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Limited herbivore migration during the Last Glacial Period of Kenya

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Eastern Africa is home to the largest terrestrial migrations on Earth. Though these migratory systems have been well studied for decades, little is known of their antiquity and evolutionary history. Serially sampled strontium stable isotopes ($^{87}Sr/^{86}Sr$) from tooth enamel can be used to track migration in mammals. Here we analyse $^{87}Sr/^{86}Sr$ for 79 bovid and equid individuals representing 18 species from four localities in Kenya to characterize prehistoric migratory systems during the Last Glacial Period (115–11.7 ka). Of the species analysed, 16 lack definitive evidence for migration, including blue wildebeest (*Connochaetes taurinus*), Thomson's gazelle (*Eudorcas thomsonii*) and plains zebra (*Equus quagga*), which are long-distance migrants today in the Greater Serengeti Ecosystem and historically in the Athi-Kapiti Plains. Only two species, the extinct wildebeests *Rusingoryx atopocranion* and *Megalotragus* sp., were migratory. These findings suggest a possible alternative narrative about ecosystem dynamics during the Last Glacial Period and shed light on the behaviour of both extant and extinct species at this time. In particular, these results indicate that migratory behaviour in extant species either emerged during the Holocene or was more spatiotemporally constrained in the past. Our results contribute to a growing body of evidence suggesting that the structure and function of geologically recent large mammal communities in eastern Africa differed considerably from those observed in the present day.

Eastern Africa hosts the largest terrestrial migrations on Earth[1]. Each year, millions of blue wildebeest (*Connochaetes taurinus*), Thomson's gazelle (*Eudorcas thomsonii*) and plains zebra (*Equus quagga*) migrate hundreds of kilometres through the Greater Serengeti Ecosystem (GSE) seeking fresh grasses and water[1]. Historically, an extension of this migratory system reached nearly to Lake Victoria[2] (Fig. 1). The same three species once migrated long distances across the Athi-Kapiti Plains in an aggregation–dispersal system[3]. All are primarily C_4 grazers tracking high-quality grass forage seasonally, typical of migrants throughout Africa[4–7]. Such migratory systems are ecologically important, and many recognize that insufficient knowledge (for example, about their timing, geography and size) is a major impediment to their conservation in the face of increasing human impacts[7,8]. However, almost nothing is known about their prehistory: What is the antiquity of Africa's migrations? How did migratory systems respond to climate change and human impacts? Which species migrated? Recent advances in mapping bioavailable

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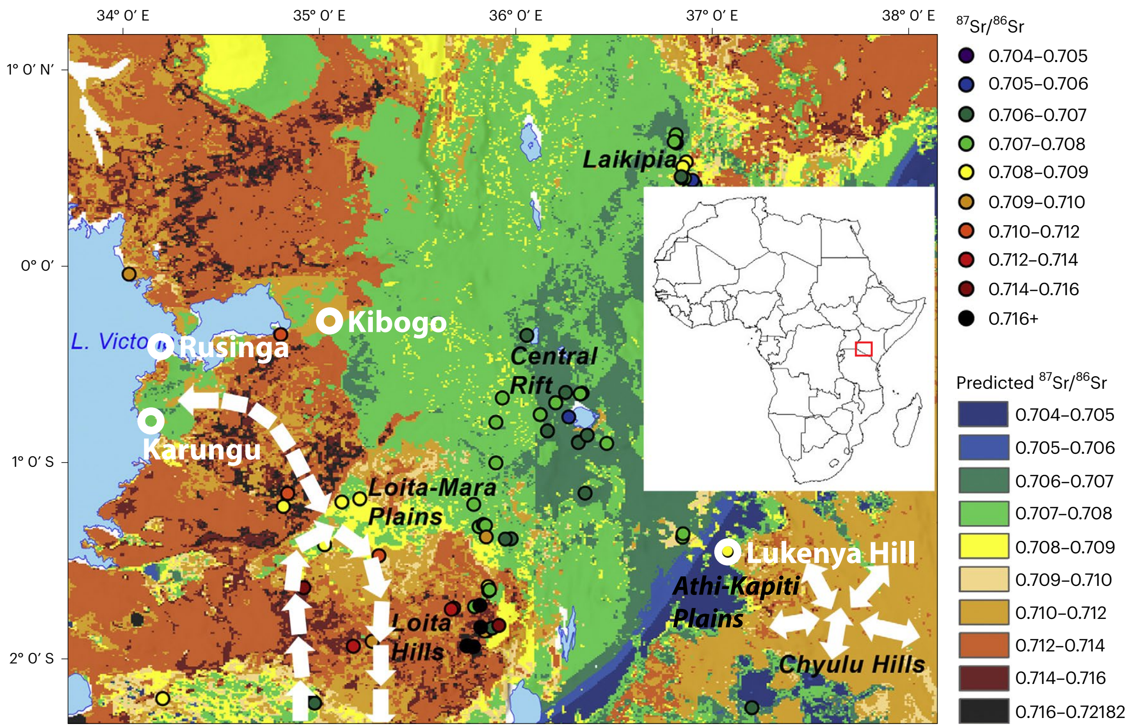

Fig. 1 | $^{87}Sr/^{86}Sr$ isoscape of southern Kenya and northern Tanzania. $^{87}Sr/^{86}Sr$ sampling localities are shown with coloured circles and fossil localities indicated with white circles. Historic migration routes in the GSE and Athi-Kapiti Plains are shown with white arrows. The position within Africa is shown in the red box in the inset. Modified from ref. 18.

strontium now allow us to make progress in understanding the prehistoric migratory systems of eastern Africa.

