

Chapter 13

Environmental Change, Ungulate Biogeography, and Their Implications for Early Human Dispersals in Equatorial East Africa

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Abstract To better understand the potential role of environmental change in mediating human dispersals across equatorial East Africa, this study examines the biogeographic histories of ungulates, including a summary of current knowledge and fossil evidence stemming from our fieldwork in the Kenyan portion of the Lake Victoria basin. Phylogeographic and paleontological evidence indicates that vegetation changes across Quaternary climate cycles mediated ungulate distributions and dispersals via the opening and closing of biogeographic barriers in equatorial East Africa. Dispersal capabilities would have been enhanced during phases of grassland expansion and diminished during phases of grassland contraction. We propose that the distribution and dispersal of diagnostic technological markers in the archaeological record may be similarly influenced by environmental changes. The Middle Stone Age record from the Lake Victoria region provides intriguing examples of possible environmentally mediated technological dispersals.

Keywords Grasslands • Lake Victoria • Late Pleistocene • Middle Stone Age • Paleoenvironments • Phylogeography • Range shift

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Introduction

The prehistory of early modern humans is characterized by massive range expansions and population dispersals. Fossil and genetic evidence indicate an African origin of our species (*Homo sapiens*) ~200 ka (McDougall et al. 2005; Campbell and Tishkoff 2010; Brown et al. 2012; but see Weaver 2012 for an alternate interpretation). These early humans later diverged into multiple genetically (Campbell and Tishkoff 2010) and morphologically diverse (Gunz et al. 2009) populations during the Late Pleistocene (126–12 ka), likely reflecting intra-African population expansions and dispersals (Soares et al. 2012). At least one of these populations migrated out of Africa ~70 ka (Campbell and Tishkoff 2010), setting the stage for the expansion of humans across the globe and the replacement of all other hominin species, including Neanderthals (*Homo neanderthalensis*) in Eurasia, and the enigmatic “hobbit” (*Homo floresiensis*) in Indonesia.

East Africa features prominently in this history of early modern humans, as it provides the earliest fossil remains of *Homo sapiens* (Omo I and II from the Kibish Formation, Ethiopia, at ~195 ka; McDougall et al. 2005; Brown et al. 2012) and the probable source populations for their Late Pleistocene dispersals out of Africa (Soares et al. 2012, 2016). Understanding the factors underlying these dispersals is the subject of intense debate spanning the fields of archaeology, paleontology, genetics, and climatology, among others (Beyin 2011). One of the more common explanatory mechanisms includes climate-driven environmental change and its effects on human demography and the opening and closing of biogeographic barriers (e.g., Forster 2004; Finlayson 2005; Vaks et al. 2007; Carto et al. 2009; Trauth et al. 2010; Compton 2011; Blome et al. 2012; Eriksson et al. 2012; Soares et al. 2012, 2016). However, the precise role of environmental change in East African human dispersals is poorly understood, stemming from a lack of well-dated archaeological sites associated with detailed paleoenvironmental

records. This is compounded by the high variability of the regional Middle Stone Age (MSA), which limits our ability to identify an archaeological signature of population movements (Tryon and Faith 2013).

While many fundamental questions concerning the role of environmental change in early human dispersals from East Africa remain unclear, a growing body of evidence indicates that Pleistocene environmental change played a central role in the biogeographic histories of associated East African faunas (e.g., Rodgers et al. 1982; Kingdon 1989; Marean 1992; Grubb et al. 1999; Wronski and Hausdorf 2008; Lorenzen et al. 2012; Faith et al. 2013). Not only does this imply that human population movements may be related to broader biogeographic patterns, but also that these insights into the relationships between changing climate, environments, and species ranges represent a useful starting point for formulating new hypotheses about human dispersals. Our aim here is to develop a framework for understanding the potential role of environmental change in Late Pleistocene human dispersals through an examination of ungulate biogeography. We focus on ungulates because they are well represented in the fossil record and because many ungulate species are clearly linked to specific habitats, making them strong candidates for exploring how environmental change mediates their biogeographic histories. This chapter provides a brief review of current knowledge together with an examination of paleontological and archaeological evidence stemming from our ongoing fieldwork in the Kenyan portion of the Lake Victoria basin.

Ungulate Biogeography

In common use, the ungulates represent a paraphyletic group of hoofed mammals, including in Africa the antelopes and buffalo (Bovidae), suids (Suidae), zebras (Equidae), giraffes (Giraffidae), rhinos (Rhinocerotidae), elephants (Elephantidae), and hippos (Hippopotamidae), among others. Ungulate diversity in Africa is exceptional (Turpie and Crowe 1994; du Toit and Cumming 1999), with the bovids (the most speciose family) alone represented by 82 extant species (IUCN 2012) and more than 100 fossil species (Gentry 2010).

The greatest diversity of African ungulates is found in equatorial East Africa (Turpie and Crowe 1994), which encompasses the boundaries between the Somalian, Sudanian, and Zambesian biogeographic regions for mammals, birds, reptiles, amphibians, and plants (Linder et al. 2012) (Fig. 13.1). These biogeographic regions, which are broadly similar to previously identified zones based on expert opinion (e.g., White 1983; Burgess et al. 2004), were statistically defined by Linder et al. (2012) using cluster analysis of species occurrences across $1^\circ \times 1^\circ$ (latitude and

longitude) cells for plants and vertebrate groups. We recognize that these zones are only a coarse measure of broad biogeographic patterns, and we use them here as a heuristic device to illustrate how biogeographic patterns changed in the past. Some of the ungulates characteristic of these regions include Grevy's zebra (*Equus grevyi*) in the xeric shrublands of the Somalian region, kob (*Kobus leche*) in the edaphic grasslands of the Sudanian region, and wildebeest (*Connochaetes taurinus*) in the secondary grasslands in the Zambesian region. All of these taxa are found in East Africa, but their ranges do not overlap, contributing to the high spatial turnover (beta diversity) observed more broadly for all East African mammals (Linder et al. 2012).

