Holocene paleoenvironmental change in southeastern Africa (Makwe Rockshelter, Zambia): implications for the spread of pastoralism

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Abstract

The paleoenvironmental conditions surrounding the origins of pastoralism and the movement of herders from eastern to southern Africa sometime between ~ 4000 to 2000 ybp have been much debated. We lack, however, detailed paleoenvironmental data from sites sampling the hunter-to-herder transition in southeastern Africa, the likely corridor from eastern to southern Africa for early pastoralists. Here we report on new paleoenvironmental data from a site in the under-sampled area of eastern Zambia, Makwe Rockshelter, which has two aggregates of archaeological horizons representing the mid-Holocene (~ 5700-5000 ybp) and the late Holocene (~ 1600-800 ybp). The mid-Holocene sediments at Makwe document a foraging society, whereas the late Holocene sediments include both wild game and domestic livestock. Using stable carbon isotopes ($\delta^{13}\text{C}$) of herbivore enamel (n=107), we show that the shift from mid-Holocene to late Holocene paleoenvironments was characterized by an increase in C_4 vegetation. These data are complemented by paleoenvironmental records from Lake Malawi that show that C_4 vegetation peaked after ~ 2000 ybp and was coincident with the onset of cooler, more arid climates. This combined paleoenvironmental record has implications for the spread of pastoralism across southeastern Africa between ~ 3000-2000 ybp and potential ‘animal disease barriers’ these early herders may have faced.

Keywords: pastoralism, southeastern Africa, Holocene, isotopes, Zambia

1. Introduction

Dedicated pastoralism emerged in eastern Africa at least ~ 4000 years before present (ybp) at sites such as Dongodien (GaJi4) and Koobi Fora Ridge (GaJi2) east of Lake Turkana (Marshall et al., 1984; Barthelme, 1985), Enkapune ya Muto in the Central Rift Valley (Marean, 1992; Ambrose, 1998), and Wadh Lang'o, Gogo Falls, and Usenge 3 near Lake Victoria (Prendergast 2010, 2011; Hildebrand and Grillo, 2012; Chritz et al., 2015). However, the earliest evidence for domesticated animals in southern Africa does not appear until ~ 2300 ybp at Leopard Cave in Namibia (Pleurdeau, et al. 2012) and slightly later at Spoegrivier, Blombos, and Kasteelberg in South Africa (Sealy and Yates, 1994; Henshilwood, 1996) and Toteng in Botswana (Robbins et al., 2005, 2008). Recent isotopic data (Chritz et al., 2015) show that a potential dispersal corridor for pastoralists in the Lake Victoria Basin was characterized by open grasslands until at least ~ 1900-1600 ybp, suggesting that the woody tsetse fly barrier to livestock waxed and waned in response to climatic conditions (Smith, 1984, 2005; Gifford-Gonzalez, 2000, 2016). New dates and sites from Lake Eyasi and the Mbulu Plateau in northern Tanzania show the appearance of domesticated animals by ~ 3000-2800 ybp (Prendergast et al., 2013, 2014), in agreement with paleoenvironmental evidence for an early, open tsetse-free corridor permitting movement of pastoralists southward. Unfortunately, however, we have very little knowledge of Holocene paleoenvironments in southeastern Africa during the spread of pastoralism across the continent.

The savannas and Highveld of Zambia are an often overlooked but critical

connection between eastern and southern Africa. Eastern Zambia in particular has produced several middle to late Holocene archaeological sites that fill a spatial gap in our understanding of the hunter-to-herder transition in sub-Saharan Africa. One such site, Makwe Rockshelter (Figure 1A), traverses this transition and may document the earliest domesticated animals and relationships between hunters and herders in the region. Here we present stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes of herbivore enamel and reconstruct middle to late Holocene paleoenvironments at Makwe. The mid-Holocene sediments of Makwe (~ 5700-5000 ybp) preserve evidence of a foraging society and are entirely composed of wild game, whereas the late Holocene sediments (~1600-800 ybp) preserve both wild game and domestic livestock. Even in the late Holocene sediments, wild game is abundant ($n = 142$) and outnumbers domesticates (wild game = 74.3% fauna), permitting paleoenvironmental inferences to be made. We ask whether the transition from the mid-Holocene to the late Holocene was characterized by a shift to more C_4 -dominated paleoenvironments, as the onset of arid conditions in the late Holocene and a decrease in woody cover has been argued to have been favorable to the spread of pastoralism (Marean, 1992; Kusimba, 2003; Gifford-Gonzalez, 2000, 2016).

1.1 Geological context

Makwe Rockshelter is located in the southwestern corner of Zambia's Katete District (14°24.8' S; 31°56.0' E) approximately 1.0 km from the international border with Mozambique (Figure 2). The rockshelter is located in the northeast side of a large granite dome known as Little Makwe kopje at 1,000-1,050 m above sea level on the grassy, well-watered plateau of the Zambian Highveld (Phillipson, 1973, 1976). The rockshelter itself

is formed by an overhang 20 m long and 9 m high extending 8.5 m into the granite dome. The presence of large boulders restricts the surface area to $\sim 45 \text{ m}^2$. A maximum depth of 2.08 m was recorded in nine stratigraphic horizons named from oldest to youngest: 1, 2i, 2ii, 3i, 3ii, 4i, 4ii, 5, and 6 (Phillipson 1973, 1976) (Figure 1B). Details of the excavations can be found in Phillipson (1976).

