Palaeogeography, Palaeoclimatology, Palaeoecology 490 (2018) 571–578

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Paleodietary change and its implications for aridity indices derived from $\delta^{18}O$ of herbivore tooth enamel

J. Tyler Faith

Natural History Museum of Utah & Department of Anthropology, University of Utah, Salt Lake City, UT 84108, USA

ARTICLE INFO

Keywords:
Aridity index
Oxygen isotopes
Non-ruminant
Ruminant
Water balance
Water dependence

ABSTRACT

A large body of research provides reconstructions of ancient water deficit—the difference between potential evapotranspiration and precipitation—using an aridity index derived from the $\delta^{18}O$ values of tooth enamel from evaporation sensitive (ES) and evaporation insensitive (EI) mammalian herbivores. The former are typically ruminants that obtain most of their water from leafy dicots (the $\delta^{18}O$ of their enamel reflects evaporation of leaf water), whereas the latter are non-ruminants dependent on surface water (the $\delta^{18}O$ of their enamel reflects local meteoric water). Use of the index requires that fossil taxa are correctly classified as ES or EI. This study examines how paleodietary change can influence such classifications. In modern ruminant ungulates, dependence on drinking water is related to the proportion of grass versus dicots in the diet. This means that paleodietary change in ruminant ungulates should be associated with shifts in drinking behavior, altering enamel $\delta^{18}O$ values and biasing the aridity index. Such bias is evident in estimates of water deficit derived from the enrichment of enamel $\delta^{18}O$ in fossil Tragelaphini relative to Hippopotamidae from East African fossil sites spanning the last ~4.4 Myr. Elevated grass consumption (measured by enamel $\delta^{13}C$) in the former is associated with reduced enrichment of enamel $\delta^{18}O$ relative to the latter, translating to lower estimates of water deficit. In conducting such analyses of fossil ungulates, the diet of those ungulates must be screened to ensure consistency with the assumptions of the method.

1. Introduction

Water availability is an important abiotic component of terrestrial ecosystems, influencing species distributions, diversity, and productivity, among many other things (e.g., Stephenson, 1990; Olff et al., 2002; Hawkins et al., 2003; Woodward et al., 2004; Bond, 2008; Huston and Wolverton, 2009). Because it is directly influenced by the interaction of several climate parameters (e.g., Chevalier and Chase, 2016), terrestrial proxies of ancient water availability are essential to those interested in the evolution of Earth's climates and its ecosystems. Of the numerous proxies at our disposal, including pollen records (e.g., Chevalier and Chase, 2016), plant macrofossils (e.g., Peppe et al., 2011), paleosols (e.g., Sheldon and Tabor, 2009), and fossil mammals (e.g., Klein, 1991; Faith, 2013) among others (e.g., Cerling, 1984; Ayliffe and Chivas, 1990; Retallack, 2005; Chase et al., 2012), one important technique for quantifying water deficit or aridity—the difference between potential evapotranspiration and precipitation—is based on the stable oxygen isotope composition ($\delta^{18}O$) of fossil herbivore teeth (Levin et al., 2006; Blumenthal et al., 2017).

In an innovative and influential study based on observations from modern East African ecosystems, Levin et al. (2006) developed an aridity index derived from the $\delta^{18}O$ values of tooth enamel from two functional groups of mammalian herbivores: those that are evaporation sensitive (ES) and those that are evaporation insensitive (EI). Though there are many climatic, dietary, and physiological variables that can influence $\delta^{18}O$ of herbivore tooth enamel (e.g., Kohn, 1996; Kohn et al., 1996), Levin et al. (2006) showed that the $\delta^{18}O$ values of ES taxa closely track evaporative enrichment relative to meteoric water. This is because they obtain most of their water from the leafy plants that they eat, and increased aridity translates to greater evaporation of leaf water and more positive $\delta^{18}O$ values, both in the leaves and in the enamel of animals that eat them. On the other hand, the enamel $\delta^{18}O$ values of EI taxa track $\delta^{18}O$ of local meteoric rainfall, primarily because a large portion of their water intake is derived from surface water. Provided that the $\delta^{18}O$ of the surface water consumed by EI taxa reflects meteoric water (i.e., the water source is not evaporated), the enrichment of enamel $\delta^{18}O$ between ES and EI taxa ($\varepsilon_{ES\text{-}EI}$) will track the enrichment of leaf water relative to meteoric water, which in turn increases as a function of water deficit (aridity). Levin et al. (2006) confirmed these relationships, and they provided regression equations that can be used to predict ancient water deficit from the enamel $\delta^{18}O$ values of ES and EI taxa in the fossil record.

