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Dietary exogenous and endogenous abrasives and tooth wear in African buffalo

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Abstract

The potential contribution of exogenous dust and grit and endogenous plant silica to tooth wear of the African buffalo in Kruger National Park was examined. Endogenous silica as percent dry matter on basalt soils (6.58%) was significantly higher than on granite soils (4.41%), and significantly higher in dry season grasses (6.64%) than in wet season grasses (4.41%). Exogenous grit on granite grasses (0.43%) had significantly higher loads than basalt grasses (0.16%) and wet season loads significantly higher (0.50%) than dry season (0.09%) loads. Grasses on granite soils were significantly tougher (0.266 J m^{-1}) than those on basalt soils (0.215 J m^{-1}). Adult buffalo were estimated to consume 10–28 kg per year of exogenous grit and 300–400 kg per year of endogenous silica. First lower buffalo molars are estimated to wear at an average rate of 1.94 mm per year with no significant difference between wear on the different soil types or between sexes. The high silica intake with no observable differences in tooth wear questions the role of silica in tooth wear. It is proposed that there is an interaction between exogenous and endogenous abrasives and that abrasion must be considered more holistically.

Keywords: Dust; Grit; Plant phytoliths; Tooth wear; African buffalo

1. Introduction

The evolution of molar crown height (hypsodonty), as herbivorous mammals shifted from browsing to a predominantly grazing diet, is a classic paradigm. Grasses are considered to be highly abrasive compared to dicotyledonous browse. The cause is usually attributed to the high levels of endogenous silica, commonly found in monocotyledonous grasses in the form of opaline phytoliths, which, in a highly cited paper, were stated to be harder than sheep tooth enamel [1]. This finding, coupled with the relatively low levels of endogenous silica in dicotyledonous plants has been widely taken to confirm the importance of grass abrasiveness in the evolution of hypsodonty (but also see Damuth and Janis [2]).

However, plants also carry an exogenous abrasive load in the form of wind or water borne dust or grit that is influenced by environment and plant height. Exogenous abrasives as a source of tooth wear has been recognized for a long time [3], and has been empirically related to sheep incisor tooth wear [4]. The specific cause in the latter case was attributed to ingested soil, which in cows was estimated as being about 1.5% of diet fresh weight over a year, and individual animals can show two-fold differences in intake [5]. It was considered unlikely that plant phytolith intake would exceed 15 g per day and be responsible for the degree of wear observed on sheep incisors of animals consuming over 200 g per day of soil [6]. Differences in phytolith mass on three New Zealand farms were not sufficiently different to explain the wear differences observed, which could be explained by differences in the amount of soil ingested. Damuth and Janis [2] concluded that typically an ungulate will consume at least as much mass of soil particles as phytoliths, if not more. However, high stocking rates on farms may not be comparable to field situations where animals can move more freely, trampling increases soil contamination and grasses are cropped while young and low in silica.

Janis [7] classified ungulates into a set of dietary divisions, modified from Hofmann and Stewart [8], to reflect habitat preference, and correlated the divisions with hypsodonty. The

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results indicated that animals feeding in open habitats, show significantly more developed hypsodonty than animals feeding in closed habitats with a greater height range of available food. The lowest hypsodonty values are not surprisingly associated with dicotyledonous plants above ground level, which might be expected to have the lowest endogenous silica and exogenous grit. The patterns were sufficiently strong to conclude that the abrasives on food are a more important determinant of hypsodonty than a diet of grass per se; a conclusion supported by Mendoza and Palmqvist [9].

Williams and Kay [10] argued that there were still no studies examining the correlation between hypsodonty and behavioural factors such as feeding height, which should influence the exogenous abrasive load. Taking this into account they concluded that both diet and exogenous abrasives "play a role" in shaping hypsodonty. The potential causes of hypsodonty have been extensively reviewed and the importance of soil ingestion noted [2]. Heuristic as these studies were, data on endogenous and exogenous loads on the above ground part of the plants, as distinct from soil intake, across dietary types, habitats and feeding heights, are still scarce.

