Earth and Planetary Science Letters 428 (2015) 84–96

Contents lists available at ScienceDirect

Earth and Planetary Science Letters

www.elsevier.com/locate/epsl

Influences on the stable oxygen and carbon isotopes in gerbillid rodent teeth in semi-arid and arid environments: Implications for past climate and environmental reconstruction

Amy Jeffrey [a,*], Christiane Denys [b], Emmanuelle Stoetzel [c], Julia A. Lee-Thorp [a]

[a] *Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, OX1 3QY, UK*
[b] *Muséum national d'Histoire naturelle, Département Systématique et Evolution – UMR 7205 ISYEB CNRS-MNHN-EPHE-UPMC, Paris, France*
[c] *Muséum national d'Histoire naturelle, Département de Préhistoire – CNRS UMR 7194, Paris, France*

ARTICLE INFO

Article history:
Received 26 March 2015
Received in revised form 6 July 2015
Accepted 6 July 2015
Available online 29 July 2015
Editor: D. Vance

Keywords:
small mammals
stable isotopes
oxygen
carbon
teeth
aridity

ABSTRACT

The stable isotope composition of small mammal tissues has the potential to provide detailed information about terrestrial palaeoclimate and environments, because their remains are abundant in palaeontological and archaeological sites, and they have restricted home ranges. Applications to the Quaternary record, however, have been sparse and limited by an acute lack of understanding of small mammal isotope ecology, particularly in arid and semi-arid environments. Here we document the oxygen and carbon isotope composition of Gerbillinae (gerbil) tooth apatite across a rainfall gradient in northwestern Africa, in order to test the relative influences of the $^{18}O/^{16}O$ in precipitation or moisture availability on gerbil teeth values, the sensitivity of tooth apatite $^{13}C/^{12}C$ to plant responses to moisture availability, and the influence of developmental period on the isotopic composition of gerbil molars and incisors. The results show that the isotopic composition of molars and incisors from the same individuals differs consistent with the different temporal periods reflected by the teeth; molar teeth are permanently rooted and form around the time of birth, whereas incisors grow continuously. The results indicate that tooth choice is an important consideration for applications as proxy Quaternary records, but also highlights a new potential means to distinguish seasonal contexts. The oxygen isotope composition of gerbil tooth apatite is strongly correlated with mean annual precipitation (MAP) below 600 mm, but above 600 mm the teeth reflect the oxygen isotope composition of local meteoric water instead. Predictably, the carbon isotope composition of the gerbil teeth reflected C_3 and C_4 dietary inputs, however arid and mesic sites could not be distinguished because of the high variability displayed in the carbon isotope composition of the teeth due to the microhabitat and short temporal period reflected by the gerbil. We show that the oxygen isotope composition of small mammal teeth strongly reflects moisture availability in semi-arid and arid environments and would provide an excellent record of palaeo-aridity in a terrestrial setting. The results illustrate that an understanding of an animal's physiology is essential for interpreting the animal's isotopic responses to external contexts, especially in arid zones.

1. Introduction

The oxygen and carbon isotope composition ($\delta^{18}O$ and $\delta^{13}C$) of fossil mammalian enamel has been widely applied to infer climate and environmental conditions such as aridity, rain water sources, climate seasonality, relative humidity and vegetation cover in the past (e.g. Ayliffe et al., 1992; Cerling et al., 1997; Hoppe, 2006; Levin et al., 2006). Small mammals are frequently abundant in archaeological and palaeontological sites, but to date have played little part in such endeavours. Their role has been largely restricted to more traditional faunal abundance methods that rely on the association of taxa with their preferred modern habitats (e.g. Fernández-Jalvo et al., 1998; Stoetzel et al., 2011). Few isotopes studies have been undertaken on small mammals because little is understood about their isotope ecology (Luz and Kolodny, 1985; Gehler et al., 2012; Royer et al., 2013). The seminal studies that first identified the links between the isotopic composition of precipitation and faunal tissues experimentally (using mostly bone and tooth phosphate), and modelled mass balance effects (Kohn, 1996), also cautioned against the effect of faster

---

[*] Corresponding author.
E-mail addresses: amy.jeffrey@rlaha.ox.ac.uk (A. Jeffrey), denys@mnhn.fr (C. Denys), stoetzel@mnhn.fr (E. Stoetzel), julia.lee-thorp@rlaha.ox.ac.uk (J.A. Lee-Thorp).

http://dx.doi.org/10.1016/j.epsl.2015.07.012

metabolism in mammals with small body sizes (Luz et al., 1984; Luz and Kolodny, 1985). Consequently most applications to fossils have been targeted at large-bodied mammals (e.g. Bryant and Froelich, 1995). These effects are not insurmountable, however, and there are several advantages in using small mammals. Advantages include the large numbers occurring in archaeological and paleontological sites, which permit statistically sound sample sizes, that the mammals have relatively small home ranges allowing inferences about local environmental conditions, and that they live in a large number of different ecological settings. Consequently, as argued by Grimes et al. (2008), the stable isotope composition of small mammal material has the potential to produce high-resolution temporal records of past environmental changes in a terrestrial setting.

Many rodents have both permanently rooted molar teeth with discrete developmental periods, and continuously growing incisor teeth, meaning that different temporal periods are reflected in each tooth type. Palaeoenvironmental reconstructions using isotopes in small mammal teeth have so far tended to focus on molar and/or incisor teeth indiscriminately with little consideration for the developmental period reflected (Hopley et al., 2006; Hynek et al., 2012). Lindars et al. (2001) suggested that post-weaning teeth should be preferred to avoid a nursing (pre-weaning) effect, but this recommendation was based on a study using only three dormice individuals, in which the stable isotope composition of molar but not incisor teeth was measured. Since these animals reproduce seasonally and have relatively short life spans the period represented by each tooth type might very well influence the isotopic composition.

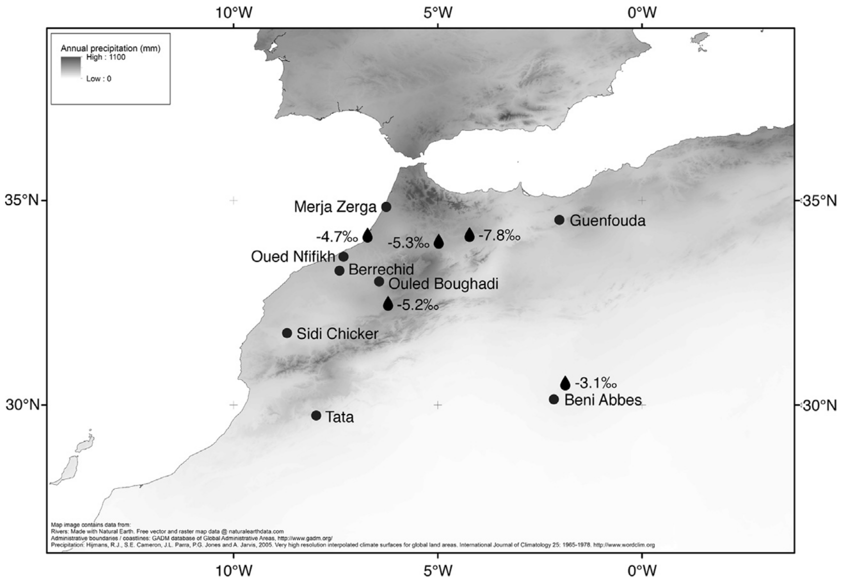
Modern analogue studies exploring the relationship between climate and the $\delta^{18}O$ composition of small mammal teeth have additionally been restricted to cool/mesic environments. Since many small mammals obtain most of their water from plants, this means that the visible effects of plant water ^{18}O-enrichment are obscured. Specific relationships between $\delta^{18}O$ of the phosphate component ($\delta^{18}O_{PO4}$) of wild Muroidea teeth and $\delta^{18}O$ local meteoric water ($\delta^{18}O_{mw}$) have been obtained for temperate Europe (D'Angela and Longinelli, 1990; Longinelli et al., 2003; Navarro et al., 2004; Royer et al., 2013). These have in turn been used to infer past $\delta^{18}O_{mw}$ and subsequently seasonal and mean annual air temperatures, based on the principle that in mid and high-latitudes mean $\delta^{18}O_{mw}$ is correlated with mean annual air temperature (e.g. Navarro et al., 2004; Tütken et al., 2006; Héran et al., 2010; Royer et al., 2014). Although the relationship between $\delta^{18}O$ in small mammal teeth and $\delta^{18}O_{mw}$ might be applicable in modern temperate Europe where plant water isotope effects are relatively small, it becomes decidedly problematic in application to the past in areas or episodes in which aridity may have been more prevalent. Ignoring the isotope effects of evapotranspiration in plant water on animal phosphate or carbonate oxygen isotope values limits efforts to reconstruct past hydrological regimes and temperatures. This problem has not gone unnoticed. Delgado Huertas et al. (1995) reported that the $\delta^{18}O_{PO4}$ of rabbit and hare bone did *not* reflect that of $\delta^{18}O_{mw}$, probably because they obtain the majority of their bodywater from food.

To our knowledge, no modern isotope studies have been undertaken on wild small mammal populations in more arid climate settings, where water from the animals' food would have a strong influence on the $\delta^{18}O$ composition of the small mammal body water, and hence their body tissues. Nor have any studies systemically explored the effects of tooth development period on the isotopic composition of rodents that have permanently rooted molar teeth and continuously growing incisor teeth. In order to address these issues, we determined the $\delta^{18}O$ and $\delta^{13}C$ composition of modern Gerbillinae (gerbil) tooth apatite across a rainfall gradient in the semi-arid and arid environments of northwestern Africa, to examine the effects of aridity and moisture availability on the isotope composition of small mammal tissues. Gerbils were chosen because they have known physiological adaptations to aridity, such as reliance on metabolic water, a low metabolic rate and large surface-area-to-volume ratio (Merritt, 2010). They are also abundant in archaeological and palaeontological sites of northwestern Africa, where they are considered to be good indicators of open and relatively dry environments (Stoetzel et al., 2011). Specifically we test whether the isotopic composition of precipitation or moisture availability exerts the primary influence on $\delta^{18}O$ composition of gerbil teeth, and the nature of local vegetation recorded in $\delta^{13}C$ of the gerbil teeth. Given the effect of aridity on C_3 plants we would expect that increasing aridity would cause $\delta^{13}C$ and $\delta^{18}O$ to co-vary and increase in the gerbil teeth. We also assess the isotopic variability between the gerbil molar and incisor teeth in order to evaluate which teeth should be used in the construction of proxy palaeo-climate and environmental records.

