Human Evolution and Migration in a Variable Environment: The Amplifier Lakes of East Africa

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The development of the Cenozoic East African Rift System (EARS) profoundly re-shaped the landscape and significantly increased the amplitude of short-term environmental response to climate variation. In particular, the development of amplifier lakes in rift basins after three million years ago significantly contributed to the exceptional sensitivity of East Africa to climate change compared to elsewhere on the African continent. These amplifier lakes respond rapidly to moderate, precessional-forced climate shifts, and as they so apply dramatic environmental pressure to the biosphere. Rift basins, when either extremely dry or lake-filled, form important barriers for migration, mixing and competition of different populations of animals and hominins. Amplifier lakes link long-term, high-amplitude tectonic processes and short-term environmental fluctuations. East Africa may have been the cradle of humankind as a consequence of this strong link between different time-scales.

The established drivers of environmental instability in East Africa are volcano-tectonic phenomena associated with the East African Rift System (EARS) and associated plateaus (time scales of 10^6 to 10^5 years), orbitally-driven changes in insolation (10^5 to 10^4 years), and variations in total solar irradiance (10^3 to 10^0 years) (Kutzbach and Street-Perrott, 1985; Nicholson, 1996; Verschuren et al., 2000; Trauth et al., 2003, 2005; Barker et al., 2004; Sepulchre et al., 2006). In addition to these direct influences, remote drivers of East African environmental changes include the uplift of the Tibetian plateau and the establishment of the African-Asian monsoon system (10^6 to 10^5 years), orbitally-driven glacial-interglacial cycles (10^4 to 10^3 years), and sea-surface temperature variations driven by ocean-atmosphere phenomena such as the Indian Ocean Dipole (IOD) and the El Niño/Southern Oscillation (ENSO) (10^4 to 10^0 years) (e.g., Kutzbach and Street-Perrott, 1985; Saji et al., 1999; Schreck and Semazzi, 2004).

Drivers of environmental changes acting on relatively long time scales have the greatest largest amplitudes and expectedly the greatest effect on the habitats of animals and hominins. For example, growth of the East African and Ethiopian plateaus are considered to be major influences in the dramatic vegetation change that has taken place on the continent during the last twenty million years (Sepulchre et al., 2006). The classic savanna hypothesis of Henry Fairfield Osborn and Raymond Dart attempted to link the evolutionary divergence of hominins and other great apes, and the emergence of bipedalism, with the forest-savanna transition in Mio-Pliocene time (e.g., Dart, 1953). Though largely disproved, the savanna hypothesis was an early attempt to link tectonic displacements, environmental change and hominin evolution.

The effects of such long-term tectonic displacements, however, can also have an influence on the magnitude of short-term environmental instabilities, thus leading to a more direct impact on the biosphere. Ancient shorelines of East African lakes, most of them reduced to salty puddles today, document orbitally-driven lake-level fluctuations of tens or hundreds of meters as a response to only moderate climate shifts (e.g., Washbourn-Kamau, 1970, 1975; Street-Perrott and Harrison; 1985; Trauth et al., 2003; Bergner et al., 2003; Garcin et al., 2009) (Fig. 1). This is related to the amplification effect, the result of a tectonically-formed graben morphology in combination with an extreme contrast between high precipitation in the elevated parts of the catchment and high evaporation in the lake area (Street-Perrott and Harrison, 1985; Bergner et al., in press).

The recent lake-level history of Lake Naivasha, and adjacent lakes in the Kenya Rift, highlights the extreme sensitivity of such *amplifier lakes* to climate changes (Fig. 2) (Washbourn, 1975; Hastenrath and Kutzbach, 1983; Bergner et al., 2003; Trauth et al., 2003, 2005; USDA/NASA/Raytheon/UMD; Ministry of Water and

Irrigation of Kenya, 2008) (see supplementary information). On the time scale of 10^0 to 10^1 years, Lake Naivasha typically varies 0-1.5 m in lake level (USDA/NASA/Raytheon/UMD; Ministry of Water and Irrigation of Kenya, 2008), whereas lake-level fluctuations on a time scale of 10^2 to 10^3 years are on the order of tens of meters (Verschuren et al., 2000). Early Holocene water-level variations reach amplitudes of up to one hundred meters (Washbourn, 1975; Hastenrath and Kutzbach, 1983; Bergner et al., 2003), whereas the lake level varied by ~150 m on a time scale of 10^4 to 10^5 years (Bergner et al., 2003; Trauth et al., 2003). Even greater water depths of more than 250 m are documented for a time scale of 10^5 to 10^6 years, after about three million years ago (Trauth et al., 2005, 2007).

Essentially, water-level changes in the Naivasha basin follow a power law where larger lake-level variations occur on longer time scales (Fig. 2). Other African lakes such as Lake Chad (Leblanc et al., 2006) and Lake Victoria (Hastenrath and Kutzbach, 1983) respond over similar time scales with significantly lower lake-level variations, whereas some lakes, e.g., Lake Ziway (Gillespie et al., 1983), Lake Nakuru (Washbourn-Kamau, 1970) or Lake Suguta (Garcin et al., 2009) demonstrate more extreme lake-level variations than Lake Naivasha. Importantly, all amplifier lakes occur in the tectonically-controlled environments of the Kenyan and Ethiopian rifts (Fig. 1 and 2). Both the basin morphology and precipitation-evaporation contrasts in the catchment area of the amplifier lakes are the result from extensional tectonic processes. Thus, this study highlights the relevance of long-term tectonic processes to short-term climate fluctuations and environmental instability.