The main factors underlying these broad biogeographic regions include the complex interactions between climate and geomorphology (e.g., tectonics, topography, soil type) and their influence on the distribution of vegetation communities, which in turn mediate the distribution of faunas (e.g., Bell 1982; O'Brien and Peters 1999; Linder et al. 2012). For example, a drier climate characterized by bimodal rainfall distinguishes the Somalian region from both the Sudanian and Zambesian regions, which are wetter and receive primarily uni-modal rainfall (O'Brien and Peters 1999). This aridity in the Somalian region translates to the presence of dry scrub vegetation inhabited by arid-adapted ungulates, including Grevy's zebra and African wild ass (*Equus africanus*). At the same time, species ranges are also influenced by geomorphological factors. In addition to mediating vegetation cover and habitat suitability through altitudinal gradients, tectonically driven uplift and rifting can create dispersal barriers to biotic communities, as evidenced

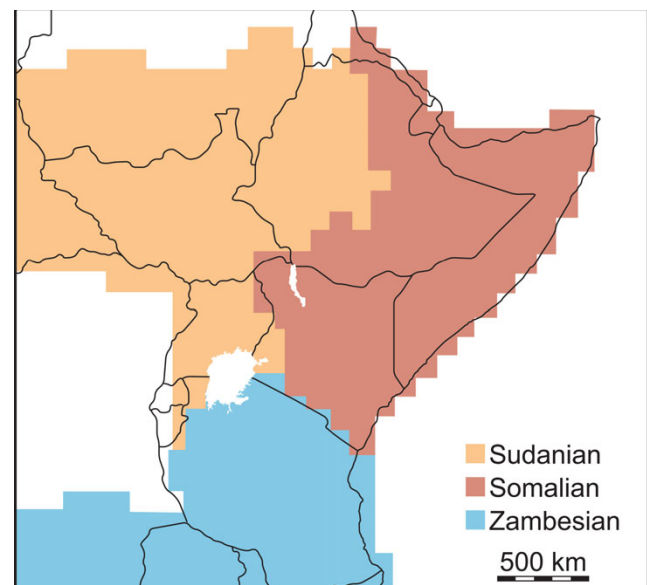


Fig. 13.1 The distribution of Sudanian, Somalian, and Zambesian biogeographic regions for mammals (after Linder et al. 2012)

by the close correspondence between the boundary of the Sudanian and Somalian regions in Ethiopia (Fig. 13.1) and the location of the Ethiopian Rift Valley, which bisects the Ethiopian highlands. Lastly, soil type can also determine broadscale biogeographic patterns. For example, the dominance of low-nutrient soils weathered from basement rock accounts for the Miombo (*Brachystegia*) woodlands and low-biomass ungulate communities characteristic of the Zambesian region, in stark contrast to the nutrient-rich volcanic soils in some portions of the Somalian region, which are associated with grasslands and high-biomass ungulate communities (Bell 1982; East 1984).

Not only does the combination of climatic and geomorphological variables in East Africa translate to biogeographic zonation of ungulate species, but the same is also true for populations within species. Lorenzen et al. (2012) show that many broadly distributed species, including warthog (*Phacochoerus africanus*), African buffalo (*Syncerus caffer*), hartebeest (*Alcelaphus buselaphus*), and giraffe (*Giraffa camelopardalis*), among others, display genetic substructuring that distinguishes between populations from the Sudanian savannas, and those in East Africa and southern Africa. Among some species there is also evidence for substructuring between East and southern African populations. The overall picture indicates that East Africa encompasses the boundaries of genetically distinct lineages from multiple regions.

A number of factors potentially contribute to this unique taxonomic and genetic diversity. High spatial variability in forage quantity and quality has been invoked as one possible driver of ungulate species richness in East Africa (du Toit and Cumming 1999), an argument supported by quantitative analyses showing extreme spatial heterogeneity in East African plant communities (Linder et al. 2012). However, this does not explain the convergence of genetically distinct lineages within species. In light of the phylogeographic evidence, Lorenzen et al. (2012) propose that environmental changes across late Quaternary glacial/interglacial cycles played an important role in the taxonomic and genetic diversity of East African ungulates. Equating glacial and interglacial conditions with dry versus humid climates, they suggest that the expansion of grassland vegetation during glacial phases would have facilitated interchange of ungulate populations throughout sub-Saharan Africa. During interglacials, the expansion of tropical forests across equatorial East Africa created a barrier that fragmented populations and restricted gene flow (see also Cowling et al. 2008). If so, then the distinct biogeographic regions and high spatial heterogeneity of biotic communities found in East Africa today (Linder et al. 2012) may be a Holocene phenomenon, with a more homogenous supercommunity characteristic of Pleistocene phases of grassland expansion.

The Fossil Record

Biogeographic evidence suggests that East Africa is a hub around which ungulate ranges expand, contract, and fragment across cycles of Quaternary environmental change. One of the key predictions generated from this is that during phases with expanded grassland cover, allopatric ungulate species from both north and south of the equator will converge in equatorial East Africa. The fossil record provides the requisite empirical evidence for testing this hypothesis. Compared to the record from southern Africa, which has been a focus of modern human origins research for decades, our understanding of the fossil history of East African ungulates over the last ~200 kyr is only beginning to come to light (Marean and Gifford-Gonzalez 1991; Marean 1992; Assefa 2006; Assefa et al. 2008; Faith et al. 2011, 2012, 2013, 2014). However, the emerging evidence provides compelling examples of climate-driven range shifts that are consistent with hypotheses derived from ungulate biogeography.

