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The Paleoenvironmental Context of Middle and Late Stone Age Behavior and Social Networks in Sub-Saharan Africa

By

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Doctor of Philosophy

Anthropology

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An abstract of
A dissertation submitted to the Faculty of the
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Abstract

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By Joshua Robert Robinson

The tempo of Middle and Late Stone Age behavioral change in Africa is integral to understanding the evolution of our species. Environmental change has been implicated in the technological changes, migratory routes and subsistence patterns that characterize the transition from the Middle to Late Stone Ages. However, we need more complete climatic and environmental data for individual archaeological sites relevant to this interval in order to understand the links between ecology and behavior.

This study tests the hypothesis that local climatic and environmental records provide a higher-resolution and locally distinct reconstruction than existing regional proxies in understanding the complex relationship between environment, behavior, and demography. Paleoenvironments at six study sites spanning this time period – Omo-Kibish and Porc Epic, Ethiopia; Lukenya Hill, Kenya; Kalemba and Makwe Caves, Zambia; Sibudu Cave, South Africa – were reconstructed through carbon and oxygen isotopic characterization and zooarchaeological analysis of fossil tooth enamel of faunal communities.

The main results suggest that the Last Glacial Maximum was the most significant continent level event in Africa during the late Pleistocene. Most study sites reflect a rapid shift towards greater aridity from the pre-Last Glacial to the Last Glacial time period. However, Omo-Kibish and Porc Epic may actually have become slightly *less arid* during the Last Glacial Maximum. In Zambia, a concurrent transition to C_3 grasslands is indicated by carbon isotopic profiles of traditional grazers, particularly equids. Such a transition is not interpreted from the data for sites in Kenya or Ethiopia, suggesting that human groups in southern Africa may have experienced more extreme shifts in local climate.

High-resolution environmental data allows for a greater appreciation of the microeconomic forces influencing behavior. Aridification of southern Africa during the Last Glacial may have had a major impact on migration and population change, altering population distributions and densities. Ethiopia with its relatively dry, but stable, environment throughout the late Pleistocene may have been a refugia for human groups and a cul-de-sac in terms of migrations out of Africa. Results of this study provide a more complete picture of regional environmental diversity for contextualizing local habitats in which humans evolved across Africa.

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Chapter 1

Introduction: The Middle and Late Stone Ages, Modern Human Behavior, and the Environment

One of the most fundamental questions in anthropology is ‘when and how did we become human?’ A key indicator of this transition is the emergence of symbolically mediated behavior, often interpreted to require cognitive abilities equivalent to modern humans (Tomasello 1999; Tennie et al. 2009; Whiten 2010; Goren-Inbar 2011). Symbolically mediated behaviors – such as in the development of composite tool technology, the use of ochre, and personal adornment in the form of shell beads, among other features – gradually appear in the archaeological record during the African Middle Stone Age, an archaeological period spanning the late Pleistocene from ~300 – 30 thousand years ago (ka) (McBrearty and Brooks 2000; Henshilwood and Marean 2003; Ambrose and Lorenz 1990; Marean and Assefa 2005). These behaviors were intensified during the subsequent Late Stone Age (~25 – 10 ka) and the transition period in between the two. It is this transition from the Middle to Late Stone Ages, roughly corresponding to the Last Glacial Maximum, which is the focus of this dissertation.

The Late Stone Age is characterized by increased population densities in parts of Africa, regional migrations out of and within Africa, and greater seasonal variation related to the origins of horticulture and agriculture (Inskeep 1967; Parkington 1972; Clark 1988; Stahl 1993; Wurz 2013; Tryon and Faith 2013). Much discussion has focused on the context and possible causal factors these behavioral events which Shea (2013) notes are complex and are obfuscated by the use of named stone tool industries giving the sense of chronological or regional homogeneity. The Last Glacial Maximum has been proposed to be a critical event in the development of behavior and exchange networks in the late Pleistocene (Castaneda et al. 2007; Claussen et al. 2013; Tryon and Faith 2013). In order to understand the role of the Last Glacial we need better site-specific environmental data for modeling the relationship between people and their environments.

For much of the twentieth century it was believed that modern human behavior developed during the European Upper Paleolithic, after 40 ka. This hypothesis was partially an artifact of strong Eurocentric bias in archaeology as well as a desire to differentially define ourselves from *Homo neanderthalensis* (see Bar-Yosef 2002 for a review). However, a few scholars championed the idea that symbolically mediated behavior developed in sub-Saharan Africa (e.g. Clark 1988; Ambrose and Lorenz 1990; Deacon and Wurz 1996). As more archaeological evidence accumulated, mostly from South Africa, but also Zambia and the Democratic Republic of the Congo, three prominent paradigms were developed to explain an African origin for modern human behavior: late Pleistocene genetic mutation (Klein 1995, 2000, 2009; Henshilwood and Dubreuil 2011); gradual emergence of modern behavioral traits as a consequence of selection leading to the evolution of our species (McBrearty and Brooks 2000; Henshilwood and Marean 2003); as a complex interplay between climate, behavior, and demography throughout the Pleistocene (Stringer 2007; d'Errico and Stringer 2011).

While the first two models are concerned primarily with the origins of modern behavior, the third can be easily adapted to other major behavioral transitions. d'Errico and Stringer (2011) conclude the discussion of their model of the relationship between climate, behavior, and demography with the following call for research:

> "…in order to make further progress in this field, we need a research strategy that allows us to model and quantify the link between environment and a particular

> past cultural adaptation, predict the response of that adaptation to climatic change and verify whether the rise and spread of innovations result in an expansion or contraction of the eco-cultural niche of a given population" (2011:1067).

It is important to note that d'Errico and Stringer, while theoretically important to this project, are writing with a focus on Eurasian climate and behavioral dynamics. This need to better contextualize the human eco-cultural niche is directly applicable to late Pleistocene Africa with its diverse array of heterogeneous environments. However, we only have a general understanding of the organization of climate, behavior, and demography during the Last Glacial period in Africa. The dissertation research reported in this volume takes the d'Errico and Stringer model as its intellectual paradigmatic framework and attempts to provide some initial responses to their call for research. As providing a satisfactory response to their questions about the relationships between climate change, demographic factors, and cultural adaptation requires a career of work, I aim to intervene at one small corner of the model, developing an approach for quantifying the link between environment and past cultural adaptation. In order to do this I seek to document and understand better the relationship between the global, regional, and local effects of a series of environmental and climatic phenomena in Africa during the transition from the Middle to Late Stone Ages—particularly in the context of the late Pleistocene glacial cycles. This paleoecological study provides the groundwork for the general agenda of my thesis and research program – evaluating human behavior in the context of environments. In this way it may be possible to identify the impacts which specific climatic regimes have on the individual archaeological sites where Late Stone Age behaviors appear, disappear, and reappear.

In the remaining portions of this introduction I will: (1) describe the current theoretical understanding for the relationship between environment and behavior; (2) provide a detailed overview of what is known about late Pleistocene environment and climate globally and in Africa; (3) introduce the archaeological test sites; (4) provide a brief overview of the study; (5) and describe how the volume will be organized.

Theoretical Relationship between Environment and Behavior

Theoretical models based on archaeological and environmental data (e.g. McBrearty and Brooks 2000; Henshilwood and Marean 2003; Tryon and Faith 2013) suggest that behavioral suites develop gradually with multiple reversals. These models generally suggest that the cognitive and physical requirements for modern behavior existed well before the appearance of symbolically mediated artifacts (see Goren-Inbar 2011). This implies that some form of selective pressure, or releaser, must have been present for early humans to begin exploiting this new adaptive landscape. Similar pressures would also be key components of cultural accumulation and social complexity during the Last Glacial (Tomassello 2009). An ongoing discussion in archaeology is that a disruption of a stable environment or climatic pattern is the ultimate explanation for behavioral change, with its effect on the demographic make-up of the population being the proximate cause. Demographic factors interacting with environmental variation in space (Binford 1968) or across time (Flannery 1972; Richerson et al. 2003; Bettinger et al. 2009) have been proposed as a pressure or releaser in social adaptation. By identifying variation in climate and vegetation this project aims to elucidate the challenges being faced by mobile human populations at the end of the Pleistocene. Some of these challenges are solved by behavioral and/or technological adaptation to equalize the niche-adaptation balance.

Hypotheses that explore behavioral adaptations to environmental stresses tend to focus on technological development. In general, these models link technological complexity and diversity with increasingly complex social and political units (Adams 1966; Boserup 1981). However, any evolutionary explanations for inventive and innovated behaviors in these models are contextualized in agricultural or early state societies. Fitzhugh (2001) provides one of the few models considering these relationships for a stone tool-based culture, and, as such, is most applicable to this study. Fitzhugh (2001) starts with the most basic question, ‘Why does technology evolve?’ Simplistic explanations include a need to solve a problem, or, alternatively, that innovation is a creative and random process. However, utilizing data from archaeological sites on the Kodiak Archipelago, Fitzhugh (2001) developed and tested an evolutionary ecology model of risk and opportunity costs. His risk sensitivity model predicts that during environmental fluctuations inventiveness would be desirable in order to increase productivity. When the environment is stable and resources are plentiful people are expected to spend less time inventing new technologies. At first this may seem contradictory, one may expect populations experiencing reduced productivity and increased environmental variability to be technologically conservative to ensure sustained resources rather than a failure of a new technology during dire times. However, technological innovation is also linked to loss of technological efficiency (Fitzhugh 2001). In other words, in dire times, when a population has little to lose, innovation is worth the risk. This idea provides the basis for models postulating that the environment is a driving factor in technological evolution.

Fitzhugh’s risk sensitivity model only gets us part of the way towards explaining the development and spread of behaviors accompanying the transition from the Middle to Late Stone Ages. The other important aspect is demography and interactions between populations. Since the early 1980s a particularly relevant subfield of anthropology, known as evolutionary culture theory (Durham 1991, 1992; Boyd and Richerson 1985, 2009), has modeled the ways in which the transmission of cultural ideas and behavioral residues are passed from generation to generation. The idea that cumulative culture, or ratcheting, (Tomasello 1999; Tennie et al. 2009), was suggested as distinguishing AMH behavioral abilities from those of great apes. As a result, evolutionary culture models began to consider population size as an important variable in creating and maintaining the ratcheting of culture (Shennan 2001; Powell et al. 2009; Richerson et al. 2009; Henrich 2001, 2004). Powell and colleagues (2009) suggest that populations reached a critical threshold approximately 100 ka which allowed ratcheting to overtake the rate of knowledge loss. Their interpretation of the loss, of some of these abilities at 70 ka is related to the stadial conditions of Oxygen Isotope Stage (OIS) 4, during which climatic deterioration led to both population decline and a dispersal of groups further away from each other (Powell et al. 2009).

Of course it is important to know if there is empirical evidence for population decline during around 70 ka. From global ice core records it is clear that OIS 4 was one of the cooler and drier periods of the last 250 ka (Chase 2010). Ambrose (1998, 2001) has proposed that the eruption of Toba at ~73 ka lead to a global volcanic winter for that has been linked to population and genetic bottlenecks in cheetahs (O’Brien et al. 1987), and Ambrose (1998) suggest that AMHs also experienced a bottleneck. If Ambrose’s Toba scenario is correct, computer simulations show that it is after human population size recovers that increased contact range and demographic growth could explain the behavioral explosion around 50 ka, rather than Klein's genetic hypothesis (Shennan 2001). Although no evidence has been discovered of a human population bottleneck directly related to Toba (Gathorne-Hardy and Harcourt-Smith 2003) or an ensuing population 'bounce back', Richerson et al. (2009) argue that the conditions of OIS 4 alone would have still fragmented AMH populations to the point that they may have experienced a loss of behavioral knowledge.

A potential flaw with employing the risk sensitivity model in explaining the origins of modern human behavior is that some authors, notably Henshilwood and Marean (2003), argue that technological innovations related to changes in the environment and resource bases are not hallmarks of modern human behavior. They prefer to attribute the abilities of modern human behavior only to those populations that produce unequivocally symbolically mediated artifacts, such as shell beads or incised ochre from sites in South Africa in response to the need for social signaling devices. However, the use of personal adornment has been hypothesized to be linked to similar forms of demographic and environmental stress. In times of uncertainty over food and water resources the use of such artifacts may provide a way to signal identity. This may lead to the formation of exchange networks through which resources, lithic technological knowledge, and other information may be transferred (Kuhn and Stiner 2007; Ambrose 2002; Deacon 1989). Whallon (1989, 2006) suggests that forager mobility/sedentism is also critical for the establishment and maintenance of social networks. These networks allow for information transfer and provide a "safety net" in periods of resource uncertainty. However, these models of mobility based on exchange of exotic goods, even in Whallon's case, has traditionally been focused on the European Upper Paleolithic. It is clear that the use of symbolically mediated artifacts as a factor of changing patterns of temporal and spatial resource availability may be just as, if not more relevant, for the MSA and early symbolic behaviors in Africa. Additionally, Goren-Inbar (2011) brings up the point that few mid-Pleistocene sites have been carefully studied with archaeological advances and techniques developed in the last decade. Nascent and/or rare evidence of symbolism from the mid-Pleistocene may have been missed due to a lack of archaeological resolution. However, even if we restrict ourselves to symbolically mediated artifacts as indicators of modern human behavior, understanding the nature of local environmental transitions remains a critical component of studies into the origins of modern human behavior.

Archaeological evidence is starting to provide initial support for d'Errico and Stringer's (2011) model based on the interaction between environmental and demographic transitions in explaining the appearance, disappearance, and reappearance of modern behavior during the Middle Stone Age (McCall 2006; Chase 2010; Richerson et al. 2009; Powell et al. 2009). However, most of these models utilize known records of global or regional environmental and climatic patterns instead of data on individual, site-level, environmental regimes. For instance, McCall (2006) offers a hypothesis for the appearance and disappearance of the precocial Howieson's Poort microlithic tool industry. Based on faunal evidence McCall argues that resource predictability abruptly decreased during OIS 4. Shifts in raw material economy are attributed to greater mobility and distances from raw material sources. As OIS 4 continued people learned how to target specific, more predictable resources, leading to the invention of the specialized microliths. However, McCall does not use any environmental proxies other than OIS stages and faunal assemblages, nor does he provide an explanation for why the “advanced” Howieson’s Poort disappears.

In their 2011 paper, d’Errico and Stringer (2011) implore future researchers to move beyond regional climatic records and to identify the relationship between behavior and environment at specific sites. Based on the above discussion, microeconomic factors and dynamics shape the ongoing response to climatic variability and long-term climate shifts. The goal here is to provide local data that is scale-relevant at individual archaeological sites rather than rely on inferring local conditions from regional proxy records. This is a first and necessary step in developing the framework for modeling and quantifying the relationship between the environment and a particular adaptive change during the Middle and Late Stone Ages.

Current State of Late Pleistocene Environmental and Climatic Knowledge

Climatic and environmental variability is intrinsically important for understanding behavioral change and cultural adaptation. It is critical to understand what is currently known about African paleoclimatic variation in time and space given the general importance of human adaptation to uncertainty. This type of paleoenvironmental study is only important to paleoanthropology if it can be appropriately situated within the context of the climate of the Pleistocene. In this way the local paleoenvironmental results can be more directly linked to issues of not only behavioral modernity, but also other behavioral questions throughout the Pleistocene.

Starting at the macro-level, both global and continental level patterns are controlled primarily by Milankovitch orbital forcing mechanisms and resulting variation in the magnitude of solar insolation. The focus of this discussion is on the period from ~175 – 10 ka. Even though the Middle Stone Age spans the timeframe from ~300 – 30 ka, the sample sites which are part of this study predominantly fall within the period ~175 – 10 ka.

It is clear that late Pleistocene environments in Africa are a result of the complex interaction between orbital forcing mechanisms (Kingston 2007; Blome et al. 2012), regional monsoon systems (Trauth et al. 2003), and more localized variables, such as sea-surface temperature and local insolation maxima (Stone et al. 2010; Moernot et al. 2010). Unfortunately, none of these variables can be directly recorded at archaeological sites and must be reconstructed through various proxies. Furthermore, it is often desirable to reconstruct other direct environmental variables, such as vegetation cover, rainfall totals, wind patterns, and lake levels, which are linked or controlled by broader orbital forcing and monsoon mechanisms. The coarsest climatic indicators or relevance here is the Marine or Oxygen Isotope Stage (OIS) framework, delineating glacial/interglacial boundaries. Briefly, the Middle Stone Age roughly spans OISs 8 – 3 (Figure 2). OIS 8, a glacial/stadial period, starts before the Middle Stone Age (although this is a dynamic boundary) at ~320 ka. This is followed by OISs 7 (~250 – 188 ka), 6 (~188 – 128 ka), 5 (~128 – 73 ka), 4 (~73 – 59 ka), and 3 (~59 – 29 ka). The Late Stone Age is primarily contained within OIS 2 (~29 – 13 ka), which is also known as the Last Glacial Maximum in a broad sense. As a general rule of thumb, even number OISs tend to be cooler and drier stadials, while odd numbered periods are warmer and wetter interstadials (Williams et al. 1988; Shackleton et al. 1990). Stadial and interstadial are typically used as designations for OISs because most periods are not true glacial/interglacial oscillations.

There is controversy regarding the relative importance of high-latitude glacial cycles, Walker circulation intensification, and ENSO/IOD variability for regional aridity, lake expansions and seasonality in equatorial regions (deMenocal, 2004; Trauth et al., 2009). Related to this uncertainty are debates about the role of orbital forcing and high-latitude millennium-scale events in driving increased environmental pressures on African ecosystems (Kingston et al. 2007; Scholz et al. 2007; Trauth et al. 2009; Armitage et al. 2011; Blome et al. 2012), and how these might have influenced resource acquisition (Reed & Rector, 2007). It is unclear how these various factors interact and mediate the local paleoenvironments in different regions or sites through time across Africa.

Coastal and deep-sea cores provide relatively continuous records of marine environments. These records have been used to reconstruct ocean circulation patterns (Schneider et al. 1995; Zhao et al. 1995; Sicre et al. 2000; Pichevin et al. 2005), upwelling cycles related to monsoon systems (van Campo et al. 1982; Rostek et al. 1997; Weldeab et al. 2007), and freshwater runoff from major river mouths (Leuschner and Sirocko 2000). Interpretations are based on sea surface temperature reconstruction which is completed through a combination of relative measures of phytoplanktonic diatoms and foraminifera and oxygen isotopic analysis of their carbonate tests (Trauth et al. 2003). Marine records may also contain data on terrestrial variables, particularly vegetation through the analysis of pollen (Tzedakis et al. 1997; Dupont et al. 2000). Offshore paleoenvironmental records are relevant to reconstructing ocean-land interactions and dynamics which, in turn may impact local responses.

Reconstructed sea-surface temperatures off the northwest coast of Africa correlate well with the OIS framework (Blome et al. 2012). Tisserand et al. (2009) and Sicre et al.

(2000) both identify a spike in temperature from 140-125 ka, the warmest period of the last true interglacial, OIS 5. Sicre et al. (2000) and Zhao et al. (1995) identify a bottoming out of temperature between 70-65 ka, corresponding with the OIS 4 stadial. Sea-surface temperature records from equatorial and southern Atlantic records also identify these OIS peaks (Schneider et al. 1995, Pichevin et al. 2005). On this basis it appears as if global cycles are the dominant force of off-shore African climate during the late Pleistocene.

However, Schneider et al. (1995) also investigated sand grain size, a proxy for upwelling and wind patterns, in cores recovered between 4ºN and 20ºS. These records revealed a 23 thousand year orbital forcing periodicity which is interpreted to be produced by a combination of variations in low latitude insolation and monsoon intensity, not necessarily global glaciation (Schenider et al. 1995; Pichevin et al. 2005). Records from the Indian Ocean provide evidence for changes in the southwest monsoon (van Campo et al. 1982; Rostek et al. 1997). Indian Ocean cores also reveal the 140-125 ka peak in sea-surface temperatures, but thereafter the Indian and Atlantic records diverge. This is interpreted to suggest that off of eastern Africa the most important contribution to environment is variation in insolation influencing the East African and Asian monsoons. Pollen records show Mediterranean species in the Arabian Sea during glacial periods, suggesting northeast trade winds and greater regional aridity during these times (van Campo et al. 1982). Overall, off-shore records appear to be influenced by the global cycles, but hints of regional diversity exist even at this continental level of analysis.

Terrestrial records are more local and specific to the sites where biological or behavioral evolution actually took place. The fact that terrestrial records tend to be discontinuous may preclude or confound attempts to develop reconstructions spanning long time periods, but as long as data exist for the biological or behavioral event under investigation it may be more insightful and relevant than ocean cores. A variety of terrestrial records have been utilized to reconstruct regional paleoenvironments. These include analysis of fauna and flora, including wood, pollen, phytoliths, leaf waxes, and biomarkers. Fauna and flora are assessed in terms of the known distributions and physical characteristics of expected modern equivalents, as well as through isotopic analyses (Kingston and Harrison 2007; Allot 2006; Assefa 2006; Faith et al. 2011; Hall 2010). Continental aridity/humidity cycles have been studied via optically stimulated luminescence dates on beach ridges and sand dunes (Bateman et al. 2004; Thomas and Shaw 2002) and migration of ancient sand ergs (Thomas and Burrough 2012, 2013). Local cycles of humidity and aridity are revealed by oxygen and carbon stable isotope analysis of speleothems and lake or spring carbonates which can be well dated by uranium/thorium techniques (Bar-Matthews et al. 2003; Vaks et al. 2007; McDermott 2004; Hillaire-Marcel et al. 1986; Bar-Matthews et al. 2010), and archaeomagnetism (Herries 2006).

In Lake Malawi, for example, periods of high eccentricity-precessionally forced cycles caused extreme periods of aridity every 11,000 years and 23,000 years (Lyons et al. 2011; Scholz et al. 2011). Trauth et al. (2003; Trauth et al. 2009) also identify a signature of regular orbital forcing on insolation in terms of 23 thousand year cycles. This is interpreted to mean that closer to the equator local insolation imparts the greatest influence on the local environment (Trauth et al. 2003). Humid/dry cycling after ~80 ka in this region varies between the lake basins (Scholz et al. 2007). These patterns have been linked to the end of the high eccentricity period. Lower orbital eccentricity reduces the degree of solar insolation, which, in turn, weakens the Asian and African cyclical monsoons (Lyons et al. 2011; Burnett et al. 2011). While the major rift valley lakes still respond to global and regional climatic cycles, lower eccentricity explains why these signals are muted after ~75 ka (Stone et al. 2010; Moernot et al. 2010).

Equatorial African paleoenvironmental and climatic indicators, including the Congo Rainforest Basin in the Democratic Republic of the Congo, are closely linked to those in East Africa. Direct, continuous records of environment from the Congo are non-existent, but based on its proximity to Lake Malawi and Lake Tanganyika it is most likely that this region also experienced drought conditions on ~11,000 and ~23,000 year cycles between ~160 – 60 ka. Pollen from the Congo River basin suggests alternating warm and humid periods with cold and dry ones on a 10,000 year cycle between 130-80 ka (corresponding to OIS substages 5e-5a). The pollen reveals rainforest expansion between 130-120 ka, 110-100 ka, and 90-80 ka, but dominance of dry woodlands at 120-110 ka, and 100-90 ka (Dupont et al. 2000). Unlike in East Africa where the droughts led to desertification and uncertain water resources, in the Congo Basin they led to an opening up of the forest canopy. Blome et al. (2012) argue that this actually made the Congo Basin more hospitable, pointing to the occupation of the Katanda site occupied during the period ~120 – 60 ka. By ~50 ka, the Congo pollen records no longer match the East Africa lake records, but instead suggest that the Kalahari expands and becomes more arid than the rest of equatorial Africa (Blome et al. 2012; Thomas and Shaw 2002). This pattern provides further support for reduced eccentricity in the later Middle Stone Age and greater localization of environmental and climatic regimes.

Paleoenvironmental data for the interior of south-central Africa are difficult to come by, but the linear dune records of the Kalahari Desert provide a glimpse into its climatic past. The modern Kalahari is made up mostly of its core in Namibia with extensions into Botswana. During the late Pleistocene, however, dunes stretched from as far south as the Pretoria Salt Pan, central South Africa, to a northern extent of the Victoria Falls area, Zambia (Thomas and Burrough 2012, 2013). Unlike the data presented above, there are no direct indictors of environmental or climatic proxies in the way of isotope analysis. Instead, direct optically stimulated luminescence dating of ancient sand dunes and ergs provides evidence of periods of extreme aridity and aeolian activity. In the northern portion of the late Pleistocene Mega-Kalahari, linear dunes surrounding Victoria Falls and the Hwange National Park (northwest Zimbabwe); suggest two short dune building events and three extended periods of aridity during the late Pleistocene. The two shorter dune building events date to ~164 – 160 ka and ~77 – 74 ka. Their geographical extent is unknown and may reflect localized events (Thomas and Shaw 2002). At ~115 – 95 ka, ~48 – 38 ka, and ~26 – 20 ka there are confirmed instances of increased aeolian Mega-Kalahari activity stretching from the Okavango Delta in north-central Botswana to Victoria Falls. These periods are separated by extended times of increased humidity reflected in fossilized woodlands and a cessation of dune activity. More recent aeolian activity seems to support the fact of lower eccentricity after ~80 ka leading to greater regionalization of climatic events. Both of the more recent desert expansions appear to be generally related to increases in northern hemisphere ice cap and glacier volume which have a direct effect on the standard surface temperature of southern hemisphere ocean water. Following the Last Glacial Maximum, this area of the

Kalahari started to reflect modern conditions—900 mm of rainfall a year with wooded grasslands (Stokes et al. 1998; Thomas and Shaw 2002; Singhvi and Wintle 1999).

From the Pretoria Salt Pan in central South Africa to the border with Botswana the Mega-Kalahari undergoes a slightly different pattern. In Botswana, at the northern extent of this region, Burrough et al. (2009) report a drought signal in the Mababe Depression between ~110-95 ka, roughly corresponding to the northern dune activity. However, less than 50 km to the south at Lobatse Cave Holmgren et al. (1994) not only report a humid period during this same time, but increasing humidity based on speleothem analysis. Drotsky's Cave, to the west of the Mababe Depression also reveals a period of humidity and reduced aeolian activity (Robbins et al. 1996). This suggests eccentricity-modulated precessional wet/dry cycles related to changes in southern hemisphere insolation which may change drastically as one moves from the interior of Botswana to the Orange River in South Africa (Burrough et al. 2009). Off-shore records imply increasing humidity for this part of the southern Africa from ~115 – 40 ka, but data from the Tswaing Crater Lake and the Pretoria Salt Pan suggest the opposite (Partridge et al. 1997, Partridge et al. 1999; Burrough et al. 2007). Bar-Matthews et al. (2010) analysis of the Pinnacle Point speleothem appears to document vegetation and rainfall shifts between 90-53 ka in concert with southern hemisphere shifts in temperature. Over this time period there is a general trend toward warmer climate, more winter-rainfall, and an increase in C_3 grasses. While the Pinnacle Point speleothem may seem to support the off-shore standard surface temperature records, it must be remembered that speleothems are inherently localized records of environmental and climatic change (Blome et al. 2012). It appears that the period from ~90 – 40 ka in southern Africa may be categorized by increasing regionalization of climatic patterns correlated by the migration of the winter-rainfall zone in the west (Lee-Thorp and Beaumont 1995; Chase and Meadows 2007) and the lower eccentricity Indian Ocean monsoon in the east (Blome et al. 2012; Thomas and Burrough 2012, 2013). All records agree that starting ~40 ka southern Africa began a steady trend towards increased humidity converging on modern day conditions. Thomas and Burrough (2012) suggest that southern Africa does not show the same well-defined cyclical aeolian events as the northern Mega-Kalahari due to the fact that it is well buffered by the ocean on three sides.

This dissertation reports primarily on data from archaeological sites dating to the period after ~75 ka. From the preceding discussion it appears that late Pleistocene environment and climate is characterized by increased regionalization and seasonality during this period. It is important to note, however, that conditions in east and central Africa seem to have been linked by high-eccentricity-modulated forced precessional cycles prior to this time period. Records from the African rift lakes of Malawi and Tanganyika do suggest temporal asynchrony of climatic events after ~40 ka (Woltering et al. 2011; Ivory et al. 2012), but the regions remain partially linked into the Last Glacial Maximum through the effect of the Congo Air Boundary on precipitation in both basins (Leroux 2001; Hely et al. 2006). Without this environmental and climatic history it would not be possible to appropriately contextualize the key events of this dissertation's focus – the Last Glacial Maximum, Heinrich 1, and the Younger Dryas.

The Last Glacial Maximum, ~27 – 13 ka, is the final major climatic event of the late Pleistocene and is characterized by the greatest expanse of the northern hemisphere ice sheets over the last ~50,000 years. In Africa, this event lead to a weakened Indian

Ocean monsoon system resulting in increased aridity across the eastern portion of the continent (Kohfeld et al. 2013). Except at the highest elevations on the continent, the Last Glacial Maximum is not typically considered to be a major cooling event in Africa. Saltre et al. (2013) and Potts et al. (2013) both claim that any shift in vegetation during the Last Glacial was altitudinal as opposed to latitudinal. Following the end of the Last Glacial Maximum *sensu lato* at ~17 ka was the Heinrich 1 event. Heinrich 1 led to extreme drought conditions in the modern Saharo-Arabian belt (Stager et al. 2011; Bouimetarhan et al. 2012). However, different regional effects of this event are reported for southeastern and central Africa. In the Lake Malawi basin, Ivory et al. (2012) characterize Heinrich 1 as a cool, but moist interval of OIS 2 with expansion of Zambezian woodlands. A brief worldwide climatic respite exists between the end of Heinrich 1 and the onset of the Younger Dryas cold-snap which lasted from ~13 – 11 ka., with a peak ~11.7 ka. The Younger Dryas was the last arid/cold event of the last glacial cycle and it has been identified in records for all parts of the planet (Broecker et al. 2010).

Regional climatic uncertainty, particularly in the period after ~75 ka, may have been a prime mover for late Pleistocene adaptation and cultural ratcheting in both Africa and Europe. Variable and unpredictable environment would provide some support to Potts' (1996, 1998, 2004) variability selection hypothesis on a macro-scale. For example, some of the hallmarks of modern behavior – composite tools, symbolic use of ochre, and long-distance exchange networks – may represent an adaptive suite in response to climatic uncertainty. Understanding the regionalization and "advancements" of the Middle and Late Stone Ages are critical for determining how Potts' variability selection hypothesis may relate to AMH origins, modern behavior, and migrations out of Africa.

Description of the Middle and Late Stone Ages

The emergence of modern human behavior during the Middle Stone Age has been a focus of archaeological research in Africa over the past decade (Barham 2000b; Henshilwood et al. 2002; d'Errico et al. 2005). There are varying opinions on when the Middle Stone Age begins. The period between ~300 – 250 ka (Scerri 2013), which predates the evidence for the first anatomically modern *Homo sapiens*, but encompasses some of the earliest evidence for blade technology and ochre use, is a common timeframe. Wurz (2013) notes that others extend this as far back as ~500 ka based on the appearance of blades in east Africa (Tryon and McBrearty 2002) and southern Africa (Wilkins et al. 2012). Recognizing the terminus of the Middle Stone Age is just as daunting, as most sites do not provide a complete stratigraphic profile from the Middle Stone Age through the transition to the Late Stone Age. At Enkapune Ya Muto, Kenya, Ambrose (1998b) argues that microliths, the defining lithic technology of the Late Stone Age, dominate the assemblage starting ~50 – 45 ka. In South Africa many sites contain a last or final Middle Stone Age stage dated to ~35 – 30 ka (Wurz 2013), and at places in Zambia the Middle Stone Age may have lasted until ~20 ka (Barham 2000b). Furthermore, the true beginning of the Late Stone Age is also in flux with most dates centering on the transition from the late Pleistocene to the early Holocene (~15 – 13 ka).

A behavioral transition period exists in all regions of Africa between the end of the Middle Stone Age and the onset of the true Late Stone Age. This transition period is extremely variable from region to region, and sometimes even between sites within a region. It is typically characterized by a mixed stone tool assemblage, usually consisting of some early microliths and backed implements. These tend to be rare early in the transition period and may disappear from the record in parts of a sequence (Barham 2000; Wurz 2013; Tryon and Faith 2013). When these form a certain percentage of the assemblage a site is commonly designated as an early or true Late Stone Age occurrence. This threshold is undefined and varies from site to site, for instance, Ambrose (1998b) uses a cut-off of 50% of the assemblage at Enkapune Ya Muto. Of course, the Late Stone Age is not defined by lithic material alone. At other sites species composition and an increase in processing ochre and shell and bone beads are utilized as hallmarks of a Late Stone Age occupation (Barham 2000). Additionally, the Late Stone Age is often thought to have different demographic, migration, and social network patterns than the Middle Stone Age. These features are not directly preserved in the archaeological record making it even more difficult to define the boundary between the Middle and Late Stone Ages.

This transition period, roughly defined as the time frame between ~45 – 15 ka, overlaps with the Last Glacial Maximum. In some parts of Africa the Late Stone Age may have begun before the onset of the Late Glacial, whereas other regions were still in what is considered to be the Middle Stone Age. This study reconstructs paleoenvironments of five late Pleistocene archaeological sites through isotopic analysis of fossil faunal tooth enamel in order to demonstrate that individual sites in east and central Africa responded differently to the Last Glacial Maximum. Figure 2 provides a visualization of the relationship between the timing of the occupation of the study sites and the global OIS framework. From the discussion of global climatic patterns above, it is expected that east and central Africa will have different environmental histories during the Last Glacial. Furthermore, my research aims to demonstrate that during the Last

Glacial individual archaeological sites within a region experience different climatic and environmental histories. This result would suggest that regional climatic records alone are not sufficient for characterizing and contextualizing late Pleistocene behavioral transitions. This multi-sited approach provides paleoenvironmental reconstructions for individual sites which can then be utilized to compare sites and develop testable hypotheses about the relationships between sites, including migrations and social networks.

Site Descriptions

In order to understand better the role of global and regional climatic events in the gradual development of modern behavioral features this dissertation reconstructions paleoenvironments for six relevant Middle and Late Stone Age archaeological sites (Figure 1). Fossil faunal tooth enamel samples were collected during the summer of 2013 from the archaeological sites of Lukenya Hill, Kenya, Omo-Kibish and Porc Epic, Ethiopia, and Kalemba Rockshelter and Makwe Caves, Zambia. Sibudu Cave, South Africa, the sixth site, is primarily occupied during OISs 4 and 3 and is included in the study as a case of behavioral modification in response to environmental change. The five sites that form the core of the thesis focus on the Last Glacial Maximum. Each of these sites were systematically excavated, contain diverse faunal assemblages, and span behaviorally relevant transitions during the Middle and Late Stone Ages. Omo-Kibish, Kalemba, and Makwe are well-dated, while new and ongoing research into the chronologies of Lukenya Hill (pers. comm. C. Tryon) and Porc Epic (pers. comm. Z. Assefa) suggests the sequences of both sites span the Last Glacial Maximum to the limits of the radiocarbon method. These sites also include well-studied lithic assemblages which may allow testing complex relationships between environment and lithic economy as part of risk aversion strategies (Fitzhugh 2001; Reed 2008) or as a response to resource availability (Nelson 1991) at a later date. Sites have been selected to encompass the entire time range of the Middle Stone Age through the Middle Stone Age/Late Stone Age transition and through the beginning of the Late Stone Age. While more details of the sites, particularly the faunal composition, are described in the chapters that follow, below I will briefly introduce each site and how it may fit into the broader regional climatic framework. These collections are curated at the National Museums of Kenya, the National Museum of Ethiopia, and the Livingstone Museum, respectively.

Figure 1. Location of sites included in this dissertation (image modified from NASA Visual Earth).

study of human-environment interactions. Fossil faunal tooth enamel samples were collected during the summer of 2011 while in the field at the University of the Witwatersrand, Johannesburg. Unlike the other sites, Sibudu does not contain a Last Glacial component, but rather dates to the preceding stadial, OIS 4. The behavioral sequence from the pre-Still Bay industry, through the Howieson's Poort, and post-Howieson's Poort periods are clearly documented and have been studied in detail (Backwell et al. 2008; Wadley and Jacobs 2004; Lombard 2008; Wadley 2007; Lombard 2006; Lombard and Phillipson 2010). While minor hiatuses do exist within the sequence, the detailed and continuous late Pleistocene technology is unique among currently excavated *and* reported South African sites. It is included here as an opportunity to directly correlate site-specific environmental conditions with relatively rapid behavioral changes during the enigmatic Howieson's Poort.

Lukenya Hill

Originally excavated by Richard Gramly in the early 1970s (Gramly and Rightmire 1973; Gramly 1976), Lukenya Hill is a gneissic inselberg in southern Kenya composed of five separate open air and rock shelter locations with both Middle Stone Age and Late Stone Age lithic assemblages. Gramly (1976) focused his excavations on site GvJm22 dividing the assemblage into two Occurrences, F and E, as defined by the bimodal distribution of stone artifacts by depth. These Occurrences have been roughly equated with the Middle and Late Stone Ages by later investigators (Marean and Gifford-Gonzalez 1991). Dating of the Middle Stone Age layers suffers from the limits of the radiocarbon method and can only be said to be older than ~40,000 years (Merrick and Brown 1984). Recent reinvestigation of the chronology at Lukenya Hill suggests that Occurrence F pre-dates the Last Glacial Maximum and that Occurrence E spans the Last

Glacial Maximum (C. Tryon pers. comm.). Marean (1990) and Marean and Gifford-Gonzalez (1991) further dived the period ~40 to 1 ka into three additional archaeological periods: late Pleistocene non-geometric (~40 – 22 ka; sites GvJm46 and GvJM62); late Pleistocene geometric (~22 – 10 ka; sites GvJm22, GvJm46, GvJm16); and Holocene (~10 – 1 ka; site GvJm19). The late Pleistocene non-geometric is considered a Middle/Late Stone Age transition grading into a true Late Stone Age site near the end of the period and into the late Pleistocene geometric. Informal scrapers, points and rare microlithic pieces appear in the Middle Stone Age (Merrick and Brown 1984). This pattern changes to an assemblage containing mostly microlithic crescents and curved backed blades during the late Pleistocene non-geometric. This is considered a transition layer because it does contain a significant amount of large blades and the percentage of geometrics is very low. Comparatively, the late Pleistocene geometric is dominated by geometrics, nongeometric microliths, and a standardized convex end scraper (Barut 1994; Kusimba 2001). For the purposes of this study the unit of analysis will be Gramly's Occurrences, roughly separating Marean's chronology between the late-Pleistocene non-geometric and late-Pleistocene geometric periods, due to the focus of the re-dating at the site (Figure 2 offers a timeline for all sites included in this dissertation).

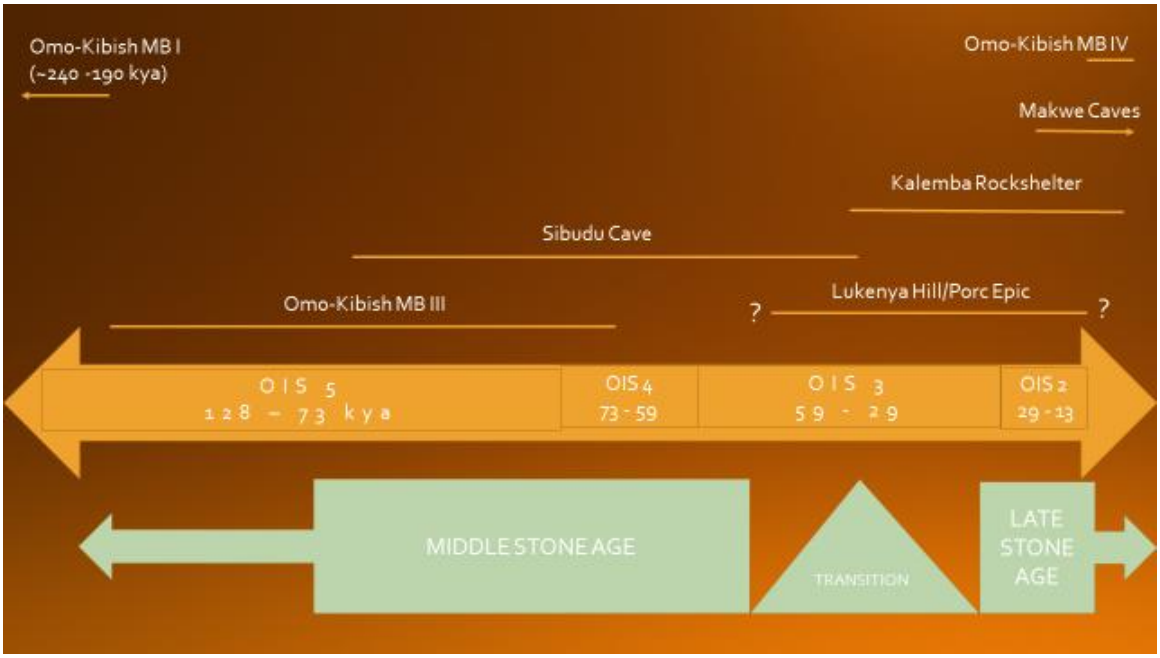

Figure 2. Timeline including sites, global OIS stages, and rough approximations of behavioral periods.

Omo-Kibish

The Omo-Kibish Formation in southwest Ethiopia is one of the more important Middle Stone Age sites for both its stone tool traditions and its early human remains. Two of the earliest fossils of modern *Homo sapiens*, dated to ~196 ka, have been recovered from the site (Fleagle et al. 2008; Brown and Fuller 2008; McDougall et al. 2008). While there has been a long and rich history of excavation at Kibish (Leakey 1969; Butzer et al. 1969), this study includes fauna from the 2001-2003 excavations (Fleagle et al. 2008; Assefa et al. 2008) only due to the lack of reliable provenience information for earlier faunal collections. The Kibish Formation is broken into 3 main members: Member I (~240 – 190 ka), Member III (~130 – 70 ka), and Member IV (~14 ka) (McDougall et al. 2005; Brown and Fuller 2008). Kibish Member I is dominated by Levallois cores discarded after the removal of a single central or “plunging” flake. Member III reflects the local Aduma Industry from the Middle Awash. The Aduma

Industry includes large cutting tools, retouched triangular points, foliate bifacial points, and small, asymmetrical discoidal cores. An important note here is that Member III at Kibish has very few retouched pieces. Member IV dates to the Late Stone Age and is similar in composition to Member III, but its lithic assemblage has not been systematically studied (Shea 2008; Fleagle et al. 2008; Sisk and Shea 2008). The environment at Omo-Kibish is interpreted to gradually shift from closed and more wet during Member I to open and more arid by Member IV through correlation with the Mediterranean sapropel record (McDougall et al. 2008). McDougall et al. (2008) suggest that the members of the Kibish Formation were formed by increased flow into the Omo River, driven by increased rainfall in the Ethiopian highlands associated with precessional cycling, which coincide with increased outflow from the Nile.

Porc Epic

A second Ethiopian site, Porc Epic Cave from the Dire Dawa region in the eastern part of the country, contains Middle Stone Age, Late Stone Age, and Neolithic archaeological layers. Only the Middle Stone Age portion is sampled as part of this study. Unfortunately, Porc Epic's stratigraphy is not very well dated, and due to a long excavation history, starting with Teilhard de Chardin (1930), some stratigraphic relationships have been lost. For these reasons, only material from Kenneth Williamson and J. Desmond Clark's excavations (Clark et al. 1984) will be considered here. Dating of Clark's stratigraphy is also complicated as at least parts of the site appear to extend beyond the capacity of the radiocarbon method. Obsidian hydration dating places the site in the time period ~77 – 61 ka (Clark et al. 1984), but radiocarbon dating of gastropod shells brackets the latest Middle Stone Age layers between ~43 – 33 ka (Assefa et al.

2008). There are issues with both of these dating techniques, specifically the accuracy of obsidian hydration dating (Anovitz et al. 1999) and the carbon reservoir effect when directly dating shell (Rick et al. 2005). There appear to be four main stratigraphic levels at Porc Epic, however, both the lithic (Pleurdeau 2003, 2005) and the faunal remains (Assefa 2002, 2006) have previously been analyzed as one unit due to the dating issue and the fact that there does not appear to be any clustering or obvious vertical breaks in the sequence. Assefa's (2002) zooarchaeological study suggests that Porc Epic was surrounded by an open-to-wooded habitat. This assessment is in agreement with its position on the edge of the rift in a rain-shadow. Pleurdeau (2003, 2005) reports that the Middle Stone Age component is mostly composed of Levallois elements, including a high percentage of retouched points and scrapers. Obsidian artifacts include bladelets, some backed and geometric in form. Pleurdeau and Assefa (pers. comm.) have recently completed new AMS and OSL dates for Porc Epic. Preliminary results show that the layer at the middle of the stratigraphic profile of the site dates to just prior to the onset of the Last Glacial Maximum. This new insight to the chronology at Porc Epic allows the site to be neatly divided between Last Glacial and pre-Last Glacial units for the purposes of this study.

Kalemba Rockshelter

Kalemba Rockshelter is located near Chadiza in eastern Zambia and was excavated by D.W. Phillipson in the early 1970s. Kalemba is known as the largest rockshelter in Zambia as well as for its extensive Holocene cave paintings and carvings. Phillipson (1973, 1976) identified thirteen stratigraphic horizons which he split into four late Pleistocene/early Holocene cultural levels: Middle Stone Age (~37 ka); a Middle to

Late Stone Age transition (~30 – 25 ka); Late Stone Age (~20 – 12 ka); and Late Stone Age (~10 - 7 ka). Concern exists over the accuracy of the 1970s radiocarbon dates, but the sequence is split almost perfectly for this study to analyze the Middle Stone Age and transition levels as pre-Last Glacial and the Late Stone Age as the Last Glacial. Kalemba's Middle Stone Age layer contains mostly retouched implements, particularly scrapers. No microliths or backed implements appear during this period. During the transition period backed convex-flakes appear in abundance with rare transverse-backed implements. By the Late Stone Age flakes show a marked reduction in size and the first geometrics of the Kalemba sequence appear. By the Late Stone Age Kalemba is dominated by a microlithic industry.

Makwe Caves

Also excavated by D.W. Phillipson, Makwe Caves is located south-west of Katete in eastern Zambia quite near Kalemba Rockshelter. Phillipson excavated eight horizons at Makwe with the majority of the site dating to the Iron Age. For this study only the fauna from Horizons 1 through 3, which represent a Late Stone Age collection dating from ~13 – 5 ka are considered. The lithic technology represented in Horizon 1 includes a variety of retouched implements and geometrics, implying that it accumulated gradually over a period from ~13 – 7 ka, and possibly even longer. Horizons 2 and 3 are both dominated by geometrics, but backed implements, including points, do not make an appearance until Horizon 3 (Phillipson 1973, 1977). Since Makwe does not include a pre-Last Glacial component it is only utilized in this study when aggregating data for regional analyses.

Sibudu Cave

The final archaeological study site is Sibudu Cave, South Africa. Sibudu Cave is a rock shelter located approximately 40 km north of present-day Durban and 15 km inland from the Indian Ocean in KwaZulu-Natal, South Africa. While discovered in the 1980s, excavations at Sibudu did not begin until the mid-1990s under the supervision of Lyn Wadley. This site is unique in terms of having a detailed and extensive Middle Stone Age sequence spanning from the pre-Still Bay (before ~77 ka) to the final Middle Stone Age (~37 ka) (Jacobs et al. 2008; Wadley and Jacobs 2006). While hiatuses do exist between these periods, the fact that several substages of the Middle Stone Age are present and were systematically excavated is a rare occurrence. The site preserves deposits from six Middle Stone Age periods: the pre-Still Bay (before ~77 ka), the Still Bay (~77-73 ka), the Howieson's Poort (~68-60 ka), the post-Howieson's Poort (~60-57 ka), the late Middle Stone Age (~50-45 ka), and the final Middle Stone Age (~40-37 ka) (Wadley and Jacobs 2004; Jacobs et al. 2008). Variations in lithic raw materials (Cochrane 2006) and archaeomagnetic data (Herries 2006) led Clark and Plug (2008) to divide to the post-Howieson's Poort Middle Stone Age into older (post-Howieson's Poort Middle Stone Age 2) and younger (post-Howieson's Poort Middle Stone Age 1) segments. The best documented transitions in tool morphology are from the Still Bay to the Howieson's Poort and from the Howieson's Poort to the post-Howieson's Poort Middle Stone Age. Bifacial lanceolate points of the Still Bay (Wadley 2007) give way to the characteristic microlithic backed segments of the Howieson's Poort (Delagnes et al. 2006; Wadley and Jacobs 2006). The post-Howieson's Poort is characterized by a shift to unifacial points and scrapers, and the concurrent disappearance of the microlithic backed segments (Cochrane 2006; Villa et al. 2005). Unifacial points are also common in the late Middle Stone Age (Wadley and Jacobs 2006). A much broader collection, including side scrapers and hollow-based points, characterize the final Middle Stone Age (Wadley 2005).