When did the amplifer lake systems evolve in East Africa? The volcano-tectonic segmentation of the Kenya Rift into smaller, partly internally drained basins began during the Pliocene and continues into the present day. Between 5.5 and 3.7 Ma, earlier halfgraben structures were antithetically faulted, thus creating a full-graben morphology in most parts of the rift (Strecker et al., 1990; KRISP Working Party, 1991; Ebinger et al., 1998; and supplementary information). The internal drainage conditions were caused by the conspiring effects of magmatic activity centered along the volcano-tectonic axis and the formation of central volcanoes during the Pleistocene. Importantly, these processes were augmented by the formation of horst and graben structures that fundamentally influenced the fluvial network of the rift. The timing of these processes coincides with a re-orientation of the extension direction from an earlier E-W to a neotectonic ESE-WNW orientation during Plio-Pleistocene (Strecker et al., 1990; and supplementary information).

The hallmark of these young extensional processes is the formation of presently isolated sub-basins that coalesced multiple times in the past during episodes of climatic changes when East Africa must have experienced greater amounts of precipitation. The combination of these tectonic movements and the existence of earlier volcanic edifices results in the distinct precipitation-evaporation contrast between the rift shoulders receiving more than 2,000 mm of mean-annual rainfall and graben areas with up to 4,000 mm of evaporation today (Garcin et al., 2009). Interestingly, the development of amplifier lake systems at that time is also documented in a distinct change in the paleo-lake character. Whereas the ~4.6-4.5 Ma old paleo-Lake Turasha in the central Kenya Rift was a relatively stable, large and shallow freshwater lake as documented by a ~90 m thick sequence of diatomites in the Naivasha basin, the younger paleo-lakes Gicheru (~1.9-1.6 Ma) and Kariandusi (~1.0-0.9 Ma) were characterized by water depths of >150 meters that varied significantly on all time scales and may thus present the transition to the amplifier-lake conditions (Trauth et al., 2005, 2007).

The switch from extensive, possibly shallow rift lakes during the early halfgraben stages to amplifier lakes Plio-Pleistocene time is important as it made this region very sensitive to climate changes. Sensitivity alone, however, does not alter the local environment as an initial change in climate is required for a response to occur. There is a growing body of geologic evidence for precession-forcing of moisture availability in the tropics, both in East Africa and elsewhere during the Plio-Pleistocene (Bush et al., 2002; Deino et al., 2006; Kingston et al., 2007; Hopley et al., 2007; Trauth et al., 2003, 2007; Cruz et al. 2005; Wang et al., 2004; Lepre et al., 2007). The precessional control on tropical moisture has also been clearly illustrated by climate modeling of Clement et al. (2004), which showed that a 180° shift in precession could change the annual precipitation in the tropics by at least 180 mm/year and induce a significant shift in seasonality, whereas precession has almost no influence on global or regional temperatures (Clement et al., 2004). A synopsis of lake-level histories in the EARS suggests that precessional forcing of moisture availability fundamentally influences the expansion and shrinkage of lakes. The first possible environmental state occurs at minimum precession and maximum insolation in the Northern Hemisphere, inducing a wetter climate over East Africa (Kutzbach and Street-Perrott, 1985).

Once a critical evaporation/precipitation threshold is passed, the amplifier lakes respond rapidly (within less than 200 years) and become very large and deep (Kutzbach and Street-Perrott, 1985; Bergner et al., 2003; Garcin et al., 2009). The presence of such large lakes affects the local environment by altering the adiabatic lapse rates leading to generally conditions, including local vegetation changes and forest expansion. Response times between climate and major vegetation changes can be as short as 50 years (Hughen et al., 2004; Maslin, 2004). Figure 3a illustrates the effect of the growth of an amplifier lake and the expansion of surrounding forest during this *Wet Period.* Once the maximum extent of rift lakes was established, on a regional basis they would have served as an east-west barrier to the migration of animals and early hominins. North-south movement between the different lake systems would have been relatively unimpeded, but with rich fertile woody environments surrounding lakes and on the rift shoulders, there would have been little or no environmental pressure to do so. As the precession cycle progresses and the insolation maximum moves towards the Southern Hemisphere, moisture availability in EARS would be reduced. The lakes initially have a muted response as their presence maintains a relative wet environment in the rift valley, until increased aridity overcomes inertia and the lakes shrink.

Modeling results and field observations suggest that East African lakes require up 2,000 years to disappear during a wet-to-dry climate transition (Bergner et al., 2003; Garcin et al., 2009). Figure 3b illustrates this *Transitional Period* and the effect of reduced rainfall and lake shrinkage on the adjacent vegetation mosaic, with forests retreat from lakeshore environments to the rift shoulders. This facilitates both north-south and east-west migration of biota. As the insolation maximum reaches the Southern Hemisphere the rift valley becomes extremely arid. Dust volume carried on the wind to both Mediterranean and Indian Ocean sites increases (deMenocal, 2004; Larrasoaña et al., 2003; Trauth et al., 2009). The effects on the environment are illustrated in Figure 3c, with small refugia of forest surviving only in the rift shoulder areas or on isolated volcanic edifices during the *Dry Period.* This effect has been seen in flightless bush crickets, which were forced into shrinken forest refugia on the rift shoulders during dry intervals, evolving into separate species (Voje et al., 2008). We postulate that a dry rift valley has acted as a major barrier, isolating animals and hominins periodically during the Plio-Pleistocene, resulting in small populations trapped in higher altitude refugia with the possibility of allopatric speciation.

