

Oscillating diachronic mobility patterns in prehistoric Eastern Sudan revealed by $^{87}\text{Sr}/^{86}\text{Sr}$ isotope analysis

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Title: Oscillating Diachronic Mobility Patterns in Prehistoric Eastern Sudan Revealed from $^{87}\text{Sr}/^{86}\text{Sr}$ Isotope Analysis

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Abstract

During the Holocene, Eastern Sudan functioned as a cultural and ecological crossroads throughout northeastern Africa. However, despite its significance, the region has remained largely unexplored in terms of human mobility studies through isotopic analyses. This research addresses this gap by analysing $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in human and faunal remains from three key archaeological sites – Upper Atbara 50 (UA50), Upper Atbara 53 (UA53), and Mahal Teglinos (K1). Spanning five cultural phases and over four millennia – UA50, Malawiya Group (second half of the 5th millennium BCE); UA53, Butana Group (late 4th millennium BCE); K1, Gash Group (early 3rd –early 2nd millennium BCE); Jebel Mokram Group (early 2nd millennium BCE–early 1st millennium CE); and Hagiz Group (first half of the 1st millennium CE) – these data offer novel insights into the diachronic patterns of mobility and interaction that shaped the Eastern Sudanese lowlands during the Mesolithic and the Neolithic. Results reveal a complex diachronic pattern of human mobility. High levels of individual mobility during the late Mesolithic likely reflect a nomadic lifestyle, which progressively shifted towards greater sedentism in the Neolithic, associated with the adoption of agriculture and animal husbandry, as well as the establishment of larger sites. In the 3rd and 2nd millennia BCE, the site K1 likely functioned as a key regional hub, facilitating interactions between different communities, as evidenced by the adoption of diverse funerary practices and the wide range of $^{87}\text{Sr}/^{86}\text{Sr}$ isotope

signatures among individuals identified as mobile. From the 2nd millennium BCE, harsher environmental conditions and shifts in socio-economic dynamics in northeastern Africa prompted a return to more nomadic pastoral lifeways. In Eastern Sudan, proximity to the Ethio-Eritrean highlands may have mitigated the effects of aridification, making this region a potential shelter region that attracted groups from the Eastern Desert, where environmental stress was likely more severe or occurred earlier.

This study establishes a preliminary isotopic baseline for Eastern Sudan and provides new insights into long-term patterns of mobility and interaction. It complements existing archaeological data and offers a robust framework for future multidisciplinary investigations into exchange networks and cultural resilience in this pivotal region of northeastern Africa.

Introduction

Isotope studies on humans and fauna in northeastern Africa have thus far focused predominantly on the Nile Valley, with particular attention to the Egyptian Nile delta [1,2], the area around the First Cataract in Egypt [3-5], and regions spanning the Second to the Sixth Cataracts in Sudan [5-23]. Collectively, these studies span a broad chronological range, from the Old Kingdom (ca. 2613–2494 BCE) to the Christian era (2nd millennium BCE). In addition, significant isotopic research has also been conducted at archaeological sites beyond the Nile corridor in Central Sudan, including Jebel Moya, dating to the 3rd millennium BCE [24], and the multi-period cemetery at al-Khiday, spanning from the Late Pleistocene to the 2nd century CE [25,26].

Nevertheless, the application of isotopic methods in the region remains limited compared to their potential, with the consequence that individuals exhibiting ‘non-local’ isotopic signatures frequently remain of uncertain origin due to the scarcity of comparative baseline data [19]. This limitation becomes even more evident when moving away from the Nile Valley into the surrounding desert landscapes, where isotopic reference profiles are particularly lacking.

Eastern Sudan, despite its long-recognised importance as a cultural and ecological crossroads throughout the Holocene, remains unexplored in isotopic research. This lack of data constrains our ability to understand long-term patterns of mobility, interaction, and adaptation in this important region. Current interpretations of these dynamics are grounded in a robust archaeological framework, developed through decades of excavations in the area between the Gash and Atbara rivers [27,28], and further supported by palaeoenvironmental reconstructions [29-31] and bioarchaeological analyses [32]. These studies have provided valuable insights into how local communities adapted to ecological variability across millennia. In particular, changes in funerary practices have proved

especially informative, reflecting the dynamic interplay between environmental change, social transformation, and cultural identity in the region [27,33-35].

Since the earliest archaeological investigations, Eastern Sudan has been recognised as a key crossroads facilitating long-distance connectivity across northeastern Africa during the Holocene. The first archaeological excavations conducted by the Italian Archaeological Mission to the Sudan (Kassala) (IAMSK) in the 1980s and 1990s focused on investigating ancient connections between the Nile Valley and the Ethio-Eritrean highlands [27,36]. More recently, the Italian Archaeological Expedition to Eastern Sudan (IAEES) has broadened its focus, aiming to reconstruct the environmental history of Eastern Sudan and explore its interactions with the Nile Valley, the Eastern Desert, the Red Sea coast, and the Ethio-Eritrean highlands.

Archaeological evidence has enabled the reconstruction of a remarkably long and continuous cultural sequence in Eastern Sudan, spanning from the 6th millennium BCE to the 2nd millennium CE, thereby offering a regional framework for interpreting cultural transformations across millennia [27,28,33,35,37]. Within this long-term trajectory, several key developments emerge: the beginning of the regional Atbai Ceramic Tradition from the 6000 BCE [27]; the presence of domestic livestock and cultivated plants in the region as early as the 4th millennium BCE; the emergence of hierarchical societies at least from the early 3rd millennium BCE; and a gradual shift toward pastoralism from the 2nd millennium BCE onwards [27,33-41]. Moreover, from the late 3rd and throughout the 2nd millennium BCE, Eastern Sudan was part of an extensive network of connections stretching from Egypt to the Ethio-Eritrean and Yemeni highlands [27,28,35]. The pivotal role of Eastern Sudan in the Neolithisation of the Ethio-Eritrean highlands is well recognized—among other aspects—as is its significance in the transmission of Sahelian crops from Africa to India via the Indian Ocean [27]. Its strategic position has led some scholars to identify the region as part of the legendary land of Punt, mentioned in Egyptian sources as a supplier of luxury goods such as aromatic resins, ebony, ivory, obsidian, animal skins, and precious metals [27,33-35,37,42].

This study presents the first comprehensive dataset of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios from human and faunal remains in Eastern Sudan, addressing a major gap in the regional isotopic record. By integrating these data with the archaeological and palaeoenvironmental framework of the Gash delta/Kassala region, the study aims to provide insights into patterns of human mobility over millennia. Our goals are to: (a) establish local strontium isotopic baselines for the reference areas; (b) assess intra-population variability and identify non-local individuals; and (c) evaluate mobility patterns in relation to changes in subsistence, social organization, and interaction spheres across Eastern Sudan.

