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# Neanderthal subsistence strategies at the Mediterranean Basin: Zooarchaeological and taphonomical study of Abric romaní, Abri du Maras and Bize-Tournal

Juan Marín

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**Juan Marín Hernando**

Le 29/07/20

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**Neanderthal subsistence strategies at the Mediterranean Basin:  
Zooarchaeological and taphonomic study of Abri Romaní, Abri du  
Maras and Bize-Tournal**

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**Doctoral Thesis**

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# Abstract

Neanderthals have been a hominin species broadly studied, that occupied and exploited a great part of the Eurasian continent, scattered during more than 300,000 years. The faunal assemblages are an essential source of information of Neanderthal life and zooarchaeological studies are a fundamental tool to interpret their behaviour. The discipline has evolved from a reductionist perspective of Neanderthal subsistence skills to the current vision in which two subsistence aspects traditionally associated with the Upper Palaeolithic and the appearance of anatomically modern humans have been broadly observed, the presence of a broad-spectrum diet and the communal mass hunting of large ungulates. This indicated that Neandertals were more complex than thought at the beginning of the discipline. However, the distribution of these behaviours on the archaeological record is not homogeneous, and these specific subsistence activities depend mainly on their regional distribution. The zooarchaeological studies emphasize the importance of meat in Neanderthal subsistence, through the effective hunting of a wide range of animals, which include from the megafauna to the small prey. However, in many archaeological sites the subsistence has been related to the exploitation of medium and large ungulates, and within them, preference over one or two species.

This doctoral dissertation has as a case of study the faunal assemblages from the level P of Abri Romaní, the level 5 of Abri du Maras and the horse assemblage of Units I, II and III in the Bize-Tournal cave. The initial objectives are establishing the origin of the accumulation, define the role of Neanderthal in their formation and establish the importance of other agents. Together with the reconstruction of mortality and anatomical profile, we will develop the study of hunting strategies, the identification of animal carcasses transport strategies. Throughout the classification of the occupation events and the function of the site, establishing the mobility strategy. Here we show that Neanderthal behaviour is characterized by variability in prey choice, element transport and in the settlement pattern. The mobility variation change in the function of the region and the chronology. Not all the archaeological sites studies in this work have permitted us to respond to the same question or study the same aspects of Neanderthal culture, it depended mainly on the archaeostratigraphic resolution.

In many Mousterian sites, the most common anatomical profile is characterized by a scarce of postcranial axial elements and compact bones and by the predominance of long bones and elements of the skull and mandibles. We evaluated the skeletal profiles from several levels of Abri Romaní and level 5 of Abri du Maras focusing on the methodology proposed by Faith and Gordon (2007). Results indicate an unconstrained

transport strategy in all levels and all size-weight categories in the Abric Romaní. The same analysis applied to Hadza assemblages revealed similar results to those found in the Abric Romaní. The most striking feature of the Hadza assemblages is the superposition of highly variable transport events. These characteristics suggest that the transport strategies used by Neanderthals in Abric Romaní are also characterized by a high degree of diversity in transport decisions. However, a trend to the transport of high-value elements could be observed in the Abric Romaní. In level 5 of Abri du Maras the transport was made maximizing the value of transported elements for all the taxa.

The degree of eruption and development of teeth and their wear stages allowed us to determine the ages of animal's death and created the mortality profiles. These results suggest that the Neanderthals employed both selective and non-selective hunting strategies. The predictability of an animal's behaviour in the environment implies that its exploitation takes place within a temporal and spatial range, which reinforces the use of a repeated hunting strategy over time and adapted to the migratory movements of each species. Neanderthals of the sites studied in this work developed specific hunting strategies considered the taxa and the age of the individual to be hunted. The hunting groups most likely employed cooperative hunting techniques, specially in the capture of large animals. Thus, is not possible to uniquely associate a single mortality profile with the predation that Neanderthals carried out within their ecological niche, and besides, we classified the hunting of Mediterranean Neanderthal as specialized in the function of age and species.

Mobility strategies of Neanderthal groups are studied through the characterization and analysis of archaeological sites and traditionally compared to the types of settlements of present-day hunter-gatherer groups, based on their mobility strategies. The faunal record of level P of Abric Romaní allowed us to study the foraging behaviour developed by Neanderthals. Through the taphonomic study of the remains and their spatial distribution, it was possible to define the characteristics of these human occupations. The analyses indicate that the assemblage was the result of at least two different types of occupations: 1) A transitory residential camp during short occupations, focusing on the exploitation of red deer; 2) A hunting camp/intermediate butchering site for the specialized capture of horses. The presence of occupations focusing on the supply of specific resources is typical of collector groups. The results of the zooarchaeological study of level P characterize the Neanderthals of Abric Romaní as groups involved in a logistic mobility system, who moved throughout the territory depending on the availability of large ungulates.

Our result permits to observe diversity in the type of settlement, hunting and transport strategies developed by Neanderthal. We observed selective and non-selective hunting

strategies depending on many cases of prey and season. An adapted transport strategy of animal carcasses in the function of the group necessities and the prey type. Besides, we found different temporary occupations: short-term and specialized occupation, like in the level P of Abri Romaní; short-term occupation with sporadic presence, like in the cave of Bize-Tournal; prolonged occupation events during a whole season, like in the level 5 of Abri du Maras. Besides, we can identify different uses of the sites for several purposes: as hunting campsite in level P for horse hunting; as a temporary halt in Bize-Tournal; has a transitory campsite in level P for the hunting of deer; as a residential campsite in level 5. Our study of the faunal assemblages of these sites adds these results to the general knowledge of Neanderthals subsistence strategies in the Mediterranean basin.



# Résumé

Les Néandertaliens sont l'une des espèces d'hominines les plus étudiées. Ils ont occupé et exploité une grande partie du continent eurasiatique pendant plus de 300.000 ans et traversant plusieurs cycles glaciaires et interglaciaires. Les assemblages fauniques et les études archéozoologiques sont une source fondamentale d'information pour comprendre les comportements de subsistance des Néandertaliens. La vision des comportements de subsistance des Néandertaliens a évolué grâce à l'archéozoologie. Ces dernières années de nombreuses découvertes ont démontré que des comportements traditionnellement associés à l'apparition des hommes anatomiquement modernes (Paléolithique Supérieur) tels qu'un régime alimentaire diversifié et des chasses collectives de masse aux grands ongulés étaient déjà l'apanage des groupes néandertaliens. Toutefois, ces activités de subsistance dépendent principalement de leur répartition régionale comme le démontrent leurs distributions hétérogènes dans le registre osseux. Les analyses archéozoologiques soulignent l'importance de la viande dans le régime alimentaire des Néandertaliens, grâce à la chasse efficace d'un de diverses espèces animales, allant de la mégafaune aux petites proies. Cependant, au sein de nombreux sites archéologiques, les comportements de subsistance ont mis au jour l'exploitation d'ongulés de taille moyenne et de grande taille, avec une sélection d'une ou deux espèces préférentiellement.

Ce travail doctoral s'est intéressé à un site espagnol et deux sites français : le niveau P de l'Abri Romaní, le niveau 5 de l'Abri du Maras et l'assemblage de chevaux des unités I, II et III dans la grotte du Bize-Tournal. Les principaux objectifs ont été d'établir l'origine de l'accumulation, de définir le rôle des Néandertaliens dans cette accumulation et d'établir l'importance des autres agents taphonomiques sur l'assemblage faunique, de reconstruire les profils de mortalités et des profils anatomiques. Sur la base de ces informations, nous développerons l'étude des stratégies cynégétiques, l'identification des stratégies de transport des carcasses des animaux et des événements d'occupation et la fonction de chaque site, ainsi nous pourrions établir la mobilité au sein des territoires.

Nous montrerons que le comportement des Néandertaliens se caractérisait par une variabilité dans la sélection des proies, le transport des éléments squelettiques. Leurs modes de peuplement et leurs mobilités au sein des territoires varient en fonction de la région et de la chronologie. L'ensemble des études de sites archéologiques étudiés dans le cadre de ce travail de thèse nous a permis de répondre à des questions diverses et complémentaires permettant d'étudier différents aspects de la culture néandertalienne en fonction de la résolution archéostratigraphique.

Dans de nombreux sites moustériens, le profil anatomique le plus courant est caractérisé par des éléments axiaux postcrâniens et des os compacts rares et par la prédominance des os longs, des éléments crâniens et des mandibules. Nous avons établi les profils squelettiques de plusieurs niveaux du site "Néandertal" de l'Abric Romaní et du niveau 5 de l'Abri du Maras en nous concentrant sur la méthodologie proposée par Faith et Gordon (2007). Les résultats indiquent une stratégie de transport sans contrainte dans tous les niveaux et pour toutes les catégories de poids et taille pour le site de l'Abric Romaní. Une analyse similaire ayant été appliquée aux assemblages Hadza a révélé des résultats proches à ceux trouvés dans l'Abric Romaní. La caractéristique la plus frappante des assemblages Hadza est la superposition d'événements de transport très variables. Ces caractéristiques suggèrent que les stratégies de transport utilisées par les Néandertaliens dans l'Abric Romaní se caractérisent également par une grande diversité dans les décisions de transport. Cependant, nous avons pu observer une tendance au transport d'éléments de grande valeur nutritive, comme dans le niveau 5 de l'Abri du Maras, où un transport préférentiel des éléments de plus grande valeur nutritive.

Le degré d'éruption et de développement des dents et leurs stades d'usure nous ont permis de déterminer l'âge de la mort de l'animal. Ces résultats suggèrent que les Néandertaliens ont utilisé des stratégies de chasse à la fois sélectives et non sélectives. La connaissance du comportement d'un animal dans son environnement implique une exploitation dans une fourchette temporelle et spatiale, renforçant l'utilisation de stratégies cynégétiques ciblées, répétées dans le temps et adaptée aux mouvements migratoires de chaque espèce. Les Néandertaliens ont développé des stratégies de chasse spécifiques tenant compte des taxons et de l'âge de l'individu qu'ils chassaient. Les groupes de chasseurs ont très probablement utilisé des techniques de chasse coopératives, en particulier pour la capture de grands animaux. Ainsi, il n'est pas possible d'associer un seul profil de mortalité à la prédation que les Néandertaliens exercent sur leur niche écologique. Par conséquent, nous avons classé la chasse des Néandertaliens méditerranéens comme étant spécialisée dans la fonction de l'âge et des espèces.

Les stratégies de mobilité des groupes de Néandertaliens sont étudiées à travers la caractérisation et l'analyse des sites archéologiques et traditionnellement comparées aux types d'occupation actuels des groupes de chasseurs-cueilleurs, en fonction de leurs stratégies de mobilité. Le registre faunique du niveau P de l'Abric Romaní est une source d'information unique pour l'analyse du comportement de subsistance, de la recherche de nourriture développée par les Néandertaliens au cours du MIS3. L'ensemble est divisé en deux sous-niveaux distincts et bien définis : Pa et Pb. L'étude taphonomique des restes et de leur répartition spatiale a permis de définir les caractéristiques de ces occupations humaines. Les analyses indiquent que l'assemblage était le résultat d'au moins deux types d'occupation différentes : 1) Un camp résidentiel



transitoire lors de courtes haltes, axé sur l'exploitation des cerfs ; 2) Un camp de chasse pour la capture spécialisée de chevaux. La présence d'occupations axées sur la disponibilité de ressources spécifiques est caractéristique des groupes de collecteurs. Les résultats de l'étude archéozoologique du niveau P ont mis en évidence que les Néandertaliens de l'Abri Romaní étaient des groupes impliqués dans un système de mobilité complexe, qui se déplacent sur tout le territoire en fonction de la disponibilité de grands ongulés.

Nos résultats ont mis en évidence la diversité des types de stratégies de peuplement, de chasse et de transport mises en place par les Néandertaliens. Nous avons démontré la présence de stratégies cynégétique sélectives et non sélectives en fonction du nombre de proies et de la saison d'abattage, c'est-à-dire une stratégie de transport des carcasses adaptée en fonction des besoins du groupe et du type de proie disponible. En outre, nous avons mis en évidence différents types d'occupations: les occupations de courte durée et spécialisée, comme dans le niveau P de l'Abri Romaní ; des présences sporadiques de courte durée, comme dans la grotte de Bize-Torunal ; des événements d'occupation prolongée pendant toute une saison, comme dans le niveau 5 de l'Abri du Maras. En outre, l'identification de différentes utilisations des sites à plusieurs fins a été mise en évidence dans le niveau P avec à la fois un campement de chasse transitoire de chasse au cerf et de chasses spécialisées aux chevaux ; une halte temporaire à Bize-Tournal un campement résidentiel dans le niveau 5 de l'Abri du Maras. Notre étude des assemblages fauniques permet d'ajouter ces résultats à la connaissance générale des stratégies de subsistance des Néandertaliens dans le bassin méditerranéen.



# List of contents

Acknowledgements .....	i
Abstract.....	iii
Résumé .....	vii
List of contents.....	xi
List of figures and tables.....	xiii
I. Introduction .....	1
Chapter 1. The state of the art .....	3
1.1. Neanderthal hunting and transport strategies.....	8
1.2. Mobility strategies .....	14
Chapter 2. Materials and methods.....	21
2.1. Materials .....	23
2.1.1. Abric Romaní .....	23
2.1.2. Abri du Maras .....	24
2.1.3. Bize-Tournal.....	25
2.2. Methods .....	26
2.2.1. Identification and abundance measurement .....	27
2.2.2. Diversity measurements .....	28
2.2.3. Determination of age of death and mortality profiles.....	29
2.2.4. Transport of ungulate carcasses.....	29
2.2.5. Fracturing and fragmentation .....	30
2.2.6. Ravaging measure.....	30
2.2.7. Taphonomic analysis .....	30
2.2.8. Taphotypes .....	31
2.2.9. Archaeostratigraphic and spatial analysis.....	31
	xi

2.2.10.	Refittings.....	32
2.2.11.	Redistribution index.....	33
Chapter 3.	Ungulate carcass transport strategies at the Middle Palaeolithic site of Abric Romaní (Capellades, Spain) .....	35
Chapter 4.	Neanderthal hunting strategies inferred from mortality profiles within the Abric Romaní sequence.....	59
Chapter 5.	Neanderthal logistic mobility during MIS3: Zooarchaeological perspective of Abric Romaní level P (Spain) .....	103
Chapter 6.	Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, Level 5 (South-eastern France).....	137
Chapter 7.	Taphonomic analysis of horse remains from Mousterian and Aurignacian Units from Bize-Tournal Cave (Aude, France).....	183
Chapter 8.	Discussion.....	233
8.1.	Assemblage formation .....	235
8.2.	Discard and transport .....	239
8.3.	Resource provisioning: prey selection and hunting .....	245
8.4.	Neandertal mobility .....	248
Chapter 9.	Conclusions .....	251
	Conclusions .....	253
	Conclusions .....	255
	References .....	257

## List of figures and tables

Figure 1 The lithostratigraphic column of the Abric Romaní Coveta Nord profile (Vallverdú i Poch, 2018) The stratigraphic column contains the temporal position of the archaeological level in accordance with the chronology of the basal boundaries of the Dansgaard-Oeschger events in the GISP2 temporal scale model (Blunier and Brook, 2001). An updated summary of the absolute ages of the Abric Romaní archaeological beds has recently been published (Vaquero et al., 2013). Legend for the lithological column: 1, organomineral grey horizon; 2, red siliciclastic and calcitic silty sand; 3, yellow calcitic sand; 4, yellow tuffaceous-travertine gravel and calcitic sand; 5, platy gravels of crystallitic travertine and calcitic sand and silt; 6, speleothems; 7, cemented sands and travertines; 8, diastem; 9, paraconformity or erosive unconformity; 10, archaeological bed. Legend for the comment columns: a, rock-fall of travertine blocks and megablocks; b, letters of the archaeological beds; c, sedimentary sequences; d, the lower boundary chronology of the Dansgaard-Oeschger events in the temporal scale model of the GISP2 core (Blunier and Brook, 2001). ..... 24

Figure 2 Vertical projection K/L band of stratigraphic levels from the East Trench (after Simon Puaud; in Moncel et al., 2019). Distinguishing the succession in three terms: from the base, a brown, organic term which can be compared to layer 5. A second silty term corresponding to layer 4 then a term superficial layer. .... 25

Figure 3 Cross-section of the filling of the northern half gallery between zones 28 and 29. Position of archaeological Unit I (Mousterian), Unit II (Mousterian), Unit III (Aurignacean) and small witness of the Unit IVC (Magdalenian final) plated centres the wall of the cavity dug by karstic erosion under the Mousterian layers (Tavoso, 1987). 26

Figure 4 %MAU distribution of horses in the main levels of Abric Romaní and Abri du Maras. .... 242

Figure 5 %MAU distribution of cervids in the main levels of Abric Romaní and Abri du Maras. .... 242

Figure 6 %MAU distribution of bovids in the main levels of Abric Romaní and Abri du Maras. .... 243

Table 1 Number of remains and percentage of long bone specimens with cut marks, anthropogenic bone breakage and carnivore tooth marks of different assemblages of Abric Romaní and Abri du Maras. .... 244



# I. Introduction

During the last 50 years, zooarchaeology has largely contributed to the increase knowledge on life of past hominins and among them, the Neanderthals. The potential of zooarchaeological and taphonomical research proportionate information on the nature of Neanderthal subsistence strategies that had been broadly proven (e.g. Stiner, 1991a; Patou-Mathis, 1993; Gaudzinski, 1996; Speth and Tchernov, 1998; Costamagno et al., 2006; Yeshurun et al., 2007; Stiner, 2013; Blasco et al., 2019a). First works of the discipline considered that Neanderthal cognitive capabilities were limited regarding Upper Palaeolithic (Binford, 1983a; Trinkaus, 1989; Bar-Yosef et al., 1992), including their capability to develop effective hunting of large ungulates (Binford, 1983b, 1988; Klein, 1989). Progressively, this image was changed from Neanderthals with mixed hunting and scavenging strategies (Stiner, 1991a, 1994, 2002a) to a vision in which Neanderthals were shown as regular hunters of adult ungulates (Stiner et al., 2009; Stiner, 2013). Few doubts persist today about Neanderthal hunting capabilities. The assemblages generated by their activities showed a regional variation in the selection of animal resources. In some assemblages, prey selection has been identified implying that Neanderthals developed a broad-spectrum diet, with the inclusion of small prey in diet, like birds, turtles and lagomorphs. It has been observed in sites of the Mediterranean basin from Levant (Stiner et al., 2000; Speth and Tchernov, 2002; Biton et al., 2017; Blasco et al., 2019b) to the Iberian Peninsula, including also the Italian Peninsula and south of France (Martínez Valle, 2009; Daujeard and Moncel, 2010a; Brown et al., 2011; Blasco and Fernández Peris, 2012; Salazar-García et al., 2013; Gabucio et al., 2014a; Blasco et al., 2016; Romandini et al., 2016; Nabais and Zilhão, 2019; Real et al., 2019b; Romandini et al., 2019). On the other hand, there are assemblages in which access or consumption of small preys has not been documented or it is very scarce, where the main food resource of Neanderthals seems to be large ungulates (Jaubert and Brugal, 1990; Patou-Mathis, 1994; Costamagno et al., 2006; Dusseldorp, 2009; Stiner et al., 2009; Daujeard and Moncel, 2010a; Lebègue et al., 2010; Patou-Mathis, 2012; Rendu et al., 2012; Rosell et al., 2012b; Valensi et al., 2012; Niven, 2013; Stiner, 2013; Smith, 2015; Rosell et al., 2017). Among these sites there is a diversity of animal procurement, including assemblages generated by communal hunting of herds (Gaudzinski and Roebroeks, 2000; Costamagno et al., 2006; Rendu et al., 2012; White et al., 2016; Daujeard et al., 2019).

This doctoral thesis aims to study the faunal resource exploitation developed by Neanderthals in the archaeological sites of Abric Romaní (Capellades, Spain), Abri du

Maras (Saint Martin d'Ardèche, France) and Bize-Tournal (Bize-Minervois, France). This work has as objectives to characterize the origin of the archaeological sites of Level P of Abric Romaní, level 5 of Abri du Maras and the horse samples of Units I, II and III of Bize-Tournal. The mortality profiles and the anatomical profiles have also been evaluated and analysed for levels E, H, I, Ja, Jb, K, L and M of Abric Romaní site. The study is focused on analysing and describing the taphonomic signal of the faunal remains recovered from these assemblages. Our main objective is to evaluate the type of exploitation of animal resources through the study of anatomical and taxonomic profiles and the age at death of the prey combined with the study of the bone surfaces. Analyses related to spatial statistics and spatial taphonomy have been applied to evaluate, in this case, the occupations of level P Abric Romaní.

This doctoral thesis is organized into nine chapters. The central research of the thesis is presented in various specific articles. The chapters framing the articles can be considered a summary, sharing the various aspects dealt within each specific investigation.

Chapter 1 presents the state of the art of the main aspects discussed in each paper. These aspects are related to Neanderthal resource procurement and management, such as the development of settlement types, hunting strategies, skeletal transport strategies and territorial mobility strategies. Chapter 2 briefly presents the archaeological assemblages studied and the methods developed for their analysis, summarizing the methods used in the various several studies. In Chapters 3 to 7 includes the SCI-SSCI paper developed during this doctoral research. Chapters 3, 4 and 5 include results obtained from the study of Abric Romaní are exposed, with three papers published in the journals *Comptes Rendus Palevol*, *PlosOne* and *Quaternary Science Reviews*. Chapter 6 corresponds to the results from the Abri du Maras level 5 analysis which has been submitted to *Quaternary Science Reviews*, and it is presented in this work in the form of a formal text for correction. Chapter 7 corresponds to an article accepted in the journal *Comptes Rendus Palevol*, based on the results of the study of the horse remains from Bize-Tournal Units I, II and III, it is presented in this work in the form of a formal text for correction since is still under editing process.

Chapter 8 includes the general discussion in which all the results of the different works are put into context. In this section, the behavioural aspects of the Neanderthal groups at these three sites are discussed and contrasted. Finally, Chapter 9 compiles the main conclusions taken of each work.



## **Chapter 1. The state of the art**



## The state of the art

The discovery in 1856 of a partial skeleton in the Feldhofer cave, in the Neander Valley, near Düsseldorf (Germany), includes the Neanderthals in the scientific discussion of human evolution (Mellars, 1996a). The assignation of this skeleton to a new human species was performed by the Irish anatomist William King in 1864. Its early discovery has contributed to Neanderthals becoming one of the more exhaustively and broadly studied human species.

Neanderthal remains have been recovered along a great part of Eurasia, from Siberia (Krause et al., 2007; Prüfer et al., 2014) to the Iberian Peninsula (Rosas et al., 2006; Walker et al., 2008). However, contexts where human remains have not been found, however, industries normally associated with Neanderthals have been identified, include northern regions of Russia (Pavlov et al., 2004) and Europe (Johansen and Stapert, 1995). Recent work extends the territorial presence of Mousterian and Middle Palaeolithic technology to the north of China in the Jinsitai cave (Li et al., 2018). However, the use of the lithic assemblages as a reference could be problematic, due to the fact that anatomical modern humans (AMH) in the Levant and Denisovans in Asia produced very similar assemblages to those attributed to Neanderthals (Shea, 2003; Douka et al., 2019; Jacobs et al., 2019; Shunkov et al., 2020).

Middle Palaeolithic material culture associated with Neanderthals was extraordinarily extensive and persistent in time (Kuhn, 2013). During over 300,000 years, Neanderthals scattered, occupied and exploited a great part of the Eurasian continent, through several glacial and interglacial cycles. According to Kuhn (2013) the factors allowing the apparent success of Mousterian technologies may also have accelerated their eventual disappearance. Remarking the small population size which allowed the persistence of their material culture but also implies very fragile cultural transmission lines and a population density very fragile (Kuhn, 2013).

Churchill (2014) proposed that Neanderthals lack technological components enough to develop complex behaviours as AMH and even less than current hunter-gatherers, as has been recently indicated by French (2019). However, nowadays it has been possible to probe that Neanderthals developed activities related to the emergence of modern human behaviour, such as practices of funerary nature (Pomeroy et al., 2017, 2020). Symbolic behaviour means the development of ornament probably related to supraregional group-type cultural assignments (Rodríguez-Hidalgo et al., 2019), it has even been proposed that Neanderthals did the first examples of parietal art (Hoffmann et al., 2018), showing Neanderthal culture was more complex than originally thought. Some researchers have argued that the direction of cultural interactions between Neanderthals and modern humans did not necessarily have to be unidirectional and that

a two-way cultural transfer between Neanderthals and AMH may have been possible (Greenbaum et al., 2019; Rodríguez-Hidalgo et al., 2019).

Anatomically Neanderthals are adapted to two rules whose predict cold adaptation (Aiello and Wheeler, 2003; Steudel-Numbers and Tilkens, 2004): Bergmann's rule (Freckleton et al., 2003) and Allen's rule (Tilkens et al., 2007). However, some researchers consider these characteristics to be primarily biomechanical adaptations, with thermoregulation as a secondary consequence (Churchill, 1998; Stewart, 2005). Neanderthals are considered to have had high demands for somatic energy, over 10% than most of the actual populations. This evidence comes from the analysis of body size and proportion (Stegmann et al., 2002; Aiello and Wheeler, 2003), as well as their activity pattern and the environments in which they developed (Stegmann et al., 2002; Aiello and Wheeler, 2003; Churchill and Rhodes, 2006; Churchill et al., 2016). Kaplan and Colleges (Kaplan et al., 2000) concluded that intelligence, increased longevity and a high-quality diet must have been developed synchronically. High energy requirements, together with a rich meat diet, may have had a significant impact on the subsistence strategies of Neanderthals, specially in terms of their food resource acquisition strategies.

There is a general agreement on the Neanderthal decline as a result of a combination of biological, cultural and environmental factors (van Andel and Davies, 2003; Finlayson, 2004; Mellars, 2004; Zilhão, 2006; Carrión Marco et al., 2019; Chazan, 2019). Two main hypotheses originated from the combination of these factors. The former is based on the idea that Neanderthals were not capable to adapt to the climatic changes at the end of the Marine Isotopic Stage (MIS 3) (Higham et al., 2014). The second defends that competence with AMH population was the main factor for their extinction (Banks et al., 2008; Gilpin et al., 2016).

In this work, we focus on Upper Pleistocene, which contains archaeological records associated with Neanderthals. This period goes from MIS 5e with the Eemian interglacial, chronology in which the assemblage from level 5 of the Abri du Maras are located, to the intermediate phase of MIS 3, chronology in which the Abric Romaní assemblages are located. This chronological range includes what some researchers have considered being Classic Neanderthals, were usually between 120,000 ka, until their extinction around 28,000 ka (Finlayson et al., 2006).

The zooarchaeology basic task is to try to reconstruct the animal resources used by ancient populations throughout the study of bone remains of the different taxa present in the archaeological record. Through this reconstruction, we pretend to shed light on behavioural aspects of the human past which includes hunting patterns, carcasses economic processes (transport, processing, consume and discard), the territorial

management through the development of different sites (including inferences about some social aspects such as group size), activities distribution, cooperation, meat sharing and also possible cultural relations that may have existed between different regions. Through zooarchaeological studies, it is also possible to interpret and reconstruct part of the ecosystems exploited by human groups, the seasonality of the occupations, the deposits formation processes and the post-depositional physical and chemical processes that could have affected the bone assemblages (e.g. Behrensmeyer, 1978; Shipman, 1981; Lyman, 1984; Andrews, 1990; Gifford-Gonzalez, 1991; Lyman, 1994). The archaeological sites are usually the result of an undetermined number of occupation events, during which materials can be incorporated or removed, depending on the use and abandonment phases of the settlements (LaMotta and Schiffer, 1999). Bailey (2006) described several types of archaeological palimpsests based mainly on the possibility of identifying occupation events and attending to the destructive processes that affect the assemblages, between the phases of contribution and loss of material.

The great archaeological sites, in which the archaeological record is conformed in many cases by thousands of specimens, indicate that reuse of certain places was a common practice of the behavioural habits of hominins population since the Lower Pleistocene (e.g. Valensi, 2000; Fernández-Peris et al., 2008; Saladié et al., 2011a, 2014, 2018; Carbonell, 2012; Niven, 2013; Romandini et al., 2014; Rodríguez-Hidalgo et al., 2015, 2017). However, several studies have proposed that the development of the base camp model, focused on structuring space around hearths, was fully developed during the Middle Palaeolithic (Rolland, 2004; Kuhn, 2012; Kuhn and Hovers, 2013; Stiner and Kuhn, 2016). Stiner (2013) proposed two models of occupation for the Mediterranean Middle Palaeolithic record based on the length of occupations. This researcher differentiated between short-term and long-term occupation events. To distinguish between these two models archaeologists have been using numerous factors: the abundance or shortage of materials (Stiner, 1991b; Maroto et al., 1996; Villaverde et al., 1996; Stringer et al., 2000; Valensi, 2000; Vaquero and Pastó, 2001; Costamagno et al., 2006; Moncel et al., 2008; Audouze, 2010; Daujeard and Moncel, 2010a; Kuntz et al., 2016; Bicho and Cascalheira, 2020); the size of the occupation area and the existence or not of a spatial organization of the occupations (Vallverdú et al., 2005; Audouze, 2010; Bicho and Cascalheira, 2020); the seasonality of occupations, whether multi-seasonal or in single-season occupations (Bridault et al., 2001; Martínez-Moreno et al., 2004; Costamagno et al., 2006; Bignon, 2008; Villaverde et al., 2017); taphonomic aspects related to human activity have also been considered, such as the frequency of burned bones (Costamagno et al., 2006; Daujeard and Moncel, 2010a; Niven et al., 2012; Marín-Arroyo, 2013; Gabucio et al., 2014b; Castel et al., 2017); and the variability on lithic assemblages, that increases as the formation processes grows (Vaquero et al., 2012; Bicho and Cascalheira, 2020).

## 1.1. Neanderthal hunting and transport strategies

The study of Steele and Baker (1993) of human predation indicates that it is necessary to consider different aspects such as the use of weapons, an elaborated communication system, social hunting, cooperation, the exploitation of large territories, transport and deferred consumption and exchange of prey. In this sense, they establish different categories to classify hunting events. These categories are separated, in the first place, by the number of hunters and hunted animals. Driver (1995) following this proposal studied the social organization and technology of the participant in hunting events. According to this author, the number of animals and the form in which they were hunted it is useful to distinguish simple predation events from sequential hunting events and mass predation events. The size and social organization of the hunting party allows distinguishing among solitary hunters, cooperative groups and communal organizations. Each of these predation types could occur in many forms depending on the hunting tactic, such as conduction, ambush, encounter, stalking or persistence hunting. Besides it could be made using many techniques as lances, spears, bow and arrows, nets or tamps (Steele and Baker, 1993; Driver, 1995; Lombard and Phillipson, 2010). Ethnoarchaeological studies of some hunter-gatherer groups show that they employ multiple hunting strategies in function of the season of the year (Yellen and Lee, 1976; Binford, 1978) and the different species hunted (Marshall, 1993, 1994).

In the archaeological sites, prey selection has been studied considering the animal species diversity, their abundance in the assemblage, the age of prey, their sex and season of death. The prey choice model (Stephens and Krebs, 1986; Kaplan and Hill, 1992; Smith and Winterhalder, 1992) assumes that human and non-human hunters decide which prey to follow considering which prey had the higher return rank (Stephens and Krebs, 1986). High-value resources, hard to acquire, implied that hunter groups possess high skills levels, knowledge, strength and coordination during the food searching (Kaplan et al., 2000). One of the bases of hunting is the knowledge about seasonal variation in animal behaviour, including diet, habitat preferences, social grouping, life development and mobility (Nelson, 1973; Lee, 1979). All these features influence prey availability, a fundamental factor in decision-making since the time spent searching for certain prey is included in the cost of capture. The prey selection pattern indicated a focus over high ranked foods, those with high ranked return rates concerning the searching and processing invested time (Stiner and Munro, 2002). Some repetitive ethological behaviours make certain species predictable and spatially restricted targets. This allows certain sites to be systematically reused (Dusseldorp, 2009). Most herbivores require daily water consumption, specially during summer, which restricts their movements around springs and other water resources (Berger, 1986; Burke, 2002). Also, seasonal migratory movements through the same corridors year after year may be

predictable (Niven et al., 2012). Therefore, the predictability of a resource added to its temporal availability in the landscape implies that its exploitation takes place within a temporal and spatial range, which reinforces the use of repeated hunting strategies over time and adapted to the migratory movements of each species (Gaudzinski and Roebroeks, 2000; Gaudzinski, 2006; Niven et al., 2012; Daujeard et al., 2019). These behaviours allowed high success rates to ambush and interception hunting (O'Connell et al., 1988a; Lupo and O'Connell, 2002; Marlowe, 2004; Hitchcock et al., 2019).

Ethnographic data has shown that when prey is acquired individually, larger animals generally have a higher value than smaller animals (Hawkes et al., 1982; Broughton and Grayson, 1993; Kelly, 1995; Lupo and Schmitt, 2005). This preference for large animals is due to a higher nutritional value and energetic rates provided, as well as a greater quantity of derived products that could be used (skin, lather, bones) (Broughton, 1994). When hunters-gatherers can kill the whole age group of a population, they prefer prime adults because these are the biggest and most profitable animals, over younger animals (Stephens and Krebs, 1986). Although, some researchers have argued that it is necessary to consider not only the size of the prey, because aspects such as the cost of processing are different even in species of the same size (Stiner et al., 1999, 2000; Stiner, 2002b; Stiner and Munro, 2002; Lupo and Schmitt, 2005). An effective way to reduce the large ungulate hunting risk is the cooperative organization of hunting parties (Stiner et al., 2009; Saladié et al., 2011a; Stiner, 2013; Rodríguez-Hidalgo, 2015; White et al., 2016; Rodríguez-Hidalgo et al., 2017) such other predators that are able to increase the maximum size of prey they hunt through cooperative hunting carried out in groups (Radloff and Du Toit, 2004). Lions, wolves, spotted hyenas and wild dogs reduce the hunting risk using cooperation, which allows them the possibility to kill animals that weights exceed theirs (Stiner et al., 2009).

During the 1980s, the first studies interested in Neanderthal subsistence strategies considered that they lacked the technology needed to capture large prey and the ability to plan hunting events (Binford, 1983a; Bar-Yosef et al., 1992; Trinkaus, 1989). These studies presented the Neanderthals as scavengers that depended on the carcass spoils abandoned by large carnivorous (Binford, 1983b, 1988; Klein, 1989). It is also showed that sites where cranial (teeth and horns) and feet remains (metapods and phalanges) were present were the result of the secondary access of hominins to the carcasses of large animals, after being exploited by hyenas and other dangerous predators. Marean and Kim (Marean and Kim, 1998) assert that these models are the result of scarce identification of the long bone shafts. Stiner's studies on Italian Middle Paleolithic sites (Stiner, 1990, 1991b, 1993) indicated that Neanderthals developed active hunting, although in comparison it was less effective than the humans of the Upper Palaeolithic. Years later, Stiner (2002a) indicated that the Neanderthal hunting specialization was

higher than previously considered, and in 2009 she postpones the big game hunting to the 400.000 years in the site of Qesem (Stiner, 2009).

Stiner (1990) defined AMH as ambush hunters, with a tendency for systematic capture of prime adults (Stiner and Kuhn, 2006). This selection implies the hunting of the reproductive core among ungulate populations. Therefore, the primed dominated and catastrophic profiles should be the most common on archaeological sites because they showed the greatest proportion of prime adults. However, the anthropogenic activity could generate a wide diversity of mortality profiles (Stiner, 1990, 2013; Blasco, 1997; Speth and Tchernov, 1998; Gaudzinski and Roebroeks, 2000; Patou-Mathis, 2000; Steele, 2004; Valensi and Psathi, 2004; Rendu, 2010). Regarding the best prey choice, Speth (2019) linked the preference of the prime adult individuals with high dependence of fat and grease in diet, because adult animals have the greatest index of fatty tissues.

The existence or not of specialized hunting strategies for Neanderthals has been a focus of debate for many authors (Mellars, 1973, 1996a, 2004; Straus, 1983; Grayson and Delpech, 2003). David and Enloe (1993) described them as specialized hunting strategies only when it is performed in the form of communal hunting of herds or of a great number, which implies the processing of great amounts of meat for their storage. This activity generated assemblages dominated by one species. Grayson and Delpech (2002) observed that the Mousterian and Aurignacian faunal groups did not differ in their degree of hunting specialization. Recently, evidence of these hunting strategies in the archaeological record has been found in the Middle Pleistocene level of TD10.2 of Gran Dolina (Atapuerca, Spain) where the communal hunting of bison has been identified (Rodríguez-Hidalgo et al., 2017). The presence of monospecific sites described as a result of communal hunting by Neanderthal is also widely known (Jaubert, 1990; Jaubert and Brugal, 1990; Brugal, 1995; Gaudzinski, 2000; Gaudzinski and Roebroeks, 2000; Beauval, 2004; Costamagno et al., 2006; Castel et al., 2017; Daujeard et al., 2019). On the other hand, Niven and colleagues (2012) identified in the French site of Jonzac a monospecific accumulation, as the reindeer exploitation. They defend that it is not possible to defend specialized hunting of this taxa, claiming it is a driven response to the availability of this resource in the environment. According to their proposals, the abundance of a taxon could not reflect selective hunting but the availability of prey by environmental restrictions (Costamagno et al., 2006; Discamps et al., 2011; Rendu et al., 2012; Castel et al., 2017). Otherwise, the studies of subsistence strategies are directly related to environmental and seasonal parameters (Rendu et al., 2019). Monospecific sites are usually located in the Atlantic and Northern Europe. In the Mediterranean basin, sites dominated by one species, in which the abundance of the taxa is not so high, are scarce (Carbonell, 2012; Romandini et al., 2014; Real et al., 2019a; Rusch et al., 2019; Pérez et al., 2020). In the Mediterranean basin, there is a greater ecosystem diversity in shorter distances, from the coastal areas, coastal plains,



fluvial valleys and mountain environments (Valensi, 2000; Aura Tortosa et al., 2002; Carbonell, 2012; Moncel and Daujeard, 2012; Finlayson et al., 2019; Mallol et al., 2019; Rusch et al., 2019). How the Neanderthals had a specialized or generalist hunting method should be conditioned by a complex number of interrelated features. These factors could be the availability of prey, the periods of the year, the size of the hunting party, the transport distance, the nature of the terrain, the technology and technique hunting, as well as the regional organization and temporal activities of Mousterian territories (Speth, 2010).

The zooarchaeological studies remark the importance of meat in Neanderthal subsistence, through the effective hunting of a wide range of animals, which include from megafauna to the small preys (Jaubert and Brugal, 1990; Stiner, 1991b; Farizy et al., 1994; Patou-Mathis, 1994; Gaudzinski and Roebroeks, 2000; Costamagno et al., 2006; Stiner and Kuhn, 2006; Fernández-Peris et al., 2008; Adler and Bar-Oz, 2009; Stiner et al., 2009; Daujeard and Moncel, 2010a; Hardy and Moncel, 2011; Blasco and Fernández Peris, 2012; Patou-Mathis, 2012; Stiner, 2013; Gabucio et al., 2014a; Rufà et al., 2014; Smith, 2015; Rufà et al., 2016).

The hominins decisions about carcasses transport to campsites and the processing of the food were guided on the need for increasing the value of the gathering or hunted food. Thus, the regular transport of the different resources to the camps created a socio-economic interaction among hominin groups (Stiner and Kuhn, 2016). The ability to transport anatomical elements from the site of acquisition to the central camps has played a key role in studies of hominid evolution (Isaac, 1978; Lee, 1979; Potts et al., 1999; Kaplan et al., 2000). Transport decisions are interesting for zooarchaeological studies since the transport or discard of bones is fundamental in the conformation of faunal assemblages. The transport of animal carcasses to archaeological sites has been studied reconstructing and analysing of skeletal profiles, through frequencies of the different anatomical parts. Based on these profiles, it is possible to classify the type of archaeological site (Leakey, 1971; Isaac, 1978).

The possible social and behavioural implications that could be extracted from transport strategies are shown in studies that have been obtained through comparison with ethnoarchaeological data, almost exclusive source of information to establish analogies concerning the behaviour of actual hunter-gatherers (Binford, 1978, 1981a, 1984a; Bunn et al., 1988; O'Connell et al., 1988b, 1990, 1992; Bunn and Ezzo, 1993; Monahan, 1998; Lupo, 2001; Marean and Cleghorn, 2003a; Cleghorn and Marean, 2004; Manuel Domínguez-Rodrigo et al., 2009). When hunter-gatherers need to transport a carcass from the kill site to their camps, they tend to selectively transport animal elements depending on the greatest quantity of meat (White, 1952, 1953a, 1954, 1955; Perkins and Daly, 1968). Binford (1978) proposed several theoretical models to

explain the transport of animal carcasses by the Nunamiut. Because body parts can be transported for specific products such as meat, marrow or fat, Binford constructed utility indices to predict the abundance of skeletal parts associated with different carcass exploitation patterns. By relating element abundances to food utility values, different utility curves are generated as a result of selective transport strategies. These investigations interpreted the abundance of skeletal elements in actual hunter-gatherer camps in relation to their nutritional return, distance from camp and group size (Binford, 1978; Metcalfe and Jones, 1988). Through these studies it is assumed that hunters try to optimize transport, balancing energy investment and return rate offered by these resources (Grayson et al., 1988; Grayson, 1989).

Since Binford's proposals (Binford, 1978) the concept of utility measured according to the amount of meat, marrow and fat associated with each anatomical element continues being the basis of analyses on transport strategies, through simplified utility indices (Metcalfe and Jones, 1988; Friesen, 2001) and utility indices adapted to different animal species (Chase, 1985; Blumenschine and Caro, 1986; Metcalfe and Jones, 1988; O'Connell and Marshall, 1989; Lyman et al., 1992; Emerson, 1993; Outram and Rowley-Conwy, 1998; Brink, 2001; Friesen, 2001). However, there could be significant problems applying utility indices to the skeletal abundances (Lyman, 1984; Grayson, 1989; Bartram, 1993; Grayson and Cannon, 1999). These can be due to destructive processes (Lyman, 1984; Metcalfe and Jones, 1988; Grayson, 1989; Lyman et al., 1992; Bunn, 1993; Oliver, 1993; Lyman, 1994; Lupo, 1998, 2001, 2001) and methodological biases in the recovery and identification of specimens (Bunn and Kroll, 1988; Marean and Frey, 1997; Bartram and Marean, 1999) that could generate false anatomical profiles or altered original abundances. According to Marean and colleagues (Marean, 1997; Marean and Cleghorn, 2003a; Cleghorn and Marean, 2004; Faith and Gordon, 2007a; Faith et al., 2009), anatomical profiles, transport and discard decisions should be evaluated based on the high-survival elements, those that are less influenced by these processes and represented by the long bones shafts and some portions of the skulls and mandibles. On the other hand, low-survival elements are highly sensitive to a whole series of attrition processes that can easily under-represent their abundance, therefore should not be used in statistical correlations.

In most of the Mousterian sites, the anatomical profiles are dominated by high survival elements, predominating long bones and heads, opposed to a scarcity of post-cranial axial elements and compact bones (e.g. Gaudzinski, 1996; Valensi and Psathi, 2004; Niven, 2013; Romandini et al., 2014). The mixing of transport events, together with post-depositional destruction processes, common in the formation of cumulative palimpsests (Bailey, 2008), could lead to inaccurate, incorrect or ambiguous analyses and interpretations of the anatomical profiles and the transport strategies that generate them (Marín et al., 2017; Yeshurun and Bar-Oz, 2018). In sites where the medium-sized

animals remain to outnumber, those of large size, it has been suggested that the anatomical profiles are the result of differential transport based on the size and weight of the animals (Patou-Mathis, 2000; Gaudzinski-Windheuser and Niven, 2009; Rendu, 2010; Rosell et al., 2012b; Romandini et al., 2014).

However, transport decisions could be based on many other factors including the type of prey, season, the number of hunters, distance and competition or not with other predators (Yellen, 1977; Binford, 1978, 1981b, 1984a; Bunn et al., 1988; Bunn and Kroll, 1988; O'Connell et al., 1988a, 1988b, 1990; Bartram, 1993; Bunn and Ezzo, 1993; Gifford-Gonzalez, 1993; Oliver, 1993; Monahan, 1998). In general, when carcasses require processing before transport, it is considered that humans will discriminate between the food utility of parts (Gifford-Gonzalez, 1993; Miracle, 1996; Outram, 2001; Lupo, 2006). Monahan (1998) describes that Hadza hunting parties have as the first objective to satisfy hunger. After that, they always try to maximize the amount of transported food, counting on parties of twelve carriers. Sometimes they discard bones that are easily processable, such as ribs or limbs, and with greater impediments, thus abandoning heavy and easily processable elements, such as heads. In most hunting events they try to reduce transport costs, so they can spend unlimited time with the hunted carcass because the carnivore risk competition is almost zero (Monahan, 1998; Lupo, 2006). Sometimes high-cost elements are transported by hunter-gatherers because they require substantial effort and time amounts to be fully processed (Marean and Cleghorn, 2003a; Lupo, 2006). Unfortunately, many of these factors are difficult to infer from the archaeological record. Another factor that could influence the anatomical profiles is the existence of an intermediate place, where the carcasses are processed and some parts are consumed before being transported to the central camp (Costamagno et al., 2006).

The transport distance from the kill site to the camp is another factor for transportation, specially relevant to the decision of head transportation (Marean, 1997). Prey choice models predict that as greater the transport distances, more likely low utility elements will be discarded at the kill site (Ugan, 2005; Bird and O'Connell, 2006). Schoville and Otarola-Castillo (Schoville and Otárola-Castillo, 2014) proposed that transport is conditioned by the number of carriers for small and medium-sized carcasses. While, for large animals, transport is mainly conditioned by the distance. These researchers observed that for Hadza groups the head is likely transported over distances very close to the camp. Using predictive equations, they calculate that beyond the 50 minutes walking distance the skulls have very little chance of being transported. It is very unlikely that entire carcasses are transported across long distances, as the ethnographic evidence indicates (Yellen, 1977; Binford, 1978; Bunn et al., 1988; O'Connell et al., 1988b, 1990; Bartram, 1993; Monahan, 1998; Abe, 2005).

In many Mousterian sites, the most common anatomical profile is characterized by a scarce of postcranial axial elements, compact bones and by the predominance of long bones and elements such as skull and mandibles (Valensi and Psathi, 2004; Romandini et al., 2014; Terlato et al., 2019). In some sites, it has been suggested that the anatomical profile is the result of a differential transport based on the selective transport of heads and feet to the shelter (Patou-Mathis, 2000; Gaudzinski-Windheuser and Niven, 2009; Rendu, 2010; Rosell et al., 2012b; Valensi et al., 2012; Romandini et al., 2014). However, the presence of post-cranial axial skeleton in the assemblage has been associated to the transport of these parts to the site, which would indicate variable transport strategies (e.g. Rendu, 2010; Niven et al., 2012; Pérez et al., 2017; Daujeard et al., 2019; Terlato et al., 2019). Although, in some cases, it has been possible to observe transport of the anatomical elements according to their utility (e.g. Valensi, 2000; Adler et al., 2006; Real et al., 2019).

## 1.2. Mobility strategies

Mobility is one of the main variables in the adaptation strategies of hunter-gatherers to their environment. It is an integral part of the socio-economic system of human groups and responds to the objective of optimizing and securing food procurement (Audouze, 2006). Following Kuhn and colleagues (2016) human group mobility is run by four phenomena related between themselves: the internal need for movement (rewards and decisions), mobility skills (biomechanical limitations), the ability to navigate (cognitive challenges of movement) and external factors. The external issues that determine movement comprise the environmental context, resources abundance and distribution and climatic and habitat changes associated, among others. According to Kelly (1992), mobility and the sites generated by current hunter-gatherers are mainly related to resource availability. Most resources are temporally and spatially restricted (Kelly, 1983, 1992) forcing groups to adopt mobile strategies for the management of these resources. Mobility enables hunter-gatherers to balance the unequal distribution of resources in the territory (Kelly, 2013), to avoid negative effects of the long-term occupation of a local ecosystem, as food deficits caused by over-hunting (Hamilton and Watt, 1970). Others benefits derived from mobility are the size group flexibility and the capability to relocate settlements near periodically abundant resources, mainly plants and animal resources and their by-products, and access to water (Lee, 1972, 1979; Tanaka, 1976; Smith, 1981; Perlman, 1985). However, hunter-gatherer groups may also develop high mobility in their territory for reasons other than water availability or irregularities in food distribution (Jones, 1983). Within any of those variants, mobility leads to a reduction of social stress and conflict between co-resident groups (Woodburn, 1972, 1980), exposure to a wider range of potentially exploitable resources (Kuhn et al., 2016) and guarantees a higher success rate in hunting (Jones, 1983). This is linked in

many cases to food management, which can range from the storage of surpluses to the equitable sharing and consumption of food obtained on a daily basis (Marshall, 1961; Lee, 1979; Binford, 1980; Gould, 1981; Jones, 1983).

To describe the movements of hunter-gatherer groups, Binford (1980) developed an approach focused on settlement patterns based on the study of the /Gwi San (Silberbauer, 1972) and the Nunamiut (Binford, 1978). He classified groups into foragers, with residential mobility, and collectors, with logistic mobility. The main difference between them is that foragers move consumers to resources with frequent residential movements, while collectors move resources to consumers, generally with fewer residential movements (Binford, 1980). Foragers make seasonal residential movements between a series of resource patches (Binford, 1980). Their residential mobility can vary significantly among sites, both in time and space, and they do not store food, but consume all the resources obtained daily. They mainly generate two types of sites, residential bases and locations. On the other hand, collectors are characterized by their logistic organization, as specialized task groups provide them with specific resources, and by the storage of food for at least part of the year (Binford, 1982). Specialized task groups leave a residential location to collect specific resources. These groups are often small and seek to procure a specific resource in a specific context. In addition to the places generated by foragers, three further possible places are used by collectors: the field camp, the station and the cache. However, the forager and collector models are not two antagonistic settlement systems, but rather a graduated series from simple to complex system, in which settlement dynamics are strongly linked to the spatial and seasonal distribution of resources in the environment (Binford, 1980). Nevertheless, not all foragers are highly mobile, nor are all collectors almost sedentary (Kelly, 2013).

Similarly, Mortensen (1972) established two models based on mobility patterns. These are the circulating model (the residential group moves in predictable seasonal rounds with a single, self-sufficient settlement type) and the radiating model (places of specific activity supply resources to residential places). Both models produce spatial and regional exploitation as one would expect from foraging and logistic models, respectively (Binford, 1980). Based on these categories, archaeological work has attempted to characterize the subsistence of past human groups.

Hunter-gatherers deal with the problem of overexploitation and resources irregular scattering through camp management and territorial movement (Binford, 1980; Kelly, 1983). Over these two points all the strategies of the human territorial organization run (Domínguez-Rodrigo, 1999). Many studies define camps as places where organized groups, usually in domestic units, live and carry out most of their daily activities (Yellen, 1977; Binford, 1978, 1980b; Jones, 1983; O'Connell et al., 1988a, 1992;

Gamble and Boismier, 1991; Kroll and Price, 1991; Bartram, 1993; Kelly, 2013). These places are used as a gathering point, binding agents of human activity, where they develop a great part of their social lives, the consumption of food and performed a wide range of technological activities and tool production (Isaac, 1978). These are the places where material remains resulting from human activity are accumulated, and therefore relevant for archaeology. The capture of large quantities of meat, the delay in consumption and transport to a place of aggregation, probably far from the kill site, must undoubtedly be related to food sharing (Isaac, 1978).

Considering that many European sites contain large accumulations resulting from repeated human activity, with high chronological ranges, it can be considered that there was an intentionality in the repeated occupation of the same space and probably also in the search for food by the Neanderthals (Dusseldorp, 2009). The information provided by detailed zoological and taphonomic studies has made possible to reconstruct characteristics of the subsistence strategies of Neanderthal groups through the establishment of prey selection, transport strategies, seasonality of occupations, carcass processing, food exchange or group cooperation. Through these capacities, it has been possible to characterize the nature of the settlements and differentiate between long and short-term occupations (e.g. Speth and Clark, 2006; Stiner y Kuhn, 2006; Faith y Gordon, 2007; Faith, 2007; Stiner et al., 2009; Saladié et al., 2011; Marín et al., 2017a, 2017b; Rodríguez-Hidalgo et al., 2017). This information, together with the studies of the lithic assemblages and the raw materials, allows us to characterize the mobility of the hominin groups according to the categorization developed for the current hunter-gatherers (e.g. Lieberman and Shea, 1994; Conard y Adler, 1997; Adler et al., 2006; Boyle, 2000; Gaudzinski, 2000; Patou-Mathis, 2000; Burke, 2004; Valensi and Psathi, 2004; Moncel 2010; Delagnes and Rendu, 2011; Carbonell, 2012; Courty et al., 2012; Daujeard and Niven et al., 2012; Turq et al., 2017).

Several aspects have allowed the study of Neanderthal mobility, such as group size (Vallverdú et al., 2010; Lalueza-Fox et al., 2011; Duveau et al., 2019), settlement type (Boyle, 2000; Patou-Mathis, 2000; Daujeard and Moncel, 2010a), raw material procurement (Fernandes et al., 2008; Gómez de Soler et al., 2019), the Neanderthal anatomy (Verpoorte, 2006; MacDonald et al., 2009; Higgins, 2014) and genetics and demographics studies of Neanderthal populations (Briggs et al., 2009; Fabre et al., 2011; Lalueza-Fox et al., 2011; Mellars and French, 2011; Dalén et al., 2012). Most parts of the research agree that Neanderthals most likely developed within small social groups in territories with low population densities (Pettit, 1997; Henrich, 2004; Vallverdú et al., 2010; Lalueza-Fox et al., 2011; Mellars and French, 2011; Duveau et al., 2019). Currently, two main hypotheses describe Neanderthal mobility. The first considers that they were exclusively capable to have a residential mobility strategy in small territories, being highly mobile groups (Verpoorte, 2006; MacDonald et al., 2009;

Roebroeks and Verpoorte, 2009; Walker and Churchill, 2014; Churchill et al., 2016). The second considers that the Neanderthals were also able to develop, in certain periods and geographical areas, settlement and mobility strategies typical of logistically organized groups within medium and large regional territories (Patou-Mathis, 2000; Vallverdú et al., 2005; Delagnes and Rendu, 2011; Niven et al., 2012; Marín-Arroyo, 2013; Turq et al., 2017).

The first hypothesis is based specially on Neanderthal physiology evidences to applied to models of optimal foraging theory of the central place. The greater robustness and heavy musculature of the Neanderthals (Porter 1999; Tattersall 1999), together with higher energy requirements (Verpoorte, 2006; MacDonald et al., 2009; Roebroeks and Verpoorte, 2009), have been considered as constraints for the cost of locomotion. Therefore, the physiological robustness of Neanderthals would have reduced their effective foraging radius, forcing these groups to increase their residential movements, indicating a type of residential mobility rather than a logistical one (Walker and Churchill, 2014; Churchill et al., 2016). The central place foraging assumes that when the effective foraging radius decreases, hunter-gatherers are forced to leave the camp. However, since the energetic requirement of Neanderthals was high, this would imply a smaller foraging radius, which forces an increase in the number of trips from the camp, but also at lower distances range because of their less efficient locomotion for long distances. This would also mean short-term occupations at each site (Steudel-Numbers and Tilkins, 2004; Weaver and Steudel-Numbers, 2005). Some authors believe that the low population density of Neanderthals forced them to exploit small territories through high residential mobility (Dusseldorp, 2009; MacDonald et al., 2009). The group requirements are conditioned by group size, the number of people per group and the energetic needs by individuals (Verpoorte, 2006). The higher per capita energy demand of Neanderthals would further reduce the number of individuals who could subsist on the same resource patch compared to AMH (Kuhn, 2013). Churchill (2014), besides, defends that Neanderthals lack of complex technology for subsistence, that would allow them to adapt to ecosystems with higher levels of risk in resource acquisition. Therefore, their food acquisition strategies were based on non-technological adaptations, such as altering group sizes or diet ranges.

Otherwise, the second hypothesis indicates that Neanderthal groups had variable mobility depending on the chronology and territory, but their features could present the variability observed in modern hunter-gatherers (Costamagno et al., 2006; Sharon, 2018). When settlement patterns are analysed, the two following interrelated issues have to be considered; the mobility patterns and settlement types (Vaquero et al., 2012). Mobility patterns are mainly characterized by the distance travelled on each trip, the total annual distance, the number of movements and the character of the movement (Kelly, 1983). The study of mobility and travel distances has traditionally been carried out in

archaeological sites through the study of raw materials catchment and the study of the faunal remains that provide information on the seasonality of the occupations (Clark, 2016).

As logistical and foraging systems differ, among other factors, in the type, number and frequency of settlements generated by hunter-gatherers as they move through the territory (Binford, 1980; Kelly, 1983, 1995) archaeological sites classifications can provide information on the type of mobility of hominin groups. The type of settlement can be known by the function of the site, depending on the type of occupation, its duration and the size of the group that occupied it. However, Burke (2002) has indicated that correlating ethnographical typologies of sites with archaeological contexts are unrealistic and that a distinction should be only made among residential and non-residential sites. This is due to palimpsest condition of most archaeological sites and the difficulty of identifying individual occupations (Vermeersch, 2001; Bailey, 2008). Despite this, there are abundant examples within the archaeological record with enough archaeo-stratigraphic visibility to interpret Neanderthal mobility (Vallverdú et al., 2005; Delagnes and Meignen, 2006; Daujeard and Moncel, 2010a; Delagnes and Rendu, 2011; Moncel and Daujeard, 2012; Vaquero et al., 2012; Soto and de Soler, 2016; Gómez de Soler et al., 2019).

In most of Western Europe, it can be considered that Neanderthals had moderate territorial and mobility ranges (Féblot-Augustins, 1993; Mellars, 1996a; Fernandes et al., 2008). Although some studies on lithic raw materials indicate local catchment ranges (<5 km) for most of the lithic material (e.g. Browne and Wilson, 2011), a trend is detected during the Middle Palaeolithic towards local procurement, however numerous examples in southern and central Europe indicated that supply was regional (100-200 km) during the Middle Palaeolithic (Féblot-Augustins, 1993; Conard and Adler, 1997; Slimak and Giraud, 2007; Spinapolice, 2012; Real et al., 2018).

In the Middle Palaeolithic sites of Near East, human groups have been related to two mobility strategies, multiseasonal logistic mobility in a radiating model related to archaic human populations and another highly seasonal residential mobility in a circulating model related to anatomically modern human populations (Lieberman and Shea, 1994; Marín-Arroyo, 2013). For the radiating model, an occupational stable model has been proposed in which the sites were used for prolonged periods and supplied through specific task sites, suggesting logistical mobility for Neanderthals (Shea, 2003). The Mediterranean region, characterized by an ecologically diverse environment, may have been an area where most resources could easily be obtained from the same place, so logistical mobility to reduce residential movements may have been developed (Shea, 2003).



In Central and Eastern Europe, the low frequency of base camps, compared to temporary camps, has been considered as an indicator of multi-directional logistical mobility strategies (Patou-Mathis, 2000). The low frequency of base camps together with the abundance of numerous sites with particular characteristics, such as temporary hunting halts (Scladina, Chokurcha I, Vindija) and kill and butchering sites (Kabazi II, Tata) has been linked by Patou-Mathis (2015) to the existence of vast supply territories and a multi-directional logistical type of mobility (Patou-Mathis, 2000).

In France, some regional variability in mobility strategies has been observed, between the Rhone valley, the south-western region of the Atlantic basin, and the south-eastern Mediterranean region. In the Rhone Valley, the classification of some sites as hunting halts, temporary campsites and others used as long-term residential camps have been associated with a far-sighted circulating model (Daujeard and Moncel, 2010a; Moncel et al., 2014). This would be similar to the proposal of Walker and Churchill (2014) who proposed that the Neanderthals developed high residential mobility together with small logistic supply mobility. However, this implies that the Neanderthals developed at a certain point a system of radiating mobility, not circulating mobility. Studies on lithic raw materials show that many deposits have regional catchment ranges (e.g. Slimak, 1999; Fernandes et al., 2008; Moncel et al., 2008b, 2014; Browne and Wilson, 2011). In south-western France, changes in the mobility strategy have been observed at a temporary level. Depending on the hunting strategies, the prey and the seasonality have been related to Quina groups and the discoid system groups with logistic mobility, while groups with laminar Levallois technologies were associated with residential mobility (Delagnes and Rendu, 2011; Niven et al., 2012; Turq et al., 2017). On the other hand, in the South-Eastern Mediterranean region of France, Neanderthal groups have been associated with a strategy of circulating mobility, where small groups scattered throughout the territory gatherer daily supplies various resources (Boyle, 2000).

In the Mediterranean basin of the Iberian Peninsula, most studies agree that Neanderthal groups were characterized by being highly mobile, developing, in most cases, accumulations resulting from repeated short-term occupations in regional territories, which could be related to a logistical mobility organization (Martínez-Moreno et al., 2004; Vallverdú et al., 2005; Zilhão and Villaverde, 2008; Rosell et al., 2017; Real et al., 2018). It is considered that in the Valencian record there was a pattern of high mobility characterised by the scattering of Neanderthal in small groups that developed short occupations in most of the sites with the alternation of carnivore occupations, as in Cova Negra and Cova Beneito (Villaverde et al., 1996; Fernández-Peris and Villaverde, 2001; Aura Tortosa et al., 2002). Level I of Abric Romaní has been defined as a result of short-term or non-residential occupation events from the activity of groups immersed within a regional mobility foraging model (Vallverdú et al., 2005, 2012; Chacón et al., 2007; Vaquero et al., 2012; Gómez de Soler et al., 2019). Depending on the studies of

lithic raw material procurement there is a certain variability in the Mediterranean basin of the Iberian Peninsula. In the central zone, some deposits reflect procurement ranges that indicate small territories (Fernández-Peris et al., 2008; Galván et al., 2008; Eixea, 2018; Álvarez-Alonso et al., 2018; Machado et al., 2019; Mallol et al., 2019). For example the sites of Abric del Pastor (Galván et al., 2008; Machado et al., 2019), El Salt (Molina, 2016; Molina et al., 2016) and Abrigo de la Quebrada (Eixea et al., 2011; Real et al., 2018). However, in the latter, the 5% of the identified flint originated over 100 km away (Eixea et al., 2011; Eixea, 2018) and at the Cova Negra site, there is a regional catchment (35-50 km) rather than local (Villaverde et al., 2014; Eixea, 2015). In the Abric Romaní the chert procurement areas are included within a regional range, approximately 16 km from the site (Gómez de Soler et al., 2019).

## **Chapter 2. Materials and methods**



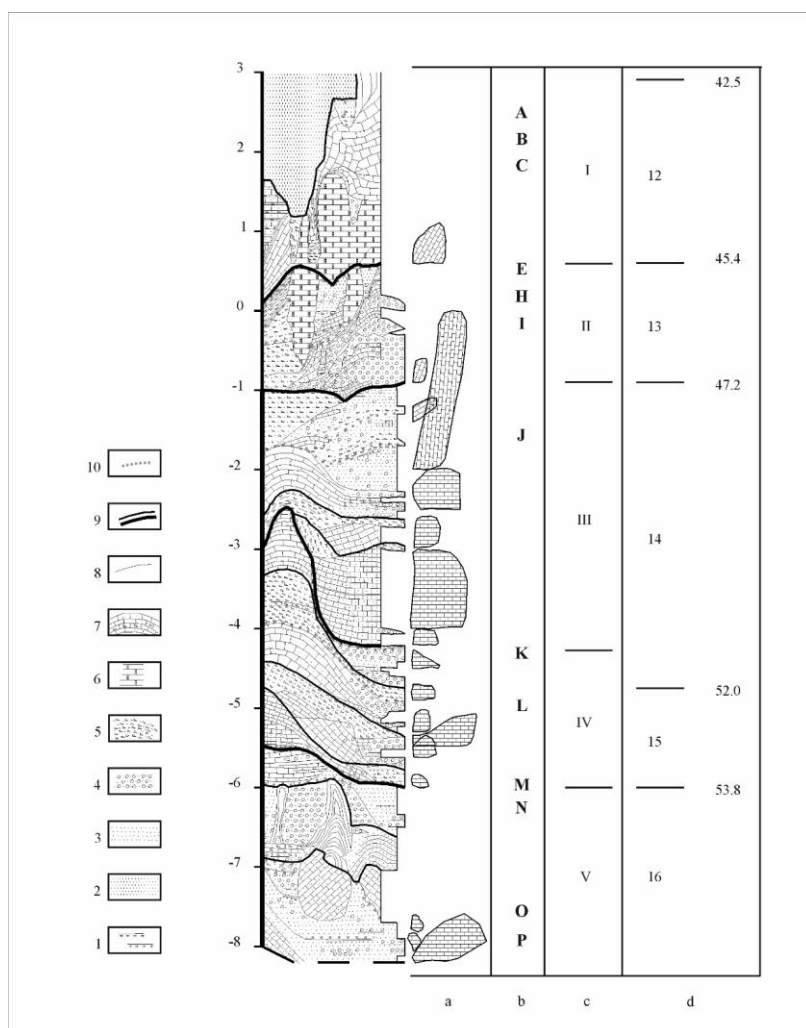
## Materials and methods

Since this work is presented in the form of a thesis compiling by five scientific papers, each one of them contains a section describing the deposits, materials and methodologies used. However, we introduce a brief compilation of the archaeological sites studied and the methods applied to the different assemblages in the different papers. The objective is to serve as a general methodological framework for all the papers.

### 2.1. Materials

#### 2.1.1. Abric Romaní

The Abric Romaní archaeological site is a rock-shelter located in the gorge of the Cinglera del Capelló, 45 km northwest from Barcelona (Spain). The stratigraphy consists of 30 m of well-stratified travertine sediments. Rock fragmentation and alluvial and biochemical sedimentary processes generate beds of consolidated stones, gravels, calcarenites and calcilutites interspersed with very thin archaeological levels (Vallverdú et al., 2010). U-series and radiocarbon dates place the Abric Romaní sequence between ~ 110 and 40 kyr (Sharp et al., 2016) (Figure 1). The sedimentation rate is estimated at around 0.6 m / kyr (Bischoff et al., 1988, 1994). The sequence comprises 17 archaeological levels (Figure 1). Except for level A, all the archaeological units of the sequence correspond to the Middle Palaeolithic. The upper levels of the sequence (A–E) were largely excavated during the previous excavations, and levels E–I were also affected by these digs, although to a lesser extent.

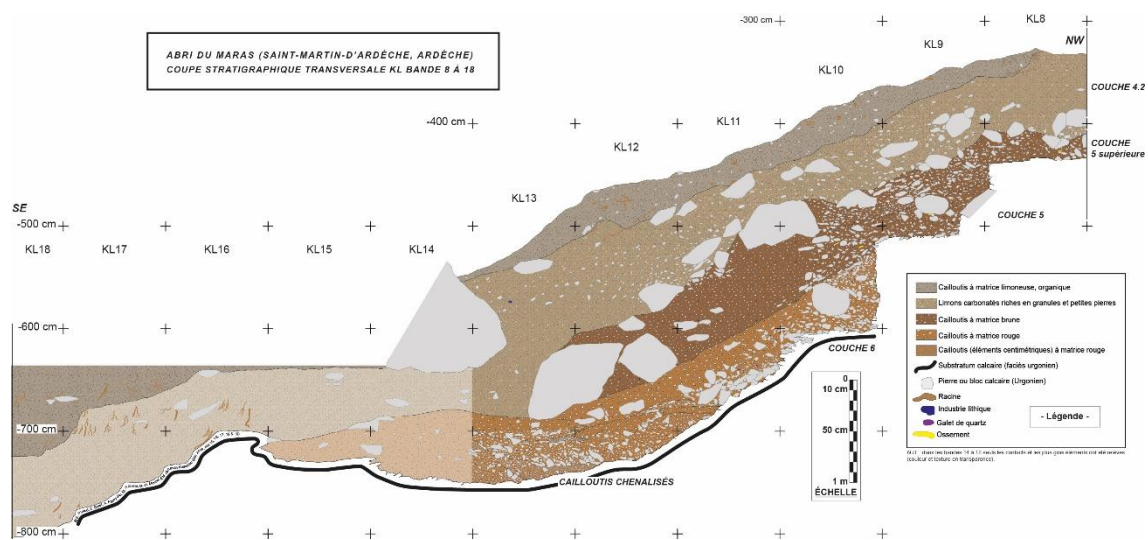


**Figure 1** The lithostratigraphic column of the Abric Romaní Coveta Nord profile (Vallverdú i Poch, 2018). The stratigraphic column contains the temporal position of the archaeological level in accordance with the chronology of the basal boundaries of the Dansgaard-Oeschger events in the GISP2 temporal scale model (Blunier and Brook, 2001). An updated summary of the absolute ages of the Abric Romaní archaeological beds has recently been published (Vaquero et al., 2013). Legend for the lithological column: 1, organomineral grey horizon; 2, red siliciclastic and calcitic silty sand; 3, yellow calcitic sand; 4, yellow tuffaceous-travertine gravel and calcitic sand; 5, platy gravels of crystallitic travertine and calcitic sand and silt; 6, speleothems; 7, cemented sands and travertines; 8, diastem; 9, paraconformity or erosive unconformity; 10, archaeological bed. Legend for the comment columns: a, rock-fall of travertine blocks and megablocks; b, letters of the archaeological beds; c, sedimentary sequences; d, the lower boundary chronology of the Dansgaard-Oeschger events in the temporal scale model of the GISP2 core (Blunier and Brook, 2001).

### 2.1.2. Abri du Maras

The Abri du Maras is located on a small valley, minor than 1 km, perpendicular to the Ardèche river valley, a tributary of Rhone river, near the locality of Saint-Martin d'Ardèche. Its elevation is 170 m above sea level, and 70 m above the Ardèche River. A geological study attests that the cave roof collapsed over time and the youngest occupations were settled under a shelter (Debard, 1988). The oldest level was named level 5 (level 8-6 of earlier excavations) and consists of an organic brown level with a sandy silt matrix, covering the limestone substratum (Figure 2). It is truncated at the front of the site and covered by a sterile level of rubble with a red clay silt matrix. The following is level 4 (Level 5-4 of earlier excavations), made up of homogeneous aeolian silt (loess) with some small blocks of limestone. It is overlain by three levels, level 3, 2 and 1, of rubble with a silty matrix and limestone slabs, like those described during previous excavations and which constrain the most recent occupations (Moncel et al., 2010). The latter also establishes a retraction in the ceiling of the shelter leading to a decrease in the location of human occupations. U-Th dating of four bone samples from

level 5 (middle of the sequence) would place this level between 70 and 90 ka ( $72 \pm 3$  ka,  $87 \pm 5$  ka,  $89 \pm 4$  ka,  $91 \pm 4$  ka), at the end of MIS 5 or the beginning of MIS 4 (Moncel and Michel, 2000). Layer 4.1 in Maras is dated to between  $40 \pm 3$  ka and  $46 \pm 3$  ka (MIS 3), while samples from Layer 4.2 provided ages ranging from  $42 \pm 3$  ka to  $55 \pm 2$  ka (MIS 3). These new ages obtained on Layers 4.1 and 4.2 indicate that the site was occupied from MIS 3, thus extending the known chronology of Abri du Maras (end of MIS 4- the beginning of MIS 5, Moncel and Michel, 2000), and one sample (AM F6-47), positioned at the top of Layer 5bis, gave an age of  $90 \pm 9$  ka (MIS 5c-b), in agreement with the previous dating study. (Richard et al., 2015).



**Figure 2** Vertical projection K/L band of stratigraphic levels from the East Trench (after Simon Puaud; in Moncel et al., 2019). Distinguishing the succession in three terms: from the base, a brown, organic term which can be compared to layer 5. A second silty term corresponding to layer 4 then a term superficial layer.

### 2.1.3. Bize-Tournal

Bize-Tournal Cave is situated in southern France, approximately 20 km north of Narbonne and 2.5 km from Bize-Minervois. Located in the foothills of the limestone massif “La Montagne Noire”, which flanks the Mediterranean Sea, the cave opens on the left side of the Cesse River. At least 11 levels have been identified in 4 units (Figure 3). Unit I is characterised by highly weathered coarse gravel, alternating with greenish plastic clays and clayey silts. The bone assemblage was strongly biased due to post-depositional water- and karst-related modification. Unit II is a 0.5 to 2 m-thick complex, formed of brown clay alternating with silts and clayey silty sands. It contains archaeological layers with very rich assemblages of large mammals and lithic series. The stratigraphy of Unit III has a lower part that comprises clayey gravelly silts and brecciated gravels with limited archaeological material, a middle part is formed of a pink breccia and yellow clayey silt and is archaeologically sub-sterile, and an upper layer is a breccia with a relatively richer archaeological assemblage. The dating of the

archaeological sequence is based on series of charcoal samples (non-calibrated dates), horse bones and teeth (uranium dating), and cervid and bovid bones (non-destructive gamma-ray spectrometry and electron spin resonance) (Yokoyama et al., 1987; Bischoff et al., 1988). Several results are unreliable because of taphonomic alteration, particularly caused by post-depositional water movement (Yokoyama et al., 1987). The most consistent results indicate that the Mousterian horizon from Unit II is dated between  $56,200 \pm 1700$  B.P. (Bischoff et al., 1988) and  $38,000 \pm 8000$  B.P. (Yokoyama et al., 1987).

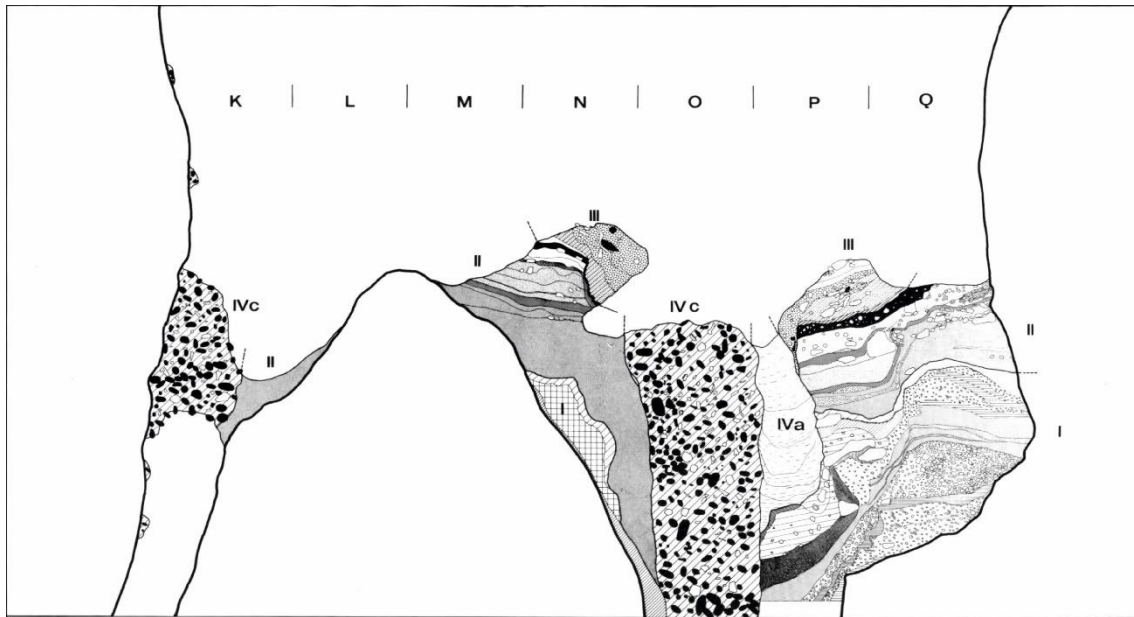


Figure 3 Cross-section of the filling of the northern half gallery between zones 28 and 29. Position of archaeological Unit I (Mousterian), Unit II (Mousterian), Unit III (Aurignacian) and small witness of the Unit IVC (Magdalenian final) plotted centres the wall of the cavity dug by karstic erosion under the Mousterian layers (Tavoso, 1987).

## 2.2. Methods

Bone assemblages are a fundamental source of information about Neanderthal subsistence. The assemblages have been studied through the zooarchaeology. It is centred in the taphonomical analysis of faunal remains. This sub-discipline of archaeology focuses on the study of the relationship between animals and humans and infer aspects of the subsistence strategies among these populations (Domínguez-Rodrigo, 1998).

Taphonomy possesses an analytical range responsible for collecting a series of data, study them and proportionate results. Besides, it has another interpretative line responsible for explaining these results in a general framework (Domínguez-Rodrigo, 1998). Researchers can observe an archaeological object and try to explore the possible links between the processes that could have generated the object and their material



products, causes and effects (Binford, 1983a). This allows us to know the interaction of biological agents that performed during the nutritional phase and the agents that acted during the sub-aerial and diagenetic phases (Capaldo, 1997, 1998; Domínguez-Rodrigo, 1998).

The ethnoarchaeology is a methodological tool specially useful for the prehistoric studies, playing a key role in the comprehension of certain anthropogenic behaviours (Gifford-Gonzalez, 2018). The objective is the use of ethnographic references to understand past human behaviors. Although some studies are exclusively descriptive, providing static references, their purpose is analytical, involving analysis based on cause-effect processes establishing diagnoses that can be applied to the archaeological record (Gifford-Gonzalez, 2018).

Some authors advise the problems and limitations associated with using strict analogies from an ethnologic context to an archaeological context (French, 2019). Although the development of the referential framework is the dominant line of taphonomic research (Bunn and Ezzo, 1993; Selvaggio, 1994, 1998; Blumenschine, 1995; Capaldo, 1998; Lupo, 1998; Lupo and O'Connell, 2002; Domínguez-Rodrigo and Barba, 2006). Indeed, the study of living populations serves us as a model to suggest hypotheses and interpret the archaeological record, although it should be taken with caution (Gifford-Gonzalez, 1991).

### 2.2.1. Identification and abundance measurement

For the anatomical and taxonomical identification, we used a series of atlas of animal anatomy (Pales and Lambert, 1971; Barone, 1976; Varela and Rodríguez, 2004; France, 2009). Besides, we have used the referential collection of the *Salle de Anatomie Comparée du Museum National d'Histoire Naturelle* in Paris (MNHN), the referential collection of the *Centre Européen de Recherches Préhistoriques de Tautavel* (EPCC-CERP) and the referential collection of the *Institut Català de Paleoecologia Humana i Evolució Social* (IPHES) in Tarragona. The features described for each specimen are element, taxa, weight size category, side (anterior, posterior, lateral or medial), portion, lateralisation (right/left) and age-at-death group. To evaluate anatomical representation, the carcasses were divided into anatomical segments: axial cranial (horns, skull, mandible, hyoid and teeth), axial postcranial (vertebrae, ribs and coxal) and appendicular (long limb bones, carpal/tarsal and phalanx). The scapula was grouped within the axial skeleton since its responses to taphonomic processes are similar to those of the axial skeleton (Yravedra and Domínguez-Rodrigo, 2009). The long bones were divided into upper appendicular bones (humerus and femur), intermediate (radius/ulna and tibia) and inferior (metapodials) (Domínguez-Rodrigo, 1997).

