**RESEARCH**

# Too good to go? Neanderthal subsistence strategies at Prado Vargas Cave (Burgos, Spain)

Héctor de la Fuente Juez[1] · Marta Navazo[1] · Alfonso Benito-Calvo[2] · Florent Rivals[3,4,5] ·
Mariano Amo-Salas[6] · Pedro Alonso-García[1]

**Abstract**
Understanding the relationship between Neanderthal groups and their environment and they it is essential to comprehending their ways of life. In this article, we use both zooarchaeology and taphonomy to study the fauna assemblages found in Level 4 of Prado Vargas Cave (Cornejo, Burgos, Spain). The results point to a site in which the main accumulating agent was Neanderthal groups, who transported small- and medium-sized animal carcasses—with deer as the dominant taxon—according to their general utility to systematically and intensely exploit the major muscle bundles, bone marrow, skin, and tendons. According to dental microwear analysis, reiterated and prolonged occupations occurred in diverse moments, suggesting that the site was used most often as a long-term campsite. We detected a minimal amount of carnivore activity, who accessed the cave during periods of human absence and modified some of the remains left by the Neanderthals. Together, this information indicates that Prado Vargas is a key site to understand the dynamics of the Neanderthals in the linking area between the Castillan Plateau and the Cantabrian Range.

## Introduction

The study of fauna plays a fundamental role in the interpretation of human occupations, given what faunal assemblages related to their activities tell us about the subsistence strategies of human groups. Anthropogenic evidence allows us to know the degree of interaction between human groups and the surrounding fauna, both prey and predators (Binford 1981). The subsistence strategies and the method of obtaining animal resources open up a wide range of possibilities that these groups could have used, from scavenging to hunting strategies (Costamagno et al. 2006; Niven et al. 2012; Rendu 2022; Selvaggio 1994; Stiner 1994) (Costamagno et al. 2006; Niven et al. 2012; Rendu 2022; Selvaggio 1994; Stiner 1994). However, both practices are not exclusive. As O'Connell et al. (1988) report, "hominids from all time periods would have welcomed the windfall of scavenging a freshly dead animal when the circumstance arose."

From an archaeological perspective, it is necessary to establish methods that allow us to assess the patterns that govern occupations in a very precise way regarding function, intensity, and organization (Blasco, 2011; Carbonell and Rosell 2004; Daujeard and Moncel 2010; Rosell 2001; Vaquero 1997). The type of occupation reflects how populations adapt to the environment in which they live and how they take advantage of their resources, being a direct evidence of the behavioral variability expressed through the acquisition and management of biotic resources and territorial mobility (Moncel and Daujeard 2012). Establishing

✉ Héctor de la Fuente Juez
  hfj0000@alu.ubu.es

1   Área de Prehistoria, Departamento de Historia, Geografía y Comunicación, Facultad de Humanidades y Comunicación, Universidad de Burgos, Paseo de los Comendadores s/n 09001, Burgos, Spain

2   Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca s/n, E-09002 Burgos, Spain

3   ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain

4   Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain

5   Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Avinguda de Catalunya 35, 43002 Tarragona, Spain

6   Department of Mathematics, Faculty of Medicine, University of Castilla-La Mancha, Camino de Moledores s/n 13071, Ciudad Real, Spain

the different types of occupation is as complex, due to the number of influencing factors and the palimpsest effect, as it is interesting as it allows us to learn more about the subsistence strategies and exploitation of the landscape they inhabited. For this reason, several authors have proposed different models. From an ethnographic point of view, Binford (1978a, b, 1980, 1983) proposes two types of groups: (1) foragers, who do not store, have greater residential mobility; and (2) collectors, who do store, have greater logistical mobility and more complex settlement patterns. Both have a base camp, which is the center of their activities. In the case of collector groups, the base camp is the place from which certain members of the group depart to places where resources are obtained (Kelly 1992). From an archaeological perspective, Carbonell and Rosell (2004) propose 4 types of occupation: (1) referential intervention centers correspond to base camps in which we observed a large quantity of remains. With respect to the fauna, herbivores dominate the assemblage, and it is common to observe differential transport of anatomical parts of the hunted animals. The remains show a large number of anthropogenic marks associated with fleshing, disarticulation, and breakage. Non-human carnivores attracted by the abandoned remains would leave their mark in times of human absence; (2) complementary intervention centers are places where specialized activities are carried out in which the accumulations of remains are smaller than in the referential intervention centers, unless the reiteration of their use produces palimpsests. Related to fauna, these sites show a great interpretative complexity, since they are usually related to traps or natural hunting grounds where the carcasses are in anatomical connections or semi-connections and show cut marks related to the first stages of the operative chain. Depending on the body size, the whole animal can be transported to a referral center. Due to the low human presence, the activity of other scavengers is high, finding tooth marks and coporlites; (3) opportunistic and marginal intervention centers are places where accumulations are very low and respond to occupations of short temporal duration. Faunal remains predominate over lithic industry, reflecting the last stages of the operational chain related to the last consumption (mainly breakage); and (4) specialized and singular intervention centers are intentional accumulations that go beyond strictly economic and substantial activities. Several Neanderthal sites have been associated with both foragers (Castel et al. 2017; Daujeard and Moncel 2010; Gaudzinski-Windheuser and Roebroeks 2011; Jauberte et al. 2008; Martínez-Moreno et al. 2004; Mellars 1996; Niven et al. 2012; Rendu et al. 2012; Rendu and Armand 2009) and collectors (Marín et al. 2019; Morin 2012; Patou-Mathis 2000; Rendu 2010; Romandini et al. 2014; Wallace and Shea 2006).

The intensity and length of time that the sites have been occupied also tell us about the function of the site. Daujeard and Moncel (2010) propose three types of sites based on these variables: (1) long-term residential camps, (2) short-term regular hunting camps, and (3) brief stopover camps. However, subsistence strategies may change seasonally, expanding the variability and complexity of occupations (Binford, 1980). In addition, it is generally accepted that nearly all sites are palimpsests, making interpretation of deposits and occupation type difficult (Bailey 2007; Lucas 2005, 2012). Long-term occupations are characterized by a high density of remains (lithic and faunal), a large settlement area, low carnivore activity, and the presence of complete operational chains (Bargalló et al. 2020; Bicho and Cascalheira 2020; Costamagno et al. 2006; Gabucio et al. 2014; Kuntz et al. 2016; Moncel and Rivals 2015; Vaquero et al. 2019). Short-term occupations are characterized by few remains, small areas, significant carnivore activity, and lithic tools configured outside the camp (Costamagno et al. 2011; Niven et al. 2012; Picin and Cascalheira 2020; Vallerdú et al. 2005; Villaverde et al. 2017). At the archaeological level, it has been possible to identify sites used as long-term camps (Bar-Yosef et al. 1992; Blasco et al. 2016; Daujeard, 2008; Morin 2012; Rendu 2010; Romandini et al. 2014), and short-term (Castel et al. 2017; Conard et al. 2012; Delagnes and Rendu 2011; Jauberte et al. 2008; Marín-Arroyo 2013; Rendu and Armand 2009; Rosell et al., 2012b; Valensi et al. 2012) and special purpose sites such as intermediate slaughter or butchering places (Costamagno et al. 2006; Rendu et al. 2012). In the Iberian Peninsula, we find numerous sites in which Neanderthals are the main accumulating agent and which are interpreted as long-term (Gabucio et al. 2014; Luret et al. 2020; Marín et al. 2019; Romero et al. 2019; Rosell et al. 2012a, b; Sañudo et al. 2016; Villaverde et al. 2017) and short-term residential sites, especially hunting camps or hunting stands (Baldeón, 1993; Bargalló et al. 2020; Martínez-Moreno et al. 2004; Moclán et al. 2021; Pérez et al. 2017a, b, 2020; Real Margalef et al. 2019; Rios-Garaizar et al. 2015; Salazar-García et al. 2013; Sánchez-Romero et al. 2020; Sanchis et al. 2019; Utrilla et al. 2010; Uzquiano et al. 2012). However, their functionality is not always known (Ready 2013; Ríos Garaizar et al. 2020; Sánchez-Hernández et al. 2019; Yravedra Sainz de los Terreros and Gómez Castanedo 2011).

Traditionally, zooarchaeological and seasonality studies do not consider the stratigraphic packages that help to distinguish possible events. To confront the problems associated with the palimpsest effect in this study, we are working on a protocol that draws from disciplines such as zooarchaeology—especially taphonomy, dental wear, and bone refits—and microstratigraphy, allowing us to distinguish events and categorize occupations. In this paper, we present the first step of this protocol, a zooarchaeological, taphonomic, and

dental wear study which provides data that sheds light on the subsistence strategies of these Neanderthals within the variability shown by the groups of the Iberian Peninsula and, particularly, of the Cantabrian range.

## Prado Vargas

The Prado Vargas cave is located in the Ojo Guareña karst complex (Burgos, Spain) (Fig. 1). Prado Vargas is a 120-m-long subhorizontal gallery interpreted as a karstic paleo-spring located in the sixth level of the complex, which would flow into the Trema river valley (Ortega et al. 2014). The cave opens on the right bank of the valley, currently located about 20 m above the Trema riverbed (Navazo et al. 2021).

Prado Vargas is the oldest karst site in Ojo Guareña and was discovered by Trinidad Torres in 1986, who excavated several trenches looking for *Ursus spelaeus* and ended up finding the Mousterian level (N4). A campaign has been active since 2006, and from 2016 to the present our interdisciplinary team has been in charge of it.

The stratigraphic sequence is composed of 9.3 m of sands, gravels, and clays that are divided into 9 lithostratigraphic units (Fig. 2). To date, layers 4 and 8 are the only ones which contain archaeological material. Unit or level 4 (N4), which is the focus of this paper, has been the only one studied so far (Alonso-García et al. 2020; Cabornero et al. 2016; de la Fuente Juez et al. 2020; Navazo et al. 2005, 2021). N4 has been dated by optically stimulated luminescence (OSL), radiocarbon dating, and AAR dating, yielding dates between 54.7 and 39.8 ka BP (Navazo et al. 2021).

Pollen analyses reflect a cold climate with a certain degree of humidity, characterized by landscapes of large arboreal spaces and some pine (*Pinus*), birch (*Betula*), and juniper coppices (*Juniperus*). This is confirmed by the macro- and micromammal fauna (Navazo et al. 2021). In previous studies, the presence of different taxa has been documented, highlighting the presence of red deer (*Cervus elaphus*) and caprines (*Capra pyrenaica* and *Rupicapra pyrenaica*), among other species, such as horses (*Equus ferus*), wild boars (*Sus scrofa*), Bos/Bison, rabbits (*Oryctolagus* sp.), cave bear (*Ursus spelaeus*), wolves (*Canis lupus*), foxes (*Vulpes vulpes*), or badgers (*Meles meles*). These animals
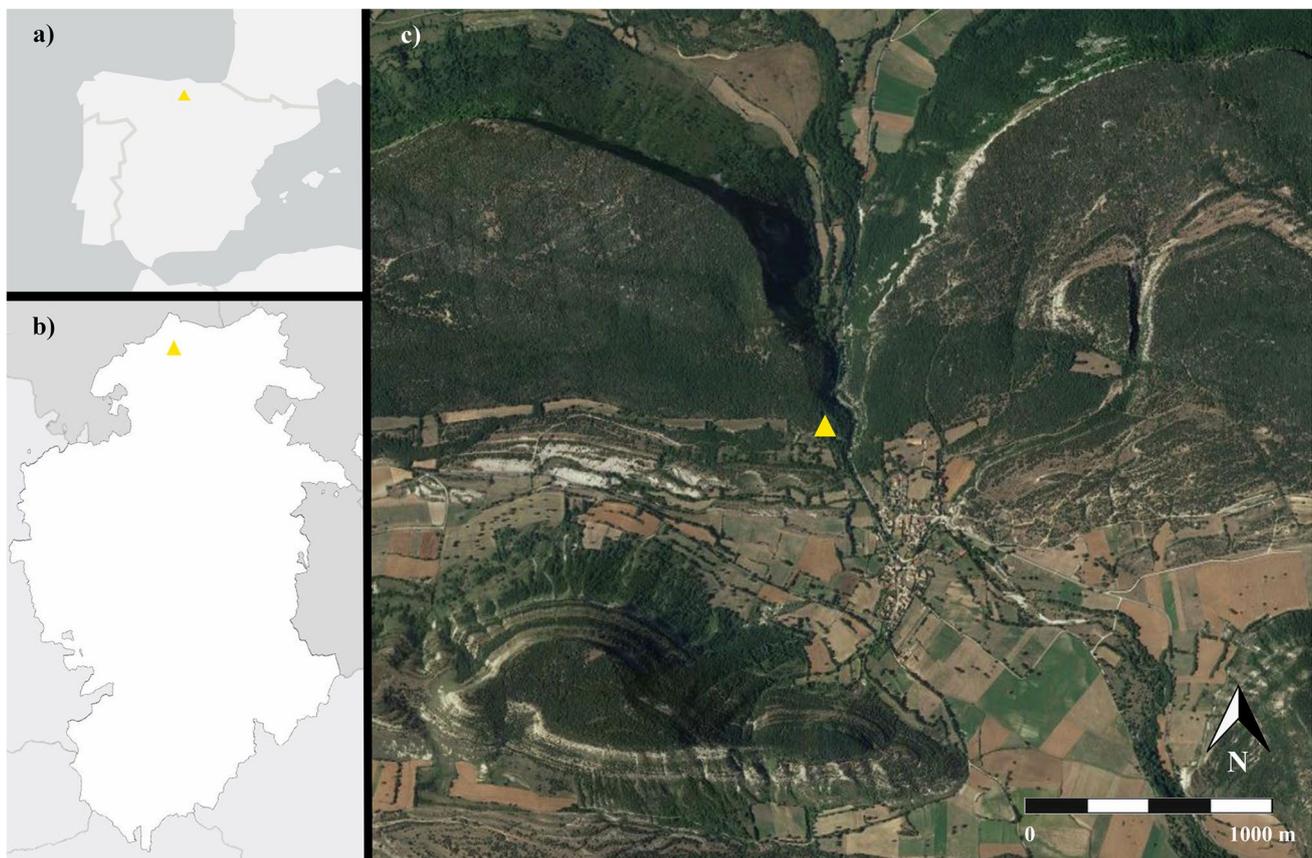