Site Synthesis

These sites have been selected to provide a local documentation of well-known global and regional climatic events. For instance, the Kibish Formation, which has the longest history of occupation of any site in this study, offers a chance to determine whether megadroughts ever reached Ethiopia. If a drought signal is recorded for the site, does it happen at the same time as the documented droughts in Kenya and Tanzania? Paleoenvironmental constructions at Porc Epic may clarify which set of dates is correct. If the site truly dates to the ~77 – 61 ka period we may expect to see increased humidity and canopy cover followed by more wooded conditions, as evidenced in Somalia and at lakes Magadi and Natron. However, if Porc Epic is more correctly dated at ~43 – 33 ka, near the beginning of the last glacial maximum, we would expect a more arid and open environment. Assefa (2006) reports higher percentages of grazing fauna which, combined with the lithic technology present, may imply the former time range. Additionally, comparisons between Kibish and Porc Epic offer a potential opportunity to investigate how regional climatic events are differentially registered at closely related sites. Lukenya Hill is closer to the true megadrought zone and can provide an assessment of the local nature of East African megadroughts. A muted megadrought signal may be expected during the Lukenya Hill Middle Stone Age due to a period of lower eccentricity, while its Late Stone Age levels should reveal increasing aridity and open environments during the Last Glacial Maximum.

Kalemba Rockshelter is occupied during both of the late Pleistocene Kalahari expansion events and should offer insight as to whether arid conditions extended from the core of dune-building activity, or if eastern Zambia was a refugia from the Mega-Kalahari. Paleoenvironmental reconstructions at Sibudu Cave may provide a signal of Kalahari Desert expansion from earlier periods. However, South Africa has often been regarded as unique among African regional climatic patterns. It seems to be affected more by off-shore currents and Antarctic air masses than the migration of the Congo Air Boundary or the Inter-tropical Convergence Zone (Marean 2010; Chase et al. 2010).

Each of the sites has undergone extensive zooarchaeological study. However, previous research has demonstrated that faunal analysis alone provides a limited understanding of past environments as similar faunal communities may exploit variable ecosystems. Isotopic analysis offers a different perspective of faunal diet and environment which may or may not conform to results based on comparisons with modern correlates (Lee-Thorp 1989; Lee-Thorp and Sponheimer 2003; Sponheimer and Lee-Thorp 1999a; Sponheimer and Lee-Thorp 1999b; Schoeninger et al. 2003; Cerling et al. 2003). Morphology may reflect diet and ecology, but it has also been hypothesized to reflect fallback foods (Crowley 2012). Additionally, it has been suggested (Kingston and Harrison 2007) that extending our knowledge of modern species studied in parks and reserves into the past may cause reconstruction errors. As a result, past feeding niches of extinct species may be much broader than fossil morphology modern analogs suggest. The multi-site longitudinal isotope analysis reported on here has the potential to more accurately reflect Pleistocene dietary guilds, potential shifts in a lineage’s diet and—in turn—local environments. By creating nuanced paleoenvironmental reconstructions for individual sites, it becomes possible to study intra-regional climatic complexity.

Overview of the Analytical and Empirical Framework

Paleoenvironmental reconstructions based on stable isotope analysis of fossil faunal tooth enamel from the five central/eastern African archaeological test sites discussed above are created in order to determine how broad regional climatic events affect environment on a local level. Stable isotopes of both carbon and oxygen are analyzed from 485 faunal enamel samples from across the five primary sites. An additional 126 faunal enamel samples were collected for the Sibudu Cave study in South Africa. Stable isotope characterization of teeth of fossil and modern fauna has been a developing approach of paleoenviromental and paleodietary research for the past twenty years. Paleoecological and paleoclimatic indicators have routinely been interpreted from carbon and oxygen isotopic profiles of African mammalian communities (Lee-Thorp 1989; Kingston 1999; Sponheimer and Lee-Thorp 1999a; Sponheimer and Lee-Thorp 1999b; Kingston and Harrison 2007; Harris et al. 2008; Codron et al. 2009; Crowley 2012). These studies focus on the carbonate fraction of bioapatite in tooth enamel, which has been shown to retain *in vivo* biogenic signals (Wang and Cerling 1994; Koch et al. 1997; Kohn et al. 1999; Lee-Thorp and Sponheimer 2003). This research proposes to infer ecological, environmental, and climatic factors based on the signatures of these feeding habits. However, this type of research must be carried out with appropriate caution. Seasonality, competition, migration, social behavior, and a variety of other factors may complicate the link between diet and environmental proxies (Caswell et al. 1973; Behrensmeyer and Hook 1992). In order to minimize these factors as best as possible, diet and paleoenvironments should be reconstructed through a community-based approach.

Carbon Isotopes and Photosynthetic Pathways

Stable carbon isotopic signatures of both modern and fossil herbivore tooth enamel is directly related to the isotopic composition of vegetation in the food chain (Tiezsen et al. 1983; Ambrose and DeNiro 1986; Cerling and Harris 1999). Terrestrial plants predominantly utilize two different photosynthetic pathways which are identified through the relative abundance of ^{12}C and ^{13}C. Trees, shrubs, and high-altitude grasses typically employ the C_3 photosynthetic pathway. Generally, there is an increase in ^{13}C in C_3 plants from wet to mesic and xeric habitats with $\delta^{13}C$ values being least negative in open, arid environments. Altitude also leads to more positive $\delta^{13}C$ values for C_3 plants (Heaton 1999; Kingston and Harrison 2007). Most grasses employ one of the C_4 subpathways, which are reflected with $\delta^{13}C$ values of between -14‰ to -11‰ (Heaton 1999; Cerling et al. 2003). Arid adapted grasses utilize the NAD-me and PEP-ck subpathways. Grasses in more mesic environments employ the classical-NADP (Hattersley 1992; Chapman 1996). Photosynthetic pathways are ideal for differentiating between browsers, grazers, and intermediate feeders since their carbon signatures reflect gross feeding strategies.

Oxygen Isotopes and Aridity

Stable oxygen isotopic profiles ($\delta^{18}O$) have also been used to reconstruct diets and climatic indicators. $\delta^{18}O$ of enamel apatite is directly related to that of body water, which in turn is a function of the $\delta^{18}O$ of drinking water, the $\delta^{18}O$ of water of ingested foods, the $\delta^{18}O$ of metabolic and atmospheric oxygen, and any behavioral or physiological water conservation mechanisms (Longinelli 1984; Koch et al. 1989; Kohn 1996; Sponheimer and Lee-Thorp 1999b). It is used here as a proxy for aridity, with the hypothesis being that in periods of drought, the lighter isotope, ^{16}O, will be preferentially evaporated compared with the heavier, ^{18}O, isotope. Drought conditions typically appear during periods of extreme heat, but similar signals are possible when ice-sheets expand and ^{16}O becomes trapped in surface ice. The result of this scenario is heavier, or ^{18}O enriched, meteoric and vegetative water sources (Kohn 1996; Levin et al. 2006). These shifts are recorded in faunal tooth enamel. Taxa which rely on leaf water show greater changes and are more evaporation sensitive than those which primarily drink from meteoric sources. Based on these patterns, Levin et al. (2006) developed an equation to calculate aridity based on the oxygen isotope values from evaporation sensitive (ES) and evaporation insensitive (EI) taxa. They determined that the δ^{18}O values of tooth apatite from ES animals increases with aridity, and the δ^{18}O of EI animals tracks values of meteoric water. Therefore, the enrichment of δ^{18}O values between ES and EI animals records the degree of ^{18}O enrichment of evaporated water and source water, which increases with environmental aridity (Levin et al. 2006).

As there is no single known taxon whose diet shifts consistently with environment, and to minimize any error due to seasonality or migration, this project will take a community based approach. To allow comparison of isotopic data across sites the sample strategy calls for as much species overlap from site to site as possible. Furthermore, some samples from Holocene and Iron Age levels at the sites will be analyzed to provide a temporally extended reconstruction. The purpose of early Holocene and Iron Age samples is to appropriately contextualize patterns interpreted from the Middle and Late Stone Ages. For example, does a signal of aridity during the Late Stone Age continue into the Iron Age or is it restricted to the Late Stone Age? Including the full range of fauna at a site will provide a check on paleoenvironmental reconstructions developed from zooarchaeological analysis. If the difference between two sites is that bushpig are absent from one, implications are uncertain. Faunal analysts may suggest that lack of bushpig is related to reduced forest understory; however, this interpretation is potentially biased by human selection choices and taphonomic processes (Caswell et al. 1973; Behrensmeyer and Hook 1992). In this case isotopic analysis can provide a more direct measure of environmental variation.

Hypotheses

The specific purpose of this research is to characterize the degree to which local paleoenvironments can be correlated with global and regional changes. It is recognized here that this study is contingent on the extent that isotopic dietary signature of fossil enamel is utilized as a proxy for environment and climate change. A secondary aspect of this research is to test whether the late Pleistocene fauna analyzed here record the same isotopic ranges as extant counterparts. With these two research goals in mind the following overarching null and alternative hypotheses drive the empirical aspect of this study.

Environmental and Climatic Set:

Null H_o: Regional environmental reconstructions are compatible with site-specific environmental/climatic changes inferred from isotopic analysis

Alternative 1: Site-specific paleoenvironmental reconstructions may reveal temporal asynchrony in the onset of regionally documented climatic shifts

Alternative 2: Regional climate regimes are manifested locally in variable ways

Faunal Set:

Null H_o: Late Pleistocene fauna with extant representatives will show similar ranges of oxygen and carbon isotopic values to those modern populations

Alternative: Sites experiencing different climatic and environmental events will reveal within-taxon differences in oxygen and carbon values between sites

This isotopic study is intended to provide a context for the ways in which late Pleistocene human groups adapted to local climatic and environmental fluctuations. Hill (1981) urged paleoecologists to move beyond data collection and to utilize their data to interpret the tempo and mode of early human biological and behavioral evolution. While each chapter provides a discussion of this study's results for human behavior, the Sibudu Cave study is a direct attempt to correlate environmental change with transitions in stone tool technology.

Sampling and Statistical Methodology

Isotopic characterization was performed on 612 total samples of powdered fossil tooth enamel (Table 1). Sampling focused on herbivores, but broadly followed the community approach advocated above, including carnivores and primates when present in sufficient quantities. Sites were divided into previously defined chronological units (described above) to ensure efficient temporal spread. All samples were taken from *in situ* or isolated molars (preferably third molars) identifiable to species. Sampling of molars limits the potentially confounding effects of weaning or juvenile dietary signals present in teeth forming during development. Special care was also made to ensure that the same taxa or community groupings were sampled in each temporal unit at each site to increase the reliability of identified patterns through time.

Enamel was carefully cleaned of any adhering sediment and weathering rinds with a high speed Brassler-type drill with tungsten-carbide bits. A vertical line of enamel was removed from each tooth, from the cementoenamel junction to the upper crown, resulting in approximately 20 mg of powdered enamel. This process is minimally destructive and ensures homogenization of intra-tooth variability. Powdered enamel was reacted for ~24 hours with ~2% sodium hypochlorite (bleach) solution in 1.5 ml microcentrifuge tubes to digest any organic material and then rinsed and centrifuged to a neutral pH with double distilled water. This was followed by sample treatment with 0.1 M acetic acid for ~4 hour to remove any secondary carbonate, rinsed to neutrality again. Mass spectrometry was performed at the Light Stable Isotope Laboratory, Department of Geosciences, University of Florida, Gainesville using a Finnigan-MAT 252 mass spectrometer interfaced with a Kiel III carbonate extraction device for the 485 samples from Lukenya Hill, Omo-Kibish, Porc Epic, Kalemba Rockshelter, and Makwe Caves. Carbon and oxygen values are reported relative to VPDB (Vienna Pee Dee Belemnite). Values were normalized by repeated analysis of the international standard NBS-19. Of the 485 total samples, 457 were successfully characterized and are confidently identified to taxa *and* temporal unit with analytical precision better than 0.05‰. Samples from Sibudu Cave were run at the Center for Scientific and Industrial Research, Pretoria, South Africa using a Finnigan-MAT 252 mass spectrometer interfaced with a Kiel III carbonate extraction device. Values were normalized by repeated analysis of the internal laboratory standard GS-35.

Site	***Total Samples***
Lukenya Hill	110
Omo-Kibish	71
Porc Epic	70
Kalemba Rockshelter	93
Makwe Caves	113
Sibudu Cave	127

Table 1. Site breakdown of 584 samples included in this study.

All statistical analyses were performed with SPSS ver. 20 software (IBM Corp.). Analysis of variance (ANOVA) tests were utilized to investigate how $\delta^{13}C$ and $\delta^{18}O$ shift over time. A two-way ANOVA design was used, with either $\delta^{13}C$ or $\delta^{18}O$ as the dependent variable and time and feeding category (browser, grazer, mixed feeder) as the independent variables. Time was assessed as two different conditions: 1) pre-Last Glacial versus Last Glacial, and 2) archaeologically-defined cultural units – Middle Stone Age, Middle/Late Stone Age transition, Late Stone Age, late Late Stone Age. In this format the main effects of contributions of each independent variable is determined in addition to the identification of any significant interaction effects between the two independent variables. Statistical analysis alone does not provide an indication of real climatic or vegetative change, but rather an indication of a difference between isotopic values for different time periods which can be further interpreted and modeled. All significant results are reported at the $p<0.05$ level. Statistical analysis of the Sibudu study has not been completed at this time. It appears as if $\delta^{18}O$ are compromised as a result of archaeological burning. A re-investigation of the Sibudu collection is under way to address these issues and to determine whether they have any effect on $\delta^{13}C$.

While care was taken to ensure that all teeth could be identified to species, bovid taxa were grouped into feeding categories as defined by Gagnon and Chew (2000). This classification scheme led to the creation of three groups: grazers, browser-grazer mixed feeders, and browsers (Table 2 offers a breakdown of which taxa fall into which feeding category). For comparison to modern taxa, the $\delta^{13}C$ ranges utilized here: grazer >2‰ to -3‰; browser-grazer intermediate -3 to -9‰; browser < -9‰. All primates were placed into a fourth group.

Table 2. Taxa sampled for this dissertation. Feeding groups as following Gagnon and Chew (2000).

	Grazers	**Mixed Feeders**	**Browsers**	**Primates**
Lukenya Hill	*Redunca fulvorufula* *Connochaetes taurinus* *Equus burchelli** *Alcelaphus buselaphus* *Damaliscus hypsodon** *Oryx gazella* *Phacochoerus africanus** *Phacochoerus aethiopicus**	*Gazella thomsonii* *Ourebia ourebi* *Taurotragus oryx*	*Madoqua kirki* *Raphicerus campestris* *Sylvicapra grimmia*	
Porc Epic	*Damaliscus lunatus* *Equus burchelli** *Kobus ellipsiprymnus* *Oryx gazella* *Phacochoerus africanus* *Pelorovis antiquus** *Redunca redunca* *Syncerus caffer*	*Aepyceros melampus* *Gazella thomsonii* *Tragelaphus strepsiceros*	*Madoqua guentheri* *Neotragus pygmaeus*	*Papio sp.*
Omo-Kibish	*Kobus ellipsiprymnus* *Connochaetes taurinus* *Equus grevyi** *Oryx gazella* *Phacochoerus africanus** *Redunca redunca* *Syncerus caffer*	*Hippopotamus amphibius** *Tragelaphus strepsiceros*	*Cephalophus weynsi* *Giraffa camelopardalis** *Madoqua kirki* *Tragelaphus scriptus*	
Kalemba Rockshelter	*Connochaetes taurinus* *Equus burchelli** *Hippotragus niger* *Kobus ellipsiprymnus* *Phacochoerus africanus**	*Gazella thomsonii* *Ourebia ourebi* *Taurotragus oryx* *Potamochoerus porcus**	*Sylvicapra grimmia* *Tragelaphus scriptus*	*Papio sp.*
Makwe Caves	*Alcelaphus buselaphus* *Connochaetes taurinus*	*Aepyceros melampus* *Taurotragus oryx*	*Oreotragus oreotragus* *Sylvicapra grimmia*	*Chlorocebus pygerythrus*

	*Equus burchelli** *Phacochoerus aethiopicus** *Syncerus caffer* *Redunca arundinum*	*Tragelaphus strepsiceros* *Potamochoerus porcus**		
Sibudu Cave	*Equus quagga** *Redunca arundinum* *Syncerus caffer* *Kobus ellipsiprymnus* *Connohaetes taurinus* *Hippotragus equinus* *Damaliscus pygargus* *Phacochoerus africanus**	*Hippopotamus amphibus** *Tragelaphus strepsiceros* *Potamochoerus larvatus** *Tragelaphus oryx*	*Philantomba monticola* *Raphicerus campesteris* *Cephalophus natalensis* *Tragelaphus scriptus*	*Chlorocebus pygerythrus* *Cercopithecus albogularis*

* = Does not appear in Gagnon and Chew. Feeding group based on other sources, including Kingdon 1997, Cerling et al. 2003, Sponheimer et al. 2003, Faith et al. 2012

Organization of the Volume

This dissertation is written in a hybrid format for reporting the data and results of the isotopic study. The individual chapters are intended as drafts of stand-alone journal articles. These chapters may repeat some of the background and methods offered in this introduction. Additionally, they do not convey the chapter-to-chapter flow of a more traditional dissertation. Despite the goal being drafts of journal articles, interesting isotopic patterns and possible explanations which are not statistically significant and/or may not be fully supported by the data are reported throughout. These chapters are not intended for publication as is. The conclusion and introduction tie together these chapters under the umbrella of contextualizing early human behavior with climatic and environmental conditions at different scales. Suggested areas for future research and further integration of isotopic techniques with other archaeological and climatological datasets is included in a conclusion which attempts to synthesize the full study and provide connections to late Pleistocene behavior. This includes a possible model for further multi-sited studies of human-environment interactions in archaeological contexts.

Chapter 2 discusses one of the main sources of bias and concern with isotopic analysis – the effect of archaeological burning on the oxygen and carbon composition of tooth enamel. Each of the study sites, and, as a result, the enamel samples, experienced some type of burning. The most heavily burned site is Sibudu Cave where there is evidence for regular burning of bedding, possibly for clearing the living surface (Goldberg et al. 2009). Experiments on modern faunal tooth enamel from the Serengeti were conducted to determine if isotopic values are altered by burning, and, if so, at what temperatures and by how much. This experiment is critical to understanding and contextualizing the results of the study, particularly in reference to Sibudu.

Chapter 3 reports individual region and site variation of the effect of the Last Glacial Maximum on aridity and vegetation cover. Each region has a unique environmental history related to the Last Glacial. Omo-Kibish and Porc Epic in Ethiopia report virtually no change in $\delta^{18}O$ throughout their occupations. Instead, they appear to be characterized by comparatively arid environments throughout the late Pleistocene. Both Lukenya Hill in Kenya and Kalemba Rockshelter in Zambia reveal a characteristic shift towards increasing aridity across the glacial maximum. However, only in Zambia is this event accompanied by a clear vegetative transition. The implications these site-specific profiles for the Last Glacial Maximum have for human behavior, particularly migrations and exchange networks is discussed. Isotopic results suggest Ethiopia may have been a stable, but arid, refugium for late Pleistocene populations during migrations within and out of Africa.

Chapter 4 delves deeper into the phytogeographic transition in Zambia. Very little is known about the regional climate and environment in central Africa outside of the Lake Malawi basin. This study provides the first insight to local paleoenvironments in Zambia and captures a particularly interesting phenomenon in the form of a photosynthetic shift from C_4 to C_3 grasslands. Similar shifts have been reported for sites in South Africa during the Last Glacial Maximum when the winter-rainfall zone may have expanded. No previous studies have revealed winter-rainfall zones in other parts of the continent or extensive C_3 grasslands below 2000 meters. This phytogeographic shift may have also had serious consequences for the origins of horticulture and agriculture in sub-Saharan Africa.

Chapter 5 is an extended case study of the Sibudu Cave site, South Africa. Unlike the rest of the sites in this study, Sibudu was carefully excavated in millimeter levels and rigorously dated through multiple trapped charge techniques. Primarily, this chapter addresses the degree to which parts of South Africa are detached, or buffered, from broader regional climatic events. Additionally, it is the only chapter in this dissertation which goes into detail about making explicit ecological-technological relationships. Specifically, it seeks to answer questions about the role of climate and environment in the appearance and subsequent disappearance of the Howieson's Poort microlithic tool technology.

Chapter 6 is the conclusion and synthesis of this dissertation, including thoughts about future research directions and how a study like this can be extended to weigh in on questions about the origins of modern behavior. It offers a discussion of the complete study and develops models of human-environment interactions for studying changes and transitions in late Pleistocene behavior. It attempts to generalize the body data, particularly from Chapters 2 and 3, to a discussion answering d'Errico and Stringer's (2011) questions about the role of environment in behavioral transitions. It builds upon Fitzhugh's (2001) risk assessment model and addresses issues relating to resource availability and foraging patterns. It is intended as a more theoretical discussion about making direct connections between environment and behavior based on the groundwork developed here.

Chapter 2
Burned by the Fire: Compromised Isotopic Results

Stable isotope analysis of fossil teeth for paleoenvironmental and paleoecological purposes has developed over the past twenty years (Lee-Thorp 1989; Sponheimer and Lee-Thorp 2007; Koch et al. 1989; Kohn 1996; Sealy et al. 1987; Sponheimer and Lee-Thorp 1999a; Sponheimer and Lee-Thorp 1999b; Schoeninger et al. 2003; Cerling et al. 2003; Kingston and Harrison 2007; Harris et al. 2008). Unlike bone, enamel bioapatite has been shown to maintain *in vivo* biogenic signals and not fossilize (Ambrose 1990; Wang and Cerling 1994; Lee-Thorp 2002; Lee-Thorp and Sponheimer 2003). For these reasons teeth are a more reliable source for reconstructing ancient environments and diets. However, instead of fossilization, there may be other factors by which enamel bioapatite undergoes diagenesis compromising isotopic values.

Burning of faunal remains, including both teeth and bone, is a common finding at many archaeological sites (White 1992; Shahack-Gross et al. 1997; Schiegl and Conard 2006; Wadley et al. 2011). It is likely that the majority of these burned remains are the result of some form of cooking or food preparation (Brain and Sillen 1988; Taylor et al. 1995), although refuse disposal or regular burning for removal or insects and other pests has also been proposed (Wadley et al. 2011). Regardless of purpose or timing of the burning event, potential exists for it to have an effect on the isotopic composition on the faunal remains. It has been demonstrated that the isotopic composition of bone bioapatite is altered through cremation and/or cooking (Pate and Hutton 1988; Ambrose 1990; Lee-Thorp 2002; Munro et al. 2007; Huls et al. 2010). Structural bone carbonate oxygen ($\delta^{18}O$) is shown to become compromised at ~250°C (Munro et al. 2007) while carbon maintains its original values up to ~675°C (Munro et al. 2007; Huls et al. 2010). Despite these experiments, little attention has been paid to whether burning has any effect on the stable isotopic behavior of enamel bioapatate.

In this study we assess any changes $\delta^{13}C$ or $\delta^{18}O$ undergo during the process of heating or burning. These experiments are intended to mimic the temperature profiles and duration of hunter-gatherer produced and controlled fires. The results are intended to reveal whether enamel is susceptible to diagenesis through burning, and, if so, do these changes occur at the same temperatures at which bone apatite is compromised. If enamel is shown to have altered $\delta^{13}C$ and $\delta^{18}O$ compositions through burning it will be critical to take this into account when interpreting isotopic values for paleoenvironmental or dietary studies.

Enamel Structure and Stable Isotopes

Enamel is a combination of inorganic hydroxyapatite and organic collagen. While bone is ~24 – 26% collagen, enamel is <1% organic. In addition to the amount of organic material, diagenesis is also related to porosity as increased pore space allows more fluids and minerals to interact with the tissue. Bone is substantially more porous than enamel at ~40‰ versus ~1‰ (Trautz 1967; Williams and Elliott 1979; Wang and Cerling 1994; Cerling and Sharp 1996; Lee-Thorp 2002; Lee-Thorp and Sponheimer 2003). Wang and Cerling (1994) discovered that enamel apatite in both open- and closed-systems retain their $\delta^{13}C$ values and can survive most diagenesis due to its characteristic low porosity. There is no indication of $\delta^{13}C$ exchange with adhering dentine. When porosity is increased, such as in bone, $\delta^{13}C$ values shift as a result of temperature, chemical and isotopic composition of solid and fluid substrates, and solid/fluid ratios. With high porosity, bone $\delta^{18}O$ values are compromised at even low temperatures than $\delta^{13}C$ as has been demonstrated by Munro et al. (2007). However, Wang and Cerling's (1994) model suggest that $\delta^{18}O$ values for low porosity material, such as enamel, would survive higher temperatures.

Bone and enamel also differ in degree of remodeling and crystal size. Bone continually undergoes replacement throughout life and also has a reduced crystal size compared to enamel. The combination of higher organic content and reduced crystal size increases the likelihood of exchange with ions in soils leading to contamination of bone (Driessens and Verbeeck 1990; Hillson and Bond 1997; Kohn et al. 1999). Enamel has been shown to resist post-mortem chemical and physical changes, including trace element contamination, in teeth more than 100 million years old (Bocherens et al. 1994). Nevertheless, enamel is not completely immune to diagenesis and alteration. Kohn et al. (1999) suggest that there may be increased secondary minerals in enamel on the order of 0.3‰. As with the Wang and Cerling (1994) study, $\delta^{13}C$ is not affected by increased secondary minerals or diagenesis whereas values of $\delta^{18}O$ may be affected depending on which site the apatite carbonate resides (Kohn et al. 1999).

Study Design

Characteristics of controlled archaeological fires are poorly known. In order to provide a baseline understanding of simple archaeological hearths Sievers and Wadley (2008) built a series of controlled fires laid directly on sand without stone walls. While their purpose was to determine the processes and conditions by which seeds are carbonized, their experiments provide some of the few documented details on the temperature and duration of archaeological simple hearths. A maximum temperature of 670°C was reached, but cooled in approximately 15 minutes to a range of 250° - 350°C which was maintained for up to 6 hours (Sievers and Wadley 2008). These results are in general agreement with Werts and Jahren's (2007) estimation of the temperatures of archaeological campfires based on analysis of soil organic matter. Both studies suggest that placement – buried in anaerobic conditions or placed in or on the fire and oxidized – is the factor determining how organic materials are affected. For comparison, ~900°C is the maximum sustained temperature for wildfires (Ice et al. 2004), although short-term flares are known to achieve much higher temperatures (Dennison et al. 2006).

Since experimental fires are difficult to control and may introduce unexpected and unknown variables, the parameters of an archaeological fire were replicated in a Thermolyne Type 2000 Muffle Furnace interfaced with a K-Type Thermocouple. Five taxa – *Giraffa camelopardalis*, *Connochaetes taurinus*, *Equus burchelli*, *Phacochoerus africanus*, and *Madoqua kirkii* – were included to address variation due to enamel thickness. All samples were modern teeth collected during surface surveys in Tanzania. An individual molar tooth for each taxa was sectioned to produce 18 samples. Samples were created with the use of a Brasseler-type dental drill with a diamond-tipped wheel. Sections, representing slivers of enamel, were cut from the cemento-enamel junction to the crown to homogenize any intra-tooth variability. Care was taken to ensure that slivers were only of enamel and any adhering dentine was removed with the use of carbide-tungsten drill bits.

Three samples of each taxa were heated to five furnace temperature settings – 300°C, 500°C, 700°C, 900°C, and 1100°C. This covers the range of experimentally created simple heaths and empirical data on wildfires (Sievers and Wadley 2008; Ice et al. 2004). The thermocouple was utilized to confirm and record the exact temperature of each trial. For each of the five temperature conditions three slivers of each taxa were burned by placement in five separate crucibles (one for each taxa). No sand or other matrix was placed on top of the samples, ensuring that the experiment mimicked aerobic or ‘in the fire’ conditions. After the furnace reached the desired temperature – determined by a steady thermocouple reading for 15 minutes – it maintained this cooking temperature for an additional 45 minutes for a total of 1 hour. At this point the furnace was shut off and allowed to cool to <100°C before removing the samples. The furnace door remained closed during the cooling process to attempt to mimic the slow cooling and leveling off of an archaeological fire. Three additional samples of each taxa were analyzed without burning as a control.

The design of enamel tooth fragments directly ‘in fire’ up to and exceeding the known sustained temperature of wildfires satisfies the most extreme possible conditions of archaeological burning. In fact, one would expect in both the case of a human-controlled fire or a wildfire that tooth enamel would be buffered slightly from the heat by surrounding cranial bone and animal flesh. Allowing the furnace to maintain maximum temperature for 1 hour is well beyond the ~15 minutes of maximum temperature observed by Sievers and Wadley (2008) in their experiments. If burning is going to have an effect on enamel isotopic composition this study is designed to discover those conditions.

Following the experimental trials all samples were crushed using an agate mortar and pestle set. While samples for isotopic analysis typically undergo pretreatment with bleach and acetic acid, no pretreatment was utilized here to avoid the introduction of any additional variables to the study. Pretreatment was also avoided in the Munro et al.

(2007) experiments. Mass spectrometry was performed on 90 total samples at the Light Stable Isotope Laboratory, Department of Geosciences, University of Florida, Gainesville using a Finnigan-MAT 252 mass spectrometer interfaced with a Kiel III carbonate extraction device. Carbon and oxygen values are reported relative to VPDB (Vienna Pee Dee Belemnite). Values were normalized by repeated analysis of the international standard NBS-19 (Table 1).

Table 1. $\delta^{13}C$ and $\delta^{18}O$ values of experimentally burned teeth.
Temperature given by thermocouple reading. Highlighted entries did not produce enough CO_2.

Species	**Tooth**	**Thermocouple**	**$\delta^{13}C$**	**$\delta^{18}O$**
Giraffa camelopardalis	Lower M2	Control	-10.3	6.1
Giraffa camelopardalis	Lower M2	Control	-10.6	8.0
Giraffa camelopardalis	Lower M2	Control	-10.4	8.1
Giraffa camelopardalis	Lower M2	313°C	-11.1	7.1
Giraffa camelopardalis	Lower M2	313°C	-11.3	7.2
Giraffa camelopardalis	Lower M2	313°C	-11.2	6.2
Giraffa camelopardalis	Lower M2	516°C	-11.4	2.9
Giraffa camelopardalis	Lower M2	516°C	-11.5	0.9
Giraffa camelopardalis	Lower M2	516°C	-10.9	2.0
Giraffa camelopardalis	Lower M2	710°C	-10.8	0.5
Giraffa camelopardalis	Lower M2	710°C	-11.6	-1.5
Giraffa camelopardalis	Lower M2	710°C	-11.3	-2.1
Giraffa camelopardalis	Lower M2	905°C	-11.0	0.1
Giraffa camelopardalis	Lower M2	905°C	-10.0	-4.4
Giraffa camelopardalis	Lower M2	905°C	-10.8	-0.9
Giraffa camelopardalis	Lower M2	1101°C	-10.7	-7.8
Giraffa camelopardalis	Lower M2	1101°C	-10.3	-8.1
Giraffa camelopardalis	Lower M2	1101°C	-10.8	-4.5
Madoqua kirkii	Upper M3	Control	-12.0	3.3
Madoqua kirkii	Upper M3	Control	-12.4	2.4
Madoqua kirkii	Upper M3	Control	-13.0	6.0
Madoqua kirkii	Upper M3	313°C	-13.5	1.5
Madoqua kirkii	Upper M3	313°C	-13.4	3.0
Madoqua kirkii	Upper M3	313°C	-13.6	0.8
Madoqua kirkii	Upper M3	516°C	-13.5	-2.0
Madoqua kirkii	Upper M3	516°C	-13.4	-3.3
Madoqua kirkii	Upper M3	516°C	-13.5	-3.4
Madoqua kirkii	Upper M3	710°C	-14.4	-9.8
Madoqua kirkii	Upper M3	710°C	-13.5	-4.0
Madoqua kirkii	Upper M3	710°C	-13.4	-4.2
Madoqua kirkii	Upper M3	905°C	-9.6	-14.3
Madoqua kirkii	Upper M3	905°C	-3.1	-23.0
Madoqua kirkii	Upper M3	905°C	-3.9	-23.9
Madoqua kirkii	Upper M3	1101°C	-12.2	-10.8
Madoqua kirkii	Upper M3	1101°C	-4.1	-18.4
Madoqua kirkii	Upper M3	1101°C	-6.6	-19.8
Equus burchelli	Upper M3	Control	-0.9	2.3
Equus burchelli	Upper M3	Control	0.1	3.1
Equus burchelli	Upper M3	Control	-0.5	2.8
Equus burchelli	Upper M3	313°C	-1.8	2.2
Equus burchelli	Upper M3	313°C	-2.0	2.1
Equus burchelli	Upper M3	313°C	-2.0	1.1
Equus burchelli	Upper M3	516°C	-1.6	-3.0

Equus burchelli	Upper M3	516°C	-1.5	-2.2
Equus burchelli	Upper M3	516°C	-1.6	-3.7
Equus burchelli	Upper M3	710°C	-1.2	-4.4
Equus burchelli	Upper M3	710°C	-1.5	-5.1
Equus burchelli	Upper M3	710 C	-2.4	-5.9
Equus burchelli	Upper M3	905°C	-1.9	-7.0
Equus burchelli	Upper M3	905°C	-2.0	-7.5
Equus burchelli	Upper M3	905°C	-1.8	-8.5
Equus burchelli	Upper M3	1101°C	-0.3	-7.3
Equus burchelli	Upper M3	1101°C	4.8	-20.4
Equus burchelli	Upper M3	1101°C	0.1	-12.6
Connochaetes taurinus	Upper M3	Control	0.7	3.6
Connochaetes taurinus	Upper M3	Control	0.1	3.1
Connochaetes taurinus	Upper M3	Control	0.5	3.2
Connochaetes taurinus	Upper M3	313°C	-0.3	2.2
Connochaetes taurinus	Upper M3	313°C	-0.2	1.1
Connochaetes taurinus	Upper M3	313°C	-0.2	1.8
Connochaetes taurinus	Upper M3	516°C	-0.7	-1.9
Connochaetes taurinus	Upper M3	516°C	-0.6	-2.0
Connochaetes taurinus	Upper M3	516°C	-0.8	-1.7
Connochaetes taurinus	Upper M3	710°C	0.4	-4.7
Connochaetes taurinus	Upper M3	710°C	1.0	-3.3
Connochaetes taurinus	Upper M3	710°C	-0.1	-4.8
Connochaetes taurinus	Upper M3	905°C	-0.5	-4.9
Connochaetes taurinus	Upper M3	905°C	-0.8	-9.0
Connochaetes taurinus	Upper M3	905°C	-0.8	-7.4
Connochaetes taurinus	Upper M3	1101°C	0.3	-10.3
Connochaetes taurinus	Upper M3	1101°C	0.3	-9.8
Connochaetes taurinus	Upper M3	1101°C	0.5	-11.5
Phacochoerus africanus	Upper M2	Control	-0.8	4.3
Phacochoerus africanus	Upper M2	Control	-0.8	4.0
Phacochoerus africanus	Upper M2	Control	-1.0	3.6
Phacochoerus africanus	Upper M2	313°C	-2.1	2.4
Phacochoerus africanus	Upper M2	313°C	-2.2	3.3
Phacochoerus africanus	Upper M2	313°C	-1.3	3.9
Phacochoerus africanus	Upper M2	516°C	-2.6	-0.5
Phacochoerus africanus	Upper M2	516°C	-1.3	-1.1
Phacochoerus africanus	Upper M2	516°C	-1.8	-1.6
Phacochoerus africanus	Upper M2	710°C	-0.8	-3.6
Phacochoerus africanus	Upper M2	710°C	-1.7	-3.8
Phacochoerus africanus	Upper M2	710°C	-0.8	-3.6
Phacochoerus africanus	Upper M2	905°C	-1.5	-5.0
Phacochoerus africanus	Upper M2	905°C	-2.0	-4.7
Phacochoerus africanus	Upper M2	905°C	-1.7	-5.6
Phacochoerus africanus	Upper M2	1101°C	-0.8	-7.1
Phacochoerus africanus	Upper M2	1101°C	-1.6	-9.0
Phacochoerus africanus	Upper M2	1101°C	-0.8	-12.3

Results

General

Faunal tooth enamel is chemically altered by burning. CO_3 yield, as measured from CO_2 gas evolved by reaction with orthophosphoric acid, is contingent on temperature and thickness of enamel (Table 1). Thin enameled taxa, especially *Madoqua kirkii*, but also *Connochaetes taurinus*, begin to lose CO_3 at 900°C. Thick enameled taxa – *Giraffa camelopardalis* and *Phacochoerus africanus* – lose CO_3 at the top temperature of 1100°C. *Equus burchelli* appears to be intermediary with one of its 900°C samples yielding almost no CO_3. At these temperatures there is so little CO_2 being produced that the results are considered unusable.

Oxygen

Burning has a substantial, but regular, effect on $\delta^{18}O$ values. Even though samples were taken to homogenize intra-tooth variability as best as possible some variation is still to be expected. Allowing for a ~2‰ range for intra-tooth variability (Kingston, unpub. data), all taxa have compromised $\delta^{18}O$ values by 500°C. At this temperature all taxa are depleted in ^{18}O. Thick enameled *Giraffa* and *Phacochoerus* appear to maintain their non-burned control $\delta^{18}O$ values at 300°C. Oxygen profiles may also be maintained at 300°C for *Equus*, *Connochaetes*, and *Madoqua* as well, but the values also may indicate a shift towards ^{18}O depletion.

Considering only those samples for which enough CO_2 was produced for valid results, the $\delta^{18}O$ shift ranges from ~ -7‰ (*Connochaetes*) to ~ -15‰ (*Madoqua*). The relationship between temperature and $\delta^{18}O$ for each taxa falls on unique linear regression lines. R^2 values for these models are generally high – ranging from 0.80 for *Madoqua* to

0.92 for *Connochaetes* and *Phacochoerus* (Figure 1). These results not only suggest that enamel undergoes chemical alteration when exposed to high temperatures, but that there is a regular and predictable process through which isotopic values are shifted.

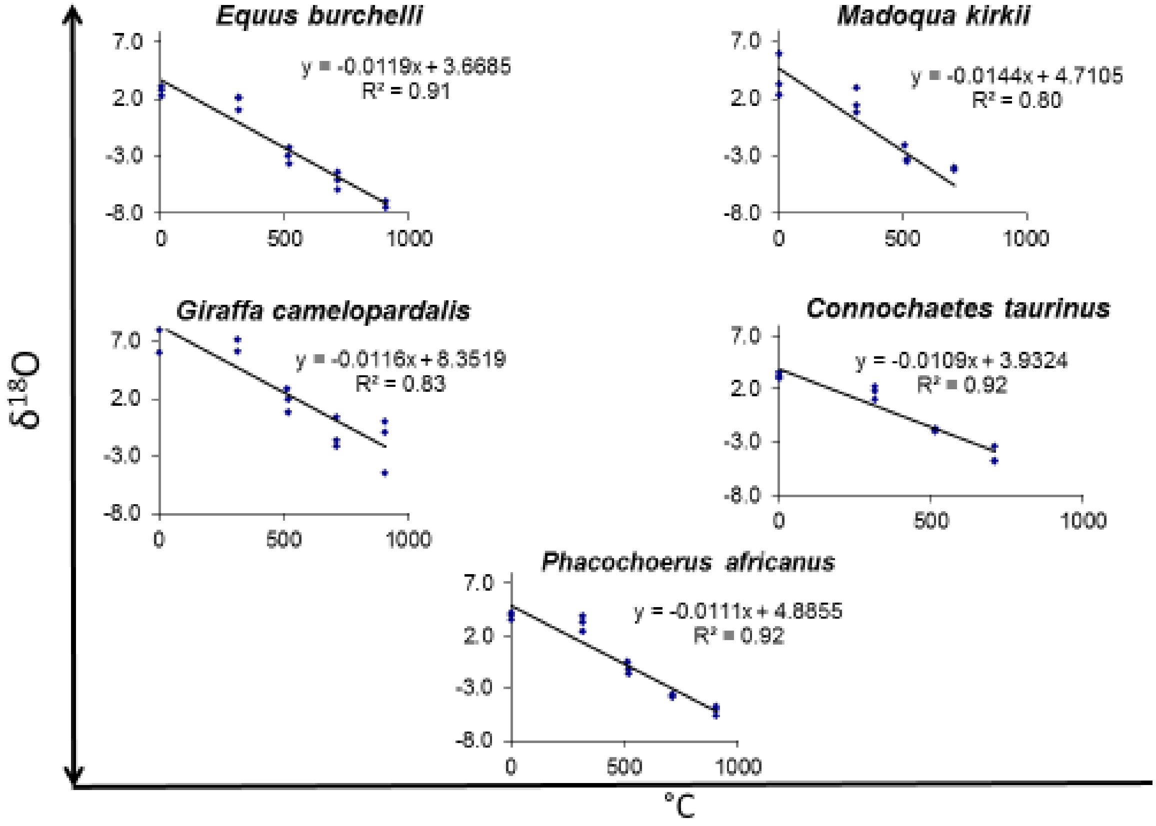

Figure 1. Regression models and R^2 values of bioapatite $\delta^{18}O$ values versus temperature for each of the five taxa. Species-specific factors, such as enamel thickness, result in different equations for each taxa.

Carbon

It does not appear as if burning has a major effect on the carbon composition of tooth enamel. All samples for which there was sufficient CO_2 produced fall within ~1.5‰ of the respective taxa's control values (Figure 2). Variation from the control values is generally in the direction of ^{13}C depletion, the opposite of what Munro et al. (2007) found with bone. Even at temperatures where the amount of structural carbonate is too low to expect reliable values (based on amount of CO_2 evolved), all taxa except

Madoqua maintain δ^{13}C close to their control values. *Madoqua* samples at 900° and 1100°C sharply shift on the order of +4‰ to +10‰.

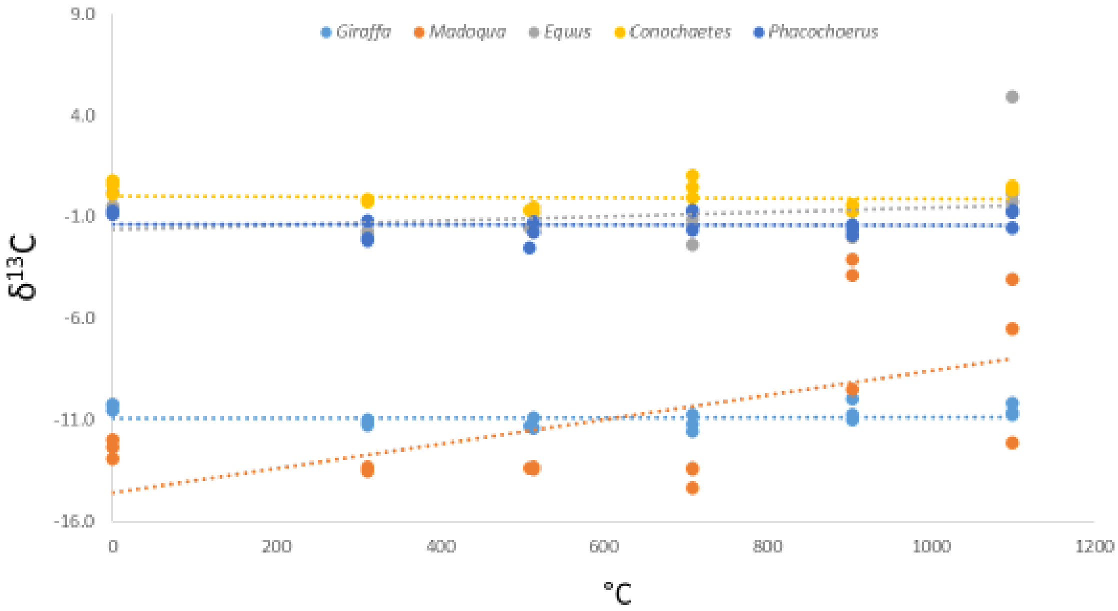

Figure 2. δ^{13}C values versus temperature for each of the five taxa. Only *Madoqua* (orange) indicates any ^{13}C enrichment with increasing temperature, otherwise δ^{13}C composition is maintained through 1100°C.

Discussion

δ^{18}O and δ^{13}C Behavior

The susceptibility of δ^{18}O and δ^{13}C isotopic composition of tooth enamel to alteration through burning are very different from each other. The overall pattern follows that of bone (Munro et al. 2007; Huls et al. 2010), but tooth enamel seems to be slightly more resistant. Larger crystal size and lower porosity creates a stronger physical structure which is able to resist the effects of burning at higher temperatures. CO_3 yields are higher at higher temperatures for enamel compared to bone and the loss of structural carbonate – as determined by the amount of CO_2 evolved – happens between 900° and

1100°C as opposed to ~650°C. Enamel thickness may have some role in resistance as the thick enameled taxa, especially *Giraffa* and *Phacochoerus*, still evolve enough CO_2 for reliable measurements at 900°C.

$\delta^{18}O$ values for all taxa are in the range of normal intra-tooth variation (Kingston unpub. data) in the control and 300°C conditions. By 500°C though all taxa have altered and compromised $\delta^{18}O$ yields. It is unclear at what temperature this alteration initially happens, but these experiments indicate enamel is slightly more resistant to burning than bone when compared to the Munro et al. (2007) study. The non-random nature of this change is most likely the result of enamel oxygen exchange with oxygen in atmospheric water. Some of the ^{18}O depletion may also be explained by fractionation due to the combustion of some of the structural carbonate during burning (Sharma and Clayton 1965; Munro et al. 2007; Huls et al. 2010).

Carbon isotope composition of tooth enamel seems to be largely unchanged by burning. Except for the taxa with the thinnest enamel, $\delta^{13}C$ values are consistent with the control condition through 1100°C. Loss of CO_3 does not lead to significant changes in isotope composition. It is somewhat unclear why or how $\delta^{13}C$ values are maintained when not enough CO_2 is evolved to give accurate readings according to conventional protocol. Munro et al. (2007) explain the ^{13}C enrichment, seen here only in *Madoqua*, as the result of ^{13}C being more tightly bonded to the bioapatite structure than ^{12}C. Changes in the $\delta^{13}C$ composition of *Madoqua* enamel does not occur until the temperature reaches 900°C, much higher than the 675°C mark for bone in the Munro et al. (2007) experiment.

Implications for Paleoenvironmental or Dietary Reconstructions

These experiments were intended to determine whether isotopic values utilized for paleoenvironmental and dietary reconstructions may be compromised due to archaeological or post-depositional burning. Many late Pleistocene archaeological sites experience some form of human-controlled fire use (James et al. 1989; Wadley et al. 2011; Sandgathe et al. 2011), but little attention has been given to whether light stable isotope values recovered from fossil human and faunal tooth enamel are affected by these fires. While $\delta^{13}C$ composition is not affected by burning at temperatures up to and included some of the hottest known wildfires, this study demonstrates that some caution may be warranted when interpreting $\delta^{18}O$ from potentially burned samples. $\delta^{18}O$ values are altered in all taxa tested here by 500°C, a temperature Sievers and Wadley (2008) have shown that simple hearths can readily reach. Their experimental simple hearths maintained temperatures at ~350°C for up to 6 hours. This combination of temperature and time may be sufficient to begin altering the $\delta^{18}O$ composition of enamel. It is likely that higher temperatures may be required to alter $\delta^{18}O$ if enamel was buried or insulated by flesh during cooking or food preparation, but it seems these temperatures were well within the abilities of late Pleistocene populations.

There are no changes in $\delta^{13}C$ composition, even after the loss of structural carbonate, up to at least 1100°C, with the sole exception being the thin-enameled *Madoqua*. *Madoqua* $\delta^{13}C$ composition is altered somewhere between 700° and 900°C. These temperatures are much higher than any of Sievers and Wadley’s (2008) experimental hearths and is near some of the highest temperatures recorded for wildfires (Ice et al. 2004). Therefore, $\delta^{13}C$ composition of fossil faunal tooth enamel from archaeological contexts which may have undergone some form of human-induced burning is resistant to alteration. $\delta^{13}C$ of thick enamel also appears to resist alteration induced by burning in wildfires.

