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Stable isotope analysis of carnivores from the Turkana Basin, Kenya: Evidence for temporally-mixed fossil assemblages

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ABSTRACT

Stable isotope palaeoecology of fossil mammals is a key research tool for understanding the environmental context of hominin evolution in the Plio-Pleistocene of Africa. Well studied mammal groups include bovids, suids, equids, proboscideans and primates, but to date there has been no in-depth study of modern and fossil carnivores. Here we produce an Africa-wide oxygen and carbon enamel isotope dataset for modern carnivores and compare it with fossil carnivore data sampled from the Plio-Pleistocene Omo Group of the Turkana Basin, Kenya. Comparison of modern carnivore carbon isotopes with satellite images of land cover indicates that carnivore $\delta^{13}\text{C}$ is related to the proportion of woody cover in the local environment. Modern carnivore oxygen isotopes are strongly influenced by the $\delta^{18}\text{O}$ of meteoric water, through drinking from standing water and through prey body fluids. Carbon isotope data from fossil carnivores shows close agreement with palaeovegetation reconstructions from $\delta^{13}\text{C}$ of palaeosol carbonates from the same geological Members, and a similar long-term trend in $\delta^{13}\text{C}$ values through time (4 Ma to 1 Ma), reflecting a gradual increase in the proportion of C_4 grasses in the Turkana Basin. This increase in the $\delta^{13}\text{C}$ of large carnivores is consistent with the evidence from other mammalian groups for an increase in the proportion of grazers compared to browsers and mixed feeders during this time interval. Two distinct trends within oxygen versus carbon isotope space indicates that the fossil carnivores lived during two distinct climatic regimes – one in which palaeo-lake Turkana was freshwater, and one in which the lake resembled its modern-day hyperalkaline state. These two climatic states most likely represent the end-members of precessionally-driven rainfall extremes over the Ethiopian Highlands. This indicates that each studied faunal assemblage from the Omo Group is a time- and climate-averaged palimpsest; this has significant implications for the interpretation of environmental signals and community palaeoecology derived from Turkana Basin fossil mammals, including early hominins.

1. Introduction

Herbivore fossils are abundant at Plio-Pleistocene fossil localities. Stable isotope analysis of herbivore enamel has provided numerous insights into the palaeodiet and palaeoenvironment of African mammals,

especially within the context of early hominin evolution (e.g. Cerling et al., 2015). Recent studies have shown that community-scale analysis of herbivore carbon isotopes does not provide a straight-forward reconstruction of African vegetation cover in either present day (Robinson et al., 2021) or past (Du et al., 2019) ecosystems. This study takes a

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novel approach to palaeoenvironmental reconstruction by focusing on the stable isotope palaeoecology of fossil carnivores.

1.1. Carnivore diets, behaviour and ecological integration

Members of the carnivore guild share a similar behavioural approach to the selection of prey (including prey abundance and the presence of competitors; Cooper et al., 2006). Prey body mass is a fundamental determinant of prey choice and predation style (Carbone et al., 1999; Hayward et al., 2007a,b), and in addition, individual species have preferences for certain prey body masses, often in direct relation to their own body mass (Tucker and Rogers, 2014). By nature of their hunting style, different carnivore species have preferred hunting habitats, for example leopards prefer to prey in dense habitats (Hayward et al., 2006) whereas lions prefer to hunt in more open country (Hayward and Kerley, 2005), often in the vicinity of water holes (Hayward and Hayward, 2012). These hunting strategies contribute to the choice of prey species, the body mass of selected prey and the dietary specialisations (and therefore carbon isotope value) of the herbivore prey.

Stable isotope palaeoecology has been used to determine the dietary preferences of fossil carnivores from the Pleistocene of Europe and the Americas. Studies of contemporaneous carnivores have yielded evidence for dietary specialisations and niche partitioning (e.g. Palmqvist et al., 2008; DeSantis et al., 2021), whereas other studies have highlighted generalist diets and overlapping niches (e.g. Feranec and DeSantis, 2014; Domingo et al., 2016). Only a limited number of studies have investigated the stable isotope ecology of modern or fossil carnivores in Africa. Most modern isotopic data derives from hair or faeces (e.g. Codron et al., 2007, 2016, 2018; Voigt et al., 2018) and occasionally bone collagen (e.g. Ambrose and DeNiro, 1986). The geographical range of these studies is small, and stable isotope measurements on tooth enamel are rare, limiting the interpretation of fossil tooth enamel isotope data. A moderate-sized dataset ($n = 55$) of Plio-Pleistocene carnivore enamel carbon isotope analyses from South Africa has been collated by Hopley and Maslin (2010), but a similar dataset for East African fossil localities is lacking.

When comparing the palaeodietary signature of the carnivore guild to that of the herbivore guild, it is fruitful to consider the role of carnivores as ecological integrators (Bump et al., 2007; Fox-Dobbs et al., 2012). The generalist diet (relative to the dietary preferences of their prey) of individual carnivores typically leads to isotopic integration of the regional vegetation through consumption of numerous herbivorous prey (e.g. Feranec and DeSantis, 2014; Domingo et al., 2016). In contrast, individual herbivores display dietary preferences, such as grazing or browsing, that may not be a true reflection of the regional vegetation, especially in mosaic environments (e.g. Robinson et al., 2021). For herbivore isotopes to inform on vegetation composition they cannot be considered on the basis of singular measurements; instead, the data from numerous individuals is averaged to represent an isotopic community, either modern or fossil (e.g. Cerling et al., 2003; Cerling et al., 2015; Robinson et al., 2021). The palaeovegetation signal derived from carnivore carbon isotopes provides additional insight into ecological structure, especially when considering the numerous taphonomic processes that impact herbivore species representation within fossil assemblages (e.g. Cutler et al., 1999; Du and Behrensmeyer, 2018).

2. Regional setting

The Turkana Basin is located within the Kenyan Rift, the deepest segment of the East African Rift System (EARS). The geology of the basin consists of a thick sequence of volcanic deposits (Rooney, 2020), lacustrine (Boes et al., 2018) and lake-margin sediments (Levin et al., 2011) accumulated within a series of half-grabens since the Oligocene (Feibel, 2011). From the earliest Pliocene onwards, the Turkana Basin developed into an integrated depositional system that fluctuated between floodplain systems associated with the ancestral Omo River

(sourced from the Ethiopian highlands to the north), and lacustrine systems during which much of the basin was inundated (Feibel, 2011; Boes et al., 2018). Plio-Pleistocene sediments from the Turkana Basin belong to the Omo Group (4.3–0.6 Ma) and are sub-divided into a number of units including the Kanapoi, Koobi Fora, Nachukui and Shungura Formations.

The Shungura Formation outcrops in the lower Omo River Valley of S.W. Ethiopia and is dominated by fluvial sedimentation associated with the ancestral Omo River. To the south of the Shungura Formation, in northern Kenya, are the Kanapoi, Koobi Fora and Nachukui formations, exposed today to the west and east of Lake Turkana. The Nachukui Formation was deposited close to the faulted margin of the half-graben, resulting in a dynamic complex of axial river deposits, lacustrine sediments, high-energy shoreline deposits and alluvial conglomerates (Harris et al., 1988). Sediments of the Koobi Fora Formation (Brown and Feibel, 1991) comprise fluvial deposits (from the palaeo-Omo river and from smaller river systems draining the eastern margins of the basin), lacustrine sediments and deltaic deposits. The Kanapoi Formation was accumulated in a deltaic environment on the margin of palaeolake Lonyumun and the proto-Kerio river (Feibel, 2003; Van Bocxlaer, B., 2020; Quinn and Lepre, 2020) to the south west of modern-day Lake Turkana.

The Plio-Pleistocene landscape of the Turkana Basin, as recorded in Omo Group deposits, can be characterised as a dynamic interplay of fluctuating lake levels, rivers, deltas and volcanoes (Feibel, 2011). This complex history can be simplified through the recognition of periods of time dominated by high lake levels (lake phases) and periods of time dominated by low lake levels (floodplain phases). Major lake phases include palaeo-lakes Lonyumun (~4.1 Ma; van Bocxlaer et al., 2020), Lokochot (~3.4 Ma; Feakins et al., 2007) and Lorenyang (~2 Ma; Lepre et al., 2007; Lepre, 2014). Further to these protracted periods of high lake levels, evidence for high-frequency lake level fluctuation within the Turkana Basin is widespread (Lepre et al., 2007; Garcin et al., 2012; Boes et al., 2018). The impact of this dynamic hydrologic environment on the water requirements and oxygen isotopic composition of Plio-Pleistocene mammals is yet to be fully resolved (Quinn, 2015).

2.1. Prior Turkana Basin stable isotope work

Carbon and oxygen isotope palaeoecological analysis of the Plio-Pleistocene sediments and fossils of the Omo Group has been extensive. Turkana Basin palaeosols, fossil molluscs and fossil mammals have all been the focus of in-depth stable isotope studies (e.g. Levin et al., 2011; Vonhof et al., 2013; Du et al., 2019). Among the fossil mammals, herbivores and hominins have been the focus of stable isotope studies (e.g. Cerling et al., 2013a, 2015); these extensive datasets have been used both as palaeodietary proxies (e.g. Cerling et al., 1999, 2013b) and as palaeoenvironmental indicators (e.g. Cerling et al., 2015; Blumenthal et al., 2017).

Comparison of contemporaneous palaeosol and tooth enamel isotopic datasets offers an opportunity to evaluate the palaeoecological signals preserved within these geochemical proxies. Du et al. (2019) undertook such a comparison for 16 east African geological members, including 12 Members from the Omo Group of the Turkana Basin. This study showed that the median carbon isotope value of fossil herbivores is typically 5–7‰ higher than that of palaeosol carbonate from the same geological unit. This offset is likely a function of the different spatio-temporal scales at which the two proxies assimilate environmental information (Du et al., 2019). Palaeosol carbonates form over a period of 100–1000 years with a restricted geographic range whereas tooth enamel forms over a period of approx. 0.1–1 year, representing a broader geographic range (dependent on the foraging range of the individual). Du and colleagues interpreted the lower carbon isotope values of palaeosol carbonate as representative of wooded floodplains, whereas the higher fossil tooth enamel values represent a broader savannah-woodland environment beyond these riparian woodlands.

This interpretation considers different spatial scales, but does not consider longer-term sedimentological or climatic controls – for example, palaeosols form during discrete time intervals within lake transgression/regression cycles and the temporal distribution of faunal assemblages within these cycles is largely unknown. The Du et al. (2019) study highlights the importance of understanding the geological biases inherent in stable isotope proxies, and the value of a multi-proxy approach, although it is clear that more interpretative work is required. With these considerations in mind, we investigate the potential of new stable isotope proxies derived from the carbon and oxygen analysis of fossil carnivores from the Turkana Basin.