We followed the weight size categories modified by Rodríguez-Hidalgo (2015) from different propositions (Brain, 1981; Bunn, 1982). We used a total of five weight categories: very large size category over 800 kg; large size category weighing between 200 and 800 kg; medium-sized category weighing between 50 and 200 kg; small category weighing between 50 and 10 kg; very small category weighing less than 10 kg.

Five measures of abundance have been used. Number of Specimens (NSP), which include the total of specimens regardless of their identification (Grayson, 1984). The number of Identified Specimens (NISP), which include the total of identified remains by taxa, as well as the number of identified specimens by anatomical elements for each taxa (Klein and Cruz-Urbe, 1984). Minimum Number of Elements (MNE), is the minimum number of skeletal elements required for the account of all samples in an assemblage (Todd and Rapson, 1988; Hill, 2008). To calculate the MNE, the superposition of anatomical landmarks, age and side have been considered (Saladié et al., 2011b). Minimum Number of Animal Units (MAU) and their standardized form (%MAU), developed by Binford (1978) to identify patterns in the bone transport and differential survival of element meaning the relative abundance of elements. And finally, the Minimum Number of Individuals (MNI) is calculated considering the laterality, size, morphology and age of the anatomical element more common in taxa (Binford, 1984; Grayson, 1984; Lyman, 1994). As a result of the good preservation of teeth, they are usually used to construct the MNI. When dental remains are not enough to construct the MNI, the estimation has been done with the most represented element.

The efforts directed to the estimation of the MNE, MNI and %MAU have as the main objective the analysis of the anatomical and mortality profiles. These estimations allow us to observe the presence or absence of bias in the anatomical representation and therefore force us to obtain explanations about the origin of the observed skeletal profiles (Egeland, 2007). In this sense, the MNE shows us the skeletal representation of these assemblages, while the %MAU reveals the deviation between what is represented and what is expected, considering the MNI.

In this work, we have calculated the Spearman correlation coefficient ( $r_s$ ) between %MAU and bone mineral density of anatomical parts confronting the values obtained for scanning sites (CT) in bison elements by Kreuzer (1992) following the recommendations of Morlan (1994a), as well as the values obtained by Lam and others (1999) in total mineral density (BMD) in  $\text{g/cm}^3$  by zones for horses and reindeer.

### 2.2.2. Diversity measurements

To establish the degree of taxonomic diversity the Shannon uniformity index (E) and the Simpson diversity index (D) on the NISP of the different identified species were

used. The Shannon diversity index ( $E$ ) =  $-(\sum p_i * \ln p_i) / \ln S$ , here  $S$  is the number of identified specimens and  $p_i$  is the standardized proportion of identified specimens by each  $i$ -nth taxon, expresses the degree of homogeneity among the species distribution. The value of the index goes from 0 to 1, the lower values indicate assemblages taxonomically not uniform, while the higher values, close to 1, are associated with assemblages where the abundance of the different taxa is similar (Magurran, 1988). Although  $E$  index is less sensible to sample size than  $H$ , we calculated the Simpson dominance index as well ( $D$ ) =  $\sum n_i (n_i - 1) / N (N - 1)$ , where  $n_i$  is the number of specimens of the  $i$ -nth taxon and  $N$  is the total number of specimens. In the Simpson index, values close to 1, indicate assemblages in which one species highlights over the others (Magurran, 1988).

### 2.2.3. Determination of age of death and mortality profiles

The age at death of the individual and the seasonality of the settlements was calculated based on the time of eruption and replacement of the teeth and the degree of wear of the occlusal surfaces (Klein and Cruz-Urbe, 1983; Mariezkurrena, 1983; Brown and Chapman, 1991; Steele and Weaver, 2002; Fernandez and Legendre, 2003; Bignon, 2006; Azorit, 2011). The birth period for red deer and horses ranged from the end of spring and the beginning of summer (horse: Levine, 1982; Burke, 2002) (deer: Clutton-Brock et al., 1982; Habermehl, 1985). Given that the period of birth and replacement of deciduous teeth occur at predictable times of the year, so it is possible to calculate the annual cycle and estimate the death season (Stiner, 1990). Horse mortality curves were created by identifying the age of death (Fernandez et al., 2006). Following Fernandez and Legendre (2003) and Fernandez et al. (2006), we calculated the parameters of life tables. Once the age of death was identified, the individuals were grouped into juveniles, prime adults and old individuals (Stiner, 1990), and plotted within triangular charts following the separation of mortality profiles proposed by Stiner (1990) and Discamps and Costamagno (2015) for red deer and horses.

### 2.2.4. Transport of ungulate carcasses

The transport strategy analysis was carried out following the method proposed by Faith and Gordon (2007), by means of the statistical correlation of Spearman's rho between the standardized food utility index (SFUI) and the %MAU and by applying the Shannon uniformity index ( $E$ ) to the anatomical profile. The following high-survival elements were considered: skull, mandible, humerus, radius/ulna, metacarpal, femur, tibia, and metatarsal (Marean and Cleghorn, 2003b). Based on the value of the anatomical parts transported, Binford (1978) established a theoretical model consisting on three different transport strategies, according to the relation between food utility and the abundance of elements: 1) bulk: maximized transport of high and moderate utility elements,

discarding low utility elements at the kill/butchering site; 2) gourmet: maximized transport of high utility elements, discarding moderate and low utility elements; 3) unbiased: body parts are transported relatively to their food utility. This makes it possible to draw a correlation between butchering and transport actions to define economic variables. Faith and Gordon (2007) added one strategy to Binford's model: 4) unconstrained: in which the animal body parts are transported regarding their abundance in a complete skeleton. In addition, the %MAU of the high-survival elements was correlated with the unsaturated marrow index (UMI) proposed by Morin (2007).

### 2.2.5. Fracturing and fragmentation

In order to establish the degree of fragmentation and the actors responsible for fragmentation processes, the method proposed by Bunn (1983) and modified by Villa and Mahieu (1991), has been followed. It had been considered the diaphysis length and circumference, the description of the delineation (longitudinal, transverse and curved / V-shape), the angle (straight, oblique or mixed) and the surface (smooth or jagged) of fracture planes.

### 2.2.6. Ravaging measure

We considered the ratio of limb bone shaft fragments (NISP) to epiphyseal specimens (Marean and Spencer, 1991; Blumenschine and Marean, 1993), and the percentage of change in the epiphysis of the long bones  $[(\text{MNE before ravaging} - \text{MNE after ravaging}) / (\text{MNE before ravaging}) * 100]$  (Blumenschine and Marean, 1993) using the total MNE according to Domínguez-Rodrigo et al. (2002), assuming that each element was represented by two epiphyses.

### 2.2.7. Taphonomic analysis

The taphonomic analysis was completed by the observation the bone surface modifications, using a binocular stereomicroscope (OPTHEC 120-Hz model). The focus of study was the changes produced during the nutritional phase (Capaldo, 1998) of modifications. Damage produced by hominins and carnivores was described according to the anatomical region and portion on which they were found. The identified anthropogenic modifications include cut marks (Binford, 1981a; Potts and Shipman, 1981; Shipman, 1981; Shipman and Rose, 1983; M. Domínguez-Rodrigo et al., 2009), and percussion marks (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994). The type, delineation, situation and position of the cut marks per element allowed us to infer butchery activities. For this, ethnoarchaeological sources (Binford, 1978; Abe, 2005), experimental data (Frison, 1974; Nilssen, 2000) and our own experiments on multiple animals were used. For percussion marks, we identified

percussion notches and pits and adhering flakes (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Vettese et al., 2017). For the study of cremations, changes in the coloration of the bones were taken into account, following the proposal of Stiner et al. (1995). The six coloration stages used are: 0) unburned; 1) small brown or black areas; 2) brown bones; 3) black bones (charred); 4) grey bones (calcined); 5) white bones (calcined). Finally, carnivore modifications identified were pits and scores (Maguire et al., 1980; Binford, 1981a; Johnson, 1985), furrowing (Brain, 1981; Haynes, 1983), and pitting (Binford, 1981a). Digested remains were identified, which present porous and softened surfaces resulting from corrosion by gastric acid (Sutcliffe, 1970). The dimensions of the pits and scores were determined using the criteria of Andrés et al. (2012) and these were compared with the experimental data of Selvaggio (1994), Delaney-Rivera et al. (2009), Andrés et al. (2012), and Saladié et al. (2013). The breakage strategies of humans and carnivores generate impact flakes that are difficult to differentiate (Brain, 1981; Bunn, 1981, 1982b; Potts, 1988b; Capaldo and Blumenschine, 1994). Although they are more common in anthropic breakage, they are not used as a diagnostic element when they do not show signs (percussion marks or tooth marks) that allowing their assignment.

### 2.2.8. Taphotypes

We followed the method developed by Domínguez-Rodrigo et al. (2015), who classified upper and intermediate long bones into different taphotypes according to the carnivore modifications (presence/absence; location of furrowing and tooth marks). This method is used to evaluate only long limb bones (humerus, femur, radius-ulna, tibia) that preserve their complete diaphyseal circumference (Domínguez-Rodrigo et al., 2015). Long bones were divided into 15 taphotypes, in order to quantify different forms of element destruction (Domínguez-Rodrigo et al., 2015). For the analysis, we compared the remains with those of horses and zebras modified by captive and wild lions from Tarangire National Park (Tanzania) and captive hyenas (Domínguez-Rodrigo et al., 2015). The statistical treatment comprised a correspondence analysis (CA) involving contingency tables per element type and taphotype, with a bootstrapped analysis of 1000 resamples. For the study of taphotypes, we used the free statistical software R ([www.r-project.org](http://www.r-project.org)), employing the “cabooters” library (Ringrose, 2012). The plots include 95% confidence ellipses, which show the overlap between the row and column categories in the contingency tables. The CA was also supported by the chi-square test.

### 2.2.9. Archaeostratigraphic and spatial analysis

A series of 25-cm-wide vertical profiles (longitudinal and transversal profiles) have been projected and analysed to identify the sublevels observed during fieldwork over

the entire surface, using ArchePlotter iv1.35.4-beta, developed by IPHES, and ArcGIS 10.4.1 (Desktop, Engine) software.

To identify the different areas of accumulation of remains, we the proposal of Romagnoli and Vaquero (2016), using combined kernel density analysis (Baxter et al., 1997) and the calculation of k-nearest neighbour distances (Baddeley et al., 2015) has been followed.

The distribution of red deer and horse remains was evaluated using Ripley's K function of the "spatstats" library of version 3.2.3 of the R software (R Core Team, 2015; Baddeley et al., 2015). This function is used to describe how a point process occurs in any specified spatial window. The curve of the observed data was interpreted as a grouping process (above the theoretical random process line), a regular process (below the theoretical random line) or CSR (complete spatial randomness) (if it is within the confidence intervals). The confidence intervals were obtained using the Monte Carlo simulation process with 30 random samples of original data. The proposal of Reeves et al. (2019) to analyse patterns of discarded material in palimpsests was used, adapting its code of analysis in R to our study. This proxy allows for the visualizing of the statistical significance of the horizontal distribution patterns of red deer and horse remains. For this, the spatial variation of a series of taxonomic representation indices is calculated using Moving Window Analysis, where each observation represents a value resulting from the calculation of that ratio in its neighbourhood. Subsequently, the statistical significance of the spatial variation of these values is tested by means of the Local and Global Moran's I test of spatial autocorrelation, leading to the identification of statistically significant concentrations of high and low values.

### 2.2.10. Refittings

Faunal remains were refitted for the spatial study, taking into consideration anatomical and mechanical refits (Marean and Kim, 1998). In all cases, distances between the refitted pieces were recorded, as well as their taphonomic modifications, being considered whether the bone had green or dry fractures, and whenever possible, the actor of bone breakage was identified. Concerning faunal refits, we followed the terminology proposed by Todd (1983, 1987) and Lyman (1994, 2006, 2008) and standardized during the subsequent analysis of different levels of Abric Romaní (Gabucio 2014; Bargalló et al. 2016; Gabucio et al. 2016). All remains longer than 2 cm were considered.

### 2.2.11. Redistribution index

To observe the redistribution of carcasses among identified activity zones, the redistribution index (RI) proposed by Jones (1983), although with modifications, has been applied. Its formula is  $RI = \text{MNIf} / (\text{MNIs} * n)$ ; where MNIf is the MNI by hearths, the MNIs is the total MNI and n is the number of hearths. Carcass distribution over a living floor surface can be related to the distribution of ungulate meat. In settlements with a high distribution of animals, the index values are approximately one. However, when animal tissues were not shared, the index is the inverse of the number of hearths. In these cases, the MNI per hearth should be similar to the MNI for the whole settlement surface, and its sum much higher than the total MNI. In cases where there is no redistribution of meat, the sum of the MNI per hearths is like the total MNI count of the assemblage. To apply the formula to level P of Abric Romaní, the index was calculated according to taxa (*Cervus elaphus* and *Equus ferus/hydruntinus*). In addition, since it is not possible to separate clearly the remains for each hearth, the MNIf was calculated for each aggregation of materials related to combustion structures. It should be noted that this only applies to sublevel Pa, where these accumulations could be discriminated in more detail.





**Chapter 3. Ungulate carcass transport strategies at  
the Middle Palaeolithic site of Abric Romani  
(Capellades, Spain)**





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## Ungulate carcass transport strategies at the Middle Palaeolithic site of Abric Romaní (Capellades, Spain)

*Stratégies de transport de carcasses d'ongulé au site Paléolithique moyen de l'Abric Romani (Capellades, Espagne)*Juan Marín<sup>a,b,c,\*</sup>, Palmira Saladié<sup>a,b,d,e</sup>, Antonio Rodríguez-Hidalgo<sup>a,b,c</sup>, Eudald Carbonell<sup>a,b,f</sup><sup>a</sup> Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Unit associated with the CSIC, C/Marcel·li i Domingo s/n, 43007 Tarragona, Spain<sup>b</sup> Àrea de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain<sup>c</sup> Equipo Primeros Pobladores de Extremadura, Casa de la Cultura Rodríguez Moñino, Avenida Cervantes s/n, 10003 Cáceres, Spain<sup>d</sup> Grupo Quaternário e Pré-História do Centro de Geociências (GQP-CG) (ul and D 73–FCT), Tomar, Portugal<sup>e</sup> Unit associated to Consejo Superior de Investigaciones Científicas (CSIC), Departamento de Paleobiología, Museo Nacional de Ciencias Naturales (MNCN), Madrid, Spain<sup>f</sup> Institute of Vertebrate Paleontology and Paleoanthropology of Beijing (IVPP), Beijing, China

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## ABSTRACT

We evaluated the skeletal profiles from several levels of the Neanderthal site of Abric Romaní, focusing on the methodology proposed by Faith and Gordon (2007): differences in the skeletal distribution of animals in accordance with their size and weight; the statistical correlation between the skeletal profiles and standard food utility index; and the anatomical diversity of size-weight categories. Results indicate an unconstrained transport strategy in all levels and all size-weight categories. However, we also found differences in the skeletal distribution of medium-sized and large animals, which may be due to different transport strategies. These characteristics suggest that the superposition of transport and occupation events could be responsible for our results. In addition, we applied the same analysis to Hadza assemblages, which revealed similar results to those found at Abric Romaní. The most striking feature of the Hadza assemblages examined is the superposition of transport events as a result of successive occupation/deposition events. This suggests that the transport strategies used by Neanderthals at Abric Romaní are also characterized by a high degree of diversity in transport decisions.

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## R É S U M É

Nous évaluons les profils squelettiques de différents niveaux du site néandertalien de l'Abric Romaní, en mettant l'accent sur la méthodologie proposée par Faith et Gordon (2007): différences de répartition des squelettes d'animaux en accord avec leur taille et leur poids; corrélation statistique entre les profils squelettiques et l'index d'utilisation de nourriture

## Mots clés :

Néandertal

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Profils anatomiques

Stratégie de transport non contraint

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standard ; diversité anatomique des catégories de poids et de tailles. Les résultats indiquent une stratégie de transport non contraint à tous les niveaux et pour toutes les catégories. Sont également trouvées des différences dans la répartition des squelettes d'animaux de moyennes et de grandes tailles, qui peuvent être dues à des différences de stratégie de transport. Ces caractéristiques suggèrent que la superposition d'événements de transport et d'occupation peut être responsable de nos résultats. En outre, nous avons appliqué la même analyse aux assemblages de Hadza, qui révèlent des résultats similaires à ceux de l'Abri Romani. Le trait le plus étonnant des assemblages de Hadza examinés est que la superposition des événements de transport est considérée comme le résultat d'événements successifs occupation/dépôt. Ceci suggère que les stratégies de transport utilisées par les Néandertaliens à l'Abri Romani sont aussi caractérisées par un haut degré de diversité dans les décisions relatives au transport.

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## 1. Introduction

The transport of animal carcasses to archaeological sites has been studied by means of the reconstruction and analyses of skeletal profiles through skeletal part frequencies, established utility ranks and theoretical transport models. Potential behavioural implications have been drawn through comparisons with ethnoarchaeological works, the exclusive source of information with which to establish analogies in relation to present-day human hunter-gatherer behaviour (e.g. Binford, 1978, 1981, 1984; Bunn and Ezzo, 1993; Bunn et al., 1988; Clerghorn and Marean, 2004; Domínguez-Rodrigo et al., 2009; Lupo, 2001; Marean and Clerghorn, 2003; Monahan, 1998; O'Connell et al., 1988a, 1988b, 1990, 1992).

With regard to the analysis of skeletal profiles, Perkins and Daly (1968) proposed that a high presence of long limb bones and heads versus a low presence of vertebrae and ribs in archaeological sites was evidence of human activities, the result of a differential transport strategy that they called the *schlep effect*. According to this proposal, the human group discarded the postcranial axial skeleton at the kill/butchering site and transported only the limbs and heads to the residential camp. More recent works have suggested that the previously proposed *schlep effect* seemed rather to be the result of an incomplete analysis of the faunal record (Clerghorn and Marean, 2004; Domínguez-Rodrigo, 1999; Marean and Clerghorn, 2003). These authors assert that the study of transport strategies based on the presence or absence of the postcranial axial skeleton can lead to misinterpretations of the archaeological record (Bunn, 1983; Clerghorn and Marean, 2004; Marean and Clerghorn, 2003; O'Connell et al., 1990, 1992). As Marean and Clerghorn (2003) have indicated, a great number of processes could result in a head and limb assemblage because these are elements with high mineral density in some of their portions, and are therefore more resistant to attritional processes. Some of these processes include human activities such as boiling, cleaning labours or fire management (Costamagno and Rigaud, 2014), which have been observed at the Abri Romani site (Gabucio et al., 2014; Vallverdú et al., 2012). So as these researchers have proposed, the analysis of skeletal profiles and transport strategies should only consider

high-survival elements (Clerghorn and Marean, 2004; Marean and Clerghorn, 2003).

One of the objectives of many ethnoarchaeological studies conducted since the 1970s has been to analyse why some specific body parts are transported while others are discarded (e.g. Binford, 1978; Bunn, 1983; O'Connell et al., 1988a, 1988b, 1990, 1992). To this end, food utility indices were created in which skeletal elements are rated based on their marrow content, intra-osseous fat content or the fleshy tissues attached to them (e.g. Binford, 1981; Emerson, 1993; Lyman, 1994; Metcalfe and Jones, 1988; Morin, 2007). Many ethnoarchaeological and methodological studies have focused on analysing and categorizing the economic value of each animal body part (e.g. Bartram, 1993a, 1993b; Bartram and Marean, 1999; Bartram et al., 1991; Binford, 1978; Emerson, 1993; Lyman, 1994; Marean and Frey, 1997; Marlowe, 2010; Metcalfe and Jones, 1988; O'Connell et al., 1988a, 1988b, 1990, 1992).

Based on the value of the anatomical parts transported, Binford (1978) established a theoretical model consisting of three different transport strategies:

- bulk: maximized transport of high and moderate utility elements, discarding low utility elements at the kill/butchering site;
  - gourmet: maximized transport of high utility elements, discarding moderate and low utility elements;
  - unbiased: body parts are transported relative to their food utility. This makes it possible to draw a correlation between butchering and transport actions in order to define economic variables.
- Faith and Gordon (2007) add a strategy to Binford's model;
- unconstrained, in which the animal body parts are transported in relation to their abundance in a complete skeleton.

Thus, large accumulations of faunal remains at archaeological sites should reveal skeletal patterns resulting from transport and/or discard decisions.

Ethnoarchaeological studies have also looked into the behavioural characteristics of present-day foragers in order to determine whether their practices are reflected in Upper and Middle Palaeolithic archaeological sites (Bunn, 1983).

According to these works, transport decisions depend on numerous social, ecological and/or economic factors (e.g. Binford, 1978; Blurton Jones et al., 1989; Hawkes et al., 2001; Lupo, 2001; Monahan, 1998; O'Connell et al., 1992). For example, Monahan (1998) refuted the hypothesis that defined the Hadza as a hunter-gatherer group that transports only heads and limbs, defended previously by Bunn et al. (1988), as well as the hypothesis that defined them as a group that always transports the postcranial axial skeleton, as O'Connell et al. (1990) claimed. Monahan (1998) concluded that archaeological assemblages do not reflect a single transport model, but rather the sum total of different overlapping transport events. This amalgamation makes it difficult to read specific events at archaeological sites, and when they are combined with the participation of other taphonomic agents, it is even more difficult to make inferences about the subsistence strategies of prehistoric hominins (Saladié et al., 2011).

Studies on the prey acquisition and transport decisions of Neanderthal groups suggest that these groups' exploitation of the herbivores in their environment was highly complex, with medium-sized and large ungulates being the most common animal remains recovered at archaeological sites (e.g. Brugal and David, 1993; Costamagno et al., 2006; Daujeard, 2004; Daujeard and Moncel, 2010; Daujeard et al., 2012; Fernández et al., 1998; Gaudzinski and Niven, 2009; Jaubert and Brugal, 1990; Moncel and Daujeard, 2012; Moncel et al., 2004; Patou-Mathis, 2000; Rendu, 2010; Rendu et al., 2012; Romandini et al., 2014; Rosell et al., 2012a, 2012b; Stiner, 1991, 1994, 2002, 2009; Voormolen, 2008). At Mousterian sites, the most common skeletal profiles are characterized by the scarcity of the postcranial axial skeleton and the predominance of the long limb bones and heads (Gaudzinski and Niven, 2009; Romandini et al., 2014; Rosell et al., 2012a, 2012b; Valensi and Psathi, 2004). At some sites, where the faunal remains of medium-sized animals outnumber those of large animals, it has been suggested that the skeletal profile is the result of a differential transport based on animal size-weight (e.g. Gaudzinski and Niven, 2009; Patou-Mathis, 2000; Rendu, 2010; Romandini et al., 2014; Rosell et al., 2012a, 2012b).

Abric Romaní consists of an extensive sequence of levels containing clear material evidence of Neanderthal occupation and activities (e.g. Carbonell, 2002, 2012; Chacón et al., 2007, 2010; Fernández-Laso et al., 2010; Gabucio et al., 2013, 2014; Rosell et al., 2012a, 2012b; Vallverdú et al., 2005; Vallverdú et al., 2012; Vaquero et al., 2001, 2012a, 2012b). The transport sequence starts with access to one or more animal carcasses and ends with the discarding of unused or exhausted animal remains (Binford, 1978). Therefore, the transport of carcasses is one of the steps undertaken during the animal butchering process. However, it is also important to explore the abandonment of some body parts, whether consumed or not, at any of the stages prior to their exhaustion. This is most likely to happen, as indicated by a large number of ethnoarchaeological works (e.g. Binford, 1978, 1981; Bunn and Kroll, 1986, 1988; Bunn et al., 1988; Hawkes et al., 2001; Hayden, 1981; Lupo, 2001; Monahan, 1998; O'Connell et al., 1988a, 1988b, 1990, 1992; Schoville and Otárola-Castillo,

2014; Yellen, 1977), as well as research conducted at archaeological sites (Domínguez-Rodrigo et al., 2009; Gaudzinski and Niven, 2009; Moncel et al., 2004; Niven et al., 2012; Patou-Mathis, 2000; Rendu, 2010; Romandini et al., 2014; Saladié et al., 2011), during the preparation of the carcass for transport from the kill/butchering site.

The transport patterns established by hominins, including modern humans, may be subject to many different variables, including social factors such as group size, or situational aspects such as the size of the animal hunted, among many others (Binford, 1978, 1981; Bunn, 1993; Bunn and Kroll, 1986, 1988; Bunn et al., 1988; Hayden, 1981; Monahan, 1998; Schoville and Otárola-Castillo, 2014). The study of what parts of the animal are brought back to camp can therefore provide insight into those social factors, or at least allow for a tangential approach towards them through inferences made about transport patterns.

In the case of the Abric Romaní Neanderthal site, medium-sized animals (the size of adult deer) are thought to have been transported whole to the central camp, and large animals (horses and aurochs adults-sized) were processed at the kill/butchering site, with only their limbs and heads carried back to camp (Cáceres et al., 1998; Fernández-Laso et al., 2011; Rosell et al., 2012a, 2012b; Saladié and Aïmene, 1998; Vallverdú et al., 2005). Our analysis of the faunal record of Abric Romaní reveals the presence of all parts of the skeleton in all the size-weight categories. For these reasons, the aim of this paper is to review the carcass transport strategies employed by the Neanderthal groups who occupied Abric Romaní and to infer the socioeconomic connotations that the strategies chosen by these hominin groups may have had. Working from this starting point, our objective is to study the skeletal profiles of the different assemblages generated by the Neanderthals at Abric Romaní in accordance with the proposals put forth by Marean et al. (Clerghorn and Marean, 2004; Marean and Clerghorn, 2003; Marean et al., 2004), i.e. analysing only the high-survival elements and relating them to the survival and nutritional value of the body parts and skeletal segments, and with those advanced by Faith and Gordon (2007), i.e. combining the correlations between utility rank indices and the anatomical diversity of the skeletal profiles to evaluate possible decisions in the transport of carcasses by Neanderthal groups. We centre our analyses on the large and medium-sized ungulates, mainly represented by deer, horses and aurochs, because they are the most common animals in the archaeozoological record of Abric Romaní, and previous works focus the discussion of Neanderthals transport strategies on these two size-weight categories.

## 2. Abric Romaní

The Abric Romaní archaeological site is a rock-shelter located on the northeastern side of the Cinglera del Capelló cliff in the town of Capellades, 45 km north-west of Barcelona, Spain. Its coordinates are 41° 32' N and 1° 41' E, its altitude is 280 m asl, and the cliff wall faces north-northeast. Its stratigraphy is made up of 20 m of well-stratified travertine sediments. Rock fragmentation and alluvial and biochemical sedimentary processes

generated boundstones, gravels, calcarenites, and calcilutites interbedded with very fine archaeological levels. U-series and radiocarbon dates put the Abric Romaní chronostratigraphy between 70 and 40 kyr. The sedimentation rate is estimated at around 0.6 m/kyr (Bischoff et al., 1988). Discovered in 1909 by Amador Romaní, the site was excavated at different periods throughout the 20th century. Ongoing excavations started in 1983 under the direction of Dr Eudald Carbonell.

Except for level A, all of the archaeological units in the sequence correspond to the Middle Palaeolithic (Fig. 1). The upper levels of the sequence (A–E) were largely excavated during the previous excavations, and levels E–I were also affected by these digs, although to a lesser extent.

The different levels of Abric Romaní are the result of the accumulation of an unknown number of occupational events. The occupation models that make up the archaeological record can be distinguished as long-term occupation events or short occupation and/or non-residential events (Vallverdú et al., 2005, 2010; Vaquero et al., 2012a). In both models, the hearths were reused, especially in long-term events, which resulted in the preservation of these structures (Vallverdú et al., 2010; Vallverdú et al., 2012). The main characteristic that differentiates these two occupation models in the record is that in the short-term or non-residential events (Table 1), areas where specific activities were performed (conservation areas for animal biomass, knapping areas, butchering areas) can be isolated and differentiated (Vallverdú et al., 2005). Meanwhile, levels characterized by long-term events exhibit overlapping of different areas and places where activities occurred and these cannot be clearly differentiated from one another (Vaquero et al., 2012b).

Therefore, the representation and superposition of occupancy models may involve the mixing of materials corresponding to different types of strategies. This effect is also observed in the lithic assemblage of Abric Romaní (Vaquero, 2008). The predominant structural category is that of flakes. Cores and retouched flakes are not abundant in the assemblages from the different levels (Chacón and Fernández-Laso, 2007; Martínez and Rando, 2000; Vaquero, 2008; Vaquero et al., 2001, 2004). The predominant raw material in the assemblage is flint, compared to other materials such as quartz or limestone. Other raw materials, like slate, sandstone, quartzite and, to a lesser extent, porphyry are also present (Table 1). Most raw materials are found in nearby sheltered environments, such as the terraces of the Anoia River and the Palaeozoic formations of the Capellades strait. Flint, however, is found in various formations located within a radius of about 28 km (Table 1) (Gómez de Soler, 2007; Morant and García-Antón, 2000). Short-duration or non-residential occupation events have been linked to the transport and abandonment of most of the retouched artefacts, notches and denticulates, whereas the exploitation of cores oriented towards the production of small flakes has been associated with long-term occupation events. The grounds for these conclusions lie in the fact that flint is the preferential raw material at the site, and it comes from reservoir outcrops not found in the immediate vicinity. Therefore, the abandonment of retouched elements has been related to less economical

occupations and the exploitation of cores to occupations that tend to maximize resources (Vallverdú et al., 2005; Vaquero et al., 2012a).

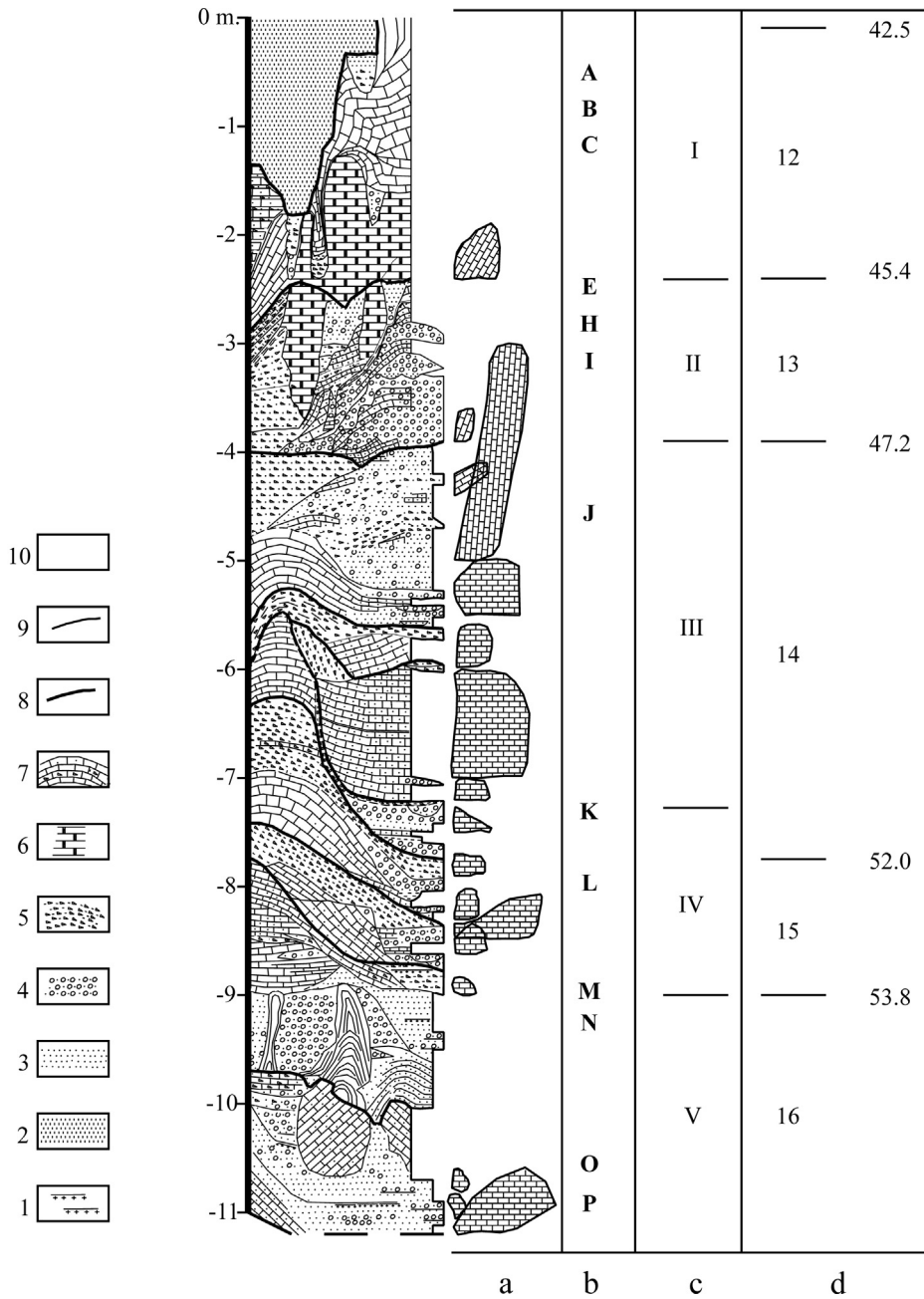
Since the 1990s, considerable importance has been placed on the zooarchaeological and taphonomic studies of the faunal remains recovered in the Abric Romaní sequence, many of them part of multidisciplinary research projects (e.g. Aïmene, 1997, 1998; Aïmene et al., 1996; Cáceres, 1998; Cáceres et al., 1998, 2012; Carbonell, 2002; Chacón and Fernández-Laso, 2007; Chacón et al., 2007, 2010; Gabucio et al., 2013, 2014; Rosell et al., 2012a, 2012b; Vallverdú et al., 2005, 2010). Faunal remains are very abundant in all of the levels of the Abric Romaní stratigraphic sequence. A total of 13 different taxa have been identified, although deer (*Cervus elaphus*) and horses (*Equus ferus*) are the most abundant animals (Table 2). Auroch remains (*Bos primigenius*) are also common at the current bottom of the sequence and chamois (*Rupicapra pyrenaica*) in the upper levels. Rhinoceros (*Stephanorhinus sp. hemitoechus*) remains have been documented in several levels, although they are scarce. In level E, a proboscidean femur shaft has been recovered. Although large herbivores predominate in all of the levels, some carnivore remains have also been recovered (Table 2) (Supplementary material).

Combustion structures are also common in all of the levels excavated at Abric Romaní to date. These structures are circular or oval in appearance and are distinct from the travertine substrate. They are characterized by a colour change, by the stratification of rufed and carbonaceous facies and by sediment compaction.

The hearth areas also contain combustion waste products, such as ashes and coals, along with other remainders of anthropic activity, such as bone and stone remains (Vallverdú, 2002; Vallverdú and Courty, 2012; Vallverdú et al., 2012). Abric Romaní has yielded fossil wood remains recovered as empty cavities in the shape and with the negative mould of the original wood surface. These remains are empty travertine imprints of completely decayed wood (Carbonell, 2002; Castro-Curel and Carbonell, 1995). The wood totally decays leaving only an imprint in the travertine when the water process stops (Castro-Curel and Carbonell, 1995). The study of these imprints has made it possible to distinguish between firewood and worked wood (Allué et al., 2012; Solé et al., 2014).

### 2.1. Zooarchaeological and taphonomical data

The data for this study were extracted from Rosell et al. (2012a, 2012b) for level J (Ja and Jb sublevels), Chacón and Fernández-Laso (2007) and Fernández-Laso et al. (2010) for level K, Chacón et al. (2007, 2010) for level L, and our own analysis of the level M assemblage. We only use the remains of the large and medium ungulates. The very large and small ungulates and the carnivore remains are not included because they are poorly represented in the Abric Romaní sequence. However, we use the presence of some bones of very large size to support some of our conclusions. These levels are not affected by the pits of the former excavations and were extensively excavated ( $\approx 250 \text{ m}^2$ ) in the recent archaeological interventions, thereby ensuring an absence of bias in the collection of the faunal remains.



**Fig. 1.** The lithostratigraphic column of the Abric Romaní Coveta Nord profile (figure elaborated and courtesy by J. Vallverdú et al., 2012). The stratigraphic column contains the temporal position of the archaeological level in accordance with the chronology of the basal boundaries of the Dansgaard–Oeschger events in the GISP2 temporal scale model (Blunier and Brook, 2001). An updated summary of the absolute ages of the Abric Romaní archaeological beds has recently been published (Vaquero et al., 2013). Legend for the lithological column: 1, organomineral grey horizon; 2, red siliciclastic and calcitic silty sand; 3, yellow calcitic sand; 4, yellow tuffaceous-travertine gravel and calcitic sand; 5, platy gravels of crystallitic travertine and calcitic sand and silt; 6, speleothems; 7, cemented sands and travertines; 8, diastem; 9, paraconformity or erosive unconformity; 10, archaeological bed. Legend for the comment columns: a: rock-fall of travertine blocks and megablocks; b: letters of the archaeological beds; c: sedimentary sequences; d: the lower boundary chronology of the Dansgaard–Oeschger events in the temporal scale model of the GISP2 core (Blunier and Brook, 2001).

**Fig. 1.** Lithostratigraphie du profil de la Coveta nord de l’Abric Romani (Vallverdú et al., 2012). La colonne stratigraphique contient la position temporelle des couches archéologiques en relation avec la chronologie des limites basales des événements avec le modèle temporel de GISP2 Dansgaard–Oeschger (Blunier et Brook, 2001). Un résumé actualisé des couches archéologiques de l’Abric Romani a récemment été publié (Vaquero et al., 2013). Légende pour la colonne lithologique : 1, horizon gris organominéral ; 2, sable limoneux silicoclastique et calcitique rouge ; 3, sable calcitique jaune ; 4, gravier travertineux et sable calcitique jaune ; 5, graviers lamellaires aplatis de travertine cristallin et sable et limon calcitiques ; 6, spéléothème ; 7, sables et travertins cimentés ; 8, diastème ; 9, paraconformités et discordances érosives ; 10, couche archéologique. Légende des commentaires : a : chute de travertins et de mégablocs gravitaires ; b : lettre des couches archéologiques ; c : séquences sédimentaires ; d : chronologie de la limite basale des événements Dansgaard–Oeschger dans le modèle d’échelle temporelle du carottage GISP2 (Blunier et Brook, 2001).

**Table 1**

Summary by layer, occupation type, lithic, wood used and previously enunciated transport strategies (Bischoff et al., 1988; Burjachs and Julià 1994; Carbonell, 2012; Chacón et al., 2007, 2010; Gómez de Soler, 2007; Rosell et al., 2012a, 2012b; Solé et al., 2014; Vallverdú et al., 2012; Vaquero et al., 2012a, 2012b).

**Tableau 1**

Résumé par niveaux, type d'occupation, lithique, bois utilisé et stratégies de transport précédemment énoncées (Bischoff et al., 1988; Burjachs et Julià 1994; Carbonell, 2012; Chacón et al., 2007, 2010; Gómez de Soler, 2007; Rosell et al., 2012a, 2012b; Solé et al., 2014; Vallverdú et al., 2012; Vaquero et al., 2012a, 2012b).

Abric Romaní	Model of occupation	Lithic		Charcoals, hearths and wood remains	Ungulate	Mortality profiles	Carcasses Transport Strategies
		Raw Material	Knapping Methods				
Level J	Residential camp: Long-term occupation	Flint (75%) outcrops to 5 km and 25 km Quartz and Limestone (10%) local 5 km	Discoid + centripetal Lithics tools: Denticulates and cores are scarce; small flakes are common	<i>Pynus sylvestris</i> (71%) <i>Pinus uncinata</i> (3.4%) Hearths = 60 Combustion and configuration. Preservation of wood is scarce, fuel wood accumulations. Pointed wooden element	<i>Cervus elaphus</i> <i>Equus ferus</i> <i>Equus hydruntinus</i> <i>Stephanorhinus sp. hemitoechus</i> <i>Bos primigenius</i> <i>Rupicapra pyrenaica</i> Proboscidea	Ja: Young = 8 Juvenile = 8 Prime Adult = 22 Old = 4 Jb: Young = 3 Juvenile = 3 Prime Adult = 8 Old = 1	Differential transport: Small and Medium animals were transported whole to the site; Large animal were processed on kill site and transport only their high food utility element
Level K	Residential camp: Short-term occupation	Local and semi-local raw materials between 15 and 20 km Flint (47.9%) Limestone (19.2%) Quartz (28%)	Discoid Lithics tools: Denticulates and cores are scarce; small flakes are common	<i>Pynus sylvestris</i> (54.51%) <i>Pinus uncinata</i> (0.4%) Hearths = 25 Combustion and configuration. Little accumulation of negative with signs of cremation	<i>Cervus elaphus</i> <i>Equus ferus</i> <i>Stephanorhinus hemitoechus</i> <i>Bos primigenius</i>	Young = 2 Juvenile = 2 Prime Adult = 8 Old = 1	Differential transport: Small and Medium animals were transported whole to the site; Large animal were processed on kill site and transport only their high food utility element
Level L	Residential camp: Short-term occupation	Local and semi-local raw materials between 15 and 20 km Flint (83.7%) Limestone (9.9%) Quartz (3.3%)	Discoid Lithics tools: Denticulates and cores are scarce; small flakes are common	<i>Pynus sylvestris</i> (63.78%) <i>Pinus uncinata</i> (2.8%) Hearths = 23 Combustion and configuration. Four accumulations grouped together to hearths	<i>Cervus elaphus</i> <i>Equus ferus</i> <i>Bos primigenius</i>	Young = 2 Juvenile = 2 Prime Adult = 4 Old = 2	Differential transport: Small and Medium animals were transported whole to the site; Large animal were processed on kill site and transport only their high food utility element
Level M	Residential camp: Long-term occupation	Local and semi-local raw materials between 15 and 20 km Flint (80%) Limestone (9.4%) Quartz (5.3%)	Discoid + centripetal Lithics tools: Denticulates, scarpers and cores are scarce; small flakes are very common	<i>Pinus Sylvestris/nigra</i> (59%) <i>Pinus uncinata</i> (1.5%) Hearths = 37 Combustion and configuration. Four accumulations grouped together to hearths	<i>Cervus elaphus</i> <i>Equus ferus</i> <i>Stephanorhinus hemitoechus</i> <i>Bos primigenius</i>	Young = 3 Juvenile = 2 Prime Adult = 11 Old = 2	Differential transport: Small and Medium animals were transported whole to the site; Large animal were processed on kill site and transport only their high food utility element



**Table 2**

Faunal taxa identified at Abric Romani and their location in the sequence by archaeological levels named from top to the base by capital letters.

**Tableau 2**

Animaux identifiés dans l'ensemble faunistique de l'Abric Romani et leur place dans la séquence par niveaux archéologiques nommés du sommet vers la base (avec lettres majuscules).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
<i>Ursus sp.</i>		X											X	
<i>Canis lupus</i>		X			X									
<i>Panthera leo spelaea</i>									X					
<i>Panthera pardus</i>				X										
<i>Lynx sp.</i>	X	X			X									
<i>Felis silvestris</i>	X	X											X	
<i>Crocuta crocuta</i>	X	X			X								X	
<i>Proboscidea indet.</i>					X									
<i>Stephanorhinus cf. hemitoechus</i>								X					X	
<i>Equus ferus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Cervus elaphus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Bos primigenius</i>					X				X	X	X	X	X	X
<i>Rupicapra pyrenaica</i>	X	X		X	X	X	X	X		X				

**Table 3**

Distribution of the number of identified specimens (NISP), total minimal number of elements (MNE), MNE of the high and low-survival elements and the minimal number of individuals (MNI) of levels Ja, Jb, K, L and M by size-weight categories. Data for levels Ja and Jb extracted from Rosell et al. (2012a, 2012b); for level K from Chacón and Fernández-Laso (2007) and Fernández-Laso et al. (2010); for level L, Chacón et al. (2007, 2010); authors' analysis for level M data.

**Tableau 3**

Répartition du nombre de spécimens identifiés (NISP), du nombre minimal total d'éléments (MNE), MNE des éléments de haute et faible survie et du nombre minimum d'individus (MNI) des niveaux Ja, Jb, K, L et M par catégories de tailles et de poids. Les données pour les niveaux Ja et Jb sont extraites de Rosell et al. (2012a, 2012b); pour le niveau K, de Chacón et Fernández-Laso (2007) et Fernández-Laso et al. (2010); pour le niveau L, de Chacón et al. (2007, 2010); pour les données de la couche M, de l'analyse de ces auteurs.

Level	Animal size	NISP	Total MNE	High-survival elements MNE	Low-survival elements MNE	MNI
Ja	Large	439	118	113	5	17
	Medium	497	171	123	48	15
Jb	Large	154	42	42	0	6
	Medium	96	52	45	7	3
K	Large	71	22	16	6	4
	Medium	335	69	49	20	9
L	Large	40	15	12	3	6
	Medium	96	37	32	5	5
M	Large	105	44	36	8	10
	Medium	711	104	71	33	7

Level Ja yielded 6738 faunal remains, of which 984 (14.6%) were identified anatomically. The taxonomic diversity of this level is high although ungulate remains predominate. Rosell et al. (2012b) identified *Equus ferus* (NISP=351), *Cervus elaphus* (NISP=497), *Bos primigenius* (NISP=88), *Stephanorhinus hemitoechus* (NISP=33), *Rupicapra pyrenaica* (NISP=6), *Ursus sp.* (NISP=1), *Lynx sp.* (NISP=1), *Canis lupus* (NISP=2) and *Vulpes vulpes* (NISP=1). This taxonomic distribution shows that medium-sized and large animals are the most abundant, while very large and small animals are scarce (Table 3). Level Ja is an anthropogenic accumulation in which the activity and disturbance of carnivores (NR=61) was extremely rare (Cáceres et al., 2012; Rosell et al., 2012a, 2012b). Lithic remains refits (262 refitting groups) and the overlapping of the hearths indicate that the level was formed in different occupational events, in long- to medium-term occupations with intercalated phases of short or non-residential occupations (Vallverdú et al., 2012; Vaquero et al., 2012a, 2012b).

In level Jb, 1722 faunal remains were recovered, 281 (16.3%) of which were identified anatomically. Rosell et al. (2012b) identified *E.ferus* (NISP=139), *C.elaphus* (NISP=96), *B.primigenius* (NISP=15), *S.hemitoechus*

(NISP=27) *R.pyrenaica* (NISP=2), *Lynx sp.* (NISP=1) and *Crocuta crocuta* (NISP=1). Level Jb also corresponds to a long-term occupation. From a zooarchaeological perspective, levels Ja and Jb exhibit the same features (Rosell et al., 2012b), but unlike the occupation of Ja, the breadth of the occupation does not cover the entire surface area, but rather is concentrated in the central area of the rock-shelter floor (Carbonell, 2012; Sañudo et al., 2012).

A total of 2564 faunal remains were recovered from level K, 406 (15.8%) of which were identified anatomically (Chacón et al., 2010). The taxa recorded in the assemblage are *C.elaphus* (NISP=335), *E.ferus* (NISP=56), and *B.primigenius* (NISP=15). As in the previous levels, the level K assemblage has been interpreted as anthropogenic in origin, but this unit has yielded more evidence of the secondary activity of carnivores on the faunal remains (NR=78) (Chacón et al., 2010; Fernández-Laso et al., 2010). Level K is the result of overlapping short-term occupations (Chacón et al., 2010, 2013).

Level L yielded 1002 faunal remains, 136 (13.6%) of which were identified anatomically (Chacón et al., 2010). The taxa identified are *C.elaphus* (NISP=96), *E.ferus* (NISP=34) and *B.primigenius* (NISP=6). Level L is characterized by a low MNI compared to the other levels

**Table 4**

Number of remains (NR) and corresponding percentage of anthropogenic and carnivore modifications in levels Ja, Jb, K, L and M (Chacón et al., 2007, 2010; Fernández-Laso et al., 2010; Rosell et al., 2012a, 2012b).

**Tableau 4**

Nombre de restes (NR) et pourcentage correspondant des modifications anthropiques dues aux carnivores dans les couches Ja, Jb, K, L et M (Chacón et al., 2007, 2010; Fernández-Laso et al., 2010; Rosell et al., 2012a, 2012b).

	Ja		Jb		K		L		M	
	NR	%	NR	%	NR	%	NR	%	NR	%
Cut marks	448	6.6	69	4	105	4.1	67	6.7	292	6.7
Percussion marks	804	11.9	149	8.6	275	10.7	34	3.4	163	3.7
Burned bones	2113	31.3	317	18.4	1301	20.7	513	51.2	1599	36.9
Tooth marks	61	0.9	4	0.2	78	3	8	0.8	13	0.3
Total	6738		1722		2564		1002		4334	

(Supplementary material), which has been related to shorter occupation events or occupations of small groups of Neanderthals. At the same time, there is less dispersion of the remains across the living floor. The lithic and faunal remain refits also suggest that level L is the product of short occupations, as most of the connections were made within the defined accumulation activity areas (Chacón et al., 2007, 2010; Fernández-Laso et al., 2010).

A total of 4334 faunal remains were recovered from level M, 836 of which have been anatomically identified. The taxa represented in this assemblage are *C. elaphus* (NISP=711), *E. ferus* (NISP=84), *B. primigenius* (NISP=31), *Stephanorhinus cf. hemitoechus* (NISP=2), *Ursus* sp. (NISP=1) and *C. crocuta* (NISP=1). The internal distribution of the faunal and lithic record, along with the intentional accumulation of firewood, has led to the suggestion that level M is the product of a reiteration of long-term occupations, showing a similar occupational pattern to level Ja. The abundance of remains as well as their dispersion and the MNI of the different animals (Table 3) seem to corroborate this hypothesis (Chacón et al., 2010, 2013; Fernández-Laso et al., 2011; Solé et al., 2014).

The most abundant modifications produced during the biostratigraphic phase (after Capaldo, 1998) are related to the exploitation of nutrients by Neanderthals (Table 4): cut marks (disarticulation, defleshing, evisceration, skinning) and bone breakage are abundant. Modifications caused by carnivores are virtually absent in the assemblages from the four levels analysed here. In levels Ja, Jb, L and M the modifications produced by carnivores affect less than 1% of the assemblage, with the exception of level K, where carnivore modifications affect 3% remains. Nevertheless, the impact of carnivores is still low throughout the assemblage, and occurs only on remains previously abandoned by Neanderthals (Chacón et al., 2010). The absence or scarcity of carnivore-induced modifications as well as the distribution of cut marks, mainly on shaft fragments, along with almost universal anthropogenic bone breakage, support the Neanderthals' primary access to the different animals documented in the various levels (e.g. Aïmène, 1997, 1998; Cáceres, 1998; Cáceres et al., 1998; Carbonell, 2002; Chacón and Fernández-Laso, 2007; Chacón et al., 2007, 2010; Rosell et al., 2012a, 2012b). Burned bones are also very common in the assemblages, possibly resulting from different processes such as food preparation, cleaning of the living floor or specific use as fuel (Cáceres, 2002; Gabucio et al., 2014).

All of the assemblages are characterized by the elevated presence of high-survival elements (skulls, jaws and fragments of shafts of the long bones of the limbs) to the detriment of low-survival elements (ribs, vertebrae, coxa, scapula, phalanges and compact bones) (Chacón and Fernández-Laso, 2007; Chacón et al., 2007, 2010; Fernández-Laso et al., 2010; Rosell et al., 2012a, 2012b; and our own analyses of Level M). It seems clear that during the occupations of Abric Romaní, deer and horses formed an important part of the Neanderthals' diet. Previous studies suggest that these skeletal profiles are associated with the differential transport of prey. Based on this model, deer were transported whole and the axial skeleton of large animals (horses, aurochs and rhinos) were abandoned at the kill/butchering site (Cáceres et al., 1998; Fernández-Laso et al., 2011; Rosell et al., 2012a, 2012b; Vallverdú et al., 2005).

### 3. Methods

As mentioned earlier, the archaeological remains at the site are the result of different accumulation events. In the case of the faunal remains, each of the different transport events that generated the final archaeological assemblage cannot be isolated (Monahan, 1998; Saladié et al., 2011). For this reason, we have used the total number of ungulate remains for each species/age classes and size-weight categories in each level with the goal of identifying the possible transport strategy that generated the entire assemblage. The minimal number of elements (MNE) and the minimal animal units (MAU) were calculated in all five assemblages considering the bone landmarks in conjunction with a repetition of regions and sides, and the anatomical position (left/right) of the bones, as described by Saladié et al. (2011). As indicated in Faith and Gordon (2007), the MNE was calculated taking into account the shaft fragments in the assemblages. We only considered the high-survival elements and did not use the low-survival elements (Marean and Clerghorn, 2003). This is because the high-survival elements are more resistant to the different attritional processes and more accurately reflect the original abundance of elements resulting from hominin transport/discard decisions. We test the correlations between the %MAU of high-survival elements of large and medium-sized animals and their bone mineral density by portions (Lam et al., 1999; Lyman, 1994), in order to consider the

**Table 5**

Distribution of taxa present in the Abric Romaní levels by size-weight categories.

**Tableau 5**

Répartition des taxons de faune présents dans les niveaux de l'Abric Romaní par catégories de tailles et de poids.

Size	Weight	Taxa
Very large	> 1000 kg	<i>Stephanorhinus cf. hemitoechus</i>
Large	300–1000 kg	<i>Equus ferus</i> adult <i>Bos primigenius</i> adult
Medium	100–300 kg	<i>Equus ferus</i> infantile <i>Bos primigenius</i> infantile <i>Cervus elaphus</i> adult
Small	< 100 kg	<i>Cervus elaphus</i> infantile <i>Rupicapra pyrenaica</i> adult

possible intervention of destructive taphonomic process as well as for these elements where densities are also variable. To compare the distribution of the elements (MNE) into the size-weight groups (large and medium-sized animals) (Table 5) of each set, we applied a Chi<sup>2</sup> test. The correlation analysis between the %MAU and the Standard Food Utility Index (SFUI) (Metcalfe and Jones, 1988) was calculated by means of Spearman's rank-order correlation coefficient ( $r_s$ ). In keeping with Faith and Gordon (2007), we used Spearman's  $r_s$  because the correlation is dependent on rank-order values and the MAU and SFUI should be treated as ordinal-scale measures. In addition, we tested the MAU with the Unsaturated Marrow Index (UMI) (Morin, 2007), with the purpose of identifying a possible preference in the transport of bones as a function of their marrow and grease content. As with the SFUI, we use Spearman's  $r_s$  to test the statistical correlation.

Our assessment of the correlation between MAU and SFUI results takes into account the possibility of type I and type II statistical errors due to the small size of most of the assemblages (Faith and Gordon, 2007). Type I errors are those in which significant correlations are found in an assemblage when no such correlation exists in the population assemblage, and type II errors are those in which no correlation is found in an assemblage despite the presence of a correlation in the population assemblage. Faith and Gordon (2007) noted that type II errors are very common in assemblages with an MNE lower than 100 and resulting from an unconstrained or bulk strategy.

Finally, and again in keeping with the proposals of Faith and Gordon (2007), we applied the Shannon Diversity Index (evenness), where evenness is equal to  $E = \sum - (P_i \times i \ln P_i) / \ln S$ .  $S$  is the number of types of elements (e.g. MNE of humeri, femora, skulls) and  $p_i$  is the standardized proportion of specimens of the  $i$ -th element. Finally, we compared the Abric Romaní assemblages using information from the faunal assemblages of the Hadza campsites of Mugugu and Tispitibe, published by Lupo (2001). The Hadza are a hunter-gatherer group that has been intensely studied with regard to different social and economic aspects, and especially concerning their animal carcass discard and transport strategies (Bunn, 1993; Bunn et al., 1988, 1991; Monahan, 1998; O'Connell, 1993; O'Connell et al., 1988a, 1988b, 1990). At these two sites, the faunal remains were collected from the surface and subsurface at a depth of 10 cm, the

MNE was calculated using all identified parts (including the diagnostic limb bone shaft), and the assemblages were formed through the overlapping of events/occupations (Lupo, 2001).

## 4. Results

### 4.1. Level Ja

The NISP and MNE show that the most abundant elements in all size-weight groups are those belonging to the skull, mandibles and the long bones (Supplementary material). Vertebrae, ribs and coxae are present in all size-weights but almost anecdotally. However, it is worth noting that according to the %MAU, they are more common among large size, except for the coxae (Fig. 2). The Chi<sup>2</sup> analysis of the MNE from medium-sized versus large animals [Chi<sup>2</sup> = 66; degrees freedom = 54;  $P(\text{same}) = 0.127$ ] revealed that there is no statistical similarity between the two size groups. The test between bone mineral density and %MAU are not statistically significant [Large size: Spearman's  $r_s = 0.205$ ;  $P(\text{same}) = 0.464$ ] [Medium size: Spearman's  $r_s = 0.339$ ;  $P(\text{same}) = 0.216$ ], this indicate that a relation between the conservation and the mineral density cannot be prove (Carbonell, 2012).

For large animals, high-survival elements had an MNE of 113. We found no statistically significant correlations between the %MAU and SFUI (Table 6; Fig. 3). With an MNE of close to 100, the Spearman's  $r_s$  of 0.404 falls within the range (95% CI) of bulk (0.275–0.964) and unconstrained (–0.732 to 0.743) transport strategies. The evenness value is 0.937, which places it within the values of a bulk strategy (0.927–0.989) (Table 6). In this case, the lack of a significant correlation between the %MAU and SFUI may be due to a type II error.

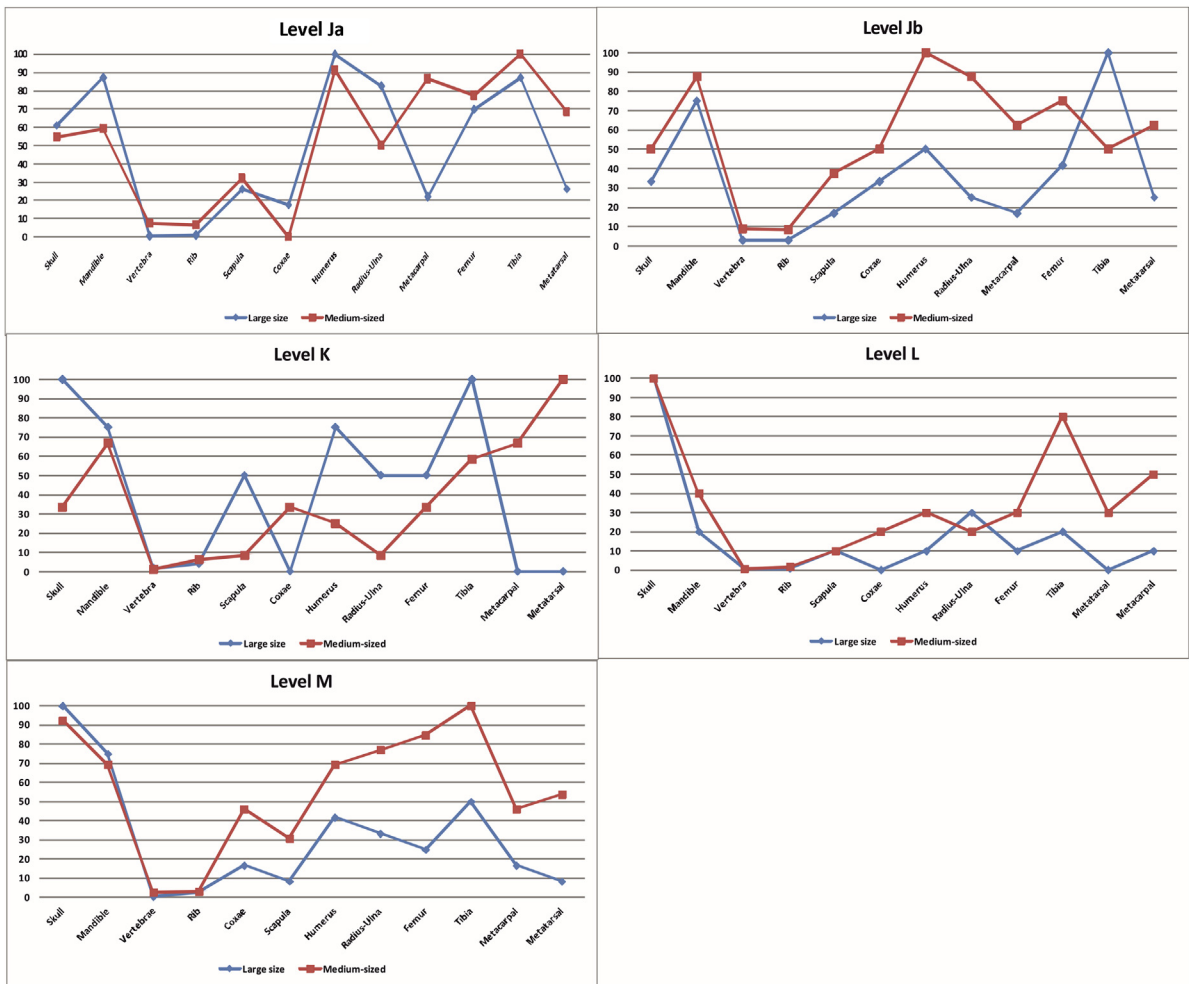
In the medium-sized animals set, the MNE of high-survival items is 123. This group did not show a statistically significant correlation between the %MAU and SFUI (Table 6) (Fig. 3). The Spearman's  $r_s$  of 0.380, with an MNE of close to 100, falls within the range (95% CI) of bulk and unconstrained transport strategies. The evenness value of 0.972 places it within the values of the bulk and unconstrained strategy (0.961–0.996).

We found statistically significant correlations between the %MAU and UMI for large and medium animals [Large size: Spearman's  $r_s = 0.711$ ;  $P(\text{same}) = 0.038$ ] [Medium size: Spearman's  $r_s = 0.677$ ;  $P(\text{same}) = 0.05$ ] (Table 6).

### 4.2. Level Jb

In the large and medium-sized animal assemblages, the most abundant bones are skulls, mandibles and long bones, according to the NISP and MNE (Supplementary material) (Table 3). The test between bone mineral density and %MAU are not statistically significant [Large size: Spearman's  $r_s = 0.068$ ;  $P(\text{same}) = 0.810$ ] [Medium size: Spearman's  $r_s = 0.167$ ;  $P(\text{same}) = 0.553$ ], this indicates that a relation between the conservation and the mineral density cannot be prove (Carbonell, 2012).

According to the %MAU, the cranial and long limb bones dominate among the large and medium-sized animals



**Fig. 2.** Distribution of the percentage of minimal animal unit (%MAU) in the main size-weight categories for levels Ja, Jb, K, L and M. Lg: Large size; Ms: Medium size.

**Fig. 2.** Répartition du pourcentage de l'unité animale minimale (% MAU) dans les principales catégories de tailles et de poids pour les couches Ja, Jb, K, L et M. Lg: grande taille; Ms: taille moyenne.

(Fig. 2), although they differ in the presence of the fore- and hind-limb elements. The bones of the forelimbs (humeri and radii-ulnae) are the most abundant in the medium-sized animal set, while in the large animals, the tibiae

are the most common elements. Humeri and femora are present in similar percentages. A comparison of the skeletal profiles of the large and medium-sized animal remains by means of a Chi<sup>2</sup> test [Chi<sup>2</sup> = 10.13; degrees freedom = 11;

**Table 6**

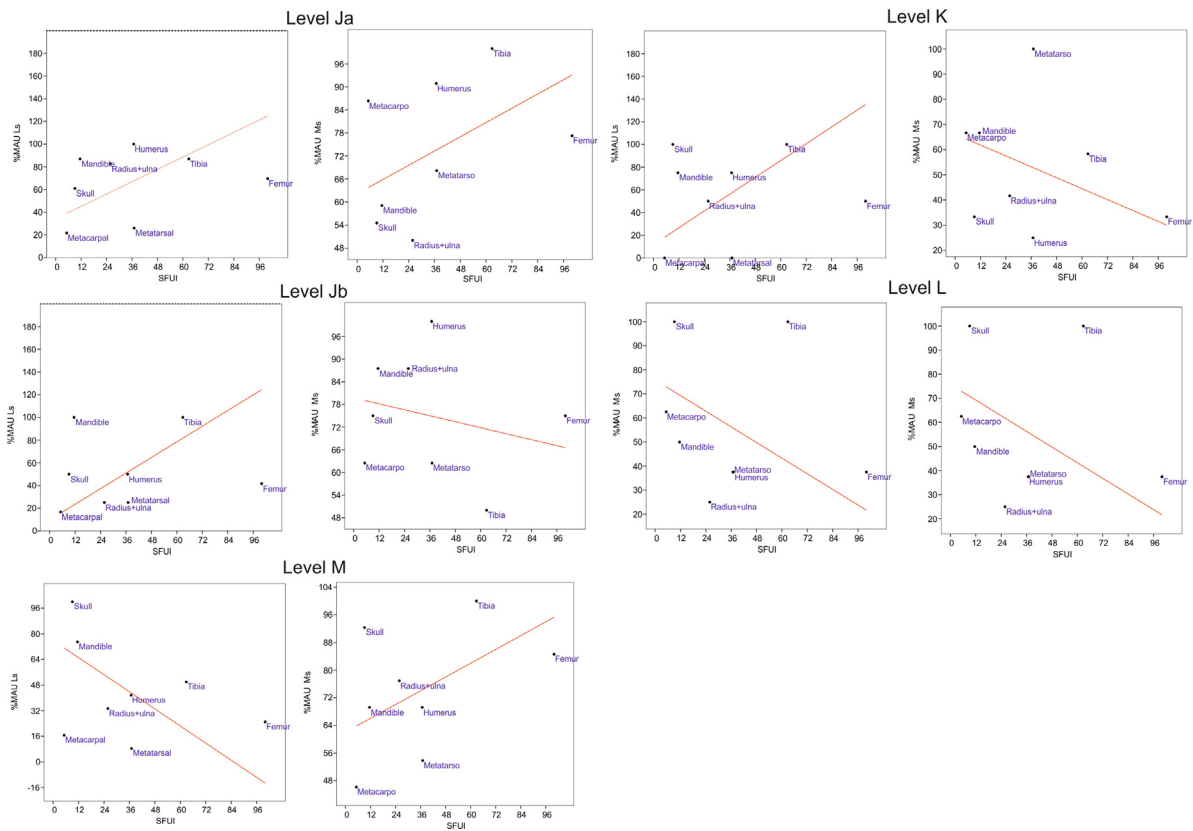
Evenness values and correlations of the different levels analysed by size-weight categories.

**Tableau 6**

Valeurs de l'Evenness et corrélations entre les différentes couches archéologiques analysées par catégories de poids.

Level/size-weight	MNE	Evenness (E)	%MAU/SFUI		%MAU/UMI	
			Spearman's (r <sub>s</sub> )	P	Spearman's (r <sub>s</sub> )	P
Ja large	113	0.937	0.404	0.326	0.711	0.003
Ja medium	123	0.972	0.380	0.359	0.677	0.05
Jb large	42	0.907	0.455	0.258	0.854	0.006
Jb medium	45	0.980	-0.169	0.699	0.548	0.13
K large	16	0.978	0.048	0.946	0.579	0.114
K medium	49	0.939	-0.168	0.695	0.753	0.023
L large	12	0.957	-0.368	0.368	0.569	0.13
L medium	32	0.959	0.306	0.460	0.762	0.023
M large	36	0.927	-0.238	0.536	0.726	0.031
M medium	71	0.983	0.407	0.316	0.899	0.002

MNE: minimum number of elements; %MAU: percentage of minimal animal unit; SFUI: standard food utility index; UMI: Unsaturated Marrow Index.



**Fig. 3.** Linear correlation of percentage of minimal animal unit (%MAU)–standard food utility index (SFUI) for large and medium size in each level.

**Fig. 3.** Corrélation linéaire de %MAU–SFUI pour la taille grande et moyenne dans chaque couche archéologique. MAU : unité animale minimum ; SFUI : index d'utilité standard de nourriture.

$P(\text{same}) = 0.518]$  supports the differing distribution of these two size-weight groups.

An MNE of 42 was found for the high-survival elements of the large animals. No statistically significant correlation was observed between the %MAU and SFUI (Fig. 3); Spearman's  $r_s$  of 0.455 is within the range (95% CI) of the bulk and unconstrained strategies obtained by Faith and Gordon (2007) (Table 6). The evenness value of 0.907 falls within the values described for bulk and unbiased strategies (Table 6). As was the case with the elements of the large size-weight assemblage in level Ja, there is a potential type II statistical error for the correlation between the %MAU and SFUI. As indicated by Faith and Gordon (2007), this error type is more common with lower MNE.

The high-survival elements of the medium-sized animal remains have an MNE of 45. No statistically significant correlation was found between the %MAU and SFUI (Fig. 3); Spearman's  $r_s$  (–0.169) falls within the range (95% CI) of an unconstrained strategy for an assemblage close to 50 MNE (Table 6). The evenness value of 0.980 is within unconstrained and bulk strategy values.

We found statistically significant correlations between the %MAU and UMI for large animals [Large size: Spearman's  $r_s = 0.854$ ;  $P(\text{same}) = 0.006$ ] and a not statistically significant correlations for medium animals [Medium size: Spearman's  $r_s = 0.548$ ;  $P(\text{same}) = 0.13$ ] (Table 6).

### 4.3. Level K

The most abundant remains in terms of NISP and MNE belong to the medium-sized animal category (Table 3). The %MAU indicates a difference in the distribution among the size groups (Fig. 2). Among the large animals, the most abundant elements are of the bones of the skull and the long bones, especially the tibiae. However, in the set of medium-sized animals, although the mandibles and tibiae are abundant, the metatarsals are the most common elements. The test between bone mineral density and %MAU are not statistically significant [Large size: Spearman's  $r_s = 0.227$ ;  $P(\text{same}) = 0.415$ ] [Medium size: Spearman's  $r_s = 0.335$ ;  $P(\text{same}) = 0.193$ ], this indicates that a relation between the conservation and the mineral density cannot be proven (Fernández-Laso et al., 2011). The  $\chi^2$  test [ $\chi^2 = 16.996$ ; degrees of freedom = 11;  $P(\text{same}) = 0.10796$ ] showed that the anatomical distribution of the two size-weight groups is not the same. The MNE of the large animal set is 16. There is no statistically significant correlation between the %MAU and SFUI (Fig. 3). Both Spearman's  $r_s$  (0.048) and the evenness value (0.978) placed this group within the ranges (95% CI) of bulk and unconstrained transport strategies (Table 6).

The medium-sized animal assemblage has an MNE of 49. There is no statistically significant correlation between the

%MAU and SFUI (Fig. 3). Spearman's  $r_s$  ( $-0.168$ ) suggests that this set is the result of an unconstrained strategy and the evenness value (0.939) indicates that it is the product of unconstrained or bulk transport strategies (Table 6).

We found no statistically significant correlations between the %MAU and UMI for large animals [Large size: Spearman's  $r_s = 0.579$ ;  $P(\text{same}) = 0.114$ ] and a high statistically significant correlation for medium animals [Medium size: Spearman's  $r_s = 0.753$ ;  $P(\text{same}) = 0.023$ ] (Table 6).

#### 4.4. Level L

As in most of the levels, medium-sized animal remains outnumber the remains of large animals (Table 3). According to the %MAU, in both size-weight categories, the most abundant elements are the skulls, while the scarcest elements in the assemblage are vertebrae and ribs (Fig. 2). The appendicular elements, especially the tibiae, are more numerous among the medium-sized animals than among the large animals. The Chi<sup>2</sup> test [Chi<sup>2</sup> = 7.248; degrees freedom = 11;  $P(\text{same}) = 0.778$ ] reveals that there is not similarity in the anatomical representation between medium-sized and large animals. The test between bone mineral density and %MAU are not statistically significant [Large size: Spearman's  $r_s = 0.04$ ;  $P(\text{same}) = 0.886$ ] [Medium size: Spearman's  $r_s = 0.297$ ;  $P(\text{same}) = 0.281$ ]; this indicates that a relation between the conservation and the mineral density cannot be proven (Fernández-Laso et al., 2011).

The MNE of the large animals is 12. There is no statistically significant correlation between the %MAU and SFUI (Fig. 3). Spearman's  $r_s$  ( $-0.368$ ) places this group as the result of an unconstrained transport strategy and the evenness value (0.957) puts it within the range (95% CI) of values of the bulk and unconstrained transport strategies (Table 6).

The medium-sized animal set has an MNE of 32. A statistically significant correlation was found between the %MAU and SFUI (Fig. 3). As for the large size-weight group, the Spearman's  $r_s$  (0.306) indicates an unconstrained strategy and the evenness value (0.959) suggests a bulk or unconstrained transport strategy (Table 6).

We found no statistically significant correlations between the %MAU and UMI for large animals [Large size: Spearman's  $r_s = 0.569$ ;  $P(\text{same}) = 0.130$ ] and a high statistically significant correlation for medium animals [Medium size: Spearman's  $r_s = 0.762$ ;  $P(\text{same}) = 0.024$ ] (Table 6).

#### 4.5. Level M

The anatomical distribution (NISP and MNE) (Supplementary material) shows a predominance of medium-sized animal remains (Table 3). According to the MNE, skulls are the most abundant and the elements of the postcranial axial skeleton are the scarcest in both weight groups. However, the two groups differ in the distribution of the long limb bones because, although a similar trend is found in both groups, the long bones are scarcer (%MAU) in the large animal set (Fig. 2). The test between bone mineral density and %MAU are statistically significant [Large size: Spearman's  $r_s = 0.436$ ;  $P(\text{same}) = 0.0024$ ] [Medium size:

Spearman's  $r_s = 0.426$ ;  $P(\text{same}) = 0.003$ ], this indicate a relation between the conservation of bone portions and their mineral density.

The Chi<sup>2</sup> test [Chi<sup>2</sup> = 8.485; degrees of freedom = 11;  $P(\text{same}) = 0.669$ ] supports the difference in distribution in the skeletal profiles of large versus medium-sized animals.

An MNE of 36 was found for the large animals in this level. There is no statistically significant correlation between the %MAU and SFUI (Fig. 3). Spearman's  $r_s$  ( $-0.238$ ) is within the range (95% CI) of an unconstrained transport strategy according to the proposals of Faith and Gordon (2007). The evenness value of 0.927 is within the range of bulk and unconstrained transport strategies (Table 6).

The medium-sized animals have an MNE of 71. There is no statistically significant correlation between the %MAU and SFUI (Fig. 3). Spearman's  $r_s$  of 0.407 falls within the range (95% CI) of bulk and unconstrained transport strategies, and the evenness value (0.983), in turn, suggests an unconstrained type strategy (Table 6).

We found statistically significant correlations between the %MAU and UMI for large and medium animals [Large size: Spearman's  $r_s = 0.726$ ;  $P(\text{same}) = 0.0316$ ] [Medium size: Spearman's  $r_s = 0.899$ ;  $P(\text{same}) = 0.002$ ] (Table 6).

#### 4.6. Hadza assemblages

In order to compare the transport models of Abric Romaní levels Ja, K, L and M, we examined correlations between the %MAU and SFUI and applied the evenness metric to the faunal assemblages recovered during the excavation of the Tispitibe and Mugugu Hadza camps (Lupo, 2001). In these assemblages the species identified by Lupo (2001) were Impala, Zebra and Alcelaphine. In order to have a sufficiently large sample with which to compare with the results of Faith and Gordon (2007) and ours, we combined the MNE of these three species. The results of these analyses of the faunal assemblages (Table 7) indicate that the assemblages at both camps are the product of an unconstrained transport strategy.

## 5. Discussion

According to the values of the correlation between the presence/absence of elements and their economic value given by Faith and Gordon (2007), two groups can be distinguished in the levels examined in this paper:

- a group composed of sets where  $r_s$  is within the range of 95% CI values obtained by Faith and Gordon (2007) for an unconstrained strategy. This group contains the assemblages of faunal remains from large animals from levels L and M (Fig. 4), and the remains the medium-sized animals of levels Jb, K, L (Fig. 4);
- a group in which  $r_s$  falls within the range of 95% CI values for bulk and unconstrained transport strategies. This group includes the large animals of levels Ja, Jb, K and the medium-sized animals of levels Ja and M (Fig. 4).

On the other hand, the evenness value for all of the sets of remains reveals a different distribution, clearly

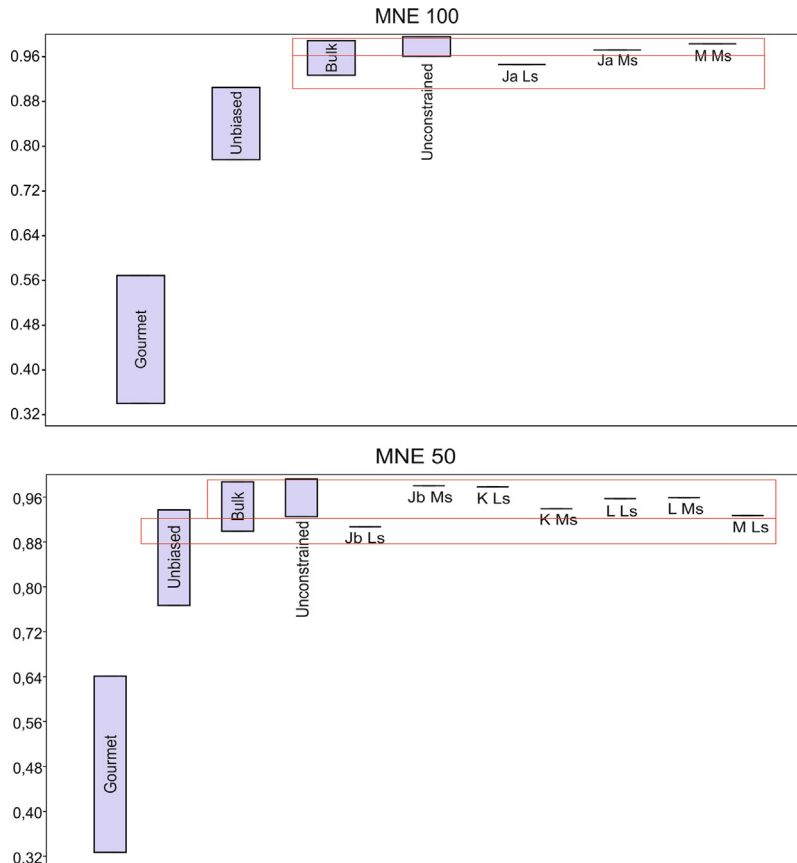
**Table 7**

Minimum number of elements (MNE), Evenness, Spearman's rank-order correlation, and transport strategy interpretation for Hadza campsite of Tispitibe and Mugugu, from Lupo (2001).

**Tableau 7**

Nombre minimum d'éléments (MNE), *Evenness*, corrélation de Spearman, et interprétation de la stratégie de transport à partir des études des campements Hadza de Tispitibe et Mugugu, de Lupo (2001).