These objectives are framed by current archaeological evidence suggesting that Malawiyya hunter-gatherers and Jebel Mokram mostly pastoral communities were highly mobile with broad resource networks, likely resulting in wide isotopic variability. In contrast, Gash Group agropastoral communities, also characterised by emerging socio-economic complexity, may have been more residential, while maintaining long-distance contacts. By linking isotopic data to these cultural trajectories, the study provides new insights into cultural connectivity and adaptive strategies in northeastern Africa throughout the Holocene.

Diachronic funerary evidence from Eastern Sudan

The fertile region between the Gash and Atbara rivers in Eastern Sudan is particularly informative from a historical and archaeological perspective, as its abundant water and soil resources – including alluvial plains, seasonal streams, and extensive grazing areas – created favourable conditions for the establishment and long-term occupation of complex settlements over time [27]. Within this area, the sites Upper Atbara 50 (UA50), Upper Atbara 53 (UA53), and Mahal Teglinos (K1) have yielded significant archaeological evidence, including both settlements and funerary contexts that span nearly four millennia – from the 5th millennium BCE to the 1st millennium CE – and encompass major cultural phases in the region (Figure 1). The archaeological and funerary evidence from these sites has been attributed to distinct cultural phases, based on diagnostic ceramic, lithic and material culture assemblages, burial features, as well as radiometric and stratigraphic evidence that anchors each phase within a well-established regional chronological framework (see Supplementary Information).

The earliest funerary evidence documented to date in the region, dated to the second half of the 5th millennium BCE, is represented by burials from site UA50, associated with the Malawiya Group, which practiced a hunter-gathering Mesolithic adaptive strategy. The following Neolithic sequence is defined by distinct groups across different sites: the earliest evidence, dated to the final centuries of the 4th millennium BCE, includes the graves of the Late Butana Group documented at site UA53; these are followed by the graves documented at site K1, including those dating to the early 3rd to early 2nd millennium BCE, attributed to the Gash Group phase (sectors XII–XIII), and those dated from the early 2nd millennium BCE to the early 1st millennium CE (sector XIV), attributed to the Jebel Mokram Group. The most recent funerary evidence from the area consists of a tumulus uncovered at K1 (sector XIV), which can likely be dated to the first half of the 1st millennium CE and attributed to the Hagiz Group or the Post-Meroitic culture [27,33,35,37]. Detailed contextual and chronological information for each site is provided in the Supplementary Information.

The human dental collections from the graveyards UA50, UA53, and K1 offer a unique opportunity to investigate human mobility and cultural interactions in Eastern Sudan diachronically, spanning five

cultural phases and more than four millennia. By integrating isotopic and archaeological evidence, and carefully acknowledging the limitations of the sample for broad population-level interpretations, this research examines individual patterns of early-life residence and mobility over time.

Results

⁸⁷Sr/⁸⁶Sr values from Eastern Sudan

The ⁸⁷Sr/⁸⁶Sr values of the 76 human samples from Eastern Sudan range from 0.70633 to 0.70709 (mean = 0.70679 ± 0.00015). Figure 2 presents a density plot of all human values, grouped by chronology and site, illustrating a distribution that varies across both time and space.

Overall, these values are consistent with the expected bioavailable Sr pool of Eastern Sudan. The region is geomorphologically dominated by sediments and waters from the tributaries of the Nile basin, exhibiting ⁸⁷Sr/⁸⁶Sr values between ~0.705 and 0.709. This range reflects mixing between two main end-members: a) low-radiogenic sediments derived from the Ethiopian Highlands, characterized by Cenozoic volcanic terrains (~0.705), and b) more radiogenic inputs from wadi sediments and desert dust (>0.709) produced through the weathering of the Sudanese Precambrian crystalline basement [16,43,44].

The Sudanese basement forms part of the Arabian-Nubian Shield, a vast Neoproterozoic orogenic province that extends from Arabia across the Red Sea into northeast Africa. Within Sudan, this basement consists of a heterogeneous assemblage of Precambrian ancient igneous and metamorphic terranes of various geochemical affinity, many of which were extensively reworked during the Pan-African orogeny (around 900-500 Ma) [43,44]. Regional geological syntheses indicate that much of northern Sudan is covered by continental clastic deposits of the Mesozoic Nubian Sandstone, representing major continental fluvial, deltaic, and marginal marine depositional cycles driven by sea-level changes and tectonic activity. In contrast, southern and central regions are dominated by Tertiary-Quaternary unconsolidated sediments. Cenozoic and younger basalts occur along the border with Ethiopia, forming part of the broader volcanic province that contributes significantly to the Sr isotope composition of the Nile and Atbara systems [16,30,43,44].

The Quaternary sediments of the study area, influenced by the Atbara and Gash rivers, are fed by intricate systems of seasonal braided streams originating from the Ethio-Eritrean highlands [30]. These riverine systems not only transport fine alluvial sediments but also play a pivotal role in the deposition of various mineral resources, including gold, agate, chalcedony, and carnelian, which naturally occur within the Atbara gravels and were historically exploited in the region [27].

Within this geological and geomorphological context, the defined local ranges for sites UA50 and UA53 (0.70682–0.70701) and site K1 (0.70666–0.70692), derived from subadult human values, align closely with the expected isotopic signatures from adjacent fluvial sediment and Nubian Sandstone exposures. While comparable values might be found elsewhere in Eastern Sudan, these site-specific ranges are strongly tied to the immediate landscapes of each site, thus providing a reliable baseline for distinguishing local from non-local/possibly non-local individuals.

Furthermore, the close agreement between subadult human and faunal values at K1 (0.70664–0.70688) strengthens the validity of using subadults as proxies for the local baseline (see below). Although the possibility of diagenetic alteration in faunal bones cannot be entirely excluded, the close overlap between faunal and subadults strongly suggests that the defined subadult range accurately reflects the local bioavailable strontium pool.

⁸⁷Sr/⁸⁶Sr values from the UA50 and UA53 graveyards

No traditional isotopic baseline data were available for the UA50 and UA53 area due to the absence of faunal remains and the impossibility of implementing a bottom-up sampling strategy on site, given the ongoing political situation in Sudan.

The ⁸⁷Sr/⁸⁶Sr human values from graveyards UA50 and UA53 span from 0.70633 to 0.70708 (mean = 0.70689 ± 0.00019; n = 18) (Supplementary Table S4). Descriptive statistics are provided in Supplementary Table S5. Tukey's interquartile range [or Tukey's fences [Q1 – k(Q3–Q1), Q3 + k(Q3–Q1)], with k = 1.5; 45] spans from 0.70649 to 0.70731, with a single individual being identified as an outlier (Supplementary Figure S2).

