**Initial Assessment of Bioavailable Strontium at Oldupai Gorge, Tanzania:
Potential for Early Mobility Studies**

Laura Tucker¹, Julien Favreau¹, Makarius Itambu^{1,2}, Fergus Larter¹, Neduvoto Mollel³, Aloyce Mwambwiga¹, Robert Patalano¹, Patrick Roberts⁴, María Soto¹, Julio Mercader^{1,4}

¹: Department of Anthropology and Archaeology, University of Calgary, 2500 University Drive, Calgary, Alberta, Canada, T2N 1N4

²: Department of History and Archaeology, University of Dar es Salaam, P.O. Box 35091, Dar es Salaam, Tanzania

³: Tropical Pesticides Research Institute, National Herbarium of Tanzania, P.O. Box 3024, Arusha, Tanzania

⁴: Department of Archaeology, Max Planck Institute for the Science of Human History, Kahlaische Str. 10, 07745 Jena, Germany

Corresponding author:

Laura Tucker

ltucker@ucalgary.ca

Department of Anthropology and Archaeology, University of Calgary
2500 University Drive NW, Calgary, Alberta, T2N 1N4

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Abstract:

Strontium isotope analysis is a useful tool for tracing mobility and migration in past populations. For it to be employed, the $^{87}\text{Sr}/^{86}\text{Sr}$ values of the landscape must be well-understood. Bioavailable strontium is a combination of geological and atmospheric strontium available for use by plants and animals. In this study we begin mapping bioavailable strontium values around the Oldupai Gorge region so that this method may be utilized on archaeological hominins and animals in the future. We analyzed three plants from 33 localities across volcanic and metamorphic bedrock, including the regional drainage sump, Olbalbal. We found that bioavailable strontium in the region is homogeneous overall, with trends towards increasing values to the north and northeast

and in Olbalbal. There was no difference between $^{87}\text{Sr}/^{86}\text{Sr}$ values of metamorphic and volcanic areas. Migrants from outside the study area with different isotopic values will be easily identifiable from the local residents.

As a proof of concept, we analyzed 7 animal teeth (hippopotamus, crocodile, and equid) from Engaji Nanyori, a Bed III and IV site at Oldupai Gorge. We found that enamel and dentine which had been acetic acid treated to remove diagenetic strontium were significantly different from one another. All animals had higher $^{87}\text{Sr}/^{86}\text{Sr}$ values than the plant values, suggesting that modern and ancient bioavailable strontium values may have been different, likely due to environmental differences.

1. Introduction

The largest contributor of strontium ions and leading cause of landscape $^{87}\text{Sr}/^{86}\text{Sr}$ variation is bedrock (Faure and Powell, 1972; Faure, 1986, Sealy et al., 1991, Bentley, 2006), though atmospheric and hydrological sources also contribute strontium (Franzén, 1980; Gosz et al., 1983; Graustein and Armstrong, 1983; Wadleigh et al., 1985; Palmer and Edmond, 1989; Andersson et al., 1990; Clow et al., 1997; Böhlke and Horan, 2000; Hosono et al., 2007; Evans et al., 2010). Bioavailable strontium is labile to plants and animals (Sillen et al., 1998; Beard and Johnson, 2000), being incorporated into their tissues after they eat and drink (Bentley, 2006). Strontium isotopes do not fractionate in biological systems, so $^{87}\text{Sr}/^{86}\text{Sr}$ values of skeletal materials directly reflect what is consumed (Capo et al., 1998; Bentley, 2006).

Strontium isotopes from skeletons provide insights into landscape use and mobility (Bentley 2006). This method has been extensively utilized for anatomically modern humans (Ericson, 1985; Knudson et al., 2005; Conlee et al., 2009; Nystrom et al., 2011; Slovak et al., 2009; Frei and Price, 2012; Wright, 2012; Perry et al., 2017), but only rarely for archaic hominins from southern Africa (Sillen et al., 1995; 1998; Copeland et al., 2011). Landscape bioavailable strontium values can be determined by analyzing waters (Frei and Frei, 2011), plants (Hartman and Richards, 2014; Copeland et al., 2016), domesticated animals (Bentley et al., 2004) rodents (Kootker et al., 2016), and land snails (Evans et al., 2009, 2010; Maurer et al., 2012). Isoscapes then allow for interpreting skeletal strontium data (e.g. Copeland et al., 2016; Evans et al., 2010; Hartman and Richards, 2014; Kootker et al., 2016).

Here, we implement a sampling strategy to build an initial map of bioavailable strontium for the Oldupai Gorge region: a site complex yielding an extraordinary record of hominin evolution (Hay, 1976; Leakey, 1971). We studied plants from 33 locations across $\sim 750 \text{ km}^2$ to outline

$^{87}\text{Sr}/^{86}\text{Sr}$ variation. The outcome underscores the potential of strontium analysis in East Africa. We argue that this method can track hominin land-use, social connectivity, and mobility; noting methodological caveats surrounding variability in bioavailable strontium unrelated to bedrock levels. We present $^{87}\text{Sr}/^{86}\text{Sr}$ data from enamel and dentine from Engaji Nanyori (Oldupai Gorge Bed III) as a proof of concept.

2. Background

2.1 Using Strontium Values at the Landscape Level

“Locals” and “non-locals” are identified by comparing archaeological values to bioavailable strontium in the region. ^{87}Sr forms from the β -decay of ^{87}Rb , gradually increasing over time, whereas ^{86}Sr remains constant (Faure and Powell, 1972; Bentley, 2006). Older, rubidium-rich rocks containing little ^{86}Sr have the highest $^{87}\text{Sr}/^{86}\text{Sr}$ values. Plants are reliable proxies of bioavailable strontium (Evans et al., 2009; Maurer et al., 2012; Copeland et al., 2016), and can be used to create isoscapes, though they may have variable $^{87}\text{Sr}/^{86}\text{Sr}$ due to differences in root depth and nutrient cycling (Poszwa et al., 2004; Maurer et al., 2012; Hartman and Richards, 2014; Flockhart et al., 2015).

Dental $^{87}\text{Sr}/^{86}\text{Sr}$ values indicate residence during tooth formation, whereas bone values indicate location later in life. Inter- and intra-tooth sampling are useful for tracing mobility over time (Britton et al., 2009, 2011; Copeland et al., 2016; cf. Balasse, 2003). Diagenesis of skeletal material is problematic, as biogenic strontium is replaced with geological values (Sillen, 1986; Bentley et al., 2004). Enamel is most resilient, followed by dentine and bone (Budd et al., 2000; Lee-Thorp and Sponheimer, 2003). The effect of diagenesis can be muted by a weak acid (Sillen

and Sealy, 1995; Lee-Thorp and Sponheimer, 2003; cf. Sillen, 1986), though it causes fossilized enamel to break down (Lee-Thorp et al., 1997).

2.2 Study Area

Oldupai Gorge is in Tanzania's Ngorongoro Conservation Area (NCA) (2° 59' 46.87" S, 35° 21' 7.50" E) along the Volcanic Highlands (NVH). North of the Gorge are metamorphic massifs, and to the east is the Olbalbal depression (Figure 2.1) (Hay, 1976). Local ecosystems are diverse and include forest, heath, and the Acacia Commiphora woodlands of the Serengeti from 1,350 to 1,850 m asl (Herlocker and Dirschl, 1972). December through April are the wettest months, and June through October are driest (Pearsall, 1957; Anderson and Talbot, 1965; Norton-Griffiths et al., 1975). Annual precipitation is 331-531 mm (Herlocker and Dirschl, 1972; Norton-Griffiths et al., 1975; Hay, 1976). Soils are shallow. Conductivity, pH, and sodium are high, and their average temperature 22 °C (Jager, 1982). Above ground temperature fluctuates from 12 °C to 33 °C. Evaporation reaches 10 mm/day (Hay, 1976). Wind is easterly (12.4 km/h). The Eastern Serengeti Plains drain into the main branch of Oldupai Gorge via the Oldupai River, from Lakes Masek and Ndutu and terminating in the Olbalbal depression (Leakey, 1978; Scoon, 2018). The Side Gorge stream originates on Lemagrut, a volcano to the south (Leakey, 1978).