Consequently, alternating wet and very dry conditions superposed on a a changing tectonically active environment in the EARS may have resulted in the formation of barriers to animal and hominin migration, both east-west and north-south. The very dry periods could have isolated populations in small refugia with the possibility of allopatric speciation. The *Transitional Periods* provide the most opportunity for migration (Fig. 3b). However, these periods are also most sensitive to extreme global climate influences, for example millennial-scale Heinrich or Dansgaard-Oeschger events or extreme El Niño/Southern Oscillation (ENSO) intervals, because the water balance of the amplifier lakes will react strongly to small changes in moisture availability. These conditions may provide the required forcing of environmental conditions that constitutes the basis of the variability selection hypothesis (Potts, 1998).

We can also speculate on the relative durations of wet periods based on the timing of the precessional cycle. Precession is sinusoidal, with intervals of little or no change in insolation, followed by intervals of a much increased rate of changes. Sinusoidal forcing results in intervals of by ~8,000 years when relatively little change in daily insolation occurs (Maslin et al., 2005), representing the *Wet Period* and *Dry Period* intervals described above. These are followed by a rapid change of about 2,500 years which 60% of the total variation in daily insolation and seasonality occurs. These intervals of rapid change correspond to the *Transitional Periods* described above. Nevertheless, without the tectonically created topographic boundary conditions these rapid and extreme changes associated with the amplifier lakes could not have occured in these local environments.

Although highly hypothetical, the close relationship between tectonics, climate, topography and superposed oscillating environmental changes on all time scales must have fundamentally influenced evolutionary processes in this tropical environment. The East African amplifier lakes are a keystone in this scenario and may help explain why East Africa became the place where early humans evolved. The further understand Plio-Pleistocene climate change in the EARS, we support proposed initiatives for scientific drilling of hominin-related sedimentary basins (e.g., Cohen, 2009).

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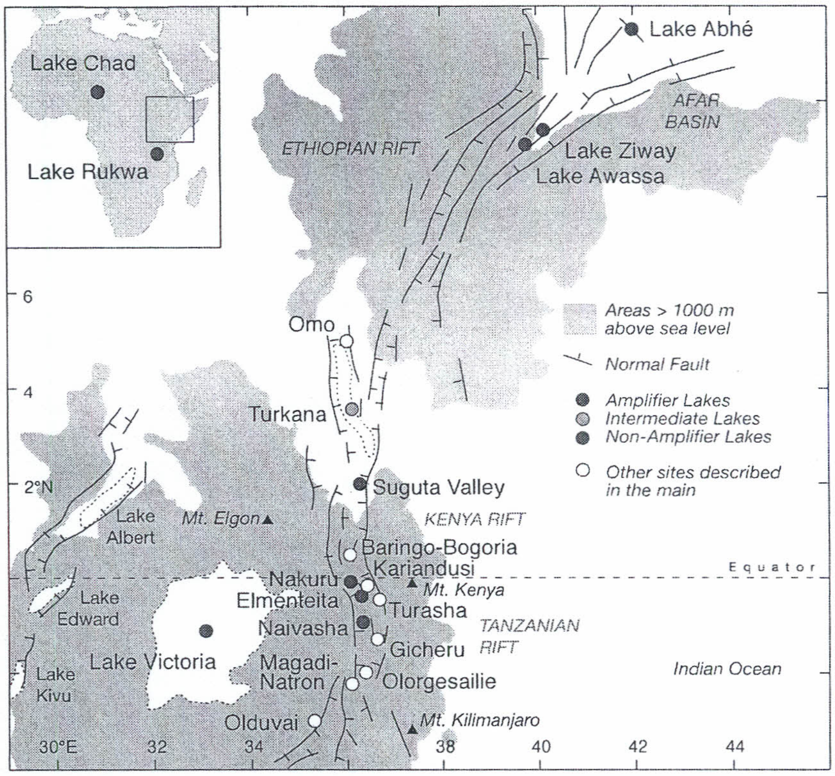
Figure Caption