	MNE	Evenness	Correlation		Strategy
			$r_s$	$p$	
Tispitibe	40	0.966	-0.163	0.707	Unconstrained
Mugugu	36	0.940	-0.390	0.344	Unconstrained



**Fig. 4.** Distribution of the Spearman's correlation values between percentage of minimal animal unit (%MAU)–standard food utility index (SFUI) for animals of levels Ja, Jb, K, L and M in relation to the values of 95% CI for the different transport strategies for a sample size of MNE 100 and MNE 50 (Faith and Gordon, 2007). Ls: Large size; Ms: Medium-sized.

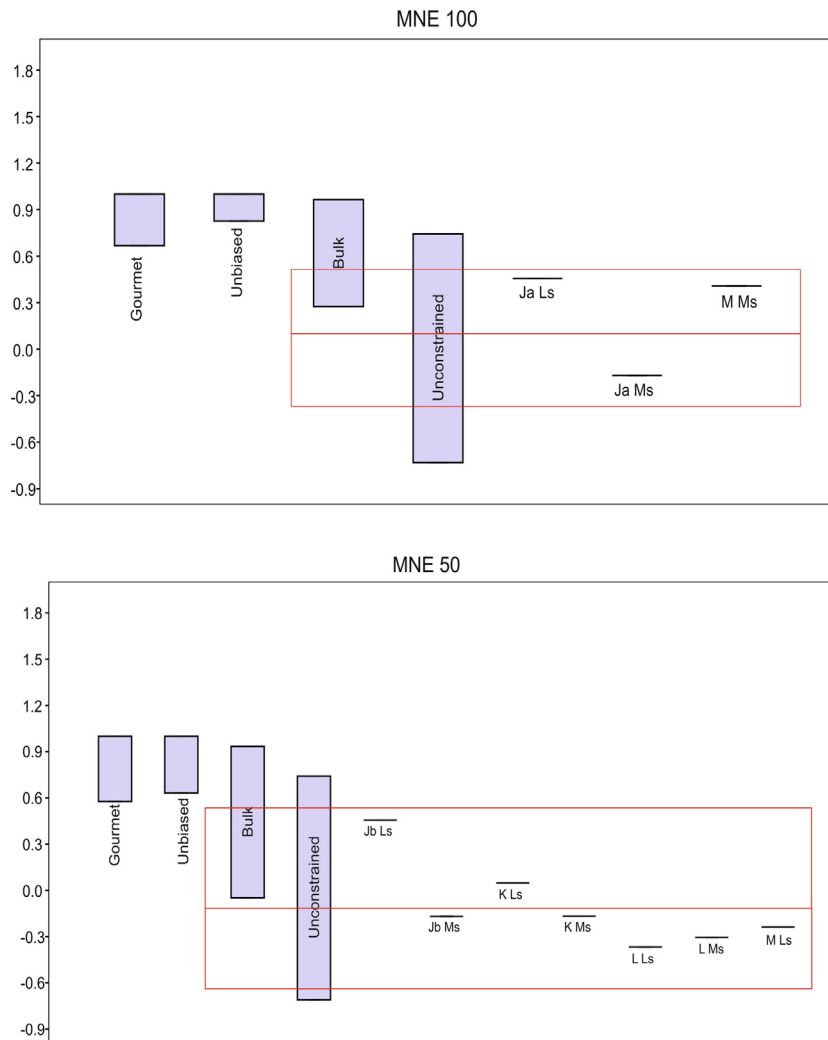
**Fig. 4.** Répartition des valeurs de corrélation de Spearman entre %MAU-SFUI pour les animaux des couches Ja, Jb, K, L et M en relation avec les valeurs de IC95 % afin de distinguer les différentes stratégies de transport pour un échantillon de MNE 100 et MNE 50 (Faith et Gordon, 2007). Ls : taille grande; Ms : taille moyenne.

corresponding to two transport strategies: the bulk strategy for the large animals of level Ja and the unconstrained strategy for the medium-sized animals of level M (Fig. 5). For the large animals of level Jb, the evenness value is within the values of the bulk and unbiased strategies (Fig. 5). For the large animals of levels K, L and M (Fig. 5) and the medium-sized animals of levels Ja, Jb, K and L (Fig. 5), the evenness values fall within the range of 95% CI values for the bulk and unconstrained strategies.

Based on these results, there are two possible statistical type II errors (in which a statistically significant correlation between the %MAU-SFUI was not observed although

the set was formed attending to the maximization of the utility elements transported): in the data for the large animals of levels Ja and Jb. In these cases, due to the size of the MNE, there might not have been a statistically significant correlation between the %MAU and SFUI because the evenness value indicates a bulk strategy for large animals in level Ja and a bulk and unbiased strategy for large animals in level Jb.

Faith and Gordon (2007) indicate that when MNE size decreases, especially for small assemblages (MNE 50), the evenness value of the bulk and unconstrained strategies overlaps. Therefore, at levels where there are no identified



**Fig. 5.** Distribution of the evenness values for the large animals of levels Ja, Jb, K, L and M in relation to the values of 95% CI for the different transport strategies for a sample size of minimum number of elements (MNE) 100 and MNE 50 (Faith and Gordon, 2007). Ls: Large size; Ms: Medium-sized.  
**Fig. 5.** Répartition des valeurs de l'Evenness pour les grands animaux des niveaux Ja, Jb, K, L et M par rapport aux valeurs de IC95% des différentes stratégies de transport pour des tailles d'échantillonnage de MNE 100 et MNE 50 (Faith et Gordon, 2007). Ls: taille grande; Ms: taille moyenne.

type II errors, the lack of a significant correlation between the %MAU and SFUI suggests an unconstrained transport strategy. According to these data, the predominant strategy among the Abric Romaní levels analysed here for medium-sized and large animals would be unconstrained. This would suggest that the body parts of the prey were transported from the kill/butchering site to the campsite according to their abundance in a complete skeleton (Faith and Gordon, 2007). In other words, these results suggest the transport of complete carcasses to the shelter, regardless of the size of the animal, meaning similar transport patterns were employed for deer, horses and aurochs. However, comparisons ( $\chi^2$  test) between the skeletal profiles of the large and medium-sized animals indicate that there are not similarities in the anatomical distributions in all of the levels studied, which points to a possible differential treatment of carcasses based on animal weight.

The analysis between bone mineral density and %MAU indicate two results. On levels Ja, Jb, K and L has not been observed differential conservation based on the mineral content of bones (Lam et al., 1999; Lyman, 1994). In contrast, in level M, we found a high statistically significant correlation between bone mineral density by portions and the %MAU of high-survival elements for large and medium size. This indicates that parts of bones with low mineral density are suffering a taphonomic process that is creating an underrepresentation of these anatomical parts. Taken into account the low alterations by carnivores and the high presence of anthropic activities, among which stand cremation and fire used (Costamagno and Rigaud, 2014; Gabucio et al., 2013, 2014; Vallverdú et al., 2012), this underrepresentation could be a combination between hominin activities.

In previous studies of these levels, some authors suggested the existence of the differential transport of



animals based on size-weight (Chacón et al., 2007, 2010; Fernández-Laso et al., 2010; Rosell et al., 2012a, 2012b). It was argued that large animals (horses and aurochs) would have been processed at the kill/butchering site with the intention of facilitating their transport to the shelter, while body parts, which were energetically not worth carrying were left behind due to their low economic value. In contrast, medium-sized animals (deer) would have been transported intact and completely exploited at the campsite (Carbonell, 2002, 2012; Chacón and Fernández-Laso, 2007; Fernández-Laso et al., 2010, 2011; Rosell, 2001; Rosell et al., 2012a, 2012b; Vallverdú et al., 2005). According to these studies, differential transport decisions were linked to the animal's weight, which is not contrary to our results. However, it was argued that this pattern is visible through a greater or lesser presence of the postcranial axial skeleton. But, having evaluated the anatomical distribution (%MAU) in the size-weight categories of the different levels (Fig. 2), it became clear that the differences proposed due to the presence of the postcranial axial skeleton are not supported. The size-weight categories of all of the levels exhibit a very similar concentration of vertebrae and ribs. In levels K, L and M, the presence of these bones for large and medium-sized animals is virtually identical. In levels Ja and Jb, although there are more vertebrae and ribs among the medium-sized animals, their presence is still scarce and they never exceed 10% of the MAU.

Valensi and Psathi (2004) note that in the Middle Palaeolithic levels of the sites of Lazaret (France), Arma delle Maine (Italy), Madonna dell'Arma (Italy), Caverna delle Fate (Italy), St. Lucia Superiore (Italy) and San Francesco (Italy) the pattern of anatomical distribution is characterized by the abundance of cranial and appendicular elements and by the scarcity of the postcranial axial skeleton, regardless of the size-weight of the animals. They indicate that this pattern suggests a primary access and a transport of complete or nearly complete carcasses into the sites (Valensi and Psathi, 2004). The same anatomical distribution was observed by Moncel et al. (2004) for medium-sized animals at the Grotte de Saint-Marcel. They said that the absence of part of the axial elements, like ribs, could be the result of a differential transport. However, the absence of the epiphyses of long bones also indicates that these underrepresentations could be result of an intensive treatment of these anatomical parts by boiling or use as fuel. Moncel et al. (2004) hypothesize that the assemblage is the result of differential transport of certain anatomical parts, but the presence, even in very small quantities, of all parts of the skeleton shows that some hunted animals were carried complete to the cave. On the other hand, Romandini et al. (2014) indicate that Grotta di Fumane was used as a habitat where the processing of carcasses was finalized after having been begun at the kill site. They infer that human groups transported to the site selected anatomical parts with high nutritional value. Gaudzinski and Niven (2009) evaluate the open-air site of Salzgitter-Lebenstedt (Germany) specializing in the hunt of *Rangifer tarandus*. It was found that the axial skeleton is always underrepresented in this assemblage, and never exceeds 20% of the MAU. Gaudzinski and Niven (2009) define the presence of long bones as result of economic decisions made by hominins.

Given this distribution, just as we observed in our study of the faunal remains of levels J, K, L and M at Abric Romaní, it seems that the trunk would be the most commonly scarce segment in all cases of transport. However, the absence of vertebrae and ribs, together with other low-survival elements may be due in part to multiple attritional processes (Lyman, 1994; Marean and Spencer, 1991), crushing of axial bones in order to collect the fat with boiling practices, and even intentional cremation during maintenance work on hearths or the cleaning of the living floor (Costamagno and Rigaud, 2014; Gabucio et al., 2014; Thery-Parisot and Costamagno, 2005; Vallverdú et al., 2005; Vallverdú et al., 2012). On the other hand, the absence of bones of the trunk is not universal in these assemblages, so their presence, although scarce, indicates that at some point some carcasses arrived the shelter intact, as for example Saladié et al. (2011) indicate for level TD-6 of Gran Dolina, Domínguez-Rodrigo et al. (2009) for FLK-Zinjanthropus 22 site or Moncel et al. (2004) for the Mousterian site of Grotte de Saint-Marcel. Therefore, the sum of attrition generated by Neanderthals and other postdepositional processes has resulted in a high degree of uniformity in the skeletal profiles of the Abric Romaní levels, characterized by the scarcity of the axial skeleton as in many Neanderthal sites, for example Grotte de Saint-Marcel (Moncel et al., 2004) or Lazaret (Valensi and Psathi, 2004).

In keeping with these proposals, the distribution of high-survival bones has to be studied to determine whether the carcasses were carried to the shelter complete, as suggested by the combination of non-correlations of %MAU and SFUI and the evenness values, relying on the proposals of Faith and Gordon (2007), or if the carcasses of animals of different weight groups were subjected to different transport strategies, as indicated by the comparison of their anatomical distribution using the Chi<sup>2</sup> test. Thus, considering the different frequencies of the %MAU, it becomes clear that the primary differences among the size-weight categories lie in the abundance of the appendicular bones. For example, in levels Jb, L, K and M, although the frequency of large and medium-sized animal skulls is similar, there are fewer long bones of large animals than of medium-sized animals (Fig. 2) (Supplementary material). This would support the hypothesis of reduced transport of the long bones of large animals from the kill/butchering site to the campsite in these levels. In level Ja, there seem to be fewer differences in this regard, particularly in terms of the frequency of the proximal appendicular bones (femora and humeri) and intermediate appendicular bones (radii-ulnae and tibiae). However, the representation of metapodials does seem to have a relationship to size-weight, as those from medium-sized animals are much more abundant than those from large animals, especially in level K (Fig. 2) (Supplementary material).

Based on these observations, it seems that the anatomical representation of the animals documented in Abric Romaní may be related to the sum of different carcass transport patterns, with animal size being one of the determining factors. Some researchers, such as Monahan (1998) and Lupo (2001), have argued that the superposition of different transport strategies makes them less visible and more difficult to relate to concrete

transportation/abandonment decisions. In fact, [Lupo \(2001\)](#) suggests that transport/abandonment decisions are more accurately reflected at a single-event kill/butchering site than in camps where overlapping masks possible differences between one event and another.

It seems that the same superposition would characterize the skeletal profiles of the most abundant animals at Abric Romaní: deer, horses and aurochs. However, the remains of a rhino in level M (one femur diaphysis) may reflect the transport of only a few bones of a carcass.

This variability of different transport models used by Neanderthals is also observed in some hunter-gatherer groups ([Binford, 1978, 1981](#); [Bunn, 1993](#); [Bunn and Kroll, 1986, 1988](#); [Bunn et al., 1988](#); [Monahan, 1998](#); [Schoville and Otárola-Castillo, 2014](#)). Therefore, different specific conditions may affect each hunting event differently. The studies conducted by [Gifford-Gonzalez \(1993\)](#) and [Monahan \(1998\)](#) indicate that some of the variables that affect the transport decisions of these groups are the weight of the animals, the number of people involved in the hunt, the number of carriers and the possibility of calling more people to help, the number of hunted animals, the anatomy of the animal itself, the cost of processing and transporting a carcass, competition with other carnivores in the environment, and the distance to the camp. Ethnographic studies of the Hadza indicate that there are even more variables in play, such as the hunger of the hunters and the toolkit they are carrying ([Bunn et al., 1988, 1991](#); [Bunn, 1993](#); [Monahan, 1998](#); [O'Connell, 1993](#); [O'Connell et al., 1988a, 1988b, 1990](#); [Oliver, 1993](#)). More recently, [Schoville and Otárola-Castillo \(2014\)](#) asserted that, for the Hadza, the most important factors in deciding which body parts are transported are the number of carriers, the size of the animal and the distance from the camp.

Based on this information, we know that the Hadza use a variety of different transport strategies for all animal size-weights ([Bunn, 1993](#); [Bunn et al., 1988, 1991](#); [Lupo, 2001](#); [Monahan, 1998](#); [O'Connell, 1993](#); [O'Connell et al., 1988a, 1988b, 1990](#)). This behaviour results in bone accumulations created by multiple transport events ([Lupo, 2001](#)). Hadza in these two camps ([Lupo, 2001](#)) and in general ([Bunn, 1993](#); [Bunn et al., 1988, 1991](#); [Monahan, 1998](#); [O'Connell, 1993](#); [O'Connell et al., 1988a, 1988b, 1990](#)) employed highly variable transport strategies for the animal carcasses brought back to camp, including the transport of complete carcasses or only a few elements. The result of the analyses of Mugugu and Tispitibe camps indicates an unconstrained transport strategy ([Table 7](#)). For this reason, the Hadza can be used to determine how a highly variable animal carcass transport pattern is reflected in the faunal record like a palimpsest result of an unconstrained transport strategy ([Table 7](#)).

The presence of most of the parts of the skeleton in all of the analysed sets suggests that the trunks, particularly of medium-sized and large animals, were wholly or partially transported to the shelter at some time. This may be consistent with the transport of complete carcasses and therefore with an unconstrained transport strategy. The result of the analyses between the %MAU and UMI, indicates that there exists a correlation between the transport of bones and their riches in marrow and grease ([Morin, 2007](#)), except for the large size of level K and L and medium size of level

Jb, which may be due to a small size of the sample. On the assemblages with high significant statistical correlations could be supported the hypotheses of a preferential transport of bones in function of the marrow riches, that is, long bones. At the same time, differences in the anatomical representation indicate that this model was not the only one used, or not necessarily the most common one used, since the skeletal profiles analysed are different by size-weights.

Carnivory and meat-sharing are central features of current hunter-gatherers, so these behaviours are critical in the evolution of hominin social relations ([Stiner, 2009](#)). The stable isotope analyses of the Neanderthal remains of Vindija, Jonzac and Marillac, among others ([Fizet et al., 1995](#); [Richards et al., 2000](#)), together with a great number of zooarchaeological researches ([Daujeard and Moncel, 2010](#); [Gaudzinski and Niven, 2009](#); [Moncel et al., 2004](#); [Patou-Mathis, 2000](#); [Rendu, 2010](#); [Rendu et al., 2012](#); [Romandini et al., 2014](#)), indicate that Neanderthals' primary food source consisted of large herbivores ([Bocherens, 2011](#); [Bocherens et al., 1999](#); [Richards et al., 2000, 2008](#)). According to [Hayden \(1981\)](#), cooperation in hunting and meat-sharing is closely related to the importance of this resource to a particular group. As shown by [Stiner \(2009\)](#) for Qesem cave, Middle Palaeolithic hominins delayed the consumption of their prey long enough to transport the animal carcasses back to camp.

Back at home base, the Neanderthal group must have shared. It is assumed that this circumstance would have been the same in levels Ja, Jb, K, L and M of Abric Romaní. The transport of numerous animal parts necessarily entailed cooperation between different individuals. The number of carriers was possibly variable, and this conditioned the transport strategies chosen. However, although many other factors could have played a key role in these decisions, they unfortunately do not have archaeological visibility.

## 6. Conclusions

The Neanderthal groups who occupied Abric Romaní during the formation of levels Ja, Jb, K, L and M developed variable transport strategies for medium-sized and large animals. The end could result in transport processes is a mixed skeletal profile, in which some of these strategies have low archaeological visibility. However, certain guidelines can be established. It seems that the postcranial axial skeleton was transported only in a few events and once inside the Abric Romaní was highly sensitive to destruction by taphonomic processes, among those are the produced by the Neanderthals. However, the decision to transport or discard at the kill/butchering site would not have been made in relation to the size-weight difference between large and medium-sized animals. The long bones and the skull bones were commonly transported, but in this case, there are differences in the distribution linked to the size-weight category, so the size of the animal itself would have been a factor of these different anatomical profiles. Therefore, evidence of an unconstrained strategy is possibly an artefact caused by the combination of different types of transport, such as in the levels of Abric Romaní. One of these transport types is the transport of the bones

richest in marrow and grease, as the high statistical correlations of MAU and UMI indicate. These conclusions can be extrapolated to other Middle Palaeolithic assemblages with similar skeletal profiles, in which human activity is the main cause of accumulation and subsequent attritional processes, are scarce. It would be desirable to extend this study with larger samples in order to test our conclusions.

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## Appendix A. Supplementary material

Supplementary material associated with this article can be found in the online version available at <http://dx.doi.org/10.1016/j.crpv.2015.11.006>.

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# Supplementary materials

NISP(MNE)	Ja		Jb		K		L		M	
	Large size	Medium size	Large size	Medium size	Large size	Medium size	Large size	Medium size	Large size	Medium size
Horn/Antler	-	9(3)	-	1(1)	-	-	-	-	-	4(1)
Skull	21(6)	5(9)	3(6)	1(3)	0(3)	4(2)	2(2)	6(4)	28(6)	62(6)
Mandible	43(23)	18(16)	11(9)	2(7)	8(3)	16(8)	9(5)	17(5)	26(9)	56(9)
Hyoids	-	3(2)	-	-	-	-	-	-	-	-
Vertebra	1(1)	7(6)	5(5)	10(10)	1(1)	9(2)	1(1)	1(1)	1(1)	18(5)
Rib	1(1)	48(15)	6(4)	19(8)	2(2)	30(9)	1(1)	4(2)	16(4)	142(5)
Scapula	4(2)	12(5)	2(2)	1(3)	4(2)	1(1)	1(1)	1(1)	3(1)	11(4)
Humerus	31(17)	47(22)	7(6)	14(8)	4(3)	19(3)	1(1)	10(3)	6(5)	61(9)
Radius-Ulna	28(17)	40(12)	3(3)	5(7)	9(5)	16(5)	3(3)	9(2)	8(4)	80(10)
Metacarpal	7(5)	71(24)	2(2)	10(5)	-	44(8)	1(1)	12(5)	3(2)	110(6)
Coxa	3(1)	1(1)	2(2)	1(2)	-	4(2)	-	1(1)	1(1)	4(3)
Carpals	-	2(2)	-	-	-	24(4)	-	-	1(1)	-
Femur	19(15)	42(20)	6(5)	7(6)	4(2)	63(7)	1(1)	4(3)	3(3)	83(11)
Patella	-	1(1)	-	-	-	-	-	-	-	-
Tibia	19(16)	51(22)	16(12)	3(4)	10(4)	-	2(2)	16(8)	15(6)	98(13)
Metatarsal	10(6)	58(22)	2(3)	21(5)	-	60(12)	-	8(3)	3(1)	63(7)
Tarsal	-	1(1)	-	2(2)	-	-	-	-	-	5(5)
Metapodial	8(4)	6(2)	4(3)	2(1)	2(2)	9(2)	1(1)	2(1)	-	-
Phalanx	-	12(10)	-	-	1(1)	10(6)	-	-	-	13(9)
Sesamoids	-	5(5)	-	3(3)	-	-	-	-	-	2(2)

SP. 1. Number of Identified Specimens and (Minimum Number of Elements) by anatomical elements for the principal weight sizes categories by levels Ja, Jb, K, L and M (Carbonell, 2012; Chacón et al., 2007, 2010; Fernández-Laso, 2011; Rosell et al., 2012a, 2012b).

Ja	MNI	MNI			
		Infantil	Juvenile	Adult	Senile
<i>Stephanorhinus cf. hemitoechus</i>	3	1	1	1	-
<i>Equus ferus</i>	15	3	2	8	2
<i>Cervus elaphus</i>	12	3	2	5	2
<i>Bos primigenius</i>	5	-	2	3	-
<i>Rupicapra pyrenaica</i>	2	-	1	1	-
<b>Total</b>	<b>37</b>	<b>7</b>	<b>8</b>	<b>18</b>	<b>4</b>

SP 2. Minimum Number of individuals by taxa and by age of death in level Ja (Carbonell, 2012; Rosell et al., 2012a, 2012b)

Jb	MNI	MNI			
		Infantil	Juvenile	Adult	Senile
<i>Stephanorhinus cf. hemitoechus</i>	2	1	-	1	-
<i>Equus ferus</i>	4	-	1	2	1
<i>Cervus elaphus</i>	4	1	-	3	-
<i>Bos primigenius</i>	2	-	1	1	-
<i>Rupicapra pyrenaica</i>	1	-	1	-	-
<b>Total</b>	<b>13</b>	<b>2</b>	<b>3</b>	<b>7</b>	<b>1</b>

SP 3. Minimum Number of individuals by taxa and by age of death in level Jb (Carbonell, 2012; Rosell et al., 2012a, 2012b).

K	MNI	MNI			
		Infantil	Juvenile	Adult	Senile
<i>Equus ferus</i>	4	1	1	2	-
<i>Cervus elaphus</i>	8	1	1	5	1
<i>Bos primigenius</i>	1	-	-	1	-
<b>Total</b>	<b>13</b>	<b>2</b>	<b>2</b>	<b>8</b>	<b>1</b>

SP 4. Minimum Number of individuals by taxa and by age of death in level K (Chacón et al., 2010; Fernández-Laso, 2011).

L	MNI	MNI			
		Infantil	Juvenile	Adult	Senile
<i>Equus ferus</i>	4	1	1	2	-
<i>Cervus elaphus</i>	5	1	1	1	2
<i>Bos primigenius</i>	1	-	-	1	-
<b>Total</b>	<b>10</b>	<b>2</b>	<b>2</b>	<b>4</b>	<b>2</b>

SP 5. Minimum Number of individuals by taxa and by age of death in level L (Chacón et al., 2010; Fernández-Laso, 2011).

M	MNI	MNI			
		Infantil	Juvenile	Adult	Senile
<i>Stephanorhinus cf. hemitoechus</i>	1	-	-	-	-
<i>Equus ferus</i>	6	-	2	4	-
<i>Cervus elaphus</i>	7	-	2	4	-
<i>Bos primigenius</i>	4	-	-	3	-
<b>Total</b>	<b>18</b>	<b>-</b>	<b>4</b>	<b>11</b>	<b>-</b>

SP 6. Minimum Number of individuals by taxa and by age of death in level M.





**Chapter 4. Neanderthal hunting strategies inferred  
from mortality profiles within the Abric  
Romaní sequence**



RESEARCH ARTICLE

# Neanderthal hunting strategies inferred from mortality profiles within the Abric Romaní sequence

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## Abstract

Ungulate mortality profiles are commonly used to study Neanderthal subsistence strategies. To assess the hunting strategies used by Neanderthals, we studied the ages at death of the cervids and equids found in levels E, H, I, Ja, Jb, K, L and M of the Abric Romaní sequence. These levels date between  $43.2 \pm 1.1$  ka BP ( $^{14}\text{C}$  AMS) and  $54.5 \pm 1.7$  ka BP (U-series). The degree of eruption and development of the teeth and their wear stages were used to determine the ages of these animals at death, and mortality profiles were constructed using these data. The equids display prime dominated profiles in all of the analyzed levels, whereas the cervids display variable profiles. These results suggest that the Neanderthals of Abric Romaní employed both selective and non-selective hunting strategies. The selective strategy focused on the hunting of prime adults and generated prime dominated profiles. On the other hand, non-selective strategies, involved the consumption of animals of variable ages, resulting in catastrophic profiles. It is likely that in the selective hunting events were conducted using selective ambushes in which it was possible to select specific prey animals. On the other hand, encounter hunting or non-selective ambush hunting may have also been used at times, based on the abundances of prey animals and encounter rates. Specific hunting strategies would have been developed accordance with the taxa and the age of the individual to be hunted. The hunting groups most likely employed cooperative hunting techniques, especially in the capture of large animals. Thus, it is not possible to uniquely associate a single mortality profile with the predation tactics of Neanderthals at Abric Romaní.

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## Introduction

Mortality profiles are an instrument traditionally used to infer the origins of fossil assemblages in archaeology and paleontology [1–6]. Kurten [4] and Voorhies [7] were pioneers in the study of paleontological assemblages. They applied principles developed by ecologists to fossil records (e.g. [8, 9]), and established the ages at death of animals in order to construct life tables, which they used to infer the population dynamics represented by the fossil record. Mortality profiles were later employed at North American Paleoindian archaeological sites [10–12]. These studies focused on bison kill sites where mass predation events occurred in order to establish hunting seasonality [10–12].

Age at death research has conventionally focused on animal dentition. Non-destructive methods have been developed for these assessments, such as the measurement of the crown heights of teeth [3, 13, 14] and analyses of occlusal surface wear [15–17]. Both methods are based on comparing the assessed tooth wear stage with reference collections that include animals whose ages at death are known. Destructive analysis methods have also been used. Cementochronology is based on counting the layers of cyclically deposited cement, which alternate between relatively thin and relatively thick and reflect a growth periodicity that generally corresponds to an annual cycle [18–20].

Two types of plots are typically used in archaeological studies with this focus: 1) Mortality profiles show the relative or absolute frequency of faunal remains within each age range [3, 5]. 2) Survivorship curves show the surviving individuals in each interval, starting with the total number in the assemblage [3, 5]. Age at death estimates are generally compiled in histograms and linear graphs (e.g. [21, 22]). Greenfield [23] introduced the use of triangular graphs in the analysis of mortality profiles, although the works of Stiner [5, 6] popularized the use of this type of diagram. The distribution of the three age groups (juvenile, prime adult and old adult) can be graphically represented to show the different mortality profiles. This makes it possible to compare the mortality profiles obtained from archaeological assemblages with profiles based on current observations. Two types of mortality profiles are characteristic of the populations of large mammals, and are commonly referred to as catastrophic (or living-structure) profiles and attritional profiles [2, 5, 7, 24]. Catastrophic mortality profiles reflect the ranges of ages that can be observed in living groups of animals, which are present in direct relation to their abundance in the ecosystem. They are produced by ambush predators (e.g. lions, leopards and tigers), by communal hunting events carried out by hominins, and by massive mortality events caused by drowning, famines, etc [2, 5, 7, 25]. Attritional mortality profiles are characterized by a high frequency of younger and older individuals, which are the weakest and most easily hunted animals, and such profiles are generally produced by cursorial hunters (e.g. cheetahs, wolves, spotted hyenas and lycaons) [2].

Using mortality profiles derived from Middle and Upper Paleolithic sites in Italy, Stiner [5] identified a progressive increase in the preference for hunting prime adult animals, an age range not exploited by other predators. This type of prey selection is ecologically complementary to cursorial predators and, to a lesser extent, ambush predators, and it allows different predators to exploit the same prey population while minimizing competition [2, 5, 6, 26]. Stiner [5] defined this hunting behavior of hominin groups as the human predatory niche. In her earliest work, Stiner [5, 6] indicated that the mortality profiles of the early Mousterian (pre-45,000 BP) are characterized by a non-selective pattern in the ages of prey. This pattern is in striking contrast to the selective pattern of the late Mousterian after 40,000 BP [5, 6], in which prime adults are more abundant. In her later work, she rejected differences between the periods mentioned above because she had observed mortality profiles that included the totality of the catastrophic and prime-dominated areas, which, on average, indicate a slight bias toward

the selection of prime adults [27]. Finally, she indicated that the presence of profiles containing prime adults during the Middle Paleolithic on different continents suggests the initial development of this behavior in the hunting of large ungulates [28].

Current opinion holds that Neanderthals were skilled hunters of large mammals, and that they had great behavioral flexibility, allowing them to exploit a wide spectrum of resources [5, 27–48]. However, the key component of Neanderthal subsistence was the exploitation of large and medium ungulates [49, 50]. In most of the Mousterian sites of the Mediterranean basin, this group of animals includes deer, horses and aurochs [33, 41–43, 48, 51].

The mortality profiles obtained from different Middle Paleolithic sites indicate that Neanderthal groups generated several types of mortality profiles. These profiles range from selective profiles like that seen at Gabasa (Spain) [52] in which juvenile animals are favored, to catastrophic profiles like that seen at Manie, Madonna and Fate (Italy) [53]. However, numerous sites show a predilection for the hunting of prime adults, as seen at Combe-Grenal (France) [52], in level E of Lazaret (France) [53], in level 7 of Pech-de-l'Aze I (France) [54], in Salzgitter Lebenstedt (Germany) [55], in Grotta Breuil (Italy) [27] and Misliya (Israel) [56], among others. This tendency has also been documented at several Lower Paleolithic sites, such as Wallertheim (Germany) [56], Qesem Cave (Israel) [57], Gran Dolina de Atapuerca (Spain) in levels TD6.2 [58] and TD10.1 [59], Cuesta de la Bajada (Spain) [60] and FLK-Zinj (Tanzania) [61, 62].

The mortality profiles determined from archaeological sites yield information on the hunting skills of the predators that occupied those sites [52]. According to optimal foraging models, hunters (human and non-human) select prey animals that provide high return rates, usually in terms of calories per unit time or per unit energy spent during foraging [63]. The availability of prey animals and the risk involved in hunting them, among other factors, affect the prey selections made by predators. Thus, the abundance of prey animals at an archaeological site provides information on the skills, techniques and hunting strategies of the hunters [52].

Steele and Baker [64] argue that discussions of human predation must include the use of tools, elaborate communication systems, social hunting, cooperation and sharing, the exploitation of large territories, the transport of prey and differing prey consumption. Thus, they established several categories into which hunting events can be classified. These categories are primarily separated in terms of the number of hunted animals and the number of hunters. Taking that proposal as a starting point, Driver [65] studied the social organization and technology of the participants in hunting events. Thus, the number of hunted animals and the way in which they are killed distinguish simple predation events from sequential or mass predation events. The size of the hunter group and its social organization might reflect individual hunters, cooperative groups or communal groups. Each of these types of predation can occur in multiple ways as a function of the tactics (e.g. hunting by driving, ambush or stalking) and techniques used (e.g., spears, bows and arrows, or nets) [64–66].

The goal of this paper is to outline the hunting strategies, including the tactics, developed by the Neanderthals of Abric Romaní over time through the reconstruction of the dental series of the equids and cervids recovered at the site and the determination of their ages at death. Abric Romaní provides the opportunity to study a 15,000-year-long sequence at a Neanderthal site, allowing us to examine the hunting strategies that the Neanderthals employed during their occupation of the rock shelter.

## The Abric Romaní

The archaeological site of Abric Romaní is a rock shelter located in the northeastern portion of the Cinglera del Capelló cliff, 45 km northwest of Barcelona, Spain. The stratigraphy is made

up of 20 m of well-stratified travertine sediments. Rock fragmentation and alluvial and bio-chemical sedimentary processes have generated beds of consolidated stones, gravels, calcarenites and calcilutites interspersed with very fine archaeological levels. Uranium-series and radiocarbon dates place the Abric Romaní deposit between 70 and 40 kyr (Table 1). The sedimentation rate is estimated to have been approximately 0.6 m/kyr [67]. Excluding level A, all of the archaeological levels correspond to the Middle Paleolithic. The Abric Romaní sequence ranges from Marine Isotope Stage (MIS) 4 (sterile levels) to the first half of MIS 3 (archaeological levels). It includes the Dansgaard-Oeschger (D-O) cycles, which extend from 19 to 12, as well as the Heinrich Stadium (HS) from 6 to 5 [68] (Table 1).

The site was discovered in 1909 by Amador Romaní and excavated during different periods throughout the 20th century. The current intervention, in which the full extent of the rock shelter (c. 300 m<sup>2</sup>) has been excavated, began in 1983. Numerous well-preserved combustion structures have been identified [69–71] in addition to wood remains, including negatives and carbonized positives [72–75].

The lithic record is typical of Middle Paleolithic assemblages. Flakes predominate, whereas cores and retouched flakes are scarce [76–81] (Table 1). Most of the raw material is derived from local sources (flint, quartz and limestone) (Table 1) [81–85].

Faunal remains are very abundant in all levels of Abric Romaní. In total, 38,228 faunal remains belonging to 13 different taxa have been recovered. Among the ungulates, cervids (*Cervus elaphus*) and equids (*Equus ferus/Equus hydruntinus*) are the most abundant animals, according to the number of identified specimens (NISP), the minimum number of elements (MNE) and the minimum number of individuals (MNI). The remains of aurochs (*Bos primigenius*) are also common in the lower levels (I, J, K, L, M, O and P), and the chamois (*Rupicapra pyrenaica*) is common in the upper levels (A, B, D, E, F, G, H and J). The remains of rhinoceros (*Stephanorhinus cf. hemitoechus*) have been documented in levels H, J and M, although they are scarce. A proboscoid femur was recovered from level E (Table 1). Zooarchaeological studies of each level indicate that the faunal record is the result of Neanderthal activity, which was characterized by primary access to animal carcasses and complete exploitation of their resources [86–89]. By means of the density of the faunal remains, as well as taphonomic analysis and anatomical refitting, it has been possible to establish areas where specific activities were performed. These analyses, along with the characterization of hearths, have resulted in the identification of sleeping areas, cleaning zones and animal processing areas in some of the levels [71, 86–93]. In all the levels, all of the activities associated with animal butchering have been documented, indicating the complete exploitation of animal resources. In addition, numerous thermoalterations have been documented. Evidence of carnivore activity is very scarce and is thought to have resulted from scavenging of the remains left by human groups [71, 73, 79, 81, 82, 86, 88–91, 94]. The faunal assemblage reflects the highly variable transport of animal carcasses. This transport ranged from complete animals to just a few elements. In general, anatomical elements that were high in unsaturated fat were preferentially transported to the rock shelter [94].

The occupation types that produced the archaeological record can be separated into two groups, long-term and short-term (and/or non-residential) occupation events [71, 73, 81, 82, 90–93, 95] (Table 1). In both of these models, all of the hearths were reused, especially during the long-term occupation events, and these structures were therefore preserved. Therefore, the materials present within the Abric Romaní correspond to the superposition of different occupational events [71, 92].

**Table 1. Summary by layer, occupation type, lithics, wood used and previously specified transport strategies [67, 68, 71, 73, 75, 81–84, 88–91, 93–95].**

Abric Romani	Model of occupation	Raw Material	Lithics	Knapping Methods	Charcoals, hearths and wood remains	Faunal Taxa	Anthropogenic / carnivore modifications	Chronology	D-O HS	MIS
<b>Level E</b>	Residential camp	Flint (90%) Limestone (5%) Quartz (3%) Others (2%)	Discoid and levallois methods. Lithic tools: Cores (2%) and retouched (4%) tools (dentifolates and noches) are scarce; small flakes (41%) and fragment flakes (49%) are most common.	Hearths = 11	Ungulate (MMU)	Canis lupus (1) Lynx sp. (1)	Anthropogenic modifications: Cut marks 7%; Percussion marks 11%	43.2 ± 1.1 ka BP (14C AMS)	12	3
<b>Level H</b>	Residential camp: Short term occupation	Flint (60%) Limestone (25%) Quartz (6%)	Discoid and levallois methods. Lithic tools: Cores (1%) and retouched (4%) tools (dentifolates and noches) are scarce; small flakes (49%) and fragment flakes (17%) are most common.	Pinus sp. = 30.4% Asteraceae = 39.3% Poaceae = 21.4% Others trees = 3.5% Hearths = 10 Preservation of wood is scarce (4 remains: 2 Pinus, 1 Juniperus)	Cervus elaphus (3) Equus ferus (2)	Crocota crocata (1) Panthera leo spelaea (1)	Anthropogenic modifications: Cut marks 2.85%	46.6 ± 1.7 ka BP (U/Th) Plat sup: 45.1 ± 3.1 ka BP (U/Th) Plat inf: 46.5 ± 1.1 ka BP (U/Th) 44.5 ± 1.2 ka (14C AMS)	13/ HSS	
<b>Level I</b>	Residential camp: Short term occupation; Highly mobile group; Linear mobility; Planning of long movement	Flint (50%) outcrops to 5km and 25 km Quartz (26%) and Limestone (21%) local 5km.	Discoid method. Lithic tools: Cores (1%) and retouched (2%) tools (dentifolates and noches) are scarce; small flakes (37%) and fragment flakes (56%) are most common.	Pinus sylvestris/nigra = 71% salzmannii = 60% Hearths = 16 Preservation of wood is scarce, fuel wood accumulations.	Cervus elaphus (7) Equus ferus (7)		Anthropogenic modifications: Cut marks 2.84%; Percussion marks 2.53% Carnivore modifications 1.5%	46 ka BP (U/Th) Plat sup: 45.1 ± 3.1 ka BP (U/Th) Plat inf: 48.6 ± 2.3 ka BP (U/Th)		
<b>Level J</b>	Residential camp: Long term occupation.	Flint (75%) outcrops to 5km and 25 km Quartz (11%) and Limestone (12%) local 5km	Discoid and Centripetal methods. Lithic tools: Dentifolates (3%) and cores (1%) are scarce; small flakes (36%) and fragment flakes (50%) are most common.	Pinus uncinata = 3.4% Hearths = 60 Preservation of wood is scarce, fuel wood accumulations. Pointed wooden element.	Equus ferus/hydrotaurinus (21) Stephanorhinus hemioechus (5) Bos primigenius (7) Rupicapra pyrenaica (4)		Anthropogenic modifications: Cut marks 11%; Percussion marks 20% Carnivore modifications 1%	Plat sup: 49.3 ± 1.6 ka BP (U-series) Plat inf: 50.4 ± 1.6 ka BP (U-series)		
<b>Level K</b>	Residential camp: Short term occupation	Local and semi-local raw materials between 15 and 20 km Flint (47.9%) Limestone (19.2%) Quartz (28%)	Discoid method. Lithic tools: Dentifolates (2%) and cores (0.7%) are scarce; small flakes (30%) and fragment flakes (34%) are most common.	Pinus uncinata = 0.4% Hearths = 25 Little accumulation of negative with signs of cremation	Cervus elaphus (11) Equus ferus (8) Bos primigenius (1)		Anthropogenic modifications: Cut marks 4.1%; Percussion marks 10.7% Carnivore modifications 3%	47 ± 2.1 ka (14C AMS) Plat sup: 50 ± 1.6 ka BP; (U-series)	14	
<b>Level L</b>	Residential camp: Short term occupation	Local and semi-local raw materials between 15 and 20 km Flint (83.7%) Limestone (9.9%) Quartz (3.3%)	Discoid method. Lithic tools: Dentifolates (2.7%) and cores (1.4%) are scarce; small flakes (46.2%) and fragment flakes (39.8%) are most common.	Pinus sylvestris = 63.78% Pinus uncinata = 2.8% Hearths = 23 Four accumulations grouped together to hearths	Cervus elaphus (7) Equus ferus (2) Bos primigenius (4)		Anthropogenic modifications: Cut marks 6.7%; Percussion marks 3.4% Carnivore modifications 0.8%	52.5 ± 1.1 ka BP (U-series)		
<b>Level M</b>	Residential camp: Long term occupation.	Local and semi-local raw materials between 10 and 30 km Flint (80%) Limestone (9.4%) Quartz (5.3%)	Discoid and centripetal methods. Lithic tools: Dentifolates (0.1%) and cores (0.02%) are scarce; small flakes (47.65%) and fragment flakes (31.25%) are most common.	Pinus sylvestris/nigra = 59% Pinus uncinata = 1.5% Hearths = 37 Four accumulations grouped together to hearths	Cervus elaphus (6) Equus ferus (4) Stephanorhinus hemioechus (1) Bos primigenius (4)	Ursus sp. (1) Crocota crocata (1) Felis silvestris (1)	Anthropogenic modifications: Cut marks 6.7%; Percussion marks 3.7% Carnivore modifications 0.3%	54.5 ± 1.7 ka BP (U-series)		

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## Materials and methods

### Materials

To determine the mortality profiles of the equids and cervids found in the Abric Romaní sequence, 486 teeth from levels E, H, I, Ja, Jb, K, L and M were examined. Of these teeth, 259 were derived from equids, and 227 from cervids. The proportions of maxillary and mandible teeth, 126:133 for the equids and 101:126 for the cervids, are very similar for both groups of animals. A large fraction of the dental remains was found isolated within the site. In some cases, fragments of maxillae and mandibles were recovered with teeth anchored in their alveoli (62 dental remains in total). The number of analyzed teeth found in each level and their integrity (in situ or isolated teeth) is reported in Table 2. To establish dental age, various methods were combined depending on the type of tooth (superior or inferior and anterior or jugal) and the taxon being considered. All materials used in this study are deposited at the Institut Català

**Table 2. Number of teeth analyzed in terms of archaeological level, species and integrity (isolated or within dental series).**

Layer	Taxa	Integrity	N	Total
E	Equids	Isolated tooth	10	10
		Tooth in bone	0	
	Cervids	Isolated tooth	2	6
		Tooth in bone	4	
H	Equids	Isolated tooth	5	9
		Tooth in bone	4	
	Cervids	Isolated tooth	4	7
		Tooth in bone	3	
I	Equids	Isolated tooth	33	39
		Tooth in bone	6	
	Cervids	Isolated tooth	3	39
		Tooth in bone	36	
Ja	Equids	Isolated tooth	77	113
		Tooth in bone	36	
	Cervids	Isolated tooth	26	45
		Tooth in bone	19	
Jb	Equids	Isolated tooth	26	26
		Tooth in bone	0	
	Cervids	Isolated tooth	1	1
		Tooth in bone	0	
K	Equids	Isolated tooth	15	19
		Tooth in bone	4	
	Cervids	Isolated tooth	20	58
		Tooth in bone	38	
L	Equids	Isolated tooth	10	10
		Tooth in bone	0	
	Cervids	Isolated tooth	5	20
		Tooth in bone	15	
M	Equids	Isolated tooth	27	33
		Tooth in bone	6	
	Cervids	Isolated tooth	25	51
		Tooth in bone	26	

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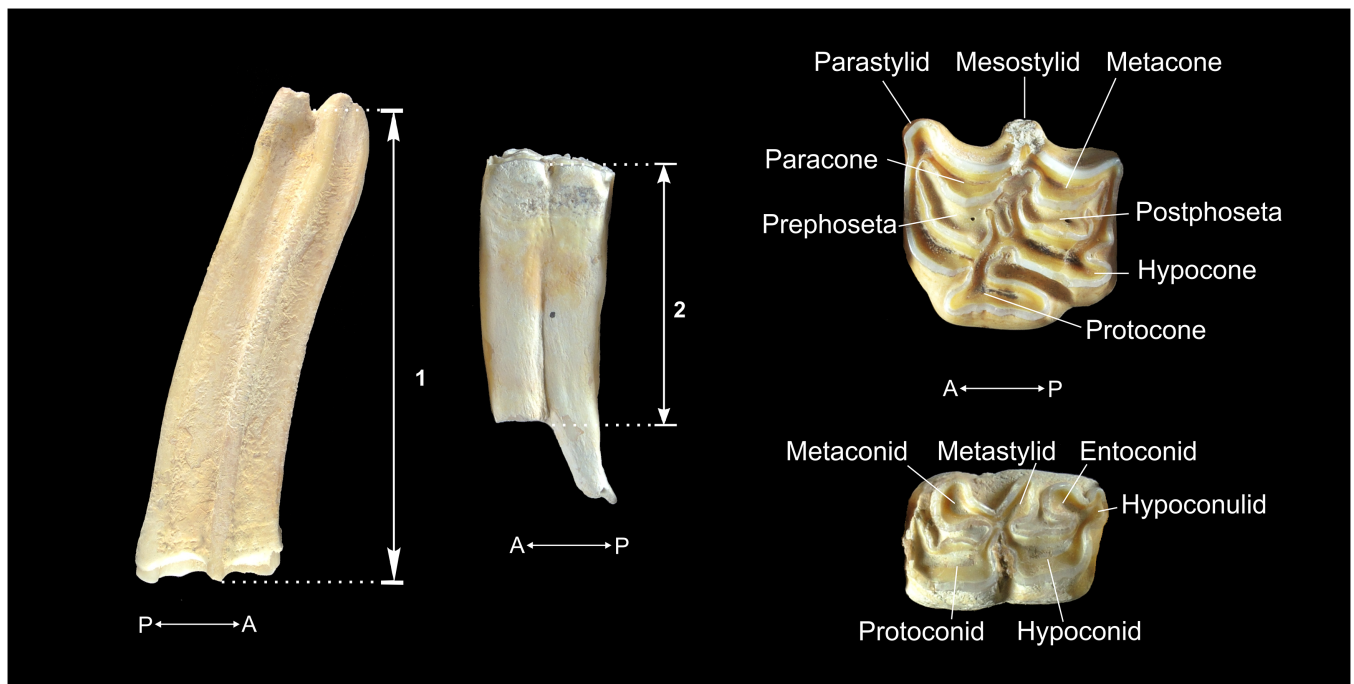


de Paleoeecologia Humana i Evolució Social (IPHES). No permits were required for the described study, which complied with all relevant regulations.

### Determination of dental age

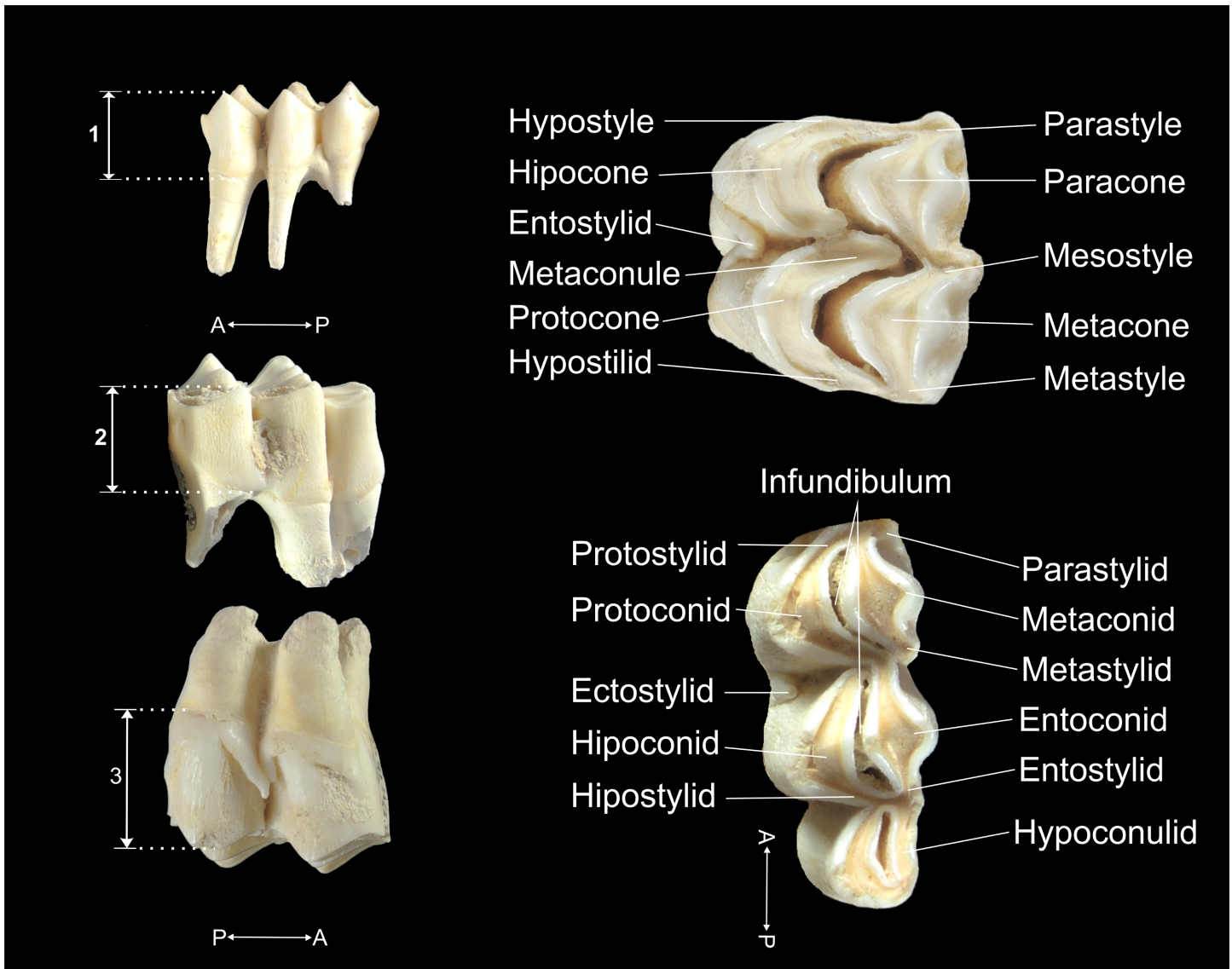
In the case of the equids, we looked at the eruption of deciduous teeth and their replacement by permanent teeth [14]. We used the nomenclature for the anatomical descriptions and for assessing the orientation of the jugal teeth established by Levine [14]. The dental ages of permanent superior and inferior premolars and molars with completely worn occlusal surfaces were calculated based on their crown heights. To estimate age, the parameters of a third-order polynomial regression that relates crown height to age were used [13]. The relevant equation is  $AGE = \sum_{k=0}^3 a_k \cdot (crown\ height)^k$ ; where  $a_k$  is the regression coefficient [13, 14, 96]. The data used in the calculation of the polynomial regression are those provided by Fernandez and Legendre [13]. In keeping with the recommendations of Fernandez et al. [22], we estimated the individual average, minimum and maximum ages as a function of the minimum error associated with each prediction equation (E) [13, 22, 96]. Crown heights were measured from the cementum-enamel junction to the highest point of the occlusal surface along the labial face (Fig 1).

To estimate the dental ages of the cervids, the eruption, replacement and wear of the jugal teeth were analyzed [15]. The anatomical nomenclature of the teeth, the designation of the worn facets and the orientations of the teeth were based on the criteria given by Brown and Chapman [15] (Fig 2). The wear stage codes established by Mariezkurrena [97] and Azorit [98] were also used. These codes were modified for *Cervus elaphus* from Payne's [16] original work with sheep and goats. To estimate the degree of wear of the maxillary dentition, an approximation was made by analogy to the attrition described by Brown and Chapman [15] for mandibular dentition, assuming that the degree of wear for maxillae is similar [99]. As a



**Fig 1. Crown height (CH) (left) and nomenclature of the cheek teeth (right) of equids.** 1 = CH of a superior tooth; 2 = CH of an inferior tooth.

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**Fig 2. Crown height (CH) (left) and nomenclature of the maxillae and mandible teeth (right) of cervids.** 1 = CH of a fourth deciduous premolar; 2 = CH of a third inferior molar; 3 = CH of a second superior molar.

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complement, the quadratic crown height method (QCHM) was applied to the mandibular and maxillary teeth ( $dP_4$ ,  $M_1$ ,  $M_2$  and  $M_3$  /  $dP^4$ ,  $M^1$ ,  $M^2$  and  $M^3$ ) to estimate dental age. The crown height was measured on the labial faces of the lower teeth and on the lingual faces of the upper teeth, on the anterior lobe between the occlusal surface and the cement-enamel junction [3, 99, 100] (Fig 2). The prediction equations applied were:  $AGE = AGE_{Ses}(\frac{CH-CH_0}{CH_0})^2$  for the fourth deciduous premolar ( $dP_4/4$ ) and  $AGE = (AGE_{pel} - AGE_e)(\frac{CH-CH_0}{CH_0})^2 + AGE_e$  for the permanent molars ( $M_1/1$ ,  $M_2/2$  and  $M_3/3$ ). Here,  $CH$  is the crown height of a tooth in mm;  $CH_0$  is the crown height of an unworn tooth in mm;  $AGE_{es}$  is the age in months, in which  $dP_4/4$  is replaced by  $P_4/4$ ;  $AGE_e$  is the eruption age in months of  $M_1/1$ ,  $M_2/2$  and  $M_3/3$ ;  $AGE_{pel}$  is the potential ecological longevity (PEL) in months.

### Estimation of the minimum number of individuals and the construction of age groups and size-weight categories

The MNE [101] for mandibles and maxillae was calculated by means of the construction of dental series, taking the side the tooth originated from (left and right) into account and estimating dental age by means of a combination of the methods described above. The sum of isolated teeth and those found anchored in alveoli with known ages provided a fairly complete dental series. Calculating the MNE can facilitate the estimation of MNI [102, 103] for each of the taxa and levels studied.

Individuals were assigned to age groups based on Bunn and Pickering’s [61] method, which uses the potential ecological longevity (PEL), and is a modification of the model described by Stiner [5]. These authors suggest dividing the PEL into five groups: young juveniles and subadult juveniles (<20% PEL), early prime adults (20–50% PEL), late prime adults (50–75% PEL) and old adults (75%>PEL). This PEL sequence is intended to correctly establish the vulnerability of the ungulates to predators, which is not clearly predicted using the age classes established by Stiner [5]. The early and late prime adult individuals are physically robust, difficult to hunt or even dangerous, whereas the young juveniles, subadult juveniles and old adults are physically weak, more vulnerable and easily hunted. These authors restructure the limits between age groups through the progression of wear stages. Thus, the event that separates young juveniles from subadult juveniles is the eruption of M<sub>1</sub> and M<sub>2</sub>. They note that, unless extraordinary preservation conditions exist, young juveniles will be excluded from the analyses. The boundary between late prime adults and old adults is the loss of the mesial infundibulum of M1 in class 3 bovids (113–340 kg) and the loss of the mesial and distal infundibulum of M2 in class 1 and 2 bovids (4.5–22.5 kg and 22.5–113 kg), which occurs at a PEL of approximately 75%. However, the method proposed by Bunn and Pickering [61] focused on bovids. That proposal has been slightly modified in our work to adapt the old adult PEL to the taxa that are most frequently encountered at the Abric Romani.

In this work, the PEL used for horses is 300 months (25 years) [35, 104] and the PEL used for cervids is 192 months (16 years) [100].

The following age groups were established for the equids: 1) Young juveniles (12 months = 4% PEL) are identified by the presence of complete deciduous dentition, which erupts between 30–40 days after birth, until the eruption of M<sub>1</sub>. 2) Subadult juveniles (60 months = 20% PEL) are characterized by wear on M1 and limited by the total loss of deciduous dentition and the eruption and initial wear of P<sub>4</sub> and M<sub>3</sub> (Levine, 1983). Finally, individuals were assigned to the last three groups, 3) early prime adults (144 months = 50% PEL), 4) late prime adult (225 months = 75% PEL), and 5) old adults (more than 225 months = 75% ≥ PEL) by measuring the crown heights of the teeth and assigning them to age groups as a function of the percentage of the PEL [14, 22, 96] (Table 3).

The cervids were divided into the following groups. 1) Young juveniles (5 months = 2.6% PEL) are identified by the presence of all deciduous dentition, which is present from birth, to the eruption and wear of M<sub>1</sub>. 2) Subadult juveniles (30 months = 20% PEL) are identified by the first wear on the mesial peak of M<sub>1</sub> to the start of wear on the distal peak of M<sub>2</sub> and the end of wear on dP<sub>2</sub>, dP<sub>3</sub> and dP<sub>4</sub>. 3) Early prime adults (78 months = 50% PEL) are identified by

**Table 3. Reference values for the age groups and crown heights used for the calculation of ages.**

Age groups	PEL Equids	Crown height (mm)											
		Mandible						Maxilla					
		P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	P <sup>2</sup>	P <sup>3</sup>	P <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>
Early prime	60–144 month	55–28	78–39	79–42	72–38	76–44	78–46	65–32	76–40	81–41	73–40	80–42	82–37
Late prime	144>225 month	28–8	39–20	42–28	38–21	44–23	46–23	32–14	40–22	41–27	40–24	42–27	37–24
Old	225≥ month	8–4	20–10	28–10	21–10	23–10	23–10	14–5	22–10	27–10	24–10	27–10	24–10

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the first stage of wear of the premolars and  $M_3$ , which occurs in *Cervus elaphus hispanicus* around 30–31 months of age, to the disappearance of the infundibulum of  $M_1$ . 4) Late prime adults (144 months = 75% PEL) are distinguished by the disappearance of the infundibulum of  $M_1$  and the appearance of the line of crown of  $M_3$ , and are limited by the attrition of the mesial and distal infundibulum of  $M_2$  and the hypoconulid of  $M_3$ . 5) Old adults ( $\sim 12$  years = 75%  $\geq$  PEL) are identified by the loss of the mesial and distal infundibulum of  $M_2$  and the hypoconulid of  $M_3$ , at approximately 144 months [15, 97, 98]. At this time, the fecundity and body fat of females decreases enormously, and the males are not able to defend their harems due to a decline in their physical strength [105–106].

The two most common weight categories at Abric Romani are large (equids) and medium-sized (cervids). However, the variation in the weight and size of animals over the course of their lives should not be ignored; taxa and weight categories are not equivalent. These variations in animal weight and size are the results of physiological changes that occur during the growth phase, which ends with sexual maturity and implies major changes in the social behavior of animals [35, 106–109].

In the case of equids, the weight of a two-year-old is equivalent to 75% of that of an adult individual, which is ultimately achieved at five years of age [108], the time at which sexual maturity is also reached by both males and females [35, 104]. Therefore, the dividing line between subadult juveniles and prime adults is considered to correspond to the dividing line between medium and large individuals. The social organization of equids is highly hierarchical. A harem is made up of one stallion and several females with their foals. At around two years of age, the male foals abandon their maternal groups to join groups of single males. Unlike males, subadult females are not forced to leave their maternal group, but they often join other harems after two years [108]. Although this behavior highly influences the composition of social groups, individuals older than two years of age have not yet reached the weight or size of an adult individual. Since the prey choices made by predators, including hominins, are primarily based on feed return rates and the difficulty of capture [63, 110, 111], the fact that male juvenile horses leave their maternal groups and join groups of single males does not necessarily change the way they are considered by predators. Therefore, two-year-old individuals are still considered subadult juvenile individuals.

The size of *Cervus elaphus* is especially variable within single populations and between populations found in different environments. Individuals usually continue to grow until they have reached seven years of age. In *Cervus elaphus*, the boundary between subadult juveniles and prime adults (30 months) coincides with two important ethological events: the abandonment of the family group by young males, and the sexual maturity of females [104]. In *Cervus elaphus* sexual maturity also corresponds to the time at which they reach their full body weight [112]. Therefore, the dividing line between subadult juveniles and prime adults is considered to correspond to the dividing line between small and medium-sized individuals. As indicated above, significant fluctuations in the size of this species have been noted within the fossil record [113, 114]. At present, it has been observed that *Cervus elaphus* in poor habitats are smaller. For example, adult males in northern France weight between 120 and 250 kg (150 kg on average) and females weight between 67 and 100 kg (80 kg on average) [115]. On the other hand, on the Iberian Peninsula, males can reach a body weight of approximately 160 kg, whereas females can reach a body weight of approximately 100 kg [106].

## Mortality analyses

Once the age profiles had been obtained, we analyzed the profiles using triangular diagrams [5]. The individuals were assigned to three age groups (young, prime and old), and the

proportion of each class was plotted on a triangular graph. To this end, the five groups were sorted into the three age categories mentioned above; Table 4 shows the correspondence between the age groups. Within the triangular graphs, the upper corner represents 100% old adults, the lower right corner indicates 100% prime adults, and the lower left corner indicates 100% young individuals. The areas representing catastrophic and attritional age structures, which occur to the left of the area indicating the dominance of prime adult and to the right of the area indicating the dominance of juveniles, respectively, are indicated on the graph. When a sample is plotted within a triangular graph, its position within one of these five zones is assumed to indicate a mortality profile [2, 5, 21, 99].

## Results

The MNI was determined to be 97 across the analyzed levels. Of these individuals, 47 are equids and 50 are cervids (Table 5).

### Equids

Based on the MNI, the level with the highest number of individuals identified is level Ja with 15 individuals, followed by levels K, I, Jb, M, E, H and L, which contain 8, 7, 6, 4, 3, 2 and 2 identified individuals (Table 5). Tables 6 and 7 show the MNE of mandibles and maxillae. Figs 3–6 show the MNI of the equids by level (S1 Table). We were able to measure the crown heights of 33 mandible teeth and 54 maxillary teeth belonging to a total of 43 individuals, which allowed us to calculate the ages of these animals (Tables 6 and 7).

A subadult juvenile individual, an early prime adult, and a late prime adult were identified in level E based on the determined age at death. Within level H, two early prime adult individuals were identified. Within level I, a subadult juvenile individual and six early prime adults were identified. Within level Ja, four subadult juvenile individuals, four early prime adults, six late prime adults and one old adult individual were identified. Within level Jb, a subadult juvenile individual, three early prime adults, and two late prime adults were identified. Within level K five early prime adults, two late prime adults and one old individual were identified. In level L two late prime adult individuals were identified. Within level M, a one subadult juvenile, two early prime adults and one late prime adult were identified. In total, 9 juveniles, 37 prime adults and 2 old adult individuals were identified (Table 5). The equids show a mortality profile that is dominated by prime adults within all levels of the sequence (Fig 7).

### Cervids

Table 5 shows the total NISP, MNE and MNI calculated for the cervids found in each of the levels studied. Tables 8 and 9 show the MNE of mandibles and maxillae in each level. Figs 8–10 show the MNI of the cervids by level. Within each level, between one and 11 individuals

**Table 4. Age group divisions based on Stiner [5] and Bunn and Pickering [61], and the estimated age of cervids and equids.**

Age groups [5]	Age groups [61]	Cervids	Equids
Young	Young juvenile	0–5 month	0-10/12 month
	Subadult juvenile	5–30 month	10/12-60 month
Prime adult	Early prime	30–78 month	60–144 month
	Late prime	78–144 month	144–225 month
Old adult	Old	≤144 month	≤225 month

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**Table 5. MNE, MNI and MNI by age group for each level of Abric Romaní.**

Level	Taxa	MNE		MNI	Juvenile	Prime adult	Old adult
		Mandible	Maxilla				
E	Equids	2	3	3	1	2	
	Cervids	2	1	3	1	2	
H	Equids	1	2	2		2	
	Cervids		3	3		3	
I	Equids	6	6	7	1	6	
	Cervids	7	4	7	5	1	1
Ja	Equids	17	12	15	4	10	1
	Cervids	7	10	10	5	5	
Jb	Equids	7	5	6	1	5	
	Cervids		1	1		1	
K	Equids	6	3	8		7	1
	Cervids	13	5	11	4	5	2
L	Equids	4	1	2		2	
	Cervids	7	1	7	2	4	1
M	Equids	4	2	4	1	3	
	Cervids	9	9	8	3	4	1
Total		92	68	97	12	41	8

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have been identified (S1 Table). Level K and level M have the most individuals, whereas level Jb contains of the fewest. It was possible to define the wear pattern of the occlusal surfaces of 63 mandible teeth belonging to 34 individuals. The identified wear patterns are indicated in Tables 8 and 9.

Based on the determined ages at death a subadult juvenile individual and two early prime adults were identified within level E. Within level H, three late prime adults were identified. Within Level I, four young juveniles, a subadult juvenile, an early prime adult and an old adult individual were identified. Within level Ja, three young juveniles, two subadult juveniles, four early prime adults and one late prime adult were identified. Within level Jb, only one early prime adult has been identified. Within level K, two young juveniles, two subadult juveniles, four early prime adults, one late prime adult and two old adult individuals were identified. Within level L, two young juveniles, three early prime adults, one late prime adult and one old adult individual were identified. Within level M, a young juvenile, two subadult juveniles, two early prime adults, two late prime adults, and one old adult individual were identified. In total, 20 juveniles, 25 prime adults and 5 old adult individuals were identified (Table 5).

For the cervids, the mortality profiles vary by level, and five different models have been identified (Fig 11): 1) a profile that is located at the intersection between the catastrophic mortality and the prime-dominated profiles in level E; 2) a profile that is dominated by prime adults within levels H and Jb; 3) a mortality profile that is dominated by juveniles in level I; 4) a profile that is positioned at the intersection between the attritional and catastrophic profiles at level Ja; 5) and a catastrophic mortality profile obtained from levels K, L and M (Fig 11).

## Discussion

To date, the deposits uncovered at Abric Romaní have yielded a sequence of 15 levels formed during the interstadial MIS 3. An exclusively anthropogenic origin for the lithic and faunal remains has been inferred for all of these levels. The mortality profiles of the main taxa indicate the existence of marked differences between the ages of the equids and cervids. The equid

**Table 6. Number of equids mandibles at Abric Romaní, indicating level, archaeological reference, MNE, size, dental series, crown height of teeth, age group according to Stiner [5] and Bunn and Pickering [61], and mean, minimum and maximum age in months.**

Level	Reference	Individual	Side	Dental series	Crown Height (mm)						Age group		Crown Height Method (Age months)			
					dp <sub>2</sub> /P <sub>2</sub>	dp <sub>3</sub> /P <sub>3</sub>	dp <sub>4</sub> /P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	[5]	[61]	Mean Age	Minimum Age	Maximum Age	
E	AR85 CIII U51 10/P58 182/AR 98 N42 1	Mand. Eq 1	Left	P3 M3 M2								Prime Adult	Early Prime			
E	AR92 T48 131/P42 19	Mand. Eq 2	Right	dp3 dp4		29.28						Juvenile	Subadult Juvenile			
H	AR 90 2.25 P49 24	Mand. Eq 1	Left	P2 P3	43.61	61.59						Prime Adult	Early Prime	87.84	75.24	100.44
I	AR92 N52 2/P49 12	Mand. Eq 1	Left	M2 M3								Prime Adult	Early Prime			
I	AR91 P49 13/K55 1/L53 1/L49 6	Mand. Eq 2	Right	M3 dp2 dp3 dp4	16.27	20.36	34.49					Juvenile	Subadult Juvenile			
I	AR 91 R30 5	Mand. Eq 3	Left	M1 M2 M3								Prime Adult	Early Prime			
I	AR 91 M49-R S/C/G60 S/C/M46 2	Mand. Eq 4	Right	P3 P4 M1 M3								Prime Adult	Early Prime			
I	AR 91 CIII S50 8/S50 9/J49 12	Mand. Eq 4	Left	P4 P3 M3								Prime Adult	Early Prime			
I	AR 91 CIII Q51 9	Mand. Eq 5	Left	P3								Prime Adult	Early Prime			
Ja	AR94 O48 35/I64 14/L56 89/L55 27/L58 44	Mand. Eq 1	Left	P2 P3 M1 M2 M3								Prime Adult	Early Prime			
Ja	AR94 K57 106/K57 81/K57 94/L48 59	Mand. Eq 1	Right	P2 P3 P4 M1 M2 M3				56.17				Prime Adult	Early Prime	81.6	61.8	101.4
Ja	AR94 L51 70/AR95 J63 4	Mand. Eq 10	Left	M2 M3 M1					34.69	31.66		Prime Adult	Late Prime	153.48	141.36	165.72
Ja	AR95 I49 110	Mand. Eq 11	Right	dp4			31.36					Juvenile	Subadult Juvenile			
Ja	AR94 N48 106/AR 93/ N44 66/AR95 K63 11	Mand. Eq 2	Right	P2 P3 P4 M1 M2 M3								Prime Adult	Early Prime			
Ja	AR93 M46 112/AR94 M48 39/AR92 M58 7	Mand. Eq 2	Left	P2 P3 P4 M1 M2 M3								Prime Adult	Early Prime			
Ja	AR95 J61 46/AR94 L55 2/AR93 J58 51/AR94	Mand. Eq 3	Right	P2 P3 P4 M1 M2 M3	36.83	49.02						Prime Adult	Early Prime	99.36	86.76	111.96
Ja	AR93 P46 1/P48 53/N50 133/AR94 K56	Mand. Eq 3	Left	M1								Prime Adult	Early Prime			
Ja	AR95 M49 80/AR93 L57 16/AR94 K59 60	Mand. Eq 4	Right	M1 P4 M2 M3			51.44		71.45			Prime Adult	Early Prime	78.24	69.36	87
Ja	AR95 R48 54/AR94 L48 23/AR94 K58 61	Mand. Eq 4	Left	P2 P3 M1 M2	33.51							Prime Adult	Early Prime	105.36	90.12	120.06
Ja	AR95 M49 80	Mand. Eq 5	Right	M1								Prime Adult	Early Prime			
Ja	AR94 O48 59/AR 96 L41 6/AR95 J62 36	Mand. Eq 5	Left	P4 M1 M2 M3								Prime Adult	Early Prime			
Ja	AR94 J58 18	Mand. Eq 6	Left	M1								Juvenile	Subadult Juvenile			

(Continued)

Table 6. (Continued)

Level	Reference	Individual	Side	Dental series	Crown Height (mm)						Age group		Crown Height Method (Age months)		
					dp <sub>2</sub> /P <sub>2</sub>	dp <sub>3</sub> /P <sub>3</sub>	dp <sub>4</sub> /P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	[5]	[61]	Mean Age	Minimum Age	Maximum Age
Ja	AR93 P47 3	Mand. Eq 7	Right	P4 M1			47.26	45.77			Prime Adult	Early Prime	101.04	75	127.08
Ja	AR94 J51 21/ AR91 H53 3	Mand. Eq 7	Left	M3							Prime Adult	Early Prime			
Ja	AR93 M55 1	Mand. Eq 8	Left	dp2 dp3 dp4 M1	11.42	10.64					Juvenile	Subadult Juvenile			
Ja	AR92 plat sup /AR95 P51 12/ AR95 J65 3	Mand. Eq 9	Left	P3		11.79					Juvenile	Subadult Juvenile			
Jb	AR95 O52 36/ N49 1/AR99 M41 107	Mand. Eq 1	Right	P2 M2 M1							Juvenile	Subadult Juvenile			
Jb	AR95 M54 130/ D46 1/M57 15	Mand. Eq 2	Left	P2 M2 M3							Juvenile	Subadult Juvenile			
Jb	AR95 M54 184/ O53 3/M57 20	Mand. Eq 3	Right	P2 M2 P3							Prime Adult	Early Prime			
Jb	AR95 M51 107/ O55 31	Mand. Eq 3	Left	M2 M3							Prime Adult	Early Prime			
Jb	AR95 O51 14	Mand. Eq 4	Left	M2											
Jb	AR95 L54 27/ M54 173	Mand. Eq 5	Left	M1 M2											
Jb	AR95 N53 79/ AR99 M42 19	Mand. Eq 7	Left	dp3		23.85					Juvenile	Subadult Juvenile			
K	AR 97 S42 93/ Q44 71	Mand. Eq 1	Right	P3 P2							Juvenile	Subadult Juvenile			
K	AR 97 P56 1	Mand. Eq 2	Right	dp4 (P4 germ) M1			12.70				Juvenile	Subadult Juvenile			
K	AR97 K58 1/I42 2/N46 9	Mand. Eq 2	Left	dp4 (P4 germ)			13.30				Juvenile	Subadult Juvenile			
K	AR97 M53 13/ R44 1	Mand. Eq 3	Left	M3							Prime Adult	Early Prime			
K	AR 96 I54 4	Mand. Eq 4	Right	M2							Juvenile	Subadult Juvenile			
K	AR 97 O45 1	Mand. Eq 5	Right	M2							Juvenile	Subadult Juvenile			
L	AR99 P42 1	Mand. Eq 1	Left	M3											
L	AR98 H58 7/ AR97 N51 7/K56 4	Mand. Eq 2	Right	M1 M2 M3			42.73				Prime Adult	Early Prime	101.88	82.08	121.68
L	AR 97 K55 1/ AR99 V48 465	Mand. Eq 3	Right	P2 P3											
L	AR99 S42 38	Mand. Eq 3	Left	P2											
M	AR00 S43 25/ S43 18/AR02 N46 14/K54 16	Mand. Eq 1	Right	dp2 dp3 dp4 M3	13.99	9.68	14.98				Juvenile	Subadult Juvenile			
M	AR02 S50 55/ S51 270	Mand. Eq 2	Right	M2 M3							Prime Adult	Early Prime			
M	AR02 L49 111/ L54 19/L52 1/ M51 2/L53	Mand. Eq 4	Left	P2 P3 P4 M1 M2 M3		53.57	56.21	43.20			Prime Adult	Early Prime	95.76	75	116.4
M	AR01/02 K48 9/ L41 13/L47 1/ K51 25	Mand. Eq 3	Left	P2 P3 P4 M1 M3	63.56			75.98		77.50	Prime Adult	Early Prime	63.6	51.84	75.24

<https://doi.org/10.1371/journal.pone.0186970.t006>



**Table 7. Number of equids maxillae at Abric Romani, indicating level, archaeological reference, MNE, size, dental series, crown height of teeth, age group according to Stiller [5] and Bunn and Pickering [61], and mean, minimum and maximum age in month.**

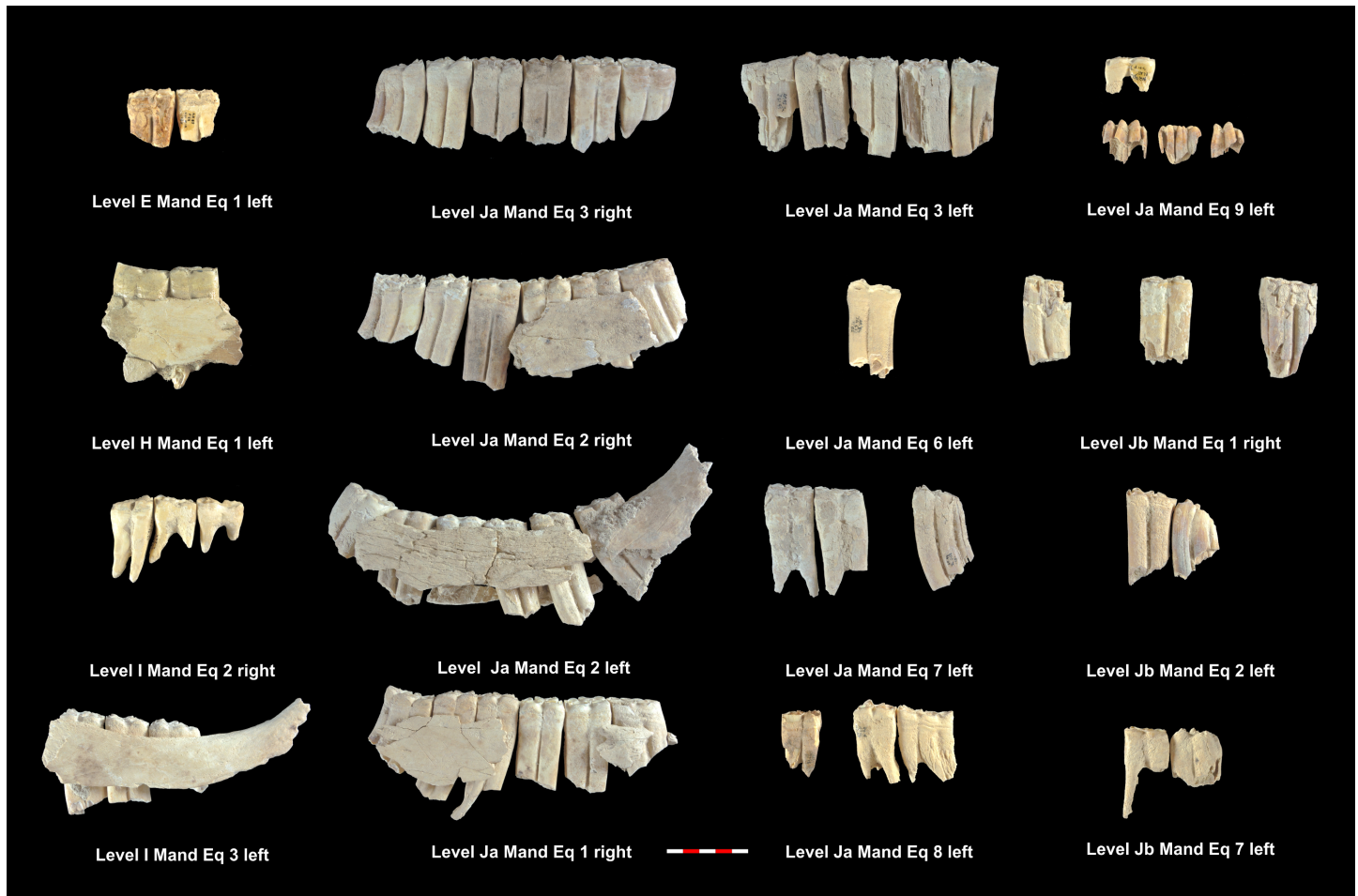
Level	Reference	Individual	Side	Dental series	Crown Height (mm)							Age group			Crown Height Method (Age months)	
					dp <sup>2</sup> /p <sup>2</sup>	dp <sup>3</sup> /p <sup>3</sup>	dp <sup>4</sup> /p <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	[5]	[61]	Mean Age	Minimum Age	Maximum Age	
E	AR84 Q48 3/ S-T/48-49 11/AR98 O42 3	Max. Eq 1	Right	P3 P4 M3		45.45	48.92					Prime Adult	Early Prime	114.12	105	123.12
E	AR92 I64 24	Max. Eq 2	Left	M2					79.61			Juvenile	Subadult Juvenile	60	45.24	62.8
E	AR92 U48 275	Max. Eq 3	Left	Indeterminate												
H	AR90 CIII 2.2.5 L54 49/M54 28	Max. Eq 1	Right	M1 M2								Prime Adult	Early Prime			
H	AR90 CIII 2.2.5 L54 2/L54 4/L56 91/K58 1	Max. Eq 1	Left	P2 P3 P4 M1 M2			81.54					Juvenile	Subadult Juvenile	47.64	35.76	59.52
I	AR91 CIII J48 2/L47 2/N48 5	Max. Eq 1	Right	P2 P3 P4								Prime Adult	Early Prime			
I	AR91 N49 1	Max. Eq 1	Left	P2 P3 P4		72.08						Prime Adult	Early Prime	70.68	64.56	76.92
I	AR91 CIII H53 2/H52 1/H53 1/S53 3	Max. Eq 2	Left	P2 P3 P4 M2					85.09			Juvenile	Subadult Juvenile	38.52	25.68	37.32
I	AR91 R58 2/M49 2/U53 5	Max. Eq 3	Right	dp2 M1 M2		26.65		88.75				Juvenile	Subadult Juvenile	24	4.2	43.92
I	AR91 M58 1/S46 N/C	Max. Eq 4	Right	P2 P4								Prime Adult	Early Prime			
I	AR94 Niv I Q58 n°8	Max. Eq 5	Left	M1		94.73						Juvenile	Subadult Juvenile	27.96	18.6	37.32
Ja	AR93 N47 14/AR95 L51 140	Max. Eq 1	Left	P4 M1			27.95	21.05				Old	Old	222.72	212.16	233.28
Ja	AR93 R46 29/AR94 L48 1/AR94 N47 14/ P48 26/R46 29	Max. Eq 2	Right	P2 P3 P4 M1		34.07		29.56				Prime Adult	Late Prime	144	132	156
Ja	AR94 P50 26/O47 117	Max. Eq 2	Left	P2 P4 P3 M1 M2		30.29			26.71			Prime Adult	Late Prime	156	144	168
Ja	AR95 I61 13/AR93 M55 2/AR93 M54 65	Max. Eq 3	Right	P2 P3 P4 M2 M3		38.69						Prime Adult	Early Prime	85.56	76.56	94.56
Ja	AR94 K55 8/AR94 F63 1/AR94 K37 107	Max. Eq 3	Left	P3 P4 M1 M2		58.48	67.35					Prime Adult	Early Prime	83.52	70.8	96.36
Ja	AR94 K54 17	Max. Eq 4	Left	P2		29.83						Prime Adult	Early Prime	133.92	120.84	147
Ja	AR94 K57 116/AR95 L49 142	Max. Eq 5	Left	dp2 M3		41.32						Prime Adult	Early Prime	113.16	100.44	126
Ja	AR98 N42 37/AR94 L57 141/AR93 N54 96	Max. Eq 6	Left	P2 P3 P4 M1 M2 M3		29.86	55.90		54.77			Prime Adult	Early Prime	110.64	99.24	121.92
Ja	AR93 K58 1/AR93 K56 1/AR96 J62 125	Max. Eq 7	Right	P2 P4 M1			53.34	60.75				Prime Adult	Early Prime	91.68	81.12	102.24
Ja	AR95 I62 15/AR94 K54 20/AR94 L57 211/ AR98 N41 7	Max. Eq 7	Left	P2 P4 M1 M2 M3			50.53	60.77	48.53	43.42		Prime Adult	Early Prime	104.52	92.88	116.28
Ja	AR93 N54 n°97	Max. Eq 8	Right	P2 P3		33.61						Prime Adult	Early Prime	124.32	114.72	133.92
Ja	AR94 N48 25/AR94 K59 72/AR94 N54 154	Max. Eq 9	Right	P2 P3 P4 M1 M2 M3		58.49		61.25	65.84			Prime Adult	Early Prime	86.64	77.16	96
Ja	AR94 S53 19	Max. Eq 9	Left	P2								Prime Adult	Early Prime			

(Continued)

Table 7. (Continued)

Level	Reference	Individual	Side	Dental series	Crown Height (mm)						Age group		Crown Height Method (Age months)			
					dp <sup>2</sup> /p <sup>2</sup>	dp <sup>3</sup> /p <sup>3</sup>	dp <sup>4</sup> /p <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	[5]	[61]	Mean Age	Minimum Age	Maximum Age	
Jb	AR95 N53 2/M48 53/L55 4	Max. Eq 1	Right	M1 M2 M3								Prime Adult	Early Prime	71.76	59.04	84.48
Jb	AR95 N51 4/M45 6/N51 58	Max. Eq 2	Left	P4M1M2M3			49.21	45.75	46.60			Prime Adult	Early Prime	113.88	95.76	132
Jb	AR95 M48 94	Max. Eq 3	Left	M3								Juvenile	Subadult Juvenile			
Jb	AR95 N49 48/N51 8	Max. Eq 4	Right	M2 M3					50.71	52.53		Prime Adult	Early Prime	103.92	91.08	116.64
Jb	AR96 L48 6	Max. Eq 5	-	germ												
K	AR96 P52 8/N52 14/N52 13	Max. Eq 1	Right	P4 M1 M2			41.21	43.05	46.88			Prime Adult	Early Prime	123.72	112.44	135
K	AR97 N53 1/O52 56/N53 3/I52 15	Max. Eq 2	Left	P4 M1 M2 M3			37.85			49.22		Prime Adult	Early Prime	123.12	110.76	135.36
K	AR96 M45 1	Max. Eq 3	Right	M3								Juvenile	Subadult Juvenile			
L	AR97 J49 4/J49 9/O52 4	Max. Eq 1	Left	dp4 P4 M1			12.29	77.42				Prime Adult	Early Prime	61.92	52.56	71.28
M	AR02 K54 3/N54 125/K54 2	Max. Eq 1	Left	P4 M1 M2 M3								Prime Adult	Early Prime			
M	AR00/02 M51 1/J53 16/N49 9/O47 2	Max. Eq 2	Right	P4 M1 M3						51.90		Prime Adult	Early Prime	98.76	85.92	111.48

<https://doi.org/10.1371/journal.pone.0186970.t007>



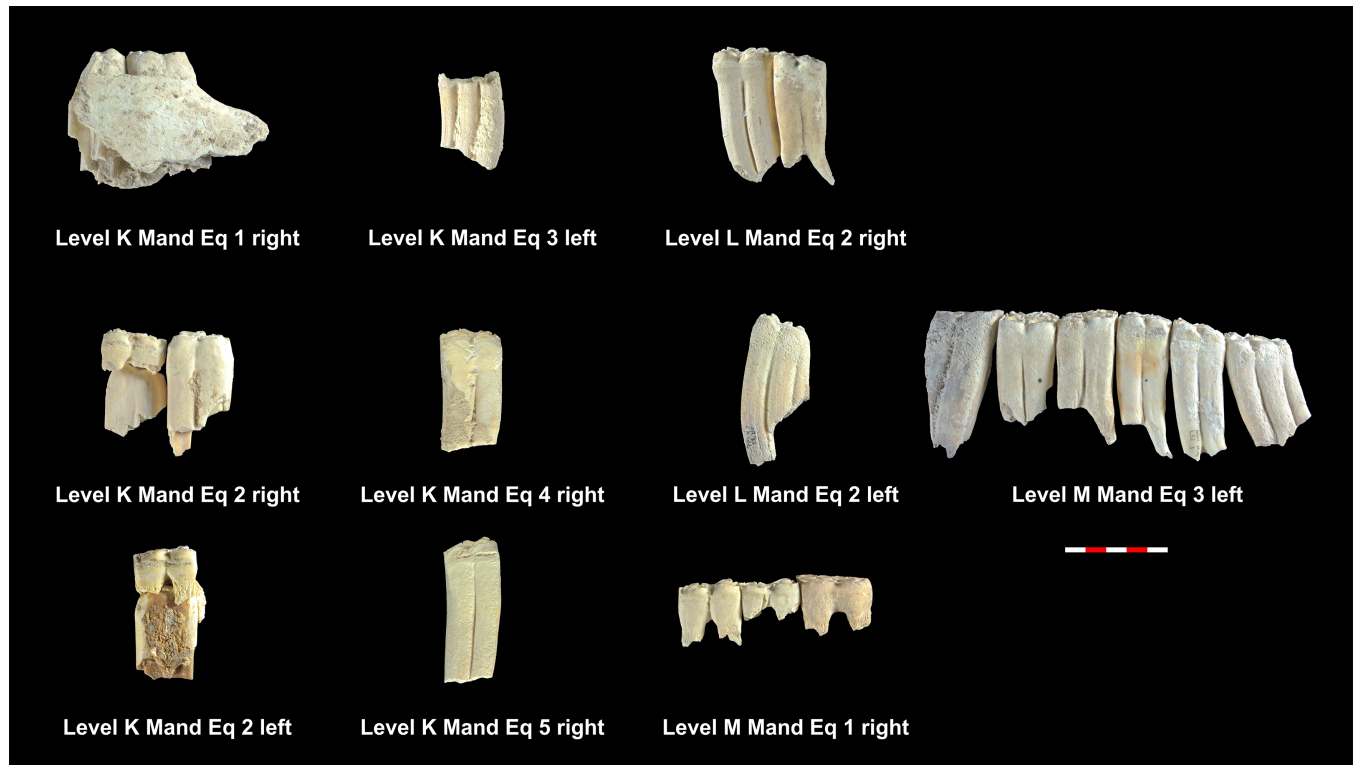
**Fig 3. MNI of equids mandibles from levels E, H, I, Ja and Jb.** Under each dental series are references to level, individual and side as shown in Table 6.