1.1. $\delta^{18}O$ and $\delta^{13}C$ in mammalian teeth

Mammalian enamel bioapatite is precipitated from blood bicarbonate, which exchanges readily with body water and together they represent the pool that determines bioapatite $\delta^{18}O$ and $\delta^{13}C$ (Passey et al., 2005). Body water $\delta^{18}O$ is controlled by the balance of oxygen inputs and outputs; inputs include drinking water, food oxygen, and atmospheric O_2 and outputs comprise of fluids (e.g sweat, urine), respired CO_2 and water vapour (Luz et al., 1984; Luz and Kolodny, 1985; Bryant and Froelich, 1995; Kohn, 1996). The physiology of the mammal influences the $\delta^{18}O$ composition of body water because of mass balance. Thus body water in mammals deriving the majority of their water from plant water (non-obligate drinkers) tends to be enriched in ^{18}O relative to mammals that drink regularly (obligate drinkers) (Kohn, 1996) because plant leaf water is relatively enriched in $H_2{}^{18}O$ compared to local environmental water due to preferential evapotranspiration of the lighter molecule ($H_2{}^{16}O$) (Gonfiantini et al., 1965). The effect of evapotranspiration is greatly enhanced under conditions of aridity and low relative humidity (Yakir et al., 1990). As arid-adapted animals, gerbil water requirements are largely met by plant water and they drink only small amounts of free water (Winkelmann and Getz, 1962; Laughlin et al., 1975). They should thus be indirectly sensitive to relative humidity.

Mammalian bioapatite $\delta^{13}C$ reflects that of ingested food and can be used to infer dietary sources of carbon, as well as ecological niche, vegetation patterning and habitat (Lee-Thorp and van der Merwe, 1987; Cerling et al., 1997). As for all mammals, gerbil tooth bioapatite $\delta^{13}C$ is influenced by the nature of local vegetation, and the relative proportions of plants using Calvin–Benson (C_3) or Hatch–Slack (C_4) photosynthesis. These pathways discriminate against ^{13}C during photosynthetic fixation of CO_2 to different extents, so that C_3 and C_4 plants have distinct $\delta^{13}C$ distributions (Park and Epstein, 1960). The global average $\delta^{13}C$ value for C_3 plants (trees, shrubs, herbs and grasses growing under temperate or shaded conditions) is about −27‰, with a large isotopic range from −23 to −36‰ since fractionation is influenced by local environmental conditions such as water availability, pCO_2, light conditions and temperature (Farquhar et al., 1989; Tieszen, 1991). C_3 plants that grow in open, arid conditions, with limited water availability tend to have higher $\delta^{13}C$ values (> -25‰). C_4 plants (mainly tropical grasses and sedges) have a narrower $\delta^{13}C$ range (−16 to −9‰). C_4 plants require high insolation in the growing (wet) season so their distribution is confined largely to environments with warm, summer growing seasons (Teeri and Stowe, 1976). They are uncommon in winter-rainfall zones. It is expected therefore that gerbil teeth from a predominantly arid, Mediterranean climate, and mostly C_3 environment such as North Africa



Map image contains data from:
Rivers: Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com
Administrative boundaries / coastlines: GADM database of Global Administrative Areas, http://www.gadm.org/
Precipitation: Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978. http://www.wordclim.org

Fig. 1. Map of northwestern Africa showing modern modelled MAP (downloaded from www.worldclim.org) (Hijmans et al., 2005). Blacks dots show the eight locations from which gerbil teeth were collected. Raindrops show the location of GNIP stations (http://www-naweb.iaea.org/) (Beni Mellal, Rabat-Cnesten, Fes Sais, Bab Bou Idir and Beni Abbes) with the weighted mean annual $\delta^{18}O_{mw}$. Darker shading indicates areas with higher MAP, while lighter shading show areas with low MAP.

should show more positive $\delta^{18}O$ and $\delta^{13}C$ composition relative to those from more mesic C_3 environments.

Thus far few studies have employed the isotopic composition of bioapatite in small mammal fossil teeth to reconstruct past conditions (Grimes et al., 2004; Hopley et al., 2006; Tütken et al., 2006; Hynek et al., 2012; García-Alix et al., 2013). To our knowledge Gehler et al. (2012) have undertaken the only modern analogue study on small mammal tooth and bone bioapatite CO_3 in a wild temperate European setting. They explored inter- and intra-specific $\delta^{18}O$ and $\delta^{13}C$ variability, but emphasised the need for further studies to understand bias due to seasonality effects and tissue formation rates. No studies to date have taken full account of the influence of drinking behaviour and plant water on small mammal bioapatite oxygen isotope composition.

2. Material and methods

2.1. Material

Modern teeth belonging to the sub-family Gerbillinae (gerbils) were collected from eight different sites across Morocco and Algeria (Fig. 1, Table 1). Large concentrations of small mammal skeletal material are found at owl nests or roosting sites through the regurgitation of pellets, and over long time periods this material is likely to become incorporated and preserved in cave or rock shelter sediments (Andrews, 1990). The hunting range of owls varies according to territory, region, season and prey availability and can range between <1 km to up to 10 km from the nest (Andrews, 1990). The barn owl (*T. alba*) is known to have a small territory (<5 km from the nest), while the large European eagle owl (*B. bubo*) also hunts in a relatively small territory (<10 km from its nest) (Mikkola, 1983). Less is known about the diet and hunting habits of the endemic North African relative of *B. bubo*, *B. ascalaphus* (Stoetzel and Denys, 2011), and we assume that it resembles the former.

Fig. 1 shows that the sites are located across a range of different bioclimatic zones (~30°–35°N) from more mesic environments on the Atlantic coast of Morocco, through to semi-arid and arid desert. Merja Zerga is a salt marsh lagoon that lies directly on the Atlantic coast of Morocco and is the most mesic site in the study receiving ~600 mm mean annual precipitation (MAP) (Table 1). Guenfouda, Oued Nfifikh, Ouled Boughadi, Berrechid and Sidi Chicker are all located north of the Atlas Mountains in the Atlantic and Mediterranean coastal zones of Morocco. Guenfouda, Sidi Chicker and Ouled Boughadi belong to semi-arid steppic environments. The vegetation at each of these sites is locally variable and includes steppe grasslands, scrub, cultivated fields and open oak forests. Tata and Beni Abbes lie south of the Atlas Mountains in the Moroccan and Algerian Sahara, both are arid sites with <200 mm MAP (Table 1).

The coastal region of North Africa has a typical Mediterranean climate with the majority of precipitation falling between October and May. Precipitation mainly originates from the Atlantic Ocean and is transported by the predominant westerly winds, but air masses can occasionally originate from the Mediterranean Sea (Ouda et al., 2005). The northern fringe of the Sahara, where both Tata and Beni Abbes are located, lies on the extreme southern edge of the mid-latitude storm track. Precipitation in this region is infrequent and variable and could be of Atlantic or even monsoon source (Knippertz et al., 2003). Observed precipitation data from Beni Abbes (source: Global Network of Isotopes in Precipitation (GNIP)) shows that precipitation tends to fall during the winter months, suggesting an Atlantic source, because mid-latitudes westerlies predominate during the winter in this region. While instrumental weather data is available in Morocco and Algeria, the weather stations are distant from the collection sites. Therefore, we used modelled climate data for each site from *WorldClim* (www.worldclim.org) (Hijmans et al., 2005). The Worldclim data is an interpolated climate surface model for global terrestrial areas at a 1-km spatial resolution, developed using observed historical MAP data (1950–2000) from global weather stations. The historical precipitation data coverage from the Mediterranean zone of North Africa is good, and in general suggests that the Worldclim MAP model has a high degree of accuracy for this region. Modelled MAP data was used as a proxy for moisture availability or aridity at each owl pellet location.

Monthly precipitation and directly measured $\delta^{18}O_{mw}$ values are available from five Global Network of Isotopes in Precipitation (GNIP) (http://www.iaea.org/water) stations in the study region (Fig. 1). The annual weighted $\delta^{18}O_{mw}$ mean from the Atlantic coast towards the Atlas appears to be consistent ($\sim -5‰$) according to observations on the coast at Rabat-Cnesten (75 m asl) and further inland at slightly higher altitudes at Fes Sais (571 m asl)

Table 1

Geographical, environmental, climate and local vegetation data for the gerbil collection sites across northwestern Africa. The modelled mean annual precipitation (MAP) data was downloaded from WorldClim (http://www.worldclim.org/), while the modelled annual $\delta^{18}O_{mw}$ is from the Isotopes in Precipitation calculator (www.waterisotopes.org).

Site name	GPS coordinates	Altitude (m asl)	Number of Gerbillinae individuals	Owl pellets/nest	Predominant local vegetation	Modelled mean annual precipitation (mm)	Modelled annual $\delta^{18}O‰_{mw(VPBD)}$	Predator
Beni Abbes, Algeria	30°07′48 N 02°09′56 W	597	10 (4 *Meriones*, 6 *Gerbillus*)	Pellets	Open desert	106	−5.0	*Tyto alba/Bubo ascalaphus?*
Tata, Morocco	29°44′34 N 07°58′21 W	690	8 (8 *Gerbillus*)	Pellets	Cultivated, open	169	−4.7	*Bubo ascalaphus*
Sidi Chicker, Morocco	31°45′39 N 08°41′26 W	209	25 (12 *Meriones*, 13 *Gerbillus*)	Nest	Steppe grassland, cultivated, open forest	263	−4.0	*Asio otus*
Guenfouda, Morocco	34°31′25 N 02°01′09 W	530	5 (4 *Meriones*, 1 *Gerbillus*)	Pellets	Steppe grassland, scarce olive-trees and pistachio-trees (indigenous), pines (invasive)	326	−5.9	*Bubo ascalaphus*
Berrechid, Morocco	33°17′45 N 07°24′30 W	219	2 (2 *Gerbillus*)	Pellets	Wheatfield and diverse cultivation (garden, potato, vegetables)	367	−4.4	*Tyto alba?*
Oued Nfifikh, Morocco	33°38′00 N 07°18′00 W	417	6 (6 *Gerbillus*)	Pellets	Wheatfield and potato cultivation, oak forest alternating with open areas	378	−4.3	*Tyto alba*
Ouled Boughadi, Morocco	33°00′18 N 06°24′34 W	844	8 (4 *Meriones*, 4 *Gerbillus*)	Pellets	Cultivated (wheat, barley), open areas, locally rocks and scarce trees/scrubs	451	−5.5	Unknown (cf. *Tyto alba?*)
Merja Zerga, Morocco	34°51′00 N 06°16′00 W	10	6 (6 *Gerbillus*)	Pellets	Woodland, scrub, grassland, humid meadow	605	-4.2	*Asio capensis?*

Table 2
Biogeographical, behavioural and ecological data for Gerbillinae used in this study. Sourced from Aulagnier and Thévenot (1986), Kowalski and Rzebik-Kowalska (1991), Kingdon (1997) and Aulagnier et al. (2009).