2.2. Extinct carnivorous species studied

Following is a summary of current interpretations of the palaeobiology and palaeoecology of the extinct carnivore species studied in this paper, including their temporal range:

2.2.1. Felidae (cats)

Dinofelis (Werdelin and Lewis, 2001) – This is a genus of machair-odont (sabertooth cat) that lacked the sabers characteristic of its relatives. Robust forelimbs for grappling and short distal limb elements show that *Dinofelis* species were likely ambush predators that preferred closed or mixed habitats. In this they resembled leopards of today but were larger (jaguar to lion-sized). Three species were present in the Omo Group: *Dinofelis petteri* (approx. 4.1 to 2.6 Ma) was of moderate size; *Dinofelis aronoki* (approx. 3.1 to 1.6 Ma) was larger; *Dinofelis piveteaui* (approx. 1.6 to 1.0 Ma) was again smaller and had narrower upper canine teeth. This more ‘saber-tooth’ appearance may have been the result of greater competition with lions and leopards after approx. 1.8 Ma. The last species is also found in South Africa.

Homoherium (Werdelin and Lewis, 2013) – This genus of sabertooths had medium-length sabers and long limbs for running. All its teeth were serrated for better cutting ability. The taxonomy within this genus has not been fully worked out for African species, but all known finds are quite similar in general appearance. The anatomical adaptations suggest a preference for open habitats and cursorial pursuit predation. *Homoherium* sp. (approx. 4.1 to 1.5 Ma) is known from all parts of Africa and is common in Omo Group sediments until ca 2 Ma after which it becomes increasingly rare.

Megantereon (Lewis and Werdelin, 2010) – A genus of sabertooths with extreme saber adaptations. Short-limbed and with very strong forequarters they were adapted for ambush predation in closed habitats. Two species are known from Omo Group sediments, *M. ekidoi* from South Turkwell (not studied here) and *M. whitei* (also known from South Africa). *Megantereon* is much less common than the previous two genera and likely more of a habitat specialist. Known in the Omo Group from approx. 3.5 to 1.5 Ma.

2.2.2. Hyaenidae (hyaenas)

Parahyaena (Werdelin, 2003; Werdelin and Manthi, 2012) – This is the genus to which the living brown hyaena (*P. brunnea*) belongs. *Parahyaena howelli* was a generalized hyaena without the extensive adaptations to scavenging seen in its living congener. It had cursorial adaptations and was likely an open habitat form. It is the most abundant carnivore at Kanapoi but is not found in slightly younger sediments of the Omo Group, such as Koobi Fora, likely having been replaced by species of *Crocota*. Age range approx. 4.3 (at Laetoli) to 3.9 Ma.

Crocota (Lewis and Werdelin, 2022) – This is the genus to which the living spotted hyaena belongs. It is a common member of the fossil record of the Omo Group, with a distinct evolutionary trajectory from small forms similar to the striped hyaena of today, to large scavenging forms with adaptations akin to those of the living brown hyaena, to the active pursuit predator (still with scavenging adaptations) of today. Three fossil forms are recognized in the Omo Group sediments: *C. venustula*, small to medium-sized forms with moderate scavenging

adaptations (approx. 4 to 1.5 Ma); *C. eturono*, large, poorly known form with dentition that was not adapted for scavenging (approx. 4 to 2.6 Ma); *C. ultra*, species of moderate to large size with distinct scavenging adaptations but lacking the hunting adaptations of the extant species (approx. 2.5 to 0.5 Ma). The first and third species are also known from South Africa.

3. Material and methods

3.1. Age and context

The carnivore taxa considered here derive from the Kanapoi Formation (Kanapoi Member), Koobi Fora Formation (Lonyumun, Tulu Bor, Upper Burgi, KBS and Okote Members) and Nachukui Formation (Natoo and Lomekwi Members) and are of comparable age to the Shungura Formation in the lower Omo Valley, as shown in Fig. 1. K/Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ dates from the sequence are derived from all four formations and many volcanic ashes are correlative between the formations. Time intervals used in this study are based on correlative marker horizons between the Koobi Fora and Nachukui Formations.

3.2. Stable isotope analysis

Modern carnivore teeth ($n = 108$) were sourced from museum collections and from local collectors. The osteological collection of the Hunterian Museum of the Royal College of Surgeons, London (RCSOM) provided 26 specimens collected between 1930 and 1947; provenance data varied in detail from country-wide to a specific locality and altitude. The Osteology Section at the National Museums of Kenya, Nairobi, provided 48 specimens collected between 1968 and 2012 with regional-scale provenance. The majority of specimens are from Kenya ($n = 79$); other countries represented are Botswana, Malawi, Nigeria, Somaliland, Tanzania and Zimbabwe. Environmental settings of the modern carnivores range from the montane forests of Mt Kilimanjaro, Tanzania, to the arid hypersaline lake-margins of Lake Rukwa, Tanzania.

Fossil carnivore teeth ($n = 52$) were sourced from the palaeontological collections of the National Museums of Kenya, Nairobi. Sampled carnivore fossils from the Omo Group of the Turkana Basin come from the Kanapoi, Koobi Fora and Nachukui Formations. Sampled formations and members are those that have yielded an abundant and diverse collection of fossil carnivores. The majority of fossil specimens ($n = 36$) could be identified to the species level; the remainder were identified to genus.

Approximately 5–7 mg of tooth enamel was sampled from each specimen using a diamond-tipped drill bit. For modern and fossil specimens, the sampled tooth (canine, incisor, molar or premolar) was chosen with the intention of minimising the impact on diagnostic tooth morphology and on the preservation of the specimen as a whole. Bulk enamel samples were usually taken longitudinally, between the cusp and the cervix, integrating at least 3–6 months of dietary signal (Green et al., 2018). The sampled enamel usually represents a post-weaning diet, although this may not be the case for some species of Hyaenidae (Binder and Van Valkenburgh, 2000).

Enamel powders were pretreated using dilute acetic acid and sodium hypochlorite or hydrogen peroxide, following the standard procedures (e.g. Lee-Thorp et al., 1997; Crowley and Wheatley, 2014). Samples were analysed using dual inlet and continuous flow mass spectrometry at the University of Utah and at University College London respectively. Results are reported in the standard permil (‰) notation relative to the Vienna Pee Dee Belemnite (VPDB) international standard. $\delta^{13}\text{C}$ values of modern enamel were corrected to the common reference time of 1750, considered to be the beginning of the Industrial Revolution, using atmospheric $\delta^{13}\text{C}$ data for the change in isotopic ratio of atmosphere due to human activities (Francey et al., 1999; Keeling et al., 2010); the $\delta^{13}\text{C}_{1750}$ value for atmospheric CO_2 is taken to be -6.3‰ .

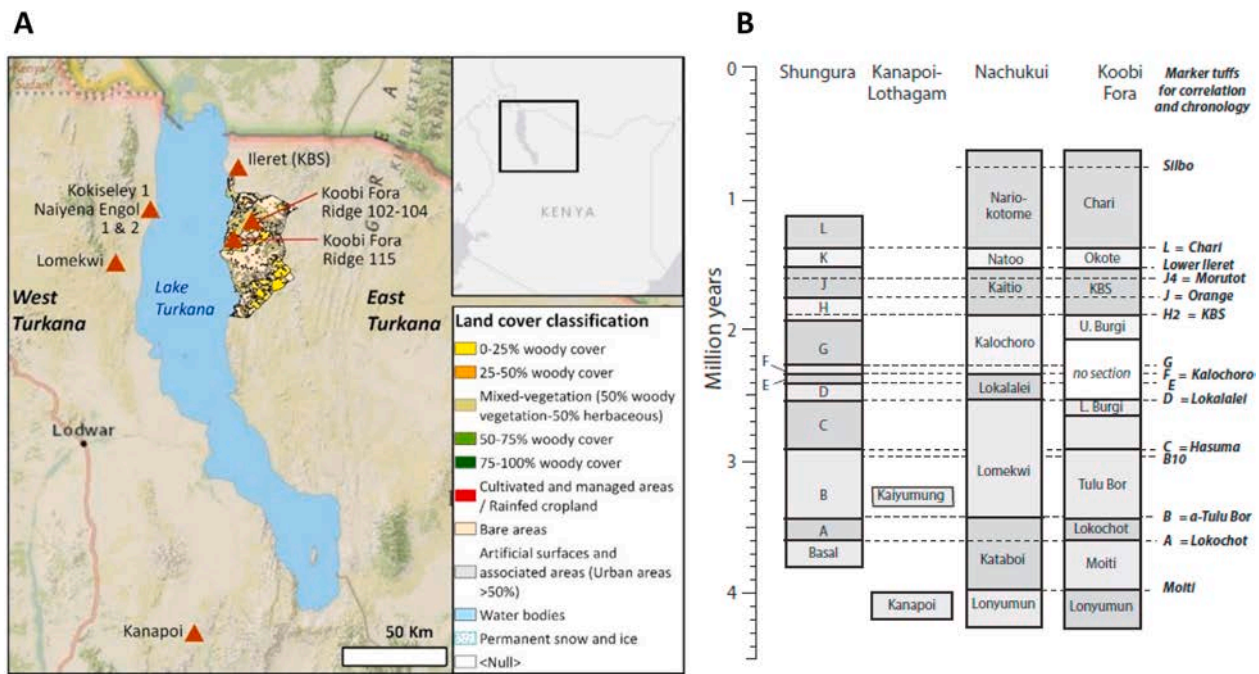


Fig. 1. (a) Map of the Turkana Basin, Kenya, showing the localities from which Plio-Pleistocene carnivores were collected. Modern carnivore specimens were collected from Sibiloi National Park; shading indicates the land cover categories used to infer woody cover for comparison with carnivore carbon isotope measurements. (b) Stratigraphic relationships in the Turkana Basin for the Shungura, Nachukui, Koobi Fora and Kanapoi Formations. Dashed lines show important volcanic ash layers (tuffs) used for correlation between formations. Stratigraphic and age information from Brown and Feibel (1986), Brown and McDougall (2011), McDougall et al. (2012) and Cerling et al. (2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. Carnivore prey preferences

The preferred prey species of extant carnivores were taken from the CarniDIET dataset of Middleton et al. (2021). CarniDIET documents all observations of prey species (as determined from scat, kills and stomach content) for African carnivores; the herbivore species that frequently constitute a high proportion ($\geq 20\%$) of an extant carnivore species diet are listed in Table 1.

Carnivore prey preferences can also be represented as a function of carnivore body size (Tucker and Rogers, 2014). Carnivore body mass estimates for extant and extinct species were taken from the CarniFOSS database (Faurby et al., 2021); *Crocota ultra* and *Crocota venustula* do not feature in the database so their body masses were calculated from molar (carnassial) length using the regression equation from Van Valkenburgh (1990). The body masses of *P. leo*, *P. pardus* and *C. Crocota* can vary with sex, locality and latitude, so the CarniFOSS data for these species should be considered as conservative estimates. Species showing adaptation to sabertooth mode (*Dinofelis piveteaui* and *Homotherium* sp.) are likely to have overestimated body masses due to the increased relative length of their carnassials. Conversely, *Megantereon whitei* is likely to have an underestimated body mass due to its small teeth, relative to body size.

Calculations of mean and maximum prey body mass were undertaken using regression equations calculated from the body masses of extant Felidae and Hyenidae and their preferred prey species, using the datasets presented in Tucker and Rogers (2014a,b). The equations used are: $\log(y) = 1.6273 \log(x) - 1.2049$ and $\log(y) = 1.6022 \log(x) - 0.7423$ for mean and maximum prey mass respectively, where x = carnivore body mass and y = prey mass. These calculations reflect hunting behaviours only, and do not account for the scavenging of large prey species; nor can they distinguish between group and solitary hunting. For these reasons, the prey body mass calculations shown in Table 1 should be viewed as broad approximations only.