E-mail address: tyler.faith@anthro.utah.edu.

https://doi.org/10.1016/j.palaeo.2017.11.045
Received 25 July 2017; Received in revised form 16 November 2017; Accepted 16 November 2017

In the 10 + years since the $\delta^{18}O$-derived aridity index (hereafter "aridity index") was published, the technique has been widely adopted by paleoecologists interested in Cenozoic climates, ecosystem change, and evolutionary processes. Because the regression equations derived by Levin et al. (2006) concerned African herbivores, most applications have focused on the African fossil record (e.g., White et al., 2009; Bedaso et al., 2010; Braun et al., 2010; Bedaso et al., 2013; Garrett et al., 2015; Lehmann et al., 2016; Robinson et al., 2016; Blumenthal et al., 2017), though others have explored $\varepsilon_{ES\text{-}EI}$ values as an index of relative aridity in a diverse range of settings, ranging from the Paleocene-Eocene Thermal Maximum (Secord et al., 2012) and Pleistocene of North America (Yann et al., 2013; Yann and DeSantis, 2014) to the late Cenozoic of China (Ciner et al., 2015). In a recent study, Blumenthal et al. (2017) expanded on the method innovated by Levin et al. (2006), providing updated regressions based on a larger sample of modern localities. Their work is sure to stimulate further interest in the use of $\varepsilon_{ES\text{-}EI}$ as a proxy for aridity in Africa and beyond.

Use of the aridity index to reconstruct ancient water deficit requires that we can accurately classify fossil taxa as ES or EI. Because we cannot directly observe the drinking behavior of fossil taxa, such classifications are based on taxonomic uniformitarianism: it is assumed that those taxa that are ES (EI) in the present were also ES (EI) in the past. Building on concerns raised by Lehmann et al. (2016), this paper describes how differences in the paleodiet of fossil organisms relative to their modern counterparts (hereafter "paleodietary change") can invalidate this assumption. Based on the relationships between diet and water dependence in modern ruminant ungulates, I argue that paleodietary change of the sort frequently observed among fossil herbivores (e.g., Faith, 2011; Uno et al., 2011; Bibi et al., 2013; Cerling et al., 2015) should influence drinking requirements, which in turn alters enamel $\delta^{18}O$ and estimates of water deficit derived from it. Drawing from previously published carbon ($\delta^{13}C$) and oxygen isotope ($\delta^{18}O$) records from East African ungulates, I document one instance where variation in reconstructed water deficit can be explained by variation in paleodiet. It follows that when applying the aridity index to the fossil record, a sensible protocol is to exclude taxa for which paleodietary change is likely to have altered drinking behavior and evaporation sensitivity.

2. Diet and water dependence in ungulates

The moisture content of the foods that ruminant ungulates (e.g., Bovidae, Cervidae, Tragulidae) consume plays an important role in determining their dependence on surface water (e.g., Taylor, 1969; Beale and Smith, 1970; Jarman, 1973; Western, 1975; Nagy and Knight, 1994; Kay, 1997; Cain et al., 2006). In general, animals that consume forage with lower water content must drink more surface water (i.e., free water) to maintain water balance. For example, Jarman (1973) showed that the intake of free water among impala (*Aepyceros melampus*) in East Africa increases as the water content of their food declines in the dry season, and Beale and Smith (1970) documented the same for pronghorn antelope (*Antilocapra americana*) in the western United States. In addition, Nagy and Knight (1994) showed that springbok (*Antidorcas marsupialis*) in southern Africa can survive without access to drinking water by preferentially consuming moisture-rich dicots, but they will consume dry grasses in abundance if they are able to supplement this low-moisture diet with drinking water.

