

The palaeoecological meaning of macromammal remains from archaeological sites exemplified by the case study of Grotta Paglicci (Upper Palaeolithic, southern Italy)

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(RECEIVED November 26, 2017; ACCEPTED May 20, 2018)

Abstract

Bone accumulation in Palaeolithic archaeological sites is often the result of activities carried out by hunter-gatherer groups. Cultural choices may have influenced prey representation in archaeological assemblages, distorting their palaeoecological meaning. We present a comparison between large mammal and small mammal assemblages from the Upper Palaeolithic sequence of Grotta Paglicci (Apulia, southern Italy) that extends from the Marginally Backed Bladelet Aurignacian (about 39,000 cal yr BP) to the Final Epigravettian (about 13,000 cal yr BP). At Paglicci, the high frequency of horse and ibex remains indicates open and dry environments for most of the Upper Palaeolithic. This is confirmed by the predominance of the common vole among small mammals. The alternation between horse and ibex, which takes place during the Upper Palaeolithic, however, looks to be more related to variations in hunting territories. Taxon frequencies change abruptly at 17,955–16,696 cal yr BP, with an increase in woodland-related ungulates together with micro-mammals, indicating a climatic evolution towards milder and more humid conditions. Results demonstrate that when the association of ungulate taxa is considered as a whole, it has a good palaeoecological signal, whilst considering taxa separately can help to better understand cultural choices of past hunter-gatherer communities.

Keywords: Grotta Paglicci; Italy; Palaeoecology; Taphonomy; Ungulates; Small mammals; Upper Palaeolithic; Zooarchaeology

INTRODUCTION

Large mammal remains are often the most common category of biological specimens from Palaeolithic archaeological sites. Basic goals of their study are the reconstruction of both hominin subsistence strategies and the palaeoenvironment. The latter has been the main focus of important studies carried out over the last decades in Italy to shed light on climatic conditions that drove changes in mammal communities during the Upper Palaeolithic (e.g., Bartolomei et al., 1977; Sala, 1983). Studies focused on ungulate taxa highlighted the influence of both climatic conditions and geomorphology on the structure of ungulate communities. In addition, a strong regionalization of the Italian Peninsula was detected, showing the Pre-Alps characterized by the presence of caprines

(*Capra ibex*, *Rupicapra rupicapra*) during more arid phases and cervids (*Cervus elaphus*, *Capreolus capreolus*, *Alces alces*) when wooded areas increased. The northern Tyrrhenian area was characterized by a generalized alternation of *Capra ibex* and *Cervus elaphus*. In the Po Plain, the most common taxon during last glacial maximum and late glaciation was probably *Bison priscus* accompanied by a limited presence of *Alces alces*. The central Apennine area was characterized by the presence of caprines (*Capra ibex*, *Rupicapra* cf. *pyrenaica*), cervid taxa (*Cervus elaphus*, *Capreolus capreolus*), and the occurrence of *Equus ferus* and *Equus hydruntinus*, which were limited to the Fucino basin in Abruzzo. The central-southern Tyrrhenian side was characterized by the presence of caprines (limited to some rocky and steep areas), wild boar (*Sus scrofa*), cervid taxa, the aurochs (*Bos primigenius*), and equids (the latter limited to lowlands, some of which emerged during periods of marine regression). Apulia was characterized by an overwhelming presence of equids and *Bos primigenius* in the plains

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(especially during the driest periods) and a great abundance of *Capra ibex* in the Gargano promontory; *Cervus elaphus* became more abundant (and sometimes the dominant species) when the climate turned to milder and more humid conditions (Sala, 1983, 2005, 2007; Boscato, 1994, 2000, 2007).

A similar regionalization was observed among small mammal populations (Berto, 2013; López-García et al., 2014; Berto et al., 2017, 2018), which differ between north and south and, especially in southern Italy, between one side of the Apennine chain and the other. In particular, arid conditions are generally believed to have prevailed in the Adriatic regions, where micromammal communities were characterized by a lower biodiversity and were dominated by few species [e.g., *Microtus arvalis* or *Microtus (Terricola) savii*]. More humid conditions are believed to have prevailed in the Tyrrhenian side, due to the high frequencies of woodland-adapted species (*Apodemus* gr. *sylvaticus-flavicollis*, *Glis glis*). The eastern (Adriatic) part of northern Italy differs from the Tyrrhenian region due to the presence of taxa coming from Eastern European regions (e.g., *Cricetus cricetus*, *Microtus oeconomus*, *Sicista* sp.) (Berto, 2013; Berto et al., 2018).

Palaeoenvironmental reconstructions based on ungulate assemblages were carried out to determine changes in species frequencies through time (e.g., Sala 1983, 2007; Boscato 1994), but the interpretations may be affected by biases due to the taphonomic pathway of remains. The relative abundance of taxa could be influenced by taphonomic agents (humans, carnivores) and taphonomic processes, such as transport to the site of selected skeletal parts; destruction of bones due to gnawing, fat extraction, and bone working; or bone attrition due to natural processes. In the case of anthropogenic bone assemblages, the choice of hunting territories on the basis of both natural and cultural constraints may also affect taxon representation. The aim of this work is to compare ungulate and small mammal assemblages from a site with a long stratigraphic record in order to understand whether changes in relative abundance of ungulate species hunted by humans may effectively reflect past climatic variations rather than particular taphonomic processes or cultural choices adopted by hunter-gatherer groups.

THE SITE

The site of Grotta Paglicci was selected to carry out our test. This cave lies on the western slope of the Gargano promontory (Apulia, southern Italy) in the municipality of Rignano Garganico (Fig. 1). It opens at an altitude of about 143 m asl and consists of a present-day cave and a rock shelter that used to be part of the same hypogean system (Crezzini et al., 2016). After the “official” discovery of the site at the end of the 1950s (the cave was already known to local people), the first field investigations were carried out

by the Natural History Museum of Verona from 1961 to 1963. From 1971 onwards, research was directed by the University of Siena in collaboration with the local heritage office (Zorzi, 1964; Palma di Cesnola, 2004a). A main trench was excavated in the cave, where a 12-m-thick stratigraphy spanning a period from the Middle Palaeolithic (layers 30–25) to the Final Epigravettian was discovered (Palma di Cesnola, 2004b). In particular, the Upper Palaeolithic sequence is one of the most complete in the whole of Europe. It comprises the Marginally Backed Bladelets Aurignacian (layer 24), the Ancient Gravettian (layers 23–22), the Evolved Gravettian (layers 21–19b), the Late Gravettian (layers 19a–18b), the Ancient Epigravettian (layers 17–12), the Evolved Epigravettian (layers 11–8), and the Final Epigravettian (layers 7–3a). As the cave was eventually obstructed by sedimentation, it was not frequented during the Romanellian, a later phase of the Epigravettian of southern Italy (Palma di Cesnola, 2001, 2004b, 2006, 2011, and references cited therein; Wierer, 2013; Ricci et al., 2016; Borgia et al., 2016). The importance of the site also derives from the presence of three human burials and several isolated Upper Palaeolithic human remains (Ronchitelli et al., 2015; Fu et al., 2016; Posth et al., 2016), as well as from Upper Palaeolithic rock paintings (the only case known in Italy to date) (Zorzi, 1963; Arrighi et al., 2012b), mobiliary art objects (Mezzena and Palma di Cesnola, 1972, 1992, 2001, 2004; Arrighi et al., 2008, 2012a), and evidence of Gravettian plant-food processing (Mariotti Lippi et al., 2015; Revedin et al., 2015).