Strontium stable isotopes are increasingly used as a proxy for tracking both modern and prehistoric migrations in North America[9–13] and Europe[14,15], but they are rarely used in Africa. The most extensive African study was conducted by Copeland et al.[16], who report on a diverse array of serially sampled herbivore teeth from South Africa. Other studies have evaluated small samples without serial sampling to evaluate lifetime mobility rather than seasonal migration[17]. The lack of progress in tracking animal mobility in eastern Africa is in part due to the former absence of fine-grained strontium isoscapes for the region. This limitation has been remedied by Janzen et al.[18], who produced an isoscape for eastern Africa, allowing us to explore prehistoric migratory systems (Fig. 1). Using this isoscape, O'Brien et al.[19] demonstrated migratory behaviour in the extinct wildebeest *Rusingoryx atopocranion* in fossil samples dating to ~100–36 ka. Here we expand on this initial work to provide a detailed picture of ungulate migrations during the Last Glacial Period (LGP; 115–11.7 ka) in eastern Africa.

In this Article, we use intra-tooth $^{87}Sr/^{86}Sr$ values from 18 herbivore species to examine migration during the LGP at four Kenyan localities: Karungu (100–36 ka), Rusinga Island (100–36 ka) and Kibogo (36–12 ka) in the north-western periphery of the GSE, and Lukenya Hill (>52–12 ka) in the Athi-Kapiti Plains—places with historical migrations[1,2] and for which prehistoric migrations have been hypothesized[3,19,20] (Fig. 1 and Table 1). To determine which species were migratory, both the raw values and variability of intra-tooth $^{87}Sr/^{86}Sr$ were considered. Because there is considerable local variation in $^{87}Sr/^{86}Sr$ across the landscape (for example, $^{87}Sr/^{86}Sr$ values in a contemporary migrant from the Serengeti are not representative of migrants from elsewhere), we identify migrants versus non-migrants using the isoscape and through comparison with select fossil species. These species include a known migrant, *Rusingoryx atopocranion*[19], as well as species whose small body sizes and specialized ecologies restrict them to small lifetime home ranges (<1 km^2) today (*Ourebia ourebi* and *Redunca* spp.). Further details on our protocol are outlined below.

Results

$^{87}Sr/^{86}Sr$ results

The isoscape model produced by Janzen et al.[18] was used as a guide for understanding local variation. For this study, the local $^{87}Sr/^{86}Sr$ range is defined as modelled values within 5 km of each locality. Based on differences in geology and other factors[18,21,22], the modelled local range in $^{87}Sr/^{86}Sr$ is ~0.707–0.708 for Karungu, ~0.707–0.712 for Kibogo and ~0.706–0.712 for Lukenya Hill. The local signature for Rusinga was not modelled by Janzen et al.[18] as Rusinga is an island, but is estimated as described in O'Brien et al.[19] using a combination of African root-rat (*Tachyoryctes splendens*) fossils from the Rusinga LGP locales of Nyamita and Wakondo and analogous geology from elsewhere in Kenya. A conservative estimate for the range of values on Rusinga is 0.704–0.708.

Raw data are given in Supplementary Table 1, and $^{87}Sr/^{86}Sr$ results for each locality are shown in Fig. 2 (see also Supplementary Figs. 1–54 for individual plots of each species). These data must be interpreted with caution. Although $^{87}Sr/^{86}Sr$ does not fractionate as it moves from bedrock sources into water and plants, there is a gradual attenuation as it is incorporated into an animal's dental tissue, with current observations suggesting that about 50% of environmental $^{87}Sr/^{86}Sr$ variation in migrants is recorded in teeth[10,23,24]. For example, for an animal evenly sampling bioavailable Sr values from 0.707 to 0.714 as it moves across the landscape, we might expect a detected Sr range of ~0.709–0.712. For the vast majority of species, the serially sampled strontium values fall within the range of the modelled isoscape values for Rusinga, Kibogo and Lukenya Hill. However, most values from Karungu are inconsistent with the modelled isoscape, including those of *Redunca arundinum*, a species with exceptionally small home ranges today and almost certainly a non-migrant in the past[25]. Thus, we conclude that the isoscape model overestimates bioavailable $^{87}Sr/^{86}Sr$ values due to low coverage in the area and the complex bedrock geology of the region. For this reason, whether or not specimens match the modelled isoscape is not considered for classification as migratory versus non-migratory at Karungu (full criteria outlined below). Individuals from Lukenya