Phillipson (1976) obtained radiocarbon dates from charcoal samples in all horizons except the earliest, Horizon 1, from which there was no charcoal, and the surface level, Horizon 6. Additionally, the sample from Horizon 5 was reported as “too young to date.” For the material that was datable, we have corrected Phillipson’s (1976) dates at 95.4% confidence using the ShCal13 curve (Hogg et al., 2013) with OxCal 4.2 (Bronk Ramsey, 2009). The corrected radiocarbon dates demonstrate a depositional hiatus in the sequence between Horizons 3ii and 4i, a gap that roughly spans from ~ 5000 ybp to ~ 1600 ybp (Table 1; Figure 1B). The earlier part of the sequence is constrained between $5717 \text{ calibrated y B.P. (calBP)} \pm 149$ in Horizon 2ii and $4950 \text{ calBP} \pm 203$ in Horizon 3ii. While there are some stratigraphic inconsistencies in the radiocarbon dates for this part of the sequence, all dates are tightly grouped between ~ 5700 - 5000 ybp. Three reliable radiocarbon dates were obtained from the upper part of the sequence: $838 \text{ calBP} \pm 66$ for Horizon 4i, and $1600 \text{ calBP} \pm 128$ and $1071 \text{ calBP} \pm 91$ for 4ii. Again, these dates are stratigraphically inconsistent, but clearly group separately from those in Horizons 2i through 3ii. For analytical purposes, we aggregate Horizons 1-3ii into a ‘mid-Holocene’ unit (~ 5700 - 5000 ybp) and Horizons 4i-5 into a ‘late Holocene’ unit (~ 1600 - 800 ybp), as they are separated by a depositional hiatus spanning several thousand years. In addition, mid-Holocene sediments preserve evidence of a foraging

society whereas the late Holocene sediments contain both wild game and domestic livestock (see below). We do not include Horizon 6 (the cave floor) in the late Holocene unit given its very young age.

1.2 Archaeological context

Phillipson (1976) named the Makwe Industry from the lithic remains of the site, although Inskeep (1979) suggested it is simply a local variation of the older Nachikufan I Industry. The Makwe Industry is present in all horizons at Makwe except the surface sediments of Horizon 6. In Horizons 4i to 5, the Makwe Industry is found with traces of the early Iron Age (Chifumbaze Industry). Phillipson (1976) provides an age estimate of ~ 10,000-8000 ybp for Horizon 1 based on similar composition of the Makwe Industry in layers of that age at the nearby site of Kalemba Rockshelter, and notes that the low artifact density in the bottom meter of the sequence may extend to the latest Pleistocene.

The Makwe Industry is characterized by reduction in artifact size from the Nachikufan I and the abandonment of the radial-core technique for single and double platform cores. Retouched implements are mostly backed microliths with few scrapers and no points. Phillipson's (1976) analysis suggests a continuous usage, but gradual development, of the Makwe Industry at the site. For instance, geometrics increase from 24% of retouched implements in Horizons 1 and 2i to 71% thereafter at the expense of backed flakes, and *petits tranchets* appear first in Horizon 3ii. Other than these minor changes, the composition of the Makwe Industry stays remarkably similar throughout the sequence. Non-chipped stone artifacts include rare and fragmentary remains of ground stone axes in Horizons 1 to 2ii. Bored stones, frequent at many sites of this age in

southcentral Africa, are absent at Makwe. Formal grinding stones appear with other early Iron Age traces in Horizon 4ii (Phillipson, 1973, 1976).

Bone bodkins and bone and stone beads are also present in the sequence. Bodkins are present in all Horizons, but conical bone points do not appear until Horizon 4i. Bead typology provides some of the most obvious changes in the sequence. Bone beads are present in Horizons 1 to 3i, being exclusively ring-shaped in Horizons 1 and 2i and exclusively tubular in Horizons 2ii and 3i. From Horizons 3ii through 5, only shell disc beads are present. With the exception of a pierced fragment of ostrich eggshell in Horizon 2ii, all shell artifacts are restricted to Horizons 3ii and above (Phillipson, 1976).

A few pieces of pottery have been recovered from Horizons 3i and 3ii in a small, isolated section of the excavation and Phillipson (1976) attributed their occurrence in these mid-Holocene layers to localized disturbance and/or stratigraphic inconsistencies. Otherwise, the earliest pottery at Makwe Rockshelter appears in Horizon 4i, becoming frequent in Horizon 4ii, and is identified as early Iron Age type. Early Iron Age pottery continues through Horizon 5 when the later Iron Age Luangwa tradition first appears (Phillipson, 1976). This chronology is consistent with other sites in Zambia, although the early Iron Age tradition may have appeared at Makwe slightly earlier than in other parts of southeastern Africa (Huffman, 1989). Metal objects first occur when pottery becomes frequent in Horizon 4ii. Copper, which is not available locally, is present in Horizon 5 (Phillipson, 1976).

Horizons 1 to 3ii preserve an exclusively wild fauna similar in composition to the fauna of southeastern Africa today (Table 2). Domestic cattle (*Bos taurus*) first appear in Horizon 4i and domestic goat or sheep (Caprini) in Horizon 4ii. While represented in all

horizons above 4i, domestic animals remain in a slight minority throughout. The wild fauna is dominated by warthog (*Phacochoerus* sp.), zebra (*Equus quagga*), bush duiker (*Sylvicapra grimmia*), and bushpig (*Potamochoerus* sp.). Larger taxa, like African buffalo (*Syncerus caffer*) and eland (*Tragelaphus oryx*), are present but rare, only occurring below Horizon 3i. Human remains consist of an incisor from Horizon 2ii, two molars and a fragment of a radius from Horizon 4i, and one molar from Horizon 4ii (Phillipson, 1976).

Phillipson's (1976) interpretation of the Makwe sequence is that the makers of the Makwe Industry continued to occupy the rockshelter from the mid-Holocene to the late Holocene, but had contact with pottery-making early pastoralist and farmers during the latter. The movement of early Iron Age technologies into eastern Zambia ~ 2000 ybp likely marks the first contact of stone-tool-using foragers with early pastoralists and farmers in this region (Phillipson, 2005). The continuity of the Makwe Industry across the depositional hiatus between Horizons 3ii and 4i suggests continual occupation by the same or a similar forager group slightly prior to contact with herders and farmers. Phillipson (1976) interprets the appearance of domestic animal remains at Makwe, although a minority of the overall faunal assemblage, as substantial inter-group contact or temporary client relationship between foragers and pastoralists.