The Records from Rusinga and Mfangano Islands

Here we highlight some of the more prominent range shifts documented in the fossil record, with an emphasis on the Late Pleistocene ungulates from Rusinga and Mfangano Islands in Kenya's Lake Victoria basin (Fig. 13.2). We focus on these sites because: (1) all of the ungulate taxa involved in major Late Pleistocene range shifts are documented here (and in some cases elsewhere); and (2) the Lake Victoria region is strategically situated along the equator in East Africa, with geological evidence documenting massive expansions and contractions in lake area, including periodic desiccation, in response to late Quaternary climate change (Stager and Johnson 2008; Stager et al. 2002, 2011; Tryon et al. in press). Seismic profiles across Lake Victoria show at least four desiccation surfaces (Johnson et al. 1996; Stager and Johnson 2008), the most recent of which correspond to extreme aridity during Heinrich Event 1 from 17 to 16 ka and again during a subsequent dry phase from 15 to 14 ka (Stager et al. 2002, 2011); the other desiccation surfaces correspond to undated phases of previous aridity and the pre-lake surface. The vegetation of the Lake Victoria region was historically characterized by bushland, thicket, and forest (White 1983), although multiple lines of evidence indicate that phases of lake contraction were associated with expanded grasslands (Kendall 1969; Talbot and Laerdal 2000; Talbot et al. 2006; Tryon et al. in press).

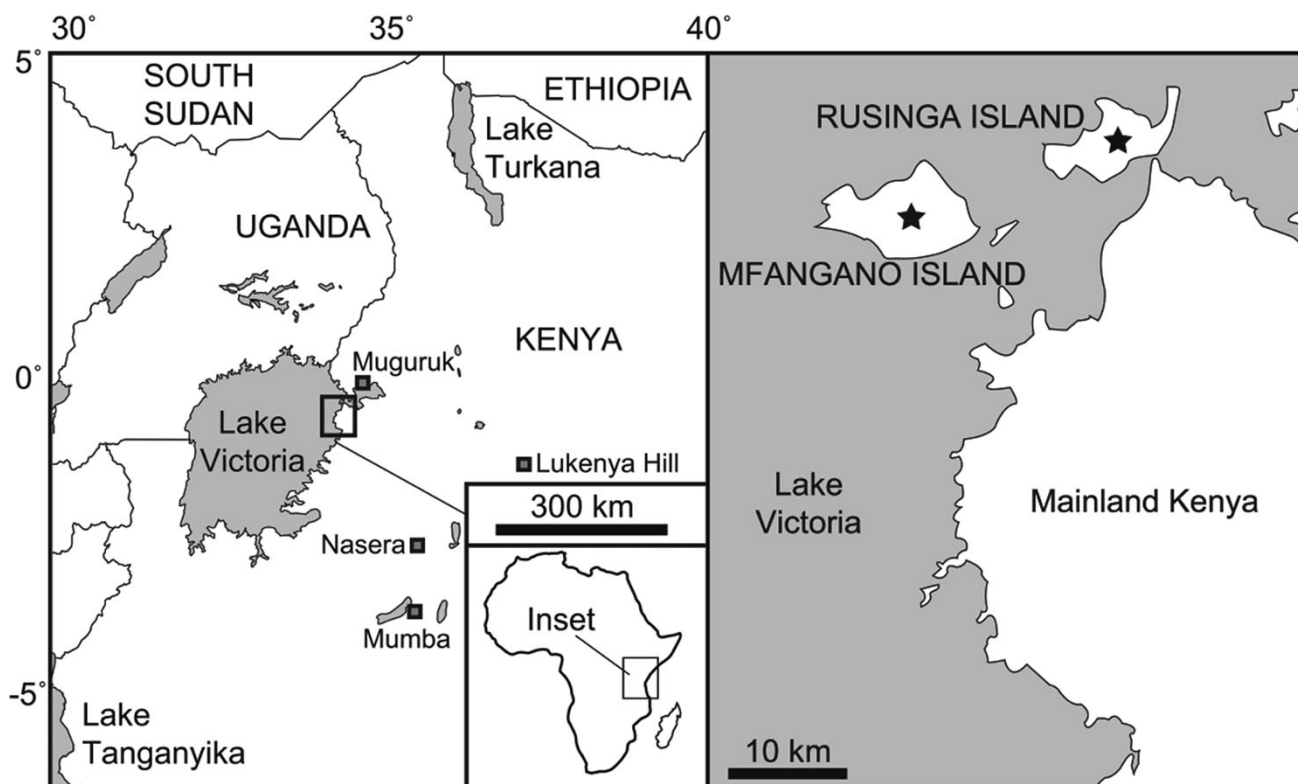


Fig. 13.2 The location of Rusinga and Mfangano islands in Kenyan Lake Victoria and nearby archaeological sites mentioned in the text

Details of our research on Rusinga Island and Mfangano Island have been published elsewhere (Faith et al. 2011, 2012, 2014; Tryon et al. 2010, 2012, 2014), and we provide only a brief summary here. Rusinga and Mfangano Islands are located within Lake Victoria (Fig. 13.2), with the former separated from the mainland by a narrow channel and the latter situated ~10 km from the mainland. On both islands, the poorly consolidated Pleistocene deposits, known as the Wasiriya Beds (Rusinga Island) and the Waware Beds (Mfangano Island), are characterized by weakly developed paleosols and tuffaceous fluvial sediments documenting a complex cut-and-fill system. The age of the Wasiriya Beds is constrained to between 100 and 33 ka, with the minimum provided by radiocarbon dates for intrusive gastropods and the maximum by geochemical analysis of tephra deposits, which suggest derivation from East African Rift System (EARS) volcanoes that began erupting ~100 ka (Blegen et al. 2015). The Waware Beds have a similar minimum age, also provided by radiocarbon age estimates for intrusive gastropods, whereas tephra correlations suggest a link to the Wasiriya Beds and a comparable maximum age (Blegen et al. 2015). The artifacts recovered from the Wasiriya Beds are typologically MSA (Fig. 13.3), and the same is likely the case for those from the Waware Beds, although a larger sample is needed to be certain.