With regard to the Upper Palaeolithic layers, 52 available radiocarbon dates indicate a quite continuous frequentation of the cave for a time period of about 26,000 yr (Table 1). Thus, Grotta Paglicci can be considered as a reference sequence for the study of the Upper Palaeolithic in southern Europe and in the Mediterranean area, and it is a key site for understanding past climatic evolution from a later phase of MIS 3 until the end of MIS 2 (in particular from 40,939–36,570 cal yr BP to 13,712–12,970 cal yr BP).

MATERIALS AND METHODS

The Epigravettian large mammal assemblage and those from the Final and Evolved Gravettian layers are still under analysis. Only a part of the remains was studied by Sala (1983) and Boscato (1994). New data presented in this paper on ungulate assemblages come from the whole Epigravettian sequence. Aurignacian and Ancient Gravettian data are from Boscato (1994), whilst Evolved and Final Gravettian data are from Sala (1983). A total amount of 18,859 Epigravettian ungulate remains were identified for the present paper, using the osteological reference collection of the University of Siena. *Rupicapra* remains have been identified only according to genus, due to the lack of specimens bearing diagnostic features able to distinguish

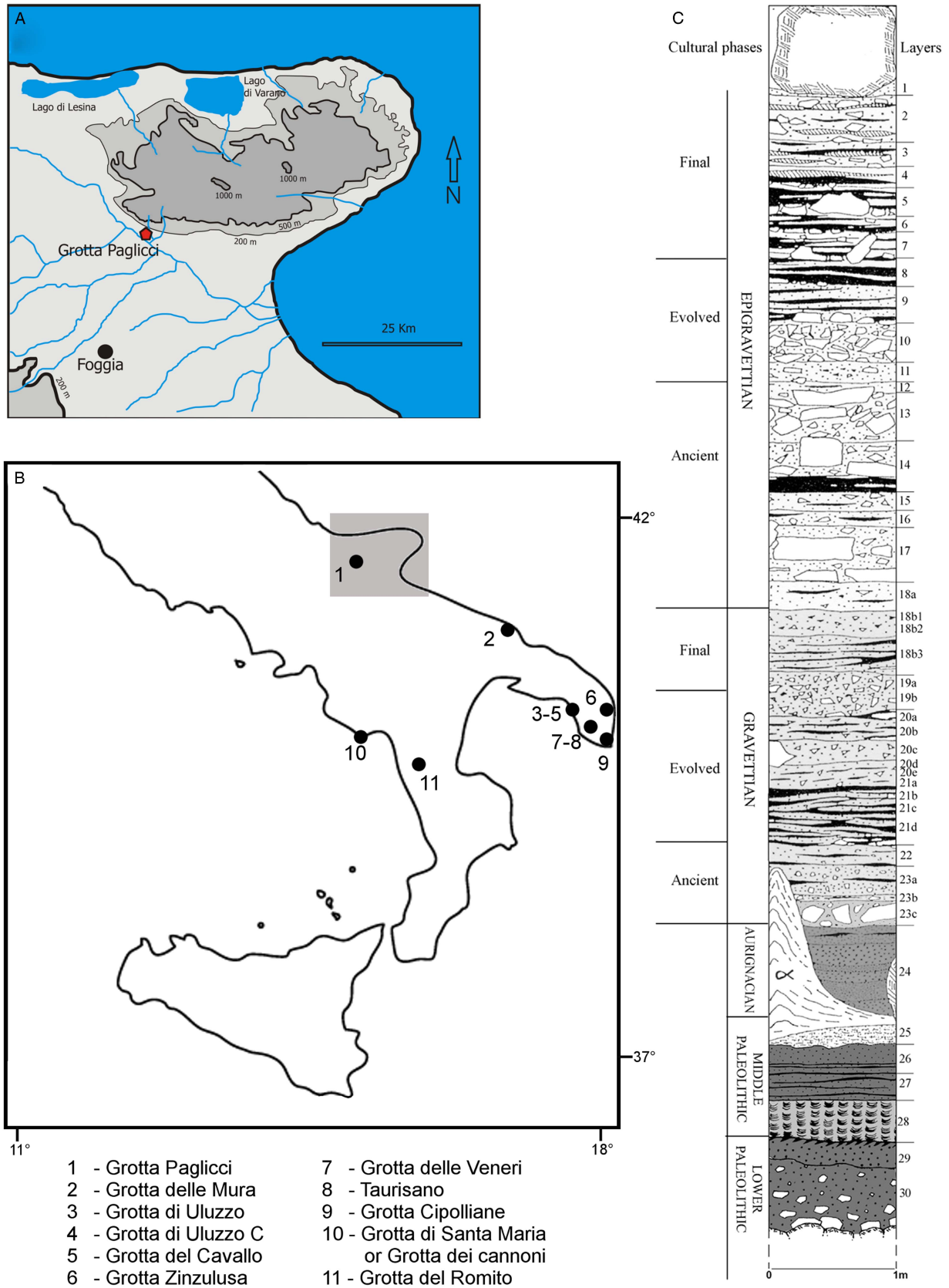


Figure 1. (A) Site location; (B) positions of sites discussed in the text; and (C) site stratigraphy.

Table 1. ^{14}C dates of the cave's stratigraphy.