<https://doi.org/10.1371/journal.pone.0186970.g003>

accumulation is dominated by prime adults, whereas the cervid accumulation presents greater variability among the different levels (Figs 7, 11 and 12).

None of the mortality profiles identified at Abric Romaní are unusual in the context of the European Middle Paleolithic record [5, 28, 37, 43, 53, 54, 116, 117]. Mortality profiles that differ according to the taxa hunted have been found at the Manie, Madonna and Lazaret sites [53]. At Manie and Madonna, aurochs present prime-dominated profiles, whereas red deer present a catastrophic profile; however, that difference only exists in one level at each site. At Lazaret, the profiles of deer and ibex change in each of the site's five levels, and neither species has a regular profile [53]. At Abric Romaní, two mortality profiles have been observed throughout the studied sequence. In addition, the atrophic character of the accumulation suggests that the mortality profiles could be considered a valid proxy that can be used to infer the hunting strategies used by the Neanderthals of Abric Romaní.

However, inferences made using mortality profiles should be taken with caution as they may not accurately reflect prey selections made by hominins [118]. Bone accumulations are affected by two key processes, specifically the possible enhanced destruction of young individual teeth and the differential transport of heads according to the weight of individual prey animals. These processes may affect the representation of juvenile individuals in a few different



**Fig 4. MNI of equids mandibles from levels K, L and M.** Under each dental series are references to level, individual and side as shown in Table 6.

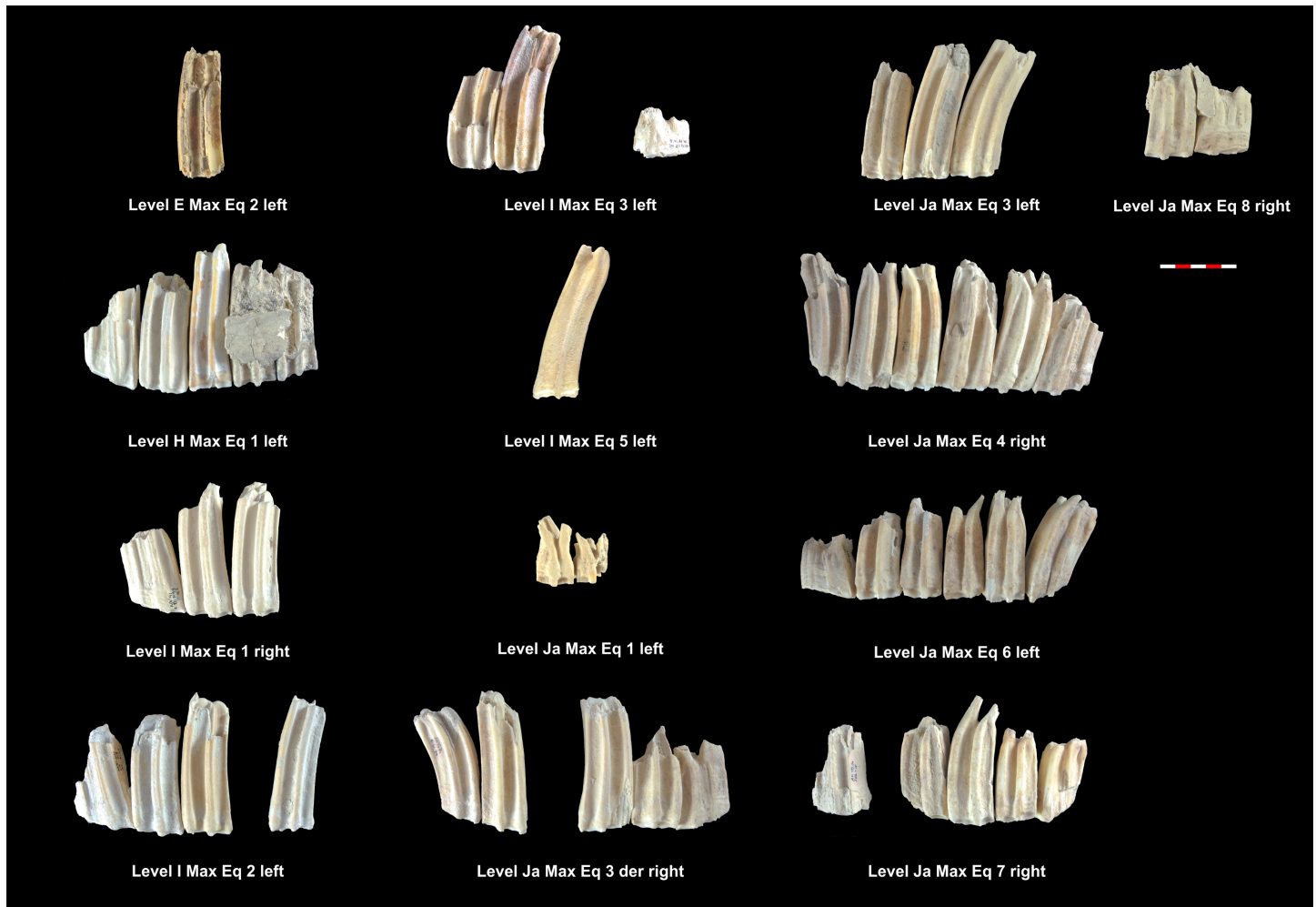
<https://doi.org/10.1371/journal.pone.0186970.g004>

ways: a) because their teeth tend to disappear easily; and b) because their lower weight means that they are more likely to have been transported whole to the site [118].

Considering the differential preservation of individual as a function of age, the scarcity of juvenile equids (17% of the sample) seems to be due to differential destruction processes. However, the high abundance of juvenile cervids (40% of the sample), whose teeth have a lower density than those of equids, indicates that the bias toward adult horses is likely not the product of differential preservation processes, because it should also have altered the deer sample.

Regarding the possible differential transport of heads, Marean [118] indicated that three interrelated factors should be considered: 1) the weight of the animal; 2) the size of the hominin group; 3) the distance between the kill site and the reference site.

Depending on the weight of the animal, many ethnoarchaeological studies indicate that hunter-gatherers faced with equal conditions usually transport more complete small animals than large animals [119–121]. In addition, the variation in the weight of an animal species throughout its life must also be considered, as it affects the decision to transport the heads of that species or not, and therefore also the composition of the mortality profiles [118]. In equids, we documented a predominance of large adult individuals (MNI = 39) over medium-sized young individuals (MNI = 8) (Table 5), while among the cervids we found no great differences between the representation of small (MNI = 20) and medium-sized individuals (MNI = 30) (Table 5). Also, the anatomical representation indicates that the cranial elements of the large animals were transported in equal proportion, or even more, to the rock shelter than cranial elements of medium-sized animals (Table 10) (Fig 13). In levels Ja, Jb, K and M the value of %MAU for skulls is 100% and in levels H and L it is equal or superior to 50%. However, for the cervids the value is 100% only in level M, and in level L the value is even



**Fig 5. MNI of equids maxillae from levels E, H, I and Ja.** Under each dental series are references to level, individual and side as shown in Table 7.

<https://doi.org/10.1371/journal.pone.0186970.g005>

under 30% (Fig 13). MNE and %MAU data for level E are not available. Thus, the weight of the animals did not appear to be a major determining factor in the transport of their heads. However, is important to consider that this circumstance could have affected the transport events [122], because the superposition of diverse transportation strategies has been identified at Abric Romaní, due to multiple conditioning factors, such as the sizes of different animals and the food utility of the transported elements [94].

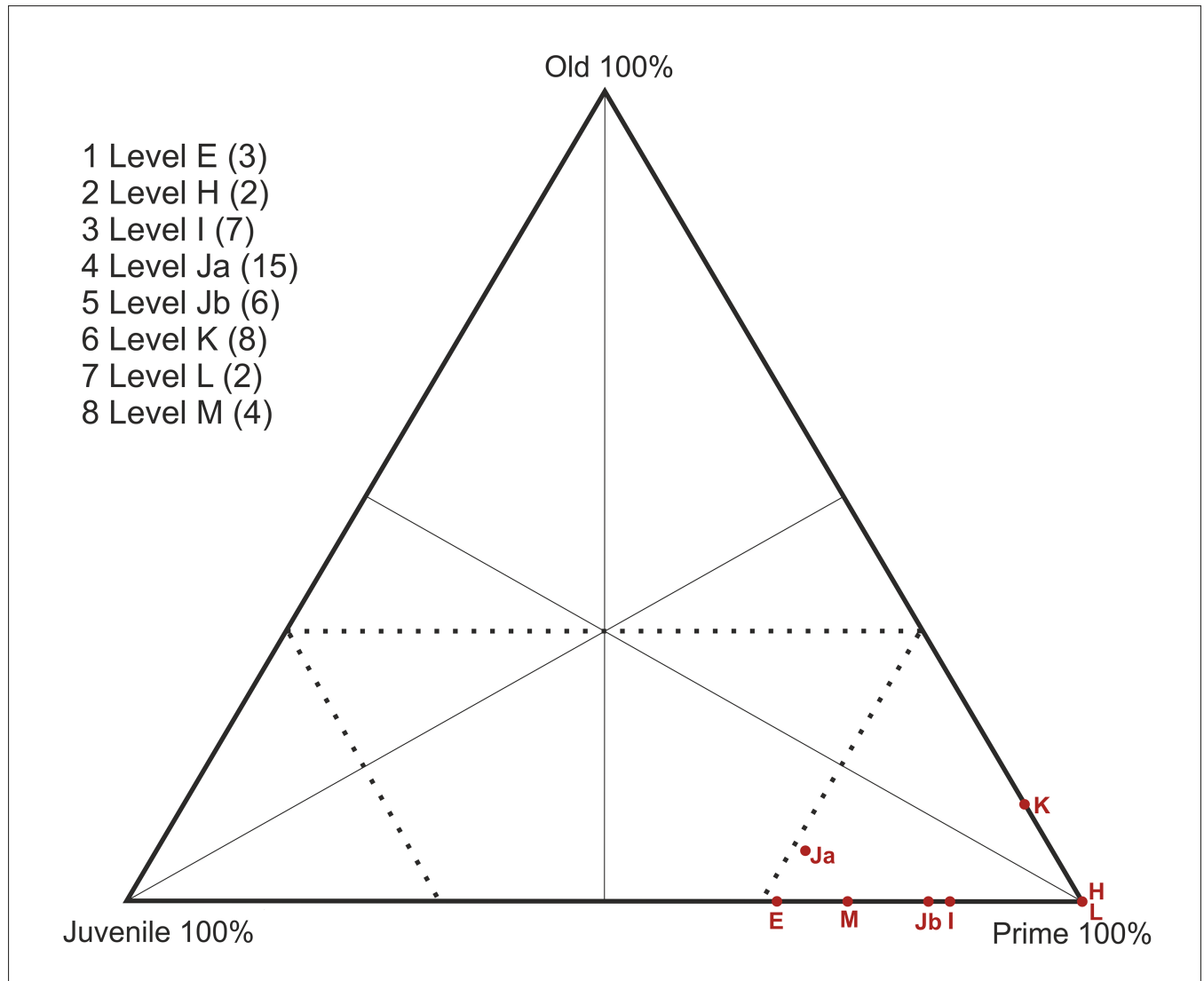
An ethnoarchaeological principle used in the study of mortality profiles indicates that, under equal conditions, within an average settling system of small groups, hunter-gatherers show greater selectivity in making transport decisions, and often abandon the heads of large animals [119, 120, 123]. On the other hand, in an average settlement system of large groups, the bias of the transport of these animals may be reduced [118–121]. The spatial patterns documented within the Abric Romaní correspond to bivouacs around isolated external hearths and to camps with many external hearths connected by reassembling, and resting and sleeping areas [78, 92, 124]. All the levels are the result of an unknown number of occupation events that occurring over hundreds to thousands of years. The levels originating from short-term or non-residential occupation events have been defined as the result of the activity of groups of hunter-gatherers immersed within a regional foraging mobility model, whereas the long-term



**Fig 6. MNI of equids maxillae from levels Jb, K, L and M.** Under each dental series are references to level, individual and side as shown in Table 7.

<https://doi.org/10.1371/journal.pone.0186970.g006>

events have been interpreted as a result of the activity of medium or large groups [70, 81, 82, 84, 91]. Levels H, I, J, K, L, and N have been defined as short-term occupation events associated with a highly mobile Neanderthal group. Analysis of the distribution and nature of the combustion structures associated with the sleeping and resting areas of level N, suggest that it could correspond to a Neanderthal group of between 8 and 12 individuals. Monahan [125] indicates that the Hadza require at least 10 to 12 porters to transport size 3 animals (113–340 kg) or greater. At Abric Romaní, the occasional transport of complete carcasses of medium-sized and large animals has been identified in all of the levels, regardless of the occupation



**Fig 7. Triangular graph showing the age distribution of equid specimens by archaeological level (MNI).**

<https://doi.org/10.1371/journal.pone.0186970.g007>

model. This indicates that hunting parties may have been sufficiently numerous to transport a complete or almost complete large animal [94], at least occasionally.

In keeping with that suggested by Marean [118], differences in the transport of heads may be present within the sequence of Abric Romaní, depending on whether small or large groups occupied the rock shelter.

Level I is the result of short-term or non-residential occupations events, in which the mobility of the group was directly related to the exploitation of hunting resources [91]. The mortality profile of cervids shows a greater number of young individuals (MNI = 5) than adults or old individuals (MNI = 1/1). The predominance of young animals may be due to selective transport, as suggested by Marean [118], in which the transport of small individuals takes precedence over the transport of the heads of adult deer. However, at this level, we see that the transport of equids is not governed by this principle. The equids are represented by one young individual and six prime adult individuals; thus, the large animals are more abundant than

**Table 8. Number of cervid mandibles at Abric Romaní, indicating level, archaeological reference, MNE, size, dental series, crown height of teeth, code of wear stage, age group according to Stiner [5] and Bunn and Pickering [61] and mean age in month.**

Level	Reference	Individual	Side	Dental series	Crown Height (mm)				Wear Stage				Age group		Quadratic Crown Height Method
					dp <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	dp <sub>4</sub>	M1	M2	M3	[5]	[61]	Age month
E	AR98 N41 209	Mand Cerv 1	Left	dp2 dp3									Juvenile	Young Juvenile	
E	AR92 T48 102	Mand Cerv 2	Left	P3 P2									Prime Adult	Early Prime	
I	AR92 L47 34	Mand Cerv 1	Right	dp2 dp3									Juvenile	Young Juvenile	
I	AR91 CIII I49 5	Mand Cerv 2	Right	dp3									Juvenile	Subadult Juvenile	
I	AR91 CIII J53 8	Mand Cerv 3	Left	P2 P3									Prime Adult	Early Prime	
I	AR92 K47 14/ K47 15	Mand Cerv 4	Left	dp2 dp3 dp4	13.74				7L				Juvenile	Young Juvenile	0,0089
I	AR92 P inf. N. C.	Mand Cerv 5	Right	dp2dp3dp4M1 M2	7.56				12L	4A	0		Juvenile	Subadult Juvenile	5,50
I	AR92 L47 38	Mand Cerv 6	Right	dp2 dp3 dp4	13.03				4C				Juvenile	Young Juvenile	0,12
I	AR92 Plat. inf. BN	Mand Cerv 7	Right	P2 P3 P4 M1 M2	4.77					15A	13B	11G	Old Adult	Old Adult Class	165,58
Ja	AR92 L47 surface/AR92 Plat. Sup.	Mand Cerv 1	Right	dp2 dp3 dp4	10.42				7L				Juvenile	Young Juvenile	1,70
Ja	AR95 I63 17/ AR98 L40 4	Mand Cerv 1	Left	dp2 dp3 dp4 M1 M2	12.43				7L	0	0		Juvenile	Young Juvenile	0,32
Ja	AR92 L47 surface/AR98 L40 3	Mand Cerv 2	Left	dp2 dp4	11.52				6L				Juvenile	Young Juvenile	0,81
Ja	AR94 P51 803/AR94 H51 1	Mand Cerv 3	Left	P3 M1 M2		16.42	23.75			6	3A		Juvenile	Subadult Juvenile	25,21
Ja	AR98 M42 12	Mand Cerv 4	Right	P2 P3 P4 M1 M2		10.70				9A			Prime Adult	Early Prime	63,58
Ja	AR92 Plat.Sup J	Mand Cerv 5	Left	dp4	8.61				6L				Juvenile	Young Juvenile	3,85
Ja	AR92 L47 surface	Mand Cerv 6	Right	dp3 dp4		6.44			11				Old adult	Late Prime	97,6
K	AR97 J47 24	Mand Cerv 1	Left	dp3 dp4	9.45				8				Juvenile	Young Juvenile	2,74
K	AR96 J44 4/ J45 4	Mand Cerv 10	Right	P2 P3 P4 M1 M2 M3	9.98					14/ 15	9	11	Old adult	Old Adult Class	110,76
K	AR97 L49 26/ K53 52	Mand Cerv 11	Left	P2 P3 P4 M1 M2 M3	9.21					9	8	9	Prime Adult	Early Prime	73,53
K	AR99 K40 s/c	Mand Cerv 2	Left	dp2 dp3 dp4			23.94		8				Juvenile	Young Juvenile	2,14
K	AR99 L43 4	Mand Cerv 2	Right	dp2 dp3 dp4					8				Juvenile	Young Juvenile	3,04
K	AR97 J45 17/ J48 15/J46 9/ J45 14	Mand Cerv 3	Right	dp2 P3 P4 M3			9.85				0		Prime Adult	Early Prime	40,21
K	AR96 U45 93	Mand Cerv 4	Right	M3		15.48	16.91				0		Juvenile	Subadult Juvenile	

(Continued)



Table 8. (Continued)

Level	Reference	Individual	Side	Dental series	Crown Height (mm)				Wear Stage				Age group		Quadratic Crown Height Method
					dp4	M1	M2	M3	dp4	M1	M2	M3	[5]	[61]	Age month
K	AR99 H41 4 /AR97 J46 25/ AR99 N42 10	Mand Cerv 5	Right	P3 M1 M3			14.88			15		11	Old Adult	Old Adult Class	122,16
K	AR99 N42 8	Mand Cerv 6	Left	M2 M3		15.77		19.61		9	6		Prime Adult	Early Prime	63,36
K	AR96 M47 34	Mand Cerv 6	Right	M2			19.59	22.25		9	6_7		Prime Adult	Early Prime	59,75
K	AR96 K54 s/c/ N45 114	Mand Cerv 7	Right	P2 P3 P4 M1 M2 M3			13.53		8	5	8	Juvenile	Subadult Juvenile	44,96	
K	AR96 N45 30	Mand Cerv 8	Left	M2 M3			8.64	10.73		5	5		Prime Adult	Early Prime	40,16
K	AR97 H45 1	Mand Cerv 9	Left	M2 M1 M3		8.33	13.93	16.50		9	8	9	Prime Adult	Early Prime	68,66
L	AR00 J42 n°8	Mand Cerv 1	Right	P2 P3 P4 M1 M2 M3		6.02	9.84	14.68		13	9	11	Prime Adult	Early Prime	94,29
L	AR97 O50 1	Mand Cerv 2	Right	P3 P4 M1 M2 M3		10.68	15.10			9	8	7	Prime Adult	Early Prime	61,05
L	AR 98 P47 4	Mand Cerv 3	Right	P2									Prime Adult	Early Prime	
L	AR99 T43 BN	Mand Cerv 4	Left	M3				4.38				12	Old Adult	Old Adult Class	175,26
L	AR00 J42 33	Mand Cerv 5	Right	dp3 dp4	10.46				1				Juvenile	Young Juvenile	1,66
L	AR98 I56 6	Mand Cerv 6	Right	dp4	11.60				1				Juvenile	Young Juvenile	0,76
L	AR99 K43 2	Mand Cerv 7	Right	M2			17.26			5			Prime Adult	Early Prime	45,90
M	AR01 T44 5 /R46 6/O45 4	Mand Cerv 1	Left	dp3 dp4	8.84				5	1			Juvenile	Young Juvenile	3,53
M	AR03 U51 638/640	Mand Cerv 2	Right	P2 P3 P4 M1		0				13			Old adult	Old Adult Class	164
M	AR00 R46 9	Mand Cerv 3	Right	P3									Prime Adult	Late Prime	
M	AR01 N46 NFC	Mand Cerv 4	Right	P3 P4 M1						1			Prime Adult	Late Prime	
M	AR01 R43 44/ L48 42/ P43 4	Mand Cerv 4	Left	P2 P3									Prime Adult	Late Prime	
M	AR02 J55 1/ AR00 N46 2/ AR02 P53 53/ K51 1	Mand Cerv 5	Left	P3 M1 M2 M3		15.58	20.31	22.33	7	5	5		Juvenile	Subadult Juvenile	37,09
M	AR02 U46 12, 13/K50 7	Mand Cerv 6	Right	P3 M1		11.10				9			Prime Adult	Early Prime	60,79
M	AR01 Q45 30	Mand Cerv 7	Left	M1						5			Prime Adult	Early Prime	
M	AR02 J52 43	Mand Cerv 8	Right	M1		19.50				4			Juvenile	Subadult Juvenile	18,19

<https://doi.org/10.1371/journal.pone.0186970.t008>

**Table 9. Number of cervid maxillae at Abric Romaní, indicating level, archaeological reference, MNE, size, dental series, crown height of teeth, code of wear stage, age group according to Stiner [5] and Bunn and Pickering [61] and mean age in months.**

Level	Reference	Individual	Side	Dental series	Crown Height (mm)				Wear Stage				Age group		Quadratic Crown Height Method
					dp <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	dp <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	[5]	[61]	Age month
E	AR92 T48/CIII/ AR98 N40 16/ N41 123	Max Cerv 1	Right	M1 M2		20.3				4A			Prime Adult	Early Prime	6.88
H	AR91 2.2.5 L59 3	Max Cerv 1	Right	M3				13.12			8A		Prime Adult	Late Prime	
H	AR91 2.2.5 L59 /L59 5	Max Cerv 2	Right	P3 P4 M1		7.8				8			Prime Adult	Late Prime	82.71
H	AR84 M45 1	Max Cerv 3	Right	M1 M2 M3			8.84				5A	3B	Prime Adult	Late Prime	67.59
I	AR91 Pinf I58/ S53 BN	Max Cerv 1	Left	P2 P3 P4 M1M2		4.37				9A			Old adult	Late Prime	124.9
I	AR92 L46 5 / M45 4 / L46 7	Max Cerv 2	Left	dp2 dp3 dp4 (P2 P3 P4) M1 M2 M3	6.62	15.67		23.27		4A	2A		Juvenile	Subadult Juvenile	20.7
I	AR92 K46 31 / K46 30	Max Cerv 3	Right	dp2 dp3									Juvenile	Subadult Juvenile	
I	AR92 M46 4	Max Cerv 4	Left	dp2 dp3 dp4	12.92					4A			Juvenile	Young Juvenile	0.27
Ja	AR95 I49 6/I49 7/ AR93 H46 12	Max Cerv 1	Right	M1M2M3		8.51	15.05	21.77		5	4A	2A	Prime Adult	Early Prime	75.12
Ja	AR93 K57 34/K57 35/L43 10/L50 352	Max Cerv 1	Left	P2 P3 M1 M2						5A			Prime Adult	Early Prime	
Ja	AR94 L50 2/AR93 M46 8/AR93 M46 6	Max Cerv 2	Right	dp2 dp4 M1	6.79	15.62			14L	4A			Juvenile	Subadult Juvenile	20.94
Ja	AR94 N53 302	Max Cerv 3	Right	dp2									Juvenile	Subadult Juvenile	
Ja	AR95 I62 65/ AR94 K59 106	Max Cerv 4	Right	M1P4		9.73				4A			Prime Adult	Early Prime	63.01
Ja	AR95 I49 8/AR93 N55 30	Max Cerv 5	Right	P2 P3									Prime Adult	Early Prime	
Ja	AR95 I49 8	Max Cerv 6	Right	P3									Prime Adult	Early Prime	
Ja	AR92 Plat. Sup./ AR 94 M49 12	Max Cerv 7	Left	dp2 dp3 dp4	14.56					4A			Juvenile	Young Juvenile	0.003
Ja	AR94 L48 13	Max Cerv 8	Right	dp3 dp4 M1	10.84	18.48				7	2A		Juvenile	Young Juvenile	10.31
Jb	AR93 N51 76	Max Cerv 1	Right	M1		8.11							Prime Adult	Late Prime	79.35
K	AR96 M45 71	Max Cerv 1	Right	P2 P3 P4 M1 M2 M3		11.03	14.68	18.83		6	4	4	Prime Adult	Early Prime	51.39
K	AR96 J47 21	Max Cerv 1	Left	M1 M3 M2		10.91	17.06	20.75		6	4	4	Prime Adult	Early Prime	52.41
K	AR96 N46 20/J49 1/J54 2	Max Cerv 2	Right	P2 M1 M2			13.03						Prime Adult	Early Prime	33.13
K	AR96 M52 5/K49 4	Max Cerv 3	Left	dp4 M1	5.22	16.63			14L	5			Juvenile	Subadult Juvenile	16.46
K	AR99 I42 4	Max Cerv 4	Left	P4									Prime Adult	Early Prime	

(Continued)

Table 9. (Continued)

Level	Reference	Individual	Side	Dental series	Crown Height (mm)			Wear Stage				Age group		Quadratic Crown Height Method	
					dp <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	dp <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	[5]	[61]	Age month
L	AR00 K42 3/ AR97 S50 2	Max Cerv 1	Left	P2 P3 M1		9.25							Prime Adult	Early Prime	67.64
M	AR00 S41 5	Max Cerv 1	Right	M1 M3 M2			11.3	18.08		5	5	1	Prime Adult	Early Prime	45.67
M	AR02 T44 47/T44 51	Max Cerv 2	Left	P2 P3 P4 M1 M2 M3		8.38	16.48	18.42				4	Prime Adult	Early Prime	76.48
M	AR00 P43 30/ M52 2	Max Cerv 3	Left	P2 P3 P4 M1 M2 M3		9.32		18.71		9	6	4	Prime Adult	Early Prime	66.95
M	AR00 S43 23	Max Cerv 4	Right	P4 M1M2		17.72	20.92			4	2		Juvenile	Subadult Juvenile	12.51
M	AR01 M41 48/ K50 20/AR02 N48 96/AR03 U49	Max Cerv 4	Left	P3 P4 M1 M2						4	2		Juvenile	Subadult Juvenile	
M	AR01 M44 12/ AR03 U50 453	Max Cerv 5	Left	P3 P4									Prime Adult	Early Prime	
M	AR01 O43 109/ N45 20	Max Cerv 6	Right	P2 P3									Prime Adult	Early Prime	
M	AR02 K54 25/ AR01 N45 23/ N46 101	Max Cerv 7	Right	P2 P3 P4 M2			6.77				9A		Prime Adult	Late Prime	89.76
M	AR00 N47 41	Max Cerv 7	Left	M2									Prime Adult	Late Prime	

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medium-sized animals. Therefore, the age representation of both species does not appear to be due to the selective transport of heads, according to the weight of the animal.

On the other hand, level J has been identified as resulting from of long-term occupation by medium or large groups composed of more than 12 individuals, and may be related to the

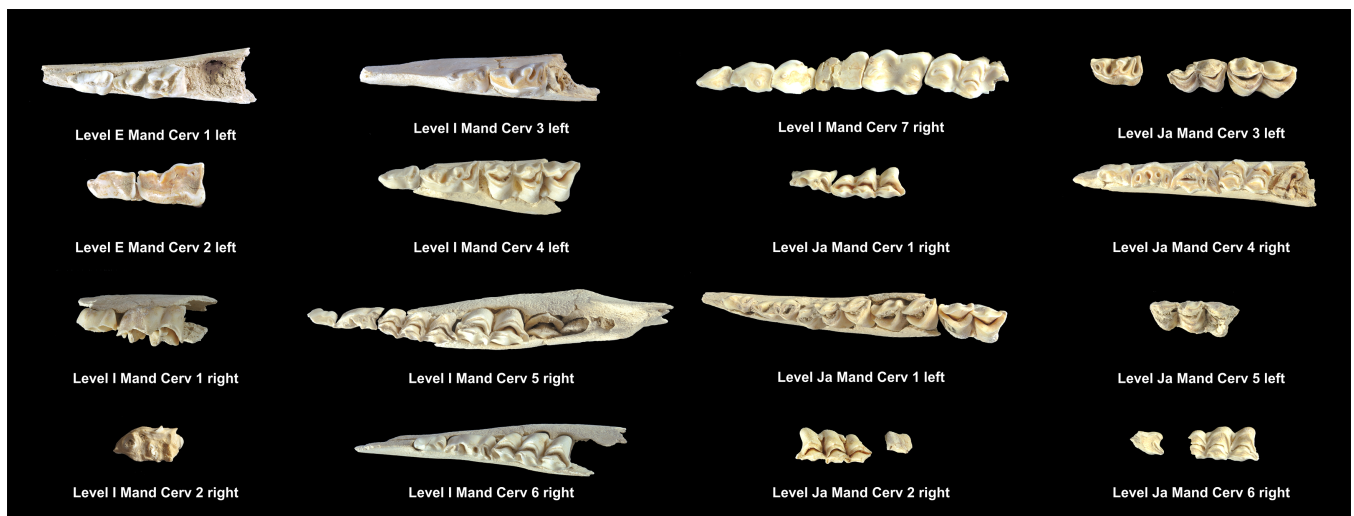
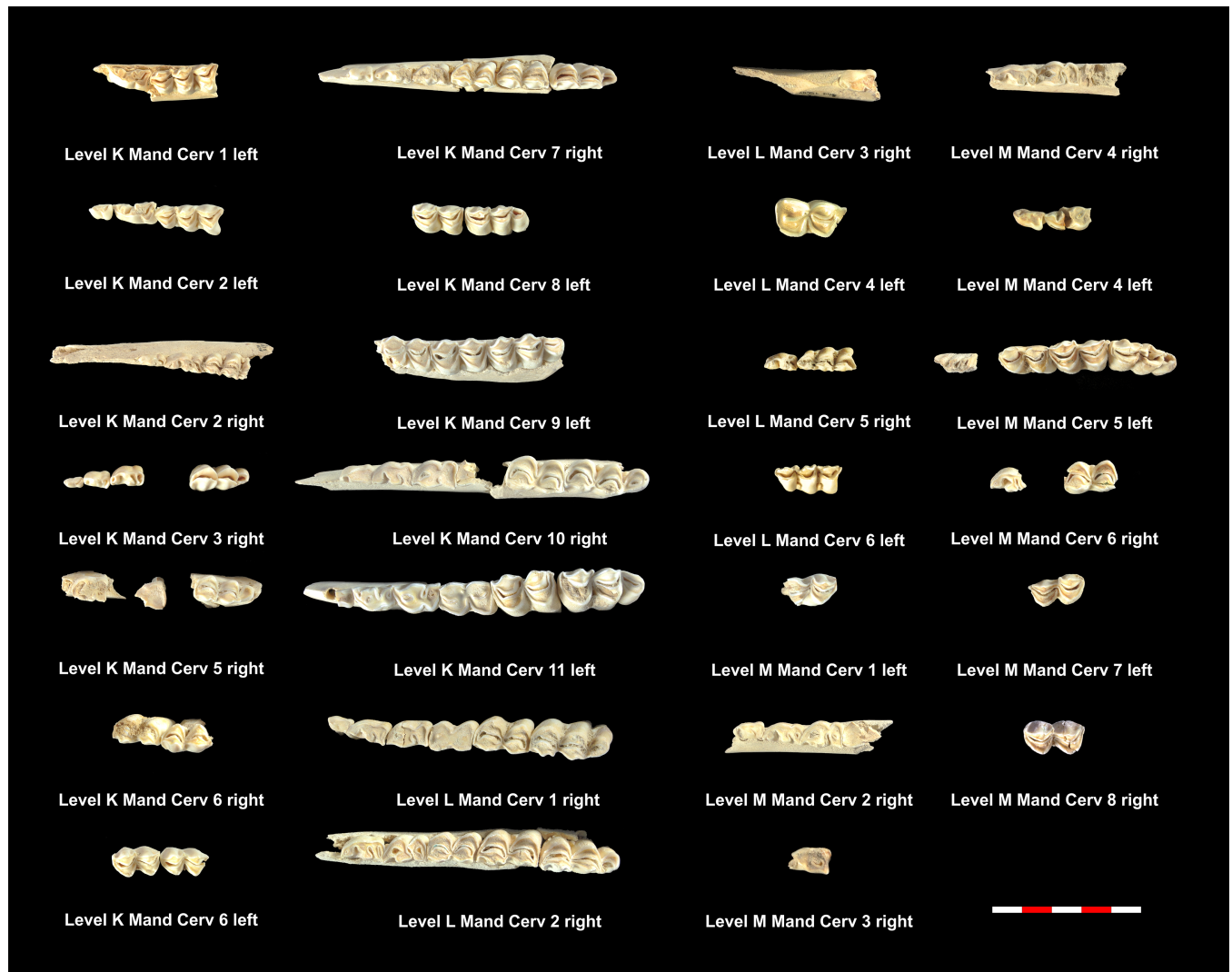


Fig 8. Cervid mandibles included in the MNI of level E, I and Ja. Under each dental series are references to level, individual and side as shown in Table 8.

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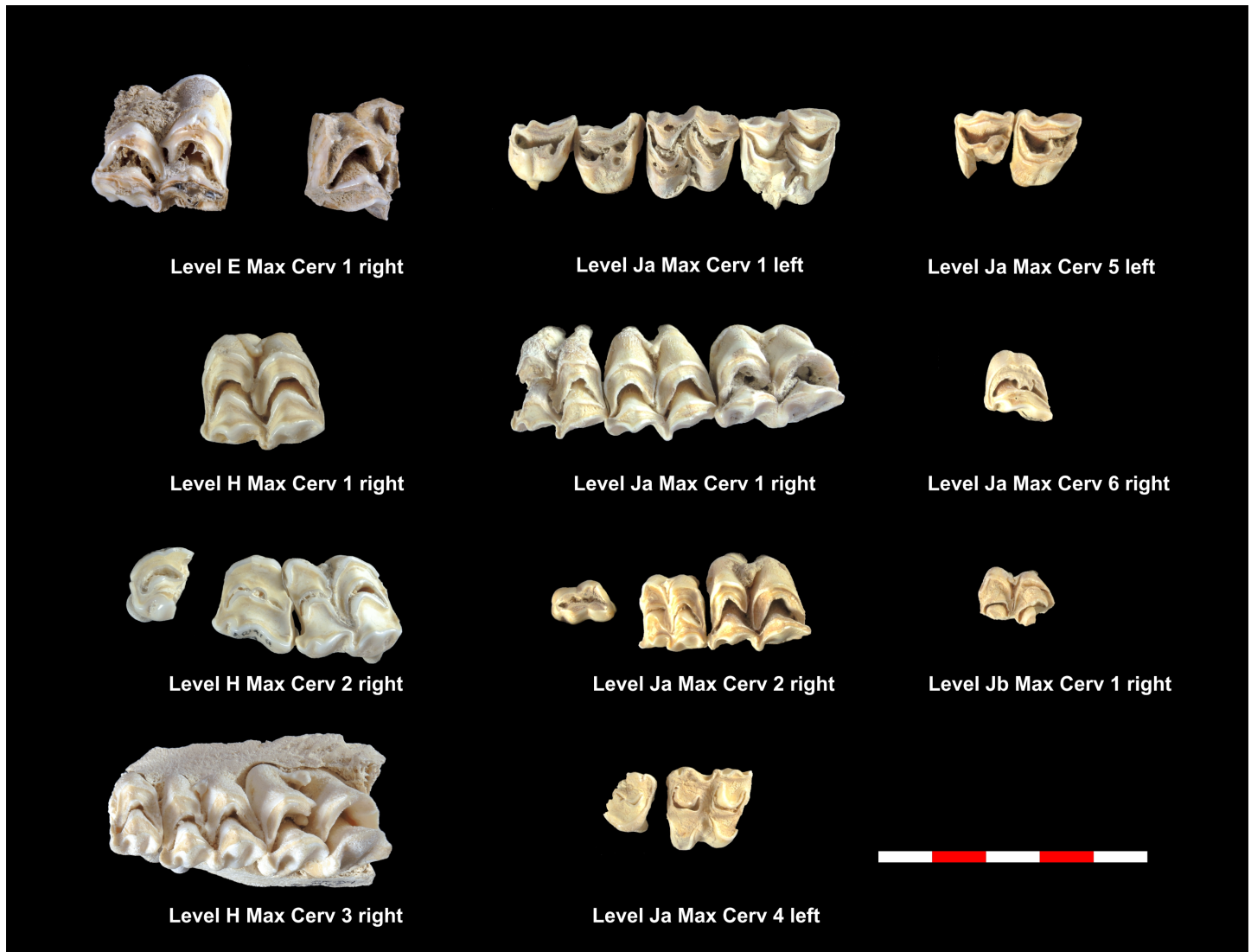


**Fig 9. Cervid mandibles included in the MNI of level K, L and M.** Under each dental series are references to level, individual and side as shown in Table 8.

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aggregation of groups of hunter-gatherers [93]. We found a balance in the representation of small and medium-sized animals among the cervids in this level. Meanwhile, the equids are dominated by large prime adults, which is common to all the levels. Thus, in spite of differences in the settlement model, age selection does not seem to be conditioned by animal size.

Finally, another factor that would condition the transport of the heads is the distance between the kill/butchering site and the reference site. The Abric Romaní is located inside an ecotone that is formed by the Anoia River, the plains that surround it, and the mountains that delimit the gorge. These features give the site strategic importance, and from it, the Neanderthals had immediate access to different biotopes and species [68, 86, 93, 126]. Biotic resources, both faunal and vegetation-based, were locally exploited [86, 89]. The selection of prey mainly focused on obtaining two types of animals, cervids and equids, which may indicate that the axis of mobility was oriented toward the open areas and the forests on the mountainsides that enclose the river valley [68, 86, 89, 93, 126]. In any case, assuming long distances from the kill/butchering site to the reference site, would favor a bias toward large animals. However, as



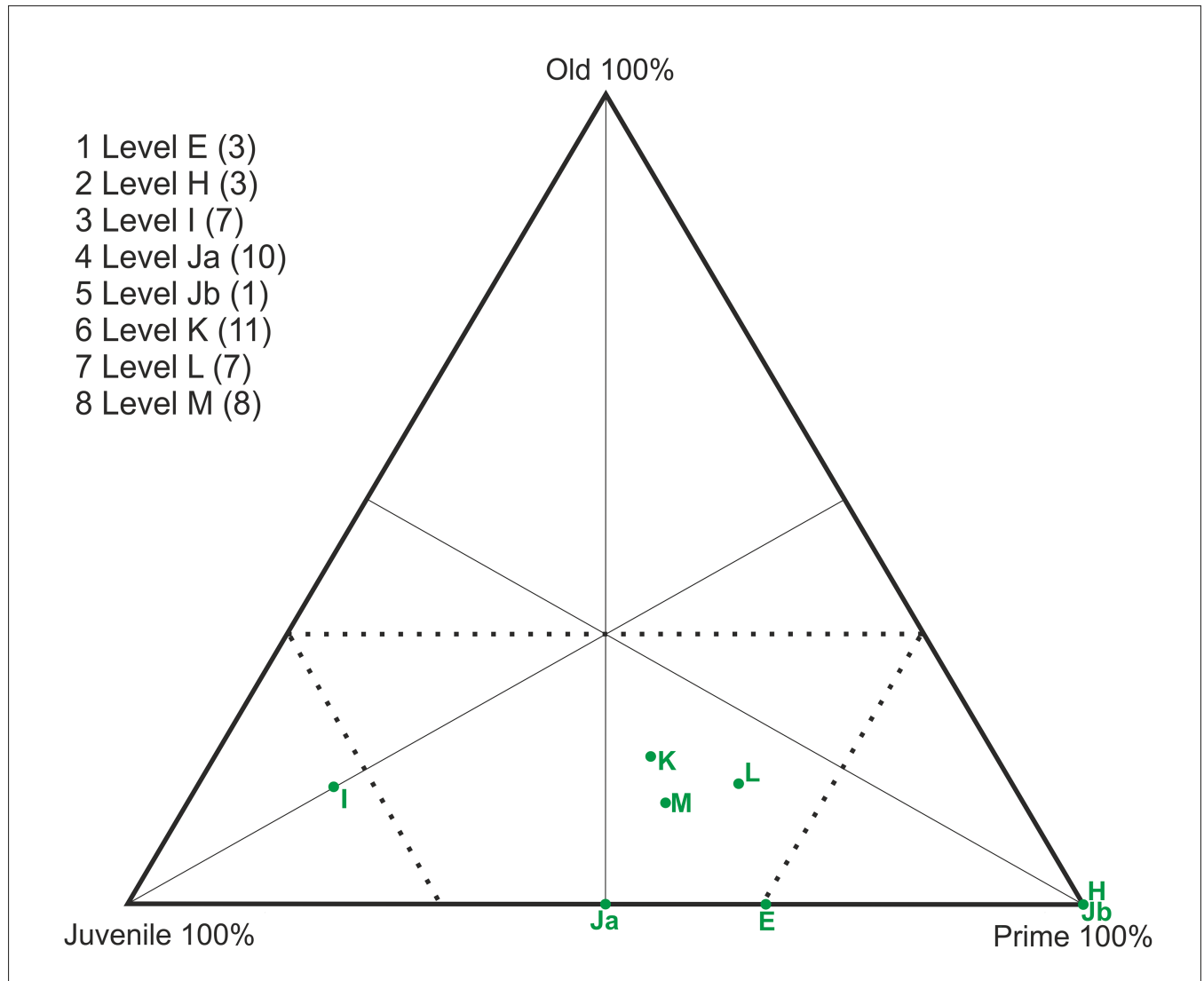
**Fig 10. Cervid maxillae included in the MNI of level E, H, Ja and Jb.** Under each dental series are references to level, individual and side as shown in Table 9.

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mentioned, the small and medium-sized cervids are represented approximately equally, whereas there is a dominance of large animals among the equids. Therefore, either the transport distance associated with the equids was shorter, or the transport of their heads did not constitute a problem.

Although the archaeological mortality profile does not necessarily correspond to the original mortality profile [118], it seems that the mortality profiles documented at Abric Romaní closely reflect the prey selection and hunting strategies and behaviors of the Neanderthals who occupied the shelter.

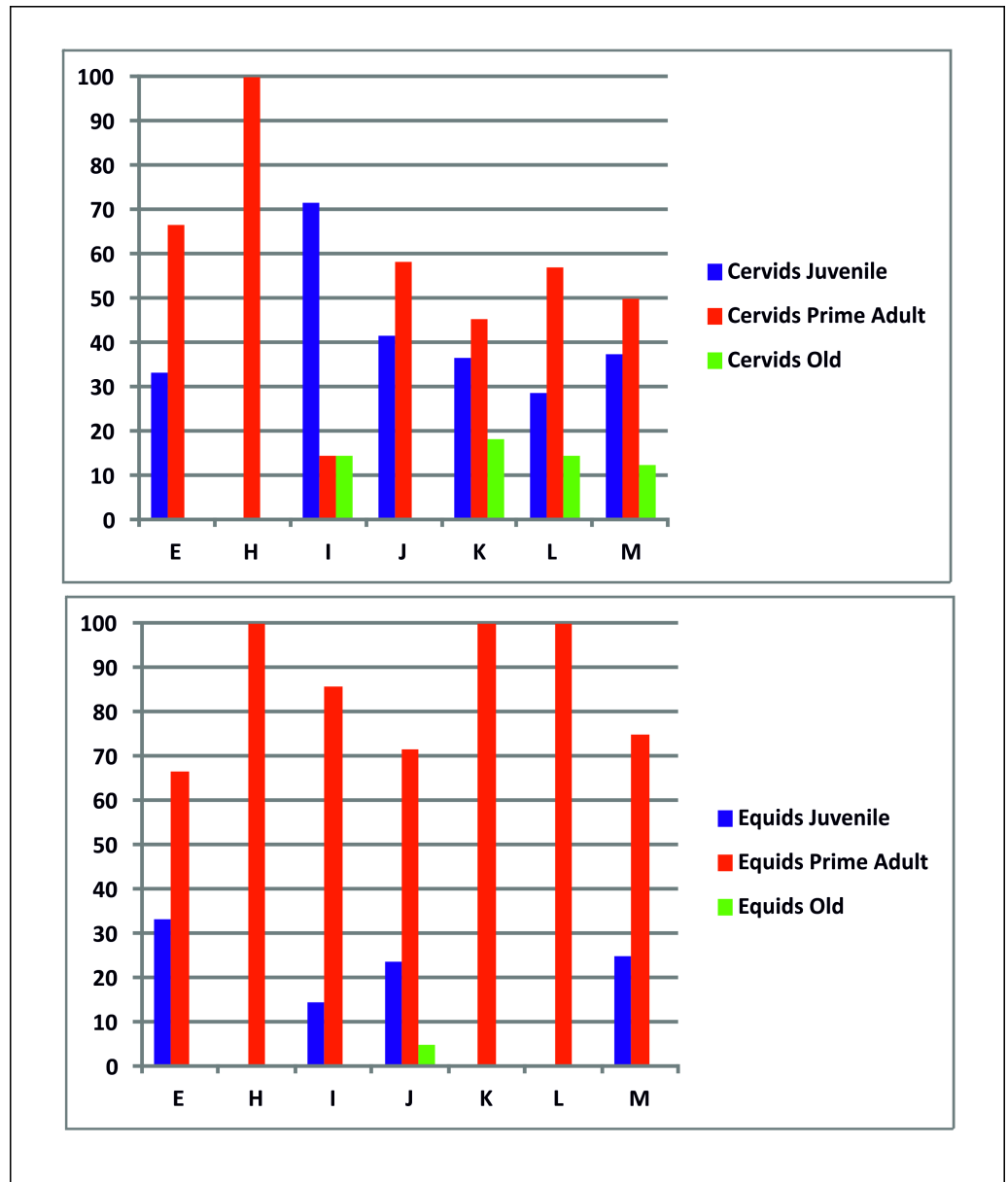
Prime-dominated profiles like those observed at Abric Romani have also been identified for different species and at numerous archaeological sites, such as equids at Cuesta de la Bajada, aurochs at Manie and Madonna, and cervids at Combe-Grenal, Lazaret E, Pech-de-l’Aze I level 7, Breuil and TD10.1 (Fig 14) [5, 27, 28, 52–54, 59, 60].



**Fig 11. Triangular graph with the age distribution of cervid specimens according to archaeological level (MNI).**

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Considering the predominance of a particular age group among the equids, we argue that individual animals may have been selectively hunted. However, Bunn and Gurtov [127] have indicated that, when a group of hunter-gatherers has sufficiently advanced technology to hunt individuals of any age group, prime adults will be captured more frequently because they are the most numerous individuals in prey populations, and not because the hunters are selective. If true, this principle should also govern the age selection of cervids. However, we observed that this premise is not fulfilled (Fig 6). Other studies have argued that the preference for prime adults reflects the objective of maximizing the return rates of predation events [63, 128]. Thus, we assume that the ability to take game from any age group would result in a preference for larger, more profitable prime adults, rather than young animals [63]. The presence of a stable predation model for equids and a variable model for cervids throughout the sequence seems to be related to the intentional selection of prime adult equids.



**Fig 12. Percentage of total age group of equids and cervids by archaeological level.**

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The identification of primary access, the immediate and recurrent access to large carcasses (over 300 kg), has been interpreted as the result of cooperative hunting [27, 28, 58, 59, 125]. In addition, this group cooperation has already been demonstrated at Abric Romaní through an analysis of the transport strategies used for animal carcasses [94]. The mortality profiles of the equids, which are dominated by large animals, support cooperative and selective hunting as the social organization of the hunting groups.

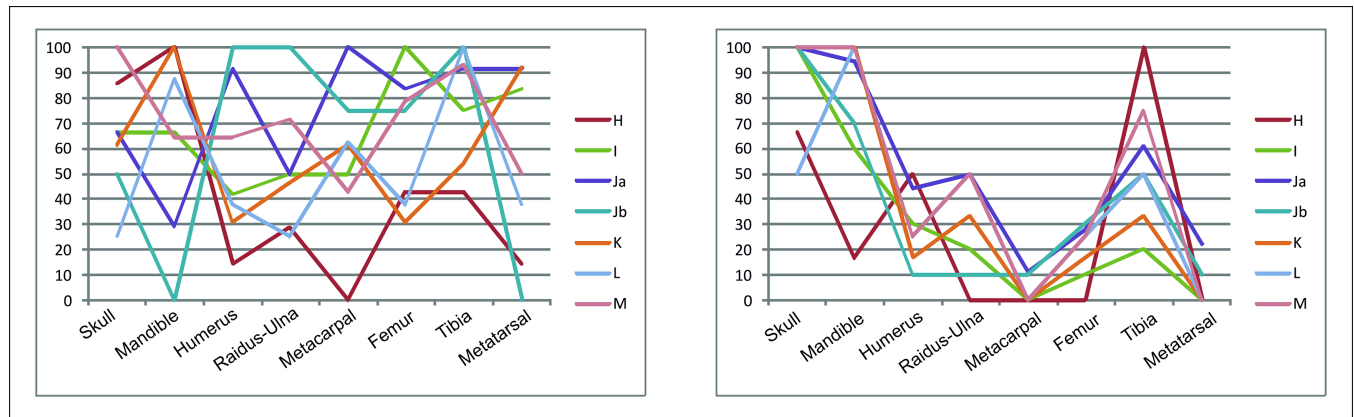
Studies of the micro-wear of the teeth of equids from Abric Romaní indicate that they were hunted for short periods of time within the same season, although not synchronously [86, 90]. Thus, we can reject the hypotheses of mass and multiple predations, and assume that simple predation events were most commonly carried out by the Neanderthal groups.

Table 10. MNE of high survival elements of the cervids and equids from the levels of Abric Romani [73, 82, 88, 90, 94].

	E		H		I		Ja		Jb		K		L		M	
	Equids	Cervids	Equids	Cervids	Equids	Cervids	Equids	Cervids	Equids	Cervids	Equids	Cervids	Equids	Cervids	Equids	Cervids
Skull	3	1	2	3	5	4	9	8	5	1	3	4	1	1	2	7
Mandible	2	2	1	7	6	8	17	7	7	0	6	13	4	7	4	9
Humerus	-	-	3	1	3	5	8	22	1	4	1	4	1	3	1	9
Radius-Ulna	-	-	0	2	2	6	9	12	1	4	2	6	2	2	2	10
Metacarpal	-	-	0	0	0	6	2	24	1	3	0	8	0	5	0	6
Femur	-	-	0	3	1	12	5	20	3	3	1	4	1	3	1	11
Tibia	-	-	6	3	2	9	11	22	5	4	2	7	2	8	3	13
Metatarsal	-	-	0	1	0	10	4	22	1	0	0	12	0	3	0	7

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**Fig 13. Anatomical profiles of the cervids (left) and equids (right) from the levels of Abric Romaní.**

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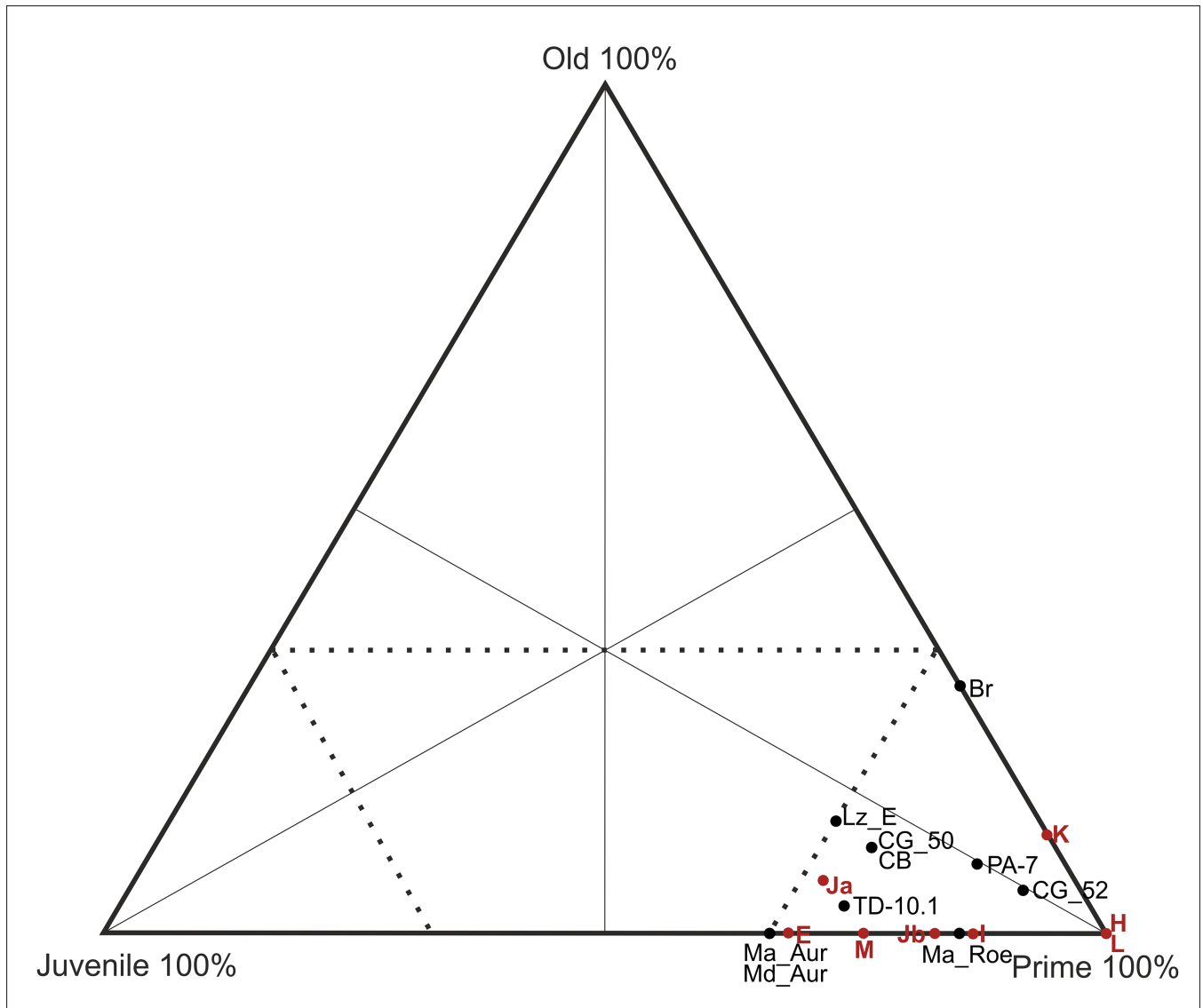
Several types of hunting techniques have been proposed that produce a prime-dominated profile. Prime-dominated profiles have been associated with selective ambush hunting in different ethnoarchaeological and archaeological studies where primary access to animal carcasses has been documented [1, 5, 24, 28, 61, 129]. Bunn and Pickering [129] have proposed ambush hunting for the FLK Zinj assemblage (Bed I of Olduvai), where the mortality profile of the great ungulates is dominated by prime adults.

Binford [24] observed that the Nunamiut generated prime-dominated profiles of caribou on certain occasions. They established hunting camps in narrow passages along the caribou migration routes, and captured the animals using bows and arrows or rifles. Thus, the hunting of prime adults was made possible by the planned use of space (i.e. the interception of prey in specific places) and by cooperative work during the acquisition of carcasses [24]. Therefore, we can argue that the hunting of horses by the Neanderthals of the Abric Romaní was accomplished by selective and cooperative hunting tactics, possibly by ambush hunting, although this conjecture cannot be demonstrated empirically.

The mortality profile of the cervids is characterized by great internal variability. Although it is widely assumed that Neanderthal activities generated prime dominated profiles, the mortality profiles of the cervids in the Abric Romaní sequence are not unusual within the Middle Paleolithic record (Fig 15). The mortality profile of the cervids shows both selective (levels E, H, I and Jb) and non-selective (levels Ja, K, L and M) patterns.

As indicated by Stiner [27], the mortality patterns generated by the hunting activities of human groups usually range from non-selective with an average towards the prime adults to heavily biased toward the prime adults. These patterns appear to be reflected in the cervid profile of level E, which is located between the intersection of the catastrophic and prime-dominated profiles (Fig 15). A prime-dominated profile has been identified at levels H and Jb (Fig 15). Although the cervids are only represented by three and one individual in these levels, respectively, which makes it difficult to defend a clear tendency in the selection of prey, prime-dominated profiles point to an age-selective hunting strategy [5].

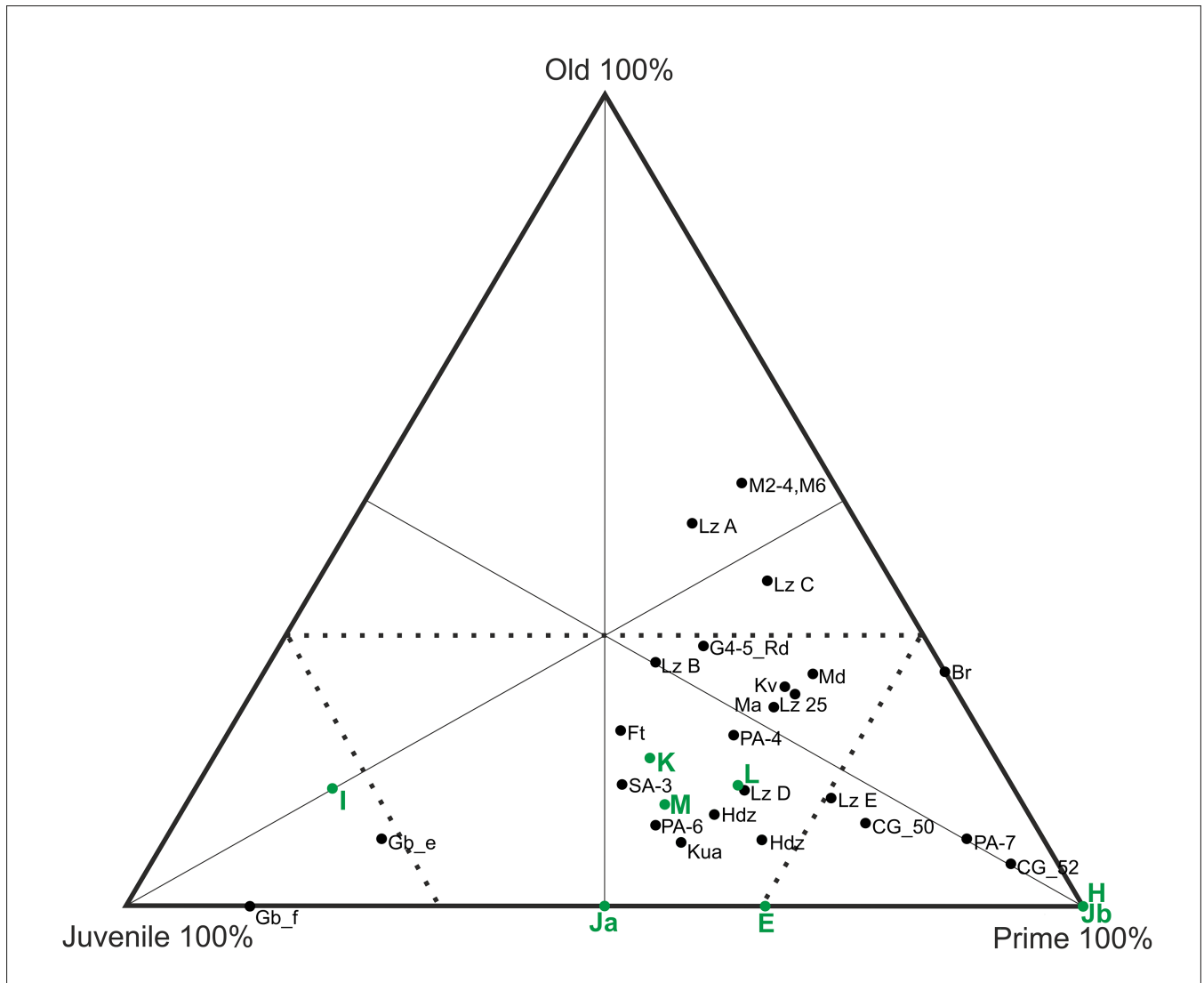
Level I yielded a mortality profile that is dominated by young individuals (Fig 14). In this scenario, the Neanderthals would have deliberately hunted younger animals, which have the lowest economic return rates [130]. The preference for the young individuals of *Cervus elaphus* is also found in other Mousterian sites, such as Cova Beneito levels XII-X (Spain) [131] and Gabasa (Spain) [52]. In the latter case, once an increase in the presence of juvenile individuals by the action of other carnivores was ruled out, Steele [52] suggested that the greater presence



**Fig 14. Triangular graph of mortality profiles of equids from different levels at Abric Romani (E, H, I, Ja, Jb, K, L and M) and from different Early and Middle Paleolithic sites.** Lz E = Lazaret [53]; Md\_Aur = Madonna aurochs [53]; Ma\_Aur, Ma\_Roe = Manie aurochs and roe deer, respectively [53]; Br = Breuil [53]; CG 50, 52 = Combe Grenal [52]; PA-7 = Pech-de-l’Aze I [54]; CB = Cuesta de la Bajada [60].

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of juvenile individuals is related to Neanderthal activity. The same behavior could account for the accumulation of cervids in level I, which includes four individuals with PEL values of less than 2.7% (less than 5 months of age). Measurement of the crown heights of these individuals indicates that two had not even passed the first month of age (Tables 8 and 9). This particular accumulation suggests a specialized seasonal hunt, perhaps during the same occupational event, indicating that hunting events were more common during cervids birthing season. Varin [132] has indicated that due to the presence of newborns, female groups display a pattern of low mobility with very specific habits in which they follow established paths at precise times of day. This behavior makes these animals extremely easy to track [54], so hunters may have waited for female groups to take their regular route and hunted them using ambushes or traps. The hunting of young individuals has been documented among current groups of



**Fig 15. Triangular graph of mortality profiles of cervids in different levels at Abric Romaní (E, H, I, Ja, Jb, K, L and M) and cervids at different Middle Paleolithic sites.** Gb e/f = Gabasa levels [52]; Ft\_Rd = Fate red deer [27]; Lz A, B, C, D, E, 25 = Lazaret levels [53]; Md = Madonna [53]; M2-4, M6 = Moscerini levels [53]; Kv = Kevara [27]; Ma = Manie [53]; Br = Breuil [53]; CG 50, 52 = Combe Grenal levels [52]; PA 4, 6, 7 = Pech-de-l’Aze levels [54]; Hdz = Hadza assemblages; K = Kua [127].

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hunter-gatherers. During the dick-dick and steenbock birthing seasons the! Kung San of the Kalahari capture young individuals by chasing them on foot or throwing clubs [133].

Binford [24] observed hunting events in which the Nunamiut (Tulekana and Kakinya) exclusively hunt young reindeer in order to obtain soft leather for clothing. Lithic use-wear analyses at Abric Romaní show that worked skins existed within the sequence, with work on fresh leather being more common [134]. In addition, lithic functionality studies in level Ja relate denticulate and notch features to the hardening of hides [81]. In the Abric Romaní sequence, although young individuals have been identified in almost all of the studied levels, they do not reach 71% of the total, as in level I. Therefore, in this level, the hunting of cervids seems to have been specifically intended to obtain this prey of low economic return, possibly to obtain their hides.

The mortality profile of level Ja is located at the intersection between the attritional and catastrophic profiles, indicating equal proportions of juvenile and prime adults, but no old adult individuals (Fig 15). The occupations took place in different events throughout the autumn and early winter, generally during a whole season, as indicated by studies of the seasonality of the ungulates [93]. Thus, the mortality profile ranged from attritional to catastrophic, indicating that Neanderthals captured individuals ranging from the weakest to the strongest over long periods of time, thus reflecting non-selective hunting.

Catastrophic mortality profiles have been identified at levels K, L and M (Fig 15). Catastrophic mortality profiles have also been observed for *Cervus elaphus* at the Mousterian sites of Pech-de-l'Aze (France) in levels 4 and 6 [54], Manie (Italy), Madonna (Italy), Fate (Italy), Lazaret (France) [53], Kebara (Israel), Sant'Agostino 3 and Guattari G4-5 (Italy) [5, 27]. Traditionally, catastrophic mortality profiles have been considered to illustrate mass communal hunting events or repeated episodes of non-selective hunting [2, 3, 5, 25, 127]. The faunal assemblages produced by mass communal hunting events are characterized by large accumulations made up of dozens of individuals of the same species, almost monospecific [25]. The systematic transport of high utility elements to the base camps has been documented in these assemblages [25]. The characteristic mortality profile of these sites is catastrophic, as determined by the age and sex of the individuals represented, with a strong trend toward seasonal or synchronous death [25]. In levels K, L and M more than three taxa are present (Table 1) with between 1 and 11 individuals of each species. The transport of the anatomical elements reveals a close correlation between the anatomical elements present and their richness in unsaturated marrow [94]. The cervids found in levels K and L were hunted over an estimated period of three months; those found in level M appear to have been hunted over an estimated period of about six months [86]. These analyses indicate that the cervids found in levels K, L and M were not hunted synchronously. Therefore, the catastrophic mortality profile of the cervids found in levels K, L, and M did not result from mass communal hunting events. As an alternative explanation for catastrophic profiles, Rendu [54] proposed that the lack of clear seasonality may be the result of a palimpsest, in which different seasonal events accumulate and finally generate a catastrophic mortality profile. However, if this explanation were to apply in the case of Abric Romani, the equids should have catastrophic profiles as well as the cervids, since the sets are the result of multiple occupational events with a broad seasonal distribution that can occupy an entire season, as in levels Ja, K, L or M [86, 91, 93]. Thus, the differences between the cervids and equids in levels Ja, K, L and M tend to support the hypothesis of the non-selective hunting of cervids, suggesting that different tactics were used to hunt different taxa and were maintained over time, and they did not result from equifinal processes.

Thus, the mortality profile generated by the Neanderthals for the cervids indicates a less selective hunting strategy regarding the age of this taxon, and is more closely related to its abundance in the environment and therefore to the rates at which hunting groups would have encountered this animal [135, 136]. In terms of the organization of hunting groups [65], once the possibility of communal hunting has been dismissed, it is impossible to determine whether the capture of the animals was accomplished by cooperative hunting parties or individuals. However, because cooperation has been established as necessary to hunt equids, it should not be ruled out for deer hunting. Unlike selective ambush hunting which would generate profiles dominated by prime adults [5, 129], Bunn and Gurtov [127] point out that non-selective ambush hunting would generate catastrophic mortality profiles. Ethnoarchaeological observations indicate that other non-selective hunting strategies also generate catastrophic mortality profiles [120, 121, 127, 137]. Middle Mississippian hunters during the Archaic period (1000–1550 BC) produced a catastrophic mortality profile of white-tailed deer in six sites through non-selective hunting by stalking [137]. The hunter groups of the Hadza and Kua generate catastrophic mortality profiles in their camps [127] (Fig 13).

Encounter hunting is the style most commonly practiced by the Hadza, although, during the dry season, they usually ambush hunt at night near water sources. In both cases, they use poisoned arrows to kill their prey [120, 121]. The Kua mainly encounter hunt, and kill with bows and arrows, although they are also effective as hunters when stalking or using persistence running and traps [133]. The non-selective mortality profiles of levels K, L and M appear to be the product of non-selective stalking. However, it cannot be completely ruled out that this profile may have been produced by non-selective ambush hunting, as with the profiles generated by other non-human ambush hunters, such as leopards or lions [5].

The results of our analysis indicate that the differences in the mortality profiles within the Abric Romani sequence are the result of various hunting strategies: 1) Selective hunting strategies were employed for equids in all levels and for cervids in levels E, H, I and Jb. 2) Non-selective hunting strategies were employed for cervids in levels Ja, K, L and M. Prime adults comprise the strongest and healthiest animals in a population. Moreover, the large size of equids implies that they pose a substantial risk to hunters. In non-human predators, this risk is reduced through cooperation, as seen in lions, wolves, spotted hyenas and lycaons. Cooperation makes it possible to hunt prey that considerably exceeds the weight of any individual predator [27]. A trend towards capturing prime and young individuals (juveniles = 2, prime adults = 5, old adult individuals = 3) has also been observed in the levels in which the other large ungulate found in this assemblage, *Bos primigenius*, is present (Ja, L, K and M). The two young individuals are subadult juveniles between 3 and 4 years of age and are very close to reaching the weight of an adult animal. Therefore, cooperative organization of hunting groups would have been an effective way to reduce risk in the capture of these large ungulates [27, 28, 58, 59, 138]. Cervid hunting may have also been cooperative, as with the equids, although it is possible that these animals were brought down by individual hunters, especially the young individuals [24, 54, 65, 135]. Depending on the number of prey animals captured during each hunting episode, equid and deer remains may have accumulated over the course of various occupational events in which Neanderthals hunted. These episodes may have occurred over several months within the same season, during the same occupation events or at different times of the year, but not synchronously, so it seems that simple predation prevails over sequential predation. In the hunting of prime adults (equids and deer), it seems that the selective ambush tactic may have been the most commonly used [1, 5, 24, 28, 128]. Young cervids can be captured in multiple ways—by traps, projectiles or pursuit [24, 54, 138]—but would not have constituted a challenge to hunters. Finally, the catastrophic profiles noted for cervids most likely resulted from encounter hunting by stalking or non-selective ambush hunting [127, 138].