2. Materials and Methods

2.1 Fossil herbivore sample

A total of 107 fossil herbivore teeth were sampled for stable carbon and oxygen isotopes from Phillipson's Makwe Rockshelter faunal collection at the Livingstone

Museum, Zambia. All nine horizons are represented in this sample, although only one specimen, a domestic cattle molar, is sampled from the surface sediments of Horizon 6 (Supplemental Information Table 1). Sampling focused on both wild and domestic fauna, ensuring to sample both wild and domestic specimens in Horizons 4i-5. Enamel samples were taken from molars (preferably third molars) to limit the potentially confounding effects of weaning (Kingston and Harrison, 2007). In attempt to minimize sampling multiple teeth from the same individual, all sampled teeth are represented by unique catalog numbers, which likely suggests that the 107 samples represent different individuals although we cannot directly confirm this based on Phillipson's (1976) data.

2.2 Stable carbon and oxygen isotopes

Stable carbon isotope analysis permits inference of the proportion of diet derived from plants using the C₃ photosynthetic pathway (trees, shrubs, and high-altitude grasses above 2000 m) and the C₄ pathway (most low elevation tropical grasses in Africa) based on the established link between the carbon isotope composition of tooth enamel and the isotopic composition of vegetation (Lee-Thorp, 1989, 2002; Wang and Cerling, 1994; Sponheimer and Lee-Thorp, 1999; Cerling et al., 2003, 2015). The carbonate fraction of tooth enamel has been shown to be minimally affected by diagenesis and, therefore, can be used as a reliable proxy for diet, which is in turn used to infer paleoenvironments (DeNiro and Epstein, 1978; Wang and Cerling, 1994; Lee-Thorp and Sponheimer, 2003). C₃ plants have $\delta^{13}\text{C}$ values ranging from -22‰ to -36‰ with a mean of $-27.4 \pm 2.0\text{‰}$ in tropical Africa and C₄ grasses have a mean of $-12.7 \pm 1.2\text{‰}$ with a range of -10‰ to -14‰ (Tieszen et al., 1979, 1983; O'Leary, 1981; Ambrose and DeNiro, 1986; Heaton,

1999; Cerling et al., 2003, 2015; Passey et al., 2005). Variability in water availability, light, and temperature, and photosynthetic recycling of respired CO₂ in closed canopy forests leads to increased isotopic variability for C₃ plants (van der Merwe and Medina, 1991; Kohn, 2010). CAM (Crassulacian acid metabolism) pathway plants, predominantly succulents, have $\delta^{13}\text{C}$ values between those of C₃ and C₄ biomass (O’Leary, 1981, 1988; Heaton, 1999). However, they are not considered in this study as it is unlikely that they composed a significant portion of herbivore diet or overall biomass in southeastern Africa during the middle or late Holocene. C₃ and C₄ plants may have isotopic yields outside of the average ranges cited above in areas such as marshes, but the general isotopic distinction between the two photosynthetic pathways is ideal for differentiating broad dietary strategies (Cerling et al., 2003; Kingston and Harrison, 2007). Carbon isotope composition is reported in δ -notation where $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$, and δ is expressed in per mil, ‰, i.e., x1000‰.

To compensate for recent changes in atmospheric CO₂, all $\delta^{13}\text{C}$ enamel values in this study are adjusted by -1.5‰ following established conversion methods (Tippie et al., 2010; Faith et al., 2015; Garrett et al., 2015). In addition to atmospheric CO₂, the fractionation between diet and enamel tissue must be considered. Tooth enamel of large mammals has been shown to be ~ +14.1‰ enriched in ${}^{13}\text{C}$ compared to their diet (Cerling and Harris, 1999; Passey et al., 2005). As such, enamel values more depleted than -9‰ characterize C₃ dominated diets, values more enriched than -2‰ suggest primarily C₄ diets, and values in between indicate mixed feeding.

In addition to descriptive and statistical analysis, the relative contribution of C₃ and C₄ biomass to diet is estimated from the $\delta^{13}\text{C}$ enamel values using a mixing model

between endmember $\delta^{13}\text{C}$ values for C_3 and C_4 plants and +14.1‰ enrichment between diet and tooth enamel (Phillips, 2012; Cerling et al., 2015; Garrett et al., 2015):

$$\delta^{13}\text{C}_{\text{measured}} = \delta^{13}\text{C}_{\text{C}_3} * f_{\text{C}_3} + \delta^{13}\text{C}_{\text{C}_4} * f_{\text{C}_4},$$

The endmember values used here are -26.0‰ for C_3 plants and $-12.7 \pm 1.2\text{‰}$ for C_4 plants, with the C_3 endmember representing an average of non-water stressed conditions ($-27.4 \pm 2.0\text{‰}$) and water-stressed conditions ($-24.6 \pm 1.1\text{‰}$) (Cerling and Harris, 1999; Cerling et al., 2003; Passey et al., 2005; Kohn, 2010). Estimates of percent C_4 consumption were rounded to the nearest 5% following Chritz et al. (2015).

Stable oxygen isotope analysis may be used as a proxy for aridity with the assumption that during arid intervals in the tropical low latitudes the lighter oxygen isotope, ^{16}O , will be preferentially lost in evaporative processes relative to the heavier, ^{18}O , isotope. The result of this scenario is heavier, or ^{18}O enriched, signals recorded in faunal tooth enamel (Kohn, 1996; Levin et al., 2006). Taxa that rely on leaf water typically exhibit greater isotopic variability and are more evaporation sensitive than those that primarily drink from meteoric/surface sources (Levin et al., 2006). While this difference between evaporation sensitive and insensitive taxa can be used to calculate an aridity index, we do not do so here because our small sample sizes do not permit comparisons of evaporation-sensitive and evaporation-insensitive taxa between the mid-Holocene and late Holocene. Furthermore, drawing direct inferences from herbivore enamel $\delta^{18}\text{O}$ is confounded by our current knowledge of this proxy's relationship to atmospheric water flux and oxygen exchange in herbivore body water (Levin et al., 2006,

2009). We therefore conservatively choose to present the $\delta^{18}\text{O}$ data without drawing conclusions from it, in the hope that future work will be able to use these data once the above mentioned complications are settled.

