Water, plants, and early human habitats in eastern Africa

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Water and its influence on plants likely exerted strong adaptive pressures in human evolution. Understanding relationships among water, plants, and early humans is limited both by incomplete terrestrial records of environmental change and by indirect proxy data for water availability. Here we present a continuous record of stable hydrogen-isotope compositions (expressed as δD values) for lipid biomarkers preserved in lake sediments from an early Pleistocene archaeological site in eastern Africa—Olduvai Gorge. We convert sedimentary leaf- and algal-lipid δD values into estimates for ancient source-water δD values by accounting for biochemical, physiological, and environmental influences on isotopic fractionation via published water–lipid enrichment factors for living plants, algae, and recent sediments. Reconstructed precipitation and lake-water δD values, respectively, are consistent with modern isotopic hydrology and reveal that dramatic fluctuations in water availability accompanied ecosystem changes. Drier conditions, indicated by lower δD values, occur in association with stable carbon-isotopic evidence for open, C4-dominated grassland ecosystems. Wetter conditions, indicated by lower δD values, are associated with expanded woody cover across the ancient landscape. Estimates for ancient precipitation amounts, based on reconstructed precipitation δD values, range between approximately 250 and 700 mm·yr⁻¹ and are consistent with modern precipitation data for eastern Africa. We conclude that freshwater availability exerted a substantial influence on eastern African ecosystems and, by extension, was central to early human proliferation during periods of rapid climate change.

paleohydrology | plant waxes | carbon isotopes

The role of water and ecosystem change in human evolution remains a subject of active debate (1–3), but experts widely acknowledge that these factors likely shaped early human (hominin) foraging strategies and diet (4) approximately 2.0–1.8 million years ago (Ma). According to marine records, this juncture occurred during an interval of protracted grassland expansion across eastern Africa (1). In contrast, coeval terrestrial records from hominin archaeological sites such as Olduvai Gorge indicate recurrent fluctuations between open-grassland and closed-woodland ecosystems (5). Although such ecosystem fluctuations are commonly interpreted in relation to aridity, grassland expansion is sensitive to multiple factors (6), and proxy signals more closely linked to meteoric waters could strengthen interpretations.

Here we use δD values for lipid biomarkers preserved in lake sediments to reconstruct source-water δD values at Olduvai Gorge during the early Pleistocene. In modern lake basins, precipitation and lake-water δD values correlate strongly with δD values for leaf- and algal-lipids, respectively, after accounting for isotopic fractionation during lipid biosynthesis (7). Present and past source-water δD values reflect the combined influences of vapor-source, transport history, and aridity, ultimately linking local hydrologic patterns to atmospheric and oceanic-circulation dynamics (8).

Sample Locality. Olduvai Gorge is incised into the eastern margin of the Serengeti Plain in northern Tanzania (Fig. 1). Gorge walls expose a thick sequence of volcaniclastic sediments and tuff accumulated in lake and lake-margin environments (9, 10). Between approximately 2.0 and 1.8 Ma, a perennial saline-alkaline lake (paleolake Olduvai) occupied the center of the closed basin (9–11). Lake-margin stratigraphy suggests paleolake Olduvai responded sensitively to local and regional precipitation patterns during this 200,000-y interval (9–12). Stable carbon-isotope compositions (expressed as δ¹³C values) of leaf-lipids preserved in the lake sediments vary by more than 15‰, suggesting that pronounced ecosystem fluctuations accompanied lake-level fluctuations (5). Here we measure leaf-lipid δD values in a subset of the same lake sediment outcrop. All samples are from locality 80 (Bed I), which accumulated near the depocenter of paleolake Olduvai (10) and was exposed by stream incision during the late Pleistocene (9).