The Neanderthals of the Abric Romani developed specific hunting strategies based on two characteristics of their prey: the taxa and the age of the individual to be hunted. Each hunting strategy gave rise to specific mortality profiles.

## Conclusions

The mortality profiles identified in the faunal assemblages of the Abric Romani are useful for studying the hunting strategies of the Neanderthals who occupied the shelter. The ages at death of the equids and cervids reflect marked differences between the two taxa. The equids are always dominated by prime adults, whereas the cervids show great diversity in the sequence. This result indicates that the observed differences in mortality profiles resulted from the use of both selective and non-selective hunting strategies.

Selective hunting strategies were employed for the equids at all levels and for the cervids found in levels E, H, I and Jb. Non-selective hunting strategies were only employed for the

cervids of levels Ja, K, L and M. The capture of equids and cervids was probably carried out by various individuals cooperatively, although individual hunting cannot be ruled out in the case of cervids. Depending on the number of prey animals caught by the hunting groups, it seems that simple predation was the most common tactic. The prime adult may have been captured by means of selective ambush hunting. The selective capture of very young individuals may have been accomplished in multiple ways, without presenting a challenge for the hunters. The tactics that generated the catastrophic profiles may have included encounter hunting by stalking or non-selective ambush hunting. Therefore, different hunting strategies have been identified within the same Neanderthal group, some of which are repeated along the sequence, as seen in the case of the equids, and others that vary according to specific behaviors, as observed in the case of the cervids.

## Supporting information

**S1 Table. Number of equids and cervids mandibles and maxillae at Abric Romaní, indicating level, archaeological reference, MNE, size, dental series, crown height of teeth and code of wear stage.**

(XLSX)

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**Chapter 5. Neanderthal logistic mobility during  
MIS3: Zooarchaeological perspective of  
Abric Romaní level P (Spain)**





## Neanderthal logistic mobility during MIS3: Zooarchaeological perspective of Abric Romaní level P (Spain)

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### ABSTRACT

Mobility strategies of Neanderthal groups are studied through the characterization and analysis of archaeological sites and traditionally compared to the types of settlements present-day hunter-gatherer groups, based on their mobility strategies. The faunal record of level P of Abric Romaní is a unique source of information for analysing the foraging behaviour developed by Neanderthals during MIS3. The assemblage is divided into two separate and well-defined sublevels: Pa and Pb. Through the taphonomic study of the remains and their spatial distribution, it was possible to define the characteristics of these human occupations. The analyses indicate that the assemblage was the result of at least two different types of occupations: 1) A transitory residential camp during short halts, focusing on the exploitation of red deer; 2) A hunting camp/intermediate butchering site for the specialized capture of horses. The presence of occupations focusing on the supply of specific resources is typical of collector groups. The results of the zooarchaeological study of level P characterize the Neanderthals of Abric Romaní as groups involved in a logistic mobility system, who moved throughout the territory depending on the availability of large ungulates.

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### 1. Introduction

According to Kuhn et al. (2016), human group mobility is driven by four interrelated phenomena: the internal need for movement (rewards and decisions), mobility skills (biomechanical limitations), the ability to navigate (cognitive challenges of movement) and external factors. The external factors that influence movement include the environmental context, distribution and abundance of resources, or the associated climatic and habitat changes, among others. Kelly (1992) argued that the mobility and settlements of modern hunter-gatherers are largely determined by the availability

of resources on which they base their survival. Most groups depend on temporally and spatially restricted resources (Kelly, 1992, 1983), forcing them to adopt mobile strategies for the management of the distribution area of these resources. Mobility enables hunter-gatherers to balance the unequal distribution of resources in the territory (Kelly, 2013), to avoid food deficits caused by over-hunting, and other negative effects of the long-term occupation of a local ecosystem (Hamilton and Watt, 1970). Other benefits of mobility include flexibility in group size and the ability to relocate settlements near periodically abundant resources, mainly plant and, animal resources and their by-products, and access to water (Lee, 1979, 1972; Perlman, 1985; Smith, 1981; Tanaka, 1976). However, foraging groups may also develop high mobility in their territory for reasons other than water availability or irregularities in

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food distribution (Jones, 1983), such as the Aché (Paraguay). In any of these variants, mobility leads to a reduction of social stress and conflict between co-resident groups (Woodburn, 1980, 1972), exposure to a wider range of potentially exploitable resources (Kuhn et al., 2016) and guarantees a higher success rate in hunting (Jones, 1983). This is linked in many cases to food management, which can range from the storage of surpluses to the equitable sharing and consumption of food obtained on a daily basis (Binford, 1980; Gould, 1981; Jones, 1983; Lee, 1979; Marshall, 1961).

Binford (1980) developed an approach focusing on settlement patterns, to describe the movements of hunter-gatherer groups, based on the study of the/Gwi San (Silberbauer, 1972) and the Nunamiut (Binford, 1978). He classified groups into foragers, with residential mobility, and collectors, with logistic mobility. The main difference between them is that foragers move consumers to resources with frequent residential movements, while collectors move resources to consumers, generally with fewer residential movements (Binford, 1980). Foragers make seasonal residential movements between a series of resource patches (Binford, 1980). Their residential mobility can vary considerably between sites, both in time and space, and they do not store food, but consume all the resources obtained daily. They mainly generate two types of places, residential bases, in which the group the entire group socialites and developed their domestic activities, and locations, where extractive tasks are exclusively carried out. On the other hand, collectors are characterized by their logistic organization, as specialized task groups provide them with specific resources, and by the storage of food for at least part of the year (Binford, 1982). Specialized task groups leave a residential location to collect a specific resource. These groups are often small and seek to procure a specific resource in a specific context. In addition to the places generated by foragers, three further possible places are used by collectors: the field camp, station, and cache. However, the forager and collector models are not two types of substantially antagonistic settlement systems, but rather a graduated series from simple to complex, in which settlement dynamics are strongly linked to the spatial and seasonal distribution of resources in the environment (Binford, 1980). Nevertheless, not all foragers are highly mobile, nor are all collectors almost sedentary (Kelly, 2013).

Similarly, Mortensen (1972) established two models based on mobility patterns. These are: the circulating model (the residential group moves in predictable seasonal rounds with a single, self-sufficient, settlement type) and the radiating model (places of specific activity supply resources to residential places). Both models produce spatial regional exploitation as one would expect from foraging and logistic models, respectively (Binford, 1980). Based on these categories, archaeological work has attempted to characterize the subsistence of past human groups.

There is no doubt that most archaeological sites are palimpsests (Bailey, 2008; Bailey and Galanidou, 2009). This means that in most cases our object of study is the result of an indeterminate number of events that can incorporate and remove materials (LaMotta and Schiffer, 1999). It is generally impossible to discriminate between or identify the length of sequences in these sequences of events (Vaquero, 2008a). On account of the overlapping of episodes of activity, it is difficult to address the duration of occupations of archaeological sites in temporal terms, although this has not led to the abandonment of these topics by archaeologists (Audouze and Enloe, 1997; Clark, 2016; Enloe, 2012; Gaudzinski, 2004; Pettitt, 1997; Riel-Salvatore et al., 2013; Spagnolo et al., 2018). Stiner (2013) proposed two models of occupation for the Middle Palaeolithic based on the function and intensity of occupations: ephemeral occupations with high mobility and relatively intense occupations with a higher input of materials. These two categories

are usually based on the density of materials, the existence of living floor structures and/or the types of modifications present on the materials.

Information from detailed zooarchaeological and taphonomic studies elucidates characteristics of Neanderthal group subsistence strategies, such as prey selection, transport strategies, seasonality of occupations, carcass processing, food exchange or group cooperation. These elements enable us to characterize the nature of settlements and differentiate between long and short occupations (e.g., Faith, 2007; Faith and Gordon, 2007; Marín et al., 2017a, 2017b; Rodríguez-Hidalgo et al., 2017; Saladié et al., 2011; Speth and Clark, 2006; Stiner et al., 2009; Stiner and Kuhn, 2006). These data, associated with the studies of lithic assemblages and raw materials, allow us to characterize the mobility of hominin groups through analogies with contemporaneous hunter-gatherers (Adler et al., 2006; Boyle, 2000; Burke, 2004; Carbonell, 2012; Conard and Adler, 1997; Courty et al., 2012; Daujeard and Moncel, 2010; Delagnes and Rendu, 2011; Gaudzinski, 2000; Lieberman and Shea, 1994; Niven et al., 2012; Patou-Mathis, 2000; Turq et al., 2017; Valensi and Psathi, 2004). As a result, mobility strategies have been proposed in Europe for Middle Palaeolithic groups, which vary mainly according to regional characteristics. Thus, for example, in Central and Eastern Europe, the low frequency of base camps in comparison to temporary camps, has been identified as an indicator of the predominance of multidirectional (radial or star pattern) logistic mobility strategies (Patou-Mathis, 2000). In the Rhone Valley (France), settlements have been associated with a far-sighted circulating models (Daujeard and Moncel, 2010; Moncel et al., 2014). In the south-western French Atlantic basin, hunting strategies, prey type and seasonality, show that groups associated with the Quina system and the discoid-denticulate system were logistically mobile, while groups with a laminar Levallois system were associated with a more residential foraging system (Delagnes and Rendu, 2011; Niven et al., 2012; Turq et al., 2017). In the south French Mediterranean basin, Neanderthal groups have been linked to a circulating mobility strategy, where small communities scattered throughout the territory sought day-to-day supplies (Boyle, 2000). In the Mediterranean basin of the Iberian Peninsula, most studies agree that Neanderthal groups are characterized by highly mobility, developing in most cases accumulations resulting from repeated occupations of short duration, which could be related to logistic organization (Martínez-Moreno et al., 2004; Real et al., 2018; Rosell et al., 2017; Vallverdú et al., 2005; Zilhão and Villaverde, 2008). In the Middle Palaeolithic sites of the Near East, hominin groups have been associated with two mobility strategies: radiating type multi-seasonal logistic mobility related to archaic populations, and a highly seasonal residential circulating mobility related to anatomically modern populations (Lieberman and Shea, 1994; Marín-Arroyo, 2013).

Although Neanderthal mobility strategies display variability, especially as regards circulating or radiating mobility, the logistic strategy it seems that it could be predominant in the Mediterranean basin of the Iberian Peninsula, France and part of Central Europe. In all these regions, group subsistence relied on the capture of large ungulates. Neanderthals in the Iberian Peninsula also based their meat economy on large ungulates, especially deer, large bovines, horses and caprines (Altuna, 1990; Arsuaga et al., 2012; Blasco, 1997; Fernández-Laso et al., 2010; Fernández-Peris et al., 2008, p.; Gabucio et al., 2018a, 2018b; 2014; Galván et al., 2001; Iturbe et al., 1993; Martínez-Moreno et al., 2004; Morin et al., 2016; Real et al., 2018; Romero et al., 2019; Salazar-García et al., 2013; Sanchis et al., 2019; Sanchis Serra et al., 2013; Steele, 2004; Utrilla et al., 2010; Villaverde et al., 2017; Yravedra et al., 2012; Yravedra and Cobos-Sánchez, 2015; Zilhão and Villaverde, 2008).



In the Abric Romaní sequence, accumulations interpreted as resulting from long-term occupation events or short-term and/or non-residential occupation events have been identified (Carbonell and Vaquero, 1998; Carbonell, 2002, 2012; Vallverdú et al., 2005, 2010; 2012a; Vaquero et al., 2012). In both scenarios, archaeological levels correspond to the superposition of an indeterminate number of occupational events (Vallverdú et al., 2005, 2010; 2012a; Vaquero et al., 2015). Through the analysis of the faunal record of the recently excavated level P (seasons 2006–2013), had conducted a study focusing on the type of occupations generated by this assemblage. To this end, have been characterized Neanderthals settlement types in the rock shelter and the associated mobility strategies.

## 2. Abric Romaní

The Abric Romaní archaeological site is a rock-shelter located in the gorge of the Cinglera del Capelló, 45 km northwest of Barcelona (Spain). The stratigraphy consists of 30 m of well-stratified travertine sediments. Rock fragmentation and alluvial and biochemical sedimentary processes generate beds of consolidated stones, gravels, calcarenites and calcilitites interspersed with very fine archaeological levels (Vallverdú et al., 2010). U-series and radio-carbon dates place the Abric Romaní sequence between ~110 and 40 kyr (Sharp et al., 2016). The sedimentation rate is estimated at around 0.6 m/kyr (Bischoff et al., 1994, 1988). Except for level A, all the archaeological units of the sequence correspond to the Middle Palaeolithic.

Discovered in 1909 by Amador Romaní, the site was excavated at different periods throughout the Twentieth century. The current excavation covers the entire extension of the rock shelter (circa 300 m<sup>2</sup>). The sequence comprises 17 archaeological levels. Numerous exceptionally well-preserved combustion structures have been documented in all the excavated levels (Vallverdú, 2002; Vallverdú et al., 2012a; Vallverdú and Courty, 2012). In addition, casts of wooden objects have also been recovered (Allué et al., 2012; Carbonell, 2012, 2002; Castro-Curel and Carbonell, 1995; Solé et al., 2013).

The lithic assemblage is characteristic of Middle Palaeolithic technological systems, with predominant flakes, and relatively sparse cores and retouched flakes (Chacón and Fernández-Laso, 2007; Martínez and Rando, 2001; Vaquero, 2008b; Vaquero et al., 2012, 2004, 2001). Chert of regional origin is the most abundant raw material in the Abric Romaní sequence (Gómez de Soler, 2016; Gómez de Soler et al., in press). In levels H, I and K, the percentage of chert drops by 70%, and is associated with an increase in raw materials of local origin; quartz in levels I and K, and limestone in level H. The fourth most represented raw material in the whole sequence of the deposit is schist, which is also from a local catchment area (Chacón et al., 2007; Gacia-Antón and Morant, 2000; Gómez de Soler, 2007; Vaquero et al., 2012).

Macro-mammal remains are very abundant in the sequence. A total of 38,228 remains belonging to 13 taxa have been recovered. Red deer (*Cervus elaphus*) and equids (*Equus ferus/Equus hydruntinus*) are the most abundant ungulates. Aurochs specimens (*Bos primigenius*) are also present in levels I, J, K, L, M, N and O and the chamois (*Rupicapra pyrenaica*) in A, B, D, E, F, G, H and J. Rare rhinoceros remains (*Stephanorhinos* cf. *hemitoechus*) have been documented in several levels. The diaphysis of a proboscidean femur was recovered in level E. The zooarchaeological studies carried out on different levels indicate that the faunal record is the result of Neanderthal activity, characterized by primary access to animal carcasses and complete processing (Fernández-Laso et al., 2010; Gabucio et al., 2014; Marín et al., 2017a, 2017b; Rosell et al., 2012b,

2012a). Specific activity areas have been identified through the analysis of the density of faunal remains, taphonomic modifications, and refits, which sometimes define sleeping areas, cleaning areas and animal processing areas (Carbonell, 2012; Gabucio et al., 2014; Vallverdú et al., 2005, 2010, 2012a). Carnivore modifications are scarce, and carnivore activity has been defined as the result of the secondary ravaging of remains abandoned by human groups (Carbonell, 2012, 2002; Rosell et al., 2012a; Vallverdú et al., 2005; Vaquero et al., 2001). Faunal anatomical profiles are the result of a highly variable transport of animal carcasses, ranging from complete animals to only a few elements. This differential transport may be related to diverse constraints, such as animal weight, tactical factors or the number of carriers (Marín et al., 2017a, 2017b).

## 3. Materials and method

Level P was excavated between 2006 and 2013 over a total area of 247 m<sup>2</sup>. This level is dated to 54.24 ± 0.42 Ka BP (top) and 55.0 ± 2.6 Ka BP (bottom) (Bischoff et al., 1994, 1988; Vallverdú et al., 2012b; Vaquero et al., 2013), and is in pollen zone 3 characterized by a cold and dry climate (Burjachs et al., 2012; Burjachs and Julià, 1994).

Level P was excavated using Cartesian coordinates on a grid divided into square metres. Two archaeological sublevels were differentiated in some areas, but it was not possible to identify them over the whole surface. A total of 4890 remains were recovered, comprising faunal specimens (1233 remains larger than 2 cm), lithic remains (2633 larger than 1 cm), malacofauna (45 remains), charcoal (950 remains) and wood casts (29 remains).

Have been projected and analysed a series of 25-cm-wide vertical profiles (longitudinal and transversal profiles), in order to identify the sublevels observed during fieldwork over the entire surface, using ArchePlotter iv1.35.4-beta, developed by IPHES, and ArcGIS 10.4.1 (Desktop, Engine) software.

Faunal remains were refitted for the spatial study, taking into consideration anatomical and mechanical refits (Marean and Kim, 1998). In all cases, distances between the refitted pieces were recorded, as well as their taphonomic modifications. Have been considered whether the bone had green or dry fractures, and whenever possible, the actor of bone breakage was identified.

To observe the redistribution of carcasses between identified activity zones, has been applied the proposed redistribution index (RI) of Jones (1983), although with modifications. The formula is:  $RI = MNIf / (MNIs \times n)$ ; where MNIf is the MNI by hearths, the MNIs is the total MNI and n is the number of hearths.

Carcass distribution over a living floor surface can be related to the distribution of ungulate meat. In settlements with a high distribution of animals, the index values are approximately one. However, when animal tissues were not shared, the index is the inverse of the number of hearths. In these cases, the MNI per hearth should be similar to the MNI for the whole settlement surface, and its sum much higher than the total MNI. In cases where there is no redistribution of meat, the sum of the MNI per hearths is similar to the total MNI count of the assemblage. To apply the formula to level P of Abric Romaní, the index was calculated according to taxa (*Cervus elaphus* and *Equus ferus/hydruntinus*). In addition, since it is not possible to clearly separate the remains for each hearth, the MNIf was calculated for each aggregation of materials related to combustion structures. It should be noted that this only applies to sublevel Pa where these accumulations could be discriminated in more detail.

To identify the different areas of accumulation of remains has been followed the proposal of Romagnoli and Vaquero (2016),

using combined kernel density analysis (Baxter et al., 1997) and the calculation of k-nearest neighbour distances (Baddeley et al., 2015).

The distribution of red deer and horse remains was evaluated using Ripley's K function of the "spatstats" library of version 3.2.3 of the R software (R Core Team, 2015; Baddeley et al., 2015). This function is used to describe how a point process occurs in any specified spatial window. The curve of the observed data was interpreted as a grouping process (above the theoretical random process line), a regular process (below the theoretical random line) or CSR (complete spatial randomness) (if it is within the confidence intervals). The confidence intervals were obtained through a Monte Carlo simulation process with 30 random samples of the original data. The proposal of Reeves et al. (2019) to analyse patterns of discarding material in palimpsests was used, adapting its code of analysis in R to our study. This proxy allows for the visualization of the statistical significance of the horizontal distribution patterns of red deer and horse remains. For this, first, the spatial variation of a series of taxonomic representation indices is calculated by means of a Moving Window Analysis, where each observation represents a value resulting from the calculation of that ratio in its neighbourhood. Subsequently, the statistical significance of the spatial variation of these values is tested by means of the Local and Global Moran's I test of spatial autocorrelation, leading to the identification of statistically significant concentrations of high and low values.

In this case, a circular window with a 2 m radius was used for the calculation of the following indices: number of *Cervus elaphus* remains/number of taxonomically identified remains; number of *Equus ferus* remains/number of taxonomically identified remains; number of remains of *Cervus elaphus*/sum of remains of *Cervus elaphus* and *Equus ferus*; number of remains of *Equus ferus*/sum of remains of *Cervus elaphus*.

Taxon, age of death, size and weight category, element, side (anterior, posterior, medial, lateral, superior and inferior) and the portion (epiphysis, metaphysis, and diaphysis) and position (left/right) were described when possible. To evaluate anatomical representation, the carcasses were divided into anatomical segments: axial cranial (horns, skull, mandible, hyoid and teeth), axial post-cranial (vertebrae, ribs and coxal) and appendicular (long limb bones, carpal/tarsal and phalanx). The scapula was grouped within the axial skeleton since its responses to taphonomic processes are similar to those of the axial skeleton (Yravedra and Domínguez-Rodrigo, 2009). The long bones were divided into upper appendicular bones (humerus and femur), intermediate (radius/ulna and tibia) and inferior (metapodials) (Domínguez-Rodrigo, 1997). Two weight categories were used: large animals weighing between 200 and 800 kg; medium-sized animals weighing between 50 and 200 kg.

Have been used four measures of abundance: Number of Specimens (NSP); Number of Identified Specimens (NISP); Minimum Number of Elements (MNE); Minimum Number of Animal Units standardized (%MAU); and Minimum Number of Individuals (MNI) (Binford, 1984; Grayson, 1984; Lyman, 1994). To calculate the MNE, has been considered the superposition of anatomical markers, and considered the age, side or landmarks. In the case of long bones, has been followed the recommendation of Marean and Spencer (1991), modified by Saladié et al. (2011). To establish the degree of taxonomic diversity, the Shannon uniformity index (E) and the Simpson diversity index (D) were used on the NISP of the different identified species.

Spearman's rank order was used to test the correlation between the %MAU and the data provided by Lam et al. (1999) for bone mineral density, taking into account the MNE of each element portion. The significance of the Spearman correlation coefficient

used in this work is 95% (0.05).

The transport strategy analysis was carried out following the method proposed by Faith and Gordon (2007), by means of the statistical correlation of Spearman's rho between the standardized food utility index (SFUI) and the %MAU and by applying the Shannon uniformity index (E) to the anatomical profile. The following high-survival elements were considered: skull, mandible, humerus, radius/ulna, metacarpal, femur, tibia, and metatarsal (Marean and Cleghorn, 2003). In addition, the %MAU of the high-survival elements was correlated with the unsaturated marrow index (UMI) proposed by Morin (2007).

The age at death of the individual and the seasonality of the settlements was calculated based on the time of eruption and replacement of the teeth and the degree of wear of the occlusal surfaces (Azorit, 2011; Bignon, 2006a; Brown and Chapman, 1991; Fernandez and Legendre, 2003; Klein and Cruz-Urbe, 1983; Mariezkurrena, 1983; Steele and Weaver, 2002). The birth period for red deer and horses was between the end of spring and the beginning of summer (horse: Levine, 1982; Burke, 2002) (deer: Clutton-Brock et al., 1982; Habermehl, 1985). Given that the period of birth and the replacement of deciduous teeth occur at predictable times of the year, it is possible to calculate the annual cycle and estimate the death season (Stiner, 1990). Once the age of death was identified, the individuals were grouped into juveniles, prime adults and old individuals (Stiner, 1990), and plotted within triangular charts following the separation of mortality profiles proposed by Stiner (1990) and Discamps and Costamagno (2015) for red deer and horses.

In order to establish the degree of fragmentation and the actors responsible for fragmentation processes, has been followed the method proposed by Bunn (1983) and modified by Villa and Mahieu (1991). For this, had been considered the diaphysis length and circumference, description of the delineation (longitudinal, transverse and curved/V-shape), angle (straight, oblique or mixed) and the surface (smooth or jagged) of fracture planes.

Taphonomic analysis was completed by the observation of bone surface modifications, through the binocular stereomicroscope (OPTHEC 120-Hz model). The focus was on the study of changes produced during the nutritional phase (Capaldo, 1998) of modifications. Damage produced by hominins and carnivores was described according to the anatomical region and the portion on which they were found. The identified anthropogenic modifications include cut marks (Binford, 1981; Domínguez-Rodrigo et al., 2009; Potts and Shipman, 1981; Shipman, 1981; Shipman and Rose, 1983), and percussion marks (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994). The type, delineation, situation and position of the cut marks per element allowed us to infer butchery activities. For this, were used ethnoarchaeological sources (Abe, 2005; Binford, 1978), experimental data (Frison, 1974; Nilssen, 2000) and our own experiments on multiple animals. For percussion marks were identified percussion notches and pits and adhering flakes (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Vettese et al., 2017). For the study of cremations, changes in the coloration of the bones were into account, following the proposal of Stiner et al. (1995). The six coloration stages used are: 0) unburned; 1) small brown or black areas; 2) brown bones; 3) black bones (charred); 4) grey bones (calcined); 5) white bones (calcined). Finally, carnivore modifications were identified through the presence of tooth marks, mainly pits and scores (Blumenschine, 1995; Bunn, 1981; Domínguez-Rodrigo and Barba, 2006; Fisher, 1995; Shipman, 1981), along with furrowing or chipping of the back edge. The breakage strategies of humans and carnivores generate impact flakes that are difficult to differentiate (Brain, 1981; Bunn, 1981; Capaldo and Blumenschine, 1994). Although they are more common in anthropic breakage, they are

not used as a diagnostic element when they show no signs (percussion marks or tooth marks) that allow their assignment.

The analysis of tooth microwear patterns (microscopic features present on the surface of the enamel) was carried out to establish the relative duration of the occupation events in the rock-shelter. The characteristics of microwear were examined for the most represented species in the assemblage, *Equus ferus* and *Cervus elaphus*. The analysis was performed following the protocol established by Solounias and Semperebon (2002) and Semperebon et al. (2004). High-resolution dental casts were observed under transmitted light with a Zeiss Stemi 2000C stereomicroscope at a magnification of 35×. The microwear features (i.e., scratches and pits) were quantified on the paracone of the upper molars or the protoconid of the lower molars. Two measurements of the variability of scratch density i.e., the standard deviation (SD) and the coefficient of variation (CV) were used to estimate the duration of the accumulation of faunal associations (Rivals et al., 2015). The integration of these two measures of variability allows for the classification of each case in one of the following three categories: [A] seasonal or shorter events, [B] events longer than a season (i.e., two or more contiguous seasons), [C] distinct events that occurred in different and non-contiguous seasons.

Finally, catchment areas were analysed in order to evaluate the mobility ratio of the Neanderthal of level P. This involved 1) a petrographic study of the predominant raw material (chert); 2) systematic geoarchaeological explorations generating specific regional mapping of the possible source areas of siliceous rocks; 3) chert abundance ratio (CAR) was applied as a quantitative approximation to estimate the availability of primary material in a territory (Soto et al., 2018).

## 4. Results

### 4.1. Archaeo-stratigraphy of level P

The separation of the two sublevels was possible over the whole surface of the rock shelter. Sublevel Pa (NR=979) contains a greater number of faunal remains than sublevel Pb (NR=254) (Fig. 1). This allowed us to develop the spatial study of faunal specimens and to distinguish possible accumulation events in the sublevel. The spatial distribution of the remains shows cluster patterns in which numerous accumulations are associated with hearths (Pa=4, Pb=3), and characterized by high densities of debris. In sublevel Pa, accumulations were discriminated from densities greater than 14–20 specimens and in Pb, at densities greater than 7–9 specimens (Fig. 2). As a result of the analysis of k-nearest neighbour distances, the z-score in the two assemblages indicates that there is a probability of less than 1% that the clustered pattern can be the result of random likelihood (Table 1). A total of seven accumulations were identified; four in Pa (1, 2, 3 and 4) and three in Pb (5, 6 and 7). Of these, four can be considered as main accumulations, located around combustion structures, three in Pa (1, 2 and 4) and one in Pb (6).

### 4.2. Taxonomic anatomy and age composition

As in the other levels in the Abric Romaní sequence, level P presents a low taxonomic diversity dominated by large and medium-sized ungulates. The best represented species is *Cervus elaphus* (Pa=63%; Pb=60% NISP), followed by *Equus ferus* (Pa=22.6%; Pb=32.2% NISP) and *Bos primigenius* (Pa=10.7%; Pb=6.7% NISP) (Table 2). The sum of the three taxa represents 96.3% NISP in sublevel Pa and 98.9% NISP in Pb. A mandible fragment belonging to an adult *Canis lupus* individual in Pa and a dozen rabbit remains between both archaeological levels complete the

assemblage. Due to the absence of anthropogenic and carnivore modifications on rabbit and wolf remains, as well as their low number, it is difficult to interpret the role of these two taxa in the assemblages. The Shannon diversity index (E: Pa=0.622, Pb=0.6506) and the Simpson index (D: Pa=0.4601; Pb=0.5048) indicate slightly diversified and relatively uniform assemblages, in which no single taxon dominates in respect to the total.

The MNE is 133 (124 of which correspond to ungulates) (Table 2), comprising to a minimum of 24 individuals, 75% of which are red deer (Pa=6; Pb=4 MNI) and horses (Pa=3; Pb=5 MNI) (Table 2). Due to the high fragmentation of long bones, a lot of remains could not be taxonomically identified, but could be assigned to a weight size category (NSP=29.6%). Approximately half of them were assigned to a weight size category. Most of them belong to medium-sized (Pa=31.9%; Pb=44.5%) and large animals (Pa=13.4%; Pb=12.2%) in accordance with the distribution of the identified specimens. A high proportion of remains are indeterminate anatomically, taxonomically and by weight size category (Pa=39.6%; Pb=27.9%).

Skeletal profiles indicate a differentiated pattern for the two most abundant taxa, red deer and horses. These patterns are broadly similar in both sublevels but present some variations (Tables A1–A4). In general, the most represented elements for red deer in Pa and Pb are long bones, especially intermediate and upper long bones. Conversely, cranial elements, especially mandibles, predominate among horse elements. The postcranial axial skeleton and small and compact bones, such as carpals, tarsals and phalanges are especially rare in both taxa and in both sublevels (Fig. 3). A more in-depth analysis of anatomical representation shows small differences by taxon and sublevel. Thus, red deer carcasses are represented by more cranial elements in Pb while the opposite occurs with the girdle portion, which is better represented in Pa. The appendicular elements show very similar pattern in both sublevels. Tibias dominate the long bones. A similar proportion of upper, intermediate and inferior appendicular elements was observed in both sublevels with the posterior appendicular elements predominating anterior elements. On the other hand, horses display a peculiar pattern, as we observe a balanced proportion of mandibles and skulls in sublevel Pb, whereas in Pa, only mandibles and hyoids were present. However, in general axial skeletal elements are scarce, although in sublevel Pb, the abundance of metatarsals and the absence of metacarpals are striking.

The estimation of the age at death of the ungulates of level P is disparate due to the lack of cranial elements for some taxa and sublevels. The cranial MNI (13 compared to the 20 individuals estimated with the postcranial skeleton), corresponds to four individuals in sublevel Pa and nine in Pb. Based on the analysis of the eruption and tooth wear sequences for the red deer, was calculated the age of five individuals, one in sublevel Pa and four in sublevel Pb. For horses, were calculated the age at death of all individuals in both sublevels. For all the ungulates, four individuals have enough dental remains to estimate the season of death. This involves two horses and two red deer (Fig. 4). The absence of aurochs dental elements did not enable us to estimate the age of the two individuals present in this group.

The mortality profile for horses indicates a predominance of prime adult individuals in both sublevels. The two identified juvenile individuals, one per sublevel, were slaughtered during the summer. In the case of red deer, sublevel Pb shows a pattern of attritional mortality. Due to the scarcity of individuals in sublevel Pa, we must interpret the mortality profile for this latter sublevel with caution. In the same way, seasonality indicates that red deer were killed in sublevel Pb during the autumn or early winter while the absence of juveniles in Pa does not allow us to establish the exact moment of death (Fig. 4).

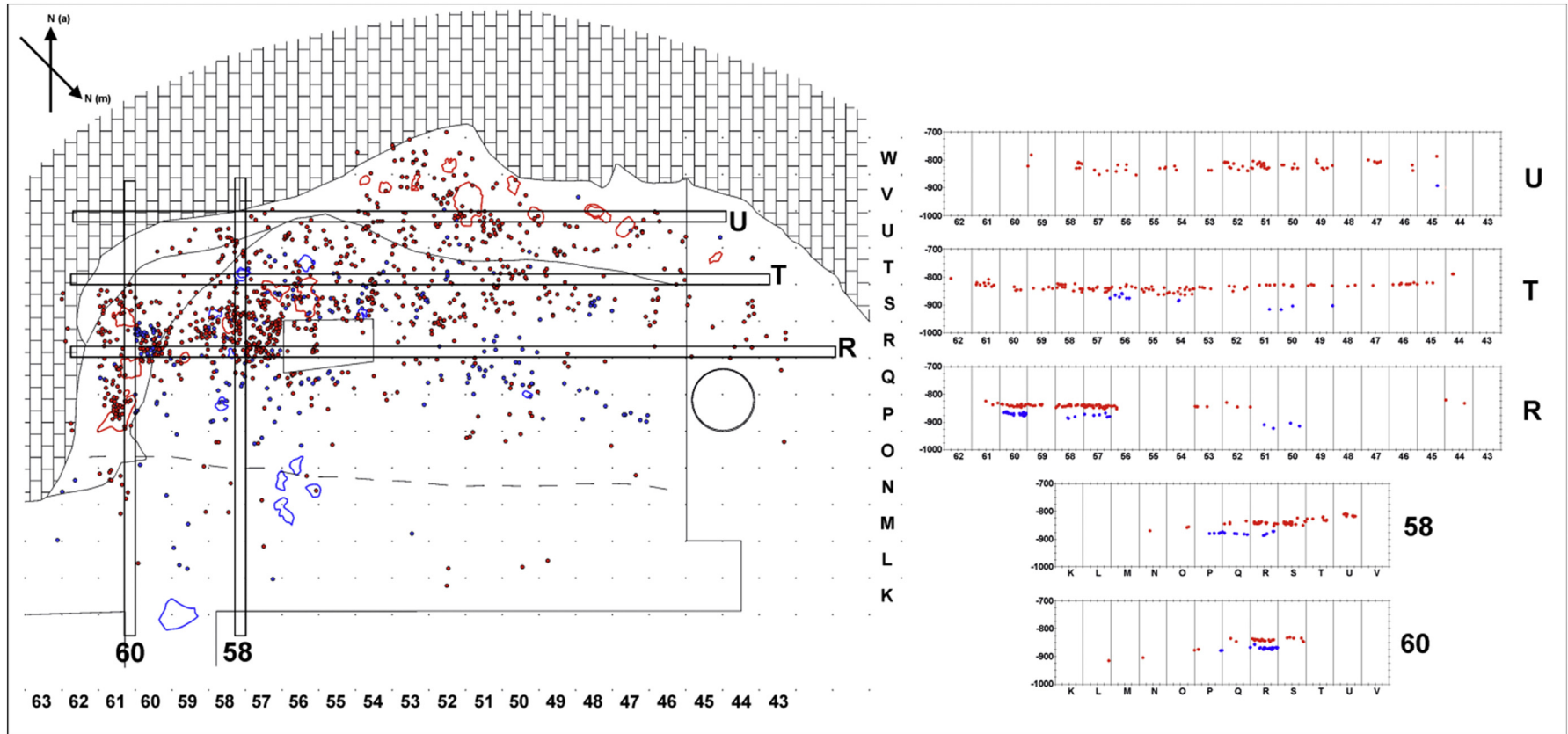


Fig. 1. Site plan (left) and sections (right) of the transversal (60 and 58) and longitudinal (U, T, R) projections developed for the identification of sublevels a (red) and b (blue) of level P. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

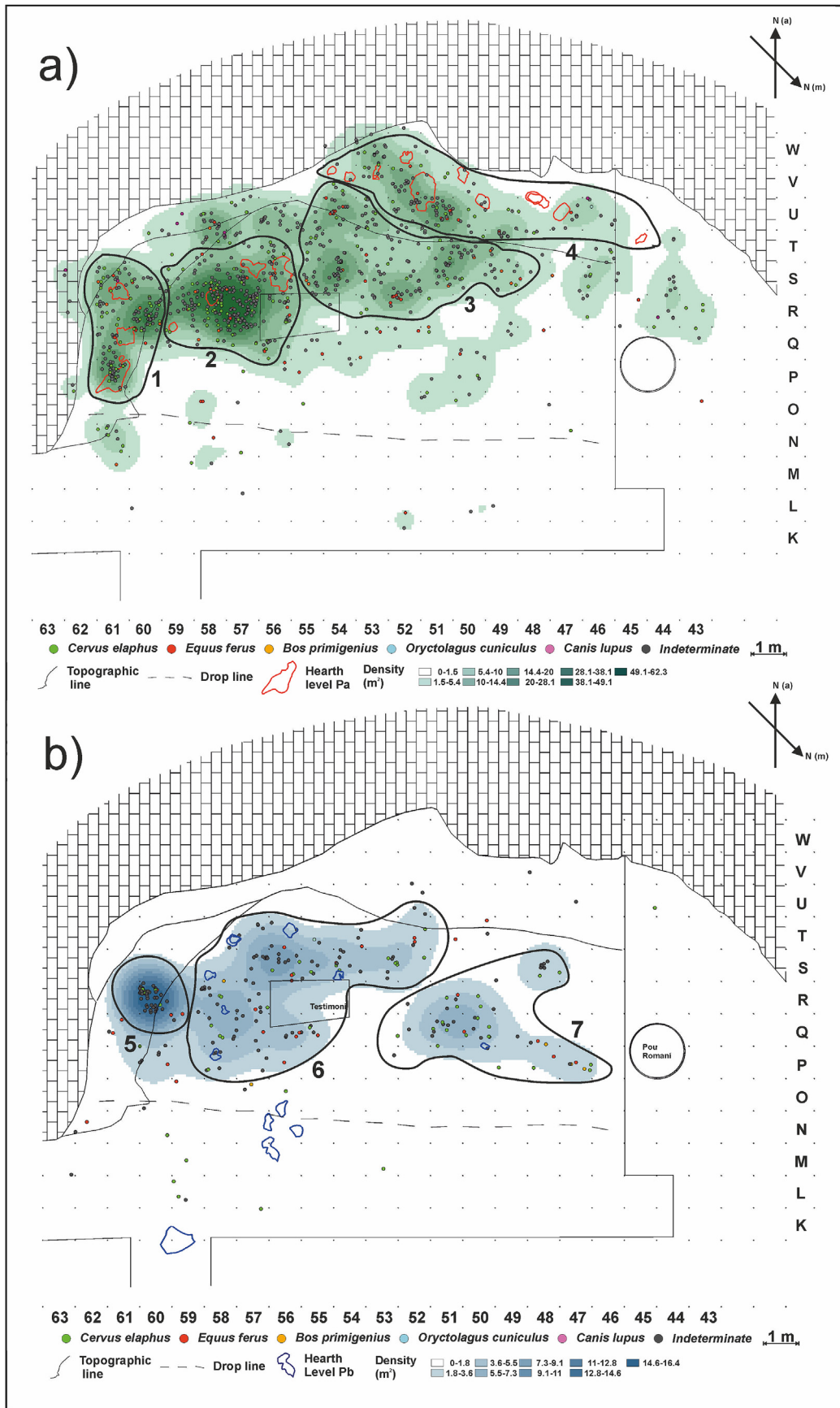


Fig. 2. Spatial distribution of faunal remains in sublevels Pa (a) and Pb (b).

**Table 1**  
Summary of the average distance to the nearest neighbour.

	Pa	Pb
Average distance observed	0.1346 m	0.2511 m
Average distance expected	0.2428 m	0.4062 m
Nearest neighbour ratio	0.554110	0.618245
z score	-26.662815	-11.570512
p value	0.000000	0.000000

The analysis of the inter-individual variation of dental micro-wear patterns in red deer and horses indicates low SD and CV values for both species, in Pa and in Pb (Table 3). These values are plotted in area [A] of the heat map indicating that the four samples correspond to animal remains accumulated during short-term events, of one season or less (Fig. 5). It is not possible to establish the season of death for the horse due to the lack of extant populations for comparison. In the case of red deer, the low scratch values, compared to extant wild populations of red deer and other cervids (Rivals et al., 2015), indicate a season of death in autumn or winter.

Correlations between (S)FUI and %MAU indicate that there is a statistical correlation for red deer in sublevel Pa. This result suggests that these animals could be subjected to unbiased or gourmet transport strategies according to the proposals of Faith and Gordon (2007) (Table 4). No other statistical correlations were identified, although the red deer shows a positive trend in sublevel Pb (Fig. 6). The values of the horse in both sublevels are inversed to bulk and unbiased strategies (Fig. 6). For the aurochs, the trend is negative in Pa and positive in Pb. There is no significant statistical correlation between the UMI and the %MAU in any of the taxa (Table 4).

The results of the Spearman coefficient between the %MAU and mineral density indicate that there are positive and statistically significant correlations in the red deer sample from Pa and Pb, in the sample of horses from Pb and the aurochs from Pa (Table 5). This indicates that there is a positive relationship, although it is low, between the representation of the anatomical parts and their mineral density.

Almost all the specimens in the faunal assemblage are fragmented (97.4%). Only 2.5% of the remains are complete, corresponding mostly to isolated teeth and articular bones. Long bone diaphysis in sublevels Pa and Pb conserve less than one third of their circumference and one quarter of their total length in 84.8% and 85.7% of the cases, respectively. The most common combination of characters in Pa sublevel is a predominance of longitudinal delineations, right angles and smooth edges (41.1%) and curved, oblique and smooth edges (36.5%). In sublevel Pb, curved, oblique

and smooth fractures are the most represented (47.05%), followed by longitudinal, straight and smooth fractures (11.2%). These patterns indicated a predominant green bone fracture at sublevel Pa and Pb.

#### 4.3. Bone surface modifications

Human-induced modifications are the most common modifications in the assemblage of level P and result from the nutritional phase of carcasses processing. Anthropogenic modifications are present on 37.2% of the bones in sublevel Pa and on 14.9% in sublevel Pb. These consist primarily of cut marks (Pa = 12.6%; Pb = 6.3%), percussion marks (Pa = 5.7%; Pb = 5.1%) and burnt bones (Pa = 26.9%; Pb = 5.1%).

Red deer is the taxon with the highest number of remains with cut marks, with 39 remains in Pa (24.4%) and 8 in Pb (16%). Nine horse specimens present cut marks in Pa (22.5%) and four in Pb (19%). Eleven aurochs specimens have cut marks in Pa (39.2%) and none in Pb. Most of the identified cut marks correspond to slicing marks (Pa = 90.3%; Pb = 87.5%). The rest of the marks are scraping marks (Pa = 8.7%; Pb = 12.5%). The identified butchery activities are defleshing (Pa = 84.3%; Pb = 100%), skinning (Pa = 10.8%), disarticulation (Pa = 3%) and periosteum removal (Pa = 2%). By species, in red deer at sublevel Pa defleshing suppose the 86.7% of butchery activities, disarticulation 8% and skinning 5.3%, and in sublevel Pb the unique butchery activity identified was defleshing. For horse in sublevel Pa the cut marks were related with the 77.8% with defleshing, 11.1% with disarticulation and the 11.1% with defleshing, in sublevel Pb the unique butchery activity identified was defleshing. For aurochs was identified remains with cut marks only in sublevel Pa, with a 50% of defleshing and a 50% of skinning, disarticulation marks were not found. In sublevel Pa for medium size animals the main activity identified was defleshing with 92.8% of cut marked remains, and disarticulation and skinning with a 3.6% each. For large animals in sublevel Pa defleshing was the 93.3% and skinning the 6.7%. In sublevel Pb for medium and large size animals the only butchery activity identified was defleshing.

Cut marks are more common on proximal appendicular elements in both sublevels, followed by intermediate appendicular elements in Pa and distal appendicular elements in Pb (Table 6). Cut marks are located mainly on midshaft portions (71.4%) of long bones, and then on the metaphysis (28.6%). Epiphyses are not cut marked.

Anthropogenic breakage marks were identified on 69 bones (NSP: Pa = 56; Pb = 13). The most common signals in this category are percussion notches (NSP: Pa = 33, Pb = 7) and followed by percussion pits (NSP: Pa = 22, Pb = 6). Related with fresh bone

**Table 2**  
NISP, NSP, MNE and MNI of taxa and weight size groups of sublevels Pa and Pb.

Taxa	P total					Pa					Pb				
	NISP	%NISP	MNE	%MNE	MNI	NISP	%NISP	MNE	%MNE	MNI	NISP	%NISP	MNE	%MNE	MNI
<i>Cervus elaphus</i>	224	62.2	64	48.1	10	170	63	37	45.1	6	54	60	27	52.9	4
<i>Equus ferus</i>	90	25.0	43	32.3	8	61	22.6	25	30.5	3	29	32.2	18	35.3	5
<i>Bos primigenius</i>	35	9.7	17	12.8	2	29	10.7	12	14.6	1	6	6.7	5	9.8	1
<i>Canis lupus</i>	1	0.3	1	0.8	1	1	0.4	1	1.2	1	0	0	0	0	0
<i>Oryctolagus cuniculus</i>	10	2.8	8	6.0	3	9	3.3	7	8.5	2	1	1.1	1	2	1
Total	360		133		24	270	100	82	100	13	90	100	51	100	11
<b>Indeterminates</b>	NSP	%NSP				NSP	%NSP				NSP	%NSP			
Medium size	299	34.2				226	31.9				73	44.5			
Large size	115	13.2				95	13.4				20	12.2			
Indeterminate	459	52.6				388	54.7				71	43.3			
Total NSP	873	100				709	100				164	100			
<b>Total</b>	1233					979					254				

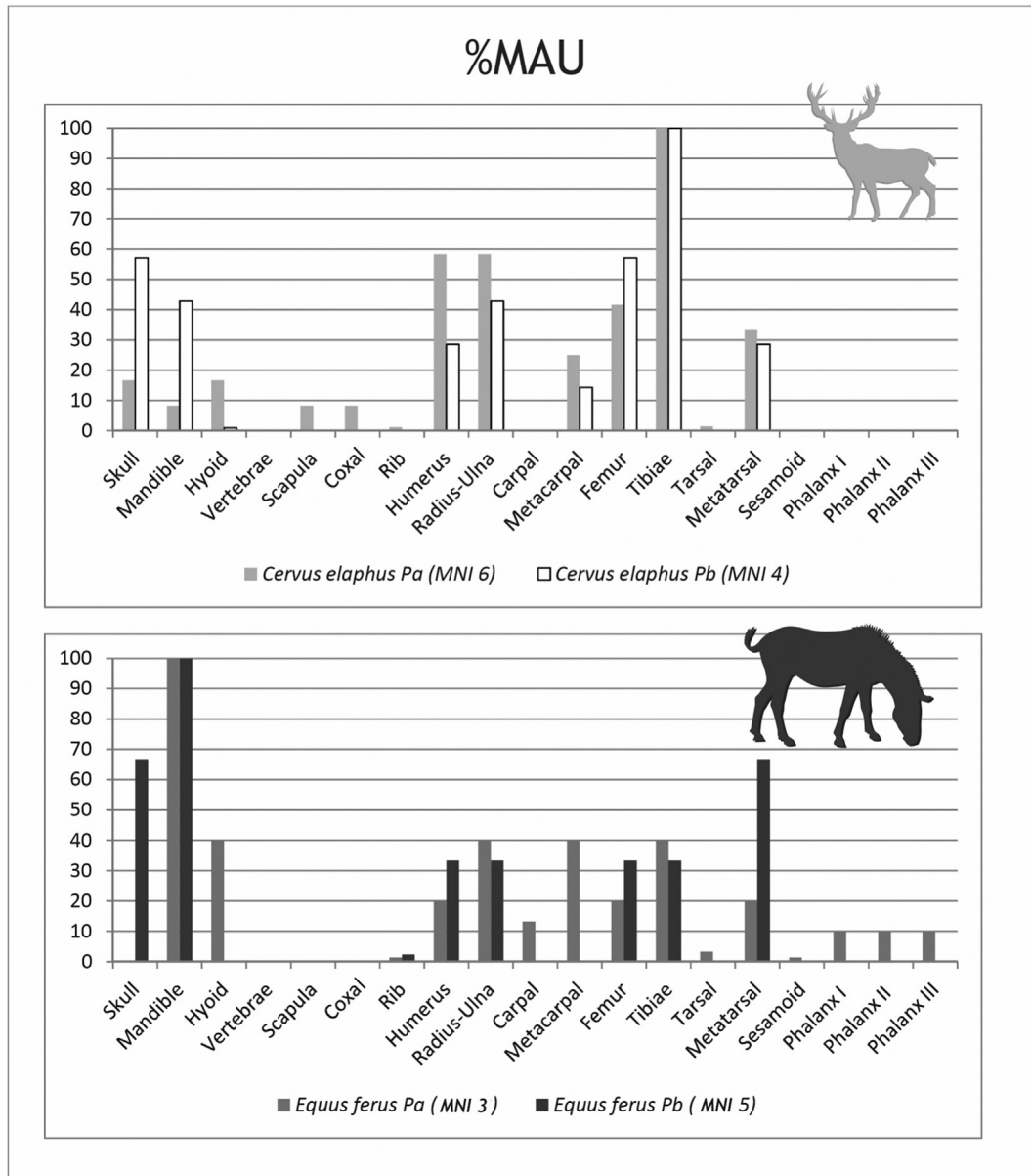


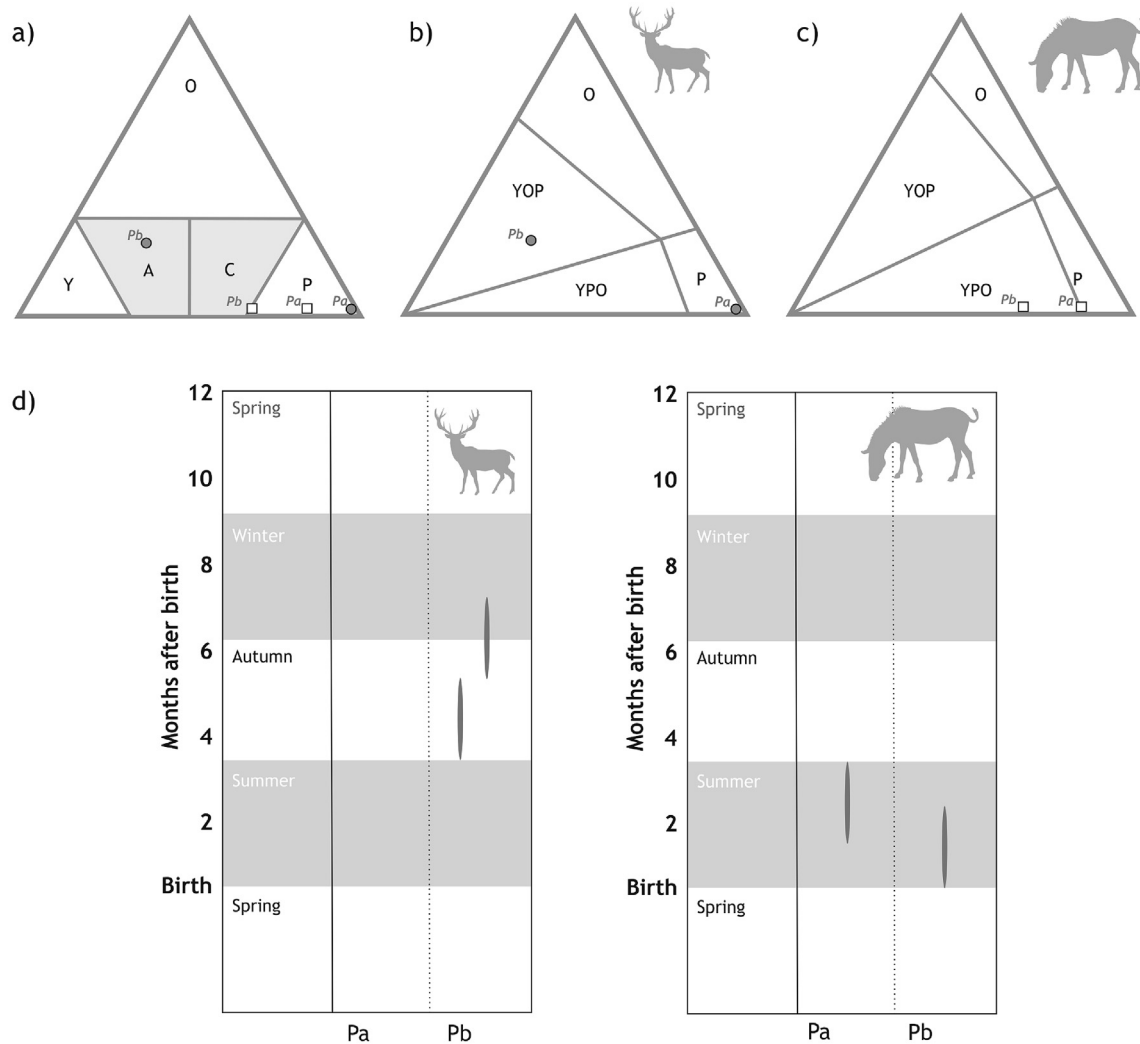
Fig. 3. %MAU of the main species of ungulates represented in sublevels Pa and Pb of Abric Romani.

breakage were impact flakes (NSP: Pa = 65, Pb = 10) and adhering flakes associated with anthropogenic marks (NSP: Pb = 1). By taxonomic distribution, the remains of red deer with anthropogenic breakage in sublevel Pa the 63.6% were percussion notches (NSP = 7) and 36.4% were percussion pits (NSP = 4), and in sublevel Pb only were identified percussion notches (NSP = 2). For horse remains with anthropogenic breakage in sublevel Pa the 75% were percussion pits (NSP = 3) and 25% percussion notches (NSP = 1), and in sublevel Pb were identified only percussion pits (NSP = 2). Remains of aurochs with anthropogenic bone breakage were identified exclusively on sublevel Pa, were 60% of percussion notches (NSP = 3) and 40% of percussion pits (NSP = 2). Anthropogenic breakage are situated on appendicular bones (98.5%), except one large-sized vertebra from sublevel Pa. Percussions notches and pits are located on the diaphysis (Pa = 71.4%, Pb = 69.2%) and metaphysis of long bones (Pa = 28.6%, Pb = 30.8%), although one percussion mark was identified on the proximal epiphyses of a horse metatarsal in sublevel Pb.

Modifications caused by fire affect 26.9% of the specimens in Pa and 5.1% in Pb. Different degrees of cremations were identified (Table 7). Single-coloured cremations are the most common and account for 88.5% of the burnt bone sample, while double or multiple colorations are relatively rare. Degree 1 (13.3%) is the most frequent, followed by degree 3 (5.1%) (Table 7).

In sublevel Pa carnivore-induced modifications are present on 5% (NR = 48) of the specimens. On 0.8% of the assemblage, carnivores were also responsible for bone breakage. In terms of taxa, red deer specimens present the most tooth marks (5.9%), followed by the horse (2.6%) and the aurochs (0.7%). In addition, a rabbit humerus with carnivore tooth marks was also identified. In sublevel Pb, carnivore tooth marks affect 3.14% (NR = 8) of the assemblage. Four remains are directly associated with fracturing caused by carnivores. The percentage of red deer remains with tooth marks is 5.5%, and 2.2% on horse specimens. No aurochs remains bear tooth marks.

A total of 12 remains, in all sublevel Pa, bear both anthropogenic



**Fig. 4.** Summary of the pattern of mortality and seasonality in level P of Abric Romani. A) Representation of the mortality of deer (grey circles) and horses (white squares) by sub-levels in a triangular plot in which the classical areas are indicated according to [Stiner \(1991\)](#). b) and c) The same results plotted on the diagrams modified by [Discamps and Costamagno, 2015](#). d) Seasonal scheme for deer and horses of the different levels of the Abric Romani P level (Y = Young; P = Prime adult; O = Old; YOP = Young-Old-Prime; YPO = Young-Prime-Old). Total MNI: deer Pa = 1, Pb = 4; horse Pa = 3, Pb = 5.

**Table 3**

Summary of microwear data for the horse and red deer assemblages from Abric Romani sublevels Pa and Pb. Abbreviations: MNI = Minimum Number of Individuals; M = Average number of pits or scratches; SD = standard deviation (for pits and scratches); CV = coefficient of variation (for scratches).

		MNI	Pits		Scratches		CV
			M	SD	M	SD	
<i>Equus ferus</i>	Pa	3	11.78	0.67	20.56	0.75	0.04
	Pb	3	15.17	1.61	21.92	0.63	0.03
<i>Cervus elaphus</i>	Pa	2	16.25	1.06	11.00	0.71	0.06
	Pb	2	14.75	1.06	13.50	1.41	0.10

and carnivore modifications. However, there is no overlapping of tooth marks on anthropogenic marks or vice versa. The cut marks identified on eleven specimens are related to filleting, and on one specimen, the slice marks are associated with the skinning of carcasses. In this assemblage, it also documents a specimen with percussion pits.

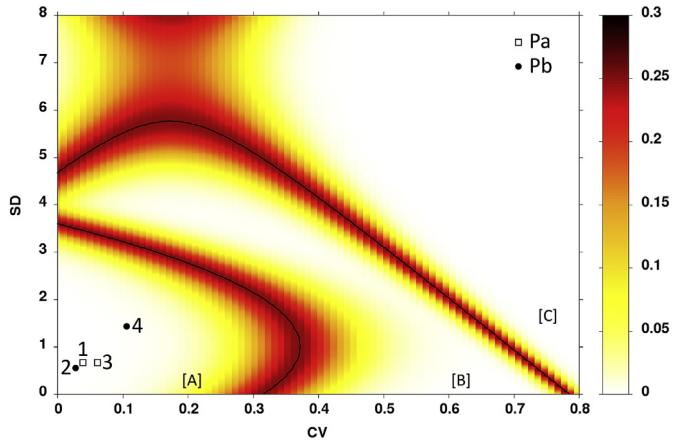
The most common post-depositional modifications in sublevel Pa are water abrasion (10.7%) and vermiculation produced by the action of plants roots (10.4%). In addition, it has been possible to identify processes of chemical dissolution (5.2%), manganese oxide

deposition (5.5%) and trampling (4.8%). In sublevel Pb, vermiculation is the most common post-depositional modification (22%), followed by manganese oxide stains (12.6%), chemical dissolutions (11%), water abrasion (7.4%) and, finally, trampling (2.7%).

#### 4.4. Faunal refitting

In total, 65 coordinated faunal remains were refitted, forming 26 refit groups ([Table 8](#)). In sublevel Pa, 23 refits were found, and only three refits come from sublevel Pb. Were distinguished between





**Fig. 5.** Boundary lines with the error probability (heat map) based on SD and CV values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separated short events (region C) and positions of the assemblages of *Equus ferus* (1–2) and *Cervus elaphus* (3–4) from Abric Romani sublevels Pa and Pb.

anatomical (Pa = 5; Pb = 1) and mechanical (Pa = 18; Pb = 2) refits, most of which are formed by two elements (NR = 16). However, in

**Table 5**  
Values of significance analysis between bone mineral density and %MAU.

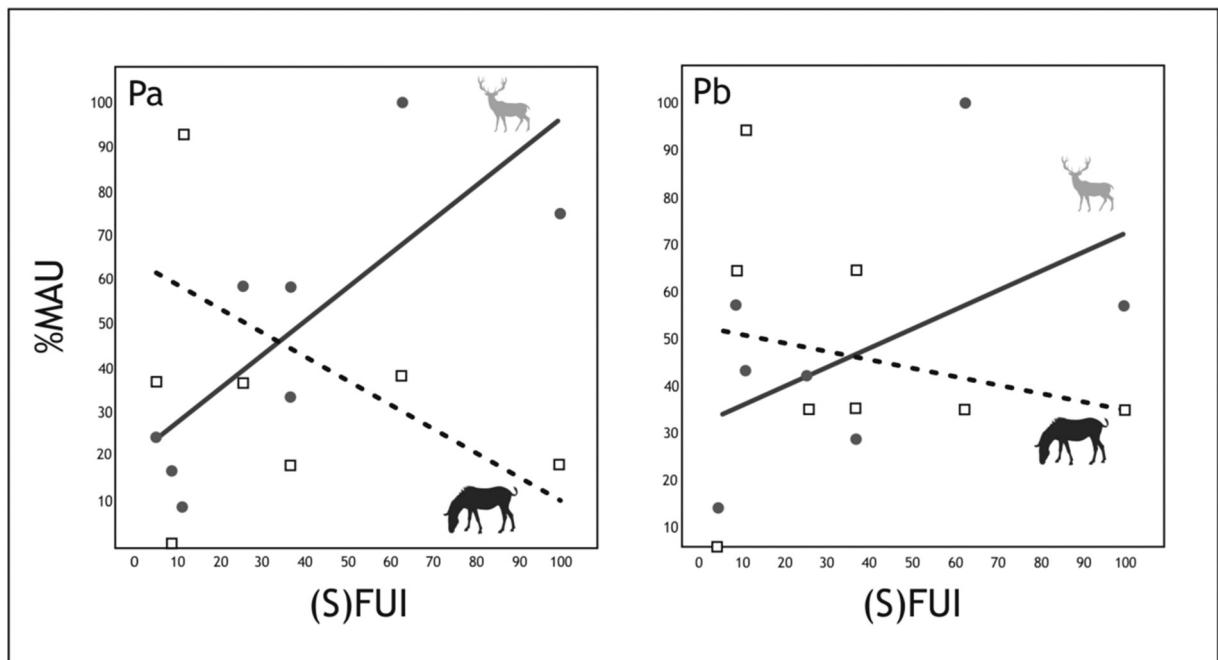
Taxa	Pa		Pb	
	Spearman's (rs)	p	Spearman's (rs)	P
<i>Cervus elaphus</i>	0.26321	0.0088306	0.32883	0.0009466
<i>Equus ferus</i>	0.18555	0.068825	0.25222	0.012693
<i>Bos primigenius</i>	0.21021	0.03877	0.12504	0.22235

five cases, three specimens were joined together, and on two occasions, four and five remains were connected. The study of refits established the existence of connections between the accumulations delimited within each sublevel (Fig. 7). In addition, it can be argued that there are no vertical movements between them.

The distances separating the refits are variable, as can be seen in Table 8. The anatomical refits from sublevel Pa display short distances between each other and belong to horse remains. However, the mechanical refits display short and long distances. They consist of three mandibles, a carpal bone plus the metacarpal, and one metatarsal plus phalanges. The details of these refits are presented in Table 8. Mechanical refits have been defined in all cases as a result of green bone breakages. In addition, in most cases, cut marks and percussion marks were observed, indicating the extraction of meat and percussion marks related to bone marrow extraction

**Table 4**  
Evenness values and correlations of the different sublevels analysed by taxa.

Taxa	Evenness	%MAU/SFUI		%MAU/UMI	
		Spearman's (rs)	P	Spearman's (rs)	P
Pa	<i>Cervus elaphus</i>	0.883	0.80241	0.021131	0.63775
	<i>Equus ferus</i>	0.908	-0.17522	0.70536	-0.09759
	<i>Bos primigenius</i>	0.971	-0.32733	0.48571	-0.29277
Pb	<i>Cervus elaphus</i>	0.928	0.46068	0.25159	0.7537
	<i>Equus ferus</i>	0.824	-0.02554	0.96429	0.67612
	<i>Bos primigenius</i>	0.595	0.50709	0.25	0.62106



**Fig. 6.** Scatter diagrams of skeletal representation in %MAU and (S)FUI for the two taxa represented in the level P faunal assemblage of the Abric Romani. The grey points represent *Cervus elaphus* and the white squares represent *Equus ferus*.

**Table 6**  
NISP (NISP%) of cut marks.

	Pa						Pb						Total
	<i>C. elaphus</i>	<i>E. ferus</i>	<i>B. primigenius</i>	Large size	Medium size	Total	<i>C. elaphus</i>	<i>E. ferus</i>	Large size	Medium size	Total		
Cranium	0/1 0	0/0 0	0/1 0	0/0 0	1/1 100	1/3 3.3	0/0 0	0/3 0	0/1 0	0/0 0	0/4 0	15.3	
Mandible	1/3 33.3	1/8 12.5	1/5 20	2/2 100	0/1 0	5/17 29.4	0/7 0	0/4 0	0/0 0	0/0 0	0/11 0	10/58 17.2	
Hyoid	0/0 0	1/1 100	0/0 0	0/0 0	0/0 0	1/1 100	0/0 0	0/0 0	0/0 0	0/0 0	0/0 0	2/2 100	
Ribs	0/4 0	0/1 0	0/0 0	1/9 11.1	0/2 0	1/16 6.3	0/0 0	0/2 0	0/1 0	0/4 0	0/7 0	2/46 4.3	
Upper limb	15/42 35.8	0/6 0	2/7 28.6	0/0 0	0/1 0	17/56 30.4	5/13 38.5	1/4 25	0/0 0	0/0 0	6/17 35.5	46/146 31.5	
Intermediate limb	20/77 26	6/16 37.5	4/9 44.4	0/0 0	0/0 0	30/102 29.4	2/23 8.7	2/5 40	0/0 0	0/0 0	4/28 14.3	68/260 26.1	
Lower limb	3/33 9.1	0/5 0	4/6 66.7	0/0 0	0/0 0	7/38 18.4	1/7 14.3	1/3 33.3	0/0 0	0/0 0	2/10 20	18/102 17.6	
Phalanx	0/0 0	1/3 33.3	0/0 0	0/0 0	0/0 0	1/3 33.3	0/0 0	0/0 0	0/0 0	0/0 0	0/0 0	2/6 33.3	
Long bone	0/0 0	0/0 0	0/0 0	10/57 17.5	22/181 12.2	32/238 13.4	0/0 0	0/0 0	1/13 0.1	1/73 0.1	2/86 2.3	68/648 10.5	
Flat bone	0/0 0	0/0 0	0/0 0	2/15 13.3	6/26 23	8/41 19.5	0/0 0	0/0 0	0/3 0	0/20 0	0/23 0	16/128 12.5	
Total	39/160 24.4	9/40 22.5	11/28 39.2	15/83 18	29/212 13.6	103/515 20	8/50 16	4/21 19	1/18 5.6	1/97 1	14/186 7.5	234/1410	

**Table 7**  
Number of burnt remains presenting some evidence of burning. The elements presenting more than one degree of alteration have been marked in each relevant category.

Burned stages	Unburned	1	2	3	4	5
NSP Pa	715	163	30	64	27	10
%NSP	70.8	16.2	3	6.3	2.7	1
NSP Pb	241	8	1	2	3	1
%NSP 256	94.2	3.1	0.4	0.8	1.1	0.4

(refits 1, 2, 7, 9, 13 and 21). In Pb, short distances separate two of the refits while the other is a long-distance refit. The first two are mechanical refits of a horse metatarsal with cut marks and a Cervidae tibia with percussion pits. The anatomical refit is an equid mandible (Table 8).

The MNI per accumulation is lower than the total MNI in both red deer and horses. Although the sum of the total MNI per area is greater than the total MNI, there is a difference of two individuals in red deer and one in horses (Table 9). In addition, the redistribution index is far from 1, and shows an inverse value to food distribution. This is an indicator of low food sharing the activity areas in sublevel Pa. In sublevel Pb, this analysis was not carried out as it was not possible to establish a clear separation between the activity areas and individual hearths.

#### 4.5. Catchment areas of lithic raw materials

The vast majority of the 2633 lithic remains larger than 1 cm, are in chert (91.1%, or 2398 remains). A petrographic study was conducted on nearly two-thirds of these (62.8%, or 1506 pieces). Lithics with strong post-diagenetic alteration (e.g., patinas, concretions, cremations), were excluded from the study, as they cannot be assigned to any specific raw material type.

Only three types of chert located within a 30 km radius of Abric Romaní, were identified in level P. The most represented chert is the Sant Martí de Tous type (SMT) with 824 pieces (54.7%), followed by the Panadella type (PAN) with 651 elements (43.2%), and finally, the Muschelkalk type (MUSCH) with 31 pieces (2.1%) (Table 10). For the first time in the sequence of Abric Romaní, SMT and PAN chert

type percentages are similar.

The near absence of chert in the main fluvial courses rules out possible procurement from secondary sources. Primary outcrops were thus defined as the main procurement source, and the CAR was calculated for a territory of about 30 km from Abric Romaní.

The regional zones with abundant siliceous outcrops are mainly located in the vicinity of Sant Martí de Tous (SMT). Consequently, the raw material procurement strategy in level P of Abric Romaní is regional for the SMT and PAN type cherts, which are located 16 km and 24 km from Abric Romaní, respectively. The use of MUSCH type chert, with primary outcrops within a local (<10 km) and regional (>10 km) radius, points to a combined local and regional procurement strategy (Fig. 8).

Due to the almost absence of chert in river courses, we calculate the Chert Abundance Ratio (CAR) to obtain a quantitative approximation of the amount of chert provided by the territory. This calculation (Soto et al., 2018), which is always approximative, gives us an overview of where the possible accumulations of raw materials are located. In this case the geological calculations for obtaining the CAR resulted in siliceous representation for the three types of chert in the territory: 16.99% for chert of SMT origin, 30.96% for MUSCH and 0.42% PAN type. The remaining 51.63% are geological formations with chert that are not represented in level P (Table B1). These data show that if the SMT uptake occurs in area of regional abundance, the presence of PAN type chert in the archaeological record responds to other aspects not related to its local abundance. The same applies to the low presence of MUSCH chert, which is not comparable to its abundance in the territory. These aspects would mark a non-random capture of the lithic raw material.

## 5. Discussion

Over the past decades, intense research at the Abric Romaní has enabled us to discuss different aspects of Neanderthal behaviour. Among them, the exploitation of resources and the type of occupation of the rock shelter have been central (Allué et al., 2017; Bargalló et al., 2016; Burjachs et al., 2012; Carrancho et al., 2016; Chacón et al., 2015; Gabucio et al., 2018a, 2018a; Romagnoli et al.,

**Table 8**

Refits from sublevels Pa and Pb. The sublevel, taxon, element, anthropogenic modifications and distance between the specimens are indicated in the table.

Refits N°	Sublevel	Taxa	Element	Number of remain	Type	Anthropic modifications	Distance	Connecting areas
Refits 1	a	<i>Cervus elaphus</i>	Tibiae	3	Mechanic	Percussion marks + burned	1 m+5 m	1–2
Refits 2	a	<i>Cervus elaphus</i>	Radius	2	Mechanic	Percussion marks + Cut marks + Burned	6 m	2–4
Refits 3	a	<i>Cervus elaphus</i>	Metatarsal	2	Mechanic	Burned	3 m	–
Refits 4	a	<i>Cervus elaphus</i>	Humerus	2	Mechanic	Cut marks + Burned	4 m	–
Refits 5	a	<i>Cervus elaphus</i>	Tibiae	2	Mechanic	Percussion marks	1 m	–
Refits 7	a	<i>Cervus elaphus</i>	Tibiae	4	Mechanic	Percussion marks + Cut marks + Burned	1 m+5 m+3 m	1–2
Refits 8	a	<i>Cervus elaphus</i>	Femur	3	Mechanic	Percussion marks + Cut marks + Burned	3 m+5 m	–
Refits 9	a	<i>Cervus elaphus</i>	Tibiae	3	Mechanic	Cut marks + Burned	1.5 m+6 m	3–4
Refits 10	a	<i>Equus ferus</i>	Radii	2	Mechanic		4 m	–
Refits 11	a	<i>Cervus elaphus</i>	Tibiae	2	Mechanic	Cut marks + Burned	>1 m	–
Refits 12	a	<i>Cervus elaphus</i>	Femur	2	Mechanic	Burned	>1 m	–
Refits 13	a	<i>Cervus elaphus</i>	Humerus	2	Mechanic	Cut marks	4 m	2–4
Refits 14	a	<i>Equus ferus</i>	Mandible	4	Anatomic		>1 m	–
Refits 16	a	<i>Equus ferus</i>	Mandible	3	Anatomic		2 m+1 m	–
Refits 17	a	Large size	Long bone	2	Mechanic		>1 m	–
Refits 18	a	<i>Equus ferus</i>	Mandible	2	Mechanic	Cut marks	>1 m	–
Refits 19	a	<i>Equus ferus</i>	Tibiae	2	Mechanic	Cut marks + Burned	1 m	–
Refits 20	a	<i>Equus ferus</i>	Femur	2	Mechanic	Burned	>1 m	–
Refits 21	a	<i>Bos primigenius</i>	Humerus	3	Mechanic	Burned	1 m+1 m	3–4
Refits 23	a	<i>Bos primigenius</i>	Tibiae	2	Mechanic	Percussion marks	1 m	–
Refits 24	a	<i>Equus ferus</i>	Metatarsal + Sesamoid + Phalanx I + II + III	5	Anatomic	Cut marks	>1 m	–
Refits 25	a	<i>Equus ferus</i>	Metacarpal + Pisiform + Trapezoid + Os Hamatum + Capitatum	5	Anatomic		>1 m	–
Refits 26	a	<i>Equus ferus</i>	Mandible	3	Anatomic		>1 m	–
Refits 6	b	<i>Cervus elaphus</i>	Tibiae	2	Mechanic		4 m	–
Refits 15	b	<i>Equus ferus</i>	Mandible	2	Anatomic		>1 m	–
Refits 22	b	<i>Equus ferus</i>	Metatarsal	2	Mechanic	Cut marks	1.5 m	–

2018, 2016; Solé et al., 2013; Vallverdú et al., 2010, 2005; Vaquero et al., 2017, 2015). The elevated sedimentation rate ( $0.6 \text{ m ky}^{-1}$ ) (Bischoff et al., 1988), the exceptional preservation of hearths (Vallverdú et al., 2012b, 2010) and activity areas (Gabucio et al., 2018b; Romagnoli and Vaquero, 2016; Vallverdú et al., 2010, 2005; Vaquero and Pastó, 2001), the extensive excavated surface (circa  $270 \text{ m}^2$ ), in addition to the assemblages resulting almost exclusively from human activity, have been key for the development of these investigations. Level P currently at the base of the archaeological sequence of this site, has been at the centre of this study.

The taxonomic uniformity of the sample, dominated by the presence of large ungulates, especially red deer and horse, as well as taphonomic modifications, together with the abundance of lithic remains and hearths in the two sublevels, show that the

assemblages are of anthropogenic origin and were hardly disturbed by other biological agents. This type of deposition has often been observed in the preceding levels of the Abric Romaní sequence (Carbonell, 2012, 2002; Fernández-Laso et al., 2010; Gabucio et al., 2014; Marín et al., 2017a; Rosell et al., 2012b). The anthropogenic modifications in sublevels Pa and Pb are the most numerous. However, only the initial and final stages of the butchering processes are represented, that is, skinning and bone breakage related to the extraction of medullar marrow, indicating intensive exploitation of ungulates. The presence and frequency of anthropogenic modifications between the two main taxa of the site are similar. However, statistically significant differences between the two anatomical profiles have been observed. These differences can be summarized by a greater presence of cranial elements in horses and a greater presence of appendicular elements in the red deer sample.

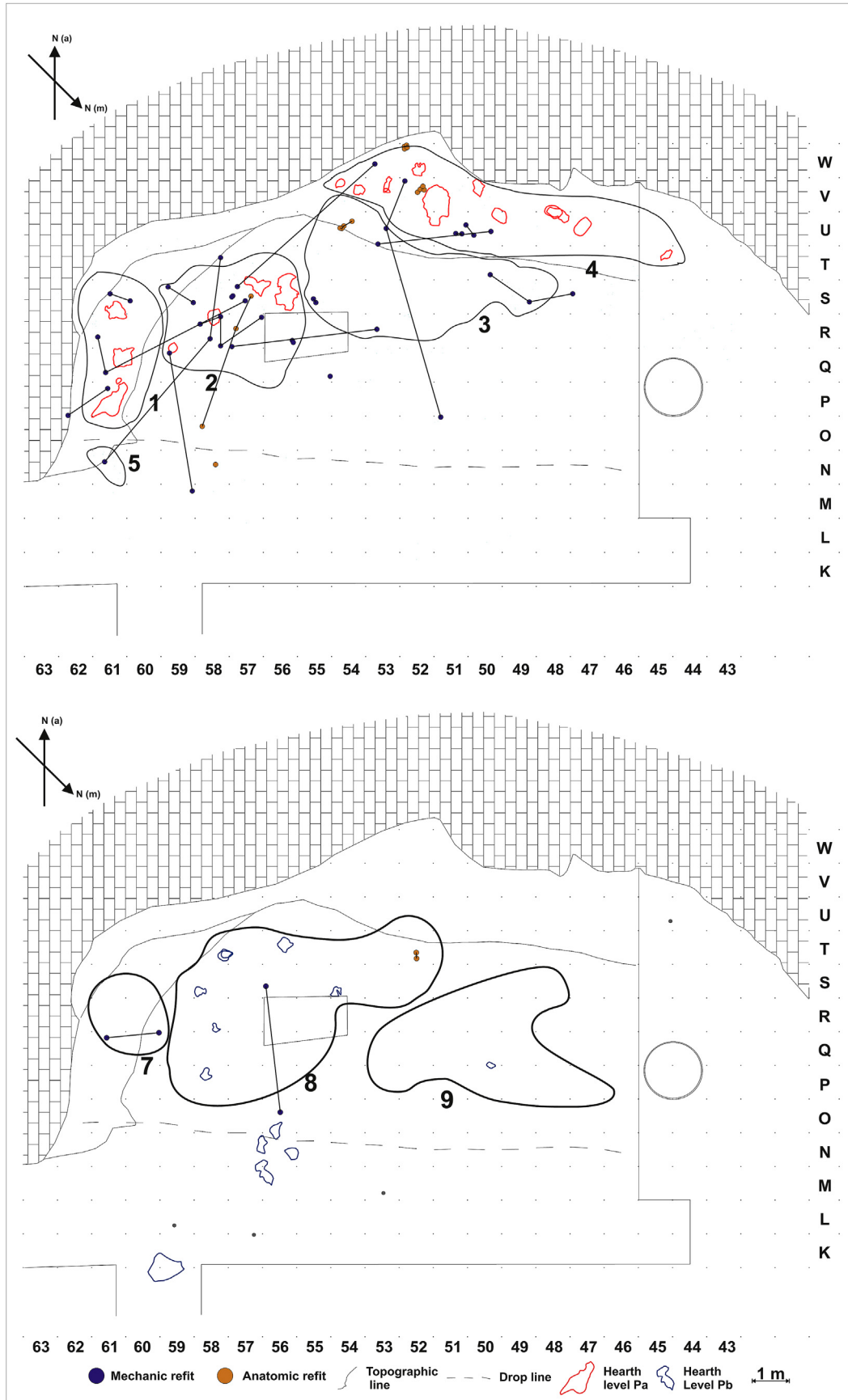


Fig. 7. Distribution of mechanical and anatomical refits in sublevel Pa (upper) and Pb (lower).

**Table 9**

MNI by accumulation area (MNif), number of hearths (n) and redistribution index (RI) for red deer and horse in Pa.