**Fig. 1** Geographic situation of Prado Vargas. **a** Location of Prado Vargas in the Iberian Peninsula. **b** Location of the site in Burgos province. **c** Location of the site at the Ojo Guareña Natural Monument
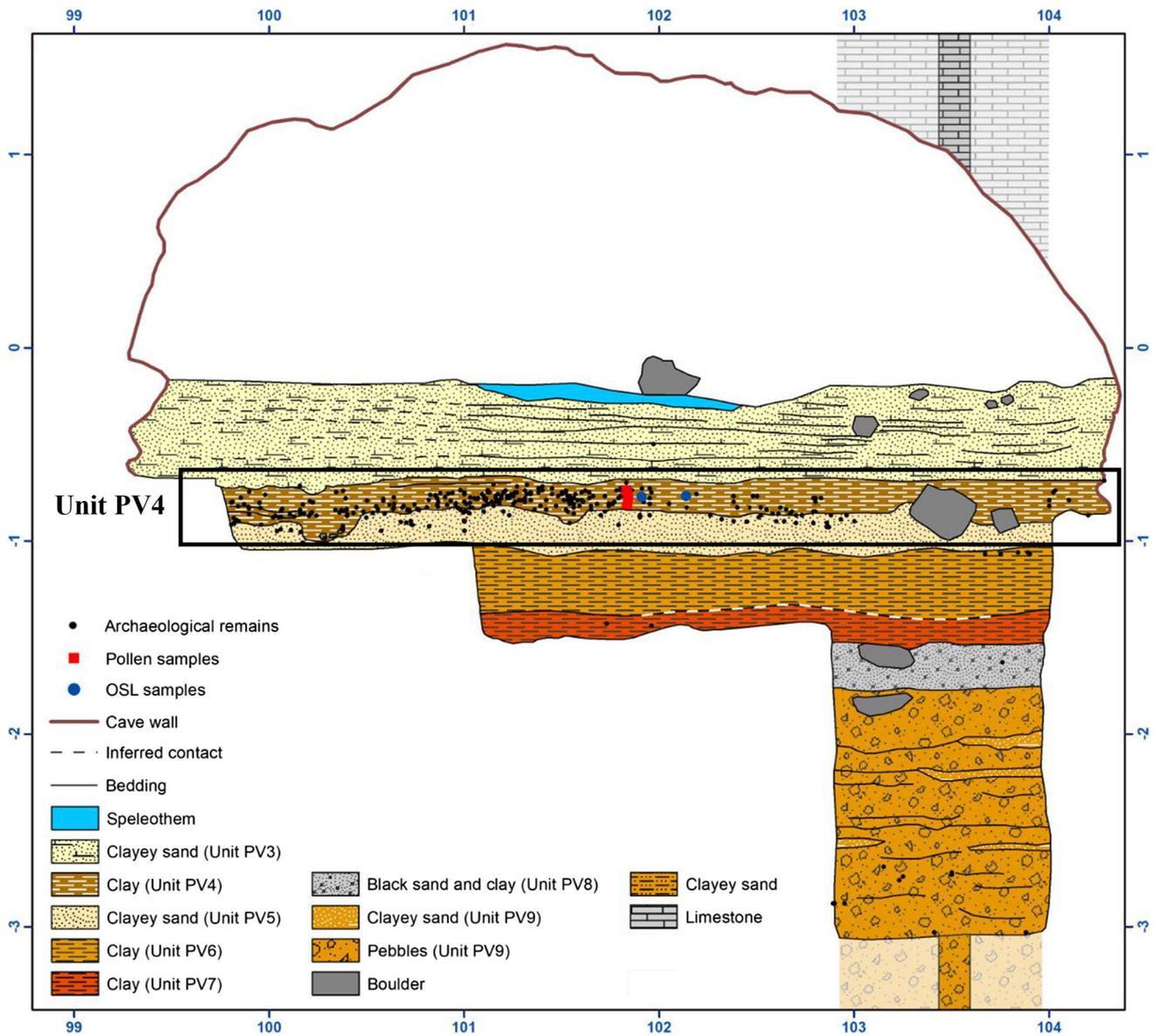
**Fig. 2** Stratigraphic sequence of Prado Vargas (modified from Navazo et al. 2021)

were transported to the cave, where the carcasses were intensively processed, from the meat to the marrow (de la Fuente Juez et al. 2020). But their use did not end there, as certain bone fragments became part of the technological sphere and were used as retouchers (Alonso-García et al. 2020).

The lithic industry is mainly made of local flint, although there are other allochthonous raw materials. All structural categories are represented, in other words, the entire reduction sequence, and exploitation is oriented towards intensive use of the material, with hierarchical discoid carving predominating. Flakes are the most representative element, cores represent 5% of the set, and the rest is formed by hammers and fragments. Discoid and Levallois are the best represented exploitation systems. The size of most retouched items is somewhat larger than that of the unretouched flakes, mostly micro- and small-sized. The most representative type is the sidescraper, followed by denticulates, notches and, with much less frequency, points and endscrapers (Navazo et al. 2005, 2021, 2022). Traceology has revealed that some tools were used for skin scraping, and meat and wood processing (Cabornero et al. 2016; Navazo et al. 2022; Santamaría Cabornero et al. 2021).

In addition, Prado Vargas 1360 deserves a special mention. This is the dental crown of a 9–10-year-old *Homo*

*neanderthalensis* infant individual with evidence of resorption, suggesting that the tooth was lost in life due to tooth replacement (Navazo et al. 2021).

## Methodology

The faunal remains from N4 have been taxonomically and anatomically classified using the reference anatomical collection of the Prehistory Laboratory of the University of Burgos and the Centro Nacional de Investigación sobre la Evolución Humana (CENIEH—National Center for Research on Human Evolution) and comparative manuals (e.g., Barone 1976; Pales and Lambert 1971; Schmid 1972). When they could not be identified, they were classified according to the size categories listed by Bunn (1986) based on studies of African mammals and adapted in later work for European sites (Cáceres 2002): very large size (VLS) > 1000 kg; large size (LS) 1000–300 kg; medium size (MS) 300–100 kg; small size (SS) 100–20 kg; very small size (VSS) < 20 kg. Likewise, small–medium size (S-MS) and large–medium size (L-MS) have been used when it has not been possible to discern to which of the two they belong. The Shannon-Wiener index and the inverse of the Simpson index were used to determine species diversity. Because Shannon's homogeneity index is more sensitive in determining the value of predominant species, Simpson's dominance index has also been used to look at the degree of specialization of hunting. Age at death was determined by bone fusion (Barone 1976) and tooth eruption and wear (e.g., Analla et al. 2002; Hillson 1990; Pérez-Barbería and Pérez-Fernández 2009; Schmid 1972; Silver 1969). To analyze mortality profiles, the ternary diagram of Stiner (1990), modified by Discamps and Costamagno (2015), was used for a more valid interpretation of the relative abundance of the different age groups in the assemblage.

For the quantification of the record, the NISP (Number of Identified Specimens), MNE (Minimum Number of Elements), and MNI (Minimum Number of Individuals) were taken into account for each taxon and body size (Lyman 1994; Pickering et al. 2003; Rodríguez Hidalgo 2015; Saladié et al. 2011; Stiner 1994). The method described by Morin (2007) was used to calculate the MNE in radius and metapodials. To assess the completeness of the record and its implications, such as biases or transport and exploitation decisions, the %MAU was calculated (Binford 1978, 1984). Various processes can lead to the disappearance of skeletal remains, with density-mediated attrition being particularly influential (R. L. Lyman 1994). In order to study differential preservation as a function of density, Spearman's correlation coefficient between %MAU and the previously described density values for different body sizes has been calculated (Lam et al. 1999; Lyman 1985; Pavao and Stahl 1999). Since

there are no values for VLS, those for LS have been used. Spearman's correlation coefficient has also been used to analyze the relationship between the selective transport of carcasses and their economic interest, through the %MAU for the different size categories and species identified and different utility indices: [S]FUI, [S]AVGFUI, [S]MAVG-MARa, [S]MAVGMARb, UMI (Emerson 1993; Metcalfe and Jones 1988; Morin 2007). To assess the transport strategy, the Shannon unit index (E) for high survival elements (Faith and Gordon 2007) was used and the "Equitability_J" function in the PAST software was employed. In order to evaluate the similarity with long-term (LT) or short-term (ST) models, a discriminant analysis (LDA) has been performed with our %MAU sample and that of other assemblages suggested as long term or short term, as continuous independent variables, with long term, short term, and Prado Vargas (PV) being considered as categorical dependent variables following Marín et al. (2019) and Moclán et al. (2021).

All the remains have been measured in millimeters and breakage has been analyzed distinguishing between green and dry (Villa and Mahieu 1991). Diagnostic elements of intentional breakage have also been documented: percussion notches, percussion pits, pseudo-notches, positive flakes, adhering flakes, flakes, microstriations and striations, and peeling (Capaldo and Blumenschine 1994; Coil et al. 2020; Pickering and Egeland 2006; Vettese et al. 2020). To discern possible breakage patterns, their specific location in the bone has been collected. Furthermore, they have been classified as isolated, opposing, correlative, and consecutive (Rosell 2001).

Bone surface modifications (BSM) were analyzed with a MOTIC SMZ-140 Series binocular loupe. Cut marks (CM) were examined according to their type, location, and morphology. (Binford 1981; Fernández-Jalvo and Andrews 2016; Shipman and Rose 1983). Thermal alterations were classified as follows: 0, no coloration; 1, dispersed brown; 2, widespread brown; 3, completely black; 4, gray and occasionally blue; 5, very pronounced gray or white (Cáceres 2002). To evaluate the relationship between coloration and position, a correspondence analysis was performed between our data and those offered by Pérez et al. (2017a, b) and the biplot representation was carried out with the categories of the variables considered, on the one hand position (2.5 cm, 5 cm, 7 cm, embers, hearth base, and flames) and on the other hand coloration (brown, black, gray, and white). That is to say, from the data provided by Perez et al. (2017a) by means of the correspondence analysis, the biplot has been generated and once the coordinates of the biplot have been obtained, the position of our sample has been represented in this biplot from the data of the same. The action of carnivores has been identified as tooth marks (TM). Classified according to their morphology, location, and purpose, we distinguished scores, pits, punctures, pitting, furrowing, or

crenulated edges, in addition to the alterations caused by digestion (Binford 1981; Domínguez-Rodrigo and Piqueras 2003; Selvaggio 1994). Carnivore identification was performed by comparing the collected pits and scores with experimental models (Andrés et al. 2012; Arilla et al. 2014, 2020; Domínguez-Rodrigo and Piqueras 2003; Saladié et al. 2013; Young et al. 2015). One-sample Student's *T*-test was used to evaluate if the means of the sample could take values provided by the literature and to be able to assume or discard the action of different agents. The normality of the data was checked using the Kolmogorov-Smirnov test. To evaluate the type of access to the carcasses, the frequency of percussion marks (PM), cut marks, and tooth marks in the different anatomical elements of the identified size categories and species was analyzed.

Other postdepositional processes such as weathering (Behrensmeyer 1978), trampling (Blasco et al. 2008; Courtenay et al. 2020), abrasion (Behrensmeyer 1990; Brett 1990; Cáceres 2002; Lyman 1994), sedimentary pressure (Shipman 1981), humidity (Coard 1999; Courty et al 1989; Fernández-Jalvo and Andrews 2000), and root action (Behrensmeyer 1978; Cáceres 2002; Fernández-Jalvo 1992) were also described.

Meso- and microwear analyses were done on all available dental remains of *Equus ferus*, *Cervus elaphus*, *Capra pyrenaica*, and *Rupicapra pyrenaica* from level 4. We selected those that were identified at the species level and whose occlusal surfaces presented facets of wear (i.e., belonging to adult individuals). Meso- and microwear will provide evidence of the dietary traits of the ungulates at two different time scales. Mesowear will inform about the annual average diet of the individuals while microwear will indicate the diet at the time of death, informing about the seasonality at the site.

Tooth mesowear is based on the analysis of the shape and relief of the tooth cusps (Fortelius and Solounias 2000). It is directly observed on the buccal or lingual side of the upper and lower molars, respectively, except for horses where only the lower teeth were analyzed. We selected all molars available and discarded those that could belong to the same individual based on size, wear stage, and laterality. Teeth from young individuals (without wear facets) and old adult individuals (with heavy wear) were discarded from the study (Rivals et al. 2007). The method is based on the classification of cusp shape and relief in seven categories, from high relief and sharp cusps (category 0) to blunt cusps with no relief (category 6) (Mihlbachler et al. 2011). The individual mesowear values were then averaged to obtain the mesowear score (MWS).

Tooth microwear was quantitatively studied according to the low-magnification method (Solounias and Semprebon, 2002). The occlusal surfaces were cleaned with acetone and then ethanol 96%. The surfaces were molded using high-resolution dental silicone (Heraeus Kulzer, PROVIL novo, Light C.D. 2 regular set) and casts were created using clear epoxy resin (C.P. Química, EP-1060A/1585B). All teeth were screened under a stereomicroscope to check and discard those presenting taphonomic alterations (King et al. 1999; Uzunidis et al., 2021). The quantification of the microwear patterns was done using a Zeiss Stemi 2000C stereomicroscope at $\times 35$ magnification. To avoid inter-observer error, the analysis was performed by a single observer (FR). Microwear features were quantified in two areas using an ocular reticule of 0.16 mm$^2$ on the paracone of the upper molars and the protoconid of the lower molars. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) which distinguish pits and scratches. The presence of some other features is recorded qualitatively (presence/absence): cross scratches, hyper-coarse scratches, gouges, large pits. Scratch texture was qualitatively evaluated using the scratch width score (SWS) which is obtained by giving a score of "0" to a surface with predominantly fine scratches, "1" to one with a mixture of fine and coarse scratches, and "2" to one with predominantly coarse. Individual scores for a sample of teeth were then averaged to obtain the SWS.