In spite of such observations and cautions, the phytolith content of grasses and the rise of grasslands is commonly exclusively linked to the evolution of hypsodonty [2]. The continued equivalence of plant silica to quartz, sand or even "ground glass" is simplistic and almost certainly misleading. Directly addressing this, Clauss et al. [11] stated there is still surprisingly little information on the differences between grass and browse in their physical and chemical characteristics and went so far as to say that the suggested differences are often "based on hearsay" (p. 48); and "the often quoted increased amount of grit adhering to grass forage is a conceptual cornerstone of many investigations on the hypsodont dentition of grazers…but has never been demonstrated quantitatively" (p.48). Hummel et al. [12] went further, arguing that even though discussion is increasingly focused on partitioning the relative effects of exogenous and endogenous abrasives, not even total levels of ingested endogenous and exogenous abrasives had been empirically correlated with hypsodonty. Total faecal silica levels were strongly correlated with hypsodonty in a sample of browsers and grazers from southern Africa [12].

Arguably, interest in the precise source of tooth abrasion has received new impetus in recent years with the finding that wear from endogenous plant silica (opaline phytoliths) may not be as simple as previously thought [13–15]. Phytoliths, at least for those measured, are not harder than sheep tooth enamel [13], contrary to the original findings of Baker et al. [1] and these findings have been largely confirmed [14,16], with some caveats, the number of species sampled is still small. However, as Lucas et al. [14], and Xia et al. [15] note, the effect of an abrasive is not just about relative hardness. Softer materials, can under certain circumstances have an impact on harder materials and the question about the potential overall contribution of plant phytoliths to wear remains in question [17].

Tooth wear is not just about the levels of abrasives in the diet. The toughness of the diet is expected to require higher chewing forces [2,7,10], presumably by driving abrasives into the tooth surface with the greater energy available. Grasses are generally considered to be particularly tough, so the higher bite forces coupled with the putatively higher abrasive levels must be considered. Roughage feeders, predominantly consumers of grass, have larger jaw muscles [18] but there are more contacts at any one time during occlusion in grazing teeth [19], so it might be as much about the number of simultaneous contacts as toughness. There is little information on the relative toughness of grasses and dicotyledonous leaves but what is known challenges the assumption that grazers always consume tougher diets [19].

Chewing forces are also a function of sharpness of tooth shearing crest, the proximity of the crests during occlusion, the area of opposing crest contact during the occlusal cycle, the velocity of the contact and the volume of food being chewed. It has been suggested that cementum thickness should reflect chewing forces to some extent [20].

Other findings emphasize the complexity of the issue. For example, Schultz et al. [21] showed that mesowear in the browser/grazer sand gazelle (*Gazella marica*) at different times of the year, when the proportions of grass and browse changed, was not reflected in measurable tooth wear. They suggested that this might be because levels of abrasives in the desert environment may have been high across seasons and food types, masking any dietary abrasive signal.

Lucas et al. [14] proposed that silica does not cause wear, sensu stricto, as no material is removed when a softer silica particle marks a tooth surface, as tooth material is "prowed" on the sides of the mark or scratch, where enamel is piled up on the margins of the mark but not removed per se. Xia et al. [15] challenged this suggestion and showed that silica may be able to form microscratches in harder enamel where tooth material is damaged during the prowing process. These studies point to a need to better understand the interactions between the different sources of abrasion, diet physical properties and the ultimate wear process.

There is very little information on the distribution of exogenous abrasive particles on plants, grass or browse, and almost none on the relative distribution of exogenous versus endogenous silica and their effect on tooth wear. This paper reports levels of exogenous abrasive particles and endogenous silica from grasses in the south of Kruger National Park (KNP). KNP is a long and narrow park along a north-south gradient. Approximately half the width is on granite-derived soils in the west and half on basalt-derived soils in the east. The study was conducted in consecutive wet and dry seasons.

In 1998, KNP authorities conducted a substantial African buffalo (*Syncerus caffer*) cull across the park as part of a bovine tuberculosis investigation. The lower jaws of 389 buffalo from the cull retained identifying labels that could be matched to records from a data base, including location, sex, condition and estimated age. Annual tooth growth rings from temperate environments are poorly developed. However, cementum rings in 157 animals were identifiable. Therefore, tooth wear can be investigated, in at least one species of grazer, in relation to the endogenous and exogenous abrasive load of