Precipitation Patterns in Eastern Africa. In eastern Africa, precipitation patterns reflect interactions between regional highlands and two convergent boundaries (Fig. 1). The Intertropical Convergence Zone (ITCZ) and closely associated African rainbelt (13) mark north–south convergence of monsoon airstreams. The Interoceanic Confluence (IOC; also referred to as the Congo Air Boundary) marks east–west convergence of air masses derived from the Indian and Atlantic Oceans (14). Both the ITCZ and IOC migrate in response to insolation-driven surface heating patterns (15), yielding two rainy seasons. In eastern Africa, the “long rains” (March to May) account for more than 50% of annual totals (15). Precipitation during the “short rains” (October to December) is more variable but correlates strongly with annual totals (16).

Precipitation δD values (δDrain) reflect the origins and histories of the related air masses that produce it. In eastern Africa, δDrain values correlate inversely with precipitation amounts due to the influences of vapor-source, transport history, and “amount” effects (17). Today the Indian Ocean is the primary vapor source to eastern Africa (13); the Atlantic Ocean and continental surface-water evaporation are important secondary sources. Transport history and amount effects result in δDrain values that differ between the rainy seasons (18). On average, δDrain values for the long rains are less negative (~20‰) than for the short rains (~28‰); in central eastern Africa, the average annual δDrain value is approximately ~22‰ (19–22).

Leaf-Lipid Apparent Fractionation Factors. Plant-water δD values reflect soil-water δD values (δD_soil) (7). Isotopic relationships between δD_soil and δDrain values can be influenced by surface vaporization in arid and semiarid regions (8), but plant-water δD


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values attenuate evaporative signals by accessing deep soil moisture and increasing productivity during rainy seasons (23).

Soil water is not fractionated significantly during uptake by plant roots, and stem-water δD values generally reflect δDsoil values (23). In contrast, leaf-water δD values can vary markedly from δDsoil values as a result of transpiration (24). The relative importance of stem-water vs. leaf-water during lipid biosynthesis remains unclear (25, 26), as does biosynthetic phenology. These factors could account for differences in apparent fractionation between source waters and lipids (δDlipid/water = [(δDlipid + 1,000)/(δDwater + 1,000)] − 1, expressed in permil (‰)) among living plants when grouped according to plant functional type (PFT).

We reevaluate a global compilation of published leaf δD values for living plants (SI Appendix) to determine representative δDlipid/water values for different PFTs relevant to this study. We target subtropical and tropical taxa in clades most representative of plants in eastern Africa since the early Paleogene (27, 28). Leaves of subtropical and tropical plants commonly contain the leaf-lipid hentriacontane (nC₃₁) (29, 30), and nC₃₁ is also abundant in lake sediments from Olduvai Gorge (5). Therefore, we use published δD values for nC₃₁ (δD₃₁) to determine δDlipid/water values applicable to sedimentary δD₃₁ values from Olduvai Gorge.

We define PFTs in terms of photosynthetic pathway and growth habit: C₃ woody plants, C₄ herbs, and C₃ graminoids. We determine representative δDlipid/water values—termed δD₃₁(model) values—from published δD₃₁ values using modeled annual δDrain values (δD₃₁(model)) (21, 22). Measured annual δDrain values rarely accompany published leaf-lipid δD values but, when available, generally coincide with δD₃₁(model) values (7, 21).

Collectively, δD₃₁(model) values average −124‰ (δAverage). Among individual PFTs the median δD₃₁(model) value for C₃ graminoids is most negative (−146‰ ± 8‰, 95% confidence interval; n = 51). The median δD₃₁(model) value for C₄ herbs (−124‰ ± 10‰; n = 24) is more negative than for C₃ woody plants (−109‰ ± 8‰; n = 84).

We calculate “landscape” apparent fractionation factors (εlandscape) using δD₃₁(model) values and relative PFT abundances (Fig. 2) estimated from δ¹³C values for nC₃₁ (δ¹³C₃₁) in lake sediments (5). Leaf-lipids represent relative PFT abundances in basins ranging from small lakes (31) to expansive river systems (32), despite differences in basin morphology, transport, and burial processes (33). We multiply each ε₃₁(model) value by relative PFT abundance (i.e., fw−woody/ fh−herb and f₃₁/fg−woody plants, herbs, and graminoids, respectively) to calculate εlandscape values:

εlandscape = fₖ−woody(−109‰) + fₖ−herb(−124‰) + f₃₁/fg− woody plants(−146‰).