The moisture content of various plant foods consumed by ungulate herbivores can vary considerably in relation to season (e.g., Jarman, 1973; Nagy and Knight, 1994), time of day (e.g., Taylor, 1969; Louw and Seely, 1982), soil drainage and topography (e.g., Jarman, 1973), and tree cover (Ludwig et al., 2004), among other things. Despite this variation, however, there are general patterns that translate to important diet-related difference in water dependence among ruminant ungulates. In particular, grasses often have a lower moisture content than dicots, a contrast that is especially prominent in environments with seasonal rainfall because grasses lose a higher proportion of water during the dry season (e.g., Young, 1970; Jarman, 1973; Nagy and Knight, 1994). This in turn means that ungulate grazers are typically more dependent on surface water than browsers (e.g., Western, 1975; Cain et al., 2006; Hempson et al., 2015); the latter are able to meet most (if not all) of their water requirements from the foods they eat.

Table 1
Water dependence across dietary classes for ruminant and non-ruminant ungulates from sub-Saharan Africa.
Data from Hempson et al. (2015).

Diet	Ruminants			Non-ruminants		
	High	Low	None	High	Low	None
Obligate grazer	6	2	0	3	0	0
Variable grazer	9	3	4	2	3	0
Browser-grazer intermediate	2	5	5	2	0	0
Generalist	0	2	4	1	2	0
Browser	2	5	12	1	0	0
Frugivore	0	0	17	0	0	0

The relationships between diet and water dependence are particularly clear among African ruminants (note: all animals are dependent on water; water dependence/independence is used here to describe dependence on *surface water*). To illustrate these relationships, I turn to functional trait data synthesized by Hempson et al. (2015) for extant sub-Saharan African ungulates (Table 1). They classified water dependence as (1) none (obtains all water from forage), (2) low (requires occasional access to surface water), and (3) high (requires daily access to surface water). They classified diet using the scheme developed by Gagnon and Chew (2000), with categories arranged on an ordinal scale according the proportion of monocots (grasses) relative to dicots and fruits: (1) obligate grazer (> 90% monocots), (2) variable grazer (60–90% monocots), (3) browser-grazer intermediate (30–70% monocots and dicots), (4) generalist (> 20% of monocots, dicots, and fruits), (5) browser (> 70% dicots), and (6) frugivore (> 70% fruits; little or no monocots). As shown in Table 1 and Fig. 1, water dependence is highly contingent on diet (chi-square test: $\chi^2 = 43.3$, $p < 0.001$). Obligate grazers are typically water dependent, whereas frugivores and browsers typically water independent. As the proportion of grasses in the diet increases, the relative number of species that are highly dependent on surface water increases (chi-square test for linear trend: $\chi^2_{\text{trend}} = 24.5$, $p < 0.001$) and the number that are water-independent decreases (chi-square test for linear trend: $\chi^2_{\text{trend}} = 29.2$, $p < 0.001$).

These relationships are remarkably consistent in light of the many other factors that can also mediate water dependence. The water dependence of a given species is influenced not only by variation in the moisture content of different plant foods (e.g., Jarman, 1973; Nagy and Knight, 1994), but also by physiological, morphological, and behavioral adaptations (Cain et al., 2006). For example, the beisa oryx (*Oryx beisa*) has a low dependence on surface water (Kingdon and Hoffman, 2013; Hempson et al., 2015) despite a diet of primarily grasses (Cerling et al., 2003). This is accomplished by occasionally supplementing the diet with succulent dicots, feeding at night when plant moisture content is typically higher, and by physiological adaptations that enhance water retention, such as limiting evaporative water loss by allowing body temperature to rise (Kingdon and Hoffman, 2013). However, despite such occasional exceptions to the rule, the strong relationship between diet and water dependence across African ruminant ungulates (Fig. 1) implies that the amount of grass consumption is a primary determinant of water dependence.

In contrast to the ruminant ungulates, among non-ruminant ungulates (e.g., Equidae, Rhinocerotidae, Hippopotamidae, Elephantidae), the influence of forage moisture content is less important. These animals tend to be water-dependent irrespective of their diet (Table 1). The likely reason is that they lack a rumen (the defining feature of the ruminants), which among other things serves as a water storage