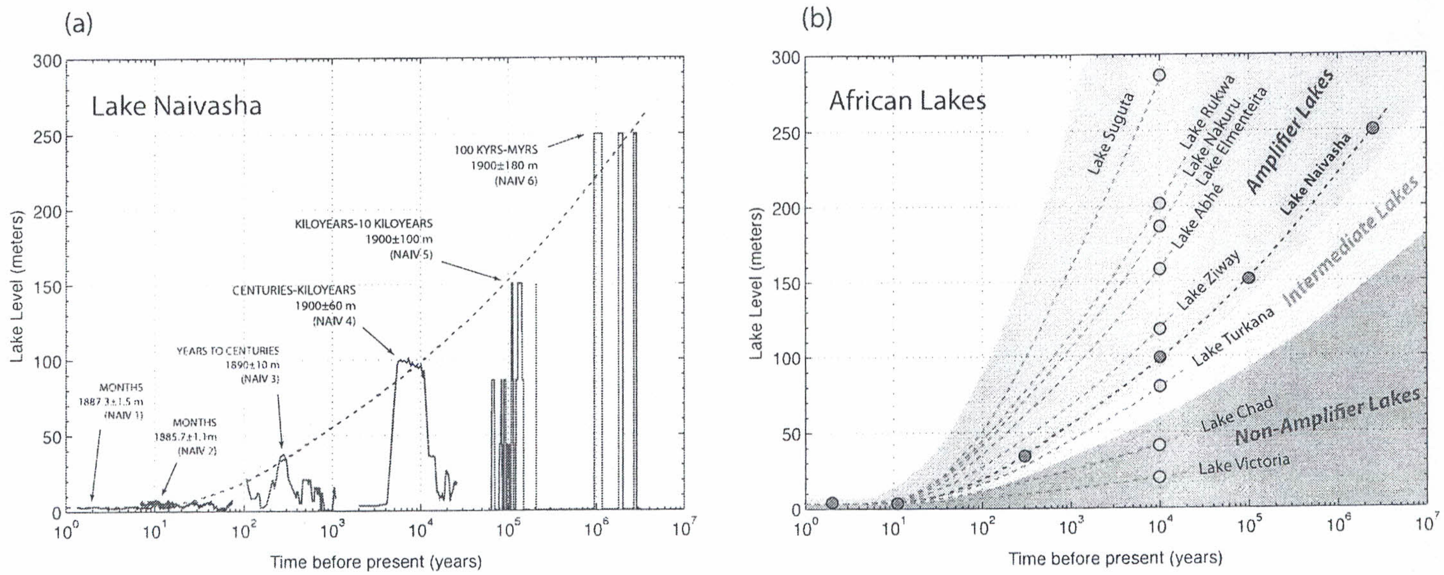
Figure 1 Map of East Africa showing topography, faults and lake basins (modified from Trauth et al., 2005). Note the location of amplifier, intermediate and non-amplifier lakes. All amplifier lakes are located in a rift environment and respond sensitively to relatively moderate climate variation.

Figure 2 (a) Lake-level change in the Naivasha basin in the Central Kenya Rift based on lake sediments and paleo-shorelines; (Naiv 1) observations (Ministry of Water and Irrigation of Kenya, 2008), (Naiv 2) satellite altimetry (USDA/NASA/Raytheon/UMD), (Naiv 3) sediment characteristics (Verschuren et al., 2000), (Naiv 4) sediment characteristics and paleo-shorelines (Richardson & Dussinger, 1986), (Naiv 5) sediment characteristics, authigenic mineral phases, diatom assemblages (Trauth et al., 2001; 2003), (Naiv 6) sediment characteristics, diatom assemblages (Trauth et al., 2005, 2007). **(b)** Compilation of lake-level variations in Africa at time scales from 10^0 to 10^7 years based on lake sediments and paleo-shorelines; Lake Victoria (Hastenrath and Kutzbach, 1983), Lake Chad (Leblanc et al., 2006), Lake Turkana (Owen et al., 1982; Hastenrath and Kutzbach, 1983), Lake Naivasha (Washbourn, 1975; Hastenrath and Kutzbach, 1983; Bergner et al., 2003; Trauth et al., 2003, 2005, 2007; USDA/NASA/Raytheon/UMD; Ministry of Water and Irrigation of Kenya, 2008), Lake Ziway (Gillespie et al., 1983), Lake Abhé (Gasse et al., 1977), Lake Nakuru-Elmenteita (Washbourn-Kamau, 1970), Lake Rukwa (+200 m) (Kervyn et al., 2006), and Lake Suguta (Garcin et al., 2009).