	<i>C. elaphus</i> /MNIs = 6			<i>E. ferus</i> /MNIs = 3		
	MNif	n	RI	MNif	n	RI
Area 1	3	3	0,2	1	3	0,1
Area 2	4	4	0,2	2	4	0,2
Area 4	2	9	0,04	1	9	0,04

Different explanations may account for these singularities. The difference between the proportion of both taxa does not seem to be related to differential preservation. In both taxonomic groups, high survival elements (Marean and Cleghorn, 2003) are the most abundant. Indeed, low density portions are scarce in the whole assemblage, independently of taxa or animal size. These data

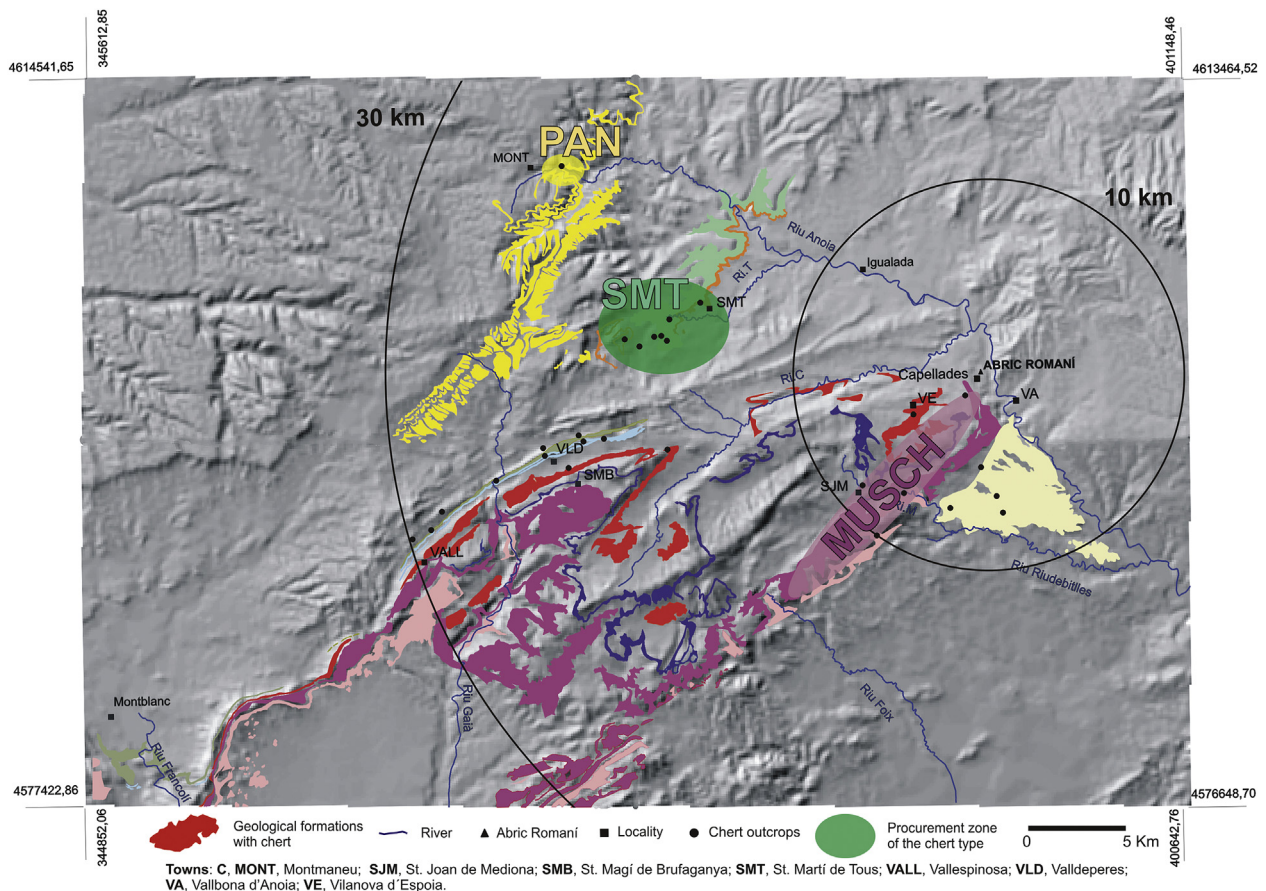
corroborate the result of the statistical correlation between bone mineral density and anatomical presentation. The low representation of these elements could be related the sum of attrition generated by Neanderthals and other post-depositional processes. The Neanderthal activities could include the systematic and deliberate destruction during consumption or by cleaning activities (Marín et al., 2017a).

This is not the first time that significant differences between the horse and red deer have been observed In the Middle Palaeolithic sequence of Abric Romani. Marín et al. (2017b) observed that the age at death of horses and red deer showed different profiles. Prime adult horses are predominant in all the sequence, resulting in a prime-dominated mortality profile. However, red deer showed higher diversity in these levels and could correspond to catastrophic profiles, dominated by young and prime adult mortality. These different mortality profiles could be related to different

**Table 10**

Technological categories by chert lithotypes in level P.

	Cores	Retouched artifacts	Flakes	Flake fragments	Fragments	Total
SMT	24	17	339	416	28	824
	2.91%	2.06%	41.14%	50.49%	3.40	54.7%
PAN	20	4	327	283	17	651
	3.07%	0.62%	50.23%	43.47%	2.61%	43.2%
MUSCH	2	2	16	11		31
	6.45%	6.45%	51.61%	35.49%		2.1%
Total	46	23	682	710	45	1506
	3.06%	1.53%	45.28%	47.14%	2.99%	100%



**Fig. 8.** Map of outcrop showing chert procurement areas within a 10- and 30-km radius, documented for level P of Abric Romani. Overlay of the digital terrain elevation model (1:50,000) with the digitization of geological formations with chert.

hunting strategies: selective ambush hunting for horses; and encounters or non-selective ambush hunting for catching red deer. Unfortunately, this disparity cannot be tested in level P due to the scarcity of red deer dental elements in the assemblage. The MNI was thus calculated based on appendicular elements. Consequently, has not been able to calculate the age of most of the red deer individuals identified in the assemblage. However, does note that prime adult horses were consistently selected as the preferred target.

In archaeological sites where one species dominates the assemblage, it is generally considered that they result from a specialized hunting strategy and that the contribution of other species was supplemental. In the sites of Jonzac, Les Padrelles, Pech de l'Aze IV, Roc de Marsal or Abri du Maras level 4.1 (Castel et al., 2017; Costamagno et al., 2006; Daujeard et al., 2019; Niven, 2013; Niven et al., 2012), the assemblages are dominated by reindeer remains, resulting from highly seasonal specialized hunting. The presence of horse and bison in these sites has been defined as a consequence of supplementary inputs; since they were locally available and not restricted by seasonal migrations. In sublevels Pa and Pb, the red deer is the best represented species (NISP, MNE and MNI), but does not dominate the assemblage, as indicated by the Shannon and Simpson index. The differences between red deer and horse cannot correspond to a scenario where horses supplemented to a subsistence strategy based on red deer hunting, and vice versa.

A possible explanation for the predominance of cranial remains and a low economic returns profile in horses elements is that these portions result from scavenging events (head and feet profile) (Trinkaus, 1989). Two strategies could be considered in this scenario: passive scavenging (Binford, 1981; Stiner, 1991), and active or confrontational scavenging (Bunn, 2001; O'Connell et al., 1988). The frequency and distribution of cut marks, which are mainly on long bone diaphysis (71.4%), joints with bone breakage marks and the low number of carnivore modifications found at Pa and Pb, indicate Neanderthals access to a large quantity of animal meat. Therefore, the passive scavenging scenario of elements abandoned by carnivores can be rejected. The other alternative is confrontational scavenging based on snatching prey from other predators. However, in assemblages with horse capture by large carnivores, especially lions, mortality profiles are dominated by the weakest animals, i.e., young and old specimens (Schaller, 1972). Stiner (1990) indicated that Mousterian sites with high proportions of scavenging showed anatomical profiles dominated by cranial remains of red deer and aurochs, with mortality profiles dominated by old individuals. The mortality profiles of sublevels Pa and Pb are dominated by prime adults, which rules out any secondary access to horse carcasses in these assemblages.

Although it is true that anatomical profiles are the best proxies for evaluating transport strategies, the results for archaeological assemblages can be ambiguous for different reasons. The differential survivorship of some elements (Marean and Cleghorn, 2003), which has already been dismissed; a low MNE (Faith and Gordon, 2007). In addition, the combination of singular events (Marín et al., 2017a). In addition, we can add the transport decisions of each individual hunting event, which could also result in variable anatomical profiles in places of consumption and deposition, such as, for example, the places in which the animals were obtained and the first carcasses were dismembered (Metcalfe and Jones, 1988; Monahan, 1998).

Other possible explanations for the divergence between deer and horse could be related to differences in animal transport strategies between the kill site and the rock-shelter. Transport strategies of animal carcasses in the upper levels of the sequence were discussed by Marín et al. (2017a). Following Faith and Gordon (2007), the results obtained indicated that the anatomical profiles

of all the weight size categories could be related to an unconstrained transport strategy, this is, the transport of all the elements of the skeleton. However, the comparison of the anatomical profiles of the levels of Abric Romaní with Hadza camps (Lupo, 2001), which generally show highly diversified types of transport, suggested that the assemblage results from mixed of transport events and various types of strategies, probably subject to different contingencies. However, in the rest of the levels, no substantial differences were observed between the different weight categories. In level P, when we examined the value of evenness with the result of the correlation between MNE and (S)FUI, following the proposal of Faith and Gordon (2007), were obtained conflicting results for both groups. These showed a positive relationship in the case of red deer and a negative relationship for horses, supporting the possibility of the existence of a reverse transport strategy for horses. In the assemblage of Pech de l'Aze IV, Niven (2013) Niven (2013) showed that there is a high representation of reindeer heads, which is, in some cases, similar to the value of upper and intermediate appendicular elements. She related this transport to the presence of fire inside the site and therefore with more efficient processing allowing for more regular transport of skulls. Although this could account for the strong presence of horse heads, it does not explain the reverse utility curve result of a lower presence of appendicular elements, nor the shortage of red deer cranial remains. Horse profiles from sublevels Pa and Pb are similar, although not equal, to the profiles expected in a kill/butchering site (Metcalfe and Jones, 1988). Enloe (2004) affirms that reverse utility curves in relation to bulk strategy values indicate the extraction of medium and high-utility elements from the kill site for later consumption in another place. The same anatomical profile and reverse utility curves have been observed in archaeological sites used as hunting camps or halts, such as the Mousterian sites of Gabasa (Blasco, 1997) and Moula-Gercy XV (Valensi et al., 2012), or the Magdalenian sites of Tureau des Gardes (Bridault, 1995) or l'Amas d'Étiolles (Bignon, 2006a). Thus, the anatomical profile observed for the horse could be the result of transport, processing, and intermediate consumption of less profitable elements inside Abric Romaní, after which the most profitable elements were transported to another aggregation site.

The differences of anatomical profiles observed between the two taxa could also be related to distinct uses of Abric Romaní as a refuge. In logistic territorial exploitation systems, the same place can be used at different moments for different purposes (Binford, 1982). Current hunter-gatherers groups develop different mobility strategies during their movements, which ultimately generate distinct occupation types (Bartram, 1993; Binford, 1980, 1978; Gamble and Boismier, 1991; Jones, 1983; Kent, 1987; Kroll and Price, 1991; O'Connell et al., 1992, 1988; Yellen, 1977). This diversity is also observed in the archaeological record of Eurasia. In most of research characterizing the logistic mobility of Neanderthal groups, this inference was made through the functionality of the archaeological sites present in a territory, with the fundamental dichotomy between long/short-term occupation sites (Boyle, 2000; Daujeard and Moncel, 2010; Delagnes and Rendu, 2011; Moncel et al., 2014; Niven et al., 2012; Patou-Mathis, 2000; Turq et al., 2017). It has thus been possible to identify sites used as long-term residential camps (Bar-Yosef et al., 1992; Carbonell, 2012; Daujeard, 2008; Daujeard and Moncel, 2010; Marín-Arroyo, 2013; Morin, 2012; Patou-Mathis, 2000; Real et al., 2018; Romandini et al., 2014; Soressi et al., 2008; Speth et al., 2012; Stiner, 2013; Villaverde et al., 2017), others as short-term camps (Daujeard, 2008; Daujeard and Moncel, 2010; Delagnes and Rendu, 2011; Marín-Arroyo, 2013; Niven et al., 2012; Patou-Mathis, 2000; Stiner, 2013; Valensi et al., 2012; Vallverdú et al., 2005), as well as special

purpose sites, such as kill sites or intermediated butchering sites (Rendu et al., 2012; Costamagno et al., 2006).

In general, it is assumed that long-term occupations generated high percentages of lithic and faunal remains, whereas short-term occupations present low quantities of remains (Bicho and Cascalheira, 2018; Costamagno et al., 2006; Daujeard and Moncel, 2010; Kuntz et al., 2016; Maroto et al., 1996; Moncel et al., 2008; Stiner, 1991; Stringer et al., 2000; Valensi et al., 2012; Vaquero and Pastó, 2001; Villaverde et al., 1996). Besides, long-term occupations usually comprise extensive occupation surfaces and diversified provisioning strategies during a long period of a season (Audouze, 2010; Bicho and Cascalheira, 2018). Conversely, short-term occupations have small surfaces, restricted provisioning strategies and multi-seasonal occupations (Costamagno et al., 2006; Martínez-Moreno et al., 2004; Niven et al., 2012; Vallverdú et al., 2005; Villaverde et al., 2017). Following these principles, the faunal assemblages of sublevels Pa and Pb correspond to short-term occupation models. Tooth microwear analysis on horse and red deer dental remains also point to of short occupations for levels Pa and Pb.

Data of Raw material procurement in level P show that the main type of chert comes from 16 km away (SMT), a distance considered as the limit of the foraging radius of the Abric Romaní Neanderthals. However, the distance of 24 km obtained for PAN chert, representing 43% of the assemblage, indicates that Neanderthals at Abric Romaní manage the logistic territory differently at different times (Gómez de Soler, 2016). The first inference of the raw material procurement of the assemblage is the unidirectionality of the mobility pattern. All the raw materials have a north-western origin. Therefore, the south-eastern origin, i.e., the coastal route, can be rejected. The second inference is that the high percentage of PAN chert and the catchment area indicate a different occupation pattern to a long-term residential camp. Binford (1982) defined three mobility patterns: 1) half-radius continuous pattern; 2) complete-radius leapfrog pattern; 3) point-to-point pattern. Has been discard the third scenario because it is typical of low biomass environments. The first scenario would be related to unidirectional mobility, in which movement from one point to another would be related to a logistic radius, as was observed during the deposition of the PAN chert. A logistic catchment radius was inferred for this lithotype, indicating occupation events associated with a logistic territory.

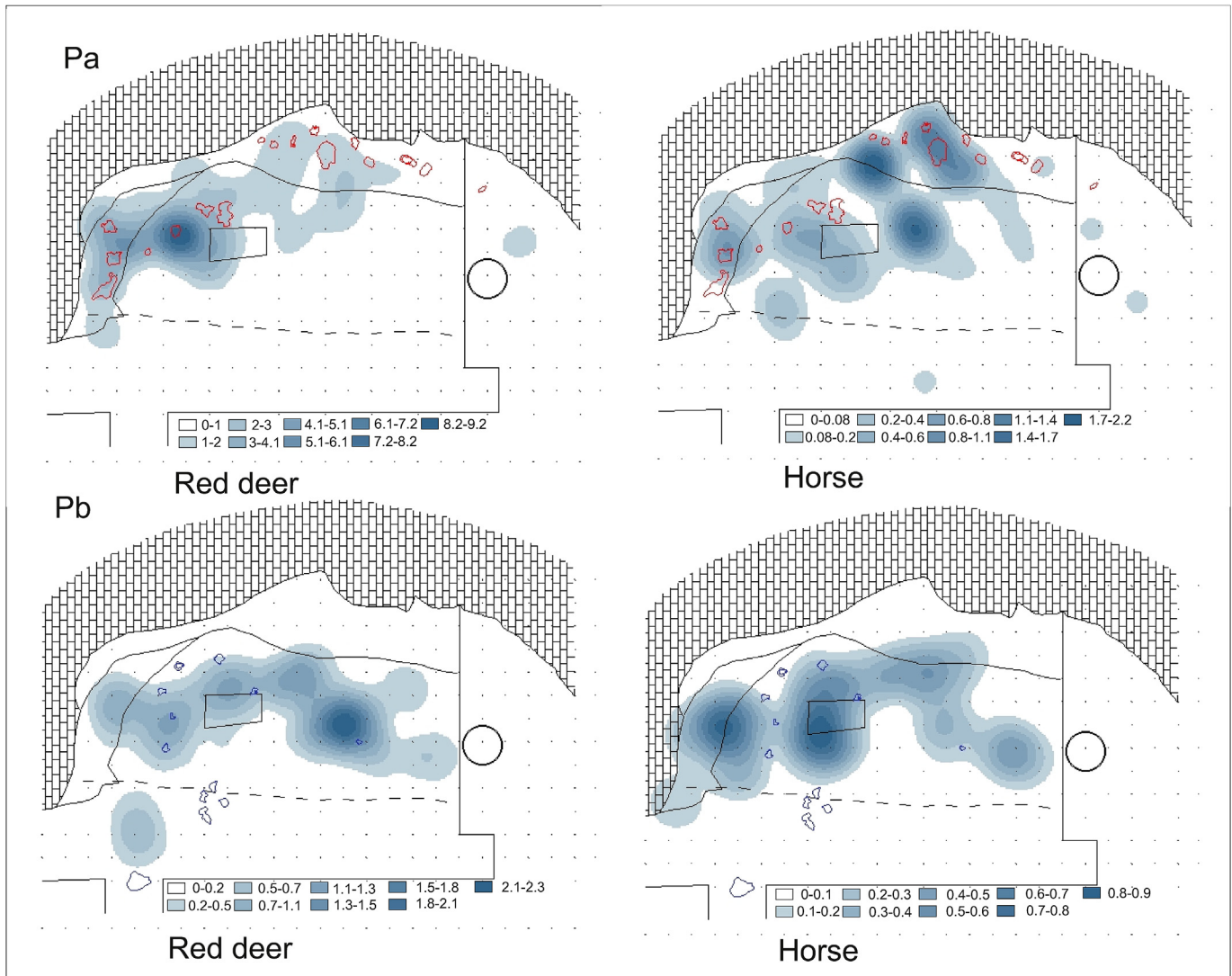
In other levels of the Abric Romaní sequence, it was possible to differentiate between long-term occupations events (e.g., levels J, M, Oa) and short-term or non-residential occupations events (e.g., levels I, H, K, L) (Carbonell, 2012, 2002; Carbonell and Vaquero, 1998; Vallverdú et al., 2012a, 2010; 2005; Vaquero et al., 2012). The main difference between these two occupation models throughout the sequence is that specific activity areas could be identified and differentiated in short-term occupation events (Vallverdú et al., 2005). Conversely, in levels resulting from long-term events, the different activity areas are superposed and cannot be differentiated from each other (Vaquero et al., 2012). However, it is not always simple to distinguish between long or short occupations in the archaeological record, since: "the locations preferred for residential camps can be expected to yield a most complex mix of archaeological remains since they were commonly also utilized logistically when the residential camps were elsewhere" (Binford, 1982:15). These occupation differences could be related to seasonal changes and with the availability of resources in the environment (Bartram, 1993; Binford, 1978; Kelly, 2013, 1983; Kroll and Price, 1991; O'Connell et al., 1992). From a taphonomic point of view, the butchering process usually show similar models in both occupations, characterized by secondary butchering

exploitation and followed by the consumption of at least part of the carcasses (Chabai et al., 2006). Besides, in the case of specialized porpoise sites, as at intermediate butchering sites, exploitation of the skeletal segment for a food input and output in the same place could be observed.

The seasonal availability of most of the resources involves temporal and spatial limitations which restrict hunter-gatherer behaviour, and are often overcome through mobility over the territory (Binford, 1980; Kelly, 1992; Speth, 1987; Speth and Spielmann, 1983). The seasonal behaviour of many hunted species determined Neanderthals mobility, and, along with the predictability of some prey movements, allowed for the use of certain sites throughout generations (e.g., Adler et al., 2006; Rivals et al., 2009; Daujeard and Moncel, 2010; Rendu, 2010; Niven et al., 2012; Stiner, 2013). The dental remains of young red deer and horse individuals in sublevels Pa and Pb are scarce, but nonetheless show that the capture season of these species do not coincide. This could be considered as an additional sign that the site was used at two periods of the year depending on the species to be exploited. Tooth microwear analysis confirms the identification of seasonality based on red deer dental eruption, indicating a season of death in the autumn or winter. In addition, our results indicate that level P is a result of multiseason occupations, which indicate short-term occupation events, as observed for the assemblages of Jonzac (Niven et al., 2012) or Abrigo de la Quebrada (Real et al., 2018). Thus, although the evidence is not individually determinant, through the sum of all of them yields more robust inferences.

The distribution of remains in sublevels Pa and Pb enables us to identify different accumulations in which the materials are concentrated around combustion structures. In the Kernell density maps, it is possible to observe that there is no overlapping between the areas of major concentrations of horse and red deer remains in either sublevel (Fig. 9). Besides, in the case of horse remains, the high concentration areas coincide with zones where anatomical refits were found. The Ripley's K test suggests that in both sublevels, horses are grouped at short distances, around 50 cm, and then regularly dispersed. The red deer remains show regular dispersion in the rock shelter for both sublevels (Fig. 10). The multitype cross function K allows us to assume spatial independence between both taxa in sublevel Pa, and a regular distribution relationship between them in sublevel Pb for distances of more than 150 cm (Figs. 11 and 12). The spatial autocorrelation Moran's I test, applied over the taxonomic representation index, confirms the pattern of the Kernell density maps. The variation in the spatial representation of taxonomically identified red deer and horse remains (Figs. C1–C3) and the relative sum ratios of both taxa (Fig. 13) showed that the significant statistical concentration areas for high and low values do not overlap in space in either sublevel.

The domestic activity areas of hunter-gatherer groups are characterized by the concentration of faunal remains, commonly reduced to small fragments that remain in the place they were produced, normally associated with hearths (Binford, 1978; Enloe et al., 1994; Gifford, 1980; Schiffer, 1983). The regular dispersion of faunal remains, in this case, could be related to the distribution of hearths on the surface. However, the spatial statistic results for sublevel Pa point to the accumulation of spatially independent horse and red deer remains. Red deer remains were found specially in accumulations 1 and 2, and horse remains in accumulations 3 and 4 (Figs. 9 and 13). For sublevel Pb, a major spatial independence exists between the red deer and horse remains, although the high-density accumulations are also independent (Figs. 9 and 13). Therefore, the distribution of faunal remains, characterized by the segregation of red deer and horses, could be related to short-term specialized occupations in search of each taxon. Otherwise, if it's take into account the results of the redistribution index (Jones,



**Fig. 9.** Kernell density maps of red deer and horse in sublevels Pa and Pb. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

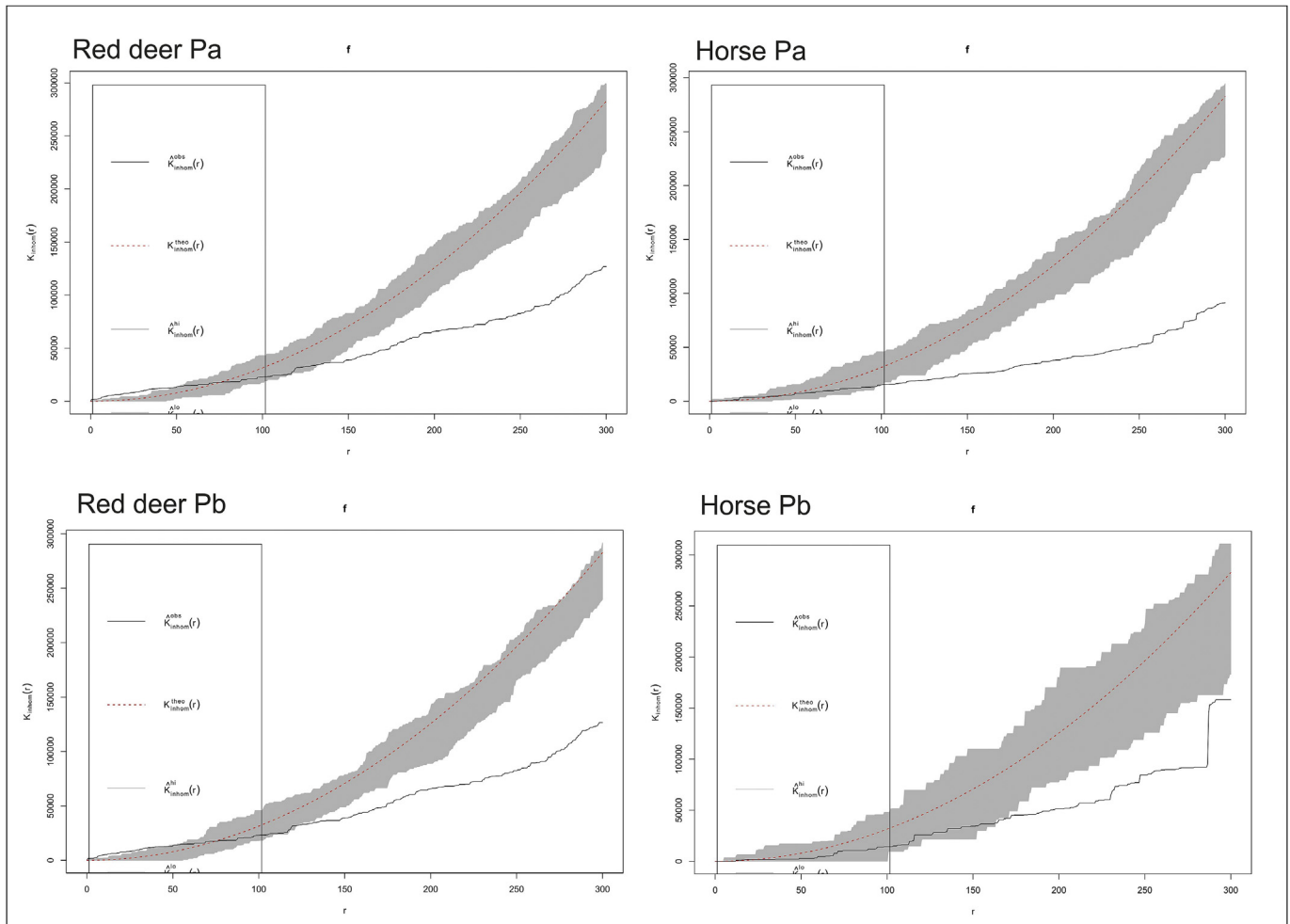
1983) for the activity areas, in sublevel Pa a low or almost null repartition of animal carcasses was found.

The indicators of the use of the site as a hunting camp for horse exploitation are multiplied if we sum up the differences between both taxa. The registered elements and their economic values show a negative correlation. This could be interpreted as the possible exportation of anatomical segments to another part of the territory. Using principal component analysis (PCA), we compared the anatomical profiles from red deer and horses of sublevels Pa and Pb with data from present-day hunter-gatherers and archaeological assemblages. The data from modern camps are from Binford (1978) for Nunamiut residential and hunting camps, and Domínguez-Solera (2017) for the Inuit hunting camp (Camp Jakob Josefsen) from West Greenland. The hunted and transported animals were caribous in both examples. The data from archaeological sites come from French Magdalenian sites, the residential campsite of Pincevent (Bignon et al., 2006) and Moulin-Neuf (Costamagno, 2000) and the hunting campsite of Tureau des Gardes (Bridault, 1995). Were selected these examples because the transported species were reindeer and horse, which allows us to compare them with the level P assemblages. The results indicate that red deer

anatomical profiles are similar in contemporary and archaeological residential camps. This shows that they are related to assemblages where the input of the elements is maximized according to their utility, mainly upper and intermediate appendicular elements. On the other hand, horse assemblages are similar to the values from hunting camps, especially in sublevel Pb (Fig. 14). This shows that the anatomical profiles of horses are the result of the extraction of the richest elements of the site. Therefore, the position of the anatomical profiles of red deer and horse with the PCA indicates opposing situations. A link was established between the archaeological sites of Turea des Gardes and Pincevent, following Bignon (2006b), in which horse carcasses were transported from the first to the second. Therefore, its opposite position within the PCA corresponds to sites with a different function. The case of Abric Romaní indicates two different uses of the same site depending on the species.

In Nunamiut hunting camps, Binford described the initial processing and consumption of the killed animals and a secondary transport from the hunting camp to a different aggregation place. Only the less useful anatomical parts were consumed, so the resulting profile is contrary to the bulk and unbiased strategies





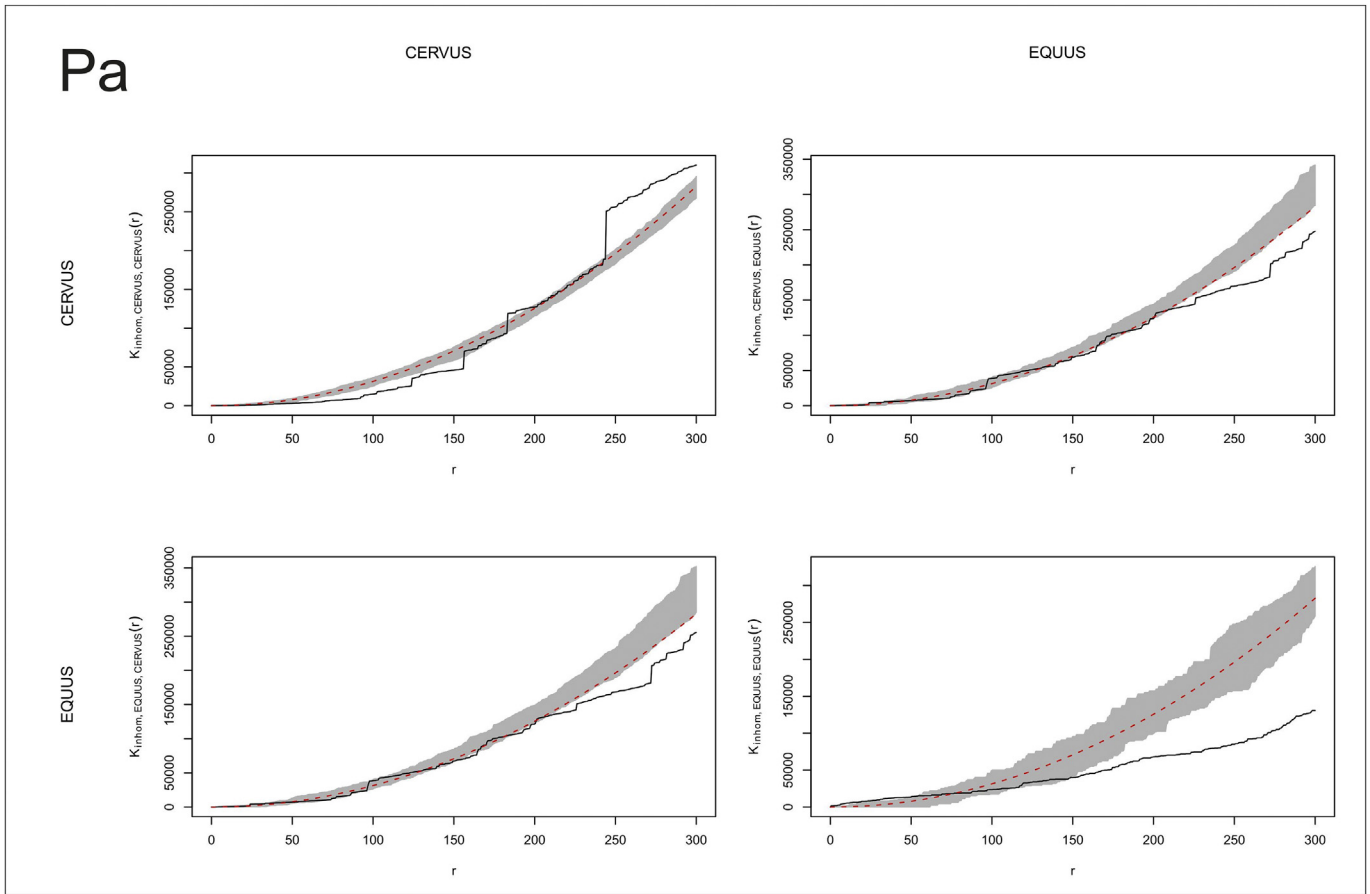
**Fig. 10.** Ripley's K test distribution of red deer and horse remains in sublevels Pa and Pb. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Binford, 1978). This pattern has also been observed in archaeological sites defined as hunting camps, such as the Mousterian site of Moulaguercy (Valensi et al., 2012), the previously mentioned Tureau des Gardes (Bridault, 1995) or the Magdalenian hunting camp of L'amas d'Etiolles (Bignon, 2006b). Therefore, the anatomical profile observed for horses could be the result of transport, processing and intermediate consumption of the less profitable elements in Abric Romaní. After that, the most useful elements were transported to another aggregation place. However, the absence of cranial elements in sublevel Pa and the abundance of metatarsals in sublevel Pb, do not strictly correspond to expectations for this type of assemblage. Therefore, cannot rule out possible events of transport and abandonment of horse remains that do not correspond to the first scenario described.

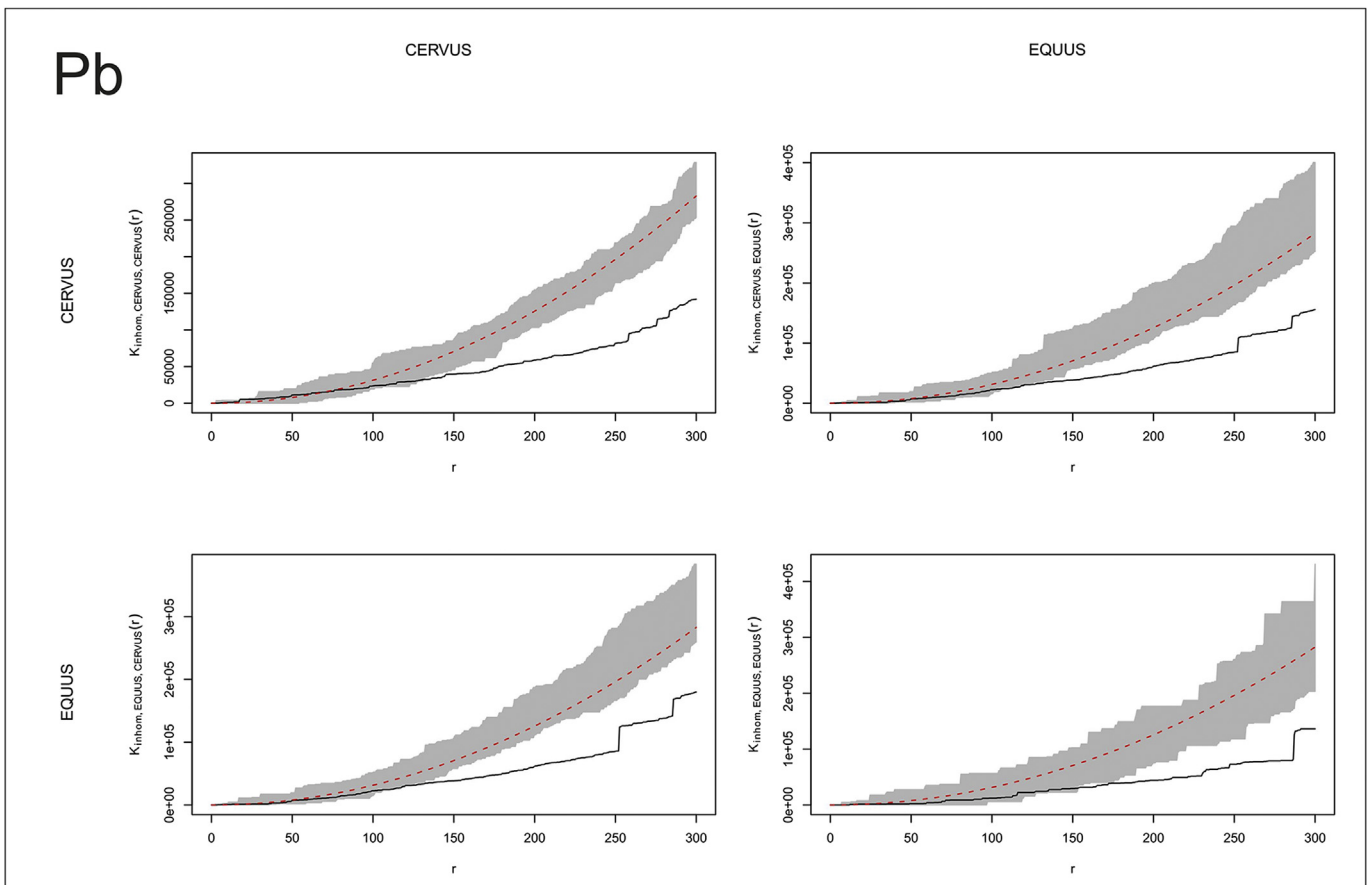
Hunting camps are usually located in places previously used as residential campsites (Binford, 1978). These places offer additional incentives for use as stopover places, such as raw material accumulations or provisions, reusable structures, such as hearths, and accumulated dry wood or deteriorated wooden structures. The best locations combine all the aforementioned features with access to a view of a vast area for searching for prey (Binford, 1978). The Abric Romaní meets these requirements for use as a preferential location for different activities. The use of the rock shelter as a residential camp has already been broadly defined (Carbonell, 2012, 2002; Vallverdú et al., 2012a, 2005; Vaquero et al., 2017), the reuse or

recycling of abandoned materials has also been documented, especially for the lithic industry (Vaquero et al., 2017, 2015). In addition, reused combustion structures and unburnt wood casts interpreted as firewood provisions for use as fuel have been recovered (Allué et al., 2017; Carrancho et al., 2016; Solé et al., 2013; Vallverdú et al., 2012a, 2010, 2005).

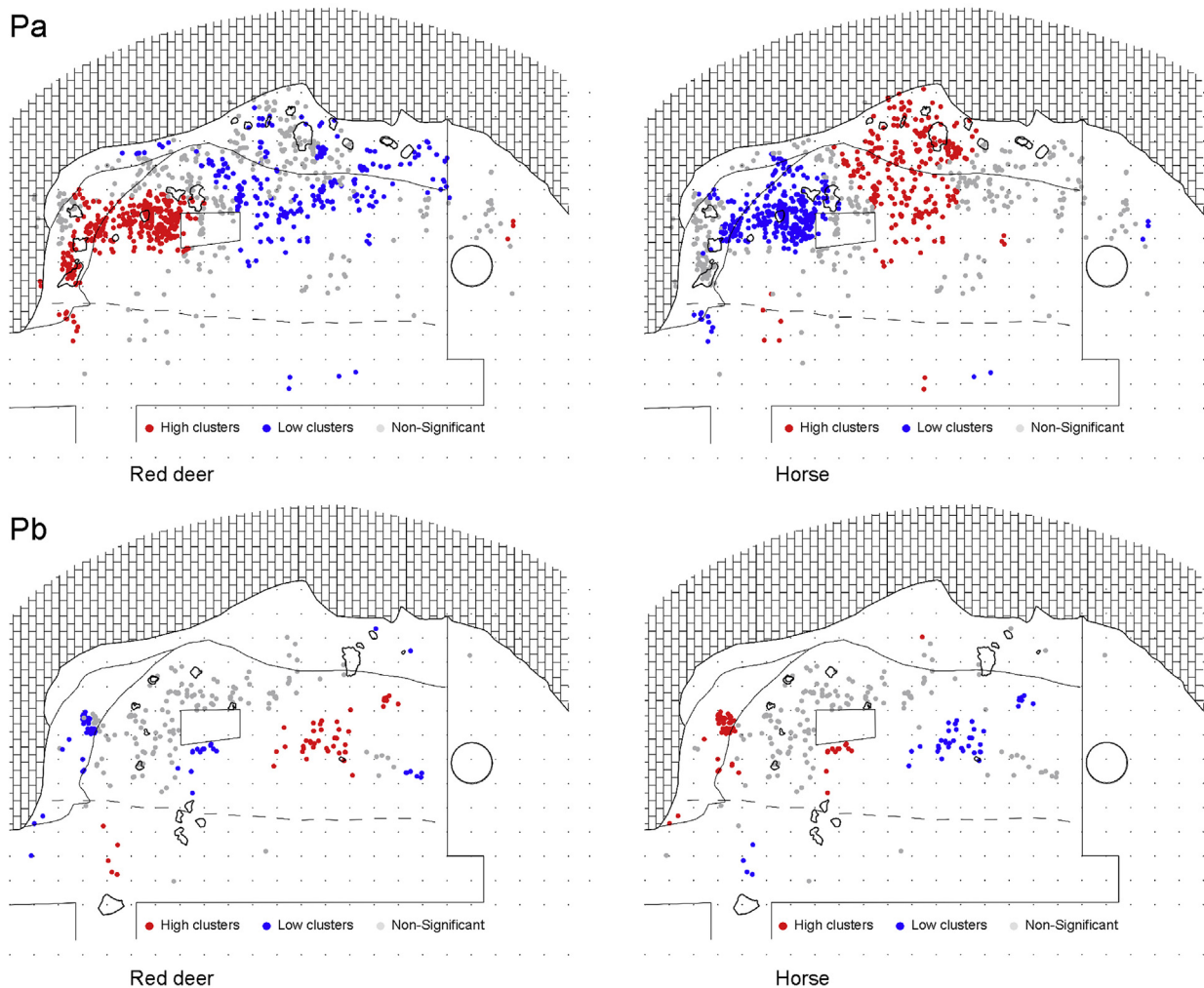
The environment exploitation system developed by Neanderthals in Abric Romaní has previously been defined as a logistic model (Vallverdú et al., 2005) where the mobility of groups was directly related to the exploitation of hunting resources. The results obtained for sublevels Pa and Pb indicate that two different types of occupations existed in a logistic mobility model. Raw material analysis supported a logistic territory of catchment for these groups. The two types of occupations were short-term occupations events, i.e., a transitory campsite with highly selective transport of red deer carcasses and a hunting camp occupation by specialized task groups for hunting horses, possibly to supply a larger residential camp. In this case, the site functioned as an intermediate butchering site. An alternative model would imply the abandonment and waste of the most nutritionally productive parts of the carcasses in the kill site, which contradicts all optimal foraging models. Finally, we must add that both types of occupation were carried out during very specific times of the year. Together with spatial distribution analysis which indicate two main areas of accumulation for each species, the result indicates that the supply of



**Fig. 11.** The multitype crossed function  $K$  of the distribution of red deer and horse remains in sublevel Pa. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 12.** The multitype crossed function  $K$  of the distribution of red deer and horse remains in sublevel Pb. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



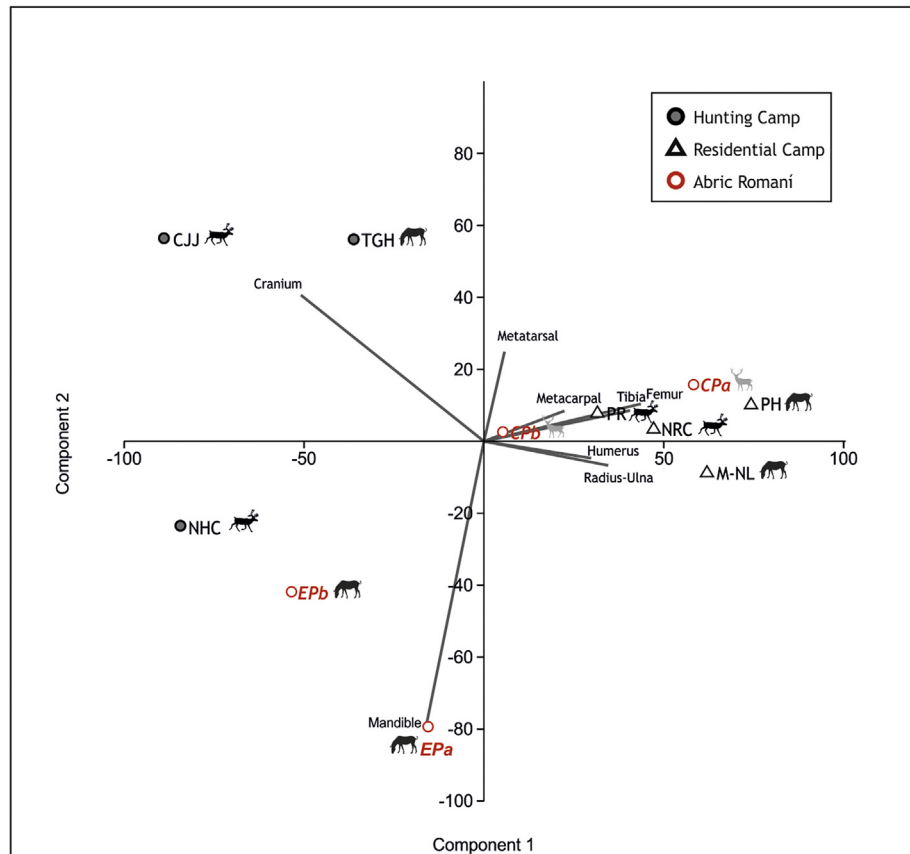
**Fig. 13.** Spatial distribution of high and low clusters associated with the ratio of Red deer and Horse to the sum of Red deer and Horse for each sublevel. High clusters (red) are areas of statistically significant high proportions of the taxon under consideration; low clusters (blue) are areas where the proportion of the taxon under consideration is statistically significantly low; grey represents nonsignificant areas. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

deer and horses by Neanderthals were mainly separate in time and space in the Abric Romaní.

The differential use of a place for distinct activities is typical of groups of collectors with logistic mobility types (Binford, 1980; Kelly, 1992). This strategy can also be identified by comparing the different uses of the rock shelter throughout the sequence. The site served as a referential site for Neanderthals for almost 35,000 years, for both high and low intensity occupations (Bargalló et al., 2016; Carbonell, 2012; Fernández-Laso et al., 2010; Gabucio et al., 2018b, 2014; Rosell et al., 2012a, 2012b; Vallverdú et al., 2005; Vaquero et al., 2012). The most intensive occupation events are related to residential camps as a result of moments of aggregation or related to more durable occupations (Fernández-Laso et al., 2010; Rosell et al., 2012a, 2012b). During short-term occupations, apart from the use as an intermediate butchering site identified in level P, other specific works have been documented. For example, at level I (short-term logistical occupations; Vallverdú et al., 2005), young red deer individuals around one month old were specifically exploited, possibly to retrieve their skins for specific uses (Marín et al., 2017b). In addition, some repetitive ethological behaviours show that certain species were predictable and spatially restricted targets, which means that particular sites could be systematically

reused. For example, seasonal migratory movements of reindeer through the same corridors (Niven et al., 2012) or the daily displacement along established pathways at precise times of day with the presence of new-borns in red deer female groups (Varin, 1980). For horses, the daily need for water, especially during the summer, restricts their movements around water spring and hydric resources (Berger, 1986; Burke, 2002).

The logistic mobility strategy has been related to a radiating type of displacement (Mortensen, 1972), characterized by the use of basecamp from which specialized task groups generate small temporary camps during the search for particular resources. This could be the mobility strategy of Neanderthals during the formation of level P, occupying the rock-shelter for specialized tasks (horse hunting), and as a temporary residential camp (deposition of the red deer). This type of mobility is not rare in the European Middle Palaeolithic record. Although there are variations, the logistic model is the most widely accepted for Neanderthal groups (Delagnes and Rendu, 2011; Martínez-Moreno et al., 2004; Moncel et al., 2014; Patou-Mathis, 2000; Vallverdú et al., 2005; Zilhão and Villaverde, 2008). The results obtained from the study of level P situate the Neanderthal groups of Abric Romaní in a regional framework in which their movements depended on the availability



**Fig. 14.** Principal component analysis of the anatomical profiles of high survival elements of horses and red deer in sublevels Pa and Pb (EPa, CPa, EPb, CPb), residential camps (NRC) and hunting camp of the Nunamiut and Inuit (CJJ; NHC) (Binford, 1978; Domínguez-Solera, 2017) and the assemblages of the Magdalenian sites of Pincevent (PH; PR), Moilin-Neuf (M-NL) and Tureau des Gardes (TGH) (Bignon et al., 2006; Bridault, 1995; Costamagno, 2000). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

of large ungulates. These displacements seem to have followed known routes, as indicated by the clear unidirectionality marked out by lithic raw material procurement and the intense reuse of the archaeological site as a place of activity.

## 6. Conclusions

Our results indicate that Neanderthal groups in level P developed two main types of low-intensity occupations: 1) a transitional residential camp; 2) a specialized hunting camp or intermediate butchering site. These occupations were closely connected to the hunting of red deer or horses. This points to a logistic mobility model close related to the exploitation of hunting resources. The seasonality and migratory behaviour approximations in this work sometimes allowed us to reaffirm the existence of differences between red deer and horses. Red deer capture was non-selective in terms of age, with transport of the anatomical parts of carcasses with a positive nutritional value to the rock shelter. On the other hand, horse hunting preferentially focused on prime adult individuals. The hunted animals were transported to the rock-shelter, where possibly after the consumption of the less useful parts, the rest was transported to a different place of aggregation. The differential use of the same place in a specialized way to obtain specific resources is characteristic of logistic behaviour.

## CRedit authorship contribution statement

**Juan Marín:** Conceptualization, Methodology, Software,

Investigation, Writing - original draft. **Antonio Rodríguez-Hidalgo:** Conceptualization, Methodology, Investigation, Writing - review & editing, Supervision. **Josep Vallverdú:** Investigation, Data curation. **Bruno Gómez de Soler:** Investigation, Data curation. **Florent Rivals:** Investigation, Data curation. **José Ramón Rabuñal:** Investigation, Data curation. **Antonio Pineda:** Investigation. **María Gema Chacón:** Investigation. **Eudald Carbonell:** Investigation. **Palmira Saladié:** Conceptualization, Methodology, Investigation, Writing - review & editing, Supervision.

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## Appendice A

**Table 1**  
NISP and MNE of faunal remains of sublevel Pa by taxa and anatomical elements.

NISP/MNE	<i>Cervus elaphus</i>	<i>Equus ferus</i>	<i>Bos primigenius</i>	<i>Canis lupus</i>	<i>Oryctolagus cuniculus</i>	Medium sized	Large size	Indet
Antler	1/1							
Cranium	1/1		1/1			1/1		
Mandible	3/1	8/5	5/1	1/1	2/2	1/1	2/1	
Isolated teeth	3/-	13/-	1/-		1/-		1/-	
Hyoid	1/1	1/1						
Vertebra						3/2	1/1	
Scapula	1/1							
Coxal	1/1							
Rib	4/2	1/1				2/1	9/2	
Humerus	21/7	4/1	6/2		1/1			
Radius + ulna	21/7	4/2	2/1		1/1			
Carpal		5/5						
Metacarpal	16/3	3/2	2/2					
Femur	24/5	4/1	1/1		2/2	1/1		
Tibia	56/12	12/2	7/2		2/1			
Tarsal								
Metatarsal	15/4	2/1	4/1					
Metapodial	2/1							
Sesamoid		1/1						
Phalanx I		1/1						
Phalanx II		1/1						
Phalanx III		1/1						
Long bone						181/-	57/-	
Flat bone						26/-	15/-	
Indeterminate						11/-	10/-	388/-

**Table 2**  
NISP and MNE of faunal remains of sublevel Pb by taxa and anatomical elements.

NISP/MNE	<i>Cervus elaphus</i>	<i>Equus ferus</i>	<i>Bos primigenius</i>	<i>Oryctolagus cuniculus</i>	Medium sized	Large size	Indet
Antler	1/1						
Cranium	/2	3/1				1/1	
Mandible	7/3	4/3	2/1				
Isolated teeth	2/-	8/-					
Vertebra	1/1				2/2		
Scapula					1/1	1/1	
Coxal			1/1				
Rib		2/1			4/1	1/1	
Humerus	7/2	2/1					
Radius + ulna	8/3	1/1					
Carpal			1/1				
Metacarpal	2/1						
Femur	6/4	2/1	1/1				
Tibia	15/7	4/1	1/1	1/1			
Tarsal							
Metatarsal	5/2	3/2					
Long bone					44/-	13/-	
Flat bone					20/-	3/-	
Indeterminate					2/-	1/-	71/-

**Table 3**  
MAU and %MAU of red deer and horse of sublevel Pa by anatomical elements.

Pa Element	<i>Cervus elaphus</i>		<i>Equus ferus</i>	
	MAU	%MAU	MAU	%MAU
Antler	0,5	8,3		
Cranium	1	16,7	0	0
Mandible	0,5	8,3	2,5	100
Hyoid	1	16,7	1	40
Vertebrae	0	0	0	0
Scapula	0,5	8,3	0	0
Coxal	0,5	8,3	0	0
Rib	0,07	1,2	0,03	1,4
Humerus	3,5	58,3	0,5	20
Radius-Ulna	3,5	58,3	1	40
Carpal	0	0	0,3	13,3
Metacarpal	1,5	25	1	40
Femur	2,5	41,7	0,5	20
Tibiae	6	100	1	40
Tarsal	0,08	1,4	0,08	3,3
Metatarsal	2	33,3	0,5	20
Sesamoid	0	0	0,04	1,4
Phalanx I	0	0	0,25	10
Phalanx II	0	0	0,25	10
Phalanx III	0	0	0,25	10

**Table 4**  
MAU and %MAU of red deer and horse of sublevel Pb by anatomical elements.

Pb Element	<i>Cervus elaphus</i>		<i>Equus ferus</i>	
	MAU	%MAU	MAU	%MAU
Antler	0,5	14,2	0	0
Cranium	2	57,1	1	66,7
Mandible	1,5	42,8	1,5	100
Vertebrae	0,03	0,92	0	0
Scapula	0	0	0	0
Rib	0	0	0,03	2,3
Humerus	1	28,5	0,5	33,3
Radius-Ulna	1,5	42,8	0,5	33,3
Metacarpal	0,5	14,2	0	0
Femur	2	57,1	0,5	33,3
Tibiae	3,5	100	0,5	33,3
Metatarsal	1	28,5	1	66,7

## Appendix B

**Table 1**  
Calculations of the chert abundance ratio within a 30-km radius. Fm. geological formation; tEV. total exposed volume; OI. occurrence index; OET. outcrop exposed thickness; EV. exposed volume; CC. chert content; CAR. chert abundance ratio. SER. chert type Sierra; MUSCH. Muschelkalk chert type; MED. Mediona chert type; PAN. Panadella chert type; SMT. St. Martí de Tous chert type; ALE. Ca l'Alemanya chert type; SAL. Cal Salvat chert type.

Chert type	Fm.	Area (km <sup>2</sup> )	Outcrops	Fm. thickness (km)	tEV (km)	OI (%)	OET (km)	EV (km <sup>3</sup> )	CC (km <sup>3</sup> )	CAR (km <sup>3</sup> )	% Chert in Fm.	% in a 30 km radius			
<b>SER</b>	<b>Serie la Guixera</b>	22.20	Canaletes	<b>.8000</b>	<b>17.76</b>	<b>.1000</b>	<b>.0040</b>	<b>.0888</b>	<b>.0004</b>	<b>.0089</b>	<b>.0500</b>	<b>29.27</b>			
	<b>Sta. Càndia</b>	16.30	Colomines	.0800	1.3040	.0500	.0040	.0652	.0002	.0033	.2500				
<b>MUSCH</b>	<b>Average Muschelkalk</b>	62.60	St. Magí	.0450	.7335	.0500	.0030	.0489	.0002	.0024	.3333				
			Brufaganya												
			La Serra	.1000	1.630	.0500	.0030	.0489	.0002	.0024	.1500				
<b>MUSCH</b>	<b>Average Muschelkalk</b>	62.60	sup.	.0850	5.3210	.0500	.0030	.1878	.0002	.0094	.1765	<b>8.96</b>			
			inf.	.0700	4.3820	.0500	.0030	.1878	.0002	.0094	.2143				
<b>MED</b>	<b>Average Mediona</b>	.1000		<b>.0775</b>	<b>4.8515</b>	<b>.0500</b>	<b>.0030</b>	<b>.1878</b>	<b>.0002</b>	<b>.0094</b>	<b>.1935</b>	<b>30.96</b>			
<b>PAN</b>	<b>Mediona</b>	.1000	Mediona	<b>.0200</b>	<b>.0020</b>	<b>.0500</b>	<b>.0020</b>	<b>.0002</b>	<b>.0001</b>	<b>.0000</b>	<b>.5000</b>	<b>.03</b>			
<b>PAN</b>	<b>Montmaneu</b>	.2400	Panadella	<b>.0500</b>	<b>.0120</b>	<b>.1500</b>	<b>.0035</b>	<b>.0008</b>	<b>.0005</b>	<b>.0001</b>	<b>1.0500</b>	<b>.42</b>			
<b>SMT</b>	<b>St. Genís</b>	5.600	Cal Calaf 1	.1000	.5600	.5500	.0020	.0112	.0011	.0062	1.1000				
			Cal Calaf 2	.1000	.5600	.5500	.0020	.0112	.0011	.0062	1.1000				
			Guinardera	.0800	.4480	.1500	.0050	.0280	.0008	.0042	.9375				
			Cal Perdut 1	.0800	.4480	.2500	.0050	.0280	.0013	.0070	1.5625				
			Cal Perdut 3	.0800	.4480	.1000	.0030	.0168	.0003	.0017	.3750				
			Guinardera 2	.0800	.4480	.1500	.0050	.0280	.0008	.0042	.9375				
			Cal Perdut 4	.0800	.4480	.1000	.0030	.0168	.0003	.0017	.3750				
			Filloi	.0100	.0560	.0800	.0020	.0112	.0002	.0009	1.6000				
			El Serral	.1000	.5600	.0800	.0020	.0112	.0002	.0009	.1600				
			Cal Perdut 2	.0800	.4480	.1000	.0020	.0112	.0002	.0011	.2500				
			<b>Average</b>	<b>.0807</b>	<b>.4517</b>	<b>.2487</b>	<b>.0037</b>	<b>.0207</b>	<b>.0009</b>	<b>.0052</b>	<b>1.1406</b>	<b>16.99</b>			
			<b>ALE</b>	<b>Bosc d'en Borràs</b>	1.790	Ca l'Alemanya	<b>.1700</b>	<b>.3043</b>	<b>.5500</b>	<b>.0020</b>	<b>.0036</b>	<b>.0011</b>	<b>.0020</b>	<b>.6471</b>	<b>6.49</b>
			<b>SAL</b>	<b>Valldepres</b>	1.580	Montclar	.0350	.0553	.3500	.0050	.0079	.0018	.0028	5.0000	
Valldepres	.0100	.0158				.1500	.0040	.0063	.0006	.0009	6.0000				
Cal Salvat	.0580	.0916				.3500	.0050	.0079	.0018	.0028	3.0172				
<b>Average</b>	<b>.0343</b>	<b>.0542</b>	<b>.2833</b>	<b>.0047</b>	<b>.0074</b>	<b>.0013</b>	<b>.0021</b>	<b>.0028</b>	<b>3.8511</b>	<b>6.89</b>					
<b>TOTAL</b>				<b>.0343</b>	<b>.0542</b>	<b>.2833</b>	<b>.0047</b>	<b>.0074</b>	<b>.0013</b>	<b>.0021</b>	<b>3.8511</b>	<b>100%</b>			

Appendice C

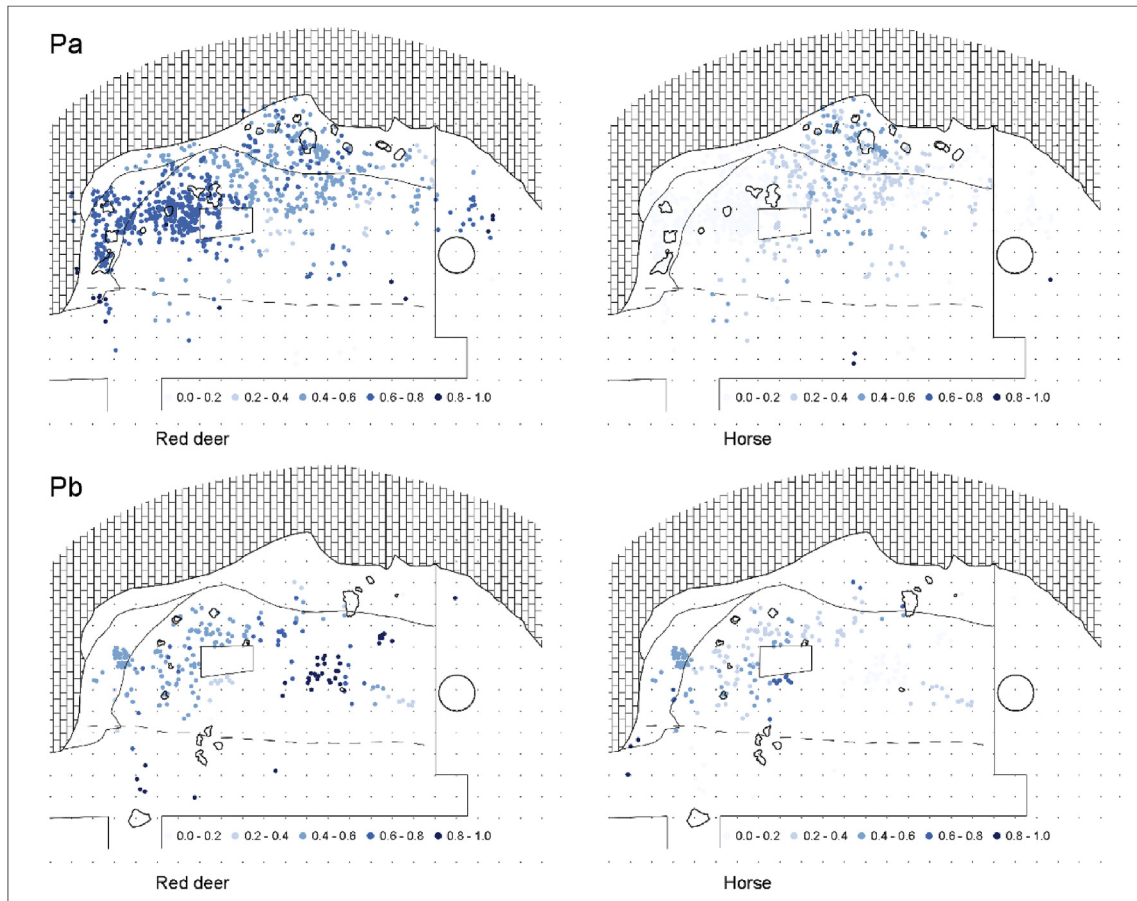
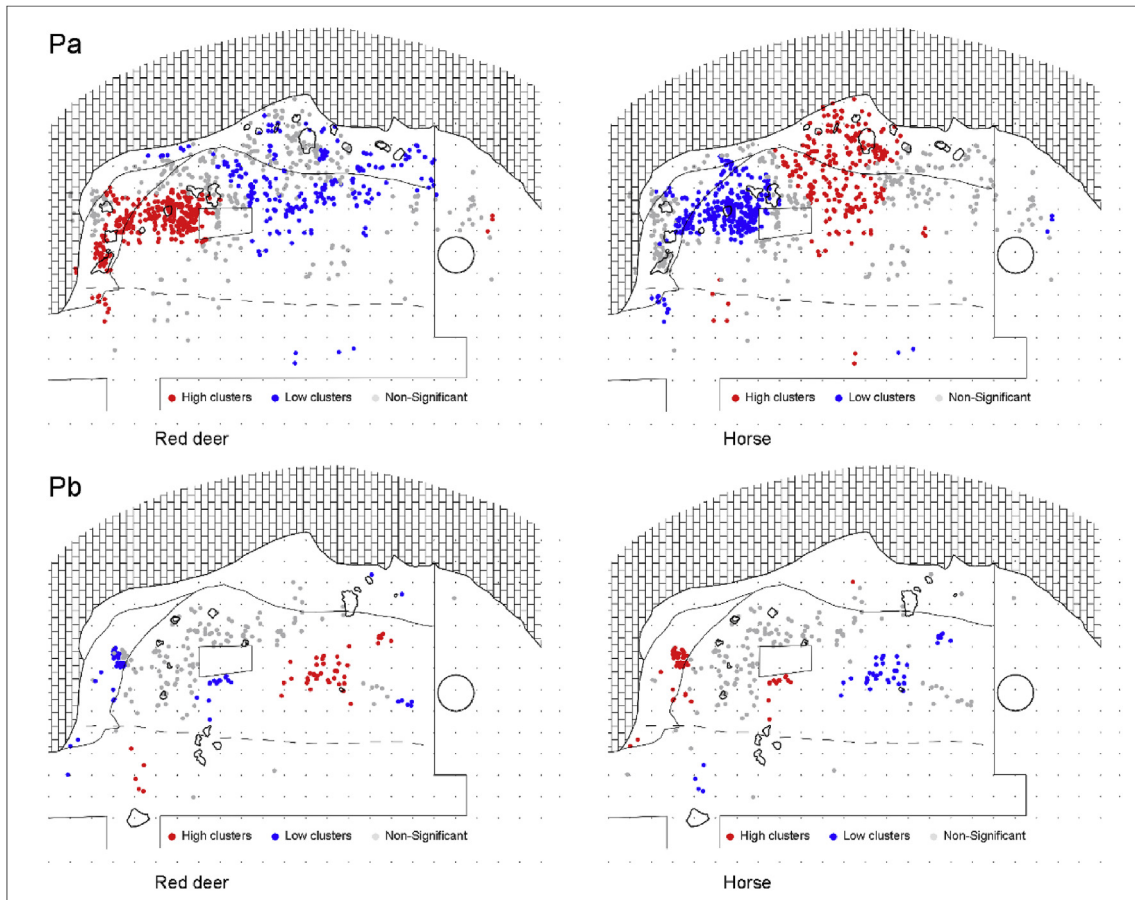
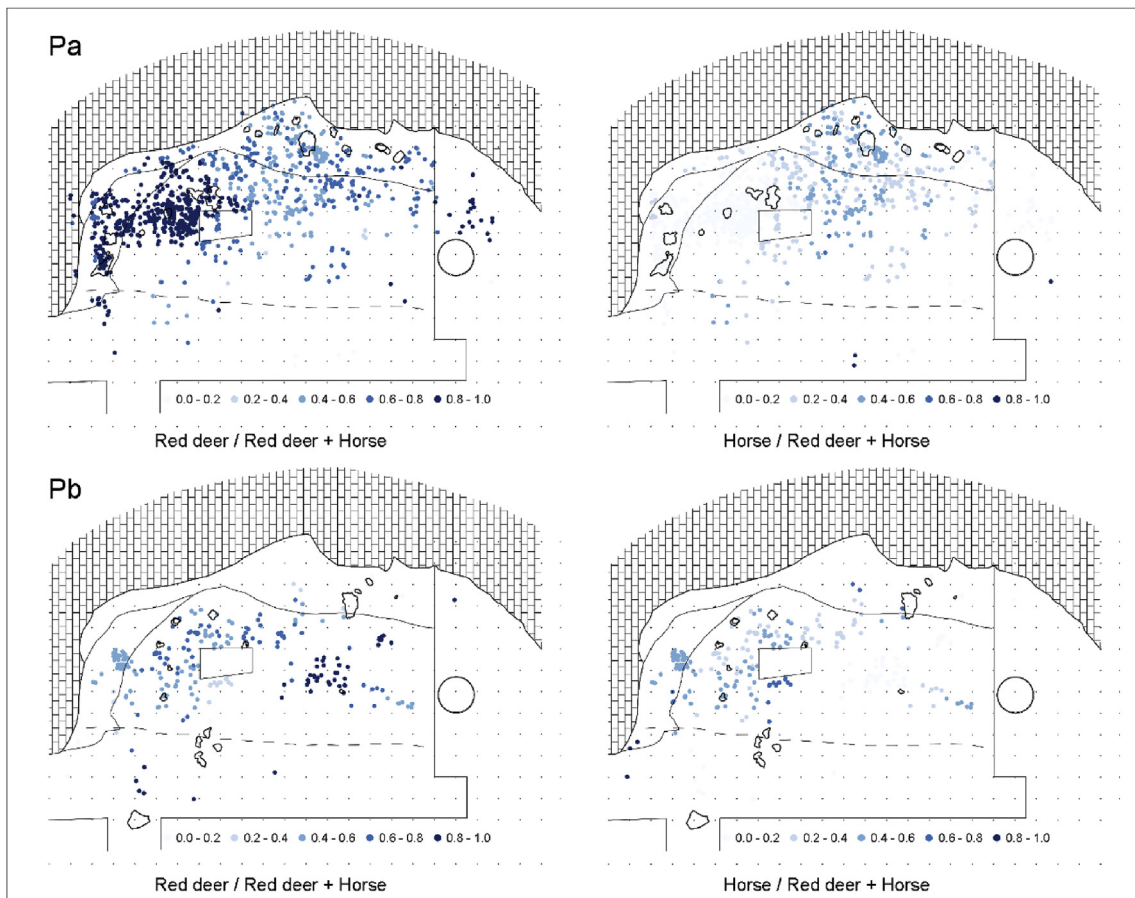


Fig. 1. Spatial distribution of the relative frequency of Red deer and Horse among the taxonomically identified remains for each archaeolevel.



**Fig. 2.** Spatial distribution of high and low clusters associated with the relative frequency of Red deer and Horse among the taxonomically identified remains for each archaeolevel. High clusters (red) are areas of statistically significant high representation of the taxon under consideration; low clusters (blue) are areas where the representation of the taxon under consideration is statistically significantly low; grey represents nonsignificant areas.



**Fig. 3.** Spatial distribution of the ratio of Red deer and Horse to the sum of Red deer and Horse for each archaeolevel.



## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.106033>.

## Founding

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**Chapter 6. Neanderthal faunal exploitation and  
settlement dynamics at the Abri du Maras,  
Level 5 (South-eastern France)**



# Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, Level 5 (South-eastern France)

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## Abstract

Over the past two decades, taphonomic and zooarchaeological studies have focused on Neanderthal settlement patterns and subsistence strategies. The south-eastern margins of the Massif Central constitute one of the regions with the most abundant archaeological evidence of Neanderthal occupations in France. The faunal record of level 5 of Abri du Maras is a unique source of information for analysing Neanderthal behaviour at the end of the MIS5. The assemblage is divided into three levels 5.1, 5.2 and 5.3, which correspond to the three main phases of human occupation of the shelter in level 5. Through the taphonomic and zooarchaeological analysis of the faunal remains, we define the characteristics of human occupation developed in the rock shelter. In this paper, we show that Neanderthal groups used the Abri du Maras as a residential campsite for long-term occupation events during a whole season, mainly summer. The intensive exploitation of the faunal resources is typical of a residential campsite, and the selective seasonal hunting strategy of medium and large ungulates,



centred on prime adults, indicates different Neanderthal subsistence patterns to the upper levels of the sequence. Here, our results document the chronological changes in occupation patterns in one of the reference sites in south-eastern France and address questions related to cultural choices and environmental constraints.

**Keywords:** Zooarchaeology; Taphonomy; Microwear; Neanderthals; Campsite; Hunting strategies; Subsistence

## 1. Introduction

Zooarchaeological studies of Middle Palaeolithic assemblages have proven to be a fundamental tool for understanding Neanderthals behaviour (Costamagno et al., 2006; Gaudzinski and Roebroeks, 2000; Niven, 2013; Niven et al., 2012; Patou-Mathis, 2000). The current state of knowledge indicates that Neanderthals were effectively hunted a wide faunal spectrum, from the megafauna to small preys (Adler and Bar-Oz, 2009; Costamagno et al., 2006; Daujeard and Moncel, 2010; Farizy et al., 1994; Fernández-Peris et al., 2008; Gabucio et al., 2014a; Gaudzinski and Roebroeks, 2000; Hardy and Moncel, 2011; Jaubert and Brugal, 1990; Patou-Mathis, 1994, 2012; Rufà et al., 2014, 2016; Smith, 2015; Stiner, 1991; Stiner et al., 2009; Stiner, 2013; Stiner and Kuhn, 2006). However, the large number of faunal remains found in Middle Palaeolithic sites indicates that the consumption of large- and medium-sized ungulates was essential for these groups (Adler et al., 2006; Brugal, 2001; Burke, 2000; Castel et al., 2017; Costamagno et al., 2006; Farizy et al., 1994; Gaudzinski, 2006; Gaudzinski and Roebroeks, 2000; Gaudzinski-Windheuser et al., 2018; Jaubert and Brugal, 1990; Stiner, 1994; Yravedra and Cobo-Sánchez, 2015). It is even more significant if we consider the importance of meat from ungulates in the Neanderthal diets suggested by numerous isotopic analysis in bone collagen over their remains (Bocherens, 2011; Bocherens et al., 2016; Jaouen et al., 2019; Morin et al., 2016; Naito et al., 2016; Richards, 2009; Richards and Trinkaus, 2009; Wißing et al., 2016).

Zooarchaeological studies, together with lithic technology studies (Delagnes et al., 2007; Delagnes and Meignen, 2006; Dibble, 1995; Eixea, 2018; Kuhn, 1992; Vaquero, 2008; Villa and Lenoir, 2009) have served as the basis for our knowledge of Middle Palaeolithic subsistence and adaptive strategies (Carrión and Walker, 2019; Marean, 2005; Speth, 2012; Stiner, 2013, 1994). Such researches explores mobility and settlement dynamics, leading to the identification of territorial organization for Middle Palaeolithic groups (Audouze, 2010; Boyle, 2000; Burke, 2000; Delagnes and Rendu, 2011; Farizy, 1994; Patou-Mathis, 2000; Turq et al., 2017). Certain areas have been widely studied, the middle right bank of the Rhone valley, the south-eastern margins of the Massif Central (Southeast France), along with tributaries, such as the Ardèche River, are some of the areas especially with particularly abundant archaeological sites. The profusion of karstic systems was conducive to the conservation of an abundant archaeological record, especially faunal remains, in caves and rock shelters (Daujeard et al., 2019; Daujeard and Moncel, 2010; Hardy et al., 2013; Moncel and Daujeard, 2012; Moncel, 2010; Moncel et al., 2019, 2004; Puaud et al., 2015; Vettese et al., 2017). A number of multidisciplinary studies have defined occupation patterns at many sites and focused on Neanderthal regional settlement and mobility. For example, were identified long-duration campsites in the site of Saint Marcel, short-term regular hunting camps in the sites of Payre, Baume Flandin, Le Figuier or Ranc Pointu and brief stopovers places in Barasses II (Balazuc) and Abri des Pêcheurs (Daujeard et al.,

2012; Daujeard and Moncel, 2010; Moncel and Daujeard, 2012; Moncel et al., 2018, 2008). In the Abri du Maras site, the fauna from level 4.1, a reindeer-dominated assemblage (88% of the NISP), indicates cooperative and planned mass hunting strategies made up of short-term hunting episodes (Daujeard et al., 2019).

The Abri du Maras rock shelter is one of the reference sites for the study of Neanderthal behaviour. The site was studied from a multidisciplinary point of view for over ten years (Daujeard et al., 2019; Hardy et al., 2020, 2013; Moncel et al., 2014, 2010; Puaud et al., 2015; Richard et al., 2015; Vettese et al., 2017). In this paper, we present the zooarchaeological analysis of the faunal assemblage from level 5 of Abri du Maras, recovered during fieldwork carried out from 2006-2018. The aim is to identify the use of the site during the formation of this level and the occupation pattern through a complete zooarchaeological and taphonomical study of the faunal assemblage. We focus on taxonomical representation, hunting and prey selection, and the transport of carcass elements to the site in order to compare level 5 with the other levels of the Middle Palaeolithic sequence of Abri du Maras and with other sites from the regional context of the Rhône valley.

## **2. The Abri du Maras Rock Shelter**

### **2.1. General description**

The Abri du Maras is located in a small dry valley, less than 1 km long, perpendicular to the Ardèche River valley, a tributary of the Rhone River, near the locality of Saint-Martin d'Ardèche. It is situated 170 m above sea level and 70 m above the Ardèche River. The rock shelter was excavated by R. Gilles and J. Combier in the 1950s and 1960s, who described sequence composed of eight archaeological levels (Combiér, 1967). In 2006, a survey at the front of the site identified two levels at the base of the sequence (named levels 4 and 5) and provided the first overview of the site (Moncel et al., 2010) (Figure 1). This survey was followed by renewed excavations.

The geological study shows that the cave roof collapsed over time and that the most recent occupations took place under a small shelter (Debard, 1988). The oldest level identified during recent excavations was named level 5 (levels 8-6 of the previous excavations) and consists of a thick organic brown level with a sandy-silty matrix, covering the limestone substratum. It is truncated in front of the site and covered by a sterile level of rubble with a red clay silt matrix. The overlying deposit is level 4 (levels 5-4 of the previous excavations), made up of homogeneous aeolian silt (loess) with some small blocks of limestone. Two phases of occupation have been identified and dated to MIS 3 (Richard et al., 2015). This level is overlain by levels 3, 2 and 1, made up of rubble with a silty matrix and limestone slabs, similar to those described during the previous excavations. These levels contain the most recent occupations (Moncel et al., 2010). The latter also significantly reduced the ceiling height of the shelter, leading to a shift in the surface of the human occupations, to the limit of the shelter roof. U-The dating of four bone samples from level 5 would place this level between 70 and 90 ka ( $72 \pm 3$  ka,  $87 \pm 5$  ka,  $89 \pm 4$  ka,  $91 \pm 4$  ka), at the end of MIS 5 or the beginning of MIS 4 (Moncel and Michel, 2000). Level 4.1 in the Abri du Maras is dated to between  $40 \pm 3$  ka and  $46 \pm 3$  ka (MIS 3), while samples from level 4.2 provided ages ranging from  $42 \pm 3$  ka to  $55 \pm 2$  ka (MIS 3). These new ages obtained on level 4.1 and 4.2 indicate that the site was occupied during MIS 3, and

thus extend the known chronology of Abri du Maras (end of MIS 4- the beginning of MIS 5, Moncel and Michel, 2000). One sample (AM F6-47), positioned at the top of level 5 upper in the western part of the site, gave an age of  $90 \pm 9$  ka (MIS 5c-b), in agreement with the previous dating study (Richard et al., 2015).

The study of large ungulates serves as an approach to paleoenvironmental evidence. Here, it indicates the development of cold weather over time and a decrease in forested areas in favour of more open steppe landscapes (reindeer succeeding deer), which is in line with sedimentological results (Debard, 1988; Moncel et al., 2018, 1994). The paleontological analysis in level 4.1 and 4.2 revealed the presence of *Rangifer tarandus*, *Equus ferus cf. germanicus*, *Cervus elaphus*, *Bison priscus*, *Capra ibex* and *Megaloceros giganteus* (Boulbes and van Asperen, 2019; Daujeard, 2008; Moncel et al., 1994). The zooarchaeological analysis of levels 4.1 and 4.2 indicates that these levels result from Neanderthal activity, characterized by a primary access to animal carcasses, systematic transport of skeletal elements to the rock shelter and a complete exploitation of animal resources (Daujeard, 2008; Daujeard et al., 2019; Moncel et al., 2018).

Lithic remains were abundant throughout the sequence. Level 4.1 and level 4.2 contain predominant Levallois production with the importation of large products and complementary in situ knapping of flakes from small nodule cores (Moncel, 1994). Technological strategies point to the fragmentation of processes in a local and semi-local perimeter around the rock shelter (Moncel et al., 2018). Large flakes, blades, and points were produced elsewhere and brought to the occupations with flint and other raw materials, nodules and fragments of slabs for in situ knapping.