Prey preferences are represented as herbivore size classes 1–5, using the scheme presented in Faith et al. (2018). On the basis of these

prey-size categories, candidate prey species and their dietary preferences (grazer, browser or mixed-feeder), are listed for each fossil carnivore species (see Supplementary Dataset 2). The temporal range of herbivore and carnivore species was taken into account when identifying potential prey species, using the data presented in Faith et al. (2018).

3.4. Remote sensing of modern vegetation

Nine case study areas were selected based on the localities (see Supplementary Information) for which isotopic data were available for a minimum of two modern carnivore specimens ($n \geq 2$). Three different land cover products were available for this study, Africover (1995–1999), Globcover (2005–2006) and Globcover (2009). When possible, contemporaneous land cover products were chosen based on the date of collection of carnivore specimens; for early and mid-20th century specimens, appropriate land cover products were chosen (see Supplementary Table 1). The Africover project provides 30 m resolution derived from Landsat-5 TM (Thematic Mapper) and Landsat-7 ETM (Enhanced Thematic Mapper) (Kalensky, 1998; Fritz et al., 2010). The Globcover land cover products offer a 300 m spatial resolution based on the MERIS 300 m Full resolution Full Swath (FRS) products (Arino, 2007; Bontemps et al., 2008). For comparison, a recent study by Robinson et al. (2021) compared herbivore carbon isotopes with woody cover at 30 m $\times$ 30 m pixel resolution averaged over the 30-year period from 1986 to 2016, using the Landsat dataset generated by Venter et al. (2018).

A land cover classification of 12 classes was defined by aggregating the original Globcover and Africover classes (see Supplementary Information). Shapefile polygons for the studied localities were extracted from the World Database on Protected Areas (WDPA), where available; the maps (see Supplementary Fig. 1) were produced in ArcGIS (version 10.1) and subsequently analysed using the software FragStats (version 4.2.1). To estimate the fraction of woody cover present at each studied

Table 1

Body mass, prey body mass and preferred prey species of extant and extinct African carnivores. ¹Summary of observed and inferred predatory style; based on ecomorphology for extinct species (Werdelin and Lewis, 2001; Palmqvist et al., 2007; Bibi, 2018; Coca-Ortega and Perez-Claros, 2019; Bobe et al., 2020). ²Estimated body masses of extant and extinct species are from the CarniFOSS dataset (Faurby et al., 2021); species absent from the dataset are indicated with an asterisk (*), and their body mass is estimated using the regression equations of Van Valkenburgh (1990). ³Mean and maximum prey body mass calculated from the carnivore body mass estimate using regression equations calculated from the Felidae and Hyaenidae data presented in Tucker and Rogers (2014a,b). ⁴Herbivore size classes for extant and extinct species are from Faith et al. (2018) and follow the widely used scheme for African mammals: Size 1 (s1): <18 kg; Size 2 (s2) = 18–80 kg; Size 3 (s3) = 80–350 kg; Size 4 (s4) = 350 to 1000 kg; Size 5 (s5) = > 1000 kg. ⁵Preferred prey species of extant African carnivores taken from the CarniDIET dataset of Middleton et al. (2021); all species that constitute ≥20% of an individual carnivore's diet (≥1% for *H. hyaena*) more than once (more than twice for *P. pardus*; once for *H. hyaena*), are listed here. Preferred prey species of extinct carnivores are based on all herbivore species of the preferred size class found within fossil assemblages from the Turkana Basin, within the known temporal range of each carnivore species (all data from Faith et al., 2018; see Supplementary Dataset); the most common (greatest number of localities) herbivore species are listed here. ⁶Herbivore dietary preferences, whether extinct (reconstructed from extant congener, stable isotopes or dental microwear) or extant (observed), are from Faith et al. (2018); classification scheme is: G, Grazer; B, Browser; MF, Mixed-Feeder.

Species	Inferred Predatory style ¹ (observed)	Body Mass Estimate (kg) ²	Predicted mean (max) Prey Body Mass (kg) ³	Bovoid Size Class ⁴ of common prey species	Preferred Prey Species ⁵ (herbivore size class ⁴)	Prey dietary preferences ⁶
<i>Panthera pardus</i>	(ambush predator, preference for woody cover)	55	42 (111)	s1-s2	<i>Aepyceros melampus</i> (s2) <i>Cephalophus natalensis</i> (s1) <i>Kobus kob</i> (s2) <i>Oreotragus oreotragus</i> (s1) <i>Potamochoerus porcus</i> (s2) <i>Procavia capensis</i> (s1) <i>Sylvicapra grimmia</i> (s1) <i>Tragelaphus strepsiceros</i> (s3)	MF B G B MF MF B B
<i>Panthera leo</i>	(pursuit predator, open country)	161	243 (622)	s2-s4	<i>Aepyceros melampus</i> (s2) <i>Connochaetes taurinus</i> (s3) <i>Equus quagga</i> (s3) <i>Kobus kob</i> (s2) <i>Oryx gazella</i> (s3) <i>Syncerus caffer</i> (s4) <i>Tragelaphus strepsiceros</i> (s3)	MF G G G G (MF) G B
<i>Crocuta crocuta</i>	(scavenger, bone cracker)	63	53 (138)	s1-s5	<i>Aepyceros melampus</i> (s1) <i>Connochaetes taurinus</i> (s3) <i>Kobus vardonii</i> (s2) <i>Loxodonta africana</i> (s5) <i>Oryx gazella</i> (s3) <i>Camelus dromedarius</i> (s4) <i>Equus africanus</i> (s3) <i>Gazella granti</i> (s2)	MF G G B G (MF) B G MF
<i>Hyaena hyaena</i>	(scavenger, bone cracker)	42	27 (72)	s2-s4	<i>Equus quagga</i> (s3) <i>Phacochoerus africanus</i> (s2) <i>Sylvicapra grimmia</i> (s1) <i>Tragelaphus strepsiceros</i> (s3)	G G B B
<i>Parahyaena brunnea</i>	(scavenger and pursuit predator)	32	18 (47)	s1-s3	<i>Aepyceros sp.</i> (s2) <i>Antidorcas recki</i> (s2) <i>Kobus sigmoidalis</i> (s3) <i>Tragelaphus sp.</i> (s3) <i>Kolpochoerus limnetes</i> (s3) <i>Metridiochoerus andrewsi</i> (s3)	MF MF G B G G
<i>Dinofelis aronoki</i> (3.1–1.6 Ma)	Ambush predator, mixed or closed habitats	108	127 (328)	s2-s3	<i>Megalotragus sp.</i> (s3) <i>Kobus sp.</i> (s3) <i>Tragelaphus strepsiceros</i> (s3) <i>Kolpochoerus limnetes</i> (s3) <i>Metridiochoerus andrewsi</i> (s3) <i>Equus sp.</i> (s3) <i>Hippopotamus aethiopicus</i> (s4)	G G B G G G G
<i>Dinofelis piveteaui</i> (1.6–1.0 Ma)	Ambush predator, mixed or closed habitats	140	194 (497)	s3-s4	<i>Aepyceros shungurae</i> (s2) <i>Megalotragus sp.</i> (s3) <i>Kobus sigmoidalis</i> (s3) <i>Tragelaphus kyaloi</i> (s3) <i>Tragelaphus rastafari</i> (s3) <i>Eurygnathohippus hasumense</i> (s3) <i>Megalotragus sp.</i> (s3) <i>Kobus sigmoidalis</i> (s3) <i>Tragelaphus cf. kyaloi</i> (s3) <i>Kolpochoerus limnetes</i> (s3) <i>Metridiochoerus andrewsi</i> (s3) <i>Eurygnathohippus hasumense</i> (s3) <i>Nyanzachoerus kanamensis</i> (s4) <i>Giraffa pygmaea</i> (s4)	MF G G B B G G G G G G G B
<i>Dinofelis petteri</i> (4.1–2.6 Ma)	Ambush predator, mixed or closed habitats	73	67 (175)	s2-s3	<i>Aepyceros sp.</i> (s2) <i>Antidorcas recki</i> (s2) <i>Megalotragus sp.</i> (s3) <i>Kobus sigmoidalis</i> (s3) <i>Tragelaphus sp.</i> (s3) <i>Kolpochoerus limnetes</i> (s3)	MF MF G G B G
<i>Homotherium sp.</i> (4.1–2.0 Ma)	Pursuit predation, open country	181	294 (750)	s3-s4	<i>Tragelaphus sp.</i> (s3) <i>Kolpochoerus limnetes</i> (s3) <i>Metridiochoerus andrewsi</i> (s3) <i>Eurygnathohippus hasumense</i> (s3) <i>Nyanzachoerus kanamensis</i> (s4) <i>Giraffa pygmaea</i> (s4)	B MF MF G G G B
<i>Megantereon whitei</i> (3.5–1.5 Ma)	Ambush predator, preference for woody cover	76	72 (187)	s2-s3	<i>Aepyceros sp.</i> (s2) <i>Antidorcas recki</i> (s2) <i>Megalotragus sp.</i> (s3) <i>Kobus sigmoidalis</i> (s3) <i>Tragelaphus sp.</i> (s3) <i>Kolpochoerus limnetes</i> (s3)	MF MF G G B G

(continued on next page)

Table 1 (continued)

Species	Inferred Predatory style ¹ (observed)	Body Mass Estimate (kg) ²	Predicted mean (max) Prey Body Mass (kg) ³	Bovid Size Class ⁴ of common prey species	Preferred Prey Species ⁵ (herbivore size class ¹)	Prey dietary preferences ⁶
<i>Parahyaena howelli</i> (4.3–3.9 Ma)	Scavenger and pursuit predator, likely open country	38	23 (61)	s1-s3	<i>Metridiochoerus andrewsi</i> (s3) <i>Eurygnathohippus ethiopicum</i> (s3) <i>Raphicerus</i> sp. (s1) <i>Gazella</i> sp. (s2) <i>Tragelaphus kyaloi</i> (s3) <i>Eurygnathohippus</i> sp. (s3)	G G B MF B G
<i>Crocota ultra</i> (2.5–0.5 Ma)	Scavenger, bone cracker	70*	63 (164)	s1-s5	Overlap with contemporaneous predators e. g. <i>D. aronoki</i> , <i>D. piveteaui</i> , <i>Homotherium</i> sp., <i>M. whitei</i> , <i>P. leo</i> .	G, B, MF
<i>Crocota venustula</i> (4.0–1.5 Ma)	Moderate scavenging adaptations	47*	33 (86)	s2	<i>Aepyceros melampus</i> (s2) <i>Aepyceros shungurae</i> (s2) <i>Antidorcas recki</i> (s2) <i>Gazella janenschii</i> (s2) <i>Gazella praethomsoni</i> (s2)	MF MF MF MF MF
<i>Crocota eturono</i> (4.0–2.6 Ma)	Scavenger and pursuit predator	85	86 (223)	s2-s3	<i>Kobus kob</i> (s2) <i>Aepyceros shungurae</i> (s2) <i>Megalotragus</i> sp. (s3) <i>Kobus sigmoidalis</i> (s3) <i>Tragelaphus kyaloi</i> (s3) <i>Tragelaphus rastafari</i> (s3) <i>Eurygnathohippus hasumense</i> (s3)	G MF G G B B G

locality, a new landscape-level variable was calculated based on the class-level metrics extracted from the land cover maps, to build an index reflecting a gradient from open-grassland-dominated landscapes to woodland/shrubland/forest dominated landscapes. This new variable, woody-cover index, was calculated based on the PLAND values (i.e. Percentage of Landscape) of the main land cover classes used in the maps (classes 1 to 5), excluding all classes with no vegetation or with vegetation of unknown nature (classes 6 to 12); see [Supplementary](#)

[Table 3](#). The fraction of woody-cover can be considered a proxy for the proportion of C₃ vegetation in the ecosystem, with the exception of high-latitude localities (e.g. Aberdares, Kenya) where C₃ grasses are dominant above ca. 2500 m ([Tieszen et al., 1979](#)).