Rusinga and Mfangano Islands have yielded some of the larger and better preserved fossil assemblages from this time period in East Africa (Table 13.1). Alcelaphine bovids and equids dominate the assemblages, indicating the presence of open grassland vegetation distinct from the historic vegetation (White 1983). Several extinct bovids are present, including *Rusingoryx atopocranion*, *Damaliscus hypsodon*, *Megalotragus* sp., *Syncerus antiquus*, and an unnamed impala, all of which are characterized by dental or postcranial adaptations to grazing in open habitats (Klein 1980, 1994; Faith et al. 2011, 2012, 2014). The presence of large gregarious grazers on Mfangano Island, some of which are migratory species, suggests a likely connection to the mainland when the deposits accumulated, requiring a ≥ 25 m reduction in lake level (Tryon et al. 2014). The precipitation decline needed to drive this would have set in motion a series of feedback mechanisms leading to a substantial reduction, if not complete desiccation, of Lake Victoria (Broecker et al. 1998; Milly 1999), leaving behind a topographically smooth grassy plain (Tryon et al. 2014). As detailed below, there is strong evidence that the expansion of grasslands and reduction in surface area of Lake Victoria facilitated interchange of ungulates from north and south of the equator.

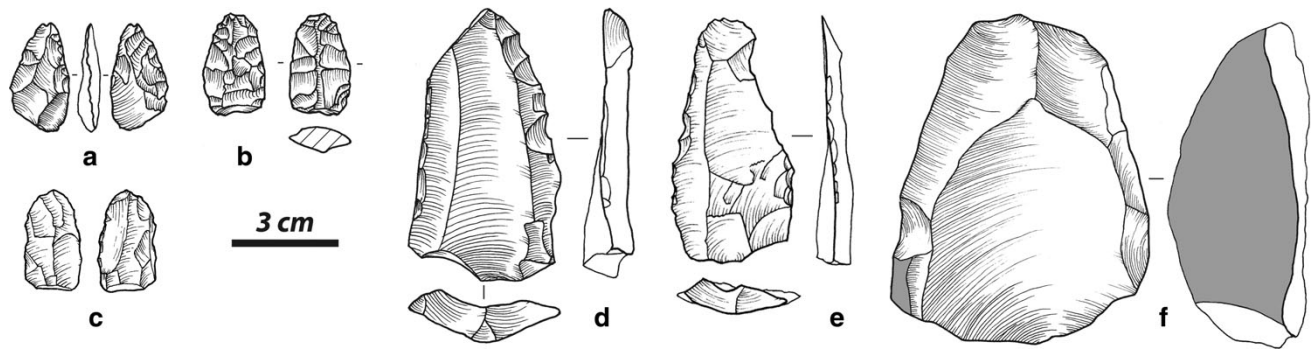


Fig. 13.3 Middle Stone Age artifacts from Rusinga and Mfangano Islands: **a–c** bifacial points, **d–e** Levallois blades variably retouched, **f** Levallois core

Table 13.1 The presence/absence of ungulate species from Rusinga and Mfangano islands as of our 2012 field season

Family	Taxon	Common name	Rusinga	Mfangano
Elephantidae	Elephantidae cf. <i>Loxodonta africana</i>	Elephant	X	–
Rhinocerotidae	<i>Ceratotherium simum</i>	White rhinoceros	X	–
Equidae	<i>Equus quagga</i>	Plains zebra	X	X
	<i>Equus grevyi</i>	Grevy's zebra	X	–
Suidae	<i>Kolpochoerus sp. †</i>	Extinct bushpig	X	–
	<i>Phacochoerus sp.</i>	Warthog	X	X
	<i>Potamochoerus sp.</i>	Bushpig	X	X
Hippopotamidae	<i>Hippopotamus sp.</i>	Hippopotamus	X	X
Bovidae	<i>Taurotragus oryx</i>	Eland	X	–
	<i>Tragelaphus scriptus</i>	Bushbuck	X	–
	<i>Tragelaphus strepsiceros</i>	Greater Kudu	X	–
	<i>Tragelaphus cf. imberbis</i>	?Lesser Kudu	X	–
	<i>Oryx beisa</i>	Oryx	X	–
	<i>Redunca fulvorufula/redunca</i>	Reedbuck	X	X
	<i>Redunca arundinum/Kobus kob</i>	Southern reedbuck/Kob	X	X
	<i>Aepyceros sp. nov. †</i>	Large extinct impala	X	–
	<i>Connochaetes taurinus</i>	Wildebeest	X	X
	<i>Damaliscus hypsodon †</i>	Small extinct alcelaphine	X	X
	<i>Megalotragus sp. †</i>	Giant wildebeest	X	–
	<i>Rusingoryx atopocranion †</i>	Extinct alcelaphine	X	X
	Alcelaphini cf. <i>Alcelaphus buselaphus</i>	Hartebeest	X	X
	<i>Sylvicapra grimmia</i>	Common duiker	X	–
	<i>Gazella thomsoni</i>	Thomson's Gazelle	X	X
	<i>Syncerus antiquus †</i>	Long-horn buffalo	X	X
	<i>Syncerus caffer</i>	African buffalo	X	X
<i>Ourebia ourebi</i>	Oribi	X	X	
<i>Oreotragus/Raphicerus</i>	Klipspringer/Steenbok	–	X	
<i>Madoqua sp.</i>	Dik-dik	–	X	

† = extinct

Grevy's Zebra (*Equus grevyi*)

Grevy's zebra historically ranged throughout arid to semi-arid grasslands and shrublands in the Horn of Africa (Fig. 13.4) (Williams 2002). Fossil remains are known from Rusinga Island (Table 13.1) and many other Middle-to-Late Pleistocene sites in southern Kenya and northern Tanzania,

including Karungu, Lukenya Hill, Lainyamok, and Kisee II, documenting a south and westward range shift or expansion of at least 500 km (Faith et al. 2013). Although the species is primarily confined to the Somalian biogeographic region, its fossil occurrences are found in areas that are today part of the Somalian, Sudanian, and Zambesian biogeographic regions. At the onset of the Holocene, Grevy's zebra disappeared from southern Kenya and northern Tanzania and

became rare in the fossil record, likely reflecting increased precipitation, the contraction of dry grassland habitats, and competition with mesic-adapted grazers (Faith et al. 2013).

Oryx (*Oryx beisa*)

The current distribution of oryx broadly corresponds to that of Grevy's zebra, but extends south into the Zambesian and northwest into the Sudanian biogeographic regions (Fig. 13.4). Oryx has a similar habitat preference as Grevy's zebra, and the two species are significantly associated in the

fossil record (Faith et al. 2013). The presence of oryx on Rusinga Island (Table 13.1) indicates a ~250 km westward range shift or expansion. Like Grevy's zebra, its range and abundance declined throughout East African fossil sites at the beginning of the Holocene (Faith et al. 2013).