The Q-Q normal plot (Supplemental Figure S3) suggests that three values deviate from the theoretically expected normal distribution. All subadults fall inside the normal distribution, indicating that this segment of the sample could serve as a proxy for the local ⁸⁷Sr/⁸⁶Sr range. By calculating Tukey's fences only on subadults' values (⁸⁷Sr/⁸⁶Sr values ranging from 0.70686 to 0.70697; mean = 0.70692 ± 0.000043; n = 5; Supplemental Table S4), it is possible to redefine the local range to 0.70682–0.70701 and identify a higher number of outliers (9), which represent 50% of the sample (Figure 3). Considering the limited number of subadults available for UA50 and UA53 (n = 5), for this area, the local ⁸⁷Sr/⁸⁶Sr baseline is treated as a conservative, internally defined reference range rather than a definitive estimate of local bioavailable strontium.

⁸⁷Sr/⁸⁶Sr values from graveyard K1

The ⁸⁷Sr/⁸⁶Sr human values from graveyard K1 span from 0.70639 to 0.70709 mean = 0.70677 ± 0.00015; n = 58) (Supplementary Table S4). Descriptive statistics are provided in Supplementary

Table S5. Tukey's interquartile range spans from 0.70656 to 0.70699, with 6 individuals being identified as outliers (Supplementary Figure S4).

The Q-Q normal plot (Supplemental Figure S5) reveals that ten values deviate markedly from the theoretically expected normal distribution. Notably, all these values represent adults, whereas subadults fall inside the normal distribution. Also in this context, this pattern supports the use of subadults' isotope values as a proxy for the local $^{87}\text{Sr}/^{86}\text{Sr}$ baseline. By calculating Tukey's fences based solely on subadults' values ($^{87}\text{Sr}/^{86}\text{Sr}$ values ranging from 0.70672 to 0.70687; mean = 0.70679 ± 0.000047 ; $n = 13$; Supplementary Table S4), it was possible to redefine the local range to 0.70666–0.70692 and identify a higher number of outliers (12) (Figure 4). It is important to note that the only subadult in the sample younger than three years of age (T.48, aged approximately 2.5 years old) – the threshold adopted for an extended breastfeeding period – exhibits an $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.70682, which falls fully within the observed subadults' range.

In addition, the presence of faunal remains at graveyard K1 supports the identification of the subadults' range as a valid local baseline interval. Indeed, Tukey's fences calculated on the faunal values ($^{87}\text{Sr}/^{86}\text{Sr}$ values ranging from 0.70664 to 0.70688; mean = 0.70674 ± 0.000047 ; $n = 13$; Supplementary Table S6) closely overlap with the human subadults' interval (Figure 4). Although diagenetic alteration may affect faunal bones, the resulting $^{87}\text{Sr}/^{86}\text{Sr}$ values likely incorporate the local diagenetic end-member, which can provide an informative proxy for the local bioavailable strontium baseline and complement the subadult human values. However, subadult and faunal values were not combined into a single range, as human and faunal mobility may reflect different ecological or management factors and should therefore be treated separately. Descriptive statistics for the faunal sample are provided in Supplementary Table S7.

Sex-specific trends in human mobility

For the second half of the 5th millennium BCE (graveyard UA50, Malawiya Group), data indicate a generally high level of individual mobility, with 83.3% of the adults (5/6) being identified as non-local/possibly non-local. This group includes the two adult males in the sample as well as three of the four females (Figure 5). Due to the limited number of individuals, it was not possible to perform statistical comparisons between sexes.

For the following phase, dated to the late 4th millennium BCE (graveyard UA53, Butana Group), the proportion of non-local/possibly non-local adults decreases to 57.1% (4/7). Mobility patterns continued to involve both sexes: 66.7% of females (2/3) and 50% of males (2/4) were identified as non-local/possibly non-local (Figure 5). However, given the small sample size, statistical comparisons between male and female mobility could not be conducted.

A notable shift emerges in the early 3rd-early 2nd millennium BCE, when overall mobility declines significantly. At the K1 graveyard during the Gash Group phase (K1 XII–XIII), only 17.9% of adults were identified as non-local or possibly non-local (7/39), comprising 9.7% of females (2/21) and 27.8% of males (5/18) (Figure 6). Although these figures suggest a potential trend toward male-dominated mobility, Fisher's exact test indicates no statistically significant difference between the sexes ($p = 0.21$).

This pattern shifts again from the early 2nd-early 1st millennium BCE, with a renewed increase in mobility during the Jebel Mokram Group phase. At graveyard K1 (K1 XIV), 80.0% of adults (4/5) were identified as non-local/possibly non-local. Notably, all females and one of the two males in the sample display non-local $^{87}\text{Sr}/^{86}\text{Sr}$ values (Figure 6). The limited number of individuals in this phase prevented statistical tests to compare mobility patterns between sexes.

Isotope analysis on human remains from the 1st millennium CE tumulus at graveyard K1, sector KIV, further supports evidence of mobility in later phases, during the Hagiz Group or Post-Meroitic phase. The adult female (Individual 1) exhibited non-local $^{87}\text{Sr}/^{86}\text{Sr}$ values, whereas the subadult (Individual 2) showed local signatures (Figure 6).

Discussion

Mobility trends and environmental adaptation in Prehistoric Eastern Sudan

Despite relatively small sample sizes for most of the chronological phases – a limitation that warrants caution in drawing broad demographic or behavioural inferences – the overall findings reveal a dynamic and multifaceted pattern of human mobility in Eastern Sudan over the millennia. Density plots of $^{87}\text{Sr}/^{86}\text{Sr}$ values clearly illustrate this diachronic variation (Figure 2). The 5th millennium BCE Mesolithic Malawiya Group hunter-gatherers and the early 2nd- to early 1st millennium BCE Jebel Mokram Group nomadic pastoralists exhibit broad, low curves spanning a wide range of strontium ratios, indicative of considerable variability in geographical origins and, by extension, potentially high levels of mobility. In contrast, Butana and Gash Group agropastoral groups show narrower distributions, reflecting a more homogeneous isotopic signal consistent with largely local populations. Nonetheless, the bimodal distribution in the late 4th millennium BCE dataset (Butana Group) and the multimodal distribution in the early 3rd-early 2nd millennium BCE dataset (Gash Group) suggest the presence of non-local/possibly non-local individuals, although the overall restricted ranges indicate a greater degree of sedentism during these central phases.