2.3 Geology and Palaeoanthropology

Oldupai Gorge is on the western flank of the Gregory Rift (Dawson, 1992; Ashley and Hay, 2002; Chorowicz, 2005). It is underlain by the metamorphic rocks from the Mozambique Belt and covered by Plio-Pleistocene materials (Anderson and Talbot, 1965; Hay, 1976; Nyamai et al., 2001; Mollel and Swisher, 2012). The Archean Tanzania Craton borders the Mozambique

Figure 2.1: Maps showing the location of the NCA and various landmarks within it. Basemap Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

Belt to the west, approximately 25 km west of Lakes Ndutu and Masek (Hay, 1976). These rocks have been stable for 2.5 Ga, and primarily consist of granitoides and greenstones (Hay, 1976; Manya et al., 2007).

The basal unit at Oldupai Gorge is the Naabi ignimbrite: pyroclastic rock from Ngorongoro volcano dated to 2.038 ± 0.005 Ma (McHenry et al., 2008; Deino, 2012; cf. Habermann et al., 2016). It is covered unconformably by the Oldupai Group, which has a maximum thickness of about 100 m and includes seven distinct sedimentary units: Bed I-IV, Masek, Ndutu, and Naisiusiu (Hay, 1976). The most recent deposits are from Oldoinyo Lengai (Hay, 1976). Oldupai Gorge has been incised for the last ~400 ka by the river (Hay, 1976).

Oldupai Gorge is famous for containing a 2-million-year record of hominin evolution (e.g. Kleindienst, 1973; Day and Molleson, 1976; Hay, 1976; Domínguez-Rodrigo et al., 1997; 2015; 2017; Fernández-Jalvo et al., 1999; McHenry et al., 2007; Blumenschine et al., 2012; de la Torre et al., 2012; Pante, 2013; Diez-Martin, et al. 2015; Hlusko et al., 2015; Organista et al., 2016). Beds I and II yield the densest archaeological assemblages and are studied the most (Hay, 1976). Bed I includes the largest Early Pleistocene archaeological sites, David's Site (Domínguez-Rodrigo et al., 2017) and FLK Zinj (Leakey, 1971). *Paranthropus boisei* (Domínguez-Rodrigo et al., 2013), *Homo habilis* (Leakey et al., 1964; Johanson et al., 1987), and *Homo erectus* (Rightmire, 1979) have been found there.

2.4 Plant and Animal Ecology

The NCA is in the Somalia-Masai floristic zone. *Acacia-Commiphora* bush and thicket is the climax vegetation and woodlands and grasslands are present, though low woodland is the most common physiognomy (Herlocker and Dirschl, 1972; Kindt et al., 2011). Grasslands can be

classified as long (dominated by *Themeda triandra*), intermediate (dominated by *Andropogon greenwayii*), and short (dominated by *Digitaria macroblephara* and *Microchloa kunthii*), which are most common (Anderson and Talbot, 1965; Herlocker and Dirschl, 1972; Norton-Griffiths et al., 1975).

Oldupai Gorge can be broken into three physiographic units: the west, the east, and the south fork tributary (Herlocker and Dirschl, 1972). The west is shallow and homogeneous in flora, featuring a low woodland of predominantly *Commiphora kua*, *Acacia mellifera*, and *Acacia tortilis*, a bushy layer comprised mainly of *Sansevieria robusta*, *Cissus quadrangularis*, and *Cissus cactiformis*, and the grasses *Sporobolus consimilis*, *Sporobolus ioclades*, *Pennisetum mezianum*, *Chloris gayana*, and *Digitaria macroblephara*. The east has steeper canyon walls, more open tree coverage, and contains many species found in the west. Additional species include *Salvadora persica*, *Lycium* spp., and *Justicia betonica*. The southern fork tributary includes the same species, plus the trees *Acacia drepanolobium* and *Acacia gerrardi*, and the grasses *Enneapogon persica*, *Themeda triandra*, and *Aristida adscensionis* (Herlocker and Dirschl, 1972). There are 32 published genera of plants near Oldupai Gorge (Herlocker and Dirschl, 1972).

Animal ecology must be considered when interpreting their $^{87}\text{Sr}/^{86}\text{Sr}$ values, as diet and ranging behaviour will impact their $^{87}\text{Sr}/^{86}\text{Sr}$ values. During the wet season there are many grazers throughout the NCA, such as Thompson's gazelles (*Gazella tomsonii*), zebra (*Equus burchelli*), and wildebeest (*Connochaetes taurinus*). They typically migrate to the northwest portion of the Serengeti in the dry season (Anderson and Talbot, 1965; Sinclair et al., 2007). Giraffes (*Giraffe camelopardalis*), various browsing antelopes, African buffalo (*Syncerus caffer*), and elephants (*Loxodonta africana*) are also present, of which giraffes and some browsing antelopes remain year-round. Predators include lions (*Panthera leo*), leopards (*Panthera pardus*), hyaenas (*Hyena*

hyaena, *Crocuta crocuta*) jackals (*Canis* spp.), and cheetahs (*Acinonyx jubatus*) (Kennedy and Kennedy, 2014). Reptiles include snakes like the black-necked spitting cobra (*Naja nigricollis*) and the black mamba (*Dendroaspis polylepis*), agama lizards (*Agama* spp.), and leopard tortoises (*Geochelone pardalis*) (Kennedy and Kennedy, 2014). Large-bodied birds include ostriches (*Struthio camelus*), secretary birds (*Sagittarius serpentarius*), and kori bustards (*Ardeotis kori*), and small-bodied birds include Kittlitz's plover (*Charadrius pecuarius*), southern ground hornbill (*Bucorvus leadbeateri*), and white-backed vultures (*Gyps africanus*) (Kennedy, 2014).

2.4 Palaeoenvironment and Palaeoclimate

During Bed I and Bed II times there was a large palaeo-lake at Oldupai (Hay, 1976). Bed I lake deposits are primarily comprised of claystone and contain authigenic minerals suggesting very saline, alkaline water (Hay, 1976). Paleosol carbonate $\delta^{13}\text{C}$ values from non-lacustrine areas imply that C_4 vegetation was expanding and temperature was increasing over the past two million years (Cerling and Hay, 1986). Variable Bed I $\delta^{18}\text{O}$ values suggest fluctuating amounts of precipitation (Sikes and Ashley, 2007).

Silicified plant parts, phytoliths, and pollen grains have been used for palaeoenvironmental reconstruction at Oldupai (Bamford, 2005, 2012; Bamford et al., 2006; 2008; Barboni et al., 2010; Albert et al., 2015). This work has focused on Beds I and II. Remains of sedges and *Typha* confirm the presence of a permanent water source in the area (Bamford, 2012). Grasses were identified (Bamford, 2012), as has *Guibourtia coleosperma*, which is not present today (Bamford, 2005). Phytoliths from FLK N and FLK Zinj suggest that vegetation was spatially heterogeneous, with wooded areas and grasslands (Bamford, 2005, 2012). Freshwater springs had denser vegetation, including palms and sedges (Barboni et al., 2010).

