

Water, plants, and early human habitats in eastern Africa

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This Feature Article is part of a series identified by the Editorial Board as reporting findings of exceptional significance.

Edited by John M. Hayes, Woods Hole Oceanographic Institution, Berkeley, CA, and approved October 31, 2012 (received for review June 6, 2012)

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 less negative δD values, occur in association with stable carbon-isotopic evidence for open, C_4 -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 $\text{mm}\cdot\text{y}^{-1}$ 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 volcanoclastic 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 $\delta^{13}\text{C}$ 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 (13), 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 (δD_{rain}) reflect the origins and histories of the related air masses that produce it. In eastern Africa, δD_{rain} 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 δD_{rain} values that differ between the rainy seasons (18). On average, δD_{rain} values for the long rains are less negative (–20‰) than for the short rains (–28‰); in central eastern Africa, the average annual δD_{rain} 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 δD_{rain} values can be influenced by surface evaporation in arid and semiarid regions (8), but plant-water δD

Author contributions: G.M.A. and K.H.F. designed research; C.R.M. performed research; C.R.M., G.M.A., and K.H.F. analyzed data; and C.R.M., G.M.A., and K.H.F. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

See Commentary on page 1144.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1209405109/-DCSupplemental.

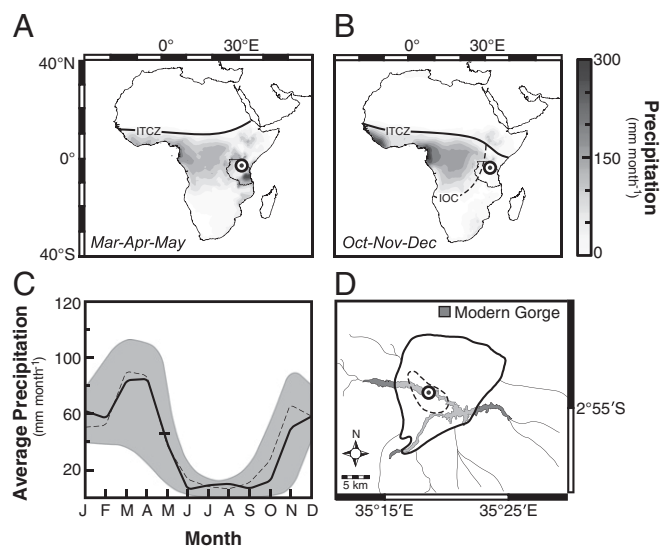


Fig. 1. Modern precipitation patterns in eastern Africa (66) during the (A) long rains (March to May) and (B) the short rains (October to December), with respect to average monthly precipitation in northern Tanzania (C) (Data courtesy of <http://climexp.knmi.nl>). In A and B, bold horizontal lines mark the position of the Intertropical Convergence Zone, whereas dashed lines mark the Inter-troceanic Confluence (13). Target symbols mark the location of Olduvai Gorge (2° 48'S, 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 Pleistocene (9). Contracted (dashed line) and expanded (bold line) lake margins are based on correlated stratigraphic sections (9–12).

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 δD_{soil} values (23). In contrast, leaf-water δD values can vary markedly from δD_{soil} 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 ($\epsilon_{lipid/water} = [(\delta D_{lipid} + 1,000) / (\delta D_{water} + 1,000)] - 1$, expressed in permil (‰) among living plants when grouped according to plant functional type (PFT).

We reevaluate a global compilation of published leaf-lipid δD values for living plants (SI Appendix) to determine representative $\epsilon_{lipid/water}$ 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 Pleistocene (27, 28). Leaves of subtropical and tropical plants commonly contain the leaf-lipid hentriacontane (nC_{31}) (29, 30), and nC_{31} is also abundant in lake sediments from Olduvai Gorge (5). Therefore, we use published δD values for nC_{31} (δD_{31}) to determine $\epsilon_{lipid/water}$ values applicable to sedimentary δD_{31} values from Olduvai Gorge.

We define PFTs in terms of photosynthetic pathway and growth habit: C_3 woody plants, C_3 herbs, and C_4 graminoids. We determine representative $\epsilon_{lipid/water}$ values—termed $\epsilon_{31/model}$ values—from published δD_{31} values using modeled annual δD_{rain} values (δD_{rain}^{model}) (21, 22). Measured annual δD_{rain} values rarely accompany published leaf-lipid δD values but, when available, generally coincide with δD_{rain}^{model} values (7, 21).