Layer	Lithic industry	Laboratory	^{14}C date (yr BP)	Cal yr BP (IntCal13)
3a	Final Epigravettian	F-94	11,440 ± 180	12,970–13,712
4	Final Epigravettian	F-95	11,950 ± 190	13,370–14,429
5 bc	Final Epigravettian	F-96	13,590 ± 200	15,841–17,021
6	Final Epigravettian	F-64	14,270 ± 230	16,696–17,955
7	Final Epigravettian	F-65	14,820 ± 210	17,551–18,541
7 c	Final Epigravettian	Ly-1628	13,720 ± 870	14,078–18,867
8	Evolved Epigravettian	F-66	15,460 ± 220	18,220–19,245
9	Evolved Epigravettian	F-67	15,270 ± 220	18,002–18,956
10	Evolved Epigravettian	F-68	15,320 ± 250	17,988–19,112
12 a	Early Epigravettian	GrN-14316	15,950 ± 350	18,549–20,133
12 c	Early Epigravettian	GrN-14317	15,730 ± 330	18,334–19,860
13 a	Early Epigravettian	GrN-14318	15,480 ± 150	18,405–19,053
13 b	Early Epigravettian	GrN-14319	16,310 ± 350	18,892–20,539
13 c	Early Epigravettian	GRN-14320	15,990 ± 160	18,901–19,683
13 d	Early Epigravettian	GRN-14321	16,030 ± 190	18,896–19,831
14 b (a)	Early Epigravettian	UtC-	15,600 ± 200	18,451–19,384
14 b (b)	Early Epigravettian	GrN-14322	15,930 ± 200	18,786–19,716
15	Early Epigravettian	UtC-	17,100 ± 300	19,929–21,491
15 a	Early Epigravettian	GrN-14323	15,570 ± 160	18,499–19,212
15 b	Early Epigravettian	GrN-14324	16,260 ± 160	19,211–20,043
16	Early Epigravettian	UtC-	17,200 ± 300	20,040–21,601
16 a3–1	Early Epigravettian	GrN-14325	16,690 ± 150	19,741–20,531
16 b3 (a)	Early Epigravettian	GrN-14326	16,450 ± 190	19,396–20,361
16 b3 (b)	Early Epigravettian	GrN-14870	16,970 ± 150	20,075–20,861
16 b5	Early Epigravettian	GrN-14871	16,750 ± 150	19,828–20,597
16 b7	Early Epigravettian	GrN-14872	16,480 ± 150	19,521–20,272
16 c2	Early Epigravettian	GrN-14873	16,850 ± 150	19,952–20,707
17 b	Early Epigravettian	GrN-14874	16,890 ± 160	19,979–20,789
17 d1	Early Epigravettian	GrN-14875	17,050 ± 160	20,136–20,989
17 e (a)	Early Epigravettian	UtC-	19,600 ± 300	22,893–24,322
17 e (b)	Early Epigravettian	GrN-14876	16,940 ± 160	20,029–20,849
17 f	Early Epigravettian	GrN-14877	16,790 ± 160	19,855–20,665
18 b2 (a)	Final Gravettian	F-44	20,200 ± 305	23,612–25,185
18 b2 (b)	Final Gravettian	R-1324	17,200 ± 150	20,355–21,191
18 b2 (c)	Final Gravettian	F-43	14,260 ± 280	16,529–18,042
18 b3	Final Gravettian	F-45	20,160 ± 310	23,555–25,157
19 a	Final Gravettian	F-46	20,730 ± 290	24,265–25,660
20 b	Evolved Gravettian	F-47	21,260 ± 340	24,643–26,184
20 c (a)	Evolved Gravettian	F-49	22,110 ± 330	25,815–27,174
20 c (b)	Evolved Gravettian	F-48	22,220 ± 360	25,870–27,290
20 de	Evolved Gravettian	F-50	22,630 ± 390	26,114–27,594
21 a	Evolved Gravettian	F-51	23,040 ± 380	26,468–27,912
21 b	Evolved Gravettian	F-57	23,470 ± 370	27,070–28,430
21 c (a)	Evolved Gravettian	F-53	23,750 ± 390	27,326–28,664
21 c (b)	Evolved Gravettian	F-54	24,210 ± 410	27,602–29,128
21 d	Evolved Gravettian	F-55	24,720 ± 420	27,871–29,749
22 b	Early Gravettian	UtC-1412	26,800 ± 300	30,493–31,330
22 f4	Early Gravettian	UtC-1413	28,300 ± 400	31,355–33,329
23 a	Early Gravettian	UtC-1414	28,100 ± 400	31,210–33,103
23 b	Early Gravettian	UtC-1415	26,300 ± 400	29,613–31,121
24 a1	Aurignacian	UtC-1789	29,300 ± 500	32,112–34,447
24 b1	Aurignacian	UtC-1790	34,300 ± 900	36,570–40,939

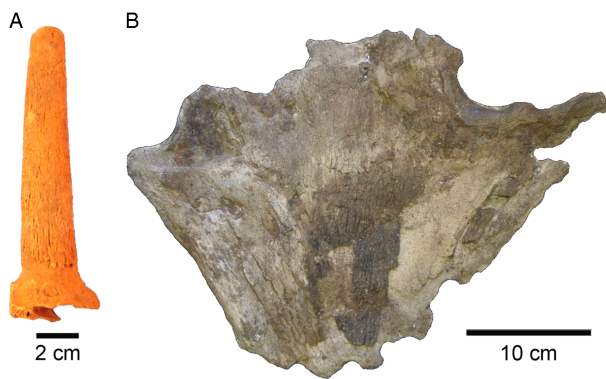


Figure 2. (color online) (A) *Rupicapra* sp., horncore (Evolved Epigravettian). This is the most relevant chamois remain from the Epigravettian sequence. (B) *Cervus elaphus*, palmated antler (Ancient Epigravettian).

between *R. rupicapra* and *R. pyrenaica* (Fig. 2A). Palmated cervid antlers were attributed to *Cervus elaphus* according to Abbazzi (1995) (Fig. 2B).

Some specimens were ascribed to categories based on animal body size alone: the category “small ungulate” comprises remains belonging to individuals similar in size to caprines, roe deer, and wild boar; the category “medium ungulate” comprises remains belonging to individuals similar in size to red deer and European ass; the category “large ungulate” comprises remains belonging to individuals similar in size to horse and cattle.

All Epigravettian specimens were analysed from a taphonomic point of view, recognizing anthropic and natural traces on bone surfaces. Striations on bone surfaces of specimens from an Ancient Gravettian layer where a hyena den was identified (Boscato, 1994; Boscato and Crezzini, 2005) were reanalysed by means of 3D microscopy using a Hirox KH-7700 digital microscope (Moretti et al., 2015; Oxilia et al., 2015; Arrighi et al., 2016). The RTF index (defined as the ratio between the breadth at the top and the breadth at the bottom of each mark’s cross section) was used as a morphometric criterion to distinguish cut marks from tooth scores. Comparative data of present-day tooth scores and experimental cut marks are from Boschín and Crezzini (2012), Crezzini et al. (2014), and Duches et al. (2016).

Relative abundance of ungulate species was calculated using NISP (Number of Identified Specimens), whilst abundance of small mammal taxa is from Berto et al. (2017). A principal component analysis (PCA) was separately performed on both large and small mammal assemblages. First and second components from the PCA carried out on ungulate assemblages were respectively labelled “PC1ung” and “PC2ung.” The first component coming from the PCA analysis on small mammal assemblages was labelled “PC1small.” Values produced by these three components were used as proxies for the reconstruction of faunal changes over time. All statistical analyses

were performed using the PAST software (Hammer et al., 2001).

Radiocarbon dates are calibrated using the software OxCal v. 4.2 (Bronk Ramsey, 2009) and the IntCal13 curve (Reimer et al., 2013).