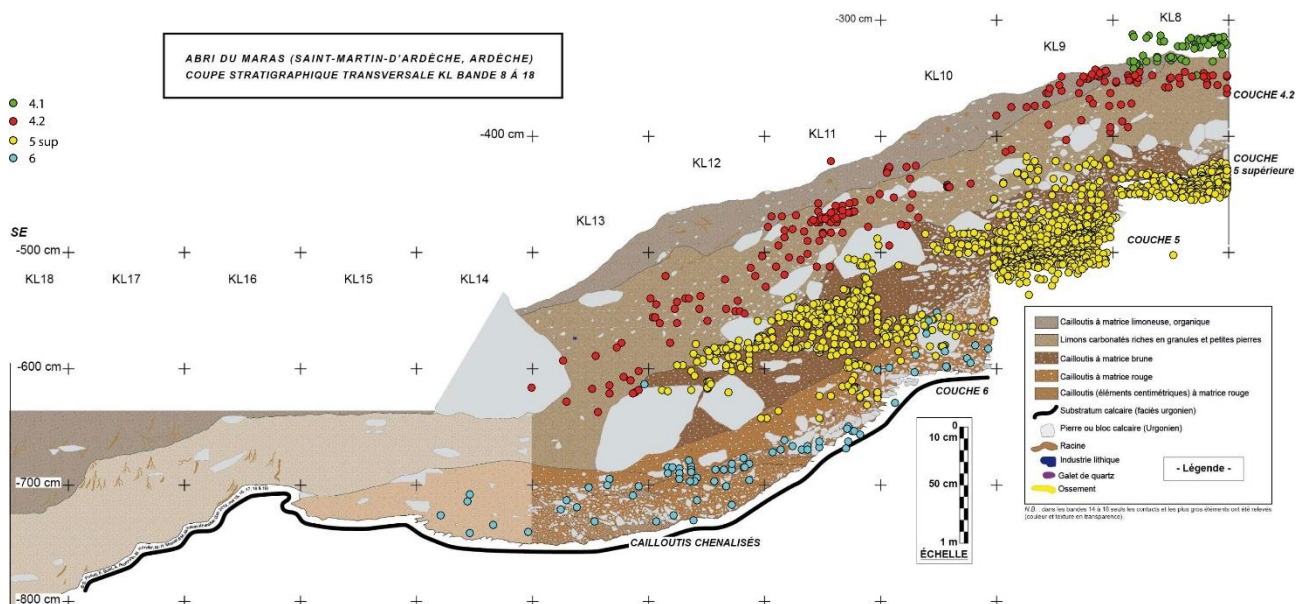


Figure 1 Vertical distribution of the archaeological material at Abri du Maras. Abri du Maras materials: green=level 4.1; red=level 4.2; yellow=level 5; blue=level 6.

## 2.2. Level 5

The upper part of level 5 is covered by a dense bed of large- and middle-sized blocks (between 50 cm and 4.5 m thick), resulting from the major collapse of the shelter. This bed delimits the level 4 from the level 5. The thickest zone of this phase of accumulation is observed in the central and eastern

parts of the site and is estimated at a thickness of 160 cm at the most. Level 5 lies on the limestone bedrock, excavated in front of the shelter, or partially covers the underlying level 6, a red and karstic deposit with some evidence of occupation. The bedrock cross-section resembles a series of steps and the infilling lies on the series of steps. Level 5 is considered as a distinct deposit in the sequence due to the similarity of the type and structure of the sediment, which consist of series of several layers of brown clay including small or large blocks resulting from the collapse of the shelter over time (Figure 1).

Three phases of occupations have been distinguished by means of the systematic plotting of the material from the sequence along 50 cm sections and by projections of spatial distributions of the material (Figure 2). Phase 5.1 corresponds to the upper part of the level, with a dense concentration of archaeological material located just under the blocks. It has been excavated over 25 m<sup>2</sup>. It can be distinguished from phase 5.2 (15 m<sup>2</sup>) by a lower density of archaeological material. The main discontinuity is observed in the lower part of the level where a sterile bed of small- and middle-sized blocks results from a minor collapse of the shelter. This bed delimits the phase of occupation phase 5.3 (15 m<sup>2</sup>) from the overlying phase 5.2. A higher diversity of core technologies, including Levallois technology, differentiates technological behaviours in level 5 from level 4. The ratio of flake tools (and diversity) is higher (around 10% as opposed to less than 5 % for level 4). Flint still dominates the corpus, associated with other stones, debitage products, some cores and entire pebbles. The flint types indicate a perimeter of procurement to the south (Orgnac plateau; 20 km approx.) and the north of the site.

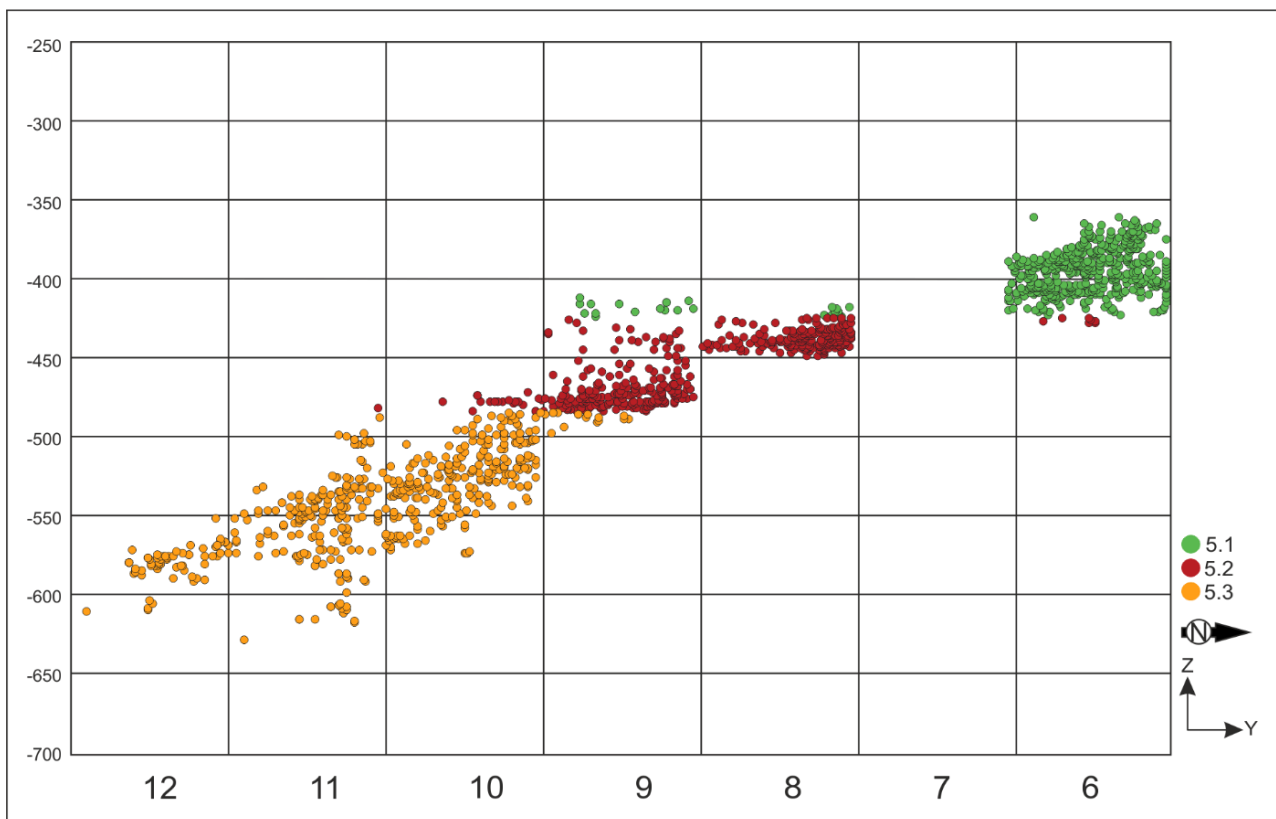


Figure 2 Vertical distribution of archaeological material of level 5 in the L line. Level 5.1=green; Level 5.2=red; Level 5.3= yellow.

### 3. Materials and Methods

A total of 5,383 faunal remains were analysed for this work: 2,511 faunal remains from level 5.1; 1,415 faunal remains from level 5.2; 1,458 faunal remains from level 5.3 were studied.

Taxon, age at death, weight category, element, side (anterior, posterior, medial, lateral, superior and inferior) and the portion (epiphysis, metaphysis and diaphysis) and position (left/right) were described when possible. Carcasses were divided into anatomical parts to estimate anatomical representation: axial cranial (horns/antlers, skull, mandible, hyoid and isolated teeth), axial postcranial (vertebrae, ribs, scapula and coxal) and appendicular (extremities). The scapula was classified with the axial skeleton because it responds to taphonomic processes in a similar way to the rest of the axial skeleton elements (Yravedra and Domínguez-Rodrigo, 2009). Long bones were divided into upper appendicular bones (humerus and femur), intermediate (radius/ulna and tibia) and inferior (metapodials) (Domínguez-Rodrigo, 1997). Three weight categories were used for the analysis of level 5: large animals weighing between 300 and 1,000 kg (horse, bison); medium-sized animals weighing between 50 and 300 kg (reindeer, red deer, wild boar, ibex); small-sized animals weighing less than 50 kg (roe deer, fallow deer, wolf).

Four measures of abundance were used in this work: Number of Identified Specimens (NISP); Minimum Number of Elements (MNE); Minimum Number of Animal Units standardized (%MAU); and Minimum Number of Individuals (MNI) (Binford, 1984; Grayson, 1984; Lyman, 1994). To calculate the MNE, the superposition of anatomical markers, the age or side were considered. For long bones, we followed the recommendation of Saladié et al. (2011). The Shannon uniformity index (E) and the Simpson diversity index (D) were used to establish the degree of taxonomic diversity.

Spearman's rank-order was used to test the correlation between the %MAU and the data provided by Lam et al. (1999) for bone mineral density, taking into account the MNE of each element. The significance of the Spearman correlation coefficient used in this work is 95% (0.05).

Transport strategy analysis was carried out following the method proposed by Faith and Gordon (2007), through the statistical correlation of Spearman's rho between the standardized food utility index (SFUI) and the %MAU and by applying the Shannon uniformity index (E) to the anatomical profile. The following high-survival elements were considered: skull, mandible, humerus, radius/ulna, metacarpal, femur, tibia, and metatarsal (Marean and Cleghorn, 2003). In addition, the %MAU of the high-survival elements was correlated with the unsaturated marrow index (UMI) proposed by Morin (2007).

The age at death of the individual and the seasonality of the formation of assemblages were calculated based on the time of eruption and replacement of teeth and the degree of wear of the occlusal surfaces (Azorit, 2011; Bignon, 2006; Bouchud, 1966; Brown and Chapman, 1991; Fernandez and Legendre, 2003; Klein and Cruz-Urbe, 1983; Mariezkurrena, 1983; C. Miller, 1974; F. L. Miller, 1974; Steele and Weaver, 2002). The birth period for reindeer and horses was between the end of spring and the beginning of summer (horse: Levine, 1982; Burke, 2002) (reindeer: Daujeard et al., 2019). Given that the period of birth and the replacement of deciduous teeth occur at predictable times of the year, it is possible to calculate the annual cycle and estimate the season of death (Stiner, 1990). Once the age

at death was identified, individuals were grouped into juveniles, prime adults and old individuals (Stiner, 1990), and plotted within triangular graph following the separation of mortality profiles proposed by Stiner (1990) and Discamps and Costamagno (2015) for reindeer and horses.

Moreover, tooth microwear was used to establish the relative duration and to confirm the seasonality of the formation of the assemblages. Tooth microwear patterns (microscopic features present on the surface of the enamel) were examined for the most represented species in the assemblage, *Rangifer tarandus* and *Equus ferus*. The analysis was performed following the protocol established by Solounias and Semprebon (2002). High-resolution dental casts were observed under transmitted light with a Zeiss Stemi 2000C stereomicroscope at 35x magnification. The microwear features (i.e., scratches and pits) were quantified on the paracone of the upper molars or the protoconid of the lower molars. Two measurements of the variability of scratch density, i.e., the standard deviation (SD) and coefficient of variation (CV) were used to estimate the duration of the accumulation of faunal associations (Rivals et al., 2015). The integration of these two measures of variability allows for the classification of each case in one of the following three categories: [A] seasonal or shorter events, [B] events longer than a season (i.e., two or more contiguous seasons), [C] distinct events that occurred in different and non-contiguous seasons. Additionally, the difference in variability among samples was tested using the Bartlett test of homogeneity of variances.

The method devised by Villa and Mahieu (1991) was followed to establish the degree of fragmentation and the agents responsible for bone breakage. For this, we considered diaphysis length and circumference, description of the delineation (longitudinal, transverse and curved / V-shape), angle (straight, oblique or mixed) and the surface (smooth or jagged) of fracture planes.

The taphonomic analysis was completed by the observation of bone surface modifications using the binocular stereomicroscope (OPTHEC 120-Hz model). We have assessed the visibility of the cortical bone surfaces based on how much surface could be studied: 0=none; 1=one third; 2=two thirds; 3=the whole surface. The study focused on modifications produced during the nutritional phase (Capaldo, 1998). Damage produced by hominins and carnivores was described according to the anatomical region and the portion on which they were found. The identified anthropogenic modifications include cut marks (Binford, 1981; Domínguez-Rodrigo et al., 2009; Potts and Shipman, 1981; Shipman, 1981; Shipman and Rose, 1983) and percussion marks (Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Vettese et al., 2020). The type, delineation, situation, and position of the cut marks per element allowed us to infer butchery activities. For this, we used ethnoarchaeological sources (Abe, 2005; Binford, 1978), experimental data (Frison, 1974; Nilssen, 2000) and our experiments on multiple animals. For the study of cremations, colour changes of the bones were taken into account, following Cáceres' proposal (2002). The six colouration stages used here are: 0) unburned; 1) small brown or black areas; 2) brown bones; 3) black bones (charred); 4) grey bones (calcined); 5) white bones (calcined). Finally, carnivore modifications were identified through the presence of tooth marks, mainly pits and scores (Blumenschine, 1995; Bunn, 1981; Domínguez-Rodrigo and Barba, 2006; Fisher, 1995; Shipman, 1981), along with furrowing and chipping of the back edges.

For the study of bone retouchers, we used the criteria detailed by Mallye et al. (2012) and Daujeard et al. (2014). We noted the taxonomic and anatomical information. Marks were classified depending on their type, location and orientation.

## 4. Results

### 4.1. Taxonomic distribution

A total of 11 species were identified (Table 1). The identification rate was high in all the levels, 26.8% in level 5.1, 19.7% in level 5.2 and 31.5% in level 5.3. The three assemblages were dominated by *Rangifer tarandus* (5.1=74%; 5.2=61.6%; 5.3=64.8%), followed in importance by *Equus ferus* (5.1=10.7%; 5.2=18.6%; 5.3=25.0%), *Cervus elaphus* (5.1=11.3%; 5.2=11.8%; 5.3=4.3%), and *Bison priscus* (5.1=2.8%; 5.2=6.5%; 5.3=5.9%). Other taxa represented less than 1% of the total. *Sus scrofa* remains were identified in levels 5.1 and 5.2, *Capreolus capreolus*, *Capra ibex*, *Equus hydruntinus* and *Oryctolagus cuniculus* in level 5.1, and *Dama dama* in level 5.2 (Table 1). A *Canis lupus* metacarpal in level 5.2 is the only carnivore bone. The levels show a uniform distribution of species, as indicated, by the evenness (Evenness: 5.1=0.4204; 5.2=0.5737; 5.3=0.6713) and the Simpson index (Simpson: 5.1=0.574; 5.2=0.433; 5.3=0.4875). Many indeterminate remains could be assigned to a weight category. Medium-sized animals dominated the three assemblages (40.2%; 41.4%; 35.5%), followed by large-sized remains (11.6%; 12.3%; 18.4%). This distribution is in keeping with the representation of reindeer, red deer and horses in the assemblages.

Taxon	5.1			5.2			5.3		
	NISP	%NISP	MNE	NISP	%NISP	MNE	NISP	%NISP	MNE
<i>Rangifer tarandus</i>	498	74.0	116	172	61.6	43	298	64.8	84
<i>Cervus elaphus</i>	75	11.3	27	33	11.8	15	20	4.3	10
<i>Dama dama</i>				1	0.4	1			
<i>Equus ferus</i>	72	10.7	25	52	18.6	19	115	25.0	42
<i>Equus hydruntinus</i>	1	0.1	1						
<i>Bison priscus</i>	19	2.8	11	18	6.5	9	25	5.9	13
<i>Capreolus capreolus</i>	4	0.6	4						
<i>Capra ibex</i>	2	0.3	1						
<i>Sus scrofa</i>	1	0.1	1	2	0.7	2			
<i>Canis lupus</i>				1	0.4	1			
<i>Oryctolagus cuniculus</i>	2	0.3	2						
Total	676		187	279		90	458		149
Large size	213	11.6		140	12.3		184	18.4	
Medium size	738	40.2		470	41.4		355	35.5	
Small size	28	1.5		10	0.9		12	1.2	
Indeterminate	858	46.7		516	45.4		449	44.9	
Total NSP	1,837			1,136			1,000		
Total	2,511			1,415			1,458		

Table 1 NISP, NSP and MNE of taxa and weight size categories in levels 5.1, 5.2 and 5.3 of Abri du Maras.

## **4.2. Anatomical distribution, bone assemblage integrity and bone transport strategy**

The minimum number of elements in level 5.1 is 187, 90 in level 5.2, and 149 in level 5.3. The distribution of NISP and MNE by taxa and elements is presented in tables S1, S2 and S3 of Supplementary materials. The anatomical distribution of reindeer in levels 5.1 and 5.2 shows a predominance of long limb bones, especially by hindlimbs (tibiae, femurs and metatarsals), with low percentages of cranial elements and even lower proportions of postcranial axial elements and compact bones (Figure 3). Conversely, reindeer cranial elements are well represented in level 5.3.

The anatomical distribution of red deer was dominated by long limb bones in levels 5.1 and 5.2. In level 5.1, percentages of tibiae, radii and humerus reached over 50% and in level 5.2 humerus, tibiae, metacarpals and femurs reached over 50%. In level 5.3, the most represented elements were skull fragments, scapulae and humerus. The rest of the long limb bones represented 50 of the total remains. The anatomical distribution of the horse is dominated by cranial elements in all the three levels. In level 5.1, mandibular remains are prevalent and in levels 5.2 and 5.3, skull remains are predominant. The representation of post-cranial axial elements is low in all three levels. In level 5.1, rib fragments were identified and level 5.2 comprised coxal elements. The post-cranial axial skeleton was best represented in level 5.3, with fragments of hyoid, rib, vertebrae, scapula and coxal bones. Long limb bones were most represented in level 5.2, with abundant femurs and tibiae and proportions of humerus and radii exceeding 60% and 50% respectively. In levels 5.1 and 5.3, none of the long limb bone %MAU proportions exceeded 30%. Bison remains were dominated by long limb bones, although cranial remains, especially mandible, and coxal remains were presented in the three levels. In level 5.1, radius and tibia percentages exceed 50%. In level 5.2 the humerus, radius and tibia are the best represented bones, and in level 5.3 the radius is predominant, followed by the humerus, cranium and mandible.



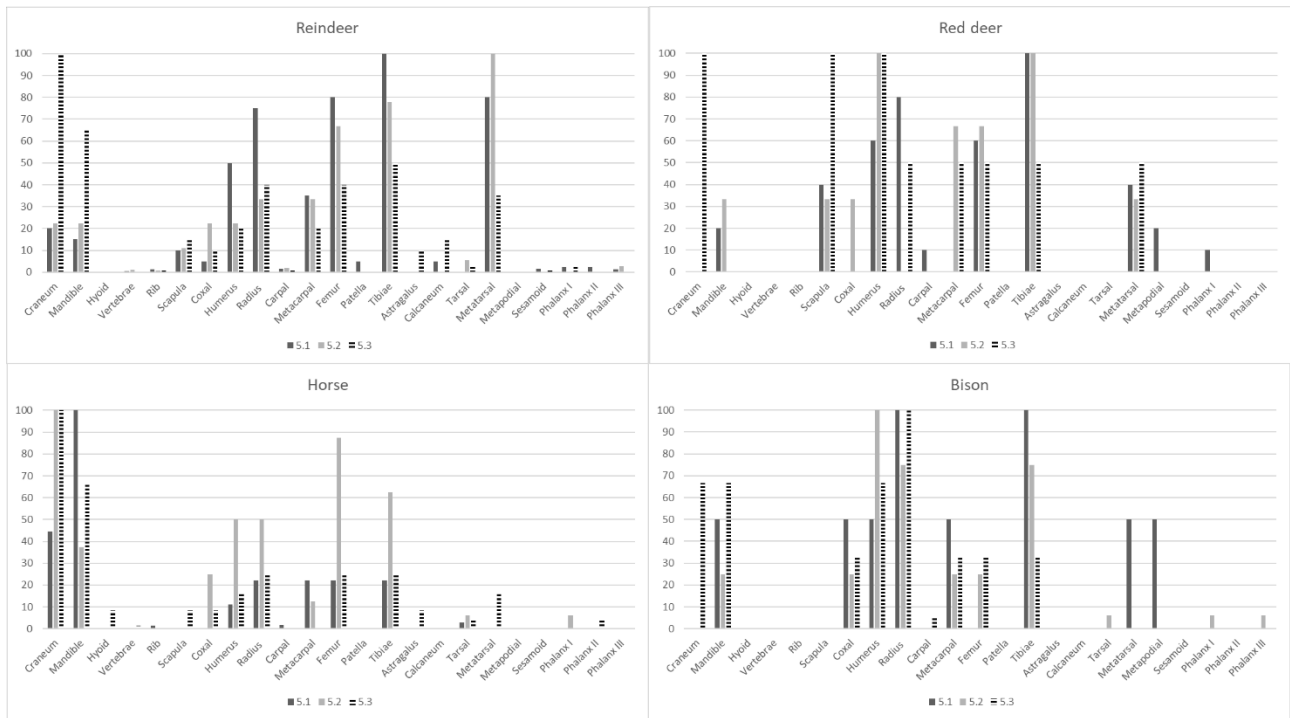


Figure 3 %MAU of the main taxa in levels 5.1, 5.2 and 5.3. Maximum values of MAU: reindeer (5.1=10; 5.2=4.5; 5.3=10); red deer (5.1=2.5; 5.2=1.5; 5.3=1); horse (5.1=4.5; 5.2=4; 5.3=6); bison (5.1=1; 5.2=2; 5.3=1.5).

The results of statistical correlations between the %MAU and bone mineral density indicated a highly significant positive correlation for medium-sized animals in the three levels and for large-sized animals in levels 5.3. No significant correlations were observed for large-sized animals in levels 5.1 and 5.2 and small animals in the three levels (Table 2).

Level	5.1		5.2		5.3	
Weight size	Spearman's (rs)	p (same)	Spearman's (rs)	p (same)	Spearman's (rs)	p (same)
Large size	0.1653	0.10011	0.16737	0.096024	0.30509	0.002025
Medium size	0.3834	8.23e-05	0.36943	1.55E-04	0.48893	2.45E-07
Small size	0.042	0.67802	0.17363	0.084048	0.001238	0.99025

Table 2 Statistical correlation between %MAU and bone mineral density (Metcalf and Jones, 1988).

Practically all the specimens in the faunal assemblage were fragmented (5.1=98.2%/; 5.2=98.6%; 5.3=93.4%). Complete elements consist of isolated teeth in the three levels (NR: 5.1=21; 5.2=14; 5.3=69), followed by articular bones (NR: 5.1=8, 5.2=5; 5.3=10) and the phalanx (NR: 5.1=2; 5.2=2; 5.3=3). In level 5.2, a complete wolf metacarpal was found and in level 5.3, a whole horse atlas and a vestigial metatarsal were recorded. A total of 83.7% of long bones in level 5.1, the 92.4% in level 5.2 and the 84.5% in level 5.3 comprised less than a third of their total circumference and a quarter of their total length (Figure 4). Breakage patterns are similar for the three samples. The most common combination of fracture types are curved, oblique and smooth and longitudinal, oblique and smooth fractures (Figure 4). These indicate that green bone breakage was predominant. Other combinations were also well represented, such longitudinal, right and smooth (5.1=16.4%; 5.2=10.1%; 5.3=13.1%), transversal, mixed and irregular (5.1=10.5%; 5.2=7.3%; 5.3=10%) (Figure 4).

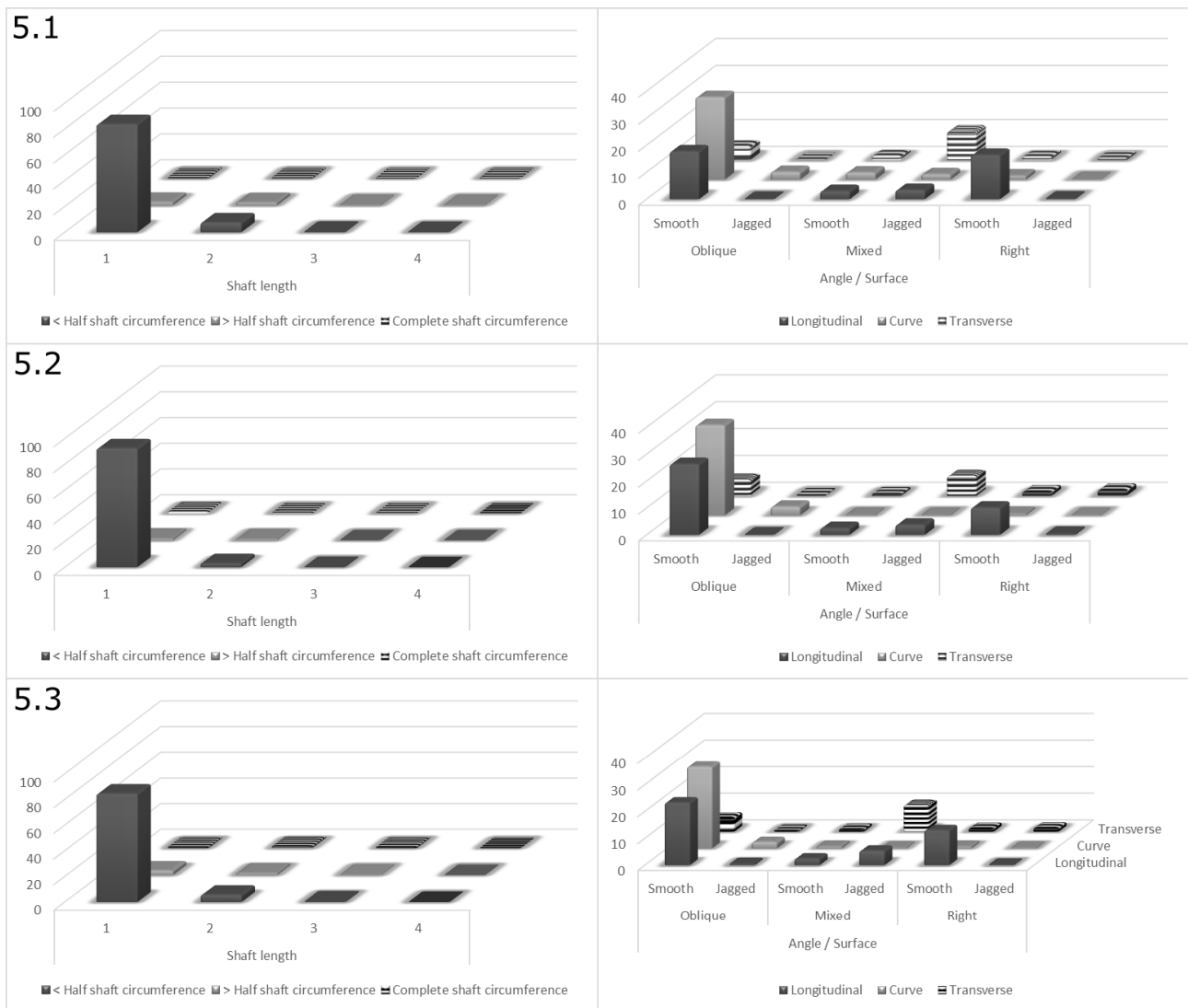


Figure 4 Fragmentation and fracture analysis of long bones for levels 5.1, 5.2 and 5.3. Frequency of the features of fracture planes in long bones (right); Frequency of shaft length and shaft circumference (left).

The evenness of the SFUI for reindeer indicated the presence of the moderate- and high-utility elements in all levels (Table 3). In level 5.1, horse elements are represented in proportionate frequencies to their utility. Bison in level 5.2 also show predominant moderate- and high-utility elements (Table 3). The statistical relation between UMI and %MAU indicates a high and positive relationship for reindeer in the levels 5.1 and 5.2. No statistical correlations were observed for the rest of the assemblages (Table 3).

Levels	Taxa	Transport strategies	Evenness	SFUI		UMI	
			%MAU	Spearman's (rs)	<i>P</i>	Spearman's (rs)	<i>P</i>
5.1	Reindeer	Bulk	0.9287	0.83834	0.013095	0.98561	0.0055556
	Red deer	Bulk/Unconstrained	0.9443	0.74704	0.040873	0.55078	0.2722
	Horse	Unbiased	0.867	-0.45661	0.27619	-0.010142	0.86667
	Bison	Bulk/Unconstrained	0.9671	0.077152	0.89524	0.24689	0.6333
5.2	Reindeer	Bulk	0.9193	0.62606	0.11012	0.84067	0.04
	Red deer	Bulk/Unconstrained	0.9513	0.43916	0.3	0.058849	0.9222
	Horse	Bulk/Unconstrained	0.9349	0.22755	0.59048	0.28989	0.5667
	Bison	Bulk	0.9105	0.23473	0.575	-0.20597	0.7111
5.3	Reindeer	Bulk	0.9286	-0.048196	0.9248	0.79446	0.1
	Red deer	Bulk/Unconstrained	0.9708	-0.068732	0.86905	-0.39279	0.6667
	Horse	Bulk/Unconstrained	0.8763	-0.036827	0.94107	0.61721	0.2333
	Bison	Bulk/Unconstrained	0.9577	-0.35044	0.40536	-0.5161	0.35

Table 3 Values of Evenness of anatomical distribution and statistical correlation between %MAU and standard food utility index (SFUI) and unsaturated marrow index (UMI).

### 4.3. Mortality profiles

The estimated MNI for all taxa in level 5.1 was 26 individuals, 16 for level 5.2 and 24 for level 5.3. For reindeer, the MNI was calculated with the tibia in level 5.1, metatarsals in level 5.2 and teeth in 5.3. For red deer, we used tibia in 5.1 and 5.2 and teeth in 5.3. For the horse, teeth were used in all levels. Finally, for bison, the radius was used in levels 5.1 and 5.3 and the humerus in level 5.2. Among the main ungulate taxa, reindeer showed the highest MNI, followed by horse, red deer and bison (Table 4). The rest of the species comprise one wild boar individual in 5.1 and another in 5.2, one individual of roe deer, european ass and rabbit in 5.1, and one fallow deer and a wolf in 5.2.

A total of 79 reindeer teeth (5.1=10; 5.2=14; 5.3=55), 96 horse teeth (5.1=32; 5.2=20; 5.3=44), 7 red deer teeth (5.1=4; 5.2=1; 5.3=2) and 10 bison teeth (5.1=4; 5.2=0; 5.3=6) were analysed (Figure 5). The number of analysed teeth found in each level and their integrity (in situ or isolated teeth) are reported in Table 4. The analysis of eruption and replacement rates and wear stages reveal the age of 15 individuals in 5.1, six individuals in level 5.2 and for 24 individuals in 5.3 (Table 4). In all three levels, prime adult individuals were the best represented group, followed by juveniles and old individuals.

Reindeer present a prime-dominated profile in all levels. Based on the ternary distribution of Discamps and Costamagno (2015), a prime-dominated profile emerges for levels 5.2 and 5.3. In level 5.1, a juvenile/prime/old profile was observed, with a predominance of prime adult (Figure 6). For horses, a catastrophic mortality profiles was observed for level 5.3 and a prime-dominated profile in levels 5.1 and 5.2. Ternary distribution (Discamps and Costamagno, 2015) presents a juvenile/prime/old profile in all levels (Figure 6). For red deer and bison, prime adult individuals were identified.

Level	Taxa	Integrity	NR	MNI	Age Group			Indeterminate
					Juvenile	Prime	Old	
5.1	Reindeer	Isolated tooth	6	10	1	2		7
		Tooth in bone	4					
	Red deer	Isolated tooth	1	3		2		1
		Tooth in bone	3					
	Equus	Isolated tooth	17	9	2	6	1	
		Tooth in bone	15					
	Bison	Isolated tooth	0	1		1		
		Tooth in bone	4					
5.2	Reindeer	Isolated tooth	8	5		2		3
		Tooth in bone	6					
	Red deer	Isolated tooth	1	2				2
		Tooth in bone	0					
	Equus	Isolated tooth	11	4	1	3		
		Tooth in bone	9					
	Bison	Isolated tooth	0	2				2
		Tooth in bone	0					
5.3	Reindeer	Isolated tooth	44	13	3	10		
		Tooth in bone	11					
	Red deer	Isolated tooth	2	1		1		
		Tooth in bone	0					
	Equus	Isolated tooth	25	8	3	4	1	
		Tooth in bone	19					
	Bison	Isolated tooth	2	2		2		
		Tooth in bone	4					

Table 4 Number of teeth analysed by species and their integrity (isolated or within dental series), total minimum number of individuals and minimum number of individuals and age at death in levels 5.1, 5.2 and 5.3.

Based on the analysis of dental eruption and replacement sequences, we assessed the season of death of young individuals. For reindeer, in level 5.1, one individual died in summer (between 15-16 months old) and in level 5.3, three young individuals also died in summer (Figure 2). For the horse, one individual in level 5.1 died at the end of summer/beginning of autumn, in level 5.2 one individual was killed at the end of spring/beginning of summer and in level 5.3, one individual died at the end of summer/beginning of autumn (Figure 6).

Tooth microwear analysis on reindeer (levels 5.1 and 5.3) and horse (levels 5.1, 5.2, 5.3) shows low SD and CV values, indicating low intra-specific variability (Table 5). Such low values usually correspond to seasonal occupations (Rivals et al. 2015). All the analysed samples plot in area A of the bivariate graph (Figure 7), indicating that the accumulation of the preys in these three levels lasted for three months or less. Additionally, there are no significant differences in variability values among the five samples (Bartlett's  $K$ -squared=2.17,  $df=4$ ,  $p=0.7015$ ), suggesting that the duration of assemblage accumulation is very similar in the three levels.

Microwear values for the reindeer are very similar for the two levels where the sample size was sufficient for microwear analysis, both in terms of pits and scratches. In comparison to microwear data from extant populations of *Rangifer tarandus* (from Rivals et al. 2015; Rivals and Semprebon 2017), our result correlate well with a summer and early autumn. These microwear results, based on adults, support the results from the dental eruption and replacement sequences (based on young individuals) and confirm that reindeer died in summer. For the horse, no microwear reference data are available for wild equids to test the dental eruption and replacement results.

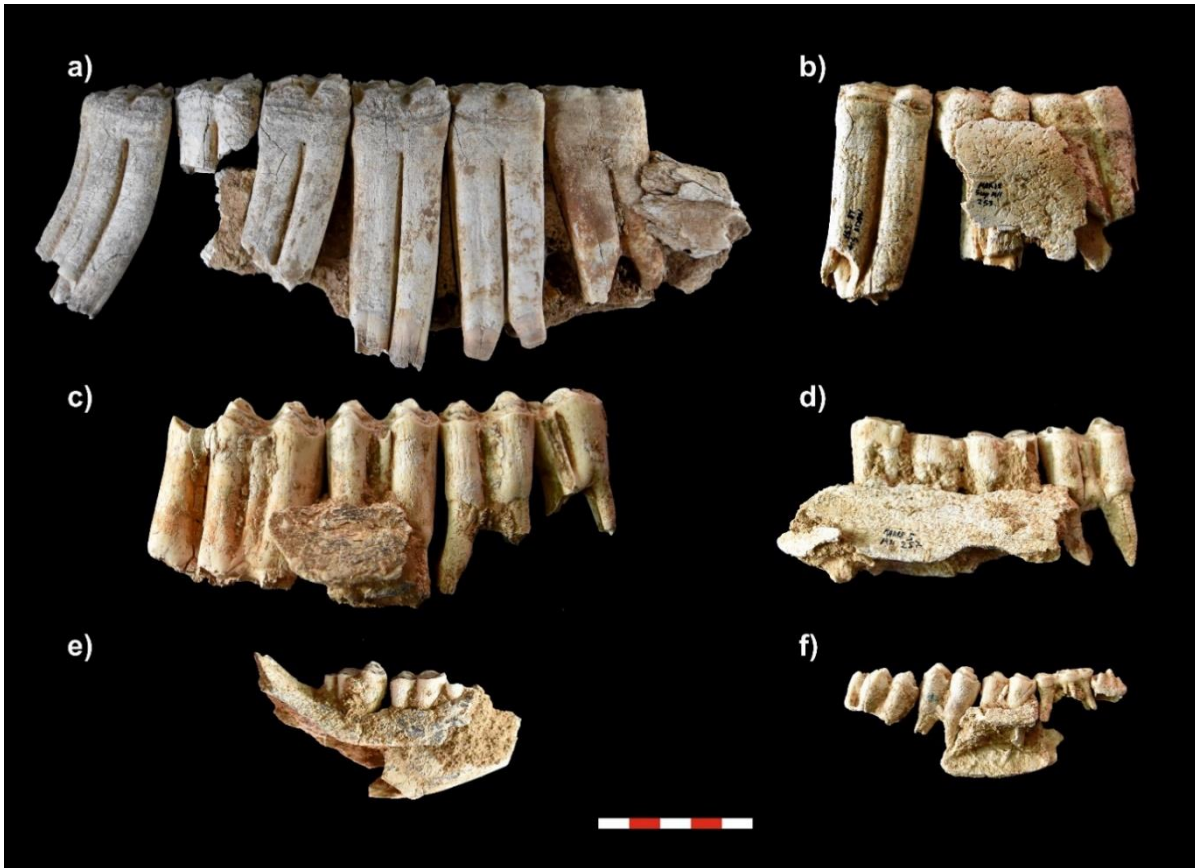


Figure 5 a) and b) mandible refits of fo prime adult horses from levels 5.3 (a) and 5.2 (b); c) and d) bison mandibles of a prime adult from level 5.3; e) reindeer mandible of a prime adult from level 5.3; f) mandible refitting of a reindeer juvenile individual from level 5.1. Scale bar = 5 cm.

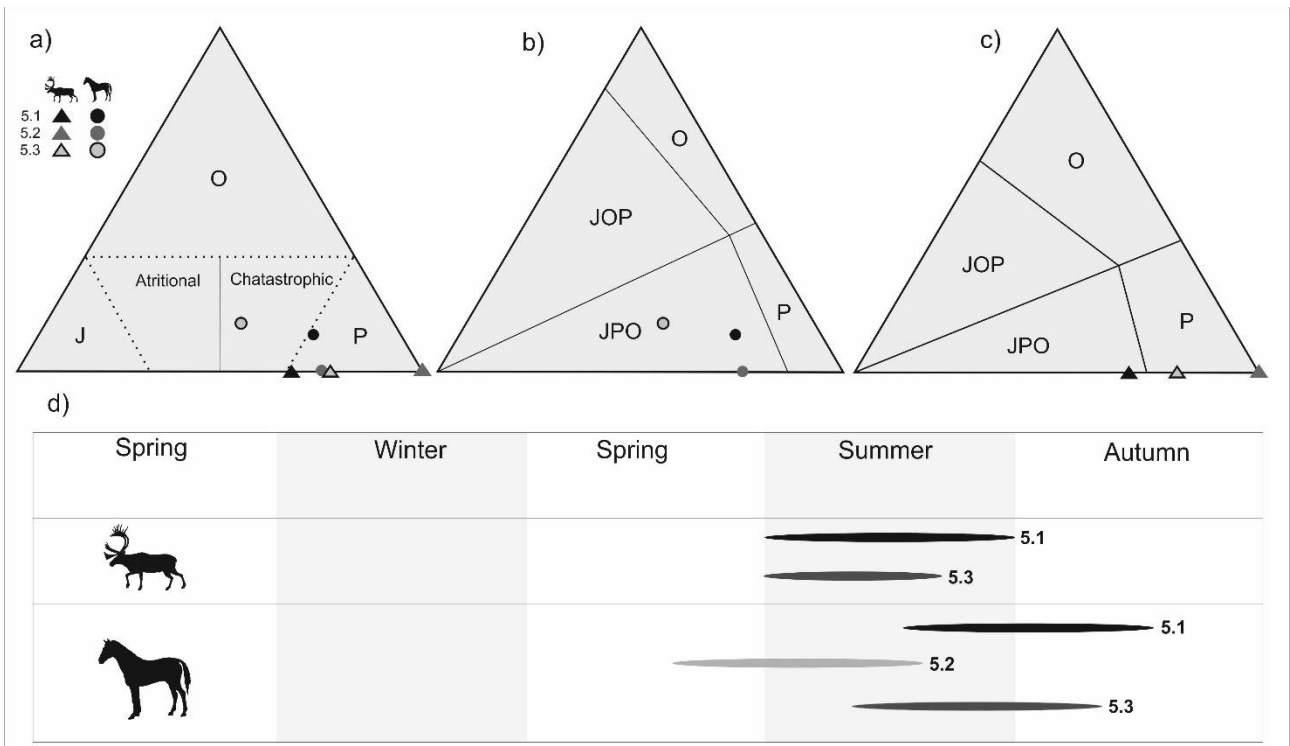


Figure 6 Ternary plot with mortality profiles for reindeer and horse from levels 5.1 and 5.2. With Stiner (1990) areas (a), and Discamp and Costamagno (2015) areas for the horse (b) and reindeer (c); (d) season of death of young individual of reindeer and horse individuals.

Level	Species	N	NP	NS	CV	SD
5.1	<i>E. ferus</i>	18	14.0	21.8	0.07	1.56
	<i>R. tarandus</i>	6	12.3	15.8	0.13	1.97
5.2	<i>E. ferus</i>	8	10.6	21.2	0.10	2.17
	<i>R. tarandus</i>	1	-	-	-	-
5.3	<i>E. ferus</i>	14	13.9	21.6	0.09	1.90
	<i>R. tarandus</i>	17	13.5	15.7	0.14	2.24

Table 5 Summarized statistics of the dental microwear results for the horse and reindeer from levels 5.1, 5.2 and 5.3 from Abri du Maras. Abbreviations: N = Number of specimens; NP = Mean number of pits; NS = Mean number of scratches; CV = Coefficient of Variation of the NS; SD = Standard Deviation of the NS.

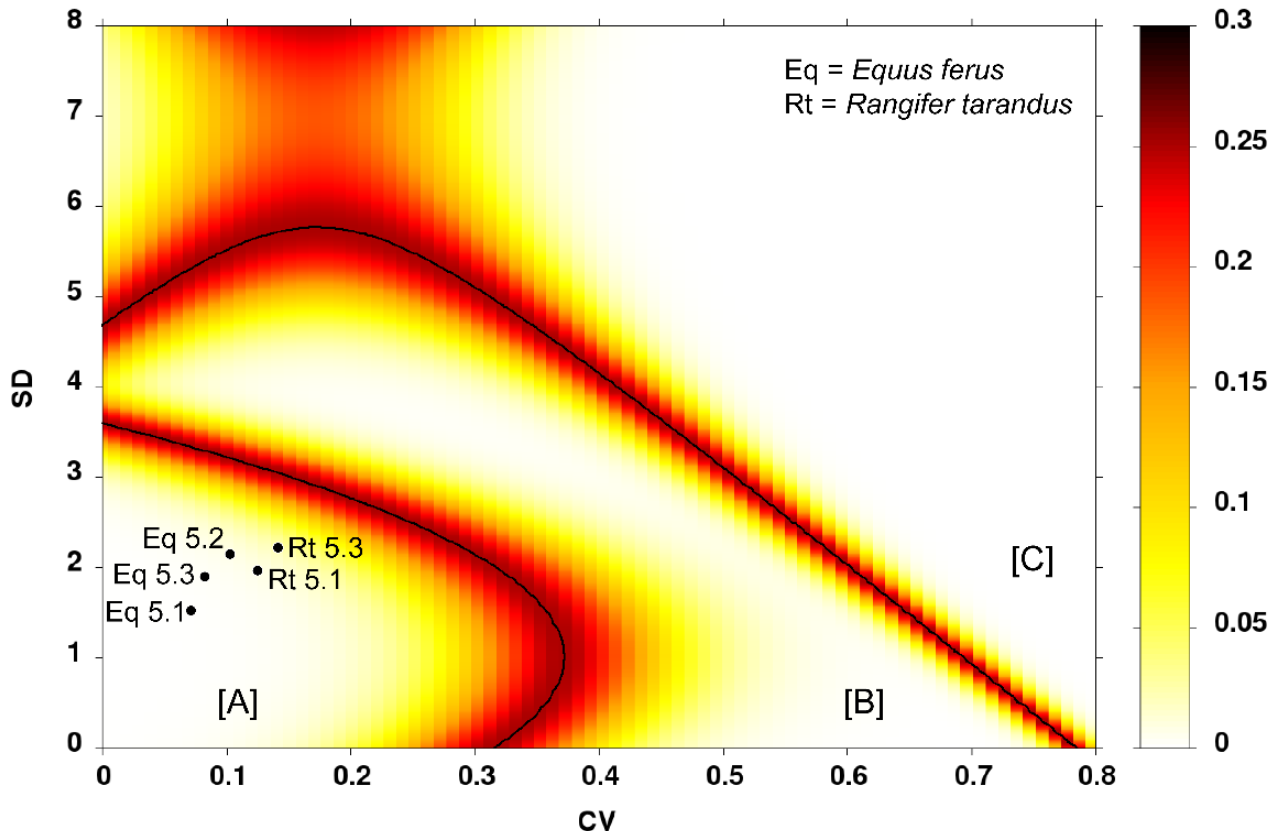


Figure 7 Boundary lines with error probability (heat map) based on SD and CV values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separate short events (region C) and positions of the horse and reindeer samples from Abri du Maras levels 5.1, 5.2 and 5.3.

## 4.4. Taphonomic signal

Overall, the visibility of cortical surfaces on the remains from levels 5.1, 5.2 and 5.3 is good. In level 5.1, more than half of the assemblage (67%) shows good cortical preservation. In level 5.2, the 44% indicate good preservation and for 41% two-thirds of the cortical surface were analysable. In level 5.3, the preservation of cortical surfaces was poorer than in the upper levels; 22.6% of remains show good preservation, for 41.1%, had two-thirds of cortical surfaces were analysable, for 31%, only one-third of the surface was analysable and 5.2% had none analysable cortical surfaces.

### 4.4.1. Post-depositional modifications

Root marks were the most widespread post-depositional alterations. In level 5.1, 28% of the remains are affected, 31.7% in level 5.2 and 52.9% in level 5.3 (Table 6). Small fissures and desquamations

were observed in the three levels, indicating periods of sub-areal exposures. Desquamations rates are low in the assemblage (5.1=8%; 5.2=4.4%; 5.3=9.2%). Black manganese oxide stains were common on bone surfaces, particularly in level 5.3 (22.4%). On the contrary, orange iron oxide precipitation marks were detected with a low rate of distribution (5.1=3.8%; 5.2=0.4%; 5.3=2.8%) (Table 5).

NR/%NR	5.1		5.2		5.3	
Fissures	371	14.8%	123	8.7%	206	14.1%
Weathering	200	8.0%	62	4.4%	134	9.2%
Roots	702	28%	448	31.7%	772	52.9%
Manganese oxide	306	12.2%	214	15.1%	327	22.4%
Iron oxide	96	3.8%	6	0.4%	41	2.8%

Table 6 Principal post-depositional modifications.

#### 4.4.2. Anthropogenic modifications

Anthropogenic modifications are the most common marks resulting from the food processing phase. In level 5.1, 8.3% of the remains bear cut marks, 8.3% of the remains present percussion marks and 32.8% show traces of burning. In level 5.2, 5.2% of bones bear cut marks, 4.1% of the remains present percussion marks and the 28.3% show traces of burning. In level 5.3, the 3.7% of the remains bear cut marks, 4.3% of the remains present percussion marks and the 8.6% show traces of cremations. In addition, we identified 30 remains used as retouchers. Carnivore modifications are extremely scarce and only affect 0.6% of the bones in level 5.1, 0.2% in level 5.2 and 0.8% in level 5.3.

The distribution, orientation and types of cut marks provide evidence of the different butchering activities. The most common types of cut marks were slicing, indicating defleshing, followed by skinning, disarticulation and periosteum removal (Table 7). Almost all the cut marks correspond to slicing marks (Figure 8). In addition, scraping marks (5.1=3.7%; 5.2=1.4%; 5.3=1.6%) and chopping marks (5.3=0.4%) were identified. The taxon with the most cut-marked remains is the reindeer (5.1=18.3%; 5.2=11%; 5.3=6.7%), followed by red deer (5.1=57.6%; 5.2=21.2%; 5.3=15%), horse (5.1=11%; 5.2=9.6%; 5.3=2.6%) and bison (5.1=31.6%; 5.2=33.3%; 5.3=14.8%). The comparison of the number of cut-marked remains with the total of NISP indicates that bison and red deer are the species with the highest percentages (Table 6).

Most of the remains with cut marks were long bones (92% in level 5.1, 88% in level 5.2 and 73% in level 5.3), followed by flat bones (7% in level 5.1, 12% in level 5.2 and 25% in level 5.3). A total of 1% and 2% of unidentified bones presented cut marks in levels 5.1 and 5.3 respectively. None of the compact bones bear cut marks. In level 5.1, 29% of upper limb bones, 22.3% of intermedia limb bones and 12% of lower limb bones, bear cut marks. In level 5.2, 26.5% of upper limb bones, 13.6% of the intermedia limb bones and the 8.8% of lower limb bones, present cut marks. Finally, in level 5.3, 7.8% of upper limb bones, 10% of the intermedia limb bones and the 8.2% of lower limb bones, bear cut marks. The total percentage of long bones shaft fragments with cut marks is not high in any of the assemblages (9.3% in the level 5.1, 5.1% in level 5.2 and a 3.9% in level 5.3). The percentage of cut marks on epiphyses is higher (12% in level 5.1, 9% in level 5.2 and 11.1% in level 5.3).

Level	5.1						5.2						5.3					
Element	Reindeer	Red deer	Horse	Bison	Large-sized	Medium-sized	Reindeer	Red deer	Horse	Bison	Large-sized	Medium-sized	Reindeer	Red deer	Horse	Bison	Large-sized	Medium-sized
Skull	0/2		0/3		0/4	0/16			0/3		1/6	0/8		0/3	0/1		0/4	0/4
%	0		0		0	0			0		16.67	0		0	0		0	0
Mandible	1/6	0/1	1/10	0/1	1/6	0/6	0/5	0/1	0/2	1/2	2/9	0/4	3/21		0/15	0/2	2/15	0/5
%	16.7	0	10	0	16.7	0	0	0	0	50	22.2	0	14.3		0	0	13.3	0
Hyoid															1/1			
%															100			
Vertebrae	0/1				0/2	0/6	1/1				0/0	0/2			1/2		0/4	0/6
%	0				0	0	100				0	0			50		0	0
Rib	1/11		3/5		1/7	3/46	1/2				0/4	2/19	0/3		0/1		3/12	2/30
%	9		60		14.2	6.52	50				0	10.5	0		0		25	6.7
Scapula	1/4	0/2			0/1		0/1	0/1				0/2	1/5	0/2	0/1		0/1	0/1
%	25	0			0		0	0				0	20	0	0		0	0
Proximal limb	29/103	4/14	1/6	2/2	3/5	1/5	6/34	2/9	4/11	4/6	1/4	1/4	2/46	2/7	0/9	2/5	0/8	0/2
%	28.1	28.5	16.7	100	60	20	17.6	22.2	36.4	66.7	25	25	4.3	28.6	0	40	0	0
Intermedia Limb	43/207	11/32	3/11	3/11	2/12	1/11	6/52	3/10	0/9	1/7	0/1	0/2	9/92	0/3	1/17	2/15	0/1	1/2
%	20.7	34.3	27.2	27.2	16.7	9	11.5	30	0	14.29	0	0	9.8	0	5.9	13.3	0	50
Distal limb	16/144	4/23	0/3	1/4		2/20	5/60	2/10	1/3	0/1		0/18	5/57	1/4	0/4	0/1	0/1	1/5
%	11.1	17.4	0	25		10	8.3	20	33.3	0		0	8.8	25	0	0	0	20
Long bones					17/141	52/542					8/94	19/364					6/100	9/251
%					12	9.5					8.5	5.2					6	3.6
Flat bones					3/24	0/80					1/12	0/47					1/22	0/35
%					12.5	0					8.3	0					4.5	0
Total	91/498	19/76	8/73	6/19			19/172	7/33	5/52	6/18			20/298	3/20	3/115	4/27		
%	18.3	25	11	31.6			11	21.2	9.6	33.3			6.7	15	2.6	14.8		

Table 7 Number of remains with cut marks, total number and percentage of remains with cut marks by the anatomical element, taxon and weight size category.

The long bones with cut marks show that the butchering processes in level 5.1 were mainly related to flesh removal (78%), skinning (16%), periosteum removal (2%) and disarticulation (1%). For level 5.2, 70.3% of the cut marks on long bones indicate defleshing, 21% skinning, the 5% disarticulation and 2.7% periosteum removal. Finally, in level 5.3, 74% of the cut marks on long bones were related to defleshing, 16% to skinning and 10% to disarticulation.



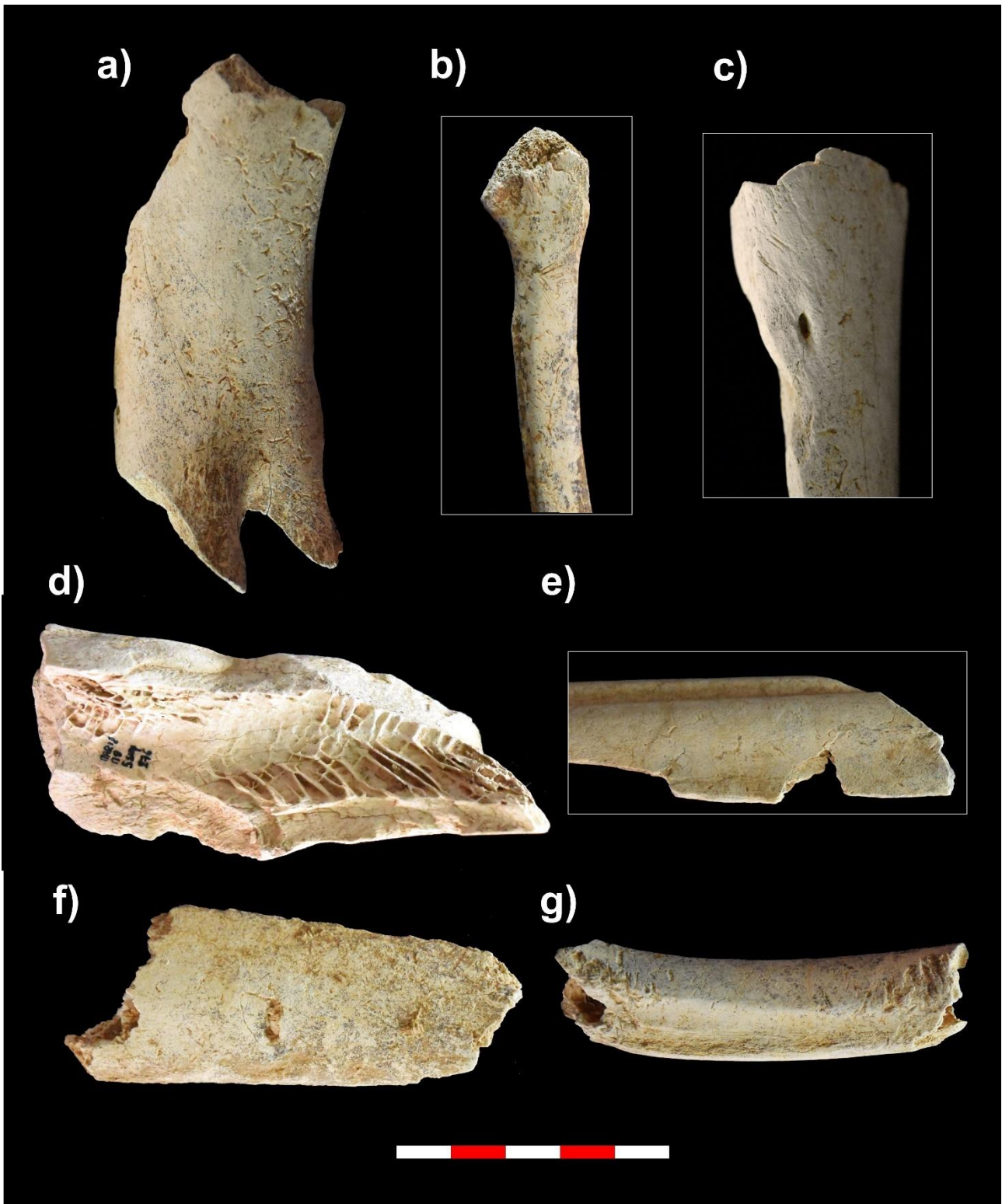


Figure 8 A) fragment of reindeer humerus with cut marks; c) horse hyoid fragment with cut marks; d) reindeer femur fragment with cut marks; d) fragment of reindeer humerus with anthropogenic bone breakage pattern; e) reindeer metatarsal with anthropogenic bone breakage pattern; f) rib fragment of a large-sized animal with carnivore tooth marks; g) rib fragment a medium-sized animals with carnivore furrowing marks. Scale bar = 5 cm.

A total of 195 remains from level 5.1, 59 remains from 5.2 and 71 from level 5.3 show anthropogenic bone breakage modifications. These were located mainly over long bones (NR: 5.1=194; 5.2=47; 5.3=58) (Figure 8). The identified anthropogenic breakage modifications were impact points (NR:

5.1=148; 5.2=49; 5.3=62), pseudo notches (NR: 5.1=22; 5.2=10; 5.3=9) and peeling (NR: 5.1=4; 5.2=1; 5.3=0). The remains of medium-sized animals present a higher number of bone breakage marks than large-sized animals. In medium-sized animals, the distribution of impact points on long limb bones is more variable in terms of their position on the bone, although there they are more common at mid-shaft. On the large-sized remains, impact points are mainly observed on the midshaft portion, except on a radius and tibia from level 5.1 and femurs from levels 5.2 and 5.3.

		Medium-sized									Large-sized								
		5.1			5.2			5.3			5.1			5.2			5.3		
Element	Face/Portion	P. 2	P. 3	P. 4	P. 2	P. 3	P. 4	P. 2	P. 3	P. 4	P. 2	P. 3	P. 4	P. 2	P. 3	P. 4	P. 2	P. 3	P. 4
Humerus	Anterior	2	5			1						1			1				
	Medial		3	1		1			2						1				
	Posterior		2	1		2			1	1					3				1
	Lateral		2	1		2	1		3										
Radius	Anterior		1		1	1			1			3			1				1
	Medial		5	1					2										
	Posterior		4					1				1	1						
	Lateral		2						1			1							
Femur	Anterior	1	6	1	1	2		1	1										
	Medial		2			1			1									1	
	Posterior		5	1		1	1		3									1	1
	Lateral		2			1			2	1		2				1			
Tibia	Anterior		5	4		1	1			1					1				1
	Medial		3	1			1	1	2			1				1			
	Posterior		7	3		2	1			1		3	1		1				
	Lateral	2	6			1			2		1	1	1						
Metapodials	Anterior	2	7	1		1				1									
	Medial		4			1				2		1							
	Posterior		4			2						1							
	Lateral		8			1				2					1				

Table 8 Number of remains with impact points for medium-sized and large-sized animals per long bone element, showing the distribution of impact points on the bone face and portion.

Traces of burning were more abundant in levels 5.1 and 5.2. In level 5.3, they were scarce compared with the overlying levels. Fire damage affects 32.8% of the remains from level 5.1, 28.3% from level 5.2 and 8.6% from level 5.3. All the degrees of burning have been identified (Table 9). In levels 5.1 and 5.2, degree 1 is the most common and the calcinated remains are the least represented. In level 5.3, charred bones (degree 3) are the most frequent. (Table 9). Single-coloured thermal alterations are prevalent in all levels, whereas double or multiple colourations are relatively rare. In level 5.1, single-coloured alterations account for 87% and in level 5.2, 90.1% of the burnt bone sample. Only single-coloured alterations were observed in level 5.3.

Levels		Burned stages					
		Unburned	1	2	3	4	5
5.1	NSP	1685	684	339	54	183	3
	%NSP	57.2	23.2	11.5	1.8	6.2	0.1
5.2	NSP	1015	250	132	206	12	1
	%NSP	62.8	15.5	8.2	12.7	0.7	0.1
5.3	NSP	1333	43	7	60	16	1
	%NSP	91.3	2.9	0.5	4.1	1.1	0.1

Table 9 Number of remains for each degree of burning per level. Remains with more than one code were indicated in each of the corresponding codes. Double colourations were included in each single code of burning.

#### 4.4.3. Carnivore modifications

A total of 16 remains from level 5.1 show carnivore modifications, three remains from level 5.2 and 12 from level 5.3. The surface modifications from level 5.1 are pits and punctures (NR=11), scores (NR=5), furrowing (NR=3), crenulated edges (NR=3) and five remains with cusps on the fractured edge (Figure 8). In level 5.2, punctures (NR=2) and tooth notches were identified on fractured (NR=2). In level 5.3, punctures (NR=6), scores (NR=5), and furrowing (NR=6: strong=5; moderate=1) were observed. The frequency of remains with carnivore modification by weight category shows that medium-sized animals was the most affected (NR: 5.1=11; 5.2=3; 5.3=8), followed by large animals (NR: 5.1=4; 5.3=4). Distribution by bone category indicates that tooth marks show similar distributions on long bones (NR=9) and flat bones (NR=8) in level 5.1, a higher proportion of flat bones in level 5.2 (NR: long=1; flat=2) and a higher proportion of long bones in level 5.3 (NR: long=9; flat=3). In level 5.1, 6% of the epiphyses bear tooth marks, none in level 5.2, and 8.3% in level 5.3. The percentage of near epiphyses affected by carnivore activity was smaller; 0.7% bear tooth marks in level 5.1 and 5.3 and none in level 5.2. Pit measurements were treated statistically for all the shaft fragments from level 5 combined due to the scarcity of measurable modifications in general. The size of the modifications suggests the action of at least one large carnivore (Andrés et al., 2012; Selvaggio and Wilder, 2001) (Figure 9). However, considering the average dimensions of the pit and puncture marks, and their 95% confidence interval, the small size of the sample did not yield a statistically significant result.

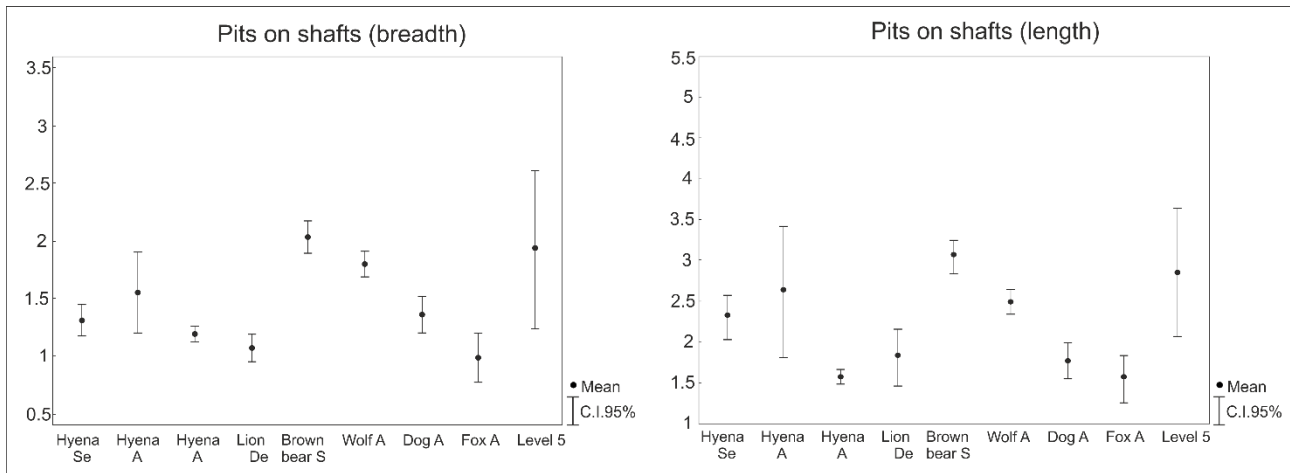


Figure 9 Mean percentages and one standard deviation of tooth pit sizes on dense cortical in function of bone according their width and length. Data for sampled/specimens marked by: Se from Selvaggio (1994); A from Andrés et al. (2012); De from Domínguez-Rodrigo and Piqueras (2003); S from Saladié et al. (2013).

One remains from level 5.3 presented human and carnivore modification, but with no overlap between them. This was a fragment of a reindeer ulna, with slicing marks on the caudal edge of the olecranon in the midshaft and on the posterior face, which also presents furrowing on the head of the ulna.

## 4.5. Bone retouchers

We identified a total of 30 bone retouchers in level 5 (Figure 10); 18 in level 5.1, 10 in level 5.2 and 2 in level 5.3 (Table 10). In level 5.1, tibia fragments were the most widely used anatomical elements for retouchers with two reindeer remains and one each for bison, horse and red deer. These were followed by two fragments of reindeer femurs and one fragment of a bison humerus. A total of eight unidentified long bone fragments were used as retouchers, six of which belong to large-sized mammals and two to medium-sized animals. In level 5.2, the most commonly used anatomical element was the tibia, with a red deer fragment and a bison fragment. In addition, we identified a horse radius fragment, a reindeer femur, a reindeer metatarsal and a fragment of a large-sized mandible. A total of four unidentified long bone fragments were used as retouchers, three from large animals and one from a medium-sized animal. In level 5.3, only two long bone remains from large animals were used as retouchers. These results indicate that large and medium-sized specimens were used as retouchers in equivalent proportions (NR: 9/9) in level 5.1. Meanwhile, in level 5.2, large-sized remains were more widely used as retouchers than medium-sized remains (NR: 8/3), and in level 5.3, only large-sized remains were used. In general, more long bone fragments were used than flat bones (NR: 5.1=18/0; 5.2=11/1; 5.3=2/0).

Bone retouchers				Type of marks			Depth of the marks			Location of blank	Position on width
Level	Element	Taxa	NR	Pits	Scores	Areas	I1	I2	I3		
5.1	Humerus	Bison	2	Triangular	Rectilinear	Hatched area		1		Apical	lateral
	Femur	Reindeer	2	Triangular	Rectilinear	Hatched area	1	2		Apical	Lateral/centred
	Tibiae	Bison	1	Triangular	Rectilinear/rough	Scaled/pitted area	1	1		External/centred	Lateral/centred
		Red deer	2	Triangular	Rectilinear	Hatched area	1	1		Apical/centred	centred
		Horse	1	Triangular	Rectilinear			1	1	Covering/centred	Apical/basal
		Reindeer	2	Triangular	Rectilinear	Hatched/ pitted area	1	1	1	centred	Apical/basal
	Metatarsal	Red deer	1	Triangular	Rectilinear	Hatched area		1		centred	Apical
	Long bone	Large size	6	Triangular	Rectilinear/smooth	Hatched/ pitted/scaled area	6	5		Apical/centred/lateral	Apical/basal
	Medium size	3	Triangular	Rectilinear	Hatched area	2	2		centred	Apical/basal	
5.2	Mandible	Large size	1	Triangular	Rectilinear	Hatched area	1			centred	centred
	Radius-Ulnae	Horse	1	Triangular	Rectilinear	Hatched area	1			Apical	centred
	Femur	Reindeer	1	Triangular	Rectilinear	Hatched area	1	2		Apical	Lateral
	Tibiae	Bison	1	Triangular	Rectilinear	Hatched area		1		centred	Apical
		Red deer	1	Triangular	Rectilinear	Hatched area	1			Apical	centred
	Metatarsal	Reindeer	1	Triangular	Rectilinear	Hatched area		1		centred	centred
	Long bone	Large size	3	Triangular	Rectilinear/smooth	Hatched/scaled area	5	4		Apical/centred	Apical/basal
		Medium size	1	Triangular	Rectilinear	Hatched area	2	2		Centred	Apical
5.3	Long bone	Large size	2	Triangular	Rectilinear/smooth	Hatched/pitted area	1	1		Apical/centred	Apical/basal

Table 10 Number of retouchers and description of used areas and types of modification by anatomical elements and taxon in the three levels.



Figure 10 Retoucher from level 5 of Abri du Maras: a) Bison humerus; b) Horse tibia; c) Bison tibia; d) Horse femur; e) Red deer tibia; f) Long bone fragment of a large-sized animal. Scale bar = 5 cm.

## 5. Discussion

In the Abri du Maras sequence, the study of the well-preserved material provides evidence of Neanderthal subsistence in south-eastern of France from the MIS 5 to the end of the MIS 3. The taxonomic diversity of the levels studied here 5.1, 5.2 and 5.3, is similar, between them as indicated by the values of Evenness and the Simpson index. The animal spectrum is centred on medium- and large-sized ungulates, a pattern commonly observed in Eurasian Neanderthal assemblages (Adler et al., 2006; Adler and Bar-Oz, 2009; Costamagno et al., 2006; Daujeard and Moncel, 2010; Farizy et al., 1994; Gaudzinski and Roebroeks, 2000; Jaubert and Brugal, 1990; Marín et al., 2017a; Moncel et al., 2004; Patou-Mathis, 2000; Real et al., 2018; Stiner, 1994; Yravedra and Cobo-Sánchez, 2015). In the three levels, large-sized animals were represented exclusively by horse and bison. The giant deer observed in level 4 was not identified in level 5 (Daujeard et al., 2019; Vettese et al., 2017).

The presence of reindeer, horse and bison indicate an open landscape. Taxa typical of forested areas, such as wild boar and roe deer, suggest the exploitation of several biotopes in levels 5.1 and 5.2. The Abri du Maras is located on an ecotone, which enabled the exploitation of the gorge of Ardèche River, the plateaus around the site and the alluvial plains of the Rhône Valley. In addition, this position provided accesses to the plateaus of the farther Massif Central, which was conducive to the exploitation of multiple environments by Neanderthals. In level 4.1 of Abri du Maras, the isotopic results and tooth wear indicated different exploitation areas for red deer and giant deer (forested), on one hand, and horse and reindeer (open lands), on the other (Daujeard et al., 2019). Similar results were shown at the site of Payre (MIS 7-6), further north on the same side of the Rhone valley, where horses were exploited in the valley and deer in the highlands (Ecker et al., 2013; Moncel et al., 2019). However, this assumption should be treated with caution on account of the ecological plasticity of ungulates, which can potentially live in diverse ecosystems and climatic conditions (Discamps et al., 2011).

In order to determine whether an assemblages as results from primary hominin accesses to animal carcasses, Domínguez-Rodrigo (1997) indicated that long bones with cut marks made by flesh removal should account for between 30% and 60% of the assemblage. The percentage of cut marks should be higher for proximal appendicular elements than for intermediate elements, which should in turn be higher than for distal elements. In central areas of long bones shafts, the percentage of cut marks should reach more than 43% (Domínguez-Rodrigo, 1997). In the levels 5.1, 5.2 and 5.3 of the Abri du Maras, most of the cut marks were identified on the long bones. Upper limb bones show a higher percentage of cut marks in levels 5.1 and 5.2 than intermedia limb bones and especially than lower limb bones. In level 5.3, the percentage of cut marks is higher for intermedia and lower limb bones than for upper limbs. More than 70% of long bones with cut marks in the central diaphysis and were related to defleshing. All these data indicate primary accesses to animal carcasses by hominins (Capaldo, 1998, p. 199; Domínguez-Rodrigo et al., 2007; Lupo and O'Connell, 2002; Selvaggio, 1998). The presence of a single carnivore remains, combined with the prevalence of anthropogenic modifications and the scarcity of modifications produced by carnivores and others taphonomic processes, such as hydric flows, show that these three assemblages result from Neanderthal activity. Carnivore activity is limited to scavenging of remains abandoned by humans.

Skeletal profiles in levels 5.1, 5.2 and 5.3 of the Abri du Maras indicated a predominance of long bones over the axial skeleton. The exception was the abundance of cranial remains for reindeer in level 5.3 and for horse in all three levels. These were related to the abundance of mandible and maxilla remains and isolated teeth. Postcranial axial skeleton remains, and compact bones were scarce for all taxa. The comparison of the results of the analysis of bone portions representation with their mineral density suggests differential attrition of the least dense elements. However, the presence of fragments of postcranial axial skeletons are present for all large-sized and medium-sized taxa, indicating that the trunk was transported some distance from the kill/butchering site. Primary accesses is characterized by the predominance of high-ranked elements with more flesh on them, which is why they were more often transported to the residential site (Binford, 1981, 1978; Bunn and Ezzo, 1993; Domínguez-Rodrigo and Pickering, 2003; Isaac, 1983; Monahan, 1998; O'Connell et al., 1992).

The analysis of transport strategies for reindeer indicated a bulk strategy in all three levels. The bulk strategy is common among present-day hunters-gatherers when demand for meat is high and they need to transport as much mass as possible to the camp (Binford, 1978; Schoville and Otárola-Castillo, 2014). The transport of reindeer carcasses privileged high-value elements in all levels, but heads were more often transported to level 5.3 than to the upper levels of the assemblage. Daujeard et al. (2019) indicated that a deficiency in the presence of isolated teeth and antler in level 4.1 could indicate that the heads were abandoned on the kill site. Often, the lack of skull bones is indicative of increased transport distances (Reynard and Henshilwood, 2017; Schoville and Otárola-Castillo, 2014). Therefore, the abundance of teeth and antler for reindeer and teeth for horse could indicate the opposite scenario, with shorter transport distances. This is all the more likely considering that all the assemblages were affected by differential destruction in the same way.

Anatomical horse profiles were dominated by skull remains in the three levels. However, the statistical analysis indicated an unbiased strategy for horses in level 5.1 and did not give clear results for levels 5.2 and 5.3, indicating a possible unconstrained or bulk strategy, probably related to a statistical error Type II (Faith and Gordon, 2007). Similar high proportions of horse skulls were observed in the Aurignacian site of Vogelherd (Niven, 2007). At the latter site, a possible different distance from the kill site (short distance), combined with the major economic utility of heads, may have favoured the transport of horse skulls to the site (Niven, 2007). Hadza groups transport complete zebra carcasses to central places more often than any of the other taxa (Lupo, 2006; Monahan, 1998). Ethnoarchaeological studies indicate that horses skulls were highly valued by hunter-gatherers, for their high quantity of tissues (O'Connell et al., 1988) and because the horse skull was less vulnerable to fat depletion compared to other parts (Levine, 1998; Lupo, 1998; Stiner, 1994). Consequently, the abundance of horse and reindeer heads in level 5.3 could be related to shorter transport distances. However, we must also bear in mind that the transport of heads could possibly represent the cooperative transport of animal carcasses, as demonstrated for other archaeological sites (Marín et al., 2017b; Rodríguez-Hidalgo et al., 2015; Saladié et al., 2011; Stiner, 2013) and by ethnographical studies (Lupo, 2001; Monahan, 1998).

The statistical analysis of the transport of red deer was not resolute in any of the levels. Anatomical distribution was similar to reindeer distribution, dominated by long limb bones in levels 5.1 and 5.2,

and dominated by cranial elements in level 5.3. For bison, the statistical analysis indicated a bulk strategy for level 5.2, but not for levels 5.1 and 5.3. Anatomical distribution was diversified, although long limb bones were abundant in three levels. Therefore, the small assemblage of red deer and bison did not identify a transport strategy in levels, but the anatomical profiles indicated that most of the skeleton parts were transported to the rock shelter at some stage.

Therefore, in the three levels, there is a tendency to transport the elements trying to optimize their economic values. This is particularly true for reindeer in levels 5.1 and 5.2, where the correlation of skeletal profiles and UMI identify a possible preference in the transport of bones in relation to their marrow and mono-unsaturated grease content. Otherwise, for reindeer from level 5.3 and horses, the transport of more complete carcasses may indicate a possible shorter distance to the kill site. In general, hunter-gatherers try the quantity of carcass products discarded at the kill/butchering site and maximize the quantity transported to a central site (Lupo, 2006).

The identification of primary access, the immediate and recurrent access to large ungulate carcasses has been interpreted as the result of cooperative hunting (Monahan, 1998; Rodríguez-Hidalgo et al., 2015; Saladié et al., 2011; Stiner, 2013; Stiner et al., 2009). Tactical hunts require cooperation between individuals for killing the animals and for storing and transporting the meat (Marean and Assefa, 1999; Monahan, 1998; Saladié et al., 2011; Stiner, 2013). Ju/'hoansi groups increase their chances in ambush hunting events by using cooperative methods (Hitchcock et al., 2019; Lee, 2012). Hayden (1981) related an increase in cooperation during hunting and meat-sharing in relation with the importance of this resource for the group. Considering the size of some of the preys captured in levels 5.1, 5.2 and 5.3, such as horse or bison, cooperative hunting was likely, as was the cooperative transport of animal carcasses. Monahan (1998) observed that when the Hadza capture a zebra-sized prey, they transport all or almost all of the animal carcass because they can organize large carrying parties. When they capture an animal, they can spend unlimited time at the kill/butchering site, and one of the hunters can stay with the carcass until additional carriers can be located to help with transport, which can require groups of 12 or more adults. In levels 5, cooperative hunting and cooperative transport strategies, which privileged the transport of elements with high nutritional values, could explain the widespread transport of heads, especially in level 5.3.

The use of certain complementary species in subsistence strategies has been proposed for sites with one predominant taxon, such as the Middle Palaeolithic sites of Jonzac, Les Pradelles, Pech de l'Aze IV and in level 4.1 of Abri du Maras (Costamagno et al., 2006; Daujeard et al., 2019; Niven, 2013; Niven et al., 2012). In the latter assemblage, hunting was centred on reindeer and the capture of horse and bison were secondary (Daujeard et al., 2019). This scenario could be maintained in levels 5.1, 5.2 and 5.3, if we consider the NISP, but differs in respect to the MNI, which is higher for horse and bison than in level 4.1. Similar percentages have been observed in levels Ja and P of Abric Romaní (Marín et al., 2019; Rosell et al., 2012), where red deer reached 50.7% of the NISP in Ja, 63% in Pa and 60% in Pb, as opposed to 35.8% of the NISP for horse in Ja, 22.6% in Pa and 32.2% in Pb, where subsistence is mainly related to the exploitation of these two species.