Finally, we apply εlandscape values to sedimentary δD₃₁ values to reconstruct δDsoil values.

The relative influences of biochemical, physiological, and environmental processes on δDlipid/water values are difficult to account for in interpretations of δD₃₁ values. For instance, our ε₃₁(model) value for C₃ woody plants does not distinguish by canopy height, despite observed differences between modern trees and shrubs (SI Appendix). Similarly, annual δDrain values do not distinguish seasonality. In eastern Africa, annual and rainy-season δDrain values can differ in excess of 20‰ (SI Appendix), although >85% of annual precipitation occurs during rainy seasons (15). Thus, to the extent that plant growth takes place in rainy seasons, annual δDrain values can overestimate δDsoil values during lipid biosynthesis.

Although propagated uncertainty in εlandscape values (SI Appendix) represents a substantial portion of the variability in modern δDsoil values across central eastern Africa (approximately 60‰), sedimentary δD₃₁ values capture space- and time-integrated signals that attenuate variability of individual plants or species (7, 31). Thus, uncertainty in εlandscape values largely reflects ecosystem-scale differences in transpiration and phenology (7), which are at least partially accounted for by ε₃₁(model) values, provided living plants are representative of their ancient counterparts. Despite some significant shortcomings in the state of the art, εlandscape values provide a useful interpretational framework to account for biological and physical influences on leaf-lipid δD values—a factor often overlooked in hydrological reconstructions.

Algal-Lipid Apparent Fractionation Factors. Aquatic photosynthetic organisms acquire hydrogen for lipid biosynthesis from ambient waters (7). Therefore, algal δD values reflect lake-water δD values—which integrate precipitation, groundwater, runoff, and evaporation—as modified by biosynthetic fractionation.

**Fig. 1.** Modern precipitation patterns in eastern Africa (68) during the (A) long rains (March to May) and (B) the short rains (October to December), with respect to average monthly precipitation in northern Tanzania (3). Data courtesy of http://climateklm.gov. In A and B, bold horizontal lines mark the position of the Intertropical Convergence Zone, whereas dashed lines mark the Interoceanic Confluence (13). Target symbols mark the location of Olduvai Gorge (2° 48’ 5”, 35° 06’ E). In C, the bold line reflects observed average monthly rainfall (1964–1984); gray envelops variation for average monthly precipitation. The dashed line reflects modeled average monthly rainfall for Tanzania (67). (D) Depositional environments surrounding paleolake Olduvai during the early Paleogene (9). Contracted (dashed line) and expanded (bold line) lake margins are based on correlated stratigraphic sections (9–12).

**Fig. 2.** Schematic depiction of ε₃₁(model) Values as a function of reconstructed ecosystem. (A) We use δ¹³C₃₁ values to estimate relative abundances for three different PFTs: C₃ graminoids, C₄ herbs, and C₃ woody plants. (B) We relate relative PFT abundances to ecosystem (5) according to United Nations Educational, Scientific, and Cultural Organization terminology (68). (C) We calculate “landscape” apparent fractionation factors (εlandscape) for deuterium by mass balance.
Biosynthetic fractionation, in turn, incorporates biological and physical factors (7). Culture studies indicate that algal $e_{lipid/water}$ values vary between species (34), but space- and time-integration seems to minimize these effects in sediments (7).

Field studies indicate that algal $e_{lipid/water}$ values vary in relation to salinity and must be accounted for when interpreting algal-lipid $\delta D$ values (35). The response of algal $e_{lipid/water}$ values to salinity is markedly consistent at $9.9^{\circ} \pm 0.2^{\circ}$ ppt$^{-1}$ (7). Heptacosane ($nC_{17}$) is a general biomarker for algae (36) and is abundant in lake sediments from Olduvai Gorge. Modern studies establish an apparent fractionation between freshwater and $nC_{17}$ equal to $\sim 172^{\circ}$ (7), and we use this value to determine algal $e_{lipid/water}$ values at different salinities—termed $e_{lake}$ values:

$$e_{lake} = 0.9(salinity) - 172^{\circ}.$$ 

We construct a basic lake-water evaporation model to constrain $e_{lake}$ values in the past (SI Appendix). Briefly, we estimate the total solute load for paleolake Olduvai on the basis of stratigraphic evidence for maximum lake area (approximately 200 km$^2$) (10) and lake level (approximately 5 m) (12) during the early Pleistocene and fossil evidence for minimum salinity (approximately 20 ppt) (9). Then, we infer changes in lake level from changes in sedimentary total organic carbon ($\%$ TOC) because these values covary in many modern lakes in eastern Africa (37).

Next, we assume a conservative solute balance and use estimates for paleolake volume to estimate salinities during lake contraction. Finally, we apply $e_{lake}$ values to sedimentary $\delta D_{lake}$ values to reconstruct lake-water $\delta D$ values ($\delta D_{lake}$). Salinity estimates for paleolake Olduvai range from approximately 20 to 100 ppt, resulting in $e_{lake}$ values that vary by up to $88^{\circ}$ from freshwater algal $e_{lipid/water}$ values.

Biosynthetic processes responsible for the influence of salinity on $\delta D_{lake}$ values are unclear (7), and not all possible mechanisms result in linear relationships. Still, $e_{lake}$ values range between $-158^{\circ}$ and $-84^{\circ}$ for paleolake Olduvai, highlighting the importance of salinity when interpreting $\delta D_{lake}$ values from sedimentary $\delta D_{17}$ values.

**Results**

Sedimentary $\delta^{13}C_{31}$ values range from $-36.3^{\circ}$ to $-21.4^{\circ}$, with an average value of $-27.8^{\circ}$ (Fig. 3). Sedimentary $\delta D_{31}$ values range from $-148^{\circ}$ to $-132^{\circ}$ and correlate weakly with $\delta^{13}C_{31}$ values ($r^2 = 0.11$) and $\%$ TOC ($r^2 = 0.08$). Reconstructed $\delta D_{soil}$ values show an increased isotopic range of 54$^{\circ}$, from $-38^{\circ}$ to $+16^{\circ}$ (Fig. 4).

Sedimentary $\delta D_{17}$ values range from $-150^{\circ}$ to $-30^{\circ}$ (Fig. 4). Measured values correlate strongly with $\delta^{13}C_{31}$ values ($r^2 = 0.83$) and $\%$ TOC ($r^2 = 0.86$). Reconstructed $\delta D_{lake}$ values show a relatively smaller isotopic range, from $+3^{\circ}$ to $+59^{\circ}$, but still correlate strongly with $\delta^{13}C_{31}$ values ($r^2 = 0.88$). Interestingly, sedimentary $\delta D_{17}$ values correlate weakly with sedimentary $\delta D_{31}$ values ($r^2 = 0.11$), but reconstructed $\delta D_{lake}$ values correlate strongly with reconstructed $\delta D_{soil}$ values ($r^2 = 0.84$).

**Interpretations and Discussion**

**Precipitation in Eastern Africa.** Historical precipitation patterns serve as a framework for interpreting reconstructed hydrologic patterns over timescales of $10^4$ to $10^5$ thousand years (38), although regional tectonism and the intensification of zonal atmospheric (Walker) circulation during the early Pleistocene could weaken this interpretational link (1, 13). Modern $\delta D_{rain}$ values reveal a regional meteoric waterline (RMWL) for eastern Africa (Fig. 5):

$$\delta D_{rain} = 7.9\delta^{18}O_{rain} + 11.3^{\circ}.$$ 

Today, annual $\delta D_{rain}$ values in eastern Africa range from approximately $-30^{\circ}$ to $-10^{\circ}$, whereas monthly $\delta D_{rain}$ values
Fig. 4. Leaf- and algal-lipid δD values and reconstructed source waters with respect to sedimentary δD_{TOC}. (A) Measured δD_{TOC} (hollow circles) and reconstructed δD_{soil} values (black circles) with respect to δD_{TOC}. A gray line marks the linear regression for values based on the average e_{18}^\text{mod} model value of −124‰. (B) Measured δD_{TOC} (hollow circles) and reconstructed δD_{lake} values (black circles) with respect to δD_{TOC}. A gray line marks the linear regression for values based on a freshwater e_{17}/water value of −172‰.