2.6 Engaji Nanyori

Engaji Nanyori (EN; also known as Juma's Korongo) is an archaeological site spanning Beds III and IV at Oldupai Gorge (1.15 to 0.8 Ma) (Hay, 1976; Manega, 1993; McHenry et al., 2007; Pante, 2013). This site formed mainly by fluvial and deltaic deposition (Hay, 1976). Faunal remains include hominids, cercopithecids, lagomorphs, rodents, carnivores, Proboscidea, Perissodactyla, Artiodactyla, crocodiles, and fish (Kleindienst, 1973; Day and Molleson, 1976). Preservation of fossils and lithics varies from extremely weathered to well-preserved (Kleindienst, 1973).

The eastern portion of the site has Beds III and IV deposits that are approximately 20 m thick, and the west side has 11 m thick deposits and represent only Bed III (Kleindienst, 1973). Leakey and Roe (1994) describe four stratigraphic layers: coarse grey sands containing artifacts, fine red sands, pink siltstone, and artifact-containing clay. Geological evidence suggests that deposits at EN were formed via back channels or stream channels moving north (Kleindienst, 1973; Leakey and Roe, 1994). These streams may have created perennial pools or supplied a marshland with water (Kleindienst, 1973).

3. Materials and Methods

3.1 Plant Sampling

Plants were collected from 33 localities over ~750 km² (Figure 3.1; Table 3.1). Localities were selected on both volcanic and metamorphic bedrock to look for geological-based variation in ⁸⁷Sr/⁸⁶Sr values. Sampling localities were primarily north of Oldupai to capture geological variability not seen to the south. Samples were collected ~3-5 km apart to identify variability in

Figure 3.1: Locations of sampling localities, their geological domains, and the lacustrine area sampled. Basemap source: Airbus, USGS, NGA, NASA, CGIAR, NLS, OS, NMA, Geodatastyrelsen, GSA, GSI and the GIS User Community.

bioavailable strontium within the geological domains. Five samples were taken from the Olbalbal depression to examine hydrological effects on strontium values. Geographical data were recorded with a Garmin eTrex 10 Global Positioning System (GPS) unit. Three plants were collected from each locality (Table 3.2). When possible, multiple types of plants and parts were collected to account for variation in $^{87}\text{Sr}/^{86}\text{Sr}$ values. Only plants that could be identified to the genus level were collected. Plants were stored in envelopes and air dried prior to identification at

Locality	Geology	Longitude	Latitude	Elevation
1	Volcanic	35.264876	-2.943339	1538.225
2	Volcanic	35.230379	-2.938182	1557.068
3	Volcanic	35.228828	-2.944456	1532.922
4	Volcanic	35.365573	-2.950064	1458.82
5	Volcanic	35.378778	-2.914144	1559.691
6	Volcanic	35.364292	-2.886326	1544.882
7	Metamorphic	35.3884	-2.880129	1586.366
8	Metamorphic	35.342504	-2.858052	1592.784
9	Metamorphic	35.320004	-2.834773	1589.259
10	Metamorphic	35.330545	-2.803343	1682.532
11	Metamorphic	35.358697	-2.740078	1810.15
12	Metamorphic	35.333732	-2.741435	1753.209
13	Metamorphic	35.323153	-2.764971	1760.194
14	Metamorphic	35.306921	-2.793945	1650.591
15	Volcanic	35.263021	-2.804032	1669.861
16	Volcanic	35.286581	-3.015409	1513.919
17	Volcanic	35.266424	-2.857492	1587.489
18	Volcanic	35.253132	-2.899225	1602.297
19	Volcanic	35.278495	-2.925186	1531.983
20	Volcanic	35.37066	-2.985356	1450.513
21	Volcanic	35.396601	-2.980115	1423.267
22	Volcanic	35.42993	-2.995884	1362.494
23	Lacustrine	35.427352	-3.01027	1313.31
24	Lacustrine	35.451995	-2.9978	1302.591
25	Lacustrine	35.467404	-2.989666	1291.68
26	Lacustrine	35.474165	-2.96554	1285.367
27	Lacustrine	35.459827	-3.022632	1292.851
28	Volcanic	35.419005	-2.976165	1358.419
29	Metamorphic	35.275396	-3.04128	1537.336
30	Volcanic	35.253204	-3.028353	1538.32
31	Volcanic	35.232917	-2.998455	1557.236
32	Volcanic	35.276675	-2.984336	1521.02
33	Volcanic	35.353044	-2.981804	1458.466

Table 3.1: Geographical and geological information for each sampling locality.

the Tropical Pesticides Research Institute in Arusha, Tanzania, and exported to the University of Calgary, Canada for strontium isotope analysis.

Sample	Locality	Family	Genus	Parts Collected
1	1	Acanthaceae	<i>Hypoestes forskoolii</i>	stems, flowers, roots
2	1	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
3	1	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
4	2	Balanitaceae	<i>Balanites aegyptiaca</i>	branches, leaves, thorns, bark
5	2	Burseraceae	<i>Commiphora sp.</i>	branches, leaves
6	2	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
7	3	Poaceae	<i>Sporobolus consimilis</i>	blades, flowers
8	3	Poaceae	<i>Pennisetum mezianum</i>	blades, flowers
9	3	Capparaceae	<i>Boscia angustifolia</i>	branches, leaves
10	4	Asparagaceae	<i>Asparagus africanus</i>	branches, leaves
11	4	Fabaceae	<i>Acacia mellifera</i>	branches, leaves
12	4	Amaranthaceae	<i>Achyranthes aspera</i>	branches, leaves, seeds
13	5	Amaranthaceae	<i>Achyranthes aspera</i>	branches, leaves
14	5	Asparagaceae	<i>Asparagus africanus</i>	branches, leaves
15	5	Poaceae	<i>Aristidia adoensis</i>	blades, flowers
16	6	Acanthaceae	<i>Barleria stuhlmannii</i>	stems, leaves, flowers
17	6	Amaranthaceae	<i>Achyranthes aspera</i>	branches, leaves, seeds
18	6	Olacaceae	<i>Ximenia caffra</i>	branches, leaves
19	7	Euphorbiaceae	<i>Euphorbia cuneata</i>	branches, leaves, fruit
20	7	Asparagaceae	<i>Asparagus africanus</i>	stems, leaves
21	7	Poaceae	<i>Enneapogon cenchroides</i>	blades, flowers
22	8	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
23	8	Acanthaceae	<i>Hypoestes forskoolii</i>	stems, leaves, flowers
24	8	Boraginaceae	<i>Heliotropium steudneri</i>	stems, leaves, flowers
25	9	Acanthaceae	<i>Hypoestes forskoolii</i>	stems, leaves, flowers
26	9	Poaceae	<i>Sporobolus panicoides</i>	blades, flowers
27	9	Acanthaceae	<i>Hypoestes forskoolii</i>	stems, leaves, flowers
28	10	Boraginaceae	<i>Cordia monoica</i>	branches, leaves
29	10	Fabaceae	<i>Acacia xanthophloea</i>	branches, thorns, leaves
30	10	Asteraceae	<i>Conyza pyrrhopappa</i>	branches, leaves
31	11	Boraginaceae	<i>Cordia monoica</i>	branches, leaves
32	11	Amaranthaceae	<i>Achyranthes aspera</i>	branches, leaves
33	11	Malvaceae	<i>Hibiscus ludwigii</i>	branches, leaves, flower, buds
34	12	Fabaceae	<i>Acacia drepanolobium</i>	branches, leaves, thorns, fruit
35	12	Burseraceae	<i>Commiphora kua</i>	leaves, branches
36	12	Asparagaceae	<i>Asparagus africanus</i>	stems, leaves
37	13	Burseraceae	<i>Commiphora merkeri</i>	branches, leaves
38	13	Boraginaceae	<i>Cordia monoica</i>	branches, leaves
39	13	Asteraceae	<i>Conyza pyrrhopappa</i>	branches, leaves
40	14	Solanaceae	<i>Withania somnifera</i>	branches, leaves
41	14	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
42	14	Acanthaceae	<i>Hypoestes forskoolii</i>	stems, leaves, flowers
43	15	Amaranthaceae	<i>Achyranthes aspera</i>	branches, leaves