White Rhinoceros (*Ceratotherium simum*)

The white rhinoceros includes two subspecies, the northern white rhinoceros (*C. simum cottoni*) and southern white rhinoceros (*C. simum simum*), although some authorities

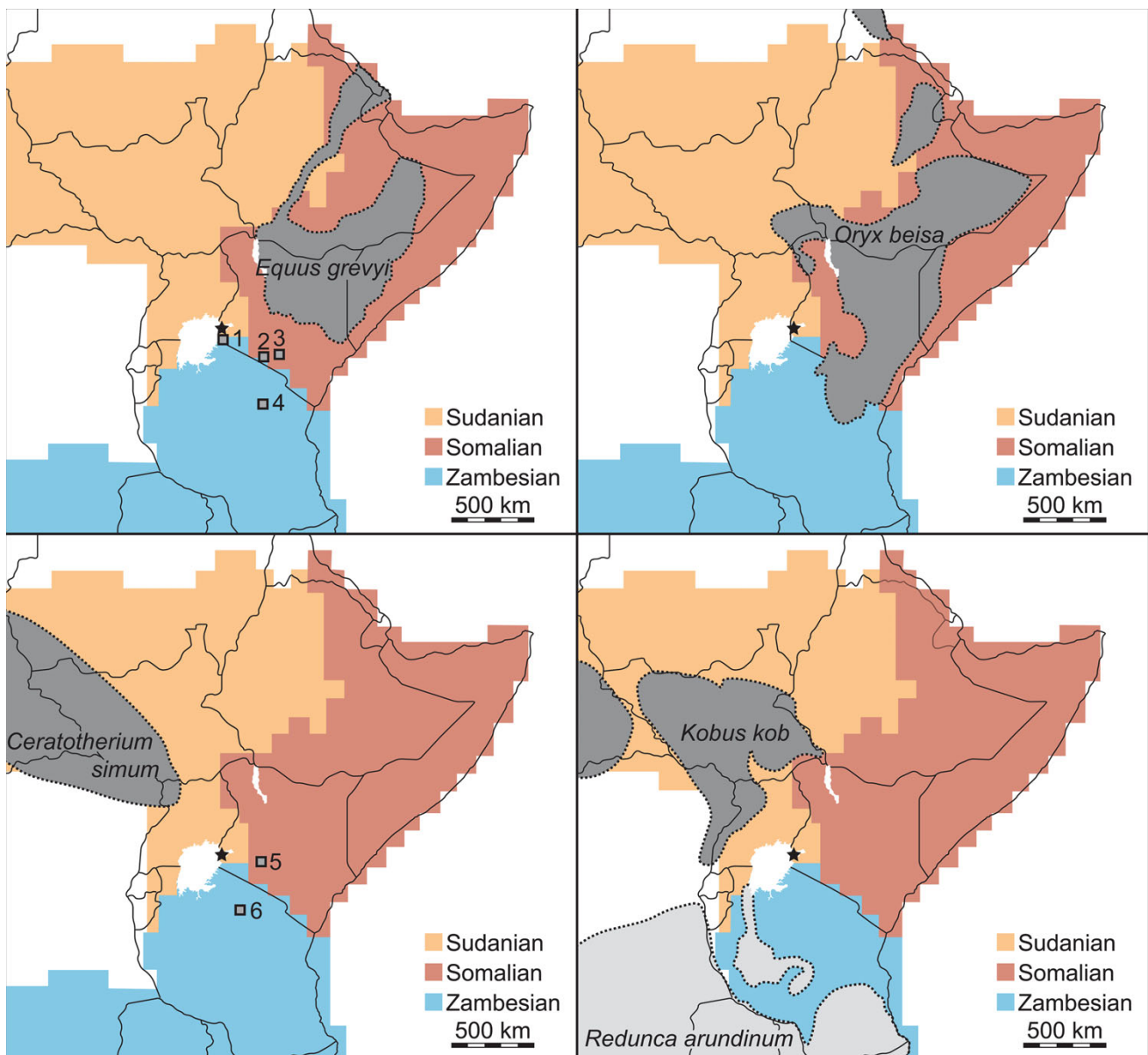


Fig. 13.4 The geographic ranges of Grevy's zebra (*Equus grevyi*), oryx (*Oryx beisa*), white rhinoceros (*Ceratotherium simum*), kob (*Kobus kob*), and southern reedbeek (*Redunca arundinum*) relative to their fossil occurrences on Rusinga and Mfangano islands (star). Range

maps are from Williams (2002) for Grevy's zebra and the IUCN Red List (2012) for all other species. Boxes correspond to fossil occurrences mentioned in the text: (1) Karungu, (2) Lainyamok, (3) Lukenya Hill, (4) Kiseke II, (5) Prolonged Drift, (6) Mumba shelter

place the former in its own species (*C. cottoni*) (Groves et al. 2010). Their geographic ranges are discontinuous, with the southern white rhinoceros historically known from southern Africa and the northern white rhinoceros known from central Africa northwest of Lake Albert (Fig. 13.4). Several white rhinoceros fossils have been recovered from Rusinga Island, ~430 km southeast of its historic range (assuming they belong to the northern taxon), with an even greater Late Pleistocene range extension (~775 km) documented at Mumba rockshelter in Tanzania (Mehlman 1989). As evidenced by an additional fossil occurrence from Prolonged Drift in central Kenya, a small and probably isolated population persisted in equatorial East Africa into the late Holocene (Gifford et al. 1980). The cause of its prehistoric disappearance from Kenya is not well understood, but could include long-term vegetation change, competition for forage and water with pastoralists and their livestock, or stochastic processes owing to small population size and isolation.