Conclusion

Tooth enamel is more resistant to the chemical and physical alterations of burning than bone. $\delta^{13}C$ composition is immune to the effects of any human-controlled burning, but $\delta^{18}O$ composition is altered between 300° and 500°C. One should be weary of highly ^{18}O depleted values from these contexts. We recommend scoring or taking notes on indicators of burning if there is suspicion that tooth enamel intended for oxygen isotopic analysis may have been burned. Use of a Munsell soil color chart has been shown to accurately reflect different stages of burned bone and teeth (Shipman et al. 1984; Devlin and Hermann 2008; Munro et al. 2007). Crystallinity Index determinations based on FTIR spectroscopy or X-ray diffraction may also provide indication if an enamel sample has been burned (Munro et al. 2007; Thompson et al. 2009, 2011). However, these analytical techniques have not been attempted or validated with tooth enamel at present. Additionally, Munro et al. (2007) report that these techniques only reveal bone alteration at temperatures above ~650°C, higher than required for alteration of $\delta^{18}O$ composition. More resistant tooth enamel may not reveal changes in Crystallinity Index until reaching even higher temperatures. Until these analytical techniques are further refined for identifying isotopic alterations, the results of these experiments demonstrate that paleoenvironmental and dietary reconstructions based on $\delta^{18}O$ composition of tooth enamel should include additional scrutiny if there is evidence of burning.

Chapter 3
Thinking Locally During the Last Glacial Maximum

The Last Glacial Maximum is the last global climatic period of the late Pleistocene, lasting from ~27,000 – 13,000 years B.P. In Africa, this time period is characterized by continental-level aridity accompanied by slight cooling (Stager et al. 2011; Bouimetarhan et al. 2012). Recent modeling suggests that increased Antarctic ice pack during the Last Glacial had a weakening effect on winds and the Indian Ocean monsoon system (Chase and Meadows 2007; Kohfeld et al. 2013), leading to increasing aridity over much of east and central Africa. This climatic event resulted in the spread of grasslands and development of migratory corridors within and out of Africa. At the same time, a new behavioral suite characterized by the development of Late Stone Age tool technology spread throughout the continent (Wurz 2013; Tryon and Faith 2013; Faith et al. 2014). It is not known if or how environment change associated with the Last Glacial Maximum played a role in the transition from the Middle to Late Stone Ages. In part, this uncertainty is a lack of site-specific studies of human-environment interaction during this time period. I argue here that it is imperative to think locally for both the behavioral transitions and the environmental conditions. By employing a multi-site approach, this study demonstrates that not only are there regional differences during the Last Glacial Maximum, but that there are also variable site-specific environments.

Within the broadly-defined Last Glacial there is a series of continental and regional-scale events. The Last Glacial Maximum *sensu lato* lasts only to ~17,000 years B.P. and is followed by the Heinrich 1 Event (~17,000 – 15,000 years B.P.) which is typically characterized by increased cooling and aridity. Heinrich 1 led to extreme drought conditions in the modern Saharo-Arabian belt (Stager et al. 2011; Boimetarhan et al. 2012). A brief worldwide climatic respite exists between the end of Heinrich 1 and the onset of the Younger Dryas cold-snap which lasted from ~13,000 – 11,000 years B.P., with a peak ~11,700 years B.P. The Younger Dryas was the last arid/cold event of the last glacial cycle and it has been identified in records globally (Broecker et al. 2010). The local ecological effects of these events in tropical Africa are currently not well known and it remains difficult to develop causal links with changes in human behavior.

The emergence of modern human behavior during the Middle and Late Stone Ages has been a focus of archaeological research in Africa over the past decade (Barham 2000; Henshilwood et al. 2002; d'Errico et al. 2005). The period from 350,000 – 25,000 years B.P. (Scerri 2013), which predates the evidence for the first anatomically modern *Homo sapiens*, but encompasses some of the earliest evidence for blade technology and ochre use, is a common timeframe for the Middle Stone Age. At most sites a transition period of mixed Middle and Late Stone Age indicators overlaps the Last Glacial (Ambrose 1998; Barham 2000b; Wurz 2013). The beginning of the Late Stone Age appears to be towards the end of the Last Glacial Maximum (~15,000 - 13,000 B.P.).

The time period of the Last Glacial, in its broadest sense, encompasses an interval of significant behavioral transition and turnover and it is not sufficient to simply state that the onset of the maximum signaled the end of the Middle Stone Age and/or the beginning of the Late Stone Age. To provide a more nuanced and specific approach to this problem, this study reconstructs paleoenvironments of five late Pleistocene archaeological sites through isotopic analysis of fossil faunal enamel in order to demonstrate that different ecosystems of East and Central Africa responded differently to the Last Glacial Maximum. In particular, the interpretation of oxygen profiles suggest that sites in Ethiopia were not strongly affected by the increased drying or aridity associated with the Last Glacial which characterizes sites further south in Kenya and Zambia. Such site-specific environmental profiles have implications for characterizing the behavioral transitions which occur at individual sites and have broader application for studying trade and social networks on the landscape.

Study Design

Fossil faunal tooth enamel samples were collected during the summer of 2013 from the archaeological sites of Lukenya Hill, Kenya, Omo-Kibish and Porc Epic, Ethiopia, and Kalemba Rockshelter and Makwe Caves, Zambia (Figure 1). These collections are curated at the National Museums of Kenya, the National Museum of Ethiopia, and the Livingstone Museum, respectively. Each of these sites were systematically excavated, contain diverse faunal assemblages, and span behaviorally relevant transitions during the Middle and Late Stone Ages. Omo-Kibish, Kalemba, and Makwe are well dated, while new and ongoing research into the chronologies of Lukenya Hill (pers. comm. C. Tryon) and Porc Epic (pers. comm. Z. Assefa)

Figure 1. Location of sites included in the study

suggests the sequences of both sites span the Last Glacial Maximum to the limits of the radiocarbon method (~57,000 B.P.). The uncertain dating of Porc Epic and hiatuses in the sequence at Omo-Kibish are real problems and inherent limitations to this study. Detailed descriptions of the excavations and archaeology of these sites can be found in the introduction to this dissertation.

Carbon and oxygen isotopic characterization was performed on 485 total samples of powdered fossil tooth enamel to constrain aspects of diet and by inference habitat and climate. Sampling focused on herbivores, but broadly followed the community approach advocated above, including carnivores and primates when present in sufficient quantities. Statistical analyses were conducted using SPSS ver. 20 (IBM Corp.), with results considered significant at $p < 0.05$. The primary interest was to investigate if $\delta^{13}C$ and $\delta^{18}O$ shift over time. To test for this a two-way ANOVA design was used, with either $\delta^{13}C$ or $\delta^{18}O$ as the dependent variable and time and feeding category (browser, grazer, mixed feeder, primate) as the independent variables. While care was taken to ensure that all teeth could be identified to species, for statistical analyses taxa were separated in four groups: browsers, grazers, mixed feeders, and primates. Time was assessed as two different conditions: 1) pre-Last Glacial versus Last Glacial, and 2) archaeologically-defined cultural units – Middle Stone Age, Middle/Late Stone Age transition, Late Stone Age, late Late Stone Age. A two-way ANOVA was employed because a secondary interest was in whether there was any interaction between time and feeding group, for instance, if browsers and grazers had different types of changes in isotopic profiles across time. Statistical analysis alone does not provide an indication of real climatic or vegetative change, but rather an indication of a difference between isotopic values for different time periods which can be further interpreted and modeled. In the case of significant main effects of time, analysis was followed up with post-hoc Tukey's tests to identify any significant shifts in isotope profiles within a site or feeding category.

Feeding categories were employed in the statistical models instead of individual species for two main reasons. First, sample sizes for individual species were quite small – some as small as three samples per species. Second, the power of the ANOVA models is increased by reducing the number of independent variables from ~30 species to 4 feeding groups. Species were grouped into feeding categories based on their primary source of consumption – grasses and sedges or tree and bush products (e.g leaves and fruit). Those which are known to consume roughly equal components of grass based and tree based projects were placed in a mixed feeding group (Gagnon and Chew 2000; Cerling et al. 2003; Sponheimer et al. 2003). All primates were placed in a separate group due to their omnivorous feeding habits and canopy browsing.

A second set of data analysis involved the calculation of aridity index (Levin et al. 2006) values for the pre-Last Glacial and Last Glacial units at three of the sites: Porc Epic, Omo-Kibish, and Kalemba Rockshelter. The index is based on the premise that some taxa are more sensitive to evaporation due to receiving most of their body water from vegetative matter, while taxa which primary drink from meteoric or surface sources are insensitive to evaporation. As a result, the difference between evaporation insensitive and sensitive taxa increases as aridity does. In theory, this eliminates the need to control for taxon-specific physiological factors affecting water consumption and retention or hydrological patterns affecting overall terrestrial aridity. The index offers a value for water deficit – a proxy for aridity – which increases from closed canopy forest to open grasslands. Levin et al. (2006) developed the aridity index as a way to compare fossil sites to modern ones with the model providing a way to estimate mean annual precipitation (i.e. Thornthwaite 1948).

Results

Oxygen

In order to address the above hypothesis concerning $\delta^{18}O$ we need to know if $\delta^{18}O$ for the pre-Last Glacial and the Last Glacial periods are different. Including all sites and faunal samples, ANOVA analysis of $\delta^{18}O$ reveals a statistically significant main effect of time across the Last Glacial at the $p<0.05$ level (Table 1). The overall shift in $\delta^{18}O$ over time is from lighter to heavier values which is indicative of increasing aridity. There is also a significant interaction of feeding category with time (Figure 2a). Post-hoc tests indicate that the feeding group effect is driven by the $\delta^{18}O$ values of browsers at Omo-Kibish and Porc Epic becoming more negative rather than the expected positive. This interaction does not invalidate the main effect as it was expected that the feeding groups at different sites may have different responses to aridity. A post-hoc explanation is that browsers in Ethiopia are predictably reflecting the fact that the environment appears to become *less* rather than *more* arid over time. Box-and-whisker plots are also provided to demonstrate the variation within the feeding categories as the interaction plots only provide single-point mean values (Figure 3a).

ANOVA analysis of individual sites, again with time and feeding group as the independent, fixed factors, reveals a statistically significant shift in $\delta^{18}O$ across the maximum in the direction of more positive $\delta^{18}O$ values at Kalemba Rockshelter and Lukenya Hill (Figure 2b, 2c). No significant interaction was identified at Kalemba or

Lukenya Hill. Neither of the Ethiopian sites, Omo-Kibish and Porc Epic, reflect this trend towards aridity over time. Post-hoc Tukey's test on the $\delta^{18}O$ values of the individual members at Omo-Kibish reveals a statistically significant difference between Member I (~240,000 – 190,000 years ago) and Member IV (~13,000 years ago) at the $p<0.05$ level implying *decreased* aridity over time (Figure 3b). A two-way ANOVA utilizing the trophic categories developed by Assefa et al. (2008) for Omo-Kibish reveals a statistically significant main effect of time in the direction of more negative $\delta^{18}O$ values (Table 1; Figure 2d). The main effect of time is *not* significant if the ANOVA is run with the feeding categories, but the trend is apparent in the interaction plot (Figure 2e). Assefa et al. (2008) choose to classify species by trophic group in an attempt to more accurately reflect the diversity of habitats that browsers and grazers occupy. For the purposes of this analysis the main division is between fresh grass feeders which exclusively consume grass and grass feeders which maintain a broader dietary range, but are primarily grass feeders (Reed 1997, 1998). Figure 2f is the interaction plot of the ANOVA analysis from Porc Epic. While there is no significant main effect of time the trend towards more negative $\delta^{18}O$ values is revealed here too.

Again, the hiatuses in the sequence of Omo-Kibish and the uncertain dating of Porc Epic may mean that the Last Glacial is not fully represented in this study. However, the broader pattern of decreasing $\delta^{18}O$ values over time is supported by the ANOVA analyses reflecting this over time, particularly in the case of the members of the Kibish Formation. Additionally, the archaeology of Porc Epic suggests that it spans the transition to the Last Glacial (Rosso et al. 2013)

Results of the individual site ANOVAs led to a reconsideration of the aridity trend across the Last Glacial considering only the sites of Lukenya Hill, Kalemba Rockshelter, and Makwe Caves. Makwe Caves was added to this analysis to provide a more complete eastern Zambia chronology. In this ANOVA design all feeding groups reflect the same statistically significant main effect of time suggesting increased aridity. Only the box-and-whisker plot is recreated here to display the full set of data (Figure 3c). No interaction effects were identified in this analysis, supporting the post-hoc explanation that the browsers from the Ethiopian sites are driving the interaction effect seen in the full study analysis.

Table 1. Results of 2-way ANOVA

Site	Effect	F	Sig.	Explanation
All Sites	*Time* *Feeding* *Time*Feeding*	5.186 3.395 3.213	**0.023** **0.018** **0.023**	δ^{18}O values become more positive
Lukenya Hill	*Time* *Feeding* *Time*Feeding*	4.760 1.283 .407	**0.031** 0.282 0.525	δ^{18}O values become more positive
Kalemba Rockshelter	*Time* *Feeding* *Time*Feeding*	12.197 .380 2.080	**0.001** 0.768 0.131	δ^{18}O values become more positive
Porc Epic	*Time* *Feeding* *Time*Feeding*	1.411 5.138 .438	0.239 **0.003** 0.733	No significant change in δ^{18}O
Omo-Kibish*	*Time* *Feeding* *Time*Feeding*	6.464 2.071 .277	**0.014** 0.081 0.759	δ^{18}O values become more negative

Bold indicates significant result ($p > 0.05$)
*Results reported on 2-way ANOVA utilizing the trophic categories developed by Assefa et al. (2008)

It remains unclear why the Ethiopian sites are so different from the rest of east and central Africa. One possible explanation is that both Porc Epic and Omo-Kibish have elevated δ^{18}O values throughout the late Pleistocene (Figure 2d). Even when the environment appears to get wetter during the Member IV period at Omo-Kibish, it is still characterized by heavier δ^{18}O values than any time period at Lukenya Hill, Kalemba, or

Makwe. As a result, the Last Glacial had no perceptible effect on aridity at either of these sites, and may, instead, have led to slightly less arid conditions.

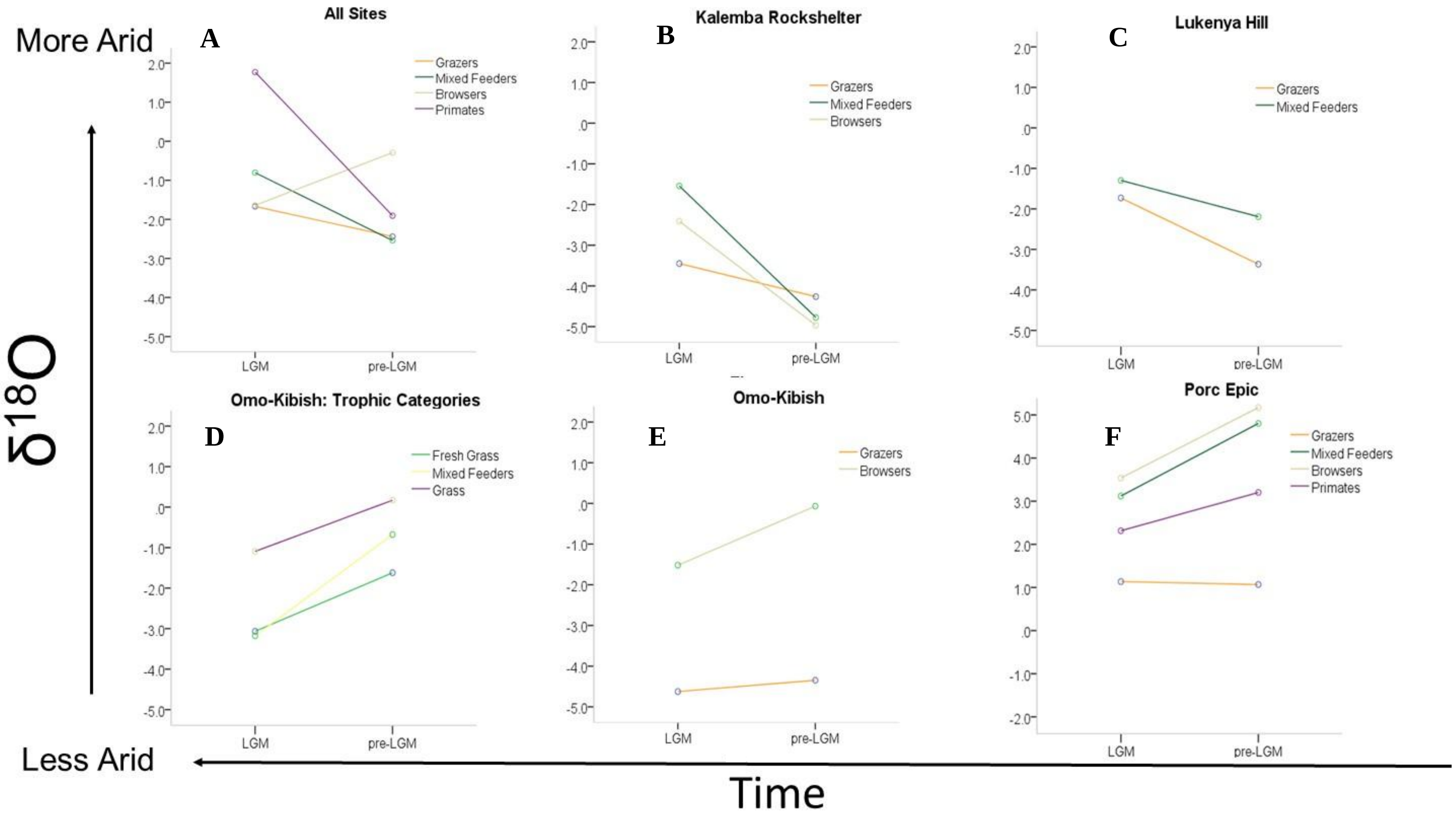

Figure 2. Interaction plots for 2-way ANOVA analyses: A) interaction plot for the fully study ANOVA showing the interaction effect of feeding group driven by the browsers; B) interaction plot for Kalemba Rockshelter showing the main effect of time and the shift towards more positive $\delta^{18}O$; C) interaction plot for Lukenya Hill showing the main effect of time and the shift towards more positive $\delta^{18}O$; D) interaction plot for Omo-Kibish utilizing trophic categories from Assefa et al. (2008); E) interaction plot for Kibish utilizing feeding categories; F) interaction plot for Porc Epic – notice that the scale for the Porc Epic plot is different from the other plots emphasizing the very positive $\delta^{18}O$ values at both time periods

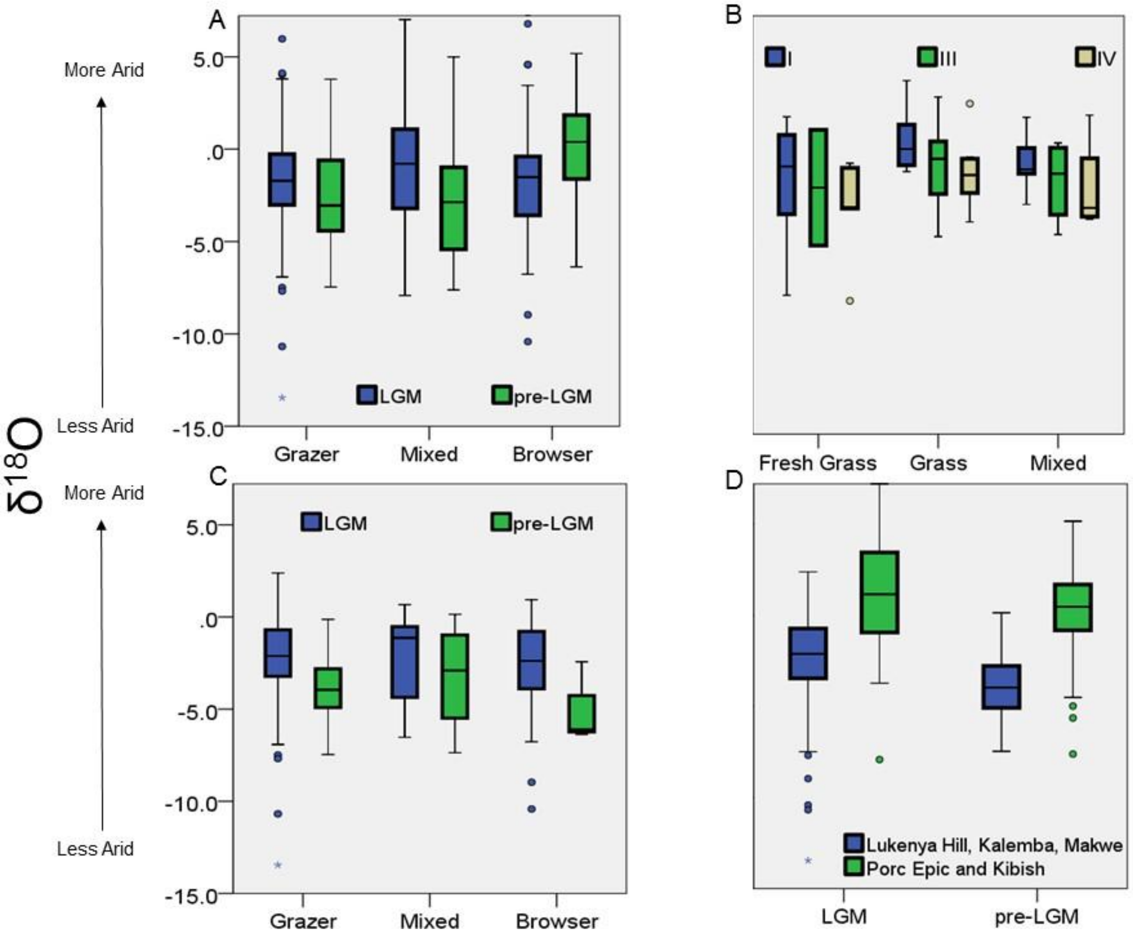

Figure 3. Box-and-whisker plots of δ^{18}O. A) δ^{18}O of all grazers, mixed feeders, and browsers from all five sites divided into LGM and pre-LGM units. B) δ^{18}O values of fresh grass feeders, grass feeders, and mixed feeders (based on Assefa et al. 2008) from Members I, III, and IV at Omo-Kibish. C) δ^{18}O of grazers, mixed feeders, and browsers from just Lukenya Hill, Kalemba Rockshelter, and Makwe Caves divided into LGM and pre-LGM units. D) Graphical representation of the difference in δ^{18}O between the Ethiopian sites and the Kenyan and Zambian sites for both the LGM and pre-LGM

Furthermore, the six most common taxa at Lukenya Hill, Kalemba, and Makwe Caves – *Alcelaphus buselaphus*, *Connochaetes taurinus*, *Equus burchelli*, *Gazella thomsonii*, *Sylvicapra grimmia*, and *Kobus ellipsiprymnus* – each individually reflect the shift in δ^{18}O from lighter values in the pre-Last Glacial period to heavier values in the Last Glacial timeframe, indicating greater evaporative regimes. Tukey's tests reveal that for all taxa except *Kobus ellipsiprymnus* these shifts are statistically significant.

Alcelaphus buselaphus: The common hartebeest is an obligate grazer and receives most of its drinking water from surface water sources. Hartebeest prefer grasslands or scrub areas and their water-retention abilities allow them to exploit some more closed areas further from permanent open water sources (Kingdon 1997). There is a clear shift in $\delta^{18}O$ over time in the combined Kenya and Zambia assemblage with the pre-Last Glacial mean at -4.3‰ and the Last Glacial mean at -2.4‰ indicating the shift towards greater aridity.

Connochaetes taurinus: Similar to the hartebeest, the blue wildebeest is also an obligate grazer which lives primarily in open grasslands. Wildebeest ranges are restricted compared to hartebeest by a dependence on large, open water sources (Kingdon 1997). The pre-Last Glacial and Last Glacial averages for samples from Lukenya Hill and Kalemba Rockshelter indicate a shift in $\delta^{18}O$ from -3.0‰ to -2.3‰. In comparison, wildebeest samples from Ethiopia have an overall average of 1.0‰ with little change across the time period under study here. However, it is important to keep in mind that absolute values are not necessarily comparable across sites – the $\delta^{18}O$ is dependent on altitude, source of precipitation, and sources of drinking water.

Equus burchelli: All species of *Equus* are considered obligate grazers preferring open, well-watered locales. Some varieties are found in shrublands, but even in these cases they feed almost exclusively on grasses (Kingdon 1997). Mean $\delta^{18}O$ for the Ethiopian equids in this study is 2.1‰, which is stable throughout time and comparable to the modern Serengeti (van der Merwe 2013). However, the pre-Last Glacial and Last Glacial means for samples from Kenya and Zambia again show a significant shift towards aridity

(-3.8‰ vs. -2.1‰).

Gazella thomsonii: Thompson’s gazelle has been classified as an intermediate feeder by Gagnon and Chew (2000), and Kingdon (1997) states that they switch from consuming grasses in the wet season to foliage, shrubs, and seeds in the dry season. *G. thomsonii* receives most of its drinking water from surface sites, but may supplement some with leafy browse in the dry season (Kingdon 1997). The means for the pre-Last Glacial, -1.9‰, and the Last Glacial, -1.5‰ reveal a slight, but statistically significant, shift towards increased aridity over time.

Sylvicapra grimmia: There is an overall lack of comparative fossil or modern datasets of $\delta^{18}O$ reported for the common duiker. Duikers live in savannahs and woodlands preferring moderately closed woodlands for shelter and safety. They primarily subsist on leaves and shoots, but include fallen fruits, flowers, and resin seasonally. They receive nearly all of their body water from leaf or fruit sources (Kingdon 1997). The effect of the maximum on the evapotranspiration in leafy and vegetative matter is well demonstrated by the $\delta^{18}O$ values for *S. grimmia.* A clear shift is signaled by the difference between the pre-Last Glacial mean of -5.0‰ and the Last Glacial mean of -2.8‰.

Kobus ellipsiprymnus: Modern waterbucks are variable grazers preferring grasses, but subsisting on browse in times of scarcity. They are typically found on the margins of savannahs and woodlands where they have access to green grass and permanent water sources. Waterbucks require surface water sources for drinking and spend a considerable amount of time in or near such sources (Kingdon 1997). Of the six taxa most common in this study, *K. ellipsiprymnus* has the smallest shift in $\delta^{18}O$ over time. This shift is not statistically significant, but it does follow the pattern of heaver $\delta^{18}O$ during the Last

Glacial (-4.7‰ vs. -4.5‰). It is possible that *K. ellipsiprymnus*' aquatic habitats provided a slight buffer against the climatic conditions of the maximum. Mean $\delta^{18}O$ for waterbuck in Ethiopia throughout the late Pleistocene is recorded as 0.2‰.

Each of the most common taxa represented in this study follows a clear and predictable pattern of increasing $\delta^{18}O$ through the transition into the LGM, regardless of dietary preference and source(s) of water. At Lukenya Hill, Kalemba Rockshelter, and Makwe Caves, all taxa reflect the overall pattern of a shift towards increased aridity from the pre-Last Glacial to the Last Glacial. The pattern is most pronounced with *S. grimmia*, which may reflect the degree of water stress that leafy vegetation faced during the maximum. These individual taxa trends hold and remain statistically significant (except for the waterbuck subset) whether samples from Makwe Caves are included or excluded from the analysis.

Aridity Index

For the purposes of this study the aridity index is used only to calculate water deficit for the pre-Last Glacial and Last Glacial time periods. Water deficit values are calculated for Omo-Kibish, Porc Epic, and Kalemba Rockshelter. Lukenya Hill is excluded from this analysis as only one specimen of an evaporation insensitive taxa (*Phacochoerus africanus*) was sampled for this study at this site. Levin et al. (2006) state that at least five samples of both the evaporation sensitive and the insensitive taxa must be included in the analysis. In order to maximize the comparability between sites, *P. africanus* (warthog) was used as the evaporation insensitive taxa at all three sites (Table 2a). At Omo-Kibish and Porc Epic, *Syncerus caffer* (African buffalo) was the evaporation sensitive taxa while *Taurotragus oryx* (eland) was the sensitive taxa at

Kalemba. As all taxa included in the calculations have modern representatives, and all samples are reasonably stratigraphically constrained, the model fits the requirements for calculating water deficit values for the pre-Last Glacial and Last Glacial time periods. The resulting water deficit calculations revealed that Kalemba Rockshelter had an increased water deficit during the maximum compared with the pre-maximum period. Omo-Kibish and Porc Epic are calculated to have a *decreased* water deficit during the Last Glacial when compared with the pre-Last Glacial at those sites. These results support the ANOVA analyses showing the Ethiopian sites as maintaining their degree of aridity, if not getting wetter, while at Kalemba the onset of the maximum coincided with increased aridity (Table 2a, 2b).

Table 2a. Calculation of Water Deficit for pre-Last Glacial time period at Omo-Kibish, Porc Epic, and Kalemba

Site	**Evaporation Insensitive Taxon**	**Evaporation Sensitive Taxon**	**Enrichment Factor**	**Water Deficit* (mm/year)**	**Modern Comparison (WD and MAP)**
Omo-Kibish	*P. africanus*	*S. caffer*	-0.50	903 mm/year	Samburu (WD = 913 mm/year; MAP = 648 mm)
Porc Epic	*P. africanus*	*S. caffer*	1.01	1142 mm/year	Amboseli (WD = 1200 mm/year; MAP = 400 mm)
Kalemba Rockshelter	*P. africanus*	*T. oryx*	-0.76	862 mm/year	Samburu (WD = 913 mm/year; MAP = 648 mm)

*Water Deficit = (Enrichment + 6.21)/0.00632; *P. africanus* regression formula from Levin et al. (2006).

Table 2b. Calculation of Water Deficit for LGM time period at Omo-Kibish, Porc Epic, and Kalemba

Site	**Evaporation Insensitive Taxon**	**Evaporation Sensitive Taxon**	**Enrichment Factor**	**Water Deficit* (mm/year)**	**Modern Comparison (WD and MAP)**
Omo-Kibish	*P. africanus*	*S. caffer*	-2.26	623 mm/year	Nanyuki (WD = 627 mm/year; MAP 759 mm)
Porc Epic	*P. africanus*	*S. caffer*	-1.15	801 mm/year	Mpala (WD = 751 mm/year; MAP = 703 mm)
Kalemba Rockshelter	*P. africanus*	*T. oryx*	0.36	1038 mm/year	Tsavo (WD = 1,059 mm/year; MAP = 549 mm)

*Water Deficit = (Enrichment + 6.21)/0.00632; *P. africanus* regression formula from Levin et al. (2006).

Carbon

ANOVA analysis of carbon followed the same design as oxygen – with the isotopic values as the dependent variable and time and feeding category as the independent fixed factors. The primary analysis with all sites and faunal samples revealed no statistically significant main effect of time (p = 0.577, F = 0.312) or interactions (Figure 4). Again, a box-and-whisker plot is provided to visually display all of the data (Figure 5a). A statistically significant main effect of feeding group is observed, but this is expected as browsers and grazers attempt to track their preferred feeding sources. As with the oxygen analysis a variety of subsets were

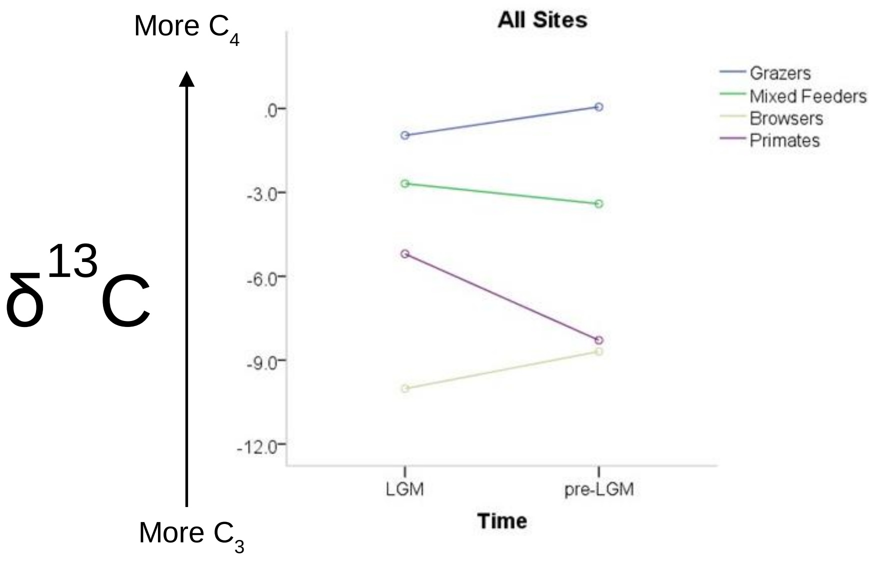

Figure 4. Interaction plot of δ^{13}C for the full study showing no significant main effect of time.

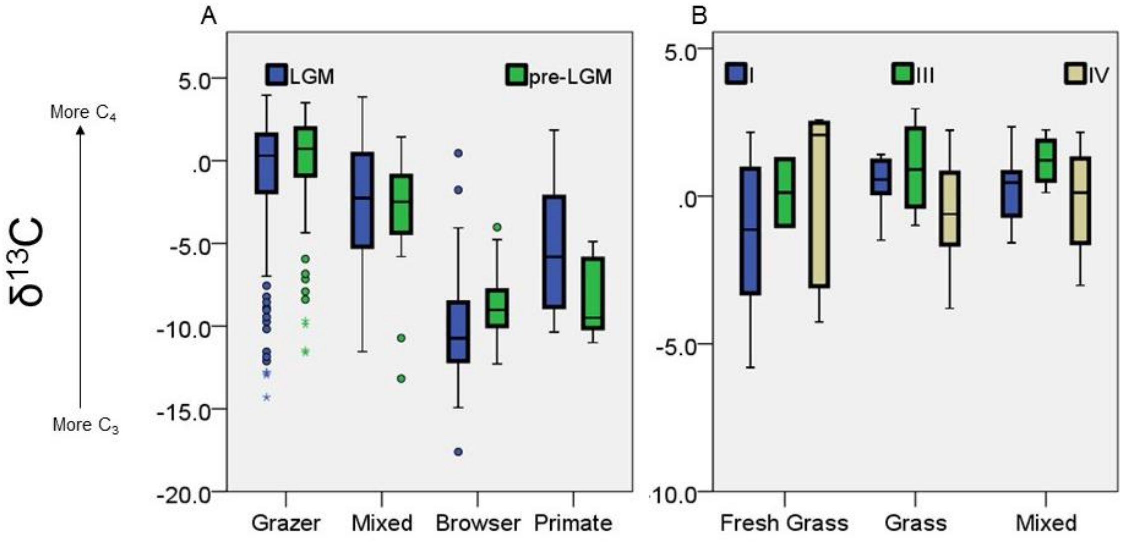

Figure 5. Box-and-whisker plots of δ^{13}C. A) δ^{13}C of all grazers, mixed feeders, browsers, and primates included in this study divided between LGM and pre-LGM units. B) δ^{13}C of fresh grass, grass, and mixed feeders (following Assefa et al. 2008) for Members I, III, and IV at Omo-Kibish.

tested to determine if there were any significant effects of time. First, subsets of fauna were tested, including running a 2-way ANOVA with the feeding categories broken down into individual species. This did not result in any significant main effects or interactions. Second, subsets of study sites were tested: removing the two Ethiopian sites, running an analysis of the two Ethiopian sites together, and running each individual site alone. Again, no significant main effect of time or interactions were discovered. For some of the individual site ANOVAs the feeding group variable was determined to be statistically significant. However, due to the fact that this main effect was expected it does not invalidate the overall result of no significant main effect of time on $\delta^{13}C$ values across the transition to the LGM.

This result is interpreted to suggest that while the Last Glacial had an effect on aridity, this shift in aridity was not large enough to cause complete changes in foraging strategies or carbon isotopic changes in preferred diets in east or central Africa. It is likely that forest and woodland environments in Kenya and Zambia retreated leaving more open habitats (Tryon and Faith 2013; Barham 2000b), but browsers were still capable of feeding on preferred C_3 dietary components.

While there may not be an overall pattern in regards to $\delta^{13}C$, Figure 4a reveals a series of outliers in the grazer feeding group during the Last Glacial. Most of these outliers are specimens of *Equus burchelli* from Kalemba Rockshelter. There are two possible explanations for this result: 1) zebras in Zambia are including significant amounts of browse in their diets; 2) they are consuming C_3 grasses following a transition from dominant C_4 grasslands to C_3 grasslands in the LGM. This phytogeographic transition is the focus of the next chapter and further discussion of it will be taken up there.

Following up on Figure 3b which shows a trend of decreasing aridity across the members of the Omo-Kibish Formation, there is interesting variability in $\delta^{13}C$ as indicated by less water stress in dietary vegetation resulting in lower $\delta^{13}C$ values (Figure 5b). The difference between Member I and IV is the starkest, but is not statistically significant. Again, the ANOVA model was run based on the trophic categories devised by Assefa et al. (2008) in order to ensure comparability to the faunal study. The obligate grazers and the mixed leaf and grass feeders show the greatest shifts from more open environments during Member I to more closed environments during Member IV. Additionally, $\delta^{13}C$ for Member III suggests it was even more open than Member I. The fresh grass group provides a less clear pattern due to the variability in $\delta^{13}C$ during Member IV.

Discussion

The Last Glacial Maximum is commonly recorded in global and continental records of past climate by more positive $\delta^{18}O$ values (Ridge et al. 2012). A similar signal is identified at some, but not all of the sites included in this study. Saltre et al. (2013) and Potts et al. (2013) both agree that any shift in vegetation during the Last Glacial was altitudinal as opposed to latitudinal. The $\delta^{13}C$ results of this study follow these expectations as the ANOVA analyses revealed minimal change in $\delta^{13}C$ values over time.

The results of this isotopic study may suggest that aridity alone is not a signal or measure of environmental suitability for herbivores. Based on the results of 2-way ANOVAs investigating the changes in $\delta^{18}O$ over time, the environment and climate at Omo-Kibish and Porc Epic appear to remain remarkably stable and relatively arid over long expanses of time. It may be time to expand or clarify Soffer's (1987) notion of an environmental refugium for humans. Rather than a lush woodland or forested area with abundant food and water resources (Soffer 1987), a refugium may also refer to an environmentally and climatically stable geographical region. Jochim's (1987) formulation of late Pleistocene and Last Glacial refugia in Europa focused on forested regions in southern Europe where specific mammalian taxa thrived during glaciation. As a result, Stewart and Stringer (2012) define a refugium as an area where a particular species can survive for an entire glacial-interglacial cycle. In fact, Stewart and Stringer (2012) suggest that refugia differed environmentally and ecologically from each other, promoting speciation at times (i.e. Neandertals vs. modern humans) and behavioral variability, which may or may not have been accompanied by genetic variability. At Lukenya Hill and Kalemba Rockshelter isotopic analysis of fossil faunal tooth enamel suggests that the onset of the Last Glacial triggered a shift toward more arid environments. This corroborates the notion that glacial periods are characterized by greater evapotranspiration, preferentially trapping ^{16}O in the atmosphere and ice-sheets (Siddall 2003). Contrary to this expected pattern, there is no perceivable shift in aridity at archaeological sites in Ethiopia. These sites appear to maintain a stable climate, although arid, throughout the late Pleistocene. If we are to discuss Middle and Late Stone Age behavior in reference to the prevailing environmental and climatic contexts, these results demonstrate that it is critical to think locally, at individual sites, even during widespread events such as the Last Glacial.

The increased aridity in Kenya and Zambia and no change, or perhaps slightly decreased aridity, in Ethiopia are in agreement with precipitation and climatic modeling for the late Pleistocene. Ray and Adams' (2001) precipitation modeling suggests that central and east Africa experienced decreased rainfall over time in the late Pleistocene, but that the horn of Africa, including Ethiopia, maintained a stable climate. These precipitation models are relatively simplistic and aggregate data over long time intervals, but they are supported by high-resolution climatic simulations carried out by Kim et al. (2008) who specifically analyzed the difference between the Last Glacial Maximum and today. The climate simulation suggests that surface temperatures over all of Africa decreased by at least 1°C, and more likely in the range of 2 -5°C, during the maximum, but that differences in topography led to specific regional and local changes in precipitation. Central Africa is projected to have had a decrease in mean annual precipitation of nearly 350 mm/year while East Africa's mean annual precipitation was reduced only 150 – 200 mm/year during the maximum. Parts of East Africa, especially the horn of Africa, experienced no change in mean annual precipitation with some areas actually experiencing an increase of 100-150 mm/year (Kim et al. 2008 - Figure 9; Kohlfeld and Harrison 2000). These values are consistent with those calculated using the δ^{18}O aridity index.

Trends in aridity from Lukenya Hill and Kalemba Rockshelter based on modeling and regional proxy data are also consistent with the $\delta^{18}O_{enamel}$ from the sites. The isotopic data map onto continental and regional records (Figure 6) spanning from just before to just after the Last Glacial (~ 40,000 – 5,000 years B.P.). The Greenland core ^{18}O curve (NGRIP) reveals a trend towards greater worldwide aridity starting ~27,000 years B.P. and lasting until ~13,000 years B.P. (NGRIP Group 2004). TEX_{86} surface temperature curves from Lakes Malawi (Woltering et al. 2011) and Tanganyika (Tierney et al. 2008) follow this pattern with temperatures decreasing from ~30,000 years B.P. until ~13,000 years B.P. Tierney et al. (2008) also report a δD C_{28}n-acid record from Lake Tanganyika, which measures the amount of terrestrial particles in a lake core. The greater amount of terrestrial particles the drier the surrounding environment must have been. The δD C_{28}n-acid record shows an increase in C_{28}n-acid in the Tanganyika core after ~25,000 years B.P., and a major spike at ~15,000 years B.P. Another proxy, BIT (branched isoprenoid tetraether) index, is an indicator of the relative contribution of soil organic matter to organic matter in marine sediments (Hopmans et al. 2004). BIT tends to decrease as aridity increases with the implication being that less surface material is eroded into the lake. The BIT curves for both Lakes Malawi (Woltering et al. 2011) and Tanganyika (Tierney et al. 2008) decrease from ~25,000 to ~17,000 years B.P., signaling increased aridity. The Tanganyika BIT record is a bit more detailed than the Malawi one and reveals a period of decreased aridity, and possibly increased precipitation, from ~17,000 to ~15,000 years B.P. This may signal the shift from the Last Glacial Maximum *sensu lato* to events like Heinrich I and alleviated conditions. Konecky et al. (2011) report δD leaf wax for two coring sites in Lake Malawi. The leaf wax curve is another measure of terrestrial material included in lake cores, and the two coring sites provide a very similar record to the BIT curve in Lake Malawi. There appears to be a general pattern towards aridity from ~25,000 to ~15,000 years B.P at which point there is a noticeable spike in the record before returning to a pattern suggesting aridity, again, perhaps separating the Last Glacial Maximum *sensu lato* from the Younger Dryas.

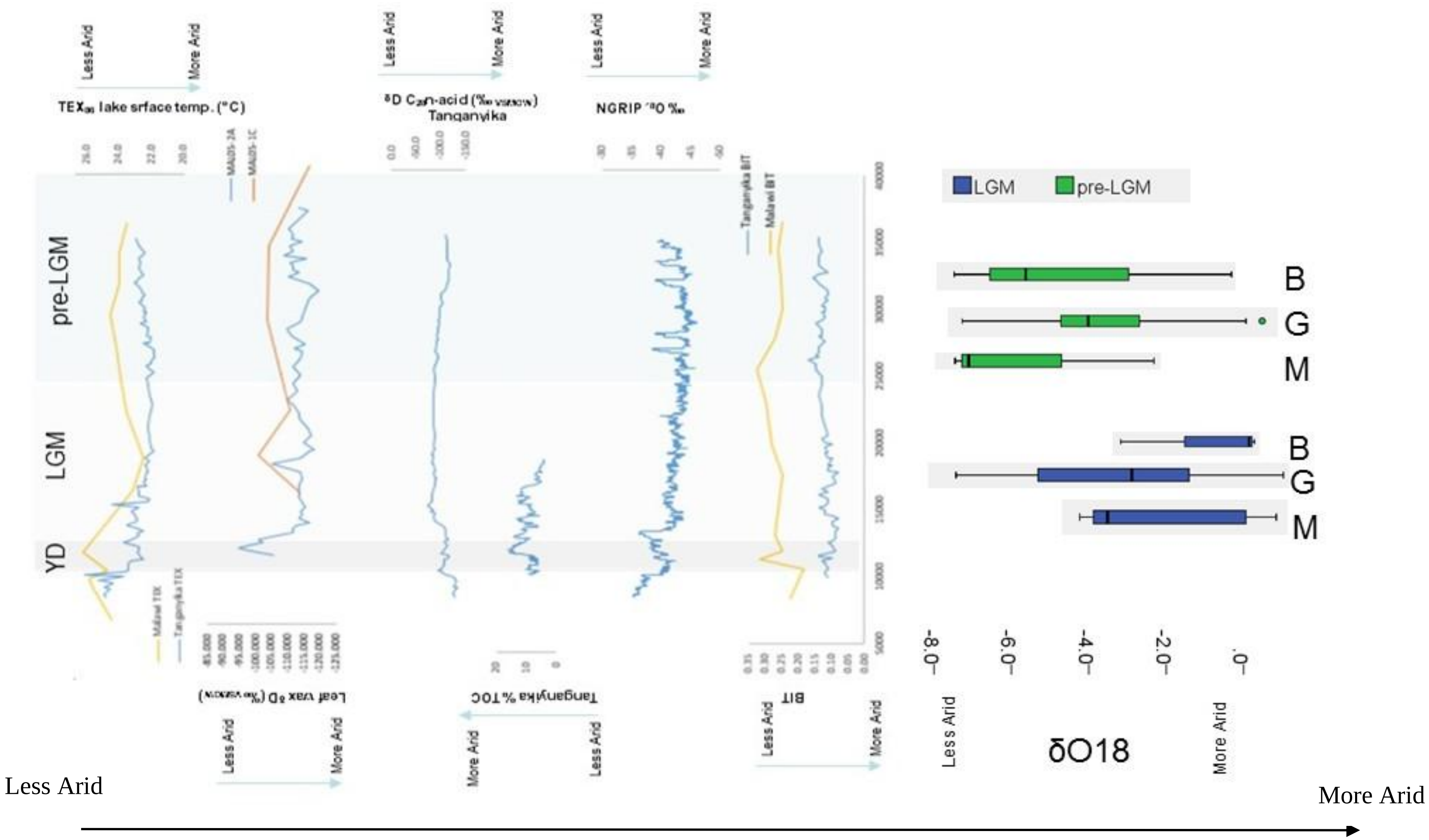

Figure 6. Global and regional curves spanning the period ~40,000 to ~5,000 years ago divided into pre-LGM and LGM periods and compared with the box-and-whisker plots of the $\delta^{18}O$ values of mixed feeders (M), grazers (G), and browsers (B) from Lukenya Hill, Kalemba Rockshelter, and Makwe Caves. Malawi TEX_{86} and BIT data from Woltering et al. 2011; Malawi leaf wax data from Konecky et al. 2011; Tanganyika TEX_{86}, BIT, and n-acid data from Tierney et al. 2008; Tanganyika TOC data from Tierney and Russell 2007; NGRIP curve from NGRIP-Members 2004. Note: except for Tanganyika TOC, all proxies/data are set to be less arid to the left and more arid to the right.

Within the Last Glacial period at Kalemba Rockshelter there appears to be a secondary shift in aridity from Horizon K within the archaeologically defined Middle to Late Stone Age transition level, ~25,000 years B.P, to the true Late Stone Age level at ~15,000 to ~10,000 years B.P. with the true Late Stone Age being more arid than the transition period (Figure 7, Appendix 1). This may be a local manifestation of the spike present in the Lake Malawi leaf wax record, the nearest temporally extensive regional record. This could be the mechanism which facilitates the phytogeographic transition from C_3 to C_4 grasslands in eastern Zambia. No mid-Last Glacial shift in aridity is detected at Lukenya Hill despite a similar spike in the Lake Tanganyika BIT curve. This may suggest that the Last Glacial and Younger Dryas periods had different local climatic profiles in Zambia, but not in Kenya. Regardless of the significance of this mid-Last Glacial shift in $\delta^{18}O$ at Kalemba, it demonstrates that not only is it critical to think locally for globally and regionally recorded events, but also that it is important to investigate the local environment and climate *during* those events.