Species	Distribution in North Africa	Habitat	Diet	Activity	Collection sites
Meriones shawii and/or *grandis*	Mediterranean semi-arid and arid bioclimate zones in North Africa.	Found in steppes and cultivated areas, sometimes in desert areas but only in gardens and oases.	Granivore that mainly feeds on cereals, but also fruits, stems, leaves and insects.	Nocturnal	Sidi Chicker, Guenfouda, Ouled Boughadi
Meriones cf. *crassus*	Saharan North Africa	Arid areas with compact sandy soils such as wadis and hamadas.	Granivore that mainly feeds on cereal, but also on stems, fruits and insects.	Nocturnal	Beni Abbes
Meriones cf. *libycus*	Saharan North Africa	Arid and semi-arid areas with sparse vegetation cover.	Feeds on fruits of legumes, grasses and chenopods.	Nocturnal or diurnal (depending on region)	Beni Abbes
Gerbillus campestris	Wide spread across North Africa including the Mediterranean and Sahara.	Cultivated areas and Mediterranean steppes. Saharan populations live in oases and rocky areas with sparse vegetation, not in sand dunes.	Granivore that mainly feeds on seeds, but also leaves, stems and fruits, as well as a significant contribution of insects.	Nocturnal	Oued Nfifikh, Sidi Chicker, Ouled Boughadi, Merja Zerga
Gerbillus gerbillus	Widespread across Saharan North Africa.	Adapted to arid habitats, mainly dunes and other large sandy areas with sparse vegetation cover.	Granivore that mainly feeds on cereal, but also on leaves, fruits and buds.	Nocturnal	Tata
Gerbillus henleyi and/or *nanus*	*G. henleyi*: Saharan areas extending east to the Arabian Peninsula. *G. nanus*: Saharan North Africa extending north to the Atlas Mountains.	*G. henleyi*: Extremely arid areas such as sand dunes, salt marshes, wadis, hamadas and stony plains. *G. nanus*: Arid regions with relatively abundant vegetation cover. Favours wadis and other habitats with sandy soil cover.	*G. henleyi*: Granivore. Feeds more on seeds than any other Gerbil species. *G. nanus*: Feeds on gramineous plants, seeds and buds.	Nocturnal	Beni Abbes, Sidi Chicker
Gerbillus tarabuli	Saharan and Sahelian areas of Northwestern Africa	Coastal steppes and inland deserts.	Seeds and fruits.		Beni Abbes

and Beni Mellal (∼468 m asl). At the higher altitude site of Bab Bou Idir (1500 m asl), $\delta^{18}O_{mw}$ is lower (∼ −7‰), reflecting an altitude effect (Dansgaard, 1964). The annual weighted $\delta^{18}O_{mw}$ mean at Beni Abbes (in the Sahara Desert), based on GNIP observations between 1966–1968, is −3.1‰, suggesting that higher temperatures and evaporation override the Rayleigh distillation (continental) isotope effect on rainfall. The mean monthly $\delta^{18}O_{mw}$ at Beni Abbes is large and ranges from +13.6 to −8.2‰, indicating frequent evaporative enrichment of precipitation in the atmosphere. In addition to greater variability, most precipitation falls within one or two months of the year.

Where there is overlap, modelled $\delta^{18}O_{mw}$ data fits well with that of observed $\delta^{18}O_{mw}$ values for each site from the GNIP stations located across Morocco and Algeria (Table 1, Fig. 1). As Sidi Chicker and Guenfouda have no current nearby GNIP station, modelled $\delta^{18}O_{mw}$ data was used from the Isotopes in Precipitation Calculator (www.waterisotopes.org) (Bowen and Revenaugh, 2003). The values used for each site are shown in Table 1.

2.2. Ecological considerations

In order to obtain sufficient samples from each location, Gerbillinae species belonging to the genera *Meriones* and *Gerbillus* were selected. Their distributions across the varied environments of North Africa differ (Table 2), but both taxa are common in archaeological and palaeontological sites. *Meriones shawii* and *Meriones grandis* are found in relatively humid biotopes in the semi-arid Mediterranean climate zone of North Africa. They were collected from sites north of the Atlas Mountains. *Meriones crassus* and *Meriones libycus* are distributed across Saharan North Africa and were collected from Beni Abbes. *Gerbillus campestris* is widely distributed across North Africa in Mediterranean and Saharan locations; it is the only *Gerbillus* sp. present at the majority of sites (Oued Nfifikh, Sidi Chicker, Ouled Boughadi, Merja Zerga). Several *Gerbillus* sp. were collected from Tata and Beni Abbes including *G. gerbillus*, *G. henleyi*, *G. nanus*, *G. tarabuli*, *G. pyramidum*.

Gerbils are classed as granivores meaning the vast majority of their diet consists of seeds and plant parts; only on rare occasions do they consume insects and other resources (Petter et al., 1984; Zaime and Gautier, 1989; Aulagnier et al., 2009; Adamou-Djerbaoui et al., 2013) (Table 2). Gerbil feeding strategies are highly variable between individuals, and they have been observed to consume a large number of plant species (Zaime and Gautier, 1989; Belabbas and Butet, 1994). Gerbil diets can vary seasonally depending on the availability of food, for example *M. shawii* diet consists almost entirely of leaves and grains during the summer months and flowering plants during the winter months (Adamou-Djerbaoui et al., 2013).

Reproduction in gerbils is strongly linked to environmental factors such as rainfall, which influences the availability and nutritional quality of the plant food available (Zaime and Gautier, 1989). Consequently their breeding season can vary from year to year. In northern Morocco, *M. shawii* generally breeds in spring and summer (between March and September), while pregnant *G. campestris* females have been captured up until November (Belabbas and Butet, 1994). In the Moroccan Saharan the gerbil breeding season may occur throughout the winter and spring months, coinciding with the winter rains and vegetation growth (Khammar and Brudieux, 1987; Zaime et al., 1992). Gerbils reach sexual maturity at approximately 40–80 days depending on the species, and they have short life-spans (Koffler, 1972). This is noteworthy for stable isotope studies because their fast body-tissue turnover times could result in hair, bone and teeth having distinctive isotope values depending on the season of formation, as shown in woodrats (Podlesak et al., 2008).

2.3. Tooth considerations

In one half of their mandible and maxilla *Meriones* and *Gerbillus* have one single incisor tooth in the anterior separated from 3 cheek teeth (1st molar, 2nd molar, 3rd, molar) by a wide diastema (Hillson, 2005). The incisors erupt when the animal is approximately 9–18 days old (Koffler, 1972; Daly, 1975) and continue to grow (and wear) throughout the individuals life. The enamel layer occurs only on the buccal surface. Studies of incisor growth rates in species of voles, rats and mice all conclude that an incisor is fully replaced within 24–50 days (Schour and Massler, 1963; Coady et al., 1967; Klevezal et al., 1990). If gerbil incisors grow at similar rates to other rodents, then these teeth reflect the last 4–8 weeks of the animal's life. In contrast, the molars are permanent rooted teeth that begin development *in utero* within days of one another. They are fully mineralised 4–8 days postnatal, except for the M3, which forms just after weaning (around 20 days) (Hiatt et al., 1974). Isotopic fractionation does not occur across the placental boundary (Fogel et al., 1989; Metcalfe et al., 2010), so tooth tissue formed in this period directly reflects the isotopic composition of the mother's body water. This may not be the case in the nursing period as fractionation may occur in the production of milk. However, there is little substantive evidence in the literature for a nursing effect in the δ^{18}O and δ^{13}C composition of animal teeth. Observations for changes in δ^{13}C of body tissues formed before and after weaning are highly variable (Fogel et al., 1989; Wright and Schwarcz, 1998; Williams et al., 2005; Fuller et al., 2006), while teeth formed during the nursing period appear to have slightly higher δ^{18}O relative to those formed post-weaning (Wright and Schwarcz, 1998; Metcalfe et al., 2010).

The stable isotope composition of the incisor and molar teeth from the same gerbil individual may differ due to the varying development times of each tooth type. Since most gerbils are born during the spring/summer months, it can be inferred that the isotopic composition of these molar teeth reflects the spring/summer season (breeding season), while the continuously growing incisor teeth are more likely to reflect the season in which the animal died. The incisor teeth could also reflect a seasonal bias if the predator hunts more often in one season, or targets specific prey in one season (Royer et al. 2014).

2.4. Methods

One gerbil mandible or maxilla was collected from separate owl pellets, and the teeth were removed. To examine inter-tooth variation within individuals δ^{18}O and δ^{13}C, measurements were undertaken on the incisor (I), 1st molar (M1) and 2nd molar (M2) of eleven *Meriones* individuals from the same side (left/right) of either the maxilla or mandible. Inter-tooth variation was more difficult to examine in *Gerbillus* because of the small size of the teeth. Where possible individual I and M1's from larger *Gerbillus* were analysed, but in order to obtain sufficient sample for isotopic measurement, tooth powder from either 2Is, 2 M1s or an M1 and M2 were combined. No attempt was made to analyse M3's for either species as they were too small. δ^{18}O and δ^{13}C measurements were carried out on seventy gerbil individuals from the eight collection sites (Fig. 1, Table 1), using one M1 from the *Meriones* and larger *Gerbillus* individuals, but either two M1's or an M1 + M2 from the smaller *Gerbillus* teeth. Molar teeth were not present in some of gerbil maxilla/mandible; therefore in a small number of individuals δ^{18}O and δ^{13}C values from incisor teeth were used to increase sample size at three sites (see Table 4).

Exterior surfaces of the teeth were cleaned with a sand blaster to remove visible dirt. The roots of the molar teeth were removed and the tooth sectioned to remove dirt from inside the tooth. The tooth was crushed using an agate mortar and pestle following the method of Gehler et al. (2012); no attempt was made to remove the dentine because of the small size of these teeth. Given the relatively short formation times for these teeth we assume that dentine apatite and enamel apatite represent the same period and conditions. The tooth samples were not pre-treated other than by mechanical cleaning. This was primarily due to their small size, and because it is extremely difficult to mechanically separate enamel and dentine in small modern teeth. Prior to these analyses, we compared the results of bulk molar and incisor material with and without standard pre-treatment methods (1.7% v/v sodium hypochlorite to remove organics, and 0.1 M acetic acid to remove secondary carbonates) (Sponheimer, 1999). The results showed no consistent differences between the pre-treated and untreated material (Table 3), but as found elsewhere, even brief (10 min) immersion in 0.1 M acetic acid dissolves up to 50% of the enamel.

Approximately 2 mg of tooth powder was reacted with 100% phosphoric acid at 70 °C in an automated Thermo Gas Bench II device, coupled with Thermo Delta V Advantage mass spectrometer, in the Stable Light Isotope Facility, University of Bradford. Data is reported in the δ-notation as per mil (‰) relative to the international reference standard VPDB for both δ^{18}O and δ^{13}C. The analytical precision for all measurements was better than 0.1‰ (1σ) for δ^{13}C and 0.2‰ (1σ) for δ^{18}O based on same-run replicates of two in-house standards, BES (tooth bioapatite enamel standard) ($\delta^{13}C = -11.1$ (VPDB), $\delta^{18}O = 25.0$ (VSMOW)) and Merck $CaCO_3$ ($\delta^{13}C = -35.45$ (VPDB), $\delta^{18}O = 13.35$ (VSMOW)). In run international standards NBS-19 gave values of 2.02 ± 0.01 for δ^{13}C and 28.76 ± 0.13 ($n = 3$ for each run), while CO-1 gave 2.44 ± 0.02 for δ^{13}C and 28.46 ± 0.09 ($n = 4$).