Table 1 | Summary of study taxa with number of sampled specimens

Taxon	Common name	Karungu	Rusinga	Kibogo	Lukenya Hill
Syncerus antiquus[a]	Long-horned buffalo	1	1	1	1
Syncerus caffer	Cape buffalo	1	1	—	—
Tragelaphus oryx	Common eland	1	—	1	1
Aepyceros sp.[a]	Lake Victoria impala	1	1	—	—
Alcelaphus buselaphus	Hartebeest	1	1	2	4
Damaliscus hypsodon[a]	Eastern African blesbok	1	1	2	4
Connochaetes taurinus	Blue wildebeest	1	1	2	4
Megalotragus sp.[a]	Giant wildebeest	1	1	2	—
Rusingoryx atopocranion[a]	Strange-headed wildebeest	1	3	—	—
Hippotragus equinus	Roan antelope	1	—	1	—
Oryx beisa	Beisa Oryx	1	1	—	1
Redunca arundinum	Southern reedbuck	1	1	1	—
Redunca fulvorufula	Mountain reedbuck	—	—	—	1
Eudorcas thomsonii	Thomson's gazelle	1	1	2	5
Nanger granti	Grant's gazelle	1	1	—	1
Ourebia ourebi	Oribi	—	1	1	1
Equus grevyi	Grévy's zebra	1	1	2	—
Equus quagga	Plains zebra	1	1	2	4

[a]Extinct species.

Hill show the most intra-tooth variation, consistent with the high local (within ~5 km) variation in modelled $^{87}Sr/^{86}Sr$ (Fig. 1).

Classification of migratory behaviour

There are no universal standards for distinguishing a migrant from a non-migrant using intra-tooth $^{87}Sr/^{86}Sr$ values, in part because observed values depend on local spatial variation in $^{87}Sr/^{86}Sr$ (for example, the degree of variation in $^{87}Sr/^{86}Sr$ for a migrant in one system may be similar to that of a non-migrant in another). Because $^{87}Sr/^{86}Sr$ variation recorded in teeth underestimates $^{87}Sr/^{86}Sr$ variation across the landscape[10,23,24], comparison of fossil values to the isoscape alone may pose difficulties for identifying migrants. To remedy this, we use three fossil taxa to facilitate identification of migrants and non-migrants: *Rusingoryx atopocranion* is used as a baseline migrant as demonstrated by O'Brien et al.[19], while *Ourebia ourebi* and *Redunca* spp. are used as baseline non-migrants, as these small-bodied species are non-migratory and have exceptionally small lifetime home ranges (<1 km^2) today and, almost certainly, prehistorically due to their body size and ecologies[25]. To be classified as a migrant, an individual must meet all three of the following criteria: (1) at least one $^{87}Sr/^{86}Sr$ value falls outside the modelled local $^{87}Sr/^{86}Sr$ variation for the locality (values within 5 km of the locality using Janzen et al.[18], with the exception of Karungu), (2) standard deviations of intra-tooth $^{87}Sr/^{86}Sr$ values are significantly greater than those of all *O. ourebi* and *Redunca* spp. from that locality (non-overlapping 95% confidence intervals) and (3) standard deviations of intra-tooth $^{87}Sr/^{86}Sr$ values are overlapping with those of *Ru. atopocranion* from that locality (note: all individuals meeting the first two criteria also meet this one; Supplementary Table 2). To be classified as a non-migrant, an individual must meet all three of the following criteria: (1) all $^{87}Sr/^{86}Sr$ values fall within the modelled local isoscape range (with the exception of Karungu), (2) standard deviations overlap with those of *O. ourebi* and *Redunca* spp. from that locality and (3) standard deviations of intra-tooth $^{87}Sr/^{86}Sr$ values are significantly lower than those of all *Ru. atopocranion* from that locality. Individuals not meeting either set of criteria will have their migratory status unclassified and are considered possible migrants. As *Ru. atopocranion* is absent at Kibogo and Lukenya Hill, individuals will need to meet both remaining criteria to be classified as either migrants or non-migrants at those localities. The classification of each individual is presented in Supplementary Table 2, and subsampling results are shown in Supplementary Figs. 55–58.

There are only five unequivocal migrants in the sample (5/79) (Fig. 3). These include the four *Ru. atopocranion* individuals previously shown to be migratory[19], as well as a single *Megalotragus* sp. from Rusinga. In contrast, the majority of individuals (63/79) are classified as non-migrants. Their observed $^{87}Sr/^{86}Sr$ values fall within the local range, and their standard deviations are indistinguishable from those of *O. ourebi* and *Redunca* spp. and below those of *Ru. atopocranion* (Supplementary Table 2). Eleven specimens are considered possible migrants, including individuals whose $^{87}Sr/^{86}Sr$ values fall within the local range but have relatively high variation (that is, overlapping with *Ru. atopocranion* and/or exceeding that of *O. ourebi* and *Redunca* spp.) (six individuals). These may represent individuals that migrated locally and to a lesser degree than *Ru. atopocranion*, or that migrated only within a similar geologic setting. Other possible migrants exhibit $^{87}Sr/^{86}Sr$ values outside the local range but with relatively little variability (that is, overlapping with *O. ourebi* and *Redunca* spp.) (three individuals), potentially representing individuals that dispersed between birth and death but moved little during the tooth formation process. Two individuals from Karungu have broad uncertainties in the standard deviations of their $^{87}Sr/^{86}Sr$ values, such that they overlap with *Ru. atopocranion* as well as *O. ourebi* and *Redunca* spp. At all localities, most or all individuals of the modern migratory species *Connochaetes taurinus*, *Eudorcas thomsonii* and *Equus quagga* were non-migrants (21/25), with a handful of individuals (4/25) being possible migrants (Supplementary Table 2).