To estimate the duration of the faunal assemblages' accumulation at Prado Vargas, we used the standard deviation (SD) and the coefficient of variation (CV) calculated on the numbers of scratches. These two values allow for the quantification of the variability of the microwear signal which is related to seasonal changes in diet and correlates to the duration of the accumulation events, e.g., hunting events (Rivals et al. 2015). The SD and CV values are plotted on a bivariate heat map to classify each sample: event lasting one season or less (zone A); events longer than a season (zone B); and separate events that occurred during non-contiguous seasons (zone C).

PAST, EXCEL, and SPSS software were used for the statistical calculations analysis carried out in this work. Throughout the work, $p < 0.05$ was considered statistically significant. With the exception of ternary plots, Student's *T*-test, diversity indices, and LDA, statistical analyses were performed using SPSS software. Diversity indices and LDA were computed using PAST software, and Student's *T*-test and ternary plots using EXCEL. Mesowear and microwear graphs were produced using R. Adobe Photoshop was used to create the artwork.

## Results

### Integrity of the faunal assemblage

A total of 6343 remains, bones, antlers, and teeth were studied. The remains were found to be highly fractured,

with the majority of the remains being less than 5 cm (see Supplementary File 1). A total of 14.98% of the remains have been identified according to their species. Most of these are ungulates (%NISP = 93.37), *Bison priscus*, *Bos primigenius*, Bos/Bison (if unable to determine which), *Equus ferus*, *Cervus elaphus*, *Dama dama*, *Capreolus capreolus*, *Capra pyrenaica*, *Rupicapra pyrenaica*, and *Sus scrofa* (Fig. 3).

Some of the remains were not identified as species and were assigned to Ungulata, Equidae, Cervidae, and Caprinae. Of the total NISP, 5.79% belong to carnivores *Ursus spelaeus*, *Panthera leo*, *Canis lupus*, *Vulpes vulpes*, *Meles meles*, and undetermined remains of Carnivora; and 0.84% belong to *Oryctolagus* sp., Leporidae, and Aves (Table 1). Simpson's index indicates a medium species diversity (1-D = 0.61), while the Shannon–Wiener index indicates a low-medium diversity (H' = 1.55).

The 88.21% of the NISP were identified according to body size, LS (8.76%), medium size (39.73%), small size (49.53%), very small size (1.14%), and VLS (0.71%). Only a total of 281 remains (NISP = 4.43%) are indeterminate. The remaining percentage are remains identified only at the anatomical level or according to bone type (long or flat).

Among ungulates, the highest MNI values are for *Cervus elaphus* (20) and *Capra pyrenaica* (14). The rest of the species obtain values between 1 and 5, except *Rupicapra pyrenaica* (7). As for carnivores, the highest values correspond to *Canis lupus* (5) and *Ursus spelaeus* (5), the rest between 1 and 3 (Table 1).

Mortality profiles indicate that most individuals are adults, except in the case of carnivores and VSS, where subadult and senile individuals are more represented.

Prime-dominated mortality profiles are evident in all taxa, although in the case of *Equus ferus* and Caprinae, whose results are not projected in the prime zone, they are close (Fig. 4).

The NISP and MNE (Supplementary Table A.1) reveal that the main sizes analyzed show a disproportion between elements of the axial skeleton and the appendicular skeleton, being the most represented elements those of the limbs. Only in the case of *Cervus elaphus* do parts of the axial skeleton, such as the mandibles and maxillae, have a significant presence. This disproportion is less marked for body sizes, so that, although there is a greater representation of limb elements, the number of elements of the axial skeleton is increased. The elements of the axial skeleton only stand out in VSS. The presence of isolated teeth stands out, although there are also complete dental series.

The %MAU confirms the asymmetry in the representation (Fig. 5; Supplementary Table A.2). To see possible biases, it has been studied the correlated correlation with between bone density and utility values by means of Spearman's correlation coefficient. As for density, *Cervus elaphus* ($\rho = 0.935$; $p$-value = $< 0.01$) and DM ($\rho = 0.915$; $p$-value = $< 0.01$) show a strong correlation. The correlation coefficient in the case of *Capra pyrenaica* has a moderate value, and although it is not statistically significant, it is close to the significance limit ($\rho = 0.538$; $p$-value = 0.058) and small size ($\rho = 0.542$; $p$-value = 0.056). With respect to utility indices, all body sizes show highly significant correlations with (S)MVGMARa and (S)MVGMARb. This happens with all main species identified, except *Bos primigenius*, *Rupicapra pyrenaica*, and *Sus scrofa*. In the case of *Equus ferus*, there is a moderate relationship which, although not statistically significant, is close to the limit of
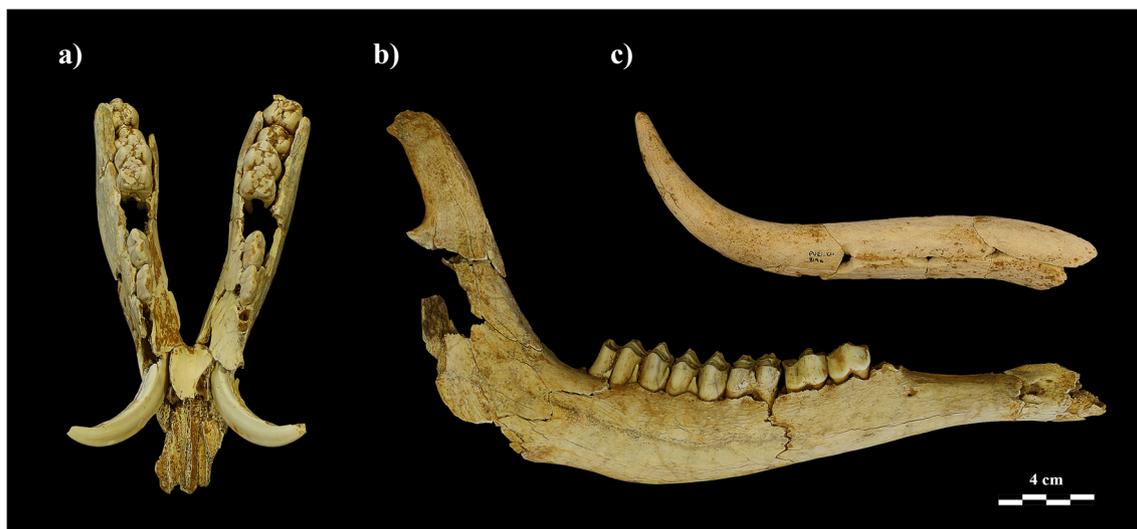


**Fig. 3** Skeletal elements found on Level 4 of Prado Vargas: **a** mandible of *Sus scrofa*; **b** mandible of *Cervus elaphus*; **c** antler of *Cervus elaphus*

**Table 1** NISP, %NISP, MNE, and NMI, general and by age, level 4 of Prado Vargas

|  | NISP | %NISP | NME | NMI | Immature | Adult | Senile |
|---|---|---|---|---|---|---|---|
| *Bison priscus* | 17 | 1.79 | 13 | 2 | 0 | 2 | 0 |
| *Bos primigenius* | 4 | 0.42 | 4 | 1 | 0 | 1 | 0 |
| Bos/Bison | 23 | 2.42 | 14 | 2 | 0 | 2 | 0 |
| Equidae | 2 | 0.21 | 2 | 1 | 0 | 1 | 0 |
| *Equus ferus* | 40 | 4.21 | 14 | 5 | 1 | 3 | 1 |
| Ungulata | 3 | 0.32 | 3 | 1 | 0 | 1 | 0 |
| Cervidae | 3 | 0.32 | 3 | 1 | 0 | 1 | 0 |
| *Cervus elaphus* | 566 | 59.52 | 281 | 20 | 1 | 18 | 1 |
| *Dama dama* | 1 | 0.11 | 1 | 1 | 0 | 1 | 0 |
| *Capreolus capreolus* | 1 | 0.11 | 2 | 1 | 0 | 1 | 0 |
| Capra | 2 | 0.21 | 2 | 2 | 1 | 1 | 0 |
| Caprinae | 19 | 2.00 | 10 | 2 | 1 | 1 | 0 |
| *Rupicapra pyrenaica* | 43 | 4.52 | 36 | 7 | 1 | 6 | 0 |
| *Capra pyrenaica* | 143 | 15.04 | 120 | 14 | 2 | 11 | 1 |
| Sus scrofa | 21 | 2.21 | 21 | 5 | 2 | 3 | 0 |
| *Ursus spelaeus* | 17 | 1.79 | 17 | 5 | 2 | 1 | 2 |
| Carnivora | 4 | 0.42 | 4 | 1 | 0 | 1 | 0 |
| *Panthera leo* | 1 | 0.11 | 1 | 1 | 0 | 1 | 0 |
| *Canis lupus* | 14 | 1.47 | 13 | 5 | 2 | 3 | 0 |
| *Vupes vulpes* | 12 | 1.26 | 12 | 3 | 1 | 2 | 0 |
| *Meles meles* | 7 | 0.74 | 7 | 2 | 0 | 2 | 0 |
| Leporidae | 3 | 0.32 | 3 | 1 | 1 | 0 | 0 |
| *Oryctolagus* | 2 | 0.21 | 3 | 1 | 0 | 1 | 0 |
| Aves | 3 | 0.32 | 3 | 2 | 0 | 2 | 0 |
| VLS | 40 | 0.71 | 3 | 1 | 0 | 1 | 0 |
| LS | 404 | 7.22 | 28 | 4 | 1 | 3 | 0 |
| M-LS | 109 | 1.95 | 20 | 4 | 1 | 3 | 0 |
| MS | 1527 | 27.29 | 83 | 10 | 1 | 9 | 0 |
| S-MS | 83 | 1.48 | 16 | 2 | 1 | 1 | 0 |
| SS | 2445 | 43.69 | 122 | 6 | 2 | 4 | 0 |
| VSS | 37 | 0.66 | 6 | 3 | 2 | 1 | 0 |

significance. Similar but less strong correlations exist with UMI, being significant in Bos/Bison, *Equus ferus*, and LS, and in *Cervus elaphus* ($\rho = 0.643$; p-value = 0.119) and medium size ($\rho = 0.679$; p-value = 0.094), where the correlations are not significant although the moderate value of the correlation coefficient, which is due to the small sample size considered in this analysis. The (S)AVGFUI yields statistically significant correlations in *Bos primigenius* and *Rupicapra pyrenaica* (Table 2).

Calculations made with the Equitability_J function indicate a low correlation with unbiased strategies and null correlation with gourmet. Most of the sizes and species identified correspond to Unbiased and Bulk strategies. However, more Unbiased values correspond ($E = 0.842$) to medium size ($E = 0.8776$), small size ($E = 0.8569$), *Equus ferus* ($E = 0.8445$), *Cervus elaphus* (E = 0.8621), and *Capra pyrenaica* ($E = 0.8666$). *Bison priscus* ($E = 0.9418$) and *Sus scrofa* ($E = 0.961$) corresponded to the Bulk strategy

($E = 0.980$), while only Bos/Bison ($E = 1$) corresponded to Unconstrained ($E = 1$). Large size values ($E = 0.9135$) are between Unbiased and Bulk. In the case of very large size, *Bos primigenius* and *Rupicapra pyrenaica*, the values obtained have not been taken into account due to the low number of samples (Fig. 6; Supplementary Table A.3). Regarding the correlation of %MAU with SFUI, only Bos/Bison ($\rho = 0.724$; p-value = 0.027) shows a statistically significant correlation. In the case of large size, *Bison priscus* and *Equus ferus*, there is a strong relationship although there is no statistically significant correlation (Supplementary Table A.4) (Tabla Correlación MAU-SFUI).

## Breakage

A total of 18,653 breakage planes were analyzed, of which the majority are curved (55.20%), oblique (80.54%), and smooth (97.72%) (Fig. 7). The presence of several
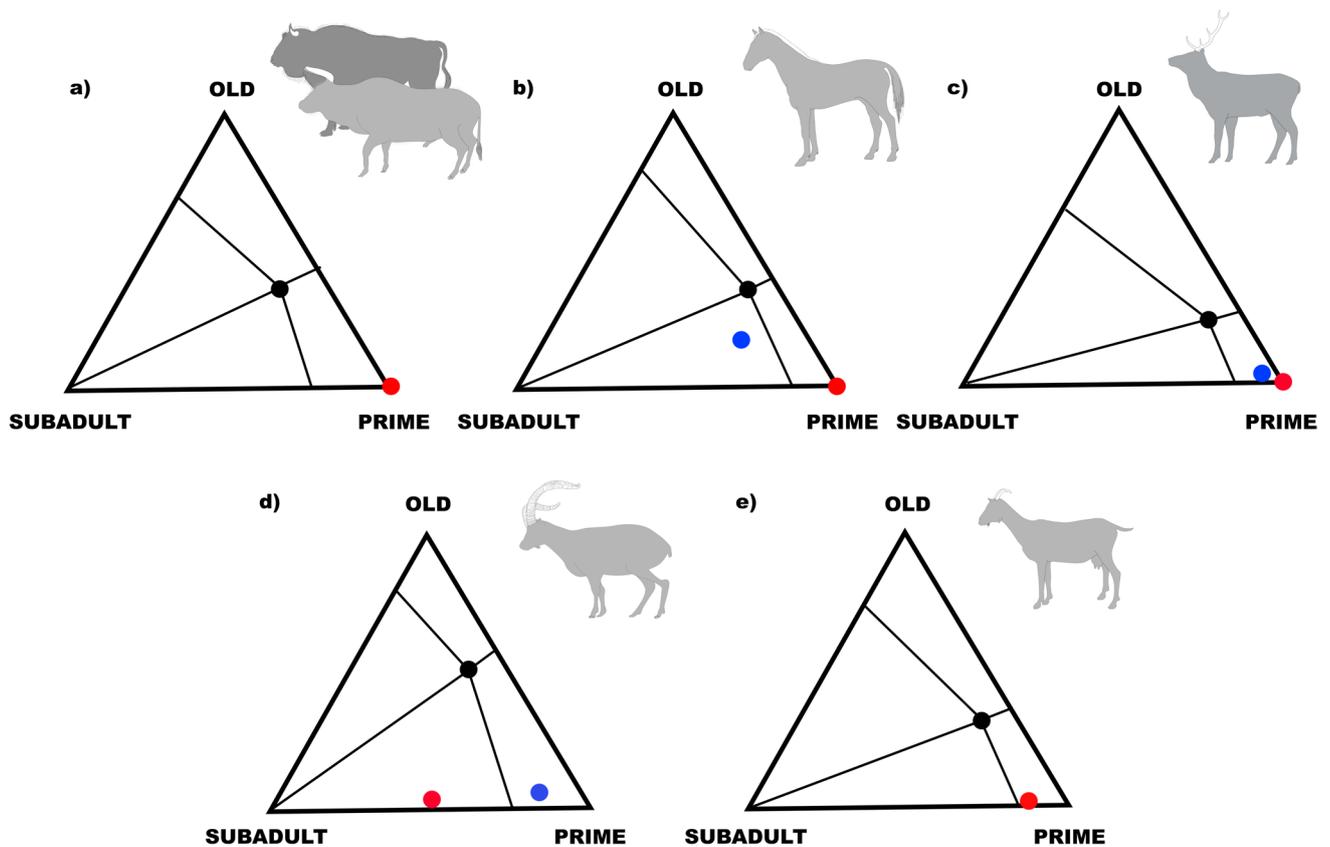
**Fig. 4** Profiles of the mortality of the main documented species. **a** Bovidae LS (*Bison priscus*, *Bos primigenius* and Bos/Bison); **b** *Equus ferus* (red) and Equidae (blue); **c** *Cervus elaphus* (blue) and Cervidae (red); **d** *Capra pyrenaica* (blue) and Caprinae (red); **e** *Rupicapra pyrenaica*