These patterns reflect shifting strategies over time: from greater movement in the earliest and latest periods to a trend toward residential stability during the intermediate phases. Statistical analysis supports this diachronic trend, with the proportion of mobile adults varying significantly across the

chronological sequence (Fisher's exact test, $p = 0.0002$). Sex-related factors may have influenced mobility, but robust comparisons were only feasible for the early 3rd-early 2nd millennium BCE phase (graveyard K1, sectors XII-XIII), where no differences between males and females were observed. Limited sample sizes precluded meaningful assessment in other phases.

These mobility trends, consistent with settlement patterns, were strongly influenced by Holocene environmental changes in Eastern Sudan. A synthesis of environmental conditions, settlement patterns, economic traits, and isotope-based evidence of mobility across the chronological phases under consideration is presented in Figure 7.

During the early to mid-Holocene African Humid Period (AHP, 14,800 – 5,500 BP), increased precipitation sustained extensive riverine and lacustrine systems, facilitating mobility across formerly desert landscapes via favourable ecological patches [31,46,47]. Evidence from UA50 and UA53 indicates that the mid-Holocene arid oscillations, well documented in the Nile Valley, were less pronounced in this region. Instead, relatively humid conditions appear to have persisted locally for a longer duration within a highly seasonal climatic regime, potentially enabling the area to function as a regional refuge during phases of broader climatic deterioration [27]. These conditions likely favoured the adoption of nomadic or semi-nomadic lifeways and interregional mobility in Eastern Sudan [30,31,47], consistent with high mobility observed at graveyard UA50 (Figures 2 and 3). Accordingly, Malawiya Group sites – small in size and characterized by shallow stratigraphy – were predominantly located in steppe environments far from the Atbara River and absent from the Gash delta, reflecting a strategy focused on exploiting locally available plant and animal resources across the humid plain [27].

Drier conditions in the region appear to have become pronounced later, from the 3rd millennium BCE onwards, partially mitigating the broader trend toward increasing aridity [27]. During this period, aridification caused the desiccation of several Nile tributaries and reduced water availability across the region [31,47]. These environmental changes prompted the concentration of settlements between the Gash and Atbara rivers and in the Gash delta, where the perennial flow of the rivers provided a relatively stable and resource-rich environment. Communities combined fishing, foraging, and early cultivation, while progressively integrating agropastoralism and adopting more sedentary lifeways [47]. Strontium isotope-based mobility trends from graveyards UA53 and K1 XII–XIII align with this shift toward more stable, sedentary settlement patterns and perhaps decreasing mobility (Figures 2-4).

The contrast between the Nile's stability and the surrounding more arid zones reinforced demographic clustering, promoting population growth and social complexity, culminating in the rise of organized

polities such as the Nubian Kingdom of Kerma [47]. In the Kassala region, a parallel process led to the rise of the Gash Group, characterized by increasing social complexity and apparently large populations, despite progressively harsher environmental conditions [27,30]. In this period, site K1 expanded to approximately 10 hectares, becoming one of the largest known sites in Eastern Sudan [28]. Correspondingly, reduced mobility at early (graveyard UA53) and full Neolithic (graveyard K1, sectors XII–XIII) phases is reflected in the predominance of local individuals (Figures 3 and 4). Nevertheless, evidence of interregional exchange – such as Red Sea shells in Late Butana Group graves at UA53 and exotic stone mace heads often crafted of exotic stones, potentially sourced from the Red Sea hills [36,48] indicates continued long-distance interactions by the end of the 4th millennium BCE [27,28].

From the 2nd millennium BCE onwards, persistent arid conditions drove renewed mobility and seasonal dispersal. Although brief humid episodes occurred [47,49,50], the period was characterized by “hyperseasonality”, with alternating dry spells and extreme flash floods generating unpredictable and often destructive conditions, unfavourable for long-term niche construction [31].

In this period, Eastern Sudan experienced profound socio-cultural changes that reshaped settlement organization, material culture, and funerary practices, marking the transition from the Gash Group to the Jebel Mokram Group [33,34,37]. Compared with Gash Group sites, Jebel Mokram settlements are generally smaller and exhibit limited stratigraphic depth, features commonly interpreted as indicative of seasonal or temporary occupation [27,34,48]. This shift was accompanied by a relocation of settlements from fertile, agriculturally suitable areas typical of the Gash Group to more marginal zones better suited for grazing [27,33,34,37,48]. Pastoralism – particularly cattle and caprine herding – emerged as the dominant adaptive strategy, as evidenced by faunal assemblages at K1 [27,51]. As a result, the Jebel Mokram Group phase is widely regarded as a key turning point in the emergence of nomadic pastoralism in Eastern Sudan [33,34,37,52]. The reorganisation of settlement patterns and subsistence strategies suggests a return to semi-nomadic lifeways, a hypothesis further supported by changes in ceramic morphology, which may have enhanced portability [34]. Although limited, strontium isotope data from this phase (K1 XIV) further support this pattern of renewed mobility (Figures 2 and 4).

Mobility, funerary practices, and social dynamics during the Gash Group

Between the mid-3rd and early 2nd millennium BCE, Eastern Sudan functioned as a pivotal crossroads connecting regions extending from Egypt to the Yemeni and the Ethio-Eritrean highlands [27,34,35]. Archaeological evidence from site K1 supports the existence of such widespread interactions during

the Gash Group: exotic goods, including imported ceramics and personal ornaments, attest to sustained contacts, particularly with the Egyptian world and the Kerma culture [35].

Within this context, despite their limited proportion, the presence of non-local/possibly non-local individuals at site K1 XII-XIII should be understood in relation to the strategic role of Eastern Sudan in northeastern Africa during this period. Notably, $^{87}\text{Sr}/^{86}\text{Sr}$ isotope analysis identified as non-local/possibly non-local some of the individuals who were not buried according to the dominant supine position, characteristic of the sector of the western Gash Group cemetery where the studied samples were collected [27,34,53].

Statistical analysis using Fisher's exact test reveals a significant association between non-local origin and deviant funerary positions ($p = 0.0016$). Specifically, among 18 burials in which deviant body positions were recorded, 6 individuals were identified as non-local/possibly non-local. In contrast, only three non-local individuals were identified among the 73 burials that adopted the dominant supine position (e.g., Grave 30, Grave 84, Grave 101). This significant correlation suggests that individuals of non-local origin were more likely to receive funerary treatments diverging from the normative supine position, characteristic of the Gash Group in this sector of the western cemetery at K1, potentially reflecting distinct social identities or cultural practices linked to their origins [35]. It is noteworthy that no spatial clustering was observed between individuals identified as non-local and those exhibiting non-normative mortuary treatment. Rather, these individuals were interspersed throughout the broader burial population, suggesting their integration within the community's funerary landscape.