RESULTS

Taphonomic agents responsible for the ungulate bone assemblage

Epigravettian ungulate remains bear anthropic marks on their surfaces. These consist of cut marks, percussion marks, and relative cones. Marks ascribable to carnivore activity (gnawing marks and corruptions) are completely absent in some of the layers and very rare in the others (Tables 2 and 3). No taphonomic data are available for the Final and Evolved Gravettian phases, but layers 21–18b are very anthropized, and no traces of carnivore frequentation were detected during the excavations (Palma di Cesnola, 2004b). With the exception of layer 22, other Ancient Gravettian and Aurignacian layers (23–24) are characterized both by anthropogenic and carnivore-related accumulations of animal remains. In particular, both anthropic marks and the presence of hyena coprolites and bones bearing carnivore-induced modifications are found in layers 23 and 24 (Boscato 1994; Boscato and Crezzini, 2005; Crezzini, 2007; Borgia and Crezzini, 2011). The largest amount of coprolites is found in layer 23c (Boscato, 1994), where striations detected on bones can be divided into two well-defined groups with different morphological characteristics: striations of anthropic origin with a V-shaped profile were indicated by high values ($N = 71$; min. = 2.3; max. = 37.5; mean = 10.2) of the ratio between the breadth at the top and the breadth at the floor of mark (defined as RTF index in Boschín and Crezzini, 2012), and tooth marks with a clear U-shaped cross section were indicated by low values of the RTF index ($N = 38$; min. = 1.4; max. = 10.1; mean = 3.3) (Fig. 3).

Epigravettian ungulate assemblages

Considering the relative abundance of ungulate taxa, the Epigravettian sequence can be divided into four main sections (Fig. 4, Table 4, Supplementary Table 1):

1. Layer 17 (ca. 20,000 cal yr BP): this phase is characterized by an overwhelming presence of ibex remains. This taxon accounts for 74.1% of ungulate NISP in the lower part of this layer (levels 17d2–h) and for 54.2% of NISP in the upper part (levels 17a–d1).
2. Layers 16 to 10b (ca. 20,000–18,500 cal yr BP): during this phase, the increase in horse remains is balanced by a decrease in those of ibex. Frequency of horse is always more than 39% of NISP and reaches a peak in layer 15b (57.8%). Abundance of ibex remains is always lower

Table 2. Anthropogenic marks on Epigravettian faunal remains (cut marks, percussion marks, and cones) according to taxonomy. Abbreviations: Bp, *Bos primigenius*; Cap, caprine; Cc, *Capreolus capreolus*; Ce, *Cervus elaphus*; Ci, *Capra ibex*; Ef, *Equus ferus*; Eh, *Equus hydruntinus*; Esp, equid; LU, large ungulate; MU, medium ungulate; Rsp, *Rupicapra* sp.; Ss, *Sus scrofa*; SU, small ungulate; Unid., unidentified.

Layers	Esp	Ef	Eh	Bp	Ci	Rsp	Cap	Ce	Cc	Ss	LU	MU	SU	Unid.
3a	—	—	1	—	—	—	—	5	2	—	1	—	—	4
4a	—	—	—	—	—	—	—	—	—	—	2	—	—	1
4b	—	—	1	—	—	—	—	—	—	—	—	—	—	2
4c	—	—	—	—	—	1	—	2	—	—	—	—	—	1
5a	—	—	—	4	—	—	—	8	—	—	9	1	—	16
5b	—	—	—	—	—	—	—	7	—	1	—	3	—	—
5c	—	—	1	1	—	—	—	12	—	—	1	1	—	2
6a	—	—	—	—	—	—	—	2	—	1	—	—	—	2
6b	—	—	—	—	—	—	—	3	—	—	—	—	—	2
6c	—	1	1	3	1	—	—	1	—	1	—	—	1	2
7a	—	—	—	—	—	—	—	—	—	—	—	—	—	1
7b	—	—	1	2	4	—	—	—	—	—	—	—	—	—
7c	—	1	—	2	2	—	—	—	—	—	1	3	—	—
8a	—	1	1	1	1	—	—	—	—	—	—	1	—	1
8b	—	1	3	1	3	—	1	—	—	—	—	—	—	3
8c	—	—	—	—	2	—	—	1	—	—	2	1	1	11
8d	—	—	—	—	—	—	—	—	—	—	5	11	2	16
9a	—	1	1	2	1	—	—	—	—	—	7	1	9	17
9b	—	1	1	—	—	—	—	—	—	—	3	—	3	4
9c	—	—	—	1	2	—	—	—	—	—	3	3	1	7
9d	—	—	—	2	1	—	—	—	—	—	1	1	10	4
10a	—	4	—	2	4	—	1	—	—	—	8	4	13	4
10b	—	—	—	—	—	—	—	—	—	—	2	—	1	5
10c	—	6	1	2	4	—	—	2	—	—	7	3	5	9
10d	—	6	—	7	2	—	—	1	—	—	16	6	6	15
10e	2	31	2	25	19	—	—	3	—	3	24	4	14	43
11a	—	6	—	4	1	—	—	2	—	—	6	1	2	12
11b	—	5	1	2	1	—	—	1	—	—	—	—	9	10
11c	—	2	—	—	—	—	—	1	—	—	9	—	3	4
12a	—	5	2	12	4	—	—	4	—	—	4	2	—	10
12d	—	4	—	3	3	—	—	—	—	—	7	3	5	47
12e	—	15	1	10	2	—	1	1	—	1	8	—	1	36
12f	—	14	1	14	3	—	1	3	—	1	6	—	7	46
12g	—	11	—	13	2	—	—	1	—	2	24	3	2	18
14a	—	1	1	—	—	—	—	—	—	—	—	—	—	6
14b	—	8	—	6	4	—	—	—	—	1	10	1	4	23
15b	—	8	—	1	1	—	—	1	—	—	—	—	—	11
16a/a1	1	5	1	12	2	—	—	—	—	1	13	—	4	11
16a2	—	1	1	2	—	—	—	2	—	—	5	—	—	8
16a3/3-1	—	—	—	2	—	—	—	—	—	—	3	1	1	4
16a3-2	—	1	—	2	—	—	—	1	—	—	5	2	3	1
16a3-3	—	4	—	6	1	—	—	2	—	—	21	1	1	3
16b	—	1	—	2	1	—	—	—	—	—	5	—	9	28
16c	—	2	—	—	—	—	—	—	—	—	—	—	—	3
17a-d1	—	1	—	—	5	—	—	—	—	—	—	—	—	—
17d2-h	—	3	1	—	7	1	—	1	—	—	—	—	—	4

than 26%, with a minimum in layer 16a/a1 (8.7%). Auroch remains increase in this phase (ranging between 37.7% in layer 16a3/a31 and 14.8% in layer 10c). Other

taxa are scarcely represented, but a clear positive trend in wild boar frequency is visible.

3. Layers 10a to 6d (ca. 18,500–18,000 cal yr BP): ibex

Table 3. Marks from carnivores on Epigravettian faunal remains. Abbreviations: Bp: *Bos primigenius*; Cap, caprine; Cc, *Capreolus capreolus*; Ce, *Cervus elaphus*; Ci, *Capra ibex*; Ef, *Equus ferus*; Eh, *Equus hydruntinus*; LU, large ungulate; MU, medium ungulate; Rsp, *Rupicapra* sp.; Ss, *Sus scrofa*; SU, small ungulate; Unid., unidentified.