Collectively, $\epsilon_{31/model}$ values average -124‰ ($\epsilon_{average}$). Among individual PFTs the median $\epsilon_{31/model}$ value for C_4 graminoids is most negative ($-146\text{‰} \pm 8\text{‰}$, 95% confidence interval; $n = 51$). The median $\epsilon_{31/model}$ value for C_3 herbs ($-124\text{‰} \pm 10\text{‰}$; $n = 24$) is more negative than for C_3 woody plants ($-109\text{‰} \pm 8\text{‰}$; $n = 84$).

We calculate “landscape” apparent fractionation factors ($\epsilon_{landscape}$) using $\epsilon_{31/model}$ values and relative PFT abundances (Fig. 2) estimated from $\delta^{13}C$ values for nC_{31} ($\delta^{13}C_{31}$) 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 $\epsilon_{31/model}$ value by relative PFT abundance (i.e., f_{woody} , f_{herb} , and f_{gram} for woody plants, herbs, and graminoids, respectively) to calculate $\epsilon_{landscape}$ values:

$$\epsilon_{landscape} = f_{woody}(-109\text{‰}) + f_{herb}(-124\text{‰}) + f_{gram}(-146\text{‰}).$$

Finally, we apply $\epsilon_{landscape}$ values to sedimentary δD_{31} values to reconstruct δD_{soil} values.

The relative influences of biochemical, physiological, and environmental processes on $\epsilon_{lipid/water}$ values are difficult to account for in interpretations of δD_{31} values. For instance, our $\epsilon_{31/model}$ value for C_3 woody plants does not distinguish by canopy height, despite observed differences between modern trees and shrubs (SI Appendix). Similarly, annual δD_{rain} values do not distinguish seasonality. In eastern Africa, annual and rainy-season δD_{rain} 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 δD_{rain} values can overestimate δD_{soil} values during lipid biosynthesis.

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

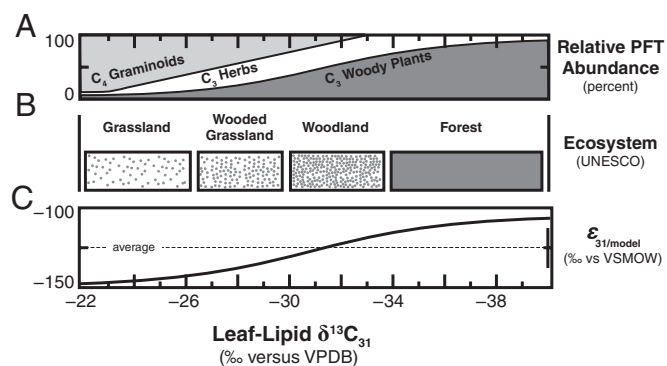


Fig. 2. Schematic depiction of $\epsilon_{31/model}$ values as a function of reconstructed ecosystem. (A) We use $\delta^{13}C_{31}$ values to estimate relative abundances for three different PFTs: C_4 graminoids, C_3 herbs, and C_3 woody plants. (B) We relate relative PFT abundances to ecosystem (5) according to United Nations Educational, Scientific, and Cultural Organization terminology (68). (C) We calculate “landscape” apparent fractionation factors ($\epsilon_{landscape}$) for deuterium by mass balance.

Biosynthetic fractionation, in turn, incorporates biological and physical factors (7). Culture studies indicate that algal $\epsilon_{\text{lipid/water}}$ values vary between species (34), but space- and time-integration seems to minimize these effects in sediments (7).

Field studies indicate that algal $\epsilon_{\text{lipid/water}}$ values vary in relation to salinity and must be accounted for when interpreting algal-lipid δD values (35). The response of algal $\epsilon_{\text{lipid/water}}$ values to salinity is markedly consistent at $0.9\text{‰} \pm 0.2\text{‰} \text{ppt}^{-1}$ (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 -172‰ (7), and we use this value to determine algal $\epsilon_{\text{lipid/water}}$ values at different salinities—termed ϵ_{lake} values:

$$\epsilon_{\text{lake}} = 0.9(\text{salinity}) - 172\text{‰}.$$

We construct a basic lake-water evaporation model to constrain ϵ_{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 ϵ_{lake} values to sedimentary δD_{17} values to reconstruct lake-water δD values (δD_{lake}). Salinity estimates for paleolake Olduvai range from approximately 20 to 100 ppt, resulting in ϵ_{lake} values that vary by up to 88‰ from freshwater algal $\epsilon_{\text{lipid/water}}$ values.