Discussion

The primary migrants during the LGP at these localities were an entirely different set of species than those that migrate today. Though a handful specimens belonging to species that are important long-distance migrants today (*Connochaetes taurinus*, *Eudorcas thomsonii* and *Equus quagga*) are classified as possible migrants (Supplementary Table 2), most of the individuals lack evidence for migratory behaviour (21/25 individuals), which is unexpected if these species were regularly involved in long-distance migration during the LGP. If this pattern holds true at other sites in the GSE, it has important implications for the antiquity of present-day migratory systems: those migrations may be of quite recent origin (that is, the Holocene). Alternatively, the migratory systems of these species may be flexible with regard to ecological conditions (for example, glacial versus interglacial environments). Just as different regions of modern Africa host populations of these species ranging from migratory to resident due to ecological variation, fossil populations varied in migratory behaviour through space and time in relation to landscape-to-regional processes that shaped herbivore access to resources across the seasonal cycle.

Additionally, we find no definitive evidence of migration among species at Kibogo or Lukenya Hill, with Kibogo including three possible migrants (out of 19 individuals) and Lukenya Hill including two possible migrants (out of 27 individuals). We only find unequivocal evidence

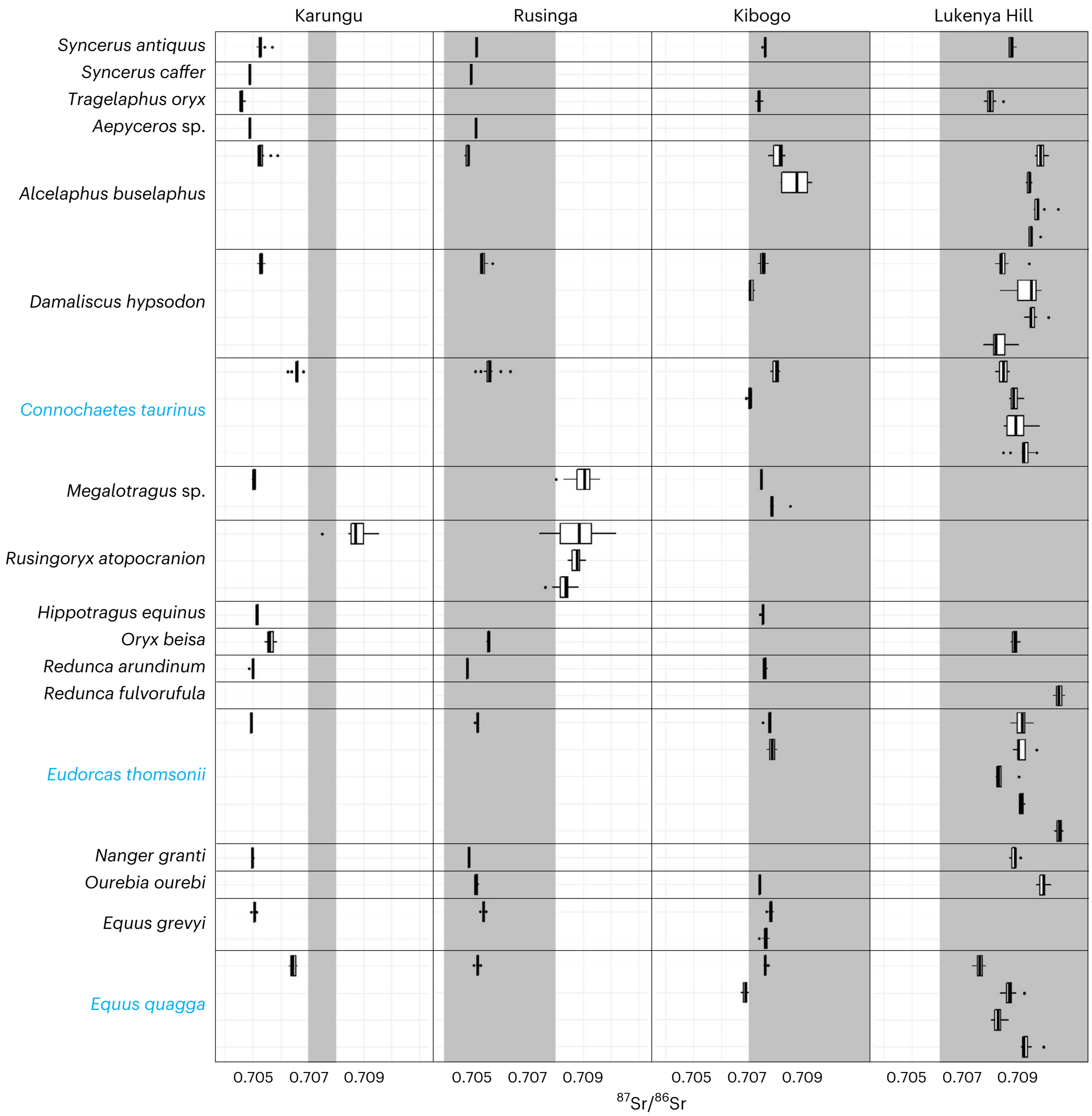

Fig. 2 | ^{87}Sr/^{86}Sr results for each individual. Modelled local ^{87}Sr/^{86}Sr range for each locality from Janzen et al.[18] is highlighted in grey. Modern long-distance migrants are shown in blue. Bounds of boxes represent interquartile range, centres represent medians, and minima and maxima represent 1.5 × interquartile range outside quartiles 1 and 3. $n = 771$ samples from 79 biologically independent animals. *Rusingoryx atopocranion* from Karungu and Rusinga and *Megalotragus* sp. from Rusinga are outliers relative to all other individuals.

of migration in the extinct wildebeests *Rusingoryx atopocranion* and *Megalotragus* sp. The ^{87}Sr/^{86}Sr values for all *Ru. atopocranion* individuals and one *Megalotragus* sp. individual from Rusinga are stark outliers at each of their respective localities, with no overlap with non-migrant individuals and high variation in ^{87}Sr/^{86}Sr (Figs. 2 and 3). These species