Fig. 5. Modern isotopic relationships for precipitation and lake waters in eastern Africa. We plot a RMWL (bold line) based on modern monthly δD_{rain} and δ^{18}O_{rain} values and single precipitation events (19–22, 39, 40): δD_{rain} = 7.9 δ^{18}O_{lake} + 11.3‰. For reference, we also plot the global meteoric waterline (dashed line). A large black circle marks the point defined by a single reconstructed δD_{soil} and published δ^{18}O_{lake} value reconstructed from minerals in closely associated lake-margin sediments (SI Appendix). Propagated uncertainties are shown (SI Appendix). For reference, a cross marks the δO value based on the average e_{17}/water value of −124‰. Modern δD_{lake} and δ^{18}O_{lake} values yield an LEL for eastern Africa (48–53): δD_{lake} = 5.6 δ^{18}O_{lake} + 11.6‰. A large black square marks the point defined by a single reconstructed δD_{lake} and published δ^{18}O_{lake} value reconstructed from authigenic clays in associated lake sediments (SI Appendix), whereas the overlying cross marks the δD value based on a freshwater e_{17}/water value of −172‰.

A large black square marks the point defined by a single reconstructed δD_{soil} and published δ^{18}O_{lake} value reconstructed from minerals in closely associated lake-margin sediments (SI Appendix). Propagated uncertainties are shown (SI Appendix). For reference, a cross marks the δO value based on the average e_{17}/water value of −124‰. Modern δD_{lake} and δ^{18}O_{lake} values yield an LEL for eastern Africa (48–53): δD_{lake} = 5.6 δ^{18}O_{lake} + 11.6‰. A large black square marks the point defined by a single reconstructed δD_{lake} and published δ^{18}O_{lake} value reconstructed from authigenic clays in associated lake sediments (SI Appendix), whereas the overlying cross marks the δD value based on a freshwater e_{17}/water value of −172‰.

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Historical data for annual δD_{rain} values (−22‰) (19, 39) and mean annual precipitation (MAP) (550 mm) (9, 15) provide a local reference point from which to project reconstructed δD_{soil} values. Because rainy seasons account for approximately 85% of MAP in northern Tanzania (15), we use an amount effect for rainy-season months to reconstruct MAP in the past:

\[
\text{MAP} = \left(\delta D_{\text{soil}} + 22‰\right) / (-0.13‰ \text{ mm}^{-1}) + 550 \text{ mm}.
\]

MAP estimates for the full range of δD_{soil} values are from −700–250 mm. This range is consistent with reconstructions based on pollen spectra (−750 mm) (46) and soil carbonates (−400 mm) (47) during wetter and drier intervals, respectively. Woody cover strongly covaries with MAP today in eastern Africa (6):

\[
f_{\text{woody}} = (0.14(MAP − 14.2)) / 100.
\]

We find a similar relationship between our estimates of MAP and woody cover (5). For instance, in the modern calibration, MAP of 700 mm yields an \(f_{\text{woody}}\) value of 0.84, which is consistent with a δ^{13}C_{clay}-derived (−36.3‰) \(f_{\text{woody}}\) value of 0.90 (5). These observations suggest amount effects influenced δD_{rain} values more than changes in vapor-source or transport history at Olduvai. The relationship between modern δD_{rain} values and amount of precipitation is difficult to evaluate in many tropical regions because of sparse measurements, but available data suggest comparable effects at seasonal, annual, and interannual timescales (44, 45). In eastern Africa, available rainy-season δD_{rain} values correlate inversely with precipitation at a slope of −0.125‰ mm\(^{-1}\) (SI Appendix). If modern sensitivity is representative for the past, and changes in vapor-source and transport history were important, then a 29‰ range in δD_{soil} values translate to 225 mm precipitation range; the full 54‰ range translates to 415-mm precipitation range.

