C_4 plants (Cerling and Harris, 1999; Francey et al., 1999; Keeling et al., 2010).

4.4.2 Sedimentary leaf wax biomarkers

Early Holocene lacustrine sediments were collected from Area 103 near Lake Turkana (Figure 4.1) in 2011. Stratigraphic correlation to previous maps of these deposits (Owen and Renaut, 1986) provides ages for the sediments (11.5 - 5.8 Kya, dates from mollusk shells *in situ*). Compound specific isotope analysis (CSIA) was completed at the Pennsylvania State University.

Eighteen leaf wax biomarker samples were extracted using an Automated Solvent Extractor in 9:1 DCM:Methanol, purified by column chromatography. The resultant polar fraction containing *n*-alkanoic acids were derivitized into fatty acid methyl esthers (FAMEs) for isotope analysis using a phthalic acid standard (Arndt Schimmelmann, U. Indiana) with a known $\delta^{13}C$ value of -73.16‰. $\delta^{13}C$ values of FAMEs were corrected to their original carbon isotopic value after methylization using a mass-balance correction of the derivitization standard. Percent C_4 input was calculated using endmember values from previously published values (-22 to -34‰) (Castañeda et al., 2009; Magill et al., 2013a).

4.5. Results

4.5.1 Lake Victoria Basin tooth enamel isotopes

Data from herbivores analyzed from archaeological sites in the Lake Victoria Basin are presented in Table 4.1 and graphically in Figure 4.3. Stable isotopes from modern comparative tooth enamel are presented as $\delta^{13}C_{1750}$ values from SW Kenya and northern Tanzania – within the Lake Victoria Basin or the greater Loita-Mara-Serengeti ecosystem, where possible. Detailed analysis of the Gogo Falls fauna is presented elsewhere (Chritz et al., 2015).

4.5.1.1. Luanda

Isotopes from tooth enamel in the early Holocene site of Luanda (9.7 – 8.5 Kya) reveal that the diets of herbivores from this site indicate that the diets of these animals were predominately dominated by C_4 resources. The exceptions are hippos (-4.2‰ ± 1.6) and bushpigs (*Potamochoerus sp.* -10.2‰ ± 2.4), which both exhibit isotope values that indicate mixed C_3/C_4 diets, but both of which are within the range of isotope values seen in these animals in modern environments.

4.5.1.2. Wadh Lang'o

Tooth enamel isotopes from herbivores at this site exhibit dietary isotopes that are all almost entirely >80% C_4. These isotope values are very similar to their modern counterparts. Interestingly, Caprini (Subfamily Caprinae; domestic sheep and goats) indicate an entirely grazing diet. This tribe includes both sheep and goats, which in modern environments are separated in dietary space into grazers (sheep) and browsers/mixed feeders (goats) (Balasse and Ambrose, 2005b; Chritz et al., 2015).

4.5.2 Lake Turkana Basin tooth enamel isotopes

Data from herbivores analyzed from archaeological sites in the Lake Turkana Basin are presented in Table 4.2 and graphically in Figure 4.4. Stable isotopes from modern comparative tooth enamel are presented as $\delta^{13}C_{1750}$ values from Turkana, from collections stored at the Turkana Basin Institute and the National Museums of Kenya's

Koobi Fora field station, and also field collected specimens.

4.5.2.1. Early Holocene sites – GaJj11, FxJj12, "Equid Site"

Isotopic data from these sites were combined due to low densities of faunal remains from these sites. All taxa analyzed for isotopes indicate diets that are primarily C_4, and all species are quite similar to their modern counterparts.

4.5.2.2. Lothagam Harpoon Site

Data from mammals at this site indicate an abundance of C_4 resources in their diet. The exception to this is an analysis of a single baboon molar (*Papio anubis*), which yields an isotope value of -6.9‰. This is more enriched than modern Turkana baboons (-10.9‰), indicating more C_4 resources in the mid-Holocene specimen, though it is still a mixed feeder.

4.5.2.3. Dongodien, GaJj2

Stable carbon isotope analysis from the abundant faunal remains at these two later Holocene pastoralist sites reveals an interesting departure from the dietary isotopes of fauna from the previous sites. Isotopes of the majority of these taxa (6/10) indicate primarily mixed C_3/C_4 feeding (<80% C_4). Looking to ecologically flexible taxa, such as Aepycerotini (impala, -7.16%), Hippopotamus (-1.55% ± 1.77), and Antilopini (gazelles, -3.24% ± 0.98), there appears to be more C_3 resources. Likewise, domestic caprines are also within the mixed C_3/C_4 dietary realm (-4.01% ± 2.33). Faunal analysis of domestic taxa from this site indicates that both sheep and goats were present (Marshall 1984), which makes these mostly mixed feeding results for both species even more intriguing.

4.5.3 Lake Turkana Basin leaf wax biomarkers

Stable carbon isotopes from leaf wax biomarkers for early Holocene deposits indicate varying inputs from C_3 and C_4 plants to the sedimentary column during the early Holocene (11.1 – 7.4 Kya, Figure 4.5). These data indicate $\%C_4$ input to range from 72% to 48% over this time period, with isotope values that are comparable to other Holocene lacustrine records in terms of range in isotopic values (Costa et al., 2014). These data reveal apparent shifts in vegetation and significantly more C_3 representation that are not apparent from the tooth enamel records for the same time period (Figure 4.5).

4.5.4 Ele Bor tooth enamel isotopes

Tooth enamel isotope data from the site of Ele Bor indicate representation of grazers (>80% C_4), mixed feeders (between 80-20% C_4), and browsers (>80% C_3) consistently across all three horizons (Table 4.3, Figure 4.6). Isotope values for archaeological herbivores are similar to their modern counterparts (Table 4.3). The modern comparative fauna for Ele Bor herbivores is a subset of teeth sampled from Turkana, since no modern faunal collections have ever been made in the area.

4.6 Discussion

4.6.1 Comparative records of ecology in the Lake Victoria Basin

Holocene records from the Lake Victoria Basin present an opportunity to understand paleoecology over the course of the Holocene using almost continuous records of pollen and $\delta^{13}C_{wax}$ values from piston cores (Figure 4.7). Similarly, these records present a unique opportunity to compare these commonly used but rarely integrated methods of understanding paleoecology (Feakins et al., 2005; Levin, 2015).

Herbivore tooth enamel isotopes from archaeological sites are depicted as integrating data across a time slice of this record (Figure 4.7), and the contrasting results of this data compilation raise intriguing questions. As has been previously noted, δD records from leaf wax biomarkers, a proxy for rainfall amount (Kahmen et al., 2013; Magill et al., 2013b; Niedermeyer et al., 2010; Polissar and Freeman, 2010; Schefuß et al., 2005), indicate gradual rather than abrupt aridification of the basin, in accordance with insolation forcing (Berke et al., 2012a), a trend also reflected in δD_{wax} from Lake Challa (Tierney et al., 2011a) and marine sediments (Niedermeyer et al., 2010).

With these caveats in mind, the tooth enamel record may be useful for determining which lacustrine proxies represent terrestrial vegetation within a certain area with more fidelity. Herbivore tooth enamel isotopes are not without their own biases, such as food selection by herbivores and taphonomic (preservation) bias at archaeological sites (Gannes et al., 1997). However, dietary isotopes still provide perspective for what resources were on the landscape, and how herbivores may have changed their diets to accommodate vegetation changes (Uno et al., 2011) (see Chapter 3). Herbivore dietary isotopes across a range of taxa, including those with more flexible diets (hippos and domestic caprines), indicate an overall abundance of C_4 plants in the Lake Victoria Basin throughout these timeslices, though some C_3 feeders are present in the early Holocene site of Luanda (Figure 4.7). The distribution of modern $\delta^{13}C_{enamel}$ from SW Kenya and northern Tanzania ("modern", Figure 4.3) from the modern counterparts of archaeological fauna indicate that most of these savanna herbivores are consuming C_4 foods, with a lower representation of C_3 browsers and C_3/C_4 mixed feeders. Indeed, isotopes of herbivore tooth enamel indicate that the diets of these herbivores have only recently included more C_3 foods, but overall are largely C_4 feeders.

Dietary trends within certain lineages reflect more ancient diets rather than modern counterparts. For example, Tragelaphini and Antilopini have a greater contribution of C_4 to their diet throughout the Holocene, only shifting to more C_3 after 1.8 kya (later than the Gogo Falls fauna). This one trend is seen in Pleistocene-aged individuals within this lineage (Cerling et al., 2015). Similarly, Neotragini are also much more enriched in ^{13}C relative to modern individuals, which could be explained by all of these samples representing oribi (*Ourebia ourebi*) rather than dik dik (*Madoqua sp.*). Hippos from Luanda (9.7 – 8.5 ka) are mixed-feeders, indicating some C_3-component to their diet that is not reflected in other herbivores (except *Potamochoerus sp.*), though returning to >80% C_4-feeding in the Gogo Falls samples. This result may indicate a higher proportion of C_3 herbaceous vegetation near the lake in the early Holocene (see Chapter 2), or the Luanda are not properly capturing the C_3 signal, as implied by the pollen record (Figure 4.7).

Reconciling these three distinct proxies is a difficult task. Herbivore tooth enamel isotopes appear to agree more with $\delta^{13}C_{wax}$ records than with pollen data (Figure 4.7). This record provides evidence that these two proxies may be similarly spatially integrated. A connection cannot yet be made between tooth enamel isotopes and paleoecology, as such a model does not yet exist, so our discussion is limited to changes in herbivore diets through time. It could also be possible that the leaf wax record is preferentially recording C_4 input to the sedimentary record, as is the case with the total soil organic pool (Wynn and Bird, 2007), though herbivore diets are still largely representative of an abundance of C_4 resources. It is clear, however, that changing climate and insolation forcing did not have an effect in forcing vegetation, as represented by the leaf waxes, or in herbivore diets, though these changes are synchronous with pollen data. It may be possible that plants in the family Moraceae are more sensitive to changes in total rainfall amount than C_4 grasses (Poaceae), or that, despite decreasing rainfall, there was no change in rainfall seasonality, thus maintaining C_4 grasses on the landscape (Hély et al., 2006).

4.6.2 Comparative records of ecology in the Lake Turkana and Ele Bor

Though the Turkana paleoecology record is discontinuous throughout the Holocene, there are still opportunities to compare proxies throughout certain intervals. The Ele Bor record will also be discussed along with the Turkana record, as they are both from northern Kenya, and present a rare opportunity to compare paleoecology from sites within a lake basin and an inland archaeological site. Though δD records do not exist for Turkana, there are direct measures of decreased rainfall via radiocarbon dated paleo-beach terraces (Garcin et al., 2012). The abrupt drop in lake level in the Turkana Basin is similar to the same observed increase in dust input to the East Atlantic during the Holocene (Figure 4.8), implying that similar climate forcing mechanisms resulting in aridity are at work in both Turkana and the Horn of Africa. The abrupt drop in lake levels indicates that Turkana responded quickly to insolation forcing and the end of the African Humid Period (deMenocal et al., 2000; Garcin et al., 2012; Tierney and deMenocal, 2013). This precipitous drop in lake level was so severe that Lake Turkana was separated into two distinct lake basins (Cerling, 1996). Tex_{86} records from Turkana from the 2P (northern basin) and 7P (southern basin) indicate increasing lake water temperatures shortly after the drop in lake level around 5 kya, either from increasing temperatures, lower water level, or both (Berke et al., 2012b). Poaceae pollen data from core 2P indicate generally high (>40%) but fluctuating levels of grass (Mohammed et al., 1995).

The Turkana tooth enamel records provide important paleoecological information for this basin. Herbivore tooth enamel isotopes from early Holocene sites all indicate mostly C_4 diets (Figure 4.8). At the site of Dongodien (Marshall et al., 1984) – the earliest pastoralist site in eastern Africa – there is a shift in the diets of herbivores towards more C_3 feeding compared to early Holocene sites. Relative to modern herbivores of the same taxa, though, dietary isotopes still indicate more C_4 biomass (Figure 4.4). These faunal assemblages are not directly comparable, as there are taxa that were not found in older assemblages at this site (Table 4.2), and likewise the presence of domestic stock (Caprini and *Bos taurus*) at Dongodien that were not present in earlier faunal assemblages. Faunal assemblages from sites within the Lake Victoria Basin, however, contain many of the same taxa at both pastoralist and fisher-hunter-gather sites (Table 4.1). The appearance of previously unseen fauna in early pastoralist sites in Turkana could indicate faunal turnover with vegetation changes within the basin, or simply be a reflection of changes in human behavior and hunting. Regardless, carbon isotopes in tooth enamel tell a story of changing herbivore diets over time, and more representation of C_3 throughout the Holocene.

The diets of tribes Antilopini and Neotragini are more C_4-dominated in the Dongodien assemblage (4.5-3.8 kya) relative to modern specimens. Once again, this is also the case with Pleistocene-ages samples of the same lineage, implying that the dietary change to more C_3 happened recently in Turkana. Dongodien caprines (either sheep or goat) likewise consumed more C_4 than modern counterparts, and even the most depleted caprines in the assemblage (which were likely goats, see Chapter 5) are not as depleted as modern Turkana goats (see Appendix D). Either early pastoralist goats were consuming less C_3 resources than modern goats by choice, or a change in herding behavior led to greater dietary separation due to herd management.

The early Holocene sedimentary $\delta^{13}C_{wax}$ values add yet another layer of complexity to the Turkana Basin record. These data indicate fluctuating C_4 input to the sedimentary record over this 4,000 year period, between 40 and 80%. It is difficult to say whether these biomarker data are in agreement with tooth enamel isotope values due to the small comparative dataset and large temporal integration. During the period over which these proxies overlap, there was a decline in $\%C_4$ indicated by the $\delta^{13}C_{wax}$ values, shortly before the 8 kyr event, an abrupt arid period (Gasse, 2000; Mayewski et al., 2004). During this event, $\%C_4$ increased to ~80%. It is possible that these herbivores (most of which exhibit dietary isotopes of >80% C_4, as well), are selectively sampling these periods of higher C_4 in Turkana. Another possibility is that decreasing less than 40% C_4 representation on the landscape is not enough of a change in terrestrial vegetation to result in a dietary shift in these mammals. Another possibility is that these leaf wax biomarkers have been transported into Turkana from outside the basin – possibly via the Omo River which drains the Ethiopian highlands and delivers up to 80% of Turkana's water and the majority of its sedimentary load in the northern basin (Cerling, 1986).

Ele Bor

The Turkana paleoecolgoical record indicates that terrestrial ecology may be sensitive to climatic changes forced by insolation. The comparative tooth enamel isotope record from Ele Bor, 200 km east and 500 m higher in elevation than Lake Turkana, is needed to address whether or not ecological changes occurred in other sites in northern Kenya, particularly outside of a lake basin. Ele Bor was an arcaheolgical habitation site with little supporting evidence for pastoral activity, providing an additional perspective on changing environments and the spread of herding communities (Gifford-Gonzalez, 2003). The fauna from Ele Bor is distinctive from that for Lake Turkana and Lake Victoria, and represents tribes of bovids (e.g., Tragelaphini, Table 4.3) and other herbivores (such as giraffe) that in modern settings are classified as browsers (Cerling et al., 2003; Gagnon and Chew, 2000). Faunal assemblages and isotopic indicators of diet are similar across all three archaeological horizons (Figure 4.5, Table 4.3). Unfortunately, other proxies of paleoecology and/or climate do not exist for Ele Bor and would be difficult to generate due to its remote location. However, the isotopes of Ele Bor herbivores indicate that the environment remained ecologically stable before and after the termination of the African Humid Period at about 5.5 kyr (deMenocal et al., 2000).

The trends in other basins for certain taxa that were more C_4 dependent on plants than modern comparative samples – Tragelaphini and Antilopini – are not present in the Ele Bor fauna, except in the oldest layer (6.5–6.2 kya). Tragelaphini are mixed feeders, then switch to diets of >80% C_3 in the 5.2–3.5 kya faunal layer, and remain that way through modern fauna. Antilopini remain mixed feeders throughout the assemblages, then consume more C_3 biomass in modern samples. Of course, this modern fauna is from the Lake Turkana Basin and may not be directly comparable, but it is intrguiging that only at Ele Bor do tragelaphines appear to consume a more modern (more C_3) diet much earlier than in either lake basin.

The fauna from Ele Bor highlights possible biases of lake basin records when reconstructing ecology over a certain time period. Large African rift lakes may have distinctive climate and environmental systems that are not representative of the region as a whole, and finding more sites outside of these basins (though challenging) would provide a rewarding opportunity to understand paleoenvironments outside of this context (Levin, 2015).

4.7.3 Paleoenvironments and advent of food production in East Africa

Within eastern Africa, there are variable records of the timing and social context in which herding first appears. As herding spread (Hildebrand and Grillo, 2012), cattle and caprines appeared by the eastern shore of NW Kenya's Lake Turkana around 4.5 Kya at GaJi4 (Dongodien) and GaJi2 (Barthelme, 1985; Marshall et al., 1984), along with wild terrestrial and aquatic fauna and novel Nderit pottery. This is accompanied both by a change in climate and a drop in lake level and also a shift in herbivore faunal assemblages with a greater representation of C_3 plants in their diets than at previous sites (Figure 4.8). In the Victoria Basin, early livestock is found with distinctive Kansyore pottery, a ceramic tradition whose roots precede herding in the region. Domesticates appear in Kansyore sites (e.g., Wadh Lang'o) ~4.4–3.3 Ka, but the small frequency of domestic fauna before ~1.9–1.8 Ka (Wadh Long'o and Gogo Falls) suggests that people initially supplemented a foraging diet with domesticates during the mid-Holocene but did not practice herding themselves until later (Dale and Ashley, 2010; Prendergast, 2010; Prendergast and Lane, 2010; Robertshaw, 1991). This is not accompanied by a large change in climate as indicated by δD or any significant shifts or trends in herbivore diets overall, or any significant change in $\delta^{13}C_{wax}$ values. Only gradually increasing δD values imply a damped increase in aridity in the region, and gradually decreasing Moraceae pollen and increasing Poaceae pollen indicate changing conditions throughout this time, though slowly (Figure 4.7).

Currently, archaeologists have proposed several possible environmental scenarios surrounding the spread of herding in East Africa. (1) Herding spread amidst worsening environmental conditions (i.e., people were “pushed” into moving their herds south to still-moist areas; migration model) or adopted livestock because fishing/hunting/gathering strategies were breaking down as climate became more arid (diffusion model). (2) It spread amidst an economic boom in a favorable climate regime (i.e., people were “pulled” south because herding was so successful it triggered an expansion; migration model). (3) Local populations saw livestock as an attractive supplement to a fairly secure fisher-hunter-gatherer subsistence strategy (diffusion model).

The paleoenvironmental research here cannot resolve migration vs. diffusion debates concerning the spread of herding, but it can refine them by clarifying the environmental context in which livestock appeared. These records indicate distinctive environmental changes associated with the archaeological records in each basin. In Turkana, around the time of the appearance of the first herders, there was a fairly abrupt (<1,000 years) change in both climate and either herbivore faunal communities and/or diet with the appearance of the first herders. At Ele Bor, there appears not to have been a distinctive change in herbivore diets over the last 6,000 years, and no evidence for any change in food producing economies. In Lake Victoria, the adoption of herding was a complicated process without a gradual and somewhat diffuse cultural transition between foragers (Kansyore) to herders (Elmenteitan) (Prendergast, 2011; 2010b), and likewise a gradual change in climate and complicated and contrasting picture of ecological change. These environmental data for these basins imply that there is no “one size fits all” model for the spread of herders southward, and that distinctive environments are only associated with the appearance of the first herders only in the Lake Turkana region, but not in the Lake Victoria region. These data call for archaeologists to refine their models concerning the spread of herders southward through East Africa, and that the environmental context of these early pastoralists must be determined on a case-by-case basis.

4.7 Conclusions

This comprehensive paleoecological dataset provides a needed comparative record for two Kenyan lake basins which record separate aspects of the spread of early food producers across East Africa during the Holocene – the northern Lake Turkana Basin and the south-western Lake Victoria Basin. The appearance of the first herders in the Lake Turkana Basin appears to coincide with both a climatological (deMenocal et al., 2000) and ecological (increasing C_3 in herbivore diets) shift. Evaluating whether this change in conditions was favorable or unfavorable (i.e., push vs. pull scenario of early herders) for the first food producers is difficult, but certainly some environmental change occurred which may have influenced their southward spread into the Turkana Basin. Similarly, no environmental change is evident from tooth enamel isotopes at the archaeological site of Ele Bor before and after the end of the African Humid Period, and likewise, there is no evidence for the presence of early herders at the site. In contrast, paleoecolgoical proxies from the Lake Victoria Basin, with a more diffuse and complex model of the adoption of early food production at archaeological sites, do not indicate any large shifts in ecology or climate. Rather, aridity set in gradually (Berke et al., 2012a), with no evidence of major ecological changes from leaf wax records or tooth enamel isotopes. These data are in contrast with pollen records, however, and there are still few paleoecological studies that combine such proxies. These Holocene paleoecolgoical records highlight the contrasting information provided by these proxies and call for further evaluation of the spatio-temporal aspects of ecology that they may sample, and caution researchers against relying on any one proxy to provide a comprehensive reconstruction of ecology.

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4.9 References

Ambrose, S.H., 1998. Chronology of the Later Stone Age and food production in East Africa. *Journal of Archaeological Science* 25 (4), 377–392.

Ambrose, S.H., DeNiro, M.J., 1989. Climate and habitat reconstruction using stable carbon and nitrogen isotope ratios of collagen in prehistoric herbivore teeth from Kenya. *Quaternary Research* 31(3), 407–422.

Ambrose, S.H., Sikes, N.E., 1991. Soil Carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. *Science* 253 (5026), 1402–1405.

Ashley, G., 2007. Orbital rhythms, monsoons, and playa lake response, Olduvai Basin, equatorial East Africa (ca. 1.85–1.74 Ma). *Geology* 35 (12), 1091–1094.

Balasse, M., Ambrose, S.H., 2005a. Mobilité altitudinale des pasteurs néolithiques dans la vallée du Rift (Kenya) : premiers indices de l'analyse du $\delta^{13}C$ de l'émail dentaire du cheptel domestique. *Anthropozoologica* 40 (1), 147–166.

Balasse, M., Ambrose, S.H., 2005b. Distinguishing sheep and goats using dental morphology and stable carbon isotopes in C_4 grassland environments. *Journal of Archaeological Science* 32 (5), 691–702.

Barthelme, J., 1985. Fisher-hunters and Neolithic pastoralists in east Turkana, Kenya. *Cambridge Monographs in Archaeology*. 363 p.

Bell, R.H., 1982. The effect of soil nutrient availability on community structure in African ecosystems. *Ecology of Tropical Savannas* 42, 193–216.

Berke, M.A., Johnson, T.C., Werner, J.P., Grice, K., 2012a. Molecular records of climate variability and vegetation response since the Late Pleistocene in the Lake Victoria basin, East Africa. *Quaternary Science Reviews* 55 (8), 59–74.

Berke, M.A., Johnson, T.C., Werner, J.P., Schouten, S., Damsté, J.S.S., 2012b. A mid-Holocene thermal maximum at the end of the African Humid Period. *Earth and Planetary Science Letters* 351–352, 95–104.

Blome, M.W., Cohen, A.S., Tryon, C.A., Brooks, A.S., Russell, J., 2012. The environmental context for the origins of modern human diversity: A synthesis of regional variability in African climate 150,000-30,000 years ago. *Journal of Human Evolution* 62(5): 563–592.

Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.J., 1996. Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. *PALAIOS* 11:306–318.

Bond, W.J., Midgley, G.F., 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* 6(8):865–869.

Bower, J., 1991. The Pastoral Neolithic of East Africa. *Journal of World Prehistory* 5, 49–82.

Buitenwerf, R., Bond, W.J., Stevens, N., 2012. Increased tree densities in South African savannas: >50 years of data suggests CO_2 as a driver. *Global Change Biology* 18(2), 675–684.

Castañeda, I.S., Mulitza, S., Schefuß, E., Santos, dos, R.A.L., Damsté, J.S.S., Schouten, S., 2009. Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. *Proceedings of the National Academy of Sciences* 106(48), 20159–20163.

Castañeda, I., Werne, J., Johnson, T., Filley, T., 2009. Late Quaternary vegetation history of southeast Africa: The molecular isotopic record from Lake Malawi. *Palaeogeography, Palaeoclimatology, Palaeoecology* 275(1-4), 100–112.

Cerling, T.E., 1986. A mass-balance approach to basin sedimentation: Constraints on the recent history of the Turkana Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 54(1-4), 63–86.

Cerling, T.E., 1996. Pore water chemistry of an alkaline lake: Lake Turkana, Kenya. in: The Limnology, Climatology and Paleoclimatology of the East African Lakes (eds. Odada, E.O. and Olago, D.O.), Gordon and Breach Publ., pp. 225–240.

Cerling, T.E., 2014. Stable Isotope Evidence for Hominin Environments in Africa. Treatise on Geochemistry, 2nd ed (eds. Holland H and Turekian, K). Elsevier Ltd., 157–167.

Cerling TA, Andanje SA, Blumenthal SA, Brown FH, Chritz KL, Harris JM, Hart J, Kirera, Kaleme P, Leakey LN, Leakey MG, Levin NE, Manthi FK, Passey BH, Uno KT. 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 million years ago. *Proceedings of the National Academy of Sciences* 112(37), 11467-11472.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120, 347–363.

Cerling, T.E., Harris, J.M., 2002. Dietary adaptations of extant and Neogene African suids. *Journal of Zoology* 256(1), 45–54.

Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy* 84(2), 456–470.

Cerling, T.E., Harris, J.M., Hart, J.A., Kaleme, P., Klingel, H., Leakey, M.G., Levin, N.E., Lewison, R.L., Passey, B.H., 2008. Stable isotope ecology of the common hippopotamus. *Journal of Zoology* 276(2), 204–212.

Cerling, T.E., Harris, J.M., Leakey, M., Mudida, N., 2003. Stable isotope ecology of northern Kenya with emphasis on the Turkana Basin. In: Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp. 583–603.

Cerling, T.E., Mbua, E., Kirera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G., Sponheimer, M., Uno, K.T. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences* 108(23), 9337–9341.

Chritz, K.L., Marshall, F.B., Zagal, M.E., Kirera, F., Cerling, T.E., 2015. Environments and trypanosomiasis risks for early herders in the later Holocene of the Lake Victoria basin, Kenya. *Proceedings of the National Academy of Sciences*. 112(12), 3674–3679.

Claussen, M., Kubatzki, C., Brovkin, V., Ganopolski, A., Hoelzmann, P., Pachur, H.J., 1999. Simulation of an abrupt change in Saharan vegetation in the mid-Holocene. *Geophysical Research Letter*s 26(14), 2037–2040.

Costa, K., Russell, J., Konecky, B., Lamb, H., 2014. Isotopic reconstruction of the African Humid Period and Congo Air Boundary migration at Lake Tana, Ethiopia. *Quaternary Science Reviews* 83, 58–67.

Coughenour, M.B., Ellis, J.E., 1993. Landscape and climatic control of woody vegetation in a dry tropical ecosystem: Turkana District, Kenya. *Journal of Biogeography* 22(4), 383–398.

Cramer, W., Bondeau, A., Woodward, F., et al. 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. *Global Change Biology* 7(4), 357–373.

Dale D and Ashley CZ (2010) Holocene hunter-fisher-gather communities: new perspectives on Kansyore using communities of western Kenya. *Azania* 45(1): 24-48.

deMenocal, P., 2011. Climate and human evolution. *Science* 331(6017), 540–542.

deMenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., Yarusinsky, M. 2000. Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. *Quaternary Science Reviews* 19, 347–361.

deMenocal, P.B., 2014. 14.8 Marine Sediment Records of African Climate Change: Progress and Puzzles. In: Treatise on Geochemistry 2nd Ed. (Cerling, T.E., Ed.) Elsevier Ltd. Pp 99–108.

Diefendorf, A.F., Freeman, K.H., Wing, S.L., 2011. Production of *n*-alkyl lipids in living plants and implications for the geologic past. *Geochimica et Cosmochimica Acta* 75(23), 7472–7485.

Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G., De Beaulieu, J.L., Hamilton, A.C., Maley, J., Marchant, R., Perez Obiol, R., Reille, M., Riollet, G., Scott, L., Straka, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F., Jonson, H., 2000. Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr bp. Journal of Biogeography. 27(3), 621–634.

Feakins, S.J., deMenocal, P., Eglinton, T.I., 2005. Biomarker records of late Neogene changes in northeast African vegetation. *Geology* 33(12), 977–980.

Feakins, S.J., Levin, N.E., Liddy, H.M., Sieracki, A., Eglinton, T.I., Bonnefille, R. 2013. Northeast African vegetation change over 12 m.y. *Quaternary Science Reviews* 73, 1–13.

Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Lagenfelds, R.L., Michel, E., Steele, L.P., 1999. A 1000-year high precision record of δ^{13}C in atmospheric CO_2. *Tellus B* 51(2), 170–193.

Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy* 81(2), 490–511.

Gannes, L.Z., O'Brien, D.M., Martinez del Rio, C., 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* 78(4), 1271–1276.

Garcin, Y., Melnick, D., Strecker, M.R., Olago, D., Tiercelin, J.-J., 2012. East African mid-Holocene wet-dry transition recorded in palaeo-shorelines of Lake Turkana, northern Kenya Rift. *Earth and Planetary Science Letters* 331-332, 322–334.

Garcin, Y., Vincens, A., Williamson, D., Buchet, G., Guiot, J., 2007. Abrupt resumption of the African Monsoon at the Younger Dryas--Holocene climatic transition. *Quaternary Science Reviews* 26(5-6), 690–704.

Gasse, F., 2000. Hydrological changes in the African tropics since the Last Glacial Maximum. *Quaternary Science Reviews* 19(1-5), 189–211.

Gifford-Gonzalez, D.P., 2000. Animal disease challenges to the emergence of pastoralism in sub-Saharan Africa. *African Archaeological Review* 17(3), 95–139.

Gifford-Gonzalez, D.P., 2003. The fauna from Ele Bor: Evidence for the persistence of foragers into the later Holocene of arid north Kenya. *African Archaeological Review* 20(2), 81–119.

Grillo, K.M., Hildebrand, E.A., 2013. The context of early megalithic architecture in eastern Africa: the Turkana Basin c. 5000-4000 BP. *Azania* 48(2), 193–217.

Hély, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M.T., Guiot, J. 2006. Sensitivity of African biomes to changes in the precipitation regime. *Global Ecology and Biogeography* 15(3), 258–270.

Hildebrand, E.A., Grillo, K.M., 2012. Early herders and monumental sites in eastern Africa: dating and interpretation. *Antiquity* 86(332), 338–352.

Hildebrand, E.A., Grillo, K.M., Shea, J., 2011. Four middle Holocene pillar sites in West Turkana, Kenya. *Journal of Field Archaeology* 36, 181–200.

Kahmen, A., Schefuß, E., Sachse, D., 2013. Leaf water deuterium enrichment shapes leaf wax *n*-alkane δD values of angiosperm plants I: Experimental evidence and mechanistic insights. *Geochimica et Cosmochimica Acta* 111(15), 39–49.

Keeling, C.D., Piper, S., Bollenbacher, A.F., Walker, S.J., 2010. Monthly atmospheric $^{13}C/^{12}C$ isotopic ratios for 11 SIO stations. accessed from: http://cdiac.ornl.gov/trends/co2/iso-sio/iso-sio.html

Kendall, R.L., 1969. An ecological history of the Lake Victoria basin. *Ecological Monographs* 39(2), 121–176.

Kingston, J.D., 2007. Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. *American Journal of Physical Anthropology*. 45, 20–58.

Kingston, J.D., 2011. Stable Isotopic Analyses of Laetoli Fossil Herbivores, in: Harrison, T. (Ed.), Vertebrate Paleobiology and Paleoanthropology, Vertebrate Paleobiology and Paleoanthropology. Springer Netherlands, Dordrecht, pp. 293–328.

Kingston, J.D., Deino, A., Edgar, R., Hill, A., 2007. Astronomically forced climate change in the Kenyan Rift Valley 2.7-2.55 Ma: implications for the evolution of early hominin ecosystems. *Journal of Human Evolution* 53, 487–503.

Kohn, M., Schoeninger, M., Valley, J., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochimica et Cosmochimica Acta* 60(20), 3889–3896.

Kohn, M., Schoeninger, M.J., Valley, J.W., 1998. Variability in oxygen isotope compositions of herbivore teeth: reflections of seasonality or developmental physiology? *Chemical Geology* 152(1-2), 97–112.

Kutzbach, J., Bonan, G., Foley, J., Harrison, S., 1996. Vegetation and soil feedbacks on the response of the African monsoon to orbital forcing in the early to middle Holocene. *Nature* 384, 623–626.

Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A., Levrard, B., 2004. A long-term numerical solution for the insolation quantities of the Earth. *Astronomy and Astrophysics* 428, 261–285.

Levin, N.E., 2015. Environment and Climate of Early Human Evolution. *Annual Review of Earth and Planetary Sciences* 43, 405–429.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. *Proceedings of the National Academy of Sciences* 103(3), 11201–11205.

Magill, C.R., Ashley, G., Freeman, K.H., 2013a. Ecosystem variability and early human habitats in eastern Africa. *Proceedings of the National Academy of Sciences* 110(4), 1167–1174.

Magill, C.R., Ashley, G., Freeman, K.H., 2013b. Water, plants, and early human habitats in eastern Africa. *Proceedings of the National Academy of Sciences* 110(4), 1175–1180.

Marshall, F., Stewart, K., Barthelme, J., 1984. Early domestic stock at Dongodien in northern Kenya. Azania 19(1), 120–127.

Marshall, F., 1990. Origins of specialized pastoral production in East Africa. *American Anthropologist* 92(4), 873–894.

Marshall, F., Hildebrand, E., 2002. Cattle Before Crops: The Beginnings of Food Production in Africa. *Journal of World Prehistory* 16(2), 99–143.

Marshall, F., Stewart, K., Barthelme, J., 1984. Early domestic stock at Dongodien in northern Kenya. *Azania* 19(1), 120–127.

Marshall, J.D., Hopley, P.J., Weedon, G.P., Herries, A.I.R., Latham, A.G., Kuykendall, K.L., 2007. High-and low-latitude orbital forcing of early hominin habitats in South Africa. *Earth and Planetary Science Letters* 256(3-4), 419–432.

Maslin, M., Christensen, B., 2007. Tectonics, orbital forcing, global climate change, and human evolution in Africa: introduction to the African paleoclimate special volume. *Journal of Human Evolution* 53(5), 443–464.

Mayewski, P., Rohling, E., Curt Stager, J., Karlén, W., Maasch, K., David Meeker, L., Meyerson, E., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R.R., Steig E.J. 2004. Holocene climate variability. *Quaternary Research* 62(3), 243–255.

Mills, A.J., Milewski, A.V., Fey, M.V., Gröngröft, A., Petersen, A., Sirami, C., 2012. Constraint on woody cover in relation to nutrient content of soils in western southern Africa. *Oikos* 122(1), 136–148.

Mohammed, M., Bonnefille, R., Johnson, T., 1995. Pollen and isotopic records in Late Holocene sediments from Lake Turkana, Kenya. *Paleogeography, Palaeoclimatology, Palaeoecology* 119(3-4), 371–383.

Moncrieff, G.R., Scheiter, S., BOND, W.J., Higgins, S.I., 2013. Increasing atmospheric CO_2 overrides the historical legacy of multiple stable biome states in Africa. *New Phytologist* 201, 908–915. doi:10.1111/nph.12551

Murphy, B.P., Bowman, D.M.J.S., 2012. What controls the distribution of tropical forest and savanna? *Ecology Letters* 15(7), 748–758.

Murphy, P.G., Lugo, A.E., 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematic*s 17, 67–88.

Niedermeyer, E.M., Schefuß, E., Sessions, A.L., Mulitza, S., Mollenhauer, G., Schulz, M., Wefer, G., 2010. Orbital- and millennial-scale changes in the hydrologic cycle and vegetation in the western African Sahel: insights from individual plant wax δD and δ^{13}C. *Quaternary Science Reviews* 29(23-24), 2996–3005.

Owen, R., Barthelme, J., Renaut, R., Vincens, A., 1982. Palaeolimnology and archaeology of Holocene deposits north-east of Lake Turkana, Kenya. *Nature* 298, 523–529.

Owen, R., Renaut, R., 1986. Sedimentology, stratigraphy and palaeoenvironments of the Holocene Galana Boi Formation, NE Lake Turkana, Kenya. *Geological Society London Special Publication*s 25, 311–322.

Passey, B.H., Cerling, T.E., Levin, N.E., 2007. Temperature dependence of oxygen isotope acid fractionation for modern and fossil tooth enamels. *Rapid Communication Mass Spectrometry* 21(17), 2853–2859.

Polissar, P.J., Freeman, K.H., 2010. Effects of aridity and vegetation on plant-wax δD in modern lake sediments. *Geochimica et Cosmochimica Acta* 74, 5785–5797.

Potts, R., 2013. Hominin evolution in settings of strong environmental variability. *Quaternary Science Reviews* 73, 1–13. doi:10.1016/j.quascirev.2013.04.003

Prendergast, M.E., 2010. Kansyore fisher-foragers and transitions to food production in East Africa: The view from Wadh Lang'o, Nyanza Province, Western Kenya. *Azania* 45(1), 83–111.

Prendergast, M.E., Lane, P., 2010. Middle Holocene fishing strategies in East Africa: zooarchaeological analysis of Pundo, a Kansyore shell midden in northern Nyanza (Kenya). *International Journal of Osteoarchaeology* 20(1), 88–112.

Prendergast, M.E., 2011. Hunters and herders at the periphery: the spread of herding in eastern Africa, in: Jousse, H., Lesur, J. (Eds.), People and Animals in Holocene Africa Recent Advances in Archaeozoology. Frankfurt. pp. 3–15.

Ratnam, J., Bond, W.J., Fensham, R.J., Hoffmann, W.A., Archibald, S., Lehmann, C.E., Anderson, M.T., Higgins, S.I., Sankaran, M., 2011. When is a "forest" a savanna, and why does it matter? *Global Ecology and Biogeography* 20(5), 653–660.

Renssen, H., Brovkin, V., Fichefet, T., Goosse, H., 2003. Holocene climate instability during the termination of the African Humid Period. *Geophysical Research Letters* 30(4), 1184–1207.

Robertshaw, P., 1991. Gogo Falls: Excavations at a complex archaeological site east of Lake Victoria. *Azania* 26(1), 63–195.

Sankaran, M., Hanan, N.P., Scholes, R., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., 2005. Determinants of woody cover in African savannas. *Nature* 438, 846–849.

Schefuß, E., Ratmeyer, V., Stuut, J.-B.W., Jansen, J.H.F., Sinninghe Damsté, J.S., 2003. Carbon isotope analyses of n-alkanes in dust from the lower atmosphere over the central eastern Atlantic. *Geochimica et Cosmochimica Act*a 67(10), 1757–1767.

Schefuß, E., Schouten, S., Schneider, R.R., 2005. Climatic controls on central African hydrology during the past 20,000 years. *Nature* 437, 1003–1006.

Schoeninger, M., Kohn, M., Valley, J., 2002. Tooth oxygen isotope ratios as paleoclimate monitors in arid ecosystems. In: Biogeochemical approaches to paleodietary analysis. Kluwer Academic, New York. Pp. 117–140.

Scholes, R., Archer, S., 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28, 517–544.

Seppä, H., Bennett, K.D., 2003. Quaternary pollen analysis: recent progress in palaeoecology and palaeoclimatology. *Progress in Physical Geography* 27(4), 548–579.

Sinninghe Damsté, J.S., Verschuren, D., Ossebaar, J., Blokker, J., van Houten, R., van der Meer, M.T.J., Plessen, B., Schouten, S., 2011. A 25,000-year record of climate-induced changes in lowland vegetation of eastern equatorial Africa revealed by the stable carbon-isotopic composition of fossil plant leaf waxes. *Earth and Planetary Science Letters* 302(1-2), 236–246.

Smith, A.B., 1992. Origins and spread of pastoralism in Africa. *Annual Review of Anthropology* 21, 125–141.

Stager, J.C., Cumming, B., Meeker, L., 2003. A 10,000-year high-resolution diatom record from Pilkington Bay, Lake Victoria, East Africa. *Quaternary Research* 59(2), 172–181.

Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology* 82(4), 881–897.

Tierney, J.E., deMenocal, P.B., 2013. Abrupt Shifts in Horn of Africa Hydroclimate Since the Last Glacial Maximum. *Science* 342(6160), 843–846.

Tierney, J., Russell, J.M., Damsté, J.S.S., Huang, Y., Verschuren, D., 2011a. Late Quaternary behavior of the East African monsoon and the importance of the Congo Air Boundary. *Quaternary Science Reviews* 30(7-8), 798–807.

Tierney, J.E., Lewis, S.C., Cook, B.I., LeGrande, A.N., 2011b. Model, proxy and isotopic perspectives on the East African Humid Period. *Earth and Planetary Science Letters* 307(1-2), 103–112.

Uno, K.T., Cerling, T.E., Harris, J.M., Kunimatsu, Y., Leakey, M.G., Nakatsukasa, M., Nakaya, H., 2011. Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proceedings of the National Academy of Sciences* 108(16), 6509–6514.

Van Der Merwe, N.J., 2013. Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. *South African Journal of Science* 109, 14 Pages.

Verschuren, D., Damsté, J., Moernaut, J., Kristen, I., Blaauw, M., Fagot, M., Haug, G., van Geel, B., de Batist, M., Barker, P., 2009. Half-precessional dynamics of monsoon rainfall near the East African Equator. *Nature* 462, 637–641.

Vincens, A., Buchet, G., Servant, M., ECOFIT Mbalang collaborators, 2010. Vegetation response to the "African Humid Period" termination in Central Cameroon (7 N) – new pollen insight from Lake Mbalang. *Climate of the Past* 6, 281–294.

Walker, M., Berkelhammer, M., Björck, S., Cwynar, L.C., Fisher, D.A., Long, A.J., Lowe, J.J., Newnham, R.M., Rasmussen, S.O., Weiss, H. 2012. Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on the Quaternary Stratigraphy (International Commission on Stratigraphy). *Journal of Quaternary Science* 27(7), 649–659.

Willis, K.J., Bennett, K.D., Burrough, S.L., Macias-Fauria, M., Tovar, C., 2013. Determining the response of African biota to climate change: using the past to model the future. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368, 20120491–20120302.

Wynn, J.G., Bird, M.I., 2007. C_4-derived soil organic carbon decomposes faster than its C_3 counterpart in mixed C_3/C_4 soils. *Global Change Biology* 13(10), 2206–2217.

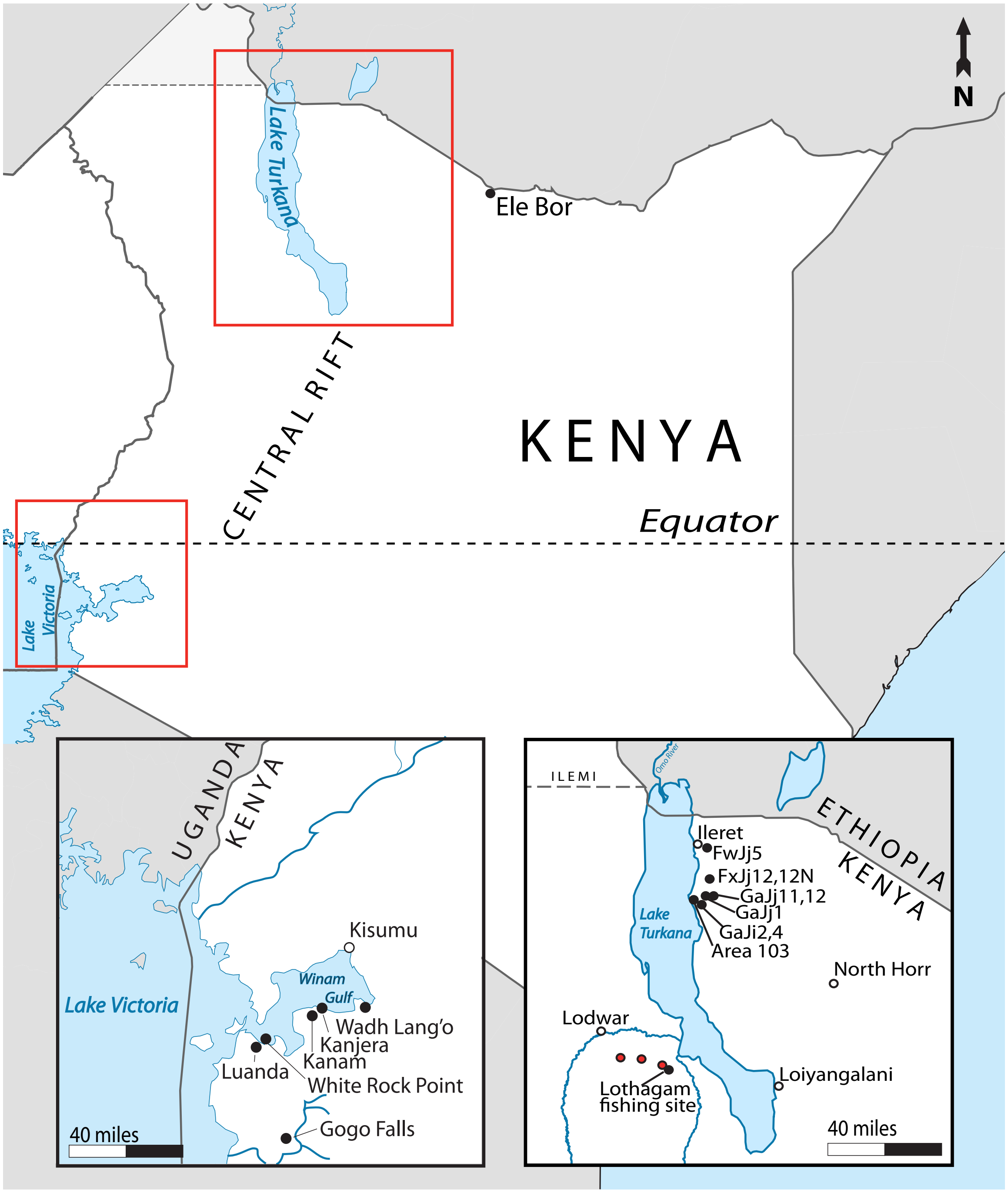


Figure 4.1: Map of the study areas. Callouts to specific sampling areas in red boxes.