share several traits with present-day migrants (for example, they are hypsodont grazers with cursorial body plans), but it is not entirely clear why they, but not other species with similar traits, were engaged in migration. However, *Ru. atopocranion* does have one additional quality shared with modern migrants: it is a dominant species in the eastern Lake Victoria Basin[26,27], and modern migrants are known to maintain relatively high population sizes in modern Africa[28].

At all four localities, there is variation in ^{87}Sr/^{86}Sr values among the non-migratory individuals, often with little overlap between individuals (for example, compare *C. taurinus*, *Eu. thomsonii* and *Oryx beisa* at Karungu). The intra-individual differences in ^{87}Sr/^{86}Sr values may result in part from time averaging. Local ^{87}Sr/^{86}Sr values change through time due to shifting geology, erosion and dust regimes, which may have contributed to small shifts in the bioavailable ^{87}Sr/^{86}Sr signals of each locality. Furthermore, as the Lukenya Hill sampled derives from a zooarchaeological assemblage accumulated primarily by human foragers[29], the animals were probably transported to the site from some distance—typically within a 10 km radius based on recent African human foragers[30,31]. Therefore, the variation in their ^{87}Sr/^{86}Sr values between individuals is perhaps in part indicative of their use of different parts of the landscape.

Our results suggest that some long-distance migratory systems observed historically are a geologically recent phenomenon, probably emerging at some point within the Holocene. Considering that herbivore migration is motivated by spatiotemporal variation in resource availability[4,25], it is reasonable to propose that there was a post-LGP shift in the timing or distribution of resources available to the species involved in present-day migrations. Possible mechanisms could include, but are not limited to, climate-driven changes in in the seasonal availability or productivity of grassy forage as well as increased competition. Although we lack the data required to tease these (and other) mechanisms apart, an intriguing hypothesis is that the emergence of today's widespread long-distance migratory systems may be related to competition with domestic livestock. During the Pleistocene and most of the Holocene, wild ungulates were one another's primary

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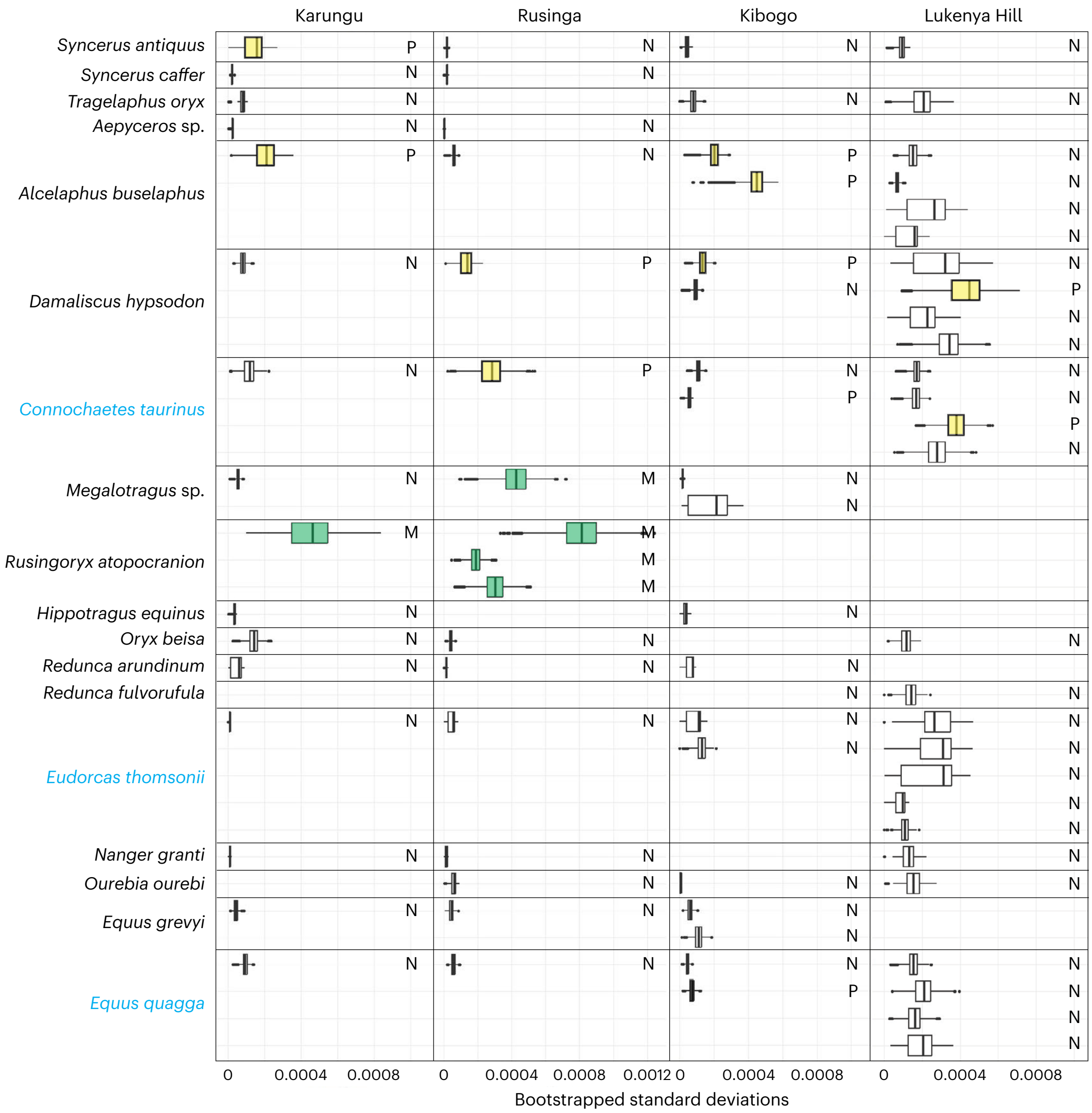