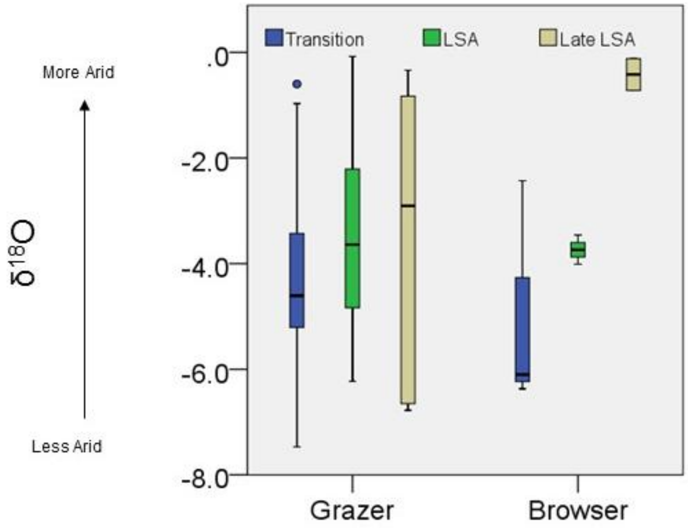

Figure 7. $\delta^{18}O$ grazers and browsers at Kalemba Rockshelter during the MSA/LSA transition period, the LSA, and the late LSA revealing more subtle shifts in $\delta^{18}O$ values than just from the pre-LGM to the LGM.

Omo-Kibish and Porc Epic are two of the most arid sites, as determined by available isotopic data, in the entire late Pleistocene. A site which is reported to have had a comparable level of aridity is Enkapune Ya Muto, Kenya. Based on a combination of carbon and nitrogen isotope analysis of tooth and bone collagen from herbivores at Enkapune Ya Muto, the climate in the late Pleistocene and early Holocene was determined to be as dry, if not drier, than the present (Ambrose and DeNiro 1989). However, unlike Omo-Kibish and Porc Epic which are reconstructed to be open acacia woodlands and grasslands, the environments at Enkapune Ya Muto are mosaics of grasslands and woodlands, perhaps with some nearby gallery forest as well. It is clear that Enkapune Ya Muto experienced more of an oscillating and variable environment through the late Pleistocene (Ambrose and DeNiro 1989). While it must be noted that the nitrogen based notion of aridity is not directly comparable with that of oxygen utilized in the current study, it appears as if Enkapune Ya Muto does not reflect the climatic pattern of decreasing aridity through the transition to the LGM revealed at Omo-Kibish and Porc Epic. The Enkapune Ya Muto reconstruction demonstrates that important climatic differences may have existed between sites in relatively small geographical areas.

The arid areas of Ethiopia may have been a type of Last Glacial refugium for humans, perhaps isolating them from other populations. It may be possible to investigate this through an analysis of the behavioral transitions, or lack thereof, at Omo-Kibish and Porc Epic. Stewart and Stringer (2012) offer the example of the stability of the Gravettian stone tool industry in modern day Belgium ~27,000 – 23,000 years B.P. as a possible isolated human refugium during the beginning of the Last Glacial Maximum. The fact that neither the lithic technology (Pleurdeau 2003, 2005) nor the stratigraphic distribution of gastropod opercula (Rosso et al. 2013) at Porc Epic reveal any major variations throughout the sequence suggest that the behavioral suite remained relatively isolated and stable. The behavioral suite at Porc Epic is not considered solely Middle or Late Stone Age, but rather an extended transition phase (Pleurdeau 2005). Similarly, at Omo-Kibish there appears to be little typo-technological variation between Members III and IV despite the fact that there is a hiatus of nearly 60,000 years (Shea 2008; Sisk and Shea 2008). The lack of behavioral change may also be related to increased residential stability and low levels of in-migration helping maintain social conformity in terms of tool technology. On the other hand, there are clear transitions between and within Middle and Late Stone Age behavioral suites, particularly in regards to lithic technology, during the late Pleistocene at Lukenya Hill (Kusimba 2001) and Kalemba Rockshelter (Phillipson 1976). At these two sites there may have been increased residential turnover and lower levels of cultural selection maintaining the prevailing behavioral suite. This does not mean Ethiopia was definitely a refugium for humans during the maximum, or that sites in Kenya and Zambia were not, but the stability of the environmental, climatic, and behavioral patterns at the Ethiopian sites fits the evolutionary culture models developed by Boyd and Richerson (1990, 2010), and Stewart and Stringer's (2012) re-imagination of refugia. More research must be done at both Porc Epic and Omo-Kibish, particularly in reference to chronology at Porc Epic and a fully study of the Member IV lithics at Omo-Kibish, in order to further develop this model of refugia and move this discussion beyond speculation.

Additionally, the isotope data reported here contradicts the climatic correlation of Omo-Kibish with the Mediterranean sapropel record. McDougall et al. (2008) attempted to constrain the age of the Omo I and II calvariae through a combination of ^{40}Ar/^{39}Ar age measurements and the sapropel record from Ocean Drilling Program Site 967 (Lourens et al. 1998). The correlation is based on the premise that increased intensity of the monsoon system increases seasonality leading to increased precipitation over eastern equatorial Africa. At these same times the discharge of the Nile would be higher allowing for the formation of the organic-rich sapropels in the Mediterranean. What McDougall et al. (2008) correlate are the ages of the members at Kibish, based on the ^{40}Ar/^{39}Ar method, and determination of the ages of the sapropel layers in the drill core from Lourens et al. (1996). The rationale behind the correlation is that if the Nile was experiencing greater flow, so must the Omo River, leading to the deposition of the members during those intervals. As a result, local environments at Omo-Kibish are hypothesized to be more wet and closed during Member I grading towards more open and arid during Member IV.

McDougall et al. (2008) argue that the expansion of Lake Turkana, which is the most likely mechanism for depositing the members, was a result almost exclusively of increased rainfall in the Ethiopian highlands feeding the Omo River. There are no independent records to support this conclusion. As a counterargument, I hypothesize that the sapropel record could be correlated with increased rainfall in the Kenyan highlands feeding Lake Turkana through smaller rivers to the south. It is difficult to determine the source(s) or contributions of different river basins to the sapropel deposits. For instance, Williams et al. (2003) argue that the same sapropels were the result of increased rainfall in the White Nile basin. Even if the hypothesis of McDougall et al. (2008) is correct, or partly correct, it does not necessarily mean that there were increased woodlands or forests at Kibish when Member I was deposited, only that increased rainfall occurred in the highlands. Correlation of the dates from the sapropel record and the members at Omo-Kibish does not necessarily directly determine the local environment at Omo.

Another potential issue with the sapropel correlation is that there are major sapropel layers which are well represented in multiple Mediterranean cores, but not at Omo-Kibish. McDougall et al. (2008) suggest that the deposits which would correlate with these missing sapropels simply aren't exposed in the part of the Omo-Kibish Formation that is part of the study, or they have been eroded away. This is certainly possible, but it may be just as likely that the reason why the formation does not correlate completely with the Mediterranean record is because of specific local environmental and climatic processes.

The existing Omo-Kibish paleoenvironmental reconstruction is also partially based on the faunal analysis by Assefa et al. (2008). Closed environments are suggested by the appearance of giant forest hog (*Hylochoerus meinertzhageni*) and duiker (*Cephalophus* sp.) remains in Member I and early in Member III, but not in the rest of Member III or Member IV. However, both the giant forest hog and the duiker remains are extremely rare, and it must be considered that the faunal collection from Member I is almost four times that from Members III and IV combined. It is possible that with more focus on Members III and IV more taxa suggesting closed environments would be identified.

It is stressed here that isotope analysis of fossil faunal tooth enamel should not be considered as the correct or only record of local climate and environment. It should be seen as only one line of *local* evidence in the discussion. Currently, the isotope data offers an alternate interpretation of paleoenvironmental trends at Omo-Kibish than the existing lines of evidence, but it should be considered alongside other local measures and measures of paleoclimate from the Ethiopian highlands as they become available.

Implications for Behavior

Behavioral transitions, which are most often archaeologically visible in the form of changes in stone tool technology, are complex events. It has been argued that these transitions are a result of a combination of environmental/climatic, demographic, and migratory factors (d'Errico and Stringer 2011; Tryon and Faith 2013). Henrich and Boyd (1998) offer a model which theorizes that cultural evolution is a balance between rates of migration and rates of cultural selection. In this model, cultural selection acts as a version of stabilizing selection maintaining a stable group which perpetuates the prevailing technology or behavior. Migrants from outside the group may bring their own behaviors with them, but unless they arrive in sufficient numbers they will ultimately conform to their new group. During periods of harsh or undesirable environmental conditions groups may become more fluid and cultural selection pressures weaken. Fitzhugh (2001) argues that it is during these periods of high risk that innovative behaviors are selected for.

This isotopic study provides only preliminary data that bears on this issue but no comprehensive answers. However, the paleoenvironmental data reported on here allows us to ask questions such as: Do trade and social networks expand or contract during periods of environmental deterioration? It is possible to see whether behavioral transitions at Omo-Kibish and Porc Epic follow expected patterns for stable environments and if behavioral transitions at Lukenya Hill and Kalemba Rockshelter match expectations for oscillating climatic conditions.

Kardulias and Hall (2008), following world-systems theory, argue that environmental deterioration is an impediment to expanding a system or incorporating new technology. During periods of stable, or productive, environments, social pressures are released and trade networks can expand. On the other hand, Rautman (1993) argues that social interactions within a region may reduce the risk of resource stress by facilitating access to resources in other areas. While Rautman was theorizing about the structure of social networks in horticultural and agricultural populations, Fitzhugh's (2001) risk sensitivity model is built on the same premise for the stone age. The risk sensitivity model predicts that during environmental fluctuations higher variance strategies and inventiveness would be desirable in order to increase productivity. Climatic stability in terms of long-term patterns of aridity and rainfall allows people to spend less time inventing new technologies and expanding social networks. With stable climatic conditions local habitats and ecosystems would be predictable and maintain a regular resource base.

These two models need not be mutually exclusive. Both productive and poor environments could precipitate the development of trade and social networks, but of different scales and types. During environmental or climatic decline populations may intensify networks in the local region for the purpose of sharing food or water resources. There would be less emphasis on maintaining extra-local or long range networks which may be related to the transfer of symbolic or prestige goods. At times of increased environmental productivity local networks may take a back seat to the development of broader trade networks. The combination of increased local, site-level, databases of environmental data provided by this study, with the advances in the technology of sourcing different artifacts, offers the possibility of starting to tease out these hypotheses in relation to the formation of trade and social networks during the late Pleistocene.

Sourcing of obsidian artifacts (Negash and Shackley 2006) and an initial investigation of possible sources for ochre (Rosso et al. 2013) at Porc Epic has already taken place. It appears as if most of the early obsidian artifacts at Porc Epic come from the source at K'one, approximately 250 km to the west, while the primary later source is Ayelu, approximately 150 km to the north-west (Negash and Shackley 2006). The spatial distribution of ochre artifacts at the site reveals a pattern of decreasing ochre use over time (Rosso et al. 2013), possibly suggesting a reduced need for ochre for exchange. If Porc Epic experienced more mild environments during the Last Glacial inhabitants may have been able to more regularly rely on local resources rather than exchange networks. It must be noted though that the hiatuses in the uncertainty in dating at Porc Epic may mean that the Last Glacial is incompletely represented in this study.

Conclusion

Site-level paleoenvironmental reconstructions built on isotopic analysis of fossil faunal tooth enamel provided here demonstrate a critical need to think locally in terms of the role of environment and climate in behavioral transitions during the Middle and Late Stone Ages. Climatic trends, particularly in regards to δ^{18}O, as inferred from the isotopic profiles of faunal communities in Ethiopia, Kenya, and Zambia suggest that the Last Glacial Maximum had variable environmental manifestations in different parts of Africa. In Kenya and Zambia there is a distinct increase in aridity at the onset of the maximum. There may be site-specific climatic trends that occur *during* the Last Glacial, specifically at Kalemba where the transition between the Middle and Late Stone Age transition period to the true Late Stone Age may be characterized by a further shift in aridity. In Ethiopia, where the climate is extremely arid throughout the late Pleistocene, the maximum does not appear to have had a major effect on local environments. Overall, this implies that not only is it important to utilize a multi-site approach to understand how global and regional events are manifested locally, but also how those events play out over time at individual sites.

Site-specific paleoenvironmental and paleoclimatic contexts allow for more direct and nuanced studies of how Middle and Late Stone Age trade and social networks were organized and what role migration may have played in behavioral transitions. For this line of inquiry to move forward we must increase the spatial and temporal spread of site-specific paleoenvironmental reconstructions and begin to consider individual sites as part of integrated social networks as opposed to isolated cases. Thinking locally has the advantage of deciphering such networks from a "ground-up" approach, and allowing perceived extra-local and regional networks to be interpreted from an empirical base. The use of empirical data offers the possibility to directly test models of behavioral and cultural evolution or to apply concepts of refugia through geographic and agent-based modeling. What this study has demonstrated is that it is not sufficient to characterize the environmental and climatic contexts within which late Pleistocene human populations lived as simply extensions of the prevailing global or regional trends. Each site is slightly different from each other, but these differences could have critical implications for social geography and behavior.

Chapter 4

Appearance and Expansion of C_3 Grasslands during the Last Glacial Maximum

Abstract

Nearly 90% of all grasses in Africa today utilize the C_4 photosynthetic pathway and dominate the continent’s tropical and subtropical savanna ecosystems. The development and expansion of grassland ecosystems have been implicated as a prime mover in discussions of human evolution. Prior to the middle to late-Miocene (>9 Ma) grasses composed only a very small percentage of vegetation cover (Strömberg 2011; Dupont et al. 2013). Isotopic analysis has been utilized to document the expansion of C_4 grasslands into C_3 dominated ecosystems during this time period. Appearance and early expansion of C_4 dominated savannas in Africa did not occur until between 9 and 7 million years ago during the late Miocene (Cerling et al. 1997; Bonnefille 2010; although, see Kingston et al. 1994 and Jacobs et al. 1999). This pattern is clearly seen in the Awash Valley of Ethiopia where Cerling et al. (2011) report that C_4 biomass appears in the mid-Miocene but that it doesn’t establish itself as the dominant ecosystem in the area until the Pliocene. The transition is complicated however, and assumes that low-altitude C_3 grasslands were not an integral part of equatorial Africa before the mid-Miocene and even subsequently as C_4 grasslands expanded and contracted.

Currently, grasses in Africa which utilize the C_3 photosynthetic pathway are limited to high-altitudes, usually above 2500 meters, or make up a small component of the biomass in wetlands, bogs, and moist closed canopy forests (Vogel et al. 1978; Tieszen et al. 1979; Kingston 2011). Stable isotopic data of the fossil faunal community from Kalemba Rockshelter, Zambia, however, suggests that extensive C_3 grasslands existed in parts of Africa below 1000 meters in the late Pleistocene and the early

Holocene during a series of events - the Last Glacial Maximum (LGM; ~26,000 – 13,000 years BP), Younger Dryas (YD; ~13,000 – 11,000 years BP), and the 8.2 kiloyear event. The appearance and spread of C_3 grasses at Kalemba is spatially and temporally complex, with replacement of C_4 grasses. Reversals are seen, particularly between the end of the Last Glacial Maximum *sensu lato* (~17,000 years BP) and the onset of the Younger Dryas, when C_4 biomass appear to dominate again. These results have implications for paleoenvironmental reconstructions at other low-latitude Africa sites which date to climatic periods that are *both* cool and arid throughout the Pliocene and Pleistocene.

Introduction

Increasingly open environments – a result of late Pleistocene glacial cycles – have been identified as a selective force in the evolution of modern human behaviors and migrations within and out of Africa associated with the Middle and Late Stone Ages (MSA and LSA, respectively) between 250,000 and 10,000 years ago (Carto et al. 2009; deMenocal 2011; Blome et al. 2012; Tryon and Faith 2013; Tryon et al. 2014). The floral taxa and photosynthetic pathways represented in grasslands have implications for overall carrying capacity (Collatz et al. 1998) and faunal grazing patterns and migration routes (Auerswald et al. 2012). In turn, human subsistence behaviors and technologies associated with hunting, trapping, and foraging would be modified in response to changes in faunal community composition (see Fitzhugh 2001; Wadley 2010). This study offers evidence for a phytogeographic event – the appearance of extensive C_3 grasslands during the late Pleistocene – which may have played a role in the technological and behavioral shifts which characterize the difference between the Middle and Late Stone Ages in central Africa.

The transition from the Middle to the Late Stone Age (~17 – 14 ka) roughly corresponds to the last of the late Pleistocene megafaunal extinctions (Faith 2011, 2014). Tryon and Faith (2013) have suggested that a shift from late Pleistocene dry grasslands to the seasonally moist short grasslands of today resulted initially in faunal range expansion and topographic shifts, and ultimately extinction, also had human consequences. Such a phytogeographic event at the late Pleistocene – early Holocene boundary may support Bettinger, Richerson, and Boyd's (2009) hypothesis that climatic and environmental conditions during the Last Glacial Maximum and Younger Dryas dictated the origins of agriculture.

Site Description

Kalemba, which is the largest known rockshelter in Zambia, was excavated by D.W. Phillipson in the early 1970s and is best known for its extensive Holocene cave paintings and carvings (Clark 1959). Phillipson (1973, 1976) carried out the first extensive mapping and study of the site. Thirteen stratigraphic horizons (a cumulative thickness of 4.3 meters) were identified in the site profile and split into four late Pleistocene/early Holocene cultural levels: MSA (~37,000 years B.P.); MSA/LSA transition (~30,000 – 25,000 years B.P.); LSA (~20,000 – 12,000 years B.P.); and late LSA (~10,000 - 7,000 years B.P.) (Table 1). Phillipson's original dates and the horizons from which dating samples were taken are shown in Table 1.

Kalemba Rockshelter is located in a steep and narrow valley near Chadiza in eastern Zambia on the south-eastern side of the Chipwete valley (Figure 1). Currently this hill country is characterized primarily by variably open woodlands and extensive grasslands with wooded biomes restricted to riverine areas (Phillipson 1973, 1977). The maximum height of the stony hill country in which Kalemba is situated is at 1350 meters above sea level with the surrounding plateau at 1180 meters above sea level.

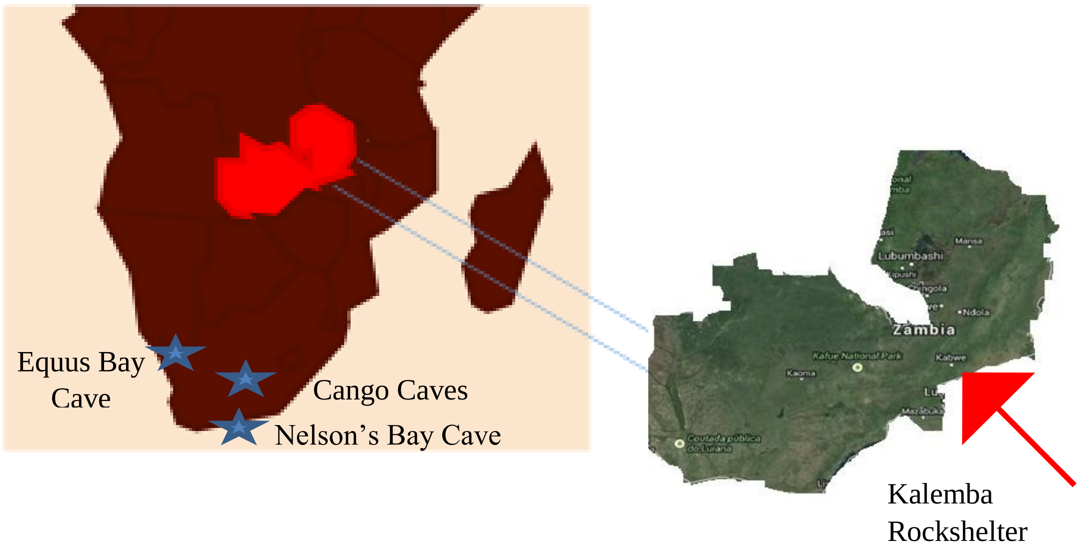

Figure 1. Location of sites mentioned in text. The inset shows Zambia and the location of Kalemba Rockshelter in south-eastern Zambia near the border with Mozambique. Terrain image from Google Maps.

Geochronology and Archaeology at Kalemba Rockshelter

Phillipson excavated a portion of the main rockshelter only, leaving sediments in the adjacent rockshelter or at the outcrops intact. The rockshelter has a maximum height of 4.5 meters and the overhang protects an area of ~100 square meters. A second, smaller, overhang is located adjacent to the main shelter covering an area of 72 square meters. Outcrops to the north- and south-west of the main shelter provide additional living area and excellent vantage points for overlooking the valley (Phillipson 1976). This study reports on the first research and data from Kalemba Rockshelter since the completion of Phillipson's excavations.

All radiocarbon dates for the sequence were obtained from bone collagen samples analyzed at the Geochron Laboratories in Cambridge, Massachusetts (Phillipson 1973, 1976). The reliability of radiocarbon dating of the organic residue of bone, particularly in the 1970s, is complicated by known mineral exchanges and recrystallization (Trueman et al. 2004; Berna et al. 2004; Bronk Ramsey and Lee 2013), especially in cave settings (Stiner et al. 2001). The amount of uncertainty in these dates is difficult to determine and Bronk Ramsey and Lee (2013) concludes that it is not practical to correct the dates based on bone collagen utilizing revised standards and techniques. However, Phillipson's dates are considered to be reasonably accurate based on the faunal composition of the site, the lithic material, and radiocarbon dates from the Holocene levels at Kalemba other eastern Zambia sites which overlap with the chronology at Kalemba (Phillipson 1976; Clark 1988; McBrearty and Brooks 2000).

Lithic material is by far the most common artifact collected from the entire sequence. Kalemba's MSA layer contains mostly retouched implements, particularly scrapers. No microliths or backed implements appear during this period at Kalemba. During the MSA/LSA transition period, backed convex-flakes appear in abundance with rare transverse-backed implements. By the LSA flakes show a marked reduction in size and the first geometrics of the Kalemba sequence appear. A short hiatus exists between the LSA and the late LSA which is characterized by a fully microlithic industry, in the early Holocene. The late LSA period also includes the majority of the non-lithic artifacts, including ochre and shell objects. Finally, two human burials and some additional isolated human skeletal material were recovered from the late LSA portion of the sequence near the surface sediments (Phillipson 1973, 1976, 1977, 2005).

Despite the uncertainty over Phillipson's original radiocarbon dates, the behavioral record supports the premise of a pre-Last Glacial Maximum MSA and transitional occupation followed by a brief hiatus and then the appearance of the LSA during the Last Glacial. The late LSA seems to be a separate occupation occurring at the end of the Pleistocene and/or the early Holocene. The placement and dating of the late LSA is identified based on the appearance of pottery and small iron implements in the immediately following Horizon Q which is dated to ~5,000 years B.P. as determined through charcoal analysis (Phillipson 1976). The patterning and timing of this behavior is comparable to the central African regional timelines developed by Clark (1988) and expanded upon by Barham (2000b).

Table 1. Geochronology of Kalemba Rockshelter and critical late Pleistocene climatic events

Archaeological Time Period or Climatic Event	**Kalemba Context (location of radiocarbon sample)**	**Radiocarbon Date (B.P.)***
Middle Stone Age	Base of sequence (G)	~37000
Last Glacial Maximum *sensu lato*	Top of Horizon H – Top of Horizon N	~26,000 – 17,000
MSA/LSA Transition	H – K (Top of Horizon H)	24650 ± 1000
Heinrich 1 Event	Middle of Horizon N	~17,000 – 15,000
Late Stone Age	K – N (Middle of Horizon N)	15380 ± 1100
Younger Dryas	Middle and Base of Horizon N	~13,000 – 11,000
8.2 kiloyear event	Top of Horizon O	8200
late LSA	O – P (Middle of Horizon O)	7965 ± 300

*Kalemba radiocarbon dates from Phillipson 1976

Late Pleistocene Climatic and Environmental Contexts in Central Africa

The Last Glacial Maximum was the last fully global climatic event of the late Pleistocene, lasting from ~26,000 – 13,000 years B.P. This period has been broken down into a series of sub-glacial events which are characterized by oscillating climatic conditions. The Last Glacial Maximum *sensu lato* lasts only to ~17,000 years B.P. and is followed by the Heinrich 1 Event (~17,000 – 15,000 years B.P.) which is typically characterized by further cooling and aridity in tropical Africa (Stager et al. 2011;

Boimetarhan et al. 2012). A brief worldwide climatic warming has been documented between the end of Heinrich 1 and the onset of the Younger Dryas cold-snap which lasted from ~13,000 – 11,000 years B.P., with a peak ~11,700 years B.P. The Younger Dryas was the last arid/cold event of the last glacial cycle and it has been identified in records for all parts of the planet (Broecker et al. 2010). The Younger Dryas was followed by an early Holocene climatic event, the 8.2 kiloyear event, which may be included in the Kalemba sequence as determined by the bone collagen radiocarbon dates. This event appears to have been a result of the final de-glaciation of the northern hemisphere leading to increased freshwater in the Atlantic Meridional Overturning Circulation (AMOC) and subsequent slowing of the system (Morrill et al. 2013). A result of the weakening of the AMOC was decreased seasonality in the Southern Hemisphere leading to abrupt weakening of the Indian Ocean monsoon system and decreased precipitation over central and southeast Africa. Each of these events have been identified in regional climatic records in low-latitude regions of Africa and have been suggested to be critical for transitions in human behavior – from the MSA to the LSA and from the LSA to the Neolithic (Renssen et al. 2009; Dixit et al. 2014). Environmental complexity in south-central Africa is part of the spatial heterogeneity and may have had complex effects on demographic and behavioral changes.

Local environment, climate, and vegetation in central and southeast Africa is sensitive to the complex interactions between the African and Indian Ocean monsoon systems, the Intertropical Convergence Zone, and the Congo Air Boundary affecting precipitation and annual seasonality (Leroux 2001; Hely et al. 2006; Ivory et al. 2012). High-resolution climatic records for the interior of central Africa during the late

Pleistocene and the Last Glacial Maximum are exceedingly rare. The geographically most relevant long-term record comes from the Lake Malawi Scientific Drilling Project (Scholz et al. 2011; Powers et al. 2011; Stone et al. 2011). While eastern Zambia is quite close to Lake Malawi, the distance between Kalemba and the coring locations in the northern basin of Malawi is over 500 kilometers. The other main source of central Africa paleoclimatic data is from study of Kalahari sand dune migration (Thomas and Goudie 1984; Thomas and Burrough 2013). Based on these records Blome et al. (2012) describe interior central Africa as wet and humid from ~35,000 – 30,000 years ago followed by an extended period of cooling and aridity accompanied by dune migration further into central Africa (see also Thomas and Burrough 2013). This is supported by the TEX_{86} record from Lake Malawi indicating a decrease of at least 3.5°C during the Last Glacial (Woltering et al. 2011) (Figure 3).

However, it is not entirely clear how the environmental and climatic shifts which accompanied the Last Glacial or related events played out locally at specific archaeological sites. Connecting these climatic events directly to human behavior documented by archaeological assemblages is difficult, due to the distance between relevant lake or ocean drilling projects and specific sites. The timing of the termination of the Last Glacial Maximum overlaps the transition from the Middle to Late Stone Ages in central Africa and these changes could have further implications for or be linked to the origins of horticulture and agriculture at the beginning of the Holocene (Phillipson 1977; Bettinger et al. 2009; Tryon and Faith 2013; Dixit et al. 2014).

Isotopic Analysis and Environmental Reconstruction

Carbon and Oxygen Stable Isotopes

Stable isotope characterization of fossil faunal, including hominin, bone and teeth for paleoenvironmental reconstruction has been a well-developed approach for over twenty years (Lee-Thorp 1989; Sponheimer and Lee-Thorp 2007; Koch et al. 1989; Kohn 1996; Sealy et al. 1987; Sponheimer and Lee-Thorp 1999a; Sponheimer and Lee-Thorp 1999b; Schoeninger et al. 2003; Cerling et al. 2003; Kingston and Harrison 2007; Harris et al. 2008). These studies primarily focus on the carbonate fraction of bioapatite in tooth enamel, which appears to be minimally affected by diagenesis and retains *in vivo* biogenic signals (Wang and Cerling 1994; Sponheimer and Lee-Thorp 1999b; Lee-Thorp 2002; Lee-Thorp and Sponheimer 2003). Stable carbon isotopic signatures of both modern and fossil herbivore tooth enamel are related to the isotopic composition of vegetation in the diet (Tiezsen et al. 1983; Ambrose and DeNiro 1986; Cerling and Harris 1999).

Terrestrial plants predominantly utilize two different photosynthetic pathways which can be differentiated based on the relative abundance of ^{12}C and ^{13}C, the two naturally occurring stable isotopes of carbon, in the plant tissues. In tropical Africa, trees, shrubs, and high-altitude grasses typically utilize the C_3 photosynthetic pathway. These plants have $\delta^{13}C$ values that range from about -23‰ to -36‰ (O'Leary 1981; Cerling et al. 2003). Kohn’s (2010) analysis of the carbon isotopic composition of C_3 plants revealed that values lower than -31‰ are due to canopy effects. Considering equatorial and midlatitude northern hemisphere C_3 biomass, Kohn estimates a global $\delta^{13}C$ average of -28.5‰, approximately 2‰ lower than commonly quoted. Generally, there is an increase in ^{13}C in C_3 plants from wet to mesic and xeric habitats, with $\delta^{13}C$ values being most positive in open, arid environments (Heaton 1999; Kingston and Harrison

2007). Most grasses employ one of the C_4 subpathways, which have $\delta^{13}C$ values ranging from -14‰ to -11‰ (Heaton 1999; Cerling et al. 2003). Arid adapted C_4 grasses utilize the NAD-me and PEP-ck subpathways (Hattersley, 1992; Chapman, 1996) with an average $\delta^{13}C$ value of -13.0±0.7‰ (Cerling et al., 2003). Grasses in mesic environments employ the classical-NADP pathway with an average $\delta^{13}C$ of -11.8±0.2‰ (Cerling et al. 2003).

Analysis of $\delta^{18}O$ of the carbonate fraction of bioapatite in fossil faunal tooth enamel provides a proxy of water flux, starting in the atmosphere and making its way through drinking/vegetative water and eventually into animal tissues (Longinelli 1984; Koch et al. 1989; Kohn 1996; Sponheimer and Lee-Thorp 1999a). It is used here as a proxy for aridity, with the general assumption that in periods of drought, the lighter oxygen isotope, ^{16}O, will be preferentially lost in evaporative processes relative to the heavier, ^{18}O, isotope. Aridity is the result of complex climatic and environmental conditions. Aridity can be accompanied by extended periods of heat with little or no rain. However, the expansion of ice-sheets and the subsequent trapping of ^{16}O in surface ice can lead to a similar isotopic result of more positive $\delta^{18}O$ (Shackleton 1987; Dayem et al. 2010). The result of this scenario is heavier, or ^{18}O enriched, meteoric and vegetative water sources (Kohn 1996; Levin et al. 2006). These shifts are recorded in faunal tooth enamel. Taxa which rely on leaf water typically exhibit greater isotopic variability and are more evaporation sensitive than those which primarily drink from meteoric/surface sources.

Photosynthetic Pathways and the C_3/C_4 Distinction

There are systematic differences between the two types of photosynthetic pathways and a suite of atmospheric variables have been proposed as adaptive factors, giving one pathway a competitive advantage over the other. C_4 plants possess a higher temperature optima (30 to 45°C) for net CO_2 exchange than C_3 plants (10 to 25°C) and their maximum rates of CO_2 uptake are substantially greater (Teeri and Stowe 1976; Tieszen et al. 1979; Paruelo and Lauenroth 1996; von Fischer et al. 2008). While moisture and/or precipitation are contributing factors, the combination of higher temperatures and lower precipitation seems to be key for the adaptive advantage of C_4 biomass relative to C_3 plants (von Fischer et al. 2008; Tipple and Pagani 2007). Sage (2004) argue that the reason why temperature is so important to the C_3/C_4 dichotomy is that C_3 vegetation has a lower water-use efficiency leading to greater carbon loss during photorespiration (Beerling and Osborne 2006; Tipple and Pagani 2007).

C_4 photosynthesis has evolved at least 9 and as many as 20 times leading to a variety of subpathways in different lineages (Edwards and Smith 2010; Strömburg 2011). Changes in $\delta^{13}C$ of atmospheric CO_2 must be considered to make quantitative interpretation and comparisons of carbon data to modern ecosystems. Industrialization has led to the addition of isotopically light CO_2 to the atmosphere (Friedli et al. 1986; Leuenberger et al. 1992; Gröcke 2002). Following Tipple et al. (2010), $\delta^{13}C$ and $\delta^{18}O$ values of atmospheric CO_2 are corrected for variation in the past, based on benthic foraminifera of the genus *Cibicidoides* were collected from Deep Sea Drilling Project sites 704 (Hodell et al. 2000) and 607 (Raymo and Ruddiman 1992), and core GeoB3004 from the German research vessel "*Meteor*" (Schmiedl and Mackensen 2006). Water temperature was estimated from the oxygen isotope composition of foraminifera based on Craig's (1965) carbonate-water isotopic temperature scale and the long-term average $\delta^{18}O$ of seawater was assumed to be 1.0‰ to account for global ice volume during the late Pleistocene. Estimates of the $\delta^{13}C$ of atmospheric CO_2 for the late Pleistocene from ~30,000 – 10,000 years ago based on an average of the three cores is -7.1±0.4‰ (Table 2). Based on the premise that modern atmospheric CO_2 has a $\delta^{13}C$ value of -8.0‰ (Keeling and Stephans 2001) a correction factor of -0.9‰ is applied to the measured values reported here to allow for comparison to modern atmosphere.

Enamel development is incremental and results in significant carbon fractionation (Allan 1967; Lee-Thorp and van der Merwe 1987; Lee-Thorp et al. 1989; Cerling and Harris 1999; Passey et al. 2005; Blumenthal et al. 2014). Lee-Thorp and van der Merwe (1991) demonstrate that this shift is on the order of 12-14‰ more positive than the vegetation that is consumed As a result of this known fractionation and the atmospheric CO_2 correction value, ranges of < -9‰ for C_3 dominated diets and > -3‰ for primarily C_4 diets will be utilized here. Photosynthetic pathways are ideal for differentiating gross feeding strategies, primarily that of browsers, grazers, and intermediate feeders.

Table 2. Location and calculated mean $\delta^{13}C$ of atmospheric CO_2 used to determine correction factor for this study.

Core Designation	**Region**	**Geographic Location**	**Mean $\delta^{13}C$ of atmospheric CO_2**
DSDP Site 704	South Atlantic	47.1 S; 8.9 E	-7.5±0.4‰
DSDP Site 607	North Atlantic	41.0 N; 33.0 W	-6.7±0.3‰
GeoB3004 *Meteor*	Gulf of Aden	14.6 N; 52.9 E	-7.1±0.3‰

Sources:
DSDP Site 707 – Hodell et al. 2000
http://hurricane.ncdc.noaa.gov/pls/paleox/f?p=519:1:::::P1_STUDY_ID:2576 (NCDC Database)
DSDP Site 607 – Raymo and Ruddiman 1992
http://hurricane.ncdc.noaa.gov/pls/paleox/f?p=519:1:::::P1_STUDY_ID:5850 (NCDC Database)
GeoB3004 *Meteor* – Schmiedl and Mackensen 2006

History of the C_3 to C_4 Grassland Transition in Africa

Fossil fauna provide a non-direct line of evidence for the existence of C_4 grasses. Morphological and isotopic analysis of members of Equidae and Elephantidae suggest that C_4 dietary grasses were available at ~8 to ~7 million years ago (Cerling et al. 1997; Edwards and Smith 2010). Suids appear to have had a later transition to C_4 diets at ~4 million years ago while other lineages, such as sivatheres, do not appear to include C_4 vegetation into their diets until the late Pliocene or the early Pleistocene (Cerling et al. 2005). Early physical microfloral evidence for C_4 grasses are chloridoid phytoliths recovered from the *Ardipithecus* site in Ethiopia at 4.4 million years ago (WoldeGabriel et al. 2009). Additionally, since differentiating between C_3 grasses and C_3 dicots in the fossil record is limited, it remains unclear whether the grassland transition documented is C_4 grasslands encroaching on C_3 woodlands or replacing C_3 grasslands. The transition was complicated and did not follow the same timing or pattern in all of Africa.

In southern Africa the phytogeographic transition appears to have occurred more recently. It is not until ~3 – 2 million years ago that C_4 biomass is suggested by dietary isotopic data from Makapansgat and Sterkfontein, although these sites are reported to have substantial C_3 grassland components as well at 1.5 million years ago (Franz-Odendaal et al. 2003; Hopley et al. 2006; Hopley et al. 2007; Lee-Thorp et al. 2007). A potentially complicating factor in South Africa relative to equatorial Africa is that the western cape of South Africa is in a winter-rainfall zone. C_3 grasses are able to propagate to a greater extent in western South Africa and outcompete C_4 grasses during variable climatic conditions, due to their unique ability to retain moisture at high rates during periods of cool temperatures (Scott 2002; Cordova and Scott 2010; Cordova 2013).

A number of studies have suggested that the South African winter-rainfall zone expanded during glacial periods, particularly the Last Glacial Maximum (van Zinderen Bakker 1967, 1976; Heine 1982; Cockcroft et al. 1987; Chase and Meadows 2007). In a recent review, Chase and Meadows (2007) conclude that previously developed models of increased Antarctic ice pack disrupting the westerly frontal system (van Zinderen Bakker 1976; Stuut et al. 2004) may have caused the winter-rainfall zone to intensify and expand northeastward. At Nelson's Bay Cave (Sealy 1996) and Equus Bay Cave (Lee-Thorp and Beaumont 1995) isotopic analysis the tooth enamel of bovids and equids have been interpreted to suggest mixed C_3/C_4 grasslands, if not grasslands dominated by C_3 varieties. Both of these sites are located well within the modern year-round, summer dominated, rain zone which has upwards of 80% C_4 grasses. C_3 grasses in this rainfall zone are restricted to higher altitudes, at least above 2000 meters and typically higher (Castaneda et al. 2007). The speleothem from Cango Caves, a site outside of the modern winter-rainfall zone, has a $\delta^{13}C$ profile which suggest the disappearance of nearly all C_4 cover by the height of the Last Glacial, ~17,000 years ago. However, the overall paleoclimatic record from the speleothem is interpreted to suggest expansive grasslands. Paleotemperature reconstruction based on the speleothem reveal a shift of -6 to -7°C during the Last Glacial compared to the present (Talma and Vogel 1992). Both the large mammal (Faith 2013) and micromammal (Avery 1982) zooarchaeological assemblages from the well-studied nearby site of Boomplaas Cave support the findings from the Cango Caves' speleothem of increased grasslands, but primarily of C_3 biomass (Faith 2013).

It appears then, at least in parts of South Africa, the expansion and relative proportions of C_3 and C_4 grasses have a complex history that potentially includes the expansion of C_3 grasslands during the Last Glacial Maximum. It remains unclear if the South African winter-rainfall zone expanded further inland into south-central Africa, including Zambia, during this time and/or subsequent cooling events, or if a South African-type winter-rainfall zone could have independently formed in south-central Africa. Such an expansion of the primary South Africa winter-rainfall zone has not been suggested or supported by present data, and the distance between the Western Cape and Kalemba, Zambia (~1500 miles or ~2500 km) makes this unlikely. However, recent vegetation and climatic modeling based on CO_2 concentration during the Last Glacial suggests the potential expansion of C_3 grasslands at the expense of established C_4 ecosystems in most tropical and subtropical parts of the planet, including Africa (Crucifix et al. 2005; Woillez et al. 2011; Claussen et al. 2013).

Materials and Methods

Carbon and oxygen isotopic characterization was performed on 93 total samples of fossil herbivore tooth enamel collected from archaeological collections at the Livingstone Museum, Zambia during the summer of 2013 (Table 3). Sampling focused on multiple herbivore guilds, but broadly followed a community approach including small mammals and primates when present in sufficient quantities. Each horizon, from G at the bottom (MSA horizon) through P at the top (late LSA horizon) of the sequence, was sampled to ensure sufficient temporal spread. All enamel samples were taken from molars (preferably third molars) identifiable to specific species. Sampling of later-forming molars limits the potentially confounding effects of weaning or juvenile dietary signals present in teeth forming during development. Special care was also made to ensure that the same taxa or community groupings were sampled in each horizon to increase the reliability of identified patterns through time.

Enamel was carefully cleaned of any adhering sediment and weathering rinds with a high speed Brassler dental drill (Forza L50k) with tungsten-carbide bits. A vertical line from the cement-enamel junction to the occlusal surface was removed from each tooth, resulting in approximately 2 mg of powdered enamel. This process is minimally destructive and ensures homogenization of intra-tooth variability. Powdered enamel was reacted for ~24 hours with ~2% bleach solution in 1.5 ml microcentrifuge tubes to digest any organic material and then rinsed and centrifuged to a neutral pH with double distilled water. This was followed by sample treatment with 0.1 M acetic acid for ~4 hour to remove any secondary carbonate, rinsed to neutrality again. Mass spectrometry was performed at the Light Stable Isotope Laboratory, Department of Geosciences, University of Florida, Gainesville using a Finnigan-MAT 252 mass spectrometer interfaced with a Kiel III carbonate extraction device. Carbon and oxygen values are reported relative to VPDB (Vienna Pee Dee Belemnite). Values were normalized by repeated analysis of the international standard NBS-19. All 93 samples were successfully characterized with analytical precision better than 0.1‰ for oxygen and 0.05‰ for carbon.

Statistical Analysis

All statistical analyses were performed with SPSS ver. 20 software (IBM Corp.). Analysis of variance (ANOVA) tests were utilized to investigate how $\delta^{13}C$ and $\delta^{18}O$ shift over time. A two-way ANOVA design was used, with either $\delta^{13}C$ or $\delta^{18}O$ as the dependent variable and time and feeding category (browser, grazer, mixed feeder) as the independent variables. Time was assessed utilizing two different temporal frameworks: 1) pre-Last Glacial versus Last Glacial, and 2) Phillipson's four defined cultural units – MSA, MSA/LSA transition, LSA, late LSA. A two-way ANOVA was employed because a secondary interest was in whether there was any interaction between time and feeding group. Statistical analysis alone does not provide an indication of real climatic or vegetative change, but rather an indication of a difference between isotopic values for different time periods which can be further interpreted and modeled. All significant results are reported at the $p<0.05$ level.

Bovid taxa were grouped into three feeding categories: grazers, browser-grazer mixed feeders, and browsers. At Kalemba most taxa fall into the grazer category, but oribi and kudu are considered mixed feeders, and bush duiker and bushbuck are browsers. Feeding categories were employed in the statistical models instead of individual species for two main reasons. First, sample sizes for individual species were quite small – some as small as three samples per species. Second, the power of the ANOVA models is increased by reducing the number of independent variables from ~15 species to 4 feeding groups. All primates were placed in a separate group due to their omnivorous dietary practices and canopy browsing. Small mammals are not included in the statistical analyses. For comparison to modern taxa, the $\delta^{13}C$ ranges utilized here: grazer >2‰ to -3‰; browser-grazer intermediate -3 to -9‰; browser < -9‰.

Table 3. Mammalian tooth enamel $\delta^{13}C$ and $\delta^{18}O$ of fossil samples from Kalemba Rockshelter. $\delta^{13}C$ values are corrected by -0.9‰* to allow comparison to modern faunal isotopic datasets.