Enamel was cleaned of adhering sediment using a high-speed Brasseler dental drill (Forza L50k) with diamond encrusted tungsten-carbide bits. Approximately 2 mg of powdered enamel was removed from broken edges of each tooth. Each powdered enamel sample was rinsed in ~ 2% hydrogen peroxide (bleach) solution for 24 h to removed organic matter and then rinsed and centrifuged to a neutral pH with deionized water. This was followed by sample treatment with 0.1 M acetic acid for ~ 4 h to remove exogenous carbonate and rinsed to neutrality again. Mass spectrometry was performed at the Light Stable Isotope Laboratory in the Department of Geosciences at the University of Florida, Gainesville in a Finnigan-MAT 252 mass spectrometer interfaced with a Kiel III carbonate extraction device. The isotopic composition of CO_2 produced was measured along with NBS-19, an international calcium carbonate standard. Replicate measurements of the standards during analysis had errors of ~ 0.1‰ for oxygen and ~ 0.05‰ for carbon.

3. Results

$\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values for individual taxa are shown in Figures 3-4 and Table 3. Overall, there is a trend to more enriched $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values going from the mid-Holocene to the late Holocene in many taxa. However, sample sizes are small for most taxa and therefore, in order to provide sufficient sample sizes for statistical comparison, taxa were aggregated into dietary classes based on observational (Kingdon

1982, 2013) and isotopic data (Harris and Cerling, 2002; Sponheimer et al., 2003; Cerling et al., 2003, 2015). The dietary classes included grazers (*Alcelaphini*, *Equus*, *Phacochoerus*, and *Aepyceros*), browsers (*Oreotragus*, *Sylvicapra*, and *Tragelaphini*), and omnivores (*Potamochoerus*). While *Aepyceros* is often described both behaviorally and isotopically as a mixed feeder (Gagnon and Chew, 2000; Cerling et al., 2003; Sponheimer et al., 2003), the diet of this taxon is variable and *Aepyceros* has been observed to have C₄-dominated diets depending on season and location (Jarman and Sinclair, 1979; Dunham, 1980a; Fritz and Bourgarel, 2013). In particular, Recent *Aepyceros* populations in southern and southeastern Africa have been show to consume between 75-90% grasses (Dunham 1980b; van Rooyen, 1992, 1993). Our Makwe data indicate C₄-dominated diets for *Aepyceros* and therefore we include this taxon with grazers. Fresh grass grazers (*Reduncini* and *Syncerus*) had small sample sizes for both the mid-Holocene (n = 3) and late Holocene (n = 3) and are not statistically analyzed.

For each dietary class, 95% confidence intervals (CI) were calculated for the mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values of each taxon by bootstrapping with replacement over 10,000 iterations. Doing so permits testing the premise that the various taxa aggregated in each dietary class have cohesive isotopic values, which, in turn, allows for identifying meaningful temporal changes in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ even if the taxa within a dietary class are not evenly sampled across the Makwe sequence. Grazers and browsers show broad overlap in the 95% CI across taxa (Table 3), meaning that differential representation of taxa within these dietary classes is unlikely to drive temporal trends. Omnivores are only represented by a single taxon, *Potamochoerus*.

3.1 Carbon

All dietary classes show overlap of the 95% CI of the means of $\delta^{13}\text{C}$ enamel for the mid-Holocene and late Holocene periods at Makwe. The CIs for grazers (mid-Holocene: -4.1‰ to -1.2‰; late Holocene: -2.7‰ to -0.7‰), however, suggests a subtle shift towards more enriched $\delta^{13}\text{C}$ enamel values. A Mann-Whitney U test shows that these differences are non-significant ($p = 0.466$) (Table 4). Omnivores also become enriched from the mid-Holocene to the late Holocene, although these differences are also non-significant ($p = 0.624$). $\delta^{13}\text{C}$ enamel values of browsers show no trends ($p = 0.620$).

All grazers and fresh grass grazers are estimated to have consumed over 70% C_4 biomass throughout the Makwe sequence (Table 5). For the grazing taxa that occur in both the mid-Holocene and the late Holocene, all show a shift towards greater C_4 consumption through time. Alcelaphini and *Equus* increase their C_4 consumption by 10%, whereas *Aepyceros* and *Phacochoerus* increase by 5%. Fresh grass grazers are represented by *Syncerus* in the mid-Holocene and Reduncini in the late Holocene, and show a 5% increase in C_4 consumption. Two of three browsers show a slight decrease in C_4 consumption from the mid-Holocene to the late Holocene (20% to 0% for Tragelaphini and 10% to 0% for *Sylvicapra*). Important to note, however, is that the mid-Holocene tragelaphin specimen is an eland (*Tragelaphus oryx*), today mixed-feeders, while the late Holocene tragelaphin specimens are greater kudu (*Tragelaphus strepsiceros*), today browsers (Kingdon 1982, 2013). *Oreotragus* is estimated to have consumed no C_4 vegetation in both the mid-Holocene and late Holocene.

Domestic livestock have C_4 -dominated diets at Makwe. Cattle are nearly pure C_4 feeders at Makwe ($\delta^{13}\text{C}$: $-0.7 \pm 1.3\text{‰}$) and are estimated to have consumed 85% C_4

vegetation. Domestic Caprini appear to be pure grazers as well ($\delta^{13}\text{C}$: $-1.3 \pm 2.9\text{‰}$) and are estimated to have 80% C_4 consumption.

3.2 Oxygen

Across dietary classes (Figure 5; Table 4), a Mann-Whitney U test indicates a significant shift in $\delta^{18}\text{O}$ enamel values for grazers ($p = 0.008$), which become more enriched from the mid-Holocene (-4.1‰ to -2.7‰) to the late Holocene (-2.4‰ to -0.6‰). A similar enrichment in $\delta^{18}\text{O}$ enamel values is evident for omnivores (mid-Holocene: -9.9‰ to -3.9‰ ; late Holocene: -5.8‰ to -2.5‰), although this is not statistically significant ($p = 0.142$), this is almost certainly due to a lack of statistical power due to the small sample size. Interpretations of the shift towards more enriched $\delta^{18}\text{O}$ values in the late Holocene for grazers and omnivores is confounded by several factors (Levin et al., 2006, 2009) and we refrain from drawing climatic or environmental interpretations on these results. Browsers are not characterized by any significant differences in $\delta^{18}\text{O}$ enamel values ($p=0.634$) and have completely overlapping CIs for the mid-Holocene and late Holocene periods.