Layers	Ef	Eh	Bp	Ci	Rsp	Cap	Ce	Ss	LU	SU	Unid.
4b	1	—	—	—	—	—	—	—	—	—	—
4c	1	—	—	—	—	—	—	—	—	—	—
5a	—	—	1	—	1	1	3	1	2	—	—
5b	—	—	—	—	—	—	—	—	—	—	1
6b	—	—	—	—	—	—	—	1	—	—	—
6c	—	1	—	—	—	—	3	1	—	—	—
6d	—	—	—	2	—	—	1	—	—	—	—
7a	—	—	—	3	—	—	—	—	—	1	—
7b	1	—	—	1	—	—	—	—	—	—	—
7c	1	—	—	1	—	—	—	—	—	—	—
8a	1	—	—	—	—	—	—	—	—	1	—
9a	—	—	—	1	—	—	—	—	—	—	—
9c	1	—	—	—	—	—	—	—	—	—	—
10a	—	—	—	—	—	1	—	—	—	—	—
10c	—	—	—	1	—	—	—	—	—	—	—
10d	2	—	—	—	—	—	—	—	—	—	—
10e	—	—	4	1	—	—	—	—	—	1	—
11a	—	—	1	1	—	—	—	—	—	—	—
11c	—	—	—	1	—	—	—	—	—	—	—
12a	1	—	—	1	—	—	—	—	—	—	—
12e	—	—	1	—	—	—	—	—	—	—	—
12f	2	1	2	1	—	—	—	—	—	—	—
12g	1	—	—	1	—	—	—	—	—	—	—
14a	1	—	—	1	—	—	—	—	—	—	—
14b	—	—	—	—	—	—	—	—	1	—	1
15b	—	—	—	—	—	1	—	—	—	—	—
16a/a1	1	—	1	—	—	—	—	—	—	—	1
16a3–2	—	—	—	—	—	1	—	—	—	—	1
16a3–3	1	—	—	—	—	—	—	—	—	—	—
17a–d1	—	—	—	1	—	—	2	—	—	—	—
17d2–h	—	—	—	1	—	—	—	—	—	—	—

increases again, reaching a relative abundance of more than 30% of NISP in most of the layers. Horse remains are fewer (<20%), and aurochs are also rarer. Wild boar remains continue to increase, together with those of red deer and European ass.

- Layers 6c to 3a (ca. 18,000–13,500 cal yr BP): the faunal turnover between layers 6d and 6c is the most important change of the whole sequence: horse and ibex frequencies decrease simultaneously and abruptly. In particular, ibex abundance decreases from 36% to 8.7%, whilst horse decreases from 16% to 1.9%. Both species continue to be very rare up to the top of the sequence. European ass remains increase, reaching a maximum abundance in layer 4b (28.9% of NISP); even if auroch percentages oscillate, their abundance

reaches a relative stability from layer 5a onwards (always more than 20%). Chamois is rare but almost always present, whilst roe deer is always represented and reaches its greatest abundance in layer 3a (7.9%). Wild boar and red deer are well represented, and at times they are the dominant species.

Comparison between ungulate and micromammal faunal assemblages (whole sequence)

For comparison of ungulate and small mammal assemblages, ungulate data from some of the layers were grouped together. Data from layer 24b were discarded due to their poor significance. A principal component analysis was then performed on both data sets (Fig. 5). As regards ungulates, the first component (PC1ung) counts for 45.9% of sample variability. Higher PC1ung values translate to greater abundance of ibex and horse remains. The second component (PC2ung) describes 29.2% of sample variability. Higher PC2ung values represent greater abundance of horse and aurochs remains, whereas lower PC2ung values reflect greater abundance of ibex remains. Values of PC1ung are quite stable: main changes are seen in an increase from layer 22f to layer 21b, a general slight decrease (with some small oscillations) from layer 20e to layer 7, and an abrupt decrease between layers 7 and 6. This last change corresponds to a similar change detected within layer 6 (6d–6c) and described in the previous section. PC2ung is characterized by much stronger oscillations, with minima corresponding to layers 22c, 20e, and 17 (Fig. 5).

As regards small mammals, most of the sample's variability (89.1%) is expressed only by one component (PC1small). Higher PC1small values indicate more abundant water vole (*Arvicola amphibius*) and Savi's pine vole [*Microtus (Terricola) savii*] remains; lower PC1small values reflect more abundant common vole (*Microtus arvalis*) remains. Even if data for layers 8, 9, and 11–16 are not representative, an abrupt change is visible between layers 7 and 6 (Fig. 5).

Because PC1ung appears to be positively influenced by open environment-related taxa and PC1small appears to be negatively influenced by continental, open, dry environment-related taxa, an expected and significant negative correlation was detected between these two factors using a linear model ($P = 4.6718 \times 10^{-7}$) (Fig. 6). In contrast, PC2ung, whose oscillations depend on the presence of lowland-related taxa versus promontory-related taxa, is not correlated with PC1small ($P = 0.3$).

DISCUSSION

At Grotta Paglicci, ungulate assemblages have been mainly deposited by humans. New taphonomic analyses confirm that part of the bone accumulation is unquestionably related to humans in addition to those layers where the strongest presence of hyena activities had been detected.

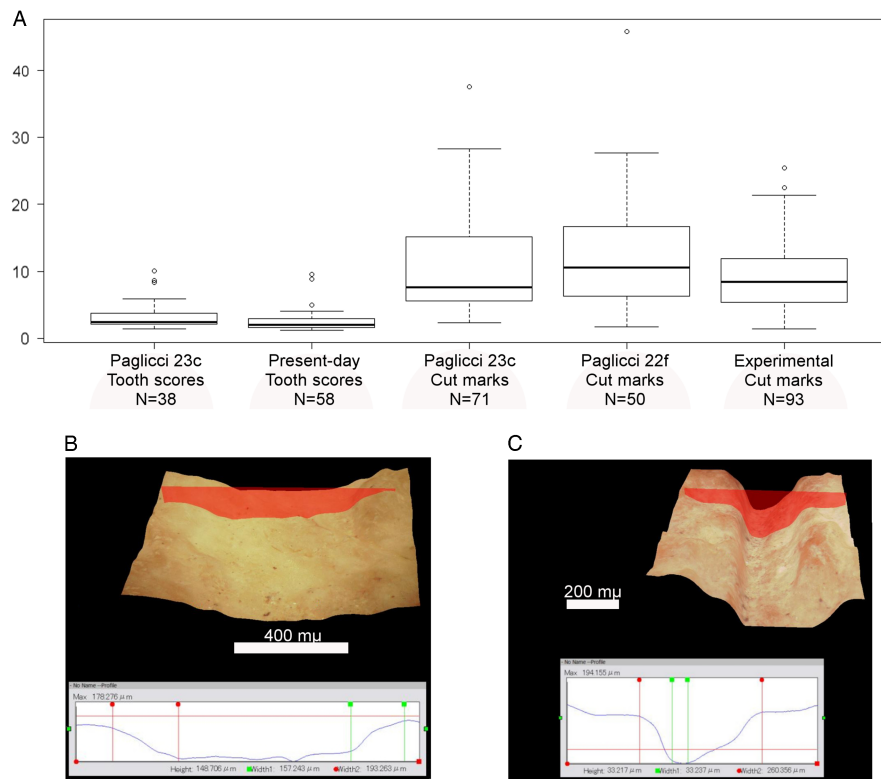


Figure 3. (color online) (A) Distribution of RTF values among five samples: marks from layer 23c interpreted as tooth scores; present-day tooth scores; marks interpreted as cut marks from layer 23c; marks interpreted as cut marks from layer 22f; experimental cut marks produced using flint implements. (B) Example of a tooth score; and (C) example of a cut mark.