Figure 4.2: Holocene paleoenvironment and archeology in Kenya **A** - Solar insolation (w/m^2) at 20 N; **B** -elevation of paleo lake terraces as a proxy for aridity (Garcin et al., 2012); **C** – deuterium leaf wax isotopes from sedimentary cores from Lake Victoria as a proxy for aridity (Berke et al., 2012a); **D** – radiocarbon dates for archaeological sites from the Turkana Basin (blue sites indicate domestic fauna present) (Barthelme, 1985; Garcin et al., 2012); **E** – radiocarbon dates from archaeological layers at Ele Bor (Gifford-Gonzalez, 2003); **F -** radiocarbon dates from archaeological sites in the Victoria Basin (Prendergast, 2010; Prendergast and Lane, 2010; Robertshaw, 1991)

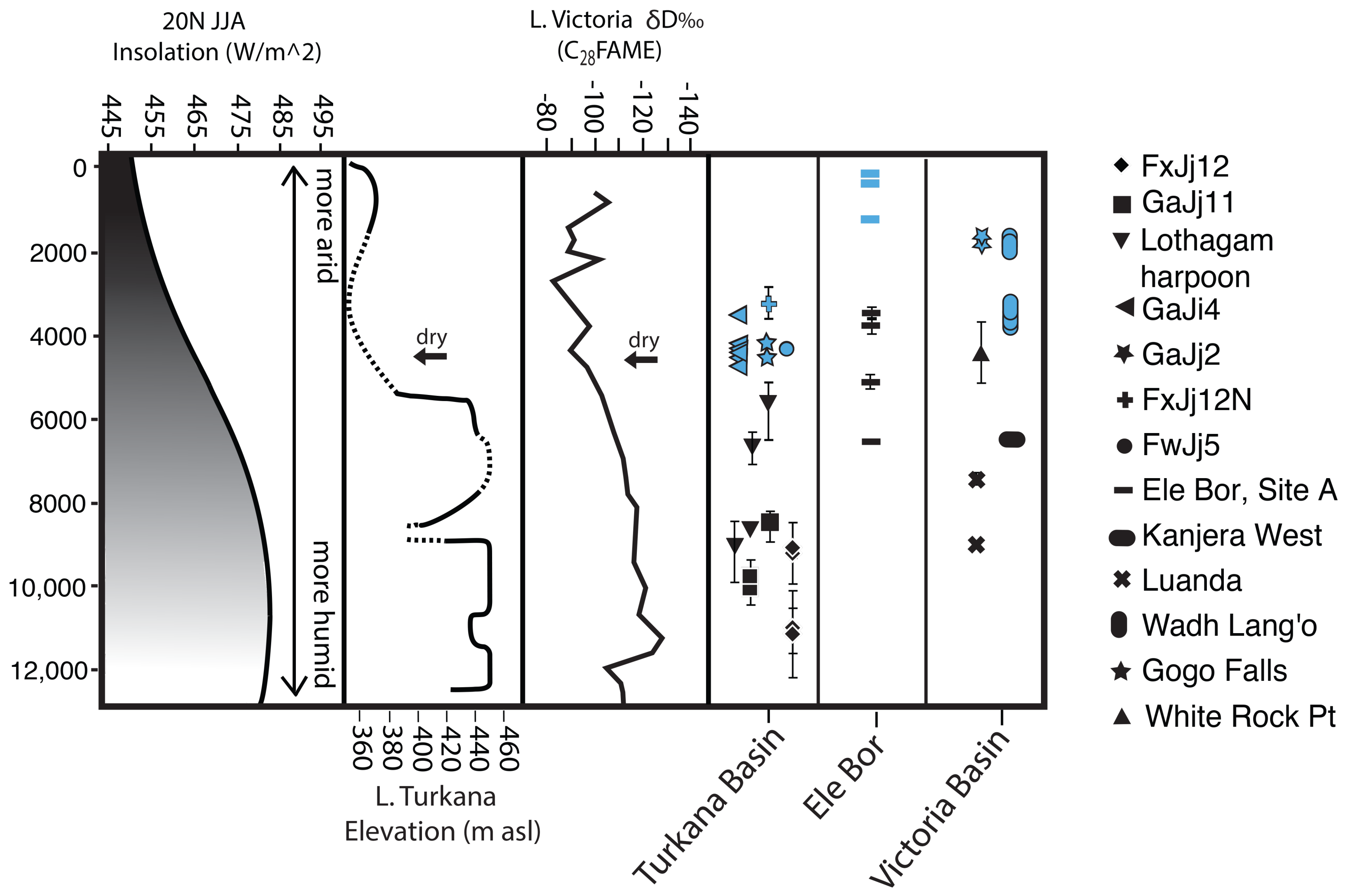

20N JJA
Insolation (W/m^2)
445
455
465
475
485
495
more arid
more humid
0
2000
4000
6000
8000
10,000
12,000
dry
L. Turkana
Elevation (m asl)
360
380
400
420
440
460
L. Victoria δD‰
(C28FAME)
-80
-100
-120
-140
dry
Turkana Basin
Ele Bor
Victoria Basin
◆ FxJj12
■ GaJj11
▼ Lothagam harpoon
◀ GaJi4
✶ GaJj2
✚ FxJj12N
● FwJj5
▬ Ele Bor, Site A
⬬ Kanjera West
✖ Luanda
⬮ Wadh Lang'o
★ Gogo Falls
▲ White Rock Pt

Table 4.1: $\delta^{13}C$ of herbivore tooth enamel from the Lake Victoria Basin.

Luanda

Family	**Tribe**	**Species**	**$\delta^{13}C$**	**+/-**	**No.**	**Citation**
Bovidae	Bovini	*Syncerus caffer*	2.1	1.5	17	this work
Bovidae	Reduncini	*Redunca sp.*	1.6	2.0	2	this work
Suidae		*Potamochoerus sp.*	-10.5	2.4	3	this work
Suidae		*Phacochoerus sp.*	0.7	0.6	2	this work
Bovidae	Reduncini	*Kobus kob*	2.0	0.9	3	this work
Bovidae	Reduncini	*Kobus ellipsiprymnus defassa*	2.3	0.8	3	this work
Hippopotamidae		*Hippoptamus amphibius*	-4.2	1.6	6	this work
Equidae			0.6		1	this work
Bovidae	Alcelaphini	*Connochaetes taurinus*	2.2	1.3	7	this work
Bovidae		class size 4	1.7	1.1	6	this work
Bovidae		class size 3	1.4		1	this work
Bovidae	Bovini		3.2		1	this work
Bovidae	Alcelaphini		2.8	0.5	2	this work

Wadh Lang'o

Family	**Tribe**	**Species**	**$\delta^{13}C$**	**+/-**	**No.**	**Citation**
Bovidae	Reduncini		2.5		1	this work
Bovidae	Reduncini	*Redunca redunca*	-0.5	2.9	3	this work
Suidae		*Phacochoerus sp.*	0.4		1	this work
Bovidae	Reduncini	*Kobus ellipsiprymnus defassa*	1.4		1	this work
Bovidae	Caprini		1.2	1.5	19	this work
Bovidae	Alcelaphini	*Connochaetes taurinus*	2.8		1	this work
Bovidae		class size 2	0.9	1.6	6	this work
Bovidae		class size 0	-0.3	2.8	2	this work
Bovidae	unk.		-0.6	0.1	2	this work
Bovidae	Bovini	*Bos taurus*	1.8		1	this work
Bovidae	Alcelaphini		2.1	1.1	6	this work

Table 4.1 (cont'd)

Gogo Falls *(from Chritz et al., 2015)*

Family	**Tribe**	**Species**	**$\delta^{13}C$**	**+/-**	**No.**
Bovidae	Tragelaphini	*Taurotragus oryx*	-6.6	2.8	5
Bovidae	Cephalophini	*Sylvicapra sp.*	-8.8		1
Bovidae	Reduncini		0.7	1.7	5
Suidae		*Potamochoerus sp.*	-3.9		1
Suidae		*Phacochoerus sp.*	-0.1	0.8	4
Bovidae	Neotragini	*Ourebia ourebi*	0.3	0.8	8
Bovidae	Hippotragini		1.2	1.4	5
Hippopotamidae		*H. amphibius*	0.6	0.6	2
Equidae			0.8	0.6	13
Bovidae	Caprini		0.3	1.4	14
Bovidae	unk.		0.5	1.3	2
Bovidae	Bovini	*Bos taurus*	1.6	1.5	11
Bovidae	Alcelaphini		1.5	1.2	15

Table 4.1: (cont'd)

modern

Family	Tribe	Species	$\delta^{13}C_{1750}$	+/-	No.	Citation
Bovidae	Tragelaphini	*Taurotragus oryx*	-10.4	2.2	18	(Cerling et al., 2003; Van Der Merwe, 2013)
Bovidae	Cephalophini	*Sylvicapra sp.**	-10.6	1.4	9	(Cerling et al., 2003)
Bovidae	Reduncini		2.5	1.4	51	(Cerling et al., 2003; Van Der Merwe, 2013)
Suidae		*Potamochoerus sp.*	-6.9	4.9	15	(Cerling and Harris, 2002)
Suidae		*Phacochoerus sp.*	1.0	1.1	56	(Bocherens et al., 1996; Cerling and Harris, 2002; Kingston, 2011)
Bovidae	Neotragini*	*Ourebia ourebi*	1.2	4.4	4	(Cerling et al., 2003)
Bovidae	Hippotragini		1.8	2.1	29	(Bocherens et al., 1996; Cerling et al., 2003; Van Der Merwe, 2013)
Hippopotamidae		*H. amphibius*	-2.3	1.7	14	(Cerling and Harris, 2002; Cerling et al., 2011)
Equidae			2.2	0.4	9	(Bocherens et al., 1996; Cerling et al., 2011; Kingston, 2011)
Bovidae	Caprini		-4.0	3.4	22	(Balasse and Ambrose, 2005a)
Bovidae	Bovini	*Bos taurus*	2.7	1.2	5	(Balasse and Ambrose, 2005a; Cerling et al., 2003)
Bovidae	Alcelaphini		3.2	1.5	93	(Cerling et al., 2003; Kingston, 2011; Van Der Merwe, 2013)

*values calculated from keratin using $\varepsilon_{\text{keratin-enamel}}$ of 11.1‰ (Cerling et al., 2003).

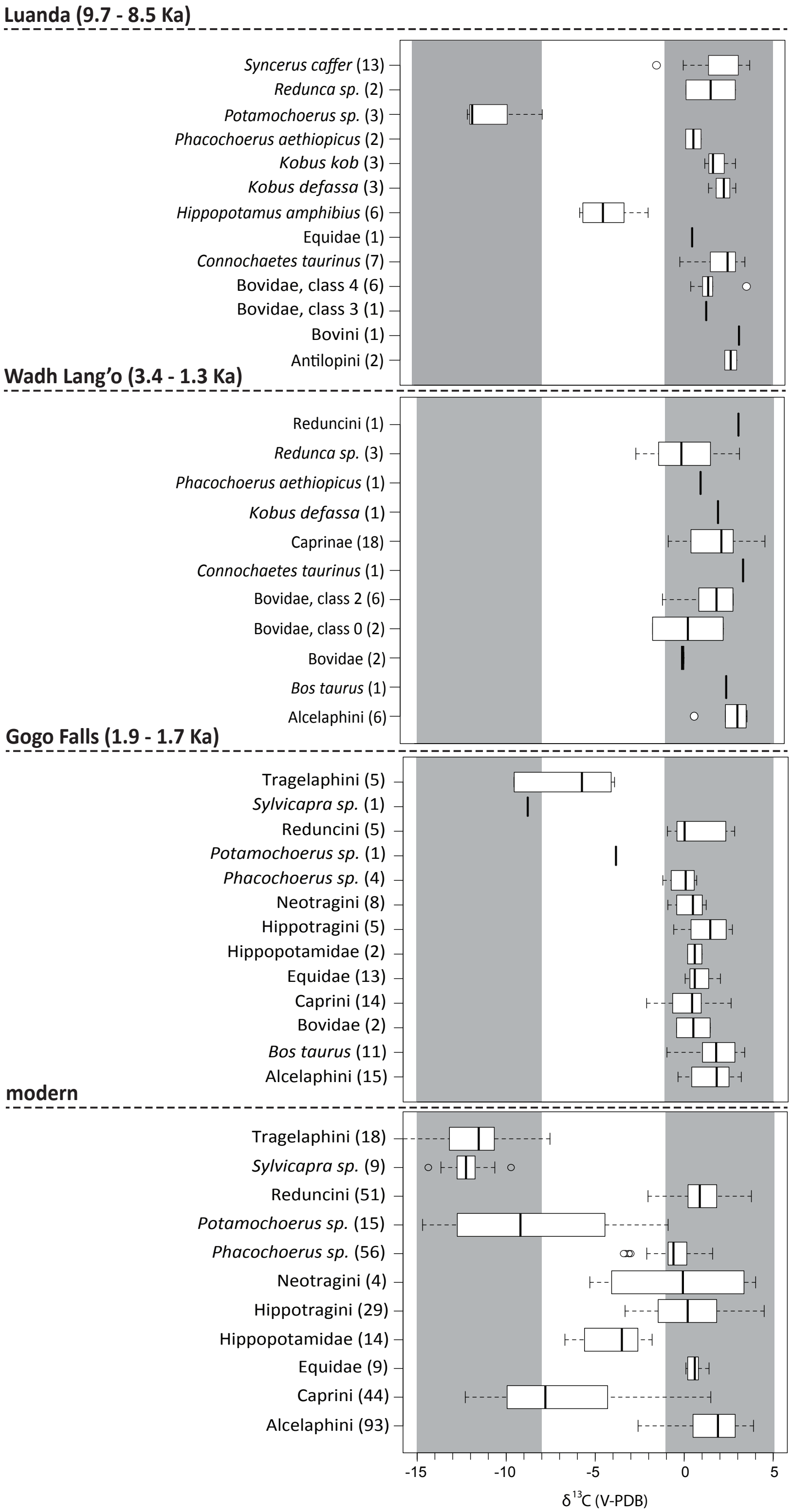


Figure 4.3: Boxplots of δ^{13}C values and dietary designations for herbivores in the Lake Victoria Basin.

Table 4.2: $\delta^{13}C$ of herbivore tooth enamel from the Lake Turkana Basin.

GaJj11, FxJj12, Equid Site

Family	Tribe	Species	$\delta^{13}C$	+/-	No.	Citation
Suidae		*Phacochoerus sp.*	0.15	0.25	2	this work
Bovidae	Reduncini		2.00		1	this work
Hippopotamidae		*Hippopotamus amphibius*	-1.02	1.53	2	this work
Equidae			-0.56	1.08	7	this work
Bovidae	unk		0.93	2.55	2	this work
Bovidae	Alcelaphini		1.28	0.76	3	this work

Lothagam Harpoon Site

Family	Tribe	Species	$\delta^{13}C$	+/-	No.	Citation
Suidae		*Phacochoerus sp.*	0.90	1.57	5	this work
Hippopotamidae		*Hippopotamus amphibius*	-0.59	0.96	5	this work
Equidae			0.61	0.58	4	this work
Cercopithecidae		*Papio anubis*	-6.87		1	this work
Bovidae	unk		0.50	1.60	9	this work

Dongodien, GaJj2

Family	Tribe	Species	$\delta^{13}C$	+/-	No.	Citation
Suidae		*Phacochoerus sp.*	-0.27	1.64	5	this work
Bovidae	Neotragini		-2.23	4.09	3	this work
Bovidae	unk.		-1.95	2.61	9	this work
Hippopotamidae		*H. amphibius*	-1.55	1.77	4	this work
Equidae			-0.24		1	this work
Bovidae	Caprini		-4.01	2.33	20	this work
Bovidae	Bovini		1.62		1	this work
Bovidae	Antilopini		-3.24	0.98	4	this work
Bovidae	Alcelaphini		-1.02	2.80	6	this work
Bovidae	Aepycerotini		-7.16		1	this work

Table 4.2:(cont'd)

Modern (data from Cerling et al., *in revision*)

Family	**Tribe**	**Species**	$\delta^{13}C_{1750}$	**+/-**	**No.**
Suidae		*Phacochoerus sp.*	0.13	2.10	4
Bovidae	Neotragini		-10.75	1.78	16
Hippopotamidae		*H. amphibius*	-0.34	2.11	8
Equidae			-2.09	3.69	14
Cercopithecidae		*Papio anubis*	-10.90		1
Bovidae	Caprini		-5.69	4.31	14
Bovidae	Bovini	*Bos taurus*	3.13	0.87	4
Bovidae	Antilopini		-8.96	4.48	3
Bovidae	Alcelaphini		3.13	0.98	6

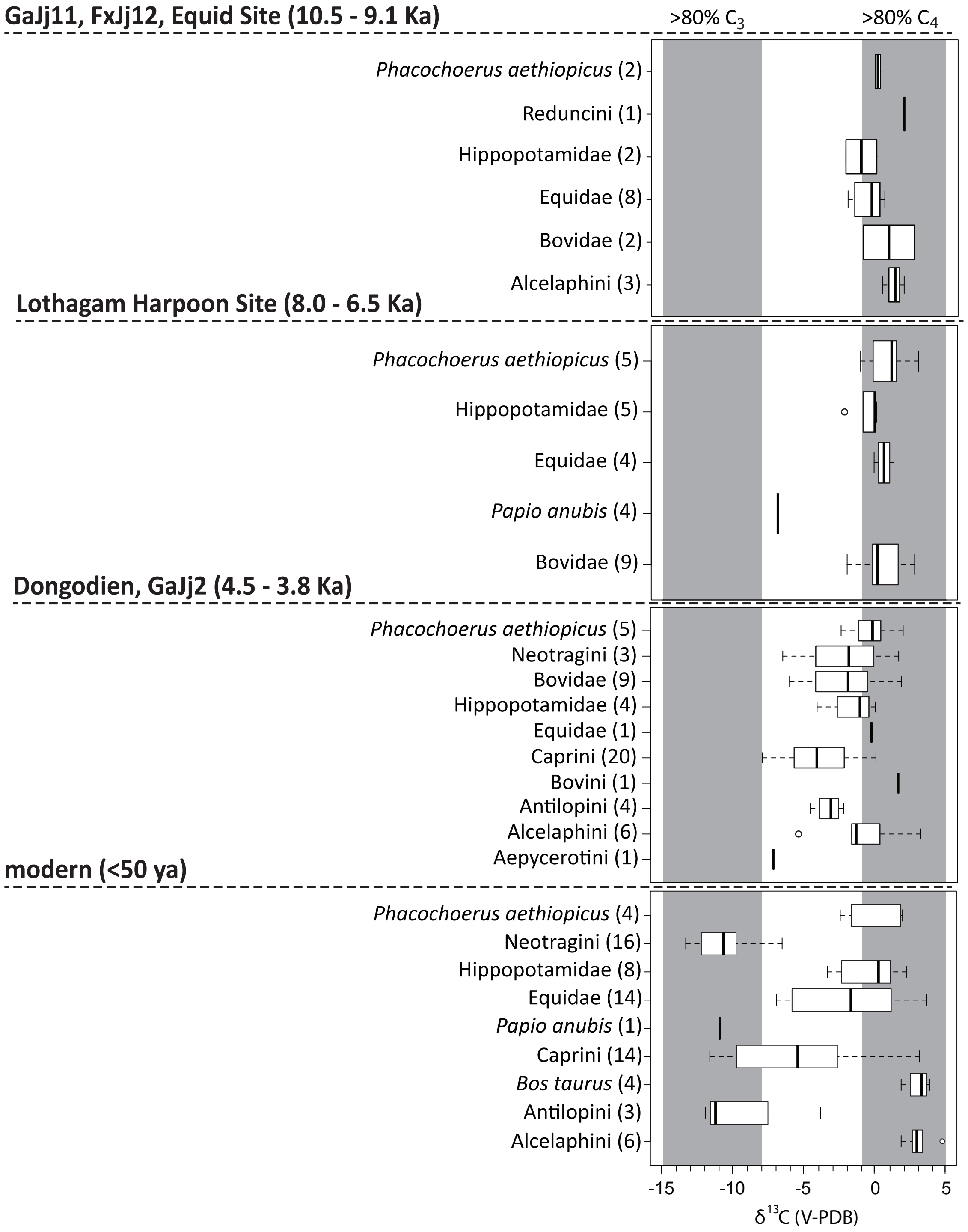


Figure 4.4: Boxplots of $\delta^{13}C$ values and dietary designations for herbivores in the Lake Turkana Basin.

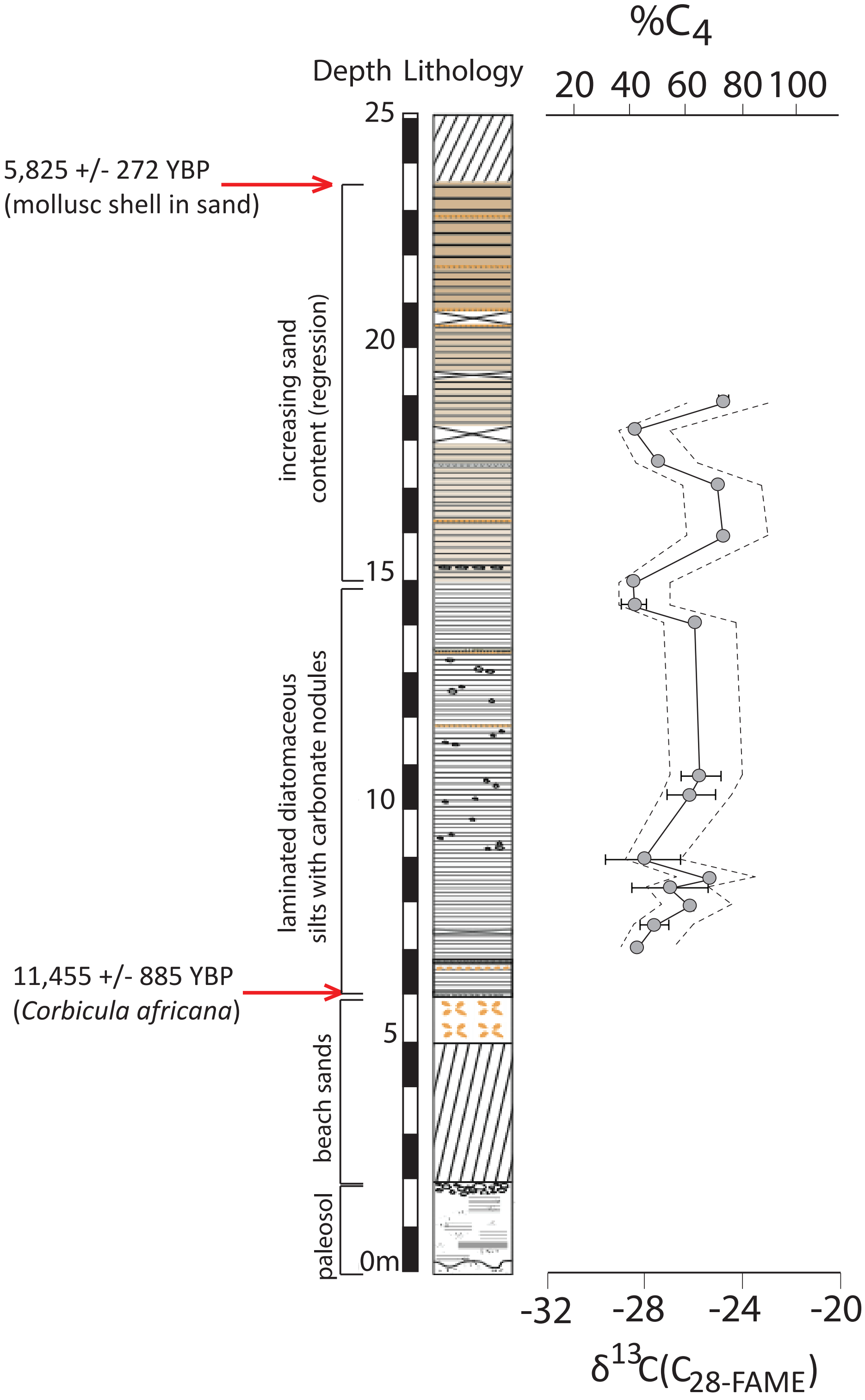


Figure 4.5: Leaf wax biomarker isotope values for terrestrial lacustrine deposits in Area 103, Turkana (dates recalibrated using OxCal 4.2 using IntCal13 from Owen and Renaut, 1986).

Table 4.3: $\delta^{13}C$ of herbivore tooth enamel from Ele Bor.

Horizon C

Family	**Tribe**	**$\delta^{13}C$**	**+/-**	**No.**	**Citation**
Bovidae		1.5		1	this work
Bovidae	Antilopini	-5.0	2.5	3	this work
Bovidae	Hippotragini	2.4		1	this work
Bovidae	Tragelaphini	-3.7	5.2	3	this work

Horizon B

Family	**Tribe**	**$\delta^{13}C$**	**+/-**	**No.**	**Citation**
Equidae		0.5	0.6	2	this work
Bovidae	Antilopini	-4.1	3.5	13	this work
Giraffidae		-12.4		1	this work
Bovidae	Neotragini	-11.8		1	this work
Bovidae	Hippotragini	1.5	2.8	8	this work
Bovidae	Cephalophini.	-2.1		1	this work
Bovidae	Tragelaphini	-10.7	1.4	4	this work

Horizon A1/A2

Family	**Tribe**	**$\delta^{13}C$**	**+/-**	**No.**	**Citation**
Bovidae	Antilopini	-2.8	3.8	7	this work
Bovidae	Neotragini	-10.7	2.4	3	this work
Bovidae	Hippotragini	1.3		1	this work

modern

Family	**Tribe**	**$\delta^{13}C_{1750}$**	**+/-**	**No.**	**Citation**
Bovidae	Neotragini	-10.8	1.8	16	Cerling et al., *in press*
Bovidae	Antilopini	-9.0	4.5	3	Cerling et al., *in press*
Bovidae	Tragelaphini	-9.8	0.8	3	Cerling et al., *in press*
Bovidae	Hippotragini	0.7	1.7	9	Cerling et al., *in press*
Equidae		-2.4	3.7	13	Cerling et al., *in press*
Giraffidae		-11.3		1	Cerling et al., *in press*

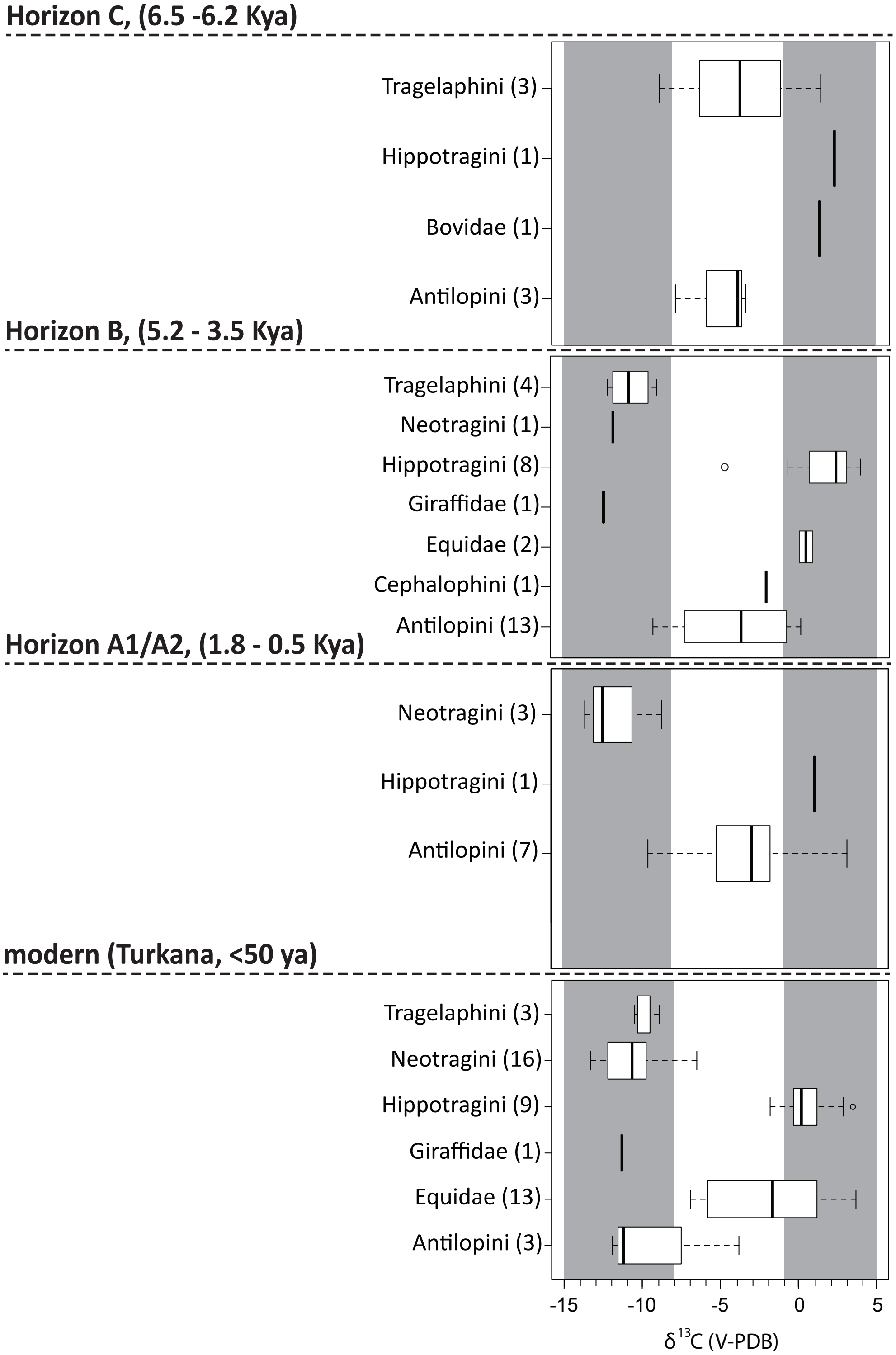


Figure 4.6: Boxplots of $\delta^{13}C$ values and dietary designations for herbivores in the Ele Bor.

Figure 4.7: Holocene paleoenvironment at Lake Victoria, Kenya. **A** – Solar summer insolation at 20 N; **B** - δD_{wax} values from sedimentary n-alkanes in piston cores from Lake Victoria (Berke et al., 2012a); **C** - $\delta^{13}C_{wax}$ values from sedimentary n-alkanes in piston cores from Lake Victoria (Berke et al., 2012a); **D** – Poaceae (grass) pollen from Pilkington Bay piston cores (Kendall, 1969); **E** – Moraceae (moist trees) pollen from Pilkington Bay (Kendall, 1969); **F** – tooth enamel isotopes from modern (see Table 4.1) archaeological sites in the Lake Victoria Basin (this study).

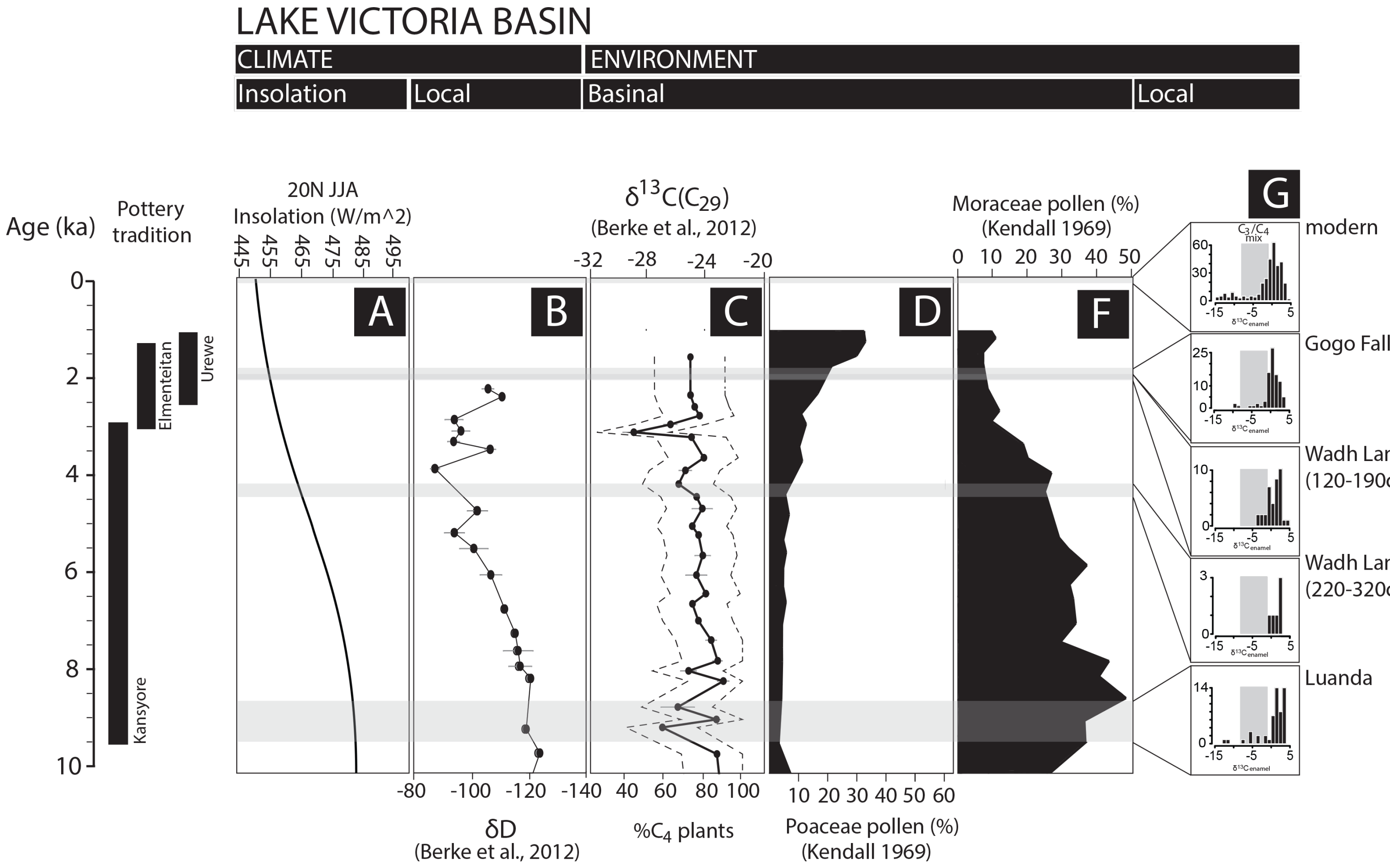
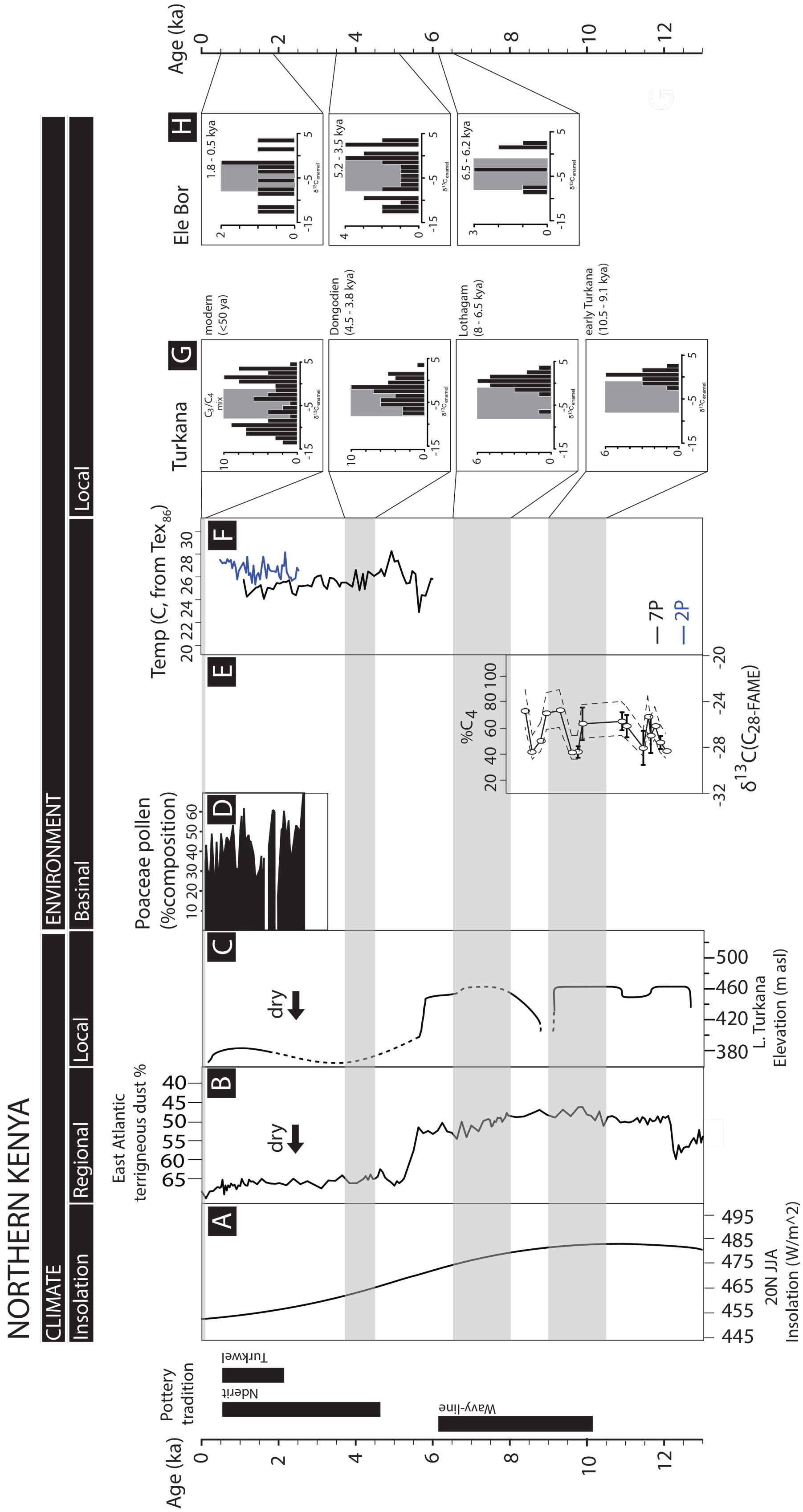

LAKE VICTORIA BASIN
CLIMATE
ENVIRONMENT
Insolation
Local
Basinal
Local
Age (ka)
0
2
4
6
8
10
Pottery tradition
Kansyore
Elmenteitan
Urewe
20N JJA Insolation (W/m^2)
445 455 465 475 485 495
A
B
δD
(Berke et al., 2012)
-80 -100 -120 -140
$\delta^{13}C(C_{29})$
(Berke et al., 2012)
-32 -28 -24 -20
C
40 60 80 100
$\%C_4$ plants
D
10 20 30 40 50 60
Poaceae pollen (%)
(Kendall 1969)
Moraceae pollen (%)
(Kendall 1969)
0 10 20 30 40 50
F
G
C_3/C_4 mix
$\delta^{13}C_{enamel}$
-15 -5 5
modern
60 30 0
Gogo Falls
25 10 0
Wadh Lang'o (120-190cm)
10 0
Wadh Lang'o (220-320cm)
3 0
Luanda
14 0

Figure 4.8: Holocene paleoenvironment at LakeTurkana and Ele Bor, Kenya. **A** – Solar summer insolation at 20 N; **B** – East Atlantic terrigneous dust input to sedimentary record from Core 231 in the Gulf of Aden (deMenocal et al., 2000); **C** – Lake Turkana paleolake terraces (Garcin et al., 2012); **D** – Poaceae (grass) pollen from core 2P (north basin)(Mohammed et al., 1995); **E** - $\delta^{13}C_{wax}$ values from sedimentary n-alkanoic acids from terrestrial lacustrine sediments (this study); **F** – Lake Turkana surface temperatures from Tex_{86} from cores 2P and 7P (Berke et al., 2012b); **G** – tooth enamel isotopes from modern (see Table 4.2) archaeological sites in the Lake Turkana Basin (this study); **H** – tooth enamel isotopes from archaeological sites from Ele Bor, Site M (this study).


NORTHERN KENYA
CLIMATE
ENVIRONMENT
Insolation
Regional
Local
Basinal
Local
Age (ka)
0
2
4
6
8
10
12
Pottery tradition
Turkwel
Nderit
Wavy-line
A
20N JJA Insolation (W/m^2)
445
455
465
475
485
495
B
East Atlantic terrigneous dust %
65
60
55
50
45
40
dry
C
L. Turkana Elevation (m asl)
380
420
460
500
dry
D
Poaceae pollen (%composition)
10 20 30 40 50 60
E
%C4
20 40 60 80 100
$\delta^{13}C(C_{28\text{-FAME}})$
-32 -28 -24 -20
F
Temp (C, from Tex86)
20 22 24 26 28 30
7P
2P
G
Turkana
modern (<50 ya)
C_3/C_4 mix
Dongodien (4.5 - 3.8 kya)
Lothagam (8 - 6.5 kya)
early Turkana (10.5 - 9.1 kya)
$\delta^{13}C_{enamel}$
-15 -5 5
H
Ele Bor
1.8 - 0.5 kya
5.2 - 3.5 kya
6.5 - 6.2 kya

CHAPTER 5

ENVIRONMENTS AND TRYPANOSOMAISIS RISKS FOR EARLY HERDERS IN THE LATER HOLOCENE OF THE LAKE VICTORIA BASIN, KENYA

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Environments and trypanosomiasis risks for early herders in the later Holocene of the Lake Victoria basin, Kenya

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Specialized pastoralism developed ∼3 kya among Pastoral Neolithic Elmenteitan herders in eastern Africa. During this time, a mosaic of hunters and herders using diverse economic strategies flourished in southern Kenya. It has been argued that the risk for trypanosomiasis (sleeping sickness), carried by tsetse flies in bushy environments, had a significant influence on pastoral diversification and migration out of eastern Africa toward southern Africa ∼2 kya. Elmenteitan levels at Gogo Falls (ca. 1.9–1.6 kya) preserve a unique faunal record, including wild mammalian herbivores, domestic cattle and caprines, fish, and birds. It has been suggested that a bushy/woodland habitat that harbored tsetse fly constrained production of domestic herds and resulted in subsistence diversification. Stable isotope analysis of herbivore tooth enamel (n = 86) from this site reveals, instead, extensive C_4 grazing by both domesticates and the majority of wild herbivores. Integrated with other ecological proxies (pollen and leaf wax biomarkers), these data imply an abundance of C_4 grasses in the Lake Victoria basin at this time, and thus little risk for tsetse-related barriers to specialized pastoralism. These data provide empirical evidence for the existence of a grassy corridor through which small groups of herders could have passed to reach southern Africa.

archaeology | carbon isotopes | food production | East Africa | livestock disease

Herding was the earliest form of food production in Africa, originating in the arid eastern Sahara ∼8 kya. Adoption of food production and increasing mobility in northeastern Africa allowed prehistoric people to manage resource availability amid a drastically changing climate (1) and transformed local populations of people and animals. Saharan herders and hunters spread southward to the Sahel, reaching eastern Africa by 4.5 kya, and eventually reaching southern Africa with sheep and cattle around 2 kya (1–8). The southern African data have been much debated, but recent genetic studies support at least limited movement of early herders from eastern to southern Africa (5, 7). Iron Age Bantu agriculturalist migrations and forager exchange processes also contributed to livestock spread. In contrast to Iron Age farmers, however, the sparse archaeological evidence suggests slow and small-scale southern pastoral migrations (9). Researchers have attributed the limited penetration of southern Africa by stone-using pastoralists to the prevalence of woodland habitats, the distribution of tsetse fly, and the influence of trypanosomiasis on livestock production from Lake Victoria and the Serengeti southward (10, 11). However, site-based paleoenvironmental data have proven difficult to obtain, and although often assumed, the proposition that ancient closed or bushy environments represented a barrier to herding has been seldom examined. Here we present stable isotope analysis of herbivore tooth enamel (n = 86) from Elmenteitan Pastoral Neolithic levels at Gogo Falls (ca. 1.9–1.6 kya) near Lake Victoria, one of the northernmost "woodland tsetse belts" modeled for Africa ca. 2,000 y ago (12, 13). Rather than providing evidence for the Lake Victoria basin as a wooded tsetse fly harboring habitat, these new fine-resolution paleoenvironmental data document extensive C_4 grazing by both domesticates and the majority of wild herbivores. A synthesis of lacustrine and terrestrial signals further supports the existence of grassy areas in the Lake Victoria basin at 2,000 B.P., indicating a change in ecology to bushy environments more recently than previously thought, and an ecosystem that would not have supported the tsetse fly around Lake Victoria.