4. Discussion

The Makwe isotope data presented here are a significant contribution to our knowledge of mid-Holocene and late Holocene paleoenvironments in Zambia and can be contrasted with those from Gogo Falls, Kenya, the only other pastoral site sampled for isotopes. The Makwe data also contribute to our knowledge of ecological change in the herbivores of southeastern Africa from the Holocene to the Recent and, more broadly,

paleoenvironmental change across the region during this time. Finally, we conclude by revisiting how the Makwe data fit into the broader picture of the movement of pastoralists from eastern to southern African during the Holocene. We discuss each of these contributions of the Makwe isotope data below.

4.1 Comparisons with Gogo Falls, Kenya

Only one other pastoralist site in Africa, the Elmenteitan layers of Gogo Falls (~1900-1600 ybp) near Lake Victoria in Kenya, has been systematically sampled for $\delta^{13}\text{C}$ isotope analysis (Chritz et al., 2015). Of the wild taxa that have been isotopically analyzed at both Makwe and Gogo Falls, all taxa at Makwe have more depleted $\delta^{13}\text{C}$ values in both the mid-Holocene and late Holocene periods. This is especially true of the browsers and *Potamochoerus*, which at Gogo Falls are estimated to have consumed between 20% and 60% C_4 biomass (Chritz et al., 2015). These direct comparisons of $\delta^{13}\text{C}$ values should be interpreted cautiously, as these comparisons may be compromised by the structural properties of the soils which underlay the vegetation herbivores consume. Serpentine soils, which cover much of the Zambian Highveld, have high levels of nickel, chromium, and copper (Vincent and Thomas, 1961; Wild, 1965), which result in grasses with lower palatability and digestibility compared with those which grow on the more fertile volcanic soils in Kenya (Bell, 1982). This soil control on grass ecosystem structure may play a role in the lower $\delta^{13}\text{C}$ values at Makwe.

The domestic livestock at Gogo Falls are also more enriched than those at Makwe. As with Gogo Falls, however, identification of the domestic Caprini remains is difficult below the tribal level and specimens cannot be confidently classified as either

sheep (*Ovis*) or goat (*Capra*) (Badenhorst and Plug, 2003). Although Brian Fagan in Phillipson (1976) identified all of the Caprini Makwe remains as *Capra*, given the difficulties differentiating sheep and goats, we conservatively identify them to the tribal level. If the Makwe remains do indeed represent goats, then they are significantly more enriched than their Recent counterparts (Recent *Capra* $\delta^{13}\text{C}$: $-7.5 \pm 2.8\text{‰}$) (Balasse and Ambrose, 2005; Chritz et al., 2015). If the Makwe remains represent sheep, then they are comparable to a sample of Recent sheep from Kenya (Recent *Ovis* $\delta^{13}\text{C}$: $-0.4 \pm 0.6\text{‰}$) (Balasse and Ambrose, 2005). Regardless of the specific identification of the Caprini teeth, the $\delta^{13}\text{C}$ enamel values still indicate high consumption of C_4 resources, suggesting a dominance of grasslands in the region during the late Holocene.

4.2 Comparisons with Recent stable isotope data

The Makwe isotope data offer a glimpse into ecological changes in the large herbivores of southeastern Africa from the Holocene to the Recent. Aggregations of the mid-Holocene and late Holocene Makwe $\delta^{13}\text{C}$ data for bovids can be compared to the Sponheimer et al. (2003) dataset of Recent $\delta^{13}\text{C}$ data from the southern African countries of South Africa, Botswana, Namibia, and Zimbabwe (Figure 6). A Mann-Whitney U test indicates that only *Aepyceros* is significantly different ($p = 0.002$) between Makwe and the Recent sample, with the Makwe sample being enriched, showing greater consumption of C_4 resources by impala during the Holocene than today in the region. In light of this statistical comparison, it is important to note that the range of Recent *Aepyceros* in the Sponheimer et al. (2003) dataset (-12.6‰ to -0.1‰) spans all isotopic dietary categories, from browsing to grazing. Furthermore, Recent *Aepyceros* populations in southern and

southeastern Africa have been shown to consume between 75-90% grasses (Dunham, 1980a, b; van Rooyen, 1992, 1993). The southern and southeastern data are consistent with Recent *Aepyceros* samples from the savannas of Akagera National Park in Rwanda, which indicate significant proportions of graze in the diets of impala (Copeland et al., 2009). As the one taxon with Recent counterparts that indicate a highly variable diet isotopically, the fact that *Aepyceros* at Makwe is predominantly a grazer is additional support for C₄-dominated environments. Non-bovid herbivores from Makwe, *Equus* and *Phacochoerus*, do not significantly differ from their Recent conspecifics (Codron et al., 2007).

4.3 Makwe's place in a regional paleoenvironmental context

Despite the paucity of isotopic data from other pastoralist sites, the Makwe $\delta^{13}\text{C}$ enamel data can be framed in the context of regional paleoenvironmental records that span the Holocene (Figure 7). Drill cores from Lake Malawi have yielded paleotemperature estimates based on TEX₈₆ (Woltering et al., 2011) and vegetation proxies, including the weighted mean *n*-alkane $\delta^{13}\text{C}$ record (Castañeda et al., 2007) and the ratio of cinnamyl to vanillyl (C/V) lignin phenols (Castañeda et al., 2009), nearby Makwe Rockshelter. Carbon isotope composition of the long-chain *n*-alkanes in plant leaf waxes have been used to successfully distinguish between C₃ and C₄ biomass (Collister et al., 1994). Castañeda et al. (2009) argued that since cinnamyl phenols are present in non-woody tissues and that vanillyl phenols are found in woody plant tissues (Hedges and Mann, 1979a, 1979b), the C/V ratio could be used to examine the contributions of non-woody vs. woody plant tissues. The Zambezi catchment record (Schefuß et al., 2011)

provides a rainfall proxy based on the hydrogen isotope composition of n -C₃₁ alkanes (δD n -C₃₁ alkane) while the carbon composition of n -C₃₁ alkanes ($\delta^{13}C$ n -C₃₁ alkane) is a vegetation proxy. The Zambezi catchment in the Indian Ocean is further away from Makwe than Lake Malawi, but major climatic and environmental shifts affecting the region are evident in the catchment record.