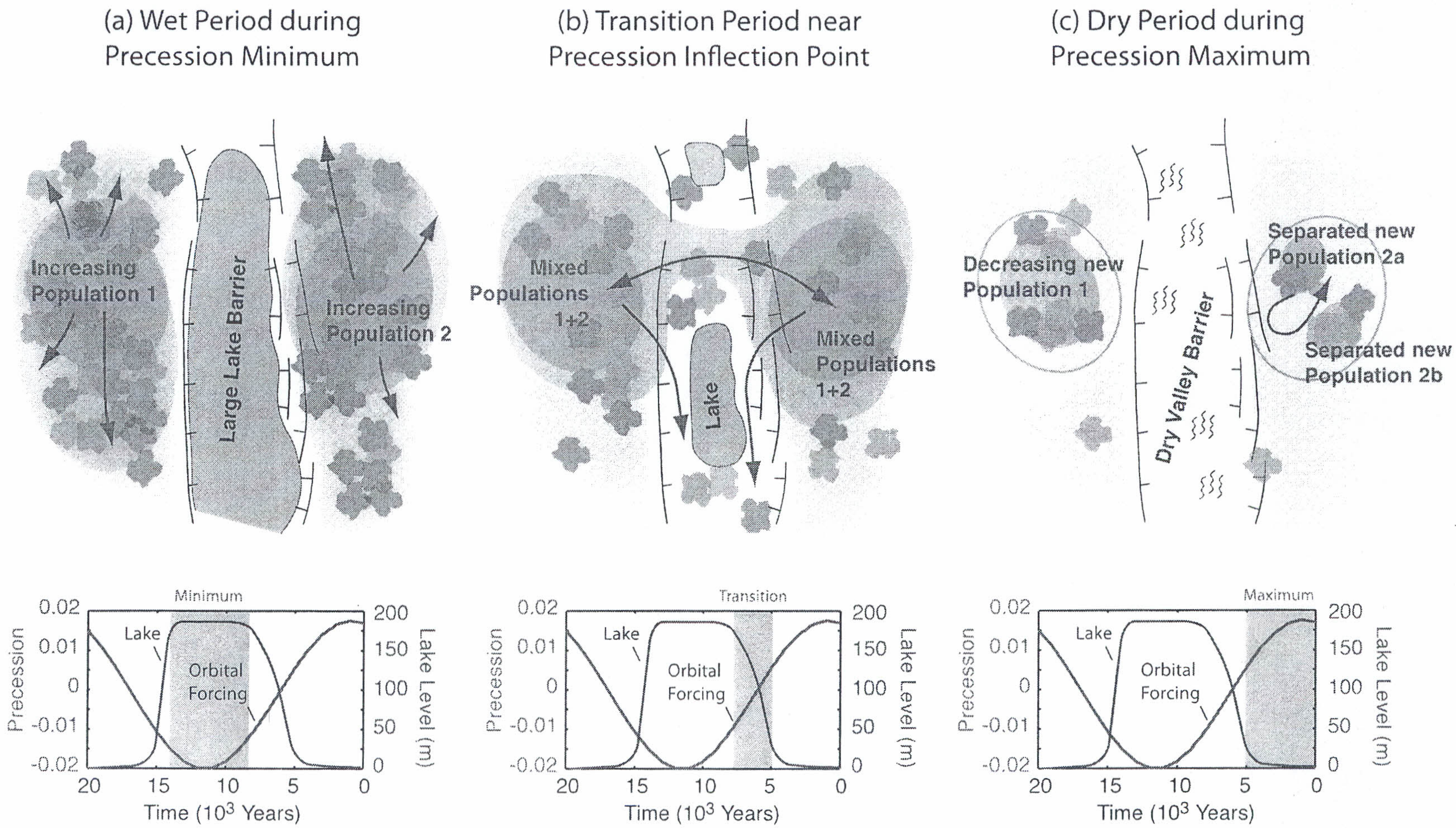
Figure 3 Conceptional model of orbitally-induced climate variation, environmental change, and population speciation and radiation in a rift environment. **(a)** During precessional minima, hence Northern Hemisphere insolation maxima, large rift lakes form natural barriers that inhibit mixing of the two separate populations 1 and 2 of animals and hominins. New species evolve independently in geographic isolation according to the model of allopatric speciation. Due to favorable environmental conditions during a wetter climate, population sizes increase, the larger populations split, and sub-populations migrate to other regions with favorable conditions. **(b)** Near the precession inflection point, favorable but deteriorating conditions foster migration of portions of the population along a corridor through the fading barrier. The populations 1 and 2 meet and compete during a gradually drying climate and limited availability of water and food. The populations utilize the margins of lakes to migrate southwards following favorable conditions in course of latitudinal climate shifts. **(c)** During the precession maximum, severe aridity creates a dry valley as a new barrier for migration of animals and early hominins forming two new populations 1 and 2. The limited availability of water and food results in a reduction of population size, and a tendency to migrate toward uplands where favorable conditions persist. Isolation of sub-populations 2a and 2b fosters allopatric speciation.



Trauth et al., Figure 1



Trauth et al., Figure 2



Trauth et al., Figure 3

Supplementary information to "Human Evolution and Migration in a Variable Environment: The Amplifier Lakes of East Africa" by Martin H. Trauth, Mark A. Maslin, Andreas G.N. Bergner, Alan Deino, Annett Junginger, Eric Odada, Daniel O. Olago, Lydia Olaka, Manfred R. Strecker

In the following, we provide a more detailed compilation of the volcano tectonic and fluvio-lacustrine history of major lake basins from the North to South (Suppl. Figs 1 and 2).

Volcano-tectonic evolution of the East African rift basins – The earliest evidence for the development of the East African Rift System (EARS) is an intense magmatic activity in Ethiopia between 45 and 35 Ma and in northern Kenya at around 33 Ma that continued to about 25 Ma, whereas the magmatic activity of the central and southern segments of the rift in Kenya and Tanzania started between 15 and 8 Ma (e.g., Ebinger et al., 1993). The driver for the magmatic activity as well as for the regional plateau uplift is the intrusion of an asthenopheric plume in East Africa (Ebinger et al., 1993). The exact timing of the development of the East African and Ethiopian plateaus is intensely discussed and ages for earliest topographic uplift range from 20 Ma (Pik et al., 2006; 2008) to 8 Ma (Spiegel et al., 2007). The tectonic uplift, however, was the first evidence for an climatic significance of the EARS and inspired the discussion about an influence of the plateau Formation, regional aridification and vegetation changes (e.g., Dart, 1953; Potts, 1998; Sepulchre et al., 2006). The plateau uplift was associated with an enormous magmatic activity in the area. In the Ethiopian Rift, volcanism started between 45 and 33 Ma, in northern Kenya at around 33 Ma and continued to about 25 Ma, whereas the magmatic activity of the central and southern segments of the rift in Kenya and Tanzania started between 15 and 8 Ma (Bagdasaryan et al., 1973; Crossley, 1979; Davidson and Rex, 1980; Crossley and Knight, 1981; McDougall and Watkins, 1987; Morley et al., 1992; Dawson, 1992; Ebinger et al., 1993; George et al., 1998).