Statistical analyses were performed using the freeware statistics package 'R' (http://www.r-project.org/). A t-test was performed to examine inter-genera variation between *Meriones* and *Gerbillus* at the site of Sidi Chicker, where high numbers of each genus were collected from an owl's nest. Low sample numbers limit the statistical exploration of inter-genera variation at the other seven sites. To evaluate whether the differences in the mean δ^{13}C and δ^{18}O composition of the gerbil molar teeth between sites was statistically significant an analysis of variance (ANOVA) was performed, followed by post-hoc tests (Tukey) for pairwise comparisons (Berrechid was not considered in the ANOVA due to small sample size). A linear model (least squares regression) was used to explore the relationship between the δ^{18}O composition of the gerbil molar teeth, MAP and $\delta^{18}O_{mw.}$

3. Results

3.1. Inter-tooth variation in δ^{18}O and δ^{13}C

Figs. 2 and 3 show the isotopic differences between left or right incisor, and 1st molar teeth, expressed as $\Delta^{18}O_{I\text{-}M1}$ ($\delta^{18}O_{incisor} - \delta^{18}O_{M1}$) and $\Delta^{13}C_{I\text{-}M1}$ ($\delta^{13}C_{incisor} - \delta^{13}C_{M1}$) in *Meriones*, and the difference between left or right incisor and molar teeth in *Gerbillus* expressed as $\Delta^{18}O_{I\text{-}M}$ ($\delta^{18}O_{incisor} - \delta^{18}O_{M}$) and $\Delta^{13}C_{I\text{-}M}$ ($\delta^{13}C_{incisor} - \delta^{13}CM$) (specific molars are not attributed in this case) (δ^{18}O and δ^{13}C values for inter-tooth analysis are provided in Supplementary Information Table 1). In *Gerbillus* $\Delta^{18}O_{I\text{-}M}$ and $\Delta^{13}C_{I\text{-}M}$ varies between individuals from ±1.1 to 5.4‰ and ±0.4 to 3.7‰, respectively (Fig. 3), while for *Meriones* $\Delta^{18}O_{I\text{-}M1}$ and $\Delta^{13}C_{I\text{-}M1}$ is ±0.1 to 2.4‰ and ±0.3 to 4.2‰ (Fig. 2). Fig. 2 also shows the isotopic difference between the 2nd molar and 1st molar, expressed as $\Delta^{18}O_{M2\text{-}M1}$ and $\Delta^{13}C_{M2\text{-}M1}$ in *Meriones*. In most *Meriones* individuals the δ^{18}O and δ^{13}C composition of M2's lies within the error range of the M1. The *Meriones* incisors tend to have lower or similar δ^{18}O and δ^{13}C composition to that recorded in the molars. This pattern is also observed in the δ^{18}O of the *Gerbillus* molar and

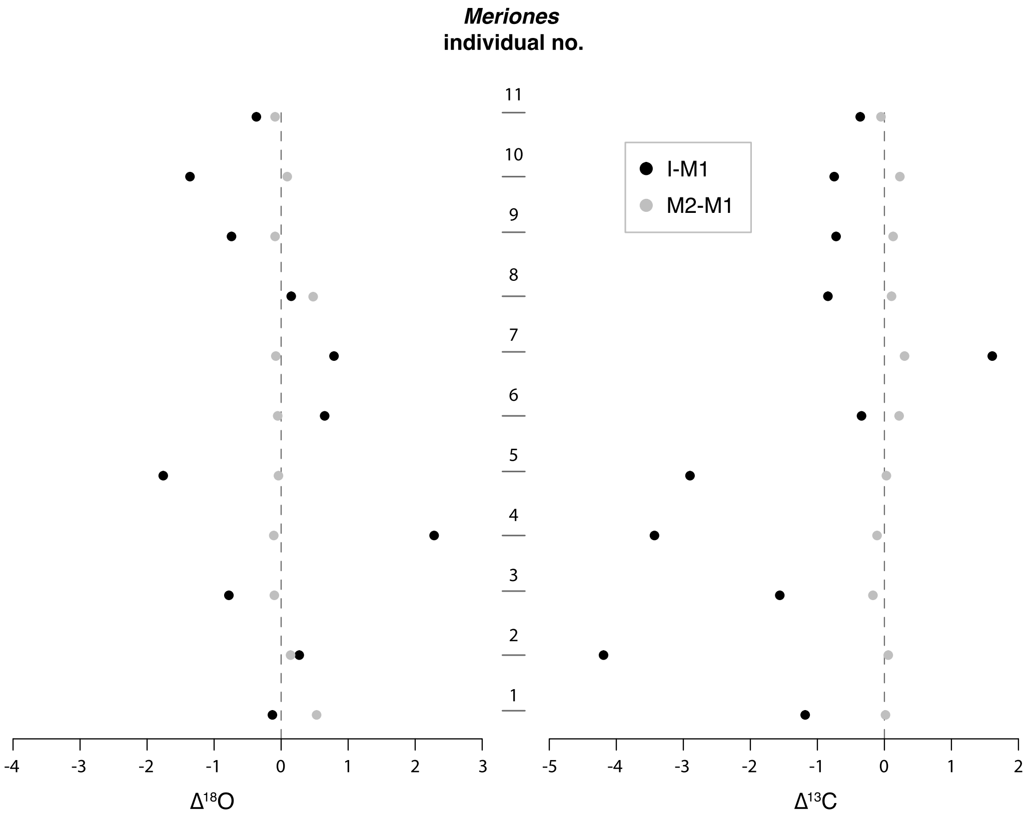


Fig. 2. Diagram showing the a) $\delta^{18}O_{incisor} - \delta^{18}O_{M1}$ (black dots) and $\delta^{18}O_{M2} - \delta^{18}O_{M1}$ (grey dots) b) $\delta^{13}C_{incisor} - \delta^{3}C_{M1}$ (black dots) and $\delta^{13}C_{M2} - \delta^{13}C_{M1}$ (grey dots) in the eleven *Meriones* individuals in which inter-tooth variation was explored. The dotted 'zero' line indicates there is no isotopic offset between the $\delta^{18}O$ and $\delta^{13}C$ composition of either the I and M1 or M2 and M1. Negative numbers indicate that the I and M2's have a lower isotopic composition in comparison to the M1, while positive numbers show that the I and M2's have a higher isotopic composition compared to the M1.

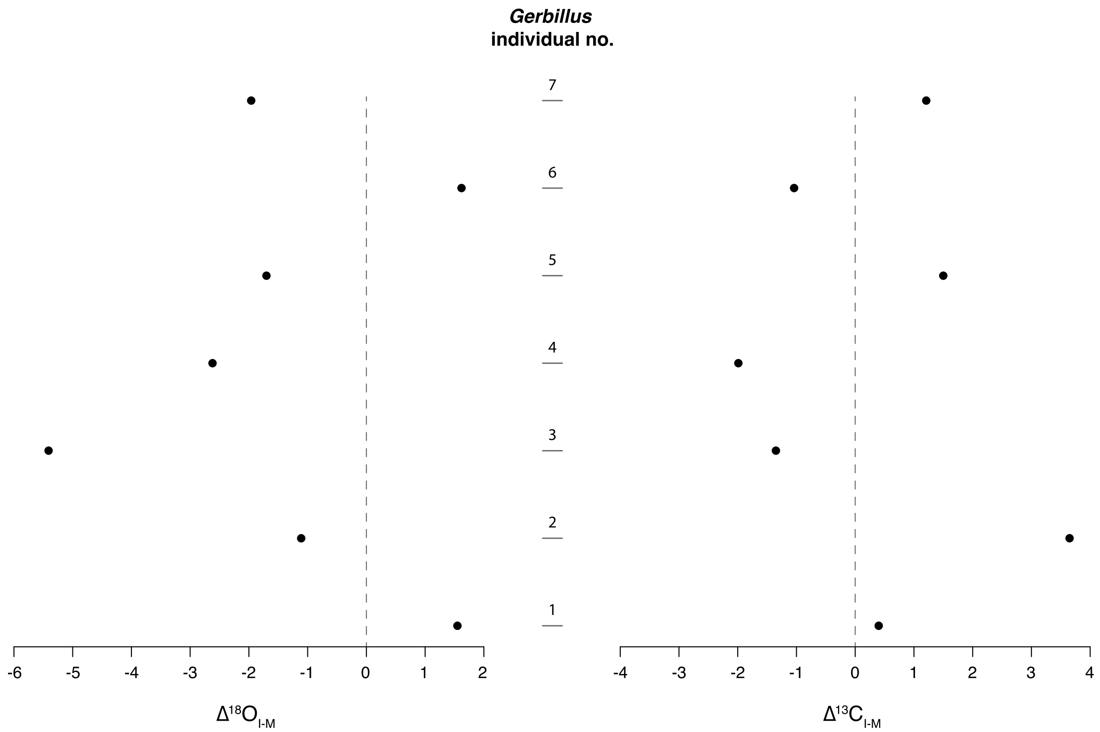


Fig. 3. Diagram showing the a) $\delta^{18}O_{incisor} - \delta^{18}O_{M}$ and the b) $\delta^{13}Cincisor - \delta^{13}C_{M}$ in the seven *Gerbillus* individuals in which inter-tooth variation was explored. The dotted 'zero' line indicates there is no isotopic offset between the $\delta^{18}O$ and $\delta^{13}C$ composition of the molar and incisor teeth. Negative numbers indicate that the incisor teeth have a lower isotopic composition in comparison to the molar teeth, while positive numbers show that the incisor teeth have a higher isotopic composition compared to the molar teeth.

Table 3

Effect of standard pretreatment methods (1.7% v/v sodium hypochlorite to remove organics, and 0.1 M acetic acid to remove secondary carbonates) on bulk molar and incisor gerbil teeth material. Four analyses for $\delta^{18}O$ and $\delta^{13}C$ were carried out on both the incisor and molar material that had underwent different pretreatments; 1) no pretreatment, 2) 1 hr NaClO, 10 mins 0.1 M acetic acid, 3) 3 hr NaClO, 10 mins 0.1 M acetic acid, 4) 6 hr NaClO, 10 mins 0.1 M acetic acid.