Biosynthetic processes responsible for the influence of salinity on δD_{17} values are unclear (7), and not all possible mechanisms

result in linear relationships. Still, ϵ_{lake} values range between -158‰ and -84‰ for paleolake Olduvai, highlighting the importance of salinity when interpreting δD_{lake} values from sedimentary δD_{17} values.

Results

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

Sedimentary δD_{17} values range from -150‰ to -30‰ (Fig. 4). Measured values correlate strongly with $\delta^{13}C_{31}$ values ($r^2 = 0.83$) and %TOC ($r^2 = 0.86$). Reconstructed δD_{lake} values show a relatively smaller isotopic range, from $+3\text{‰}$ to $+59\text{‰}$, but still correlate strongly with $\delta^{13}C_{31}$ values ($r^2 = 0.88$). Interestingly, sedimentary δD_{17} values correlate weakly with sedimentary δD_{31} values ($r^2 = 0.11$), but reconstructed δD_{lake} values correlate strongly with reconstructed δD_{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 10^1 to 10^3 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 δD_{rain} values reveal a regional meteoric waterline (RMWL) for eastern Africa (Fig. 5):

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

Today, annual δD_{rain} values in eastern Africa range from approximately -30‰ and -10‰ , whereas monthly δD_{rain} values

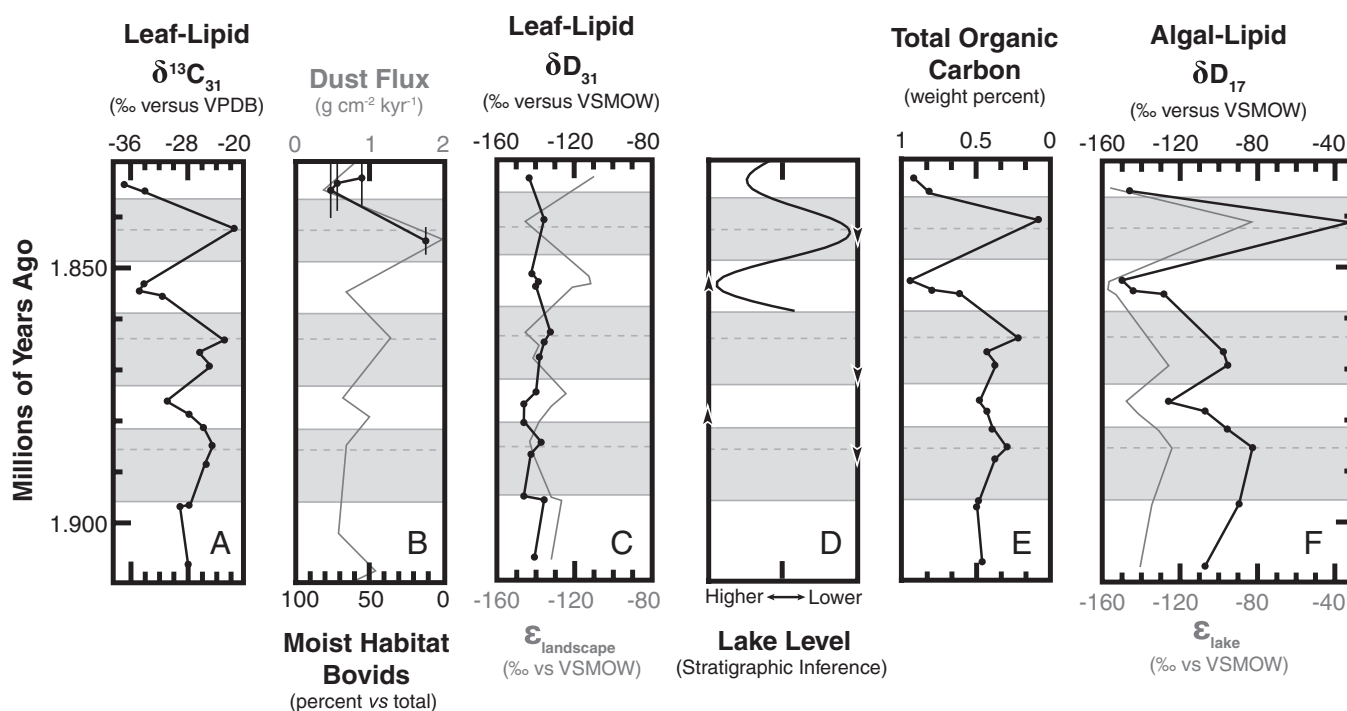


Fig. 3. Relationships between leaf- and algal-lipid δD values and ancillary proxy data for Olduvai Gorge. (A) Sedimentary $\delta^{13}C_{31}$ values (5). (B) Dust fluxes into the Arabian Sea (gray line) and closed- or moist-habitat bovids by percentage of total bovids (black circles) (1, 69). (C) Sedimentary δD_{31} values (black circles) alongside $\epsilon_{\text{ecosystem}}$ values (gray line). (D) Stratigraphic evidence for lake levels (9–12). Horizons that contain faunal evidence for low (down arrows) or high (up arrows) lake levels are also shown (12). (E) Sedimentary total organic carbon. (F) Sedimentary δD_{17} values (black circles) alongside ϵ_{lake} values (gray line).

Gorge and highlight the importance of using $\epsilon_{\text{landscape}}$ values to reconstruct hydrologic patterns from leaf-lipid δD values.

Lake-Water Evaporation in Eastern Africa. Loss of lighter isotopic species (H_2^{16}O) during evaporation progressively enriches residual lake waters in DH^{16}O and H_2^{18}O . In eastern Africa, lake-water δD values ($\delta\text{D}_{\text{lake}}$) and $\delta^{18}\text{O}$ values ($\delta^{18}\text{O}_{\text{lake}}$) 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 $\delta\text{D}_{\text{lake}}$ and $\delta^{18}\text{O}_{\text{lake}}$ values yield an LEL for eastern Africa:

$$\delta\text{D}_{\text{lake}} = 5.6\delta^{18}\text{O}_{\text{lake}} + 1.6\text{‰}$$

