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Resource and niche differentiation mechanisms by sympatric Early Pleistocene ungulates: the case study of Coste San Giacomo

Flavia Strani [a, b, *], Daniel DeMiguel [c, d, **], Raffaele Sardella [a, b], Luca Bellucci [b, e]

[a] Dipartimento di Scienze della Terra, Sapienza - Università di Roma, P.le Aldo Moro 5, 00185, Roma, Italy
[b] Istituto Italiano di Paleontologia Umana, Piazza R. Bonghi 2, 03012, Anagni, Frosinone, Italy
[c] Institut Català de Paleontologia Miquel Crusafont, Edifici Z, C/ de les Columnes s/n, Universitat Autònoma de Barcelona, 08193, Cerdanyola del Vallès, Barcelona, Spain
[d] Departamento de Ciencias de la Tierra, Área de Paleontología, Universidad de Zaragoza, Zaragoza, Spain
[e] Polo museale Sapienza, Sapienza – Università di Roma, P.le Aldo Moro 5, 00185, Roma, Italy

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Resource competition and niche partitioning among the exceptionally high number of sympatric ungulates of the Early Pleistocene site of Coste San Giacomo (Central Italy) is here examined through the study of their dietary proclivities and body size. The main aim of this study is to investigate the niche differentiation mechanisms that let the fossil ungulates coexist in the same region. We also provide information about the complementarity of two different methodologies that observe diet variation at a different time scales (inner and outer mesowear) in the study of dental wear patterns of fossil ungulates. Results from analyses of dental wear degree and body masses predictions show that a wide range of feeding behaviours were adopted by the taxonomical groups (i.e., cervids, bovids and equids) in order to avoid competition. Among larger ungulates diet ranges from strict browsing (*Eucladoceros* sp., *Gazellospira torticornis*), to mixed feeding (*Gallogoral meneghinii*, *Leptobos* sp.) to pure grazing (*Equus stenonis*), whereas smaller taxa are more selective feeders (*Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*) with only one exception (*Gazella borbonica*). When taxa with the same feeding behaviour occurred in the same habitat, competition was minimised by differences in body size.

1. Introduction

Competition between species occurs when species occupy the same habitat, use the same resources and when said resources are limiting. Ungulates can directly compete for shared resources of food or space, or can interfere against resources used by another species (interference competition) (Latham, 1999). Niche differentiation mechanisms, such as habitat segregation, differences in body weights and specialized dietary adaptations as well as beneficial interactions (facilitation), can however minimize competition allowing the co-existence of different sympatric ungulate in a region, (De Boer and Prins, 1990; Klein and Bay, 1994; Latham, 1999; Prins et al., 2006; Sietses et al., 2009). Such ecological mechanisms in fossil assemblages are often difficult to investigate, but they are indeed important to understand interspecific relationship among taxa, especially in those localities where multiple fossil ungulates occurred and overlapped. In extant herbivore ungulates, diet quality and body size are strongly related (Henley and Ward, 2006; Codron et al., 2007), with the former decreasing when body size increases (Mysterud, 1998; references within; Codron et al., 2007) and with animals of similar body mass and digestive system foraging on similar foods (Henley and Ward, 2006). This is because larger herbivores require larger quantities of food, and the more abundant plants parts (e.g. stems or twigs) are generally of lower nutritional quality than less abundant, higher-quality parts (e.g. leaves, fruits or forbs). Contrarily, smaller herbivores require smaller quantities of food, and they are generally selective feeders adapting to use mostly high quality forage (Clauss et al., 2013). As a result, herbivores exhibiting different body size and different dietary preferences can coexist in the same ecosystem (Prins and Olff,

* Corresponding author. Dipartimento di Scienze della Terra, Sapienza - Università di Roma, P.le Aldo Moro 5, 00185, Roma, Italy.
** Corresponding author. Institut Català de Paleontologia Miquel Crusafont, Edifici Z, C/ de les Columnes s/n, Universitat Autònoma de Barcelona, 08193, Cerdanyola del Vallès, Barcelona, Spain.
E-mail addresses: flavia.strani@uniroma1.it (F. Strani), daniel.demiguel@icp.cat (D. DeMiguel).

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1998).

The Early Pleistocene large mammal assemblage of Coste San Giacomo (herein referred as CSG) in Anagni (Central Italy), recently dated around 2.1 Ma (Bellucci et al., 2014), is characterized by an unusual abundance of herbivore taxa, mostly represented by artiodactyls and perissodactyls (Bellucci et al., 2012; Strani et al., 2015). Among these, three fossil cervids (*Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus* and *Eucladoceros* sp.), four bovids (*Gallogoral meneghinii*, *Gazella borbonica*, *Gazellospira torticornis* and *Leptobos* sp.), and one equid (*Equus stenonis*) have been identified (Bellucci et al., 2012; Bellucci and Sardella, 2015). These taxa have been recently studied from a paleodietary point of view in order to gain new information about the palaeoclimate and palaeoenvironmental conditions that prevailed in Central Italy during the Gelasian (Early Pleistocene) through the analysis of their dental wear degree (mesowear) and molar crown height (hypsodonty) (Strani et al., 2015).