A large black square marks the point defined by a single reconstructed δD_{soil} and published δ^{18}O_{lake} value reconstructed from minerals in closely associated lake-margin sediments (SI Appendix). Propagated uncertainties are shown (SI Appendix). For reference, a cross marks the δO value based on the average e_{17}/water value of −124‰. Modern δD_{lake} and δ^{18}O_{lake} values yield an LEL for eastern Africa (48–53): δD_{lake} = 5.6 δ^{18}O_{lake} + 11.6‰. A large black square marks the point defined by a single reconstructed δD_{lake} and published δ^{18}O_{lake} value reconstructed from authigenic clays in associated lake sediments (SI Appendix), whereas the overlying cross marks the δD value based on a freshwater e_{17}/water value of −172‰.
Lake-Water Evaporation in Eastern Africa. Loss of lighter isotopic species (H$_2^{16}$O) during evaporation progressively enriches residual lake waters in DH$_2^{18}$O and H$_2^{18}$O. In eastern Africa, lake-water $\delta$D values ($\delta$D$_{lake}$) and $\delta^{18}$O values ($\delta^{18}$O$_{lake}$) define an isotopic trajectory—called a local evaporation line (LEL)—with a slope that is lower than that of the RMWL (8). LEL slopes are primarily a function of relative humidity ($h$); in general, very low $h$ values (e.g., 0.25) result in slopes close to 4, whereas higher $h$ values result in slopes closer to 6 (8). Modern $\delta$D$_{lake}$ and $\delta^{18}$O$_{lake}$ values yield an LEL for eastern Africa:

\[
\delta_{D_{lake}} = 5.68 \delta^{18}O_{lake} + 1.6\%e.
\]

Modern $\delta$D$_{lake}$ values range from approximately $-30\%e$ in humid regions of eastern Africa to $+80\%e$ or higher in extremely arid regions (48–53).

The LEL defines source-water composition at its intersection with the RMWL. For modern waters in eastern Africa, LEL and RMWL intersect at a source-water $\delta$D value of $-22\%e$ (Fig. 5), which closely matches historical data (19–22). In closed basins, lake waters derive primarily from precipitation (54).

Tracing Isotopic Hydrology at Olduvai Gorge. To compare modern and ancient lakewaters, we pair reconstructed $\delta$D$_{lake}$ values with published $\delta^{18}$O$_{lake}$ values that were determined from authigenic clays (12) in associated sediments (SI Appendix). Reconstructed $\delta$D$_{lake}$–$\delta^{18}$O$_{lake}$ values show close agreement with the modern LEL (Fig. 5). Further, reconstructed $\delta$D$_{lake}$ and $\delta^{18}$O$_{lake}$ values strongly correlate, suggesting lake-water compositions shifted largely owing to changes in precipitation. Evaporation rates decrease at high salinity because of the decreased activity of water in high ionic-strength solutions. As a result, potential evaporation can exceed lake-water evaporation by up to 100-fold (54). Thus, although reconstructed $\delta$D$_{lake}$ values vary only slightly more than $\delta^{18}$O$_{lake}$ values, changes in source-water and amount of precipitation would have been accompanied by large changes in potential evaporation. Reconstructed lake evaporation relative to meteoric input ($E/I$) based on our data suggest higher evaporation during intervals of reduced precipitation ($E/I < 2.9$) than during increased precipitation ($E/I > 1.3$) and are consistent with historical and modeled $E/I$ values for eastern Africa (SI Appendix).

Water Availability and Ecosystem Dynamics. Reconstructed $\delta$D$_{rain}$ and $\delta$D$_{lake}$ values reveal strong relationships between water and carbon-isotopic data for ecosystem type. Lower $\delta$D$_{rain}$ and $\delta$D$_{lake}$ values, which reflect increased MAP and decreased evaporation, respectively, correspond with increased woody cover ($f_{woody} = 0.90$). Although the organic carbon-derived indicators we use to determine $e_{landscape}$ and $e_{lake}$ values may be codependent (55), reconstructed values for $f_{woody}$ and lake level are consistent with independent indicators for ecosystem type and paleolake level (Fig. 3). Much like today (6), aridity was a dominant control on ecosystem change in eastern Africa during the Pleistocene.