Kob (*Kobus kob*) or Southern Reedbuck (*Redunca arundinum*)

Both Rusinga and Mfangano Islands yield dental remains of a medium-sized reduncine, larger than Bohor reedbuck (*Redunca redunca*), but smaller than waterbuck (*Kobus ellipsiprymnus*), that are morphologically similar to and overlap in size with modern kob and southern reedbuck. Both taxa have a similar habitat requirement for fresh grasses and year-round access to water, which is consistent with the fluvial nature of the fossil deposits. The ranges of these two reduncines are allopatric (Fig. 13.4), with kob occurring north and west of Lake Victoria in the Sudanian savannas and southern reedbuck ranging from southern Africa to just south of the Lake Victoria basin. Although it is unclear whether the fossil specimens belong to kob, southern reedbuck, or both, the occurrence of either implies a ~350 km range shift to the southeast (kob) or northeast (southern reedbuck).

A Non-Analog Supercommunity

The convergence of various ungulate species with historically allopatric ranges on Rusinga and Mfangano Islands supports the notion of a homogenous East African supercommunity during Pleistocene phases of grassland expansion. It follows that the distinct biogeographic zonation found in East Africa today (Fig. 13.1; Linder et al. 2012) is ephemeral—probably limited to the Holocene—and closely linked to climate and its effects on vegetation structure.

Other variables that contribute to the establishment of biogeographic zonation in East Africa (e.g., tectonics, topography, and soil type), unquestionably contributed to Late Pleistocene vegetation structure, but these are expected to be relatively stable over the timescale examined here, leaving climate as the most likely driver of first-order vegetation change.

While the non-analog supercommunity is consistent with enhanced ungulate dispersal capabilities related to expanded grasslands and a smaller Lake Victoria, it is also possible that environments at the time were highly productive and uniquely suited to supporting ungulate diversity. Across a range of East and southern African ecosystems, ungulate diversity and biomass peaks between 700 and 800 mm annual precipitation (Coe et al. 1976; East 1984; Faith 2013). A decline in annual precipitation from the ~1000 to 1200 mm/yr observed today, which is supported by the inferred decline of Lake Victoria (Tryon et al. 2014), could further underpin the diversity of the Late Pleistocene ungulate community. Reduced atmospheric CO₂ concentrations may have also contributed to the diversity, by enhancing foraging nutrient content, in turn supporting higher biomass large herbivore communities (Faith 2011).

The presence of extinct grazing bovids characterized by massive body mass (*Syncerus antiquus* and *Megalotragus* sp.) or extreme hypsodonty (*Damaliscus hypsodon*, *Rusingoryx atopocranion*, and the unnamed impala), of which *D. hypsodon* and *R. atopocranion* are dominant, also implies the presence of non-analog environments. We have previously interpreted their presence, together with that of Grevy's zebra and oryx, as evidence for aridity (Tryon et al. 2010, 2012; Faith et al. 2011, 2013), although this is at odds with the high diversity (see Faith 2013). A more detailed exploration of this conflict is beyond the scope of this study, but possible explanations could include the presence of a complex Late Pleistocene grazing succession (e.g., Brink and Lee-Thorp 1992) or an extinct migratory system (e.g., Marean 2010; Faith and Thompson 2013).

Climatic and Tectonic Drivers

Range shifts documented on Rusinga and Mfangano Islands illustrate the importance of vegetation change, particularly the expansion of grassland vegetation, in the biogeographic histories of ungulate populations. The mechanisms responsible for the expansion and contraction of grassland vegetation in equatorial East Africa during the Pleistocene include moisture availability, atmospheric CO₂ concentrations, and tectonically driven topographic shifts. The complex interaction of these variables would have played an important role in the opening and closing of dispersal

corridors for ungulate populations, and we provide a summary of these mechanisms below.

Changes in moisture availability are sometimes equated with glacial versus interglacial climates, which are typically generalized as reflecting more arid (glacial) versus more humid (interglacial) conditions. However, although changes in global moisture availability across glacial/interglacial cycles may influence equatorial East African climate, we caution that this oversimplification ignores the complexities of regional climate dynamics. Moisture availability in equatorial East Africa is driven by the complex interplay between orbital forcing, the position of the Intertropical Convergence Zone (ITCZ), high-latitude climate events, tropical ocean temperature gradients, and regional tectonics (e.g., DeMenocal 1995, 2004, 2011; Trauth et al. 2003, 2005, 2007, 2009; Feakins et al. 2005, 2013; Sepulchre et al. 2006; Verschuren et al. 2009; Blome et al. 2012). In addition to these global and regional drivers, local factors may also play an important role in vegetation change. For example, today as much as 90% of water loss in Lake Victoria is due to evaporation and 80% of the input is from direct precipitation (rather than inflow from streams and rivers) (Piper et al. 1986; Crul 1995), such that precipitation change plays a key role in lake size and moisture availability (Broecker et al. 1998; Milly 1999). This sensitivity to precipitation means that small changes in local rainfall patterns could translate to more pronounced aridification and vegetation change in the Lake Victoria region compared to other areas of East Africa.

In addition to moisture availability, reduced atmospheric CO₂ concentrations during Pleistocene glacial phases may also facilitate the expansion of grasslands due to the competitive advantage of C₄ plants under such conditions (Prentice et al. 2011). For example, the paleoenvironmental record from Lake Challa on the Kenya/Tanzania border shows that both humid and arid intervals from 12 to 25 ka were dominated by C₄ vegetation, most of which are probably grasses, whereas C₃ vegetation only expands at the onset of the Holocene (Sinninghe Damsté et al. 2011). This may indicate that the past distribution of grassland habitats in equatorial East Africa is more sensitive to atmospheric CO₂ than to precipitation.