Fig. 3 | Subsampled standard deviations of $^{87}Sr/^{86}Sr$ for each individual. Migratory behaviour is indicated: M, migrant (highlighted in green); P, possible migrant (highlighted in yellow); N, non-migrant. Modern long-distance migrants are shown in blue. Bounds of boxes represent interquartile range, centres represent medians, and minima and maxima represent 1.5 × interquartile range outside quartiles 1 and 3. n = 771 samples from 79 biologically independent animals. Only *Rusingoryx atopocranion* and one *Megalotragus* sp. are classified as migrants.

competitors for resources in eastern Africa. However, the spread of pastoralism into Kenya around 5 ka introduced domestic cattle, sheep and goats as a new guild of competitors[32,33]. Because spatiotemporal variation in domestic herbivore foraging is controlled by pastoralists, herd management strategies can concentrate livestock on different parts of the landscape (for example, in relation to pastoralist settlements) across the seasonal cycle[34]. This could translate to spatiotemporal variation in competition and resource availability, potentially setting the stage for migration among wild herbivores seeking to optimize foraging returns. However, this is just one of many possibilities, and both testing this hypothesis and identifying the origins of historical migratory systems will require analysis of younger fossil samples paired with additional palaeoecological and archaeological data.

Our analysis also allows us to ground truth Janzen et al.'s[18] Sr isoscape. At Rusinga, Kibogo and Lukenya Hill, the vast majority of measured $^{87}Sr/^{86}Sr$ values closely match those of the modelled isoscape, falling well within the range of local predicted values. Fossil values for most animals from Karungu are lower than those of the isoscape model by ~0.002, including for *Ourebia ourebi* and *Redunca arundinum*, the species most likely to be indicative of local conditions due to their characteristically small home ranges[25]. Some of this difference may be due to the resolution of the model, which was limited in the eastern Lake Victoria Basin. However, the differences may also be due to changes over the past 100 kyr. Though this is a relatively short time geologically speaking, this is a tectonically and volcanically active area, and some change is to be expected. Additionally, the refilling of Lake Victoria shortly after ~36 ka (ref. 35), which had been desiccated for much of the LGP, would have also impacted dust regimes, potentially altering the $^{87}Sr/^{86}Sr$ values measured around parts of the lake today.

Finally, these results have implications for human behaviour. Some models of early human mobility are based on modern analogues of migratory systems, but our data force a rethink of this; two of the four localities had no detectable migration during the LGP. In light of this, our interpretation of archaeological sites needs to be revisited. For example, Marean[3,29] argues that localities like Lukenya Hill were used by humans to intercept migratory game, particularly *Damaliscus hypsodon*, in the Late Pleistocene. Our results indicate that most *D. hypsodon* individuals at Lukenya Hill were non-migratory, and only one was a potential migrant. Such assumptions of migratory behaviour will require revisitation at other sites as well, including Nasera Rockshelter[36].

Though the information presented here has broad implications for herbivore behavioural dynamics in the LGP, it is just the start of applying serially sampled ^{87}Sr/^{86}Sr to the fossil record of eastern Africa. In particular, we encourage further research into grounding fossil patterns with modern migrants and non-migrants. Due to multiple factors, foremost among them that the historical migrations of the eastern Lake Victoria Basin no longer exist and those within the Athi-Kapiti Plains are considerably reduced in size, we have been unable to use modern comparatives. However, it would be possible to integrate modern and fossil data from sites within the GSE of Tanzania (for example, Nasera Rockshelter[36]), and we see this as a key potential avenue for future research.