diagnostic elements of intentional breakage has been documented (%NISP = 17.22). Of these, 52.20% are percussion notches (*n* = 814) and 26.92% are positive flakes (*n* = 294). Percussion pits (*n* = 92), cortical flakes (*n* = 35), flakes (*n* = 88), and pseudo-notches (*n* = 88) were also observed. Most of them are found in the diaphysis (*n* = 950; 93.05%) and are isolated (*n* = 445; 68.25%), although there are also overlapped notches (*n* = 77; 11.81%) and opposed (*n* = 46; 7.06%). The main species identified (*Bison priscus*, Bos/Bison, *Equus ferus*, *Cervus elaphus*, *Capra pyrenaica*, *Rupicapra pyrenaica*, and *Sus scrofa*) and all body sizes except VSS show some of these elements (Table 4). *Cervus elaphus* is the species that is most present (NISP = 132), while the levels of sizes that are most present are small size (NISP = 373) and medium size (NISP = 310). According to anatomical elements, long bones are the most present, with the humerus (NISP = 82) standing out, followed by the tibia (NISP = 56), the metatarsus (NISP = 54), the radius (NISP = 57), and the femur (NISP = 41). The presence of percussion notches in a 1st phalanx and a 2nd phalanx is noteworthy. The presence of diagnostic elements of intentional breakage has also been

documented in elements of the axial skeleton, in skulls (NISP = 2), ribs (NISP = 5), scapula (NISP = 1), and indeterminate flat bones (NISP = 5).

The sides on which the diagnostic elements of intentional breakage are located are very similar in the different species and body sizes, with some exceptions. In the case of medium-size metapodials, they are preferentially located on the anterior side, a tendency that is repeated in *Cervus elaphus*, while in the case of medium-size humeri on the anterior and exterior sides (Table 3).

## Bone surface modifications

Bone surface modification (BSM) has been documented in most of the identified remains, with alterations produced by fossildiagenetic and postdepositional processes (e.g., trampling, roots, chemical corrosion) (Fig. 8). A total of 592 remains were identified with cut marks (%NISP = 9.33), especially in ungulates (*Bison priscus*, Bos/Bison, *Equus ferus*, *Cervus elaphus*, *Capra pyrenaica*, and *Rupicapra pyrenaica*). The species with the highest number of identified cut marks was *Cervus elaphus* (*n* = 94), followed by *Capra*
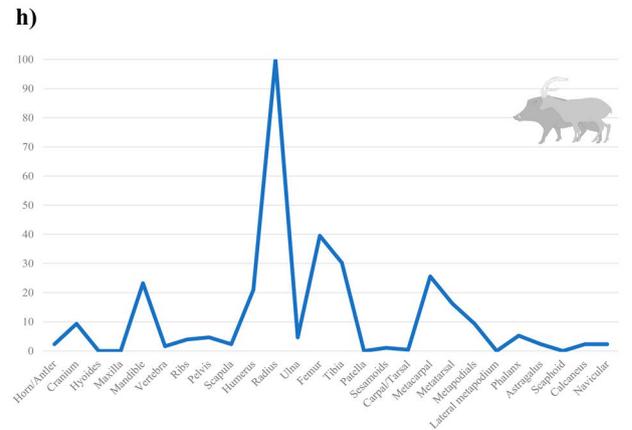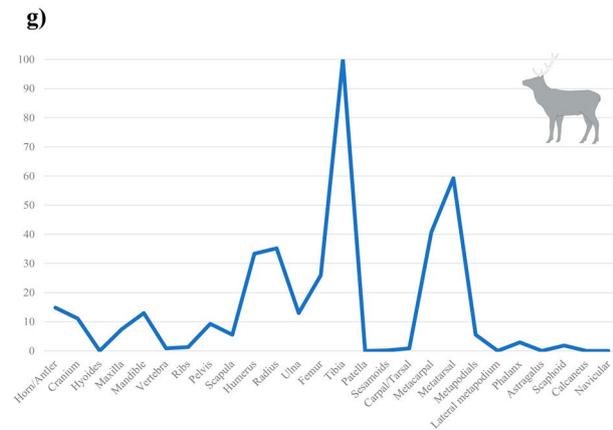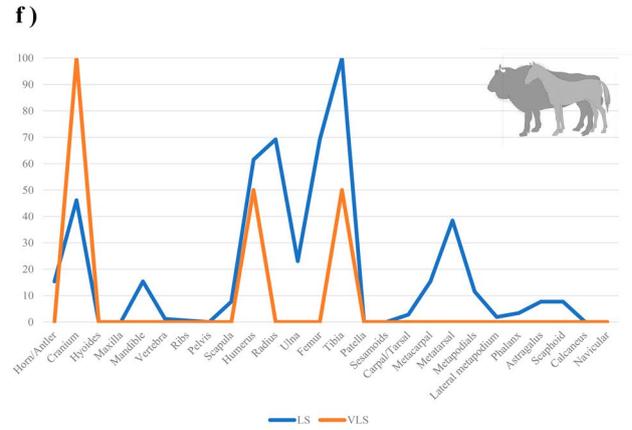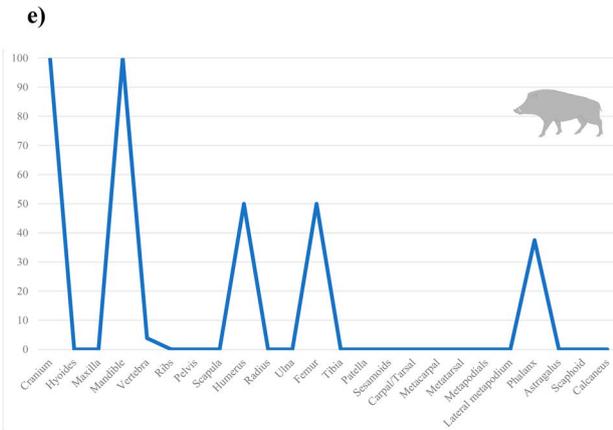
a) 



b)
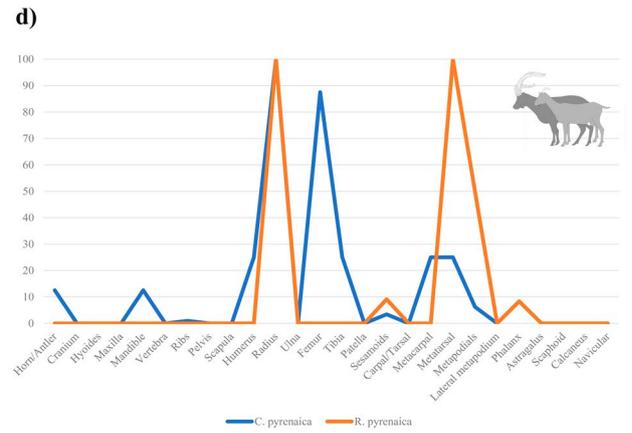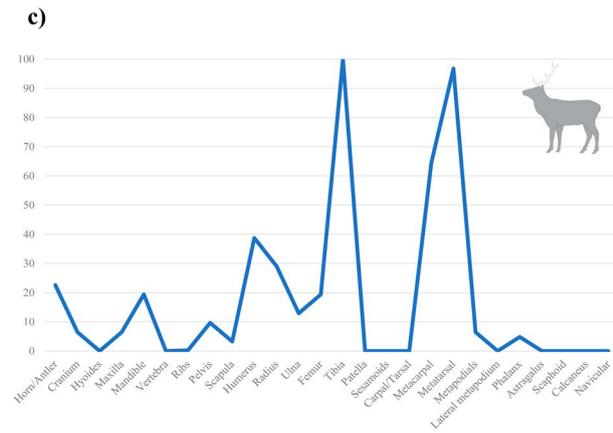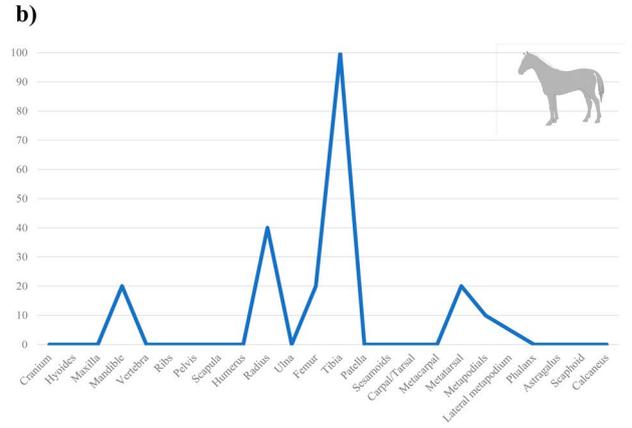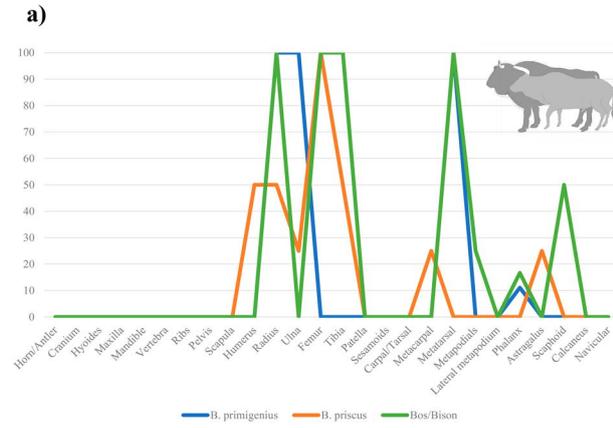


c)



d)



e)



f )



g)



h)

◄**Fig. 5** %MAU of the main documented species and sizes. **a** Bovidae LS (*Bison priscus*, *Bos primigenius*, and Bos/Bison; **b** *Equus ferus*; **c** *Cervus elaphus*; **d** *Capra pyrenaica* and *Rupicapra pyrenaica*; **e** *Sus scrofa*; **f** LS; **g** MS; **h** SS

*pyrenaica* (NSP = 9). Cut marks have been documented in all body sizes, with more in small size (NSP = 230; 38.85%) and in medium size (NSP = 170; 28,72%).

At the anatomical level, cut marks are mainly found in the elements of the appendicular skeleton. They are mostly documented in unidentified long bones (NSP = 319), tibiae (NSP = 46), humeri (NSP = 45), metatarsals (NSP = 42), and radii (NSP = 39). However, they are also documented in unidentified flat bones (NSP = 10), ribs (NSP = 9), mandible (NSP = 8), vertebra (NSP = 4), coxal (NSP = 3), and scapula (NSP = 1). Flat bones with cut marks are from *Cervus elaphus*, *Rupicapra pyrenaica*, large size, medium size, and small size (Table 4).

In terms of typology, the majority of cut marks are incisions (%NSP = 93), followed by sawing (%NSP = 2.65), chop (%NSP = 2.65), and scraping marks (%NSP = 1.7). Occasionally, more than one type of markings are present in the same remains.

A total of 239 remains were identified with tooth marks (%NISP = 3.77), especially in ungulates (*Cervus elaphus*, *Capra pyrenaica*, *Rupicapra pyrenaica*, and Caprinae), although there is one carnivore remains, *Vulpes vulpes*, with tooth marks. The species most in which tooth marks have been most frequently identified are *Cervus elaphus* (NSP = 23) and *Capra pyrenaica* (NSP = 5). In the different sizes, tooth marks are also documented in large size (NSP = 21), medium size (NSP = 67), small size (NSP = 101), and VSS (NSP = 1). In addition, they are documented in 14 indeterminate remains.

At the anatomical level, tooth marks are identified especially in unidentified long bones (NSP = 137). We did not observe a significant difference between the bones identified with percussion marks: elements of the appendicular and axial skeleton were similar. Radii (NSP = 20) and tibiae (NSP = 16) stand out. It is worth noting the presence of two horns with percussion marks (Table 4). The measurements of the tooth marks are detailed in Supplementary Table A.5. In addition to pits and scores, remains with digestion (NSP = 34), pitting (NSP = 30), crenulated edges (NSP = 18), furrowing (NSP = 4), and diaphyseal cylinder (NSP = 1) have been documented.

In 9 remains cut marks and tooth marks overlaps have been found, always in long bones, especially medium size (NSP = 6) and small size (NSP = 3). Only two of them could be identified, a tibia of small size and a metopodial of Caprinae. All but one of the superpositions are Human-Carnivore. It should be noted that 4 of them show percussion marks.