44	15	Boraginaceae	<i>Heliotropium steudneri</i>	branches, leaves
45	15	Asparagaceae	<i>Asparagus africanus</i>	stems, leaves
46	16	Burseraceae	<i>Commiphora sp.</i>	branches, leaves
47	16	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
48	16	Poaceae	<i>Sporobolus panicoides</i>	blades, flowers, roots
49	17	Poaceae	<i>Sporobolus panicoides</i>	blades, flowers, roots
50	17	Poaceae	<i>Digitaria macroblephara</i>	blades, flowers, roots
51	17	Poaceae	<i>Digitaria macroblephara</i>	blades, flowers, roots
52	18	Olacaceae	<i>Ximenia caffra</i>	branches, leaves
53	18	Boraginaceae	<i>Heliotropium steudneri</i>	branches, leaves
54	18	Fabaceae	<i>Acacia mellifera</i>	branches, leaves
55	19	Acanthaceae	<i>Barleria eranthemoides</i>	stems, leaves, flowers
56	19	Acanthaceae	<i>Justicia betonica</i>	stems, leaves
57	19	Poaceae	<i>Sporobolus panicoides</i>	blades, flowers
58	20	Olacaceae	<i>Ximenia caffra</i>	branches, leaves
59	20	Burseraceae	<i>Commiphora merkeri</i>	branches, leaves
60	20	Fabaceae	<i>Acacia mellifera</i>	branches, leaves
61	21	Vitaceae	<i>Cissus quadrangularis</i>	branches
62	21	Asphodelaceae	<i>Aloe secundiflora</i>	leaves
63	21	Asparagaceae	<i>Asparagus africanus</i>	branches, leaves
64	22	Balanitaceae	<i>Balanites aegyptiaca</i>	branches, leaves, thorns
65	22	Fabaceae	<i>Acacia mellifera</i>	branches, leaves
66	22	Olacaceae	<i>Ximenia caffra</i>	branches, leaves
67	23	Balanitaceae	<i>Balanites aegyptiaca</i>	branches, leaves
68	23	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
69	23	Poaceae	<i>Sporobolus panicoides</i>	blades, flowers
70	24	Balanitaceae	<i>Balanites aegyptiaca</i>	branches, leaves
71	24	Balanitaceae	<i>Balanites aegyptiaca</i>	branches, leaves
72	24	Fabaceae	<i>Acacia tortilis</i>	branches, leaves
73	25	Fabaceae	<i>Acacia mellifera</i>	branches, leaves
74	25	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
75	25	Poaceae	<i>Pennisetum mezianum</i>	blades, flowers, roots
76	26	Amaranthaceae	<i>Achyranthes aspera</i>	branches, leaves
77	26	Fabaceae	<i>Acacia xanthophloea</i>	branches, leaves
78	26	Balanitaceae	<i>Balanites aegyptiaca</i>	branches, leaves
79	27	Capparaceae	<i>Cadaba farinosa</i>	branches, leaves
80	27	Fabaceae	<i>Acacia tortilis</i>	branches, leaves
81	27	Solanaceae	<i>Lycium europaeum</i>	branches, leaves
82	28	Amaranthaceae	<i>Achyranthes aspera</i>	branches, leaves
83	28	Burseraceae	<i>Commiphora sp.</i>	branches, leaves
84	28	Balanitaceae	<i>Balanites aegyptiaca</i>	branches, leaves
85	29	Salvadoraceae	<i>Salvadora persica</i>	branches, leaves
86	29	Asparagaceae	<i>Asparagus africanus</i>	stems, leaves
87	29	Poaceae	<i>Aristidia adoensis</i>	blades, roots, flowers

88	30	Asparagaceae	<i>Asparagus africanus</i>	branches, leaves
89	30	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
90	30	Asparagaceae	<i>Asparagus africanus</i>	branches, leaves, fruit
91	31	Asparagaceae	<i>Asparagus africanus</i>	branches, leaves
92	31	Fabaceae	<i>Acacia tortilis</i>	branches, leaves, thorns
93	31	Fabaceae	<i>Senna italica</i>	leaves, flowers, stems, fruits
94	32	Poaceae	<i>Digitaria macroblephara</i>	blades, flowers, roots
95	32	Poaceae	<i>Sporobolus panicoides</i>	blades, flowers, roots
96	32	Convolvulaceae	<i>Ipomoea sp.</i>	branches, leaves
97	33	Boraginaceae	<i>Cordia monoica</i>	branches, leaves
98	33	Poaceae	<i>Cynodon dactylon</i>	blades, roots
99	33	Acanthaceae	<i>Barleria eranthemoides</i>	branches, leaves

Table 3.2: Species and parts of plants sampled from each locality

3.2 Excavation

All teeth were excavated by the Stone Tools, Diet, and Sociality (SDS) team at EN in July 2017 (Figure 3.2). Teeth were found in or near six geotrenches. These include isolated teeth from equids (n=2), crocodiles (n=3), and a hippopotamus (n=1) (Table 3.3). The outer surface of EN6 was cracked all over and flaking. The remaining teeth were in better condition. EN7 was encased in rock with the crown exposed. The teeth were exported to the University of Calgary.

3.3 Plant Laboratory Methods

In the SDS Preparations Laboratory at the University of Calgary, ~1 g of each plant was cut into small pieces. The three plants from each locality were combined in sample bags. Cutting implements were cleaned with 99% isopropyl alcohol to avoid cross-contamination. The plants were ashed in sterile, covered crucibles at 400 °C for 48 hours in the Tropical Archaeology Laboratory (TAL) at the University of Calgary. In the Isotope Science Laboratory (ISL) at the University of Calgary, 10-15 mg of ash was placed in 1.5 mL centrifuge tubes, digested in 500 µL of 3M HNO₃ for two hours, and centrifuged at 3000 rpm for 3 minutes.

Figure 3.2: Topographical map of Engaji Nanyori and the locations of trenches excavated.

Specimen	Taxon	Tooth Type	Provenance
EN1	Equid	Molar	South of E
EN2	Crocodile	Unknown	B
EN3	Crocodile	Unknown	D
EN4	Crocodile	Unknown	F
EN5	Crocodile	Unknown	B
EN6	Equid	Molar	D
EN7	Hippopotamus	Molar	D

Table 3.3: Teeth sampled and their provenance at EN.

247 3.4 Tooth Preparation

248 In the Preparation Laboratory, the teeth were brushed to remove surface sediment, then
249 grazed with a Dremel Engraver tool with a 1.2 mm diamond-tipped bit on medium speed to remove
250 remaining contaminants. The Dremel was used to remove ~10 mg each of enamel and dentine.
251 The bit was cleaned with 99% isopropyl between samples and teeth. When sampling EN7 low
252 speed was used to keep the concretion intact.