3.5. Oxygen isotopes in meteoric water

A reference database of oxygen isotopes in meteoric waters (river,

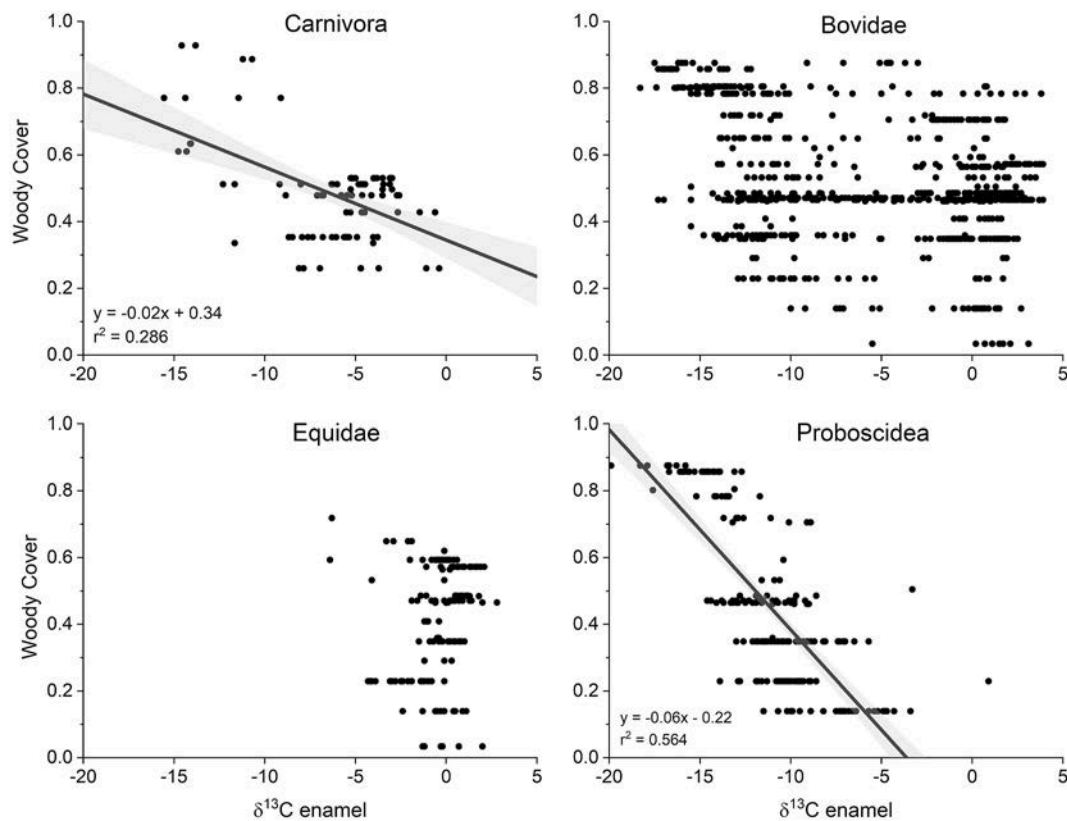


Fig. 2. Relationship between modern African carnivore $\delta^{13}\text{C}$ enamel and the fraction of woody cover in the local ecosystem, as determined from remote sensing data (see supplementary info). Modern carnivore localities are from Kenya, Malawi and Tanzania. Comparable datasets for African herbivore $\delta^{13}\text{C}$ enamel are from [Robinson et al. \(2021\)](#). Linear regression lines, equations and 95% confidence bands (grey shading) are shown for significant relationships.

lake, groundwater and ice) from the modern carnivore localities was collected from the literature (Cerling et al., 1988; Bergonzini et al., 2001; Thompson et al., 2002; Levin et al., 2009; Blumenthal et al., 2017; Kang'ethe, 2019; Banda et al., 2020; Bode et al., 2020); see Supplementary Dataset. The two leopard individuals from Mount Mulanje in Malawi (RCSOM/A 116.151 & 116.152) were collected in 1947, most likely from within the confines of the Mount Mulanje Forest Reserve (established in 1927) where the forested slopes range from an altitude of 800–1800 m. The plains surrounding the mountain are at an altitude of 600–700 m, including the local river water and groundwater localities analysed for oxygen isotopes (Banda et al., 2020). From this dataset, the oxygen isotopic composition of rainfall at an average altitude of 1300 m was estimated using the tropical isotopic lapse rate of -0.18‰ per 100 m of increased elevation, as quoted in Otte et al. (2016).

4. Results

4.1. Carbon isotopes and woody cover

There is a weak correlation ($r^2 = 0.286$) between modern carnivore $\delta^{13}\text{C}$ and the woody-cover fraction for the ecosystem from which they were collected (see Fig. 2). This is an equivalent relationship to that observed for woody cover and the enamel $\delta^{13}\text{C}$ of African Proboscidea ($r^2 = 0.564$) by Robinson et al. (2021), although proboscideans show a steeper gradient and a stronger preference for closed environments. The shallower gradient for carnivores implies no preference for open or closed environments. Carnivore prey taxa, such as the Bovidae and Equidae, do not show a significant relationship with woody-cover (see Fig. 2); Bovid $\delta^{13}\text{C}$ is independent of woody cover, whereas the Equidae are more commonly found in open environments. These datasets imply that African carnivores, like proboscideans, are effective integrators of vegetation (Robinson et al., 2021). Proboscideans are ecological integrators due to their dietary flexibility (browsing and some grazing) and their large body sizes; carnivores integrate through the consumption of multiple herbivore prey species (browsers and grazers) selected on the basis of abundance and catchability (Balme et al., 2007).

Robinson et al. (2021) reanalyse their dataset by removing forested (>80% woody cover) and high-elevation (>2000 m) localities, using the argument that Plio-Pleistocene fossil localities from East Africa are rarely, if ever, associated with either forested or high-elevation environments. A key reason for removing these datapoints is that high-elevation localities (such as Aberdares, Kenya) can contain C_3 grasses (with low $\delta^{13}\text{C}$ values) which herbivorous grazers, such as buffalo, will preferentially consume, distorting the relationship between $\delta^{13}\text{C}$ and woody cover. Unlike herbivores, carnivores are not selective feeders, so the impact of high-elevation C_3 grasses on the isotopic results is reduced. Just 4 out of the 108 modern carnivore teeth sampled are from localities with significant amounts of C_3 grasses (all Aberdares). An additional 4 samples are from high-elevation localities (Mt Mulanje, Malawi, and Mt Kilimanjaro, Tanzania) that have a high fraction of woody cover. These datapoints are valuable contributions to the dataset because they represent spatially restricted areas of forest, irrespective of altitude, when compared with the low spatial resolution of carnivore provenance within the low altitude localities. Restricted areas of low altitude forest are common in modern day east Africa, often as riparian corridors, and are likely to have been present during the Plio-Pleistocene; the high elevation localities included in this study function as an analogue for these environments.

4.2. Carnivore prey preferences

The CarniDIET dataset (Middleton et al., 2021) indicates that modern leopards (*Panthera pardus*) in Africa have a preference for browsing and mixed-feeding herbivore species; this contrasts with the preference of modern lions and hyaenas for grazing and mixed-feeding species (see Table 1). This is in agreement with behavioural observations of leopards

hunting at woodland margins (Hayward et al., 2006; Balme et al., 2007), lions hunting in relatively open habitats in the proximity of water sources (de Boer et al., 2010) and the significant dietary overlap between hyaenas and lions (Hayward, 2006). Due to recent contractions in the historical range of these species (e.g. Jacobson et al., 2016; de Manuel et al., 2020), it is likely that the dietary observations from select nature reserves are not representative of prey preferences across the entirety of their late Holocene sub-Saharan range.

The modern leopard carbon isotope dataset is distinct from that of the modern lion and the modern spotted hyaena (Fig. 4; Supplementary Fig. 2). *P. pardus* shows a clear preference for C_3 -browsing prey species ($\delta^{13}\text{C}$ mean = -10.4‰ ; min = -14.0‰ ; max = -3.5‰ ; $n = 27$), although some individuals do consume a significant proportion of grazing prey. Four *P. pardus* individuals are from high-altitude (C_3 dominated) localities (Mt Kilimanjaro, Tanzania and Mt Mulanje, Malawi), and five high-altitude *P. leo* individuals are from Aberdares, Kenya; these high-altitude individuals are not responsible for the observed carbon isotopic differences between the two modern species, although they should be considered when comparing the modern dataset with the persistent low-altitude environments of the Turkana Basin fossil localities. There is a dearth of evidence for *P. pardus* prey preferences over time, however carbon isotope values from Swartkrans Member 1 at approximately 1.8 Ma (Lee-Thorp et al., 2000) indicate a similar preference for browsing prey, including the occasional individual that consumes grazers ($\delta^{13}\text{C}$ mean = -7.6‰ ; min = -9.8‰ ; max = -2.2‰ ; $n = 7$). This indicates that while leopards have a preference for browsers, both in the modern day and in the Pleistocene, they exhibit predatory opportunism in their response to fluxes in prey abundance and prey species in space and through time. The two other modern carnivores featured in this study, *Panthera leo* and *Crocota Crocuta*, show a similar $\delta^{13}\text{C}$ range to the leopard, but their mean $\delta^{13}\text{C}$ values are higher (-3.8‰ , $n = 59$; -4.3‰ , $n = 29$ respectively), indicating more frequent hunting/scavenging in an open environment, in agreement with behavioural observations (Hayward and Kerley, 2005; Hayward, 2006; Middleton et al., 2021). A similar distribution of $\delta^{13}\text{C}$ values (mean = -5.3‰ ; min = -10.3‰ , max = -0.5‰) is seen among the 13 *P. leo* individuals from the Plio-Pleistocene of South Africa (Lee-Thorp et al., 2000, 2007). For further discussion of dietary niche partitioning and stock-raiding among modern carnivores, see Supplementary Information.