The adult males from Grave 6 and Grave 117 were placed in a contracted position on their right side, while the adult male from Grave 59 was buried in an extended position on his left side. Additional non-local/possible non-local adults were found in two double graves (i.e., Grave 78 and Grave 101). Notably, Grave 78 contained a non-local male (Individual 1) and a local female (Individual 2), buried together with their legs contracted, facing each other, and their heads close (Figure 8). The left arm of the male encircled the woman – a posture suggesting a close personal bond between the two individuals [53]. In Grave 101, the remains of a non-local female (Individual 1) were recovered alongside an adult whose skeletal preservation was insufficient to allow for a reliable sex assessment (Individual 2). The absence of preserved dental remains precluded isotope and proteomic analyses for this individual. Both individuals were closely associated in the burial, but the available evidence does not allow for any further interpretation regarding their relationship.

The evidence from Grave 78 – and possibly from Grave 101 – may reflect broader social dynamics, such as patterns of individual mobility linked to marriage alliances, seasonal movements, or other

forms of socially embedded migration. Instances of intermarriage between individuals originating from different groups could have served as mechanisms for alliance-building, the reinforcement of exchange networks, and/or the avoidance of inbreeding. Furthermore, the presence of both male and female mobile individuals indicates that mobility was not confined to a single sex, but involved a variety of strategies, highlighting the complexity of social dynamics in the early 3rd–early 2nd millennium BCE Eastern Sudan.

The multimodal distribution of human $^{87}\text{Sr}/^{86}\text{Sr}$ values observed among individuals in the Gash Group sample (Figures 2 and 4) provides evidence in favour of the interpretation of Manzo (2020), suggesting that, between the mid-3rd and early 2nd millennium BCE, site K1 likely functioned as a central hub, a gathering place facilitating interactions among diverse communities [35]. In this light, the presence of non-local/possibly non-local individuals buried in graves with atypical body positions could suggest that the variation observed in funerary practices was shaped, at least in part, by the expression of different social or cultural identities.

Excavations in the central sector of site K1, right in between the eastern and western cemeteries, have revealed an area characterised by a high concentration of fire pits and pits containing local and imported pottery, animal bones, and archaeobotanical remains – evidence consistent with ritualised feasting activities [35,54]. Particularly notable is the presence of large, locally made ceramic trays – reminiscent of modern griddles used in Sudan, Ethiopia, and Eritrea to bake flat, fermented bread [55] – alongside Egyptian Marl A3 jars, which are typically associated with long-term storage [56]. These finds have led to the hypothesis that imported foodstuffs may have been consumed alongside local dishes at K1, in a context of intercultural commensality [54]. The discovery of administrative devices – sealings and possible tokens – in the same area suggests that such events were not only ceremonial but also tied to the site's administrative functions, potentially reinforcing social cohesion through shared practices [54].

How the complex interactions among different groups documented in the archaeological record are reflected in the funerary context remains difficult to determine. Despite the archaeological evidence pointing to intense intercultural contact at site K1, the relatively narrow range of $^{87}\text{Sr}/^{86}\text{Sr}$ values (Figures 4 and 6) suggests that the western cemetery was primarily used by the local group(s) from the region during the Gash Group period. This apparent discrepancy raises important questions about the relationship between the society of the living and the community of the dead.

One possible interpretation is that foreigners who participated in ritual or economic activities at K1 did not necessarily settle there or were not buried within the western cemetery sector where the studied samples were collected. Alternatively, albeit with a few documented exceptions, burial within

the cemetery may have been largely restricted to individuals belonging to the local regional communities. In this sense, the funerary sphere might reflect a more bounded or ideologically constructed conception of social group(s), one that does not necessarily correspond to the broader interregional networks of interaction evident in the wider archaeological record.

This discrepancy underscores the need to consider funerary contexts not simply as passive reflections of social reality but as socially and culturally constructed spaces, shaped by specific logics that do not always mirror the complexity of lived experience [57,58].

Socio-cultural transformations in Eastern Sudan during the 2nd millennium BCE

From around 1800 BCE, the cultural shift from the Gash Group to the Jebel Mokram tradition in Eastern Sudan has often been interpreted as the result of interactions between the region and neighbouring regions, particularly the Eastern Desert and the Nile Valley [52,59]. In particular, based on shared features in material culture and burial practices, the Jebel Mokram Group tradition has been linked to the Pan-Grave horizon – typical of nomadic groups likely originating in the Eastern Desert and present in the Nile Valley between 1800 and 1500 BCE [33,34,37,52,60-63].

The concurrent emergence of Pan-Grave features in Eastern Sudan, Egypt, and Lower Nubia points to a shared catalyst for the spread of nomadic groups across these regions, likely related to increasing aridity documented in northeastern Africa since the 3rd millennium BCE [47]. The Semna dispatches from the reign of Amenemhat III (ca. 1831–1786 BCE) further contextualise these changes, reporting drought and famine in the Eastern Desert [64,65].

Such environmental pressures likely contributed to growing mobility during this period. Genetic studies on modern populations [66-69] and biodistance analyses [70-74] suggest sustained, bidirectional gene flow between Egypt and Nubia from the 2nd millennium BCE onward. These biological connections are further supported by linguistic evidence indicating a high degree of ethno-linguistic diversity in ancient Nubia and Sudan, shaped by the movement of nomadic pastoralists and broader population dynamics [75].

Recent geoarchaeological studies revealed that, despite certain regional variations, environmental stressors also affected Eastern Sudan during the early 2nd millennium BCE [29-31]. The disappearance of larger mammal species in favour of savannah-adapted fauna, such as various gazelle species, provides an ecological marker of these changes [28]. In addition, bioarchaeological data, including dental calculus analysis, suggest increasing dietary diversity and adaptive subsistence strategies, reflecting resilient responses to both environmental and socio-economic pressures of this period [32].

However, the shift toward arid conditions in northeastern Africa was marked by substantial regional and local variability [47]. In the case of Eastern Sudan, the proximity to the Ethio-Eritrean highlands may have still mitigated the advance of aridification, allowing relatively humid conditions to persist longer than in neighbouring regions. These more favourable ecological conditions may have transformed Eastern Sudan into a refuge zone, attracting groups from the Eastern Desert that were more severely or precociously affected by environmental stress [28,34]. This scenario is supported by isotope analyses, which reveal high levels of mobility during the Mokram Group period, with 80% of non-local/possibly non-local adults being identified within the sample from graveyard K1 (sector XIV) (Figures 2 and 4).

Archaeological evidence from site K1 documents the transition from the Gash Group to the Jebel Mokram Group phase around 1800 BCE [33,34,37]. From a funerary perspective, contracted inhumations became dominant, replacing the greater variability of body positions documented in earlier phases. At the same time, stelae were supplanted by stone circles, which likely served as markers for tumuli [27,34]. A distinctive feature of Jebel Mokram Group graves is the placement of a stone beneath the head of the deceased [53].