Early herders in northern Kenya relied on sheep, goats, fish, and diverse wild vertebrates (1, 14). Research in western Kenya, and specifically the Lake Victoria basin (Fig. 1), has revealed southwestward movement of Elmenteitan herders into an area populated by complex ceramic-using, fishing hunter-gatherers and a more varied process of adoption of food production. Domestic sheep and goats appear in low numbers starting around 3.7 kya at Wadh Lang'o, and perhaps also at Gogo Falls and Usenge 3 (15), but not at other sites such as Siror (16), suggesting patchy adoption of herding. Specialized dependence on livestock in Africa is first documented in Elmenteitan sites, which date at the earliest to 3.1 kya at Njoro River Cave, east of Lake Victoria (17, 18). Elmenteitan sites occur to the north in Laikipia, on the Mau Escarpment, on the southern end of the Loita Hills and the northern Mara Plains, and at Gogo Falls (the westernmost extent) (18). Despite opportunities for hunting, fauna from Elmenteitan sites on the Mara plains are >90% domestic (19, 20). The exception to this is the site of Gogo Falls, which has a diverse and abundant faunal assemblage, including

Significance

Herding was the earliest form of African food production and transformed local populations of people and animals. Herders migrated from eastern to southern Africa around 2,000 years ago, but only in small numbers. Zoonotic disease vectors, specifically the tsetse fly, which carries sleeping sickness, are thought to have impeded these movements. Archaeologists have argued that the presence of tsetse flies around Lake Victoria, Kenya, created a barrier that prevented migration and forced subsistence diversification. This study, using stable isotope analysis of animal teeth, reveals the existence of ancient grassy environments east of Lake Victoria, rather than tsetse-rich bushy environments. This overturns previous assumptions about environmental constraints on livestock management in a key area for southward movement of early herders.

Author contributions: K.L.C. designed research; K.L.C. and M.E.Z. performed research; F.K. provided samples; T.E.C. contributed new reagents/analytic tools; K.L.C., F.B.M., M.E.Z., F.K., and T.E.C. analyzed data; and K.L.C., F.B.M., and T.E.C. wrote the paper.

The authors declare no conflict of interest.

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Fig. 1. Location of Gogo Falls in relation to other Holocene archaeological sites (●) and towns (○) in the Lake Victoria basin.

fish and wild herbivores (21). The unique faunal assemblages from Elmenteitan levels at Gogo Falls and from Prolonged Drift (22), which has a mixed Savanna Pastoral Neolithic stone tool assemblage, have sparked considerable debate over the significance of subsistence variability for understanding environmental risks and the dynamics of frontier pastoral-hunter-gather subsistence during the spread of food production. Foragers in the process of adopting herding, loss of stock by pastoralists, and environmental and disease constraints have all been considered possible factors leading to heavy reliance on wild resources (21–24). South of the Mara plains and Lake Victoria, ancient herders left fewer material traces, leading to arguments regarding the existence of a long-term pastoral-forager frontier, south of which herders did not thrive (25–27).

The presence of tsetse flies in eastern Africa has been used as an explanation for observed patterns of subsistence diversity among early pastoralists in the Lake Victoria basin (21, 28) and for limited southward movement (15, 20, 29, 30). A range of zoonoses posed threats for early herders, but trypanosomiasis risks have an especially widespread effect on human communities, even today (10, 12, 13, 30). Mesic, bushy/wooded environments that may have harbored large numbers of tsetse fly (*Glossina* spp.) would have been poorly suited to extensive cattle stock-keeping. The tsetse fly carries trypanosome parasites that transfer to hosts during blood meals and eventually cause often-fatal sleeping sickness in ungulates (predominately domesticates) and humans. In modern and precolonial times, herders have controlled tsetse fly numbers by heavy grazing, burning and destruction of woody areas, and managed livestock to avoid areas with abundant tsetse (10, 31, 32). It is not unreasonable to assume, then, that bushy, tsetse-rich environments would have impeded heavy reliance on livestock by early herders and may have even created a boundary beyond which it was difficult for large numbers of herders to settle (20, 33). Despite an abundance of archaeological sites, however, terrestrial paleoecological data for the Holocene in Kenya are scarce and have been based primarily on lacustrine archives, rather than sites themselves. Pollen and leaf wax biomarkers from lacustrine records from Lake Victoria yield somewhat conflicting paleoenvironmental interpretations: pollen data indicate decreasing moist tree and shrub presence (indicated by Moraceae pollen) in the Lake Victoria basin until ∼2 kya, when grass pollen (Poaceae) increased (Fig. 2) (34), contrasting with stable carbon isotopes from lacustrine leaf wax biomarkers, which indicate persistence of C_4 grasses throughout the last 6 kya, with only a sharp decrease in C_4 around 3 kya (Fig. 2) (35). These contrasting results could be explained by differences in spatial integration, with lipids recording a more localized signal within the catchment and pollen recording a more regional vegetation signal (36), and likely also point to varied, fluctuating input from C_4 grasses during this period. Even so, pollen evidence suggests only minor (∼10%) moist forest in the region compared with ∼20–30% input from

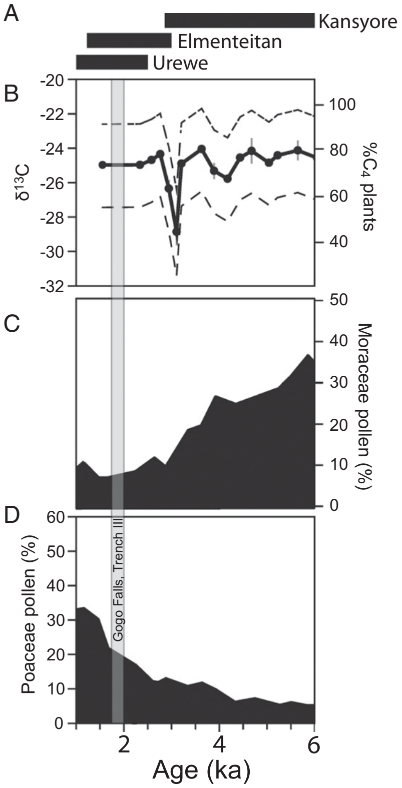

Fig. 2. (*A*) Holocene pottery traditions present at archaeological sites in the Victoria basin. (*B*) Leaf wax $\delta^{13}C$ and modeled $\%C_4$ from lacustrine sedimentary cores in Lake Victoria (35). (*C*) Moraceae (tropical mesic trees and shrubs) pollen counts from lacustrine sedimentary cores in Lake Victoria (data from ref. 34). (*D*) Poaceae (grass) pollen counts from lacustrine sedimentary cores in Lake Victoria (data from ref. 34). *B*, *C*, and *D* modified with permission from Elsevier; www.sciencedirect.com/science/journal/02773791.

grasses. These records offer the important wider ecological context of regional (pollen) and basinal (leaf waxes) ecology, yet they are too coarse to understand specialized pastoralist expansions, and especially for local evidence (site-based reconstruction) of habitats harboring tsetse.

To determine whether or not shifting tsetse-rich environments were present at particular locales during specific periods, direct stable isotope-based paleoecological analysis at archaeological sites can provide a complement to faunal analysis (21, 37–39). Isotopic measurements of enamel carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) can be used to understand diet, habitat, and climate (40, 41). Although bone and tooth collagen have been previously used to assess paleoenvironment at Holocene archaeological sites in Kenya (42), tooth enamel is preferred, as it resists digenetic alteration and can be easily compared with fauna from older periods of geologic time (43). In some instances, faunal tooth enamel isotopes may provide our best estimates of environmental change over time, because these signals are less temporally and spatially attenuated than other proxies, such as leaf wax biomarkers (44), which may be influenced by reservoir effects during catchment transport before deposition (45, 46). The environmental context of the Elmenteitan layers of Gogo Falls has been previously interpreted as a grassland/bushland mosaic, based on analysis of wild species diversity and the presence of modern browsing taxa such as roan or sable antelope (Tragelaphini) and bushpig (*Potamochoerus*), as well as grazers such as oribi (21). The relatively low proportions of domestic stock were interpreted as reflecting environmental constraints on pastoral productivity in the region. The presence of the tsetse fly in a presumed seasonally mesic, bushy/woody environment, it was argued, prevented herders from relying exclusively on domesticates, which resulted in seasonal fishing and hunting of large wild ungulates (21). These interpretations have not yet been ground-truthed with a local, terrestrial paleoecological indicator.

Results

Isotopic data are presented in in Fig. 3 and *SI Appendix*, Tables S1 and S3. For comparison, a compilation of modern comparable herbivore $\delta^{13}C_{1750}$ values, primarily from southern Kenya and northern Tanzania, are presented in Fig. 4 (*SI Appendix*, Table S2) (47–53). The average $\delta^{13}C$ values indicate a diet with >80% C_4 grass for 10 of 13 taxa from Gogo Falls. *Potamochoerus sp.* ($\delta^{13}C = -3.86‰$; $n = 1$), *Sylvicapra sp.* ($\delta^{13}C = -8.81‰$; $n = 1$), and Tragelaphini ($\delta^{13}C = -6.6‰$; $n = 5$) are the most ^{13}C-depleted herbivores in the assemblage, but they are more ^{13}C-enriched than their modern counterparts (Fig. 4; *SI Appendix*, Table S2). Modern hippos average −2.3 ± 1.7‰, whereas hippos at Gogo Falls average 0.6 ± 0.6‰. The presence of both large migratory and small, local bovids provides further evidence for both locally and basinally grassy environments (21).

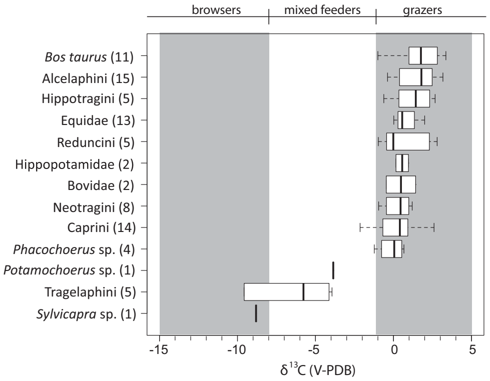

Fig. 3. Box plots of $\delta^{13}C$ tooth enamel values from archaeological tooth enamel, Trench III, Gogo Falls.

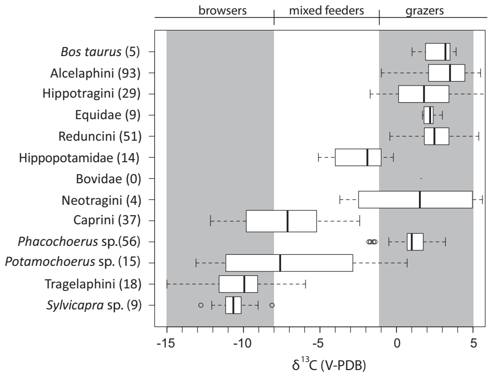

Fig. 4. Box plot of $\delta^{13}C_{1750}$ tooth enamel values from modern comparative fauna from Kenya and Tanzania. *Neotragini and *Sylvicapra sp.* values were calculated to tooth enamel values from keratin, using $\varepsilon_{\text{keratin-enamel}}$ values of 11.1‰ because of a lack of enamel values in the literature.

Domestic fauna are pure C_4 feeders at Gogo Falls. *Bos taurus* is within the range of pure C_4 diet at both Gogo Falls and in the modern environment. Tribe Caprini (Subfamily Caprinae), which includes both goats and sheep, is again overwhelmingly within the range of a pure C_4 diet (1.6 ± 1.4‰). Modern goat $\delta^{13}C_{1750}$ values from locations across Kenya range from −2.6‰ to −12.3‰, whereas modern sheep range from −0.3‰ to −1.5‰ (*SI Appendix*, Fig. S1 and Table S4) because of the different dietary preferences of sheep and goats. Sheep are primarily grazers, whereas goats are mixed feeders that tend to browse, as their highly efficient digestive physiology confers an advantage for consuming low-quality woody forage (50, 54–57). Criteria for distinguishing domestic sheep and goat teeth have not been considered reliable in Africa (58), and Gogo Falls samples, at the time of identification, were simply identified as sheep or goat. Future studies may distinguish teeth and postcranial bones in African samples (59). If both sheep and goats were present at Gogo Falls, then these isotopic results indicate a much higher consumption of C_4 resources by modern goats than is typically observed (50, 56, 60). If the isotope data represent values exclusively from sheep, which is more likely, this level of C_4 intake is not unusual, yet the presence of sheep only at this site is unusual compared with current herding practices in East Africa.

Discussion

In comparison with the present day, isotopic analyses of herbivores indicate that during the Elmenteitan occupation at Gogo Falls, there were few C_3 browsers or mixed C_3–C_4 feeders, suggesting a landscape dominated by C_4 grasses. This interpretation is in general agreement with $\delta^{13}C_{\text{wax}}$ values (Fig. 2) from lacustrine cores in Lake Victoria (which likely indicate vegetation locally, within the lake catchment), and to a lesser extent with pollen records, which indicate mixed environments regionally. These three lines of evidence, taken together, strongly imply an abundance of C_4 grasses in the basin during this period. Vegetation in and around the Winam Gulf today has been characterized as "evergreen and semi-evergreen bushland and thicket," "edaphic wooded grasslands and grasslands on drainage impeded or seasonally flooded soils," and "moist combretum wooded grassland" (which comprises the ecology area around the Kuja River, where the Gogo Falls is located) (61). Faunally based interpretations, primarily the presence of grazers and modern browsers such as Tragelaphini and *Potamochoerus* sp., of the ancient environment at Gogo Falls suggested a woodland/grassland/bushland mosaic that is climatologically and ecologically similar to today (21), which would have supported tsetse flies. This bushland interpretation is not supported by the isotopic data, which are dominated by C_4-grazing taxa with few C_3-browsing taxa, contradicting long-held assumptions of modern climate and ecology persisting over the last 3 millennia in most regions of eastern Africa (19, 21, 24).

Given the resolution of data available, it is not yet possible to quantify the relative proportions of grassy and woody vegetation; however, abundant C_4 grasses must have been present. Abundant grassy vegetation may have been the result of changes in rainfall seasonality in the later Holocene (62, 63), changes in total rainfall in the Lake Victoria basin, increased burning, or ecological factors, such as heavy grazing by domesticates or wild herbivores. Controlled grazing by cattle, sheep, and goats can stimulate new grass growth where grazing herbivores thrive (64, 65). Overgrazing, however, makes environments more bushy and reduces grass height (66). Burning promotes new grass and may have maintained grasslands if herders were regularly burning savanna for livestock, as is a common practice in modern eastern Africa (67–69). The presence of megaherbivores maintains grasslands as well, and when both burning and elephant or giraffe populations are high, grasslands expand (67, 68, 70). Given such complex environmental interactions in African grasslands today, the question arises whether ancient herders in the Lake Victoria basin helped create grasslands through grazing and fire, or whether they were created and maintained by other ecological and climatological factors (71, 72).

The isotopic data from Gogo Falls and leaf wax data from the Lake Victoria basin reveal an ideal environment for large grazing herds of domesticates in the immediate Lake Victoria basin catchment, one rich in C_4 grasses. Such grasslands were not an ideal environment for tsetse flies, which calls into question the maintenance of long-term areas of hunter-gatherer-pastoral interaction and the inhibition of southward movements of herders by stable and extensive bands of tsetse bush (2). This study fits with the findings of recent genetic research including Y-chromosome, lactase persistence, and livestock data that point to some migration of herders from eastern to southern Africa (5–7). Archaeologists arguing for successful early pastoral migrations from eastern to southern Africa have pointed to some similarities between Elmenteitan pottery and early herder ceramics in southern Africa (73). Our data imply that a tsetse-rich barrier preventing herders from moving through the Lake Victoria basin into northern Tanzania and other parts of sub-Saharan Africa (9, 24, 33, 74) was not widespread 2,000 y ago, bolstering the possibility of such connections.

On a local level, our data show that Elmenteitan herders at Gogo Falls were not forced into hunting and fishing because of ecological constraints on stock-keeping. The Elmenteitan mammalian fauna at Gogo Falls are made up of 53.5% domestic livestock comprising cattle and sheep (based on isotopes). Fishing was also a significant activity (21). Recent research in the Lake Victoria basin has shown that the nearby site of Wadh Lang'o shares similar dates of 1,950 ± 35 y B.P. for early Elmenteitan levels (27, 75) and a number of similarities with Gogo Falls: Wadh Lang'o is also a large open-air site with a long sequence containing Kansyore, Elmenteitan, and Iron Age horizons (27, 75). It is situated in a similar environmental setting, on the banks of a river flowing into Lake Victoria. There are as yet no direct paleoecological proxies from this site, but according to lacustrine paleoenvironmental archives (Fig. 2), it was also likely situated in a grassy environment. Fishing is a significant activity at both sites; however, the mammals in the Elmenteitan faunal horizons in Trench 1, Wadh Lang'o (below datum 140–190 cm), are predominantly (89–91%) domestic, suggesting limited hunting (75). Alcelaphines are represented, but the zebra and oribi present at Gogo Falls are absent at Wadh Lang'o. Herding strategies also differed between Wadh Lang'o and Gogo Falls, with cattle making up 1% or less of the domestic fauna at Wadh Lang'o (n = 88 below datum 140–190 cm; n = 156 below datum 140–160 cm; *SI Appendix*, Table S5) compared with 32% (n = 328) at Gogo Falls. In strong contrast with these sites in the Lake Victoria basin, there is no fishing and very little hunting in Elmenteitan sites on the plains of southern Kenya (19, 20). Cattle, sheep, and goats make up 97–100% of the fauna at the open air settlement sites in the Lemek-Mara, including Ngamuriak, Sugenya, and Oldorotua, as well as the Central Rift Valley rock shelter of Maasai Gorge (*SI Appendix*, Table S5). Reliance on cattle and some small stock, combined with fishing and significant hunting at Gogo Falls, is an unexpected contrast with nearby Elmenteitan sites and does not fit a typical Elmenteitan subsistence pattern. Nor do the fauna, material culture, and organization of this site suggest hunter-gatherers in the process of adopting herding. Gogo Falls appears to have been populated by a unique group of people, potentially a small group of herders, who took flexible approaches to subsistence opportunities and interactions with hunter-gatherer-fishers as they followed grassy corridors in eastern Africa.

Conclusions

Our results provide much-needed late Holocene paleoenvironmental data for the Lake Victoria basin and demonstrate that substantial ecological changes occurred over the last 2,000 y. Isotopic data reveal that the fauna were dominated by C_4 grazers with very few C_3 browsing taxa, suggesting a grassy paleoecological setting for the unique Elmenteitan site of Gogo Falls. This challenges interpretations based on macrofaunal remains and models of disease-depressed livestock production (21). The isotopic findings also draw attention to herder relations with hunter-gatherers, rather than ecology, in consumption of large wild ungulates in western Kenya. This suggests that social factors may have played a greater role than previously thought in subsistence diversity during the spread of pastoralism in Eastern Africa. High levels of hunting at Gogo Falls can no longer be attributed to closed or bushy habitats that inhibited livestock production and southward movement of herders (21) and contributed to long-term frontier interactions between pastoralists and hunter-gatherers (25, 27, 74). These data raise interesting questions about the interplay among herders, environmental management and adaptation, and ecological drivers for grassland maintenance. Finally, in light of the isotope data from Gogo Falls and lacustrine leaf wax data (35), the Lake Victoria basin may have been the setting for grassy corridors through which demic migration of pastoralists occurred out of eastern Africa and toward southern Africa (30).

Materials and Methods

Site Description. The archaeological site of Gogo Falls is located on the banks of the Kuja River by a dam that bears the same name (34°21′E, 0°34′S; Fig. 1). The area receives ~1,060 mm/y in rainfall, with bimodal rainfall seasonality, with rains occurring in March–May and October–November (28). At this time, the area surrounding the site has been ecologically altered by farming, but natural vegetation is characterized as a wooded grassland (61). Nearby local wild fauna include roan antelope, zebra, and giraffe, and historically, a diverse mammalian population including elephant, lion, cheetah, and rhinoceros (61). Browsers are rare, and thus woodland and thicket encroachment has been occurring in the area (76).

Gogo Falls was excavated by Robertshaw in 1980 and 1983 (28, 77), and teeth analyzed for this article were uncovered during the 1983 excavation.

Five noncontinuous trenches were dug in the study area, each yielding abundant faunal remains, artifacts, and potsherds spanning three cultural traditions: Kansyore, Elmenteitan, and Urewe (28). The stratigraphic details of Trench III is presented by Robertshaw (28), but the highlight of this excavation is a 1.5-m ash and dung midden layer containing Elmenteitan pottery exclusively, which Robertshaw interpreted as a stock-keeping area. Radiocarbon dating of charcoal near the top of Trench III gave an uncalibrated age of 1,770 ± 80 y B.P., and another date from the bottom of the trench gave an age of 1,990 ± 80 y B.P. (28), with no evidence of stratigraphic mixing. These dates calibrate to 1,646 calibrated y B.P. (calBP) ± 96 and 1,900 calBP ± 100 at 95.4% confidence using ShCal13 (78).

Teeth were selected from faunal analysis by Marshall and Stewart (21). All the faunal material excavated from the 1.5-m ash midden is in excellent preservation. The fauna from this trench are diverse, containing fish, avian, and mammalian remains. Domestic caprines (goat and sheep) constitute the largest proportion of the assemblage (36.4%), followed by cattle (17.1%), topi/hartebeest (presented here at the tribal level of identification, "Alcelaphini"; 15.2%), oribi (presented as "Neotragini"; 11.8%), zebra (11.3%), reedbuck ("Reduncini"; 2.8%), warthog (1.8%), and eland and roan/sable ("T. oryx" and "Hippotragini", respectively; 1.1%) (21). Stable isotope analysis was carried out on a subset of these teeth, including samples from rarer fauna as well (i.e., *Potamochoerus* sp. and *Sylvicapra sp.*).

Laboratory Analysis. Following the sampling procedures outlined by the National Museums of Kenya, teeth were photographed and sampled along broken edges, using a Dremel tool and diamond drill bit. About 1 mg enamel powder was drilled from each sample. Enamel powder was prepared and analyzed at the University of Utah. Enamel powders were treated with 0.1 M buffered acetic acid (pH ~5.3) for 30 min to remove labile carbonates (79, 80). After acid treatment, powders were rinsed three times with distilled water and dried at 60 °C overnight. Sample powders were weighed into silver capsules and dried under vacuum at 200 °C for 2 h before analysis. Samples were analyzed for $\delta^{13}C$ and $\delta^{18}O$ on a Finnigan MAT 252 coupled to a Carboflo dual-inlet carbonate device (common phosphoric acid bath at 90 °C for 15 min reaction time). Stable isotope ratios are reported as delta (δ) values relative to the international carbon isotope standard, Vienna Pee Dee Belemnite, using the standard permil (‰) notation, where $\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1{,}000$ and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the sample and standard, respectively. SD of an internal carbonate standard (Carrara marble) was ±0.1‰.

Dietary designations for herbivores are based on estimated consumption of C_4 plants (tropical grasses) and C_3 plants (trees, shrubs, herbs), which is calculated using a hypothetical 100% C_4 diet and an isotope enrichment (ε^*) between diet and herbivore tooth enamel of 14.1‰ (81). Estimated carbon isotope composition of tooth enamel for a 100% C_4 diet is based on the average isotopic value of modern C_4 plants in eastern and central Africa (−12.9‰; $n = 764$) (82). Changes in the isotopic composition of atmospheric CO_2 resulting from the combustion of fossil fuels between modern environments and preindustrial Holocene (presented here as $\delta\ ^{13}C_{1750}$) were accounted for by adding 1.6‰ to the modern average $\delta^{13}C$ of C_4 plants (81, 83, 84).

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1. Marshall F, Hildebrand E (2002) Cattle Before Crops: The Beginnings of Food Production in Africa. *J World Prehist* 16(2):99–143.
2. Smith AB (1992) Origins and spread of pastoralism in Africa. *Annu Rev Anthropol* 21:125–141.
3. Sadr K (1998) The First Herders at the Cape of Good Hope. *Afr Archaeol Rev* 15(15):101–132.
4. Pleurdeau D, et al. (2012) "Of sheep and men": Earliest direct evidence of caprine domestication in southern Africa at Leopard Cave (Erongo, Namibia). *PLoS ONE* 7(7):e40340.
5. Ranciaro A, et al. (2014) Genetic origins of lactase persistence and the spread of pastoralism in Africa. *Am J Hum Genet* 94(4):496–510.
6. Stock F, Gifford-Gonzalez DP (2013) Genetics and African Cattle Domestication. *Afr Archaeol Rev* 30:51–72.
7. Henn BM, et al. (2008) Y-chromosomal evidence of a pastoralist migration through Tanzania to southern Africa. *Proc Natl Acad Sci USA* 105(31):10693–10698.
8. Schweitzer FR (1974) Archaeological evidence for sheep at the Cape. *The South African Archaeological Bulletin* 29(115-116):75–82.
9. Smith AB (2014) *The Origins of Herding in Southern Africa: Debating the "Neolithic" model* (Lambert Academic Publishing, Saarbrucken).
10. Gifford-Gonzalez DP (2000) Animal disease challenges to the emergence of pastoralism in sub-Saharan Africa. *Afr Archaeol Rev* 17(3):95–139.
11. Smith AB (2005) *African Herders: Emergence of Pastoral Traditions* (AltaMira Press, Walnut Creek, CA).
12. Ford J (1971) *The Role of the Trypanosomaises in African Ecology: A Study of the Tsetse Fly Problem* (Clarendon Press, Oxford).
13. Cecchi G, Mattioli RC, Slingenbergh J, de la Rocque S (2008) Land cover and tsetse fly distributions in sub-Saharan Africa. *Med Vet Entomol* 22(4):364–373.
14. Marshall F, Stewart K, Barthelme J (1984) Early domestic stock at Dongodien in northern Kenya. *Azania* 19(1):120–127.
15. Prendergast ME (2011) Hunters and herders at the periphery: The spread of herding in eastern Africa. *People and Animals in Holocene Africa Recent Advances in Archaeozoology*, eds Jousse H, Lesur J (Africa Magna Verlag, Frankfurt), pp 43–58.
16. Dale D, Ashley CZ (2010) Holocene hunter-fisher-gatherer communities: new perspectives on Kansyore Using communities of Western Kenya. *Azania* 45(1):24–48.
17. Merrick HV, Monaghan MC (1984) The date of the cremated burials in Njoro River Cave. *Azania* 19(1):7–11.
18. Robertshaw P (1988) The elmenteitan: An early food-producing culture in East Africa. *World Archaeol* 20:57–69.
19. Marshall F (1990) Origins of specialized pastoral production in East Africa. *Am Anthropol* 92:873–894.
20. Marshall F, Grillo K, Arco L (2011) Prehistoric Pastoralists and Social Responses to Climatic risk in East Africa. *Sustainable Lifeways: Cultural Persistence in an Ever-changing Environment*, eds Miller NF, Moore KM, Ryan K (University of Pennsylvania Press, Philadelphia), pp 74–105.
21. Marshall F, Stewart K (1994) Hunting, fishing and herding pastoralists of western Kenya: The fauna from Gogo Falls. *Archaeozoologia* 7:7–27.
22. Gifford-Gonzalez DP, Isaac GL, Nelson CM (1980) Evidence for predation and pastoralism at Prolonged Drift: a Pastoral Neolithic site in Kenya. *Azania* 15(1):57–108.
23. Prendergast ME, Mutundu KK (2009) Late Holocene zooarchaeology in East Africa: Ethnographic analogues and interpretive challenges. *Documenta Archaeobiologiae* 7:203–232.
24. Gifford-Gonzalez DP (1998) Early pastoralists in East Africa: Ecological and social dimensions. *J Anthropol Archaeol* 17(2):166–200.
25. Prendergast ME, et al. (2013) Pastoral Neolithic sites on the southern Mbulu Plateau, Tanzania. *Azania* 48(4):498–520.
26. Bower J (1991) The pastoral neolithic of East Africa. *J World Prehist* 5(1):49–82.
27. Lane P (2004) The "moving frontier" and the transition to food production in Kenya. *Azania* 39(1):243–264.
28. Robertshaw P (1991) Gogo Falls: Excavations at a complex archaeological site east of Lake Victoria. *Azania* 26(1):63–195.
29. Hanotte O, et al. (2002) African pastoralism: genetic imprints of origins and migrations. *Science* 296(5566):336–339.
30. Smith AB (1984) Environmental limitations on prehistoric pastoralism in Africa. *Afr Archaeol Rev* 2:99–111.
31. Kjekshus H (1996) *Ecology Control and Economic Development in East African History: The Case of Tanganyika, 1850-1950* (Ohio University Press, Athens, OH).
32. Lamprey R, Waller R (1990) The Loita-Mara Region in Historical Times: Patterns of Subsistence, Settlement and Ecological Change. *Early Pastoralists of South-Western Kenya*, ed Robertshaw P (British Institute of Eastern Africa, Nairobi), pp 16–35.
33. Smith AB (1992) Origins and spread of pastoralism in Africa. *Annu Rev Anthropol* 21:125–141.
34. Kendall RL (1969) An ecological history of the Lake Victoria basin. *Ecol Monogr* 39(2):121–176.
35. Berke MA, et al. (2012) Molecular records of climate variability and vegetation response since the Late Pleistocene in the Lake Victoria basin, East Africa. *Quat Sci Rev* 55(8):59–74.
36. Farrimond P, Flanagan RL (1996) Lipid stratigraphy of a Flandrian peat bed (Northumberland, UK): Comparison with the pollen record. *Holocene* 6(1):69–74.
37. Lane P, et al. (2007) The transition to farming in eastern Africa: new faunal and dating evidence from Wadh Lang'o and Usenge, Kenya. *Antiquity* 81(311):62–81.
38. Gifford-Gonzalez DP (1985) Faunal Assemblages from Masai Gorge Rockshelter and Marula Rockshelter. *Azania* 20(1):69–88.
39. Marean CW (1992) Hunter to herder: Large mammal remains from the hunter-gatherer occupation at Enkapune Ya Muto rock-shelter, Central Rift, Kenya. *Afr Archaeol Rev* 10(1):65–127.
40. Lee-Thorp JA, Sponheimer M, Luyt J (2007) Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. *J Hum Evol* 53(5):595–601.
41. Levin NE, Cerling TE, Passey BH, Harris JM, Ehleringer JR (2006) A stable isotope aridity index for terrestrial environments. *Proc Natl Acad Sci USA* 103(30):11201–11205.
42. Ambrose SH, DeNiro MJ (1989) Climate and habitat reconstruction using stable carbon and nitrogen isotope ratios of collagen in prehistoric herbivore teeth from Kenya. *Quat Res* 31(3):407–422.
43. Kohn MJ, Cerling TE (2002) Stable isotope compositions of biological apatite. *Rev Mineral Geochem* 48:455–488.

44. Kingston JD (2007) Shifting adaptive landscapes: Progress and challenges in reconstructing early hominid environments. *Am J Phys Anthropol* 50(Suppl 45):20–58.
45. Uchida M, et al. (2005) Age discrepancy between molecular biomarkers and calcareous foraminifera isolated from the same horizons of Northwest Pacific sediments. *Chem Geol* 218(1-2):73–89.
46. Matsumoto K, Kawamura K, Uchida M (2007) Radiocarbon content and stable carbon isotopic ratios of individual fatty acids in subsurface soil: Implication for selective microbial degradation and modification of soil organic matter. *Geochem J* 41: 483–492.
47. Cerling TE, et al. (2011) Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Natl Acad Sci USA* 108(23):9337–9341.
48. Harris JM, Cerling TE (2002) Dietary adaptations of extant and Neogene African suids. *Journal of Zoology* 256(1):45–54.
49. Cerling TE, Harris JM, Passey BH (2003) Diets of East African Bovidae based on stable isotope analysis. *J Mammal* 84(2):456–470.
50. Balasse M, Ambrose SH (2005) Distinguishing sheep and goats using dental morphology and stable carbon isotopes in C$_4$ grassland environments. *J Archaeol Sci* 32(5): 691–702.
51. Van Der Merwe NJ (2013) Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. *S Afr J Sci* 109(11-12):1–14.
52. Bocherens H, Koch PL, Mariotti A, Geraads D, Jaeger JJ (1996) Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. *Palaios* 11(4):306–318.
53. Kingston JD (2011) Stable isotopic analyses of Laetoli fossil herbivores. *Geology, Geochronology, Paleoecology and Paleoenvironment*, Paleontology and Geology of Laetoli: Human Evolution in Context, ed Harrison T (Springer, Dordrecht, The Netherlands), Vol 1, pp 293–328.
54. Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia* 78:443–457.
55. Silanikove N (2000) The physiological basis of adaptation in goats to harsh environments. *Small Rumin Res* 35(3):181–193.
56. Ambrose SH, DeNiro MJ (1986) The isotopic ecology of East African mammals. *Oecologia* 69:395–406.
57. Migongo-Bake W, Hansen RM (1987) Seasonal diets of camels, cattle, sheep, and goats in a common range in eastern Africa. *J Range Manage* 40(1):76–79.
58. Badenhorst S, Plug I (2003) The archaeozoology of goats, *Capra hircus* (Linnaeus, 1758): their size variation during the last two millennia in southern Africa (Mammalia: Artiodactyla: Caprini). *Ann Transvaal Mus* 40:91–121.
59. Zeder MA, Pilaar SE (2010) Assessing the reliability of criteria used to identify mandibles and mandibular teeth in sheep, *Ovis*, and goats, *Capra*. *J Archaeol Sci* 37: 252–242.
60. Balasse M, Ambrose SH (2005) Mobilité altitudinale des pasteurs néolithiques dans la vallée du Rift (Kenya) : Premiers indices de l'analyse du δ^{13}C de l'émail dentaire du cheptel domestique. *Anthropozoologica* 40(1):147–166.
61. Lillesø J-PB, et al. (2011) The atlas. *Potential Natural Vegetation of Eastern Africa (Ethiopia, Kenya, Malawi, Rwanda, Tanzania, Uganda and Zambia)*, Forest and Landscape Working Papers (Forest & Landscape, University of Copenhagen, Frederiksberg, Denmark), Vol 1, No 61/2011.
62. Tierney JE, Lewis SC, Cook BI, LeGrande AN, Schmidt GA (2011) Model, proxy and isotopic perspectives on the East African Humid Period. *Earth Planet Sci Lett* 307(1-2): 103–112.
63. Thompson LG, et al. (2002) Kilimanjaro ice core records: evidence of holocene climate change in tropical Africa. *Science* 298(5593):589–593.
64. Odadi WO, Karachi MK, Abdulrazak SA, Young TP (2011) African wild ungulates compete with or facilitate cattle depending on season. *Science* 333(6050):1753–1755.
65. Veblen KE, Young TP (2010) Contrasting effects of cattle and wildlife on the vegetation development of a savanna landscape mosaic. *J Ecol* 98(5):993–1001.
66. Treydte AC, Baumgartner S, Heitkönig IM, Grant CC, Getz WM (2013) Herbaceous forage and selection patterns by ungulates across varying herbivore assemblages in a South African Savanna. *PLoS ONE* 8(12):e82831.
67. Dublin HT (1995) Vegetation Dynamics in the Serengeti-Mara Ecosystem: The Role of Elephants, Fire, and Other Factors. *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*, eds Sinclair ARE, Acrese P (University of Chicago Press, Chicago), pp 71–90.
68. Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and Fire as Causes of Multiple Stable States in the Serengeti-Mara Woodlands. *J Anim Ecol* 59(3):1147–1164.
69. Archibald S, Bond WJ (2004) Grazer movements: Spatial and temporal responses to burning in a tall-grass African savanna. *Int J Wildland Fire* 13(3):377–385.
70. Lamprey RH, Reid RS (2004) Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *J Biogeogr* 31(6):997–1032.
71. Good SP, Caylor KK (2011) Climatological determinants of woody cover in Africa. *Proc Natl Acad Sci USA* 108(12):4902–4907.
72. Sankaran M, et al. (2005) Determinants of woody cover in African savannas. *Nature* 438(7069):846–849.
73. Smith AB (2009) Pastoralism in the Western Cape Province, South Africa: A retrospective review. *Journal of African Archaeology* 7(2):239–252.
74. Clark JD (1980) Early human occupation of African savanna environments. *Human Ecology in Savanna Environments*, ed Harris DR (Academic Press, London), pp 41-72.
75. Prendergast ME (2010) Kansyore fisher-foragers and transitions to food production in East Africa: The view from Wadh Lang'o, Nyanza Province, Western Kenya. *Azania* 45(1):83–111.
76. Muriuki GW, Njoka TJ, Reid RS (2003) Tsetse, wildlife and land-cover change in Ruma National Park, South-western Kenya. *J Hum Ecol* 14(4):229–235.
77. Collett DP, Robertshaw P (1980) Early Iron Age and Kansyore Pottery: Finds from Gogo Falls, South Nyanza. *Azania* 15(1):133–145.
78. Hogg AG, et al. (2013) SHCal$_{13}$ Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* 55(2):1–15.
79. Lee-Thorp JA, Van der Merwe NJ (1987) Carbon isotope analysis of fossil bone apatite. *S Afr J Sci* 83:712–715.
80. Koch PL, Tuross N, Fogel M (1997) The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. *J Archaeol Sci* 24(5): 417–430.
81. Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120(3):347–363.
82. Cerling TE (2014) 14.12 Stable Isotope Evidence for Hominin Environments in Africa. *Treatise on Geochemistry*, ed Cerling TE (Elsevier, Amsterdam), 2nd Ed, pp 157–167.
83. Francey RJ, et al. (1999) A 1000-year high precision record of δ^{13}C in atmospheric CO2. *Tellus B Chem Phys Meterol* 51(2):170–193.
84. Keeling CD, Piper S, Bollenbacher AF, Walker SJ (2010) Monthly atmospheric 13C/12C isotopic ratios for 10 SIO stations. Available at cdiac.ornl.gov/trends/co2/iso-sio/iso-sio.html. Accessed October 1, 2014.

SI Appendix

Table S1: $\delta^{13}C$ tooth enamel values (average and standard deviation) from archaeological tooth enamel, Trench III, Gogo Falls.

Family	**Tribe**	**Species**	**$\delta^{13}C$**	**Std. dev.**	**no. samples**
Bovidae	Bovini	*Bos taurus*	1.6	1.5	11
Bovidae	Alcelaphini		1.5	1.2	15
Bovidae	Hippotragini		1.2	1.4	5
Equidae		*Equus sp.*	0.8	0.6	13
Bovidae	Reduncini		0.7	1.7	5
Hippopotamidae		*Hippopotamus amphibius*	0.6	0.6	2
Bovidae	unk.		0.5	1.3	2
Bovidae	Neotragini	*Ourebia ourebi*	0.3	0.8	8
Bovidae	Caprini		0.2	1.4	14
Suidae		*Phacochoerus sp.*	-0.1	0.9	4
Suidae		*Potamochoerus sp.*	-3.9		1
Bovidae	Tragelaphini	*Taurotragus oryx*	-6.6	2.8	5
Bovidae	Cephalophini	*Sylvicapra sp.*	-8.8		1

Table S2: $\delta^{13}C_{1750}$ tooth enamel values (average and standard deviation) from modern comparative fauna from Kenya and Tanzania. *Neotragini and *Sylvicapra* values were calculated to tooth enamel values from keratin using $\varepsilon_{\text{keratin-enamel}}$ values of 11.1‰ because of a lack of enamel values in the literature.

Family	**Tribe**	**Species**	**$\delta^{13}C$**	**std. dev. (±)**	**no. samples**	**Ref.**
Bovidae	Bovini	*Bos taurus*	2.7	1.2	5	(1, 2)
Bovidae	Alcelaphini		3.2	1.5	93	(3-6)
Bovidae	Hippotragini		1.8	2.1	29	(3-5)
Equidae		*Equus sp.*	2.2	0.4	9	(5, 7, 8)
Bovidae	Reduncini		2.5	1.4	51	(3, 4)
Hippopotamidae		*Hippopotamus amphibius*	-2.3	1.7	14	(7, 9)
Bovidae	Neotragini*	*Ourebia ourebi*	1.3	4.4	4	(3)
Bovidae	Caprini		-4.0	3.4	22	(10)
Suidae		*Phacochoerus sp.*	1.0	1.1	56	(5, 6, 9)
Suidae		*Potamochoerus sp.*	-6.9	4.9	15	(9)
Bovidae	Tragelaphini	*T. oryx*	-10.4	2.2	18	(3, 4)
Bovidae	Cephalophini	*Sylvicapra sp.**	-10.6	1.4	9	(3)

Table S3: δ^{13}C and δ^{18}O tooth enamel values from Gogo Falls fauna. Calculated %C_4 has been rounded to the nearest 5% to account for uncertainty in the dietary model.