PCA results allow us to quantify the ecological significance of ungulate associations: PCA1_{lung} and PCA1_{small} have a clear palaeoenvironmental meaning in terms of open versus closed environments and/or dry versus humid conditions. In both cases, the abrupt change from layer 7 to layer 6 (Fig. 5) is clearly visible, and a significant correlation between these two factors was detected. This is very important, if we consider that accumulations of small mammal and large mammal bones are related to two completely independent agents that act on territories of different size: nocturnal and diurnal birds of prey or small carnivores, and human hunters (or hyenas), respectively.

The composition of ungulate assemblages indicates the persistence of open environment-related taxa (steppes and forest steppes) for a long time, and more precisely from the Aurignacian up to the Final Epigravettian. This long phase was characterised by small-amplitude oscillations towards more humid and milder conditions. Large mammal remains from such oscillations show a slight decrease in horse and ibex balanced by an increase in auroch and chamois. This is the case in layers 22f, 16, 11, and 8c, where palaeoclimatic reconstructions indicate an increase in woods and open woodlands (Berto et al., 2017). The climate change towards more humid and milder conditions (and generally from a continental climate to a Mediterranean one) detected by Berto et al. (2017) from the final part of the Gravettian onwards is confirmed by a general positive

trend, visible first in wild boar and later in other taxa, such as red deer and roe deer, and by a decrease in ibex and horse. This change is completed at the boundary between layers 6d and 6c (or between layers 7 and 6 when some levels are grouped together). It is worth noting how shifts towards more Mediterranean conditions are generally accompanied by a replacement of horse with European ass among equids.

This change is probably related to a regional climatic shift also detectable in other sites: at Taurisano (southern Apulia) during the Final Epigravettian, the decrease in equids was balanced by an increase in aurochs; a similar situation was observed at Grotta di Uluzzo, which is close to Taurisano (Palma di Cesnola, 1993; Borzatti von Löwenstern, 1963); at Grotta del Romito (Calabria, Tyrrhenian side), ibex decreases during the Evolved-Final Epigravettian, whilst red deer and wild boar increase (Bertini Vacca, 2012). The palaeoecological meaning of this change was also confirmed by the study of micromammal remains and chronostratigraphy from the same site (López-García et al., 2014; Blockley et al., 2018). At Grotta di Santa Maria (Campania, Tyrrhenian side), ibex and aurochs decrease during the Epigravettian, whilst wild boar and red deer increase (Boscato, 2000). In addition, palaeoclimatic reconstructions based on mammal assemblages at Paglicci are confirmed by isotopic studies that indicate a climate amelioration and an increase in humidity during the late

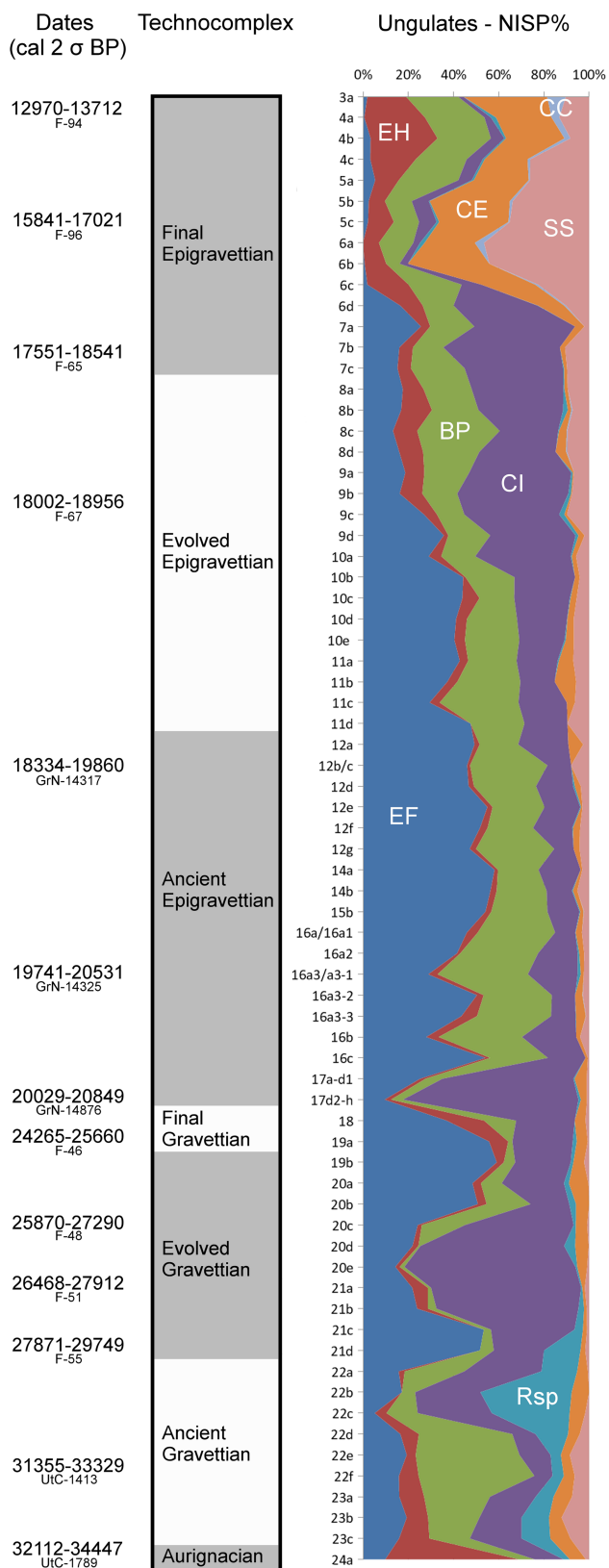


Figure 4. (color online) Relative abundance of ungulate taxa (NISP %) through the sequence. Abbreviations: BP, *Bos primigenius*; CC, *Capreolus capreolus*; CE, *Cervus elaphus*; CI, *Capra ibex*; EF, *Equus ferus*; EH, *Equus hydruntinus*; Rsp, *Rupicapra* sp.; SS, *Sus scrofa*. ^{14}C dates are calibrated with the Oxcal v. 4.2 software (Bronk Ramsey, 2009) using the IntCal13 curve (Reimer et al., 2013).

glacial (Abbazzi et al., 1996; Delgado Huertas et al., 1997; Iacumin et al., 1997).