A total of 348 (%NISP = 5.49) burned remains were documented. The dimensions of these remains are 74.43% smaller than 25 mm. At the taxonomic level, only 10 remains were identified: *Bison priscus* (NISP = 1), *Capra pyrenaica* (NISP = 3), *Rupicapra pyrenaica* (NISP = 1), *Cervus elaphus* (NISP = 4), and *Ursus spelaeus* (NISP = 1). They have been identified in all body sizes, large size (NISP = 14), medium size (NISP = 83), M-LS (NISP = 2), small size (NISP = 191), small–medium size (NISP = 7), very large size (NISP = 2), and very small size (NISP = 1). Most of the burned remains are unidentified long bones (NISP = 297). Burned elements of the axial and appendicular skeleton were identified, most notably the humeri (NISP = 4), metacarpals (NISP = 4), ribs (NISP = 4), and metatarsals (NISP = 3). According to the portion of the bone, 72.13% belonged to the diaphysis, 12.93% to the metaphysis, and 1.72% to the epiphysis. Regarding the degree of cremation, most of them show grade 2 (NISP = 231) and grade 3 (NISP = 274), followed by grade 4 (NISP = 108). It should be noted that 25 remains show percussion marks, 19 cut marks, and 40 tooth marks.

Other postdepositional alterations have been documented, most notably manganese oxide (%NISP = 79.58), fissures (%NISP = 64.40), polishing (%NISP = 61.22%), rounding (%NISP = 58.98), trampling (%NISP = 48.29), and vermiculations (%NISP = 42.39) (Supplementary Table A.6).

## Dental mesowear and microwear

A total of 112 teeth were molded and cast. For the mesowear, 47 teeth (i.e., 42%) were discarded due to taphonomic issues (mainly broken cusps). The preservation of the microwear pattern on the ungulate teeth at Prado Vargas is better than that of mesowear. After screening, 23 teeth were discarded (i.e., 20.5%) due to taphonomic damages (weathering, erosion, etc.). The final sample is made of 65 teeth for mesowear and 89 for microwear.

*Cervus elaphus*, with a mesowear score of 1.52, overlaps with values reported for the extant leaf browsers and mixed feeders (Table 5; Fig. 9). The microwear pattern is characterized by an intermediate number of pits and scratches, a high proportion of individuals with large pits and gouges, a mixture of fine and coarse scratches, and the absence of cross scratches (Table 5). Compared with extant ungulates with known diets, it fits with the range of the leaf browsers (Fig. 10).

*Capra pyrenaica* has the lowest mesowear score among all the ungulates analyzed (Table 5). The mesowear score (MWS) indicates a diet with low abrasiveness. The mesowear score fits with values of the extant leaf browsers and mixed feeders (Fig. 9). The microwear pattern shows a low number of scratches and the highest number of pits

**Table 2** Spearman's correlation coefficients and p-values between %MAU and utility indexes (Emerson 1993; Metcalfe and Jones 1988; Morin 2007)

| | | B. primigenius | B. priscus | Bos/Bison | Equus ferus | C. elaphus | C. pyrenaica | R. pyrenaica | Sus scrofa | LS | MS | SS | VLS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SFUI | Correlation coefficient | −0.373 | 0.275 | 0.239 | 0.244 | 0.025 | 0.007 | −0.373 | −0.017 | 0.165 | 0.091 | 0.028 | 0.259 |
| | p-value | 0.233 | 0.386 | 0.454 | 0.445 | 0.940 | 0.982 | 0.233 | 0.959 | 0.609 | 0.779 | 0.931 | 0.416 |
| UMI | Correlation coefficient | 0.020 | 0.356 | 0.777* | 0.842* | 0.643 | 0.394 | 0.020 | −0.299 | 0.775* | 0.679 | 0.393 | 0.316 |
| | p-value | 0.966 | 0.434 | 0.040 | 0.017 | 0.119 | 0.382 | 0.966 | 0.515 | 0.041 | 0.094 | 0.383 | 0.490 |
| (S)AVGFUI | Correlation coefficient | −0.612* | 0.275 | 0.275 | 0.102 | −0.249 | −0.108 | −0.612* | 0.192 | 0.032 | −0.210 | −0.063 | 0.259 |
| | p-value | 0.034 | 0.386 | 0.386 | 0.752 | 0.436 | 0.739 | 0.034 | 0.550 | 0.922 | 0.513 | 0.846 | 0.416 |
| (S)MAVGTF | Correlation coefficient | −0.447 | 0.110 | −0.020 | −0.165 | −0.418 | −0.268 | −0.447 | 0.167 | −0.214 | −0.364 | −0.287 | 0.097 |
| | p-value | 0.145 | 0.733 | 0.951 | 0.607 | 0.177 | 0.400 | 0.145 | 0.604 | 0.503 | 0.244 | 0.365 | 0.763 |
| (S)MVGMARa | Correlation coefficient | 0.172 | 0.816** | 0.683* | 0.547 | 0.695* | 0.715** | 0.172 | 0.231 | 0.862** | 0.732** | 0.711** | 0.587* |
| | p-value | 0.594 | 0.001 | 0.014 | 0.066 | 0.012 | 0.009 | 0.594 | 0.470 | 0.000 | 0.007 | 0.009 | 0.045 |
| (S)MVGMARb | Correlation coefficient | 0.172 | 0.848** | 0.683* | 0.547 | 0.772** | 0.762** | 0.172 | 0.231 | 0.816** | 0.789** | 0.789** | 0.587* |
| | p-value | 0.594 | 0.000 | 0.014 | 0.066 | 0.003 | 0.004 | 0.594 | 0.470 | 0.001 | 0.002 | 0.002 | 0.045 |

(Table 5). It also records a high percentage of individuals with large pits and gouges and a texture dominated by relatively large scratches. In comparison with extant ungulates, it corresponds to a browsing diet (Fig. 10).

*Rupicapra pyrenaica* shows a mesowear score very similar to that of the red deer (Table 5; Fig. 9) indicating a diet corresponding to the extant leaf browsers and mixed feeders. Microwear patterns are also similar to that of *Cervus elaphus* indicating a leaf browsing diet at the time of death (Fig. 10).

*Equus ferus* is represented by a low sample size; however, some trends can be highlighted. The mesowear score is the highest among the four taxa studied here, but it reflects an intermediate level of abrasion (Table 5). It overlaps with extant grazers and grass-dominated mixed feeders (Fig. 9). The microwear pattern, observed on a slightly higher number of individuals, shows an intermediate number of scratches, a low number of pits, absence of large pits, and low percentage of individuals with large pits (Table 5). On the bivariate plot (Fig. 2), the sample falls in between the confidence ellipses for the extant leaf browsers and grazers, i.e., they would below to the mixed feeders.

When the NMIs (Table 5) are considered, the assemblage comprises 41 individuals belonging to the leaf browsers or browse-dominated leaf browsers (*C. elaphus*, *C. pyrenaica*, and *R. pyrenaica*) and 5 to the grazers (*E. ferus*). The ungulates analyzed through dental wear are dominated at 89.1% by the leaf browsers or browse-dominated leaf browsers and only 10.9% were grazers.

The CV and SD values computed on the numbers of scratches for each sample show different patterns. Two samples, *Equus ferus* and *Rupicapra pyrenaica*, have very low values (Table 1) that fall in zone A of the heat map (Fig. 11). These low values indicate that all the individuals died at a single season. *Cervus elaphus* and *Capra pyrenaica* have higher values (Table 1) that would indicate a longer duration for the accumulation of these animals in the cave. *Cervus elaphus*, however, falls on the boundary between zones B and C where the probability of error is too high. For *Capra pyrenaica*, the high values indicate the animals died and were brought back to the cave during a period that lasted longer than a single season (Fig. 11).

## Discussion

In level 4 of Prado Vargas, we observed a certain diversity of represented taxa, documenting remains of all body sizes, which indicates a varied meat diet centered on ungulates. We observed a predilection for *Cervus elaphus*, as this was the most represented taxon. However, the presence of a greater number of small size remains leads us to believe that taxa such as *Capra pyrenaica* were also highly consumed. This

**Fig. 6** Values of *E* at 95% CI for the main identified species and sizes and the different transport strategies (Faith and Gordon 2007)
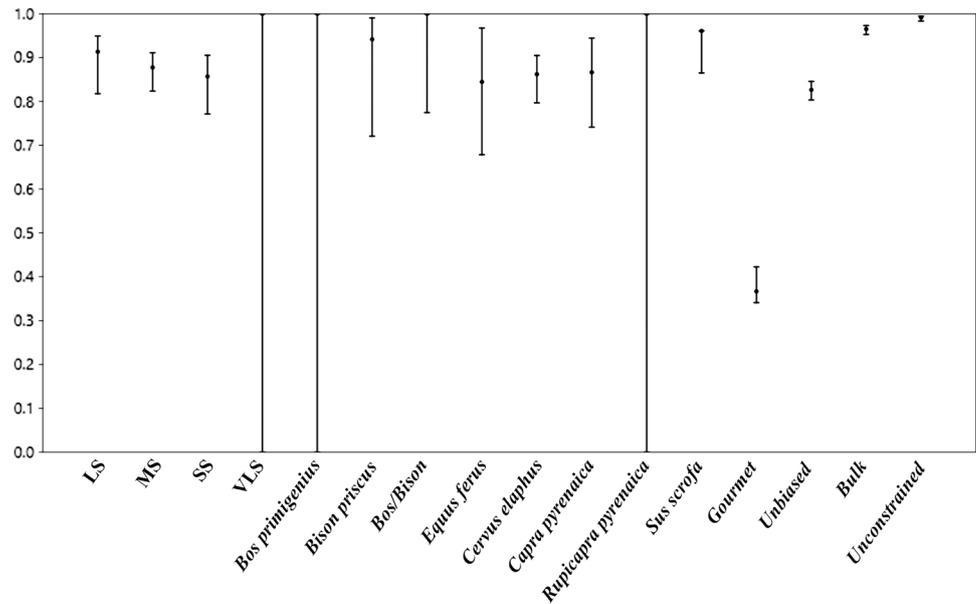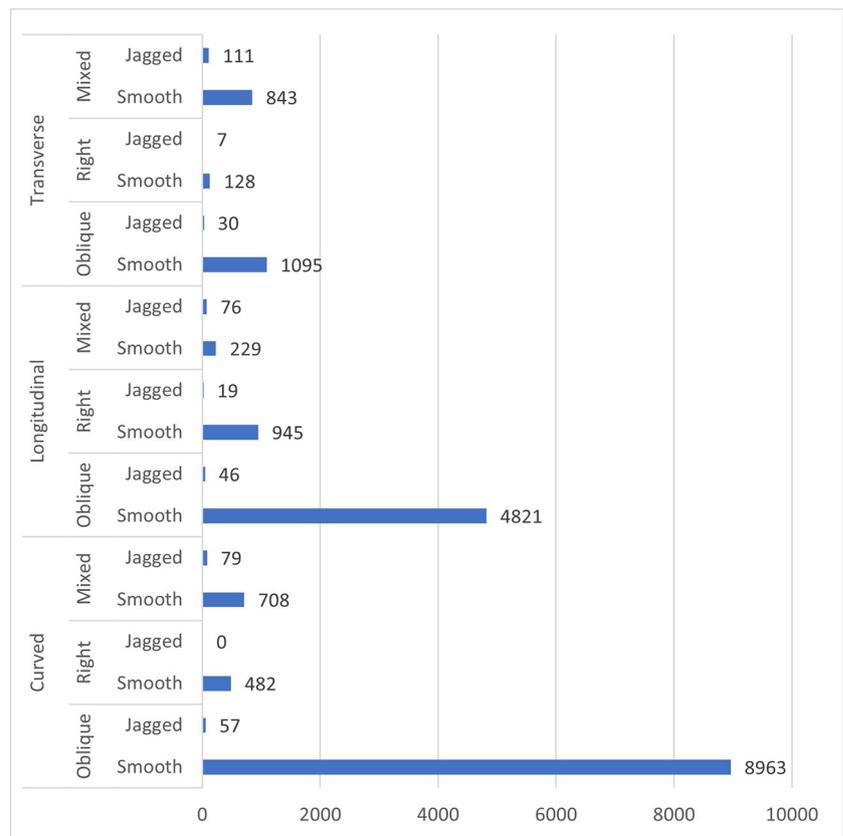


**Fig. 7** Summary of the characteristics of the different breakage planes according to the criteria of Villa and Mahieu (1991)



is consistent with what has been observed in the Cantabrian range in similar chronologies, where the main ungulates exploited are *Cervus elaphus* (Altuna 1971; Castaños 2005; Fuentes Vidarte 1980; Luret et al. 2020; Pike-Tay et al. 1999) and caprines (Baldeón, 1993; Castaños 2005; Urquijo et al. 2005). The comparison of meso- and micro dental wear of these ungulates at the time of their deaths indicates a diet based on plants with low abrasion (low phytolith concentration). In total, 90% of the individuals hunted and transported into the cave were leaf browsers (*Capra pyrenaica*, *Cervus elaphus*, and *Rupicapra pyrenaica*), i.e., they fed on herbaceous plants and leaves of shrubs or trees. This indicates an