We have characterized herbivore migration during the LGP in the largest analysis of serially sampled ^{87}Sr/^{86}Sr undertaken on African fossils, providing insight into the lives of prehistoric animals that would have been intractable just a few years ago. We analyse enamel ^{87}Sr/^{86}Sr from 18 bovid and equid species from Kenya and find unambiguous migratory signals in two extinct and no extant species. This suggests that the present-day migratory behaviours of *C. taurinus*, *Eu. thomsonii* and *Eq. quagga* were either spatially limited in the past or arose only recently. This changes our understanding of the ecology of these species and demonstrates that some of the migratory systems observed in eastern Africa today have geologically recent origins. This contributes to a growing body of evidence demonstrating that the structure and function of Pleistocene ecosystems differed considerably from those observed in present-day Africa[37].

Methods

Materials

Fossils from four localities in western and southern Kenya (Fig. 1) dating from ~100–12 ka were sampled (Table 1; see Supplementary Table 1 for details). The eastern Lake Victoria Basin of western Kenya, a region with a historical connection to the GSE[2], includes three sampling localities: Karungu, Rusinga and Kibogo. The Pleistocene archaeology, palaeontology and geology of these localities have been investigated by the Lake Victoria Prehistory Project since 2009, continuing to today. Rusinga is an island in Lake Victoria that was connected to the mainland during the LGP when Lake Victoria was desiccated[35], with Pleistocene exposures yielding abundant faunal remains alongside Middle Stone Age (MSA) artefacts. Specimens have been collected ~~v~~ ~100–36 ka (ref. 38). Karungu is a set of multiple MSA-bearing exposures correlated to those at Rusinga but lies on the Kenyan mainland, dating to 100–36 ka (ref. 27). The younger site of Kibogo is one of the few Pleistocene localities in the region that includes Later Stone Age (LSA) artefacts, and its sediments are constrained to between ~36 and 12 ka (ref. 39). Located in southern Kenya's Athi-Kapiti plains south-east of Nairobi, Lukenya Hill hosts a rich zooarchaeological record[40]. Among the many archaeological sites at Lukenya Hill, GvJm-22 has a large and well-dated faunal assemblage including both MSA and LSA artefact-bearing strata in three occurrences: E, dating to 52–12 ka, and F and G, dating to >52 ka (refs. 41–43). It was first excavated from 1970 to 1973 by Richard M. Gramly, and the faunal remains were evaluated by Marean[29]. All specimens sampled in this study were from the Gramly excavations.

The specimens from these four localities are curated in the Palaeontology and Archaeology Divisions of the Earth Sciences Department at the National Museums of Kenya in Nairobi, Kenya. For each species from each locality, second and third molars capturing the entire growth axis of the tooth without substantial cracks or other damage were selected for sampling. First molars were avoided as their mineralization typically occurs during gestation or while nursing, potentially altering geochemical signals[44]. Bovids and equids were targeted due to both their abundance and their diversity of roles in modern African migratory systems, including several likely non-migrant bovids providing local isotopic signals (for example, *Ourebia ourebi* and *Redunca* spp.[25]). Additionally, ungulate teeth are relatively slow-growing, with a single unworn molar representing 1–2 years of growth, though this varies by taxonomy and body size[45–49]. Each tooth was compared with modern and fossil specimens to confirm identification. Multiple specimens from different individuals of each species were sampled whenever possible from each of the four localities. In total, the 18 species chosen for analysis represent 93% of the number of identified ungulate specimens of the Lake Victoria Basin localities and 94% of those for GvJm-22. This robust coverage allows for migration to be compared between species and across space.

Analysis

To prepare specimens for processing, each molar was cleaned with acetone and cotton swabs. Next, the outermost enamel layer was removed using a handheld drill (1.2 mm diameter). Approximately 8 mg of enamel was then extracted with the drill as powder into a microcentrifuge tube. Sampling lines varied by specimen size but were typically ~5 mm long with a depth of ~1 mm. Drilling was repeated multiple times (3–18) for each molar in ~3–5 mm increments along the growth axis from apex to cervix, depending on crown height. Samples were then shipped to the University of Utah for processing. There, 2–5 mg were weighed for ^{87}Sr/^{86}Sr analysis, with the remainder reserved for future isotopic analyses.

Elemental ratios and ^{87}Sr/^{86}Sr isotope ratios were measured in the ICP-MS Strontium Laboratory in the University of Utah Department of Geology and Geophysics following the methods of Mackey and Fernandez[50] and O'Brien et al.[19]. Samples were digested in concentrated nitric acid, combined with indium, and diluted with 2.4% nitric acid. Elemental concentrations were then measured using an inductively coupled plasma mass spectrometer (ICP-MS) Agilent. Using calculated strontium concentration, dissolved enamel solutions were diluted to a minimum of 200 ppb Sr and purified using a PrepFAST automated inline purification system. Finally, samples were dried, dissolved in 2.4% nitric acid and run on a multicollector ICP-MS to measure ^{87}Sr/^{86}Sr isotope ratios.