Using the n -alkane $\delta^{13}C$ record and C/V ratio vegetation proxies in tandem, paleoenvironmental records from Lake Malawi show that major shifts in basal vegetation were coincident with shifts in temperature. Castañeda et al. (2007, 2009) documented a pulse of increased C₃ in the Malawi Basin ~ 7700-2000 ybp. The lowest contribution of C₄ vegetation to the n -alkane $\delta^{13}C$ record during the mid and late Holocene is ~ 40% at 4900 ybp, and the lowest C/V ratio, indicating more woody plant tissues, occurred at 4000 ybp (Castañeda et al., 2007, 2009). At roughly the same time, between ~ 7700 and ~ 5000 ybp, the TEX₈₆ record indicates a temperature increase of ~ 4°C (Woltering et al., 2011). Both the n -alkane $\delta^{13}C$ record and the C/V ratio indicate a shift back towards more C₄ vegetation after 4000 ybp with estimated contribution of C₄ vegetation to the n -alkane $\delta^{13}C$ record peaking at >55% about 1000 ybp (Castañeda et al., 2007, 2009). These indicators of increased C₄ vegetation are accompanied by a decrease in late Holocene temperatures (Woltering et al., 2011). Castañeda et al. (2009) argue that these combined records suggest cooler and more arid conditions in the Lake Malawi basin over the last 2000 years.

In the Zambezi catchment, depleted δD n -C₃₁ alkane values, indicating wetter conditions, are associated with stronger evidence for C₄ vegetation in the $\delta^{13}C$ n -C₃₁ alkane values (Schefuß et al., 2011). Schefuß et al. (2011) argue that this unexpected

correlation is due to a shift in the hydrological source area. When there is greater rainfall in the floodplain on the coast, more C₄ plant waxes from further upstream are able to reach the coast while lower rainfall transport only C₃ plant waxes from coastal vegetation. A general trend towards more C₄ vegetation from the mid to the late Holocene is apparent in the $\delta^{13}\text{C}$ *n*-C₃₁ alkane values and, as described above, likely reflects an overall change in regional vegetation. The δD *n*-C₃₁ alkane values, as expected in this scenario, indicate greater rainfall over the Zambezi catchment area during the late Holocene than in the mid-Holocene (Schefuß et al., 2011). From this record it is difficult to assess aridity in the Zambian Highveld around Makwe Rockshelter, but it does seem as if there is an overall regional shift to more C₄ vegetation, supporting the record from Lake Malawi.

The Lake Malawi and Zambezi catchment data are complemented by a pollen record from Ishiba Ngandu on the northern Zambian Plateau ~ 450 km to the north of Makwe Rockshelter. The Ishiba Ngandu record, despite poor chronological control, has been interpreted to indicate a decline of moist evergreen forest taxa at ~ 3000 ybp coincident with an increase in C₄ grasses (Livingstone, 1971; Hamilton, 1982). Livingstone (1971) argues that this change in pollen may be related to a combination of slightly more arid climatic conditions and the entry of Iron Age herders and pastoralists using fire to clear areas. The expansion of forests during the mid-Holocene associated with humid conditions has also been identified in the record from Lake Rukwa, Tanzania (Vincens et al., 2005) and has been associated to a strengthened African monsoon (deMenocal et al., 2000). As with the records from Lake Malawi, the Zambezi catchment, and Ishiba Ngandu, increasingly arid conditions and expansion of grasses are indicated in

the Lake Rukwa record over the last 4000 years (Vincens et al., 2005). The vegetation change from C₃-dominated conditions to C₄-dominated conditions occurred as southeastern Africa shifted from warm mid-Holocene temperatures to cooler late Holocene temperatures (Woltering et al., 2011), and is consistent with the $\delta^{13}\text{C}$ enamel data from Makwe, which document mixed C₃/C₄ paleoenvironments during the mid-Holocene and a shift to more C₄-dominated paleoenvironments during the late Holocene.

4.4 Makwe's implications for the spread of pastoralism

The new Makwe isotope data throw light on the paleoenvironmental conditions that facilitated the spread of pastoralism across sub-Saharan Africa during the late Holocene. Dedicated pastoralism emerged in eastern Africa at least ~ 4000 ybp based on sites in Kenya (Marshall et al., 1984; Barthelme, 1985; Marean, 1992; Ambrose, 1998; Prendergast 2010, 2011; Hildebrand and Grillo, 2012; Chritz et al., 2015). Pastoralism first reached southern Africa by ~ 2300 ybp, as evinced by domestic Caprini teeth from Leopard Cave, Namibia (Pleurdeau, et al. 2012), although this finding has been linked with a western route of movement for pastoralists into southern Africa. If an eastern route was taken, then the movement of pastoralists into eastern Zambia likely occurred ~ 3000-2000 ybp (Phillipson, 2005). This date is based on sites from Lake Eyasi and the Mbulu Plateau in northern Tanzania that date to ~ 3000-2800 ybp (Prendergast et al., 2013, 2014) and the earliest pastoral sites in South Africa that date to ~ 2000 ybp (Sealy and Yates, 1994; Henshilwood, 1996). While the late Holocene sediments of Makwe (~ 1600-800 ybp) postdate the initial movements of herders across the region, our data are within hundreds of years of this event and it is possible, if not likely, that similar environments

persisted at that earlier time. This is especially true when contrasted with the mid-Holocene, which hosted a diversity of both C₃ and C₄ consuming herbivores. Our $\delta^{13}\text{C}$ enamel data suggest that by the late Holocene C₄-dominated environments characterized eastern Zambia and would have provided a route for pastoralists and livestock to southern Africa. Taxa that today are almost exclusively grazers (*Phacocoerus* and *Equus*) evince mixed-feeding during the mid-Holocene but shift to C₄-dominated diets in the late Holocene.