With this new updated information of their dietary preferences, this research relies on the working hypothesis that the extraordinary number of herbivore ungulates werw forced to exhibit different mechanisms in CSG in order to avoid strong direct competition, partition the niche space and optimize exploitation of the available vegetation. We consider indeed CSG as an exceptional case study to do this because of the wide spectrum of diets and body sizes exhibited, and the occurrence of different taxonomic groups in the same assemblage. To do so, we focus on new traits of ecological relevance (e.g., body size) and more precise dietary inferences also adopting the new inner mesowear approach (Solounias et al., 2014) to better understand how niche and resource partitioning work in fossil communities. Importantly, and given the abundant dietary data provided by the CSG mammal community, here we also aim to examine the complementary nature of two proxy methods based on the dental wear degree (inner and outer mesowear) comparing the obtained results and test their combined use in paleoecological studies.

2. Material and methods

The studied fossil material belongs to the Early Pleistocene (Gelasian) locality of Coste San Giacomo (CSG) near the town of Anagni (Frosinone, Central Italy). Extensive fieldwork has been carried out since 1978 by researchers of the Italian Institute of Human Palaeontology (IsIPU) (Segre Naldini et al., 2009; Bellucci et al., 2014 and references therein). The material is currently housed at the IsIPU laboratory in Anagni (Frosinone, Central Italy). The updated faunal list of CSG (Bellucci et al., 2014) comprises 19 large and 7 micromammal taxa. Among them, the fossil material here studied consists of 102 dental (molar) specimens of the following ungulate taxa: *Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*, *Eucladoceros* sp., *Gazella borbonica*, *Gazellospira torticornis*, *Gallogoral meneghinii*, *Leptobos* sp. and *Equus stenonis*.

2.1. Body mass estimation

Herbivore body mass is an important ecological trait in niche repartitioning as it influences diet choices (Henley and Ward, 2006). Mammalian body size is usually predicted by proximal limb bones (Scott, 1983, 1990), cranial (MacFadden and Hulbert, 1990) or dental (Janis, 1990) measurements. Due to the lack of well represented post-cranial and cranial remains for most of the CSG ungulates, only dental measurements were taken. The occlusal lengths of upper second (M2) or lower first (m1) molars were used to estimate body size following the procedure described by Janis (1990). The intercepts and slopes of prediction equations for the different cranio-dental measurements for 1) perissodactyls, 2) cervids only and 3) bovids only were taken from Janis (1990). That is, in order to predict the weight of the CSG taxa, we used the provided slopes and intercepts of the linear regressions based on log M2 and log m1 occlusal length, form the "Perissodactyls and hyracoids only" group (for *E. stenonis*), from the "Cervids only group" (for *Axis* cf. *lyra*, *Croizetoceros* cf. *ramosus*, *Eucladoceros* sp.), and from the "Bovids only group" (for *Gazella borbonica*, *Gazellospira torticornis* and *Gallogoral meneghinii*). The inverse logarithm was calculated to obtain the body mass for each animal.

The results were compared with modern taxa listed in Janis (1990). Note that body size estimation for *Leptobos* sp. was not performed due to the lack of both M2 and m1 specimens for this taxon.

2.2. Dental mesowear

Mesowear is considered a good dietary indicator in herbivore species, as it represents the cumulative effects of the items ingested (both foods and exogenous particles such as dust and grit) on the dental morphology that are produced in a long period of time compared to the lifespan of the animal (Fortelius and Solounias, 2000).

Traditional mesowear (Fortelius and Solounias, 2000), referred as "outer mesowear" (Solounias et al., 2014; Danowitz et al., 2016), analyses the sharpness (i.e., morphology) of the cusps and the height of the occlusal relief of the most labial enamel bands of upper molars and the most lingual of the lower ones (Kaiser and Solounias, 2003; DeMiguel et al., 2012). In Strani et al. (2015), occlusal relief (high or low) and cusp shape (sharp, rounded or blunt) of the apex of the paracone and metacone of the M1-M3 and the metaconid and entoconid of the m1–m3 were examined and scored, and data compared with those of a database of extant ungulates with known diets (Fortelius and Solounias, 2000). The variables were also converted to a score following Rivals et al. (2009) as follows: (0) teeth showing a combination of high relief and sharp cusps; (1) teeth with high relief and rounded cusps; (2) teeth with low relief and rounded cusps; (2.5) teeth with low relief and sharp cusps; and (3) teeth with low relief and blunt cusps.

The inner mesowear method, recently developed by Solounias et al. (2014), analyses instead the second enamel band that forms the lingual margin of the metacone or paracone from an occlusal view, which is generally more frequently preserved in fossil specimens. Inner mesowear reflects dietary preferences that are intermediate in time (days-weeks; Danowitz et al., 2016) between outer mesowear (months-years; Fortelius and Solounias, 2000; Mihlbachler et al., 2011; Sánchez-Hernández et al., 2016) and dental microwear (days-hours; Solounias and Semprebon, 2002). For inner mesowear, the enamel band is scored on the mesial and distal sides of the metacone using a 4 point scaling system described by Solounias et al. (2014) and Danowitz et al. (2016): (1) flat and planar with no gouges or indentations on the surface of the enamel; (2) nearly flat with several gouges that traverse the surface from either edge—the labial and lingual edges of the enamel band are somewhat rounded; (3) similar to score 2, but more rounded with less defined edges and more gouges; and (4) rounded—the surface is smooth without gouges, and there are no well-defined edges. The junction of the mesial and distal sides termed J is similarly scored: (1) it joins at a sharp, well-defined junction; (2) it is somewhat sharp, and often contains a gouge; (3) it is rounded, but the mesial and distal sides appear as distinct, separate surfaces; and (4) the J point lacks a discrete apex, and the mesial and distal sides of the enamel band form one continuous surface. The method was originally applied by Solounias et al. (2014) only on upper second molars (M2), and here it has been extended to M1 and M3 molars of different individuals in order to widen the sample and

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