Palaeoecological analysis of the prey-size preferences of extinct African carnivores (see Table 1) suggests that all studied species were likely to consume a similar mixture of grazing, browsing and mixed-feeding herbivores. There is no obvious (palaeo)ecological distinction between the reconstructed dietary preferences of hunting and scavenging carnivores (see Table 1), nor is there a meaningful difference between the two Carnivora families, Felidae and Hyaenidae, or reconstructed predator body size (see Table 1). Carbon isotope results show an overlap between the $\delta^{13}\text{C}$ values of extinct carnivore species and the $\delta^{13}\text{C}$ values of modern *P. leo* and *C. crocuta* (see Fig. 4). There are no distinct species-specific patterns among the extinct carnivores, and no palaeoecological equivalent of the modern leopard (see Fig. 4). *Parahyaena howelli* (all specimens from Kanapoi, at approx. 4.1 Ma) has the lowest mean $\delta^{13}\text{C}$ values, suggesting a slight preference for browsing and mixed-feeding herbivores. However, C_3 vegetation was prevalent within the Pliocene ecosystem at Kanapoi (Manthi et al., 2020), so the *P. howelli* isotopic data may be a reflection of sampling from a single locality, rather than a distinct dietary preference of this species through time and space. Only one carnivore specimen, *Crocota ultra* (KNM-ER 358) from the KBS Member of the Koobi Fora Formation, has a $\delta^{13}\text{C}$ value (-10.9‰) indicative of a diet exclusively of browsing herbivores.

4.3. Carnivore water consumption

Studies of carnivore water requirements are rare, and observations are often anecdotal. Hayward and Hayward (2012) demonstrate that

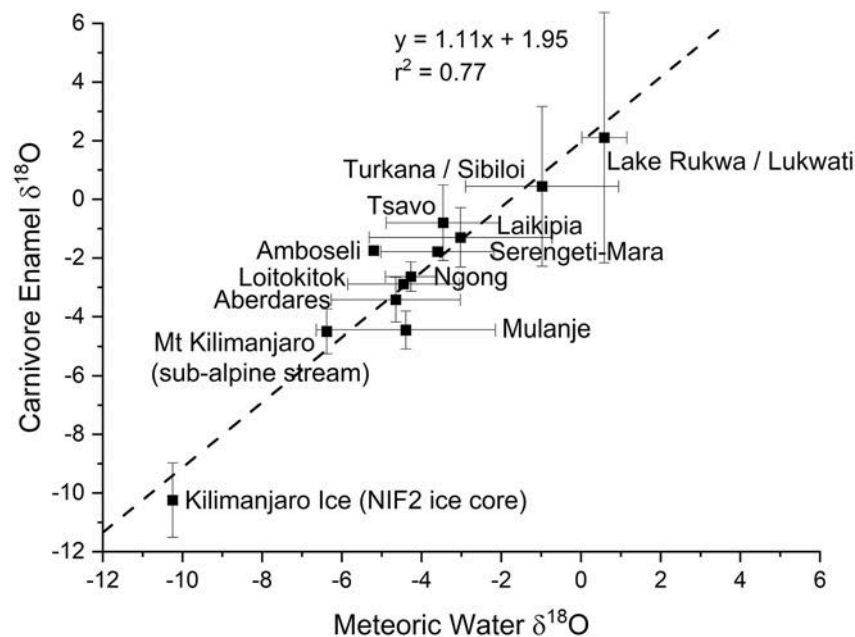


Fig. 3. Relationship between oxygen isotope values in modern carnivore enamel and local meteoric water. Meteoric water data from published sources (see Supplementary Dataset 1). Error bars indicate 1 s.d.

Panthera leo and *Crocuta crocuta* have low water needs, relative to water-dependant herbivores, and that they predominantly drink from waterholes at night. de Boer et al. (2010) found that lion kills occur within the vicinity of water sources, presumably due to the increased availability of prey at these localities. It is thought that carnivores are required to drink every few days (Clarke and Berry, 1992). In the arid conditions of Etosha National Park, Namibia, drinking was found to comprise 40% of lion water influx (Clarke and Berry, 1992), whereas in the Umfolozi Game Reserve in South Africa, lions showed seasonality in their water intake: ~50% from drinking in the warm summer months and ~10% from drinking in the colder winter months (Green et al., 1984). In this same study, spotted hyaenas ($n = 3$) were found to have negligible requirements for drinking water. Stock-raiding carnivores obtain some of their body water from farmed animals that drink from a broad range of water sources, including shallow wells and harvested rainwater (Njarui et al., 2014).

Results from the present study indicate a wide range in the $\delta^{18}\text{O}$ value of modern carnivores (-10.2 to $+3.2\text{‰}$). Mean carnivore $\delta^{18}\text{O}$ values per locality correlate strongly ($r^2 = 0.77$) with the mean $\delta^{18}\text{O}$ value of environmental water (see Fig. 3). Mean $\delta^{18}\text{O}_{\text{carnivore}}$ values are marginally higher than those of the local environmental waters. This may be due to the collection of water isotope data from substantial water bodies (e.g. lakes/streams), and the paucity of isotopic data from evaporatively-enriched sources such as ephemeral pools and leaf water (obtained by carnivores from herbivorous prey). This small isotopic offset indicates that the $\delta^{18}\text{O}$ of African carnivore tooth enamel is a high-fidelity proxy for the $\delta^{18}\text{O}$ of local environmental water. This is in agreement with the prediction (Kohn, 1996) and observation among North American felids (Pietsch and Tütken, 2016) that the $\delta^{18}\text{O}$ of carnivore biapatite tracks $\delta^{18}\text{O}$ of meteoric water. The environmental water dataset (see Supplementary Data #1) contains two sources of environmental water on Mt Kilimanjaro, Tanzania, each with distinct oxygen isotope compositions: sub-alpine stream water, collected in 2014–2015, with a mean annual $\delta^{18}\text{O}$ value of -6.4‰ and a Sep–Oct minimum of -7‰ (Bode et al., 2020), and mountain glaciers with a median $\delta^{18}\text{O}$ value of -10.2‰ (Thompson et al., 2002). The two leopards collected in 1946 from the cedar forests on the western slopes of Mt Kilimanjaro (see Supplementary Information) lived at a time when glacial extent and glacier retreat were greater than today (Cullen et al.,

2006). It is likely that the glacial meltwater contribution to sub-alpine streams in the 1940s was greater than during the 2014–2015 water isotope study of Bode et al. (2020), perhaps approaching values of -10‰ . If so, a more extreme seasonal variation in the $\delta^{18}\text{O}$ values of local water sources could explain the measured $\delta^{18}\text{O}_{\text{carnivore}}$ values of -10.2‰ (RCSOM/G 139.71) and -4.5‰ (RCSOM/G 16.51).

Modern carnivores living in the vicinity of alkaline lakes (Sibilo near Lake Turkana and Lukwati near Lake Rukwa) show the highest $\delta^{18}\text{O}$ values (min = -1.9 , max = 3.2 , mean = 0.8 , $n = 10$). At Sibilo National Park, bordering the eastern shore of Lake Turkana, lion ($n = 3$) and spotted hyaena ($n = 5$) show distinct $\delta^{18}\text{O}$ values: mean of $+2.6\text{‰}$ and -0.9‰ respectively. Hyaena values are similar to local river sources (-1.5‰), and lion values are approaching those of modern-day Lake Turkana water $\delta^{18}\text{O}$ values of $+5.8\text{‰}$ (Cerling et al., 1988, 2008; Cerling, 1996). This is consistent with the suggestion that hyaenas have a lower drinking need than lions (Green et al., 1984) and that they are well adapted to restricted water intake (Skinner et al., 1992). This data also indicates that the alkaline Lake Turkana waters offer a valuable drinking source for some carnivore species.

Oxygen isotope values of fossil carnivores from the Turkana Basin range from -6.3 to $+2.3\text{‰}$. This is equivalent to the range of values for low-altitude modern (all-Africa) carnivore $\delta^{18}\text{O}$ of -6.7 to $+3.2\text{‰}$ (excluding the 9 specimens from high-altitude localities: Mt Kilimanjaro, Aberdares and Mt Mulanje); this is an appropriate comparison, as high-altitude localities are rarely represented in the east African fossil record (e.g. Robinson et al., 2021). The Turkana Basin fossils have a much wider range of $\delta^{18}\text{O}$ values than modern carnivores from the Turkana Basin (Sibilo: -1.9 to $+3.2$, $n = 8$), representing a broader range of environmental waters than the alkaline lake and arid hinterland of today.

Comparable $\delta^{18}\text{O}$ measurements from fossil carnivores are rare. Palmqvist et al. (2008) present a small range of bone $\delta^{18}\text{O}$ values (min = -5.2 , max = -2.3 , $n = 10$) for Felidae and Hyaenidae from the Early Pleistocene of Spain; bone and enamel $\delta^{18}\text{O}$ values differ in their susceptibility to diagenetic alteration (Zazzo et al., 2004), making comparison difficult. Carnivores from the Late Pleistocene of California (Trayler et al., 2015) show possible site-specific enamel $\delta^{18}\text{O}$ trends in relation to altitude. Intra-tooth isotope analysis of two *Smilodon fatalis* canines (Feranec, 2004) shows seasonal change in $\delta^{18}\text{O}$ of up to 4‰ .

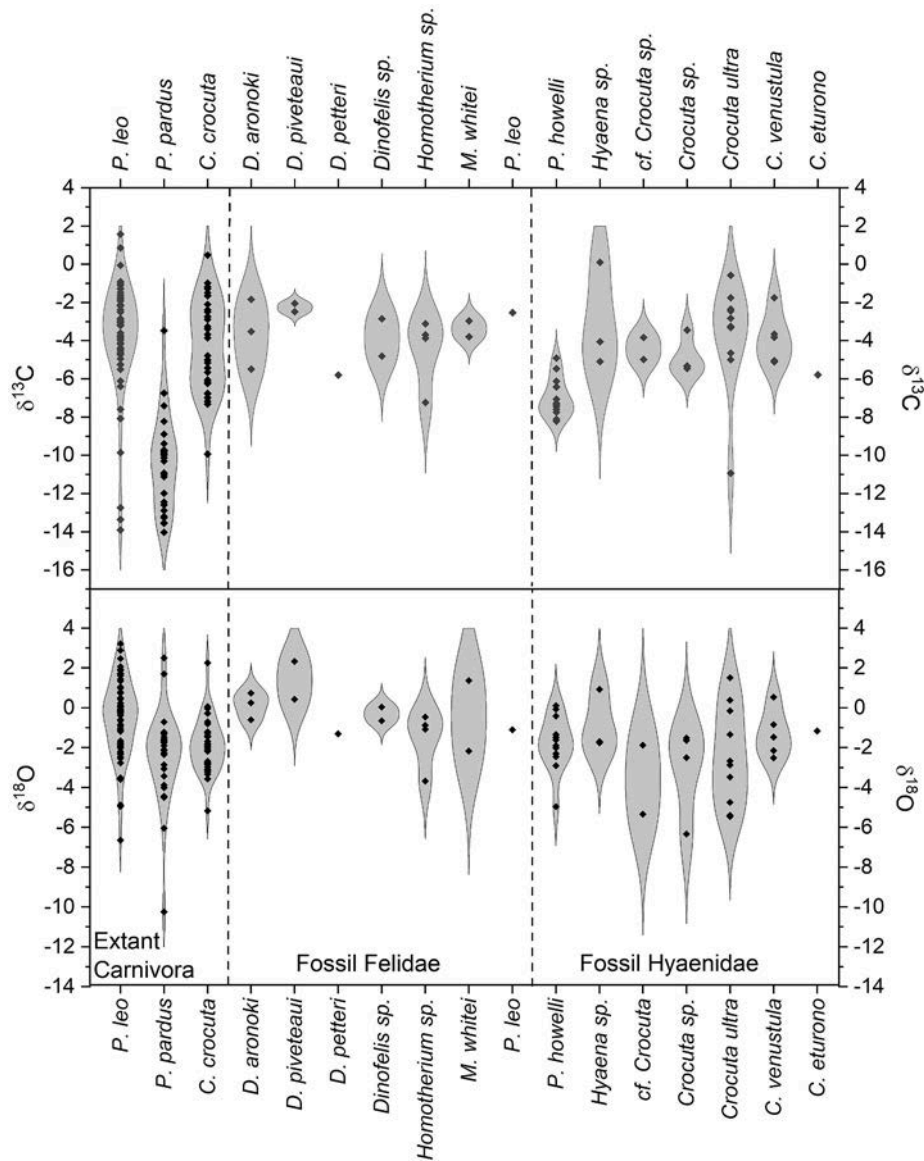


Fig. 4. Carbon and oxygen isotope values for fossil Felidae and Hyaenidae species from the Plio-Pleistocene of the Turkana Basin. Stable isotope values for extant species from modern localities across Africa are shown for comparison. See Supplementary Dataset 1.