Taxon	Horizon	$\delta^{13}C$	$\delta^{18}O$	Cultural Period	Tooth	Stratigraphic Designation
Bovidae (41)						
Antilopini (1)						
Gazella thomsonii	Horizon O	-10.4	-0.8	Late LSA (~10 - 7 kya)	Upper M1/2	KLB H 14 - 11
Alcelaphini (9)						
Connochaetes taurinus	Horizon H	-4.2	-2.2	Transition (~ 30 - 25 kya)	Upper M3	KLB I 17 - 40
Connochaetes taurinus	Horizon H	1.6	-0.6	Transition (~ 30 - 25 kya)	Molar	KLB I 17 - 40
Connochaetes taurinus	Horizon I	-0.2	-3.5	Transition (~ 30 - 25 kya)	Upper M1	KLB H 17 - 37
Connochaetes taurinus	Horizon I	0.4	-4.4	Transition (~ 30 - 25 kya)	Upper M3	KLB H 16 - 36
Connochaetes taurinus	Horizon J	2.3	-4.3	Transition (~ 30 - 25 kya)	M3	KLB I 16 - 34
Connochaetes taurinus	Horizon K	-0.9	-3.4	Transition (~ 30 - 25 kya)	Lower M3	KLB H 16 - 31
Connochaetes taurinus	Horizon I	-0.2	-3.6	Transition (~ 30 - 25 kya)	Lower M3	KLB H 17 - 38
Connochaetes taurinus	Horizon I	1.1	-6.5	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 16 - 36
Connochaetes taurinus	Horizon K	-0.1	-4.6	Transition (~ 20 - 12 kya)	M1/2	KLB I 16 - 27
Cephalophini (7)						
Sylvicapra grimmia	Horizon I	-13.2	-6.1	Transition (~ 30 - 25 kya)	Lower M2	KLB I 17 - 36
Sylvicapra grimmia	Horizon J	-10.5	-6.4	Transition (~ 30 - 25 kya)	Lower M2	KLB I 16 - 35
Sylvicapra grimmia	Horizon K	-10.9	-2.4	Transition (~ 30 - 25 kya)	Upper M1	KLB H 17 - 28
Sylvicapra grimmia	Horizon L	-14.3	-3.7	Transition (~ 20 - 12 kya)	Upper M3	KLB I 16 - 23
Sylvicapra grimmia	Horizon L	-9.9	-3.5	Transition (~ 20 - 12 kya)	Lower M3	KLB H 17 - 25
Sylvicapra grimmia	Horizon M	-5.0	-4.0	Transition (~ 20 - 12 kya)	M1/2	KLB I 17 - 21
Sylvicapra grimmia	Horizon Q	-13.0	-0.1	Late LSA (~10 - 7 kya)	M1/2	KLB I 14 – 6
Hippotragini (1)						

Hippotragus niger	Horizon J	0.0	-5.2	Transition (~ 30 - 25 kya)	Upper M3	KLB H 17 - 34
Neotragini (1)						
Ourebia ourebi	Horizon O	-9.7	-0.6	Late LSA (~10 - 7 kya)	Upper M2/3	KLB H 14 - 13
Reduncini (17)						
Kobus ellipsiprymnus	Horizon I	-7.7	-5.1	Transition (~ 30 - 25 kya)	Lower Molar	KLB I 16 - 36
Kobus ellipsiprymnus	Horizon I	1.1	-2.3	Transition (~ 30 - 25 kya)	Upper M3	KLB I 16 - 38
Kobus ellipsiprymnus	Horizon I	0.7	-3.4	Transition (~ 30 - 25 kya)	Lower Molar	KLB H 17 - 39
Kobus ellipsiprymnus	Horizon J	1.7	-3.9	Transition (~ 30 - 25 kya)	Lower M3	KLB H 17 - 34
Kobus ellipsiprymnus	Horizon J	0.6	-5.8	Transition (~ 30 - 25 kya)	Lower Molar	KLB H 17 - 34
Kobus ellipsiprymnus	Horizon J	0.8	-5.7	Transition (~ 30 - 25 kya)	Lower M3	KLB H 16 - 35
Kobus ellipsiprymnus	Horizon J	1.0	-5.7	Transition (~ 30 - 25 kya)	M1/2	KLB H 16 - 34
Kobus ellipsiprymnus	Horizon J	-2.4	-5.1	Transition (~ 30 - 25 kya)	Lower M3	KLB H 17 - 32
Kobus ellipsiprymnus	Horizon K	-0.2	-5.4	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 16 - 28
Kobus ellipsiprymnus	Horizon K	0.9	-3.6	Transition (~ 20 - 12 kya)	Lower M2/3	KLB I 17 - 26
Kobus ellipsiprymnus	Horizon K	0.0	-5.1	Transition (~ 20 - 12 kya)	Lower M1	KLB I 17 - 26
Kobus ellipsiprymnus	Horizon L	0.2	-6.2	Transition (~ 20 - 12 kya)	Upper M3	KLB H 16 - 24
Kobus ellipsiprymnus	Horizon N	0.1	-3.2	Transition (~ 20 - 12 kya)	M1/2	KLB I 15 - 15
Redunca arundinum	Horizon K	2.4	-1.3	Transition (~ 30 - 25 kya)	M1/2	KLB I 17 - 39? (31/32)
Redunca arundinum	Horizon K	1.0	-4.4	Transition (~ 30 - 25 kya)	Upper M3	KLB I 17 - 30
Redunca arundinum	Horizon L	-0.3	-1.2	Transition (~ 20 - 12 kya)	M1/2	KLB H 16 - 26
Redunca arundinum	Horizon N	-9.5	-0.1	Transition (~ 20 - 12 kya)	M2	KLB I 15 - 14
Tragelaphini (5)						
Taurotragus oryx	Horizon G	-11.6	-5.8	MSA (~37000 B.P.)	Molar	KLB H 16 - 46
Taurotragus oryx	Horizon I	-1.7	-1.2	Transition (~ 30 - 25 kya)	Upper M2/3	KLB I 17 - 38

Taurotragus oryx	Horizon K	-14.1	-7.4	Transition (~ 30 - 25 kya)	Molar	KLB H 16 - 29
Taurotragus oryx	Horizon M	-12.4	-4.0	Transition (~ 20 - 12 kya)	Lower M3	KLB I 16 - 22
Tragelaphus scriptus	Horizon O	-10.3	-0.7	Late LSA (~10 - 7 kya)	Lower M1	KLB H 14 - 12
Cercopithecidae (3)						
Papio sp.	Horizon I	-10.4	-5.6	Transition (~29 – 22 kya)	Upper M3	KLB I 16 - 37
Papio sp.	Horizon J	-11.9	-5.1	Transition (~29 – 22 kya)	Lower M1	KLB H 17 - 35
Papio sp.	Horizon K	-11.0	-5.1	Transition (~29 – 22 kya)	Lower M3	KLB H 17 – 30
Suidae (14)						
Phacochoerus africanus	Horizon I	-5.0	-2.7	Transition (~ 30 - 25 kya)	Molar	KLB I 17 - 36
Phacochoerus africanus	Horizon I	-8.8	-5.1	Transition (~ 30 - 25 kya)	Molar	KLB I 17 - 36
Phacochoerus africanus	Horizon K	-1.3	-4.2	Transition (~ 30 - 25 kya)	Molar	KLB H 16 - 29
Phacochoerus africanus	Horizon L	-4.0	-5.9	Transition (~ 20 - 12 kya)	M2/3	KLB H 17 - 26
Phacochoerus africanus	Horizon O	-1.9	-2.9	Late LSA (~10 - 7 kya)	M2/3	KLB I 14 - 13
Potamochoerus porcus	Horizon I	-0.7	-1.0	Transition (~ 30 - 25 kya)	Lower P4	KLB I 16 - 37
Potamochoerus porcus	Horizon I	-10.8	-2.8	Transition (~ 30 - 25 kya)	Molar	KLB I 16 - 37
Potamochoerus porcus	Horizon I	-9.3	-2.3	Transition (~ 30 - 25 kya)	Lower M3	KLB I 17 - 37
Potamochoerus porcus	Horizon J	-1.9	-5.9	Transition (~ 30 - 25 kya)	Molar	KLB H 17 - 34
Potamochoerus porcus	Horizon J	-12.4	-7.3	Transition (~ 30 - 25 kya)	Lower M2	KLB H 16 - 32
Potamochoerus porcus	Horizon J	0.5	-4.8	Transition (~ 30 - 25 kya)	M1	KLB I 17 - 33
Potamochoerus porcus	Horizon K	-12.5	-7.5	Transition (~ 30 - 25 kya)	Lower M3	KLB H 17 - 31
Potamochoerus porcus	Horizon O	-7.1	-6.8	Late LSA (~10 - 7 kya)	M2/3	KLB I 14 - 12
Potamochoerus porcus	Horizon P	-10.3	-6.6	Late LSA (~10 - 7 kya)	Lower M1/2	KLB H 14 - 10
Equidae (34)						

Equus burchelli	Horizon G	-1.2	-2.3	MSA (~37000 B.P.)	Molar	KLB H 16 - 45
Equus burchelli	Horizon I	-0.1	-2.1	Transition (~ 30 - 25 kya)	Upper M1/2	KLB I 17 - 39
Equus burchelli	Horizon I	-1.7	-1.8	Transition (~ 30 - 25 kya)	Molar	KLB I 17 - 39
Equus burchelli	Horizon I	-3.3	-2.9	Transition (~ 30 - 25 kya)	Upper M2/3	KLB I 17 - 36
Equus burchelli	Horizon I	-0.7	-3.6	Transition (~ 30 - 25 kya)	Molar	KLB I 17 - 36
Equus burchelli	Horizon I	-3.7	-4.2	Transition (~ 30 - 25 kya)	Upper M3	KLB I 17 - 36
Equus burchelli	Horizon I	-1.5	-3.3	Transition (~ 30 - 25 kya)	Molar	KLB I 17 - 37
Equus burchelli	Horizon I	0.6	-5.4	Transition (~ 30 - 25 kya)	Molar	KLB H 17 - 38
Equus burchelli	Horizon I	0.3	-4.9	Transition (~ 30 - 25 kya)	Molar	KLB H 17 - 38
Equus burchelli	Horizon I	-10.6	-4.6	Transition (~ 30 - 25 kya)	Lower M3	KLB H 17 - 38
Equus burchelli	Horizon J	0.0	-4.8	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 17 - 34
Equus burchelli	Horizon J	-0.1	-5.1	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 17 - 34
Equus burchelli	Horizon J	-2.4	-4.7	Transition (~ 30 - 25 kya)	Upper M3	KLB H 17 - 34
Equus burchelli	Horizon J	-1.9	-4.9	Transition (~ 30 - 25 kya)	Molar	KLB H 17 - 34
Equus burchelli	Horizon J	-3.5	-4.3	Transition (~ 30 - 25 kya)	Molar	KLB H 17 - 34
Equus burchelli	Horizon J	-5.3	-4.6	Transition (~ 30 - 25 kya)	Upper M2/3	KLB H 16 - 33
Equus burchelli	Horizon J	-8.1	-4.6	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 16 - 32
Equus burchelli	Horizon J	-1.3	-3.9	Transition (~ 30 - 25 kya)	Upper M1/2	KLB I 17 - 33
Equus burchelli	Horizon J	-1.8	-5.7	Transition (~ 30 - 25 kya)	Upper M3	KLB I 17 - 33
Equus burchelli	Horizon J	1.1	-5.0	Transition (~ 30 - 25 kya)	Lower M1/2	KLB H 17 - 33
Equus burchelli	Horizon J	-1.6	-5.7	Transition (~ 30 - 25 kya)	Upper M1/2	KLB I 16 - 35
Equus burchelli	Horizon J	-6.8	-5.8	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 16 - 34
Equus burchelli	Horizon J	-0.8	-5.6	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 17 - 32
Equus burchelli	Horizon J	-0.7	-4.9	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 17 - 32
Equus burchelli	Horizon J	0.9	-5.1	Transition (~ 30 - 25 kya)	Lower M1/2	KLB H 17 - 32
Equus burchelli	Horizon K	-2.5	-6.1	Transition (~ 30 - 25 kya)	Lower M1/2	KLB H 17 - 30
Equus burchelli	Horizon K	-4.3	-3.9	Transition (~ 30 - 25 kya)	Upper M1/2	KLB H 17 - 30

Equus burchelli	Horizon K	0.4	-2.1	Transition (~ 30 - 25 kya)	Upper M1/2	KLB I 17 - 30
Equus burchelli	Horizon L	-4.3	-4.0	Transition (~ 20 - 12 kya)	Upper M1/2	KLB I 17 - 23
Equus burchelli	Horizon N	-2.0	-2.0	Transition (~ 20 - 12 kya)	Lower M1/2	KLB H 14 - 13
Equus burchelli	Horizon N	-0.4	-2.4	Transition (~ 20 - 12 kya)	Lower M1/2	KLB I 15 - 17
Equus burchelli	Horizon O	-5.8	-2.9	Late LSA (~10 - 7 kya)	Lower M1/2	KLB H 15 - 13
Equus burchelli	Horizon O	-9.1	-0.3	Late LSA (~10 - 7 kya)	Lower M1/2	KLB H 14 - 12
Equus burchelli	Horizon O	-8.5	-0.8	Late LSA (~10 - 7 kya)	Upper M1/2	KLB I 14 - 11
Hystricidae (1)						
Hystrix. sp.	Horizon O	-9.8	-0.7	Late LSA (~10 - 7 kya)	Molar	KLB H 14 - 11

*Correction calculated from Tipple et al. (2010): $\delta^{13}C_{CO_2(g)} = \left|\frac{\delta^{13}C_{DIC} + 10^3}{\left(\epsilon_{DIC-CO_2(g)}/10^3\right) + 1}\right| - 10^3$

Table 2 contains estimates for the δ^{13}C of atmospheric CO_2 of three ocean cores based on the above equation. The mean of these estimates, -7.1‰, was compared to the modern value of δ^{13}C for atmospheric CO_2 from Keeling et al. (2001) of -8.0‰ to arrive at the correction factor.

Results

In Africa the Last Glacial Maximum has been described as an aridity event more so than a cooling event (but see models by Crucifix et al. 2005; Claussen et al. 2013) due to the weakening effect it is predicted to have had on winds and the Indian Ocean and African monsoon systems (Kohfeld et al. 2013). Regardless, it likely had overall effects of increasing aridity and decreasing temperature. Therefore, the Last Glacial Maximum is commonly recorded in global and continental records of past climate by more positive $\delta^{18}O$ values, as O^{16} is preferentially evaporated and trapped in ice sheets (Ridge et al. 2012; Mangerud et al. 2013). Without existing data or models suggesting a full-scale transition in central African grasslands from C_4 to C_3 varieties, any shifts in vegetation were expected to be altitudinal and result in minimal shifts in enamel $\delta^{13}C$ (Saltre et al. 2013; Potts et al. 2013). It was hypothesized that $\delta^{18}O$ would indicate a clear shift across the Last Glacial and related events while there would be minimal change in $\delta^{13}C$ values. Another way to think of this is that animals can consciously track their preferred dietary resources, but would be unable to mitigate the effects of increased water stress which may have been widespread. Changes in $\delta^{13}C$ at a single site are typically small and related to water stress and amount of solar insolation as opposed to different photosynthetic pathways. However, significant shifts were noted for *both* $\delta^{18}O$ and $\delta^{13}C$ at Kalemba Rockshelter, Zambia.

Oxygen

ANOVA analysis of $\delta^{18}O$ at Kalemba Rockshelter reveals a statistically significant main effect of time across the Last Glacial ($p = 0.01$, $F = 12.197$). The shift is towards greater aridity signaled by a transition from lighter to heavier $\delta^{18}O$ values across the Last Glacial (Figure 2, 3a). There are no significant main effect of feeding group (*p* = 0.768, *F* = 0.380) or interactions between feeding group and time (*p* = 0.131, *F* = 2.080). Archaeologically, or behaviorally, the Last Glacial Maximum interval separates the MSA/LSA transition period from the true LSA. As a result, these data suggest that the LSA developed during a period that was more arid than the transition phase and perhaps reflects an arid adapted foraging strategy.

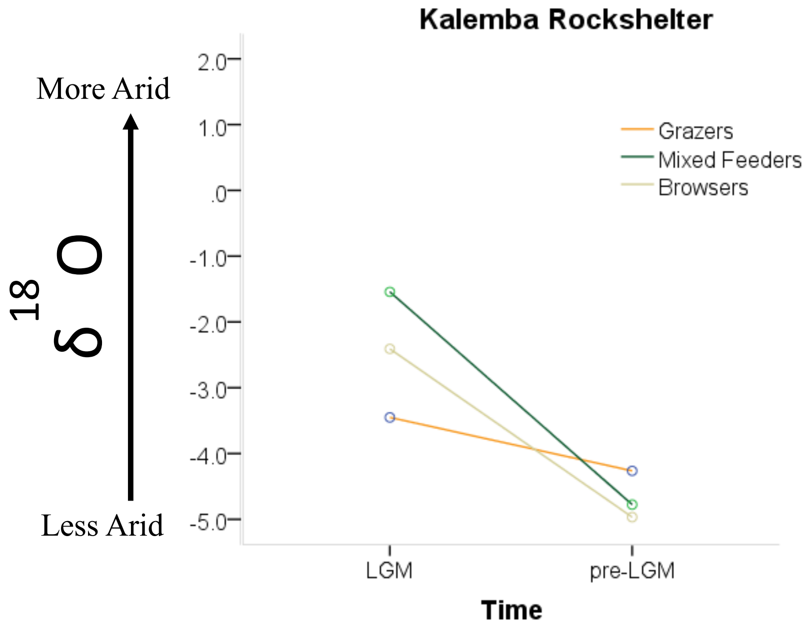

Figure 2. Interaction plot of 2-way ANOVA for Kalemba Rockshelter showing a statistically significant shift from lighter to heavier δ^{18}O values.

This statistically significant shift holds for two of the most abundant species at Kalemba: *Equus burchelli* (zebra) and *Sylvicapra grimmia* (common duiker). All taxa with more than three pre-LGM and three LGM samples reflect this trend, although they are not statistically significant. Only wildebeest, bushpig, and warthog suggest a shift from heavier to lighter δ^{18}O values, but these trends are not significant and represent small pre-LGM and LGM sample sizes.

The δ^{18}O for modern *E. burchelli* from Lukwati and Serengeti is -3.1‰ and 1.1‰ respectively (van der Merwe 2013). Mean δ^{18}O for Kalemba equids is -4.4‰ for the pre-Last Glacial period and -2.1‰ for the Last Glacial. This difference is significant at the $p<0.05$ level as determined by a student's t-test (N = 34; p = 0.0002). Despite a small sample size, *S. grimmia* shows a similar δ^{18}O shift of -5.0‰ in the pre-Last Glacial to -2.8‰ during the Last Glacial Maximum (N = 7; p = 0.033). Since the common duiker is an obligate browser which receives most of its body water from vegetation sources, this may reflect the degree of water stress that leafy vegetation faced during the Last Glacial in Zambia.

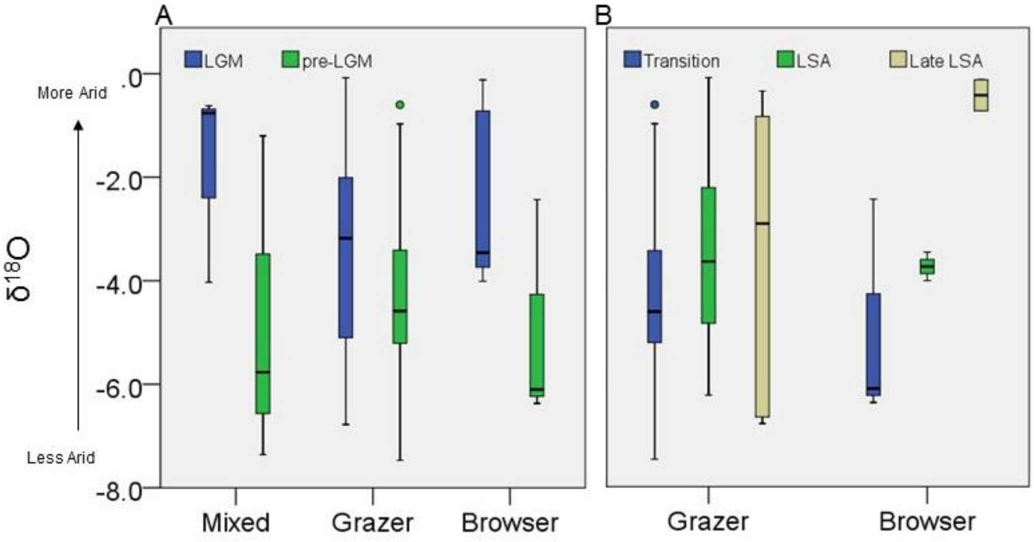

Figure 3. Box-and-whisker plots of δ^{18}O at Kalemba Rockshelter. A) δ^{18}O of mixed feeders, grazers, and browsers showing a shift towards more arid conditions from the pre-Last Glacial to Last Glacial time periods. B) δ^{18}O of browsers and grazers at Kalemba Rockshelter showing a shift in aridity from the transition period to the late LSA.

Mid-Last Glacial shifts in aridity are also apparent in more specific stratigraphic context for the fauna collected at the Kalemba Rockshelter. Breaking the Kalemba sequence into the four archaeologically defined cultural periods identifies two potential shifts in δ^{18}O *during* the Last Glacial (Figure 3b, Figure 4). Post-hoc Tukey's tests reveal that late LSA period is statistically different from the transition period ($p = 0.001$). Additional post-hoc tests suggest that this shift is being driven primarily by the browser feeding group ($p = 0.42$, $F = 6.352$), although the grazers also reflect this trend. The shift from the MSA/LSA transition unit to the LSA and the shift from the LSA to the true LSA follows this pattern of more positive δ^{18}O values, but are not statistically significant. There are no significant main effects of feeding group or significant

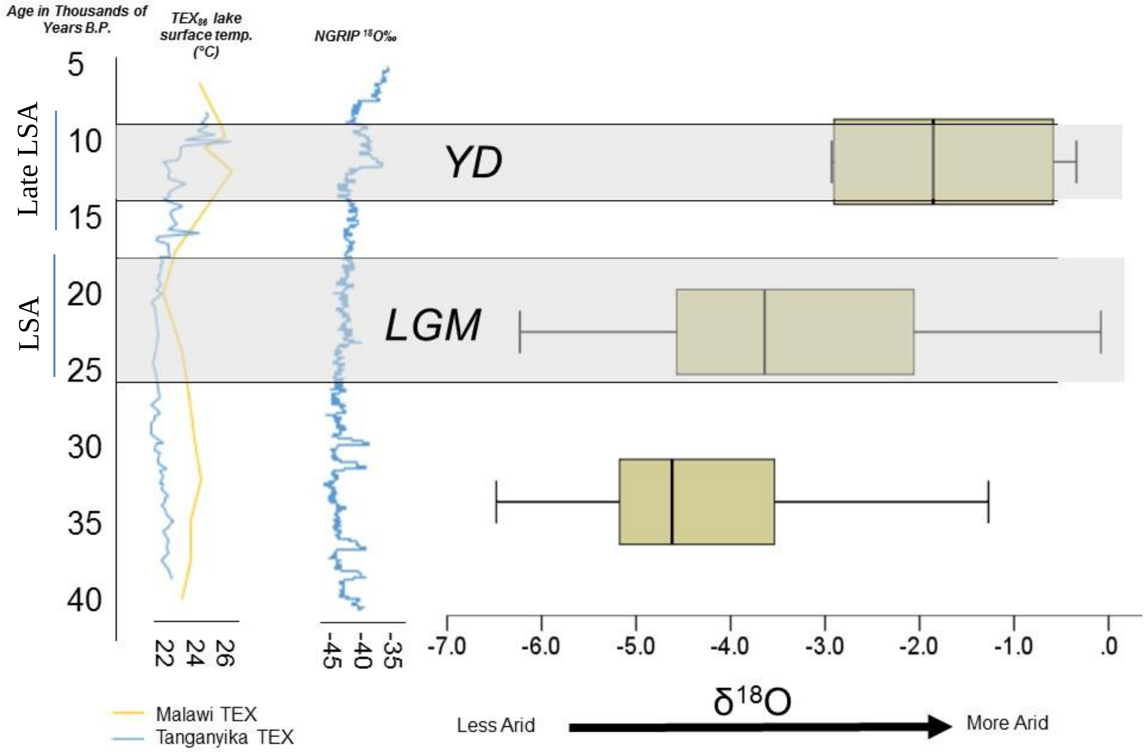

Figure 4. Box-and-whisker plots of δ^{18}O of all grazers at Kalemba Rockshelter broken down into the MSA/LSA transition, LSA, and late LSA archaeological units. A shift toward more enriched δ^{18}O is seen over time with the LSA unit roughly corresponding to the Last Glacial Maximum *sensu lato* and the late LSA roughly corresponding to the Younger Dryas (YD). These events can also be seen in the global NGRIP ice core record (NGRIP Members 2004) and the TEX_{86} temperature curves from Lakes Malawi (Woltering et al. 2011) and Tanganyika (Tierney et al. 2008).

interactions between feeding group or time when the analysis is based on the cultural units. This shift is penecontemporaneous to decreasing temperatures in Lakes Malawi and Tanganyika (Figure 4).

Shifts in $\delta^{18}O$ values across the transition to the LGM alone does not reveal anything specific about changes in the taxonomy of overall vegetation cover. Combined with models which suggest a decrease in temperature in tropical and sub-tropical Africa of ~2 - 5ºC (Kim et al. 2008; Woillez et al. 2011; Claussen et al. 2013), increased local aridity may have been the mechanism by which a transition from C_4 dominated to C_3 dominated grasslands took place.

Carbon

ANOVA analysis of carbon followed the same design as oxygen – with the isotopic values as the dependent variable and time and feeding category as the independent fixed factors. The full dataset analysis with the time condition as pre-LGM vs. LGM revealed no statistically significant main effects (time: $p = 0.644$, $F = 0.215$) or interactions (Figure 5a). Restricting the analysis to just the grazers also does not result in any statistically significant main effects (time: $p = 0.154$, $F = 2.072$) or interactions. However, the mid-Last Glacial shift in $\delta^{18}O$ suggests that the archaeologically defined cultural units may be more relevant time units for this analysis.

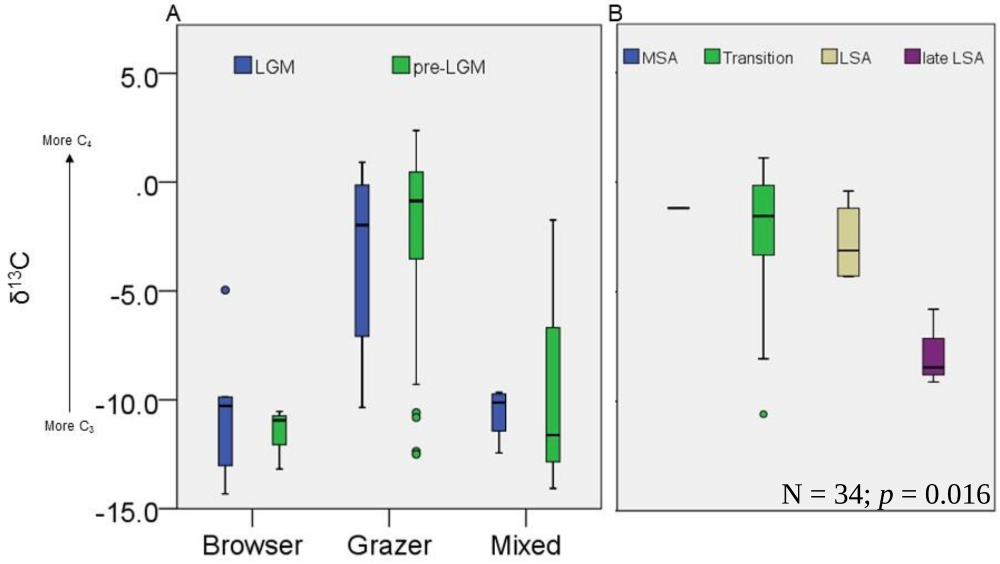

Figure 5. δ^{13}C at Kalemba Rockshelter. A) δ^{13}C of feeding groups. B) δ^{13}C of *Equus burchelli* with the major shift in δ^{13}C seen between the LSA and late LSA periods.

Considering only the grazers, which account for 75 of the 93 faunal samples at Kalemba, a very clear and statistically significant transition from more positive to more negative δ^{13}C values is apparent for grazers overall ($p = 0.018$, $F = 3.572$) and zebra, in particular (Figure 5b). It is best seen as a gradual shift building from the MSA/LSA transition period to the late LSA. Post-hoc Tukey's tests reveal that the δ^{13}C values for the late LSA are statistically significantly different at the $p<0.05$ level from both the MSA/LSA transition period ($p = 0.01$) and the LSA ($p = 0.001$). However, the MSA/LSA transition period and the LSA are not statistically different from each other ($p = 0.941$). It seems that despite the overall shift in aridity across the Last Glacial the transition in grasslands is not a simple pre-Last Glacial versus Last Glacial event.

Zebra provides the best example of the phytogeographic transition as it appears in all four time periods (Figure 5b). Mean δ^{13}C for zebra in the MSA at -1.2‰ falls between the modern ranges reported at Serengeti (0.5‰ to 1.2‰) and Lukwati (-0.7‰ to -3.1‰) by van der Merwe (2013). During the transition and LSA periods δ^{13}C falls to

-2.1‰ and -2.7‰, although this is still within the conservative range of grazers. As with the general grazer pattern, a statistically significant shift is seen with the onset of the late LSA. The $\delta^{13}C$ of zebra for this period ranges from -5.8‰ to -9.1‰ with a mean of -7.8‰. Based on post-hoc Tukey's tests, $\delta^{13}C$ values for late LSA zebra are significantly different for those from the MSA/LSA transition ($p = 0.006$) and the LSA ($p = 0.045$). At Equus Cave, Lee-Thorp and Beaumont (1995) report comparable values for *Equus quagga*, including one at -5.2‰ (corrected to -6.1‰), where they argue C_3 grasses existed in the period shortly before 10,000 years ago.

The shift in $\delta^{13}C$ at Kalemba coincides with increased aridity, as determined by $\delta^{18}O$ values, during the Last Glacial Maximum. Additionally, the overall zooarchaeological analysis of the Kalemba Rockshelter assemblage is interpreted as representing an open woodland to grassland ecosystem throughout the sequence, with the most open grasslands appearing in the LSA and late LSA periods (Phillipson 1976). With these two factors combined, the most parsimonious explanation for the ~ -5.7‰ shift in mean $\delta^{13}C$ for zebra from the transition/LSA to the late LSA is that of expanded C_3 grasslands at and below 1000 meters.

Redunca arundinum, an obligate grazer preferring grass valleys (Kingdon 1997), shows an initial shift from the transition period to the LSA of -6.6‰, from a mean of 1.7‰ to a mean of -4.9‰. The sample size for the southern reedbuck is too small (N = 4) for this difference to reach the level of statistical significance. Sponheimer et al. (2003) report a modern range of 2.5‰ to -0.7‰ for this taxon. The transition value most likely reflects obligate grazing of C_4 grasses, but the LSA value of -4.9‰ has never been recorded for *R. arundinum*. While no samples of *R. arundinum* were collected from the late LSA these values may suggest that the emergence of C_3 grasses below 1000 meters in eastern Zambia had begun by ~15,000 years ago. These mid-Last Glacial shifts in $\delta^{13}C$ may correspond with events like Heinrich 1 and/or the Younger Dryas providing a mechanism to explain the nature of the appearance and expansion of C_3 grasslands.

Discussion

Despite its distance from the modern South African winter-rainfall zone, and a maximum paleoaltitude at 1350 meters, it appears that C_3 grasses underwent a substantial expansion around Kalemba Rockshelter in Zambia during the Last Glacial and perhaps the Younger Dryas. A shift in $\delta^{18}O$ towards aridity from ~30,000 years B.P. to ~10,000 years B.P. seems to be the ultimate mechanism by which a grassland transition took place. Overall, $\delta^{18}O_{enamel}$ values are quite depleted relative to contemporary populations in east Africa and modern samples. This appears to be a result of the comparatively depleted meteoric and groundwater sources of central Africa. Data from the Ndola, Zambia and Hararre, Zimbabwe International Atomic Energy Agency and World Meteorological Organization isotope composition stations consistently yield some of the most depleted water sources on the continent (Rozanski et al. 1993; IAEA 2013). It is possible that this is a result of the distance over which moisture from the Indian Ocean must traverse before reaching south-central Africa, becoming progressively depleted. While the interpreted increase in aridity during the Last Glacial is a global event, the specific effects it had on the composition of grasslands in central Africa is not apparent from existing regional records.

Expansion of C_3 grasses below 1000 meters in eastern Zambia may have occurred at or around 23,000 years ago with small pockets of C_3 grasses persisting through the

LSA and major expansion towards the end of the LSA and lasting into the late LSA. Both the Younger Dryas and the 8.2 kiloyear event have been identified as rapid increases in aridity leading to greatly reduced vegetation cover in much of central Africa (Zhao et al. 2000; Broecker et al. 2010; Morrill et al. 2013). Existing chronology for the site makes identifying or distinguishing between these two events difficult. The Younger Dryas appears to overlap with the end of the LSA at Kalemba while the 8.2 kiloyear event appears to occur towards the later stages of the late LSA. Therefore, the Younger Dryas may be the event which allows C_3 grasses to establish and expand in the late Pleistocene. The 8.2 kiloyear event may have had a role in helping C_3 grasses maintain a competitive advantage over C_4 grasses into the Holocene. Analysis of the Lake Malawi cores suggest this period is characterized by a return to a combination of drier and cooler conditions with increased northeasterly winds (Powers et al. 2005; Brown et al. 2007; Woltering et al. 2011; Ivory et al. 2012).

Ivory et al. (2012) divided the period from 18,100 to 9,500 years B.P. into three zones and six sub-stages (two stages per zone) based on pollen composition in the MAL05-2A core from the northern basin of Lake Malawi. The first subzone, 18,100 to 16,400 years B.P., appears to capture the peak of the Last Glacial Maximum *sensu lato* with widespread grasses near the lake and aquatic taxa suggesting the proximity of the shoreline to the core location. While Zambezian woodlands and tropical seasonal forest start expanding by the end of this subzone, grasslands dominate throughout the three zones. At the beginning of the Younger Dryas period (phase one of subzone 2b at 13,000 to 12,300 years B.P.) tropical forests reach their maximum. However, as the Younger Dryas continues grasses reach their peak values by ~10,000 years B.P. The expansion of woodlands and tropical forests is an important finding, but seems to be quite subtle as grasses account for increasing levels of pollen throughout the record (Table 4).

Table 4. Expansion of grasslands during the late Pleistocene as determined by pollen count in Lake Malawi (Ivory et al. 2012).

Zone	**Time Period**	**% Poaceae pollen**
1:subzone 1a	18,100 – 16,400 years ago	36%; 520 grains/cm^2/year
2:subzone 2a	14,700 – 13,000 years ago	45%; 650 grains/cm^2/year
3:subzone 3a	11,800 – 10,700 years ago	54%; 691 grains/cm^2/year

The period from 18,100 to 15,500 years B.P. is characterized by cool lowland temperatures, perhaps freezing temperatures at altitude, which allowed high-altitude taxa to grow at lower elevations. Wu et al. (2007) suggest that montane taxa, including C_3 grasses, may have thrived at elevations as low as 600 meters.

Based on the pollen record, C_3 grasses expanded in the period 14,700 – 13,800 years B.P., but this was short-lived as increasing moisture during the period immediately following forced these grasses back to higher altitudes (Ivory et al. 2012). This complicated series of environmental and climatic reversals during the period ~16,000 – 13,000 years B.P. may explain why $\delta^{13}C$ values for the LSA period at Kalemba reveal little to no difference from the transition period. Although, a series of outliers for both the transition and LSA imply that some patches of C_3 grasses must have been present. With the onset of the Younger Dryas (13,000 – 12,300 years B.P.) cooler, drier conditions return to Lake Malawi and once again higher-latitude vegetation expands below 1000 meters. Ivory et al. (2012) describe the second half of the Younger Dryas (12,300 – 11,800 years B.P.) as the period of the greatest extent of grasslands in the Malawi basin. These interpretations are consistent with other indicators of aridity and increased dry season severity. A southward movement of the Intertropical Convergence Zone coupled with decreasing temperature and enhanced northeasterly tradewinds has been modeled as the reason for increased moisture stress during the Younger Dryas (Gasse 2000; Hely et al. 2006). Grasslands are projected to have continued expanding in the Lake Malawi basin through 9,500 years B.P. (Ivory et al. 2012). This part of the core appears to correlate with the end of the LSA and the beginning of the late LSA in Zambia.

Castaneda et al. (2007) report that these were most likely C_4 grasses based on n-alkane records. This may be a situation where the distance between the core and Kalemba Rockshelter has an effect on environmental interpretations and modeling. Despite the drought conditions, the Lake Malawi region would be significantly more protected and buffered than the Chipwete Valley in Zambia. At this time period lake effect hydrological patterns, including increased precipitation compared to sites further away from the lake, may have held C_3 grasses at altitude. While C_4 grasslands expanded around Lake Malawi in the early Holocene, the combined effects of increased aridity and decreased temperatures without lake buffering seem to have allowed C_3 grasses to expand and thrive inland and away from the lake. This is a clear situation where the regional records are out of sync with what human populations were experiencing.

Further support for expanded C_3 grasslands in the Kalemba Rockshelter area, particularly during the end of the LSA and into the late LSA period, comes from species composition. Phillipson (1973, 1977) reports that the zooarchaeological assemblage at Kalemba is dominated by grazers and concludes that the number of equids suggests that

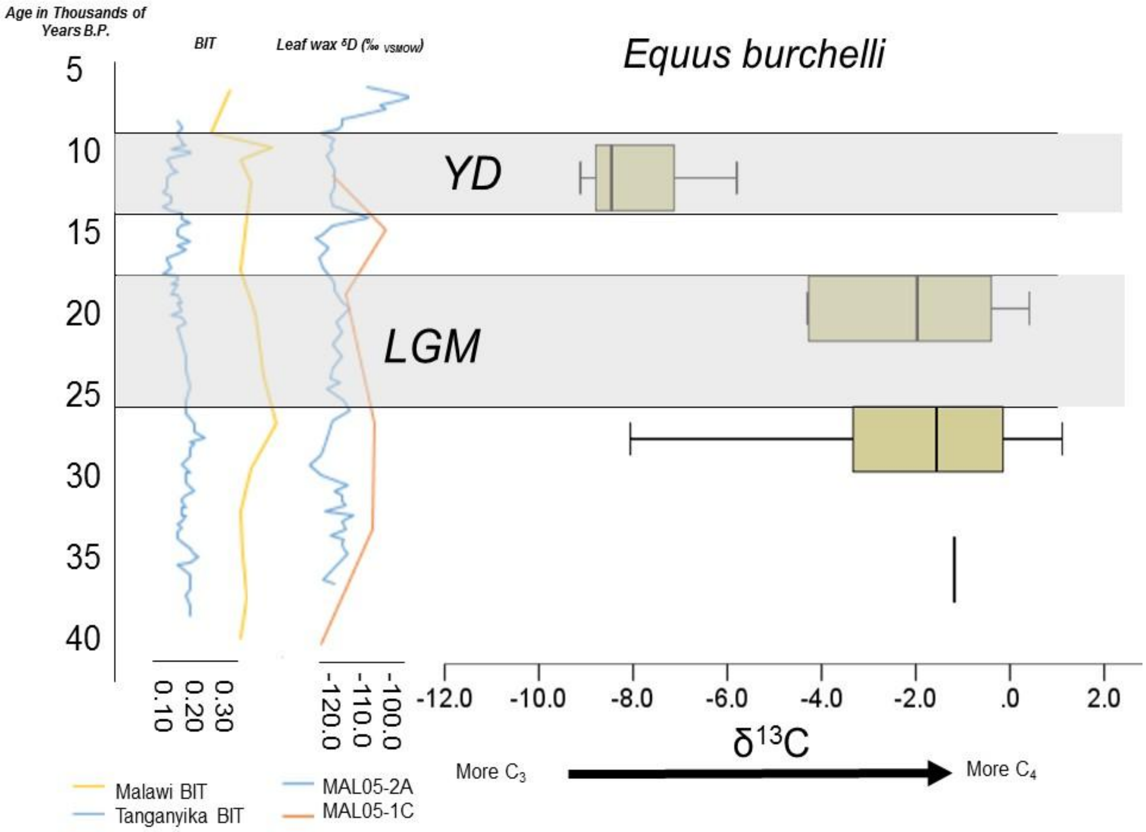

Figure 6. Box-and-whisker plots of $\delta^{13}C$ of *Equus burchelli* at Kalemba Rockshelter broken down into the MSA/LSA transition, LSA, and late LSA archaeological units. A shift toward more depleted $\delta^{13}C$ is seen over time with the LSA unit roughly corresponding to the Last Glacial Maximum *sensu lato* and the late LSA roughly corresponding to the Younger Dryas (YD). These events can also be seen in the BIT records from Lakes Malawi (Woltering et al. 2011) and Tanganyika (Tierney et al. 2008) and the leaf wax records from the Lake Malawi cores (Konecky et al. 2011).

the environment surrounding the site must have progressively opened up from grassy woodlands to open grasslands through time. Interestingly, the isotope study reveals that this expanded grassland consisted of an increased proportion of C_3 grasses. Concurrent shifts in the BIT records from Lakes Malawi and Tanganyika and the leaf wax record from Lake Malawi suggest that some broader climatic event is occurring at the same time (Figure 6).

While the samples size are not large enough to test statistical significance, the decrease in species diversity is supported by the fact that C_3 grasses typically have a lower carrying capacity than C_4 grasses (Collatz et al. 1998). This is related to the reduced ability C_3 grasses have in fixing CO_2 compared to C_4 grasses. Reduced CO_2 leads to lower productivity and a lower total biomass as a result. At Kalemba Rockshelter, once C_3 grasses became the dominant component of the ecosystem it seems as if zebra outcompeted other grazers for a decreasing resource base. A possible modern example of this is in Mongolian steppe grasslands during seasons when C_3 grasses expand. At these times equids, which are considered hyper-grazers, are disproportionally represented to the exclusion of other grazers. However, in seasons and years when C_4 grasses make up the bulk of the biomass a more even species composition occurs (Auerswald et al. 2012).

ANOVA analyses of both $\delta^{18}O$ and $\delta^{13}C$ reveal that the main transition towards more arid conditions and the expansion of C_3 grasslands took place between the LSA and the late LSA. This more subtle shift is mirrored by the environmental and climatic complexity in the Lake Malawi core between ~17,000 years B.P. and ~9,000 years B.P. (Ivory et al. 2012). The fact that there is no statistically significant shift in $\delta^{13}C$ when considering time as aggregated pre-LGM and LGM units suggests that a phytogeographic transition temporally lagged behind the climatic shift revealed by $\delta^{18}O$ values. A secondary shift in $\delta^{18}O$ between the LSA and late LSA may have been a catalyst for the expansion of C_3 grasslands from earlier pockets to a larger area, making the transition more archaeologically visible. The phytogeograhic transition at Kalemba Rockshelter in the late Pleistocene is also supported by the regional signal of cooler temperatures and decreased BIT in the Lake Malawi and Lake Tanganyika basins which would have been advantageous to C_3 grasses in competition with C_4 grasses.

Implication for Agriculture and Mobility

V.G. Childe (1951) was the first to suggest an environmental cause for the origins of agriculture when he theorized that agriculture became necessary due to environmental degradation during the Last Glacial. Following Childe, McCorriston and Hole (1991) identified the Younger Dryas as *the* climatic event which was the driving mechanism for the origins of agriculture across the world. They argued that population size had been growing throughout the late Pleistocene and relied upon a stable resource base, but during the Younger Dryas this hunting and foraging resource base disappeared. Agriculture was invented in order to support this large population which no longer had a predictable food source. Since this time models have shifted from environmental degradation being the prime mover of agricultural origins to environmental amelioration allowing agriculture to flourish.

Bettinger, Richerson, and Boyd (2009) have argued that the origins of agriculture were constrained by the climatic conditions of the late Last Glacial and the Younger Dryas. The complex and abrupt shifts in climate and environment, such as those identified by Ivory et al. (2012), which characterized this time period prevented agriculture from taking hold. The shift to C_3 grasslands during the LGM identified in this study may have been a forcing factor towards intensified human-plant interaction. Early attempts at horticulture and plant production are attested to in Natufian contexts in the Middle East during the Epipaleolithic, but they disappear during the Younger Dryas (Feynman and Ruzmaikin 2007). The combination of increased aridity and lower atmospheric CO_2 would have had the effect of decreasing overall plant productivity, regardless of photosynthetic pathway. This lower level of productivity may have led populations in south-central Africa to attempt to enhance the productivity of their surroundings, resulting in some of the technological changes seen in the transition from the MSA to the LSA.

Agriculture in Africa, outside of the Nile Valley, is not definitively identified until ~6,000 years B.P. (Marshall and Hildebrand 2002). This is a lag time of approximately 4,000 – 2,000 years from the end of the Younger Dryas and the 8.2 kiloyear event, but during that intervening period early horticulture and preferential plant selection may have begun. Phillipson (1968) and Clark (1976) argue that pottery was used as mass storage for grains and grasses in south-central Africa as early as the end of the Late Stone Age/early Iron Age (~8,000 years B.P.). Even if full-blown agriculture did not begin until much later, Bettinger, Richerson, and Boyd’s (2009) thesis that it wasn’t possible until after the Younger Dryas may still be valid. Even if the climatic conditions prevented agriculture from taking hold until the mid-Holocene, the expansion of C_3 grasses below 1000 meters in south-central Africa during the Younger Dryas identified in this study may have been a mechanism toward increased human protection and selection of certain plants. Preferentially selecting plants and minor horticultural practices may have provided a sufficient resource base, and intensification was not required until much later. Ultimately, early horticulture may be part of differentiating between MSA and LSA technological assemblages and behavioral suites.

Conclusion

Expansion of C_3 grasslands from their current high-altitude or winter-rainfall niche during periods of increased aridity, specifically the Last Glacial Maximum, has been suggested by modelers (Crucifix et al. 2005; Kim et al. 2008; Claussen et al. 2013) and paleoclimatologists (van Zinderen Bakker 1967, 1976; Cockcroft et al. 1987). Archaeologists in South Africa have recovered paleoenvironmental data from fossil faunal enamel (Lee-Thorp and Beaumont 1995; Sealy 1996) and speleothems (Talma and Vogel 1992; Faith 2013) which suggest that the modern winter-rainfall zone in South Africa expanded northward during the Last Glacial. However, the expansion of the winter-rainfall zone, or development of independent winter-rainfall zones, further into south-central Africa has not been previously proposed or tested. The data reported here supports the notion of the existence of a winter-rainfall zone leading to the replacement of C_4 grasslands by C_3 grasslands in eastern Zambia during the Last Glacial Maximum and subsequent late Pleistocene/early Holocene climatic events.

Isotopic analysis of fossil faunal enamel yields $\delta^{18}O$ values which are enriched during the Last Glacial indicating increasing aridity. At the same time TEX_{86} data from Lake Malawi (Powers et al. 2005; Woltering et al. 2011) reveals a decrease in surface temperatures of at least 3.5°C. Together, the increased aridity and reduced temperature would create favorable conditions for C_3 vegetation, including grasses, to outcompete the existing C_4 flora which dominated ecosystems in the Kalemba Rockshelter area. Interpretation of $\delta^{13}C$ data supports a complex but gradual phytogeographic transition from C_4 to C_3 grassland ecosystems. Unlike the $\delta^{18}O$ data, analysis of $\delta^{13}C$ does not yield a simple pre-Last Glacial to Last Glacial shift. $\delta^{13}C$ for grazers as a whole, and zebra in particular, suggests that C_3 grasses may have started encroaching on elevations below 1200 meters by ~23,000 years B.P. (the end of the MSA/LSA transition at Kalemba). However, a more complete transition is not identified until the end of the LSA and the beginning of the late LSA (~10,000 – 8,000 years ago). While a similar complex and gradual pattern is also reflected in the Lake Malawi core (Ivory et al. 2012) it fails to reveal the specific climatic and environmental contexts of individual sites where critical demographic and behavioral transitions were happening.

The Younger Dryas appears to have been the proximate mechanism in the sudden expansion of C_3 grasslands. Although it could be argued that the Last Glacial Maximum *sensu lato* also promoted some patches of C_3 grasses at or below 1000 meters in the Chipwete Valley surrounding Kalemba Rockshelter. Expanded C_3 grassland ecosystems persisted in the region at least through the 8.2 kiloyear event. Analysis of zebra offers the greatest insight to this transition as a $\delta^{13}C$ shift of ~ -5.6‰ is recorded for the LSA and late LSA periods respectively at Kalemba. $\delta^{13}C_{enamel}$ values of fossil zebra are well outside of the conservative range for grazers at > -3‰. Carbon isotopic values for zebra recorded at the end of the LSA and into the late LSA are more negative and in the C_3 vegetation direction more so than any modern equid datasets and most fossil datasets post-dating the initial expansion of C_4 grasses in the late Miocene. Interestingly, one of the only datasets with comparable values is that of *Equus quagga* at Equus Cave, also during the Last Glacial and Younger Dryas which has also been interpreted to suggest extensive C_3 grasslands in southern Africa (Lee-Thorp and Beaumont 1995). Support for the expansion of C_3 grasses, as opposed to zebra feeding on C_3 browse as an explanation for the shift in $\delta^{13}C$, comes from the fact that the zooarchaeological assemblage is almost exclusively grass-feeding grazers during the late LSA. The resulting late Pleistocene environmental reconstruction of the area is as a grassy woodland grading to open grassland over time. This is very similar to the vegetation surrounding Kalemba Rockshelter today. Furthermore, the loss of obligate grazer taxa towards the end of the LSA is not accompanied by an increase in browser diversity, implying that zebra outcompeted other grazers on the lower productivity biomass of C_3 grasses.

Finally, this transition to C_3 grasslands in south-central Africa during the late Pleistocene/early Holocene may have had some effect on the origins of agriculture in the region. The replacement of C_4 grasses suggest cooler and more arid conditions and lower primary productivity possibly leading to early forms of horticulture, including the selection and protection of certain preferred plants. It appears that the expansion of C_3 grasslands lasted well into the mid-Holocene through the 8.2 kiloyear event. If this was the case the combination of the prevailing cool and arid environment and the effect of generations of C_3 grasses on the soil substrate in the area may have made it difficult for full scale agriculture to take hold until later.

Regardless of the mechanism or process it appears that the aridity and cooling of the Last Glacial Maximum had a significant effect on the distribution and physiology of vegetation in south-central Africa in the late Pleistocene and affected how early Holocene populations interacted with their environments. Technological and behavioral shifts characteristic of the transition between the MSA and LSA may be directly related to different foraging opportunities created by the grass transition. Changes in prey distribution and resource availability may have required new hunting and trapping technologies and had an effect on the degree of sedentism and migration. LSA microlithic technologies may suggest the need for more seasonal mobility and/or the requirement for more generalized tools for mobile hunting groups. Furthermore, these results demonstrate that global and regional records of environmental and climatic change are not sufficient by themselves in contextualizing late Pleistocene behaviors and migrations. The next step is to further supplement the high-resolution global and regional records with additional site-specific reconstructions which could yield further insights to the local conditions in which our ancestors lived.

Chapter 5
Sibudu Cave: South African Archaeology in Context

Goodwin and van Reit Lowe (1929) developed a lithic-based chronology for the African continent based on a series of sites they excavated in southern Africa. It is in this article that the term Middle Stone Age (MSA) first appears. Cautiously, they described the MSA as the period within which behavioral modernity first appeared based on the association of MSA archaeological horizons with the remains of anatomically modern humans (AMH). As more MSA sites were discovered across Africa, many without skeletal remains, Goodwin and van Reit Lowe's descriptions of the artifacts as a modern behavioral suite, but not their chronology, fell out of favor (Clark 1988). The MSA designation was seen as nothing more than Africa's equivalent of Europe's Middle Paleolithic, a period certainly important for human evolution, but not for behavioral modernity or AMH.

Fifty years after publishing their chronology, Goodwin and van Reit Lowe were vindicated. While archaeology and paleoanthropology in most of the rest of Africa focused on earlier hominin origins, excavation of MSA and later sites in South Africa continued. In the 1970s the excavation of Klasies River Mouth once again brought the MSA to the forefront of the discussion of AMH origins. Fragmentary pieces of AMH remains were carefully excavated in association with lithic artifacts suggesting some form of behavioral modernity (Butzer 1978). The excavation reignited ideas that the MSA was critically important to identifying the origin of modern human behavior and culture. Advancements in trapped-charge dating methods, including electron-spin resonance, optically stimulated luminescence (OSL), thermoluminescence, and a series of other techniques, during the past fifteen years has established the chronology of the MSA in Africa as spanning the period from roughly 250,000 to 30,000 years ago (Woodborne and Vogel 1997; Jacobs et al. 2003; Jacobs et al. 2006; Jacobs et al. 2008).