Specimen ID	Common/ Species name	Family/Sub-Family	Tribe	δ^{13}C	δ^{18}O	%C4
KKC13-E-296	*Bos taurus*	Bovidae	Bovini	-1.0	1.0	80
KKC13-E-297	*Bos taurus*	Bovidae	Bovini	-0.8	-2.7	80
KKC13-E-298	*Bos taurus*	Bovidae	Bovini	1.9	1.8	100
KKC13-E-299	*Bos taurus*	Bovidae	Bovini	1.5	1.2	100
KKC13-E-300	*Bos taurus*	Bovidae	Bovini	1.8	0.3	100
KKC13-E-301	*Bos taurus*	Bovidae	Bovini	2.9	1.7	100
KKC13-E-302	*Bos taurus*	Bovidae	Bovini	2.7	2.8	100
KKC13-E-303	*Bos taurus*	Bovidae	Bovini	0.6	0.5	90
KKC13-E-304	*Bos taurus*	Bovidae	Bovini	3.4	2.3	100
KKC13-E-305	*Bos taurus*	Bovidae	Bovini	3.2	2.1	100
KKC13-E-306	*Bos taurus*	Bovidae	Bovini	1.3	2.5	95
KKC13-E-307	*Bos taurus*	Bovidae	Bovini	1.8	0.7	100
KKC13-E-342		Bovidae	Alcelaphini	0.2	1.4	90
KKC13-E-343		Bovidae	Alcelaphini	0.1	1.5	90
KKC13-E-345		Bovidae	Alcelaphini	3.2	2.4	100
KKC13-E-350		Bovidae	Alcelaphini	-0.4	-0.4	85
KKC13-E-351		Bovidae	Alcelaphini	1.3	0.3	95
KKC13-E-352		Bovidae	Alcelaphini	3.0	1.9	100
KKC13-E-353		Bovidae	Alcelaphini	0.6	0.1	90
KKC13-E-354	*Damaliscus spp.*	Bovidae	Alcelaphini	2.7	1.5	100
KKC13-E-355	*Damaliscus spp.*	Bovidae	Alcelaphini	3.0	1.9	100
KKC13-E-356	topi/hartebeest	Bovidae	Alcelaphini	2.1	-2.1	100
KKC13-E-357	*Damaliscus spp.*	Bovidae	Alcelaphini	0.6	-0.3	90
KKC13-E-358	*Damaliscus spp.*	Bovidae	Alcelaphini	2.2	1.3	100
KKC13-E-346*	*Alcelaphus/ Damaliscus*	Bovidae	Alcelaphini	0.0	-0.3	85
KKC13-E-348*		Bovidae	Alcelaphini	2.2	1.3	100
KKC13-E-377	topi/hartebeest	Bovidae	Alcelaphini	0.3	1.1	90
KKC13-E-349	roan/sable	Bovidae	Hippotragini	-0.6	-2.7	85
KKC13-E-373	roan/sable	Bovidae	Hippotragini	1.4	-2.1	100
KKC13-E-376	roan/sable	Bovidae	Hippotragini	2.3	0.4	100
KKC13-E-372*	roan	Bovidae	Hippotragini	2.7	0.2	100
KKC13-E-374*	roan/sable	Bovidae	Hippotragini	0.9	2.4	95
KKC13-E-317	*Equus burchelli*	Equidae		1.5	1.9	100
KKC13-E-318	*Equus burchelli*	Equidae		2.0	1.4	100
KKC13-E-319	*Equus burchelli*	Equidae		1.3	0.0	100
KKC13-E-320	*Equus burchelli*	Equidae		0.8	1.3	95

Specimen ID	Common/ Species name	Family/Sub-Family	Tribe	$\delta^{13}C$	$\delta^{18}O$	%C4
KKC13-E-315	*Equus spp.*	Equidae		0.1	1.0	90
KKC13-E-316	*Equus spp.*	Equidae		1.6	2.4	100
KKC13-E-321	*Equus spp.*	Equidae		0.6	1.2	90
KKC13-E-323	*Equus spp.*	Equidae		0.5	-0.4	90
KKC13-E-324	*Equus spp.*	Equidae		0.0	-0.3	90
KKC13-E-312*	*Equus spp.*	Equidae		0.1	1.4	90
KKC13-E-314*	*Equus spp.*	Equidae		0.0	0.6	90
KKC13-E-367	kob/waterbuck	Bovidae	Reduncini	2.8	0.9	100
KKC13-E-378	kob/waterbuck	Bovidae	Reduncini	2.3	1.3	100
KKC13-E-368*		Bovidae	Reduncini	-0.4	-0.3	85
KKC13-E-370*		Bovidae	Reduncini	-1.0	-0.2	80
KKC13-E-371*		Bovidae	Reduncini	1.0	-2.6	95
KKC13-E-330	*H. amphibius*	Hippopotamidae		0.2	-2.6	90
KKC13-E-331	*H. amphibius*	Hippopotamidae		-0.5	0.7	85
KKC13-E-309*	unk	Bovidae		1.4	0.8	100
KKC13-E-347	unk	Bovidae		1.0	0.7	95
KKC13-E-333	*Ourebia ourebi*	Bovidae	Neotragini	0.0	-1.1	95
KKC13-E-334	*Ourebia ourebi*	Bovidae	Neotragini	0.9	-3.0	94
KKC13-E-335	*Ourebia ourebi*	Bovidae	Neotragini	-0.6	0.9	85
KKC13-E-336	*Ourebia ourebi*	Bovidae	Neotragini	-0.9	2.1	80
KKC13-E-337	*Ourebia ourebi*	Bovidae	Neotragini	-0.3	1.9	85
KKC13-E-338	*Ourebia ourebi*	Bovidae	Neotragini	1.2	0.5	95
KKC13-E-339	*Ourebia ourebi*	Bovidae	Neotragini	0.9	0.8	95
KKC13-E-340	*Ourebia ourebi*	Bovidae	Neotragini	0.9	0.7	95
KKC13-E-283*	goat/sheep	Caprinae		-0.4	1.9	85
KKC13-E-280	goat/sheep	Caprinae		2.2	3.0	100
KKC13-E-281	goat/sheep	Caprinae		0.2	1.9	90
KKC13-E-282	goat/sheep	Caprinae		-2.0	1.6	75
KKC13-E-284	goat/sheep	Caprinae		-0.8	3.2	80
KKC13-E-285	goat/sheep	Caprinae		0.5	4.3	90
KKC13-E-288	goat/sheep	Caprinae		1.7	1.3	100
KKC13-E-289	goat/sheep	Caprinae		-0.7	-2.8	80
KKC13-E-290	goat/sheep	Caprinae		0.5	3.8	90
KKC13-E-291	goat/sheep	Caprinae		-2.1	-0.6	70
KKC13-E-292	goat/sheep	Caprinae		2.6	2.9	100
KKC13-E-293	goat/sheep	Caprinae		0.7	1.6	90
KKC13-E-286*	goat/sheep	Caprinae		0.3	3.3	90
KKC13-E-287*	goat/sheep	Caprinae		-1.2	-1.9	80
KKC13-E-326	*Phacochoerus sp.*	Suidae		0.7	1.4	90
KKC13-E-327	*Phacochoerus sp.*	Suidae		0.4	1.7	90
KKC13-E-328	*Phacochoerus sp.*	Suidae		-0.3	-0.2	85

Specimen ID	**Common/ Species name**	**Family/Sub-Family**	**Tribe**	**$\delta^{13}C$**	**$\delta^{18}O$**	**%C4**
KKC13-E-332	*Potamochoerus sp.*	Suidae		-5.8	2.3	45
KKC13-E-360	*Taurotragus oryx*	Bovidae	Tragelaphini	-9.6	-0.8	20
KKC13-E-363	*Taurotragus oryx*	Bovidae	Tragelaphini	-3.9	0.0	60
KKC13-E-364	*Taurotragus oryx*	Bovidae	Tragelaphini	-4.1	1.2	60
KKC13-E-361*	*Taurotragus oryx*	Bovidae	Tragelaphini	-9.6	2.0	20
KKC13-E-362*	*Sylvicapra sp.*	Bovidae	Cephalophini	-8.8	-1.1	25

**sample was run untreated due to low sample volume*

Table S4: Modern caprine $\delta^{13}C_{1750}$ tooth enamel data.

Common/Species name	Locality	$\delta^{13}C_{1750}$	Citation
sheep	Naivasha Basin	0.1	(10)
sheep	Naivasha Basin	0.3	(10)
sheep	Naivasha Basin	-0.9	(10)
sheep	Naivasha Basin	0.2	(10)
sheep	Naivasha Basin	-0.6	(10)
sheep	Naivasha Basin	-1.5	(10)
sheep	Central Rift valley	-0.7	(2)
sheep	Central Rift valley	-0.4	(2)
goat	Baragoi	-7.9	this study
goat	Baringo	-10.2	this study
goat	Borana Maua	-10.7	this study
goat	Ciakariga	-10.9	this study
goat	Emuhaya	-10	this study
goat	Kainauk	-8.5	this study
goat	Kibwezi	-6.3	this study
goat	Kilungu	-9.7	this study
goat	Kilungu	-10.1	this study
goat	Kimende	-4.7	this study
goat	Lamu	-12.3	this study
goat	Lodwar	-3.5	this study
goat	Loyangalani	-9.5	this study
goat	Maimanti	-9.7	this study
goat	Malaral	-4.1	this study
goat	Mandera	-5.6	this study
goat	Marimanti	-11.7	this study
goat	Matiiri	-6	this study
goat	Maua	-9.5	this study
goat	Mericho	-3.6	this study
goat	Nanyuki	-6.3	this study
goat	Nariokotome	-5.4	this study
goat	Ndaragwa	-3.5	this study
goat	South Horr	-10.3	this study
goat	Suguta Malmar	-4.4	this study
goat	Tharaka	-11.2	this study
goat	Tunyai	-11.6	this study
goat	Naivasha Basin	-6.3	(10)
goat	Naivasha Basin	-7.4	(10)
goat	Naivasha Basin	-7.2	(10)
goat	Naivasha Basin	-6.1	(10)
goat	Naivasha Basin	-6.5	(10)

Common/Species name	Locality	$\delta^{13}C_{1750}$	Citation
goat	Naivasha Basin	-5.9	(10)
goat	Naivasha Basin	-3.4	(10)
goat	Naivasha Basin	-2.6	(10)
goat	Naivasha Basin	-8.5	(10)

Table S5: Comparison of wild vs. domestic fauna at Neolithic sites in Kenya

Site	**Tradition**	**wild %**	**domestic**	**N (NISP)**	**Ref.**
Narosura	SPN*	7	93	1215	(11)
Crescent Island Main	SPN	18	82	526	(11)
Prolonged Drift	SPN	79.9	20.1	1491	(12)
Ngamuriak	Elmenteitan	0.5	99.56	4653	(13, 14)
Sugenya	Elmenteitan	1.9	98.1	1774	(15)
Oldorotua	Elmenteitan	1.6	98.4	2127	(15)
Maasai Gorge	Elmenteitan	4.3	96.7	115	(11)
Gogo Falls	Elmenteitan	46.5	53.5	612	(16)
Wadh Lango 140-160	Elmenteitan	10.9	89.1	156	(17)
Wadh Lango 160-190	Elmenteitan	10	90	88	(17)

**SPN = Savanna Pastoral Neolithic*

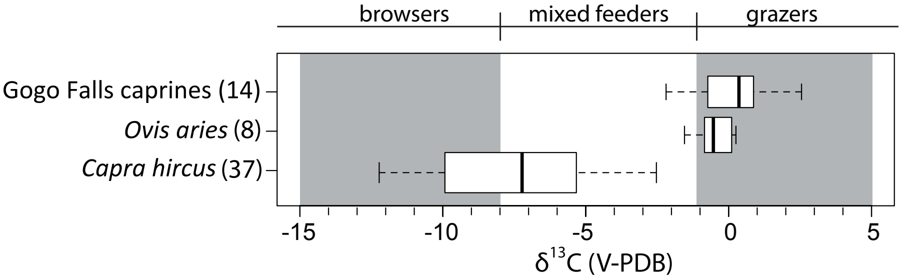


Figure S1: Boxplots of $\delta^{13}C_{1750}$ tooth enamel values of modern goat, *Capra hircus* (Table S4), modern sheep, *Ovis aries* (Table S4), and Gogo Falls caprines (Table S3).

SI References

1. Cerling TE, Harris JM, Leakey M, Mudida N (2003) Stable isotope ecology of northern Kenya with emphasis on the Turkana Basin. *Lothagam: The Dawn of Humanity in Eastern Africa*, eds Leakey MG, Harris JM (Columbia University Press, New York), pp.583–603.

2. Balasse M, Ambrose SH (2005) Mobilité altitudinale des pasteurs néolithiques dans la vallée du Rift (Kenya) : premiers indices de l'analyse du δ^{13}C de l'émail dentaire du cheptel domestique. *Anthropozoologica* 40(1):147–166.

3. Cerling TE, Harris JM, Passey BH (2003) Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy* 84(2):456–470.

4. Van Der Merwe NJ (2013) Isotopic ecology of fossil fauna from Olduvai Gorge at ca 1.8 Ma, compared with modern fauna. *South African Journal of Science* 109(11/12):1-14.

5. Bocherens H, Koch PL, Mariotti A, Geraads D, Jaeger JJ (1996) Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. *PALAIOS* 11(4):306–318.

6. Kingston JD (2011), Stable isotopic analyses of Laetoli herbivores, *Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 1: Geology, Geochronology, Paleoecology and Paleoenvironment*, ed Harrison T (Springer Netherlands, Dordrecht), pp 293–328.

7. Cerling TE et al. (2011) Diet of *Paranthropus boisei* in the Early Pleistocene of East Africa. *Proceedings of the National Academy of Science* 108(23):9337-9341.

8. Kingston JD, Harrison T (2007) Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: implications for early hominin paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243(3-4):272–306.

9. Cerling TE, Harris JM (2002) Dietary adaptations of extant and Neogene African suids. *Journal of Zoology* 256(1):45–54.

10. Balasse M, Ambrose SH (2005) Distinguishing sheep and goats using dental morphology and stable carbon isotopes in C_4 grassland environments. *Journal of Archaeological Science* 32(5):691-702.

11. Gifford-Gonzalez DP (1998) Early pastoralists in East Africa: Ecological and social dimensions. *Journal of Anthropological Archaeology* 17(2):166–200.

12. Gifford-Gonzalez DP, Isaac GL, Nelson CM (1980) Evidence for predation and pastoralism at Prolonged Drift: a Pastoral Neolithic site in Kenya. *Azania* 15(1):57-108.

13. Marshall F (1990) Origins of specialized pastoral production in East Africa.

American Anthropologist 92(4):873–894.

14. Marshall F, Grillo K, Arco L (2011) Prehistoric pastoralists and social responses to climatic risk in East Africa. *Sustainable Lifeways: Cultural Persistence in an Ever-changing Environment*, eds. Miller NF, Moore KM, Ryan K(University of Pennsylvania Press, Philadelphia), pp 74-105.

15. Simons A (2004) The development of early pastoral societies in south-western Kenya: A study of the faunal assemblages from Sugenya and Oldorotua 1 (La Trobe Univeristy, Melbourne). Ph.D. dissertation.

16. Marshall F, Stewart K (1994) Hunting, fishing and herding pastoralists of western Kenya: the fauna from Gogo Falls. *Archaeozoologia* 7(1):7-27.

17. Prendergast ME (2010) Kansyore fisher-foragers and transitions to food production in East Africa: The view from Wadh Lang'o, Nyanza Province, Western Kenya. *Azania* 45(1):83–111.

APPENDIX A

RAW HIPPO CANINE ISOTOPE DATA AND FIGURES

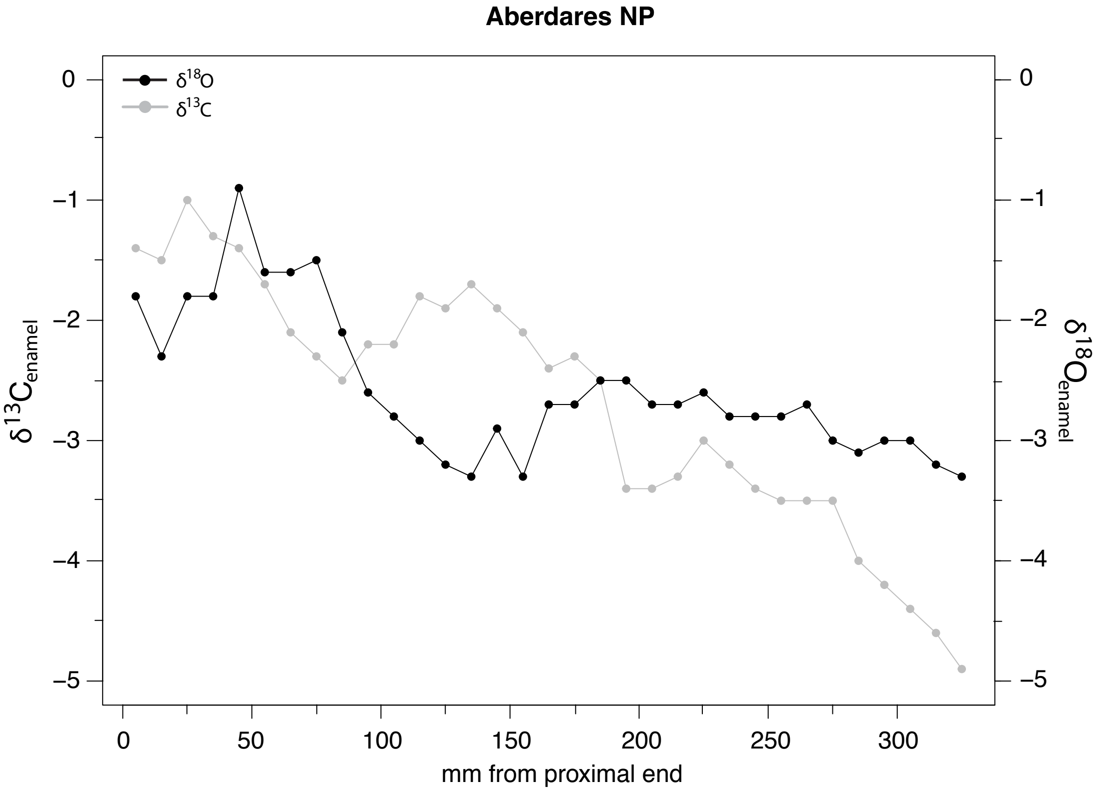


Figure A.1: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Aberdares NP hippo (0mm = death).

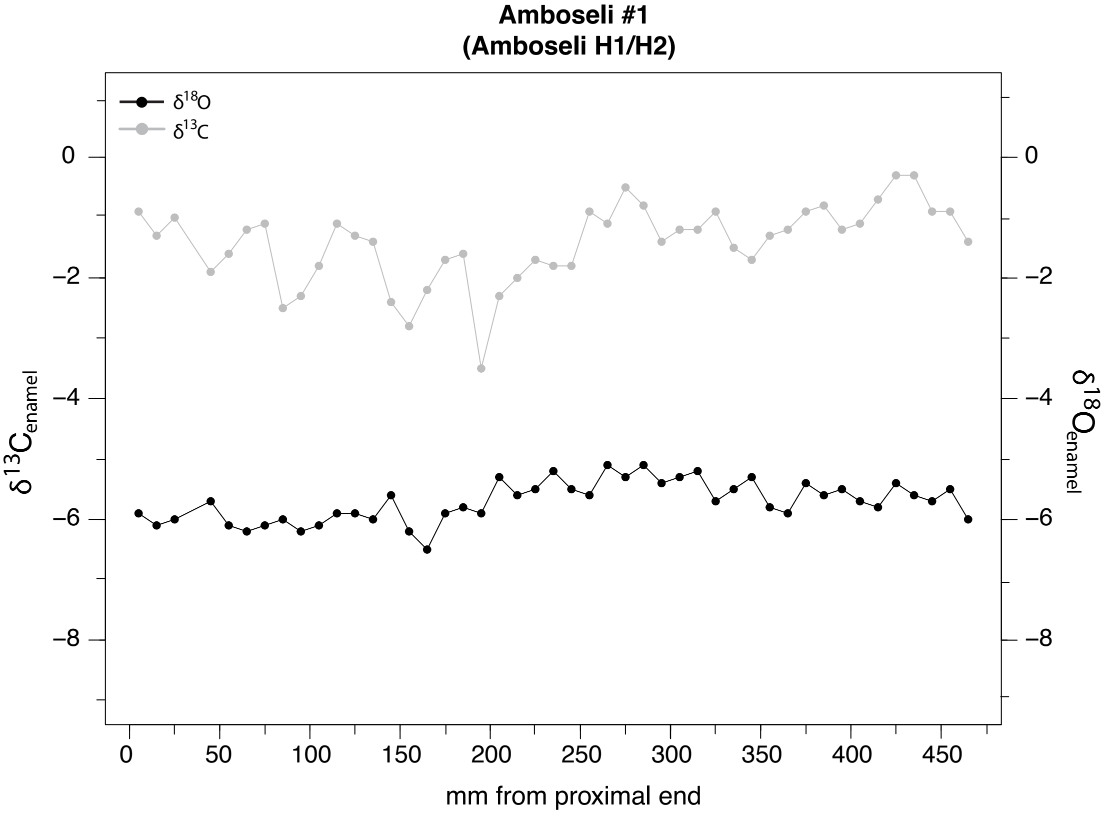


Figure A.2: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Amboseli #1 hippo (0mm = death).

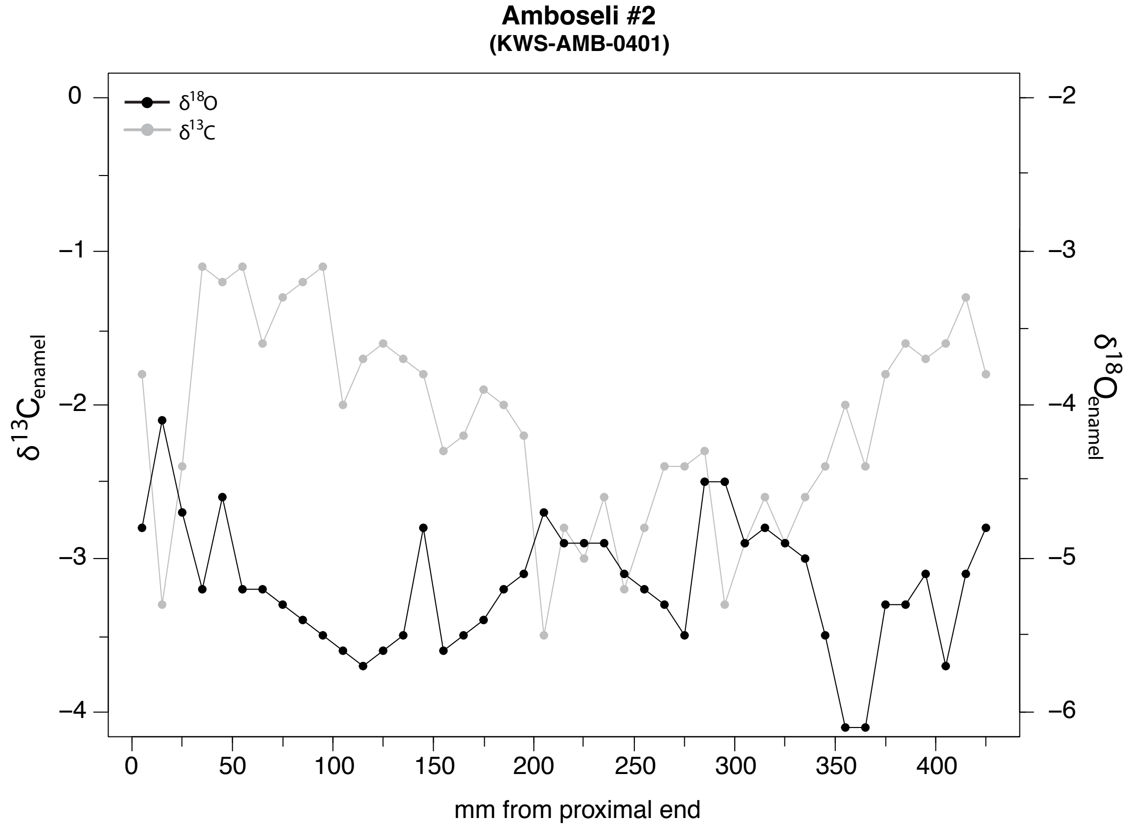


Figure A.3: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Amboseli #2 hippo (0mm = death).

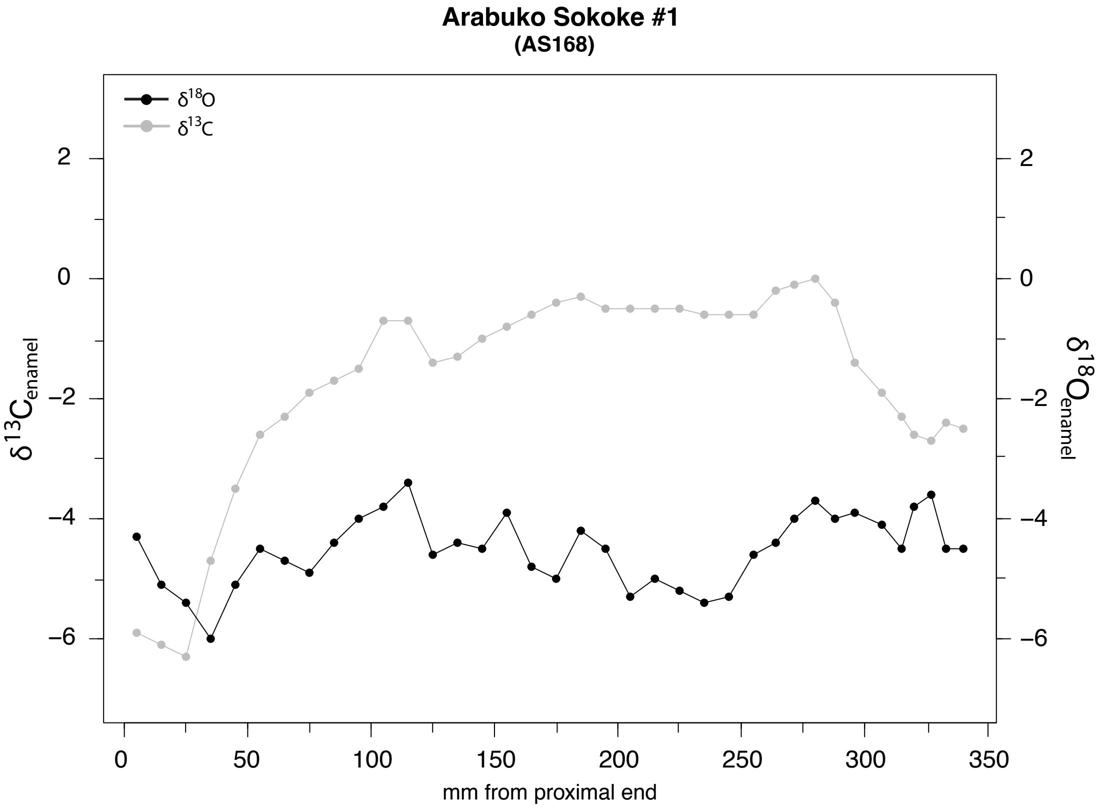


Figure A.4: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Arabuko Sokoke #1 hippo (0mm = death).

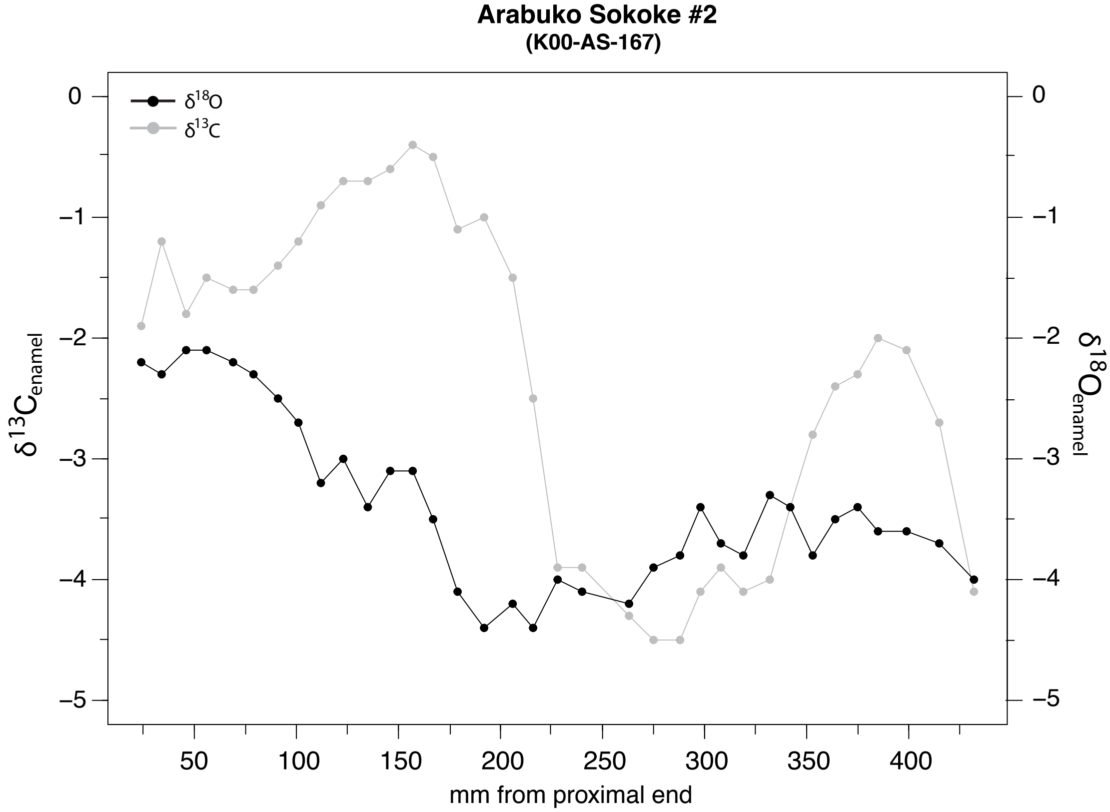


Figure A.5: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Arabuko Sokoke #2 hippo (0mm = death).

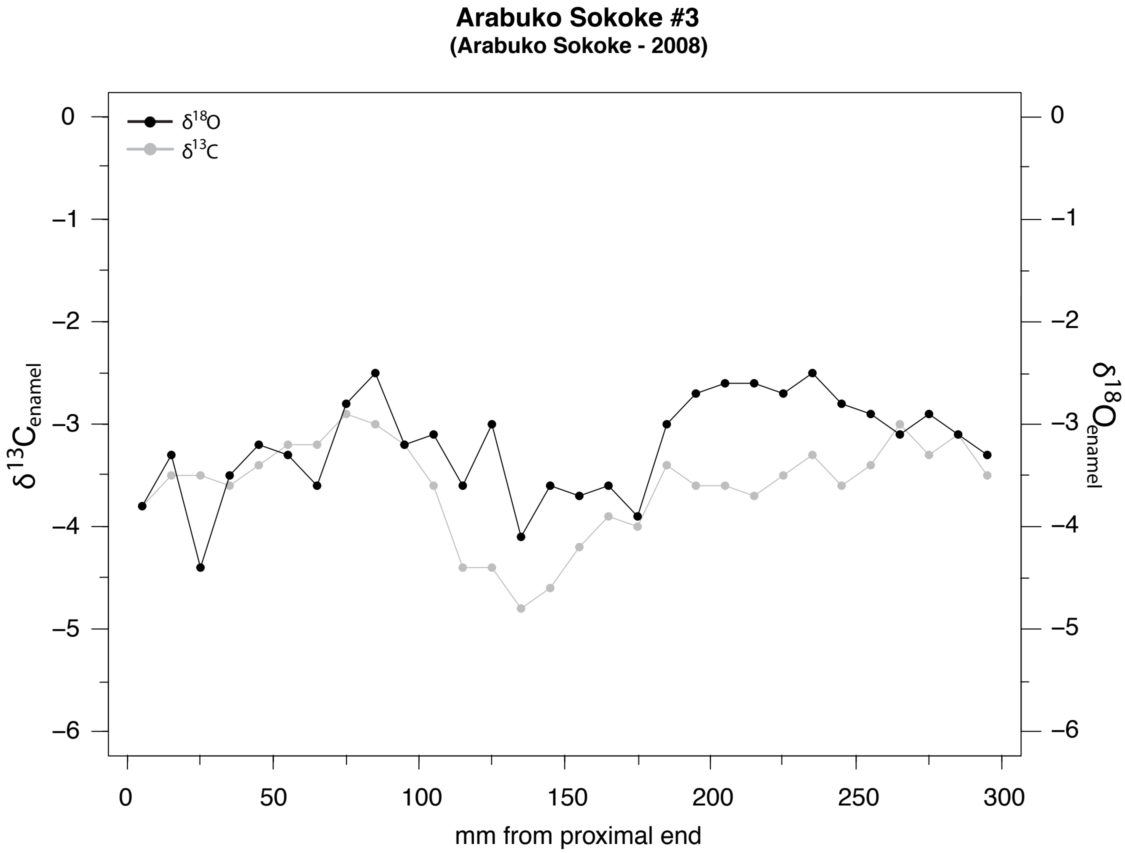


Figure A.6: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Arabuko Sokoke #3 hippo (0mm = death).

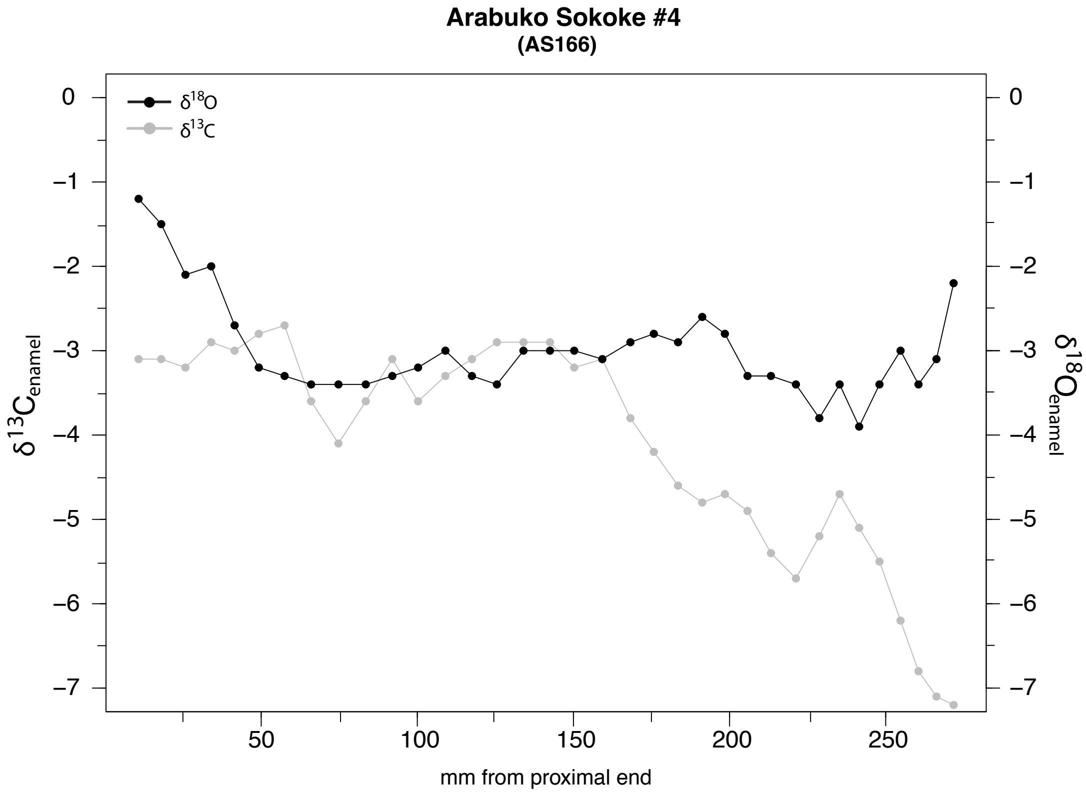


Figure A.7: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Arabuko Sokoke #4 hippo (0mm = death).

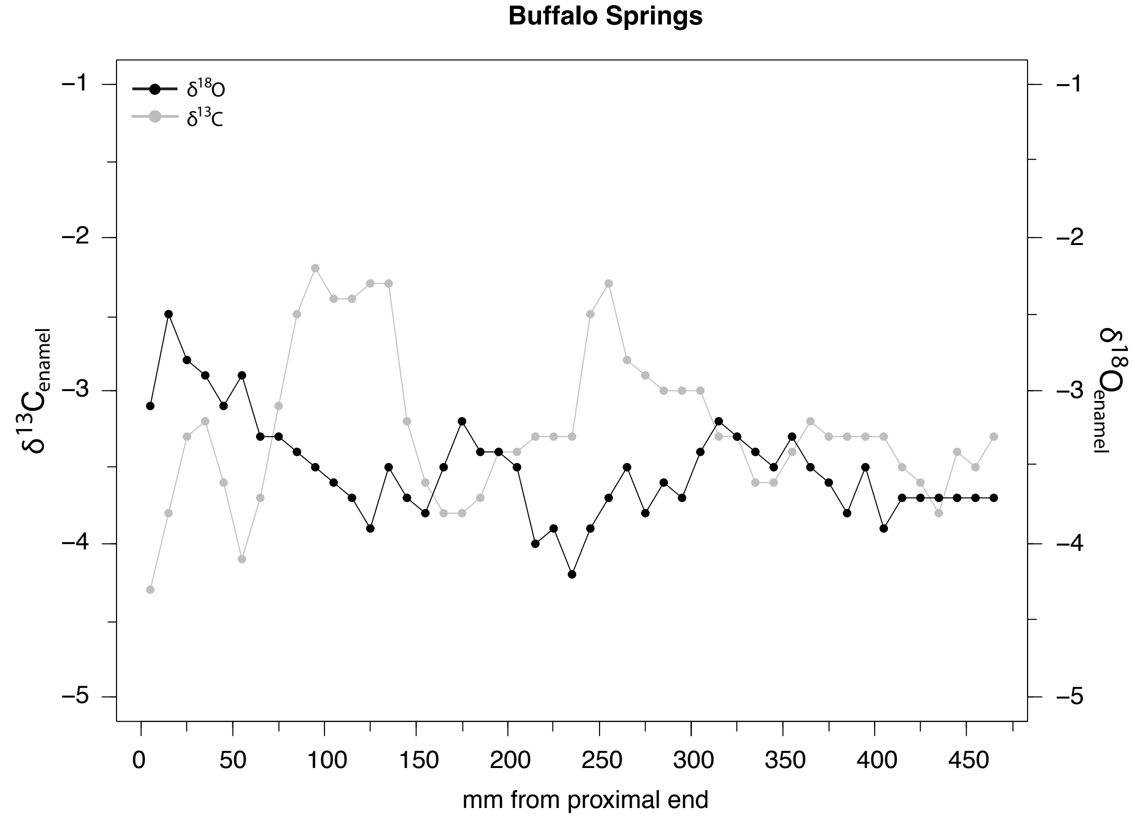


Figure A.8: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Buffalo Springs hippo (0mm = death).

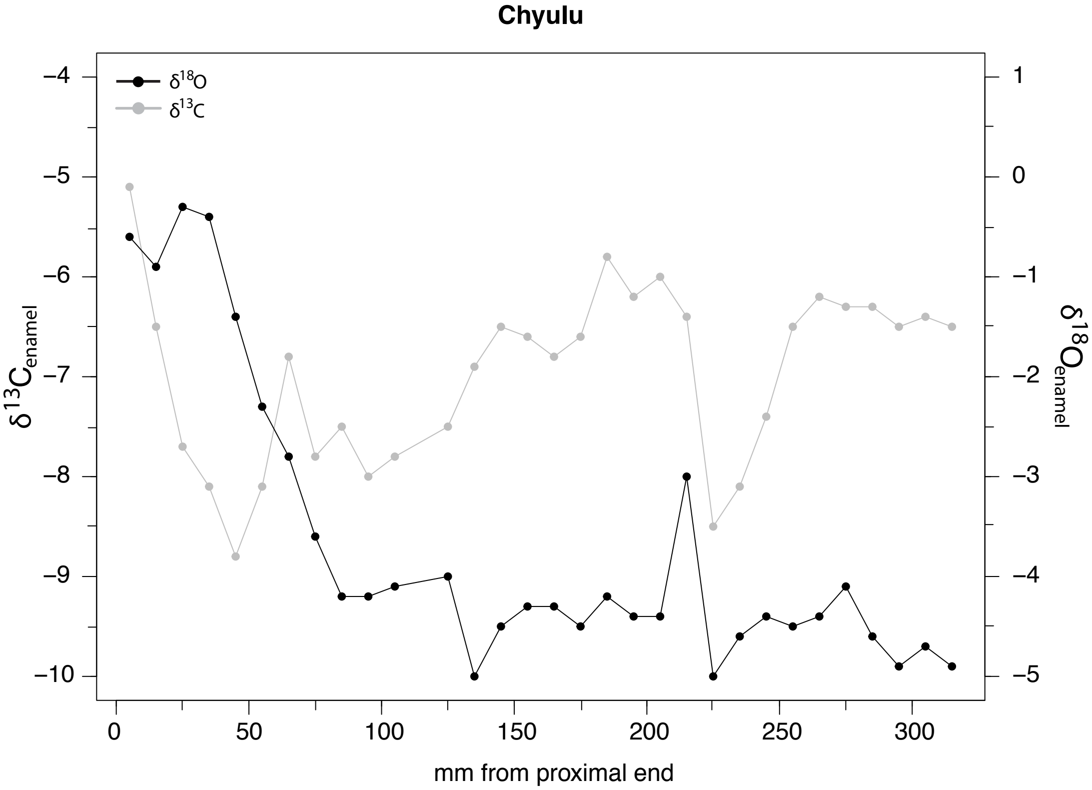


Figure A.9: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Chyulu hippo (0mm = death).

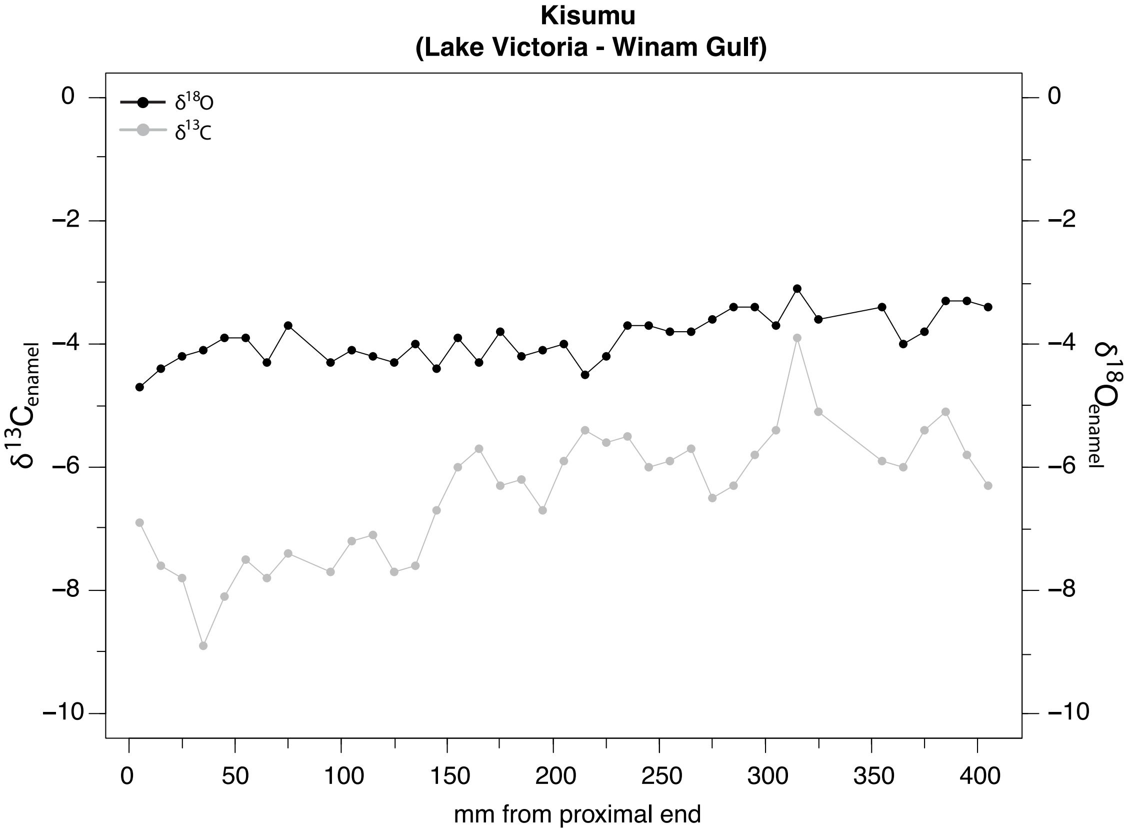


Figure A.10: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Kisumu hippo (0mm = death).

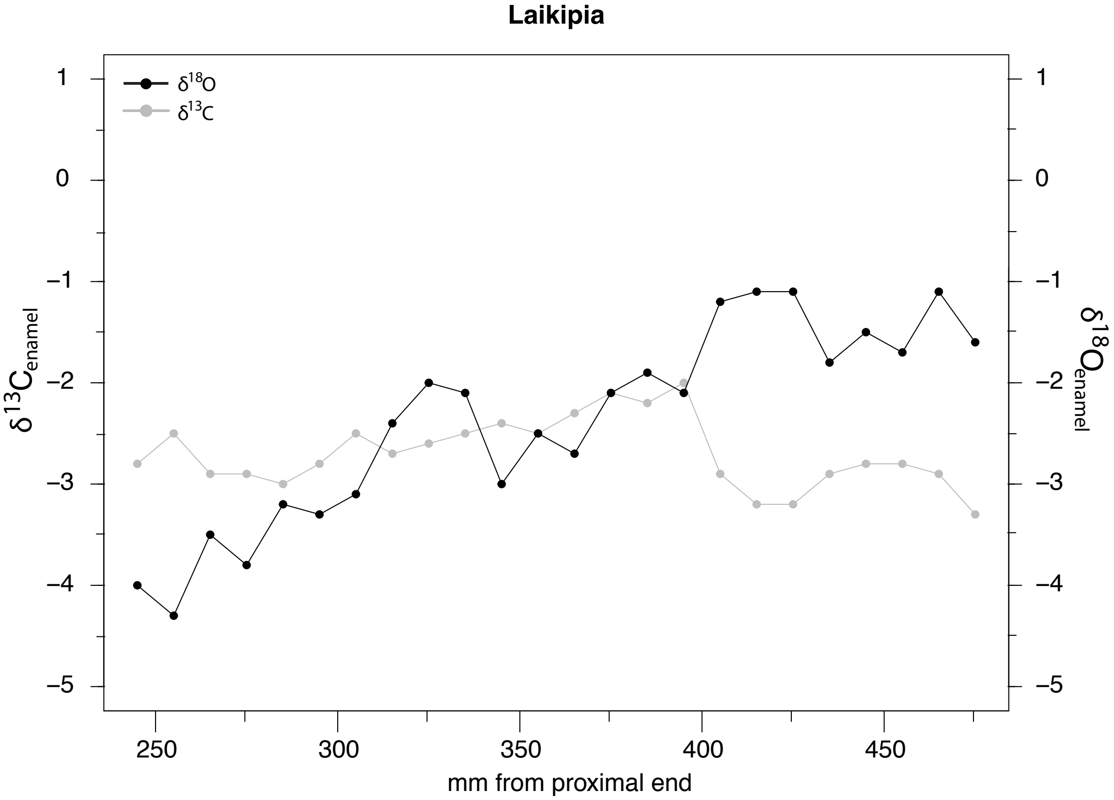


Figure A.11: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Laikipia hippo (0mm = death).