This is likely due to increased evapotranspiration in the summer months, and demonstrates the sensitivity of fossil carnivore enamel $\delta^{18}\text{O}$ to the isotopic composition of environmental waters.

4.4. Comparison with other proxies

$\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of fossils carnivores from the Omo Group were compared with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from associated palaeosols (collated from [Levin, 2013](#); [Du et al., 2019](#); [Quinn and Lepre, 2020](#)) and fossil herbivore tooth enamel (collated from [Du et al., 2019](#); [Manthi](#)

Table 2

Comparison of median stable isotope values for palaeosol carbonate, fossil carnivores and fossil herbivores from members within the Kanapoi, Koobi Fora and Nachukui Formations of the Turkana basin.

Member	Age (Ma)	Palaeosol Carbonate			Fossil Carnivores				Fossil Herbivores		
		Median $\delta^{13}\text{C}$	Median $\delta^{18}\text{O}$	n	Median $\delta^{13}\text{C}$	Median $\delta^{18}\text{O}$	n analyses	n taxa	Median $\delta^{13}\text{C}$	n analyses	n taxa
Okote	1.5	-4.65	0.29	12	-2.27	-0.34	8	7	-0.60	93	17
KBS	1.8	-5.63	-2.58	28	-3.48	-1.70	12	4	-0.40	181	21
Upper Burgi	2.0	-5.90	-3.40	34	-3.84	-0.97	8	3	-0.10	181	21
Kaitio	1.7	-6.21	-1.42	13	-5.10	-1.70	1	1	-0.10	36	12
Lomekwi	3.4–2.5	-5.90	-4.37	13	-5.32	-4.88	5	2	-1.55	108	19
Tulu Bor	3.2	-7.39	-2.00	31	-5.79	-1.17	1	1	-2.40	17	9
Lonyumun	3.8	-8.17	-5.14	2	-5.68	0.51	2	1	-6.90	81	14
Kanapoi	4.1	-8.20	-4.10	53	-7.25	-1.55	14	3	-5.10	110	25

et al., 2020), see Table 2 and Fig. 6. A positive correlation ($R^2 = 0.72$) between $\delta^{13}\text{C}_{\text{carnivore}}$ and $\delta^{13}\text{C}_{\text{palaeosol}}$ indicates close agreement between these two complementary vegetation proxies, albeit with a small offset of 1.6‰. This is a far closer agreement than the approx. 5–7‰ offset found between $\delta^{13}\text{C}_{\text{herbivore}}$ and $\delta^{13}\text{C}_{\text{palaeosol}}$ by Du et al. (2019) at east African Plio-Pleistocene localities.

4.5. Statistical analyses

The FlexMix finite mixture model package in R (Leisch, 2004) was used to identify clusters within the isotopic datasets, and to determine their regression equations (see Fig. 8). The modern carnivores represent a single population ($\delta^{18}\text{O} = 0.26 \times \delta^{13}\text{C} + 0.16$, $\sigma = 1.51$), whereas the fossil carnivore dataset consists of two distinct populations (population 1: $\delta^{18}\text{O} = 0.25 \times \delta^{13}\text{C} + 0.29$, $\sigma = 1.21$ and population 2: $\delta^{18}\text{O} = 0.64 \times \delta^{13}\text{C} - 2.35$, $\sigma = 0.32$). The first fossil population overlaps with the modern dataset, although $\delta^{13}\text{C}$ values $< -8\text{‰}$ are rare. The second fossil population is characterised by distinctly low $\delta^{18}\text{O}$ values and a steeper regression line.

5. Discussion

5.1. Comparison with fossil herbivores and palaeosols

The fossil carnivores used in this analysis are derived from the same (sub)Members of the Omo Group, and from indistinguishable sedimentological and taphonomic contexts, as the fossil herbivores. The observed disagreement between their palaeovegetation reconstructions is striking and must relate to the distinct ecological context of their dietary behaviours. The carbon (and oxygen) isotope ecology of individual carnivores has been demonstrated to reflect the woody cover and hydrological conditions of their local environment (see Figs. 3 and 4); no such relationship has been established between modern herbivores and their environment (Robinson et al., 2021; Quinn, 2015). This is because the diet of an individual herbivore is highly selective (browser/-grazer/mixed feeder) and the average environment represented by a fossil herbivore assemblage is highly dependent on skeletal part representation over space and time. Our finding that $\delta^{13}\text{C}_{\text{herbivore}}$ at the (sub) Member level reconstructs a more open C_4 environment than $\delta^{13}\text{C}_{\text{carnivore}}$ can be explained in a number of ways (1) herbivore migratory

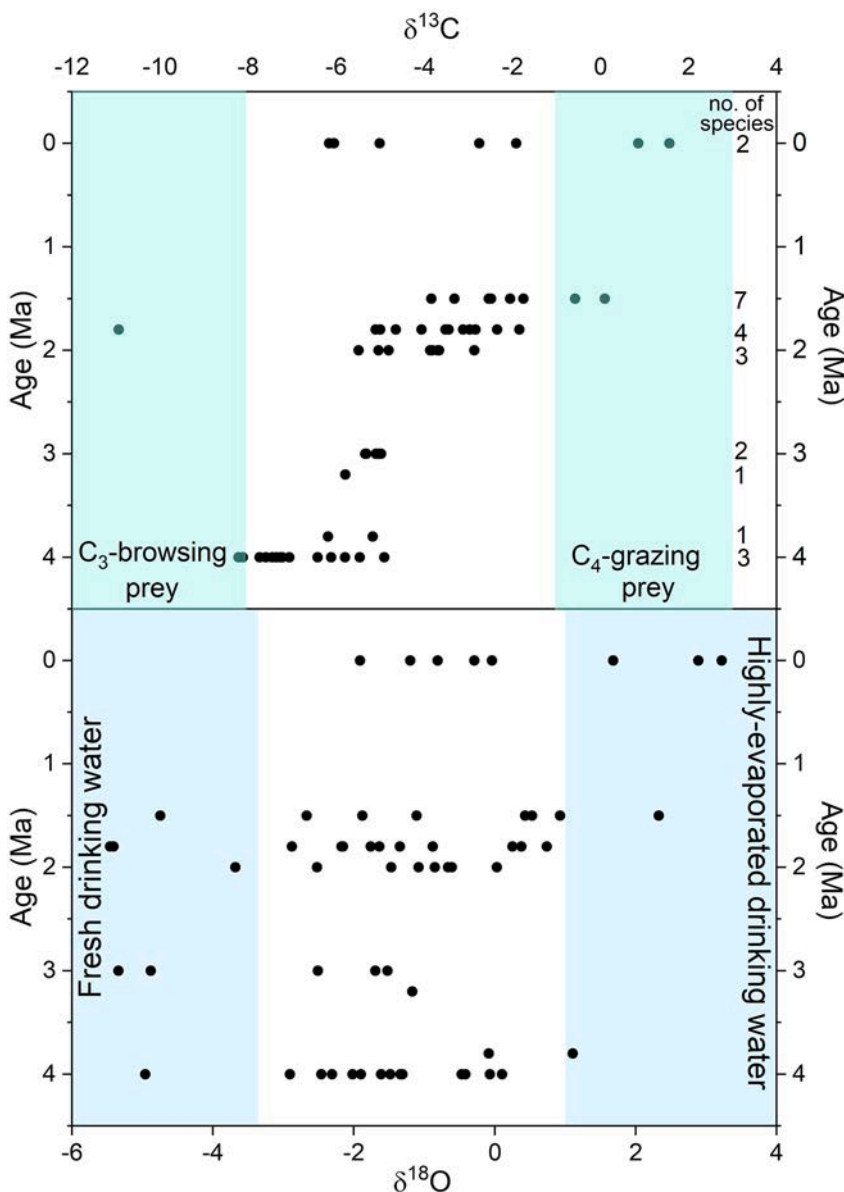


Fig. 5. Turkana Basin carnivore enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ through time. Green shading represents the carbon isotope values of C_3 -browsers and C_4 -grazers (Cerling et al., 2015); it is assumed that this isotopic signature is passed on to carnivorous predators with negligible isotopic fractionation (Bocherens and Drucker, 2003). Blue shading represents low and high extremes of evaporation; $>1\text{‰}$ $\delta^{18}\text{O}$ represents evaporatively-enriched water sources such as alkaline lakes and some water holes (Cerling et al., 1988), $<3.5\text{‰}$ $\delta^{18}\text{O}$ represents fresh water sources, such as rivers and lakes, that have undergone little evaporation and are close to meteoric water values (Lemmen et al., 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