Modern $\delta\text{D}_{\text{lake}}$ values range from approximately -30‰ in humid regions of eastern Africa to $+80\text{‰}$ 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 δD value of -22‰ (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 lake-waters, we pair reconstructed $\delta\text{D}_{\text{lake}}$ values with published $\delta^{18}\text{O}_{\text{lake}}$ values that were determined from authigenic clays (12) in associated sediments (*SI Appendix*). Reconstructed $\delta\text{D}_{\text{lake}} - \delta^{18}\text{O}_{\text{lake}}$ values show close agreement with the modern LEL (Fig. 5). Further, reconstructed $\delta\text{D}_{\text{lake}}$ and $\delta\text{D}_{\text{soil}}$ 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 $\delta\text{D}_{\text{lake}}$ values vary only slightly more than $\delta\text{D}_{\text{soil}}$ 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 $\delta\text{D}_{\text{rain}}$ and $\delta\text{D}_{\text{lake}}$ values reveal strong relationships between water and carbon-isotopic data for ecosystem type. Lower $\delta\text{D}_{\text{rain}}$ and $\delta\text{D}_{\text{lake}}$ values, which reflect increased MAP and decreased evaporation, respectively, correspond with increased woody cover ($f_{\text{woody}} = 0.90$). Although the organic carbon-derived indicators we use to determine $\epsilon_{\text{landscape}}$ and ϵ_{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 $\delta^{13}\text{C}$ 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_4 -like $\delta^{13}\text{C}$ 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 δD 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 δD values with corresponding $\delta^{13}\text{C}$ values to account for physiological and environmental influences on reconstructed precipitation δD values. We use a basic lake-water evaporation model to account for the influence of salinity on algal-lipid δD values and reconstructed lake-water δD values. Sedimentary leaf- and algal-lipid δD values show a weak relationship, but “corrected” values correlate strongly. We compare reconstructed precipitation and lake-water δD values with isotopic data for environmental waters in modern eastern African 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 δD values were measured by gas chromatography–isotope ratio monitoring–mass spectrometry. Hydrogen gas of known δD value was used as reference. Samples were coinjected with internal standards of known δD values ($n\text{C}_{41}$, androstane, and squalane). Uncertainty (1σ SD) for $n\text{C}_{41}$ was 4‰.

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

ACKNOWLEDGMENTS. We thank the Ngorongoro Conservation Area Authority for field permits to R. Blumenshine and F. Masao. This study was supported by the Winston Churchill Foundation, Carbon Educators and Researchers Together for Humanity (CarbonEARTH) (National Science Foundation Grant Division of Graduate Education 0947962), and the Tanzania Antiquities Department. Samples were collected by G. Ashley and R. Renaut (National Science Foundation Grant Earth Sciences 9903258).

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