253 In the TAL the samples were subdivided into two 3-5 mg subsamples. One set of enamel
254 and dentine from each tooth was soaked in 500 μL of 0.1 M acetic acid for 30 minutes to remove
255 diagenetic strontium. The other half were left untreated to see if diagenetic strontium was removed.
256 The tubes were filled with RODI water, centrifuged at 5000 rpm for 5 minutes, and the supernatant
257 removed. The samples were rinsed to neutrality and dried overnight under a heat lamp. Next,
258 samples were transferred into sterile Teflon jars, dissolved in 500 μL of 5M HNO_3 and 50 μL of
259 H_2O_2 , and heated overnight on a hotplate at 60 $^\circ\text{C}$. To leach strontium, 500 μL of 3M HNO_3 was
260 added and allowed to react for two hours.

261

262 3.4 Isotope Analyses

263 All samples were analyzed in the ISL. 100 μL of Eichrom Sr Resin (50-100 μm) was put
264 into glass ion exchange columns, pre-cleaned with 3 mL of Milli-Q H_2O , and pre-conditioned with
265 500 μL of 3M HNO_3 . The supernatants from the plants and all of the dental samples were placed
266 into the columns and dissolved in 500 μL of 3M HNO_3 . The resin was rinsed twice with 1 mL of
267 3M HNO_3 , then the strontium was eluted with 500 μL of Milli-Q H_2O and collected in 1.5 mL
268 centrifuge tubes. Samples were dried under a heat lamp for 48 hours.

The samples were analysed on a Thermo-Fisher Triton thermal ionization mass spectrometer (TIMS). Each carousel was run with the international standard NIST SRM 987 to ensure external precision, yielding an analytical reproducibility of ± 0.000013 . Two duplicate samples were prepared for each carousel. $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were calculated 150 times, and measurements within two standard deviations of the mean were used to calculate the final values. ^{85}Rb was monitored to correct for interference from ^{87}Rb . All $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were normalised against instrumental mass bias using the ratio $^{88}\text{Sr}/^{86}\text{Sr}=8.375209$.

3.3 Data Analyses

Google Earth Pro, ArcGIS Desktop 10.6, and Adobe Photoshop Creative Cloud 2015 generated our maps and figures. Microsoft Excel 2016 facilitated descriptive statistics and graphs. Nonparametric statistical tests were run due to small sample sizes and differences in group size. Kruskal-Wallis and Dunn's Post-Hoc tests compared $^{87}\text{Sr}/^{86}\text{Sr}$ values in several types of bedrock and plant covers. Spearman's rho tests correlated geographical variables and $^{87}\text{Sr}/^{86}\text{Sr}$ values. Wilcoxon Signed Rank tests were used to compare dental tissues of the same tooth with and without acid-treatment, and Mann-Whitney U tests were used to observe variation between localities where different plant types were collected, and compare enamel and dentine results. These tests were run using PAST 3.19 (<https://folk.uio.no/ohammer/past/>).

To create our isoscape, sample coordinates were imported in ArcGIS 10.5.1 as point shapefiles. The related database showed $^{87}\text{Sr}/^{86}\text{Sr}$ values associated with each locality. Resulting georeferences for $^{87}\text{Sr}/^{86}\text{Sr}$ values were subject to Empirical Bayesian Kriging (EBK): a random interpolation method that calculates predicted $^{87}\text{Sr}/^{86}\text{Sr}$ ratios across the landscape from known

values. Simulations reached 100 semi-variograms. The results were classified into ten geometric intervals, yielding a regional isoscape.

Full datasets are available at the Federated Research Data Repository (doi: 10.20383/101.0157) and a preprint of this manuscript has been made available online with the Open Science Framework (doi: xxx).

4. Results

4.1 Bioavailable Strontium

4.1.1 Geological variation

See Table 4.1 for the full list of $^{87}\text{Sr}/^{86}\text{Sr}$ results for each locality, the geological domain, and the types of plants collected and Figure 4.1 for the isoscape of the region. The range in $^{87}\text{Sr}/^{86}\text{Sr}$ values for all localities was 0.70424 to 0.70476. Summary statistics for each geological domain are in Table 4.2. There was a significant difference between $^{87}\text{Sr}/^{86}\text{Sr}$ values for localities from differing bedrock types (Kruskal-Wallis Test, $P < 0.01$), but only between lacustrine ($n=5$; median=0.70471) and metamorphic areas ($n=9$; median=0.70449) (Dunn's Post-Hoc Test, $P < 0.01$) and lacustrine and volcanic areas ($n=19$; median=0.70449) (Dunn's Post-Hoc Test, $P < 0.001$).

4.1.2 Geographical variation

Graphs of $^{87}\text{Sr}/^{86}\text{Sr}$ values plotted against geographic variables are presented in Figure 4.2. See Table 4.3 for Spearman's correlation coefficients describing relationships between geographical variables and $^{87}\text{Sr}/^{86}\text{Sr}$ values. There is a moderate negative correlation between $^{87}\text{Sr}/^{86}\text{Sr}$ and elevation for all localities (Spearman's correlation, $R=-0.370$). There is no correlation

Locality	$^{87}\text{Sr}/^{86}\text{Sr}$	2 SE ^a	Plant types collected ^b
1	0.704539	0.000006	TTG
2	0.704513	0.000006	TTT
3	0.704523	0.000006	SGG
4	0.704324	0.000006	SSG
5	0.704241	0.000004	SGG
6	0.704443	0.000002	SSG
7	0.704381	0.000006	TGG
8	0.704563	0.000006	TGG
9	0.704427	0.000012	GGG
10	0.704402	0.000014	TSS
11	0.704493	0.000004	SSS
12	0.704268	0.000016	SSG
13	0.704485	0.000010	SSS
14	0.704648	0.000004	TSG
15	0.704435	0.000004	SGG
16	0.704555	0.000004	TSG
17	0.704379	0.000004	GGG
18	0.704630	0.000006	SSG
19	0.704490	0.000006	GGG
20	0.704488	0.000004	TSS
21	0.704488	0.000010	SSG
22	0.704476	0.000008	TSS
23	0.704639	0.000004	TTG
24	0.704738	0.000008	TTT
25	0.704714	0.000008	TSG
26	0.704758	0.000012	TTS
27	0.704684	0.000004	TSS
28	0.704375	0.000004	SSS
29	0.704601	0.000004	TGG
30	0.704518	0.000004	TGG
31	0.704599	0.000024	TGG
32	0.704477	0.000010	GGG
33	0.704480	0.000004	SGG

Table 4.1: $^{87}\text{Sr}/^{86}\text{Sr}$ results and the type of plants analyzed for each locality.

^a 2 SE: Standard error is the internal precision of the TIMS measurements for each sample.

^b Plant type codes: T = tree, S = shrub, G = grass. Small herbs (e.g. *Asparagus africanus*) are included with grasses, and large succulents (e.g. *Aloe secundiflora*) are included with shrubs.

Figure 4.1: Isoscape showing the approximate spatial distribution of bioavailable strontium values across the landscape.

	N	Mean	Median	Minimum	Maximum	SD
Volcanic	19	0.70447	0.70449	0.70424	0.70463	0.00001
Metamorphic	9	0.70447	0.70449	0.70427	0.70465	0.00012
Lacustrine	5	0.70471	0.70471	0.70464	0.70476	0.00001
All	33	0.70451	0.70449	0.70424	0.70476	0.00013

Table 4.2: Summary statistics of $^{87}\text{Sr}/^{86}\text{Sr}$ values of volcanic, metamorphic, lacustrine, and all localities.

between elevation and metamorphic areas, volcanic areas, or volcanic and metamorphic combined.

The correlation coefficient for Olbalbal was strongly negative (Spearman's correlation, $R=-0.700$).