At K1, the ceramic assemblage associated with the Jebel Mokram Group reflects a synthesis of long-standing local traditions, innovative local practices, and external influences from the Pan-Grave horizon [33,34,37]. This led to the suggestion that the Jebel Mokram Group likely represented the southernmost node of wider socio-cultural networks extending from Lower Nubia to Egypt, and possibly including regions of the Eastern Desert. These networks likely developed in response to broader dynamics – particularly the above-mentioned environmental changes – that influenced both short-term seasonal mobility and favoured the long-term displacement of human groups across the region [33,34,37].

From an archaeological perspective, the spread of exotic ceramic traits in the 2nd millennium BCE ceramic production of the Eritrean-Sudanese lowlands has been interpreted as the result of the movement and/or exchange of women between groups. This hypothesis is based on the idea that women – often responsible for pottery production in many African societies – may have brought with them specific stylistic or technological traditions when they joined new communities through marriage or other forms of social integration [34,76].

The presence of such vessels at site K1 – particularly bowls and cups associated with food consumption – may further support this interpretation [34]. If, as ethnographic parallels from various African regions suggest, pottery production was predominantly a female activity, embedded in domestic and gendered spheres of knowledge transmission, then the spread of these ceramics may

reflect the movement of women, potentially in the context of exogamous marriage practices [34,76,77]. Ethnographical studies on pottery-making in Niger, Sudan, Burkina Faso, Ivory Coast, Nigeria, Ghana, Cameroon, Rwanda, Malawi, and South Africa consistently document the central role of women in pottery-making, typically carried out within female-controlled domestic spaces [78-81]. Despite the limited size of the Jebel Mokram Group sample, isotope data appear to support this scenario, with all adult females from this phase exhibiting non-local strontium signatures (Figure 6). This finding gains further significance when considered in contrast to the preceding Gash Group phase, during which only a small proportion of females exhibited non-local $^{87}\text{Sr}/^{86}\text{Sr}$ signatures (2/21; 9.5%) (Figure 6). Although the small sample size precludes statistically robust comparisons between sexes, the data may indicate shifting social dynamics, possibly associated with the growing adoption of exogamous marriage practices and increased female mobility within wider networks of interaction and exchange. Such practices are also well documented in Neolithic Europe, where they were typically embedded within broadly patrilocal kinship systems [82-85].

Some scholars suggest that mobile extended kin groups from different areas – including the Pan-Grave communities, inhabitants of the Red Sea Hills, the Gash delta, and the Nile Valley – likely gathered at strategic locations across the landscape to facilitate both the exchange of goods and the formation/establishment of marital alliances [16]. The growing influence of the Upper Nubian Nile Valley, particularly that of the Kerma culture, further underscores the complexity of the socio-economic networks operating during this period [35,86].

At the site of Tombos, in the area of the Third Cataract, the architectural features, mortuary practices, biodistance analysis, and $^{87}\text{Sr}/^{86}\text{Sr}$ isotope analysis revealed a mixed ethnic identity among the population, which was composed of local Nubians, Egyptian immigrants, and individuals of mixed ancestry [8,10,70,87]. The coexistence of different burial traditions among both male and female individuals has been interpreted as indicative of intermarriage between Nubians and Egyptians [8,70,87].

Further insight into female mobility in the latest phase covered by this study is offered by the 1st millennium CE tumulus from K1, sector XIV [53]. The adult female buried here (Individual 1) exhibits non-local $^{87}\text{Sr}/^{86}\text{Sr}$ values, while the child buried with her shows local signatures (Individual 2). Although the absence of aDNA data limits certainty, isotope evidence, together with the fact that the two individuals were buried together, suggests a possible relationship between them.

While based on a single case, this finding highlights the broader pattern of female mobility and suggests that such movements may have played a role in shaping community composition and facilitating interregional connections, even in later periods.

Conclusions

This study represents the first strontium isotope-based investigation of human mobility in Eastern Sudan, a region largely overlooked in isotopic research despite its central role as a cultural and ecological crossroads in northeastern Africa throughout the Holocene. By analysing $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in human and faunal remains from three key graveyards (UA50, UA53, and K1), spanning five cultural phases from the 5th millennium BCE to the 1st millennium CE, this research offers new elements that may help improve our understanding of the long-term dynamics of mobility and interaction across the Eastern Sudanese lowlands.

A clear diachronic trend emerges in the proportion of mobile individuals, likely reflecting shifts in mobility strategies and socio-political integration. When considering the mobility patterns revealed by this study in the context of environmental changes, it becomes evident that the climatic trajectory in Eastern Sudan – and in the broader Nile Valley – played a profound role in shaping human mobility and settlement strategies throughout prehistory.

(a) Humid conditions during the 5th millennium BCE sustained lacustrine and riverine systems, creating a resource-rich environment that facilitated seasonal movements and flexible subsistence strategies. High levels of individual mobility during this period likely reflect a nomadic lifestyle, characterised by frequent movements across the landscape and the use of temporary settlements in the plains between the Gash and Atbara rivers.

(b) From the late 4th millennium BCE, the Neolithic transition is marked by a gradual decline in mobility, consistent with the rise of agriculture and animal husbandry. This shift is also reflected in the emergence of more permanent settlements and increasing social differentiation, as evidenced by changes in material culture and funerary practices. Within this context, site K1 stands out as a key landmark in Eastern Sudan, gaining strategic importance between the 3rd and 2nd millennia BCE as a node at the intersection of local and long-distance interaction networks. At K1, the burial of non-local/possibly non-local individuals in atypical body positions, alongside the marked variability in their $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, points to the presence of people from diverse geographical and cultural backgrounds. Such diversity suggests the coexistence of multiple social identities, expressed through distinct funerary practices within a relatively homogeneous local population.

(c) From the early 2nd millennium BCE, environmental and socio-economic pressures prompted a cultural transformation, evidenced by changes in settlement patterns, material culture, burial practices, and mobility patterns, marking a return to more mobile, nomadic lifeways. In Eastern Sudan, the nearby Ethio-Eritrean highlands appear to have delayed the onset of aridification, allowing

relatively humid conditions to persist longer than in surrounding regions. Consequently, Eastern Sudan functioned as a refuge zone, attracting groups displaced from both the Nile Valley and the Eastern Desert, where environmental stress was more severe or occurred earlier. This scenario is supported by isotopic data, revealing renewed increased mobility compared to the previous phase and a wide distribution of $^{87}\text{Sr}/^{86}\text{Sr}$ values among mobile individuals.