While these early stages of rifting were characterized by updoming and downwarping in the later rift sectors, faulting progressed from north to south. Major faulting in Ethiopia between 20 to 14 Ma was followed by the generation of east-dipping faults in Kenya between 12 and 7 Ma on NNW striking and E dipping normal faults during SW-SE extension, creating a half graben with a rollover monocline (Williams et al., 1983; Baker et al., 1988, Blisniuk and Strecker, 1990; Strecker and Bosworth, 1991; Ebinger et al., 2000). These early half grabens were subsequently faulted antithetically between about 5.5 and 3.7 Ma during a slightly rotated stress field with WSW-ESE orientation, which generated a full-graben morphology (Baker et al., 1988, Blisniuk and Strecker, 1990). The earliest evidence for lakes in a half/early-full graben setting is a ~90 m thick diatomite sequence that overlies ~4.6 Ma old trachytic lava flows and is overlain by 4.5-3.4 Ma old Kinangop tuffs exposed in the valley of the Turasha River on the present Kinangop Plateau East of the modern Naivasha basin (Trauth et al., 2007). The diatom assemblages indicate a shallow freshwater environment rather than the conditions in a large and deep lake (Trauth et al., 2007). In cannot excluded, however, that the Turasha deposits represent the sediments of larger, but relatively shallow lake that expanded towards the North and South along the axis of the rift.

Prior to the full-graben stage, the large Aberdare volcanic complex with elevation in excess of 4,000 m was established (Baker et al., 1972; Williams et al., 1983) (Suppl. Fig. 1). Since then, the Aberdare range in the East of the modern Naivasha basin together with the Mau Escarpment, more than 3,000 m high, to the West form important orographic barriers in Kenya that form a rainshadow for moisture-bearing winds from both the Indian Ocean and the Atlantic Ocean via the Kongo basin. Between 3.6 and 2.7 Ma, ongoing WSW-ESE extension created W- to WSW-dipping normal faults with dextral components creating the Aberdare escarpment along the Sattima fault (Strecker et al., 1991). By 2.6 Ma, the graben was further segmented in the Central Kenya Rift by West dipping faults, creating the 30 km wide intrarift Kinangop Plateau and the tectonically active 40-km-wide inner rift (Baker et al., 1988; Strecker et al., 1990). The central graben depression in the Naivasha area between the Kinangop Plateau and the Mau escarpment went through a phase of subsidence after 2.6 Ma before voluminous trachyte eruptions occurred that did not overlap with the plateau after 1.9 Ma during W-E extension. The inner rift was subsequently covered by trachytic, basaltic, and rhyolithic lavas and continues to be affected by normal faulting leading to further segmentation of the rift floor (Strecker et al., 1990; Bosworth and Strecker, 1997). There is no unambiguous evidence from sedimentation patterns in the Magadi-Natron and Olduvai basins, however, that major fault-bounded basins existed at that time (Foster et al., 1997). Major normal faulting in these regions occurred at 1.2 Ma and produced the present-day rift escarpments (Foster et al., 1997). Subsequent Late Quaternary structural en-echelón segmentation during west-northwest to east-southeast oriented extension created numerous sub-basins in the individual rift sectors that repeatedly hosted smaller lakes (Baker et al., 1988).

The magmatic and tectonic evolution of the Kenyan rift segments shows that conditions for the establishment of large lakes existed by approximately 3 Ma. However, continued faulting and en-echelón segmentation during WNW-ESE oriented extension created numerous smaller sub-basins that repeatedly hosted lakes during the Pleistocene (Strecker et al., 1990; Bosworth and Strecker, 1997).

Examples for variable environments on all time scales – East African lakes fluctuated on all time scales (Suppl. Fig. 2). The chronology of Plio-Pleistocene lake-level variations in East Africa indicates consistent wetter and more seasonal conditions every ca. 0.8 Ma, with periods of precessional-forced extreme climate variability at ca. 4.7-4.3 Ma, 4.2-3.8 Ma, ~3.6-3.4 Ma, ~3.2-2.90 Ma, 2.7-2.5 Ma, 1.9-1.7 Ma and 1.1-0.9 Ma and after ca. 0.2 Ma before present (Trauth et al., 2003, 2005, 2007; Maslin and Trauth, 2009). On shorter time scales, the history of these large lakes reveal rapid (less than one thousand years) and large-magnitude fluctuations (up to ~300 meters, Garcin et al., 2009). The internal variability of the large-lake episodes is best documented for the Plio-Pleistocene Chemeron Formation (3.5 to 1.7 Ma) in the Tugen Hills (Deino et al., 2006; Kingston et al., 2007), the Mid Pleistocene Olorgesailie Formation in the Southern Kenya Rift (1.2 to 0.5 Ma) (Behrensmeyer et al., 2002; Owen et al., 2008), and the Late Pleistocene Ol Njorowa Gorge Formation in the Central Kenya Rift (<0.2 Ma) (Trauth et al., 2001, 2003). The revised analyses of terrestrial dust records from marine sediments by Trauth et al. (2009) has recently shown that African climate is mostly influenced by low-latitude climate transitions such as the closure of the Indonesian Seaway (Cane and Molnar, 2001) and associated reduced heat flow to the tropics and the onset of the Walker Circulation near 1.9 Ma (Ravelo et al., 2005; Trauth et al., 2009) rather than the intensification of the Northern Hemisphere glaciations as a result of the closure of the Panama Isthmus (deMenocal, 1995, 2004).