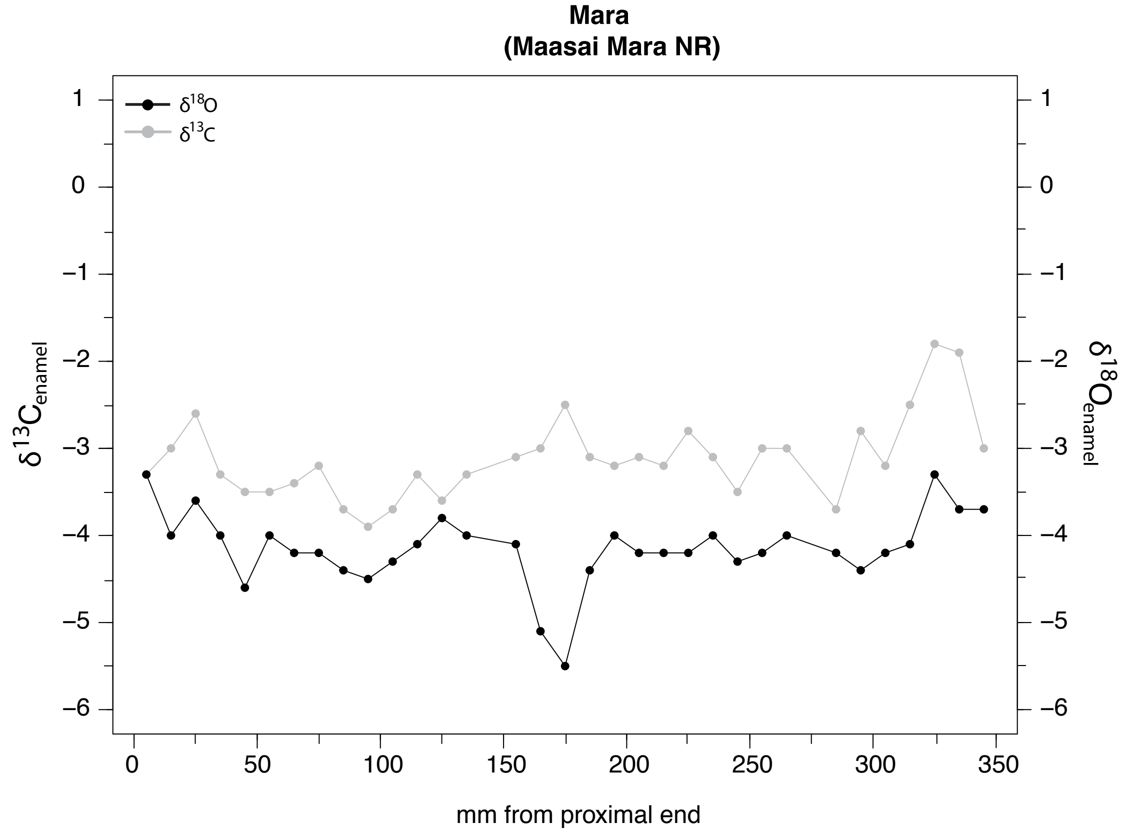


Figure A.12: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Mara hippo (0mm = death).

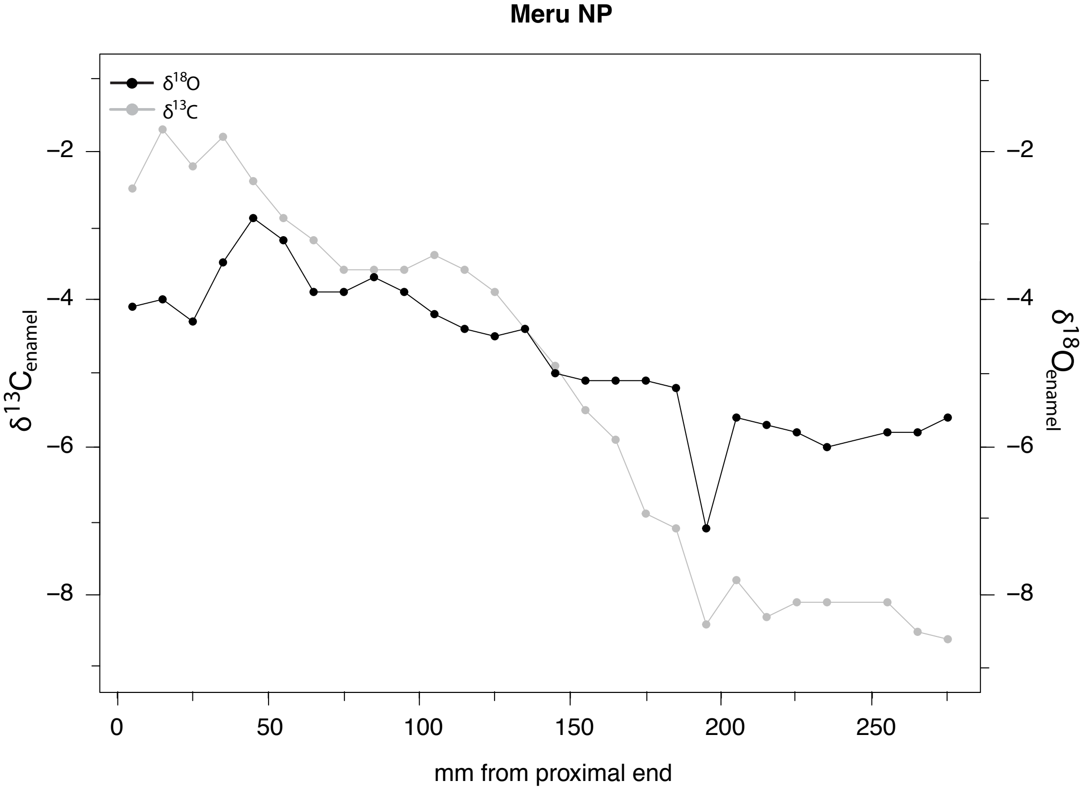
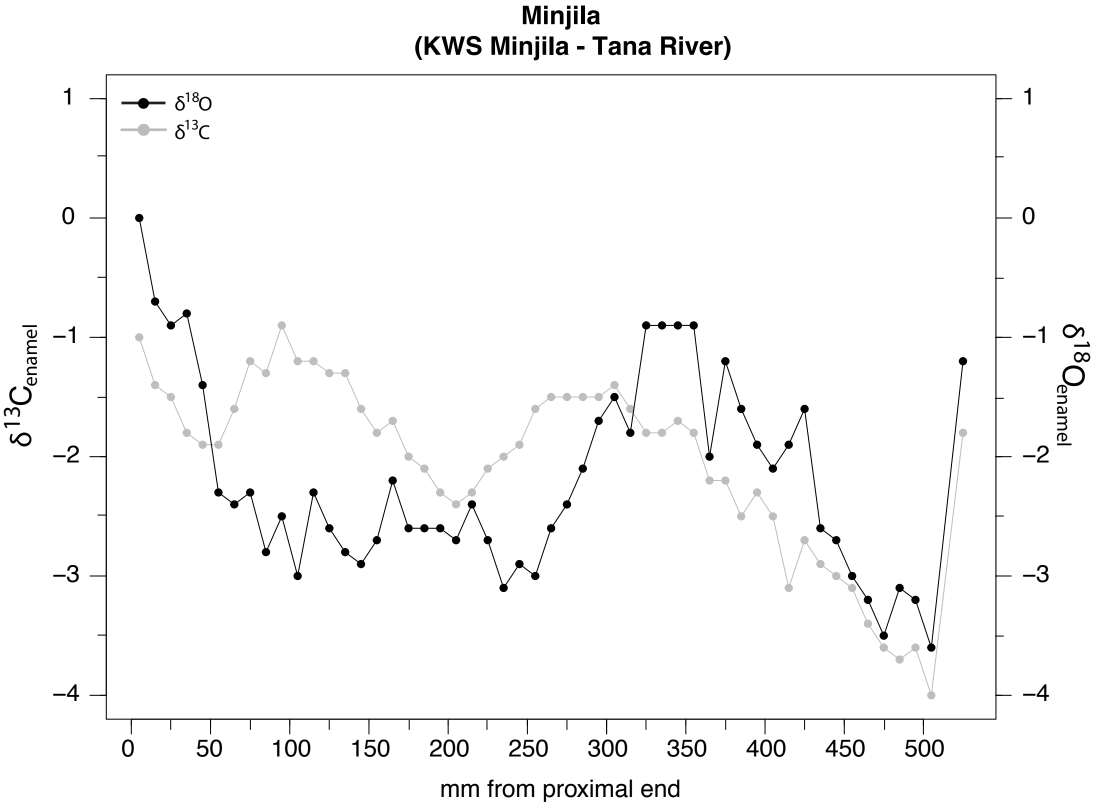
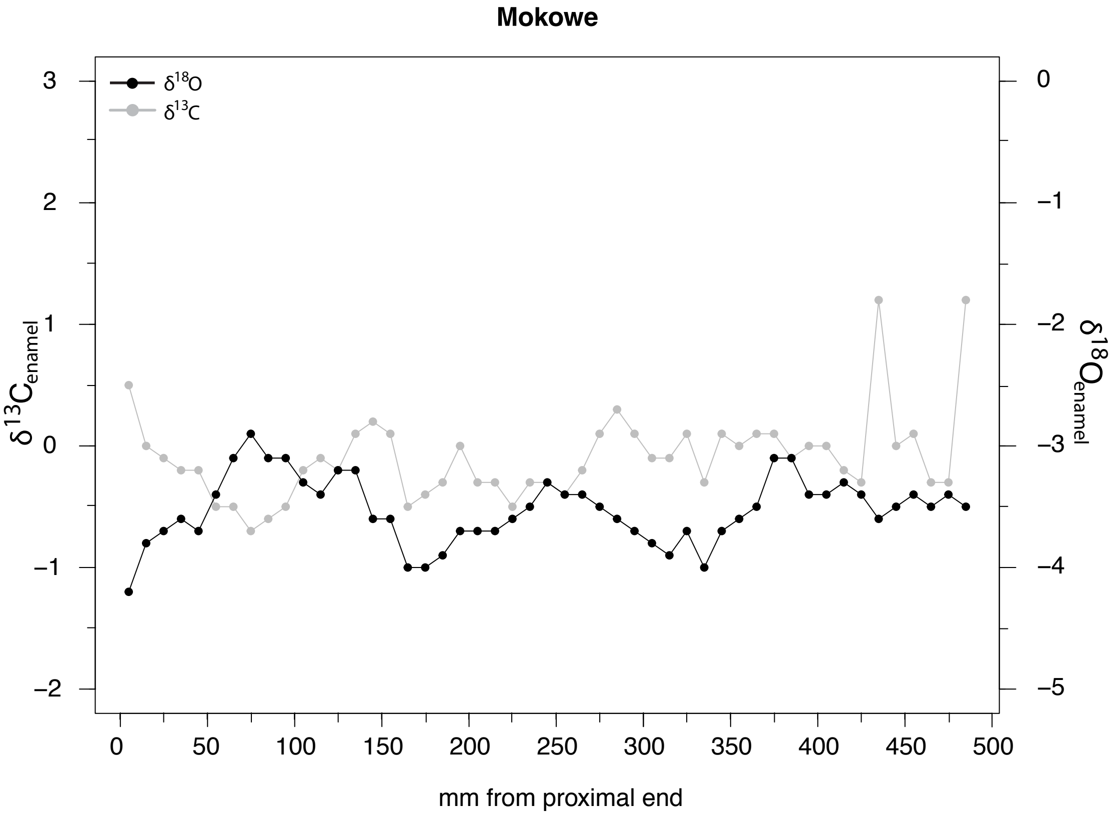


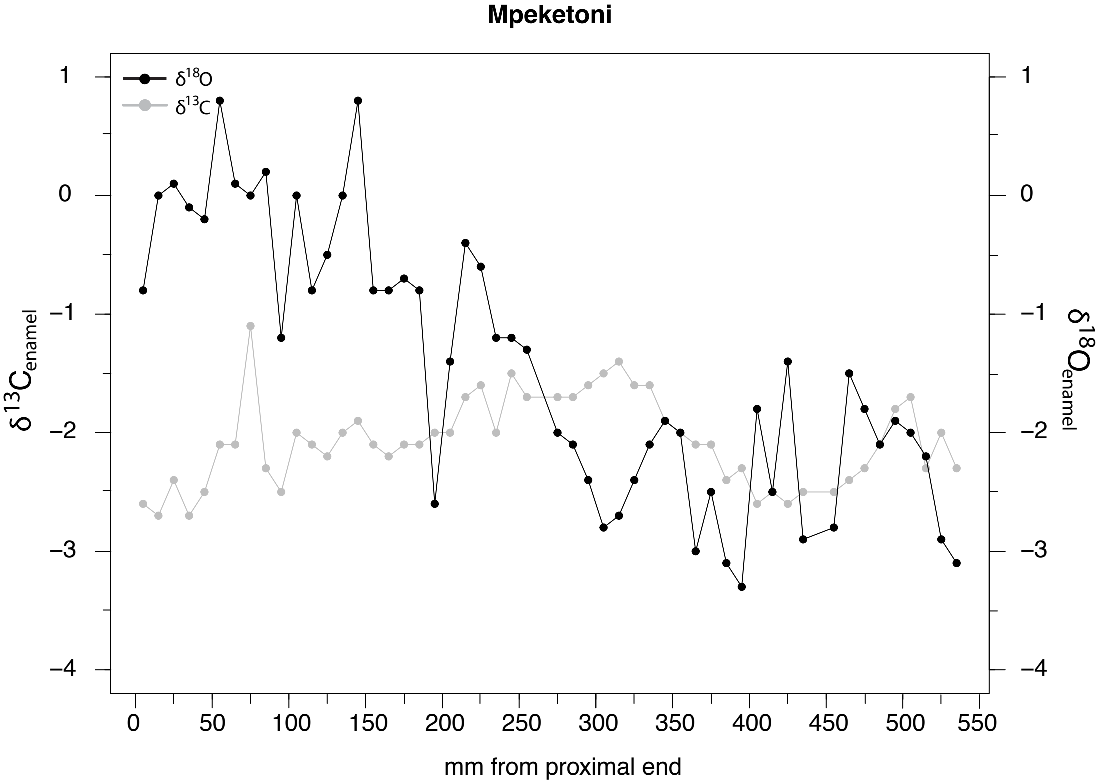
Figure A.13: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Meru NP hippo (0mm = death).



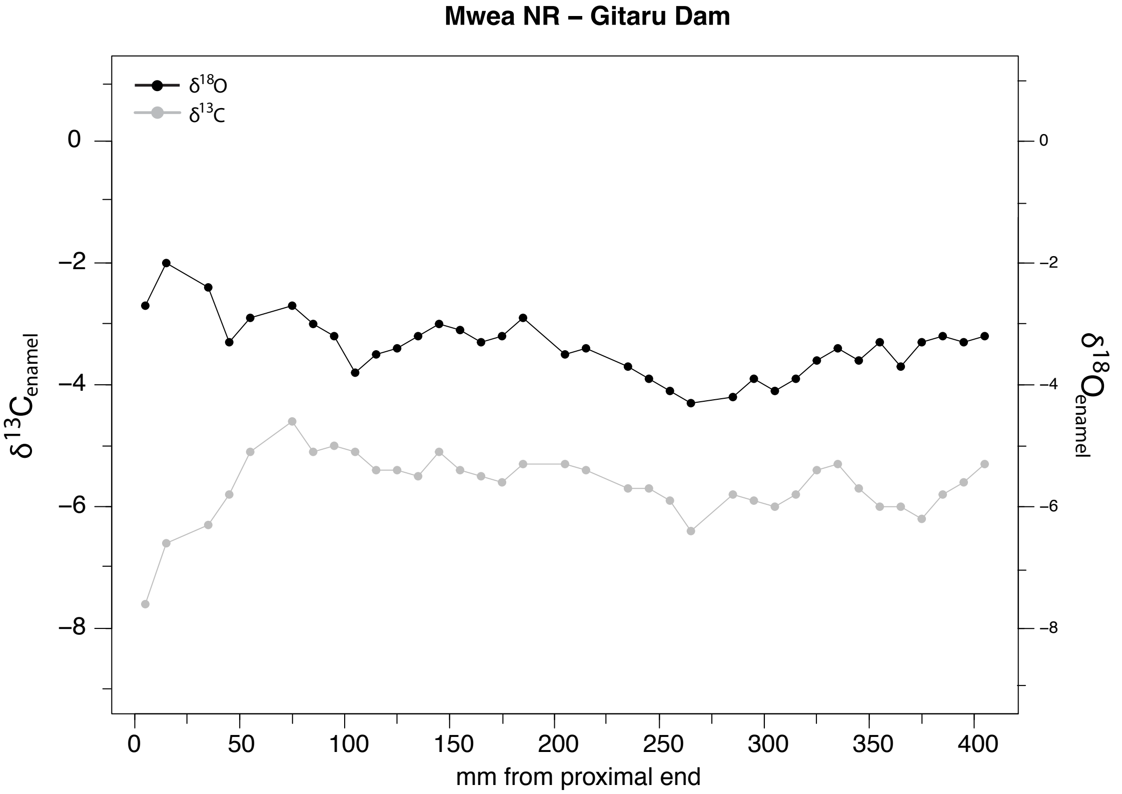
Appendix Figure 14: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Minjila hippo (0mm = death).



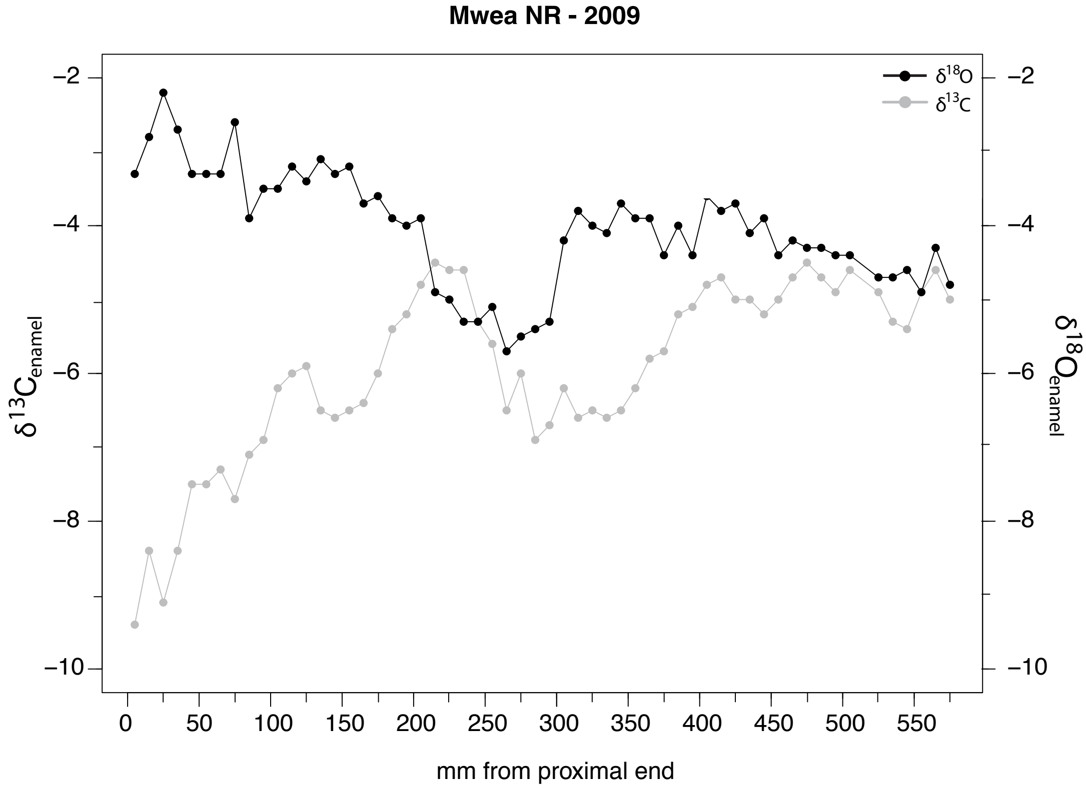
Appendix Figure 15: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Mokowe hippo (0mm = death).



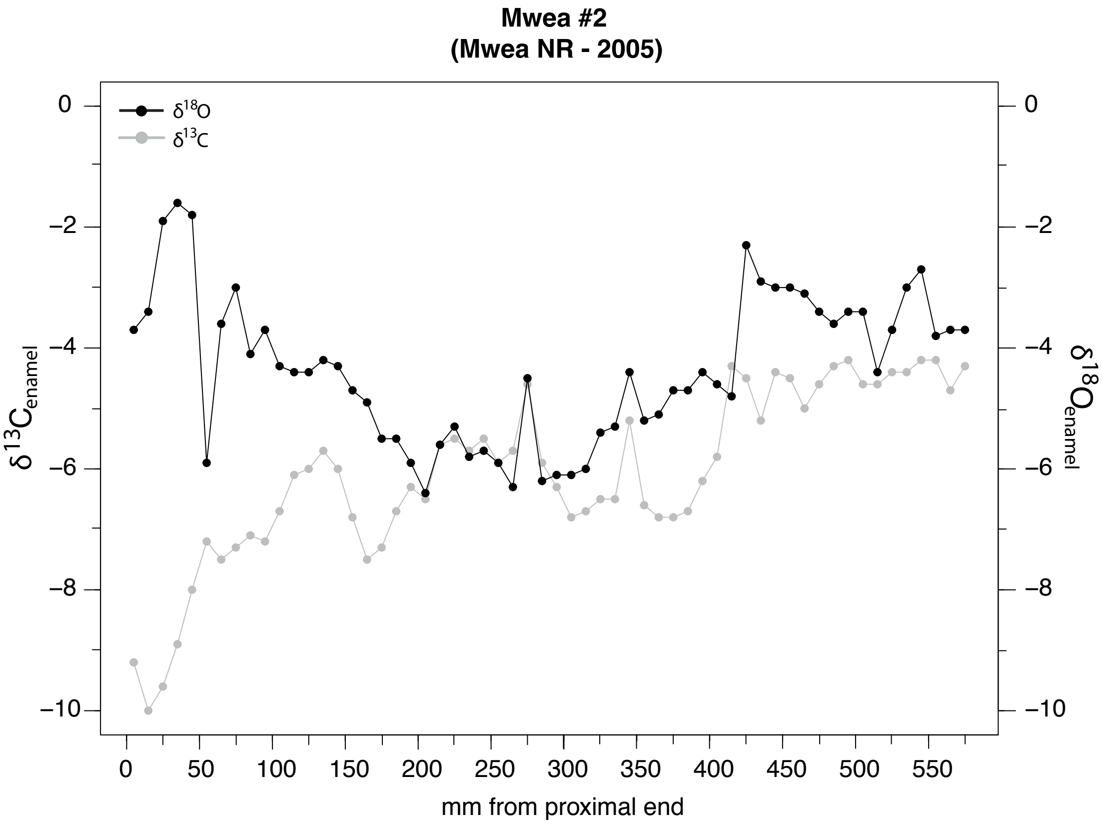
Appendix Figure 16: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Mpeketoni hippo (0mm = death).



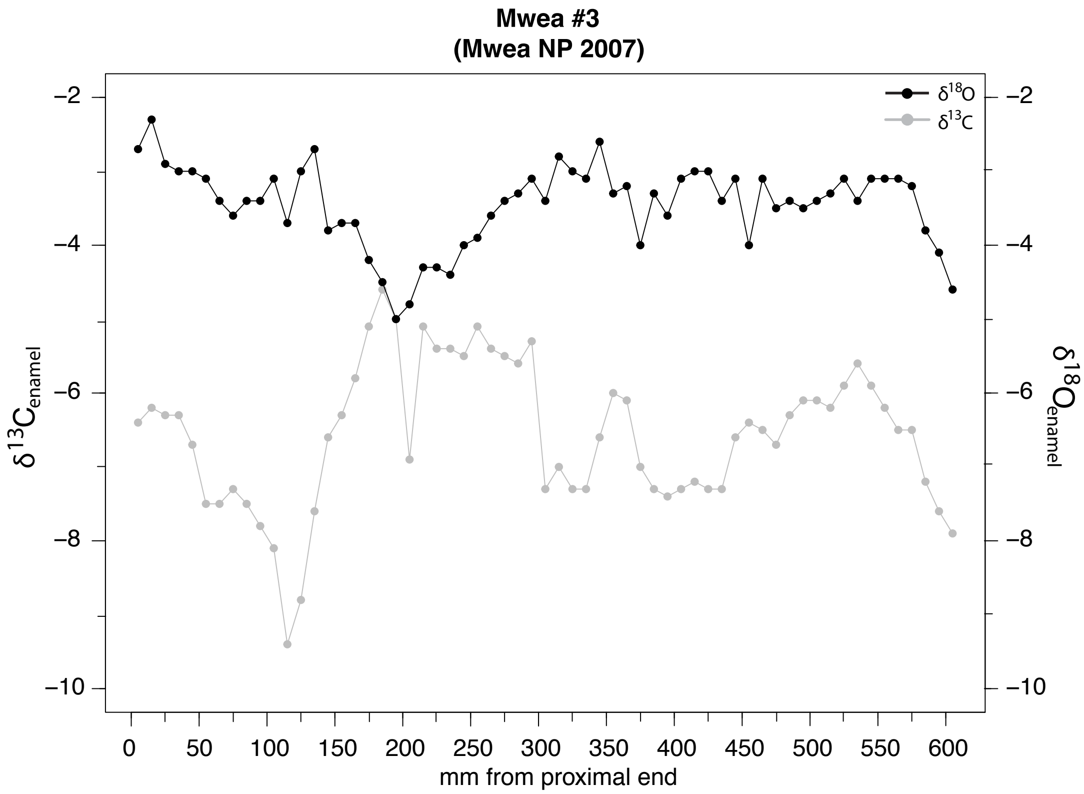
Appendix Figure 17: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Mwea – Gitaru Dam hippo (0mm = death).



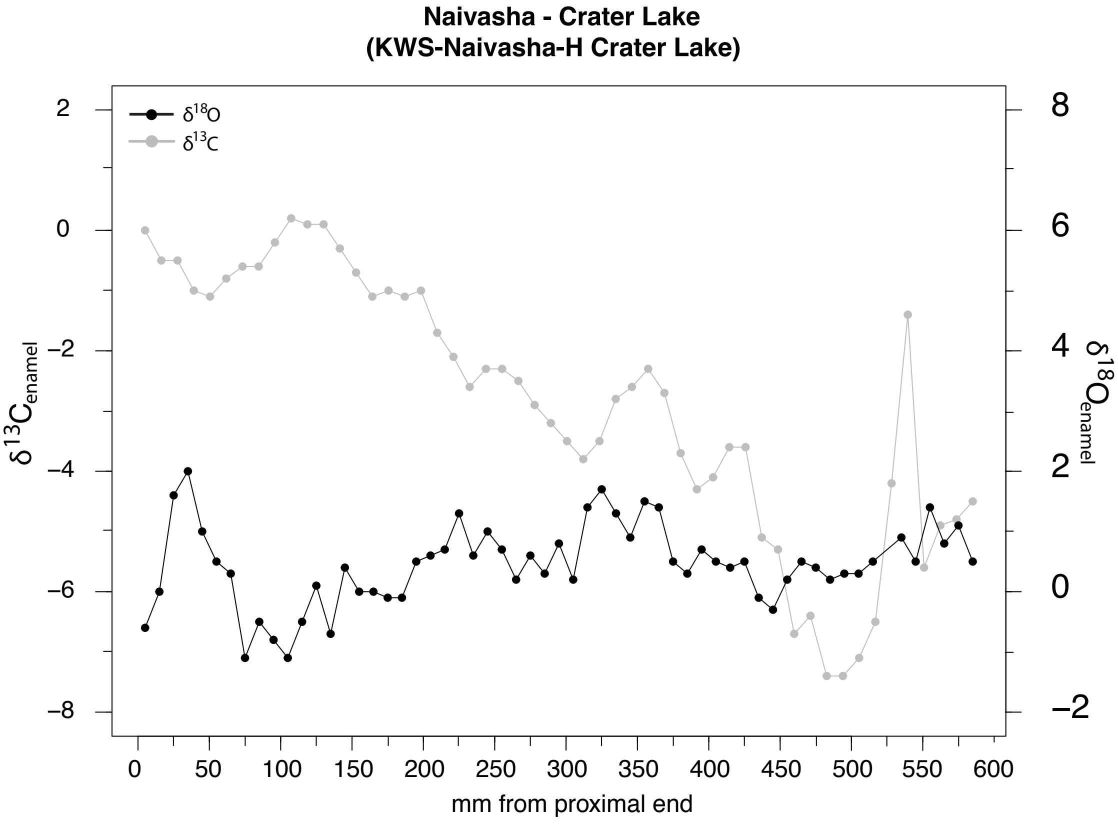
Appendix Figure 18: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Mwea #1 hippo (0mm = death).



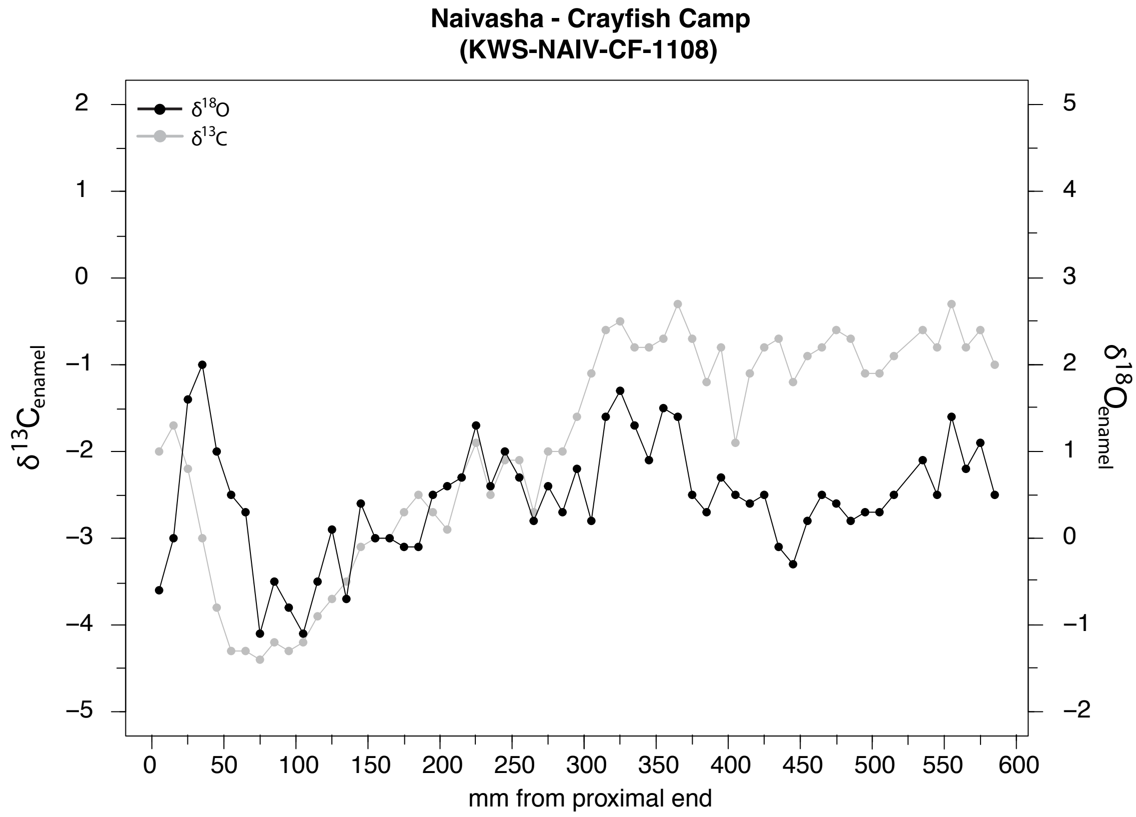
Appendix Figure 19: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Mwea #2 hippo (0mm = death).



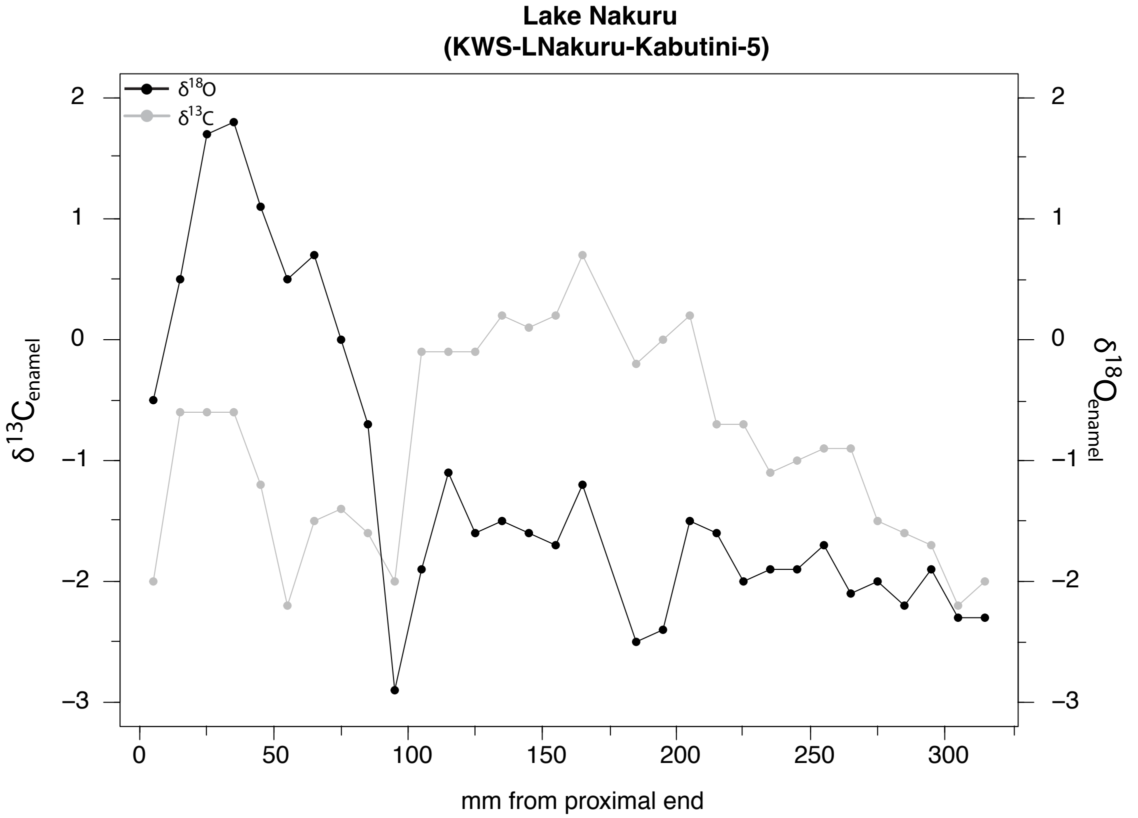
Appendix Figure 20: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Mwea #3 hippo (0mm = death).



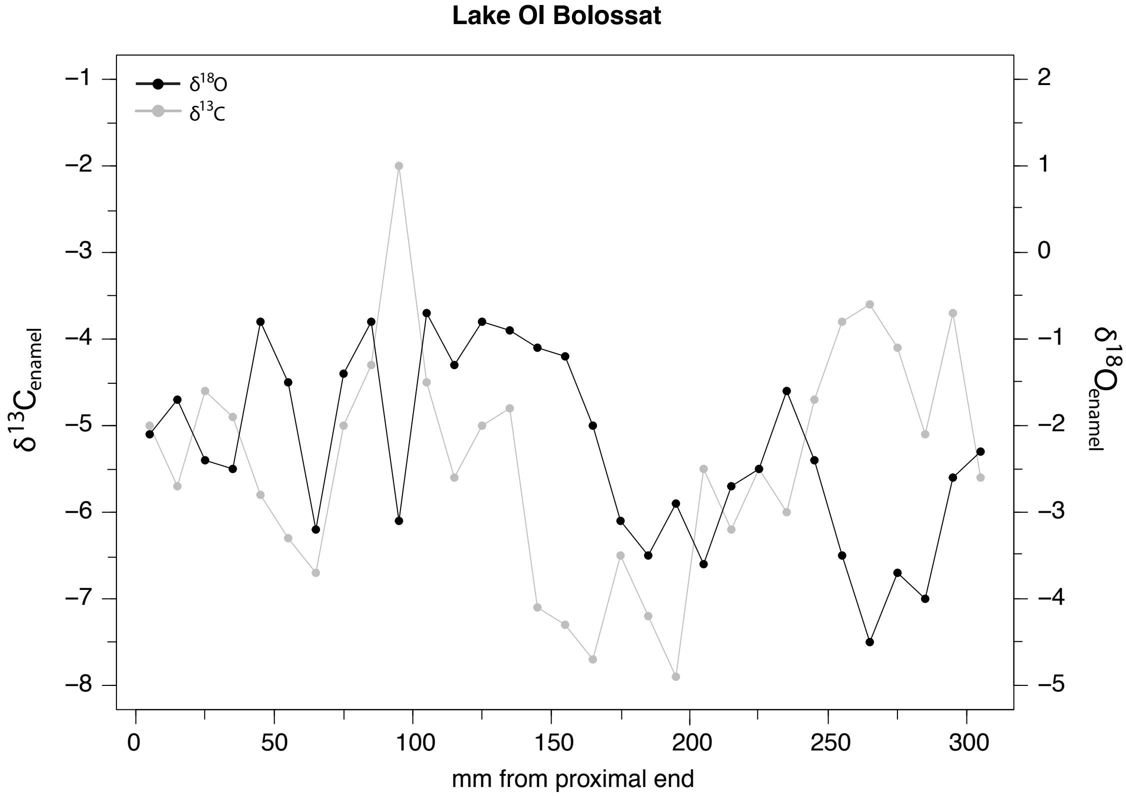
Appendix Figure 21: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Naivasha hippo (0mm = death).



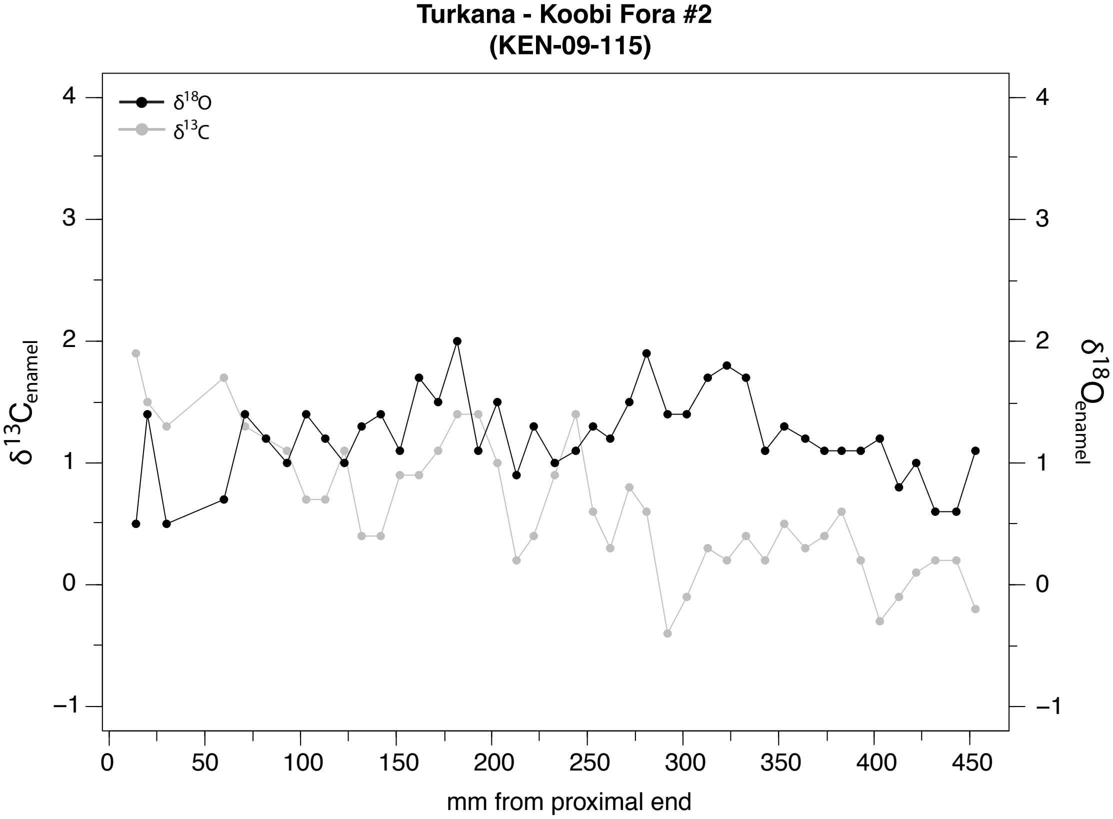
Appendix Figure 22: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Naivasha hippo (0mm = death).



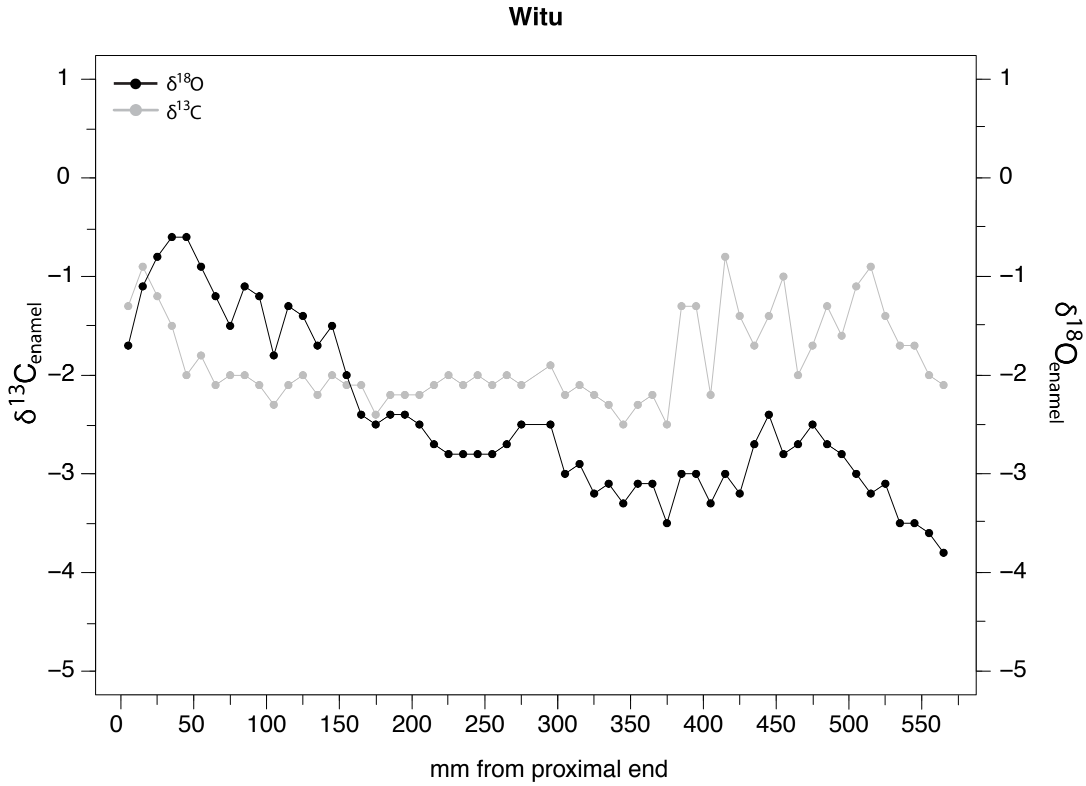
Appendix Figure 23: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Lake Nakuru hippo (0mm = death).



Appendix Figure 24: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Lake Ol Bolossat hippo (0mm = death).



Appendix Figure 25: $\delta^{13}C$ and $\delta^{18}O$ (V-PDB) canine enamel profile plot of Turkana – Koobi Fora 2 hippo (0mm = death).



Appendix Figure 26: δ^{13}C and δ^{18}O (V-PDB) canine enamel profile plot of Witu hippo (0mm = death).

Table A.1: Aberdares NP hippo isotope values.