With due consideration of the sample's limitations for drawing population-wide conclusions, these findings highlight the complex interplay between cultural transformation, environmental adaptation, and long-distance interaction that shaped mobility strategies in Prehistoric Eastern Sudan, positioning the region as a key crossroads for interaction and exchange between local populations and external groups. By providing the first isotopic dataset for this region, this study establishes a reference framework that will support future research in deepening our understanding of mobility, exchange networks, and adaptive strategies in one of northeastern Africa's most archaeologically rich regions.

Further research, integrating spatially resolved $^{87}\text{Sr}/^{86}\text{Sr}$ isotope analysis through LA-ICP(MC)MS, will be undertaken to refine our understanding of the timing, extent, and nature of mobility and connectivity within Eastern Sudan.

Materials and Methods

The human and faunal sample

Since 2010, excavations in Eastern Sudan have documented 180 inhumations across the sites UA50, UA53, and K1. These include single, double, and multiple burials, accounting for a total of 202 individuals, buried in varied body positions and orientations [27,34,53,88,89]. Detailed information is reported in Supplementary Table S1.

For this study, only individuals with preserved enamel from a first permanent molar (M1) were selected for $^{87}\text{Sr}/^{86}\text{Sr}$ analysis, as the isotope ratios recorded in the M1 enamel predominantly reflect the geochemical environment experienced during early postnatal life.

The M1 begins forming at the very end of gestation or shortly after birth [90]. While a limited portion of enamel (i.e., the cuspal region) may form in utero, the lateral enamel mineralises entirely postnatally [90]. To avoid potential prenatal signals, only the lateral portion of the dental crown was sampled in this study. Within this framework, breastfeeding-related strontium inputs are unlikely to affect M1s' $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in a manner that compromises the identification of local versus non-local individuals. Human breast milk contains low absolute concentrations of strontium, and any maternal contribution is progressively diluted with the introduction of complementary foods during weaning [91–95]. Moreover, physiological processes do not induce significant fractionation of the $^{87}\text{Sr}/^{86}\text{Sr}$

ratio; breast milk therefore transmits the maternal dietary and environmental strontium signature rather than producing a distinct isotopic offset in the infant. In addition, any mass-dependent effects are further corrected analytically during analysis, via internal normalisation to a constant $^{88}\text{Sr}/^{86}\text{Sr}$ ratio [96,97]. Consequently, in contexts where mothers and infants exploit the same habitual landscape, breastfeeding is unlikely to result in spurious non-local assignments.

The final dataset includes 76 individuals (Supplementary Table S2). Specifically, in the Upper Atbara graveyards, 9 individuals (6 adults and 3 subadults) were analysed from site UA50 (second half of the 5th millennium BCE, Malawiya Group), and another 9 individuals (6 adults and 2 subadults) from site UA53 (late 4th -early 3rd millennium BCE, Butana Group). At site K1, a total of 58 individuals were sampled. Of these, 50 (39 adults and 11 subadults) from sectors K1 XII–XIII are associated with the early 3rd-early 2nd millennium BCE phase (Gash Group); 6 (5 adults and 1 subadult) from sector K1 XIV belong to the early 2nd-early 1st millennium BCE phase (Jebel Mokram Group); and 2 individuals (1 adult and 1 subadult) come from a tumulus in sector K1 XIV, dating to the first half of the 1st millennium CE (Hagiz Group).

Moreover, 13 faunal bone samples – including remains from 3 ovicaprids and 10 rodents – were collected from site K1 (Supplementary Table S3). No faunal remains were available for sampling from the Upper Atbara graveyards at UA50 and UA53.

All necessary permits for this study were obtained from the National Corporation for Antiquities and Museums (NCAM), under the framework of a research agreement with the University of Naples “L’Orientale” and the Associazione Internazionale di Studi sul Mediterraneo e l’Oriente (ISMEO). All sampled materials are currently stored at the University of Naples “L’Orientale”, Italy.

Osteological analysis

Osteological sex estimation in adults was performed through the observation of sexually dimorphic features in the skull and pelvis [98,99]. The individuals were classified as males (M), probably males (M?), females (F), probably females (F?), and indeterminate (IND).

Age-at-death estimation in subadults was based on three main criteria: (a) the formation and eruption stages of primary and permanent dentition [90]; (b) the developmental and growth stages of long bones [100]; and (c) the degree of epiphyseal fusion [100]. Age-at-death estimation in adult individuals was performed using multiple skeletal and dental indicators: (a) tooth wear patterns [99]; (b) degenerative changes in the sternal end of the ribs [102,103]; (c) morphological features of the pubic symphysis [104]; and (d) the auricular surface of the ilium [105]. The individuals were categorized into the following age groups: infants (I; 0–1 year), young children (YC; 1–5 years), older

children (OC; 5–10 years), juveniles (J; 10–15 years), adolescents (AD; 15–20 years), young adults (YA; 20–40 years), and mature adults (MA; >40 years). When it was not possible to define a more precise age class for adult individuals, these were categorized as ‘generic adults’ (GA; >20 years).

For isotope analysis, we considered two main biosocial classes: subadults (from birth to 15 years of age) and adults (above 15 years of age). The reason for including still-growing adolescent individuals among the latter category is that they may have already acquired the adult social role [106,107].

⁸⁷Sr/⁸⁶Sr analysis

Strontium isotope analyses were carried out at the MeGic lab of the Department of Chemical and Geological Sciences at the University of Modena and Reggio Emilia.

Fragments of lateral enamel (approximately 0.05 g) were obtained by cutting each tooth with a flexible diamond-edged rotary wheel mounted on a DREMEL model 300. All adhering contaminants, including soil, sediment, and dentine residues, were removed using a dental bur. After rinsing with MilliQ water, approximately 5 mg of each sample was dissolved in 3M HNO₃. The chromatographic separation of Sr was performed through Teflon columns filled with 30 µl of Eichrom Sr spec resin [108]. After cleaning with MilliQ water, the dissolved samples were loaded, and cations (not Sr) were desorbed by percolating 3M HNO₃ to eliminate all possible isobaric interferences. Sr was then eluted using MilliQ water. The Sr samples were diluted with 4% HNO₃ and measured at the Centro Interdipartimentale Grandi Strumenti of the University of Modena and Reggio Emilia using a Neptune MC-ICPMS. ⁸²Kr, ⁸³Kr, ⁸⁴Sr, ⁸⁵Rb, ⁸⁶Sr, ⁸⁷Sr and ⁸⁸Sr m/z were collected with 10¹¹ and 10¹² (for ⁸²Kr, ⁸³Kr and ⁸⁴Sr) Ω resistors. Background subtraction and Rb correction were performed with routine methods [97]; similarly, mass bias normalisation used an exponential law and an ⁸⁸Sr/⁸⁶Sr ratio of 8.375209 [109]. Individual ⁸⁷Sr/⁸⁶Sr ratios were reported to an accepted NIST-SRM 987 value of 0.710248 [110].