	Bulk tooth material	No pretreatment (VPDB ‰)	1 hr NaClO 10 min 0.1 M acetic acid (VPDB ‰)	3 hr NaClO 10 min 0.1 M acetic acid (VPDB ‰)	6 hr NaClO 10 min 0.1 M acetic acid (VPDB ‰)
$\delta^{13}C$	Incisor	−15.1	−15.4	−15.5	−15.6
	Molar	−14.3	−17.0	−14.6	−14.4
$\delta^{18}O$	Incisor	0.4	0.4	0.1	0.4
	Molar	0.8	−1.4	1.1	1.3

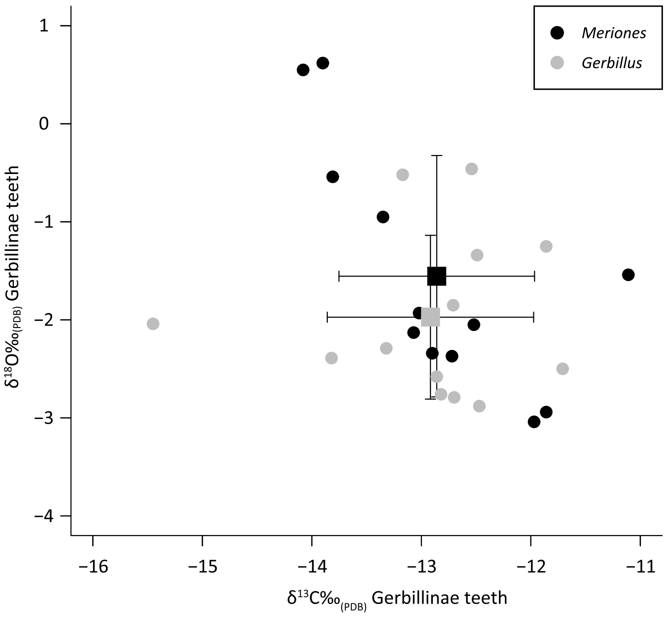


Fig. 4. The $\delta^{18}O$ and $\delta^{13}C$ composition of *Gerbillus* ($n = 13$) and *Meriones* ($n = 12$) molar teeth at Sidi Chicker (small dots). The large squares show the mean and standard deviation (1σ) of each genus.

incisor teeth, but it is not as clear in the $\delta^{13}C$ values of the *Gerbillus* teeth.

3.2. Inter-genera variation in $\delta^{18}O$ and $\delta^{13}C$ of gerbil molars

Comparison of means for *Meriones* ($\delta^{18}O = -1.6‰ \pm 1.2$, $\delta^{13}C = -12.9‰ \pm 0.9$, n = 12) and *Gerbillus* ($\delta^{18}O = -2.0‰ \pm 0.8$, $\delta^{13}C = -12.9‰ \pm 0.9$, n = 13) molars at Sidi Chicker show that they are similar and statistically indistinguishable (based on T-tests $p =< 0.05$ in both cases) (Fig. 4). Given these similarities we combined the isotope data for the two genera in subsequent analyses.

3.3. $\delta^{18}O$ and $\delta^{13}C$ composition of Gerbillinae molar teeth in northwestern Africa

Summary statistics for the $\delta^{18}O$ and $\delta^{13}C$ composition of gerbil molar teeth ($\delta^{18}O_{mt}$ and $\delta^{13}C_{mt}$) for each of the eight sites across northwestern Africa are listed in Table 4 ($\delta^{18}O$ and $\delta^{13}C$ values for each tooth are provided in Supplementary Information Table 2). Variation in $\delta^{18}O$ for all the gerbil molars ranges from −5.2‰ to 3.8‰. Mean $\delta^{18}O_{mt}$ values at each site are 1.8‰ ± 1.9 (Beni Abbes), −0.9‰ ± 0.6 (Tata), −1.8‰ ± 1.0 (Sidi Chicker), −2.7‰ ± 1.2 (Guenfouda), −3.7‰ ± 0.7 (Berrechid), −3.7‰ ± 0.9 (Oued Nfifikh), −3.5‰ ± 0.8 (Ouled Boughadi) and −4.5‰ ± 0.6 (Merja Zerga). Intra-site variation in $\delta^{18}O$ ranges from 1.0‰ at Berrechid to 4.3‰ at Beni Abbes. Higher intra-site variation at Beni Abbes is consistent with the highly variable rainfall at this site. An analysis of variance (ANOVA) shows significant differences in $\delta^{18}O_{mt}$ between Beni Abbes, Tata, Sidi Chicker, Guenfouda, Oued Nfifikh, Ouled Boughadi and Merja Zerga ($F = 30.94$, $P =< 0.01$). A post hoc Tukey test shows significant differences between the $\delta^{18}O_{mt}$ at the arid sites with <300 mm MAP (Beni Abbes, Tata and Sidi Chicker) and the mesic sites that have >400 mm MAP (Oued Nfifikh, Ouled Boughadi and Merja Zerga) ($P =< 0.01$). Beni Abbes, the site with highest $\delta^{18}O_{mt}$, differs significantly from all six other sites (Tukey test, $P =< 0.01$). There are no significant differences between sites with >300 mm MAP (Guenfouda, Oued Nfifikh, Ouled Boughadi and Merja Zerga). Overall, these analyses show significant differences in $\delta^{18}O_{mt}$ between arid and mesic sites, but not between sites with similar MAP.

Variation in $\delta^{13}C$ for all gerbil molars ranges from −16.3‰ to −4.6‰. Mean $\delta^{13}C$ values for each site are −13.4‰ ± 1.4 (Beni Abbes), −8.0‰ ± 3.4 (Tata), −12.9‰ ± 0.9 (Sidi Chicker), −14.8‰ ± 1.2 (Guenfouda), −14.8‰ ± 0.5 (Berrechid), −12.9‰ ± 2.7 (Oued Nfifikh), −14.9‰ ± 0.5 (Ouled Boughadi) and −14.0‰ ± 1.3 (Merja Zerga). Beni Abbes, Sidi Chicker, Guenfouda, Berrechid, Ouled Boughadi, Merja Zerga all have relatively low intra-site $\delta^{13}C_{mt}$ variation of 0.6 to 4.6‰, whereas the intra-site variation at Tata and Oued Nififikh is large (8.9‰ and 7.6‰, respectively) (Fig. 5). An analysis of variance (ANOVA) shows there are significant differences in $\delta^{13}C_{mt}$ between Beni Abbes, Tata, Sidi Chicker, Guenfouda, Oued Nfifikh, Ouled Boughadi and Merja Zerga ($F = 14.92$, $P =< 0.01$). A post hoc Tukey test shows that the $\delta^{13}C_{mt}$ at Tata is significantly different to that from all other sites ($P =< 0.01$).

Using the experimentally observed carbon isotope fractionation between tooth enamel bioapatite and diet in rodents of 11.5‰ (Passey et al., 2005), we infer that the gerbils at Beni Abbes, Sidi Chicker, Guenfouda, Berrechid, Ouled Boughadi, Merja Zerga and most individuals at Oued Nfifikh had C_3 diets with average $\delta^{13}C$ compositions from ∼ −28 to −22‰. At Tata $\delta^{13}C_{mt}$ values range from ∼ −5 to −13‰, indicating some contribution of C_4 plants to the diet. A single individual at Oued Nfifikh shows a clear C_4 contribution (Fig. 5). Amongst the gerbils that consumed a pure/predominantly C_3 diet, generally higher $\delta^{13}C$ values (∼ −12 to −14‰) are recorded at the arid sites (Beni Abbes, Tata and Sidi Chicker), than at the more mesic sites of Guenfouda, Oued Nfifikh, Ouled Boughadi, Berrechid and Merja Zerga where $\delta^{13}C$ values are tend to be lower (∼ −16 to −14‰), although these differences are not statistically significant. Gerbils at Oued Nfifikh and Merja Zerga have $\delta^{13}C_{mt}$ values that span those recorded at both the mesic and arid sites (Fig. 5).

4. Discussion

4.1. Inter-tooth variation in $\delta^{18}O$ and $\delta^{13}C$

Variation in $\delta^{18}O$ and $\delta^{13}C$ of continuously growing incisors and permanent, rooted molars amongst small mammals has been poorly documented to date. The only existing study to explore this issue (as far as we are aware) documents inter-tooth variation within *Arvicola terrestris*, a species that has both continuously

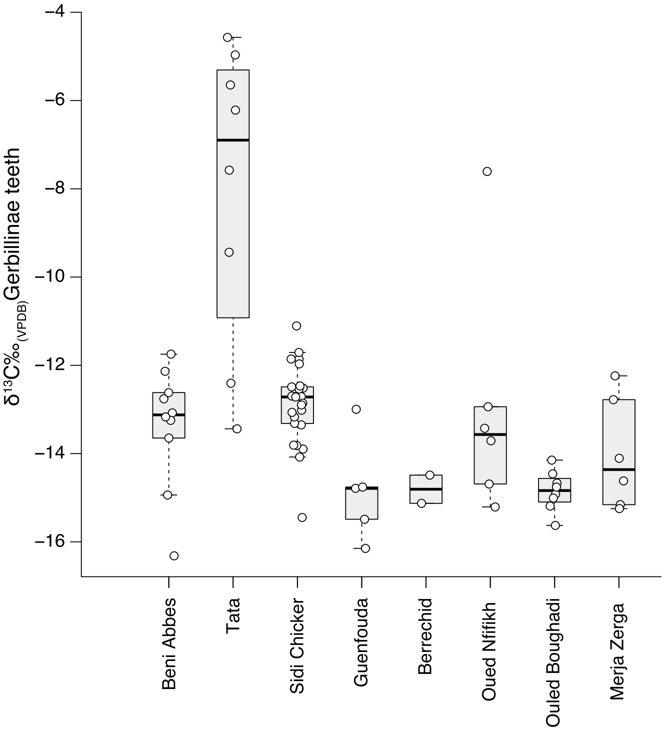


Fig. 5. Boxplot showing the δ^{13}C composition of Gerbillinae molar teeth from the eight sites across NW Africa. The δ^{13}C composition of each individual tooth (white dots) is also marked the graph to demonstrate the intra-site variation at each site.

growing molar and incisor teeth (Gehler et al., 2012). Gehler et al. (2012) reported inter-tooth ranges between M1, M2 and M3 in *Arvicola terrestris* of ±0.2 to 1.0‰ for δ^{18}O, and 0.1 to 0.6‰ for δ^{13}C, slightly higher than the inter-molar range recorded in *Meriones* of ±0.0 to 0.5‰ and ±0.0 to 0.2‰ respectively (see Fig. 2). The overall inter-tooth range (I, M1, M2 and M3) in *Arvicola terrestris* increased with the inclusion of the incisor tooth to 0.3 to 1.9‰ in δ^{18}O and 0.3 to 1.5‰ in δ^{13}C, lower than the isotopic differences between incisors and molar teeth in both *Meriones* and *Gerbillus*.