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**
Aberdares	Aberdares NP	5	-1.4	-1.8
Aberdares	Aberdares NP	15	-1.5	-2.3
Aberdares	Aberdares NP	25	-1.0	-1.8
Aberdares	Aberdares NP	35	-1.3	-1.8
Aberdares	Aberdares NP	45	-1.4	-0.9
Aberdares	Aberdares NP	55	-1.7	-1.6
Aberdares	Aberdares NP	65	-2.1	-1.6
Aberdares	Aberdares NP	75	-2.3	-1.5
Aberdares	Aberdares NP	85	-2.5	-2.1
Aberdares	Aberdares NP	95	-2.2	-2.6
Aberdares	Aberdares NP	105	-2.2	-2.8
Aberdares	Aberdares NP	115	-1.8	-3.0
Aberdares	Aberdares NP	125	-1.9	-3.2
Aberdares	Aberdares NP	135	-1.7	-3.3
Aberdares	Aberdares NP	145	-1.9	-2.9
Aberdares	Aberdares NP	155	-2.1	-3.3
Aberdares	Aberdares NP	165	-2.4	-2.7
Aberdares	Aberdares NP	175	-2.3	-2.7
Aberdares	Aberdares NP	185	-2.5	-2.5
Aberdares	Aberdares NP	195	-3.4	-2.5
Aberdares	Aberdares NP	205	-3.4	-2.7
Aberdares	Aberdares NP	215	-3.3	-2.7
Aberdares	Aberdares NP	225	-3.0	-2.6
Aberdares	Aberdares NP	235	-3.2	-2.8
Aberdares	Aberdares NP	245	-3.4	-2.8
Aberdares	Aberdares NP	255	-3.5	-2.8
Aberdares	Aberdares NP	265	-3.5	-2.7
Aberdares	Aberdares NP	275	-3.5	-3.0
Aberdares	Aberdares NP	285	-4.0	-3.1
Aberdares	Aberdares NP	295	-4.2	-3.0
Aberdares	Aberdares NP	305	-4.4	-3.0
Aberdares	Aberdares NP	315	-4.6	-3.2
Aberdares	Aberdares NP	325	-4.9	-3.3

Table A.2: Adhi Dam (Boni NR) hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
KWS-Adhidam	Adhi Dam	5	-7.9	-1.6
KWS-Adhidam	Adhi Dam	15	-7.1	0.3
KWS-Adhidam	Adhi Dam	25	-5.7	-0.2
KWS-Adhidam	Adhi Dam	35	-5.5	0.1
KWS-Adhidam	Adhi Dam	45	-5.7	-0.7
KWS-Adhidam	Adhi Dam	55	-6.8	-1.2
KWS-Adhidam	Adhi Dam	65	-7.2	-1.7
KWS-Adhidam	Adhi Dam	75	-7.0	-1.6
KWS-Adhidam	Adhi Dam	85	-7.0	-1.4
KWS-Adhidam	Adhi Dam	95	-6.2	-1.2
KWS-Adhidam	Adhi Dam	105	-5.7	-1.3
KWS-Adhidam	Adhi Dam	115	-5.4	-1.1
KWS-Adhidam	Adhi Dam	125	-5.3	-2.0
KWS-Adhidam	Adhi Dam	135	-5.5	-1.9
KWS-Adhidam	Adhi Dam	145	-5.5	-2.2
KWS-Adhidam	Adhi Dam	155	-5.5	-1.7
KWS-Adhidam	Adhi Dam	165	-5.2	-1.9
KWS-Adhidam	Adhi Dam	175	-6.2	-1.6
KWS-Adhidam	Adhi Dam	185	-5.0	-1.4
KWS-Adhidam	Adhi Dam	195	-6.2	-1.6
KWS-Adhidam	Adhi Dam	205	-6.6	-1.6
KWS-Adhidam	Adhi Dam	215	-7.2	-1.7
KWS-Adhidam	Adhi Dam	225	-7.0	-1.8
KWS-Adhidam	Adhi Dam	245	-7.7	-1.7
KWS-Adhidam	Adhi Dam	255	-7.0	-2.0
KWS-Adhidam	Adhi Dam	265	-6.7	-1.6
KWS-Adhidam	Adhi Dam	275	-6.3	-1.5
KWS-Adhidam	Adhi Dam	285	-6.4	-1.6
KWS-Adhidam	Adhi Dam	295	-6.4	-1.6
KWS-Adhidam	Adhi Dam	305	-7.0	-1.8
KWS-Adhidam	Adhi Dam	315	-6.7	-2.2
KWS-Adhidam	Adhi Dam	325	-7.0	-2.1
KWS-Adhidam	Adhi Dam	335	-7.0	-3.1
KWS-Adhidam	Adhi Dam	345	-6.8	-2.9
KWS-Adhidam	Adhi Dam	355	-6.5	-3.4
KWS-Adhidam	Adhi Dam	365	-6.5	-3.1
KWS-Adhidam	Adhi Dam	375	-5.6	-3.7
KWS-Adhidam	Adhi Dam	385	-5.1	-3.5
KWS-Adhidam	Adhi Dam	395	-3.9	-2.7
KWS-Adhidam	Adhi Dam	405	-3.0	-2.5

Table A.2: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
KWS-Adhidam	Adhi Dam	415	-2.3	-1.3
KWS-Adhidam	Adhi Dam	425	-2.4	-1.7
KWS-Adhidam	Adhi Dam	455	-2.3	-1.1
KWS-Adhidam	Adhi Dam	465	-2.3	-1.4
KWS-Adhidam	Adhi Dam	475	-2.0	-1.9
KWS-Adhidam	Adhi Dam	485	-2.5	-1.4
KWS-Adhidam	Adhi Dam	495	-2.9	-1.8

Table A.3: Amboseli #1 hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**
Amboseli-H1-H2	Amboseli #1	5	-0.9	-5.9
Amboseli-H1-H2	Amboseli #1	15	-1.3	-6.1
Amboseli-H1-H2	Amboseli #1	25	-1.0	-6.0
Amboseli-H1-H2	Amboseli #1	45	-1.9	-5.7
Amboseli-H1-H2	Amboseli #1	55	-1.6	-6.1
Amboseli-H1-H2	Amboseli #1	65	-1.2	-6.2
Amboseli-H1-H2	Amboseli #1	75	-1.1	-6.1
Amboseli-H1-H2	Amboseli #1	85	-2.5	-6.0
Amboseli-H1-H2	Amboseli #1	95	-2.3	-6.2
Amboseli-H1-H2	Amboseli #1	105	-1.8	-6.1
Amboseli-H1-H2	Amboseli #1	115	-1.1	-5.9
Amboseli-H1-H2	Amboseli #1	125	-1.3	-5.9
Amboseli-H1-H2	Amboseli #1	135	-1.4	-6.0
Amboseli-H1-H2	Amboseli #1	145	-2.4	-5.6
Amboseli-H1-H2	Amboseli #1	155	-2.8	-6.2
Amboseli-H1-H2	Amboseli #1	165	-2.2	-6.5
Amboseli-H1-H2	Amboseli #1	175	-1.7	-5.9
Amboseli-H1-H2	Amboseli #1	185	-1.6	-5.8
Amboseli-H1-H2	Amboseli #1	195	-3.5	-5.9
Amboseli-H1-H2	Amboseli #1	205	-2.3	-5.3
Amboseli-H1-H2	Amboseli #1	215	-2.0	-5.6
Amboseli-H1-H2	Amboseli #1	225	-1.7	-5.5
Amboseli-H1-H2	Amboseli #1	235	-1.8	-5.2
Amboseli-H1-H2	Amboseli #1	245	-1.8	-5.5
Amboseli-H1-H2	Amboseli #1	255	-0.9	-5.6
Amboseli-H1-H2	Amboseli #1	265	-1.1	-5.1
Amboseli-H1-H2	Amboseli #1	275	-0.5	-5.3
Amboseli-H1-H2	Amboseli #1	285	-0.8	-5.1
Amboseli-H1-H2	Amboseli #1	295	-1.4	-5.4
Amboseli-H1-H2	Amboseli #1	305	-1.2	-5.3
Amboseli-H1-H2	Amboseli #1	315	-1.2	-5.2
Amboseli-H1-H2	Amboseli #1	325	-0.9	-5.7
Amboseli-H1-H2	Amboseli #1	335	-1.5	-5.5
Amboseli-H1-H2	Amboseli #1	345	-1.7	-5.3
Amboseli-H1-H2	Amboseli #1	355	-1.3	-5.8
Amboseli-H1-H2	Amboseli #1	365	-1.2	-5.9
Amboseli-H1-H2	Amboseli #1	375	-0.9	-5.4
Amboseli-H1-H2	Amboseli #1	385	-0.8	-5.6
Amboseli-H1-H2	Amboseli #1	395	-1.2	-5.5
Amboseli-H1-H2	Amboseli #1	405	-1.1	-5.7

Table A.3: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**
Amboseli-H1-H2	Amboseli #1	415	-0.7	-5.8
Amboseli-H1-H2	Amboseli #1	425	-0.3	-5.4
Amboseli-H1-H2	Amboseli #1	435	-0.3	-5.6
Amboseli-H1-H2	Amboseli #1	445	-0.9	-5.7
Amboseli-H1-H2	Amboseli #1	455	-0.9	-5.5
Amboseli-H1-H2	Amboseli #1	465	-1.4	-6.0

Table A.4: Amboseli #2 hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
KWS-Amb-0401	Amboseli #2	5	-1.8	-4.8
KWS-Amb-0401	Amboseli #2	15	-3.3	-4.1
KWS-Amb-0401	Amboseli #2	25	-2.4	-4.7
KWS-Amb-0401	Amboseli #2	35	-1.1	-5.2
KWS-Amb-0401	Amboseli #2	45	-1.2	-4.6
KWS-Amb-0401	Amboseli #2	55	-1.1	-5.2
KWS-Amb-0401	Amboseli #2	65	-1.6	-5.2
KWS-Amb-0401	Amboseli #2	75	-1.3	-5.3
KWS-Amb-0401	Amboseli #2	85	-1.2	-5.4
KWS-Amb-0401	Amboseli #2	95	-1.1	-5.5
KWS-Amb-0401	Amboseli #2	105	-2.0	-5.6
KWS-Amb-0401	Amboseli #2	115	-1.7	-5.7
KWS-Amb-0401	Amboseli #2	125	-1.6	-5.6
KWS-Amb-0401	Amboseli #2	135	-1.7	-5.5
KWS-Amb-0401	Amboseli #2	145	-1.8	-4.8
KWS-Amb-0401	Amboseli #2	155	-2.3	-5.6
KWS-Amb-0401	Amboseli #2	165	-2.2	-5.5
KWS-Amb-0401	Amboseli #2	175	-1.9	-5.4
KWS-Amb-0401	Amboseli #2	185	-2.0	-5.2
KWS-Amb-0401	Amboseli #2	195	-2.2	-5.1
KWS-Amb-0401	Amboseli #2	205	-3.5	-4.7
KWS-Amb-0401	Amboseli #2	215	-2.8	-4.9
KWS-Amb-0401	Amboseli #2	225	-3.0	-4.9
KWS-Amb-0401	Amboseli #2	235	-2.6	-4.9
KWS-Amb-0401	Amboseli #2	245	-3.2	-5.1
KWS-Amb-0401	Amboseli #2	255	-2.8	-5.2
KWS-Amb-0401	Amboseli #2	265	-2.4	-5.3
KWS-Amb-0401	Amboseli #2	275	-2.4	-5.5
KWS-Amb-0401	Amboseli #2	285	-2.3	-4.5
KWS-Amb-0401	Amboseli #2	295	-3.3	-4.5
KWS-Amb-0401	Amboseli #2	305	-2.9	-4.9
KWS-Amb-0401	Amboseli #2	315	-2.6	-4.8
KWS-Amb-0401	Amboseli #2	325	-2.9	-4.9
KWS-Amb-0401	Amboseli #2	335	-2.6	-5.0
KWS-Amb-0401	Amboseli #2	345	-2.4	-5.5
KWS-Amb-0401	Amboseli #2	355	-2.0	-6.1
KWS-Amb-0401	Amboseli #2	365	-2.4	-6.1
KWS-Amb-0401	Amboseli #2	375	-1.8	-5.3
KWS-Amb-0401	Amboseli #2	385	-1.6	-5.3
KWS-Amb-0401	Amboseli #2	395	-1.7	-5.1

Table A.4: (cont'd)

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**
KWS-Amb-0401	Amboseli #2	405	-1.6	-5.7
KWS-Amb-0401	Amboseli #2	415	-1.3	-5.1
KWS-Amb-0401	Amboseli #2	425	-1.8	-4.8

Table A.5: Arabuko Sokoke #1 hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	5	-5.9	-4.3
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	15	-6.1	-5.1
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	25	-6.3	-5.4
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	35	-4.7	-6.0
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	45	-3.5	-5.1
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	55	-2.6	-4.5
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	65	-2.3	-4.7
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	75	-1.9	-4.9
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	85	-1.7	-4.4
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	95	-1.5	-4.0
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	105	-0.7	-3.8
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	115	-0.7	-3.4
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	125	-1.4	-4.6
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	135	-1.3	-4.4
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	145	-1.0	-4.5
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	155	-0.8	-3.9
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	165	-0.6	-4.8
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	175	-0.4	-5.0
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	185	-0.3	-4.2
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	195	-0.5	-4.5
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	205	-0.5	-5.3
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	215	-0.5	-5.0
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	225	-0.5	-5.2
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	235	-0.6	-5.4
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	245	-0.6	-5.3
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	255	-0.6	-4.6
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	264	-0.2	-4.4
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	271.5	-0.1	-4.0
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	280	0.0	-3.7
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	288	-0.4	-4.0
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	296	-1.4	-3.9
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	307	-1.9	-4.1
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	315	-2.3	-4.5
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	320	-2.6	-3.8
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	327	-2.7	-3.6
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	333	-2.4	-4.5
Arabuko-Sokoke-AS-168	Arabuko Sokoke #1	340	-2.5	-4.5

Table A.6: Arabuko Sokoke #2 hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
K00-AS-167	Arabuko Sokoke #2	24	-1.9	-2.2
K00-AS-167	Arabuko Sokoke #2	34	-1.2	-2.3
K00-AS-167	Arabuko Sokoke #2	46	-1.8	-2.1
K00-AS-167	Arabuko Sokoke #2	56	-1.5	-2.1
K00-AS-167	Arabuko Sokoke #2	69	-1.6	-2.2
K00-AS-167	Arabuko Sokoke #2	79	-1.6	-2.3
K00-AS-167	Arabuko Sokoke #2	91	-1.4	-2.5
K00-AS-167	Arabuko Sokoke #2	101	-1.2	-2.7
K00-AS-167	Arabuko Sokoke #2	112	-0.9	-3.2
K00-AS-167	Arabuko Sokoke #2	123	-0.7	-3.0
K00-AS-167	Arabuko Sokoke #2	135	-0.7	-3.4
K00-AS-167	Arabuko Sokoke #2	146	-0.6	-3.1
K00-AS-167	Arabuko Sokoke #2	157	-0.4	-3.1
K00-AS-167	Arabuko Sokoke #2	167	-0.5	-3.5
K00-AS-167	Arabuko Sokoke #2	179	-1.1	-4.1
K00-AS-167	Arabuko Sokoke #2	192	-1.0	-4.4
K00-AS-167	Arabuko Sokoke #2	206	-1.5	-4.2
K00-AS-167	Arabuko Sokoke #2	216	-2.5	-4.4
K00-AS-167	Arabuko Sokoke #2	228	-3.9	-4.0
K00-AS-167	Arabuko Sokoke #2	240	-3.9	-4.1
K00-AS-167	Arabuko Sokoke #2	263	-4.3	-4.2
K00-AS-167	Arabuko Sokoke #2	275	-4.5	-3.9
K00-AS-167	Arabuko Sokoke #2	288	-4.5	-3.8
K00-AS-167	Arabuko Sokoke #2	298	-4.1	-3.4
K00-AS-167	Arabuko Sokoke #2	308	-3.9	-3.7
K00-AS-167	Arabuko Sokoke #2	319	-4.1	-3.8
K00-AS-167	Arabuko Sokoke #2	332	-4.0	-3.3
K00-AS-167	Arabuko Sokoke #2	342	-3.4	-3.4
K00-AS-167	Arabuko Sokoke #2	353	-2.8	-3.8
K00-AS-167	Arabuko Sokoke #2	364	-2.4	-3.5
K00-AS-167	Arabuko Sokoke #2	375	-2.3	-3.4
K00-AS-167	Arabuko Sokoke #2	385	-2.0	-3.6
K00-AS-167	Arabuko Sokoke #2	399	-2.1	-3.6
K00-AS-167	Arabuko Sokoke #2	415	-2.7	-3.7
K00-AS-167	Arabuko Sokoke #2	432	-4.1	-4.0

Table A.7: Arabuko Sokoke #3 hippo isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
Arabuko-Sokoke-08	Arabuko Sokoke #3	5	-3.8	-3.8
Arabuko-Sokoke-08	Arabuko Sokoke #3	15	-3.5	-3.3
Arabuko-Sokoke-08	Arabuko Sokoke #3	25	-3.5	-4.4
Arabuko-Sokoke-08	Arabuko Sokoke #3	35	-3.6	-3.5
Arabuko-Sokoke-08	Arabuko Sokoke #3	45	-3.4	-3.2
Arabuko-Sokoke-08	Arabuko Sokoke #3	55	-3.2	-3.3
Arabuko-Sokoke-08	Arabuko Sokoke #3	65	-3.2	-3.6
Arabuko-Sokoke-08	Arabuko Sokoke #3	75	-2.9	-2.8
Arabuko-Sokoke-08	Arabuko Sokoke #3	85	-3.0	-2.5
Arabuko-Sokoke-08	Arabuko Sokoke #3	95	-3.2	-3.2
Arabuko-Sokoke-08	Arabuko Sokoke #3	105	-3.6	-3.1
Arabuko-Sokoke-08	Arabuko Sokoke #3	115	-4.4	-3.6
Arabuko-Sokoke-08	Arabuko Sokoke #3	125	-4.4	-3.0
Arabuko-Sokoke-08	Arabuko Sokoke #3	135	-4.8	-4.1
Arabuko-Sokoke-08	Arabuko Sokoke #3	145	-4.6	-3.6
Arabuko-Sokoke-08	Arabuko Sokoke #3	155	-4.2	-3.7
Arabuko-Sokoke-08	Arabuko Sokoke #3	165	-3.9	-3.6
Arabuko-Sokoke-08	Arabuko Sokoke #3	175	-4.0	-3.9
Arabuko-Sokoke-08	Arabuko Sokoke #3	185	-3.4	-3.0
Arabuko-Sokoke-08	Arabuko Sokoke #3	195	-3.6	-2.7
Arabuko-Sokoke-08	Arabuko Sokoke #3	205	-3.6	-2.6
Arabuko-Sokoke-08	Arabuko Sokoke #3	215	-3.7	-2.6
Arabuko-Sokoke-08	Arabuko Sokoke #3	225	-3.5	-2.7
Arabuko-Sokoke-08	Arabuko Sokoke #3	235	-3.3	-2.5
Arabuko-Sokoke-08	Arabuko Sokoke #3	245	-3.6	-2.8
Arabuko-Sokoke-08	Arabuko Sokoke #3	255	-3.4	-2.9
Arabuko-Sokoke-08	Arabuko Sokoke #3	265	-3.0	-3.1
Arabuko-Sokoke-08	Arabuko Sokoke #3	275	-3.3	-2.9
Arabuko-Sokoke-08	Arabuko Sokoke #3	285	-3.1	-3.1
Arabuko-Sokoke-08	Arabuko Sokoke #3	295	-3.5	-3.3

Table A.8: Buffalo Springs hippo isotope values.

Specimen	Locality	Position	δ^{13}C (V-PDB)	$\delta\ ^{18}$O (V-PDB)
Buffalo-Springs	Buffalo Springs NR	5	-4.3	-3.1
Buffalo-Springs	Buffalo Springs NR	15	-3.8	-2.5
Buffalo-Springs	Buffalo Springs NR	25	-3.3	-2.8
Buffalo-Springs	Buffalo Springs NR	35	-3.2	-2.9
Buffalo-Springs	Buffalo Springs NR	45	-3.6	-3.1
Buffalo-Springs	Buffalo Springs NR	55	-4.1	-2.9
Buffalo-Springs	Buffalo Springs NR	65	-3.7	-3.3
Buffalo-Springs	Buffalo Springs NR	75	-3.1	-3.3
Buffalo-Springs	Buffalo Springs NR	85	-2.5	-3.4
Buffalo-Springs	Buffalo Springs NR	95	-2.2	-3.5
Buffalo-Springs	Buffalo Springs NR	105	-2.4	-3.6
Buffalo-Springs	Buffalo Springs NR	115	-2.4	-3.7
Buffalo-Springs	Buffalo Springs NR	125	-2.3	-3.9
Buffalo-Springs	Buffalo Springs NR	135	-2.3	-3.5
Buffalo-Springs	Buffalo Springs NR	145	-3.2	-3.7
Buffalo-Springs	Buffalo Springs NR	155	-3.6	-3.8
Buffalo-Springs	Buffalo Springs NR	165	-3.8	-3.5
Buffalo-Springs	Buffalo Springs NR	175	-3.8	-3.2
Buffalo-Springs	Buffalo Springs NR	185	-3.7	-3.4
Buffalo-Springs	Buffalo Springs NR	195	-3.4	-3.4
Buffalo-Springs	Buffalo Springs NR	205	-3.4	-3.5
Buffalo-Springs	Buffalo Springs NR	215	-3.3	-4.0
Buffalo-Springs	Buffalo Springs NR	225	-3.3	-3.9
Buffalo-Springs	Buffalo Springs NR	235	-3.3	-4.2
Buffalo-Springs	Buffalo Springs NR	245	-2.5	-3.9
Buffalo-Springs	Buffalo Springs NR	255	-2.3	-3.7
Buffalo-Springs	Buffalo Springs NR	265	-2.8	-3.5
Buffalo-Springs	Buffalo Springs NR	275	-2.9	-3.8
Buffalo-Springs	Buffalo Springs NR	285	-3.0	-3.6
Buffalo-Springs	Buffalo Springs NR	295	-3.0	-3.7
Buffalo-Springs	Buffalo Springs NR	305	-3.0	-3.4
Buffalo-Springs	Buffalo Springs NR	315	-3.3	-3.2
Buffalo-Springs	Buffalo Springs NR	325	-3.3	-3.3
Buffalo-Springs	Buffalo Springs NR	335	-3.6	-3.4
Buffalo-Springs	Buffalo Springs NR	345	-3.6	-3.5
Buffalo-Springs	Buffalo Springs NR	355	-3.4	-3.3
Buffalo-Springs	Buffalo Springs NR	365	-3.2	-3.5
Buffalo-Springs	Buffalo Springs NR	375	-3.3	-3.6
Buffalo-Springs	Buffalo Springs NR	385	-3.3	-3.8
Buffalo-Springs	Buffalo Springs NR	395	-3.3	-3.5

Table A.8: (cont'd)

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**$\delta\ ^{18}$O (V-PDB)**
Buffalo-Springs	Buffalo Springs NR	405	-3.3	-3.9
Buffalo-Springs	Buffalo Springs NR	415	-3.5	-3.7
Buffalo-Springs	Buffalo Springs NR	425	-3.6	-3.7
Buffalo-Springs	Buffalo Springs NR	435	-3.8	-3.7
Buffalo-Springs	Buffalo Springs NR	445	-3.4	-3.7
Buffalo-Springs	Buffalo Springs NR	455	-3.5	-3.7
Buffalo-Springs	Buffalo Springs NR	465	-3.3	-3.7

Table A.9: Chyulu hippo isotope values

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
Chyulu	Chyulu	5	-5.1	-0.6
Chyulu	Chyulu	15	-6.5	-0.9
Chyulu	Chyulu	25	-7.7	-0.3
Chyulu	Chyulu	35	-8.1	-0.4
Chyulu	Chyulu	45	-8.8	-1.4
Chyulu	Chyulu	55	-8.1	-2.3
Chyulu	Chyulu	65	-6.8	-2.8
Chyulu	Chyulu	75	-7.8	-3.6
Chyulu	Chyulu	85	-7.5	-4.2
Chyulu	Chyulu	95	-8.0	-4.2
Chyulu	Chyulu	105	-7.8	-4.1
Chyulu	Chyulu	125	-7.5	-4.0
Chyulu	Chyulu	135	-6.9	-5.0
Chyulu	Chyulu	145	-6.5	-4.5
Chyulu	Chyulu	155	-6.6	-4.3
Chyulu	Chyulu	165	-6.8	-4.3
Chyulu	Chyulu	175	-6.6	-4.5
Chyulu	Chyulu	185	-5.8	-4.2
Chyulu	Chyulu	195	-6.2	-4.4
Chyulu	Chyulu	205	-6.0	-4.4
Chyulu	Chyulu	215	-6.4	-3.0
Chyulu	Chyulu	225	-8.5	-5.0
Chyulu	Chyulu	235	-8.1	-4.6
Chyulu	Chyulu	245	-7.4	-4.4
Chyulu	Chyulu	255	-6.5	-4.5
Chyulu	Chyulu	265	-6.2	-4.4
Chyulu	Chyulu	275	-6.3	-4.1
Chyulu	Chyulu	285	-6.3	-4.6
Chyulu	Chyulu	295	-6.5	-4.9
Chyulu	Chyulu	305	-6.4	-4.7
Chyulu	Chyulu	315	-6.5	-4.9

Table A.10: Kisumu (Lake Victoria) hippo isotope values

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**
Kisumu	Kisumu	5	-6.9	-4.7
Kisumu	Kisumu	15	-7.6	-4.4
Kisumu	Kisumu	25	-7.8	-4.2
Kisumu	Kisumu	35	-8.9	-4.1
Kisumu	Kisumu	45	-8.1	-3.9
Kisumu	Kisumu	55	-7.5	-3.9
Kisumu	Kisumu	65	-7.8	-4.3
Kisumu	Kisumu	75	-7.4	-3.7
Kisumu	Kisumu	95	-7.7	-4.3
Kisumu	Kisumu	105	-7.2	-4.1
Kisumu	Kisumu	115	-7.1	-4.2
Kisumu	Kisumu	125	-7.7	-4.3
Kisumu	Kisumu	135	-7.6	-4.0
Kisumu	Kisumu	145	-6.7	-4.4
Kisumu	Kisumu	155	-6.0	-3.9
Kisumu	Kisumu	165	-5.7	-4.3
Kisumu	Kisumu	175	-6.3	-3.8
Kisumu	Kisumu	185	-6.2	-4.2
Kisumu	Kisumu	195	-6.7	-4.1
Kisumu	Kisumu	205	-5.9	-4.0
Kisumu	Kisumu	215	-5.4	-4.5
Kisumu	Kisumu	225	-5.6	-4.2
Kisumu	Kisumu	235	-5.5	-3.7
Kisumu	Kisumu	245	-6.0	-3.7
Kisumu	Kisumu	255	-5.9	-3.8
Kisumu	Kisumu	265	-5.7	-3.8
Kisumu	Kisumu	275	-6.5	-3.6
Kisumu	Kisumu	285	-6.3	-3.4
Kisumu	Kisumu	295	-5.8	-3.4
Kisumu	Kisumu	305	-5.4	-3.7
Kisumu	Kisumu	315	-3.9	-3.1
Kisumu	Kisumu	325	-5.1	-3.6
Kisumu	Kisumu	355	-5.9	-3.4
Kisumu	Kisumu	365	-6.0	-4.0
Kisumu	Kisumu	375	-5.4	-3.8
Kisumu	Kisumu	385	-5.1	-3.3
Kisumu	Kisumu	395	-5.8	-3.3
Kisumu	Kisumu	405	-6.3	-3.4

Table A.11: Laikipia hippo isotope values (tusk still in skull – estimated 240mm missing).

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**
K01-LAI-191	Laikipia	245	-2.8	-4.0
K01-LAI-191	Laikipia	255	-2.5	-4.3
K01-LAI-191	Laikipia	265	-2.9	-3.5
K01-LAI-191	Laikipia	275	-2.9	-3.8
K01-LAI-191	Laikipia	285	-3.0	-3.2
K01-LAI-191	Laikipia	295	-2.8	-3.3
K01-LAI-191	Laikipia	305	-2.5	-3.1
K01-LAI-191	Laikipia	315	-2.7	-2.4
K01-LAI-191	Laikipia	325	-2.6	-2.0
K01-LAI-191	Laikipia	335	-2.5	-2.1
K01-LAI-191	Laikipia	345	-2.4	-3.0
K01-LAI-191	Laikipia	355	-2.5	-2.5
K01-LAI-191	Laikipia	365	-2.3	-2.7
K01-LAI-191	Laikipia	375	-2.1	-2.1
K01-LAI-191	Laikipia	385	-2.2	-1.9
K01-LAI-191	Laikipia	395	-2.0	-2.1
K01-LAI-191	Laikipia	405	-2.9	-1.2
K01-LAI-191	Laikipia	415	-3.2	-1.1
K01-LAI-191	Laikipia	425	-3.2	-1.1
K01-LAI-191	Laikipia	435	-2.9	-1.8
K01-LAI-191	Laikipia	445	-2.8	-1.5
K01-LAI-191	Laikipia	455	-2.8	-1.7
K01-LAI-191	Laikipia	465	-2.9	-1.1
K01-LAI-191	Laikipia	475	-3.3	-1.6

Table A.12: Maasai Mara hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
Mara	Maasai Mara	5	-3.3	-3.3
Mara	Maasai Mara	15	-3.0	-4.0
Mara	Maasai Mara	25	-2.6	-3.6
Mara	Maasai Mara	35	-3.3	-4.0
Mara	Maasai Mara	45	-3.5	-4.6
Mara	Maasai Mara	55	-3.5	-4.0
Mara	Maasai Mara	65	-3.4	-4.2
Mara	Maasai Mara	75	-3.2	-4.2
Mara	Maasai Mara	85	-3.7	-4.4
Mara	Maasai Mara	95	-3.9	-4.5
Mara	Maasai Mara	105	-3.7	-4.3
Mara	Maasai Mara	115	-3.3	-4.1
Mara	Maasai Mara	125	-3.6	-3.8
Mara	Maasai Mara	135	-3.3	-4.0
Mara	Maasai Mara	155	-3.1	-4.1
Mara	Maasai Mara	165	-3.0	-5.1
Mara	Maasai Mara	175	-2.5	-5.5
Mara	Maasai Mara	185	-3.1	-4.4
Mara	Maasai Mara	195	-3.2	-4.0
Mara	Maasai Mara	205	-3.1	-4.2
Mara	Maasai Mara	215	-3.2	-4.2
Mara	Maasai Mara	225	-2.8	-4.2
Mara	Maasai Mara	235	-3.1	-4.0
Mara	Maasai Mara	245	-3.5	-4.3
Mara	Maasai Mara	255	-3.0	-4.2
Mara	Maasai Mara	265	-3.0	-4.0
Mara	Maasai Mara	285	-3.7	-4.2
Mara	Maasai Mara	295	-2.8	-4.4
Mara	Maasai Mara	305	-3.2	-4.2
Mara	Maasai Mara	315	-2.5	-4.1
Mara	Maasai Mara	325	-1.8	-3.3
Mara	Maasai Mara	335	-1.9	-3.7
Mara	Maasai Mara	345	-3.0	-3.7

Table A.13: Meru NP hippo isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
Meru	Meru NP	5	-2.5	-4.1
Meru	Meru NP	15	-1.7	-4.0
Meru	Meru NP	25	-2.2	-4.3
Meru	Meru NP	35	-1.8	-3.5
Meru	Meru NP	45	-2.4	-2.9
Meru	Meru NP	55	-2.9	-3.2
Meru	Meru NP	65	-3.2	-3.9
Meru	Meru NP	75	-3.6	-3.9
Meru	Meru NP	85	-3.6	-3.7
Meru	Meru NP	95	-3.6	-3.9
Meru	Meru NP	105	-3.4	-4.2
Meru	Meru NP	115	-3.6	-4.4
Meru	Meru NP	125	-3.9	-4.5
Meru	Meru NP	135	-4.4	-4.4
Meru	Meru NP	145	-4.9	-5.0
Meru	Meru NP	155	-5.5	-5.1
Meru	Meru NP	165	-5.9	-5.1
Meru	Meru NP	175	-6.9	-5.1
Meru	Meru NP	185	-7.1	-5.2
Meru	Meru NP	195	-8.4	-7.1
Meru	Meru NP	205	-7.8	-5.6
Meru	Meru NP	215	-8.3	-5.7
Meru	Meru NP	225	-8.1	-5.8
Meru	Meru NP	235	-8.1	-6.0
Meru	Meru NP	255	-8.1	-5.8
Meru	Meru NP	265	-8.5	-5.8
Meru	Meru NP	275	-8.6	-5.6

Table A.14: Minjila hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
KWS-Minjila	Minjila	5	-1.0	0.0
KWS-Minjila	Minjila	15	-1.4	-0.7
KWS-Minjila	Minjila	25	-1.5	-0.9
KWS-Minjila	Minjila	35	-1.8	-0.8
KWS-Minjila	Minjila	45	-1.9	-1.4
KWS-Minjila	Minjila	55	-1.9	-2.3
KWS-Minjila	Minjila	65	-1.6	-2.4
KWS-Minjila	Minjila	75	-1.2	-2.3
KWS-Minjila	Minjila	85	-1.3	-2.8
KWS-Minjila	Minjila	95	-0.9	-2.5
KWS-Minjila	Minjila	105	-1.2	-3.0
KWS-Minjila	Minjila	115	-1.2	-2.3
KWS-Minjila	Minjila	125	-1.3	-2.6
KWS-Minjila	Minjila	135	-1.3	-2.8
KWS-Minjila	Minjila	145	-1.6	-2.9
KWS-Minjila	Minjila	155	-1.8	-2.7
KWS-Minjila	Minjila	165	-1.7	-2.2
KWS-Minjila	Minjila	175	-2.0	-2.6
KWS-Minjila	Minjila	185	-2.1	-2.6
KWS-Minjila	Minjila	195	-2.3	-2.6
KWS-Minjila	Minjila	205	-2.4	-2.7
KWS-Minjila	Minjila	215	-2.3	-2.4
KWS-Minjila	Minjila	225	-2.1	-2.7
KWS-Minjila	Minjila	235	-2.0	-3.1
KWS-Minjila	Minjila	245	-1.9	-2.9
KWS-Minjila	Minjila	255	-1.6	-3.0
KWS-Minjila	Minjila	265	-1.5	-2.6
KWS-Minjila	Minjila	275	-1.5	-2.4
KWS-Minjila	Minjila	285	-1.5	-2.1
KWS-Minjila	Minjila	295	-1.5	-1.7
KWS-Minjila	Minjila	305	-1.4	-1.5
KWS-Minjila	Minjila	315	-1.6	-1.8
KWS-Minjila	Minjila	325	-1.8	-0.9
KWS-Minjila	Minjila	335	-1.8	-0.9
KWS-Minjila	Minjila	345	-1.7	-0.9
KWS-Minjila	Minjila	355	-1.8	-0.9
KWS-Minjila	Minjila	365	-2.2	-2.0
KWS-Minjila	Minjila	375	-2.2	-1.2
KWS-Minjila	Minjila	385	-2.5	-1.6
KWS-Minjila	Minjila	395	-2.3	-1.9

Table A.14: (cont'd)

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**$\delta\ ^{18}$O (V-PDB)**
KWS-Minjila	Minjila	405	-2.5	-2.1
KWS-Minjila	Minjila	415	-3.1	-1.9
KWS-Minjila	Minjila	425	-2.7	-1.6
KWS-Minjila	Minjila	435	-2.9	-2.6
KWS-Minjila	Minjila	445	-3.0	-2.7
KWS-Minjila	Minjila	455	-3.1	-3.0
KWS-Minjila	Minjila	465	-3.4	-3.2
KWS-Minjila	Minjila	475	-3.6	-3.5
KWS-Minjila	Minjila	485	-3.7	-3.1
KWS-Minjila	Minjila	495	-3.6	-3.2
KWS-Minjila	Minjila	505	-4.0	-3.6
KWS-Minjila	Minjila	525	-1.8	-1.2

Table A.15: Mokowe hippo isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
Mokowe	Mokowe	5	0.5	-4.2
Mokowe	Mokowe	15	0.0	-3.8
Mokowe	Mokowe	25	-0.1	-3.7
Mokowe	Mokowe	35	-0.2	-3.6
Mokowe	Mokowe	45	-0.2	-3.7
Mokowe	Mokowe	55	-0.5	-3.4
Mokowe	Mokowe	65	-0.5	-3.1
Mokowe	Mokowe	75	-0.7	-2.9
Mokowe	Mokowe	85	-0.6	-3.1
Mokowe	Mokowe	95	-0.5	-3.1
Mokowe	Mokowe	105	-0.2	-3.3
Mokowe	Mokowe	115	-0.1	-3.4
Mokowe	Mokowe	125	-0.2	-3.2
Mokowe	Mokowe	135	0.1	-3.2
Mokowe	Mokowe	145	0.2	-3.6
Mokowe	Mokowe	155	0.1	-3.6
Mokowe	Mokowe	165	-0.5	-4.0
Mokowe	Mokowe	175	-0.4	-4.0
Mokowe	Mokowe	185	-0.3	-3.9
Mokowe	Mokowe	195	0.0	-3.7
Mokowe	Mokowe	205	-0.3	-3.7
Mokowe	Mokowe	215	-0.3	-3.7
Mokowe	Mokowe	225	-0.5	-3.6
Mokowe	Mokowe	235	-0.3	-3.5
Mokowe	Mokowe	245	-0.3	-3.3
Mokowe	Mokowe	255	-0.4	-3.4
Mokowe	Mokowe	265	-0.2	-3.4
Mokowe	Mokowe	275	0.1	-3.5
Mokowe	Mokowe	285	0.3	-3.6
Mokowe	Mokowe	295	0.1	-3.7
Mokowe	Mokowe	305	-0.1	-3.8
Mokowe	Mokowe	315	-0.1	-3.9
Mokowe	Mokowe	325	0.1	-3.7
Mokowe	Mokowe	335	-0.3	-4.0
Mokowe	Mokowe	345	0.1	-3.7
Mokowe	Mokowe	355	0.0	-3.6
Mokowe	Mokowe	365	0.1	-3.5
Mokowe	Mokowe	375	0.1	-3.1
Mokowe	Mokowe	385	-0.1	-3.1
Mokowe	Mokowe	395	0.0	-3.4

Table A.15: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
Mokowe	Mokowe	405	0.0	-3.4
Mokowe	Mokowe	415	-0.2	-3.3
Mokowe	Mokowe	425	-0.3	-3.4
Mokowe	Mokowe	435	1.2	-3.6
Mokowe	Mokowe	445	0.0	-3.5
Mokowe	Mokowe	455	0.1	-3.4
Mokowe	Mokowe	465	-0.3	-3.5
Mokowe	Mokowe	475	-0.3	-3.4
Mokowe	Mokowe	485	1.2	-3.5

Table A.16: Mpeketoni hippo isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
Mpeketoni	Mpeketoni	5	-2.6	-0.8
Mpeketoni	Mpeketoni	15	-2.7	0.0
Mpeketoni	Mpeketoni	25	-2.4	0.1
Mpeketoni	Mpeketoni	35	-2.7	-0.1
Mpeketoni	Mpeketoni	45	-2.5	-0.2
Mpeketoni	Mpeketoni	55	-2.1	0.8
Mpeketoni	Mpeketoni	65	-2.1	0.1
Mpeketoni	Mpeketoni	75	-1.1	0.0
Mpeketoni	Mpeketoni	85	-2.3	0.2
Mpeketoni	Mpeketoni	95	-2.5	-1.2
Mpeketoni	Mpeketoni	105	-2.0	0.0
Mpeketoni	Mpeketoni	115	-2.1	-0.8
Mpeketoni	Mpeketoni	125	-2.2	-0.5
Mpeketoni	Mpeketoni	135	-2.0	0.0
Mpeketoni	Mpeketoni	145	-1.9	0.8
Mpeketoni	Mpeketoni	155	-2.1	-0.8
Mpeketoni	Mpeketoni	165	-2.2	-0.8
Mpeketoni	Mpeketoni	175	-2.1	-0.7
Mpeketoni	Mpeketoni	185	-2.1	-0.8
Mpeketoni	Mpeketoni	195	-2.0	-2.6
Mpeketoni	Mpeketoni	205	-2.0	-1.4
Mpeketoni	Mpeketoni	215	-1.7	-0.4
Mpeketoni	Mpeketoni	225	-1.6	-0.6
Mpeketoni	Mpeketoni	235	-2.0	-1.2
Mpeketoni	Mpeketoni	245	-1.5	-1.2
Mpeketoni	Mpeketoni	255	-1.7	-1.3
Mpeketoni	Mpeketoni	275	-1.7	-2.0
Mpeketoni	Mpeketoni	285	-1.7	-2.1
Mpeketoni	Mpeketoni	295	-1.6	-2.4
Mpeketoni	Mpeketoni	305	-1.5	-2.8
Mpeketoni	Mpeketoni	315	-1.4	-2.7
Mpeketoni	Mpeketoni	325	-1.6	-2.4
Mpeketoni	Mpeketoni	335	-1.6	-2.1
Mpeketoni	Mpeketoni	345	-1.9	-1.9
Mpeketoni	Mpeketoni	355	-2.0	-2.0
Mpeketoni	Mpeketoni	365	-2.1	-3.0
Mpeketoni	Mpeketoni	375	-2.1	-2.5
Mpeketoni	Mpeketoni	385	-2.4	-3.1
Mpeketoni	Mpeketoni	395	-2.3	-3.3
Mpeketoni	Mpeketoni	405	-2.6	-1.8

Table A.16: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**
Mpeketoni	Mpeketoni	415	-2.5	-2.5
Mpeketoni	Mpeketoni	425	-2.6	-1.4
Mpeketoni	Mpeketoni	435	-2.5	-2.9
Mpeketoni	Mpeketoni	455	-2.5	-2.8
Mpeketoni	Mpeketoni	465	-2.4	-1.5
Mpeketoni	Mpeketoni	475	-2.3	-1.8
Mpeketoni	Mpeketoni	485	-2.1	-2.1
Mpeketoni	Mpeketoni	495	-1.8	-1.9
Mpeketoni	Mpeketoni	505	-1.7	-2.0
Mpeketoni	Mpeketoni	515	-2.3	-2.2
Mpeketoni	Mpeketoni	525	-2.0	-2.9
Mpeketoni	Mpeketoni	535	-2.3	-3.1

Table A.17: Mwea – Gitaru Dam hippo isotope values

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**
Mwea-Gitaru	Mwea - Gitaru Dam	5	-7.6	-2.7
Mwea-Gitaru	Mwea - Gitaru Dam	15	-6.6	-2.0
Mwea-Gitaru	Mwea - Gitaru Dam	35	-6.3	-2.4
Mwea-Gitaru	Mwea - Gitaru Dam	45	-5.8	-3.3
Mwea-Gitaru	Mwea - Gitaru Dam	55	-5.1	-2.9
Mwea-Gitaru	Mwea - Gitaru Dam	75	-4.6	-2.7
Mwea-Gitaru	Mwea - Gitaru Dam	85	-5.1	-3.0
Mwea-Gitaru	Mwea - Gitaru Dam	95	-5.0	-3.2
Mwea-Gitaru	Mwea - Gitaru Dam	105	-5.1	-3.8
Mwea-Gitaru	Mwea - Gitaru Dam	115	-5.4	-3.5
Mwea-Gitaru	Mwea - Gitaru Dam	125	-5.4	-3.4
Mwea-Gitaru	Mwea - Gitaru Dam	135	-5.5	-3.2
Mwea-Gitaru	Mwea - Gitaru Dam	145	-5.1	-3.0
Mwea-Gitaru	Mwea - Gitaru Dam	155	-5.4	-3.1
Mwea-Gitaru	Mwea - Gitaru Dam	165	-5.5	-3.3
Mwea-Gitaru	Mwea - Gitaru Dam	175	-5.6	-3.2
Mwea-Gitaru	Mwea - Gitaru Dam	185	-5.3	-2.9
Mwea-Gitaru	Mwea - Gitaru Dam	205	-5.3	-3.5
Mwea-Gitaru	Mwea - Gitaru Dam	215	-5.4	-3.4
Mwea-Gitaru	Mwea - Gitaru Dam	235	-5.7	-3.7
Mwea-Gitaru	Mwea - Gitaru Dam	245	-5.7	-3.9
Mwea-Gitaru	Mwea - Gitaru Dam	255	-5.9	-4.1
Mwea-Gitaru	Mwea - Gitaru Dam	265	-6.4	-4.3
Mwea-Gitaru	Mwea - Gitaru Dam	285	-5.8	-4.2
Mwea-Gitaru	Mwea - Gitaru Dam	295	-5.9	-3.9
Mwea-Gitaru	Mwea - Gitaru Dam	305	-6.0	-4.1
Mwea-Gitaru	Mwea - Gitaru Dam	315	-5.8	-3.9
Mwea-Gitaru	Mwea - Gitaru Dam	325	-5.4	-3.6
Mwea-Gitaru	Mwea - Gitaru Dam	335	-5.3	-3.4
Mwea-Gitaru	Mwea - Gitaru Dam	345	-5.7	-3.6
Mwea-Gitaru	Mwea - Gitaru Dam	355	-6.0	-3.3
Mwea-Gitaru	Mwea - Gitaru Dam	365	-6.0	-3.7
Mwea-Gitaru	Mwea - Gitaru Dam	375	-6.2	-3.3
Mwea-Gitaru	Mwea - Gitaru Dam	385	-5.8	-3.2
Mwea-Gitaru	Mwea - Gitaru Dam	395	-5.6	-3.3
Mwea-Gitaru	Mwea - Gitaru Dam	405	-5.3	-3.2

Table A.18: Mwea #1 isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta\ ^{18}O$ (V-PDB)
Mwea-09	Mwea #1	5	-9.4	-3.3
Mwea-09	Mwea #1	15	-8.4	-2.8
Mwea-09	Mwea #1	25	-9.1	-2.2
Mwea-09	Mwea #1	35	-8.4	-2.7
Mwea-09	Mwea #1	45	-7.5	-3.3
Mwea-09	Mwea #1	55	-7.5	-3.3
Mwea-09	Mwea #1	65	-7.3	-3.3
Mwea-09	Mwea #1	75	-7.7	-2.6
Mwea-09	Mwea #1	85	-7.1	-3.9
Mwea-09	Mwea #1	95	-6.9	-3.5
Mwea-09	Mwea #1	105	-6.2	-3.5
Mwea-09	Mwea #1	115	-6.0	-3.2
Mwea-09	Mwea #1	125	-5.9	-3.4
Mwea-09	Mwea #1	135	-6.5	-3.1
Mwea-09	Mwea #1	145	-6.6	-3.3
Mwea-09	Mwea #1	155	-6.5	-3.2
Mwea-09	Mwea #1	165	-6.4	-3.7
Mwea-09	Mwea #1	175	-6.0	-3.6
Mwea-09	Mwea #1	185	-5.4	-3.9
Mwea-09	Mwea #1	195	-5.2	-4.0
Mwea-09	Mwea #1	205	-4.8	-3.9
Mwea-09	Mwea #1	215	-4.5	-4.9
Mwea-09	Mwea #1	225	-4.6	-5.0
Mwea-09	Mwea #1	235	-4.6	-5.3
Mwea-09	Mwea #1	245	-5.3	-5.3
Mwea-09	Mwea #1	255	-5.6	-5.1
Mwea-09	Mwea #1	265	-6.5	-5.7
Mwea-09	Mwea #1	275	-6.0	-5.5
Mwea-09	Mwea #1	285	-6.9	-5.4
Mwea-09	Mwea #1	295	-6.7	-5.3
Mwea-09	Mwea #1	305	-6.2	-4.2
Mwea-09	Mwea #1	315	-6.6	-3.8
Mwea-09	Mwea #1	325	-6.5	-4.0
Mwea-09	Mwea #1	335	-6.6	-4.1
Mwea-09	Mwea #1	345	-6.5	-3.7
Mwea-09	Mwea #1	355	-6.2	-3.9
Mwea-09	Mwea #1	365	-5.8	-3.9
Mwea-09	Mwea #1	375	-5.7	-4.4
Mwea-09	Mwea #1	385	-5.2	-4.0
Mwea-09	Mwea #1	395	-5.1	-4.4