Assessing the local Sr baseline

Due to the location of the Upper Atbara and the Mahal Teglinos graveyards in an area affected by instability, it was not possible to recently collect vegetation, water, and soil samples for building local Sr baselines as recommended in the literature [111–114]. Given this limitation, the assessment of the local ⁸⁷Sr/⁸⁶Sr range in both ecological areas was based on alternative approaches.

For graveyard K1, the local baseline was inferred using three main criteria: (a) the range of ⁸⁷Sr/⁸⁶Sr values observed in faunal remains [113,115]; (b) the shape of the distribution of human isotope values [116–118]; (c) the ⁸⁷Sr/⁸⁶Sr values of the youngest individuals (aged below 15), whose isotopic

signatures were assumed to be indicative of local values, as children are generally less likely to have participated in long-distance mobility [115, 119-123]. For UA50 and UA53 graveyards, only criteria (b) and (c) could be applied, as faunal data were not available. Given their geographic proximity (ca 0.5 km of distance as the crow flies), these sites were considered together in this assessment.

The use of $^{87}\text{Sr}/^{86}\text{Sr}$ values from the youngest individuals as indicators of the local isotopic baseline is well established in the bioarchaeological literature, where subadults have consistently proven to be reliable proxies for local environmental signatures [115, 119-123]. Although it is acknowledged that certain socioeconomic or cultural contexts may involve higher levels of family mobility, including children, available evidence indicates that such cases represent exceptions rather than common patterns [16,124]. As a result, in our study, the combination of multiple independent criteria allows for the definition of a reliable local baseline for reconstructing mobility. ‘Local’ implies isotopic consistency, during the first 2-3 years of life, within the habitual landscape exploited by a community.

Statistical analysis

Statistical analysis and data visualisation were performed using the R environment for statistical computing (version 4.5.2) [125]. Outlier isotope values were identified using Tukey’s interquartile range [$1.5 \times \text{IQR}$ beyond Q1 or Q3; 45].

Data availability

All the data are available in this article and its Supplementary Information file.

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Author contributions

Conceptualization: G.C., A.M.; Formal analysis: G.C., A.M.; Funding acquisition: A.M.; Investigation: G.C., A.S., H.I.A., F.L.; Methodology: F.L.; Resources: A.S., H.I.A., F.L., A.C., A.N., A.M.; Supervision: A.S., L.B., A.N., A.M.; Writing—original draft: G.C.; Writing—review and editing: All authors contributed equally.

Competing interests

The authors declare no competing interests.

Figure legends

Figure 1. Map of eastern Sudan showing the locations of sites Upper Atbara 50 (UA50), Upper Atbara 53 (UA53), and Mahal Teglinos (K1). The map was created by Stefano Costanzo using QGIS version 3.44.5 (QGIS Development Team, 2025; <https://www.qgis.org>) and public domain satellite imagery accessed through the QuickMapServices plugin (NextGIS, 2025; <https://nextgis.com>).

Figure 2. Density plots of the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope values across the chronological phases considered in this study. The grey dashed line indicates the density distribution of all human $^{87}\text{Sr}/^{86}\text{Sr}$ values. The individuals dating to the second half of the 5th millennium BCE (red curve) and to the early 2nd–early 1st millennium BCE (orange curve) exhibit broad, low distributions spanning a wide range of values, reflecting high isotopic variability. Conversely, the green and blue curves correspond to the individuals dating to the late 4th millennium BCE (graveyard UA53) and the early 2nd millennium BCE (graveyard K1 XII-XIII) and display narrower distributions. Within these, isotope values for individuals from graveyard UA53 follow a bimodal distribution, whereas those for individuals from graveyard K1 XII-XIII are multimodally distributed, indicating internal heterogeneity in both samples.

Figure 3. Kernel density plot of $^{87}\text{Sr}/^{86}\text{Sr}$ human values from the Upper Atbara graveyards (UA50 and UA53). Considering all 18 human values (the dashed grey line), the mode peak corresponds to

individuals likely born locally, whereas the smaller modal peaks towards less radiogenic values suggest other groups of individuals, possibly originating from elsewhere. The dashed lines indicate the local Sr range (as 0.70682–0.70701), defined through Tukey's interquartile range calculated solely on subadults' values. The 9 individuals whose $^{87}\text{Sr}/^{86}\text{Sr}$ values fall outside this range are considered possibly non-locals.

Figure 4. Kernel density plot of $^{87}\text{Sr}/^{86}\text{Sr}$ human values from graveyard K1. Considering all 58 human values (the dashed grey line), the mode peak corresponds to individuals likely born locally, whereas the smaller modal peaks towards both less and more radiogenic values suggest the presence of other groups of individuals, possibly originating from elsewhere. The red dashed lines indicate the local Sr range (as 0.70666–0.70692), defined through Tukey's interquartile range calculated solely on subadults' values. The 12 individuals whose $^{87}\text{Sr}/^{86}\text{Sr}$ values fall outside this range are considered possibly non-locals.

Figure 5. $^{87}\text{Sr}/^{86}\text{Sr}$ human values from the Upper Atbara graveyards (UA50 and UA53), plotted by chronology, sex, and age class. The yellow dashed lines indicate the local Sr range (as 0.70682–0.70701), defined through Tukey's interquartile range calculated solely on subadults' values. (5) Of the 18 total individuals, 9 fall outside the local range.

Figure 6. $^{87}\text{Sr}/^{86}\text{Sr}$ human values from graveyard K1 plotted by chronology, sex, and age class. The orange dashed lines indicate the local Sr range (as 0.70666–0.70692), defined through Tukey's interquartile range calculated on non-adult values (13). The green dashed lines indicate the Sr range (as 0.70664–0.70688), defined through Tukey's interquartile range calculated on faunal values (13). Of the 58 total values, 12 fall outside the local range.

Figure 7. Schematic synthesis of mobility trends and environmental adaptation in Prehistoric Eastern Sudan. The figure summarises key environmental circumstances, settlement patterns, economic traits, and isotope-based evidence of mobility across the chronological sequence considered in this study.

Figure 8. Grave 78 from graveyard K1 (early 3rd-early 2nd millennium BCE, Gash Group phase), with two adults placed with contracted legs, facing each other, and with their heads close. The arm of the non-local male (Individual 1, on the left) encircles the local female (Individual 2, on the right), suggesting a close relationship between the two individuals.