Recent work by Andrew Hill, John Kingston and colleagues on the upper Chemeron Formation (3.5 to 1.7 Ma) exposed in the Tugen Hills (western Baringo-Bogoria Basin) revealed a sequence of five major diatomites (Deino et al., 2006; Kingston et al., 2007) (Suppl. Fig. 2a). Single-crystal $^{40}Ar/^{39}Ar$ determinations show they occur between 2.66 and 2.56 Ma at ~20 kyr intervals (Deino et al., 2006). Detailed mapping and stratigraphic analysis suggest that these cycles with precessional periodicity are not due to local tectonic movements but reflect climate changes (Deino et al., 2006). First investigations of the diatom flora contained in these diatomites indicate the existence of large deep lakes between 2.66 and 2.56 Ma (Owen, 2002). The lake episode recorded in the Chemeron Formation correlates with several important lake episodes observed in the Afar Basin and the Ethiopian Rift (Williams et al., 1979).

The Olorgesailie Formation has been intensely studied by the team of Rick Potts since the 80's (e.g., Potts, 1999; Behrensmeyer et al., 2002; Owen et al., 2008) (Suppl. Fig. 2b). The Olorgesailie Formation records the Formation of a closed-basin environment shortly before 0.992 Ma, alternating between lacustrine and subaerial conditions for a period of ~500 kyr but no episodes of major erosion (Behrensmeyer et al., 2002; Owen et al., 2008). The most important lake period occurred between 0.992 and 0.974 Ma as documented by the deposition of the main diatomite bed (Behrensmeyer et al., 2002; Owen et al., 2008). After 0.500 Ma, the basin experienced phases of valley cutting associated with base-level fluctuations of around 50 m over periods of 10^4 to 10^5 years (Potts, 1988; 1998; Behrensmeyer et al., 2002; Owen et al., 2008). The stratigraphy of the Olorgesailie Formation, however, has recently been the matter of discussions (see Trauth et al., 2005; Owen et al., 2008; Trauth and Maslin, 2009; Owen et al., 2009). According to the newest interpretation by Owen et al. (2008), the Olorgesailie basins has no environmental record during much of the time between 1.2 and 0.49 Ma. Owen et al. (2008) proposed relatively short periods of full lacustrine conditions, whereas soil formation, reworking and erosion are the predominant processes during much of the time between 1.2 and 0.49 Ma. Instead, we propose a more straightforward interpretation of the Olorgesailie record based on the raw stratigraphic evidence and lake-level record as published by Behrensmeyer et al. (2002), the Ar/Ar chronology published by Deino et al. (1990; 1992) and the additional Ar/Ar age of 1.2 Ma near the base of the section provided by Owen et al. (2008) (Suppl. Fig. 2b). A robust stratigraphy independent from any assumptions about sedimentation rates, the character of the deposits and the occurrence of reworked or eroded material was obtained by simple linear interpolation of the lake-level record Behrensmeyer et al. (2002) taking into account the Ar/Ar ages by Deino et al. (1990; 1992) and Owen et al. (2008). The large error bar of the Ar/Ar age near 1.0 Ma and the large undated interval between ~1.2 and 1.0 Ma introduces some degree of uncertainty that allows to shift the earliest lake episode by ~0.1 Ma towards older times. The lake-level record in the Olorgesailie basin then perfectly matches the earth's eccentricity cycle and therefore suggest that indeed a large, but fluctuating lake occurred in the southern Kenya rift during a relatively long period of time. As already stated in Trauth et al. (2005, 2007), however, the lake-level was subjected to considerable fluctuations all the time, as also indicated by the analysis of diatom assemblages (Owen et al., 2008). The lake episode recorded in the Olorgesailie Formation also correlates nicely with fluctuating paleo-lakes in the Central Kenya Rift (Trauth et al., 2005, 2007), the

Suguta Valley (Dunkley et al., 1993), the Omo-Turkana basin (Feibel et al., 1991) and in the Afar Basin (Gasse, 1990).

The Ol Njorowa Gorge Formation in the southern Naivasha basin shows five highstands and intermittent lowstand recurring at half-precessional (ca. 11 kyr) cyclicities (Trauth et al., 2001, 2003) consistent with the concept of low-latitude orbital forcing and climate (Berger et al., 1997, 2006) (Suppl. Fig. 2c). The Late Pleistocene Lake Naivasha was characterized by the deposition of up to 4 m thick diatomites containing a mixed planktonic and benthic-epiphytic diatom community that indicate alternating freshwater and highly alkaline conditions (Trauth et al., 2001, 2003). Additional evidence for the paleo-water depths of these young lakes comes from the altitude of paleo-shorelines and sediment outcrops (Trauth et al., 2001, 2003). Basin reconstructions and hydrological modeling suggests that the highest lake levels reached ca. 150 m during the peak of the wet episode between ca. 145 and 60 kyr before present (Bergner et al., 2003, 2004). The Ol Njorowa Gorge Formation also contains evidence for remarkable droughts in the Central Kenya Rift similar to the ones reported from the Malawi basin by Brown et al. (2007). The corresponding sediments contain authigenic silicates such as zeolites that document chemical weathering of silicic volcanic glass in an extremely alkaline lake environment. No lake, however, indicates the complete absence of lake sediments. The sedimentary record of basin contains fluvial or eolian deposits, and primarily deposited, impact craters of pumice lapilli on mud surfaces or reworked pyroclastic material. The lake episode recorded in the Ol Njorowa Gorge Formation also correlates with the Kibish Formation in the Omo along the Omo River (Butzer et al., 1969; Brown et al., 2008). Uranium-series ages for hydrothermal deposits recording geothermal activity in the Suguta Valley (Northern Kenya Rift) suggest elevated water tables and increased availability of meteoric water associated with more humid climate as early as 133±11 kyr BP (Sturchio et al., 1993). High lake levels can be inferred from shorelines in the Magadi-Natron Basin in the southern part of the rift, where littoral stromatolites provide U-series ages of 135 kyr BP (Hillaire-Marcel et al., 1986).