As part of historical and ongoing research on archaeological sites in South Africa, this chapter assesses the role of environmental conditions on the development of technological innovations, including the bow and arrow, at Sibudu Cave, KwaZulu-Natal, South Africa from ~80,000 – 30,000 years B.P. Sibudu's detailed stratigraphy has been dated by OSL methods to identify faunal, floral, and lithic transitions with high temporal resolution (Jacobs et al. 2008). Detailed dating, combined with the careful excavation methods described by Wadley and Jacobs (2006), offers centimeter-level control for the association of faunal, floral, and artifactual remains. The local environments interpreted through time at Sibudu will be compared with the dominant southern African events of this time period, including the arid/wet cycles of the expansion and contraction of the Kalahari Desert (Thomas and Goudie 1984; Barham 2000; Partridge 1999; Thomas and Burrough 2013). Sibudu's location is over one thousand kilometers from the Kalahari Desert, meaning that the Kalahari cycles must have had a significant impact on regional climate if they are to be detected at Sibudu. The goal here is twofold: to identify the local environmental and climatic shifts affecting the Sibudu area during the MSA and to provide a preliminary assessment of any relation to regional events despite its great distance from the core of the Kalahari. I close the chapter with a consideration of the environmental shifts' effects upon behavioral transitions based on the turnover of lithic technologies at Sibudu Cave.

Geological and Archaeological Context

Sibudu Cave is a rock shelter located approximately 40 km north of present-day

Durban and 15 km inland from the Indian Ocean in KwaZulu-Natal, South Africa (Figure 1). It currently is twenty meters above the Tongati River on a forested cliff; however, downcutting of the river into the bedrock has exaggerated this distance over time (Allott 2005) and at the time of formation it may have existed at the river surface level. Additional fluvial events carved pockets into the sandstone and shale cliff, leaving the largest of these chambers, Sibudu at fifty-five meters long by eighteen meters deep. Sibudu is unique in that the stratigraphy preserves a detailed and extensive MSA sequence, spanning from the pre-Still Bay archaeological period (before ~77,000 years ago) to the final MSA (~38,000 years B.P.) (Jacobs et al. 2008; Wadley and Jacobs 2006). While hiatuses do exist between these periods, the fact that several substages of the MSA are present and were systematically excavated is rare. Excellent preservation of seeds, bone, and other organic materials—also uncommon at MSA sites—has allowed for multi-faceted environmental reconstructions for many of the substages of the MSA represented at the site (Wadley and Jacobs 2004, 2006; Allot 2006; Clark and Plug 2008). The comprehensive excavations at this site provides a unique opportunity to explore the extent to which the environment acted as a selective pressure for the behavioral variability seen during the MSA, including transitions in lithic technology and subsistence practices.

Figure 1. Location of Sibudu Cave in South Africa with other sites mentioned in the text (modified from Clark 2009).

Archaeological periods are defined or inferred for the sequence at Sibudu based on differences in the lithic assemblage (Wadley and Jacobs 2006; Wadley 2005, 2007; Lombard 2008). The site preserves deposits from six MSA periods: the pre-Still Bay (before ~77,000 years ago), the Still Bay (~77,000 – 73,000 years B.P.), the Howieson's Poort (HP; ~68,000 – 60,000 years B.P.), the post-HP (~60,000 – 57,000 years B.P.), the late MSA (~50,000 – 45,000 years B.P.), and the final MSA (~40,000 – 37,000 years B.P.) (Wadley and Jacobs 2004; Jacobs et al. 2008). Figure 2 provides a detailed composite stratigraphy section. Variations in lithic raw materials (Cochrane 2006) and archaeomagnetic data (Herries 2006) led Clark and Plug (2008) to divide the post-HP MSA into older (post-HP MSA 1) and younger (post-HP MSA 2) segments. The MSA sequence at Sibudu temporally correlates with several distinctive shifts in global climate. For instance, the pre-Still Bay appears mainly to be contained within Oxygen Isotope Stage (OIS) 5, the Still Bay runs through the end of OIS 5 (~73,000 years B.P.), the HP is completely within OIS 4 (~73,000 – 58,000 years B.P.), and the post-HP through the final MSA coincide mainly with OIS 3 (~58,000 – 27,000 years B.P.) (Figure 2). OIS 5 and OIS 3 are warmer periods, while OIS 4 represents a glacial period. Herries' (2006) archaeomagnetic data revealed higher coercivity minerals, a signal of colder, glacial climates, within the post-HP MSA 2. This led him to hypothesize that the post-HP MSA deposits preserve the shift from OIS 4 to OIS 3 (Herries 2006). Further evidence suggests that the OIS 3 interstadial can be broken into two distinct periods, one from ~60,000 – 45,000 year B.P., during which climate was similar to that of today, and another colder, drier period from ~45,000 – 30,000 years B.P. (Lambeck et al. 2002). This period of instability neatly divides the late from the final MSA at Sibudu. Isotope data collected from fauna across the sequence will allow for more accurate environmental and climatic reconstructions for each of the occupational phases and may also confirm the placement of the OIS4/OIS 3 transition in the sequence. High-resolution isotope data can also provide an indication of the importance of climatic factors in mediating or driving behavioral shifts.

Furthermore, detailed study of backed stone tools revealed changes within the HP lithic assemblage in terms of raw material, dimensions, and possibly hafting techniques (Lombard 2008; Wadley and Mohapi 2008) (see Table 1 for detailed stratigraphy and chronology). Quartz and hornfels artifacts dominate in the two oldest HP layers (PGS and GS2/GS), while dolerite is the main raw material in the youngest HP level (GR2/GR). The dimensions of these segments range from short, narrow quartz segments in PGS to long, wide, and thick dolerite tools in GR2/GR and it has been proposed that the earlier quartz segments were hafted as transverse arrowheads while the later dolerite tools may have been spearheads (Wadley and Mohapi 2008).

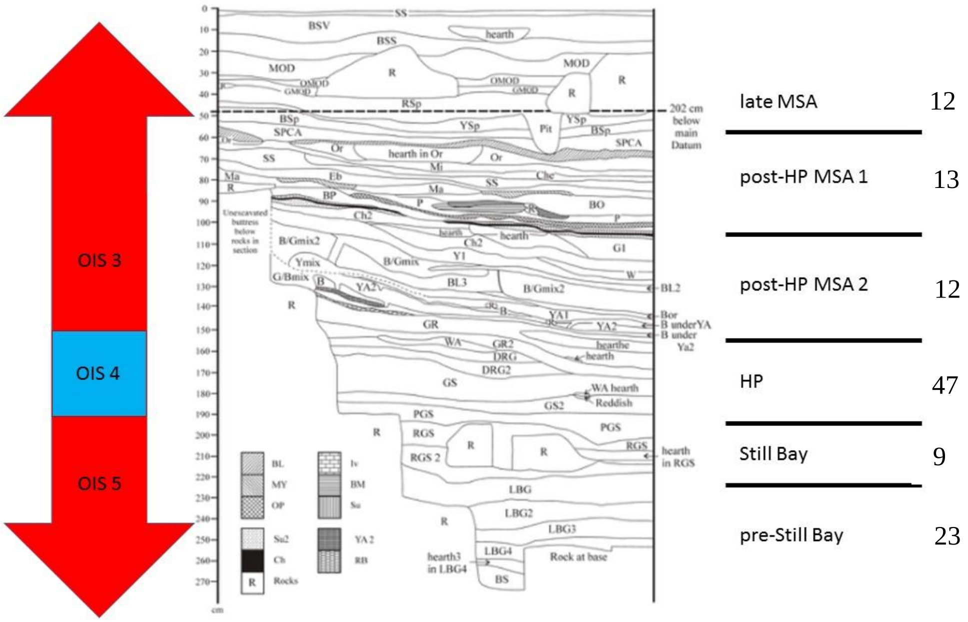

Figure 2. Composite stratigraphic profile of the North Wall of Sibudu Cave with both the global Oxygen Isotope Stage framework and the site MSA timeline provided for comparison. Faunal tooth enamel sample numbers are provided for each MSA period. Note that the final MSA (10 samples) and Iron Age levels are not represented in this profile. Profile drawing modified from Wadley and Jacobs 2006.

Lombard and Pargeter (2008) and Lombard (2008) interpreted different hafting orientations for HP segments from impact and residue analysis. The oldest segments (from PGS) appear to have been hafted in longitudinal, transverse, or back-to-back formations. A shift to diagonal or end-on hafting is seen for the intermediary layer (GS2/GS), with no specific configurations dominating in the final HP layer (GR2/GR) (Lombard and Pargeter 2008; Lombard 2008). Such changes in stone tool technology within a relatively short period may be related to shifts in hunting practices and resource distribution due to unstable climatic and environmental transitions throughout OIS 4.

Table 1. Stratigraphic Layers, Abbreviations, and OSL Dates (dates from Jacobs et al. 2008)

Archaeological Period	**Stratigraphic Designations**	**Abbreviation**	**OSL Date (thousands of years)**
Howieson's Poort	Grey Rocky	GR; GR2	61.7 ± 2.0
	Dark Reddish Grey	DRG; DRG2	
	Grey Sand	GS; GS2	63.8 ± 2.8
	Pinkish Grey Sand	PGS	64.7 ± 2.3
Still Bay	Reddish Grey Sand	RGS, RGS2	70.5 ± 2.3
pre-Still Bay	Light Browinish Grey	LBG; LBG2;	72.5 ± 2.5
		LBG3; LBG4	73.2 ± 2.7
	Brown Sand	BS	77.3 ± 2.7

Environmental Context

Southern Africa is often described as having supported a unique variety of ecosystems and vegetation regimes distinct from the rest of Africa. The Cape Floral Kingdom, representing ~60% of the floral diversity of Africa, has often been described as a late Pleistocene refuge for *Homo sapiens* (Marean 2010). South Africa has a complicated and incomplete regional paleoenvironmental record. In Botswana, Burrough et al. (2007, 2009) report signs of a megadrought between ~110,000 – 95,000 years B.P., slightly later than the megadroughts of eastern/equatorial Africa. However, less than 50 km to the south, at Lobatse Cave, Holmgren et al. (1994) not only report a humid period during this same time, but increasing precipitation based on speleothem analysis. This suggests eccentricity-modulated precessional wet/dry cycles related to changes in southern hemisphere insolation (Burrough et al. 2007). A second event that may have affected southern African wet/dry cycles is the expansion and contraction of the Kalahari Desert during the late Pleistocene. Thomas and Goudie (1984) map out these patterns by determining the times when ancient sand ergs were active. Their results imply that the Kalahari expanded from its modern extent twice during the MSA, between ~140,000 – 100,000 years B.P. and from ~50,000 – 30,000 years B.P. Both periods would be characterized by extreme aridity, perhaps a result of the megadroughts described above. The second period may be identified at Sibudu. The Bar-Matthews et al. (2010) speleothem from Pinnacle Point is the closest high-resolution climatic record to Sibudu. It appears to document vegetation and rainfall shifts between ~90,000 – 53,000 years B.P. in concert with southern hemisphere shifts in temperature. Over this time period there is a general trend toward warmer climate, with more winter rainfall and an increase in C_3 grasses. However, the Pinnacle Point speleothem also reveals periods of rapid environmental change not recorded in marine or regional lake core records. One of these periods is at 72,000 years B.P. when there is an abrupt shift from winter rainfall and C_3 grass dominance to summer rainfall and C_4 grass dominance. This period also corresponds with shifts in lithic technology in the southern Cape leading to the Still Bay industry (Bar-Matthews et al. 2010). It is important to note that Still Bay technology does not appear at the same time in all locations across southern Africa (Jacobs et al. 2008), suggesting that the event recorded in the speleothem may represent a local timescale of a broader South African climatic phenomenon.

Within the modern southern African microcosm, Sibudu Cave is situated in the summer rainfall region with average temperatures between 22 – 25 degrees Celsius. While most of the natural vegetation around the site has been destroyed by farming and modernization, the cliff face preserves a high diversity of Cape Floral vegetation (Wadley and Jacobs 2004; Allott 2005). The Tongati River, a perennial water source, supports forest growth on the cliff face and in the valley, while the rain shadow slopes opposite the shelter are home to Acacia woodlands. Wadley (2006) contends that a similar mosaic of habitats was present throughout the occupation of the site.

Environmental changes within and between the South African MSA archaeological periods have been identified using faunal and botanical data (Jacobs et al. 2008). Climatic and environment shifts occur *within* OISs on the scale of a few hundred or a thousand years. For example, floral and faunal datasets have been utilized to explore the nature of environmental change across the transition from the HP to the post-HP MSA, occurring *within* OIS 4. The HP fauna is comprised of species that preferentially inhabit closed environments, while the fauna from the younger portion of the post-HP MSA suggests a more open, savanna-like environment (Clark and Plug 2008). The charcoal data also reveal a turnover from closed forested environments during the HP to more open, dry conditions in the post-HP MSA 1 (Allott 2006). However, the faunal data from the post-HP MSA 2 (a more recent period) indicate that this transition was a gradual one, with the most abrupt environmental changes taking place *during* the course of the archaeologically defined post-HP MSA (unfortunately, no charcoal data from the post-HP MSA 2 are currently available). This has been further supported by Herries' (2006) archaeomagnetic data from the site.

Isotope Background

Stable isotope characterization of teeth of fossil and modern fauna has been a developing approach of paleoenviromental and paleodietary research for the past twenty years. Paleoecological and paleoclimatic indicators have been interpreted from carbon and oxygen isotopic profiles of African mammalian communities (Lee-Thorp 1989; Kingston 1999; Sponheimer and Lee-Thorp 1999a; Sponheimer and Lee-Thorp 1999b; Kingston and Harrison 2007; Harris et al. 2008; Codron et al. 2009; Crowley 2012). These studies focus on the carbonate fraction of bioapatite in tooth enamel, which has been shown to retain *in vivo* biogenic signals (Wang and Cerling 1994; Koch et al. 1997; Kohn 1999; Lee-Thorp and Sponheimer 2003). This approach classifies large-bodied mammalian herbivores as grazers, browsers, and intermediate or mixed feeders based on the carbon isotopic signature derived from tooth enamel. This research proposes to infer ecological, environmental, and climatic factors based on the signatures of these feeding habits. However, this type of research must be carried out with appropriate caution. Seasonality, competition, migration, social behavior, and a variety of other factors may complicate the link between diet and environmental proxies (Caswell et al. 1973; Behrensmeyer and Hook 1992). In order to minimize these factors as best as possible, diet and paleoenvironments should be reconstructed through a community based approach which includes all foraging guilds (grazers, browsers, and mixed feeders).

Stable carbon isotopic signatures of both modern and fossil herbivore tooth enamel is related to the isotopic composition of vegetation in the food chain (Tiezsen et al. 1983; Ambrose and DeNiro 1986; Cerling and Harris 1999). Terrestrial plants predominantly utilize two different photosynthetic pathways which are identified through the relative abundance of ^{12}C and ^{13}C. Trees, shrubs, and high-altitude grasses typically employ the C_3 photosynthetic pathway. Generally, there is an increase in ^{13}C in C_3 plants from wet to mesic and xeric habitats with $\delta^{13}C$ values being least negative in open, arid environments. Altitude also leads to more positive $\delta^{13}C$ values for C_3 plants (Heaton 1999; Kingston and Harrison 2007). Most grasses employ one of the C_4 subpathways, which are reflected with $\delta^{13}C$ values of between -14‰ to -11‰ (Heaton 1999; Cerling et al. 2003). Arid adapted grasses utilize the NAD-me and PEP-ck subpathways. Grasses in more mesic environments employ the classical-NADP (Hattersley 1992; Chapman

1996). Photosynthetic pathways are ideal for differentiating between browsers, grazers, and intermediate feeders since their carbon signatures reflect gross feeding strategies.

Methods

Fossil faunal tooth enamel samples were collected during the summer of 2011 in the archaeological laboratory at the University of the Witwatersrand, Johannesburg. Samples were gathered from each field season at Sibudu Cave, including April 2011. This allowed for a representative species sample spanning the stratigraphic profile of the site. Each sampled tooth corresponded with a strict stratigraphic description of its placement within the entire profile. Teeth from all field seasons prior to April 2011 were previously identified to taxonomic level, but were confirmed prior to sampling. Specimens from the April 2011 field season and any teeth from previous years with uncertain or dubious identification were reassessed using the comparative zooarchaeological collection at the Ditsong (formally Transvaal) Museum, Pretoria.

In almost all cases, molar enamel was analyzed, limiting the potentially confounding effects of weaning or juvenile dietary signals present in teeth forming during development. Enamel was carefully cleaned of any adhering sediment and weathering rinds with a high speed Brassler-type drill with tungsten-carbide bits. A vertical line of enamel was removed from each tooth, from the cementoenamel junction to the upper crown, resulting in approximately 2 mg of powdered enamel. This process is minimally destructive and ensures homogenization of intra-tooth variability. Powdered enamel was reacted for ~24 hours with ~2% bleach solution in 1.5 ml microcentrifuge tubes to digest any organic material and then rinsed and centrifuged to a neutral pH with double distilled water. This was followed by sample treatment with 0.1 M acetic acid for ~4 hour to remove any secondary carbonate, rinsed to neutrality again, and baked at 25°C to burn off any residual organics. Mass spectrometry was performed at the Center for Scientific and Industrial Research (CSIR) Palaeo-Science and Isotope Laboratory in Pretoria using a Finnigan-MAT 252 mass spectrometer interfaced with a Kiel III carbonate extraction device. Carbon and oxygen values are reported relative to VPDB (Vienna Pee Dee Belemnite). Precision was better than ±0.05‰ for $\delta^{13}C$ ratios.

$\delta^{18}O$ values appear to have been compromised by the extensive archaeological burning at the site (Wadley et al. 2011) and are only referenced here as broad trends. In a controlled experiment with modern faunal tooth enamel it is evident that burning affects $\delta^{18}O$ but not $\delta^{13}C$ values (Robinson and Kingston, unpub. data and see Chapter 2 of this dissertation). Burning appears to result in a regular pattern of $\delta^{18}O$ regression based on temperature, which potentially allows for the comparison of such values within the assemblage but complicates comparisons with other sites. Re-investigation of the faunal tooth enamel samples is underway to determine possible corrections or interpretation of these values.

Statistical Analysis

Due to the compromised $\delta^{18}O$ values only preliminary statistical analysis was carried out with $\delta^{13}C$ values. Analyses were performed with SPSS ver. 20 software (IBM Corp.). Analysis of variance (ANOVA) tests were utilized to investigate how $\delta^{13}C$ shift over time, but only within the Howieson's Poort and from the Howieson's Poort to the post-HP period. A two-way ANOVA design was used with $\delta^{13}C$ as the dependent variable and time and species as the independent, fixed variables. Species is utilized here instead of feeding group due to the negatively shifted $\delta^{13}C$. It is unclear whether traditional grazing, browsing, and mixed feeding categories would be appropriate in this case. The two-way ANOVA is employed to determine if there are any significant interactions effects between time and species.

Results

General

A total of 126 representative enamel samples of 19 herbivore taxa, all identified to species, were analyzed isotopically from multiple stratigraphic horizons, corresponding to each of the six major archaeological periods, within the Sibudu Cave succession (see Figure 2 for sample distribution). Dietary guilds are defined primarily on assessments of relative dietary intake of C_3 and C_4 biomass as revealed by the $\delta^{13}C$ variation in enamel.

In general, $\delta^{13}C$ results from Sibudu indicate significant variation in diet between and within the fossil taxa. No taxa yielded signals reflecting obligate or pure C_4 grazing. The equids, white rhinoceros, wildebeest, and other herbivores typically classified as grazers have $\delta^{13}C$ enamel values consistent with more mixed feeding (Figure 3). There are a couple of possible explanations for these results. First, the vicinity of the Tongati River and associated gallery forest may have led to expanded dietary breadth for many taxa compared to modern relatives, with a relatively greater cumulative browsing strategy. Second, the winter-rainfall pattern which has been interpreted to exist during Oxygen Isotope Stage 4, combined with an apparent decrease in temperatures, favored C_3 grasses over C_4 biomass. C_3 grasslands are known to have expanded in southern Africa during the Last Glacial Maximum under similar conditions (Lee-Thorp and Beaumont 1995; Sealy 1996; this dissertation). Due to the compromised $\delta^{18}O$ values preventing an assessment of temperature or aridity at the site, both explanations are considered plausible with a combination of the two presently favored. It does not appear as if $\delta^{13}C$ are compromised in anyway. Overall environmental patterns, despite the light values, match trends inferred from other paleoenvironmental proxies. Additionally, isotopic distinctions between traditional browsers and grazers have overlapping $\delta^{13}C$ ranges, ruling out any artificial shift in values due to burning or technical error.

The carbon isotopic values reported here are the most negatively shifted of any sub-Saharan archaeological site for the Pleistocene. However, the Pliocene site of Langebaanweg, South Africa offers a possible comparison. Equids and reduncines (waterbuck) which are adapted for grass grazing also have $\delta^{13}C$ enamel values that would be considered consistent with mixed feeding strategies, including substantial browsing. Franz-Odendaal et al. (2002) conclude based on the isotopic results and detailed palynology that these data instead reveal extensive C_3 grasslands associated with a winter-rainfall pattern. While Sibudu has not be reconstructed as an open grassland area, the combination of C_3 grasses and a canopy effect could produce the isotopic results seen here.

Primates, indicative of forested or wooded habitats, are abundant in the Still Bay and HP layers, but disappear during the earliest part of the post-HP period. Additionally, equids and other obligate grazers are absent in the sequence until the later part of the post-HP period (Clark and Plug 2008). Isotopic analysis of the faunal community suggests greater amounts of C_4 vegetation are included in the diet through time from the pre-Still Bay to the final MSA,

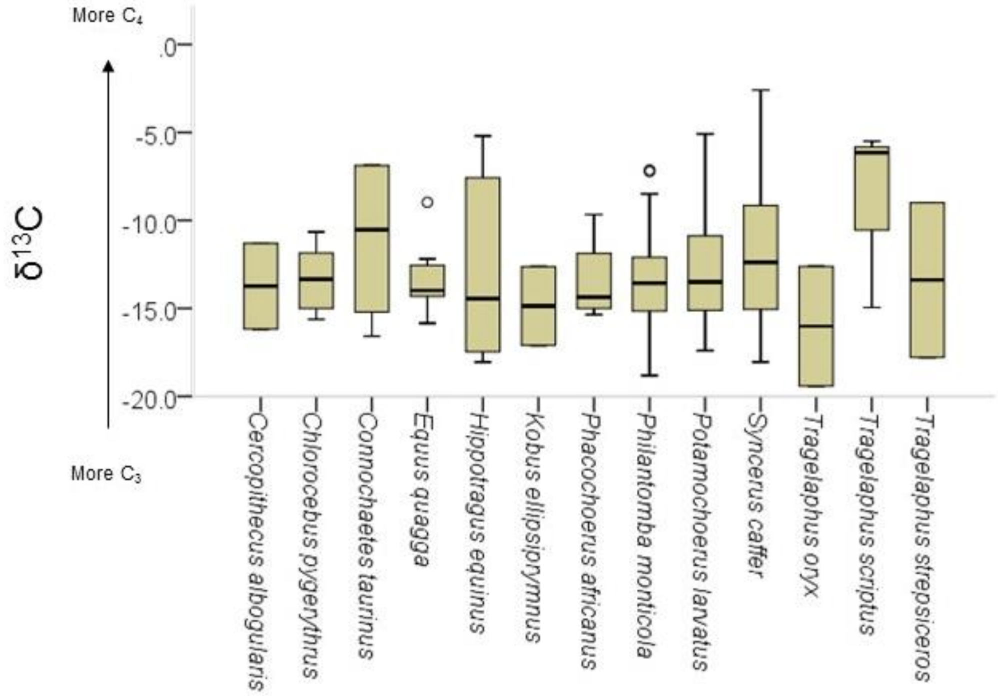

Figure 3. $\delta^{13}C$ ranges for the most common species in the isotope study.

supporting the faunal patterns. It is possible that equids fed on a combination of C_4 and C_3 grasses as the environment opened up but retained some humid-adapted, C_3, grasses in forested areas (Vogel et al. 1978; Tieszen et al. 1979; Kingston 2011).

The main effect of time between the HP and post-HP periods is statistically significant ($p = 0.007$, $F = 8.064$) in ANOVA analyses. There are no statistically significant interactions effects or main effects of species. The trend revealed is from more negative $\delta^{13}C$ values in the HP to more positive values in the post-HP (Figure 4a). This suggests that the closed woodlands of the HP may have opened up slightly in the post-HP period.

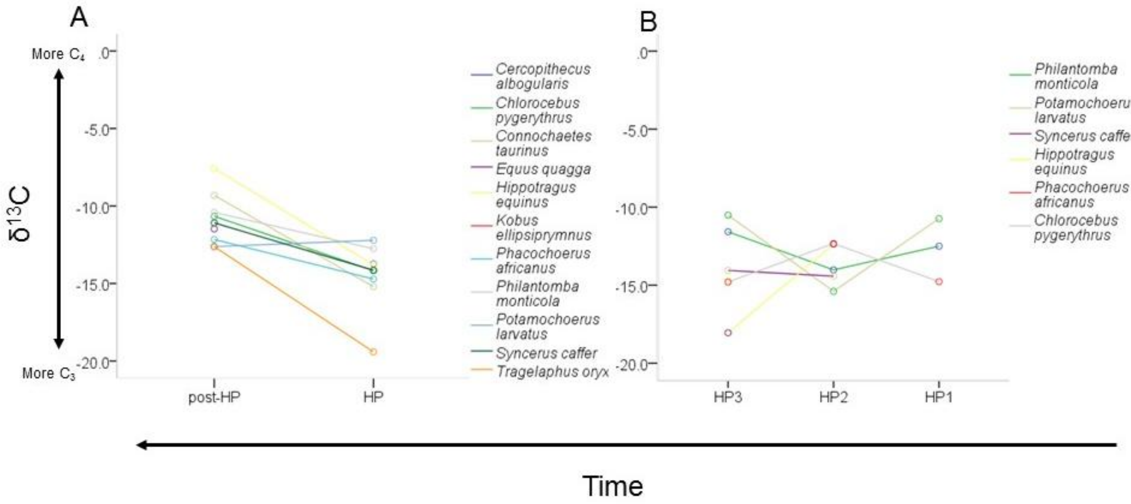

Figure 4. Interaction plots for two-way ANOVAs: A) time condition – HP vs. post-HP is statistically significant; B) time condition – three HP periods is not statistically significant.

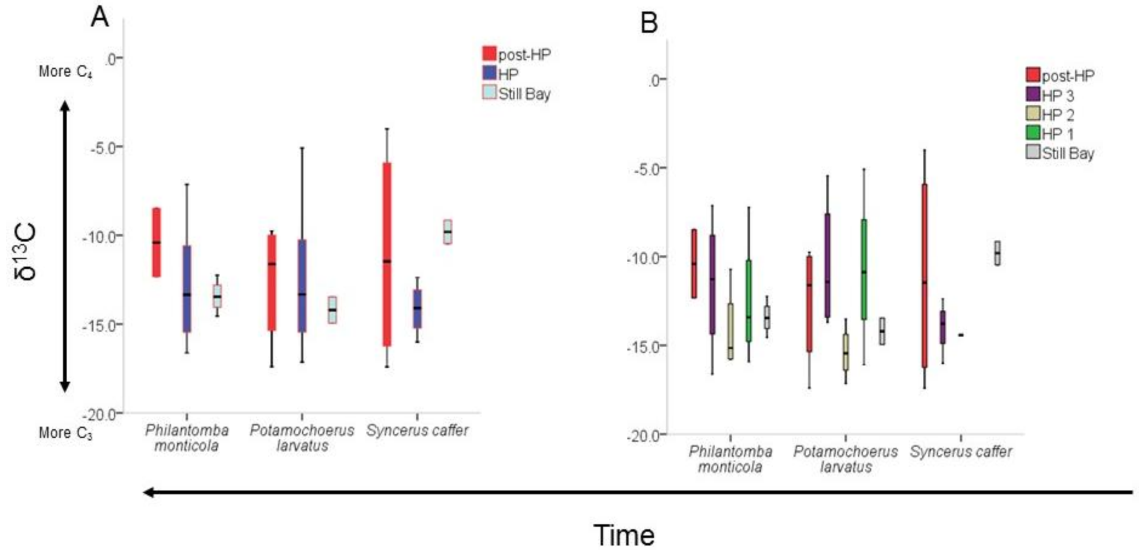

Figure 5. Box-and-whisker plots for the three most common species in the Still Bay, HP, and post-HP: A) the three HP time intervals collapsed into one; B) the three HP time intervals as separate units.

Dividing the HP into three periods based on the lithic analysis reveals a more nuanced pattern. $\delta^{13}C$ values are shifted in a C_3 direction during the Still Bay and the first two HP periods. A shift towards the C_4 end of the spectrum appears in the final HP phase, but returns in the C_3 direction during the post-HP MSA 2. The pattern is more obvious when collapsing the three HP periods into one unit (Figure 5a, 5b). Box-and-whisker plots are provided to show the distribution of the isotopic data. It is important to note here though that ANOVA analysis did not reveal any significant main effects (time: $p = 0.962$, $F = 0.039$) or interactions within the HP (Figure 4b).

While the Tongati River may support a gallery forest and associated wetland grasses throughout the period in which the sequence is deposited, it appears that what were mostly closed woodlands from the pre-Still Bay through the first two-thirds of the HP rapidly became open woodlands with some open grassy patches. This mosaic environment seems to be the environment that dominates the recent portion of the sequence, with varying proportions of C_3 and C_4 grasses and wooded components.

Bovidae

Introduction

Bovids are the most populous large-bodied herbivore family in Africa and are known to have diverged and adapted into a variety of environments and ecological niches. Due to their ubiquity, bovids have been a main component of paloenvironmental research (Sponheimer et al. 1999; Sponheimer and Lee-Thorp 2007; Clark and Plug 2008). While many studies have focused on zooarchaeological analysis and comparison with modern correlates, isotopic study has been less prominent due to the difficulty of securely identifying isolated teeth and fragments and the uncertain nature of taxonomic relationships within the family. However, bovids are by far the most common taxa in the Sibudu assemblage, representing ~55% of all identifiable elements and ~80% of skeletal remains that cannot be identified to species (Clark and Plug 2008). As such a critical group for interpreting paleoenvironmental characteristics, isotopic analysis focused on teeth which could be identified to species in seven bovid tribes.

Tragelaphini

Tragelaphines (*Taurotragus oryx*, *Tragelaphus scriptus*, and *Tragelaphus strepsiceros*) are mixed feeders that have adapted to browse with low-crowned molars and unique digestive tracts. Ancestral forms are thought to have preferred moist woodlands and forests with moderate to heavy cover (Kingdon 1997; Kappelman et al. 1997). Most tragelaphines are variable to obligate browsers, but *T. oryx* is more properly identified as a mixed feeder (Cerling et al. 2003; Sponheimer et al. 2003). δ^{13}C values for eland from the post-HP and HP are -12.6‰ and -19.4‰, respectively. One sample of kudu, also from the post-HP deposits, yields a δ^{13}C value of -17.8‰. Such negative values may also be suggestive of a canopy effect whereby environmental conditions under a dense canopy are known to result in depletion of ^{13}C abundance in plants compared to open contexts (Craig 1954). These changes in of ^{13}C abundance are also known to be passed along to large herbivore consumers (Drucker et al. 2008). More positive δ^{13}C values come from one sample of bushbuck and one of kudu from the late MSA with yields of -5.5‰ and -9.0‰, respectively. Small sample sizes prevent interpreting patterns or shifts in δ^{13}C through time.

Alcelaphini

Alcelaphines from Sibudu studied here include *Connochaetes taurinus* and *Damaliscus pygargus*. Modern forms are variable or obligate grazers suggesting open woodland or grassy habitats. Alcelaphine ranges are restricted by their need for regular access to permanent surface water sources. (Kingdon 1997; Estes 1991). Alcelaphines from the later post-HP and late MSA, include one sample of bontebok and three samples of wildebeest. Samples from these two horizons have an intermediate C_3/C_4 profile with $\delta^{13}C$ values ranging from -6.8‰ to -7.2‰ and one outlier at -14.1‰. Two wildebeest samples from the pre-Still Bay and HP yield very negative $\delta^{13}C$ values at -15.2‰ and -16.6‰, indicating a C_3 dominated diet. Given the adaptations for gramnivory, it is probably likely they were feeding on C_3 grasses. This difference is further added evidence for the existence of C_3 grasslands in the Sibudu region during the MSA. It may also signify that alcelaphines living near riverine forests included some browse in their diets, or were also affected by the canopy effect.

Hippotragini

Kingdon (1997) describes modern hippotragines as preferring dry and grassy localities with few competitors. They are known to subsist primarily on grasses, but can include substantial amounts of browse in their diets during the dry season. The appearance of abundant specimens of *Hippotragus equinus* in the Sibudu sequence is at odds with the lack of evidence of grasslands near or around the site during the MSA (Wadley 2006). However, hippotragines from Laetoli have $\delta^{13}C$ values ranging from -2‰ to -9‰ (Kingston and Harrison 2007) and those from Sterkfontein have values of $\delta^{13}C$ ranging from -1.1‰ to -10.2‰ (Luyt and Lee-Thorp 2003). These data indicate that fossil forms maintained a much greater dietary breadth than modern counterparts and inhabited a greater variety of environs.

Roan antelope is present in both the HP and post-HP deposits at Sibudu. The HP samples have $\delta^{13}C$ values ranging from -5.2‰ to -18.1‰ with an average of -13.8‰. One sample from the post-HP yields a value of -7.6‰. More positive values reflect the more open habitats of the late HP and post-HP periods while some of the most negative values are indicative of closed canopy conditions. In addition to C_3 grasses it is possible that hippotragines were able to compete in browsing and mixed feeding niches during the more severe periods of OIS 4, particularly since the area around Sibudu appears to lack obligate browsers such as giraffids and elephantids.

Neotragini

Identified neotragines are exceedingly rare in the Sibudu assemblage and exist only in the last and final MSA periods (Clark and Plug 2008). Neotragines are adapted to warm, dry conditions and typically inhabit open plains and stony savannas. Despite this habitat, neotragines are dedicated browsers feeding mostly on roots, tubers, and shoots. They can survive long periods without water as they receive most it from their food sources (Kingdon 1997). The single *Raphicerus campesteris* tooth analyzed from the final MSA provided a $\delta^{13}C$ of -16.6‰ which is on the far end of the range of modern forms (Cerling et al. 2003).

Reduncini

Typically considered obligate to variable grazers, modern reduncines yield positive $\delta^{13}C$ values reflecting a C_4 dominated diet. Nevertheless, Cerling et al. (2003) caution that most modern reduncine samples come from populations that are well established in grassy national parks which may complicate the picture when comparing modern examples to archaeological and fossil samples. Three reduncine teeth are included here from Sibudu: one *Redunca arundinum* and two *Kobus ellipsiprymnus*. With $\delta^{13}C$ yields of -12.6‰ to -17.1‰, well outside the modern range, and more negative than any values reported for other fossil localities, reduncines provide evidence for the existence of C_3 grasslands at Sibudu. However, it is unlikely that open C_3

grasslands could result in values like -17.1‰ alone. It must be considered that reduncines engaged in some browsing behaviors and that $\delta^{13}C$ values may reflect canopy effects.

Cephalophini

Cephalophines dominate the bovid assemblage at Sibudu and may well be the most represented mammalian group throughout the sequence (Clark and Plug 2008). Both *Cephalophus natalensis* and *Philantomba monticola* are present and sampled here. These two species are forest dwellers preferring closed canopy forest and subsisting on fallen fruits and other vegetative matter. Modern examples consistently yield $\delta^{13}C$ values < -15‰, indicating heavily closed canopy with essentially a C_3 vegetation composition.

At Sibudu, 31 samples of cephalophines are included in the isotopic study. Table 2 provides the $\delta^{13}C$ ranges and means for the blue duiker in each of the MSA horizons. It is one of only two taxa, along with African buffalo, present in each of the MSA periods in the sequence. The number of samples of blue duiker allows for a unique view of environmental and climatic change over time. The single sample of the red forest duiker comes from the late MSA and yields a $\delta^{13}C$ value of -16.1‰. The general trend is from more negative values in the pre-Still Bay deposits to more positive values in the post-HP. Both the late and final MSA horizons, represented by small sample sizes, yield $\delta^{13}C$ values more negative than the HP and post-HP means. The overall trend may suggest a shift to more open environments during the end of the HP and the beginning of the post-HP.

Table 2. $\delta^{13}C$ ranges and means for the blue duiker in each MSA horizon at Sibudu Cave.

MSA Horizon (sample size)	**$\delta^{13}C$ Range (‰)**	**$\delta^{13}C$ Mean (‰)**
pre-Still Bay (5)	-10.2 to -18.8	-15.2
Still Bay (4)	-12.3 to -14.6	-13.5
Howieson's Poort (16)	-4.9 to -16.6	-12.3
post-HP (2)	-8.5 and -12.3	-10.4
late MSA (1)	-14.7	
final MSA (2)	-13.4 and -17.3	-15.4

Bovini

Only a single species of bovini, *Syncerus caffer*, exists at Sibudu. This species is known mainly as a variable grazer preferring forest or thickets. They require access to surface water and can live in open savannas only by becoming immobile to avoid overheating (Kingdon 1997). African buffalo often yield positive $\delta^{13}C$ values, signaling a nearly pure C_4 diet (Cerling et al. 2003). However, a lesser known subspecies, *S. c. nanus*, is a forest dweller found in closed canopy forest ranging from the Ituri Forest to South Africa. This subspecies prefers low-level browse and waterlogged grasses in glades. Unfortunately, it is nearly impossible to distinguish between subspecies of *S. caffer* even when a substantial portion of skeletal anatomy is preserved, let alone isolated teeth (Kingdon 1997; Vrba 2009).

African buffalo is the second most commonly sampled bovid in the Sibudu assemblage. The isotopic trend is from more negative values during the pre-Still Bay and HP to more positive values during the late and final MSA. The small sample sizes and wide ranges make further interpretation difficult (Table 3). It must also be considered that both the forest dwelling and savanna dwelling varieties are sampled throughout the sequence, perhaps being reflected in the wide $\delta^{13}C$ ranges. Additionally, both variants of *S. caffer* are known to successfully subsist on C_3 browse in environments which lack a suitable C_4 substrate (Kingdon 1997).

Table 3. δ^{13}C ranges and means for the African buffalo in each MSA horizon at Sibudu Cave.

MSA Horizon (sample size)	**δ^{13}C Range (‰)**	**δ^{13}C Mean (‰)**
pre-Still Bay (2)	-14.8 and -15.3	-15.1
Still Bay (2)	-9.2 and -10.5	-9.9
Howieson’s Poort (4)	-12.4 to -16.0	-14.2
post-HP (4)	-4.0 to -17.4	-11.1
late MSA (3)	-2.6 to -10.8	-7.8
final MSA (2)	-5.3 and -18.1	-11.7

Summary

Unlike samples of modern bovids, which tend to reflect specialization as C_3 browsers or C_4 grazers, most specimens from Sibudu reflect some form of mixed C_3/C_4 profile. These results suggest two possibilities: (1) the fossil bovids at Sibudu inhabited a more generalized ecological niche than their modern counterparts, or (2) the existence of C_3 grasslands. C_3 grasslands may have existed at Sibudu either as a result of cooling and aridity during OIS 4, as marsh adapted varieties, or some combination of both. Additionally, it is also most likely that the δ^{13}C values for the bovids sampled at Sibudu are also affected by a canopy effect leading to the negative shift seen in many of the taxa.

The Pinnacle Point speleothem suggests that C_3 grasses were wide-spread in southern Africa during the MSA (Bar-Matthews et al. 2010). Since the faunal assemblage is dominated by forest and closed canopy species, particularly the cephalophines, C_3 grasses may have primarily been varieties that thrive in closed-canopy and/or waterlogged areas. While for some of the bovid tribes here it is possible to interpret their δ^{13}C ranges as a result of mixed feeding and browsing, modern reduncines are not known to include leaves, fruit, or shoots in their diets. It is almost certain that some patches of C_3 grass must have existed to support reduncine groups. Isotope values seem to suggest that environments became more open at Sibudu during the late and final MSA periods.

Rhinocerotidae

Ceratotherium simum is the only member of this family unequivocally identified at Sibudu. It appears highly fragmentary throughout the end of the HP and into the post-HP period. At Sibudu only a single molar from the middle-third of the HP sequence was suitable for isotopic analysis. *Ceratotherium* is believed to have diverged from *Diceros* during the late Miocene (Harris and Leakey 2003). Its appearance has also been linked to the expansion of grasslands and progressive grazing (Carroll 1988). Isotopic analysis of modern *Ceratotherium* evidences its linkage to grasslands, typically revealing a variable to obligate C_4 grazing signal (Bocherens et al. 1996; Cerling et al. 2003). However, some early *Ceratotherium* specimens from the Lower Nawata Formation (7.4-6.5 Ma) (Cerling et al. 2003), and from Chad (4-3.5 Ma) (Zazzo et al. 2000) show a mixed-feeding dietary pattern. *Ceratotherium* from Laetoli indicate a range in feeding ecology from variable browsing (some reflecting pure C_3 browse) to intermediate browsing-grazing (Kingston and Harrison 2007). Sibudu's single specimen falls in the C_3 end of the spectrum. This categorization may be a result of Sibudu being surrounded by extensive forest in the middle of the HP as the $\delta^{13}C$ trends indicate. Another explanation is that *Ceratotherium* did not achieve its modern obligate grazing niche until more recently. Kingston and Harrison (2007) demonstrated an 86% probability that fossil *Ceratotherium* maintained a significantly greater dietary breadth than its modern counterpart. If *Ceratotherium* truly had an opportunistic feeding strategy its $\delta^{13}C$ could be used to compare vegetation cover between sites. In comparison to the described fossil sites, Sibudu would have been more wooded than Kenya and Chad while sharing comparable vegetation cover with tuffs 1 and 6 at Laetoli. In the context of this study though, it is more likely that *Ceratotherium* subsisted on abundant C_3 grasses around the riverine forest.

Hippopotamidae

A single fragmentary *Hippopotamus* tusk was sampled from the final MSA at Sibudu. Without any corresponding molars it is difficult to interpret the results since the formation and physiological patterns of tusks remain somewhat unclear. A tusk sample may be averaged over a long period, even a lifetime, or may represent a specific, shorter-term event (Passey and Cerling 2002). *Hippopotamus* was once thought to be an obligate grazer, but Cerling et al. (2008) discovered a range of $\delta^{13}C$ values in modern samples. These ranges were interpreted to be the result of including some browse in the diet in addition to water-logged C_3 grasses and other vegetation. The Sibudu tusk indicates a C_3 dominated ecosystem, although it is difficult to reconstruct this level of ecological detail on a single tooth.

Primate

Besides *Homo*, four primates have been identified at Sibudu: *Cercopithecus albogulais*, *Chlorocebus pygerythrus*, *Papio,* and *Galago*. These primates disappear from the archaeological record following the earliest post-HP (Clark and Plug 2008). Only *C. albogularis* and *C. pygerythrus* are represented in the isotope study. Both of these species are highly adaptable and can be found in environments ranging from savannas to closed-canopy forests (Kingdon 1997). In this study the $\delta^{13}C$ values of both species suggests that they prefer moderately closed forest canopy and subsist primarily on C_3 vegetation.

Eight samples of vervet monkey spanning the pre-Still Bay through the earliest post-HP are included here. Three pre-Still Bay $\delta^{13}C$ values range from -11.6‰ to -

15.6‰. This range overlaps with four samples from the HP deposits with a range of -12.3‰ to -15.2‰. Based on these values it seems clear that Sibudu was surrounded by a closed woodland or forested regime prior to ~65 ka. Two samples of Syke's monkey yield similar $\delta^{13}C$ values for the HP at -11.3‰ and -16.2‰. A single vervet monkey molar from the post-HP has a $\delta^{13}C$ value of -10.7‰, providing support for a transition to more open environs after ~60 ka.

Equidae

Only one species of equid has been identified at Sibudu, *Equus quagga*. Genetic data suggests that *E. quagga* is a variant of *Equus burchelli*, diverging from the original stock between ~290,000 and 120,000 years ago (Higuchi et al. 1987; Bhoora et al. 2010). Equid diets are hypothesized to have been C_4 dominated since the Miocene global expansion of C_4 biomass (Cerling et al. 1997). Earlier in the Miocene, around 10 Ma, isotopic analysis of equid enamel yields a dietary signal of C_3 browsing or perhaps grazing on C_3 grasses (Cerling et al. 2003; Kingston 1999). Equid enamel analyzed from sites in Africa dating to the last five Myr have yielded $\delta^{13}C$ values confined to -2‰ to 3‰ (Bocherens et al. 1996; Kingston 1999; Cerling et al. 2003).

Assuming that equids are obligate grazers, the relatively depleted values from Sibudu provides clear evidence for the presence of C_3 grasslands. The seven samples of quagga from Sibudu date to the late post-HP period, the late MSA, and the final MSA. $\delta^{13}C$ values stay fairly consistent through time: post-HP -9.0‰ and -14.0‰; late MSA -12.2‰, -12.9‰, and -15.9‰; final MSA -14.2‰ and -14.4‰. These values are more negative than any other archaeological collection of equids, and are interpreted here to be a result of a combination of a closed canopy effect and C_3 grasses.

Lee-Thorp and Beaumont (1995) report yields of -5.2‰ for an assemblage of equids from the Last Glacial site of Equus Cave, Cape Province, South Africa. A possible explanation for the appearance of these C_3 grasses are shifts in or development of winter-rainfall regimes during stadial periods. Equids seem to provide the best evidence at Sibudu in support of Bar-Matthews et al. (2010) interpretation of the Pinnacle Point speleothem showing an expansion of C_3 grasslands. However, the speleothem record ends at ~53,000 B.P., before the post-HP, late MSA, and final MSA at Sibudu or the Last Glacial at Equus Cave. Regardless, Lee-Thorp and Beaumont (1995) argue that the pattern at Equus Cave must represent at least short periods of increased winter-rainfall which would support C_3 grasses. This scenario would also result in a decrease of seasonality – preventing C_4 grasses from having a competitive advantage over C_3 varieties – based on the fact that summer and winter rainfall regimes would be nearly similar (Vogel et al. 1978). Furthermore, the assemblage at Equus Cave dates to roughly the same time as the later portion of the sequence at Sibudu (Lee-Thorp and Beaumont 1995).

Suidae

Due to their omnivorous diet, suids are often considered as a relevant proxy for interpreting hominin paleobiology and complex adaptive strategies (Bishop et al. 1999; Harris and Cerling 2002). Two species are present at Sibudu, *Phacochoerus africanus* and *Potamochoerus larvatus*. *P. larvatus* is the more common of the two with cranio-dental morphology suggesting understory browsing in woodland or forested habitats consistent with modern representatives (Bishop et al. 1999). On the other hand, *P. africanus* is a large-bodied suid with large tusks, both features interpreted as predatordefense useful in more open environments. The dominance of *P. larvatus* in the assemblage alone would suggest a heavily forested environment; however, it has also been suggested that fossil forms of *P. africanus* maintained morphological properties consistent with open woodland dwelling (Bishop et al. 1999).

Analysis of 30 *P. larvatus* enamel samples throughout the Sibudu sequence resulted in a range of $\delta^{13}C$ values from -5‰ to -17.4‰, suggestive of a mixed feeding to C_3 browse dietary preference. Similar to previously discussed taxa, *P. larvatus* shows an overall shift towards a greater C_3 signal in the HP, particularly during the second part of the HP, with the average peaking at -15.5‰. $\delta^{13}C$ yields in this range would imply a heavily canopied forest. Enrichment of ^{13}C is present in enamel dating to the final portion of the HP, with values around -11.5‰. Isotopic carbon yields reflecting more open environments continues through the post-HP period and the late MSA. With only four samples of *P. africanus* the patterns are not as strong, but it is evident that the HP, with an average of -14.5‰, was a more forested time than the post-HP, with an average of -12‰. Warthogs are generally considered grazers, but are known to consume substantial amounts of browse during dry periods (Kingdon 1997). With this in mind the $\delta^{13}C$ yields for the suids probably reflect mixed feeding on C_3 browse and grass. As eclectic and flexible feeders, their dietary patterns would be contingent on the floral composition of the local ecosystem. As a result, Sibudu must have been highly wooded during the HP, but underwent an opening up of woodlands with sparsely distributed C_4 grasses.