The correlation between $^{87}\text{Sr}/^{86}\text{Sr}$ values and latitude for all localities is significant and moderately negative (Spearman's correlation, $R=-0.454$). A moderately negative correlation exists between latitude and volcanic $^{87}\text{Sr}/^{86}\text{Sr}$ values (Spearman's correlation, $R=-0.340$). There was no correlation between metamorphic localities and latitude. Lacustrine localities and latitude have a strongly positive correlation (Spearman's correlation, $R=0.800$).

Longitude is the strongest geographical predictor of $^{87}\text{Sr}/^{86}\text{Sr}$ values. There was a moderately negative correlation between volcanic $^{87}\text{Sr}/^{86}\text{Sr}$ values and longitude (Spearman's correlation, $R=-0.540$), and for metamorphic localities and longitude (Spearman's correlation, $R=-0.517$). When volcanic and metamorphic localities are combined there is a moderately negative correlation (Spearman's correlation, $R=-0.481$). There is a strongly positive correlation between longitude and $^{87}\text{Sr}/^{86}\text{Sr}$ values of lacustrine localities (Spearman's correlation, $R=0.700$). There was not a significant correlation when all localities were combined.

4.1.3 Variation between plant types

The range of $^{87}\text{Sr}/^{86}\text{Sr}$ values for each type of vegetation at localities where they were collected versus localities in which they were not is in Figure 4.3. For only metamorphic and volcanic areas, see Figure 4.4. There was a significant difference in $^{87}\text{Sr}/^{86}\text{Sr}$ value medians

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Figure 4.2: Graphs of $^{87}\text{Sr}/^{86}\text{Sr}$ for each geological domain plotted against the various geographic variables.

between localities where trees were sampled ($n=17$; median=0.70456; see Table 4.4) and where only grasses and shrubs were sampled ($n=16$; median=0.70446) (Mann-Whitney U Test, $P < 0.01$).

All lacustrine samples ($n=5$) included trees, and all but one had higher $^{87}\text{Sr}/^{86}\text{Sr}$ than any other locality, so the test was re-run with only metamorphic and volcanic localities. There was still a significant difference between localities where trees were sampled ($n=12$; median=0.70453) and where they were not ($n=16$; median=0.70446) (Mann-Whitney U Test, $P < 0.05$). There was not a

	N	Elevation		Latitude		Longitude	
		Coefficient	<i>P</i>	Coefficient	<i>P</i>	Coefficient	<i>P</i>
All Localities	33	-0.38*	<0.04*	-0.46*	<0.01*	-0.07	0.72
Volcanic	19	0.15	0.55	-0.34*	0.15	-0.54*	<0.02*
Metamorphic	9	-0.15	0.68	-0.17	0.64	-0.52*	0.16
Lacustrine	5	-0.70*	0.23	0.80*	0.08	0.70*	0.23
Volcanic and Metamorphic	28	0.02	0.93	-0.28	0.14	-0.54*	<0.01*

Table 4.3: Spearman's correlation coefficients describing relationships between $^{87}\text{Sr}/^{86}\text{Sr}$ values and geographic variables.

* Significant results ($\alpha=0.05$) and correlations stronger than $|0.3|$

Figure 4.3: Range of $^{87}\text{Sr}/^{86}\text{Sr}$ for each type of vegetation at localities where they were collected versus where that type was not.

significant difference between shrubs and no shrubs or grass and no grass at all localities or only metamorphic and volcanic areas.

There was a significant difference in median $^{87}\text{Sr}/^{86}\text{Sr}$ values between localities of all types where trees were sampled ($n=9$; median=0.70456) and where shrubs were sampled ($n=12$; median=0.70446) (Mann-Whitney U Test; $P < 0.01$; see Table 4.5) Localities where both were

Figure 4.4: $^{87}\text{Sr}/^{86}\text{Sr}$ for each type of vegetation at localities where they were collected versus where they were not (volcanic and metamorphic only).

sampld were excluded from this analysis. The result is not significant when only metamorphic and volcanic localities are examined. There was no significant difference between localities with shrubs and grasses for all localities and metamorphic and volcanic localities, nor for trees and grasses for either condition. When overlapping localities are included, there is no significant difference between medians of $^{87}\text{Sr}/^{86}\text{Sr}$ values where trees, shrubs, and grasses were collected (Kruskal-Wallis Test; $P=0.084$). When lacustrine samples are excluded from this test the result is not significant either (Kruskal-Wallis Test; $P=0.173$). For these analyses, herbs were included with grasses, and large succulents were included with shrubs.

4.2 Dental Results

All Localities								
$^{87}\text{Sr}/^{86}\text{Sr}$								
Plant Type	N	Mean	Median	SD	Minimum	Maximum	Z-score	P
Trees	17	0.704577	0.704563	0.000111	0.704381	0.704758	3.31	<0.01*
No Trees	16	0.704435	0.704460	0.000010	0.704241	0.704630		
Shrubs	20	0.704496	0.704487	0.000140	0.704379	0.704758	-0.83	0.41
No Shrubs	13	0.704528	0.704518	0.000103	0.704241	0.704738		
Grasses	23	0.704484	0.704490	0.000122	0.704241	0.704714	-0.72	0.47
No Grasses	10	0.704541	0.704491	0.000136	0.704375	0.704758		
Metamorphic and Volcanic Only								
$^{87}\text{Sr}/^{86}\text{Sr}$								
Plant Type	N	Mean	Median	SD	Minimum	Maximum	Z-score	P
Trees	12	0.704524	0.704529	0.000008	0.704381	0.704648	-2.41	<0.02*
No Trees	16	0.704435	0.704460	0.000010	0.704241	0.704630		
Shrubs	17	0.704456	0.70448	0.000111	0.704241	0.704648	-1.13	0.26
No Shrubs	11	0.704499	0.704513	0.000008	0.704379	0.704601		
Grasses	19	0.704471	0.704484	0.000010	0.704241	0.704630	0.40	0.75
No Grasses	7	0.704462	0.704485	0.000005	0.704375	0.704513		

Table 4.4: Mann-Whitney U Test results and summary statistics for plant types vs. localities where they were not collected.

* Results significant ($\alpha=0.05$)

All dental $^{87}\text{Sr}/^{86}\text{Sr}$ values were higher than any bioavailable strontium results (range=0.70513–0.70547) (Figure 4.5; Table 4.6). There was a significant difference between the median $^{87}\text{Sr}/^{86}\text{Sr}$ values of acid-treated enamel (median=0.70530) and dentine (median=0.70534) (Wilcoxon Signed Rank Test, $P < 0.05$; Table 4.7). There were no significant differences between any other tissues in either condition.