Table A.18: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
Mwea-09	Mwea #1	405	-4.8	-3.6
Mwea-09	Mwea #1	415	-4.7	-3.8
Mwea-09	Mwea #1	425	-5.0	-3.7
Mwea-09	Mwea #1	435	-5.0	-4.1
Mwea-09	Mwea #1	445	-5.2	-3.9
Mwea-09	Mwea #1	455	-5.0	-4.4
Mwea-09	Mwea #1	465	-4.7	-4.2
Mwea-09	Mwea #1	475	-4.5	-4.3
Mwea-09	Mwea #1	485	-4.7	-4.3
Mwea-09	Mwea #1	495	-4.9	-4.4
Mwea-09	Mwea #1	505	-4.6	-4.4
Mwea-09	Mwea #1	525	-4.9	-4.7
Mwea-09	Mwea #1	535	-5.3	-4.7
Mwea-09	Mwea #1	545	-5.4	-4.6
Mwea-09	Mwea #1	555	-4.9	-4.9
Mwea-09	Mwea #1	565	-4.6	-4.3
Mwea-09	Mwea #1	575	-5.0	-4.8

Table A.19: Mwea #2 hippo isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
Mwea-NR-MAR-2005	Mwea #2	5	-9.2	-3.7
Mwea-NR-MAR-2005	Mwea #2	15	-10.0	-3.4
liMwea-NR-MAR-2005	Mwea #2	25	-9.6	-1.9
Mwea-NR-MAR-2005	Mwea #2	35	-8.9	-1.6
Mwea-NR-MAR-2005	Mwea #2	45	-8.0	-1.8
Mwea-NR-MAR-2005	Mwea #2	55	-7.2	-5.9
Mwea-NR-MAR-2005	Mwea #2	65	-7.5	-3.6
Mwea-NR-MAR-2005	Mwea #2	75	-7.3	-3.0
Mwea-NR-MAR-2005	Mwea #2	85	-7.1	-4.1
Mwea-NR-MAR-2005	Mwea #2	95	-7.2	-3.7
Mwea-NR-MAR-2005	Mwea #2	105	-6.7	-4.3
Mwea-NR-MAR-2005	Mwea #2	115	-6.1	-4.4
Mwea-NR-MAR-2005	Mwea #2	125	-6.0	-4.4
Mwea-NR-MAR-2005	Mwea #2	135	-5.7	-4.2
Mwea-NR-MAR-2005	Mwea #2	145	-6.0	-4.3
Mwea-NR-MAR-2005	Mwea #2	155	-6.8	-4.7
Mwea-NR-MAR-2005	Mwea #2	165	-7.5	-4.9
Mwea-NR-MAR-2005	Mwea #2	175	-7.3	-5.5
Mwea-NR-MAR-2005	Mwea #2	185	-6.7	-5.5
Mwea-NR-MAR-2005	Mwea #2	195	-6.3	-5.9
Mwea-NR-MAR-2005	Mwea #2	205	-6.5	-6.4
Mwea-NR-MAR-2005	Mwea #2	215	-5.6	-5.6
Mwea-NR-MAR-2005	Mwea #2	225	-5.5	-5.3
Mwea-NR-MAR-2005	Mwea #2	235	-5.7	-5.8
Mwea-NR-MAR-2005	Mwea #2	245	-5.5	-5.7
Mwea-NR-MAR-2005	Mwea #2	255	-5.9	-5.9
Mwea-NR-MAR-2005	Mwea #2	265	-5.7	-6.3
Mwea-NR-MAR-2005	Mwea #2	275	-4.6	-4.5
Mwea-NR-MAR-2005	Mwea #2	285	-5.9	-6.2
Mwea-NR-MAR-2005	Mwea #2	295	-6.3	-6.1
Mwea-NR-MAR-2005	Mwea #2	305	-6.8	-6.1
Mwea-NR-MAR-2005	Mwea #2	315	-6.7	-6.0
Mwea-NR-MAR-2005	Mwea #2	325	-6.5	-5.4
Mwea-NR-MAR-2005	Mwea #2	335	-6.5	-5.3
Mwea-NR-MAR-2005	Mwea #2	345	-5.2	-4.4
Mwea-NR-MAR-2005	Mwea #2	355	-6.6	-5.2
Mwea-NR-MAR-2005	Mwea #2	365	-6.8	-5.1
Mwea-NR-MAR-2005	Mwea #2	375	-6.8	-4.7
Mwea-NR-MAR-2005	Mwea #2	385	-6.7	-4.7
Mwea-NR-MAR-2005	Mwea #2	395	-6.2	-4.4

Table A.19: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
Mwea-NR-MAR-2005	Mwea #2	405	-5.8	-4.6
Mwea-NR-MAR-2005	Mwea #2	415	-4.3	-4.8
Mwea-NR-MAR-2005	Mwea #2	425	-4.5	-2.3
Mwea-NR-MAR-2005	Mwea #2	435	-5.2	-2.9
Mwea-NR-MAR-2005	Mwea #2	445	-4.4	-3.0
Mwea-NR-MAR-2005	Mwea #2	455	-4.5	-3.0
Mwea-NR-MAR-2005	Mwea #2	465	-5.0	-3.1
Mwea-NR-MAR-2005	Mwea #2	475	-4.6	-3.4
Mwea-NR-MAR-2005	Mwea #2	485	-4.3	-3.6
Mwea-NR-MAR-2005	Mwea #2	495	-4.2	-3.4
Mwea-NR-MAR-2005	Mwea #2	505	-4.6	-3.4
Mwea-NR-MAR-2005	Mwea #2	515	-4.6	-4.4
Mwea-NR-MAR-2005	Mwea #2	525	-4.4	-3.7
Mwea-NR-MAR-2005	Mwea #2	535	-4.4	-3.0
Mwea-NR-MAR-2005	Mwea #2	545	-4.2	-2.7
Mwea-NR-MAR-2005	Mwea #2	555	-4.2	-3.8
Mwea-NR-MAR-2005	Mwea #2	565	-4.7	-3.7
Mwea-NR-MAR-2005	Mwea #2	575	-4.3	-3.7

Table A.20: Mwea #3 hippo isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
Mwea-NP-2007	Mwea #3	5	-6.4	-2.7
Mwea-NP-2007	Mwea #3	15	-6.2	-2.3
Mwea-NP-2007	Mwea #3	25	-6.3	-2.9
Mwea-NP-2007	Mwea #3	35	-6.3	-3.0
Mwea-NP-2007	Mwea #3	45	-6.7	-3.0
Mwea-NP-2007	Mwea #3	55	-7.5	-3.1
Mwea-NP-2007	Mwea #3	65	-7.5	-3.4
Mwea-NP-2007	Mwea #3	75	-7.3	-3.6
Mwea-NP-2007	Mwea #3	85	-7.5	-3.4
Mwea-NP-2007	Mwea #3	95	-7.8	-3.4
Mwea-NP-2007	Mwea #3	105	-8.1	-3.1
Mwea-NP-2007	Mwea #3	115	-9.4	-3.7
Mwea-NP-2007	Mwea #3	125	-8.8	-3.0
Mwea-NP-2007	Mwea #3	135	-7.6	-2.7
Mwea-NP-2007	Mwea #3	145	-6.6	-3.8
Mwea-NP-2007	Mwea #3	155	-6.3	-3.7
Mwea-NP-2007	Mwea #3	165	-5.8	-3.7
Mwea-NP-2007	Mwea #3	175	-5.1	-4.2
Mwea-NP-2007	Mwea #3	185	-4.6	-4.5
Mwea-NP-2007	Mwea #3	195	-5.0	-5.0
Mwea-NP-2007	Mwea #3	205	-6.9	-4.8
Mwea-NP-2007	Mwea #3	215	-5.1	-4.3
Mwea-NP-2007	Mwea #3	225	-5.4	-4.3
Mwea-NP-2007	Mwea #3	235	-5.4	-4.4
Mwea-NP-2007	Mwea #3	245	-5.5	-4.0
Mwea-NP-2007	Mwea #3	255	-5.1	-3.9
Mwea-NP-2007	Mwea #3	265	-5.4	-3.6
Mwea-NP-2007	Mwea #3	275	-5.5	-3.4
Mwea-NP-2007	Mwea #3	285	-5.6	-3.3
Mwea-NP-2007	Mwea #3	295	-5.3	-3.1
Mwea-NP-2007	Mwea #3	305	-7.3	-3.4
Mwea-NP-2007	Mwea #3	315	-7.0	-2.8
Mwea-NP-2007	Mwea #3	325	-7.3	-3.0
Mwea-NP-2007	Mwea #3	335	-7.3	-3.1
Mwea-NP-2007	Mwea #3	345	-6.6	-2.6
Mwea-NP-2007	Mwea #3	355	-6.0	-3.3
Mwea-NP-2007	Mwea #3	365	-6.1	-3.2
Mwea-NP-2007	Mwea #3	375	-7.0	-4.0
Mwea-NP-2007	Mwea #3	385	-7.3	-3.3
Mwea-NP-2007	Mwea #3	395	-7.4	-3.6

Table A.20: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
Mwea-NP-2007	Mwea #3	405	-7.3	-3.1
Mwea-NP-2007	Mwea #3	415	-7.2	-3.0
Mwea-NP-2007	Mwea #3	425	-7.3	-3.0
Mwea-NP-2007	Mwea #3	435	-7.3	-3.4
Mwea-NP-2007	Mwea #3	445	-6.6	-3.1
Mwea-NP-2007	Mwea #3	455	-6.4	-4.0
Mwea-NP-2007	Mwea #3	465	-6.5	-3.1
Mwea-NP-2007	Mwea #3	475	-6.7	-3.5
Mwea-NP-2007	Mwea #3	485	-6.3	-3.4
Mwea-NP-2007	Mwea #3	495	-6.1	-3.5
Mwea-NP-2007	Mwea #3	505	-6.1	-3.4
Mwea-NP-2007	Mwea #3	515	-6.2	-3.3
Mwea-NP-2007	Mwea #3	525	-5.9	-3.1
Mwea-NP-2007	Mwea #3	535	-5.6	-3.4
Mwea-NP-2007	Mwea #3	545	-5.9	-3.1
Mwea-NP-2007	Mwea #3	555	-6.2	-3.1
Mwea-NP-2007	Mwea #3	565	-6.5	-3.1
Mwea-NP-2007	Mwea #3	575	-6.5	-3.2
Mwea-NP-2007	Mwea #3	585	-7.2	-3.8
Mwea-NP-2007	Mwea #3	595	-7.6	-4.1
Mwea-NP-2007	Mwea #3	605	-7.9	-4.6

Table A.21: Naivasha – Crater Lake hippo isotope values.

Specimen	Locality	Pos.	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
KWS-Naivasha-CraterL	Naivasha - Crater Lake	15	0.0	-1.7
KWS-Naivasha-CraterL	Naivasha - Crater Lake	25	-0.5	-2.2
KWS-Naivasha-CraterL	Naivasha - Crater Lake	35	-0.5	-2.2
KWS-Naivasha-CraterL	Naivasha - Crater Lake	45	-1.0	-2.7
KWS-Naivasha-CraterL	Naivasha - Crater Lake	55	-1.1	-2.9
KWS-Naivasha-CraterL	Naivasha - Crater Lake	65	-0.8	-3.5
KWS-Naivasha-CraterL	Naivasha - Crater Lake	75	-0.6	-4.0
KWS-Naivasha-CraterL	Naivasha - Crater Lake	85	-0.6	-4.3
KWS-Naivasha-CraterL	Naivasha - Crater Lake	95	-0.2	-4.2
KWS-Naivasha-CraterL	Naivasha - Crater Lake	105	0.2	-4.8
KWS-Naivasha-CraterL	Naivasha - Crater Lake	115	0.1	-5.1
KWS-Naivasha-CraterL	Naivasha - Crater Lake	125	0.1	-5.5
KWS-Naivasha-CraterL	Naivasha - Crater Lake	135	-0.3	-5.1
KWS-Naivasha-CraterL	Naivasha - Crater Lake	145	-0.7	-5.2
KWS-Naivasha-CraterL	Naivasha - Crater Lake	155	-1.1	-5.2
KWS-Naivasha-CraterL	Naivasha - Crater Lake	165	-1.0	-4.7
KWS-Naivasha-CraterL	Naivasha - Crater Lake	175	-1.1	-5.0
KWS-Naivasha-CraterL	Naivasha - Crater Lake	185	-1.0	-5.1
KWS-Naivasha-CraterL	Naivasha - Crater Lake	195	-1.7	-4.8
KWS-Naivasha-CraterL	Naivasha - Crater Lake	205	-2.1	-4.7
KWS-Naivasha-CraterL	Naivasha - Crater Lake	215	-2.6	-4.6
KWS-Naivasha-CraterL	Naivasha - Crater Lake	225	-2.3	-4.5
KWS-Naivasha-CraterL	Naivasha - Crater Lake	235	-2.3	-4.4
KWS-Naivasha-CraterL	Naivasha - Crater Lake	245	-2.5	-4.5
KWS-Naivasha-CraterL	Naivasha - Crater Lake	255	-2.9	-4.7
KWS-Naivasha-CraterL	Naivasha - Crater Lake	265	-3.2	-4.4
KWS-Naivasha-CraterL	Naivasha - Crater Lake	275	-3.5	-4.5
KWS-Naivasha-CraterL	Naivasha - Crater Lake	285	-3.8	-3.9
KWS-Naivasha-CraterL	Naivasha - Crater Lake	295	-3.5	-4.0
KWS-Naivasha-CraterL	Naivasha - Crater Lake	305	-2.8	-3.9
KWS-Naivasha-CraterL	Naivasha - Crater Lake	315	-2.6	-3.8
KWS-Naivasha-CraterL	Naivasha - Crater Lake	325	-2.3	-3.3
KWS-Naivasha-CraterL	Naivasha - Crater Lake	335	-2.7	-3.9
KWS-Naivasha-CraterL	Naivasha - Crater Lake	345	-3.7	-3.0
KWS-Naivasha-CraterL	Naivasha - Crater Lake	355	-4.3	-2.9
KWS-Naivasha-CraterL	Naivasha - Crater Lake	365	-4.1	-2.8
KWS-Naivasha-CraterL	Naivasha - Crater Lake	375	-3.6	-3.4
KWS-Naivasha-CraterL	Naivasha - Crater Lake	385	-3.6	-3.1
KWS-Naivasha-CraterL	Naivasha - Crater Lake	395	-5.1	-2.8
KWS-Naivasha-CraterL	Naivasha - Crater Lake	405	-5.3	-2.4

Table A.21: (cont'd)

Specimen	**Locality**	**Pos.**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
KWS-Naivasha-CraterL	Naivasha - Crater Lake	415	-6.7	-2.1
KWS-Naivasha-CraterL	Naivasha - Crater Lake	425	-6.4	-2.4
KWS-Naivasha-CraterL	Naivasha - Crater Lake	435	-7.4	-2.1
KWS-Naivasha-CraterL	Naivasha - Crater Lake	445	-7.4	-2.3
KWS-Naivasha-CraterL	Naivasha - Crater Lake	455	-7.1	-2.3
KWS-Naivasha-CraterL	Naivasha - Crater Lake	465	-6.5	-3.0
KWS-Naivasha-CraterL	Naivasha - Crater Lake	475	-4.2	-3.9
KWS-Naivasha-CraterL	Naivasha - Crater Lake	485	-1.4	-3.6
KWS-Naivasha-CraterL	Naivasha - Crater Lake	495	-5.6	-3.0
KWS-Naivasha-CraterL	Naivasha - Crater Lake	505	-4.9	-3.3
KWS-Naivasha-CraterL	Naivasha - Crater Lake	515	-4.8	-3.4
KWS-Naivasha-CraterL	Naivasha - Crater Lake	525	-4.5	-3.8

Table A.22: Naivasha – Crayfish hippo isotope values.

Specimen	Locality	Position	δ^{13}C (V-PDB)	δ^{18}O (V-PDB)
KWS-NAIV-1108	Naivasha - Crayfish	5	-2.0	-0.6
KWS-NAIV-1108	Naivasha - Crayfish	15	-1.7	0.0
KWS-NAIV-1108	Naivasha - Crayfish	25	-2.2	1.6
KWS-NAIV-1108	Naivasha - Crayfish	35	-3.0	2.0
KWS-NAIV-1108	Naivasha - Crayfish	45	-3.8	1.0
KWS-NAIV-1108	Naivasha - Crayfish	55	-4.3	0.5
KWS-NAIV-1108	Naivasha - Crayfish	65	-4.3	0.3
KWS-NAIV-1108	Naivasha - Crayfish	75	-4.4	-1.1
KWS-NAIV-1108	Naivasha - Crayfish	85	-4.2	-0.5
KWS-NAIV-1108	Naivasha - Crayfish	95	-4.3	-0.8
KWS-NAIV-1108	Naivasha - Crayfish	105	-4.2	-1.1
KWS-NAIV-1108	Naivasha - Crayfish	115	-3.9	-0.5
KWS-NAIV-1108	Naivasha - Crayfish	125	-3.7	0.1
KWS-NAIV-1108	Naivasha - Crayfish	135	-3.5	-0.7
KWS-NAIV-1108	Naivasha - Crayfish	145	-3.1	0.4
KWS-NAIV-1108	Naivasha - Crayfish	155	-3.0	0.0
KWS-NAIV-1108	Naivasha - Crayfish	165	-3.0	0.0
KWS-NAIV-1108	Naivasha - Crayfish	175	-2.7	-0.1
KWS-NAIV-1108	Naivasha - Crayfish	185	-2.5	-0.1
KWS-NAIV-1108	Naivasha - Crayfish	195	-2.7	0.5
KWS-NAIV-1108	Naivasha - Crayfish	205	-2.9	0.6
KWS-NAIV-1108	Naivasha - Crayfish	215	-2.3	0.7
KWS-NAIV-1108	Naivasha - Crayfish	225	-1.9	1.3
KWS-NAIV-1108	Naivasha - Crayfish	235	-2.5	0.6
KWS-NAIV-1108	Naivasha - Crayfish	245	-2.1	1.0
KWS-NAIV-1108	Naivasha - Crayfish	255	-2.1	0.7
KWS-NAIV-1108	Naivasha - Crayfish	265	-2.7	0.2
KWS-NAIV-1108	Naivasha - Crayfish	275	-2.0	0.6
KWS-NAIV-1108	Naivasha - Crayfish	285	-2.0	0.3
KWS-NAIV-1108	Naivasha - Crayfish	295	-1.6	0.8
KWS-NAIV-1108	Naivasha - Crayfish	305	-1.1	0.2
KWS-NAIV-1108	Naivasha - Crayfish	315	-0.6	1.4
KWS-NAIV-1108	Naivasha - Crayfish	325	-0.5	1.7
KWS-NAIV-1108	Naivasha - Crayfish	335	-0.8	1.3
KWS-NAIV-1108	Naivasha - Crayfish	345	-0.8	0.9
KWS-NAIV-1108	Naivasha - Crayfish	355	-0.7	1.5
KWS-NAIV-1108	Naivasha - Crayfish	365	-0.3	1.4
KWS-NAIV-1108	Naivasha - Crayfish	375	-0.7	0.5
KWS-NAIV-1108	Naivasha - Crayfish	385	-1.2	0.3
KWS-NAIV-1108	Naivasha - Crayfish	395	-0.8	0.7

Table A.22: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
KWS-NAIV-1108	Naivasha - Crayfish	405	-1.9	0.5
KWS-NAIV-1108	Naivasha - Crayfish	415	-1.1	0.4
KWS-NAIV-1108	Naivasha - Crayfish	425	-0.8	0.5
KWS-NAIV-1108	Naivasha - Crayfish	435	-0.7	-0.1
KWS-NAIV-1108	Naivasha - Crayfish	445	-1.2	-0.3
KWS-NAIV-1108	Naivasha - Crayfish	455	-0.9	0.2
KWS-NAIV-1108	Naivasha - Crayfish	465	-0.8	0.5
KWS-NAIV-1108	Naivasha - Crayfish	475	-0.6	0.4
KWS-NAIV-1108	Naivasha - Crayfish	485	-0.7	0.2
KWS-NAIV-1108	Naivasha - Crayfish	495	-1.1	0.3
KWS-NAIV-1108	Naivasha - Crayfish	505	-1.1	0.3
KWS-NAIV-1108	Naivasha - Crayfish	515	-0.9	0.5
KWS-NAIV-1108	Naivasha - Crayfish	535	-0.6	0.9
KWS-NAIV-1108	Naivasha - Crayfish	545	-0.8	0.5
KWS-NAIV-1108	Naivasha - Crayfish	555	-0.3	1.4
KWS-NAIV-1108	Naivasha - Crayfish	565	-0.8	0.8
KWS-NAIV-1108	Naivasha - Crayfish	575	-0.6	1.1
KWS-NAIV-1108	Naivasha - Crayfish	585	-1.0	0.5

Table A.23: Lake Nakuru hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
KWS-LNakuru-Kabutini	Nakuru	5	-2.0	-0.5
KWS-LNakuru-Kabutini	Nakuru	15	-0.6	0.5
KWS-LNakuru-Kabutini	Nakuru	25	-0.6	1.7
KWS-LNakuru-Kabutini	Nakuru	35	-0.6	1.8
KWS-LNakuru-Kabutini	Nakuru	45	-1.2	1.1
KWS-LNakuru-Kabutini	Nakuru	55	-2.2	0.5
KWS-LNakuru-Kabutini	Nakuru	65	-1.5	0.7
KWS-LNakuru-Kabutini	Nakuru	75	-1.4	0.0
KWS-LNakuru-Kabutini	Nakuru	85	-1.6	-0.7
KWS-LNakuru-Kabutini	Nakuru	95	-2.0	-2.9
KWS-LNakuru-Kabutini	Nakuru	105	-0.1	-1.9
KWS-LNakuru-Kabutini	Nakuru	115	-0.1	-1.1
KWS-LNakuru-Kabutini	Nakuru	125	-0.1	-1.6
KWS-LNakuru-Kabutini	Nakuru	135	0.2	-1.5
KWS-LNakuru-Kabutini	Nakuru	145	0.1	-1.6
KWS-LNakuru-Kabutini	Nakuru	155	0.2	-1.7
KWS-LNakuru-Kabutini	Nakuru	165	0.7	-1.2
KWS-LNakuru-Kabutini	Nakuru	185	-0.2	-2.5
KWS-LNakuru-Kabutini	Nakuru	195	0.0	-2.4
KWS-LNakuru-Kabutini	Nakuru	205	0.2	-1.5
KWS-LNakuru-Kabutini	Nakuru	215	-0.7	-1.6
KWS-LNakuru-Kabutini	Nakuru	225	-0.7	-2.0
KWS-LNakuru-Kabutini	Nakuru	235	-1.1	-1.9
KWS-LNakuru-Kabutini	Nakuru	245	-1.0	-1.9
KWS-LNakuru-Kabutini	Nakuru	255	-0.9	-1.7
KWS-LNakuru-Kabutini	Nakuru	265	-0.9	-2.1
KWS-LNakuru-Kabutini	Nakuru	275	-1.5	-2.0
KWS-LNakuru-Kabutini	Nakuru	285	-1.6	-2.2
KWS-LNakuru-Kabutini	Nakuru	295	-1.7	-1.9
KWS-LNakuru-Kabutini	Nakuru	305	-2.2	-2.3
KWS-LNakuru-Kabutini	Nakuru	315	-2.0	-2.3

Table A.24: Lake Ol Bolossat hippo isotope values.

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**
Olbolossat	Olbolossat	5	-5.0	-2.1
Olbolossat	Olbolossat	15	-5.7	-1.7
Olbolossat	Olbolossat	25	-4.6	-2.4
Olbolossat	Olbolossat	35	-4.9	-2.5
Olbolossat	Olbolossat	45	-5.8	-0.8
Olbolossat	Olbolossat	55	-6.3	-1.5
Olbolossat	Olbolossat	65	-6.7	-3.2
Olbolossat	Olbolossat	75	-5.0	-1.4
Olbolossat	Olbolossat	85	-4.3	-0.8
Olbolossat	Olbolossat	95	-2.0	-3.1
Olbolossat	Olbolossat	105	-4.5	-0.7
Olbolossat	Olbolossat	115	-5.6	-1.3
Olbolossat	Olbolossat	125	-5.0	-0.8
Olbolossat	Olbolossat	135	-4.8	-0.9
Olbolossat	Olbolossat	145	-7.1	-1.1
Olbolossat	Olbolossat	155	-7.3	-1.2
Olbolossat	Olbolossat	165	-7.7	-2.0
Olbolossat	Olbolossat	175	-6.5	-3.1
Olbolossat	Olbolossat	185	-7.2	-3.5
Olbolossat	Olbolossat	195	-7.9	-2.9
Olbolossat	Olbolossat	205	-5.5	-3.6
Olbolossat	Olbolossat	215	-6.2	-2.7
Olbolossat	Olbolossat	225	-5.5	-2.5
Olbolossat	Olbolossat	235	-6.0	-1.6
Olbolossat	Olbolossat	245	-4.7	-2.4
Olbolossat	Olbolossat	255	-3.8	-3.5
Olbolossat	Olbolossat	265	-3.6	-4.5
Olbolossat	Olbolossat	275	-4.1	-3.7
Olbolossat	Olbolossat	285	-5.1	-4.0
Olbolossat	Olbolossat	295	-3.7	-2.6
Olbolossat	Olbolossat	305	-5.6	-2.3

Table A.25: Tsavo #1 hippo isotope values.

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**
K01-TSW-291	Tsavo #1	5	-7.4	-0.9
K01-TSW-291	Tsavo #1	15	-6.8	-0.4
K01-TSW-291	Tsavo #1	25	-5.6	-1.9
K01-TSW-291	Tsavo #1	35	-5.6	-3.2
K01-TSW-291	Tsavo #1	45	-6.3	-3.8
K01-TSW-291	Tsavo #1	55	-7.9	-3.8
K01-TSW-291	Tsavo #1	65	-8.5	-3.9
K01-TSW-291	Tsavo #1	75	-5.7	-4.5
K01-TSW-291	Tsavo #1	85	-4.5	-4.4
K01-TSW-291	Tsavo #1	95	-4.4	-4.4
K01-TSW-291	Tsavo #1	105	-3.7	-4.4
K01-TSW-291	Tsavo #1	115	-3.1	-4.7
K01-TSW-291	Tsavo #1	125	-3.0	-4.2
K01-TSW-291	Tsavo #1	135	-2.6	-4.5
K01-TSW-291	Tsavo #1	145	-3.1	-4.8
K01-TSW-291	Tsavo #1	155	-2.6	-4.6
K01-TSW-291	Tsavo #1	165	-2.3	-4.1
K01-TSW-291	Tsavo #1	175	-2.0	-4.4
K01-TSW-291	Tsavo #1	185	-1.7	-4.6
K01-TSW-291	Tsavo #1	195	-1.9	-4.6
K01-TSW-291	Tsavo #1	205	-2.1	-4.7
K01-TSW-291	Tsavo #1	215	-2.7	-4.5
K01-TSW-291	Tsavo #1	225	-3.4	-4.0
K01-TSW-291	Tsavo #1	235	-2.8	-4.2
K01-TSW-291	Tsavo #1	245	-2.1	-4.0
K01-TSW-291	Tsavo #1	255	-2.3	-4.1
K01-TSW-291	Tsavo #1	275	-2.8	-4.5
K01-TSW-291	Tsavo #1	285	-2.9	-4.3
K01-TSW-291	Tsavo #1	295	-2.5	-4.4
K01-TSW-291	Tsavo #1	305	-2.5	-3.8
K01-TSW-291	Tsavo #1	315	-2.5	-4.0
K01-TSW-291	Tsavo #1	325	-2.5	-4.5
K01-TSW-291	Tsavo #1	335	-2.5	-4.9
K01-TSW-291	Tsavo #1	345	-2.6	-4.7
K01-TSW-291	Tsavo #1	345	-2.5	-4.3
K01-TSW-291	Tsavo #1	355	-2.4	-4.8
K01-TSW-291	Tsavo #1	355	-2.3	-4.7
K01-TSW-291	Tsavo #1	365	-2.0	-4.6
K01-TSW-291	Tsavo #1	365	-1.9	-4.4
K01-TSW-291	Tsavo #1	375	-2.1	-4.6

Table A.25: (cont'd)

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta\ ^{18}O$ (V-PDB)
K01-TSW-291	Tsavo #1	375	-1.8	-4.3
K01-TSW-291	Tsavo #1	385	-1.5	-4.3
K01-TSW-291	Tsavo #1	385	-1.5	-4.5
K01-TSW-291	Tsavo #1	395	-1.3	-4.2
K01-TSW-291	Tsavo #1	405	-1.6	-4.4
K01-TSW-291	Tsavo #1	415	-1.5	-4.0
K01-TSW-291	Tsavo #1	425	-1.8	-3.8
K01-TSW-291	Tsavo #1	435	-2.0	-4.1
K01-TSW-291	Tsavo #1	445	-2.2	-3.7
K01-TSW-291	Tsavo #1	455	-2.3	-4.0
K01-TSW-291	Tsavo #1	465	-1.9	-4.6
K01-TSW-291	Tsavo #1	475	-2.3	-4.4
K01-TSW-291	Tsavo #1	485	-2.3	-4.7
K01-TSW-291	Tsavo #1	495	-2.7	-4.9
K01-TSW-291	Tsavo #1	505	-3.2	-5.2
K01-TSW-291	Tsavo #1	515	-3.6	-4.9
K01-TSW-291	Tsavo #1	525	-3.7	-4.9
K01-TSW-291	Tsavo #1	535	-3.4	-5.0
K01-TSW-291	Tsavo #1	545	-3.1	-4.7
K01-TSW-291	Tsavo #1	555	-3.1	-5.0
K01-TSW-291	Tsavo #1	565	-3.4	-5.1
K01-TSW-291	Tsavo #1	575	-3.3	-4.7
K01-TSW-291	Tsavo #1	585	-2.8	-4.6
K01-TSW-291	Tsavo #1	595	-2.8	-4.7
K01-TSW-291	Tsavo #1	605	-2.3	-4.5

Table A.26: Tsavo #2 hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**
Tsavo-09	Tsavo #2	5	-2.4	-3.6
Tsavo-09	Tsavo #2	15	-3.5	-3.3
Tsavo-09	Tsavo #2	25	-4.2	-3.3
Tsavo-09	Tsavo #2	35	-4.2	-3.5
Tsavo-09	Tsavo #2	45	-3.8	-3.1
Tsavo-09	Tsavo #2	55	-3.3	-4.1
Tsavo-09	Tsavo #2	65	-3.1	-4.1
Tsavo-09	Tsavo #2	75	-3.3	-4.5
Tsavo-09	Tsavo #2	85	-3.5	-4.6
Tsavo-09	Tsavo #2	95	-3.3	-4.6
Tsavo-09	Tsavo #2	105	-3.2	-4.3
Tsavo-09	Tsavo #2	115	-3.4	-4.7
Tsavo-09	Tsavo #2	125	-3.0	-4.8
Tsavo-09	Tsavo #2	135	-2.8	-4.3
Tsavo-09	Tsavo #2	145	-3.6	-4.2
Tsavo-09	Tsavo #2	155	-3.6	-4.6
Tsavo-09	Tsavo #2	175	-3.1	-4.5
Tsavo-09	Tsavo #2	185	-3.3	-4.5
Tsavo-09	Tsavo #2	195	-3.1	-4.3
Tsavo-09	Tsavo #2	205	-3.5	-4.7
Tsavo-09	Tsavo #2	215	-3.9	-4.8
Tsavo-09	Tsavo #2	225	-4.5	-4.3
Tsavo-09	Tsavo #2	235	-4.6	-4.5
Tsavo-09	Tsavo #2	245	-4.6	-5.0
Tsavo-09	Tsavo #2	255	-4.6	-5.3
Tsavo-09	Tsavo #2	265	-3.3	-5.3
Tsavo-09	Tsavo #2	275	-2.6	-5.6
Tsavo-09	Tsavo #2	285	-3.7	-5.6
Tsavo-09	Tsavo #2	295	-3.6	-5.1
Tsavo-09	Tsavo #2	305	-3.1	-4.8
Tsavo-09	Tsavo #2	315	-2.7	-4.6
Tsavo-09	Tsavo #2	325	-2.5	-4.6
Tsavo-09	Tsavo #2	335	-2.2	-4.7
Tsavo-09	Tsavo #2	345	-2.2	-4.7
Tsavo-09	Tsavo #2	355	-2.7	-4.7
Tsavo-09	Tsavo #2	365	-2.8	-4.9
Tsavo-09	Tsavo #2	375	-3.2	-3.9
Tsavo-09	Tsavo #2	385	-3.5	-4.2
Tsavo-09	Tsavo #2	395	-2.7	-4.4
Tsavo-09	Tsavo #2	405	-2.6	-4.2

Table A.26: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**δ ^{18}O (V-PDB)**
Tsavo-09	Tsavo #2	415	-2.4	-4.1
Tsavo-09	Tsavo #2	425	-2.6	-4.6
Tsavo-09	Tsavo #2	435	-2.6	-4.2
Tsavo-09	Tsavo #2	445	-2.1	-4.0
Tsavo-09	Tsavo #2	455	-2.5	-4.1
Tsavo-09	Tsavo #2	465	-3.3	-4.6
Tsavo-09	Tsavo #2	475	-3.5	-4.5
Tsavo-09	Tsavo #2	485	-3.5	-4.3
Tsavo-09	Tsavo #2	495	-3.3	-4.1
Tsavo-09	Tsavo #2	505	-3.5	-5.1
Tsavo-09	Tsavo #2	515	-2.9	-4.3
Tsavo-09	Tsavo #2	525	-2.3	-3.9
Tsavo-09	Tsavo #2	535	-2.6	-3.5
Tsavo-09	Tsavo #2	545	-2.5	-4.2
Tsavo-09	Tsavo #2	555	-3.1	-4.5
Tsavo-09	Tsavo #2	565	-3.5	-4.3
Tsavo-09	Tsavo #2	575	-3.2	-3.9
Tsavo-09	Tsavo #2	585	-3.2	-4.2
Tsavo-09	Tsavo #2	595	-2.3	-3.4

Table A.27: Tsavo #3 hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
K08-201	Tsavo #3	5	-2.8	-3.3
K08-201	Tsavo #3	15	-2.9	-3.1
K08-201	Tsavo #3	25	-2.9	-1.4
K08-201	Tsavo #3	35	-3.3	-0.3
K08-201	Tsavo #3	45	-3.7	0.8
K08-201	Tsavo #3	55	-5.6	1.8
K08-201	Tsavo #3	65	-5.5	1.0
K08-201	Tsavo #3	75	-5.4	0.7
K08-201	Tsavo #3	85	-4.7	0.3
K08-201	Tsavo #3	95	-5.3	-1.6
K08-201	Tsavo #3	105	-5.7	-1.5
K08-201	Tsavo #3	115	-4.5	-1.2
K08-201	Tsavo #3	125	-4.5	-1.2
K08-201	Tsavo #3	135	-3.9	-1.6
K08-201	Tsavo #3	145	-3.6	-1.5
K08-201	Tsavo #3	155	-3.3	-1.7
K08-201	Tsavo #3	165	-2.7	-2.1
K08-201	Tsavo #3	175	-2.5	-1.9
K08-201	Tsavo #3	185	-2.9	-1.4
K08-201	Tsavo #3	195	-2.7	-1.3
K08-201	Tsavo #3	205	-2.3	-1.9
K08-201	Tsavo #3	215	-2.1	-2.2
K08-201	Tsavo #3	225	-2.1	-1.7
K08-201	Tsavo #3	235	-2.3	-0.8
K08-201	Tsavo #3	245	-2.6	-0.9
K08-201	Tsavo #3	255	-2.2	-1.2
K08-201	Tsavo #3	265	-2.2	-1.2
K08-201	Tsavo #3	275	-2.0	-1.1
K08-201	Tsavo #3	285	-1.7	-2.3
K08-201	Tsavo #3	295	-2.0	-2.4
K08-201	Tsavo #3	305	-2.4	-2.1
K08-201	Tsavo #3	315	-2.4	-1.5
K08-201	Tsavo #3	325	-2.4	-1.2
K08-201	Tsavo #3	335	-2.8	-1.6
K08-201	Tsavo #3	345	-4.4	-3.0
K08-201	Tsavo #3	355	-5.8	-2.8
K08-201	Tsavo #3	365	-7.3	-2.9
K08-201	Tsavo #3	375	-7.5	-3.0
K08-201	Tsavo #3	385	-7.8	-3.3
K08-201	Tsavo #3	395	-9.4	-2.9

Table A.27: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
K08-201	Tsavo #3	405	-10.0	-4.3
K08-201	Tsavo #3	415	-9.7	-3.3
K08-201	Tsavo #3	425	-8.5	-3.4
K08-201	Tsavo #3	435	-8.9	-4.4
K08-201	Tsavo #3	445	-9.4	-3.9
K08-201	Tsavo #3	455	-9.4	-4.3
K08-201	Tsavo #3	465	-7.7	-4.1
K08-201	Tsavo #3	475	-7.2	-4.2
K08-201	Tsavo #3	485	-6.6	-4.4
K08-201	Tsavo #3	495	-6.3	-4.6
K08-201	Tsavo #3	505	-5.4	-3.9
K08-201	Tsavo #3	515	-4.8	-3.8
K08-201	Tsavo #3	525	-4.7	-4.0
K08-201	Tsavo #3	535	-6.2	-4.2

Table A.28: Turkana – Koobi Fora 1 hippo isotope values.

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
K11-KF	Turkana - Koobi Fora 1	15	1.0	0.9
K11-KF	Turkana - Koobi Fora 1	25	1.2	1.5
K11-KF	Turkana - Koobi Fora 1	35	0.6	1.2
K11-KF	Turkana - Koobi Fora 1	45	0.7	1.3
K11-KF	Turkana - Koobi Fora 1	52	0.4	2.9
K11-KF	Turkana - Koobi Fora 1	54	0.5	2.9
K11-KF	Turkana - Koobi Fora 1	56	0.4	2.2
K11-KF	Turkana - Koobi Fora 1	58	0.3	2.3
K11-KF	Turkana - Koobi Fora 1	60	0.4	2.7
K11-KF	Turkana - Koobi Fora 1	62	0.4	2.8
K11-KF	Turkana - Koobi Fora 1	64	0.6	2.7
K11-KF	Turkana - Koobi Fora 1	66	0.6	2.6
K11-KF	Turkana - Koobi Fora 1	68	0.8	2.2
K11-KF	Turkana - Koobi Fora 1	70	1.1	2.8
K11-KF	Turkana - Koobi Fora 1	72	1.0	2.1
K11-KF	Turkana - Koobi Fora 1	74	1.1	2.1
K11-KF	Turkana - Koobi Fora 1	76	0.9	2.2
K11-KF	Turkana - Koobi Fora 1	78	1.0	2.3
K11-KF	Turkana - Koobi Fora 1	80	0.8	2.3
K11-KF	Turkana - Koobi Fora 1	82	0.3	1.2
K11-KF	Turkana - Koobi Fora 1	84	0.6	2.0
K11-KF	Turkana - Koobi Fora 1	86	0.4	1.4
K11-KF	Turkana - Koobi Fora 1	88	0.4	1.5
K11-KF	Turkana - Koobi Fora 1	90	-0.1	1.1
K11-KF	Turkana - Koobi Fora 1	92	0.3	1.5
K11-KF	Turkana - Koobi Fora 1	94	0.1	1.5
K11-KF	Turkana - Koobi Fora 1	96	0.2	1.5
K11-KF	Turkana - Koobi Fora 1	98	0.1	1.0
K11-KF	Turkana - Koobi Fora 1	100	0.1	1.7
K11-KF	Turkana - Koobi Fora 1	102	0.3	2.5
K11-KF	Turkana - Koobi Fora 1	104	0.3	2.2
K11-KF	Turkana - Koobi Fora 1	106	0.4	2.5
K11-KF	Turkana - Koobi Fora 1	108	0.4	2.5
K11-KF	Turkana - Koobi Fora 1	110	0.4	2.4
K11-KF	Turkana - Koobi Fora 1	112	0.5	2.2
K11-KF	Turkana - Koobi Fora 1	114	0.6	2.5
K11-KF	Turkana - Koobi Fora 1	116	0.6	2.2
K11-KF	Turkana - Koobi Fora 1	118	0.7	2.0
K11-KF	Turkana - Koobi Fora 1	120	0.7	1.6
K11-KF	Turkana - Koobi Fora 1	122	1.0	1.9

Table A.28: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
K11-KF	Turkana - Koobi Fora 1	124	1.1	2.0
K11-KF	Turkana - Koobi Fora 1	126	1.2	1.8
K11-KF	Turkana - Koobi Fora 1	128	1.3	1.7
K11-KF	Turkana - Koobi Fora 1	130	1.4	1.4
K11-KF	Turkana - Koobi Fora 1	132	0.7	2.2
K11-KF	Turkana - Koobi Fora 1	134	1.2	2.3
K11-KF	Turkana - Koobi Fora 1	136	1.4	2.2
K11-KF	Turkana - Koobi Fora 1	138	1.1	1.8
K11-KF	Turkana - Koobi Fora 1	140	1.2	1.8
K11-KF	Turkana - Koobi Fora 1	142	1.4	2.0
K11-KF	Turkana - Koobi Fora 1	144	1.5	2.0
K11-KF	Turkana - Koobi Fora 1	146	1.5	2.1
K11-KF	Turkana - Koobi Fora 1	148	1.2	2.4
K11-KF	Turkana - Koobi Fora 1	150	1.2	2.1
K11-KF	Turkana - Koobi Fora 1	151	0.2	0.6
K11-KF	Turkana - Koobi Fora 1	153	0.0	0.9
K11-KF	Turkana - Koobi Fora 1	155	0.1	0.7
K11-KF	Turkana - Koobi Fora 1	157	0.4	1.1
K11-KF	Turkana - Koobi Fora 1	159	0.3	1.3
K11-KF	Turkana - Koobi Fora 1	161	0.5	1.0
K11-KF	Turkana - Koobi Fora 1	163	0.5	1.2
K11-KF	Turkana - Koobi Fora 1	165	0.7	1.3
K11-KF	Turkana - Koobi Fora 1	167	0.7	1.4
K11-KF	Turkana - Koobi Fora 1	169	0.7	1.7
K11-KF	Turkana - Koobi Fora 1	171	0.9	1.5
K11-KF	Turkana - Koobi Fora 1	173	1.2	1.2
K11-KF	Turkana - Koobi Fora 1	175	0.9	0.9
K11-KF	Turkana - Koobi Fora 1	177	1.1	1.1
K11-KF	Turkana - Koobi Fora 1	179	0.9	0.6
K11-KF	Turkana - Koobi Fora 1	181	1.0	0.7
K11-KF	Turkana - Koobi Fora 1	183	0.8	0.0
K11-KF	Turkana - Koobi Fora 1	185	1.3	0.4
K11-KF	Turkana - Koobi Fora 1	187	0.9	-0.2
K11-KF	Turkana - Koobi Fora 1	189	0.7	0.3
K11-KF	Turkana - Koobi Fora 1	191	0.8	0.7
K11-KF	Turkana - Koobi Fora 1	193	0.4	0.5
K11-KF	Turkana - Koobi Fora 1	195	0.5	0.9
K11-KF	Turkana - Koobi Fora 1	197	0.3	0.6
K11-KF	Turkana - Koobi Fora 1	199	0.3	0.5
K11-KF	Turkana - Koobi Fora 1	201	0.0	0.4

Table A.28: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
K11-KF	Turkana - Koobi Fora 1	203	0.0	0.8
K11-KF	Turkana - Koobi Fora 1	205	-0.1	0.6
K11-KF	Turkana - Koobi Fora 1	207	0.2	1.0
K11-KF	Turkana - Koobi Fora 1	209	0.0	0.6
K11-KF	Turkana - Koobi Fora 1	211	0.1	0.3
K11-KF	Turkana - Koobi Fora 1	213	0.3	0.6
K11-KF	Turkana - Koobi Fora 1	215	0.0	0.9
K11-KF	Turkana - Koobi Fora 1	217	-0.1	0.8
K11-KF	Turkana - Koobi Fora 1	219	0.0	0.9
K11-KF	Turkana - Koobi Fora 1	221	-0.1	0.9
K11-KF	Turkana - Koobi Fora 1	223	-0.2	1.0
K11-KF	Turkana - Koobi Fora 1	225	-0.4	0.5
K11-KF	Turkana - Koobi Fora 1	227	-0.5	0.6
K11-KF	Turkana - Koobi Fora 1	229	-0.7	1.1
K11-KF	Turkana - Koobi Fora 1	231	-0.3	1.1
K11-KF	Turkana - Koobi Fora 1	233	-0.1	0.9
K11-KF	Turkana - Koobi Fora 1	235	0.1	0.3
K11-KF	Turkana - Koobi Fora 1	237	0.1	0.5
K11-KF	Turkana - Koobi Fora 1	239	0.2	1.1
K11-KF	Turkana - Koobi Fora 1	241	0.1	0.7
K11-KF	Turkana - Koobi Fora 1	243	0.2	1.1
K11-KF	Turkana - Koobi Fora 1	245	0.3	1.1
K11-KF	Turkana - Koobi Fora 1	247	0.3	0.9
K11-KF	Turkana - Koobi Fora 1	249	0.2	0.9
K11-KF	Turkana - Koobi Fora 1	250	1.1	2.3
K11-KF	Turkana - Koobi Fora 1	252	1.0	2.2
K11-KF	Turkana - Koobi Fora 1	254	1.1	2.2
K11-KF	Turkana - Koobi Fora 1	256	1.0	2.2
K11-KF	Turkana - Koobi Fora 1	258	1.0	1.7
K11-KF	Turkana - Koobi Fora 1	260	0.9	1.7
K11-KF	Turkana - Koobi Fora 1	262	0.7	1.7
K11-KF	Turkana - Koobi Fora 1	264	0.9	1.7
K11-KF	Turkana - Koobi Fora 1	266	0.9	1.2
K11-KF	Turkana - Koobi Fora 1	268	0.8	1.6
K11-KF	Turkana - Koobi Fora 1	270	0.9	1.0
K11-KF	Turkana - Koobi Fora 1	272	0.6	1.3
K11-KF	Turkana - Koobi Fora 1	274	0.9	1.3
K11-KF	Turkana - Koobi Fora 1	276	1.0	1.4
K11-KF	Turkana - Koobi Fora 1	278	1.1	1.5
K11-KF	Turkana - Koobi Fora 1	280	1.0	1.7

Table A.28: (cont'd)

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)
K11-KF	Turkana - Koobi Fora 1	282	1.1	1.5
K11-KF	Turkana - Koobi Fora 1	284	1.0	1.4
K11-KF	Turkana - Koobi Fora 1	286	1.2	1.8
K11-KF	Turkana - Koobi Fora 1	288	1.3	1.9
K11-KF	Turkana - Koobi Fora 1	290	1.2	2.0
K11-KF	Turkana - Koobi Fora 1	292	1.1	2.0
K11-KF	Turkana - Koobi Fora 1	294	1.3	2.2
K11-KF	Turkana - Koobi Fora 1	296	1.4	2.7
K11-KF	Turkana - Koobi Fora 1	298	1.0	1.0
K11-KF	Turkana - Koobi Fora 1	300	1.2	1.7
K11-KF	Turkana - Koobi Fora 1	302	1.2	1.4
K11-KF	Turkana - Koobi Fora 1	304	1.3	1.3
K11-KF	Turkana - Koobi Fora 1	306	1.3	1.4
K11-KF	Turkana - Koobi Fora 1	308	1.5	1.8
K11-KF	Turkana - Koobi Fora 1	310	1.6	1.9
K11-KF	Turkana - Koobi Fora 1	312	1.4	1.6
K11-KF	Turkana - Koobi Fora 1	314	1.2	1.4
K11-KF	Turkana - Koobi Fora 1	316	1.3	1.3
K11-KF	Turkana - Koobi Fora 1	318	1.2	0.9
K11-KF	Turkana - Koobi Fora 1	320	1.4	1.1
K11-KF	Turkana - Koobi Fora 1	322	1.6	1.1
K11-KF	Turkana - Koobi Fora 1	324	1.4	0.8
K11-KF	Turkana - Koobi Fora 1	326	1.5	0.7
K11-KF	Turkana - Koobi Fora 1	328	0.7	0.3
K11-KF	Turkana - Koobi Fora 1	330	1.3	0.7
K11-KF	Turkana - Koobi Fora 1	332	1.4	0.9
K11-KF	Turkana - Koobi Fora 1	334	1.3	0.8
K11-KF	Turkana - Koobi Fora 1	336	1.2	1.3
K11-KF	Turkana - Koobi Fora 1	338	1.3	1.1
K11-KF	Turkana - Koobi Fora 1	340	1.3	0.9
K11-KF	Turkana - Koobi Fora 1	342	1.7	1.5
K11-KF	Turkana - Koobi Fora 1	344	1.4	1.7
K11-KF	Turkana - Koobi Fora 1	346	1.3	1.0
K11-KF	Turkana - Koobi Fora 1	348	1.1	1.8
K11-KF	Turkana - Koobi Fora 1	350	1.6	1.6
K11-KF	Turkana - Koobi Fora 1	355	1.3	0.0
K11-KF	Turkana - Koobi Fora 1	365	1.3	1.1
K11-KF	Turkana - Koobi Fora 1	375	1.4	1.0
K11-KF	Turkana - Koobi Fora 1	385	1.3	1.2
K11-KF	Turkana - Koobi Fora 1	395	1.1	1.1

Table A.28: (cont'd)

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ ^{18}O (V-PDB)**
K11-KF	Turkana - Koobi Fora 1	405	1.2	0.8
K11-KF	Turkana - Koobi Fora 1	415	1.4	2.0
K11-KF	Turkana - Koobi Fora 1	425	1.4	1.2
K11-KF	Turkana - Koobi Fora 1	435	1.1	0.6
K11-KF	Turkana - Koobi Fora 1	445	1.4	0.9
K11-KF	Turkana - Koobi Fora 1	455	1.0	1.2
K11-KF	Turkana - Koobi Fora 1	465	0.7	0.9
K11-KF	Turkana - Koobi Fora 1	475	0.7	2.2
K11-KF	Turkana - Koobi Fora 1	485	0.5	2.4

Table A.29: Turkana – Koobi Fora 2 hippo isotope values.