Discussion

Isotopic data from Sibudu offers a unique perspective on faunal foraging strategies both during specific periods of the MSA and throughout the archaeological sequence. The majority of the taxa are characterized as variable to obligate C_3 consumers, with the $\delta^{13}C$ values of equids and reduncines, suggesting that C_3 grasses were an important part of the diet (and landscape). From the above review it appears as if C_4 grasslands may have become a more important part of the landscape after ~50,000 years ago, but that C_3 grasses persisted through the late and final MSA periods. It is possible that the expansion of C_3 grasslands was a response to changing climate linked to the expansion of the Kalahari. Cooler and wetter conditions are known to give C_3 grasses a competitive advantage over C_4 types (Teeri and Stowe 1976; Paruelo and Lauenroth 1996; Tipple and Pagani 2007). In fact, Chase (2010) argues that it is under exactly these types of conditions that the Howieson's Poort spread during OIS 4. *Ceratotherium*, *P. africanus*, *S. caffer*, and *H. equinus*, all believed to be variable to obligate grazers, also yield isotopic signatures indicating some consumption of C_3 grasses.

While modern correlates tend to offer the best insight into the ecology of fossil faunal taxa, it is clear from this study that MSA lineages maintained a more eclectic dietary guild than extant counterparts. Cerling et al. (2003) and Sponheimer et al. (2003) both provide extensive lists of $\delta^{13}C$ ranges for modern taxa in East and South Africa. Very few of their results imply intermediate feeding adaptations, which are typical at Sibudu as well as at many of the other fossil sites discussed above (Sealy 1996; Franz-Odendaal et al. 2002; Kingston and Harrison 2007). Fossil herbivore lineages sampled and/or foraged differently in these environments than their modern representatives, and, as such, maintained fundamentally different feeding niches. In addition to C_3 and C_4 grasses, it is likely that many taxa sampled here also included browse in their diets.

Modern species may have been forced to become specialists as a result of increasing competition for less quality resources, whereas isotopic signatures of fossil forms reflect shifting niche partitioning as competing taxa become extinct or experience adaptive radiations (Kingston and Harrison 2007).

Shifting environments and land cover, as indicated by changing diets in the various herbivore guilds, are evident at Sibudu throughout the sequence. This is especially true for those species recovered from most (if not all) of the MSA archaeological units. *P. monticola*, *P. larvatus*, and *S. caffer* all clearly show a trend of increase in closed canopy cover – either through increased consumption of browse or consumption of closed-canopy adapted grasses – during the first two parts of the HP (~68,000 – 63,000 years B.P.) followed by a rapid opening of environments during the final stage of the HP and the post-HP period (~61,000 – 56,000 years B.P.). Other strata in the sequence appears to reflect these more open environments, perhaps with some added woodlands or forests around the Tongati River. The isotopic results suggest that ^{13}C depletion was a result of a combination of expanded forests and shifts in winter-rainfall patterns supporting C_3 grasslands and/or more closed canopy conditions. The shift towards more open environments at other times is supported by the shift in the faunal assemblage as well, consisting of more open-habitat, grazing forms such as alcelaphines, tragelaphines, and equids after the earliest post-HP period (Clark and Plug 2008). Isotopic signatures of these taxa indicating ^{13}C enrichment may signify a greater presence of C_4 grasslands in the late and final MSA at Sibudu, an increase in aridity. It does seem that by the post-HP Sibudu habitats were locally grassier than prior to ~60,000 years ago and that new habitats were available.

In comparison with modern correlates, the grazers from Sibudu, particularly *P. africanus*, *E. quagga*, and *H. equinus*, have greater intra-specific carbon isotopic variability. This could connote greater ecological diversity leading to more varied feeding niches and increased C_3 grass consumption due to shifts in resource availability. Morphological analysis and comparison with modern examples of these grazers led Clark and Plug (2008) to conclude that the post-HP period was characterized by some open grasslands. If so, it is likely these were primarily C_3 grasslands. Shifts in resource availability does not only affect faunal diets, but are also a driving mechanism in hominin behavioral changes as evidenced in shifting lithic assemblages during the HP (Lombard 2006, 2008). Kingston and Harrison's (2007) assertion that a single taxon could never be an "isotopic ecological indicator" is confirmed by the above results. It is clear that fossil lineages were more flexible and variable than expected based on modern examples, and that the fossil taxa maintained greater dietary breadth through times of environmental and climatic change.

Overall, Sibudu was dominated throughout the MSA by a woodland ecosystem that, perhaps anchored by the Tongati River, became heavily closed and forested during the HP. The presence of the river and forest along with cool and moist climates encouraged the growth C_3 grasses. From the last part of the HP onwards Sibudu was characterized by a more open woodland environment which may have supported some extensive C_4 grassy areas. The proportion of C_3 and C_4 grasses during this later period at Sibudu is currently unknown. Regardless, throughout the sequence, and compared with modern herbivore isotopic profiles, the Sibudu cumulative dietary spectrum is heavily weighted towards C_3 biomass. At present it isn't possible to correlated $\delta^{18}O$ trends with the interpreted shifts in vegetation due to apparent fractionation of the oxygen values.

Conclusions

The dietary ecology inferred for the vast majority of the 19 herbivore taxa representing 6 families reveal an eclectic and flexible diet and the appearance of C_3 grasslands during OIS 4. Compared with fossil sites and modern correlates, Sibudu isotopic enamel signatures exhibit complex and variable foraging patterns, reflecting dynamic intrinsic biotic and external climatic forces on the ecosystem. For instance, the community of *S. caffer*, *P. monticola, C. taurinus,* and *C. pygerythrus,* which dominate the assemblage through time, displays clear shifts in carbon values across MSA archaeological boundaries. Heavily forested environs of the pre-Still Bay slowly shift through time to open woodlands and grasslands. As the HP has been dated to ~68,000 – 60,000 years B.P., well before the Kalahari expansion of ~50,000 years ago, it suggests that Sibudu was not significantly affected by this event, but instead reflects some of the patterns evident in the Bar-Matthews et al. (2010) speleothem. It is also possible that the Sibudu area did not fully recover from the first Kalahari expansion between ~140,000 and 100,000 years B.P. (Thomas and Goudie 1984; Thomas and Burrough 2013). Without material from earlier in the Pleistocene from Sibudu it is impossible to know if the area was affected by a major arid event which continued between the two desert expansion events with my data simply picking up local variation. More data from Sibudu and other sites is required to clear up any relationship to the Pinnacle Point speleothem or Kalahari expansion.

Shifts in $\delta^{13}C$ isotopic values during the HP appear to correlate with transitions in stone tool technology and strategies. Situating hominins within a woodland or woodland-forest mosaic has recently become the norm (Kingston and Harrison 2007; White et al. 2009; Potts 2012). This shift from the savanna as the preferred habitat of hominins requires new adaptive explanations for tool use and manufacture within the unique selective pressures of environments like those inferred for Sibudu. The appearance of bow-and-arrow technology at 64,000 years B.P. is correlated with the opening of the canopy forest near the end of the HP. Sellet et al. (2006) argue that bow-and-arrow technology would have been most useful in moderately closed to open forested and woodland environments. In these environments bow technology would have allowed a greater build-up of kinetic energy for a projectile in restricted areas. More open environments may also be tied to shifts in resource availability (Nelson 1991) and risk aversion strategies (Fitzhugh 2001), leading to innovation. When the climate changed at the end of the Still Bay period and the forests around Sibudu opened up, the traps and snares, which Wadley (2010) argues were used in the Still Bay, were less effective. However, the appearance and development of backed microliths does not appear to be related to the environmental patterns. Sibudu is interpreted to maintain a forested environment from the pre-Still Bay period through the late HP. During this time the technological assemblage shifts from large unifacial lanceolate points to the backed microliths with no discernable environmental prompting. It is possible though that microliths were not an adaptation to changing environments at Sibudu, but rather brought to Sibudu by mobile groups migrating to the coast from the interior during OIS 4. At Sibudu the larger population size and increased interaction with these mobile groups may have led to experimenting with different raw materials and hafting techniques (Lombard 2008; Wadley and Mohapi 2008) as the environment shifted throughout the HP time period. Utilizing the results of the isotopic analysis from the other sites included in this dissertation, the conclusion offers a more detailed discussion of how changing and unstable environments combined with greater residential mobility may have led to the spread, development, and, at times, disappearance, of mircolithic tool technology.

Chapter 6
Synthesis, Conclusions, and Future Research

This dissertation has studied the ways in which known global and regional climatic events are differentially recorded at individual archaeological sites which were locations of human occupation and behavioral transitions. With the exception of Sibudu Cave, careful evaluation of the chronology of the remaining sites shows that my study came to focus primarily on the time period ~40,000 – 10,000 years B.P., which encompasses the Last Glacial Maximum, broadly defined as Oxygen Isotope Stage 2 and lasting from ~27,000 – 13,000 years B.P. Based on an investigation of the stable isotope values of fossil faunal tooth enamel from the sites of Lukenya Hill, Kenya, Omo-Kibish and Porc Epic, Ethiopia, and Kalemba Rockshelter and Makwe Caves, Zambia, I argue that there were important climatic and environmental differences between modern Kenya, Ethiopia, and Zambia during the late Pleistocene. These differences include the lack of a shift towards increasing aridity in Ethiopia at the onset of the Last Glacial and a phytogeographic transition in grasslands in Zambia as a result of changing climatic conditions. In the case of Sibudu Cave it appears as if climatic instability during Oxygen Isotope Stage 4 may correlate with changes in the raw materials and hafting techniques of the Howieson's Poort. It is possible that a phytogeograhic transition occurred here as well, supporting the contention that pockets of C_3 grasslands were a common feature of glacial periods. I have suggested that these site-specific climatic and environmental profiles played a critical role in the development of modern human behaviors, the organization of trade and social networks, the formation of refugia, and the nature of migratory routes within and out of Africa.

In Chapter 1, I presented the following research hypotheses:

Environmental and Climatic Set:

Null H_o: Regional environmental reconstructions are compatible with site-specific environmental/climatic changes inferred from isotopic analysis

Alternative 1: Site-specific paleoenvironmental reconstructions may reveal temporal asynchrony in the onset of regionally documented climatic shifts

Alternative 2: Regional climate regimes are manifested locally in variable ways

Faunal Set:

Null H_o: Late Pleistocene fauna with extant representatives will show similar ranges of oxygen and carbon isotopic values to those modern populations

Alternative: Sites experiencing different climatic and environmental events will reveal within-taxon differences in oxygen and carbon values between sites

I now attempt to provide succinct responses to these hypotheses and to provide a broader framework to consider human-environment interactions.

Environmental and Climatic Hypotheses

Regional climatic records for the Last Glacial Maximum and the period just preceding it are based primarily on speleothems, marine and lake cores, and offshore pollen records. These records reveal increased fluvial activity and precipitation during Dansgaard-Oeschger cycle 11 (~43,000 years ago) which is correlated with increased Northern Hemisphere insolation (Revel et al. 2013; Wolff et al. 2010). By ~35,000 years B.P. the eccentricity-modulated cycles which dominated much of the late Pleistocene were dampened leading to global cooling which may have also slowed the North Atlantic thermohaline circulation. Over time this event reduced the land-sea thermal gradient and shifted the location of the Inter-Tropical Convergence Zone. In Africa, both the West African and Indian Ocean monsoon systems were reduced resulting in increased aridity in the eastern and central portions of the continent and helping usher in the Last Glacial (Vidal and Arz 2004; Tierney et al. 2008). Based on this reconstruction one would expect a clear shift in $\delta^{18}O$ from lighter to heavier values over time signaling aridity. Changes in $\delta^{13}C$ across the maximum are expected to be minimal. Modeling of vegetation during this time period suggests primarily altitudinal as opposed to latitudinal shifts in Africa (Saltre et al. 2013; Potts et al. 2013). Furthermore, any minor shifts in vegetation may not be identifiable in the isotope study as animals may simply track their preferred food sources along those altitudinal gradients. These are the conditions which would support the null hypothesis. However, considering all five sites in the primary study, there is strong scientific support for the alternative hypothesis.

At Lukenya Hill the predicted $\delta^{18}O$ shift is seen and accompanied by no perceivable change in $\delta^{13}C$. If this was the only site included in the study we would probably accept the null hypothesis. A slight shift in $\delta^{13}C$ is apparent in the mixed feeder category at Lukenya Hill suggesting the inclusion of more C_4 vegetation in the diet over time. However, the mixed feeding category contains a variety of taxa with different physiological characteristics and relying on this as proof of a major phytogeographic transition is not advisable.

The predicted $\delta^{18}O$ shift towards aridity is also seen in Zambia, whether Kalemba Rockshelter is considered alone or Makwe Caves is included to create a broader eastern Zambia chronology. At Kalemba though there *is* a major phytogeographic transition. By the peak of the Last Glacial (~17,000 years B.P.) high-latitude C_3 grasses appear. Unlike the models of Saltre et al. (2013) and Potts et al. (2013), this is more than just an altitudinal shift as the maximum elevation of the site is 1300 meters above sea-level, well below where C_3 grasses normally exist in Africa. Increased aridity and decreased temperatures, also present in the Lake Malawi drill core records (Woltering et al. 2011; Ivory et al. 2012), throughout the late Pleistocene and into the Younger Dryas allowed C_3 grasslands to expand. The Last Glacial is also correlated with one of the last great expansions of the Mega-Kalahari desert to the north and east maintaining the arid conditions of central Africa (Thomas and Burrough 2013).

While in both Kenya and Zambia part of the condition for the null hypothesis appears to be true, there is no such shift in $\delta^{18}O$ at either Omo-Kibish or Porc Epic. These sites have the heaviest $\delta^{18}O$ values throughout the late Pleistocene, but the values remain remarkable stable through time. At Omo-Kibish there is actually a slight shift towards lighter $\delta^{18}O$ from Member I to Member IV. It is difficult to say if this shift is the result of any real increase in precipitation, although overall $\delta^{13}C$ move slight towards the C_3 end of the spectrum over this same time period. Porc Epic does not have any perceivable shifts in $\delta^{18}O$ or $\delta^{13}C$ throughout its occupation. One issue to consider is that the exact chronology of Porc Epic is still unclear. Recent study suggests that the sequence spans the Last Glacial (Z. Assefa pers. comm.), but others have concluded that it only contains a short-lived occupation from ~43,000 – 32,000 years B.P. (i.e. Rosso et al. 2013). Regardless of the chronological discrepancy, the isotope study clearly demonstrates the fact that both sites were characterized by heavy $\delta^{18}O$ throughout the late

Pleistocene and that there may have been some increased precipitation in the Omo region during the broadly defined Last Glacial.

Oxygen Isotope Stage 4 in South Africa has been described as a wet, cool, stadial. Models of vegetation cover suggest that there was little change in the proportion of forests and grasslands (McCall 2006; Chase 2010). At Sibudu archaeological burning has compromised the validity of the $\delta^{18}O$ values so it is not possible to test whether there are temporal shifts in aridity. However, the $\delta^{13}C$ values appear to be unaffected by burning and tell a surprising story. Almost all fossil faunal tooth enamel samples from Sibudu are shifted in the C_3 direction, including the grazers. Without the $\delta^{18}O$ values it is difficult to interpret these results, but it is likely that the $\delta^{13}C$ values are the result of a combination of increased browsing by traditional grazers and the appearance of pockets of C_3 grasses. With evidence for C_3 grasses at other South African sites during the later Last Glacial stadial (Lee-Thorp and Beaumont 1995; Faith 2013), it wouldn’t be surprising if C_3 grasses also appeared and expanded during prior stadials. Further investigation of the Sibudu site and re-consideration of the enamel samples are planned to clarify what is happening in eastern South Africa.

At present, the data reported here must be interpreted to reject the null hypothesis. Alternative hypothesis 2 – global and regional climatic regimes are manifested locally in variable ways – is the best supported by the current analysis. Alternative hypothesis 1, which allows for temporal asynchrony in terms of the onset of specific global and regional events is rejected by the lack of climatic and environmental change in Ethiopia. Paleoenvironments at the site of Moche Borago in Ethiopia are also interpreted to be warm and very arid after the end of the eccentricity-modulated precessional cycles

(Fisher 2010; Brandt et al. 2012). However, no direct isotopic analyses of fauna have been done at this site to provide a comparative dataset. Furthermore, the phytogeographic shift apparent in Zambia appears to be a local phenomenon, although it is known that C_3 grasslands expanded in South Africa during this time as well (Lee-Thorp and Beaumont 1995; Sealy 1996). South Africa has an established modern winter-rainfall zone with C_3 grasslands in abundance while no C_3 grasses exist below 1500 meters above sea level in Zambia today (Chase and Meadows 2010). Similarly, Sibudu Cave is outside of the winter-rainfall zone in a region where C_3 grasses are not known to exist at all (Vogel et al. 1978). Unless new evidence from Ethiopian sites, in particular Omo-Kibish and Porc Epic, reveal the expected shifts to aridity with the onset of the maximum, it seems evident that regional climatic records are not sufficient for characterizing the environmental context of individual archaeological sites.

Faunal Hypotheses

The vast majority of taxa sampled as part of this study are extant. Two exceptions to this rule are *Damaliscus hypsodon* sampled at Lukenya Hill and *Pelorovis antiquus* sampled at Porc Epic and Omo-Kibish. Generally, the $\delta^{18}O$ and $\delta^{13}C$ values reported here fall within the ranges reported for modern examples of these taxa (Cerling et al. 2003; Sponheimer et al. 2003; van der Merwe 2013). As a general rule $\delta^{18}O$ values are under-reported and establishing a true range for some taxa is not possible at the current time. It is also well known that $\delta^{18}O$ shift over a broader range than $\delta^{13}C$ simply for the fact that animals have no way of knowing, or any known care, for the isotopic composition of their water. Despite the complexity of water flux through the atmosphere it is more directly an indicator of the environment than carbon (Lee-Thorp and

Sponheimer 2007; Crowley 2012). This would seem to suggest that the null hypothesis is accepted. However, there are important exceptions which imply that certain environmental and climatic conditions lead to within-taxa differences between sites – the alternative hypothesis.

In this study the preeminent example of these within-taxa differences is of *Equus burchelli*. The common zebra is sampled at all sites in this study, most often at Lukenya Hill and Kalemba Rockshelter. At Lukenya Hill all *Equus burchelli* specimens fall within or very near the modern range of $\delta^{13}C$. The majority of samples from Kalemba also fall in this range and reflect obligate C_4 grazing. However, a handful of samples of *Equus burchelli* from the Last Glacial portion of the sequence at Kalemba are more negative and towards the C_3 part of the vegetation spectrum. Other grazers at Kalemba, including *Redunca arundinum* and *Kobus ellipsiprymnus*, also reflect feeding on C_3 vegetation during the maximum. Additionally, most grazers from Sibudu – *Equus quagga*, *Syncerus caffer*, *Connochaetes taurinus*, *Kobus ellipsiprymnus*, and *Redunca arundinum* – are shifted in the direction of lighter $\delta^{13}C$. Ranges for *Equus* sp. and *Redunca arundinum* from Kalemba and Sibudu are comparable. Such values for these taxa are not recorded at the other sites in the study or in any modern datasets.

Despite far fewer modern datasets of $\delta^{18}O$, quite a few taxa show generally lighter ranges than are reported today. The implications of this finding are difficult to interpret partially due to the fact that most modern datasets come from managed game parks and preserves with restricted, and sometimes human-supplemented, water sources (Cerling et al. 2003; Crowley 2012). Taking the archaeological and modern ranges on face value it appears that the late Pleistocene may have been slightly wetter than modern ecosystems –

which in isotopic studies tend to be east African game reserves such as the Serengeti. It is simply possible that this is not a valid comparison. Other possibilities are that the source of precipitation was different in the late Pleistocene than it is today, or even that the source of precipitation at certain sites in the study does not match that over modern isotope study sites. This appears to be the case in Zambia where modern water sources have lighter $\delta^{18}O$ values than those in east Africa (IAEA 2013). Without comparative modern isotopic datasets from central Africa it is unclear if there is any difference between archaeological and modern animals.

Even with these uncertainties, within-taxa differences both within and between sites in this study are apparent. At both Lukenya Hill and Kalemba Rockshelter most taxa reveal shifts from lighter to heavier $\delta^{18}O$ over time. Mean values for *Damaliscus hypsodon* during the pre-Last Glacial and the Last Glacial time period are statistically significantly different from each other at the $p<0.05$ level. Values for *Equus burchelli*, *Connochaetes taurinus*, *Sylvicapra grimmia*, *Gazella thomsonii*, and *Kobus ellipsiprymnus* are not statistically significantly different, but all reveal major shifts over time. It is clear that prevailing environmental and climatic conditions have implications for the isotopic values recorded in faunal tooth enamel.

With these data and patterns in mind, the alternative faunal hypothesis is best supported by this dissertation research. I stress that this does not mean archaeological representatives necessarily had different feeding and/or drinking habitats than modern animals. Even in the case of *Equus* sp. and other grazers at Kalemba and Sibudu it appears that they continued to consume grasses, but the photosynthetic properties of those grasses changed. There is no indication that any modern grazers were engaging in substantial browsing in the late Pleistocene. This result does support Crowley's (2012) contention that isotopic analyses can reveal more about an animal's diet and habitat than zooarchaeological and mesowear analysis alone. It appears as if certain taxa displayed broader dietary and habitat breadth than their modern forms (i.e. Kingston and Harrison 2007; Kingston 2011). More importantly, this is another conclusion in support of intensive, site-specific, paleoenvironmental reconstructions through time. Based on faunal community composition the sites of Lukenya Hill and Kalemba Rockshelter would have been interpreted to have nearly identical climatic and environmental conditions. Without the isotopic study of *Equus burchelli* the phytogeographic transition and its implications for human-environment interactions would have not been identified.

Isotope Study in Broader Perspective

In 1981 Andrew Hill posed the question "Why study paleoecology?" This was not an antagonistic question, but rather his way to force researchers to move beyond data collection and to develop testable hypotheses for studying human evolutionary history. In many ways Hill's questions and challenges remain relevant today. In partial response to this, Kingston (2007) describes a hierarchical classification system for paleoecology which considers the importance of different scales of relevant data. He states that the "emphasis of…evolutionary paleoecology revolves on developing 'snapshot' habitat reconstructions for specific…localities" (2007:29). Kingston also notes that relying on a singular image to interpret adaptive trends is fraught with uncertainties. This dissertation takes the 'snapshot' approach a step further by creating a small "album" in an attempt to circumvent the issues of developing adaptive perspectives based on a single site. In fact, this approach demonstrates that a singular ‘snapshot’ is most likely a unique occurrence as opposed to a generalized condition.

In the previous chapters I have provided some suggestions as to the role Last Glacial and Oxygen Isotope Stage 4 environments and climates may have played in late Pleistocene human behavioral or cultural evolution. Here I attempt to provide a synthesis of how mobility patterns, subsistence strategies, social organization, and tool technology may have varied in response to the paleoenvironmental uncertainty of the Last Glacial Maximum based on the “album” approach. Demography and behavior do not develop in a vacuum, but are inherently tied to the transmission of cultural ideas and residues passed from generation to generation and from group to group (Durham 1991, 1992; Boyd and Richerson 1985, 2009). In an attempt to model the relationship between environment and behavior I borrow some ideas from the field of evolutionary culture theory, particularly the importance of population size (Shennan 2001; Powell et al. 2009; Richerson et al. 2009; Henrich 2001, 2004). It is important to note these models are typically considered at a more fine grained level than here, but it is possible to apply the logic of these theories and models to the late Pleistocene.

In order to respond to d’Errico and Stringer’s (2011) call for a research strategy which links the environment and cultural adaptation it is necessary to borrow from evolutionary culture theory an understanding of the conditions under which there may be a change in behavior. Theoretical models of behavioral change developed by Boyd and Richerson (1990), Henrich and Boyd (1998), and Henrich (2004) identify rates of migration or interaction as the principal component in the stability of social conformity. The size of a migration or degree of inter-group interaction must be sufficiently large to tip the balance of cultural selection *and* to maintain or ratchet the new behavior (Tomasello 2009; Tennie et al. 2009). Powell and colleagues (2009) suggest that populations reached a critical threshold approximately 100 ka which allowed for ratcheting to overtake the rate of knowledge loss. Modern hunter-gatherers are known to disperse and migrate when encountered with unpredictable environments or living conditions. It is during these times that they adopt more flexible behavioral strategies and are more likely to invent or borrow new tools or behaviors to exploit varying ecological resources (Yellen 1977; Fitzhugh 2001).

In the context of stadial climates it would be expected that human populations would disperse and move about the landscape as aridity set in and their resource base migrated to more stable environments. For instance, stadials earlier in the Pleistocene are known to have shrunk the Congo rainforest at the expense of grasslands (Dupont et al. 2000). The sites of Kalemba Rockshelter and Lukenya Hill appear to be less densely occupied at the height of the Last Glacial ~17,000 years B.P. (Phillipson 1976; Marean and Gifford-Gonzalez 1991). It is likely that during the driest period occupants at Kalemba would have migrated to the east towards Lake Malawi. Late examples of Middle Stone Age technology have recently been (re)discovered at the Airport and Mwanganda’s Village sites along the northern lake catchment area (Thompson et al. 2013; Wright et al. 2014). Similarly the occupants of Lukenya Hill may have also sought out a refuge near a permanent water source which buffered them from the environmental conditions.

It is clear from the isotope analysis that $\delta^{18}O$ values were heavier, signaling aridity, throughout time at Omo-Kibish and Porc Epic than in any other region included in this study. Despite this environment human groups lived at these Ethiopian sites, perhaps as a result of rivers which received fresh input from the highlands. During the Last Glacial these sites appear to be remarkably climatically stable while locations to the south and north experience severe drying. While the small lakes in Ethiopia and Somalia contracted and dried up during the late Pleistocene and early Holocene (Hildebrand 2003), rivers continued to be feed by highland precipitation (McDougall et al. 2008). Additionally, both the Omo-Kibish and Porc Epic sites are located at the intersection of different ecotones providing a variety of habitats and resources (Assefa et al. 2008; Assefa 2006). Inhabitants of these sites may have been restricted in their movement due to severe drought conditions in adjacent areas, but were able to survive in these perennially arid regions due to predictable resources. It is also for these reasons that Ethiopia may have been a type of refugia for human populations during the Last Glacial and acted as a cul-de-sac of migrations within and out of Africa.

The relationship between environment, social interactions, and technology has been modeled in many different contexts. In general, these models link technological complexity and diversity with increasingly complex social and political units (Adams 1966; Boserup 1981). For example, Rautman (1993) argues that social networks within a region may reduce the risk of resource stress by facilitating access to resources in other areas. On the other hand, a world-systems theory approach argues that environmental deterioration is an impediment to expanding an exchange system or incorporating new technologies (Kardulias and Hall 2008). However, any evolutionary explanations for inventive and innovated behaviors in these models are contextualized in agricultural or early state societies. Fitzhugh (2001) provides one of the few models considering these relationships for a stone tool-based culture, and, as such, is most applicable to this study.

Building on Fitzhugh's (2001) risk-sensitivity model it is during periods of uncertain and oscillating environmental conditions that innovative behaviors or technologies would be adopted. At both Kalemba Rockshelter and Lukenya Hill the period of reduced occupation is accompanied by changes in the stone tool industry, namely Late Stone Age microliths. It is unclear whether microliths are related to more mobile or more sedentary populations. Microliths require substantial time investment hafting and developing mounts for composite tools (Belfer-Cohen and Goring-Morris 2002). Lombard and Phillipson (2010) suggest that microliths at Sibudu Cave are utilized to in bow-and-arrow technology which would be more conducive to closed wooded environments (Sellet et al. 2006). This is often considered to be the functional approach (Becker and Wendorf 1993; Odell 1994). At the same time though, it has been suggested that microliths involve greater mobility as they are less resource intensive, lightweight, and amenable to multi-component designs (Shott 1986; Ambrose 2002; Whallon 2006). Tool maintenance would be more efficient with a standardized form and interchangeable components (Bar-Yosef and Kuhn 1999). The ability to have a cache of microliths on hand provides greater flexibility with regards to raw material access and in controlling risk (Bamforth and Bleed 1997). After having reviewed these arguments I believe the mobility viewpoint is most applicable to this study. It is most likely that adaptation of microliths is variable in different parts of the world and different times based on local conditions – and I do not advocate here that mobility is a single-factor explanation for the appearance of microliths throughout the world. Instead, I believe that the adaptation of microliths during the LGM in central Africa is an evolutionary response to unstable and uncertain environments leading to greater seasonal or residential mobility.

Microliths do not first appear in the Late Stone Age, but rather have Middle Stone Age origins. In southern Africa the Howieson's Poort microlithic toolkit existed during Oxygen Isotope Stage 4. It then disappears from the archaeological record (Ambrose and Lorenz 1990; Jacobs et al. 2008; Chase 2010). However, the late Pleistocene archaeological record for interior parts of South Africa, Zimbabwe, and Zambia is too sparse to conclusively say microliths completely disappeared from southern African toolkits. In fact, it is not even clear where the Howieson's Poort came from to begin with.

Looking to the future the Howieson's Poort provides an interesting test case for the mobility model of microlith adaptation. Perhaps mobile populations in the Mega-Kalahari had been using microliths for thousands of years before they made their way to the South African coasts during Oxygen Isotope Stage 4. If mobile desert populations were forced towards the coast at this time the test implication would be that they brought their lithic technology with them and, based on Henrich and Boyd's (1998) argument, tipped the balance of cultural selection in their favor. Interestingly, the size of occupation at Sibudu is interpreted to have only decreased slightly (Wadley and Jacobs 2006, 2008). Based on my data the environment in the interior of the continent was becoming progressively unpredictable. Mobile groups may have merged with more sedentary populations at Sibudu, or at least engaged in social and exchange networks. We would expect to see through population modeling (Shennan 2001) increased coastal population size and increased migratory density into a specific region in the models of Powell et al.

(2009). As conditions ameliorated during Oxygen Isotope Stage 3, as my data suggests, South African coastal populations became more sedentary again and the interior and desert areas returned to being hospitable. Those who remained at Sibudu re-adopted characteristic Middle Stone Age tools, but those who returned in-land may have retained a degree of mobility and may have continued the use of microliths.

Similarly, during the Last Glacial some of these mobile populations may have moved eastward to Kalemba and Makwe Caves where they brought their microlithic technology with them. Support for this explanation comes from very early microliths, perhaps as old as ~200,000 years, at the Zambian site of Twin Rivers. At this time the Mega-Kalahari expanded to its greatest northeastward extent during the late Pleistocene and occupation of Twin Rivers was very low and probably only utilized by mobile groups (Barham 2000). Kalemba does not contain archaeological material from Oxygen Isotope Stage 4 and there are no other known Middle Stone Age sites in Zambia. If such a site was discovered it would be expected to contain microliths as a result of increased mobility and interaction between groups. Microliths do not reappear for almost another 100,000 years in the form of the Howieson’s Poort in South Africa.

In eastern Africa microliths appear as early as ~48,000 years B.P. at Enkapune Ya Muto (Ambrose 1998, 2001). Test implications for the mobility model in eastern Africa would be mobile groups from elsewhere bringing microlithic technology to a more settled area, or at least a more archaeologically visible rockshelter. Microliths spread across parts of modern day Kenya and Tanzania throughout Oxygen Isotope Stage 3 (Clark 1988; McBrearty and Brooks 2000; McBrearty 2001). However, as my data shows, by the height of the Last Glacial they are widespread in eastern Africa.

Interestingly, both of the Ethiopian sites included in this study, Omo-Kibish and Porc Epic, are completely devoid of intentionally formed microliths (Shea 2008; Leplongeon 2013). This would suggest that the groups at these sites remained fairly sedentary and cohesive and that very few migrants came into the area. The fact that this study reveals environments at Omo-Kibish may as becoming increasingly less arid as the late Pleistocene progressed would promote low residential mobility. This increased moisture at Omo-Kibish in the Member IV time period may be a result of the African Humid Period (~15,000 – 5,000 years B.P.) which is interpreted to have led to greater precipitation in northern Africa while other parts of the continent still experienced Last Glacial arid conditions (deMenocal et al. 2000; Renssen et al. 2006).

It must be noted here that the archaeological, behavioral, and environmental interpretations in Ethiopia based on the isotopic analysis is complicated by the major depositional hiatuses at Omo-Kibish (Fleagle et al. 2008) and the uncertainty in Porc Epic's chronology (Assefa 2006; Assefa et al. 2008). Other Ethiopian sites, including Moche Borago (Fisher 2010; Brandt et al. 2012) and Goda Buticha (Pleurdeau et al. 2014), do contain substantial microlithic assemblages as early as ~42,000 years B.P. Both of these sites have chronological hiatuses from ~30,000 – 6,000 years B.P., although it is currently unclear whether these hiatuses are due to poor environmental conditions or some other factor. Many other sites in the horn of Africa – Midhishi 2, Laas Geel, Aladi Springs, K'one, Lake Besaka, and Ziway-Shala Basin – also appear to be un-occupied during this time period (Gossa et al. 2012; Kurashina 1978; Pleurdeau et al. 2014; Menard et al. 2014). It is certainly possible that the reason no shift in δ^{18}O is seen at Omo-Kibish or Porc Epic is because very little, if any, of the Last Glacial

Maximum is represented in the faunal samples. Regional climatic proxies, most notably potassium composition of the Chew Bahir Basin core from southern Ethiopia, appear to pick up increased aridity during the Last Glacial, Heinrich I, and Younger Dryas (Foerster et al. 2012). Perhaps as opposed to no shift towards increased aridity the Last Glacial was so overwhelmingly arid that people left these sites completely.

Regardless, at the present time I stand by my initial conclusions. The fact that Goda Buticha is less than 30 km away from Porc Epic, and has a microlithic industry while Porc Epic does not, suggest that there may be more complex local environmental and climatic factors at play. Many of these other sites in the horn which have microliths but are missing the Last Glacial Maximum in their stratigraphy have been reconstructed as moderately closed woodlands and forests (Fisher 2010; Pleurdeau et al. 2014). These habitats may have only been seasonally available, or existed for relatively short periods of time, disappearing during more arid periods. Porc Epic and Omo-Kibish, located in perennial and predictable open habitats and with access to adjacent ecotones, could have been more stable bases for some of these other sites which were occupied by more mobile groups. This interpretation also implies complex organization of social and exchange networks on the landscape which contracted and expanded in response to climatic conditions.

The above discussion of microliths suggests that late Pleistocene human groups had a complex social geography, perhaps verging on regionalization as seen in modern hunter-gatherers (Yellen 1977). Invention and development of microlithic tool technology and other behaviors accompanying the transition to the Late Stone Age does not necessarily require larger population sizes, but rather greater inter-group interaction.

It stands to reason if sedentary groups dispersed and became more mobile they may have a greater chance of intensive social interaction with other mobile groups than if they remained isolated and sedentary. While microliths in and of themselves may not represent a “higher skill complexity,” the way in which they are combined in composite tools could be a result of intensified inter-group interactions. Furthermore, the use of ochre, shell, and other artifacts as objects of personal adornment may have been of greater use to mobile groups as signaling devices. In simple terms, they could display to each other if they were friendly or not (i.e. Nowell 2006, 2010). Of course, similar artifacts could be utilized by sedentary groups as a form of trade currency or as symbols of prestige of stature. These are all topics for future research and provide additional test implications for the mobility model of microlith adaptation.

Conclusions and Future Directions

This dissertation has provided the first detailed multi-sited paleoenvironmental reconstruction of late Pleistocene archaeological sites. The results of the isotopic study demonstrate that individual sites experienced different and unique climatic and environmental conditions despite well-studied regional and global events. These site-specific environmental profiles have implications for the development and spread of late Pleistocene human behavioral features – including migratory strategies, subsistence economy, social and trade networks, and stone tool technologies. It appears as if late Pleistocene refugia, or cul-de-sacs, existed in unexpected areas. The significant aridity experienced by human populations in many other parts of the continent during the Late Glacial led to a period of increased mobility, which may have resulted in the development of the Late Stone Age behavioral suite, and ultimately set the climatic and demographic stage for the origins of agriculture in the early Holocene.

With the exception of this study, there have been very few high-resolution isotopic studies of late Pleistocene archaeological sites. Many questions remain and the development of additional datasets is needed to further flesh out some of the conclusions discussed in this chapter. At present, Hill's (1981) call for a more thorough synthesis of paleoecological research and evolutionary adaptive theory is inadequately addressed, but it is becoming possible to ask the following questions:

- What role do local environments have in site-specific behavioral development and transitions? Are these site-specific events part of a larger pattern or are they the result of a series of unique circumstances?
- Were different sites on the landscape inhabited/utilized by the same group of people or is every site a unique occupation? If sites like Porc Epic and Goda Buticha were utilized by the same population was it a seasonal cycle?
- If environmental change is so important, why is it only in the late Pleistocene that we have regional behavioral variability? Climatic oscillations have occurred throughout human evolutionary history.
- What were the migratory pathways, both within and out of Africa, created by late Pleistocene climatic conditions?

Some researchers are beginning to explore these types of questions (see Chase 2010; Fisher 2010; Brandt et al. 2012; Tryon and Faith 2013 and references therein), but we still lack sufficient paleoenvironmental reconstructions. Isotopic analysis is only one avenue, but riverine coring projects (i.e. Foerster et al. 2012) and detailed palynological studies (i.e. Ivory et al. 2012) are becoming more common and help provide additional high-resolution lines of evidence for basinal, if not more local scales. The integration of these different proxies with archaeological evidence will allow for a more holistic evaluation of human behavior in the context of environment.

How did late Pleistocene human populations contend with greater aridity and environmental instability? Were there areas that were protected from or less affected by these climatic changes? My interpretation of the isotopic data suggests that at sites like Lukenya Hill and Kalemba Rockshelter where environments became less stable during the Last Glacial human populations became more mobile. These groups developed mobile and generalized technological toolkits, namely microliths, and increased inter-group interactions on the landscape led to greater sharing of ideas and subsequent innovation and ratcheting. A similar sequence of events may have occurred at Sibudu Cave during Oxygen Isotope Stage 4, although in this case Sibudu was the location or region to which mobile groups migrated. At sites like Porc Epic and Omo-Kibish where environments remained stable throughout the late Pleistocene populations remained sedentary and may have been isolated from intensified inter-group interactions.

I emphasize here that some of these more speculative interpretations may end up not being accurate. I am more than happy for them to be incorrect as long as they spur the development of testable hypothesis by myself and other researchers. In specific reference to this study, further research must be done at Omo-Kibish, Porc Epic, and Lukenya Hill to accurately date the human occupations and determine whether there are additional archaeological deposits which date to the late Pleistocene. Continued study of the Sibudu faunal collection and re-investigation of the isotopic results may lead to useful $\delta^{18}O$ data for a more detailed interpretation of the Howieson's Poort during Oxygen Isotope Stage 4. Re-investigation and possible re-excavation of David Phillipson's 1970s excavations and surveys in eastern Zambia would provide material for modern dating methods, and perhaps additional sites to further develop the regional chronology. It would also be of interest to try and sort through the collections and records of the Livingstone Museum which currently are in extreme disarray (Figures 1, 2). It is most likely that additional Middle and Late Stone Age archaeological sites have been previously explored and curated collections or old-field notes stored at the museum may provide important clues identifying potential sites in this under-appreciated part of the continent.

Figure 1. One of the better aisles in the Livingstone Museum's storage rooms. Even the lights work!

Figure 2. What most aisles in the Livingstone Museum look like. Stacked high with broken and upturned and unlabeled boxes in rubble piles of bone, stone, and pottery. Most of the collections room doesn't have working electricity and extensive water damage affects boxes and bones which deteriorate to the touch.

In reference to Hill's call for deeper integration and theoretical consideration of paleoecological data I would propose the use of Geographic Information System (GIS) and agent-based modeling technology. It is through these tools that it becomes possible to try to tease out what the paleoenvironmental reconstructions of this isotope study reveal about social networks and organization. An initial study could test whether the models of Henrich and Boyd (1998), Powell et al. (2009), and others can be modified to determine the rate of skill acquisition and innovation in a situation of highly mobile populations. Such models could lead to testable hypotheses about the relationship between the people at sites like Porc Epic and Goda Buticha in Ethiopia. Modeling of mobile populations allows for a test of the development of Late Stone Age microliths and/or composite tool technologies. How do two groups of people interact when coming from two entirely different environmental contexts? What about how late Pleistocene exchange and social networks of a single site were affected by changes in environmental and climatic transitions? These models can (1) test the relationship between environment and the organization of exchange networks, (2) develop an understanding of which economic conditions lead human communities to engage in risky strategies of shifting subsistence regimes and adapting new technology, and (3) determine if and how exchange networks contract or expand in different environmental conditions. Agent-based models can be used for generating archaeologically testable hypotheses which would then require a combination of laboratory, museum, and field based research to investigate.

It is through these types of investigations that we can begin doing what Hill (1981) proposed over 30 years ago. I do not view this dissertation as the completion of the study, but rather as laying the groundwork for addressing d’Errico and Stringer’s (2011) call for determining the responses of cultural adaptation to climate change and identifying the affect it had on the eco-cultural niche of human populations.

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Appendix 1. Mammalian tooth enamel δ^{13}C and δ^{18}O of fossil samples in this study. These are raw values - no correction for pre-industrial atmospheric CO_2 has been applied.