Enamel $^{87}\text{Sr}/^{86}\text{Sr}$ values changed the most with acid for EN1 (difference=0.000257). For all other teeth the absolute difference in $^{87}\text{Sr}/^{86}\text{Sr}$ values of enamel was 0.000038 or less, averaging 0.000054 when EN1 is included and 0.000020 when it is not. Dentine had larger differences between acid-treated and non acid-treated samples. EN1 again had the largest absolute difference (0.000240), followed by EN3 (0.000181). The average absolute difference in dentine was

All Localities								
$^{87}\text{Sr}/^{86}\text{Sr}$								
Plant Type	N	Mean	Median	SD	Minimum	Maximum	Z-score	P
Trees	9	0.704566	0.704563	0.000010	0.704381	0.704738	-2.67	<0.01*
Shrubs	12	0.704432	0.704462	0.000003	0.704241	0.704630		
Trees	7	0.704580	0.704513	0.000143	0.704402	0.704758	-1.94	0.05
Grass	13	0.704431	0.704443	0.000107	0.704241	0.704630		
Shrubs	8	0.704520	0.704487	0.000133	0.704375	0.704758	-0.29	0.77
Grass	11	0.704510	0.704518	0.000009	0.704379	0.704639		
Metamorphic and Volcanic Only								
$^{87}\text{Sr}/^{86}\text{Sr}$								
Plant Type	N	Mean	Median	SD	Minimum	Maximum	Z-score	P
Trees	7	0.704531	0.704539	0.000007	0.704381	0.704601	-2.16	<0.01*
Shrubs	12	0.704432	0.704462	0.000003	0.704241	0.704630		
Trees	4 [†]	0.704470	0.704482	0.000005	0.704402	0.704513	n.d.	n.d.
Grass	13	0.704431	0.704443	0.000107	0.704241	0.704630		
Shrubs	6	0.704453	0.704481	0.000005	0.704375	0.704493	-1.25	0.212
Grass	10	0.704497	0.704504	0.000008	0.704379	0.704601		

Table 4.5: Descriptive statistics and Mann-Whitney U Test results for localities with certain types of plants collected. No localities with overlapping vegetation types are included here (e.g. when comparing trees and shrubs no localities are included where both trees and shrubs were sampled). * Results significant ($\alpha=0.05$)

[†] Sample size not large enough to run Mann-Whitney U Test.

0.000094 when EN1 is included and 0.000070 when it is not. Including EN1, the average change in dentine was almost double that of enamel, and when excluded the average change is more than triple that of enamel. Enamel $^{87}\text{Sr}/^{86}\text{Sr}$ values increased after acid treatment except EN5 and EN7. Dentine $^{87}\text{Sr}/^{86}\text{Sr}$ values changed more unexpectedly, with four decreases and three increases.

The highest (0.70543) and lowest (0.70513) acid-treated enamel values were crocodiles, and the hippopotamus is between the crocodile and equid values (Table 4.8). Thus, there appears to be no difference between aquatic and terrestrial fauna.

Figure 4.5: Acid-washed dental $^{87}\text{Sr}/^{86}\text{Sr}$ values versus bioavailable values

Enamel $^{87}\text{Sr}/^{86}\text{Sr}$				
Tooth	Family	Acid	No Acid	Difference
EN1	Equidae	0.705339	0.705082	0.000257
EN2	Crocodylidae	0.705245	0.705207	0.000038
EN3	Crocodylidae	0.705296	0.705264	0.000032
EN4	Crocodylidae	0.705433	0.705412	0.000021
EN5	Crocodylidae	0.705133	0.705143	-0.000010
EN6	Equidae	0.705252	0.705246	0.000006
EN7	Hippopotamidae	0.705313	0.705324	-0.000011
Dentine $^{87}\text{Sr}/^{86}\text{Sr}$				
Tooth	Family	Acid	No Acid	Difference
EN1	Equidae	0.705466	0.705226	0.000240
EN2	Crocodylidae	0.705270	0.705329	-0.000059
EN3	Crocodylidae	0.705428	0.705237	0.000191
EN4	Crocodylidae	0.705415	0.705423	-0.000008
EN5	Crocodylidae	0.705138	0.705185	-0.000047
EN6	Equidae	0.705289	0.705200	0.000089
EN7	Hippopotamidae	0.705340	0.705367	-0.000027

Table 4.6: $^{87}\text{Sr}/^{86}\text{Sr}$ results for the acid washing experiment. The difference column is calculated as difference = acid – no acid.

Tissue	N	Median	Z-score	W-value	p-value
Enamel (A)	7	0.705296	-1.521	23	0.12819
Enamel (N)	7	0.705246			
Dentine (A)	7	0.705340	0.6761	18	0.49896
Dentine (N)	7	0.705237			
Enamel (A)	7	0.705296	2.0284	26	0.04252
Dentine (A)	7	0.705340			
Enamel (N)	7	0.705246	1.1832	21	0.23672
Dentine (N)	7	0.705237			
Both (A)	14	0.7053045	1.1614	71	0.24549
Both (N)	14	0.7052415			

Table 4.7: Wilcoxon Signed Rank test results from the acid treatment experiment. Significant results are bolded ($\alpha=0.05$). A=acid, N=no acid.

Enamel $^{87}\text{Sr}/^{86}\text{Sr}$					
Family	N	Minimum	Maximum	Mean	SD
Equidae	2	0.705252	0.705339	0.705296	0.000006
Crocodylidae	4	0.705143	0.705433	0.705277	0.000124
Hippopotamidae	1	0.705313	0.705313	0.705313	N/A
Dentine $^{87}\text{Sr}/^{86}\text{Sr}$					
Family	N	Minimum	Maximum	Mean	SD
Equidae	2	0.705289	0.705466	0.705378	0.000125
Crocodylidae	4	0.705138	0.705428	0.705313	0.000137
Hippopotamidae	1	0.705340	0.705340	0.705340	N/A

Table 4.8: Descriptive statistics for acid-washed dental $^{87}\text{Sr}/^{86}\text{Sr}$ results by family.

5. Discussion

5.1 Sources of Variation

5.1.1 Bedrock

There was a small range in $^{87}\text{Sr}/^{86}\text{Sr}$ values, despite sampling over approximately 750 km² and varying geology. Therefore, it will be easy to see animals from outside the area, but difficult to trace movement within the region. $^{87}\text{Sr}/^{86}\text{Sr}$ values of metamorphic inselbergs and volcanic areas were statistically indistinguishable from one another. The metamorphic rocks are either similar isotopically to the volcanic ones, or atmospheric strontium obscures their differences. The

Mozambique Belt rocks are likely more radiogenic than the volcanics, so atmospheric strontium likely provides much of the bioavailable strontium reservoir.

5.1.2 Atmospheric strontium

Oldupai receives rain in the wet season, though it likely has low strontium concentrations (Andersson et al., 1990; Stewart et al., 2001). Mean annual rainfall is about 50 cm and precipitation evaporates rapidly (Hay, 1976), so rain is probably not a significant contributor of strontium. Dust storms are common and a likely contributor of strontium, potentially leading to homogeneity in bioavailable strontium. Wind is typically easterly, carrying ash from Oldoinyo Lengai and loosely-packed soil constituted largely of volcanic ash (Anderson and Talbot, 1965).

5.1.3 Hydrological strontium

Rivers may have different $^{87}\text{Sr}/^{86}\text{Sr}$ values than the rest of the landscape (Wadleigh et al., 1985; Palmer and Edmond, 1989). Olbalbal has higher $^{87}\text{Sr}/^{86}\text{Sr}$ values than all but one locality. The Oldupai river ends there and is likely carrying strontium from Lakes Masek and Ndutu, the volcanic landscape in between, and riverbed basalts from Ngorongoro (Hay, 1976). Ngorongoro lavas have $^{87}\text{Sr}/^{86}\text{Sr}$ values ranging from ~0.704 to 0.708 (Mollet et al., 2008; 2011; Figure 5.1). As well, the Tanzania Craton is highly radiogenic, possibly contributing strontium to the river via groundwater or dust (Copeland et al., 2012).

5.1.4 Geographical factors

Areas of high elevation experience increased weathering and often have $^{87}\text{Sr}/^{86}\text{Sr}$ ratios closer to bedrock than atmospheric values, particularly in rivers (Bentley, 2006; Brennan et al.,

Figure 5.1: $^{87}\text{Sr}/^{86}\text{Sr}$ values for various materials from volcanoes of the Ngorongoro Volcanic Highland.