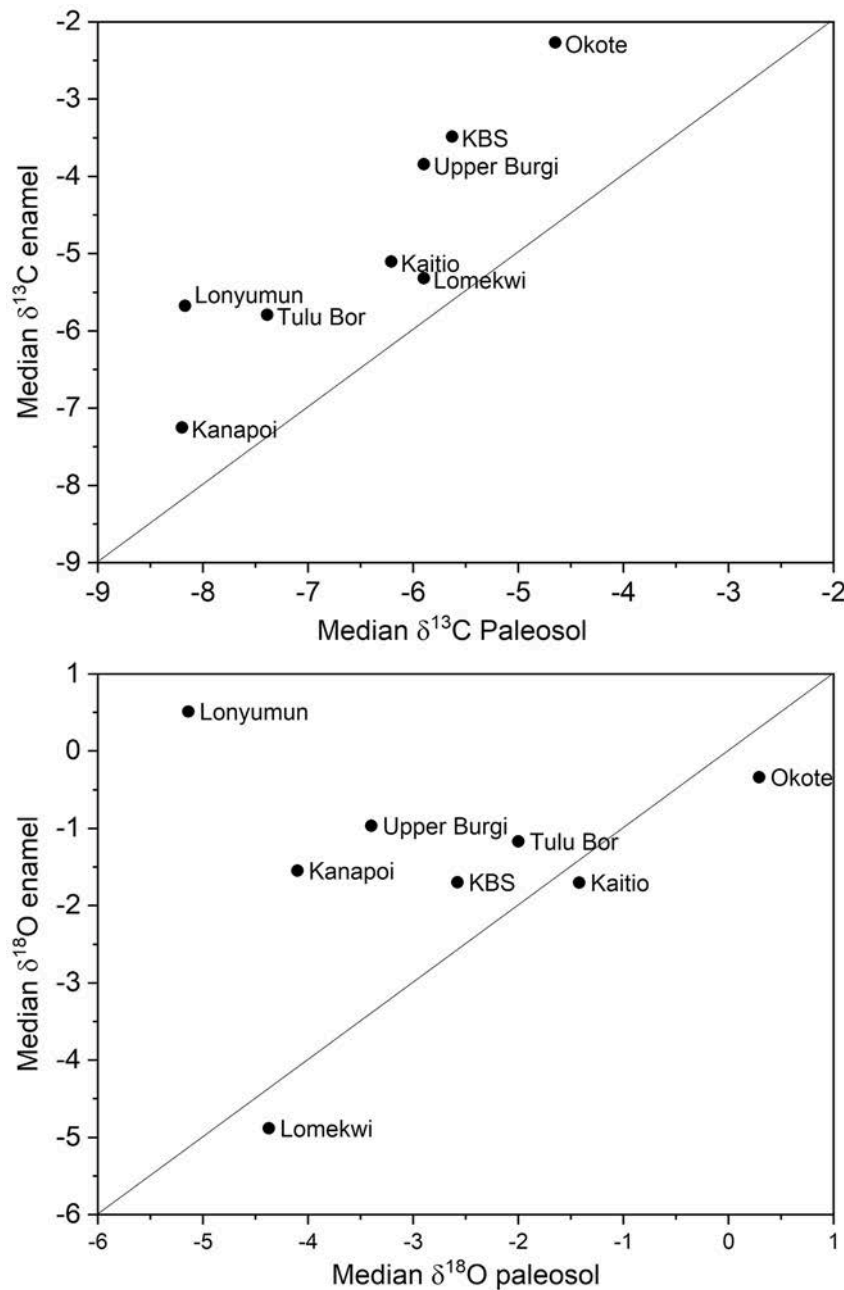


Fig. 6. Comparison of carnivore and palaeosol stable isotopes within geological members of the Omo Group, Turkana Basin. Carnivore $\delta^{13}\text{C}$ and palaeosol $\delta^{13}\text{C}$ show close agreement, indicative of a shared palaeovegetation signal. Carnivore $\delta^{18}\text{O}$ and palaeosol $\delta^{18}\text{O}$ are not related, implying different hydrological settings.

behaviour means that some of the analysed tooth enamel may have formed many miles from the fossil recovery site (2) a herd of grazing herbivores may be ephemeral on the landscape, but may contribute a significant proportion of skeletal material to a fossil assemblage (i.e. mass death event) (3) the fluvio-lacustrine setting of most fossil-bearing sediments may lead to a preferential preservation of grazing herbivores from open environments. In contrast, carnivores typically inhabit a proximal home range (i.e. non-migratory) and, as discussed above, they are ecological integrators.

The small offset observed between $\delta^{13}\text{C}_{\text{carnivore}}$ and $\delta^{13}\text{C}_{\text{palaeosol}}$ implies that both proxies are reliable palaeovegetation indicators (Fig. 6). $\delta^{13}\text{C}_{\text{palaeosol}}$ reconstructs a marginally higher proportion of C_3 vegetation than $\delta^{13}\text{C}_{\text{carnivore}}$, a pattern that was also recognized in a comparison between plant wax biomarkers and palaeosol carbonate (Uno et al., 2016). As suggested by Du et al. (2019), this may be due to the

preferential formation of palaeosol carbonates in woodland floodplains or riparian corridors. This may be the case, however it is also worth considering the temporal context of these two proxies. In lake-margin environments, the stable grassland-woodland conditions required to form palaeosol carbonates will not be a permanent fixture in the environment – changes in precipitation and corresponding lake level changes will result in the cessation of palaeosol carbonate growth. In contrast, we argue here that the Omo Group faunal assemblages contain individuals that lived during all phases of the precessional cycle. It may be that the palaeosol carbonates are forming during discrete periods of time that experience higher than average rainfall and woody cover.

5.2. Evidence for freshwater palaeolakes

A subset of Plio-Pleistocene carnivores has lower (-6.3 to -3.7‰)

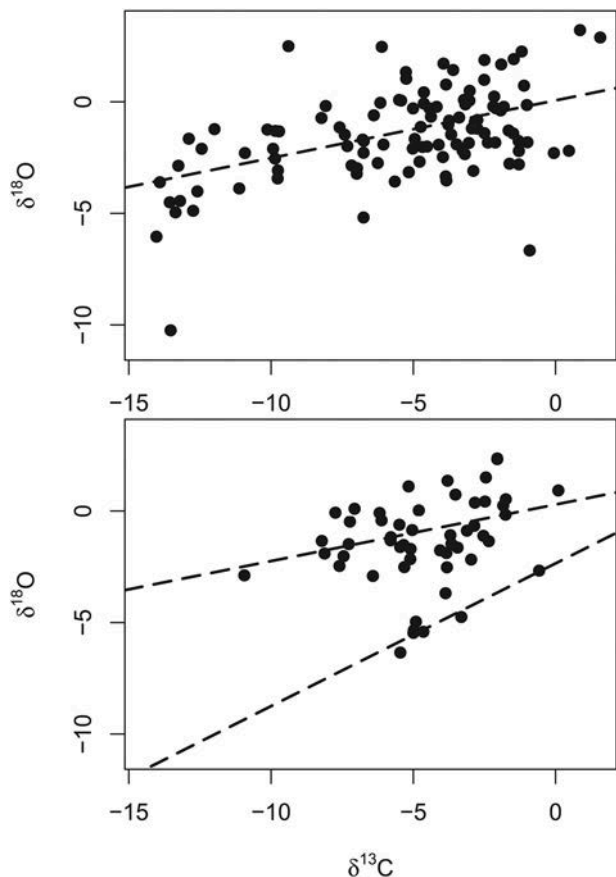


Fig. 7. Comparison of oxygen and carbon isotope values of modern carnivores (all Africa) and fossil carnivores (Turkana Basin). The modern dataset contains a single data population, the fossil dataset contains two. Low $\delta^{13}\text{C}$ values (indicative of C_3 diet) are rare in the fossil dataset; low $\delta^{18}\text{O}$ values (indicative of freshwater sources) are rare in the modern dataset. Data clusters identified, and regression lines drawn, using the FlexMix (Leisch, 2004) package in R.

$\delta^{18}\text{O}$ values than their modern Turkana Basin equivalents (see Fig. 5). The low $\delta^{18}\text{O}$ values indicate carnivores drinking from a water source with a $\delta^{18}\text{O}$ value of -7.4 to -4.9‰ , based on the regression equation between modern carnivores and environmental water (see Fig. 3). This is equivalent to the freshwater values that have been recorded at 3.27 Ma in palaeolake Hadar (Sidi Hakoma Member, Ethiopia (mean = -6.7 , min = -8.41 , max = -4.99‰ , $n = 17$; Hailemichael et al., 2002). Souron et al. (2012) demonstrate that at ~ 2.8 Ma, an individual of *Hippopotamus protamphibius* from the riverine setting of the Shungura Fm had a mean $\delta^{18}\text{O}$ value of -5.5‰ ($n = 20$), ranging from -6.7‰ to -4.4‰ . Levin et al. (2004) show that $\delta^{18}\text{O}$ values of palaeosols across E. Africa can be substantially lower than those recorded in the modern day. By the Olduvai Subchron (~ 1.8 Ma), $\delta^{18}\text{O}$ of lake-dwelling bivalve shells is $> -4\text{‰}$ (Vanhof et al., 2013). Meteoric water sources with low $\delta^{18}\text{O}$ values were clearly common in the Plio-Pleistocene of East Africa.

Candidate sources of Plio-Pleistocene freshwater include lakes, rivers and groundwater-fed springs. Groundwater can be an important source of drinking water for African mammals, including carnivores, (Hayward and Hayward, 2012; Lundgren et al., 2021), and may have contributed to the low $\delta^{18}\text{O}$ values reported in this study. Groundwater sources can persist through orbital extremes, constituting a larger proportion of surface water sources during dry periods (Cuthbert et al., 2017). Recharge of groundwaters in eastern Africa typically occurs during intense rainfall events (Taylor et al., 2012; Cuthbert et al., 2019) when $\delta^{18}\text{O}_{\text{rainfall}}$ values are likely to be low, due to the amount effect (Tindall et al., 2009). If drinking from groundwater sources is responsible for the low Plio-Pleistocene carnivore $\delta^{18}\text{O}$ values, then this is likely to occur

during relatively dry phases, in contrast to wet phases when additional drinking-water sources (such as lakes and rivers) are available. Under this scenario, both dry and wet phases could yield low carnivore $\delta^{18}\text{O}$ values, a pattern inconsistent with the wide range of $\delta^{18}\text{O}$ values observed throughout the Plio-Pleistocene (Fig. 5). Other sources of low $\delta^{18}\text{O}$ drinking water, such as freshwater lakes, should also be considered.

Past periods of lower than modern day $\delta^{18}\text{O}_{\text{lake-water}}$ values for east African freshwater lakes are well understood. Ricketts and Johnson (1996) used an isotopic mass balance model of Lake Turkana to show that long term (millennial-scale) trends in $\delta^{18}\text{O}$ are controlled by regional changes in the $\delta^{18}\text{O}$ value of meteoric water input, not by changes in lake level. The most likely cause of these lower isotopic values are changes in the amount and/or source (Lemma et al., 2020) of precipitation in the Ethiopian Highlands in response to the migration of the Congo Air Boundary (CAB) and changes in the proportion of moisture derived from the Indian Ocean (Levin et al., 2009; Kebede and Travi, 2012; Vanhof et al., 2013). This interpretation is supported by isotope-enabled GCM simulations for the early Holocene precessional maxima of east Africa, as recorded in rainfall patterns and lake levels (Tierney et al., 2011).

It is likely that palaeo-freshwater lakes were maintained by increased river input, and perhaps reduced evapotranspiration, experienced during wet phases. The subordinate regression line in Fig. 7 demonstrates that periods of freshwater (as indicated by low $\delta^{18}\text{O}_{\text{lake-water}}$ values) in the Lake Turkana basin experience only a modest increase in C_3 woody vegetation (as indicated by lower $\delta^{13}\text{C}$ values). This indicates that the local vegetation in the vicinity of palaeo-lake Turkana is not strongly influenced by the presence of a large body of standing water, nor does the high rainfall experienced in the Ethiopian Highlands translate into significantly higher rainfall/moisture within the Turkana basin, presumably due to rainshadow effects, high temperatures and high levels of evapotranspiration (Sepulchre et al., 2006; Nicholson, 2016). This reconstruction of a large freshwater lake surrounded by an arid hinterland (see Fig. 8) is supported by Van Bocxlaer (2020) who, based on a study of Pliocene freshwater molluscs, concluded that swampy or ephemeral backwaters were rare in these Turkana palaeolakes. There is clearly a long-term trend (4–1 Ma) in carnivore $\delta^{13}\text{C}$ due to increasing proportions of C_4 vegetation in the Turkana Basin (see Fig. 5), as observed in other mammalian groups (e.g. Cerling et al., 2015; Blumenthal et al., 2017), but no clear evidence from the present study for large orbital-scale fluctuations in vegetation structure (i.e. forest indicators are rare).