Site	Taxon	δ^{13}C	δ^{18}O	Tooth	Cultural/Time Unit	Stratigraphy/Location
Lukenya Hill[1]	**Bovidae (100)**					
	Antilopini (10)					
	Gazella thomsoni	-2.3	-0.1	Lower Left M	MSA	GvJm 19 2114
	G. thomsoni	0.8	-4.7	Upper Right M1	MSA	GvJm 19 2704
	G. thomsoni	-3.0	-0.4	M	LPNG	GvJm 22
	G. thomsoni	-2.5	-2.8	M	LPNG	GvJm 22
	G. thomsoni	-0.3	-0.3	M	LPNG	GvJm 46 6627
	G. thomsoni	-3.5	0.1	Lower Right M3	LPG	GvJm 62 2027
	G. thomsoni	1.4	-3.0	M	Holocene	GvJm 46 3902
	G. thomsoni	-0.4	0.1	M	Holocene	GvJm 46 6676
	Gazella gazella	-5.5	0.6	M	LPNG	GvJm 22
	Madoqua kirki	-8.7	0.9	Upper Right M3	MSA	GvJm 19 4302
	Alcelaphini (72)					
	Alcelaphus buselaphus	2.6	-1.9	M3	MSA	GvJm 19 2826
	A. buselaphus	0.7	-2.7	M	MSA	GvJm 22
	A. buselaphus	2.5	-1.4	M	MSA	GvJm 22
	A. buselaphus	2.8	-2.6	M	MSA	GvJm 22
	A. buselaphus	-0.3	-2.4	M	LPNG	GvJm 19 2600
	A. buselaphus	0.7	-1.9	M	LPNG	GvJm 19 2784
	A. buselaphus	-0.8	-4.0	M	LPNG	GvJm 19 4855
	A. buselaphus	-2.4	-3.6	M	LPNG	GvJm 22
	A. buselaphus	2.2	-3.5	M	LPNG	GvJm 22
	A. buselaphus	2.3	-3.3	M	LPNG	GvJm 22
	A. buselaphus	2.5	-4.6	M	LPNG	GvJm 22
	A. buselaphus	2.3	-3.8	M	LPNG	GvJm 22
	A. buselaphus	1.5	-1.3	M	LPNG	GvJm 22
	A. buselaphus	-0.6	-3.0	M	LPNG	GvJm 22
	A. buselaphus	2.8	-3.5	Upper Right M2	LPG	GvJm 62 2016

	A. buselaphus	2.9	-4.4	Upper Right M1/2	LPG	GvJm 62 2251
	A. buselaphus	1.1	-5.2	Upper Right M3	LPG	GvJm 62 2314
	A. buselaphus	-0.3	-5.7	Upper Right M3	LPG	GvJm 62 340
	Connochaetes taurinus	1.7	1.7	M2	MSA	GvJm 19 2424
	C. taurinus	2.4	-3.2	M2	MSA	GvJm 19 2774
	C. taurinus	3.6	-1.7	M	MSA	GvJm 22
	C. taurinus	3.3	-2.7	M	MSA	GvJm 22
	C. taurinus	0.8	-3.2	M3	LPNG	GvJm 19 1345
	C. taurinus	1.7	-3.2	M	LPNG	GvJm 19 2434
	C. taurinus	3.1	1.5	M	LPNG	GvJm 22
	C. taurinus	1.8	-2.9	M	LPNG	GvJm 22
	C. taurinus	1.3	-1.1	M	LPNG	GvJm 22
	C. taurinus	1.0	-2.3	M	LPNG	GvJm 22
	C. taurinus	1.1	-0.1	Upper Right M	LPG	GvJm 62 341
	Damaliscus hypsodon	0.8	-2.0	M	LPNG	GvJm 19 406
	D. hypsodon	1.7	-0.5	M	LPNG	GvJm 22
	D. hypsodon	3.3	-2.4	M	LPNG	GvJm 22
	D. hypsodon	1.3	0.2	M	LPNG	GvJm 22
	D. hypsodon	1.6	-0.7	M	LPNG	GvJm 22
	D. hypsodon	3.5	-1.2	M	LPNG	GvJm 22
	D. hypsodon	-0.3	-0.7	M	LPNG	GvJm 22
	D. hypsodon	1.1	-1.6	M	LPNG	GvJm 22
	D. hypsodon	2.7	-4.4	M	LPNG	GvJm 22
	D. hypsodon	0.0	-3.5	M	LPNG	GvJm 22
	D. hypsodon	1.5	-3.2	M	LPNG	GvJm 22
	D. hypsodon	0.7	-3.9	M	LPNG	GvJm 22
	D. hypsodon	3.4	-2.3	M	LPNG	GvJm 22
	D. hypsodon	1.0	-0.3	M	LPNG	GvJm 22
	D. hypsodon	2.6	-1.9	M	LPNG	GvJm 22
	D. hypsodon	0.5	-0.3	M	LPNG	GvJm 22
	D. hypsodon	1.7	-2.1	M	LPNG	GvJm 22
	D. hypsodon	0.7	-1.7	M	LPNG	GvJm 22

	D. hypsodon	0.7	0.7	M	LPNG	GvJm 22
	D. hypsodon	0.7	-2.0	M	LPNG	GvJm 22
	D. hypsodon	2.5	-4.6	Lower M	LPG	GvJm 62 1978
	D. hypsodon	2.3	-4.1	Lower Left M3	LPG	GvJm 62 1985
	D. hypsodon	1.5	-4.2	Lower Right M1/2	LPG	GvJm 62 2012
	D. hypsodon	1.9	-4.6	Lower Right M3	LPG	GvJm 62 2274
	D. hypsodon	2.1	-2.2	Lower M	LPG	GvJm 62 2285
	D. hypsodon	2.0	-3.2	M	Holocene	GvJm 46 3369
	D. hypsodon	2.8	-4.0	M	Holocene	GvJm 46 3372
	D. hypsodon	-0.2	-3.2	M	Holocene	GvJm 46 3557
	D. hypsodon	2.8	-4.4	M	Holocene	GvJm 46 3590
	D. hypsodon	0.7	-3.4	M	Holocene	GvJm 46 3688
	D. hypsodon	2.6	-1.4	M	Holocene	GvJm 46 3950
	D. hypsodon	2.1	-5.9	M	Holocene	GvJm 46 4101
	D. hypsodon	2.6	-5.0	M	Holocene	GvJm 46 4102
	D. hypsodon	2.4	-3.7	M	Holocene	GvJm 46 4516
	D. hypsodon	2.8	-2.8	M	Holocene	GvJm 46 4902
	D. hypsodon	3.5	-2.5	M	Holocene	GvJm 46 4916
	D. hypsodon	2.8	-3.2	M	Holocene	GvJm 46 4917
	D. hypsodon	2.6	-3.9	M	Holocene	GvJm 46 4949
	D. hypsodon	2.8	-4.4	M	Holocene	GvJm 46 4951
	D. hypsodon	1.3	-4.0	M	Holocene	GvJm 46 4963
	D. hypsodon	2.5	-3.6	M	Holocene	GvJm 46 6519
	D. hypsodon	1.2	-1.4	M	Holocene	GvJm 46 6788
	D. hypsodon	3.2	-2.6	M	Holocene	GvJm 46 6891
	Cephalophini (2)					
	Sylvicapra grimma	-8.0	-0.4	Upper Right M1/2	LPNG	GvJm 19 4164
	S. grimma	-4.9	-1.8	Upper Left M3	LPNG	GvJm 19 3904
	Hippotragini (3)					
	Oryx gazella	-1.2	-0.7	Lower Right M	MSA	GvJm 19 2765
	O. gazella	1.1	-2.5	M	MSA	GvJm 22
	O. gazella	1.0	-1.0	M	LPNG	GvJm 22

	Neotragini (11)					
	Ourebia ourebi	-0.3	-0.8	Upper Left M2/3	MSA	GvJm 19 2035
	O. ourebi	-7.8	-0.3	Lower Right M3	MSA	GvJm 19 2673
	O. ourebi	-3.5	-3.4	Lower Right M2	LPNG	GvJm 19 2632
	O. ourebi	-1.7	-0.8	M	LPNG	GvJm 22
	O. ourebi	0.6	0.6	M	LPNG	GvJm 46 6620
	O. ourebi	-4.5	-3.8	M	LPNG	GvJm 46 6623
	Raphicerus campestris	-11.4	-2.4	Upper Left M1/2	MSA	GvJm 19 2758
	Raphicerus fulvorufula	0.3	-3.2	Upper Right M3	MSA	GvJm 19 2478
	R. fulvorufula	-1.6	0.4	Lower Right M1/2	LPNG	GvJm 19 10587
	R. fulvorufula	0.0	-3.2	Upper M3	LPNG	GvJm 19 2567
	R. fulvorufula	1.1	0.2	M	LPNG	GvJm 22
	Tragelaphini (2)					
	Taurotragus oryx	-9.5	-2.2	M	LPNG	GvJm 22
	T. oryx	-8.6	-1.4	M	LPNG	GvJm 22
	Suidae (4)					
	Potamochoerus porcus	-8.9	-0.4	Upper Right M3	MSA	GvJm 19 2724
	P. porcus	-12.9	-7.5	M	LPNG	GvJm 22
	Phacochoerus aethiopicus	-1.2	-0.9	Upper Right M3	LPNG	GvJm 19 2599
	Phacochoerus africanus	0.0	0.6	M	LPNG	GvJm 22
	Equidae (15)					
	Equus burchelli	0.5	1.9	M	MSA	GvJm 19 1489
	E. burchelli	-1.2	-1.0	M	MSA	GvJm 19 2126
	E. burchelli	-1.2	-0.6	M	LPNG	GvJm 19 2792
	E. burchelli	-1.9	-0.1	M	LPNG	GvJm 22
	E. burchelli	-0.4	-5.0	M	LPNG	GvJm 22
	E. burchelli	-1.9	-1.8	M	LPNG	GvJm 22
	E. burchelli	2.1	-1.5	M	LPNG	GvJm 22
	E. burchelli	1.0	-3.8	M	LPNG	GvJm 22
	E. burchelli	0.9	-2.6	M	LPNG	GvJm 22
	E. burchelli	-0.9	-1.9	Upper Left M1/2	LPG	GvJm 62 1342
	E. burchelli	0.4	-3.4	Upper Right M3	LPG	GvJm 62 1703

	E. burchelli	-1.1	-3.4	Upper Right M1/2	LPG	GvJm 62 2031
	E. burchelli	-2.6	-2.0	Lower Left M3	LPG	GvJm 62 2301
	E. burchelli	2.3	-0.9	M	Holocene	GvJm 46 4915
	E. burchelli	0.6	-4.1	M	Holocene	GvJm 46 6602
Porc Epic[2]	**Bovidae (41)**					
	Aepycerotini (3)					
	Aepyceros melampus	-1.5	-0.3	Lower M1		2503
	A. melampus	-0.4	1.5	Lower M3		828
	A. melampus	-3.5	5.0	Lower M3		B2819
	Antilopini (3)					
	Gazella cf. granti	-1.4	2.9	Upper M3		836
	Gazella spp.	-3.1	3.5	Upper M		1279
	Madoqua cf. guentheri	-6.8	6.8	Lower M3		B2476
	Alcelaphini (3)					
	Damaliscus lunatus	-0.6	1.6	Upper M1		341B
	D. lunatus	2.5	3.3	Upper M		982
	Damaliscus cf. lunatus	2.5	0.1	Upper M		2122
	Bovini (14)					
	Pelorovis sp. antiquus	-4.8	4.6	Lower M3		2285
	Pelorovis sp. antiquus	-4.9	3.9	Upper M		2631
	Pelorovis sp. antiquus	-6.1	-2.0	Upper M		2445
	Pelorovis sp. antiquus	-3.1	4.0	Lower M3		B1852
	Pelorovis sp. antiquus	-5.9	7.0	Lower M2		2426
	Syncerus caffer	-4.1	0.8	Lower M1		B2037
	S. caffer	-4.3	3.5	Lower M1		2059
	S. caffer	2.0	1.6	Lower M2		2014
	S. caffer	3.1	2.1	Lower M2		B2118
	S. caffer	3.5	-2.7	Lower M		B2118
	S. caffer	1.0	0.7	Upper M1		1176
	S. caffer	3.0	-1.5	M		300
	S. caffer	-0.1	-0.2	Upper M2		B2320
	S. caffer	2.9	2.4	Lower M2		1049Z

	Hippotragini (1)					
	O. gazella	0.5	-0.9	Lower M1		B1851
	Neotragini (2)					
	Neotragus spp.	-8.5	4.6	Lower M		1828
	Raphiceros spp.	-8.6	7.4	Upper M		B2411
	Reduncini (8)					
	Kobus ellipsiprymnus	1.6	-3.7	M		2251
	K. ellipsiprymnus	-1.5	2.4	Lower M		2506
	Kobus spp.	-0.8	2.8	Lower M2		1648
	Redunca redunca	-2.6	1.6	Lower M3		1849
	R. redunca	0.6	-0.2	Lower M2		1259
	Redunca sp. redunca	-2.9	1.1	Lower M2		5104Z
	Redunca sp. redunca	1.5	-1.2	Lower M2		5000(Z)
	Redunca spp.	1.9	1.5	Lower M		748
	Tragelaphini (7)					
	Tragelaphus strepsiceros	-7.0	4.6	Upper M		671
	T. strepsiceros	-7.4	5.2	Lower M2		683
	T. strepsiceros	-4.2	2.3	Lower M2		B2017
	T. strepsiceros	-4.4	2.6	Lower M3		B1965
	Tragelaphus cf. strepsiceros	-5.3	3.5	Upper M1		651
	Tragelaphus spp.	-7.2	-0.4	Lower M3		444
	Tragelaphus spp.	0.4	0.6	M		B1965
	Cercopithecidae (7)					
	Cercopithecinae	-4.9	4.4	Lower M1		876
	Papio sp.	-9.8	4.2	Upper M1		1279
	Papio spp.	-0.1	-0.2	Lower M		534
	Papio spp.	-5.9	2.0	Lower M3		5013Z
	Papio spp.	-4.2	4.1	Lower M3		2409
	Papio spp.	-5.8	1.7	Lower M3		1994
	Papio spp.	-7.8	3.2	Lower M		B2302
	Suidae (14)					
	P. africanus	-1.7	1.7	Lower M3		B1905

	P. africanus	-7.0	6.0	M		2065
	P. africanus	0.0	3.0	Lower M3		2065
	P. africanus	-2.3	2.9	Lower M		2059
	P. africanus	-0.2	-1.6	Lower M3		5018Z
	P. africanus	0.2	4.1	M		B1831
	P. africanus	-9.7	0.4	Lower M		621
	P. africanus	-1.7	-0.4	M3		B2242
	P. africanus	-2.1	0.3	M2		B2242
	P. africanus	-2.6	0.8	Lower M3		194
	P. africanus	-0.4	0.5	M		1724
	P. africanus	0.3	-0.3	Upper M3		1486
	P. africanus	-0.4	2.3	M3		B1949
	Potamochoerus spp.	-4.0	-1.8	Lower M		B2041
	Equidae (5)					
	E. burchelli	**-1.5**	**3.8**	**Lower M**		**1966**
	E. burchelli	0.5	2.1	Lower M		931
	E. burchelli	-2.5	0.1	Upper M3		B2360
	Equus cf. burchelli	-0.4	4.0	Lower M1		1989
	Equus cf. grevyi	0.6	1.6	Upper M3		1696
	Procaviidae (2)					
	Procavia capensis	-2.2	5.9	Upper M1		B2470
	P. capensis	-3.7	4.6	Lower M3		B2679
Omo-Kibish	**Bovidae (45)**					
	Bovidae	2.6	-0.9	Lower Left M3	Member 4	Kib 026
	Antilopini (1)					
	Madoqua cf. kirkii	-8.4	-0.6	Lower Right M3	Member 1	Kib 149
	Alcelaphini (2)					
	Alcelaphini indet.	-3.3	0.9	Upper Right M3	Member 1	Kib 103
	cf. Connochates	2.0	1.0	Lower Left M3	Member 3	Kib 166
	Bovini (25)					
	S. caffer	-3.9	-0.9	Right Upper M2	Unknown	Kib 023
	S. caffer	2.1	1.1	Lower Left M3	Unknown	Kib 169

	S. caffer	1.3	-5.9	Upper Right M2	Unknown	Kib 047
	S. caffer	-0.2	-2.6	Lower Right M1	Unknown	Kib 072
	S. caffer	-4.0	-0.3	Lower Right M3	Unknown	KIB 119
	S. caffer	0.6	0.0	Upper Left M1/M2	Unknown	KIB 087
	S. caffer	1.4	-4.3	Right M1	Unknown	kib 068
	S. caffer	-0.2	1.9	Upper M1/2	?3?1	Kib 075
	S. caffer	-2.4	-3.4	Upper M1/2	1/4?	Kib 185
	S. caffer	2.3	1.2	Upper Left M1/M2	Member 1	Kib 106
	S. caffer	-0.2	-0.8	Lower Left M1/M2	Member 1	Kib 106
	S. caffer	-1.6	-1.3	Upper Left M2	Member 1	Kib 106
	S. caffer	0.5	1.8	Upper M1/2	Member 1	Kib 106
	S. caffer	1.1	-2.8	Lower Right M3	Member 1	Kib 052
	S. caffer	-1.1	-0.9	Lower M	Member 1	Kib 152
	S. caffer	0.6	-1.0	Lower Left M1	Member 1	Kib 069
	S. caffer	0.9	-4.4	Lower Left M1	Member 3	Kib 066
	S. caffer	2.2	-2.3	Lower Left M2	Member 3	Kib 066
	S. caffer	-3	-3.3	Lower Left M3	Member 4	Kib 115
	S. caffer	2.2	-3.6	Upper Left M3	Member 4	Kib 172
	S. caffer	0.4	-2.6	Upper Left M1/2	Member 4	Kib 019
	Syncerus caffer/Pelorovis?	0.1	0.5	Lower Left M1	Member 3	Kib 018
	Syncerus cf. caffer	1.5	0.0	Lower Right M	Member 3	Kib 146
	Bovini	2.2	0.7	Upper Right M	Member 1	Kib 139
	Bovini indet.	-1.3	0.8	Upper M	?3?1	Kib 075
	Cephalophini (1)					
	Cephalophus cf. weynsi	-9.4	0.5	Upper M	Member 1	Kib 149
	Hippotragini (3)					
	Oryx cf. gazella	2.5	2.9	Lower Left M3	Member 3	Kib 124
	Oryx cf. gazella	3.0	-2.4	Lower Right M3	Member 3	Kib 166
	Oryx cf. gazella	2.2	-2.4	Lower Right M3	Member 4	Kib 019
	Reduncini (9)					
	K. ellipsiprymnus	0.9	1.8	Lower Right M3	Member 1	Kib 006
	K. ellipsiprymnus	1.7	1.9	Lower Left M3	Member 1	Kib 064

	K. ellipsiprymnus	1.2	-5	Upper Left M	Member 3	Kib 166
	K. ellipsiprymnus	-1.0	1.2	Lower Right M1/2	Member 3	Kib 018
	Kobus cf. ellipsiprymnus	-3.1	-0.6	Lower Left M1/2	Member 4	Kib 019
	Kobus cf. ellipsiprymnus	2.8	0.0	Lower Left M3	Unknown	Kib 072
	Kobus cf. ellipsiprymnus	2.5	-0.7	Upper Left M1/2	Unknown	Kib 031
	R. redunca	2.1	-3.0	Left Lower eM1	?4	Kib 170
	Redunca cf. redunca	2.5	-2.9	Lower Right M1/2	Member 4	Kib 172
	Tragelaphini (3)					
	Tragelaphus cf. scriptus	-11.5	-0.8	Right Lower M3	?3?1	KIB 082
	Tragelaphus cf. scriptus	-10.0	1.9	Upper M.	Member 1	Kib 106
	Tragelaphus strepsiceros	-8.3	1.0	Right Lower M3	?3?1	Kib 171
	Suidae (27)					
	P. africanus	1.3	0.1	Lower M	?3?1	Kib 074
	P. africanus	-0.2	-1.1	M	Member 1	Kib 064
	P. africanus	0.4	0.3	M	Member 1	Kib 006
	P. africanus	-1.5	-0.7	Lower M3	Member 1	Kib 061
	P. africanus	1.1	1.3	M	Member 1	kib 093
	P. africanus	0.6	0.0	M	Member 1	Kib 103
	P. africanus	-0.1	-0.1	M	Member 1	KIB 103
	P. africanus	0.3	-0.8	M	Member 1	KIB 103
	P. africanus	0.5	1.3	Upper Left M3	Member 1	Kib 141
	P. africanus	1.4	1.6	M	Member 1	Kib 147
	P. africanus	0.5	-4.5	M	Member 3	Kib 018
	P. africanus	-1.0	-0.8	Upper M3	Member 3	Kib 024
	P. africanus	-1.0	-2.0	M	Member 3	Kib 048
	P. africanus	0.3	0.1	M	Member 3	Kib 062
	P. africanus	-2.1	-2.0	Upper M3	Member 4	Kib 019
	P. africanus	1.6	2.6	M	Member 4	Kib 019
	P. africanus	-1.2	-0.4	M	Member 4	Kib 115
	P. africanus	-0.1	-3.7	M	Member 4	Kib 115
	P. africanus	-1.0	-0.9	Upper M3	Member 4	Kib 126
	P. africanus	-0.2	-0.3	M	Member 4	Kib 126

	P. africanus	-3.8	-1.6	M	Member 4	Kib 126
	P. africanus	0.3	1.2	M	Unknown	Kib 001
	P. africanus	0.8	-0.1	Lower Left M3	Unknown	Kib 016
	P. africanus	-2.5	-0.2	Molar	Unknown	Kib 051
	P. africanus	0.1	0.9	Lower M2	Unknown	Kib 156
	P. porcus	-1.0	-1.1	Left M	Member 1	Kib 117
	P. porcus	-0.8	0.5	Left M	Member 1	Kib 117
	Equidae (5)					
	Equus cf. burchelli	1.0	-0.7	Upper Right M3	Member 1	Kib 006
	Equus cf. grevyi	1.4	3.8	Lower Left M3	Member 1	Kib 006
	Equus cf. grevyi	1.3	2.9	Lower Left M2	Member 1	Kib 006
	Equus cf. grevyi	-1.3	1.5	Lower Right M3	Member 2	Kib 113
	Equus cf. grevyi	1.6	0.7	Upper Right M3	Unknown	Kib 051
	Rinocerotidae (1)					
	Cerathorium simum	-0.7	-1.0	Lower Left M1	Unknown	Kib 092
	Giraffidae (3)					
	Giraffa camelopardalis	-8.6	1.8	Upper M	?3?1	Kib 174
	G. camelopardalis	-4.8	2.2	Lower M	Member 1	Kib 006
	G. camelopardalis	-4.0	0.3	Upper Right M1/2	Member 1	Kib 106
	Hippopotamidae (8)					
	Hippopotamus amphibius	-5.8	-3.3	M	Member 1	Kib 073
	H. amphibius	-5.1	-2.3	Upper Left M1/2	Member 1	Kib 086
	H. amphibius	-4.3	-7.9	M	Member 4	Kib 126
	Hippopotamos cf. amphibius	-6.0	-5.6	Incisor/Tusk	Unknown	KIB 099
	Hippopotamus cf. amphibius	-2.2	-7.6	M	Member 1	Kib 052
	Hippopotamus cf. amphibius	0.2	-2.9	M	Member 1	Kib 061
	Hippopotamus cf. amphibius	-1.0	-5.6	Incisor/Tusk	Member 1	Kib 103
	Hippopotamus cf. amphibius	-10.1	-4.2	M	Unknown	KIB 091
Kalemba Rockshelter	**Bovidae (41)**					
	Antilopini (1)					
	G. thomsonii	-10.4	-0.8	Upper M1/2	Late LSA (~10 - 7 kya)	Horizon O

	Alcelaphini (9)					
	C. taurinus	-4.2	-2.2	Upper M3	Transition (~ 30 - 25 kya)	Horizon H
	C. taurinus	1.6	-0.6	Molar	Transition (~ 30 - 25 kya)	Horizon H
	C. taurinus	-0.2	-3.5	Upper M1	Transition (~ 30 - 25 kya)	Horizon I
	C. taurinus	0.4	-4.4	Upper M3	Transition (~ 30 - 25 kya)	Horizon I
	C. taurinus	2.3	-4.3	M3	Transition (~ 30 - 25 kya)	Horizon J
	C. taurinus	-0.9	-3.4	Lower M3	Transition (~ 30 - 25 kya)	Horizon K
	C. taurinus	-0.2	-3.6	Lower M3	Transition (~ 30 - 25 kya)	Horizon I
	C. taurinus	1.1	-6.5	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon I
	C. taurinus	-0.1	-4.6	M1/2	Transition (~ 20 - 12 kya)	Horizon K
	Cephalophini (7)					
	S. grimmia	-13.2	-6.1	Lower M2	Transition (~ 30 - 25 kya)	Horizon I
	S. grimmia	-10.5	-6.4	Lower M2	Transition (~ 30 - 25 kya)	Horizon J
	S. grimmia	-10.9	-2.4	Upper M1	Transition (~ 30 - 25 kya)	Horizon K
	S. grimmia	-14.3	-3.7	Upper M3	Transition (~ 20 - 12 kya)	Horizon L
	S. grimmia	-9.9	-3.5	Lower M3	Transition (~ 20 - 12 kya)	Horizon L
	S. grimmia	-5.0	-4.0	M1/2	Transition (~ 20 - 12 kya)	Horizon M

	S. grimmia	-13.0	-0.1	M1/2	Late LSA (~10 - 7 kya)	Horizon Q
	Hippotragini (1)					
	Hippotragus niger	0.0	-5.2	Upper M3	Transition (~ 30 - 25 kya)	Horizon J
	Neotragini (1)					
	O. ourebi	-9.7	-0.6	Upper M2/3	Late LSA (~10 - 7 kya)	Horizon O
	Reduncini (17)					
	K. ellipsiprymnus	-7.7	-5.1	Lower Molar	Transition (~ 30 - 25 kya)	Horizon I
	K. ellipsiprymnus	1.1	-2.3	Upper M3	Transition (~ 30 - 25 kya)	Horizon I
	K. ellipsiprymnus	0.7	-3.4	Lower Molar	Transition (~ 30 - 25 kya)	Horizon I
	K. ellipsiprymnus	1.7	-3.9	Lower M3	Transition (~ 30 - 25 kya)	Horizon J
	K. ellipsiprymnus	0.6	-5.8	Lower Molar	Transition (~ 30 - 25 kya)	Horizon J
	K. ellipsiprymnus	0.8	-5.7	Lower M3	Transition (~ 30 - 25 kya)	Horizon J
	K. ellipsiprymnus	1.0	-5.7	M1/2	Transition (~ 30 - 25 kya)	Horizon J
	K. ellipsiprymnus	-2.4	-5.1	Lower M3	Transition (~ 30 - 25 kya)	Horizon J
	K. ellipsiprymnus	-0.2	-5.4	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon K
	K. ellipsiprymnus	0.9	-3.6	Lower M2/3	Transition (~ 20 - 12 kya)	Horizon K
	K. ellipsiprymnus	0.0	-5.1	Lower M1	Transition (~ 20 - 12 kya)	Horizon K
	K. ellipsiprymnus	0.2	-6.2	Upper M3	Transition (~ 20 - 12 kya)	Horizon L

	K. ellipsiprymnus	0.1	-3.2	M1/2	Transition (~ 20 - 12 kya)	Horizon N
	R. arundinum	2.4	-1.3	M1/2	Transition (~ 30 - 25 kya)	Horizon K
	R. arundinum	1.0	-4.4	Upper M3	Transition (~ 30 - 25 kya)	Horizon K
	R. arundinum	-0.3	-1.2	M1/2	Transition (~ 20 - 12 kya)	Horizon L
	R. arundinum	-9.5	-0.1	M2	Transition (~ 20 - 12 kya)	Horizon N
	Tragelaphini (5)					
	T. oryx	-11.6	-5.8	Molar	MSA (~37000 B.P.)	Horizon G
	T. oryx	-1.7	-1.2	Upper M2/3	Transition (~ 30 - 25 kya)	Horizon I
	T. oryx	-14.1	-7.4	Molar	Transition (~ 30 - 25 kya)	Horizon K
	T. oryx	-12.4	-4.0	Lower M3	Transition (~ 20 - 12 kya)	Horizon M
	T. scriptus	-10.3	-0.7	Lower M1	Late LSA (~10 - 7 kya)	Horizon O
	Cercopithecidae (3)					
	Papio sp.	-10.4	-5.6	Upper M3	Transition (~29 – 22 kya)	Horizon I
	Papio sp.	-11.9	-5.1	Lower M1	Transition (~29 – 22 kya)	Horizon J
	Papio sp.	-11.0	-5.1	Lower M3	Transition (~29 – 22 kya)	Horizon K
	Suidae (14)					
	P. africanus	-5.0	-2.7	Molar	Transition (~ 30 - 25 kya)	Horizon I
	P. africanus	-8.8	-5.1	Molar	Transition (~ 30 - 25 kya)	Horizon I

	P. africanus	-1.3	-4.2	Molar	Transition (~ 30 - 25 kya)	Horizon K
	P. africanus	-4.0	-5.9	M2/3	Transition (~ 20 - 12 kya)	Horizon L
	P. africanus	-1.9	-2.9	M2/3	Late LSA (~10 - 7 kya)	Horizon O
	P. porcus	-0.7	-1.0	Lower P4	Transition (~ 30 - 25 kya)	Horizon I
	P. porcus	-10.8	-2.8	Molar	Transition (~ 30 - 25 kya)	Horizon I
	P. porcus	-9.3	-2.3	Lower M3	Transition (~ 30 - 25 kya)	Horizon I
	P. porcus	-1.9	-5.9	Molar	Transition (~ 30 - 25 kya)	Horizon J
	P. porcus	-12.4	-7.3	Lower M2	Transition (~ 30 - 25 kya)	Horizon J
	P. porcus	0.5	-4.8	M1	Transition (~ 30 - 25 kya)	Horizon J
	P. porcus	-12.5	-7.5	Lower M3	Transition (~ 30 - 25 kya)	Horizon K
	P. porcus	-7.1	-6.8	M2/3	Late LSA (~10 - 7 kya)	Horizon O
	P. porcus	-10.3	-6.6	Lower M1/2	Late LSA (~10 - 7 kya)	Horizon P
	Equidae (34)					
	E. burchelli	-1.2	-2.3	Molar	MSA (~37000 B.P.)	Horizon G
	E. burchelli	-0.1	-2.1	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	-1.7	-1.8	Molar	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	-3.3	-2.9	Upper M2/3	Transition (~ 30 - 25 kya)	Horizon I

	E. burchelli	-0.7	-3.6	Molar	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	-3.7	-4.2	Upper M3	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	-1.5	-3.3	Molar	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	0.6	-5.4	Molar	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	0.3	-4.9	Molar	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	-10.6	-4.6	Lower M3	Transition (~ 30 - 25 kya)	Horizon I
	E. burchelli	0.0	-4.8	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-0.1	-5.1	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-2.4	-4.7	Upper M3	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-1.9	-4.9	Molar	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-3.5	-4.3	Molar	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-5.3	-4.6	Upper M2/3	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-8.1	-4.6	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-1.3	-3.9	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-1.8	-5.7	Upper M3	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	1.1	-5.0	Lower M1/2	Transition (~ 30 - 25 kya)	Horizon J

	E. burchelli	-1.6	-5.7	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-6.8	-5.8	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-0.8	-5.6	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-0.7	-4.9	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	0.9	-5.1	Lower M1/2	Transition (~ 30 - 25 kya)	Horizon J
	E. burchelli	-2.5	-6.1	Lower M1/2	Transition (~ 30 - 25 kya)	Horizon K
	E. burchelli	-4.3	-3.9	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon K
	E. burchelli	0.4	-2.1	Upper M1/2	Transition (~ 30 - 25 kya)	Horizon K
	E. burchelli	-4.3	-4.0	Upper M1/2	Transition (~ 20 - 12 kya)	Horizon L
	E. burchelli	-2.0	-2.0	Lower M1/2	Transition (~ 20 - 12 kya)	Horizon N
	E. burchelli	-0.4	-2.4	Lower M1/2	Transition (~ 20 - 12 kya)	Horizon N
	E. burchelli	-5.8	-2.9	Lower M1/2	Late LSA (~10 - 7 kya)	Horizon O
	E. burchelli	-9.1	-0.3	Lower M1/2	Late LSA (~10 - 7 kya)	Horizon O
	E. burchelli	-8.5	-0.8	Upper M1/2	Late LSA (~10 - 7 kya)	Horizon O
	Hystricidae (1)					
	Hystrix. sp.	-9.8	-0.7	M	Late LSA (~10 - 7 kya)	Horizon O
	Bovidae (72)					

Makwe Caves	**Aepycerotini (8)**					
	A. melampus	-10.6	-0.7	M1/2	< 13 - 7 ka	Horizon 1
	A. melampus	0.4	0.7	Lower Right M3	~ 2000 ya - Present	Horizon 5
	A. melampus	0.4	-0.9	Upper M1/2	~ 2000 ya - Present	Horizon 5
	A. melampus	2.3	-6.5	M1/2	~ 7000 - 5150 ya	Horizon 2i
	A. melampus	0.1	-1.1	Lower M3	~ 7000 - 5150 ya	Horizon 2i
	A. melampus	0.9	-4.9	Upper M2	~ 7000 - 5150 ya	Horizon 2ii
	A. melampus	1.9	-5.7	Upper M1/2	~ 7000 - 5150 ya	Horizon 3i
	A. melampus	3.9	-2.9	Upper M1/2	Hiatus ~4000 - 2000 ya	Horizon 3ii
	Alcelaphini (8)					
	A. buselaphus	-2.0	-1.9	M1/2	~ 7000 - 5150 ya	Horizon 2ii
	C. taurinus	-3.2	-5.6	Lower Right M1	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	C. taurinus	3.2	-3.2	Upper M1/2	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	C. taurinus	3.1	-4.3	M1/2	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	C. taurinus	1.4	0.1	M1/2	~ 2000 ya - Present	Horizon 4ii
	C. taurinus	3.2	-1.3	M1/2	~ 2000 ya - Present	Horizon 4ii
	C. taurinus	1.6	-2.4	Lower M3	~ 7000 - 5150 ya	Horizon 2i
	C. taurinus	3.2	-2.1	M1/2	~ 7000 - 5150 ya	Horizon 2i
	Bovini (17)					
	S. caffer	-0.1	-0.3	Upper M1/2	~ 7000 - 5150 ya	Horizon 3i
	S. caffer	3.0	-1.5	Upper M1/2	< 13 - 7 ka	Horizon 1
	S. caffer	0.4	-2.3	Lower P4	< 13 - 7 ka	Horizon 1
	Bos taurus	1.5	-1.2	Upper M1/2	~ 2000 ya - Present	Horizon 4ii
	B. taurus	1.8	1.4	M1/2	~ 2000 ya - Present	Horizon 4ii
	B. taurus	-0.9	-0.5	M2/3	~ 2000 ya - Present	Horizon 4ii
	B. taurus	-0.1	0.7	Upper M1	~ 2000 ya - Present	Horizon 5
	B. taurus	2.2	-0.8	Upper M2	~ 2000 ya - Present	Horizon 5
	B. taurus	1.9	-2.4	Upper M3	~ 2000 ya - Present	Horizon 5
	B. taurus	-1.8	-1.0	M1/2	~ 2000 ya - Present	Horizon 5

	B. taurus	-1.2	-1.3	Upper M	~ 2000 ya - Present	Horizon 5
	B. taurus	2.0	-0.8	M1/2	~ 2000 ya - Present	Horizon 5
	B. taurus	0.8	-2.0	Upper M1/2	~ 2000 ya - Present	Horizon 5
	B. taurus	1.3	-1.1	Lower Left M2	~ 2000 ya - Present	Horizon 5
	B. taurus	1.1	-1.7	Upper M1	~ 2000 ya - Present	Horizon 5
	B. taurus	1.4	-1.8	Lower M2	~ 2000 ya - Present	Horizon 5
	B. taurus	4.0	-0.3	Upper Left M2	~ 2000 ya - Present	Horizon 6
	Caprini (5)					
	Capra hircus	-20.3	-13.5	Lower Left M3	~ 2000 ya - Present	Horizon 4ii
	C. hircus	3.3	-0.2	P4	~ 2000 ya - Present	Horizon 4ii
	C. hircus	-2.6	1.9	M1/2	~ 2000 ya - Present	Horizon 4ii
	C. hircus	-2.0	-2.7	Upper M1/2	~ 2000 ya - Present	Horizon 5
	C. hircus	2.2	0.6	Lower M3	~ 2000 ya - Present	Horizon 5
	Cephalophini (18)					
	S. grimmia	-8.4	-2.5	Lower Right M1/2	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	S. grimmia	-10.5	-0.9	Upper Left M2	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	S. grimmia	-12.6	-3.0	Upper M3	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	S. grimmia	-12.2	-4.0	M1/2	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	S. grimmia	-11.4	-3.5	Upper Left M3	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	S. grimmia	-11.3	-1.6	Lower M3	~ 2000 ya - Present	Horizon 4ii
	S. grimmia	-11.6	-0.6	Lower M3	~ 2000 ya - Present	Horizon 4ii
	S. grimmia	-11.7	-0.8	Upper M2	~ 2000 ya - Present	Horizon 5
	S. grimmia	-11.3	-2.6	Upper Left M1	~ 2000 ya - Present	Horizon 5
	S. grimmia	-11.9	-1.8	Upper M3	~ 7000 - 5150 ya	Horizon 2i
	S. grimmia	-12.0	-4.3	Upper M3	~ 7000 - 5150 ya	Horizon 2ii
	S. grimmia	-12.2	-4.7	Upper M3	~ 7000 - 5150 ya	Horizon 2ii
	S. grimmia	-1.8	-1.0	Upper M3	~ 7000 - 5150 ya	Horizon 2ii
	S. grimmia	-11.1	-1.5	Upper M2	~ 7000 - 5150 ya	Horizon 3i

	S. grimmia	-12.4	-6.8	Upper M3	~ 7000 - 5150 ya	Horizon 3i
	S. grimmia	-12.1	-5.6	M1/2	~ 7000 - 5150 ya	Horizon 3i
	S. grimmia	-11.5	-3.3	M3	< 13 - 7 ka	Horizon 1
	S. grimmia	-11.1	-3.9	Lower Right M3	Hiatus ~4000 - 2000 ya	Horizon 3ii
	Neotragini (9)					
	Oreotragus oreotragus	-10.7	-2.4	Lower M2	~ 7000 - 5150 ya	Horizon 3i
	O. oreotragus	-17.6	-10.4	Lower Right M1	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	O. oreotragus	-10.7	-1.2	Upper M2	~ 2000 ya - Present	Horizon 4ii
	O. oreotragus	-12.5	0.9	Upper M3	~ 5150 - 4300 ya	Horizon 3ii
	O. oreotragus	-12.3	-6.6	M	~ 7000 - 5150 ya	Horizon 3i
	O. oreotragus	-13.5	-2.4	Lower Left M1	Hiatus ~4000 - 2000 ya	Horizon 3ii
	O. oreotragus	-10.2	-2.5	Upper Left M3	Hiatus ~4000 - 2000 ya	Horizon 3ii
	O. oreotragus	-13.7	-5.0	M1/2	Hiatus ~4000 - 2000 ya	Horizon 3ii
	O. oreotragus	-12.1	-0.2	Left M3	Hiatus ~4000 - 2000 ya	Horizon 3ii
	Reduncini (3)					
	R. arundinum	0.9	-1.9	M1	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	R. arundinum	1.9	-2.3	M1/2	~ 2000 ya - Present	Horizon 4ii
	R. arundinum	2.5	0.0	Upper M1/2	~ 2000 ya - Present	Horizon 4ii
	Tragelaphini (4)					
	T. oryx	-7.3	-5.1	M1/2	~ 7000 - 5150 ya	Horizon 2ii
	T. strepsiceros	-13.4	-1.2	M1/2	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	T. strepsiceros	-13.2	-5.4	Lower Right M1	~ 2000 ya - Present	Horizon 5
	T. strepsiceros	-14.9	-9.0	Lower M3	~ 2000 ya - Present	Horizon 5
	Cercopithecidae (1)					

	Chlorocebus aethiops	-10.4	-1.5	Lower Right M3	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	Suidae (27)					
	Phacochoerus aetheopicus	-4.7	-3.2	Lower M3	~ 7000 - 5150 ya	Horizon 3i
	P. aetheopicus	-2.9	-3.0	Lower Right M3	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	P. aetheopicus	-6.2	-1.2	M	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	P. aetheopicus	-1.3	-4.2	M3	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	P. aetheopicus	0.3	-0.6	M3	~ 2000 ya - Present	Horizon 4ii
	P. aetheopicus	1.8	-1.3	M3	~ 2000 ya - Present	Horizon 4ii
	P. aetheopicus	0.0	0.3	M	~ 2000 ya - Present	Horizon 4ii
	P. aetheopicus	-0.4	-4.4	M	~ 2000 ya - Present	Horizon 4ii
	P. aetheopicus	-5.0	0.2	Upper Right M2	~ 2000 ya - Present	Horizon 5
	P. aetheopicus	-0.9	0.8	M3	~ 2000 ya - Present	Horizon 5
	P. aetheopicus	1.3	2.4	M3	~ 2000 ya - Present	Horizon 5
	P. aetheopicus	2.4	-2.1	M3	~ 2000 ya - Present	Horizon 5
	P. aetheopicus	-5.2	-2.7	M3	~ 7000 - 5150 ya	Horizon 2i
	P. aetheopicus	-1.2	-5.5	M3	~ 7000 - 5150 ya	Horizon 2ii
	P. aetheopicus	0.1	-6.3	M	~ 7000 - 5150 ya	Horizon 2ii
	P. aetheopicus	-1.9	-0.9	M	~ 7000 - 5150 ya	Horizon 2ii
	P. aetheopicus	-1.8	-4.3	M	~ 7000 - 5150 ya	Horizon 2ii
	P. aetheopicus	1.7	-2.9	M3	~ 7000 - 5150 ya	Horizon 3i
	P. porcus	-12.8	-3.6	M	~ 2000 ya - Present	Horizon 4ii
	P. porcus	-10.2	-3.7	Lower Right M3	~ 2000 ya - Present	Horizon 5
	P. porcus	-11.6	-1.5	Upper Left M1	~ 2000 ya - Present	Horizon 5
	P. porcus	-9.0	-5.2	M	~ 2000 ya - Present	Horizon 5
	P. porcus	-12.1	-6.8	Upper Right M3	~ 2000 ya - Present	Horizon 5
	P. porcus	-5.1	-2.8	Upper Right M1	~ 5150 - 4300 ya	Horizon 3ii
	P. porcus	-14.3	-10.7	Lower Left M1	~ 5150 - 4300 ya	Horizon 3ii
	P. porcus	-12.8	-7.7	Lower Right M3	~ 5150 - 4300 ya	Horizon 3ii

	P. porcus	-11.9	-6.9	M	~ 7000 - 5150 ya	Horizon 3i
	Equidae (9)					
	E. burchelli	-2.0	-2.7	M	~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	E. burchelli	0.5	-3.7	Lower M1/2	~ 2000 ya - Present	Horizon 4ii
	E. burchelli	1.1	0.4	Lower M3	~ 2000 ya - Present	Horizon 5
	E. burchelli	-0.6	0.6	Lower M	~ 2000 ya - Present	Horizon 5
	E. burchelli	-0.6	-3.3	Upper M1/2	~ 5150 - 4300 ya	Horizon 3ii
	E. burchelli	-0.3	-4.1	Lower M3	~ 5150 - 4300 ya	Horizon 3ii
	E. burchelli	-4.2	-3.2	Upper M1/2	Hiatus ~4000 - 2000 ya	Horizon 3ii
	E. burchelli	-5.4	-2.4	M	Hiatus ~4000 - 2000 ya	Horizon 3ii
	E. burchelli	0.4	-3.0	Upper M1/2	Hiatus ~4000 - 2000 ya	Horizon 3ii
	Other (4)					
	? Bush/Tree Rat	-10.7	-1.4	Lower Right M3	Hiatus ~4000 - 2000 ya	Horizon 3ii
	? Bush/Tree Rat	-9.7	0.2	Upper Right M3	Hiatus ~4000 - 2000 ya	Horizon 3ii
	Clarias gariepinus (catfish)	-4.9	-0.6		~ 2000 ya - Present	Horizon 4i (Early Iron Age)
	Clarias gariepinus (catfish)	-10.5	-3.6		~ 5150 - 4300 ya	Horizon 3ii
Sibudu Cave	**Bovidae (71)**					
	Bovidae	-15.0		M	pre-Still Bay	Light Browish Grey II
	Alcelaphini (7)					
	C. taurinus	-15.2		Upper M	HP	Grey Rocky I (Under Rock)
	C. taurinus	-6.8		Upper M2	Late MSA	Oreo
	C. taurinus	-7.0		M	post-HP	Black Under Yellow Ash 1
	C. taurinus	-6.9		Upper M	post-HP	Brown Speckled
	C. taurinus	-14.1		M	post-HP	Mustard

	C. taurinus	-16.6		M	pre-Still Bay	Light Browish Grey III
	Damaliscus pygargus	-7.2		Upper M2	post-HP	Mahogany
	Bovini (17)					
	S. caffer	-13.8		Lower M2	Final MSA	Coffee
	S. caffer	-5.3		Lower M2	Final MSA	Light Brown Mottled
	S. caffer	-12.4		Upper Right M2	HP	Grey Rocky II
	S. caffer	-13.8		Upper Right M1	HP	Grey Rocky II
	S. caffer	-16.0		Lower Right M3	HP	Grey Rocky II (Under Hearth 2)
	S. caffer	-14.4		Lower Left M1	HP	Grey Sand II
	S. caffer	-10.1		Lower M1	Late MSA	Cadbury Under Rock
	S. caffer	-2.6		Upper M1	Late MSA	Mottled Deposit
	S. caffer	-10.8		Upper M2	Late MSA	Orange Mottled
	S. caffer	-17.4		Lower M2	post-HP	Brown Speckled
	S. caffer	-15.1		Lower M2	post-HP	Ebony
	S. caffer	-4.0		Upper M3	post-HP	Mustard
	S. caffer	-7.9		Upper P3	post-HP	Spotty Camel
	S. caffer	-14.8		Lower Right M1	pre-Still Bay	Brown Sand II
	S. caffer	-15.3		Lower Left M1	pre-Still Bay	Brown Sand V (Base near sandbags)
	S. caffer	-9.2		Upper M1	Still Bay	Reddish Grey Sand I
	S. caffer	-10.5		M1	Still Bay	Reddish Grey Sand I
	Cephalophini (31)					
	Cephalophus natalensis	-16.1		Lower M1	Late MSA	Mottled Deposit
	Philantomba monticola	-13.4		Lower M2	Final MSA	Coffee
	P. monticola	-4.9		Lower Right M3	HP	Grey Sand I (Hearth II)
	P. monticola	-17.3		Lower M2	Final MSA	Buff
	P. monticola	-12.1		Upper M	HP	Grey Rocky I (Under Rock)
	P. monticola	-7.1		Lower Left M3	HP	Grey Rocky II
	P. monticola	-16.6		Lower Left M3	HP	Grey Rocky II

	P. monticola	-10.5		Lower Left M3	HP	Grey Rocky II (Under Rock)
	P. monticola	-12.7		Upper Right M1	HP	Grey Sand I
	P. monticola	-10.7		M	HP	Grey Sand I (Hearth II)
	P. monticola	-15.8		Lower Right M1	HP	Grey Sand II
	P. monticola	-15.2		Upper Right M2	HP	Grey Sand II
	P. monticola	-15.8		Upper Left M1	HP	Grey Sand II
	P. monticola	-10.2		Lower Right M3	HP	Pinkish Grey Sand
	P. monticola	-14.8		Lower Right M2	HP	Pinkish Grey Sand
	P. monticola	-13.4		M	HP	Pinkish Grey Sand
	P. monticola	-13.5		Upper Left M3	HP	Pinkish Grey Sand
	P. monticola	-15.9		M	HP	Pinkish Grey Sand
	P. monticola	-7.2		Upper Left M2	HP	Pinkish Grey Sand (Hearth I)
	P. monticola	-14.7		Lower M1	Late MSA	Mottled Deposit
	P. monticola	-8.5		M	post-HP	Black Under B/G Mix
	P. monticola	-12.3		M	post-HP	Yellow Ash
	P. monticola	-10.2		Lower Left M2	pre-Still Bay	Brown Sand III
	P. monticola	-18.8		Lower Left M3	pre-Still Bay	Brown Sand V
	P. monticola	-15.0		Lower Left M2	pre-Still Bay	Brown Sand V (Base)
	P. monticola	-14.9		Lower Right M3	pre-Still Bay	Brown Sand XI
	P. monticola	-16.9		M	pre-Still Bay	Light Browish Grey II
	P. monticola	-12.3		Lower Left M3	Still Bay	Reddish Grey Sand I
	P. monticola	-14.6		Upper M1	Still Bay	Reddish Grey Sand I
	P. monticola	-13.6		M	Still Bay	Reddish Grey Sand I (First Scrape)
	P. monticola	-13.4		M	Still Bay	Reddish Grey Sand I (Second Scrape)
	Hippotragini (5)					
	Hippotragus equinus	-7.6		M	post-HP	Brown Speckled
	H. equinus	-18.1		Lower Left M3	HP	Grey Rocky I
	H. equinus	-5.2		Lower Left M2	HP	Grey Sand I

	H. equinus	-17.5		Lower Left M3	HP	Grey Sand I
	H. equinus	-14.5		Lower M1	HP	Grey Sand II
	Neotragini (1)					
	R. campesteris	-16.7		Lower M1	Final MSA	Buff
	Reduncini (3)					
	K. ellipsiprymnus	-17.1		Upper M2	Final MSA	Buff
	K. ellipsiprymnus	-12.6		Lower M1	post-HP	Black Layer
	R. arundinum	-18.1		Upper M2	Final MSA	Coffee
	Tragelaphini (6)					
	T. oryx	-19.4		Upper M	HP	Grey Rocky I (Hearth III)
	T. oryx	-12.6		Lower M	post-HP	Brown Pox
	T. scriptus	-5.5		Lower M1	Late MSA	Yellow Speckled
	T. scriptus	-6.2		Upper M1	Still Bay	Reddish Grey Sand I
	T. strepsiceros	-9.0		Upper M2	Late MSA	Yellow Speckled
	T. strepsiceros	-17.8		M	post-HP	Flame
	Cercopithecidae (10)					
	Cercopithecus albogularis	-11.3		Upper M3	HP	Pinkish Grey Sand
	C. albogularis	-16.2		Lower M1	HP	Pinkish Grey Sand
	Chlorocebus pygerythrus	-10.7		Upper M	post-HP	Hearth 1 in Yellow Ash - Top
	C. pygerythrus	-12.3		Lower M3	HP	Grey Sand I
	C. pygerythrus	-15.2		Lower M3	HP	Dark Reddish Grey II
	C. pygerythrus	-14.4		M2	HP	Dark Reddish Grey II
	C. pygerythrus	-14.8		Lower M1	HP	Pinkish Grey Sand
	C. pygerythrus	-11.6		Upper Left M2	pre-Still Bay	Brown Sand V
	C. pygerythrus	-15.6		M	pre-Still Bay	Light Browish Grey III
	C. pygerythrus/C. albogularis	-12.1		Lower Left M2	pre-Still Bay	Brown Sand V
	Suidae (36)					
	P. africanus	-15.4		Lower Left M2	HP	Grey Rocky I (Hearthe Base)

	P. africanus	-14.1		Lower M1	HP	Grey Rocky I (Hearth e Top)
	P. africanus	-14.7		M	post-HP	Black Under Yellow Ash 1
	P. africanus	-9.7		M2	post-HP	Hearth 2 in Yellow Ash 2
	Potamochoerus larvatus	-9.7		M	HP	Grey Rocky I
	P. larvatus	-13.7		M	HP	Grey Rocky I
	P. larvatus	-5.5		M	HP	Grey Rocky I (Hearth III)
	P. larvatus	-13.1		M	HP	Grey Rocky II
	P. larvatus	-15.3		M	HP	Grey Sand I
	P. larvatus	-13.5		M	HP	Grey Sand I
	P. larvatus	-15.7		M	HP	Grey Sand II
	P. larvatus	-17.1		M	HP	Grey Sand II
	P. larvatus	-5.1		M	HP	Pinkish Grey Sand
	P. larvatus	-10.8		M	HP	Pinkish Grey Sand
	P. larvatus	-16.1		M	HP	Pinkish Grey Sand (Hearth I)
	P. larvatus	-11.0		M	HP	Pinkish Grey Sand (Hearth)
	P. larvatus	-7.8		M	Late MSA	Yellow Speckled
	P. larvatus	-10.0		M	post-HP	Brown Organic Above Yellow Ash
	P. larvatus	-9.8		M2	post-HP	Reddish Brown
	P. larvatus	-15.4		M	post-HP	Yellow Ash
	P. larvatus	-17.4		M	post-HP	Yellow Ash 2
	P. larvatus	-13.2		M	post-HP	Yellow Ash 2
	P. larvatus	-10.0		M	post-HP	Yellow Ash 2
	P. larvatus	-16.3		M	pre-Still Bay	Brown Sand I
	P. larvatus	-13.5		M	pre-Still Bay	Brown Sand I
	P. larvatus	-13.9		M	pre-Still Bay	Brown Sand I
	P. larvatus	-12.4		Lower Right M3	pre-Still Bay	Brown Sand XII

	P. larvatus	-13.6		M	pre-Still Bay	Brown Sand XIV
	P. larvatus	-13.4		M	pre-Still Bay	Light Browish Grey I (Under Rock)
	P. larvatus	-14.0		M	pre-Still Bay	Light Browish Grey II
	P. larvatus	-13.9		M	pre-Still Bay	Light Browish Grey II
	P. larvatus	-17.4		M	pre-Still Bay	Light Browish Grey II (Under Rock)
	P. larvatus	-13.7		P4/M	pre-Still Bay	Light Browish Grey III (Hearth a)
	P. larvatus	-11.3		M	pre-Still Bay	Light Browish Grey III (Under Rock)
	P. larvatus	-15.0		Upper M3	Still Bay	Reddish Grey Sand I
	P. larvatus	-13.5		M	Still Bay	Reddish Grey Sand II (North Wall)
	Equidae (7)					
	Equus quagga	-14.4		Upper M2	Final MSA	Coffee
	E. quagga	-14.2		Upper M2	Final MSA	Coffee
	E. quagga	-12.2		M	Late MSA	Black Lens II Below Orange Mottled III
	E. quagga	-12.9		Lower Right M1	Late MSA	Brown Mod
	E. quagga	-15.9		Upper M3	Late MSA	Mottled Deposit
	E. quagga	-9.0		Upper M3	post-HP	Brown Speckled
	E. quagga	-14.0		Lower Right M1	post-HP	Yellow Ash 2
	Rinocerotidae (1)					
	C. simum	-13.1		Lower Left M1	HP	Grey Sand I
	Hippopotamidae (1)					
	H. amphibus	-16.0		Tusk	Final MSA	Light Brown Mottled

[1] LPNG – Late Pleistocene Non-Geometric; LPG – Late Pleistocene Geometric (Marean and Gifford-Gonzalez 1991)

[2] No culture/time unit designations are specified for Porc Epic as none have been formally determined. In this dissertation time at Porc Epic is assessed by stratigraphic layer/depth (following Assefa 2006).