Differences between the inter-molar isotopic ranges in the gerbils and *Arvicola terrestris* are best explained by considering the respective tooth formation times. In *Meriones*, the M1 and M2 mineralise within days of each other after birth (Hiatt et al., 1974) and therefore form from the same body water and bicarbonate pools, whereas in *Arvicola terrestris* molars grow continuously, and potentially at different rates. In that case seasonal dietary and environmental differences may be reflected. Overall inter-tooth variation (including the molar and incisor teeth) in the gerbils (up to ∼5‰ in δ^{18}O and ∼4‰ in δ^{13}C; Figs. 2 and 3) is higher than that observed in *Arvicola terrestris*. This difference is partly explained by the differences in developmental times of the various teeth. Gerbil molars form only in the spring/summer breeding season whereas incisors grow continuously throughout life (Schour and Massler, 1963; Coady et al., 1967; Klevezal et al., 1990); in the latter case the isotopic composition may reflect any season. In contrast *Arvicola terrestris* incisors and molars both grow continuously and are thus less likely to show inter-tooth δ^{18}O and δ^{13}C disparity.

Isotopic offsets in δ^{18}O and δ^{13}C between the gerbil molar and incisor teeth show that as predicted, each tooth type reflects a different temporal period. There are advantages and disadvantages to using permanent molar, or continuously growing incisor teeth, for palaeoclimate reconstructions. Although molars reflect a short time-span i.e. the breeding season, the δ^{18}O and δ^{13}C results are more consistent with less variation. Continuously growing incisor teeth are inherently more variable in that they are not seasonally restricted, although they may provide annually resolved information. The incisor teeth may also record a seasonal prey bias if owls tend to hunt gerbils preferentially in a particular season. The tendency for higher δ^{18}O and δ^{13}C values in molars relative to incisors in gerbils hints at the potential for construction of seasonally resolved palaeorecords. Whether or not this potential is achieved, our results show careful consideration must be given to tooth choice when applying an isotope approach to the construction of proxy climate records.

4.2. Inter-genera variation in δ^{18}O and δ^{13}C of molar teeth

The results show that there is no inter-genera variation in $\delta^{18}O_{mt}$ and $\delta^{13}C_{mt}$ between *Meriones* sp. and *Gerbillus* sp. at Sidi

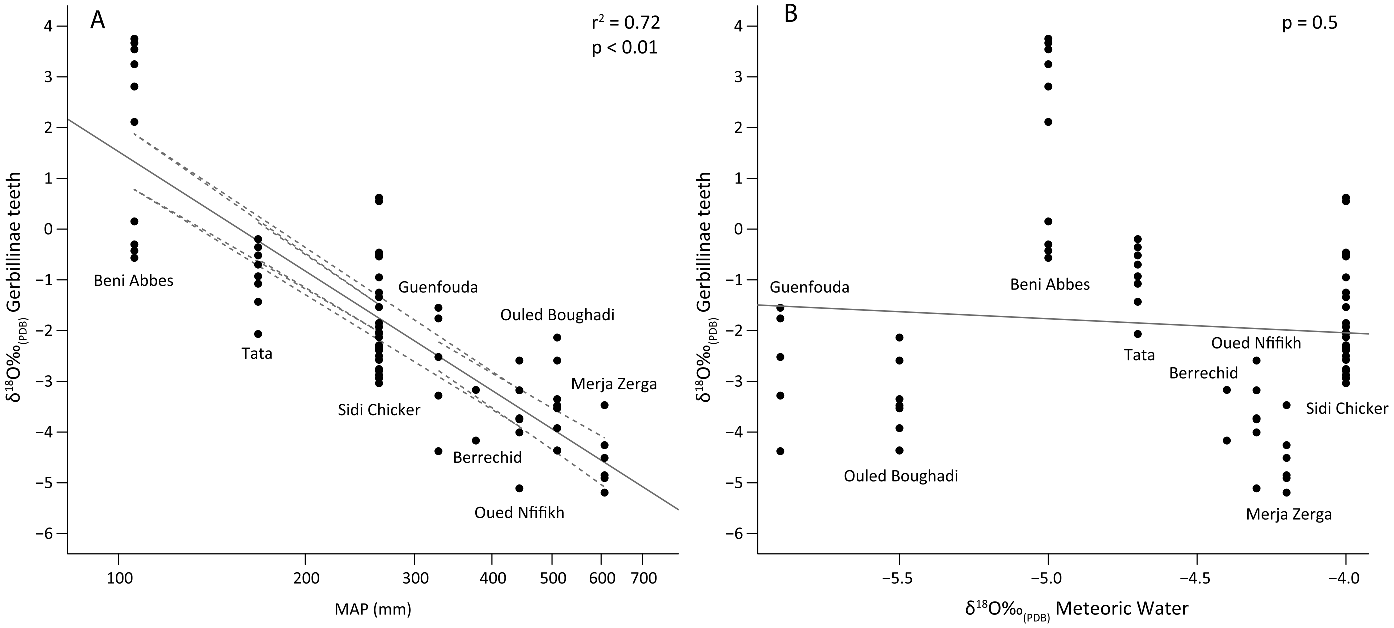


Fig. 6. Relationship between $\delta^{18}O_{mt}$ and A) MAP; B) $\delta^{18}O_{mw}$ from the eight sites across NW Africa.

Table 4
Summary statistics for the δ^{18}O and δ^{13}C composition of gerbil molar teeth from the eight sites across NW Africa. * indicate the number of incisor teeth used at each site.

Site	Number of molar teeth from individuals	$\delta^{18}O_{(VPBD)}$ Mean (‰)	Standard deviation (1σ)	Minimum (‰)	Maximum (‰)	Range (‰)	$\delta^{13}C_{(VPBD)}$ Mean (‰)	Standard deviation (1σ)	Minimum (‰)	Maximum (‰)	Range (‰)
Beni Abbes	*10	1.8	1.9	−0.6	3.8	4.3	−13.4	1.4	−16.3	−11.8	4.6
Tata	***8	−0.9	0.6	−2.1	−0.2	1.9	−8.0	3.4	−13.4	−4.6	8.9
Sidi Chicker	25	−1.8	1.0	−3.0	0.6	3.7	−12.9	0.9	−15.5	−11.1	4.3
Guenfouda	5	−2.7	1.2	−4.4	−1.6	2.8	−14.8	1.2	−16.2	−13.0	3.2
Berrechid	2	−3.7	0.7	−4.2	−3.2	1.0	−14.8	0.5	−15.1	−14.5	0.6
Oued Nfifikh	*6	−3.7	−0.9	−5.1	−2.6	2.5	−12.9	2.7	−15.2	−7.6	7.6
Ouled Boughadi	8	−3.5	0.8	−4.4	−2.1	2.2	−14.9	0.5	−15.6	−14.2	1.5
Merja Zerga	6	−4.5	0.6	−5.2	−3.5	1.7	−14.0	1.3	−15.3	−12.2	3.0

**indicates number of incisor teeth in sample.*

Chicker (Fig. 4). This is not entirely unexpected because *Meriones* and *Gerbillus* belong to the same sub-family (Gerbillinae) and have similar behaviours, diets and habitat preferences (Table 2). The species at Sidi Chicker (*M. shawii/grandis* and *G. campestris*) are all classed as granivores with very similar diets (Table 2). Likewise, they have comparable habitat preferences and can be found in Mediterranean steppes, cultivated areas and oases (Table 2). Thus similarities in δ^{18}O and δ^{13}C compositions likely reflect similar moisture conditions and dietary pools, as well as suggesting that both species have closely similar physiology and drinking behaviours. As *Meriones* and *Gerbillus* have similar isotope ecologies it allows us to combine the data from both genera, and all species, for the purposes of examining geographic/climate response variability.

4.3. δ^{18}O and δ^{13}C composition of Gerbillinae molar teeth in northwestern Africa

There is a significant inverse correlation between $\delta^{18}O_{mt}$ and MAP ($p =< 0.01$, $R^2 = -0.72$), but no significant relationship between $\delta^{18}O_{mt}$ and the interpolated $\delta^{18}O_{mw}$ ($p = 0.5$) (Fig. 6). The relationship between $\delta^{18}O_{mt}$ and MAP improves when average δ^{18}O values from each site are used ($p =< 0.01$, $R^2 = -0.94$) (Fig. 7). The linear regression shows that when MAP is <300 mm, moisture availability is more closely correlated with $\delta^{18}O_{mt}$ but at the sites where MAP is >400 mm, moisture availability has a lesser effect. At the more mesic sites of Berrechid, Oued Nfifikh and Ouled Boughadi the $\delta^{18}O_{mt}$ are not strongly enriched over local $\delta^{18}O_{mw}$, and at Merja Zerga with ∼600 mm MAP the $\delta^{18}O_{mt}$ appears to be approximately similar to that of $\delta^{18}O_{mw.}$ Therefore, as moisture availability decreases, $\delta^{18}O_{mt}$ increases, but in more mesic settings aridity has less of an effect on the $\delta^{18}O_{mt}$ and these values more likely reflect that of $\delta^{18}O_{mw}$. Because there is a strong relationship between $\delta^{18}O_{mt}$ and MAP, it suggests that any possible physiological signal (from nursing for example) is overprinted by the climate signal in the gerbil molar teeth.

The observation that $\delta^{18}O_{mt}$ reflects moisture availability in semi-arid and arid environments such as these rather than $\delta^{18}O_{mw}$, as is commonly assumed, most likely reflects the gerbil's reliance on water from food and the effect of aridity on this water pool. This contribution of water and oxygen from the diet is perhaps greater than anticipated for good reasons. For instance, an experimental study of woodrats reported that 56% of drinking water and 15% food were responsible for the oxygen in bodywater (Podlesak et al., 2008). These results, however, cannot be interpolated easily to semi-arid and arid settings. Grains make up the largest component of gerbils' diet and in order to conserve water, gerbils store grains in their more humid, cool burrows to absorb soil moisture into the grain (Merritt, 2010). Soil and surface waters are likely to be enriched in ^{18}O compared to meteoric water due to evaporative effects (Gat and Airey, 2006). Gerbils also eat plant leaves, which are known to be highly sensitive to evaporative enrichment in ^{18}O (Gonfiantini et al., 1965; Yakir et al., 1990). Modelled annual δ^{18}O leaf water values show that values in Mediterranean North Africa are high (∼12‰), and on the periphery of the Sahara, where Beni Abbes and Tata are located, modelled leaf water values are extremely high (∼22‰) (West et al., 2008). The evaporative effects may not be as strong in nocturnal gerbils as in diurnal animals, because the δ^{18}O of leaf water is lower at night (Förstel, 1978), but its effects will still be evident. Relationships between the δ^{18}O composition of mammal body tissues and aridity/relative humidity in areas with high moisture deficits have been similarly observed in several 'evaporation sensitive' large mammals (Cormie et al., 1994; Iacumin and Longinelli, 2002; Levin et al., 2006).