The terminal Pleistocene/Early Holocene sediments and shorelines of Lakes Naivasha and Nakuru Elmenteita are also well-studied lakes for the last precessional cycle and associated high-lakes levels (Washbourn-Kamau, 1970; 1975; 1977; Richardson and Dussinger, 1986; Trauth et al., 2003; Dühnforth et al., 2006) (Suppl. Fig. 2d). Between ca. 13 and 5 kyr before present the lake level was 110 m (Lake Naivasha) and 180 m (Lake Nakuru-Elmenteita) above the modern lakes. High lakes with similar amplitudes were also reported from many other East African lake basins, such as Lake Abhé (+160 m) (Gasse et al., 1977), Lake Ziway (+112 m) (Gillespie et al., 1983), Lake Suguta (+280 m) (Garcin et al., 2009), Lake Turkana (+80 m) (Owen et al., 1982; Hastenrath and Kutzbach, 1983; Vincens et al., 1989), Lake Nakuru-Elmenteita (+180 m) (Washbourn-Kamau, 1967; 1970), Lake Naivasha (+100 m) (Washbourn, 1975; Hastenrath and Kutzbach, 1983) and Lake Rukwa (+200 m) (Kervyn et al., 2006) that mark the so-called African Humid Period (spanning ca. 15,500-5,500 cal. yrs BP) (e.g., Gasse, 2000; Barker et al., 2004). The abruptness of the onset and termination of the African Humid Period and associated environmental shifts is a matter of debate (deMenocal et al., 2000; Kröpelin et al., 2008a, 2008b; Brovkin and Claussen, 2008; deMenocal, 2008; Cole et al., 2009). Also intensely debated is the relative importance of high-latitude glacial shifs and reduced thermohaline circulation during Heinrich and Younger Dryas events during that time interval (Trauth et al., 2003; Brown et al., 2007; Tierney et al., 2008; Garcin et al., 2009).

During the last millenium, Lake Naivasha fluctuated considerably by ~30 m during decades (Verschuren et al., 2000) (Suppl. Fig. 2e). The water level variations were reconstructed using sediment stratigraphy, diatom assemblages and fossil midge assemblages. According to these reconstructions, East Africa as significantly drier than today during the Medieval Warm Period (MWP, AD 1000–1270) and wetter during the Little Ice Age (LIA, AD 1270–1850) which was interrupted by three prolonged dry episodes. The humidity changes in the Naivasha basin correlate with long-term changes in solar radiation suggesting that decade-scale rainfall variations are largely controlled by solar forcing (Verschuren et al., 2000). The Naivasha record as a record of climate changes during the last millenium, however, was also subject to intense discussions (see summary in Gasse et al., 2002). Six ice cores from Kilimanjaro providing an ~11.7-thousand-year record of Holocene climate and environmental variability for eastern equatorial Africa suggest substantial cooling (Thompson et al., 2002). These and other records of East African climate changes during the last millennium illustrate the spatial complexity of environmental changes on relatively short times scales (e.g., Gasse et al., 2002; Thompson et al., 2006; Russell et al., 2007).

The modern lake-level fluctuations of Lake Naivasha based on satellite altimetry and observations are in the range of a few (1 to 6) meters (Data from Ministry of Water and Irrigation of Kenya, 2008, and Vincent et al., 1979; Åse, 1987). The present climate patterns in East Africa include several major air streams and convergence zones, superimposed upon regional factors associated with topography, large lakes, and maritime influence (Nicholson, 1996). Regional wind and pressure patterns include the Congo air stream with westerly and southwesterly air flow, as well as the NE and SE monsoons. In contrast to the Asian SW monsoon, both monsoons over East Africa are relatively dry. In contrast, the Congo air stream is humid and associated with rainfall. These major air streams are separated by the Intertropical Convergence Zone (ITCZ) and the Congo Air Boundary. Rainfall in East Africa is mainly linked to the passage of the ITCZ causing a strongly bimodal annual cycle (Nicholson, 1996). The period during April-May is considered to be the 'long rains' while the October-November period is called the 'short rains', following the latitudinal position of the overhead sun with a time lag of about 4-6 weeks. Fluctuations in the intensity of precipitation are linked to E-W adjustments in the zonal Walker circulation associated with the Indian Ocean Dipole and the El Niño/ Southern Oscillation (Saji et al., 1999; Moy et al., 2002) (Suppl. Fig. 2f).

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