Over longer timescales (>100 kyr) through the Pleistocene, changes in ungulate ranges may also have been influenced by regional tectonics. Extension and uplift associated with the EARS has dramatically altered the East African landscape since the Oligocene by creating large rift lakes such as Lakes Malawi, Tanganyika, Kivu, Albert and Edwards, causing the opening and closure of connections between major lakes, changing flow directions of major

ivers, and creating significant differences in topography (e.g., Rosendahl 1987; Chorowicz 2005). Lake Victoria, though not a true rift lake, was created when extension and uplift of the western and east arms of the EARS caused backponding of rivers into a topographic low between the two branches of the rift ~1.6–0.4 Ma (e.g., Kent 1944; Bishop and Trendall 1967; Ebinger 1989; Johnson et al. 1996; Talbot and Williams 2009). After its formation, continued rifting caused the lake basin to shift as much as 50 km eastward (Doornkamp and Temple 1966; Stager and Johnson 2008). Through the creation of rift-influenced lakes and significant topographic variability across the landscape, the rifting of the EARS may have influenced ungulate biogeographic histories by opening and closing potential dispersal corridors. Although precipitation and atmospheric CO₂ concentrations are the primary drivers of vegetation change, tectonically driven topographic changes probably also contributed to habitat fragmentation and variability across East Africa, which could have affected the ranges of ungulate taxa throughout the Pleistocene.

There is little doubt that climate and tectonics strongly influence East African paleoenvironments during the Pleistocene. However, as emphasized by Blome et al. (2012), determining the precise nature of environmental changes and their underlying mechanisms in the Lake Victoria basin and across East Africa will require improved chronological control and more refined paleoenvironmental records.

Implications for Early Human Dispersals

Biogeographic evidence suggests that climate-driven vegetation changes across equatorial East Africa played an important role in mediating the distribution of ungulate species, with the expansion of grasslands facilitating interchange across East Africa (Lorenzen et al. 2012). This is corroborated by the fossil records from Rusinga and Mfangano Islands, which show that ungulate species with historically allopatric ranges converged in equatorial East Africa at a time when Lake Victoria was much reduced, if not desiccated, and grasslands were widespread (Tryon et al. 2014). Presumably, the loss of grasslands and expansion of the equatorial forest belt at the onset of the Holocene and during previous humid intervals with high atmospheric CO₂ concentrations (Cowling et al. 2008) would have prompted range shifts and fragmentations in species distributions approaching those observed historically. What are the implications of these patterns for early modern human dispersals?

In the Paleolithic archaeological record, diagnostic lithic technology represents one of the few means of tracking human dispersals. On its own, the extent to which the movement of technological markers reflects the dispersal of human populations (and their genes) is uncertain, but it at least documents the dispersal of human behavioral repertoires. There is abundant ethnographic evidence showing that the subsistence behaviors and associated technologies of historic hunter-gatherers are very closely linked to the environment (Oswalt 1973; Kelly 1995; Binford 2001; Collard et al. 2005), in which case it is reasonable to suppose that the movement of technological markers linked to specific environments might parallel the broader patterns observed in the ungulates. Below we explore some possible links between the distributions of technologies in the Lake Victoria region in relation to paleoenvironmental change.

The Lake Victoria MSA

Previous discussions of distinct technological markers from the Lake Victoria region have focused on the Lupemban industry, which represents one of the more distinct MSA regional variants, characterized by the presence of large (>10 cm), thin, bifacially flaked lanceolate points. These lanceolates are well known from central Africa (Barham 2000; Mercader 2002), although their distribution extends to the eastern margins of Lake Victoria, including near-shore islands (Leakey and Owen 1945; Nenquin 1971; McBrearty 1988; Tryon et al. 2012; Taylor 2016). Where paleoenvironmental records are available, the Lupemban is typically associated with forested vegetation (Barham 2000; Mercader 2002; Taylor 2016).

The vegetation of the Lake Victoria region today represents a mosaic of endemic taxa from neighboring regions (White 1983), attesting to the past expansion and contraction of vegetation communities, a model consistent with the implications of the ungulates from Rusinga and Mfangano Islands (Table 13.1), the distribution of modern faunas (e.g., Kingdon 1989; Wronski and Hausdorf 2008), and paleo-vegetation models (e.g., Cowling et al. 2008). To the extent that the distribution of Lupemban artifacts is tied to forested paleoenvironments, we expect that its easternmost occurrences in the Lake Victoria basin to be associated with an expanded equatorial forest belt. As shown in Fig. 13.5, all of the Lupemban sites in the eastern portion of the Lake Victoria basin lie along now submerged portions of major rivers that traversed the basin prior to peak lake size sometime during the Middle or Late Pleistocene (Temple 1966;

Scholz et al. 1998). These sites represent the easternmost limits of the Lupemban, and include Muguruk on the Winam Gulf in Kenya (McBrearty 1988), sites reported by Leakey and Owen (1945) in the Yala River valley of Kenya, and on Bugaia Island in Uganda (Nenquin 1971). The nearby rivers would have likely provided naturally wooded corridors facilitating the expansion of forest-adapted taxa and technologies, perhaps including the Lupemban, around the margins of Lake Victoria.

The MSA assemblages from the Wasiriya and Waware Beds of Rusinga and Mfangano Islands are typologically distinct from Lupemban assemblages in the Lake Victoria region or elsewhere, which is not surprising given the associated grassy paleoenvironment. In light of the evidence from ungulate biogeography, it is possible that the expansion of grasslands would facilitate the movement of people or technological traditions associated with these environments from broad East African regions north or south of the equator. In previous studies (Tryon et al. 2012; Tryon and Faith 2013), we identified one possible example of this. The lithic assemblages from Rusinga and Mfangano Islands (Fig. 13.3) include very small (2–4 cm in length) bifacially flaked points that overlap in size with those from MSA sites throughout the East African Rift System. These include the Late Pleistocene MSA or MSA/LSA assemblages from Nasera Rockshelter in Tanzania (~290 km southeast), site GvJm-16 at Lukenya Hill in Kenya (~340 km east southeast), and Aduma in Ethiopia (~1,390 km northeast). At all of these sites, the associated faunas or other paleoenvironmental records indicate grassland vegetation comparable to that inferred for Rusinga and Mfangano Islands, raising the possibility that these small points represent either a human population or (more likely) a technology associated with Late Pleistocene tropical grasslands. This possible connection to Rift Valley sites is further supported by the rare presence of obsidian from the Wasiriya Beds, the nearest outcrops of which are from Rift Valley sources ~250 km to the east.