2016). A weak negative correlation exists between elevation and $^{87}\text{Sr}/^{86}\text{Sr}$ values when all localities were included, likely driven by the lacustrine samples. Lower parts of Olbalbal hold river water for longer, so plants growing there receive more water. One water source is stream water from Lemagrut, approximately 1,500 m in height (Hay, 1976) and likely weathered faster than lower areas. Its $^{87}\text{Sr}/^{86}\text{Sr}$ values are ~ 0.7047 to 0.7052 (Mollet et al., 2011), so the stream is probably partly responsible Olbalbal's values.

A negative relationship between exists latitude and $^{87}\text{Sr}/^{86}\text{Sr}$ for all localities except Olbalbal, but longitude is a stronger predictor. No correlation exists between $^{87}\text{Sr}/^{86}\text{Sr}$ values and longitude for all localities, likely due to Olbalbal as this test responds only to monotonic relationships. These trends for metamorphic and volcanic localities may be caused by Oldoinyo Lengai. Its extrusions have $^{87}\text{Sr}/^{86}\text{Sr}$ values of ~ 0.70412 to 0.70522 , though most had values less than 0.70450 (Bell and Simonetti, 1996; Kalt et al., 1997). These values are close to the

bioavailable ones, particularly in the north and east. It may therefore possible to identify animals or hominins that originated near the volcano.

5.1.5 Plant types

Ligneous plants have deeper roots and use more bedrock strontium, whereas shallower-rooted plants may use more atmospheric strontium (Whipkey et al., 2000; Maurer et al., 2012; Hartman and Richards, 2014). Localities with trees had higher $^{87}\text{Sr}/^{86}\text{Sr}$ values (descriptive statistics; tree mean=0.70458, shrub mean=0.70450, grass mean=0.70448), so bedrock strontium may be more radiogenic than atmospheric strontium. We attempted to collect a grass, shrub, and tree from every locality in case of differences between plant types, but this was impossible due to homogeneity of flora in some areas (Figure 5.2).

5.2 Dental Tissues

5.2.1 Diagenesis

Untreated enamel and dentine $^{87}\text{Sr}/^{86}\text{Sr}$ values from the same tooth did not differ significantly from one another. However, dentine $^{87}\text{Sr}/^{86}\text{Sr}$ values were significantly higher than enamel values when acid treated. On average, dentine $^{87}\text{Sr}/^{86}\text{Sr}$ values changed more than enamel, suggesting they were more altered. However, changes were small, so diagenesis may not be strong at the site. Copeland et al. (2012) found similar $^{87}\text{Sr}/^{86}\text{Sr}$ results for most Bed I fauna, ranging ~0.70450-0.70650. Consistency in values from Bed I to Bed III but with interindividual variation suggests that biogenic values are preserved.

Figure 5.2: Plant landscapes near Oldupai Gorge; a) an elevated view of Lemagrut (left) and Naibor Soit (right) facing southwest from near the top of Engelosin showing patchy wooded areas (uphill from Locality 5); b) open grassland showing sparse covering with short grasses northwest of Naibor Soit (Locality 30); c) a patch of *Acacia xanthophloea* on the outskirts of the Olbalbal depression (Locality 26); d) *Sansevieria robusta* and *Commiphora merkeri* at Granite Falls, the western limit of Oldupai Gorge (Locality 3).

5.2.2 Taxonomy and migration

Dental results were higher than bioavailable values. Crocodiles were most variable (0.70513-0.70543) but had the largest sample size. Nile crocodiles' (*Crocodylus nilotica*) home ranges are less than 30 km² (Caverley and Downs, 2015), though they may hunt non-local prey and have unusual ⁸⁷Sr/⁸⁶Sr ratios. This variation is probably not from land use, unless some teeth were transported fluvially from elsewhere. Rather, it could be from consuming different prey. The crocodiles also may have lived at different times, as EN spans 315 ka and the stratigraphy is not

well-dated. Hippopotamus (*Hippopotamus amphibius*) are semi-aquatic, are rarely more than 2-3 km from water, and eat primarily herbivorous foods (Bakker et al., 2016). Therefore, they should yield local $^{87}\text{Sr}/^{86}\text{Sr}$ values. The hippopotamus sampled had a $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of 0.70531, which was higher than all but one zebra and one crocodile.

Zebras (*Equus quagga*) migrate up to 500 km seasonally (Lee et al., 2016; Naidoo et al., 2016). The zebra teeth analysed here are close to the hippopotamus; therefore, appearing local. Most zebras today migrate north to the Serengeti (Estes, 2014), though some are resident. Copeland et al. (2012) found that the northern and western parts of the Serengeti have high $^{87}\text{Sr}/^{86}\text{Sr}$ values, but ~80 km northwest of Oldupai had bioavailable strontium values like those found here. If zebras were migrating within this area, they would be indistinguishable from residents. Alternatively, they may have been sedentary in the past. In Bed III times EN may have been wet enough to support animals year-round, or they may not have travelled as far for resources. No Bed I Antilopini and Alcelophini had non-local $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Copeland et al., 2012), so environmental differences in the past may have allowed animals to be resident. If so, non-local $^{87}\text{Sr}/^{86}\text{Sr}$ values may indicate dispersal rather than migration.

5.3 Modern vs. Ancient Bioavailable Strontium

Bioavailable strontium in the past may have been different, as the archaeological values do not align with the modern plants, possibly due to the environment because the region was wetter than the present in Bed III times (Kleindienst, 1973). Rainwater sources may have been different; for example: Lake Victoria formed about 50 ka and is a source of meteoric water around Oldupai today, but it was not around in Bed III times (van der Merwe, 2013). Beginning 1.15 Ma, the main drainageways passed through EN to end 5 km north of the site (Kleindienst, 1973; Hay, 1976).

These streams likely originated near Lemagrut and Sadiman volcanoes. The $^{87}\text{Sr}/^{86}\text{Sr}$ values of their rocks encompass the values of the teeth analyzed here. The streams were likely a major water source for flora and fauna and would have contributed to the area's bioavailable strontium.

Volcanism appears not to have been responsible for the differences in bioavailable strontium. The active volcanic centre in the NVH shifted gradually southwest to northeast, and $^{87}\text{Sr}/^{86}\text{Sr}$ values of the volcanoes decrease moving northeast from about 0.706 to 0.704 (Manega, 1993; Mollel et al., 2011). Bed III tuffs were likely deposited by Embagai and Loolmalasin (Manega, 1993; Mollel and Swisher, 2012; Greenwood, 2014). We found no data on Loolmalasin's $^{87}\text{Sr}/^{86}\text{Sr}$ values, but it is near Embagai and Olmoti which have lavas ranging from ~0.7041 to 0.7050 (Mollel, 2007), close to those of Oldoinyo Lengai today.

6. Conclusion

While $^{87}\text{Sr}/^{86}\text{Sr}$ variation in this region is limited, trends exist which may be related to environmental factors. It would be impossible to re-trace small-scale movements, but Copeland et al. (2012) found much higher values in Manyara and Serengeti National Parks, so large-scale dispersals over hundreds of kilometers will be observable. This isoscape should be expanded to connect with areas sampled by Copeland et al. (2012) and to include the diverse volcanic rocks of the NVH.

Preliminary archaeological $^{87}\text{Sr}/^{86}\text{Sr}$ results suggest that diagenesis can be reversed with weak acetic acid, and that modern and ancient bioavailable strontium differ. Sequential sampling of teeth and a multi-isotope approach ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) could refine interpretations of mobility by accounting for vegetation and precipitation patterns (e.g. Bentley et al., 2008; Widga et al., 2010).

Future studies should note how palaeoenvironments differ from modern ones when interpreting isotopic data and consider how this may have impacted hominin and animal behaviour.

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