Contrasting proxy records have fueled debate about the pace and patterns of environmental change in eastern Africa during the Pleistocene. Pollen and fossil abundance records suggest expansion of arid-adapted species beginning near 2.0 Ma and culminating around 1.8 Ma (56, 57). Marine dust-flux records and soil-carbonate $^{13}$C values also suggest shifts toward more arid conditions around 1.8 Ma (1), although geomorphic evidence suggests regionally wetter conditions (1).

Lipid biomarkers from Olduvai Gorge point to rapid changes in plants and water between approximately 2.0 and 1.8 Ma, and we suggest this environmental variability both influenced and can reconcile proxy records. For instance, increased seasonality can lead to C$_4$ graminoid expansions (58) but can also lead to unrepresentatively positive C$_3$-like $\delta^{13}$C values in soil carbonates (59). Similarly, rapid wet-to-dry transitions can simultaneously produce both increased dust and elevated lake-levels (60). Over the past several million years, modulation of marine dust-flux records from the Arabian Sea has been tightly coupled with orbital eccentricity, resulting in distinct intervals of exceptionally high-amplitude variability during orbital-eccentricity maxima (1). We hypothesize that high-amplitude, orbital precession-paced environmental variability, as opposed to gradual or stepwise aridification, characterized eastern Africa during the early Pleistocene.

Water and Early Human Evolution. In semiarid regions, precipitation primarily determines water availability (15). Today, water availability shapes primate behaviors through its influence on vegetation and resource distributions (4, 61). For example, regions with MAP <700 mm do not support chimpanzee populations (62). Water likely shaped behavioral adaptations in the genus Homo (63). Our evidence for dramatic variability is consistent with water as a strong selective pressure in human evolution (1, 2). However, thermoregulatory and dietary constraints function at microhabitat scales (64), and many hominin fossil sites—including Olduvai Gorge (9)—are associated with ephemeral or saline water sources (65). Our reconstructions of precipitation and lake-chemistry indicate that, even during maximum lake expansion, lake waters at Olduvai Gorge were likely not potable (12). Groundwater-fed freshwater springs could have aided hominin existence and proliferation (65).

Conclusions

This study presents a continuous record of $\delta$D values for lipid biomarkers from lake sediments at Olduvai Gorge that were deposited during a key juncture in human evolution, ~2.0–1.8 Ma. We pair sedimentary leaf-lipid $\delta$D values with corresponding $\delta^{13}$C values to account for physiological and environmental influences on reconstructed precipitation $\delta$D values. We use a basic lake-water evaporation model to account for the influence of salinity on algal-lipid $\delta$D values and reconstructed lake-water $\delta$D values. Sedimentary leaf- and algal-lipid $\delta$D values show a weak relationship, but “corrected” values correlate strongly. We compare reconstructed precipitation and lake-water $\delta$D values with isotopic data for environmental waters in modern eastern Africa to estimate ancient precipitation amounts and evaporative losses, respectively. Our results indicate Olduvai Gorge received approximately 250 mm of MAP during arid intervals and ~700 mm during wetter intervals. Given the magnitude and variability in water availability revealed by our reconstructions, we hypothesize freshwater springs were important for hominin subsistence in highly variable environments.

Materials and Methods

Lipid Extraction and Purification. Lipid biomarkers in lake sediments were extracted and separated according to Magill et al. (5).

Isotopic Analysis. Lipid $\delta$D values were measured by gas chromatography–isotope ratio monitoring–mass spectrometry. Hydrogen gas of known $\delta$D value was used as reference. Samples were coinjected with internal standards of known $\delta$D values (nC$_{41}$, androstane, and squalane). Uncertainty (1σ SD) for nC$_{41}$ was $4\%e$.

Age Model. Our age model is constrained using previously published $^{40}$Ar/$^{39}$Ar, magnetic stratigraphy, and tuff correlation dates (5).

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