**Table 3** Distribution of notches according to anatomical element of the main species and sizes

|  |  | Anterior | Posterior | Interior | Exterior | Lateral |
|---|---|---|---|---|---|---|
| *Bison priscus* | Femur | 1 | 1 | 0 | 1 | 0 |
|  | Radius | 0 | 0 | 1 | 1 | 0 |
|  | Tibia | 0 | 0 | 1 | 0 | 0 |
| Bos/Bison | Radius | 0 | 0 | 1 | 0 | 0 |
|  | Metatarsal | 1 | 1 | 0 | 0 | 0 |
| *Equus ferus* | Tibia | 0 | 2 | 0 | 1 | 0 |
|  | Humerus | 0 | 1 | 0 | 0 | 0 |
|  | Radius | 0 | 0 | 0 | 1 | 0 |
| *Cervus elaphus* | Femur | 0 | 5 | 2 | 2 | 0 |
|  | Tibia | 3 | 7 | 1 | 5 | 0 |
|  | Metatarsal | 19 | 2 | 13 | 1 | 8 |
|  | Humerus | 9 | 4 | 2 | 9 | 0 |
|  | Radius | 4 | 3 | 1 | 0 | 0 |
|  | Metacarpal | 12 | 0 | 4 | 3 | 6 |
| *Capra pyrenaica* | Femur | 0 | 1 | 1 | 1 | 0 |
|  | Tibia | 0 | 0 | 2 | 0 | 0 |
|  | Metatarsal | 0 | 2 | 1 | 0 | 0 |
|  | Radius | 1 | 2 | 0 | 0 | 0 |
| *Rupicapra pyrenaica* | Radius | 1 | 0 | 0 | 0 | 0 |
|  | Metacarpal | 1 | 0 | 0 | 0 | 0 |
| *Sus scrofa* | Femur | 0 | 1 | 0 | 1 | 0 |
|  | Humerus | 1 | 0 | 0 | 0 | 0 |
| Humerus | LS | 3 | 4 | 3 | 3 | 3 |
|  | MS | 13 | 8 | 6 | 13 | 4 |
|  | SS | 4 | 3 | 3 | 3 | 3 |
|  | Total | 20 | 15 | 12 | 19 | 10 |
| Radius | LS | 0 | 0 | 2 | 2 | 0 |
|  | MS | 7 | 6 | 4 | 3 | 3 |
|  | SS | 6 | 6 | 4 | 4 | 4 |
|  | Total | 13 | 12 | 10 | 9 | 7 |
| Metacarpal | LS | 0 | 0 | 0 | 0 | 0 |
|  | MS | 14 | 2 | 6 | 5 | 8 |
|  | SS | 3 | 2 | 2 | 2 | 2 |
|  | Total | 17 | 4 | 8 | 7 | 10 |
| Femur | LS | 2 | 2 | 1 | 2 | 1 |
|  | MS | 3 | 8 | 5 | 5 | 3 |
|  | SS | 3 | 5 | 4 | 5 | 3 |
|  | Total | 8 | 15 | 10 | 12 | 7 |
| Tibia | LS | 3 | 5 | 4 | 4 | 3 |
|  | MS | 7 | 11 | 5 | 9 | 4 |
|  | SS | 0 | 0 | 2 | 0 | 0 |
|  | Total | 10 | 16 | 11 | 13 | 7 |
| Metatarsal | LS | 1 | 1 | 0 | 0 | 0 |
|  | MS | 20 | 3 | 14 | 2 | 9 |
|  | SS | 0 | 2 | 1 | 0 | 0 |
|  | Total | 21 | 6 | 15 | 2 | 9 |

exploitation of forest environments by Neanderthal groups. According to pollen and microfauna data (Navazo et al. 2021), the surrounding of the site was covered with sparse forested areas with pine, birch and juniper, and large open meadows. This would suggest a preference by Neanderthals

**Fig. 8** Taphonomic alterations documented in Level 4 of Prado Vargas. **a** Cut marks in the first phalanx of *Capra pyrenaica*; **b** cut marks in *Cervus elaphus* maxilla; **c** cut marks in femur of small size; **d** cut marks in *Cervus elaphus* metatarsal; **e** percussion notch in *Cervus elaphus* metatarsal; **f** percussion notch in large-size femur; **g** diaphyseal cylinder generated in small-size radius
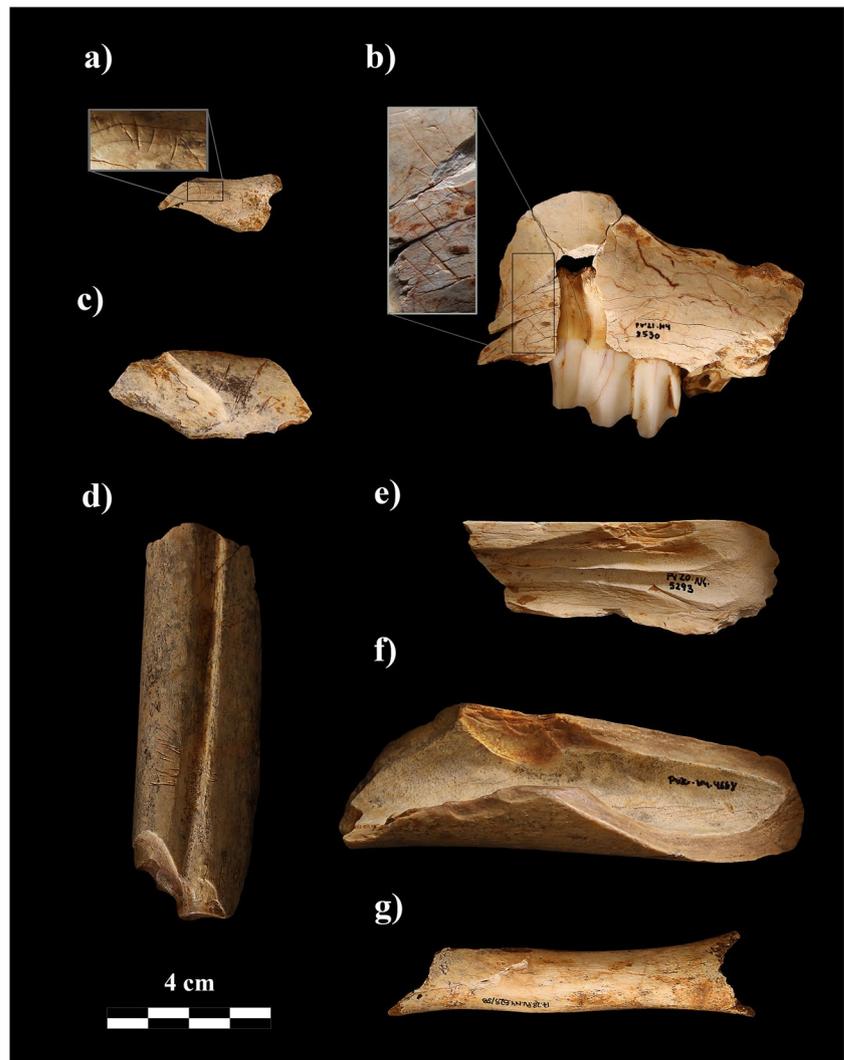


for hunting in the more forested areas rather than in open habitats.

Mortality patterns of the main taxa identified indicate a selection of adult or juvenile-adult individuals. This prime-dominated mortality profile is linked to the hunting practices of hominids, a practice observed in several European sites (e.g., Castel et al. 2017; Niven et al. 2012; Rendu et al. 2012; Romandini et al. 2014; Starkovich 2017) as well as peninsular sites (e.g., Marín et al. 2019; Moclán et al. 2021; Ríos Garaizar et al. 2020; Salazar-García et al. 2013; Sánchez-Romero et al. 2020). According to the ethology of certain species, we can estimate the time of year in which they died through the study of dental eruption. The remains of *Ursus spelaeus* suggest they died between January and April; *Sus scrofa* between September and December; *Capra pyrenaica* between June and October; and *Rupicapra pyrenaica* between January and June. The bears seem to have encountered death during hibernation, since they show no anthropogenic or carnivore evidence of predation or transport.

But the other taxa do, so their predation could have taken place throughout the year, from January to December. However, only in certain months they are available at once, this being the months between June and October. This suggests an occupation of the cave by hominids between spring and autumn.

The uneven presence of anatomical elements may be due to carcass transport decisions or postdepositional processes. The presence of isolated teeth and other taphonomic processes can tell us about the differential destruction of elements of lower skeletal survival. The correlation with density indices indicates that there is differential preservation in *Cervus elaphus* and medium size, which cannot be ruled out in *Capra pyrenaica* and small size. Large size, however, does not seem to show it. The significant amounts of polishing and rounding in the cortical and medular sides of remains suggest the presence of water currents. However, there are anatomical elements that should be transported immediately (Behrensmeyer 1975; Voorhies 1969).

**Table 4** Number of specimens of BSM in the main species and sizes according to anatomical element

| Element | | B. priscus | Bos/Bison | Equus ferus | C. elaphus | C. pyrenaica | R. pyrenaica | Caprinae | Sus scrofa | Vulpes vulpes | LS | MS | SS | VLS | VSS | Indet |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Horn/antler | CM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | PM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Cranium | CM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | TM | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - | - |
| | PM | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - |
| Mandible | CM | - | - | - | 2 | - | 1 | - | - | - | 2 | 1 | 2 | - | - | - |
| | TM | - | - | - | 1 | - | - | 1 | - | 1 | - | - | - | - | - | - |
| | PM | - | - | - | - | - | - | - | - | - | 1 | - | 1 | - | - | - |
| Vertebra | CM | - | - | - | - | - | - | - | - | - | 1 | 1 | 3 | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 | - | - | - |
| | PM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Ribs | CM | - | - | - | - | - | - | - | - | - | 1 | 2 | - | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | - | - | 5 | - | 1 | - |
| | PM | - | - | - | - | - | - | - | - | - | 1 | 1 | 3 | - | - | - |
| Pelvis | CM | - | - | - | 2 | - | - | - | - | - | 1 | 1 | 3 | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | - | 1 | 3 | - | - | - |
| | PM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Scapula | CM | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - |
| | PM | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - |
| Humerus | CM | - | - | 1 | 11 | - | - | - | - | - | 7 | 16 | 10 | - | - | - |
| | TM | - | - | - | 2 | - | - | - | - | - | 1 | 5 | 2 | - | - | - |
| | PM | - | - | 1 | 24 | 1 | - | - | 1 | - | 12 | 23 | 20 | - | - | - |
| Radius | CM | 1 | - | 2 | 7 | 4 | - | - | - | - | 5 | 7 | 13 | - | - | - |
| | TM | - | - | - | 3 | 2 | - | - | - | - | 3 | - | 12 | - | - | - |
| | PM | 1 | 1 | 1 | 8 | 3 | 1 | - | - | - | 4 | 15 | 13 | - | - | - |
| Ulna | CM | - | - | - | 2 | - | - | - | - | - | 1 | 2 | 1 | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - |
| | PM | - | - | - | - | - | 1 | - | - | - | 1 | - | - | - | - | - |
| Femur | CM | - | - | 1 | 5 | 3 | - | - | - | - | 1 | 14 | 6 | - | - | - |
| | TM | - | - | - | 2 | - | - | - | - | - | 1 | 2 | 4 | - | - | - |
| | PM | 4 | 1 | - | 9 | 2 | - | - | 1 | - | 5 | 8 | 11 | - | - | - |

**Table 4** (continued)

| | | B. priscus | Bos/Bison | Equus ferus | C. elaphus | C. pyrenaica | R. pyrenaica | Caprinae | Sus scrofa | Vulpes vulpes | LS | MS | SS | VLS | VSS | Indet |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tibia | CM | 1 | 2 | - | 13 | - | - | - | - | - | 6 | 17 | 7 | - | - | - |
| | TM | - | - | - | 3 | 1 | - | - | - | - | 1 | 7 | 3 | - | - | - |
| | PM | 1 | - | 3 | 18 | 2 | - | 1 | - | - | 7 | 19 | 6 | - | - | - |
| Metacarpal | CM | - | - | - | 18 | - | - | - | - | - | 1 | 1 | 3 | - | - | - |
| | TM | - | - | - | - | 1 | - | - | - | - | - | - | 1 | - | - | - |
| | PM | - | - | - | 24 | - | - | - | - | - | - | 3 | 3 | - | - | - |
| Metatarsal | CM | - | 2 | - | 33 | - | 2 | - | - | - | 3 | 2 | - | - | - | - |
| | TM | - | - | - | 7 | - | 1 | - | - | - | - | - | - | - | - | - |
| | PM | - | 2 | - | 44 | 2 | 1 | - | - | - | 1 | 4 | - | - | - | - |
| Metapodials | CM | - | - | - | 1 | 1 | 1 | - | - | - | - | - | 3 | - | - | - |
| | TM | - | - | - | 1 | - | - | 1 | - | - | - | 1 | 2 | - | - | - |
| | PM | - | - | - | 3 | - | - | - | - | - | 1 | 3 | 3 | - | - | 1 |
| 1ª phalanx | CM | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - |
| | TM | - | - | - | 2 | - | - | 1 | - | - | - | - | - | - | - | - |
| | PM | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - |
| 2ª phalanx | CM | - | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | PM | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - |
| 3ª phalanx | CM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | TM | - | - | - | 1 | 1 | - | - | - | - | - | - | - | - | - | - |
| | PM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Long bones | CM | - | - | - | - | - | - | - | - | - | 30 | 105 | 171 | 5 | - | 8 |
| | TM | - | - | - | - | - | - | - | - | - | 14 | 49 | 71 | - | 1 | 2 |
| | PM | - | - | - | - | - | - | - | - | - | 74 | 231 | 310 | 8 | - | 76 |
| Flat bones | CM | - | - | - | - | - | - | - | - | - | - | 1 | 5 | - | - | 4 |
| | TM | - | - | - | - | - | - | - | - | - | 1 | 1 | - | - | - | 2 |
| | PM | - | - | - | - | - | - | - | - | - | - | 2 | 2 | - | - | 1 |
| Indet | CM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | TM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 10 |
| | PM | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

**Table 5** Summary of the microwear data for the ungulates from level 4 of Prado Vargas

| | Mesowear | | Microwear | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *N* | MWS | *N* | Npit | Nscr | SDscr | CVsrc | %LP | %G | SWS | %XS |
| *E. ferus* | 3 | 3.33 | 5 | 12.92 | 17.42 | 0.80 | 0.05 | 0 | 16.7 | 1.2 | 0 |
| *C. elaphus* | 31 | 1.52 | 35 | 22.01 | 14.30 | 4.77 | 0.33 | 88.6 | 65.7 | 1.6 | 0 |
| *C. pyrenaica* | 26 | 1.27 | 40 | 36.25 | 13.09 | 3.16 | 0.24 | 97.5 | 75.0 | 1.4 | 0 |
| *R. pyrenaica* | 5 | 1.60 | 8 | 24.94 | 16.00 | 0.76 | 0.05 | 100 | 87.5 | 1.3 | 0 |

*N*, number of specimens; *M*, mean; *SD*, standard deviation (for $N \geq 4$); *CV*, coefficient of variation; *MWS*, mesowear score; *Npit*, average number of pits; *Nscr*, average number of scratches; *SDscr*, standard deviation of the number of scratches; *CVscr*, coefficient of variation of the number of scratches; *%LP*, percentage of individuals with large pits; *%G*, percentage of individuals with gouges; *SWS*, scratch width score; *%XS*, percentage of individuals with cross scratches