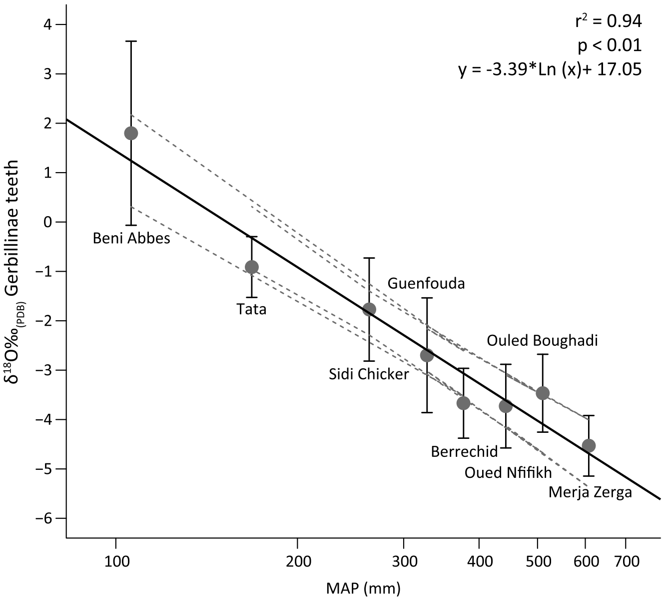


Fig. 7. Relationship between the mean $\delta^{18}O_{mt}$ and MAP from each sites across NW Africa. The error bars show standard deviation (1σ) It should be noted that there were only two teeth were analysed from Berrechid.

The low daily water requirements of small mammals compared to larger mammals suggests that small mammal body waters are generally more sensitive to evaporative loss and therefore enrichment in ^{18}O compared to large mammals. Laboratory studies have shown that even when free water is available gerbils drink extremely small amounts (Winkelmann and Getz, 1962; Laughlin et al., 1975) and they can survive for several days without water by relying on metabolic and food water (Edwards et al., 1983). Although gerbils have several adaptive strategies to avoid over-heating and prevent water loss, a controlled laboratory study has shown that evaporative loss increases with temperature in *Meriones unguiculatus* (Buffenstein and Jarvis, 1985). Therefore, in the high temperature arid environments of Beni Abbes and Tata the gerbils' bodywater will undergo a higher level of evaporative enrichment in ^{18}O in comparison to those gerbils in the more mesic environments on the Atlantic coast. All of these factors contribute to the strong effects of reduced moisture availability and increased temperatures on gerbil bodywater $\delta^{18}O$ values.

Although the arid sites tend to have higher $\delta^{13}C_{mt}$ relative to the more mesic sites they do not differ significantly (with the exception of Tata where the gerbils consumed C_4 plants in their diet). This suggests that $\delta^{13}C_{mt}$ does partly reflect the isotopic effects of water deficit on the predominantly C_3 vegetation consumed by the gerbils, but there is high $\delta^{13}C_{mt}$ variability resulting from the gerbils microhabitat and short time period recorded by the teeth (Fig. 5). The results show that the $\delta^{13}C$ composition of small mammal teeth reflects C_3/C_4 vegetation inputs in arid and semi-arid settings. Care should be taken when interpreting $\delta^{13}C$ composition of small mammal teeth in proxy climate records because of the high $\delta^{13}C$ variability from the reflected microhabitats.

5. Conclusion

We have shown that the isotopic composition of molars and incisors from the same rodent individual differs, consistent with the different temporal periods reflected by the teeth; molar teeth are permanently rooted and form around the time of birth, whereas incisors grow continuously. Therefore, careful consideration should be given to the signal reflected by each tooth when selecting to build proxy palaeo-climate and environmental records. The data also indicates that molar and incisor teeth could also be potentially used as a means to distinguish seasonal contexts. We have demonstrated a robust relationship between $\delta^{18}O_{mt}$ and MAP resulting from the gerbils' reliance on food water. Predictably the $\delta^{13}C_{mt}$ recorded the gerbils diet reflecting both C_3 and C_4 dietary inputs. Gerbil teeth are generally more ^{13}C-depleted in mesic areas compared to arid ones, reflecting the isotopic effects of water deficit on the predominantly C_3 vegetation, however there is high variability in $\delta^{13}C_{mt}$ due to the microhabitat reflected by the gerbil. The results indicate that the $\delta^{18}O$ composition of small mammal teeth strongly reflects aridity in semi-arid and arid environments and would make an excellent proxy for terrestrial palaeo-aridity in this setting. $\delta^{13}C$ data should be used to compliment the $\delta^{18}O$ data, but care should be taken during interpretation due to the microhabitat and short temporal period reflected by small mammals. Stable isotopes in small mammal teeth accurately record local climate and environmental conditions, but close attention to the developmental periods, and behaviour of the animals' is required in order to make their climate and environmental interpretation meaningful.

Acknowledgements

We thank Chris Green, Andrew Gledhill and Peter Ditchfield for technical assistance, Erika Nitsch for statistics advice, Tom Frankland for help in producing the graphics and Andrew Jeffrey for proof reading. Owl pellets were collected thanks to Francis Petter (Tata), Stéphane Aulagnier (INRA Toulouse, France) (Sidi Chicker), Francis Petter (Tata), Watik Hamdine (Beni Abbes), ANR-09-PEXT-004 MOHMIE project for Berrechid, Ouled Boughadi, Merja Zerga and Guenfouda and the RHOI (NSF) project for Oued Nfifikh (with the help of Abdeslam Rihane, University of Casablanca). We would like to thank Aurélien Royer and two anonymous reviewers whose helpful comments significantly improved the manuscript. This research was funded by NERC training grant NE/K500811/1, the Boise Trust Fund and St Cross College.

Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.epsl.2015.07.012.

References

Adamou-Djerbaoui, M., Denys, C., Chaba, H., Seid, M.M., Djelaila, Y., Labdelli, F., Adamou, M.S., 2013. Étude du régime alimentarie d'un rongeur nuisible (*Meriones shawii* Duvernoy, 1842, Mammalia, Rodentia) en Algerie. Leban. Sci. J. 14, 15–32.

Andrews, P., 1990. Owls, Caves and Fossils. Natural History Museum Publications, London.

Aulagnier, S., Thevenot, M., 1986. Catalogue des mammifères sauvages du Maroc. Trav. l'Institut Sci. Rabat, Série Zool. 41, 1–164.

Aulagnier, S., Haffner, P., Mitchell-Jones, A.J., Moutou, F., Zima, J., 2009. Mammals of Europe, North Africa and the Middle East. A&C Black, London.

Ayliffe, L.K., Lister, A.M., Chivas, A.R., 1992. The preservation of glacial–interglacial climatic signatures in the oxygen isotopes of elephant skeletal phosphate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 99, 179–191.

Belabbas, S., Butet, A., 1994. The diet of *Meriones shawii*, in the nature reserve of Mergueb, Algeria. Pol. Ecol. Stud. 20, 293–303.

Bowen, G.J., Revenaugh, J., 2003. Interpolating the isotopic composition of modern meteoric precipitation. Water Resour. Res. 39, 1299. http://dx.doi.org/10.1029/2003WR002086.

Bryant, D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochim. Cosmochim. Acta 59, 4523–4537. http://dx.doi.org/10.1016/0016-7037(95)00250-4.

Buffenstein, R., Jarvis, J.U., 1985. Thermoregulation and metabolism in the smallest African gerbil, *Gerbillus pusillus*. J. Zool. 205, 107–121.

Cerling, T.E., Harris, J.M., Macfadden, B.J., Leakey, M.G., Quadek, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153–158.

Coady, J.M., Toto, P.D., Santangelo, M.V., 1967. Histology of the mouse incisor. J. Dent. Res. 46, 384–388. http://dx.doi.org/10.1177/00220345670460021201.

Cormie, A.B., Luz, B., Schwarcz, H.P., 1994. Relationship between the hydrogen and oxygen isotopes of deer bone and their use in the estimation of relative humidity. Geochim. Cosmochim. Acta 58, 3439–3449.

D'Angela, D., Longinelli, A., 1990. Oxygen isotopes in living mammal's bone phosphate: further results. Chem. Geol. Isot. Geosci. Sect. 86, 75–82. http://dx.doi.org/10.1016/0168-9622(90)90007-Y.

Daly, M., 1975. Early use of solid food by a leaf-eating gerbil (*Psammomys obesus*). J. Mammaol. 56, 509–511.

Dansgaard, W., 1964. Stable isotopes in precipitation. Tellus 16, 436–468.

Delgado Huertas, A., Iacumin, P., Stenni, B., Sánchez Chillón, B., Longinelli, A., 1995. Oxygen isotope variations of phosphate in mammalian bone and tooth enamel. Geochim. Cosmochim. Acta 59, 4299–4305. http://dx.doi.org/10.1016/0016-7037(95)00286-9.

Edwards, B.A., Donaldson, K., Simpson, P., 1983. Water balance and protein intake in the Mongolian gerbil (*Meriones unguiculatus*). Comp. Biochem. Physiol. A 76, 807–815.

Farquhar, G.D., Ehleringer, J.D., Hibick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 503–537.

Fernández-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998. Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). J. Hum. Evol. 34, 137–172. http://dx.doi.org/10.1006/jhev.1997.0188.

Fogel, M., Tuross, N., Owsley, D., 1989. Nitrogen Isotope Tracers of Human Lactation in Modern and Archaeological Populations, vol. 88. Carnegie Institute, New York.

Förstel, H., 1978. The enrichment of ^{18}O in leaf water under natural conditions. Radiat. Environ. Biophys. 15, 323–344.

Fuller, B., Fuller, J., Harris, D., Hedges, R.E., 2006. Detection of breastfeeding and weaning in modern human infants with carbon and nitrogen stable isotope ratios. Am. J. Phys. Anthropol. 129, 279–292.

García-Alix, A., Delgado Huertas, A., Martín Suárez, E., Freudenthal, M., 2013. Environmental conditions vs. landscape. Assessment of the factors that influence small mammal fauna distribution in Southern Iberia during the latest Messinian by mean of stable isotopes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 492–500. http://dx.doi.org/10.1016/j.palaeo.2013.06.017.

Gat, J.R., Airey, P.L., 2006. Stable water isotopes in the atmosphere/biosphere/lithosphere interface: scaling-up from the local to continental scale, under humid and dry conditions. Glob. Planet. Change 51, 2533. http://dx.doi.org/10.1016/j.gloplacha.2005.12.004.

Gehler, A., Tütken, T., Pack, A., 2012. Oxygen and carbon isotope variations in a modern rodent community – implications for palaeoenvironmental reconstructions. PLoS ONE 7, e49531. http://dx.doi.org/10.1371/journal.pone.0049531.

Gonfiantini, R., Gratziu, S., Tongiorgi, E., 1965. Oxygen isotopic composition of water in leaves. In: Isotopes and Radiation in Soil-Plant Nutrition Studies. International Atomic Energy Commission, Vienna, pp. 405–410.

Grimes, S.T., Collinson, M.E., Hooker, J.J., Mattey, D.P., Grassineau, N.V., Lowry, D., 2004. Distinguishing the diets of coexisting fossil theridomyid and glirid rodents using carbon isotopes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 208, 103–119. http://dx.doi.org/10.1016/j.palaeo.2004.02.031.