^{87}Sr/^{86}Sr values were consistent through multiple runs of each specimen, with a mean standard deviation of 9.6×10^{-6} between runs (range 4.6×10^{-6}–2.0×10^{-5}). Ten serial samples belonging to specimen LVPP-KIB-18-305 were processed from start to finish twice to further test the analytic precision of the ICP-MS measurements, with results showing strong consistency: samples only differed by an average of 1.3×10^{-5} (Supplementary Fig. 59). Additionally, elemental ratios of 28 elements relative to calcium were compared to ^{87}Sr/^{86}Sr values from each locality to detect signs that diagenesis altered observed ^{87}Sr/^{86}Sr values. We find many examples of correlations between ^{87}Sr/^{86}Sr and elemental ratios, some of which are probably geographic in origin and others diagenetic. Select elemental ratios are shown in Supplementary Figs. 60–83, and all values are given in Supplementary Table 1. However, all correlations are weak. r^2 is <0.2 for all correlations and is >0.1 for only three: U/Ca is significantly correlated with ^{87}Sr/^{86}Sr at Lukenya Hill ($r^2 = 0.196$, $P < 0.0001$), Mn/Ca is significantly correlated with ^{87}Sr/^{86}Sr at Rusinga ($r^2 = 0.173$, $P < 0.0001$) and Fe/Ca is significantly correlated with ^{87}Sr/^{86}Sr at Kibogo ($r^2 = 0.103$ $P < 0.0001$). Regarding the former result, no specimens from Lukenya Hill are classified as migrants (see below), so this does not alter our conclusions. The latter two results are probably just artefacts of geographic differences in Mn and Fe concentrations correlating with the ^{87}Sr/^{86}Sr isoscape. All other results from elements indicative of diagenesis (for example, rare-earth elements) have weak correlations with ^{87}Sr/^{86}Sr. Thus, we find no reason to think that diagenesis would have altered our interpretations.

We note that there is not a 1:1 correspondence between where an animal is and the ^{87}Sr/^{86}Sr values recorded in its teeth. Therefore, we assume that detected strontium range is a fraction of the total range of the parts of the isoscape through which an animal migrated. Past studies indicate that ~50% of environmental ^{87}Sr/^{86}Sr variation is reflected in herbivore apatite ^{87}Sr/^{86}Sr due to delayed attenuation[10,23,24].

To compare movement across individuals, the standard deviations of intra-tooth ^{87}Sr/^{86}Sr values across each tooth were considered in comparison with those of the present, and almost certainly past, non-migrants *Ourebia ourebi* and *Redunca* spp., which have modern home ranges of <1 km (ref. 25). Due to different sampling effort across specimens, standard deviations from a subsampling method were used for classifying individuals as migrants or non-migrants rather than amplitude. In this procedure, five serial samples were selected at random for each tooth, and the standard deviation of $^{87}Sr/^{86}Sr$ values was calculated. This procedure was repeated 10,000 times per individual, so the range of standard deviations could be plotted. This provides a uniform standardization of all specimens, regardless of how many times they were actually sampled (as we expected a greater number of samples to lead to greater variance in $^{87}Sr/^{86}Sr$). If the 95% confidence interval of standard deviations was less than or overlapped with that of *O. ourebi* or *Redunca* spp., we conclude that that individual moved little during the period of tooth formation and can be classified as a non-migrant as long as its values are in the range of local variation. For Karungu and Rusinga, we also compared subsampled standard deviations with *Rusingoryx atopocranion*, an established migrant in O'Brien et al.[19]: if the 95% confidence interval was greater than or overlapped with the subsampled standard deviations of *Ru. atopocranion* from that locality and had values falling outside the local range of variation, we concluded that that individual was a migrant.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All raw data associated with this work are available in supplementary tables.

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Author contributions

K.O. and J.T.F. conceived the project. K.O., J.T.F., C.A.T. and T.E.C. provided funding. K.O., L.A., T.E.C., K.P. and D.P.F. conducted stable isotope analyses. K.O. wrote the paper. All authors provided paper feedback and gave final approval for paper publication.

Competing interests

The authors declare no competing interests.

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Study description	Stable isotope analysis of fossil herbivore teeth
Research sample	79 fossil herbivore teeth from the Last Glacial Period of Kenya. This is the largest possible dataset of teeth to be serially drilled for stable isotopes.
Sampling strategy	Maximum number of specimens per locality
Data collection	KO and LA collected all data at the National Museums of Kenya
Timing and spatial scale	Sampling took place in Summer of 2022.
Data exclusions	Species for which no high-quality second or third molars were present were excluded from the study.
Reproducibility	Replications were done for one Connochaetes taurinus tooth, and 87Sr/86Sr was accurate to the 6th decimal.
Randomization	Specimens were grouped by locality
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Specimen provenance

All specimens were collected in previous years. They are housed at the National Museums of Kenya and were accessed with permission through NACOSTI (license NACOSTI/P/22/17029)

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All specimens are accessible in the Palaeontology collections at the National Museums of Kenya

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