**Fig. 9** Mesowear scores (MWS) for the ungulates from the level 4 of Prado Vargas compared with the dietary categories in extant ungulates (i.e., leaf browsers, mixed feeders, and grazers). Error bars correspond to the standard error of the mean (± 1 SEM) for each sample
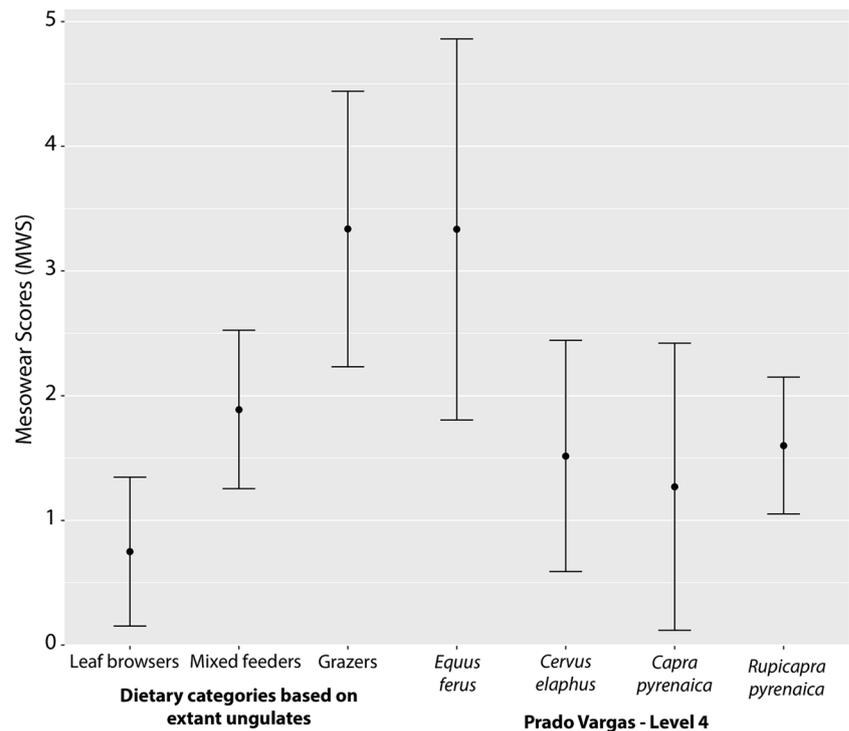


Regarding food utility indices, we only observed that *Bos primigenius* and *Rupicapra pyrenaica* are exploited according to their general utility. However, all body sizes and the main species identified (*Bison priscus*, Bos/Bison, *Cervus elaphus*, *Equus ferus*, and *Capra pyrenaica*) show a correlation with the medular fat indices. The Equitability_J function indicates that our samples correspond to unbiased and bulk transport strategies, related to the selective transport of the most economically useful and the maximization of all but the least useful elements. Thus, differential conservation seems to be due to the economic interest of the carcasses, with a systematic selection of the parts with high nutritional value.

Although the first stages of the processing sequence are carried out at the place where the prey is obtained, the carcasses are intensively exploited at the site under study. Most of the cut marks are located in the long bones of all the sizes and main documented species, showing evidence of disarticulation and exploitation of the large muscle bundles. The presence of cut marks in jawbones of *Cervus elaphus*, *Rupicapra pyrenaica*, large size, medium size, and small size is evidence of the consumption of the muscular bundles of the masticatory apparatus. Skinning is documented in Bos/Bison, *Cervus elaphus*, *Capra pyrenaica*, *Rupicapra pyrenaica*, large size, medium size, medium size, and small size, with cut marks observed in the metapodials and first phalanges. In the case of metapodials, the cut marks identified also indicate the removal of the tendons of the anterior and posterior sides. The presence of scrapings in the long bones is also evidence of the removal of the periosteum to facilitate breakage, as observed by Binford (1981), Blasco et al. (2014), Marean and Assefa (1999), or Vettese et al.

**Fig. 10** Bivariate plot of the average numbers of pits and scratches for the ungulates from the level 4 of Prado Vargas. Error bars correspond to standard error of the mean (± 1 SEM) for each sample. Plain ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers (LB) and grazers (G) based on the reference database from Solounias and Semprebon (2002)
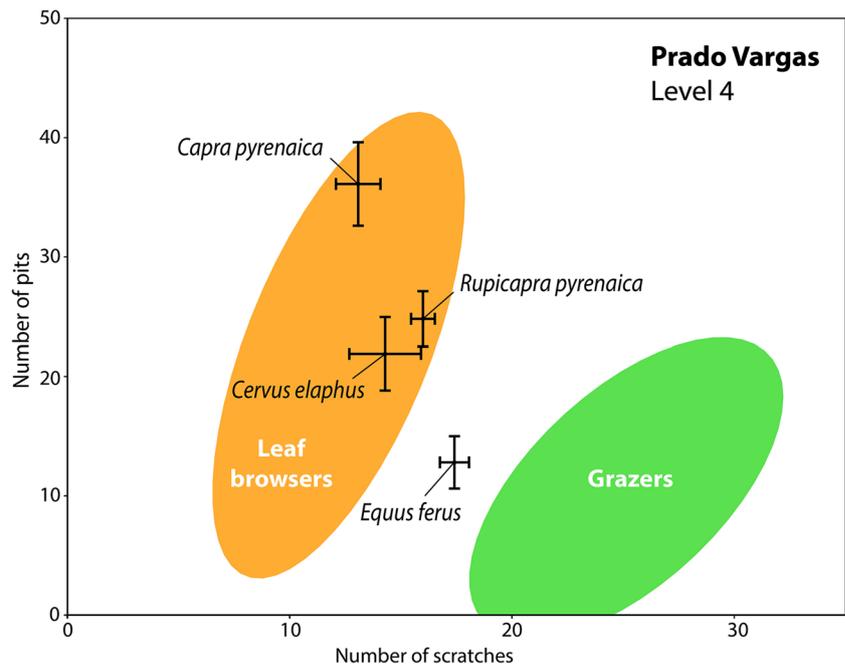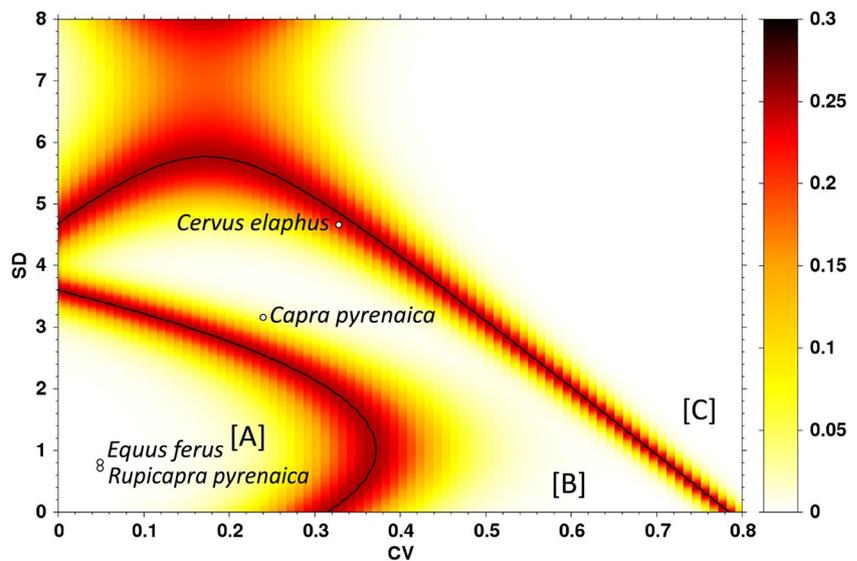


**Fig. 11** Boundary lines with an error probability (heat map) based on standard deviations (SD) and coefficient of variation (CV) values of microwear data used for the classification of Prado Vargas samples into short events (region A), long-term events (region B), or two separate short events (region C)



(2020). We observed the presence of evisceration and dismemberment in almost all sizes and in *Cervus elaphus*. This indicates that, although evisceration may be carried out inside or outside the site, on certain occasions the prey are transported in their entirety to be to be processed in the site. Although cut marks are accidents and there are certain activities that lead to their underrepresentation, we did not observe any specialization in any particular activity.

The high fragmentation of our assemblage is a typical feature of anthropogenic exploitation, since it is the result of the exploitation of bone marrow, as noted by Stiner (1994), Vettese et al. (2020), and Villa and Mahieu (1991).

The breakage of the bone in its fresh state and the presence of percussion marks show that hominids consumed this resource once the muscle bundles were consumed. All body sizes and the main species identified show this consumption in elements of the axial and appendicular skeleton. Some authors have tried to discern certain patterns in the breakage (e.g., Blasco et al. 2013; Vettese et al. 2017); however, we were not able to identify any pattern.

The identified tooth marks have been measured and compared with reported in the literature (Andrés et al. 2012; Arilla et al. 2014, 2020; Domínguez-Rodrigo and Piqueras 2003; Saladié et al. 2013; Young et al. 2015), so

**Table 6** Means and *p*-values obtained from the Student *T*-test (Andrés et al. 2012; Arilla et al. 2014, 2020; Domínguez-Rodrigo and Piqueras 2003; Saladié et al. 2013; Young et al. 2015)

| | Pits cancellous | | Pits diaphysis | | Scores cancellous breadth | | Scores cancellous length | | Scores diaphysis breadth | | Scores diaphysis length | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | P-value | Mean | P-value | Mean | P-value | Mean | P-value | Mean | P-value | Mean | P-value |
| Hyena | 2.9000 | <0.001 | 1.5500 | <0.001 | - | - | - | - | - | - | - | - |
| Hyena | 1.6400 | <0.001 | 1.1900 | 0.2689 | 0.6600 | <0.001 | 3.6000 | <0.001 | 0.6000 | <0.001 | 3.0000 | <0.001 |
| Wolf | 2.7000 | <0.001 | 1.8000 | <0.001 | 2.9200 | <0.001 | 10.7600 | <0.001 | 1.6800 | 0.6348 | 8.6200 | <0.001 |
| Fox | 1.8800 | <0.001 | 0.9900 | <0.001 | 0.6500 | <0.001 | 3.7100 | <0.001 | 0.4200 | <0.001 | 3.6400 | <0.001 |
| Maasai | 0.9100 | 0.0005 | 0.7600 | <0.001 | 0.4600 | <0.001 | 2.3400 | <0.001 | 0.5600 | <0.001 | 1.9100 | <0.001 |
| Dog | 1.9000 | <0.001 | 1.3600 | 0.1150 | 0.8100 | 0.0002 | 5.9500 | <0.001 | 0.6600 | <0.001 | 5.0600 | <0.001 |
| Lion | 4.0500 | <0.001 | 1.7000 | <0.001 | 2.7000 | 0.0163 | 10.6800 | <0.001 | 0.9600 | <0.001 | 9.3200 | <0.001 |
| Hyenas | 5.3200 | <0.001 | 2.2400 | <0.001 | 4.5900 | <0.001 | 13.4000 | <0.001 | 1.2900 | <0.001 | 7.3400 | <0.001 |
| Bears | 3.7300 | <0.001 | 1.8800 | <0.001 | 2.1900 | <0.001 | 10.6400 | <0.001 | 1.6500 | 0.4070 | 10.9200 | <0.001 |
| Dogs | 3.3400 | <0.001 | 2.3800 | <0.001 | 1.7700 | 0.2777 | 12.8000 | <0.001 | 1.5000 | 0.0115 | 12.8000 | <0.001 |
| Lions | 4.3200 | <0.001 | 2.2000 | <0.001 | 4.9500 | <0.001 | 23.7000 | <0.001 | 2.2000 | <0.001 | 8.4000 | <0.001 |
| Fox metaphysis | 1.1000 | 0.7520 | 0.9000 | <0.001 | 1.5500 | 0.6823 | - | - | 1.4000 | <0.001 | - | - |
| Fox epiphyses | 1.5000 | 0.0072 | - | - | 2.4000 | <0.001 | - | - | - | - | - | - |
| Badger (captive) | 2.0000 | <0.001 | 2.0000 | <0.001 | 0.9100 | <0.001 | 3.5700 | <0.001 | 0.9100 | <0.001 | 3.5700 | <0.001 |
| Fox | 0.9200 | 0.0890 | 0.9200 | 0.0001 | 0.9600 | <0.001 | 6.0300 | <0.001 | 0.9600 | <0.001 | 6.0300 | <0.001 |
| Human | - | - | - | - | - | - | - | - | 0.7400 | <0.001 | 0.7400 | <0.001 |
| Human total metaphysis | 1.5500 | 0.0025 | 1.2400 | 0.7517 | 0.4400 | <0.001 | 0.4400 | <0.001 | - | - | - | - |
| Human total epiphyses | 2.3400 | <0.001 | - | - | 1.7800 | 0.2491 | 1.7800 | <0.001 | - | - | - | - |
| Human raw metaphysis | 1.5700 | 0.0017 | 1.2800 | 0.7517 | - | - | - | - | - | - | - | - |
| Human raw epiphyses | 2.4900 | <0.001 | - | - | - | - | - | - | - | - | - | - |
| Human cooked metaphysis | 1.5300 | 0.0039 | 1.2100 | 0.4293 | - | - | - | - | - | - | - | - |
| Human cooked epiphyses | 2.2000 | <0.001 | - | - | - | - | - | - | - | - | - | - |
| Bear (large) metaphysis | 1.6254 | <0.001 | - | - | 0.2626 | <0.001 | - | - | - | - | - | - |
| Bear (large) epiphyses | 2.2921 | <0.001 | - | - | | | - | - | - | - | - | - |
| Bear (small) metaphysis | 2.8602 | <0.001 | - | - | 1.1900 | 0.0059 | - | - | - | - | - | - |
| Bear (small) epiphyses | 2.7638 | <0.001 | - | - | | | - | - | - | - | - | - |

as to discern the responsible agent (see Supplementary File 2). Since our sample coincides with a large number of carnivores and the total data are not available, the means of our values (see Supplementary Table A.7) were compared with those obtained in the literature by means of the Student *T*-test (Table 6). In this way, we seek to rule out those species for which there is statistically significant evidence that the means are different. We note that we cannot statistically rule out that in cancellous bone affect foxes, bears, dogs, and humans, and in diaphysis, foxes, hyenas, and humans. Thus, they could have altered some remains and made others disappear. The digested bones can be attributed to *Canis lupus*, since they measure less than 40 mm, although some of greater length could have been the result of the action of hyenas.