The small MSA points found on Rusinga and Mfangano Islands and in the Rift Valley are rare to the west of Lake Victoria, reported only from Kibwera in Tanzania (Reid and Njau 1994), although unfortunately no illustrations or photographs are provided (Fig. 13.5). Assuming that points and other artifacts produced by hunter-gatherers are to some extent a reflection of the environment in which they were used, the geographic limits of different types of MSA point (small points versus Lupemban lanceolates) along the margins of present-day Lake Victoria (Fig. 13.5) is consistent with the hypothesis that this area is a nexus of environmental changes that facilitated the movement of people and their technological markers.

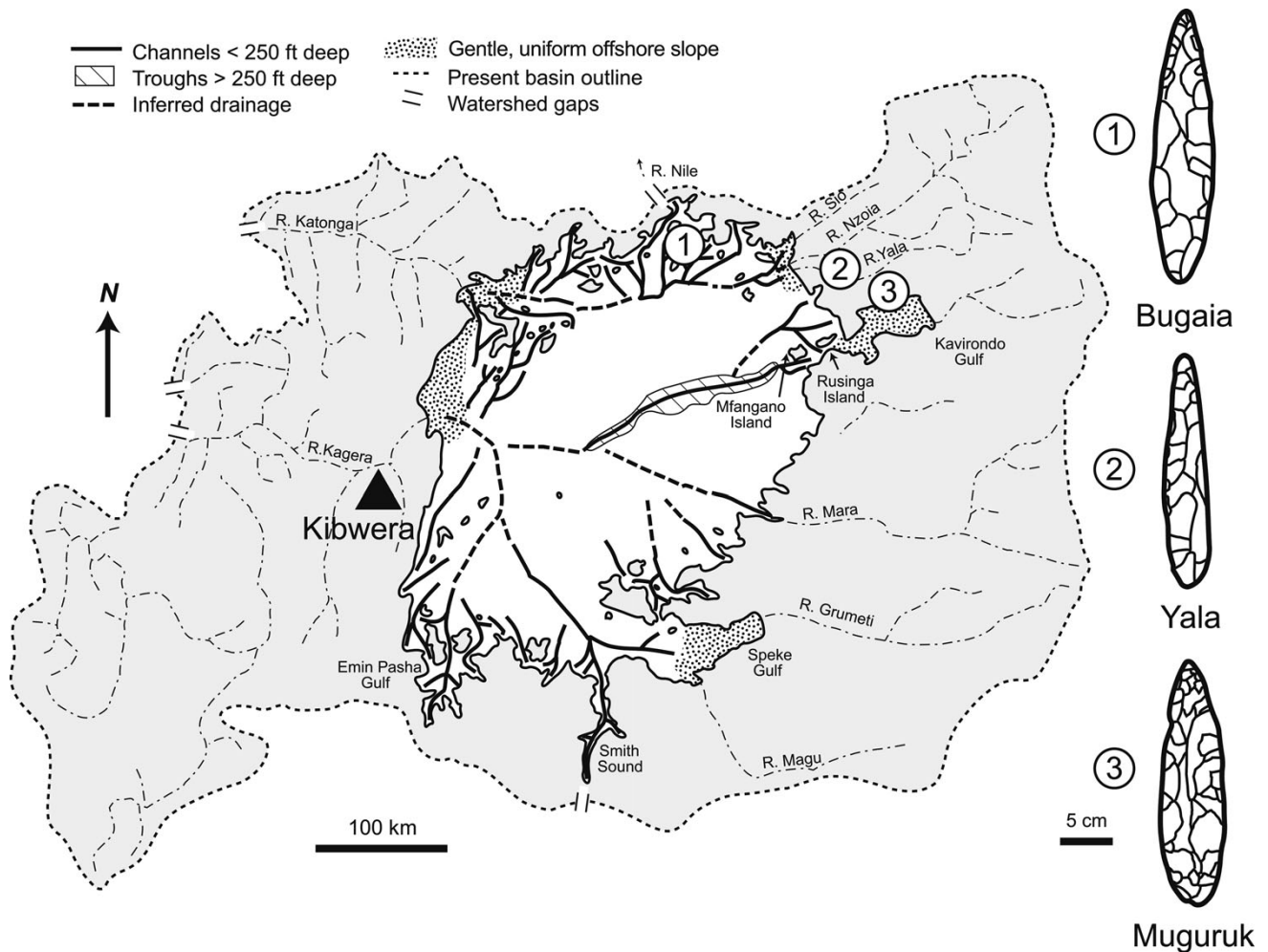


Fig. 13.5 Buried river channels across the Lake Victoria basin, simplified after Temple (1966). Note the proximity of the easternmost Lupemban lanceolate sites to major east-west flowing rivers that traverse the basin. Smaller MSA points are not reported in the western

portion of the Lake Victoria basin except at Kibwera (illustrations unavailable). Artifact sketches after Leakey and Owen (1945), Nenquin (1971), and McBrearty (1988), and illustrated at same scale

Conclusions

Biogeographic evidence provides a compelling argument that environmental changes across late Quaternary climate cycles mediated the distributions and dispersals of ungulate species via the opening and closing of barriers and dispersal corridors in equatorial East Africa. For a broad range of savanna ungulates, dispersal capabilities would have been enhanced during phases of grassland expansion and diminished during phases of grassland contraction, leading to repeated range expansions and fragmentations.

These patterns are of importance to human origins research, as genetic evidence documents multiple East African dispersals of early modern humans during the Late Pleistocene, both within and out of Africa (Campbell and Tishkoff 2010; Soares et al. 2012, 2016). We propose that, as is clearly the case for ungulates, the distribution and

dispersals of diagnostic technological markers in the archaeological record may also be mediated by environmental changes. The archaeological record from the Lake Victoria region provides some intriguing examples of possible environmentally mediated technological dispersals, but it is clear that a better sampled archaeological record and improved chronology is crucial to fleshing out these patterns. Although such limitations are an ever-present problem that can only be resolved through further fieldwork, the patterns explored here provide an initial framework for exploring the dispersal of early human populations migrations and expansions during a critical stage in human evolution.

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