5.3. Mixed (time-averaged) faunal assemblages

The importance of orbital-scale (precessional) vegetation and rainfall changes in the Plio-Pleistocene of Africa has been highlighted by numerous studies of marine sediments (e.g. deMenocal and Bloemendal, 1995; Feakins et al., 2005; Caley et al., 2018) and terrestrial archives (e.g. Hopley et al., 2007; Magill et al., 2013; Lupien et al., 2018). Given the ubiquitous presence of Plio-Pleistocene precessional cycles, it is notable that they have yet to be identified within or between faunal assemblages of this age. Hopley and Maslin (2010) suggested that this was because the vast majority of terrestrial mammal fossil assemblages lack the temporal resolution (approx. <5500 years) required to recognise precessional-scale environmental change. The implication is that fossils from the wetter and drier end-members of the precessional cycle become mixed within a single fossil assemblage that is both time- and climate-averaged.

While the climate-averaging concept (Hopley and Maslin, 2010) seems to be a plausible scenario for the accumulation of fossil assemblages from the Plio-Pleistocene of East Africa (Stern, 1994; Cerling et al., 2013), it has yet to be conclusively demonstrated. The current study provides compelling evidence in support of temporally mixed faunal assemblages. In Fig. 7 we show that there are two distinct $\delta^{18}\text{O}$ vs

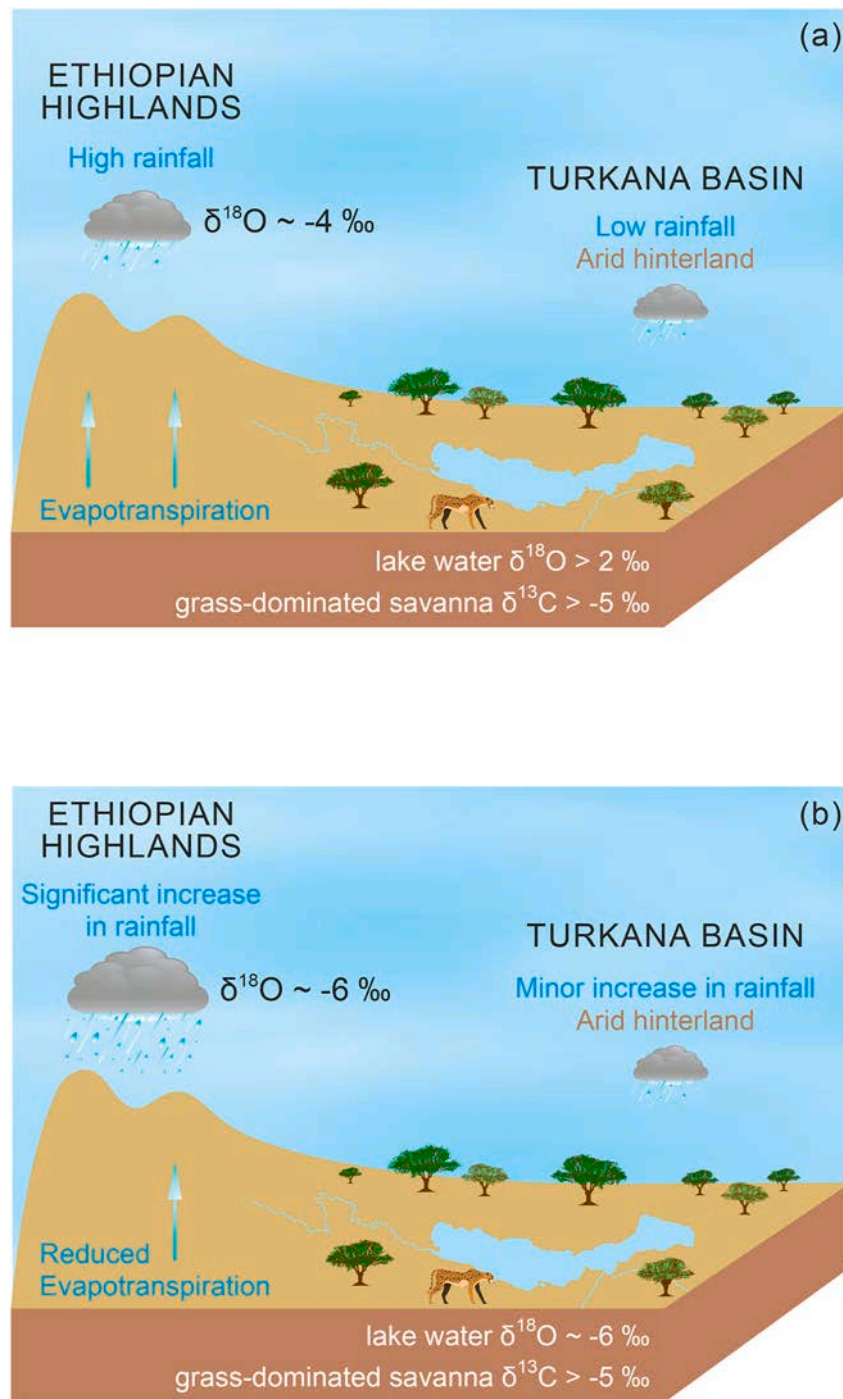


Fig. 8. Sketch to illustrate rainfall controls on the $\delta^{18}\text{O}$ value of Lake Turkana water and carnivore enamel isotopes. (a) precessional minimum scenario, as observed in the present day. Ethiopian Highland rainfall has low $\delta^{18}\text{O}$ values (Levin et al., 2009; Lemma et al., 2020), Lake Turkana water (Cerling, 1996; Cerling et al., 2008) is evaporatively enriched ($\delta^{18}\text{O}$ is $> 2 \text{ ‰}$) and the hinterland is arid (Mbaluka and Brown, 2016; Nicholson, 2016), with a high proportion of C_4 vegetation ($\delta^{13}\text{C} > -5 \text{ ‰}$). (b) precessional maximum scenario. With reduced evapotranspiration, lake water is fresh ($\delta^{18}\text{O}$ is $\sim -6 \text{ ‰}$) yet the hinterland remains arid ($\delta^{13}\text{C} > -5 \text{ ‰}$). This results in two different $\delta^{13}\text{C}$ vs $\delta^{18}\text{O}$ relationships within the Plio-Pleistocene carnivore enamel dataset from the Turkana Basin, as shown in Fig. 7. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

$\delta^{13}\text{C}$ trends within the fossil carnivore isotopic dataset. The predominant trend is comparable to the modern carnivore isotopic dataset, whereas the subordinate trend shows a steeper gradient and unusually low $\delta^{18}\text{O}$ values (see Fig. 7). The low $\delta^{18}\text{O}$ values do not represent species-specific behaviours or a discrete period of environmental change within the Turkana Basin because representative datapoints are found among four different species from the Kanapoi, Lomekwi, Upper Burgi, KBS and Okote Members, spanning the time interval from 4 to 1.5 Ma (see Supplementary Table 4). This indicates that each of these depositional units contains carnivores living under two temporally distinct hydrological regimes.

5.4. Implications for the interpretation of East African faunal assemblages

As demonstrated above, the fossil carnivore isotope data confirms that Turkana Basin faunal assemblages were accumulated during periods of both reduced and enhanced rainfall, representing more than one phase of a precessional cycle ($> \sim 5500$ years). This has a number of implications for the study of East African fossil assemblages and for our understanding of the environmental context of early hominin evolution. Most prior work on African Plio-Pleistocene palaeoenvironments has been conducted under the implicit assumption that time-averaging of faunal assemblages is minimal; when time-averaging is acknowledged (e.g. Stern, 1994), it is often assumed to take place under static environmental conditions (e.g. Du and Behrensmeyer, 2018; Du et al., 2019),

again with minimal impact on palaeoecological interpretations. With the evidence presented in this study for both time- and climate-averaging, the full range of implications must be considered.

Studies that attempt to reconstruct palaeoenvironmental conditions by compiling evidence from numerous individuals or species within a faunal assemblage are producing reconstructions of average orbital-scale conditions (e.g. Patterson et al., 2017; Bobe et al., 2020), not a single time-slice of a living palaeo-community. The typical reconstruction of “a woodland environment surrounded by savannah grassland with a wetland component” must be reconsidered within the context of a temporally-mixed assemblage forming under a rapidly changing environment. While it is clear from modern analogue studies that environmental mosaics are common in East Africa (e.g. Reynolds et al., 2015), the appearance of ubiquitous mosaic environments is being exaggerated by the process of climate averaging. Supporting evidence for temporally-mixed faunal assemblages comes from evidence for non-analogue Plio-Pleistocene trophic structures (e.g. Cerling et al., 2015; Faith et al., 2019), the ubiquitous savannah-mosaic environmental reconstructions and the broad dietary variability of mixed-feeding individuals (e.g. Scott et al., 2005; Sponheimer et al., 2006). Going forward, temporally-mixed faunal assemblages must be considered the default scenario for the Plio-Pleistocene of Africa, and attempts to falsify this assumption should be considered on a case-by-case basis.

Future work will focus on disentangling these mixed faunal assemblages by striving to identify contemporaneous individuals or species associations. For example, indicators of association, such as fossil footprints (e.g. Roach et al., 2016), predator bitemarks (e.g. Njau and Blumenshine, 2006) or stone tool cutmarks (e.g. Braun et al., 2010) may aid the identification of contemporaneous species and individuals. Conventional isotopic tools, such as carbon and oxygen isotope analysis, are currently insufficient to identify individual or species associations, but a suite of new isotopic proxies may lead to advances in this area.

6. Conclusions

This study has shown that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in modern carnivore enamel faithfully reproduces African local vegetation structure (proportion of woody cover) and the isotopic composition of local meteoric water sources respectively. These integrated environmental signals are mediated through the carbon isotope composition of multiple herbivorous prey individuals and species, and through the oxygen isotopic composition of multiple water sources (e.g. lakewater, riverwater and prey bodywater). Application of these techniques to Plio-Pleistocene carnivores from the Turkana basin demonstrates that there are two isotopic populations, independent of age and species, that reflect two distinct environmental regimes most likely marked by the presence, and absence, of a freshwater palaeolake. Isotopic evidence for the presence of fresh and alkaline water sources during the accumulation of each faunal assemblage is compelling evidence for time- and climate-averaged faunal assemblages. This is the first quantitative demonstration that Turkana Basin fossil assemblages accumulated during more than one phase of a precessional cycle (>5500 years) and that prior assumptions of discrete palaeocommunities living during singular and static environmental conditions will need to be reconsidered.

Author contributions

PJH, LW and TEC designed the research. LW performed taxonomic identification; LC undertook the remote-sensing work; PJH and TEC collected the stable isotope samples and made the isotopic measurements; OM, FKM and LNL undertook fieldwork, collected the specimens and provided stratigraphic context; all authors wrote and reviewed the manuscript.

7. Data availability

All data is available in the main text and the supplementary information.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2022.04.004>.

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