Grimes, S.T., Collinson, M.E., Hooker, J.J., Mattey, D.P., 2008. Is small beautiful? A review of the advantages and limitations of using small mammal teeth and the direct laser fluorination analysis technique in the isotope reconstruction of past continental climate change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 266, 39–50. http://dx.doi.org/10.1016/j.palaeo.2008.03.014.

Héran, M.-A., Lécuyer, C., Legendre, S., 2010. Cenozoic long-term terrestrial climatic evolution in Germany tracked by δ^{18}O of rodent tooth phosphate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 285, 331–342. http://dx.doi.org/10.1016/j.palaeo.2009.11.030.

Hiatt, J.L., Gartner, L.P., Provenza, D.V., 1974. Molar development in the mongolian gerbil (*Meriones unguiculatus*). Am. J. Anat. 141, 1–22. http://dx.doi.org/10.1002/aja.1001410102.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. http://dx.doi.org/10.1002/joc.1276.

Hillson, S., 2005. Teeth. Cambridge University Press, Cambridge.

Hopley, P.J., Latham, A.G., Marshall, J.D., 2006. Palaeoenvironments and palaeodiets of mid-Pliocene micromammals from Makapansgat Limeworks, South Africa: a stable isotope and dental microwear approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 233, 235–251. http://dx.doi.org/10.1016/j.palaeo.2005.09.011.

Hoppe, K., 2006. Correlation between the oxygen isotope ratio of North American bison teeth and local waters: implication for paleoclimatic reconstructions. Earth Planet. Sci. Lett. 244, 408–417. http://dx.doi.org/10.1016/j.epsl.2006.01.062.

Hynek, S.A., Passey, B.H., Prado, J.L., Brown, F.H., Cerling, T.E., Quade, J., 2012. Small mammal carbon isotope ecology across the Miocene–Pliocene boundary, northwestern Argentina. Earth Planet. Sci. Lett. 321–322, 177–188. http://dx.doi.org/10.1016/j.epsl.2011.12.038.

Iacumin, P., Longinelli, A., 2002. Relationship between δ^{18}O values for skeletal apatite from reindeer and foxes and yearly mean δ^{18}O values of environmental water. Earth Planet. Sci. Lett. 201, 213–219.

Khammar, F., Brudieux, R., 1987. Seasonal changes in testicular contents and plasma concentrations of androgens in the desert gerbil (*Gerbillus gerbillus*). J. Reprod. Fertil. 80, 589–594.

Kingdon, J., 1997. The Kingdon Field Guide to African Mammals. A&C Black, London.

Klevezal, G.A., Pucek, M., Sukhovskaja, L., 1990. Incisor growth in voles. Acta Theriol. 35, 331–344.

Knippertz, P., Christoph, M., Speth, P., 2003. Long-term precipitation variability in Morocco and the link to the large-scale circulation in recent and future climates. Meteorol. Atmos. Phys. 88, 67–88. http://dx.doi.org/10.1007/s00703-002-0561-y.

Koffler, B.R., 1972. Meriones crassus. Mammal. Species 9, 1–4. http://dx.doi.org/10.1126/science.95.2469.427-b.

Kohn, M.J., 1996. Predicting animal δ^{18}O: accounting for diet and physiological adaptation. Geochim. Cosmochim. Acta 60, 4811–4829.

Kowalski, K., Rzebik-Kowalska, B., 1991. Mammals of Algeria. Polish Academy of Sciences, Krakow.

Laughlin, M.E., Donovick, P.J., Burright, R.G., 1975. Consummatory behavior in meadow voles (*Microtus pennsylvanicus*) and mongolian gerbils (*Meriones unguiculatus*). Physiol. Behav. 15, 185–189.

Lee-Thorp, J.A., van der Merwe, N.J., 1987. Carbon isotope analysis of fossil bone apatite. South Afr. J. Sci. 83, 712–713.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. Proc. Natl. Acad. Sci. USA 103, 11201–11205. http://dx.doi.org/10.1073/pnas.0604719103.

Lindars, E., Grimes, S., Mattey, D., Collinson, M., Hooker, J., Jones, T., 2001. Phosphate δ^{18}O determination of modern rodent teeth by direct laser fluorination: an appraisal of methodology and potential application to palaeoclimate reconstruction. Geochim. Cosmochim. Acta 65, 2535–2548.

Longinelli, A., Iacumin, P., Davanzo, S., Nikolaev, V., 2003. Modern reindeer and mice: revised phosphate–water isotope equations. Earth Planet. Sci. Lett. 214, 491–498. http://dx.doi.org/10.1016/S0012-821X(03)00395-9.

Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. Earth Planet. Sci. Lett. 75, 29–36. http://dx.doi.org/10.1016/0012-821X(85)90047-0.

Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochim. Cosmochim. Acta 48, 1689–1693.

Merritt, J.F., 2010. The Biology of Small Mammals. The John Hopkins University Press, Maryland.

Metcalfe, J.Z., Longstaffe, F.J., Zazula, G.D., 2010. Nursing, weaning, and tooth development in woolly mammoths from Old Crow, Yukon, Canada: implications for Pleistocene extinctions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 298, 257–270. http://dx.doi.org/10.1016/j.palaeo.2010.09.032.

Mikkola, H., 1983. Owls of Europe. Calton, Poyser.

Navarro, N., Lécuyer, C., Montuire, S., Langlois, C., Martineau, F., 2004. Oxygen isotope compositions of phosphate from arvicoline teeth and Quaternary climatic changes, Gigny, French Jura. Quat. Res. 62, 172–182. http://dx.doi.org/10.1016/j.yqres.2004.06.001.

Ouda, B., El Hamdaoui, A., Ibn Majah, M., 2005. Isotopic composition of precipitation at three Moroccan stations influenced by Oceanic and Mediterranean air masses. In: Isotopic Composition of Precipitation in the Mediterranean Basin in Relation to Air Circulation Patterns and Climate. International Atomic Energy Commission, Vienna, pp. 125–140.

Park, R., Epstein, S., 1960. Carbon isotope fractionation during photosynthesis. Geochim. Cosmochim. Acta 21, 110–126.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breadth CO$_2$, and bioapatite in different mammals. J. Archaeol. Sci. 32, 1459–1470.

Petter, F., Lachiver, F., Chekir, R., 1984. Les adaptations des rongeurs Gerbilidés à la vie dans les régions arides. Bull. Société Bot. Fr. 131, 365–373. http://dx.doi.org/10.1080/01811789.1984.10826676.

Podlesak, D.W., Torregrossa, A.-M., Ehleringer, J.R., Dearing, M.D., Passey, B.H., Cerling, T.E., 2008. Turnover of oxygen and hydrogen isotopes in the body water, CO$_2$, hair, and enamel of a small mammal. Geochim. Cosmochim. Acta 72, 19–35. http://dx.doi.org/10.1016/j.gca.2007.10.003.

Royer, A., Lécuyer, C., Montuire, S., Amiot, R., Legendre, S., Cuenca-Bescós, G., Jeannet, M., Martineau, F., 2013. What does the oxygen isotope composition of rodent teeth record? Earth Planet. Sci. Lett. 361, 258–271. http://dx.doi.org/10.1016/j.epsl.2012.09.058.

Royer, A., Lécuyer, C., Montuire, S., Primault, J., Fourel, F., Jeannet, M., 2014. Summer air temperature, reconstructions from the last glacial stage based on rodents from the site Taillis-des-Coteaux (Vienne), Western France. Quat. Res. 82, 420–429. http://dx.doi.org/10.1016/j.yqres.2014.06.006.

Schour, I., Massler, M., 1963. The teeth. In: Farris, E.J., Griffith, J.Q. (Eds.), The Rat in Laboratory Investgations. Hafner Publishing Co, New York, pp. 104–165.

Sponheimer, M., 1999. Isotopic ecology of the Makapansgat Limeworks fauna. Rutgers University.

Stoetzel, E., Denys, C., 2011. Les microvertébrés d'Afrique du Nord: synthèse des travaux en néo- et paléotaphonomie. In: Laroulandie, V., Mallye, J.B., Denys, C. (Eds.), Taphonomie des Petits Vertébrés: Référentiels et Transferts aux Fossiles, Actes de la Table Ronde du RTP Taphonomie, Talence 20–21 Octobre. British Archaeological Reports. Archaeopress, Oxford, pp. 23–32.

Stoetzel, E., Marion, L., Nespoulet, R., El Hajraoui, M.A., Denys, C., 2011. Taphonomy and palaeoecology of the late Pleistocene to middle Holocene small mammal succession of El Harhoura 2 cave (Rabat-Témara, Morocco). J. Hum. Evol. 60, 1–33. http://dx.doi.org/10.1016/j.jhevol.2010.07.016.

Teeri, J.A., Stowe, L.G., 1976. Climatic patterns and the distribution of C4 grasses in North America. Oecologia 23, 1–12.

Tieszen, L., 1991. Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. J. Archaeol. Sci. 18, 227–248. http://dx.doi.org/10.1016/0305-4403(91)90063-U.

Tütken, T., Vennemann, T.W., Janz, H., Heizmann, E.P.J., 2006. Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim basin, SW Germany: a reconstruction from C, O, and Sr isotopes of fossil remains. Palaeogeogr. Palaeoclimatol. Palaeoecol. 241, 457–491. http://dx.doi.org/10.1016/j.palaeo.2006.04.007.

West, J.B., Sobek, A., Ehleringer, J.R., 2008. A simplified GIS approach to modeling global leaf water isoscapes. PLoS ONE 3, e2447. http://dx.doi.org/10.1371/journal.pone.0002447.

Williams, J., White, C., Longstaffe, F., 2005. Trophic level and macronutrient shift effects associated with the weaning process in the Postclassic Maya. Am. J. Phys. Anthropol. 128, 781–790.

Winkelmann, J.R., Getz, L.L., 1962. Water balance in the Mongolian gerbil. J. Mammal. 43, 150–154.

Wright, L.E., Schwarcz, H.P., 1998. Stable carbon and oxygen isotopes in human tooth enamel: identifying breastfeeding and weaning in prehistory. Am. J. Phys. Anthropol. 106, 1018.

Yakir, D., DeNiro, M.J., Ephrath, J.E., 1990. Effects of water stress on oxygen, hydrogen and carbon ratios in two species of cotton plants. Plant Cell Environ. 13, 949–955.

Zaime, A., Gautier, J.Y., 1989. Comparaison des regimes alimentaires de trois especes sympatriques de Gerbillidae en milieu saharien. Rev. d'Ecologie (La Terre la Vie) 4, 153–163.

Zaime, A., Laraki, M., Gautier, J.-Y., Garnier, D.H., 1992. Seasonal variations of androgens and of several sexual parameters in male *Meriones shawii* in Southern Morocco. Gen. Comp. Endocrinol. 86, 289–296.