Specimen	**Locality**	**Position**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**
KEN-09-115	Turkana - Koobi Fora 2	14	1.9	0.5
KEN-09-115	Turkana - Koobi Fora 2	20	1.5	1.4
KEN-09-115	Turkana - Koobi Fora 2	30	1.3	0.5
KEN-09-115	Turkana - Koobi Fora 2	60	1.7	0.7
KEN-09-115	Turkana - Koobi Fora 2	71	1.3	1.4
KEN-09-115	Turkana - Koobi Fora 2	82	1.2	1.2
KEN-09-115	Turkana - Koobi Fora 2	93	1.1	1.0
KEN-09-115	Turkana - Koobi Fora 2	103	0.7	1.4
KEN-09-115	Turkana - Koobi Fora 2	113	0.7	1.2
KEN-09-115	Turkana - Koobi Fora 2	123	1.1	1.0
KEN-09-115	Turkana - Koobi Fora 2	132	0.4	1.3
KEN-09-115	Turkana - Koobi Fora 2	142	0.4	1.4
KEN-09-115	Turkana - Koobi Fora 2	152	0.9	1.1
KEN-09-115	Turkana - Koobi Fora 2	162	0.9	1.7
KEN-09-115	Turkana - Koobi Fora 2	172	1.1	1.5
KEN-09-115	Turkana - Koobi Fora 2	182	1.4	2.0
KEN-09-115	Turkana - Koobi Fora 2	193	1.4	1.1
KEN-09-115	Turkana - Koobi Fora 2	203	1.0	1.5
KEN-09-115	Turkana - Koobi Fora 2	213	0.2	0.9
KEN-09-115	Turkana - Koobi Fora 2	222	0.4	1.3
KEN-09-115	Turkana - Koobi Fora 2	233	0.9	1.0
KEN-09-115	Turkana - Koobi Fora 2	244	1.4	1.1
KEN-09-115	Turkana - Koobi Fora 2	253	0.6	1.3
KEN-09-115	Turkana - Koobi Fora 2	262	0.3	1.2
KEN-09-115	Turkana - Koobi Fora 2	272	0.8	1.5
KEN-09-115	Turkana - Koobi Fora 2	281	0.6	1.9
KEN-09-115	Turkana - Koobi Fora 2	292	-0.4	1.4
KEN-09-115	Turkana - Koobi Fora 2	302	-0.1	1.4
KEN-09-115	Turkana - Koobi Fora 2	313	0.3	1.7
KEN-09-115	Turkana - Koobi Fora 2	323	0.2	1.8
KEN-09-115	Turkana - Koobi Fora 2	333	0.4	1.7
KEN-09-115	Turkana - Koobi Fora 2	343	0.2	1.1
KEN-09-115	Turkana - Koobi Fora 2	353	0.5	1.3
KEN-09-115	Turkana - Koobi Fora 2	364	0.3	1.2
KEN-09-115	Turkana - Koobi Fora 2	374	0.4	1.1
KEN-09-115	Turkana - Koobi Fora 2	383	0.6	1.1
KEN-09-115	Turkana - Koobi Fora 2	393	0.2	1.1
KEN-09-115	Turkana - Koobi Fora 2	403	-0.3	1.2
KEN-09-115	Turkana - Koobi Fora 2	413	-0.1	0.8
KEN-09-115	Turkana - Koobi Fora 2	422	0.1	1.0

Table A.29: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**
KEN-09-115	Turkana - Koobi Fora 2	432	0.2	0.6
KEN-09-115	Turkana - Koobi Fora 2	443	0.2	0.6
KEN-09-115	Turkana - Koobi Fora 2	453	-0.2	1.1

Table A.30: Witu hippo isotope values.

Specimen	Locality	Position	$\delta^{13}C$ (V-PDB)	$\delta\ ^{18}O$ (V-PDB)
Witu	Witu	5	-1.3	-1.7
Witu	Witu	15	-0.9	-1.1
Witu	Witu	25	-1.2	-0.8
Witu	Witu	35	-1.5	-0.6
Witu	Witu	45	-2.0	-0.6
Witu	Witu	55	-1.8	-0.9
Witu	Witu	65	-2.1	-1.2
Witu	Witu	75	-2.0	-1.5
Witu	Witu	85	-2.0	-1.1
Witu	Witu	95	-2.1	-1.2
Witu	Witu	105	-2.3	-1.8
Witu	Witu	115	-2.1	-1.3
Witu	Witu	125	-2.0	-1.4
Witu	Witu	135	-2.2	-1.7
Witu	Witu	145	-2.0	-1.5
Witu	Witu	155	-2.1	-2.0
Witu	Witu	165	-2.1	-2.4
Witu	Witu	175	-2.4	-2.5
Witu	Witu	185	-2.2	-2.4
Witu	Witu	195	-2.2	-2.4
Witu	Witu	205	-2.2	-2.5
Witu	Witu	215	-2.1	-2.7
Witu	Witu	225	-2.0	-2.8
Witu	Witu	235	-2.1	-2.8
Witu	Witu	245	-2.0	-2.8
Witu	Witu	255	-2.1	-2.8
Witu	Witu	265	-2.0	-2.7
Witu	Witu	275	-2.1	-2.5
Witu	Witu	295	-1.9	-2.5
Witu	Witu	305	-2.2	-3.0
Witu	Witu	315	-2.1	-2.9
Witu	Witu	325	-2.2	-3.2
Witu	Witu	335	-2.3	-3.1
Witu	Witu	345	-2.5	-3.3
Witu	Witu	355	-2.3	-3.1
Witu	Witu	365	-2.2	-3.1
Witu	Witu	375	-2.5	-3.5
Witu	Witu	385	-1.3	-3.0
Witu	Witu	395	-1.3	-3.0
Witu	Witu	405	-2.2	-3.3

Table A.30: (cont'd)

Specimen	**Locality**	**Position**	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**
Witu	Witu	415	-0.8	-3.0
Witu	Witu	425	-1.4	-3.2
Witu	Witu	435	-1.7	-2.7
Witu	Witu	445	-1.4	-2.4
Witu	Witu	455	-1.0	-2.8
Witu	Witu	465	-2.0	-2.7
Witu	Witu	475	-1.7	-2.5
Witu	Witu	485	-1.3	-2.7
Witu	Witu	495	-1.6	-2.8
Witu	Witu	505	-1.1	-3.0
Witu	Witu	515	-0.9	-3.2
Witu	Witu	525	-1.4	-3.1
Witu	Witu	535	-1.7	-3.5
Witu	Witu	545	-1.7	-3.5
Witu	Witu	555	-2.0	-3.6
Witu	Witu	565	-2.1	-3.8

Table A.31: Bonferroni corrected *P*-values, Wilcoxan rank-sum test (**bold = significant**).

Locality, Isotope	*Bonferroni corrected P-values*
Naivasha, C	1.000
Naivasha, O	1.000
AdhiDam, C	1.000
AdhiDam, O	0.162
Turkana09, C	0.122
Turkana09, O	1.000
Amboseli0401,C	1.000
Amboseli0401,O	1.000
Tsavo07, C	1.000
Tsavo07, O	1.000
Tsavo96, C	**0.002**
Tsavo96, O	**0.002**
AS167, C	1.000
AS167, O	0.139
Minjila, C	1.000
Minjila, O	0.169
Nakuru, C	1.000
Nakuru, O	**0.006**
Mwea09, C	**0.002**
Mwea09, O	**0.009**
MweaNR, C	**0.002**
MweaNR, O	0.950
Mwea05, C	1.000
Mwea05, O	0.169
MweaGitaru, C	1.000
MweaGitaru, O	0.182
NaivashaH, C	0.317
NaivashaH, O	0.193
AmboseliH, C	1.000
AmboseliH, O	0.577
AS08, C	1.000
AS08, O	1.000
Chyulu, C	1.000
Chyulu, O	**0.005**
Kisumu, C	**0.014**
Kisumu, O	1.000
Mara, C	1.000
Mara, O	1.000
Meru, C	**0.000**
Meru, O	**0.032**

Table A.31: (cont'd)

Locality	*Bonferroni corrected P-values*
Mokowe, C	1.000
Mokowe, O	1.000
Mpeketoni, C	0.162
Mpeketoni, O	**0.007**
Olbolossat, C	1.000
Olbolossat, O	1.000
Witu, C	1.000
Witu, O	**0.003**
AS168, C	**0.008**
AS168, O	1.000
AS166, C	0.154
AS166, O	1.000
Koobi Fora, C	1.000
Koobi Fora, O	0.376
Buffalo Springs, C	0.517
Buffalo Springs, O	**0.002**
Aberdares, C	**0.010**
Aberdares, O	**0.014**

APPENDIX B

RAW ISOTOPE DATA FROM QUEEN ELIZABETH NATIONAL PARK HIPPOS

Table B.1: Raw isotope values of QEP hippos through time.

Specimen	Cal. Year	Length (mm from prox. end)	$\delta^{13}C$ (V-PDB)	$\delta\ ^{18}O$ (V-PDB)	%C_4
KL	1970.59	5	-0.2	0.6	85
KL	1970.29	45	0.0	-0.5	85
KL	1969.99	75	0.6	0.5	90
KL	1969.69	95	0.7	-0.8	90
KL	1969.39	105	0.9	-0.8	95
KL	1969.09	115	0.7	-2.6	90
KL	1968.79	125	0.7	-1.1	90
KL	1968.49	135	0.8	-0.7	95
KL	1968.19	145	-0.4	-0.4	85
KL	1967.89	155	0.3	-0.6	90
KL	1967.59	165	-0.5	0.3	85
KL	1967.29	175	-0.8	-0.3	80
KL	1966.99	185	-1.1	-0.6	80
KL	1966.69	195	0.5	0.3	90
KL	1966.39	205	-0.7	-0.1	82
KL	1966.09	215	-1.0	-1.0	80
KL	1965.79	225	-0.2	0.5	85
KL	1965.49	235	-0.2	0.4	85
KL	1965.19	245	-0.1	0.5	85
KL	1964.89	255	-0.1	0.9	85
KL	1964.59	265	-0.7	0.3	80
KL	1964.29	275	-0.1	0.6	85
KL	1963.99	285	0.5	1.4	90
KL	1963.69	295	-0.1	0.4	85
KL	1963.39	305	0.0	0.3	85
KL	1963.09	315	-0.2	0.4	85
KL	1962.79	325	0.0	0.3	85
KL	1962.49	335	0.2	0.4	90
KL	1962.19	345	0.3	-0.5	90
KL	1961.89	355	-0.2	-0.4	85
KL	1961.59	365	-0.3	-0.3	85
KL	1961.29	375	-0.1	1.1	85
KL	1960.99	385	-0.2	1.3	85
Queen VIC	1982.87	15	-3.5	-1.9	60
Queen VIC	1983.10	25	-3.0	0.6	65
Queen VIC	1983.32	45	-3.0	-0.5	65
Queen VIC	1983.55	65	-3.8	-1.7	60
Queen VIC	1983.77	75	-3.2	-2.2	65
Queen VIC	1984.00	85	-3.3	-2.1	65
Queen VIC	1984.23	95	-4.0	-1.0	60

Table B.1: (cont'd)

Specimen	**Cal. Year**	**Length (mm from prox. end)**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**	**%C_4**
Queen VIC	1984.45	105	-3.2	-1.2	65
Queen VIC	1984.68	115	-1.6	-0.9	75
Queen VIC	1985.13	135	-3.6	-0.4	60
Queen VIC	1985.58	155	-3.0	-1.7	65
Queen VIC	1985.81	165	-2.8	-1.2	65
Queen VIC	1986.03	175	-3.3	-0.8	65
Queen VIC	1986.26	185	-3.2	-0.9	65
Queen VIC	1986.71	205	-3.5	-0.8	65
Queen VIC	1986.94	225	-3.0	-0.6	65
Queen VIC	1987.39	245	-3.3	-0.1	65
Queen VIC	1987.61	255	-3.0	0.1	65
Queen VIC	1987.84	265	-3.3	-0.7	65
Queen VIC	1988.06	275	-3.3	-1.0	56
Queen VIC	1988.29	285	-3.5	-1.7	60
Queen VIC	1988.52	295	-4.0	-1.9	60
Queen VIC	1988.74	305	-4.0	-1.6	60
Queen VIC	1988.97	315	-3.5	-0.8	65
Queen VIC	1989.19	325	-3.4	-0.7	65
Queen VIC	1989.42	335	-4.1	-1.5	60
Queen VIC	1989.65	345	-3.6	0.2	60
Queen VIC	1989.87	355	-3.6	-0.9	60
Q-09-KL	2000.00	5	-2.7	1.2	70
Q-09-KL	1999.77	15	-2.3	1.0	70
Q-09-KL	1999.55	25	-3.0	0.4	65
Q-09-KL	1999.32	35	-3.4	-0.5	65
Q-09-KL	1999.10	45	-3.2	-0.4	65
Q-09-KL	1998.87	55	-3.1	-0.1	65
Q-09-KL	1998.65	65	-3.6	-0.3	60
Q-09-KL	1998.42	75	-3.4	-1.8	65
Q-09-KL	1998.19	85	-3.2	-1.5	65
Q-09-KL	1997.97	95	-3.3	-2.5	65
Q-09-KL	1997.74	105	-3.1	-2.4	65
Q-09-KL	1997.52	115	-3.0	-3.5	65
Q-09-KL	1997.29	125	-2.7	-4.1	70
Q-09-KL	1997.06	135	-2.8	-4.2	65
Q-09-KL	1996.84	145	-2.9	-4.9	65
Q-09-KL	1996.61	155	-2.7	-5.6	70
Q-09-KL	1996.39	165	-2.5	-4.3	70
Q-09-KL	1996.16	175	-2.4	-2.8	70
Q-09-KL	1995.94	185	-2.3	-3.3	70

Table B.1: (cont'd)

Specimen	**Cal. Year**	**Length (mm from prox. end)**	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**	**%C_4**
Q-09-KL	1995.71	195	-2.6	-2.8	70
Q-09-KL	1995.48	205	-2.5	-2.2	70
Q-09-KL	1995.26	215	-2.5	-2.1	70
Q-09-KL	1995.03	225	-2.4	-1.8	70
Q-09-KL	1994.81	235	-2.4	-2.3	70
Q-09-KL	1994.58	245	-2.4	-2.0	70
Q-09-KL	1994.36	255	-1.9	-2.9	75
Q-09-KL	1994.13	265	-2.9	-1.3	65
Q-09-KL	1993.9	275	-2.8	-2.5	65
Q-09-KL	1993.68	285	-2.1	-2.1	70
Q-09-KL	1993.45	295	-2.5	-1.7	70
Q-09-KL	1993.23	305	-2.5	-2.5	70
Q-09-KL	1993.00	315	-2.6	-2.3	70
Q-09-KL	1992.77	325	-2.7	-2.5	70
Q-09-KL	1992.55	335	-2.6	-2.4	70
Q-09-KL	1992.32	345	-2.5	-2.0	70
Q-09-KL	1992.1	355	-2.3	-1.0	70
Q-09-KL	1991.87	365	-2.6	-2.2	70
Q-09-KL	1991.65	375	-2.5	-1.7	70
Q-09-KL	1991.42	385	-2.6	-0.9	70
Q-09-KL	1991.19	395	-2.8	-1.5	65
Q-09-KL	1990.97	405	-2.8	-2.0	65
Q-09-KL	1990.74	415	-2.8	-1.4	70
Q-09-KL	1990.52	425	-3.2	-1.9	65
Q-09-KL	1990.29	435	-3.4	-1.7	65
Q-09-KL	1990.06	445	-3.4	-1.4	65
Q-09-KL	1989.84	455	-4.1	-1.9	60
Q-09-KL	1989.61	465	-4.0	-1.7	60
Q-09-KL	1989.39	475	-4.4	-1.7	55
Q-09-KL	1989.16	485	-4.3	-1.8	55
Q-09-KL	1988.94	495	-3.9	-1.2	60
Q-09-KL	1988.71	505	-3.9	-1.4	60
Q-09-KL	1988.48	515	-4.0	-1.3	60
Q-09-KL	1988.26	525	-3.4	-1.7	65
Q-09-KL	1988.03	535	-3.2	-2.2	65
Q-09-KL	1987.81	545	-3.2	-2.5	65
Q-09-KL	1987.58	555	-3.0	-1.2	65
Q-09-KL	1987.36	565	-3.0	-1.7	65
Q-09-KL	1987.13	575	-2.8	-2.4	65
Q-09-KL	1986.9	585	-2.6	-1.7	70

Table B.1: (cont'd)

Specimen	Cal. Year	Length (mm from prox. end)	$\delta^{13}C$ (V-PDB)	$\delta^{18}O$ (V-PDB)	%C_4
Q-09-KL	1986.68	595	-2.9	-1.5	65
Q-09-KL	1986.45	605	-3.0	-1.6	65
Q-09-KL	1986.23	615	-3.0	-1.7	65
Q-09-KL	1986.00	625	-3.1	-2.3	65
Q-09-KL	1985.77	635	-3.1	-1.8	65
Q-09-KL	1985.55	645	-3.0	-1.5	65
Q-09-KL	1985.32	655	-2.9	-1.5	65
Q-09-KL	1985.10	665	-2.9	-2.0	65

APPENDIX C

RAW ISOTOPE VALUES OF ARCHAEOLOGICAL TOOTH ENAMEL AND LEAF WAX BIOMARKERS

Table C.1: Isotope values of Luanda (9.7 – 8.5 Kya) fauna.

Specimen	$\delta^{13}C$ (V-PDB)	$\delta\ ^{18}O$ (V-PDB)	KLC ID	NMK ID	Tooth
Alcelaphini	3.1	0.3	KKC13-E-191	L/691/BS/3	LI2
Alcelaphini	2.4	-2.8	KKC13-E-178	L/583/FS/7	frag
Bovini	3.2	-1.2	KKC13-E-190	L/691/OB/0	LI
BVD 3	1.4	-0.2	KKC13-E-189	L/691/OB/0	M0
BVD 4	1.7	-2.0	KKC13-E-151	L/414/BR/6	frag
BVD 4	1.2	-3.4	KKC13-E-154	L/414/OB/1	frag
BVD 4	0.5	2.3	KKC13-E-157	L369/BS/2	P4
BVD 4	1.7	-1.0	KKC13-E-166	L/256/OB/1	frag
BVD 4	1.3	-1.5	KKC13-E-174	L/828/BH/7	frag
BVD 4	3.6	-0.8	KKC13-E-205	L/828/BH/8	frag
Connochaetes taurinus	-0.1	0.4	KKC13-E-158	L/369/BS/3	M1
Connochaetes taurinus	2.6	-0.3	KKC13-E-164	L/256/OB/1	I1
Connochaetes taurinus	1.6	-0.7	KKC13-E-171	L/828/OB/1	M2
Connochaetes taurinus	3.4	0.2	KKC13-E-193	L/533/OB/2	P3
Connochaetes taurinus	1.6	0.0	KKC13-E-196	L/607/BS2/4	LM0
Connochaetes taurinus	2.6	0.6	KKC13-E-200	L/639/BS/3	LM1
Connochaetes taurinus	3.6	-0.5	KKC13-E-201	L/639/GM	UM3
Equus spp.	0.6	-0.6	KKC13-E-152	L/414/BS/5	LP3/4
H. amphibius	-1.9	-3.1	KKC13-E-155	L/369/BS/3	UM3
H. amphibius	-3.4	-3.0	KKC13-E-167	L/369/OB/0	Um2
H. amphibius	-5.5	-2.3	KKC13-E-172	L/828/BH/7	frag
H. amphibius	-5.7	-4.1	KKC13-E-173	L/828/BH/7	tusk
H. amphibius	-3.2	-2.8	KKC13-E-185	L/583/GM/8	frag
H. amphibius	-5.5	-4.6	KKC13-E-188	L/583/GM/8	frag
Kobus defassa	2.4	-4.7	KKC13-E-176	L/533/BS/5	M0
Kobus defassa	1.5	-1.2	KKC13-E-202	L/828/BH/8	LM1
Kobus defassa	3.0	-0.1	KKC13-E-203	L/828/BH/8	LM0
Kobus kob	1.8	-1.0	KKC13-E-148	L/414/OB/1	M3
Kobus kob	3.0	0.0	KKC13-E-149	L/583/GM/8	M2
Kobus kob	1.3	-1.4	KKC13-E-150	L/828/BH/8	M1,2?
Potamochoerus spp.	-12.0	-5.2	KKC13-E-181	L/583/FS/7	frag
P. aethiopicus	1.1	1.4	KKC13-E-198	L/639/OB/0	LM3
P. aethiopicus	0.2	-0.6	KKC13-E-206	L/828/BH/8	LM3
Potamochoerus spp.	-7.8	-4.2	KKC13-E-179	L/583/FS/7	LM3
Potamochoerus spp.	-11.8	-5.5	KKC13-E-180	L/583/FS/7	M2
Redunca spp.	0.3	0.0	KKC13-E-147	L/414/OB/1	UM3
Redunca spp.	3.0	-1.5	KKC13-E-192	L/756/OB/0	UM3
Syncerus caffer	0.7	0.5	KKC13-E-153	L/414/OB/1	M0
Syncerus caffer	-1.4	0.3	KKC13-E-194	L/756/BS/3	LM0
Syncerus caffer	0.1	-0.6	KKC13-E-159	L/369/OB/1	M2

Table C.1: (cont'd)

Specimen	**$\delta^{13}C$ (V-PDB)**	**$\delta\ ^{18}O$ (V-PDB)**	**KLC ID**	**NMK ID**	**Tooth**
Syncerus caffer	0.5	-0.7	KKC13-E-170	L/828/OB/0	M0
Syncerus caffer	1.5	-3.3	KKC13-E-177	L/533/BS/5	I1
Syncerus caffer	1.9	-1.7	KKC13-E-163	L/256/OB/1	M3
Syncerus caffer	1.9	-0.1	KKC13-E-175	L/533/OB/3	M2
Syncerus caffer	2.1	-0.9	KKC13-E-187	L/583/OB/2	M3
Syncerus caffer	2.3	-2.1	KKC13-E-160	L/369/BS/3	M3
Syncerus caffer	2.9	-1.3	KKC13-E-168	L/828/OB/0	M0
Syncerus caffer	3.0	-2.5	KKC13-E-197	L/607/GS/7	M3
Syncerus caffer	3.1	-2.3	KKC13-E-161	L/256/OB/1	M0
Syncerus caffer	3.2	-2.8	KKC13-E-169	L/828/OB/0	M3
Syncerus caffer	3.4	-1.8	KKC13-E-199	L/639/OB/0	frag
Syncerus caffer	3.7	-1.6	KKC13-E-184	L/583/FS/7	LP2
Syncerus caffer	3.7	-3.2	KKC13-E-162	L/256/OB/1	M0
Syncerus caffer	3.8	-1.9	KKC13-E-204	L/828/BH/8	P0

Table C.2: Isotope values of Wadh Lang'o (~3 Kya) fauna.

Specimen	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**	**KLC ID**	**NMK ID**	**Tooth**
BVD 2	2.2	-2.4	KKC13-E-240	208	UM1
Caprini	2.7	1.1	KKC13-E-245	280	LM3
Caprini	-0.1	0.1	KKC13-E-254	2945	LM1/2
Connochaetes taurinus	2.8	1.9	KKC13-E-244	281	UM0
Kobus defassa	1.4	2.6	KKC13-E-243	181	LM0
Phacochoerus aethiopicus	0.4	-0.1	KKC13-E-257	2944	frags

Table C.3: Isotope values of Wadh Lang'o (~2 Kya) fauna.

Specimen	**$\delta^{13}C$ (V-PDB)**	**$\delta^{18}O$ (V-PDB)**	**KLC ID**	**NMK ID**	**Tooth**
Alcelaphini	3.0	5.2	KKC13-E-215	2916	UM3
Alcelaphini	0.0	4.0	KKC13-E-213	2929	UP4
Alcelaphini	2.7	4.1	KKC13-E-214	2915	UP4
Alcelaphini	2.2	2.8	KKC13-E-216	2921	frag
Alcelaphini	3.0	3.6	KKC13-E-217	2909a	M3?
Alcelaphini	1.8	1.3	KKC13-E-218	2909b	M2
Bos taurus	1.8	3.6	KKC13-E-238	4448	M2
BVD 0	1.7	-0.5	KKC13-E-227	2914	frag
BVD 0	-2.3	2.1	KKC13-E-228	16626-28	frag
BVD 2	2.2	5.7	KKC13-E-251	2870	Lm3
BVD 2	-1.8	0.2	KKC13-E-255	2894	ind
BVD 2	0.6	1.2	KKC13-E-256	5246	UM3
BVD 2	2.0	2.5	KKC13-E-262	n/a	frag
BVD 2	0.3	3.1	KKC13-E-263	n/a	frag
BVD 2-3	-0.6	4.7	KKC13-E-253	2939	frag
BVD 3-4	-0.7	2.2	KKC13-E-242	1612	M3
Caprini	0.1	1.6	KKC13-E-237	2886	M
Caprini	3.1	4.7	KKC13-E-247	2878	UM3
Caprini	1.6	4.1	KKC13-E-252	1702	LM3
Caprini	2.8	5.4	KKC13-E-208	2926	LM2
Caprini	4.0	5.0	KKC13-E-209	2928	M3
Caprini	1.1	2.6	KKC13-E-210	2927	DUP4
Caprini	2.2	-2.4	KKC13-E-219	2908	UM2
Caprini	-0.3	1.7	KKC13-E-220	2911	UM2
Caprini	2.2	-0.3	KKC13-E-222	2910	LM2
Caprini	-0.2	2.0	KKC13-E-223	2924	UM3
Caprini	-1.4	0.1	KKC13-E-230	4537	UM3
Caprini	1.7	3.9	KKC13-E-241	1615a	M3
Caprini	-0.5	4.3	KKC13-E-249	2871	M2
Caprini	2.1	4.1	KKC13-E-250	2876	M0
Caprini	2.0	3.7	KKC13-E-258	5096	M1
Caprini	-0.7	2.1	KKC13-E-260	2888	LM12
Caprini	-2.2	4.2	KKC13-E-235	2865	P4
Redunca redunca	-0.7	1.7	KKC13-E-221	2912	UM2
Redunca redunca	-3.3	-1.6	KKC13-E-224	2918	UM0
Redunca redunca	2.6	0.7	KKC13-E-225	2923	UM0
Reduncini	2.5	0.4	KKC13-E-226	2913	UM0

Table C.4: Lothagam faunal isotopes (8.3 Kya).

Specimen	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**	**Site**	**Age**	**KLC ID**	**NMK ID**	**Tooth**
Alcelaphini	0.5	3.0	"Equid site"	10.5	KC12-9AA		M
Alcelaphini	2.0	3.2	FxJj12	9.5-8.3	KKC10-16F	"area 116"	P1/P2?
Alcelaphini	1.4	-1.8	FxJj12	9.5-8.3	KKC10-11	FxJj12-46	M2
Bovidae	-0.9	2.1	"Equid site"	10.5	KC12-2T		M
Bovidae	2.7	2.5	GaJj11	10.2-9.9	KKC13-E-1	73	M3
Equidae	-1.1	1.7	"Equid site"	10.5	KC12-11AX		M
Equidae	-2.0	1.1	"Equid site"	10.5	KC12-13Y		M
Equidae	-1.9	-2.5	"Equid site"	10.5	KC12-14AE		M
Equidae	0.6	1.2	"Equid site"	10.5	KC12-2S		M
Equidae	0.6	5.8	"Equid site"	10.5	KC12-7N		M
Equidae	-0.3	2.3	"Equid site"	10.5	KC12-7O		M
Equidae	0.0	2.4	"Equid site"	10.5	KC12-7P		M
H. amphibius	-2.1	-2.0	GaJj11	10.2-9.9	KKC11-41	188	C
H. amphibius	0.1	-2.3	GaJj11	10.2-9.9	KKC13-E-2	199	frag
Reduncini	2.0	2.8	"Equid site"	10.5	KC12-10AZ		frag
Suidae	0.3	3.1	"Equid site"	10.5	KC12-11AW		M
Suidae	0.0	3.0	"Equid site"	10.5	KC12-6AB		M

Table C.5: Later Holocene faunal isotopes (8.3 Kya); isotopes relative to V-PDB.

Specimen	$\delta^{13}C$	$\delta^{18}O$	Site	Age	KLC ID	NMK ID	Tooth
Aepycerotini	-7.2	2.3	GaJj2	4.9-4.4	KKC13-E-23	187	M
Alcelaphini	-5.4	3.9	GaJj2	4.9-4.4	KKC13-E-31	110	M
Alcelaphini	-1.6	3.4	Dongodien	4.5-3.4	KKC13-E-6	357	M
Alcelaphini	-1.4	2.4	GaJj2	4.9-4.4	KKC13-E-28	122	M
Alcelaphini	-1.3	4.5	Dongodien	4.5-3.4	KKC11-6	GaJi4-27	M2
Alcelaphini	0.3	2.8	Dongodien	4.5-3.4	KKC13-E-8	1089	M frag
Alcelaphini	3.2	0.5	GaJj2	4.9-4.4	KKC13-E-29	114	M
Antilopini	-4.5	0.6	Dongodien	4.5-3.4	KKC13-E-48	214	M3 frag
Antilopini	-3.3	3.8	Dongodien	4.5-3.4	KKC13-E-35	103	M3
Antilopini	-3.0	4.1	Dongodien	4.5-3.4	KKC11-6F	GaJi4-430	M2
Antilopini	-2.2	4.0	Dongodien	4.5-3.4	KKC13-E-5	306	M
Bovini	1.6	3.6	Dongodien	4.5-3.4	KKC13-E-52	1013	P2
Caprini	-7.9	3.2	Dongodien	4.5-3.4	KKC13-E-4	329	M
Caprini	-7.5	1.5	Dongodien	4.5-3.4	KKC13-E-39	951	M2
Caprini	-6.8	5.2	Dongodien	4.5-3.4	KKC13-E-40	601	I
Caprini	-6.0	1.7	GaJj2	4.9-4.4	KKC13-E-33	112	M
Caprini	-5.9	4.4	Dongodien	4.5-3.4	KKC10-22F	GaJi4-212	M
Caprini	-5.5	4.7	Dongodien	4.5-3.4	KKC13-E-42	822	M3 frag
Caprini	-5.4	2.4	Dongodien	4.5-3.4	KKC13-E-51	240	M2
Caprini	-5.3	4.8	Dongodien	4.5-3.4	KKC13-E-36	822	M
Caprini	-4.8	5.1	Dongodien	4.5-3.4	KKC13-E-41	864	I
Caprini	-4.5	6.0	Dongodien	4.5-3.4	KKC10-20F	GaJi4-1013	M2
Caprini	-3.7	2.1	Dongodien	4.5-3.4	KKC13-E-10	61	M3
Caprini	-3.4	4.9	Dongodien	4.5-3.4	KKC13-E-37	836	M3
Caprini	-3.1	4.4	Dongodien	4.5-3.4	KKC13-E-45	478	M2
Caprini	-2.9	6.7	Dongodien	4.5-3.4	KKC10-18F	GaJi4-573	M
Caprini	-2.3	4.6	Dongodien	4.5-3.4	KKC13-E-38	1029	I
Caprini	-2.1	5.1	Dongodien	4.5-3.4	KKC13-E-49	1193	M2
Caprini	-1.6	4.6	Dongodien	4.5-3.4	KKC11-2	GaJi4-378	M2
Caprini	-1.5	5.8	Dongodien	4.5-3.4	KKC13-E-46	614	M
Caprini	0.0	4.1	Dongodien	4.5-3.4	KKC13-E-43	1029	M
Caprini	0.1	3.6	Dongodien	4.5-3.4	KKC13-E-47	272	jaw
Equidae	-0.2	0.6	Dongodien	4.5-3.4	KKC13-E-55	104149	P2

Table C.5: (cont'd)

Specimen	$\delta^{13}C$	$\delta^{18}O$	Site	Age	KLC ID	NMK ID	Tooth
H. amphibius	-4.1	-0.6	GaJj2	4.9-4.4	KKC13-E-19	80	M frag
H. amphibius	-1.2	0.5	GaJj2	4.9-4.4	KKC13-E-34	176	M frag
H. amphibius	-0.9	-1.4	GaJj2	4.9-4.4	KKC13-E-27	62	frag
H. amphibius	0	0.4	Dongodien	4.5-3.4	KKC11-7	GaJi4-422	C serial
indet	-6	5.3	Dongodien	4.5-3.4	KKC10-19F	GaJi4-1029	M
indet	-4.4	2.2	GaJj2	4.9-4.4	KKC13-E-24	238	M
indet	-4.2	3.5	Dongodien	4.5-3.4	KKC11-5	GaJi4-891	M
indet	-2.3	5	Dongodien	4.5-3.4	KKC13-E-50	914	PM4
indet	-1.9	1.4	GaJj2	4.9-4.4	KKC13-E-18	109	M
indet	-1.4	1.8	Dongodien	4.5-3.4	KKC11-1	GaJi4-763	M
indet	-0.5	1.9	Dongodien	4.5-3.4	KKC13-E-9	338	M frag
indet	1.3	4.1	GaJj2	4.9-4.4	KKC13-E-16	132	M frag
indet	1.9	3.8	GaJj2	4.9-4.4	KKC13-E-22	8	M frag
Neotragini	-6.5	2.6	GaJj2	4.9-4.4	KKC13-E-21	188	M frag
Neotragini	-1.9	-0.3	GaJj2	4.9-4.4	KKC13-E-30	111	M3
Neotragini	1.7	2	GaJj2	4.9-4.4	KKC13-E-25	25	M3
Suidae	-2.4	-1.4	GaJj2	4.9-4.4	KKC11-38	GaJj2-110	C
Suidae	-1.2	0.6	GaJj2	4.9-4.4	KKC13-E-32	186	?
Suidae	-0.2	1.7	GaJj2	4.9-4.4	KKC11-37	GaJj2-35	M
Suidae	0.4	1	FxJj12N	3.8-3.0	KKC11-40	FxJj12-152	M
Suidae	2	1.2	GaJj2	4.9-4.4	KKC13-E-26	175	tusk

Table C.6: EBA, Horizon C faunal isotope values.

Specimen	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**	**KLC ID**	**NMK ID**	**Tooth**
Antilopini	-7.8	1.4	KKC13-E-113	100367	frag
Antilopini	-3.8	2.7	KKC13-E-112	100803	M2
Antilopini	-3.3	3.7	KKC13-E-115	100622	M1
Bovidae	1.5	2.7	KKC13-E-109	101012	M frag
Hippotragini	2.4	4.1	KKC13-E-108	102010	M0
Tragelaphini	-8.9	5.6	KKC13-E-104	100897	M0
Tragelaphini	-3.7	1.5	KKC13-E-105	100375	M0
Tragelaphini	1.5	1.1	KKC13-E-107	102014	M0

Table C.7: EBA, Horizon B faunal isotopes.

Specimen	$\delta^{13}C$ (V-PDB)	$\delta\ ^{18}O$ (V-PDB)	KLC ID	NMK ID	Tooth
Antilopini	0.2	1.6	KKC13-E-63	104107	M3
Antilopini	-0.2	2.3	KKC13-E-76	102873	M3
Antilopini	-0.8	3.6	KKC13-E-64	103339	M2
Antilopini	-0.8	5.3	KKC13-E-65	102974	M1
Antilopini	-1.4	4.2	KKC13-E-66	104070	M3
Antilopini	-1.7	2.8	KKC13-E-70	104177	M2
Antilopini	-3.7	1.8	KKC13-E-68	103256	M1
Antilopini	-5.8	-2.8	KKC13-E-71	200001	M2
Antilopini	-6.5	2.5	KKC13-E-72	104121	M3
Antilopini	-7.3	5.0	KKC13-E-69	103372	M3
Antilopini	-7.6	1.5	KKC13-E-75	104068	M3
Antilopini	-9.1	0.7	KKC13-E-74	103301	M3
Antilopini	-9.3	5.5	KKC13-E-67	104062	M3
Cephalophini	-2.1	1.8	KKC13-E-83	104172	M0
Equidae	0.9	1.1	KKC13-E-56	104106	M3
Equidae	0.1	1.3	KKC13-E-60	104093	frag
Giraffidae	-12.4	5.4	KKC13-E-61	101919	frag
Hippotragini	4.0	2.9	KKC13-E-96	104160	M0
Hippotragini	3.4	-0.8	KKC13-E-92	102887	frag
Hippotragini	2.7	0.6	KKC13-E-94	101650	P2
Hippotragini	2.6	0.2	KKC13-E-93	104148	P2
Hippotragini	2.2	2.2	KKC13-E-90	104263	M3
Hippotragini	2.1	1.6	KKC13-E-88	104363	frag
Hippotragini	-0.7	3.2	KKC13-E-95	103300	M0
Hippotragini	-4.7	2.8	KKC13-E-89	104072	M0
Neotragini	-11.8	1.6	KKC13-E-86	103252	M1
Tragelaphini	-9.0	5.1	KKC13-E-77	103254	M0
Tragelaphini	-10.1	6.3	KKC13-E-78	104264	M0
Tragelaphini	-11.5	3.2	KKC13-E-80	102100	M0
Tragelaphini	-12.2	7.0	KKC13-E-79	104079	P0

Table C.8: EBA Horizons A1 and A2 isotope values.

Specimen	**δ^{13}C (V-PDB)**	**δ^{18}O (V-PDB)**	**KLC ID**	**NMK ID**	**Tooth**
Antilopini	3.3	2.7	KKC13-E-101	100198	M2
Hippotragini	1.3	-0.1	KKC13-E-91	102763	M1
Antilopini	-1.2	1.0	KKC13-E-98	101530	M0
Antilopini	-1.5	3.3	KKC13-E-100	100142	M3
Antilopini	-2.5	-0.3	KKC13-E-103	101014	P4
Antilopini	-3.8	-4.3	KKC13-E-102	100850	P3
Antilopini	-5.5	3.5	KKC13-E-97	104203	P4
Neotragini	-7.9	1.4	KKC13-E-84	102879	P2
Antilopini	-8.7	1.8	KKC13-E-99	101506	M0
Neotragini	-11.5	3.6	KKC13-E-87	102479	P4
Neotragini	-12.6	0.1	KKC13-E-85	104162	M2

Table C.9: C_{28} FAME leaf wax biomarker values. %C_4 calcuated using endmember values from -22 to -34‰, rounded to the nearest 5% to account for uncertatinty (Castañeda et al., 2009; Magill et al., 2013a).

Depth in Section	**$\delta^{13}C$ - C_{28} (V-PDB)**	**%C_4**
7.0	-28.4	0.50
7.5	-27.7	0.55
7.9	-26.3	0.65
8.3	-27.1	0.55
8.5	-25.4	0.70
8.9	-28.1	0.50
10.3	-26.2	0.65
10.7	-25.8	0.65
14.0	-26.1	0.65
14.4	-28.5	0.45
14.9	-28.5	0.45
15.9	-24.9	0.75
17.0	-25.1	0.70
17.5	-27.5	0.55
18.2	-28.5	0.45
18.8	-24.9	0.75