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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

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A B S T R A C T

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

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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