The disappearance of horse remains in the final part of the sequence of Grotta Paglicci does not mean that the taxon became extinct in Apulia: its remains are present in the Epigravettian layers of a number of more southerly sites: Grotta del Cavallo (Nardò, Lecce), Grotta Cipolliane (Lecce) (Palma di Cesnola, 1963), Grotta di Uluzzo, Grotta di Uluzzo C (Borzatti von Löwenstern, 1963, 1965), Grotta Zinzulusa (Castro, Lecce) (Cardini, 1962), and Grotta delle Veneri (Parabita, Lecce) (Sala, 1983). At Grotta delle Mura in Apulia, the horse survived until the early Holocene (Bon and Boscato, 1993).

The disappearance of horses at Paglicci could be due to an increase in humid areas across the plain at the foot of the Gargano promontory, which forced horses to move south. Open environments, probably still present in the rocky area of the promontory, which is characterized by a permeable limestone substratum, represented an environment suitable for the European ass, which increased at Paglicci during the Final Epigravettian.

PCA points out another intriguing issue: the first component, PC1small, accounts for most of the micromammal sample variability and indicates an exclusively palaeoecological meaning of small mammal assemblages. However, PC1ung, which is supposed to be environmentally related, accounts for much less variability within the ungulate sample. A quite large portion of the sample variability is described by the second principal component (PC2ung), the values of which may indicate the alternate exploitation by humans of two different territories, both not far from Paglicci: the plain and the promontory. In fact, both horse and ibex occur in similar (dry) climatic conditions, but they inhabit very different landscapes. A similar dichotomy could also be hypothesized for aurochs and chamois during periods when the climate became more humid and open woodlands covered the territory. When PC2ung reaches its extreme values, it is indicative of a selective exploitation of particular taxa (as it is the case of ibex in layer 17).

CONCLUSIONS

This paper demonstrates that analysis of changes in ungulate composition can represent a valuable tool for the reconstruction of past climatic shifts, even if taxon representation in anthropogenic accumulation of animal remains can be influenced by both cultural choices and different taphonomic pathways. In the case of a long-term stratigraphy, the analysis of relative abundance of taxa appears to be more sensitive than the examination of presence/absence data. In any case, collected data must be discussed in light of the geographic and geomorphological characteristics of territories around the site, especially in a diverse region like the Italian Peninsula. The comparison of ungulate data with those from the study of small mammal remains allows us to

Table 4. Epigravettian ungulate assemblages (NISP%). Abbreviations: Bp, *Bos primigenius*; Cap, caprine; Cc, *Capreolus capreolus*; Ce, *Cervus elaphus*; Cer, cervid; Ci, *Capra ibex*; Ef, *Equus ferus*; Eh, *Equus hydruntinus*; Eq, equid; Rsp, *Rupicapra* sp.; Ss, *Sus scrofa*.

Layer	NISP%											Σ NISP
	Eq	Ef	Eh	Bp	Ci	Rsp	Cap	Ce	Cc	Cer	Ss	
3a	2.8	1.9	16.2	21.8	2.3	0.0	2.3	35.2	7.9	0.0	9.7	216
4a	0.0	0.6	26.7	26.1	2.8	2.3	0.6	24.4	3.4	0.0	13.1	176
4b	0.0	3.3	28.9	23.1	5.9	0.7	1.8	25.3	2.6	0.4	8.1	273
4c	0.0	3.2	19.7	22.0	7.0	0.9	2.0	18.6	1.2	0.0	25.5	345
5a	0.4	5.4	10.4	26.1	5.9	0.9	0.6	24.0	0.6	0.0	25.9	541
5b	1.3	2.5	7.1	11.7	7.5	0.4	0.0	35.0	1.3	0.0	33.3	240
5c	0.6	2.2	11.3	11.0	7.7	1.1	0.3	30.4	0.6	0.0	34.8	362
6a	0.0	0.0	7.0	15.0	3.0	2.0	1.0	22.0	4.0	0.0	46.0	100
6b	2.1	0.7	9.2	5.7	3.5	0.0	1.4	34.8	0.0	0.0	42.6	141
6c	1.0	1.9	18.0	23.2	8.7	0.0	0.3	23.5	1.3	0.0	22.2	311
6d	1.8	16.0	9.6	13.2	36.0	0.3	1.3	11.2	0.8	0.0	9.9	394
7a	1.5	25.1	4.0	19.1	43.7	0.0	0.5	4.0	0.0	0.0	2.0	199
7b	3.6	15.6	5.8	12.9	49.8	0.0	0.0	2.2	0.0	0.0	10.2	225
7c	1.2	14.8	5.8	23.0	42.4	0.4	1.2	1.2	0.0	0.4	9.5	243
8a	2.7	16.6	8.6	20.0	38.2	0.5	3.2	1.4	0.0	0.0	8.9	440
8b	2.6	16.0	12.9	19.4	35.4	2.0	3.4	1.4	0.0	0.0	6.9	350
8c	3.2	12.7	10.2	34.9	24.6	0.4	1.8	3.2	0.0	0.0	9.2	284
8d	2.8	15.1	10.0	23.5	31.9	0.0	2.8	4.4	0.4	0.0	9.2	251
9a	2.2	17.7	8.0	18.7	42.8	0.7	3.2	0.5	0.0	0.0	6.3	603
9b	4.3	15.2	9.4	14.5	46.1	1.2	2.0	0.4	0.0	0.0	7.0	256
9c	7.0	23.5	5.0	10.5	36.5	2.0	6.0	1.0	0.0	0.0	8.5	200
9d	3.6	32.3	1.8	16.8	34.1	1.2	6.0	2.4	0.0	0.0	1.8	167
10a	2.6	26.6	5.0	13.8	38.6	0.4	5.9	1.7	0.0	0.0	5.2	458
10b	3.0	42.6	1.0	20.8	25.7	0.0	1.0	2.0	0.0	0.0	4.0	101
10c	1.0	42.3	7.2	14.8	23.6	0.3	3.0	2.6	0.0	0.0	5.2	305
10d	2.8	39.4	4.6	21.2	21.2	0.1	1.5	2.7	0.0	0.0	6.5	741
10e	2.3	39.1	4.5	23.2	19.4	0.6	0.9	3.5	0.0	0.1	6.4	1631
11a	1.6	41.5	3.6	20.7	17.6	0.5	1.6	6.2	0.0	0.0	6.7	193
11b	1.8	36.0	4.3	26.8	14.6	0.0	1.8	9.1	0.0	0.0	5.5	164
11c	2.6	28.7	4.3	33.9	20.9	0.0	0.0	3.5	0.0	0.0	6.1	115
11d	0.0	47.6	0.0	23.8	19.0	0.0	0.0	0.0	0.0	0.0	9.5	21
12a	1.9	47.5	2.2	16.4	21.4	0.0	1.9	6.3	0.0	0.0	2.5	318
12b/c	0.0	46.1	1.3	34.2	10.5	0.0	0.0	0.0	0.0	0.0	7.9	76
12d	1.5	45.9	2.3	26.9	16.2	0.8	0.3	2.6	0.0	0.0	3.6	390
12e	0.8	53.7	2.3	22.4	15.4	0.4	1.7	0.6	0.0	0.0	2.8	531
12f	0.8	50.6	3.3	19.6	16.9	0.4	1.4	3.1	0.0	0.0	3.9	850
12g ossaio	1.2	46.1	2.7	33.8	8.4	0.0	1.2	2.5	0.0	0.0	4.1	512
14a	3.6	56.1	1.4	17.3	18.0	0.0	0.0	0.7	0.0	0.0	2.9	139
14b	1.1	55.1	2.7	21.5	11.0	0.4	1.3	1.9	0.0	0.0	5.1	474
15b	0.0	57.8	1.1	20.7	14.4	0.7	1.1	1.1	0.0	0.0	3.0	270
15b ossaio	0.7	49.6	3.9	28.2	13.7	0.0	0.4	1.8	0.4	0.0	1.4	284
16a/16a1	2.0	44.7	4.7	33.2	8.7	0.2	0.8	2.6	0.0	0.0	3.1	1171
16a2	1.0	39.7	1.4	32.9	16.8	0.7	3.4	2.1	0.0	0.0	2.1	292
16a3/a3-1	2.6	27.3	3.9	37.7	20.8	1.3	3.0	1.3	0.0	0.0	2.2	231
16a3-2	2.8	48.3	2.8	28.9	9.9	0.0	1.4	3.0	0.2	0.0	2.6	495
16a3-3	3.1	41.7	6.6	31.3	10.4	0.2	1.3	4.1	0.1	0.0	1.3	876
16b	2.8	26.7	5.2	35.1	22.9	0.0	1.9	1.6	0.0	0.0	3.8	633
16c	3.0	51.7	2.0	24.4	15.9	0.0	1.0	1.0	0.0	0.5	0.5	201
17a-d1	1.7	23.6	2.2	7.0	54.2	0.5	4.7	5.0	0.0	0.0	1.0	402
17d2-h	0.4	9.1	2.7	5.1	74.1	1.0	3.9	2.5	0.0	0.1	0.9	668