The Makwe isotope data, combined with other paleoenvironmental records (Figure 7), are consistent with hypotheses regarding the importance of late Holocene aridity and grasslands in facilitating the movement of pastoralists out of eastern Africa (Marean, 1992; Kusimba, 2003; Gifford-Gonzalez, 2000, 2016). The combined record suggests that the movement of pastoralists from eastern to southern Africa during the late Holocene was coincident with regional aridity and a shift to C₄-dominated paleoenvironments. The reduction of bushy environments as mesic conditions waned and C₃ vegetation decreased would have led to a decrease in disease risk to livestock from tsetse flies (Smith, 1984, 2005; Gifford-Gonzalez, 2000, 2016). Although the expansion of C₄ grasslands during the late Holocene may be the product of burning by pastoralists, the Lake Malawi paleoenvironmental records suggest that the abundance of C₄ vegetation is also a product of regional aridity and temperature change. Future $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel isotopic data from other pastoralist sites and field work in southeastern Africa, especially eastern Zambia with its rich Holocene record, will provide much-needed additional data on the spread of pastoralism across the region. These data may provide evidence for

intensive human-modification of landscapes (e.g., pastoralist burning) or a natural transition to cooler temperatures and C₄-dominated vegetation during the late Holocene.

5. Conclusions

The new $\delta^{13}\text{C}$ enamel data from Makwe Rockshelter document a shift to more grassy paleoenvironments during the late Holocene (~ 1600-800 ybp) of eastern Zambia. These data are consistent with hypotheses regarding the importance of C₄ grasslands to the spread of pastoralism from eastern to southern Africa (Marean, 1992; Kusimba, 2003; Gifford-Gonzalez, 2000, 2016) and provide evidence for a grassy route across southeastern Africa during this time. Paleoenvironmental records from Lake Malawi and elsewhere show that C₄ vegetation peaked after ~ 2000 ybp with the onset of cooler, more arid climates. Future work on other Holocene sites in southeastern Africa are much-needed to further refine our understanding of the paleoenvironmental context of the hunter-to-herder transition, and the Makwe data provide a starting point for this work.

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Figure Captions

Figure 1. (A) Map of southeastern Africa with the location of Makwe Rockshelter noted by the gold star and (B) cross-section through the Makwe deposits (adapted from Phillipson, 1976) with radiocarbon dates shown as black circles and lines depicting error bars. [Page Width]

Figure 2. Detailed map of the area surrounding Makwe Rockshelter with areas above 1075m shaded (adapted from Phillipson, 1976). [1/2 Page Width]

Figure 3. Boxplots of stable carbon ($\delta^{13}\text{C}$) isotopes of the Makwe fauna at the tribal/genus level. $\delta^{13}\text{C}$ values are corrected as described in the text. The $\delta^{13}\text{C}$ values span the spectrum of browsers (green) to grazers (brown). Dotted lines denote breaks between browsers and mixed-feeders (green dotted line) and mixed-feeders and grazers (brown dotted line). [1/2 Page Width]

Figure 4. Boxplots of stable oxygen ($\delta^{18}\text{O}$) isotopes of the Makwe fauna at the tribal/genus level. [1/2 Page Width]

Figure 5. Boxplots of stable oxygen ($\delta^{18}\text{O}$) isotopes of the Makwe fauna by dietary class. While all dietary classes show enriched $\delta^{18}\text{O}$ values for the late Holocene, this trend is statistically significant for grazers ($p = 0.008$). [1/2 Page Width]

Figure 6. Boxplots of stable carbon ($\delta^{13}\text{C}$) isotopes of the Makwe bovids compared with Recent $\delta^{13}\text{C}$ isotope data from southern Africa. Only *Aepyceros* differs significantly ($p = 0.002$) between the Makwe and Recent samples. Recent $\delta^{13}\text{C}$ isotope data from Sponheimer et al. 2003. [Page Width]

Figure 7. Compilation of regional paleoenvironmental records that span the age of the Makwe deposits: Lake Malawi TEX_{86} record (Woltering et al., 2011), Lake Malawi weighted mean $\delta^{13}\text{C}$ of *n*-alkanes (Castañeda et al., 2007), Lake Malawi cinnamyl to vanillyl (C/V) lignin phenols ratio (Castañeda et al., 2009), and Zambezi catchment hydrogen (δD) and carbon ($\delta^{13}\text{C}$) isotopes of *n*- C_{31} alkanes (Schefuß et al., 2011). [Page Width]

Table 1. Phillipson's (1976) charcoal radiometric dates corrected with ShCal13 curve (Hogg et al., 2013) with OxCal 4.2 (Bronk Ramsey, 2009). Note that all dates in the text are based on the ShCal13 calibration.

Horizon	Square	Level	1976 Age (in y B.P.)	ShCal13 (calBP)	Lab Number
5	C 9	3	"too young to date"	---	SR-212
4ii	C 12	6	1200 ± 80	1071 ± 91	SR-207
4ii	B 12	6	1730 ± 110	1600 ± 128	GX-1551
4i	C 11	7-8	970 ± 70	838 ± 66	SR-206
4i*	B 12	8	5430 ± 140	6160 ± 153	GX-1552
3ii	C 12	11	4380 ± 130	4950 ± 203	N-903
3ii	B 12	11	4645 ± 110	5292 ± 172	GX-1553
3ii	C 13	12	4920 ± 130	5621 ± 159	N-904
3i	B 12	12	4580 ± 90	5177 ± 148	SR-205
3i	B 12	13	4485 ± 110	5085 ± 158	GX-1554
3i	B 11	10	4985 ± 100	5695 ± 118	SR-208
2ii	B 11	12	5010 ± 90	5717 ± 103	SR-204
2i	B 13	14	4815 ± 120	5495 ± 149	GX-1555

*Phillipson notes that this sample was incompletely pretreated for removal of contaminants due to a small size of the sample

Table 2. Faunal list of the Makwe sequence; numbers represent number of identifiable specimens (NISP) (adapted from Phillipson, 1976).