The presence of carnivore bones and their marks indicates their access to some remains. The presence of bears may be due to their death in hibernation or to predation, since they are mostly senile or sub-adult individuals. Hyenas and wolves may perform repeated predation on bears hibernating in a cave (Stiner, 1998), although they may also scavenge bear carcasses (Daschek and Mester 2020). Taphonomic analysis suggests that these bears died naturally during hibernation, since no carnivore or hominid action was observed in the recovered remains. The presence of trampling could be the result of bear movements during hibernation, as observed by Diedrich (2011) and Sauqué et al. (2015), although trampling could also be the result of the transit of the Neanderthals themselves. Bears and small carnivores such as *Vulpes vulpes* and *Meles meles* have been shown to be potential set modifiers (Arilla et al. 2014, 2020), like wolves and hyenas (Binford 1978, 1981). Of the latter two, remains of mainly adult and subadult individuals of *Canis lupus* have been found. Their ability to accumulate remains in caves is limited and circumstantial (Sanchís et al. 2019), although the scarce presence of digested bones and remains of subadult individuals may indicate a more intense use of the cave as breeding dens. The existence of

**Fig. 12** Analysis of correspondences between the color and position data according to their degree of cremation and location of Pérez et al. (2017a, b) and representation in the biplot of our sample (PV)
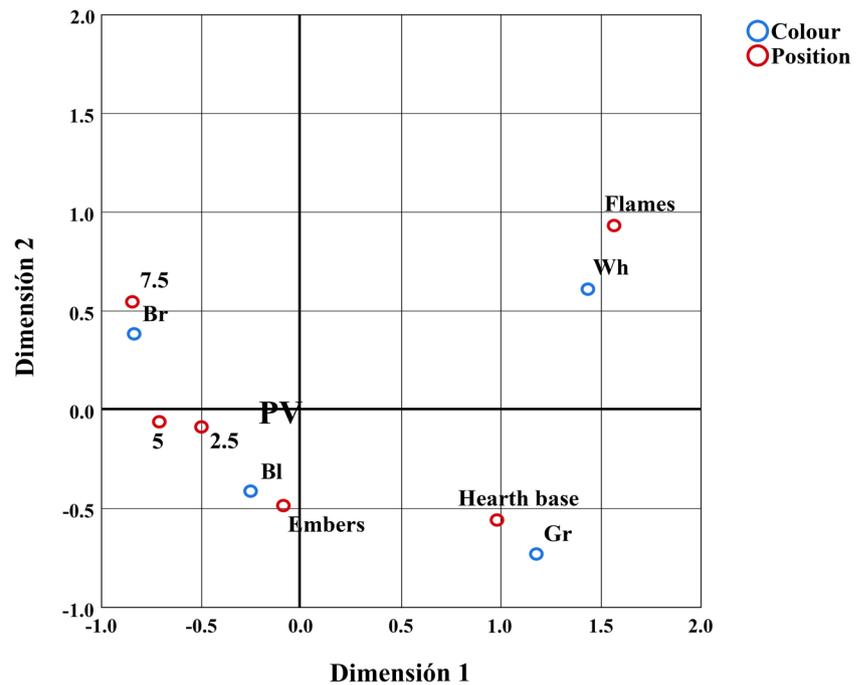


manganese and concretion indicates the presence of humid conditions in the cave (Fernández-Jalvo 1992; Fernández-Jalvo and Andrews 2000), which would make it more habitable at certain times of the year for cave carnivores than hominids following Sanchis et al. (2019). However, the low percentage of tooth marks would indicate that Prado Vargas would correspond more to a referential intervention center as defined by Carbonell and Rosell (2004).

However, the presence of cut marks-tooth marks overlaps indicates that carnivores are not the main accumulating agent, but that, in the case where they are responsible, they were able to access the remains left by hominids. Although some authors propose that if tooth marks affect the same species and body sizes, carnivore access to remains is rapid (Rusch et al. 2019), and access does not appear to be immediate, as some remains are incorporated into the technological sphere, being used as retouchers (Alonso-García et al. 2020).

The presence of burned bones is evidence of the use of fire by Neanderthals. The study of the relationship or association between the grades of cremation and their position indicates that some remains seemed to have been in contact with the embers. The absence of epiphyses and metaphyses, or spongy tissues in general, may be related to the hearths, and bone may have been used as fuel. In addition, other remains indicate that the burned remains could have acquired a brown and black coloration (grades 2 and 3) after having been buried between 2.5 cm and 5 cm beneath a hearth (Fig. 12). The reuse of hearths (Vallverdú et al. 2012) and the accumulation of burned remains or different combustion events are typical of long-term occupations. Thus,

there seems to be evidence of an intense and recurrent use of the cave by Neanderthals at different times.

Hominids are the main accumulating agent of level 4, although we must not lose sight of the fact that, like most archaeological sites, this is a palimpsest in which occupations (of Neanderthals and Neanderthals-carnivores) are superimposed with remains that may have undergone modifications in respect to their original positions. In order to see to which model of occupation level 4 would correspond, a linear discriminant analysis (LDA) was performed comparing the %MAU of *Bos primigenius*, *Bison priscus*, Bos/Bison, *Equus ferus*, *Cervus elaphus*, *Capra pyrenaica*, *Rupicapra pyrenaica*, large size, medium size, and small size, with levels and deposits catalogued as long term (Bignon et al. 2006; Blasco et al., 2016; Fernádez Laso et al. 2010; Marín et al. 2019; Romandini et al. 2014; Rosell et al. 2012a, b) or short term (Costamagno 2000; Fernádez Laso et al. 2010; Marín et al. 2019; Moclán et al. 2021; Real Margalef et al. 2019; Rosell et al. 2012a, b; Rosell et al. 2017) (Fig. 13). Once we have plotted the data and created the convex hulls, we observed that there is a very significant difference between long term and short term. Our sample does not coincide with either of the two, our sample does not coincide with either of the two, since the convex hulls do not intersect, but if correlated with either, it would do so with long term. However, the ambiguity of the terms makes its classification difficult. Dental microwear provides information on the duration of hunting events. *Capra pyrenaica* and perhaps *Cervus elaphus* were hunted during several seasons of the year, indicating either a long-term occupancy of the site or repeated occupations at different seasons during the
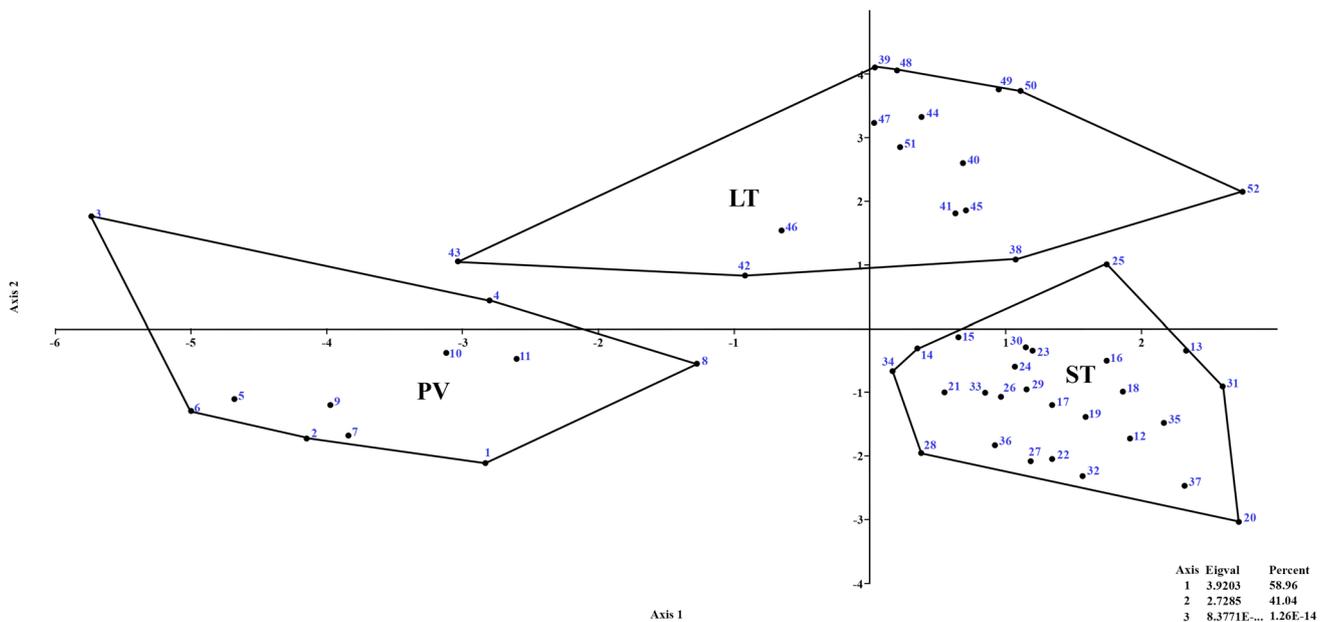
**Fig. 13** LDA between the %MAU of our sample (PV) and suggested sets such as LT and ST. (1) *Bos primiegnius*; (2) *Bison priscus*; (3) Bos/Bison; (4) *Equus ferus*; (5) *Cervus elaphus*; (6) *Capra pyrenaica*; (7) *Rupicapra pyrenaica*; (8) *Sus scrofa*; (9) LS; (10) MS; (11) SS; (12) *Equus ferus* Pa Abric Romaní; (13) *Equus ferus* Pb Abric Romaní; (14) Caprinae Abrigo de la Quebrada IV; (15) Cervidae Abrigo de la Quebrada IV; (16) Equidae Abrigo de la Quebrada; (17) IV *Saiga tatarica* Moulin-Neuf (Gironde); (18) *Rangifer tarandus* Moulin-Neuf (Gironde); (19) *Equus caballus* Moulin-Neuf (Gironde); (20) Bovinae Moulin-Neuf (Gironde); (21) Bovinae Navalmaillo; (22) *Equus ferus* Navalmaillo; (23) Cervidae Navalmaillo; (24) *Cervus elaphus* Navalmaillo; (25) VLS Navalmaillo; (26) LS Navalmaillo; (27) MS Navalmaillo; (28) SS Navalmaillo; (29) Equidae Ja Abric Romaní; (30) Equidae Jb Abric Romaní; (31) Equidae M Abric Romaní; (32) Equidae Teixoneres III; (33) Cervidae Teixoneres III; (34) Bovidae Teixoneres III; (35) LS Teixoneres III; (36) MS Teixoneres III; (37) SS Teixoneres III; (38) LS Quesem; (39) MS Quesem; (40) SS Quesem; (41) *Cervus elaphus* Pa Abric Romaní; (42) *Cervus elaphus* Pb Abric Romaní; (43) *Rangifer tarandus* Pincevent; (44) *Equus* Pincevent; (45) Bovidae M Abric Romaní; (46) Cervidae M Abric Romaní; (47) *Cervus elaphus* Grotta di Fumane A9; (48) *Capreolus capreolus* Grotta di Fumane A9; (49) Bovidae Ja Abric Romaní; (50) Cervidae Ja Abric Romaní; (51) Bovidae Jb Abric Romaní; (52) Cervidae Jb Abric Romaní

formation of level 4. Less represented species, such as *Equus ferus* and *Rupicapra pyrenaica*, were hunted during short and seasonal events. These results indicate that Neanderthal groups took advantage of specific resources when they were available in the environment.

These results would correspond with other diagnostics of long-term occupations. The high density of remains (Gabucio et al. 2014) is a diagnostic feature that we observed in level 4, where in a large area of 80 m² more than ten thousand archaeological remains have been recovered. The lithic industry is 90% local flint and complete operational chains have been recovered (Navazo et al. 2021), i.e., there is no evidence of the introduction of tools configured outside the site, something typical of short term. In addition, the traceological analysis indicates hide scraping, wood processing, and meat processing, so we see that the activities carried out at the site go beyond those carried out in short-term occupations. The presence of burnt flint, such as that found at Prado Vargas, is also a long-term feature (Rusch et al. 2019). Likewise, the presence of a left Ldm1 of Homo Neanderthalensis (Navazo et al. 2021) indicates the presence of children in the group,

something that would not necessarily be expected in short-term or hunting camps, as opposed to long-term or more residential camps.

Subsequent work will allow us to further clarify the functionality and seasonality of the site, by means of spatial analysis and refits, since the spatial relationship of the remains is fundamental to try to individualize events and more accurately identify the type of occupation.

## Conclusions

Several analytical methods and techniques were applied to the zooarchaeological assemblage of the level 4 of Prado Vargas: anatomical and taxonomical identification, taphonomic analysis, and tooth wear analysis. The zooarchaeological and taphonomic analysis of level 4 at Prado Vargas suggests that the site was used repeatedly by Neanderthal groups as a camp more akin to a long-term than a short-term camp, in which intensive use of animal resources was made. Also the microwear indicates either a long-term occupancy of the site or

repeated occupations at different seasons during the formation of level 4.

They hunted primarily adult animals and transported their carcasses according to their usefulness, although sometimes they transported them whole. There may have been hydraulic transport of some remains, but this does not appear to have affected the whole assemblage, and differential preservation is due to utility interest. Once at the site, they exploited all the food resources, from the muscle packs and marrow to other elements such as skin and tendons, incorporating the resulting remains into the technological sphere by using them as retouchers. The presence of burn remains is evidence of use of fire by Neandertals, who may have been using bones as fuel. The correlation between color and position of burn remains seems to evidence an intense and recurrent use of the cave.

Competition with carnivores was low; few remains are affected by their activity. Although some of them are digested, we cannot rule out that some of the tooth marks were produced by humans. The low percentage of tooth marks, assuming they are all produced by non-human carnivores, and the presence of cut marks-tooth marks overlaps would indicate that these would have affected the assemblage when the hominins were not in the cave, accessing their remains at times when the cave was less habitable.

All the results shown here (zooarchaeological, taphonomic, and dental wear) and the conclusions we draw from them make Prado Vargas Cave a key site for understanding the dynamics of these penultimate Neanderthals, who were found in a place of transition between the Cantabrian region and the interior of the Iberian Peninsula.

## Declarations

## References

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