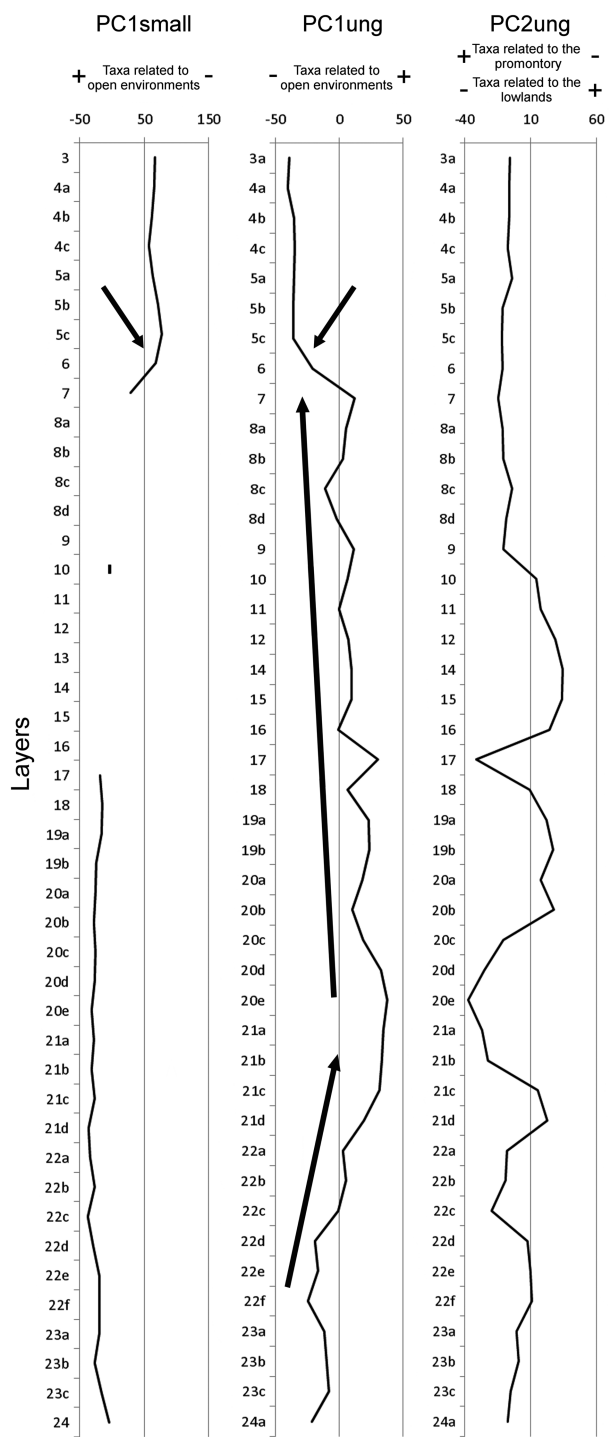


Figure 5. Diachronic trend of PC1small, PC1ung, and PC2ung over time.

distinguish between environmental and anthropic influences on the faunal composition. Finally, the results from such multivariate analysis, if integrated with studies on raw material procurement strategies and human mobility, can represent a powerful tool to shed light on diachronic changes in hunting territories and on how the environment was exploited by humans through time.

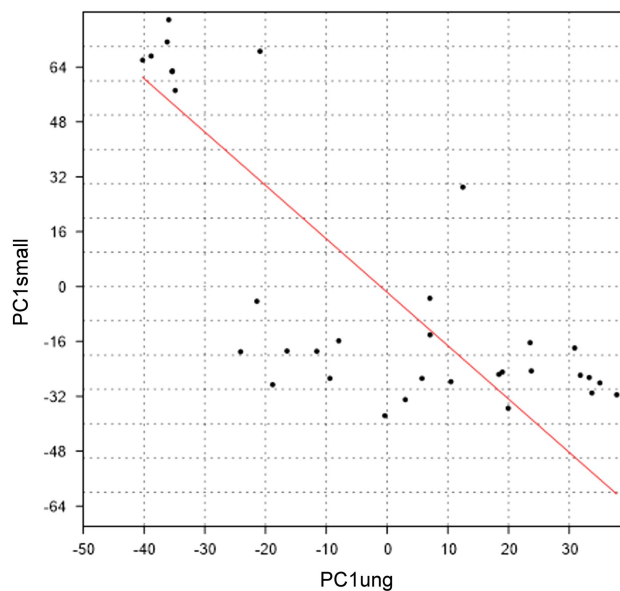


Figure 6. Linear model describing a correlation between PC1ung and PC1small. Both factors are environment related.

ACKNOWLEDGMENTS

The authors thanks the Soprintendenza Archeologia, Belle Arti e Paesaggio per le provincie di Barletta–Andria–Trani e Foggia for supporting research at Grotta Paglicci, Prof. A. Palma di Cesnola for his studies of the site, and dott. Sem Scaramucci for his revision of the text.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit <https://doi.org/10.1017/qua.2018.59>

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