Order	Family	Tribe	Species	Makwe 5	Makwe 4ii	Makwe 4i	Makwe 3ii	Makwe 3i	Makwe 2	Makwe 1
Artiodactyla	Bovidae	Aepycerotini	<i>Aepyceros melampus</i>	2	0	0	0	1	3	1
Artiodactyla	Bovidae	Alcelaphini	<i>Alcelaphus buselaphus</i>	0	0	0	0	0	1	0
Artiodactyla	Bovidae	Alcelaphini	<i>Connochaetes taurinus</i>	0	2	3	0	0	2	0
Artiodactyla	Bovidae	Bovini	<i>Bos taurus</i>	35	10	2	0	0	0	0
Artiodactyla	Bovidae	Bovini	<i>Syncerus caffer</i>	0	0	0	0	3	2	2
Artiodactyla	Bovidae	Caprini	Caprini sp.	2	2	0	0	0	0	0
Artiodactyla	Bovidae	Cephalophini	<i>Sylvicapra grimmia</i>	2	2	6	1	6	4	1
Artiodactyla	Bovidae	Neotragini	<i>Oreotragus oreotragus</i>	0	1	1	5	2	0	0
Artiodactyla	Bovidae	Reduncini	<i>Redunca arundinum</i>	0	2	1	0	0	0	0
Artiodactyla	Bovidae	Tragelaphini	<i>Tragelaphus oryx</i>	0	0	0	0	0	1	0
Artiodactyla	Bovidae	Tragelaphini	<i>Tragelaphus strepsiceros</i>	3	0	2	0	1	0	0
Artiodactyla	Suidae		<i>Phacochoerus</i> sp.	25	17	5	3	8	25	1
Artiodactyla	Suidae		<i>Potamochoerus</i> sp.	8	2	4	1	3	0	0
Perissodactyla	Equidae		<i>Equus quagga</i>	7	1	4	10	2	1	1

Table 3. Enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ means and 95% confidence intervals for individual taxa. $\delta^{13}\text{C}$ values are corrected by -1.5‰ as detailed in the text.

Taxon/Dietary Class	<i>n</i>	$\delta^{13}\text{C}$	95% CI	$\delta^{18}\text{O}$	95% CI
Grazers					
Alcelaphini	8	-0.6	-3.1 to 1.7	-2.7	-4.4 to -1.0
<i>Aepyceros melampus</i>	8	-1.6	-4.8 to 0.6	-2.8	-4.6 to -1.0
<i>Equus quagga</i>	9	-2.7	-4.3 to -1.4	-2.4	-3.4 to -1.2
<i>Phacochoerus</i> sp.	18	-2.8	-4.1 to -1.7	-2.2	-3.3 to -1.1
Fresh Grass Grazers					
Reduncini	3	0.3	-0.6 to 1.0	-1.4	-2.3 to 0.0
<i>Syncerus caffer</i>	3	-0.4	-1.7 to 1.6	-1.4	-2.3 to -0.3
Browsers					
Tragelaphini	4	-13.7	-16.4 to -8.8	-5.2	-9.0 to -1.2
<i>Oreotragus oreotragus</i>	9	-14.1	-15.7 to -12.8	-3.3	-5.8 to -1.2
<i>Sylvicapra grimmia</i>	18	-12.5	-13.3 to -11.2	-2.9	-3.8 to -2.1
Omnivores					
<i>Potamochoerus</i> sp.	9	-12.6	-14.2 to -10.7	-5.4	-7.4 to -3.6
Domesticated					
<i>Bos taurus</i>	13	-0.7	-1.5 to 0.0	-1.0	-1.5 to -0.4
Caprini	4	-1.3	-4.1 to 1.8	-0.1	-2.7 to 1.9

Table 4. Mann-Whitney U tests (p-values) and 95% confidence intervals of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enamel values for feeding guilds. $\delta^{13}\text{C}$ confidence intervals are calculated based on corrected values as described in the text.

Dietary Class	Carbon ($\delta^{13}\text{C}$)			Oxygen ($\delta^{18}\text{O}$)		
	M-W	Mid-Holocene (<i>n</i>)	Late Holocene (<i>n</i>)	M-W	Mid-Holocene (<i>n</i>)	Late Holocene (<i>n</i>)
Browsers	0.620	-13.7 to -11.1 (17)	-14.9 to -12.6 (14)	0.634	-4.3 to -2.3 (17)	-5.0 to -1.9 (14)
Grazers	0.466	-4.1 to -1.2 (21)	-2.7 to -0.7 (22)	0.008	-4.1 to -2.7 (21)	-2.4 to -0.6 (22)
Omnivores	0.624	-15.4 to -8.3 (4)	-13.9 to -11.3 (5)	0.142	-9.9 to -3.9 (4)	-5.8 to -2.5 (5)

Table 5. Estimated mean percent C₄ vegetation consumed by individual taxa for the mid-Holocene (M) and late Holocene (L) rounded to the nearest 5%.

Taxon/Dietary Class	<i>n</i> (M/L)	Overall %C₄	Mid-Holocene %C₄	Late Holocene %C₄
Grazers				
Alcelaphini	8 (3/5)	90	80	90
<i>Aepyceros melampus</i>	8 (6/2)	75	75	80
<i>Equus quagga</i>	9 (4/5)	70	65	75
<i>Phacochoerus</i> sp.	18 (7/11)	70	65	70
Fresh Grass Grazers				
Reduncini	3 (0/3)	90	---	90
<i>Syncerus caffer</i>	3 (3/0)	85	85	---
Browsers				
Tragelaphini	4 (1/3)	5	20	0
<i>Oreotragus oreotragus</i>	9 (7/2)	0	0	0
<i>Sylvicapra grimmia</i>	18 (9/9)	5	10	0
Omnivores				
<i>Potamochoerus</i> sp.	9 (4/5)	5	10	0
Domesticates				
<i>Bos taurus</i>	13	85	---	85
Caprini	4	80	---	80