The results of mortality profile construction indicate a preference for the capture of prime adult individuals for all species, for the three levels. The mortality profiles of reindeer are dominated by



prime adults, prime-dominated for horses in levels 5.1 and 5.2 and catastrophic in 5.3. Finally, although red deer and bison individuals are rare, all the animals for which age could be identified were prime adults. Stiner (1990) defines humans as ambush predators with a tendency to systematically capture prime adult individuals. Besides, prime-dominated profiles have been proposed in different ethnoarchaeological and archaeological studies as a result of primary accesses, (Binford, 1978; Bunn and Gurtov, 2014; Bunn and Pickering, 2010a, 2010b; Frison, 1984; Gaudzinski and Roebroeks, 2000; Patou-Mathis, 2000; Stiner, 1990, 2013). Stiner and Kuhn (2006) propose that humans are the only predators who frequently targets the reproductive core of animal populations, this is prime adults. Speth (2019) linked the preference for prime adults, with the highest overall fat levels, to a high dependence on these resource for the calorific supply of Neanderthals groups. Bunn and Gurtov (2014) specify that high rates of prime adults as a result of non-selective ambush hunting result in assemblages with more than 70% of prime adult individuals because prime adult animals predominate in the ecosystem. The mortality profiles identified in this work are dominated by prime adults, with 78.5% in level 5.1, 83.3% in level 5.2 and a 71% in level 5.3. These are over the 70% limit defined by Bunn and Gurtov (2014).

According to the zones developed by Discamps and Costamagno (2015), the reindeer profiles in levels 5.2 and 5.3 indicate prime adults and reindeer in level 5.1 and horse in all levels into the JPO zone, related to L-shaped profiles. However, the JPO zone could not be systematically linked to non-selective hunting, as a result of the variation of the curve of the living-structure profile related to environmental changes or the response to predation pressure (Discamps and Costamagno, 2015). The seasonal data for reindeer suggests a specific capture window during summer for levels 5.1 and 5.3. Unfortunately, there were no data for young reindeer individuals in level 5.2. Data for horse indicated the use of the site during summer in the three levels, although levels 5.1 and 5.3 also point to site use during part of the autumn and level 5.2 for part of spring (Figure 5). Therefore, animals were mainly killed in summer, at a period when ungulate populations comprise a high proportion of juvenile individuals. Levine (1983) indicated that the active hunting of bachelor groups of male horses generated profiles with a higher proportion of prime adults. Although prime adults predominate for the horse in the Abri du Maras, young individuals were also present in the assemblages, especially for in level 5.3, which indicates that groups of females with their foals were also exploited. For reindeer, the predominance of prime adults is even higher than for the horse and they were killed during the same season. Therefore, if hunting was non-selective, we could expect a higher percentage of juvenile reindeer individuals, especially if we consider Damuth's rule which proposes that population densities are inversely related to body size in animal communities (Morin and Ready, 2013). Therefore, these could be related to ambush hunting preferentially killing prime adults. As for the question of whether the prime-dominated profile was the result of selective hunting or simply a statistic issue related to the abundance of prime animals, we opt for a selective tendency, especially in the case of reindeer. For the FLK Zinj assemblage, Bunn and Pickering (2010a) suggest that ambush hunting by projectiles generated a prime-dominated profile. The presence of the projectile technology was clearly identified in the European archaeological record after the discovery of wooden spears at the Middle Pleistocene sites of Schöningen (Schoch et al., 2015; Thieme, 1997) and Clacton-on-Sea (Allington-Jones, 2015; Oakley et al., 1977). This indicates that the spears productions existed

in the Neanderthals lineage. This technology was previously identified at Abri du Maras by Hardy et al. (2013) through the study of projectile point fractures.

A lot of research defines campsites as places where groups generally organized in domestic units live and develop most of their activities (Bartram, 1993; Binford, 1980, 1978; Gamble and Boismier, 1991; Jones, 1983; Kelly, 2013; Kent, 1987; Kroll and Price, 1991; O'Connell et al., 1992, 1988; Yellen, 1977). Isaac's proposals (Isaac, 1978) regarding campsites and livings floors for Pleistocene Hominins are useful for describing Neanderthals sites if we consider the social-related aspect. These include the capture of large quantities of meat, for delayed consumption, and transport to a different place, probably at some distance from the kill/butchering site, undoubtedly related to food-sharing events. The occupation of Abri du Maras during the formation of levels 5.1, 5.2 and 5.3 could correspond to the typical features of a residential camp where high quantities of food were transported and processed in situ, during cooperative events. This feature could explain the higher ratio of flake tools and of some Quina scrapers and bifacial scrapers made on thin flint slabs collected on the southern plateau.

The Middle Palaeolithic record from the south-eastern Rhône valley region has been widely studied, and Abri du Maras is one of the main reference sites (Daujeard et al., 2019; Daujeard and Moncel, 2010; Moncel and Daujeard, 2012; Moncel, 2010; Moncel et al., 2019, 2004). Daujeard and Moncel (2010) identified three main types of sites in the area: 1) Type I: Long-term residential camps characterized by recurrent human accumulation (high rate of anthropogenic modifications), seasonal selective hunting with a specialized hunting spectrum, transport of whole carcasses or best pieces, presence of bone retouchers, complete or mostly complete lithic sequences on local stones, a low percentage of tools; 2) Type II: Short-term regular camps, with recurrent human accumulation interspersed with carnivore visits, seasonal selective hunting with a varied herbivore spectrum, with scavenging events, particularly of very big animals, some retouchers, mostly complete lithic sequence on flint, exogenous flint, a moderate number of tools; 3) Type III: Brief stopping-places: natural or carnivore accumulations with some human occupations, very scarce or absent burnt bones, scarce or absent retouchers, mostly complete lithic sequences, high proportions of tools and low density of lithic remains. This regional analysis enabled us to interpret the regional land use pattern of Neanderthal groups as a farsighted circulating model, with recurrent base camps and satellite hunting camps. In this classification, Abri du Maras was defined as an archaeological type I site (Daujeard and Moncel, 2010). In more recent work, the occupation of level 4.1 was described as a campsite for short but repeated occupations, in which Neanderthal groups developed hunting centred on the mass killing of reindeer herds, probably when they crossed the Ardèche River during the autumn migration (Daujeard et al., 2019).

As shown above, levels 5.1, 5.2 and 5.3 were the result of the Neanderthal activity. In the upper levels of Abri du Maras (level 4.1 and 4.2), the accumulations were also described as resulting from Neanderthal activity, with inexistent carnivore activity was inexistent (Daujeard et al., 2019; Vettese et al., 2017). These features have also been identified in other Middle Palaeolithic sites used as residential camps (Cáceres et al., 2012; Castel et al., 2017; Chacón et al., 2010; Gabucio et al., 2014b; Niven, 2013; Real et al., 2018; Yeshurun et al., 2007), where similar accumulations were observed,

such as Saint Marcel, where the 40% of the remains show anthropogenic modifications, or in Baume des Peyrards where 18.2% of all remains were modified by hominins. In addition, carnivore modifications were particularly rare in these sites (NR%: Saint Marcel=4%; Baume des Peyrards=0.8%).

The high degree of burning has been related to high intensity or repeated occupations, whereas low levels of fire damage indicate low intensity occupations (Castel et al., 2017; Costamagno et al., 2006; Gabucio et al., 2014b; Marín-Arroyo, 2013; Niven et al., 2012). At Wanderer's Cave (Australia), analysis of the burning signal indicated that the majority of the faunal specimens were unintentionally burned (Asmussen, 2009), and that more intensive human occupation led to increased frequencies of thermal modification events. Conversely, short occupation events have been related to less evidence of human occupation or cooking opportunities (Asmussen, 2009). Levels 5.1 and 5.2 comprise a high percentage of burned remains, whereas level 5.3 presents low rates of burning. These could be related to low-intensity occupation in levels 5.3, which could indicate differences between the level 5 occupations, although the taxonomic composition and anthropogenic activities seem to indicate the contrary. We also have to keep in mind that the topographical aspect of the shelter differed over time during the infilling of level 5. The deposit indicates that the shelter was large and possibly extended over two sides of the small valley. Over time, the roof collapsed, and the shelter is now only visible on the right side of the valley. We can infer from quantity of blocks in the level 5 deposit that the shelter roof also slowly decreased in size before the big collapse between levels 4 and 5.

Long-term occupations usually comprise diversified provisioning strategies over one or several seasons (Audouze, 2010; Bicho and Cascalheira, 2020), whereas short-term occupations show restricted provisioning strategies and multi-seasonal occupations (Costamagno et al., 2006; Martínez-Moreno et al., 2004; Niven et al., 2012; Vallverdú et al., 2005; Villaverde et al., 2017). However, this assumption should be considered carefully, as in some archaeological sites related to short-term occupation events, only one occupation season is observed, such as the French sites of Abri du Maras level 4.1 (Daujeard et al., 2019), les Pradelles (Costamagno et al., 2006), Grotte du Bison (Bouchard, 2016) or Pech de l'Azé IV level 4 (Niven, 2013), or the Spanish sites of Abrigo de la Quebrada (Real et al., 2019). In levels 5.1, 5.2 and 5.3, the site was especially occupied in summer for reindeer, although the horse showed certain variability, including autumn kills in levels 5.1 and 5.3 and spring slaughter in 5.2, and therefore could indicate long-term (seasonal) occupation events. It is important to highlight that young individuals (from dental eruption and replacement patterns) and adults (from tooth microwear) display evidence of the same seasonal dynamic.

Finally, the percentage of retouchers is higher at sites used as residential camps (Daujeard and Moncel, 2010). In level 5.1, the percentage of bone retouchers was 2.6% and for level 5.2, 1.6%. In level 5.3, only two retouchers were found. These proportions are similar to those recorded at other MIS 5 sites in region used as long-term campsites, such as of Baume des Peyrards (2%) or Saint Marcel (3%). On the other hand, sites from MIS 4 comprise lower percentages of retouchers, such as level 4.1 of Abri du Maras (<1%), Barasses (1%) or Grotte du Figuier (1%) (Daujeard and Moncel, 2010).

Ethnoarchaeological studies indicate that the choice of hunting places was generally linked to contexts where prey behaviour could be predicted, such as migration routes, near streams, lakes, springs or ridges, among others (Binford, 1978; Hitchcock et al., 2019). Despite the differences between levels 4.1 and levels 5 of Abri du Maras, the repeated use of the site as a campsite indicates the importance of the rock shelter for Neanderthal subsistence strategies. This repeated use may be due to the position of the site which offered refuge and easy accesses to different types of habitats (Daujeard and Moncel, 2010; Moncel and Daujeard, 2012). The results from levels 5.1, 5.2 and 5.3 classify the Abri du Maras level 5 occupation as a residential camp used repeatedly for a complete season, especially in summer, for the exploitation of large ungulates, namely cervids, horse and bison.

## **6. Conclusions**

As a result of our analysis, we can confirm that during the formation of levels 5.1, 5.2 and 5.3, Neanderthal groups used the Abri du Maras rock shelter as a seasonal campsite for long-term occupation events, especially in summer. The taxonomical distribution in level 5 could indicate a more temperate climate, with the presence of forest species, and an open landscape, with taxa typical of plains. Neanderthals intensively exploited faunal resources around the shelter, located in a small valley close to the Ardèche River. The type of occupation, i.e., a long-term residential habitat, appears different from that of level 4.1 (MIS 3), which highlights short-term episodes of reindeer hunting. In level 5, the lithic assemblage shows a higher ratio of flake tools, including some large scrapers, possibly a limited introduction of already worked products and a higher quantity of whole pebbles in diverse stones collected along the Ardèche River. They indicate strategies adapted to long-term occupations with various domestic activities. Mortality profiles indicate preferential selection of prime-dominated reindeer, red deer and horse, mainly killed during the summer. However, horses were also killed during the autumn, which could indicate different seasonal events. Our data indicate that the most probable hunting strategy was cooperative ambush hunting. After capture, the transport of animal carcasses optimizes the food values of the transported elements, which is a typical pattern for sites used as residential camps. However, the high percentage of cranial remains for reindeer in level 5.3 and horses in all levels seems to indicate that the transport distance or the number of carriers facilitated the repeated transport of this anatomical element. Future isotopic analyses and studies of micro and meso wear will indicate the type of feeding and mobility of reindeer and horse in levels 5. Considering the ecological behaviour of these species and the data discussed above, the expected scenario would be the exploitation of the plain for reindeer and horses and the plateau for red deer and other forest species. In the future, it would be interesting to compare occupation dynamics and subsistence strategies with other sites of the region and especially with the upper levels 4.1 and 4.2 of Abri du Maras.

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# Supplementary materials

	<i>Rangifer tarandus</i>		<i>Cervus elaphus</i>		<i>Equus ferus</i>		<i>Bison priscus</i>		<i>Capreolus capreolus</i>		<i>Sus scrofa</i>		<i>Oryctolagus cuniculus</i>		Medium size		Large size	
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
5.1																		
Cranium	2	2			3	2				1					16	1	4	1
Mandible	6	3	1	1	10	9	1	1							6	2	6	1
Isolated teeth	8		2	1	18				1									
Vertebrae	1	1													6	5	2	1
Rib	11	4			5	2									46	5	7	1
Scapula	4	2	2	2													1	1
Coxal	1	1					1	1							1	1	4	3
Humerus	41	10	9	3	1	1	2	1	1	1					2	1	4	1
Radius	48	11	12	3	4	2	4	2							1	1	1	1
Radius/ulna	13	4	2	1														
Ulna	11	8			1	1	1	1							1	1		
Carpal	2	2	14	3	1	1			1	1								
Metacarpal	21	7			3	2	1	1	1	1					2	1		
Femur	62	16	5	3	5	2							1	1	2	1	1	1
Patella	1	1																
Tibiae	135	20	18	5	6	2	6	2							7	2	11	2
Astragalus																		
Calcaneum	1	1											1	1				
Tarsal					1	1												
Metatarsal	115	16	7	2			2	1			1	1			5	1		
Metapodial	8		2	1			1	1							15	2		
Sesamoid	2	2																
Phalange I	2	2	2	2														
Phalange II	2	2																
Phalange III	1	1																
Fragment of teeth					15										6		7	
Long bone															542		141	
Flat bone															80		24	
Total	498	116	76	27	73	25	19	11	4	4	1	1	2	2	738	24	213	13

Table S1 Number of identified specimens and minimal number of elements by anatomical elements for the principal taxa and weight sizes categories of level 5.1.

	<i>Rangifer tarandus</i>		<i>Cervus elaphus</i>		<i>Equus ferus</i>		<i>Bison priscus</i>		<i>Sus scrofa</i>		<i>Dama dama</i>		<i>Canis lupus</i>		Medium size		Large size		Small size		
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	
5.2																					
Craneum	0	1			3	4										8	1	6	1		
Mandible	5	2	1	1	2	3	2	1								4		9	1		
Isolated teeth	8				11																
Hyoid																					
Vertebrae	1	1														3	2				
Rib	2	1														19	3	4	1	2	1
Scapula	1	1	1	1												2	1				
Coxal	3	2	1	1	2	1										1	1				
Humerus	10	2	6	3	4	2	6	2								1	1	3	1		
Radius	12	3							1	1								1	1		
Radius/ulna	5	1			4	1	1	1													
Ulna	4	1	1	1					1	1											
Carpal																					
Metacarpal	11	3	5	2	1	1	1	1					1	1		2	1				
Femur	24	6	3	2	7	2	1	1								3	1	1	1		
Patella																					
Tibiae	31	7	9	3	5	2	6	2								3	1				
Astragalus																					
Calcaneum																					
Tarsal	2	2			2	2					1	1									
Metatarsal	47	9	5	1												7	1				
Metatarsal vest																					
Metapodial	2				2											9					
Sesamoid																					
Phalange I					1	1	1	1													
Phalange II																					
Phalange III	1	1					1	1													
Fragment of teeth	2		1		8											15		10		2	
Long bone																346		94		5	
Flat bone																47		12			
Total	171	43	33	15	52	19	19	10	2	2	1	1	1	1	470	13	140	6	9	1	

Table S2 Number of identified specimens and minimal number of elements by anatomical elements for the principal taxa and weight sizes categories of level 5.2.

5.3	<i>Rangifer tarandus</i>		<i>Cervus elaphus</i>		<i>Equus ferus</i>		<i>Bison priscus</i>		Medium size		Large size		Small size	
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Craneum	3	10		1	1	6		1	4	1	7	1		
Mandible	21	13			15	8	2	2	5	1	15	1		
Isolated teeth	50		4		26									
Hyoid					1	1								
Vertebrae					2	2			6	2	4	2		
Rib	3	2			2	1			30	6	12	3		
Scapula	5	3	2	2	1	1			1	1	1	1		
Coxal	6	2			1	1	1	1						
Humerus	18	4	5	2	2	2	4	2			6	1		
Radius	23	6	1	1	1	1	7	2						
Radius/ulna	10	2			4	2								
Ulna	5	2			2	2	4	3						
Carpal	1	1					1	1						
Metacarpal	11	4	1	1			1	1						
Femur	28	8	2	1	7	3	1	1			2	1		
Patella														
Tibiae	54	10	2	1	10	3	4	1	2	1	1	1		
Astragalus	2	2			1	1								
Calcaneum	3	3												
Tarsal	2	2			2	2								
Metatarsal	41	7	3	1	4	2			3	1				
Metatarsal vest					3	3								
Metapodial	5								2		1	1		
Sesamoid	1	1												
Phalange I	2	2												
Phalange II					1	1								
Phalange III														
Fragment of teeth	4				28				14		13		5	
Long bone											100		5	
Flat bone											22		1	
Total	298	84	20	10	114	42	27	15	67	13	184	12	11	0

Table S3 Number of identified specimens and minimal number of elements by anatomical elements for the principal taxa and weight sizes categories of level 5.3.

**Chapter 7. Taphonomic analysis of horse remains  
from Mousterian and Aurignacian Units  
from Bize-Tournal Cave (Aude, France)**



# **Taphonomic analysis of horse remains from Mousterian and Aurignacian Units from Bize-Tournal Cave (Aude, France)**

## **Analyse taphonomique des restes de chevaux des unités moustériennes et aurignaciennes de la grotte de Bize-Tournal (Aude, France)**

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## **Abstract**

Caves were systematically used as shelter by carnivores and hominins groups. The study of ungulate assemblages is essential for understand hominins and carnivore behavior, as well as their interactions when the two agents shared the space. For this reason, many studies involve the taphonomic analysis of faunal remains, focusing on the identification of the various biotic actors. This study looks at the horse assemblages from Mousterian and Aurignacian Units I, II and III from Bize-Tournal cave with the aim to characterizing the nature of this accumulation. Here we show that the horse remains in this units are mainly the consequence of carnivore activity. Unit II also clearly evidences the fact that the assemblage is the result of hyena activity. Our analysis indicates a predominance of cranial remains and lower long limb bones (metapodials). The mortality profiles of the three units are different, although two are classic of a cursorial predator. Taphonomical

and statistical analysis indicated that carnivores were the main modifying agent at the three units. Our results demonstrate that hominins played a minor role in horse accumulation. Additionally, it seems that there was little difference in the exploitation of this species by Mousterian and Aurignacian groups, and this probably took place during short, sporadic hominin occupations.

## Résumé

Les grottes étaient systématiquement utilisées comme abri par les carnivores et les groupes d'hominidés. L'étude des assemblages d'ongulés est essentielle pour comprendre le comportement des hominidés et des carnivores, ainsi que leurs interactions lorsque les deux agents se sont partagé l'espace. Pour cette raison, de nombreuses études impliquent l'analyse taphonomique des restes de faune, en se concentrant sur l'identification des différents acteurs biotiques. Cette étude examine les assemblages de chevaux des Unités I, II et III (moustériennes et aurignaciennes) de la grotte de Bize-Tournal dans le but de caractériser la nature de cette accumulation. Nous montrons ici que les restes de cheval dans ces unités sont principalement la conséquence de l'activité carnivore. L'Unité II met également en évidence le fait que l'assemblage est le résultat de l'activité de l'hyène. Notre analyse indique une prédominance des restes crâniens et des os de membres inférieurs longs (métapodes). Les profils de mortalité des trois Unités sont différents, bien que deux soient classiques d'un prédateur *cursorial*. Des analyses taphonomiques et statistiques ont montré que les carnivores étaient le principal agent modificateur dans les trois unités. Nos résultats démontrent que les hominines ont joué un rôle mineur dans l'accumulation des restes de chevaux. De plus, il semble qu'il y ait eu peu de différences dans l'exploitation de cette espèce par les groupes moustériens et aurignaciens, et cela s'est probablement passé pendant des occupations courtes et sporadiques d'hominines.

Keywords: Mousterian; Aurignacian; Carnivore; Taphotype; Hyena; Horse

Mots clés: Moustérien ; Aurignacien ; Carnivore ; Carnivore ; Taphotype ; Hyène ; Cheval

## 1. Introduction

In the Palaearctic area, caves were the focus for occupation by various species, including hominins and carnivores. In fact, these taxa shared several characteristics that included diet (importance/dependence on ungulates), social organisation (except solitary predators), the types of food resource catchment zones, and the use of shelters (Brugal and Fosse, 2004). These common features must have led them to interact fairly frequently (Capaldo, 1997; Daujeard and Moncel, 2010; Egeland et al., 2004; Patou-Mathis, 2012; Selvaggio, 1998). Carnivores were actively involved in the accumulation and modification of bone assemblages at the large majority of Pleistocene sites. For this

reason, understanding the role of carnivores as taphonomic agents has been crucial in zooarchaeological studies focused on reconstructing site formation (Faith and Behrensmeyer, 2006; Kruuk, 1970; Lacruz and Maude, 2005; Mills and Mills, 1977).

With the aim of characterising the accumulations generated by carnivores and the type of modifications present in them, a large number of actualistic studies have been developed (e.g., Andrés et al., 2012; Arriaza et al., 2016; Cruz-Uribe, 1991; Domínguez-Rodrigo et al., 2012; Domínguez-Rodrigo and Piqueras, 2003; Fourvel et al., 2012; Gidna et al., 2015; Pokines and Peterhans, 2007; Selvaggio, 1994). Understanding the ethology of these animals is also fundamental for assessing their ability to modify bones and accumulate remains (Binford, 1981; Brugal and Fosse, 2004; Domínguez-Rodrigo et al., 2012; Kruuk, 1970).

Just as in the study of hominin accumulations, carnivore assemblages are analysed to determine: mortality profiles for identifying the selected prey (Bunn and Pickering, 2010; Fosse, 1996; Klein, 1982; Klein and Cruz-Uribe, 1983; Stiner, 1990); anatomical profiles for establishing the transport of elements (Arriaza et al., 2016; Blumenshine and Marean, 1993; Brugal and Fosse, 2004; Stiner, 2002); the taphonomic signal that allows us to establish the sequence of access to animal carcasses (Blumenshine et al., 2007; Egeland et al., 2004) and identify the distinct agents involved (Blumenshine, 1986; Grayson, 1989; Klein, 1982; Marean et al., 2004), as well as, sometimes, the specific type of carnivore involved (Andrés et al., 2012; Binford, 1981; Fosse, 1995; Stiner, 1991a)

All carnivorous mammals modify the bones of their prey to some degree, but not all generate accumulations. Large canids (tribe *Canini* or wolf-like canids; genera *Canis*, *Lycaon*, and *Cuon*) have been studied as significant bone modifiers (Binford, 1981; Sala et al., 2012); some authors have characterised them as bone accumulators (Binford, 1981; Fourvel et al., 2012; Mallye et al., 2012; Stiner, 2002), while others classify them as agents of carcass dispersal (Yravedra et al., 2012, 2011). Several studies converge on the limited capability of the large and medium felids (genera *Panthera*, *Puma*, and *Acinonyx*) to modify bones. As recently proved, medium-sized felids, like the puma and leopard (Sauqué et al., 2018, 2014; Sauqué and Sanchis, 2017), are true bone accumulators, although lions can to be bone accumulators under determined conditions (Arriaza et al., 2016; Brain, 1981; Stiner et al., 2012). However, their position in the food web and their gregarious behaviour indicate that this species is not a typical bone collector (Schaller, 1972). Other carnivores commonly present in Pleistocene assemblages were the various species of bear (Pinto et al., 2005; Pinto and Andrews, 2004; Sala et al., 2014; Stiner, 2010; Stiner et al., 1998, 1996). Their remains are particularly abundant as the result of death during hibernation, meaning bear skeletons are common at sites used as hibernation dens (Stiner, 2010). Actualistic studies of brown and black bears indicate that these carnivores were bone modifiers but not bone accumulators (McNamee, 1990; Rogers, 1981). The taphonomic signal generated by these taxa has been described in both actualistic (Arilla et al., 2014; Sala and Arsuaga, 2013; Saladié et al., 2013) and



archaeological contexts (Fernández-Jalvo and Andrews, 2011; Pinto and Andrews, 2004; Stiner, 2010).

The three species of extant hyena, brown hyena (*Parahyaena brunnea*) (Lacruz and Maude, 2005; Mills and Mills, 1977; Skinner and Aarde, 1991), striped hyena (*Hyaena hyaena*) (Becker and Reed, 1993; Kempe et al., 2006), and spotted hyena (*Crocuta crocuta*) (Egeland et al., 2008; Faith, 2007; Fourvel et al., 2015; Mills and Mills, 1977; Skinner et al., 1986) are the most studied species from a taphonomic point of view, appearing in 125 works (Lyman, 2018), because they are among the highest-volume bone accumulators (Cruz-Uribe, 1991; Kuhn et al., 2010; Lam, 1992; Pickering, 2002; Skinner et al., 1986; Stiner, 1991a). A series of criteria have been proposed and revised that, in combination, could be used to distinguish accumulations generated by humans from those of hyenas (Cruz-Uribe, 1991; Kuhn et al., 2010; Pickering, 2002; Stiner, 1991a). These taxa are the greatest bone modifiers, and can consume and digest bone tissues (Kruuk, 1972, 1970). The assemblages formed by hyenas present abundant bone breakage, characterised by the presence of long limb bones with complete or near-complete shafts and almost no epiphyses, forming numerous cylinders (Pickering, 2002). In addition, digested bones and distinctive damage, such as scores, pits, punctures, furrowing, and scooping-out are common (Cruz-Uribe, 1991). However, this damage and modification of faunal remains has also been found in assemblages generated by other carnivores (Binford, 1981; Brain, 1981; Lyman, 1994; Njau and Blumenshine, 2006), so their presence cannot be taken as a unique indicator of hyena activity. Another criterion used is the mortality profile of the prey: U-shaped profiles are associated with cursorial predators; and L-shaped profiles with ambush predators (Bunn and Pickering, 2010; Stiner, 1990). The two most reliable criteria to clarify an accumulation as being generated by hyena are the abundance of coprolites and juvenile hyena remains (Cruz-Uribe, 1991; Kuhn et al., 2010; Stiner, 1991a). According to the proportions of hyena remains from juvenile, adult, and old individuals it is possible to distinguish between cub-raising dens, with a dominance of juvenile remains (more than 50%); communal dens with equal proportions of the ages or even a tendency towards more adult and old remains; and prey depot dens, dominated by adult remains (Diedrich, 2011a, 2012). All these criteria have been applied in taphonomic studies of Pleistocene hyena dens (Bourdillat, 1999; Brain, 1981; Cruz-Uribe, 1991; Diedrich, 2014, 2011b, 2010; Diedrich and Zák, 2006; Fosse, 1996; Fourvel et al., 2015; Guadelli, 1989; Saladié et al., 2017). However, Saladié et al. (2017) and Prendergast and Domínguez-Rodrigo (2008) concluded that these accumulations could be taphonomically very variable. This variability could be related to the ethology of the animals and the activity of other taphonomic actors and processes on the fossil assemblages (Saladié et al., 2017).

This paper focuses on a complete zooarchaeological and taphonomic analysis of the horse remains from the Mousterian and Aurignacian levels of Bize-Tournal Cave. Our goal is to clarify the origin of the horse accumulations and their taphonomic history, a point of special interest is identifying the role played by humans and carnivores in the

accumulation of this species. The horse assemblage of Bize-Tournal constitutes a good sample in which to investigate the carnivore/hominin procurement of this species, considering the large number of remains recovered from this cave. In addition, we try to identify possible differences in horse management between Mousterian and Aurignacian hominin groups.

## 2. Bize-Tournal

Bize-Tournal Cave is situated in southern France (43°20'N 2°52'E), approximately 20 km north of Narbonne and 2.5 km from Bize-Minervois. Located in the foothills of the limestone massif "La Montagne Noire", which flanks the Mediterranean Sea, the cave opens on the left side of the Cesse River. Discovered and excavated by P. Tournal beginning in 1827, the site became a reference for the first prehistoric and taphonomic studies (Tournal, 1829, 1828, 1827). The last excavations of the Pleistocene horizons were conducted between 1970 and 1987 by A. Tavano in a preserved area of approximately 75m<sup>2</sup>. He found a well-stratified sequence of deposits from the Mousterian to the Magdalenian period, which provides record to the regional transition from the Middle to Upper Palaeolithic (Tavano, 1987a, 1987b).

At least 11 levels have been identified in 4 units. Unit I (level A) is characterised by highly weathered coarse gravel, alternating with greenish plastic clays and clayey silts. The bone assemblage was strongly biased due to post-depositional water- and karst-related modification. Unit II (level B/C and D1/D2) is a 0.5 to 2 m-thick complex, formed of brown clay alternating with silts and clayey silty sands. It contains archaeological layers with very rich assemblages of large mammals and lithic series. The stratigraphy of Unit III is clearer: the lower part comprises clayey gravelly silts and brecciated gravels with limited archaeological material (level E1, after Tavano, 1987a; F1-F2, after Patou-Mathis, 1994); the middle part is formed of a pink breccia and yellow clayey silt and is archaeologically sub-sterile (level E2, sub-sterile); the upper layer is a breccia with a relatively richer archaeological series (level E3, after Tavano, 1987a; F3-F4, after Patou-Mathis, 1994). The lowest layers comprise fine gravel with a silty matrix whereas the upper ones are hard breccia. Archaeological levels G and H (Unit IV) are characterised by abundant lithic and faunal remains. Unit IV contains the most significant archaeological records and belong to Magdalenian cultural period.

The dating of the archaeological sequence is based on series of charcoal samples (non-calibrated dates), horse bones and teeth (uranium dating), and cervid and bovid bones (non-destructive gamma-ray spectrometry and electron spin resonance (ESR)) (Bischoff et al., 1988; Yokoyama et al., 1987). Several results are unreliable because of taphonomic alteration, particularly caused by post-depositional water movement (Yokoyama et al., 1987). The most consistent results indicate that the Mousterian horizon from Unit II is between 56,200 ± 1700 B.P. (Bischoff et al., 1988) and 38,000 ± 8000 B.P. (Yokoyama

et al., 1987). The Aurignacian horizon from Unit III is dated as 29,000 B.P. and 35,800 B.P. (Yokoyama et al., 1987) (Table 1).

Period	Unit	Level		Dates
Aurignacian	III	E3 <sup>a</sup>	F3F4 <sup>b</sup>	
		E2 <sup>a</sup>	F1F2 <sup>b</sup>	>29 a B.P. (Ly1895) (14C)
		E1 <sup>a</sup>		>35.8 a B.P. (Ly1898) (14C)
Mousterian	II	D1/D2 <sup>a</sup>		33.6±1.2 B.P. (Ly1676) ( <sup>14</sup> C)
		B/C <sup>a</sup>		38±8 a (ESR) 56.2± 1.7 a (U-series)
	I	A <sup>a</sup>		

Table 1 Archaeological levels included on this study of Bize-Tournal Cave. Units from: <sup>a</sup>=Tavoso (1987a); <sup>b</sup>=Patou-Mathis (1994); Dating from Yokoyama et al. (1987). Ages in ka B.P., radiocarbon dates uncalibrated.

Tableau 1 Niveaux archéologiques inclus dans cette étude de la grotte Bize-Tournal. Unités de: <sup>a</sup>=Tavoso (1987a); <sup>b</sup>=Patou-Mathis (1994); Dating de Yokoyama et al (1987). Âges en ka B.P., dates radiocarbone non calibrées.

The lithic tools from Units I and II correspond to denticulate Mousterian with non-laminar Levallois flakes, with practically no technological and typological variations (Chacón, 2009; Lumley and Isetti, 1965; Lumley, 1971; Tavoso, 1987b). From Unit III, an early Aurignacian technology with Dufour bladelets has been recovered, and there is a typical Aurignacian layer dominated by end scrapers (Sacchi, 1986; Tavoso, 1987b).

A total of seven ungulate species and seven carnivore taxa (Magniez, 2009)(Table 2) have been identified from the Mousterian levels. The most numerous ungulates in Units I, II and III is *Equus ferus*, followed by *Rangifer tarandus* and *Bos/Bison* sp. (Table 2). *Ursus spelaeus* was the most abundant carnivore taxon in all the units, followed by *Panthera pardus* (Unit I), and *Crocuta crocuta spelaea* (Units II and III) (Table 2). The Mousterian phase involved short-term, recurrent hominin occupations, essentially focused on the exploitation of horse, reindeer, and large bovids, through collective hunting, while giant deer, red deer, ibex, and wild boar remains were accumulated by carnivores, especially the cave hyena (Magniez, 2009, 2010; Magniez and Boulbes, 2014).

Taxa	Unit I		Unit II		Unit III	
	NISP	%NISP	NISP	%NISP	NISP	%NISP
<i>Bos primigenius / Bison priscus</i>	2	2.2	190	10.3	27	5.0
<i>Capra praepyrenaica / Capra pyrenaica</i>	1	1.1	143	7.7	8	1.5
<i>Megaloceros giganteus</i>	-	-	50	2.7	-	-
<i>Cervus elaphus</i>	1	1.1	41	2.2	-	-
<i>Rangifer tarandus</i>	24	25.8	194	10.5	170	31.3
<i>Sus scrofa</i>	-	-	14	0.8	-	-
<i>Equus ferus germanicus</i>	51	54.8	767	41.4		
<i>Equus ferus gallicus</i>					266	48.9
<i>Caelodonta antiquitatis</i>	-	-	10	0.5	1	0.2
<i>Ursus spelaeus</i>	11	11.8	299	16.1	32	5.9
<i>Ursus arctos</i>	1	1.1	8	0.4	1	0.2
<i>Crocota crocuta spelaea</i>	-	-	91	4.9	23	4.2
<i>Canis lupus</i>	-	-	20	1.1	7	1.3
<i>Vulpes vulpes</i>	-	-	18	1.0	9	1.7
<i>Panthera leo spelaea</i>	-	-	4	0.2	-	-
<i>Panthera pardus</i>	2	2.2	1	0.1	-	-
<i>Lynx lynx</i>	-	-	2	0.1	-	-
Total	93	100	1852	100	544	100

Table 2 NISP and %NISP of large mammals in Bize-Tournal Cave. Data from Magniez (2009).

Tableau 2 NRdt et %NRdt des grands mammifères de la grotte de Bize-Tournal. Données de Magniez (2009).

The horse from Tournal corresponds to a medium-sized horse with “heavy” proportions and broad muzzle. The skeleton shows a clear decrease in body size through the stratigraphy (Magniez and Boulbes, 2014). The remains from units I and II correspond to the chrono-subspecies *Equus ferus germanicus*, those from unit III (and unit IV) can be attributed to *E. f. gallicus*. Body mass estimations vary between 400 and 480 kg in the unit II and 380-450 kg in the unit III. Another particular feature of Tournal horse is the strong diaphysis robustness of the metapodials. This pattern corresponds to an ecomorphological trait correlated to the high level of humidity (Boulbes and van Asperen, 2019).

### 3. Materials and methods

The *Equus ferus* remains analysed come from the Tavoso excavation, focused on the three first units: the Mousterian Unit I (NISP=51) and Unit II (NISP =767); and the Aurignacian Unit III (NISP =266) (Table3). In this study were included coordinate bone splinters identified as horse remains after a survey of the unidentified remains of the faunal assemblages, which allows to have a more complete corpus to discuss the impact the different taphonomic agents.

The features described for each specimen are element, taxa, size, side (anterior, posterior, lateral or medial), portion, lateralisation (right/left), landmarks, and age-at-death group.

We have used four abundance measurements: number of identified specimens (NISP); minimum number of elements (MNE); the standardised expression of the number of animal units (%MAU); and the minimum number of individuals (MNI) (Binford, 1984; Grayson, 1984). Following Domínguez-Rodrigo (Domínguez-Rodrigo, 1997), to represent skeletal parts, the carcasses were divided into anatomical segments: head (cranium, mandible, hyoid, and teeth); axial (vertebrae, ribs); and appendicular (limb bones). Long bones were divided into upper limb bones (humerus and femur), intermediate limb bones (radius/ulna and tibia), and lower limb bones (metapodials).

Age of death and seasonality was determined through a study of the teeth, considering the time of eruption, replacement of teeth, and the degree of occlusal surface wear and root development (Fernandez and Legendre, 2003; Forsten and Moigne, 1998). Isolated teeth were analysed together with the dental series. Anatomical refitting was performed based on lateralisation, wear, and size, and this permitted an accurate MNE and MNI to be obtained for the mandibles and maxillae. The horse birthing period, between spring and early summer, has been taken as standard (Burke, 2002; Levine, 1983). Horse mortality curves were created by identifying age of death (Fernandez et al., 2006). Following Fernandez and Legendre (2003) and Fernandez et al. (2006), we calculated the parameters of life tables: the frequency ( $f_x$ ) of the individuals in each successive age group using the percentage of the dental NISP; the mortality rate ( $q_x$ ) during the interval  $x$  to  $x+1$ , through the ratio of  $f_x$  and  $l_x$ :  $q_x = (f_x/l_x) * 100$ ; and the survival rate ( $l_x$ ) from birth to age ( $x$ ). By convention, the value of the first age group was often set at 100 or 1000 to proportionally increase the values using  $l_{x+1} = l_x - f_x$ ; individual killing factor (*k-factor*) values obtained for each age group were compared over the lifespan. By summing  $k_x$ , one obtains an additive index  $K$ , that indicates the “intensity” of mortality generated by different factors (e.g., predation). The calculation was:  $Abs(k_x) = \log_{10}(f_x) - \log_{10}(f_{x+1})$ . Once the age of death had been identified, the individuals were grouped into the groups juvenile, prime adult, and old (Stiner, 1990), and plotted on triangular graphs following the separation of different mortality profiles according to Stiner (1990) and the modified ternary plot for horses (Discamps and Costamagno, 2015).

We used the Spearman’s rank-order to test the correlation between %MAU of each portion of the elements and bone mineral density (Lam et al., 1999), to identify any possible differential destruction of less dense portions of bones.

Following Bunn (Bunn, 1983) and Villa and Mahieu (Villa and Mahieu, 1991), shaft circumference, shaft length, and the fracture outline, angle and edge were listed to explore the nature of the fragmentation observed in the assemblage. We considered the ratio of limb bone shaft fragments (NISP) to epiphyseal specimens (Blumenschine and Marean, 1993; Marean and Spencer, 1991), and the percentage of change in the epiphysis of the long bones [ $(MNE \text{ before ravaging} - MNE \text{ after ravaging}) / (MNE \text{ before ravaging}) * 100$ ] (Blumenschine and Marean, 1993) using the total MNE according to Domínguez-Rodrigo et al. (2002), assuming that each element was represented by two epiphyses.

Carnivore- and hominin-induced modifications were described according to anatomical region and the portion of bone on which the alterations were found. The carnivore modifications identified were pits and scores (Binford, 1981; Johnson, 1985; Maguire et al., 1980), furrowing (Brain, 1981; Haynes, 1983), and pitting (Binford, 1981). Digested remains were identified, which present porous and softened surfaces resulting from corrosion by gastric acid (Sutcliffe, 1970). The dimensions of the pits and scores were determined using the criteria of Andrés et al. (2012) and these were compared with the experimental data of Selvaggio (1994), Delaney-Rivera et al. (2009), Andrés et al. (2012), and Saladié et al. (2013). Only one type of cut mark was identified: slicing marks (Domínguez-Rodrigo et al., 2009; Shipman and Rose, 1983). The type, delineation, location, and positions of the cut marks on the bones allowed the identification of butchering activities (Binford, 1981; Galán and Domínguez-Rodrigo, 2013; Nilssen, 2000).

We followed the method of Domínguez-Rodrigo et al. (2015), who classified upper and intermediate long bones into different taphotypes according to the carnivore modifications (presence/absence; location of furrowing and tooth marks). This method is used to evaluate only long limb bones (humerus, femur, radius-ulna, tibia) that preserve their complete diaphyseal circumference (Domínguez-Rodrigo et al., 2015). The long bones were divided into 15 taphotypes, in order to quantify different forms of element destruction (Domínguez-Rodrigo et al., 2015). For the analysis, we compared the remains with those of horses and zebras modified by captive and wild lions from Tarangire National Park (Tanzania) and captive hyenas (Domínguez-Rodrigo et al., 2015). The statistical treatment comprised a correspondence analysis (CA) involving contingency tables per element type and taphotype, with a bootstrapped analysis of 1000 resamples. For the study of taphotypes, we used the free statistical software R ([www.r-project.org](http://www.r-project.org)), employing the “cabooters” library (Ringrose, 2012). The plots include 95% confidence ellipses, which show the overlap between the row and column categories in the contingency tables. The CA was also supported by the chi-square test.

The post-depositional modifications identified were rounding, polishing, fissures, concretions, and manganese oxides stains, and these were recorded as being present or absent for each specimen.

## 4. Results

Unit II contained the largest number of horse remains according the NISP and MNE, followed by Unit III, and finally Unit I (Table 3). According to the NISP, the most numerous remains in all layers were isolated teeth, followed by long limb bones (humerus in Unit I and metapodials in Units II and III) (Table 3). The anatomical distribution of %MAU used to estimate the anatomical profiles indicated a predominance of skulls (cranium and mandible) in Unit I, followed in importance by coxa and humerus remains, with values of less than 20%. Unit II presented the greatest values of %MAU for

mandibles, followed by cranium remains, metatarsal and metacarpal. After these elements, the next most important were: tibia, radius/ulna, and femur. The post-cranial axial skeleton presented an irregular distribution, with a value of around 40% for coxa and values of less than 10% for scapula, ribs and vertebrae. From the carpals and tarsals were better represented astragalus and calcaneus bones (Figure 1). Unit III was dominated by skull elements, followed astragalus, tibia, metacarpal and coxal bones (Figure 1).

	Unit I		Unit II		Unit III	
	NISP	MNE	NISP	MNE	NISP	MNE
Cranium	-	7	19	25	1	10
Mandible	4	7	30	37	12	23
Isolated teeth	35	-	341	-	171	-
Vertebra	-	-	6	4	1	1
Rib	-	-	11	7	3	1
Scapula	2	2	8	4	-	-
Coxal bone	-	-	31	19	5	4
Humerus	3	2	20	9	5	2
Radius/ulna	-	-	29	20	7	3
Carpal	-	-	3	3	3	3
Metacarpal	-	-	55	35	13	5
Metacarpal vestigial	-	-	7	7	3	3
Femur	1	1	30	16	8	3
Patella	1	1	4	4	-	-
Tibia	-	-	52	23	9	5
Astragalus	1	1	18	16	6	6
Calcaneum	-	-	12	11	1	1
Tarsal	-	-	7	7	3	3
Metatarsal	3	1	49	40	4	4
Metatarsal vestigial	-	-	3	3	-	-
Sesamoid	-	-	3	3	1	1
Phalanx I	-	-	9	8	4	3
Phalanx II	-	-	8	8	3	3
Phalanx III	1	1	12	10	3	3
Total	51	23	767	319	266	87

*Table 3 Estimated NISP, MNE, and %MAU of horse elements by archaeological unit at Bize-Tournal.*

*Tableau 3 Estimation du NRdt, du NME et du %UAM des éléments du chevaux par Unité archéologique de Bize-tournal.*

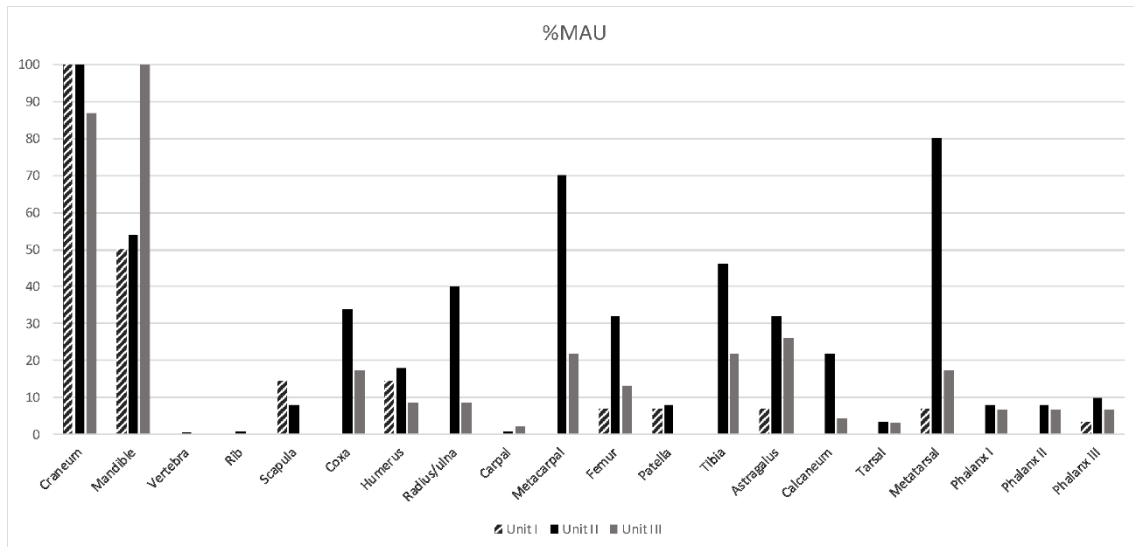


Figure 1 %MAU distribution by elements of horse remains from Units I, II, and III from Bize-Tourmal.

Figure 1 Répartition du %UAM par éléments pour les restes de chevaux des Unités I, II et III de Bize-Tourmal.

The percentages of dental preservation between the right and left teeth clearly indicate good preservation of the original deposits (Table 4).

Cultural Attribution	Unit	Tooth/Dental NISP(MNI)	Left teeth	Right teeth	Total expected	Differential preservation (%)
Aurignacian	Unit III	97 (14)	36	61	122	79.5
Mousterian	Unit II	342 (25)	164	178	356	96.06
	Unit I	34 (7)	17	16	34	97.05

Table 4 The total sample NISP and MNI, the frequency of right and left teeth and the differential preservation rate.

Tableau 4 Échantillon total du NRdt et NMI et fréquence des dents droites et gauches et taux de préservation différentiel.

For MNI, the unit with most individuals was Unit II (MNI=25), followed by Unit III (MNI=14), and then Unit I (MNI=7) (Table 5). Units I and III were dominated by prime-adult individuals. In Unit II, juveniles were the most numerous, although there was also a significant number of prime adults.

The juvenile individuals identified in Unit I must have died during the summer/autumn. In Unit II, the wear and eruption of the juvenile teeth indicates that they were killed in all seasons; some individuals with deciduous dentition were recovered with no wear, and in some cases the dentition was not completely formed, indicating that these animals died in their first weeks of life, in addition to individuals with deciduous dentition with all degrees of wear. Unit III presented a similar seasonal pattern to that found in Unit II, with multi-seasonal death, including the birth period (Table 5).



The mortality profiles differ significantly between the units. In terms of frequency ( $f_x$ ), the proportion of juvenile individuals was similar in Units II and III, but these are less well represented in Unit I; in contrast, the proportion of adults was more important in Units I and III than Unit II. Old individuals were better represented in Units II and III, with none present at all in Unit I (Figure 2). Indeed, Unit I contained no remains of adults older than 15 years (Table 6). The mortality based on life tables indicated for Unit I shows an increase in animals between 9 and 15 years old, with no older individuals. Unit II presents a moderate L-shaped mortality curve (Figure 2). In Unit III, individuals aged between 0-3 and 6-12 years were the best represented, with a bias towards individuals aged 3-6 years. An exponential increase in mortality rates ( $q_x$ ) was identified for adult individuals in Units I and III, and a regular increase in mortality in Unit II for all age groups (Figure 2). The survivorship ( $l_x$ ) obtained for all the samples corresponds to a regular decrease in the successive groups, most highlighted in Unit I from the age of 6 and accentuated in Unit III from 9 years old. In contrast, the curve for Unit II shows a slowly linear decrease (Figure 2). Predation considered in the Killing Factor ( $K_x$ ) indicated higher values of  $K$  in Units I ( $K=1.8$ ) and III ( $K=3.6$ ) and lower values in Unit II ( $K=0.9$ ), revealing a more stable predation structure.

The mortality profiles indicate a prime-adult dominated profile in Unit I, an attritional profile in Unit II, and a catastrophic profile in Unit III (Figure 3). All the mortality profiles fall into the juvenile/prime/old areas, designed by Discamps and Costamagno (Discamps and Costamagno, 2015), which include primarily L-shaped and part of the U-shaped traditional profiles. These results indicate that the differences in mortality profiles in the traditional areas of ternary diagrams should be taken with caution. A prime adult dominated profile is not always an indicator of selective hunting, this can be dependent on the hunted groups. In Unit I, the prime-adult dominated profile may be related to hunting episodes when adult male horses aggregated, at the beginning of autumn (Denzau and Denzau, 1999; Klimov, 1988). In addition, it is not always possible to confidently distinguish L-shaped and U-shaped profiles on a ternary diagram (Discamps and Costamagno, 2015). Therefore, the results from Units II and III, which also demonstrate a similar seasonality, indicate that there were similarities in the choice of prey.

Cultural Attribution	Unit	MNI (MNI%)				Seasonality	Mortality
		Juvenile	Prime adult	Old	Total		
Aurignacian	Unit III	4 (28.57)	8 (57.14)	2 (14.29)	14	Annual	Catastrophic
Mousterian	Unit II	11 (44)	9 (36)	5 (20)	25	Annual	Attritional
	Unit I	1 (14.29)	5 (71.43)	1 (14.29)	7	Seasonal (Summer-Fall)	Prime-dominated

Table 5 MNI by age categories, frequencies (%), seasonality, and interpreted mortality.

Tableau 5 MNI par catégories d'âge, fréquences (%), saisonnalité et interprétation de la mortalité.

Age group	Frequency (fx)			Mortality (qx)			Survival (lx)			Killing factor (kx)		
	Unit I	Unit II	Unit III	Unit I	Unit II	Unit III	Unit I	Unit II	Unit III	Unit I	Unit II	Unit III
0-3	6.89	20.43	23.18	6.89	20.43	23.18	100	100	100	0.39	0.11	0.9
3-6	17.24	15.69	2.89	18.51	19.72	3.77	93.10	79.56	76.81	0.38	0.019	0.81
6-9	41.37	16.42	18.84	54.54	25.71	25.49	75.86	63.86	73.91	0.12	0.05	0.18
9-12	31.03	14.59	28.98	90	30.76	52.63	34.48	47.45	55.07	0.95	0.22	0.3
12-15	3.44	8.75	14.49	100	26.67	55.56	3.44	32.84	26.08	0	0.06	0.39
15-18	0	10.21	5.79	0	42.42	50	0	24.08	11.59	0	0.27	0.6
18-21	0	5.47	1.44	0	39.47	25	0	13.86	5.79	0	0.18	0.47
21-25	0	8.39	4.34	0	100	100	0	8.39	4.34	0	0	0.9

Table 6 Life tables of horses from Units I, II, and III

Tableau 6 Tables de survie des chevaux des Unités I, II et III.

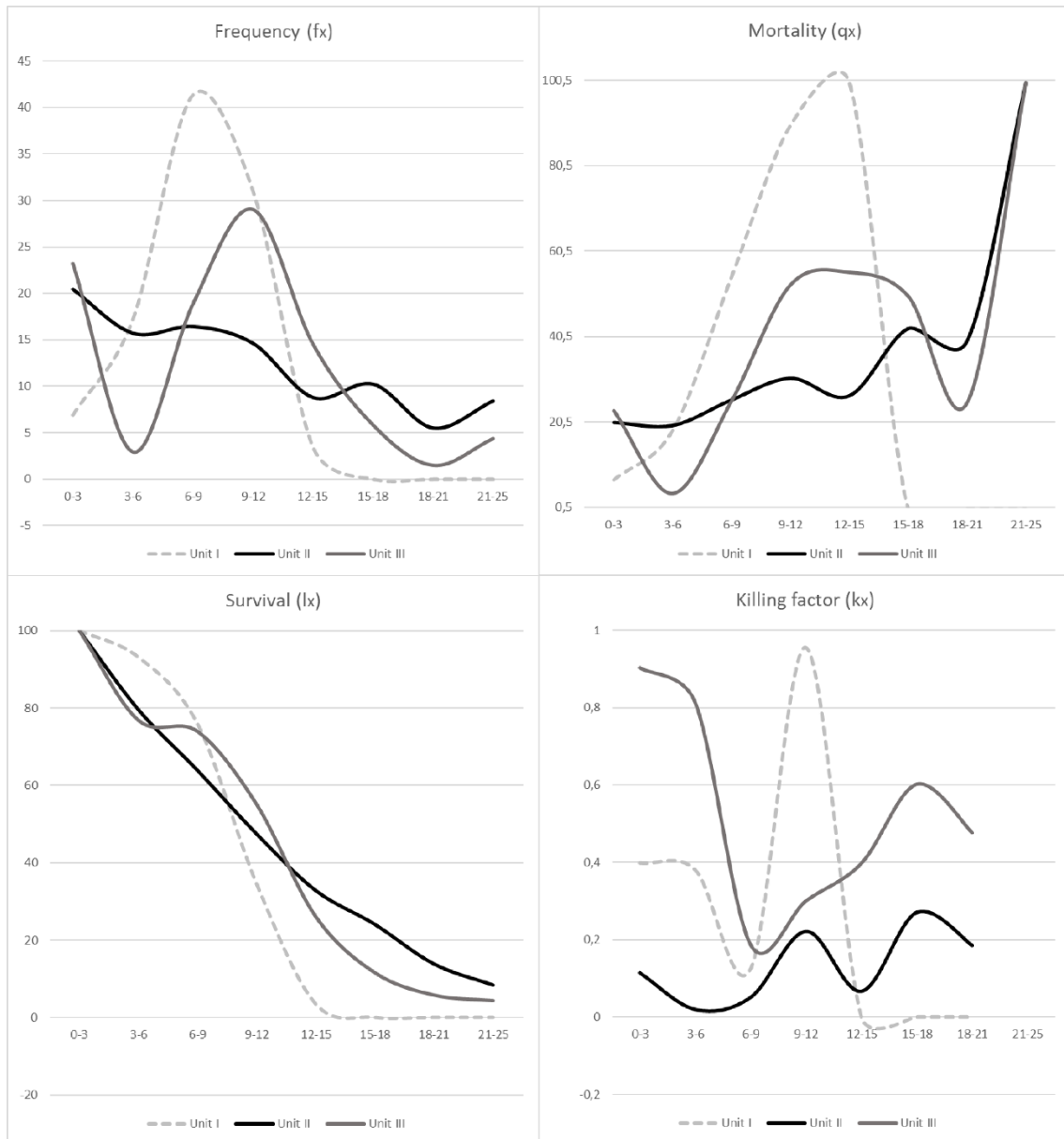


Figure 2 Mortality and survivorship curves. The abscissa axis indicates frequency values and the ordinate axis indicates age groups. J=Juvenile; P=Prime-adult; O=Old; JOP=Juvenile/Old/Prime; JPO=Juvenile/Prime/Old.

Figure 2 Courbes de mortalité et de survie. L'axe des abscisses indique les valeurs de fréquence pour le tableau 2 et l'axe des ordonnées indique les groupes d'âge.

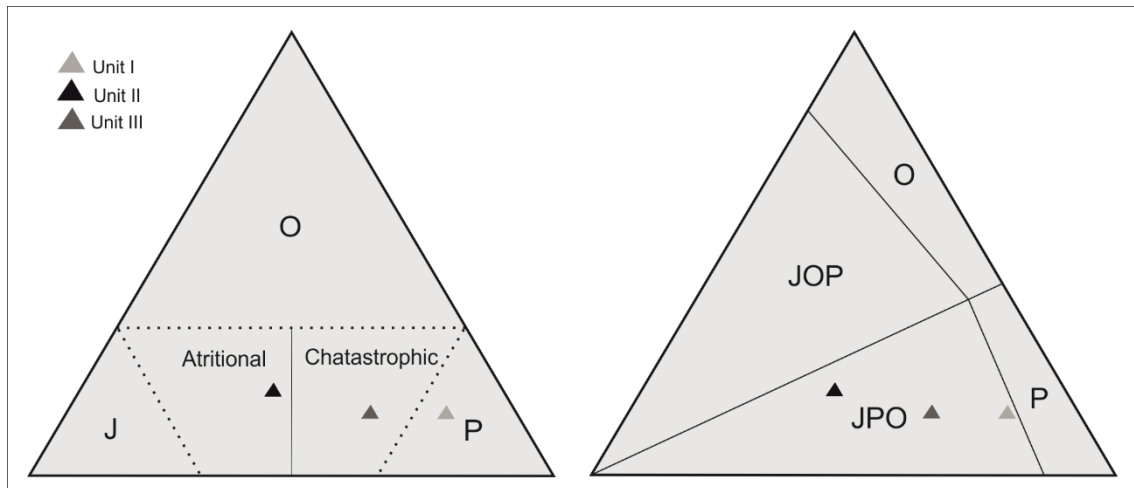


Figure 3 Mortality profiles for horse samples. Ternary classification from Stiner (1990) and Discamps and Costamagno (2015).

Figure 3 Profils de mortalité pour les échantillons de chevaux. Diagrammes ternaires de Stiner (1990) et Discamp et Costamagno (2015). J=Jeunes ; P=Adulte ; O=Âgés; JOP=Jeunes/Âgés /Adulte; JPO=Jeunes/Adulte/Âgés.

In Units II and III we identified a significant and positive statistical correlation between the bone mineral density of anatomical portions and their %MAU (Unit II:  $r_s=0.394$ ,  $p=0.0001$  / Unit III:  $r_s=0.3$ ,  $p=0.003$ ) (Figure 4). In Unit I there was no significant correlation between %MAU and bone density ( $r_s=0.160$ ,  $p=0.128$ ). These results indicate bone-mediated attrition of less dense parts in Units II and III.

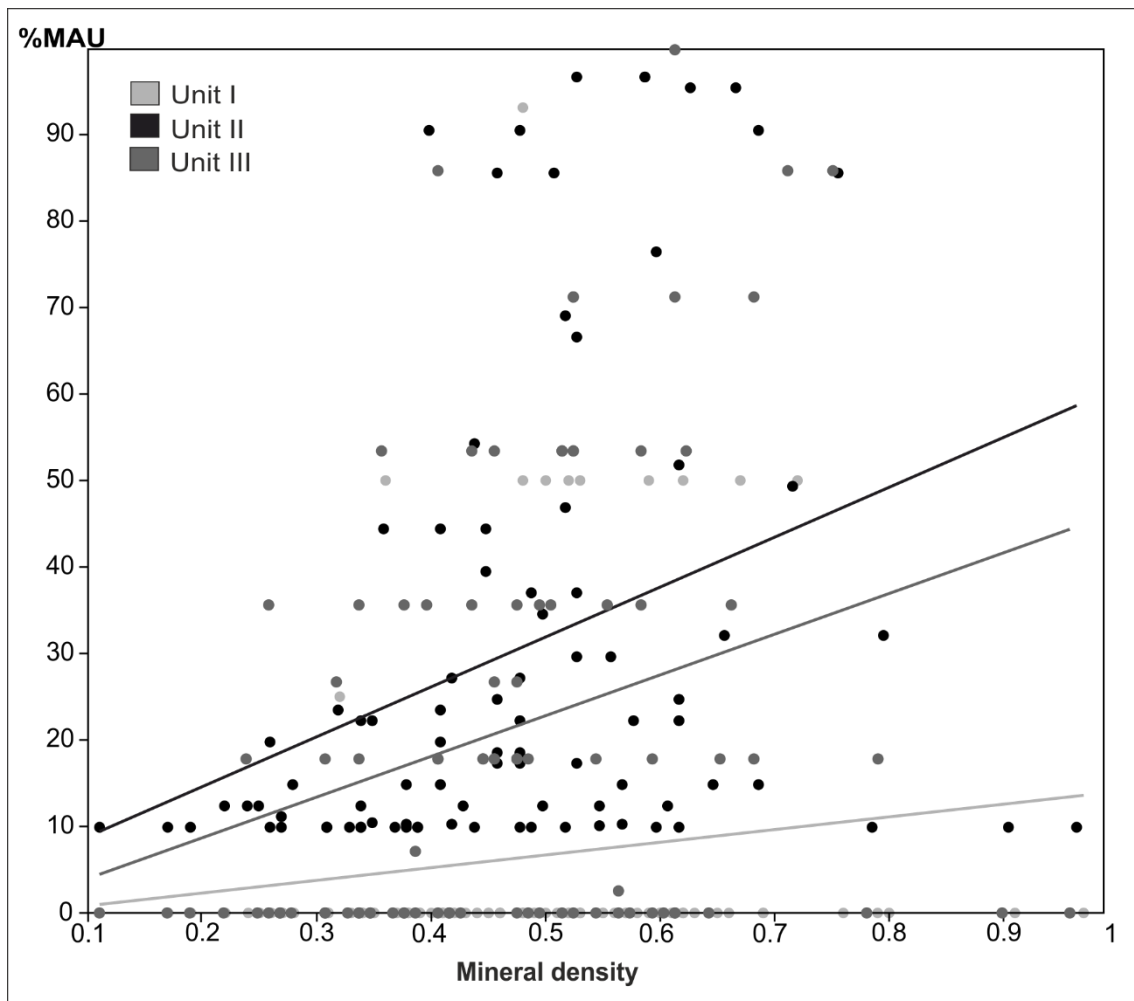


Figure 4 Statistical correlation between %MAU and bone mineral density.

Figure 4 Corrélation statistique entre le %MAU et la densité minérale osseuse.

With regard to fragmentation, a high percentage of complete remains was found in all the units (Unit I=68.6%; Unit II=51%; Unit III=50.6%). Of these, the majority were dental remains (Unit I=88.5%; Unit II=72.4%; Unit III=84.4%), follow by articular bones (Unit I=2.8%; Unit II=7.6%; Unit III=10.6%), and phalanges (Unit I=8.5%; Unit II=4.8%; Unit III=4.6%). An elevated percentage of long limb bones were complete in Units II and III. From Unit II, a total of 54 complete metapodials (metacarpal=28 (50.9%); metatarsal=26 (52%)) two radius (8%) and one tibia 52 (1.9%) were recovered. In Unit III, three complete metapodials (metacarpal=2 (15.3%); metatarsal=1 (25%)) were found. No complete long bones were recorded from Unit I.

The percentage of long limb bone diaphyses with less than one-quarter of their original length preserved were 37.5% in Unit I, 34.8% in Unit II, and 55.8% in Unit III; those with less than one third of their original circumference were 37.5% in Unit I, 39.4% in Unit II, and 51.1% in Unit III. This indicates a moderate degree of fragmentation and is related to the high number of complete bones and those remains that preserve the complete length and circumference of the shaft, formally mid-shaft cylinders (Unit I=37.5%; Unit II=47.1%; Unit III=34.8%).

Analysis of long limb bone breakage indicated that the most common combination of fracture edge features in all levels were transversal delineations, mixed angles, and smooth surfaces (Unit I=28.5%; Unit II=25.8%; Unit III=35.8%), indicating that the fractures predominantly occurred when the bones were dry. The second most frequent combination of fractures were: curve delineations, oblique angles, and jagged surfaces in Unit I (21.4%); longitudinal, oblique, and smooth surfaces in Unit II (15.1%); and longitudinal, right, and smooth in Unit III (16.4%). The combination of curve delineation and oblique angles were recorded in 7.1% of the long limb bones from Unit I, 12.1% from Unit II, and 8.9% from Unit III; these could be related to green bone breakage.

During the analysis of MNE it was possible to appreciate an imbalance in the representation of certain parts of limb bones (Figure 5). In Unit I, fragments of epiphyses and near epiphyses were better represented than humerus, femur, and metatarsal mid-shaft portions. In Unit II, only humerus and femur bones presented a large proportion of mid-shaft fragments with near epiphyses and proximal and distal ends. Fewer distal epiphyses were found for tibia remains. Radius and metapodial bones were represented in equal proportions in all bone portions. The sample from Unit III was more diverse: the portions of humerus, femur and metapodial remains were similarly represented; no tibia distal epiphysis fragments were found, and no fragments of the proximal ends and shafts of radius bones were found (Figure 5). The disappearance of epiphyses may also be related to the low proportion of axial skeleton remains.

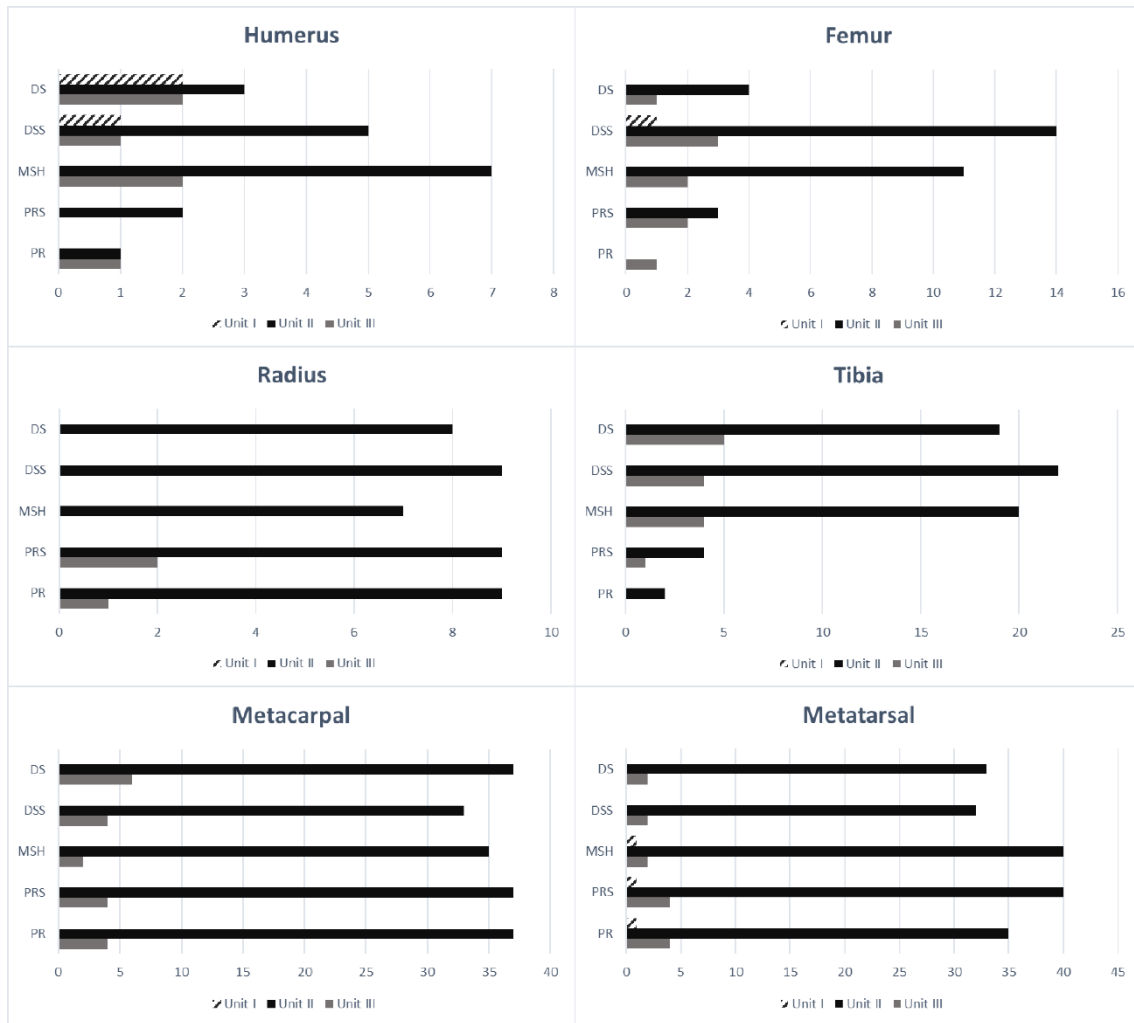


Figure 5 Portions MNEs for limb bones by body size class. DS=Distal end; DSS=Distal shaft; MSH=Medium shaft; PRS=Proximal shaft; PR=proximal end.

Figure 5 Portions d'MNEs pour les os des membres par classe de taille corporelle. DS= Extrémité distale; DSS= Diaphyse distale; MSH= Diaphyse moyenne; PRS= Diaphyse proximale; PR= Extrémité proximale.

The percentage of change and the epiphysis-shaft ratio indicate a significant underrepresentation of epiphyses in Unit II (%change=70.6; Epiphysis/Shaft= 0.3). These factors also reveal that about half the epiphyses were missing in both Unit I (%change=66.7; Epiphysis/Shaft: 0.5) and Unit III (%change=58.3; Epiphysis/Shaft=0.5). Positive percentages of change values indicate severe epiphysis loss, and low values for the Epiphysis/Shaft ratio indicate the intensity of carnivore bone destruction, in addition to a high level of competition between scavengers (Blumenschine and Marean, 1993).

For the Peninj sites, Domínguez-Rodrigo et al. (2002) related repeated hominid visits with the obtaining and processing of animal carcasses, and for the hyena den of Syokimau, Egeland et al. (2008) indicated that a negative and highly significant relationship for the linear regression between values of percentage of change and the Epiphysis:Shaft ratio indicated intense ravaging by carnivores. When the result of the Bize-Tournal Cave units is plotted with those of the Peninj sites and Syokimau, the results

of the linear regression indicate intense carnivore ravaging, especially in Unit II, with more moderate activity in Unit III (Figure 6).

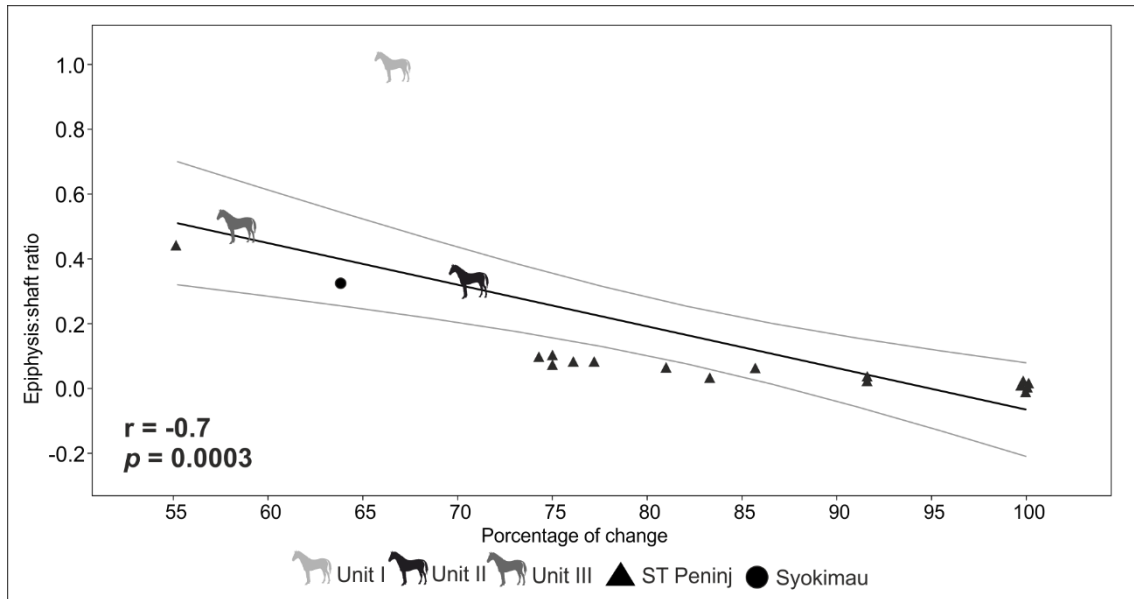


Figure 6 Distribution of epiphysis:shaft ratio and percentage of change from Bize-Tournal data, Peninj (Domínguez-Rodrigo et al., 2002) and hyena den of Syokimau (Egeland et al., 2008).

Figure 6 Distribution du ratio épiphyses/diaphyses et pourcentage de changement d'après les données de Bize-Tournal, Peninj (Domínguez-Rodrigo et al., 2002) et repaire d'hyène de Syokimau (Egeland et al., 2008).

## 4.1. Bone Surface Modifications

In Units I, II, and III, carnivore-induced modification was the most commonly seen on horse bones. Tooth marks and carnivore bone breakage were the most numerous modifications (Table 7). If we exclude isolated teeth when generating the percentages, the rates of carnivore-modified bone increases to 25% in Unit I, 52.8% in Unit II, and 11.8% in Unit III. Anthropogenic modifications were identified exclusively in Units II and III, through the presence of cut marks. In addition, within Unit II, some remains presenting cut marks show a modification coincidence with carnivore tooth marks. This appointed the predominance of carnivore-related modifications in the Mousterian and Aurignacian Units.

Surface Modification	Unit I		Unit II		Unit III	
	NISP	%NR	NR	%NR	NR	%NR
Pits and scores	4	7.8	234	30.5	10	3.8
Digested	0	0	17	2.2	0	0.0
Carnivore bone breakage	1	2	74	9.6	15	5.6
Cylinders	0	0	68	8.9	4	1.5
Cut-marked	0	0	6	0.8	5	1.9

Table 7 Total number and percentage of remains by carnivore and human surface modifications.

Tableau 7 Nombre total et pourcentage de restes avec modifications de surface d'origine carnivore et anthropique.



The distribution of tooth marks on the anatomical portions indicated that in Unit I, 33.3% of appendicular elements (NISP: 4/12) had carnivore modifications, while the axial and cranial elements did not. In Unit II, 60.34% of the axial remains (NISP: 35/58), 54.31% of appendicular elements (NISP: 170/313), and 41.67% of cranial elements (NISP: 20/48) bore carnivore modifications. In Unit III, 25% of the axial remains (NISP: 2/8), and 17.02% of appendicular elements (NISP: 8/47) displayed carnivore alterations, while none of the cranial specimens did. With regard to the distribution of tooth marks on long bone portions, the remains from Unit I presented carnivore modifications on 33.3% of the near epiphyses (NISP: 1/3), 25% on the shaft fragments (NISP: 1/4), and there were none on the epiphyses. In Unit II, 66.3% of shaft fragments presented modifications (NISP: 59/89), as did 46.03% of the near epiphyses (NISP: 29/63), and 7.7% of the epiphyses (NISP: 1/13). Additionally, 59.7% of the complete long bones evidenced carnivore modifications (NISP: 34/57). Finally, in Unit III, 25% of near epiphyses (NISP: 3/12) presented some type of tooth marks, as did 14.29% of the epiphyses (NISP: 1/7), and 13.1% of the shafts (NISP: 3/23). Cylinders were especially numerous in Unit II (NISP=68). Tooth marks were abundant on compact bones, especially phalanx remains (NISP: Unit I=2; Unit II=23; Unit III=1). These modifications could explain the lower presence of these types of bones in the assemblage, as they were probably consumed by carnivores (Cruz-Uribe, 1991; Marean, 1991). Digested bones were identified exclusively in Unit II, with a total of 17 specimens, comprising 11 complete remains and six bone fragments. The complete remains were: 6 isolated teeth corresponding to the superior and inferior dentition of juvenile and adult individuals; two proximal and two medial phalanges; and one petrosal bone. The fragmented specimens with evidence of digestion were: one tibia fragment; one metapodial; the head of a rib; one calcaneus fragment; and two long bone fragments. The degree of digestion was moderate in 10 remains, strong in 6, and extreme in the tibia fragment.

With regard to the type of carnivore modification in Unit I, scores and pits were identified on long bone shafts (Table 8). In Unit II, tooth marks were identified on all the elements and portions of the horse carcasses. It was possible to verify the presence of pits, scores, punctures, and pitting (Table 8) (Figure 7). On long bones, the modifications were more abundant on shaft fragments. On flat bones, such as the coxa, pitting modifications were the most abundant (Figure 89). Compact bones showed high degrees of modification, particularly phalanx remains, where 82.1% of the total presented tooth marks. In Unit III pits and pitting were identified on the shafts of long bones (Table 8). Furrowing was well represented, especially on long bone epiphyses (Table 9). Furrowing was the most abundant modification in Unit II, particularly on femur distal epiphyses and tibia proximal epiphyses (Table 9). In Unit III, furrowing was present on proximal humerus, and proximal and distal femur remains (Table 9).

Unit I						
	Long bones			Flat bones		Articular bones
	Prox. Ep.	Shaft	Dist. Ep.	Cortical	Cancellous	Compact bone
Pits	0	0	0	0	0	0
Scores	0	16.7	0	0	0	0
Punctures	0	0	0	0	0	0
Pitting	0	50	0	0	0	0
Unit II						
	Long bones			Flat bones		Articular bones
	Prox. Ep.	Shaft	Dist. Ep.	Cortical	Cancellous	Compact bone
Pits	0.9	7.6	0	3.4	1.7	0
Scores	2.2	15.6	2.2	19	0	10
Punctures	0.4	0.9	0	0	1.7	2.5
Pitting	0.9	20.4	2.7	74.1	0	27.5
Unit III						
	Long bones			Flat bones		Articular bones
	Prox. Ep.	Shaft	Dist. Ep.	Cortical	Cancellous	Compact bone
Pits	0	14.3	0	0	0	0
Scores	0	0	0	0	0	0
Punctures	0	0	0	0	0	0
Pitting	0	57.1	0	100	0	0

Table 8. Frequency of remains with carnivore modifications by type of bones and anatomical part.

Tableau 8. Fréquence des restes avec modifications liées aux carnivores par type d'os et partie anatomique.

	Humerus prox	Humerus dist	Radius prox	Radius dist	Ulna prox	Femur prox	Femur dist	Tibia prox	Tibia dist	Metapodial prox	Metapodial dist
Unit II	5/9 (55.6)	4/8 (50)	4/11 (36.4)	3/11 (27.3)	1/2 (50)	9/12 (75)	7/19 (36.8)	11/17 (64.7)	3/24 (12.5)	28/74 (37.8)	36/76 (47.4)
Unit III	1/2 (50)	0/2 (0)	0/2 (0)	0/0 (0)	0/2 (0)	1/6 (16.7)	1/3 (33.3)	0/2 (0)	0/5 (0)	0/6 (0)	1/9 (11.1)

Table 9 Number of remains with furrowing on long bones by section. Numerators are for the number of elements with damage. Denominators are for the total number of elements (sections). Frequency are in brackets.

Tableau 9 Nombre de restes avec stries et rainures sur les os longs par section. Les numérateurs correspondent au nombre d'éléments endommagés. Le dénominateurs correspondent au nombre total d'éléments (sections). La fréquence est entre parenthèses.



*Figure 7 Horse remains from Unit II modified by carnivore activity: a) humerus with pitting and carnivore breakage; b) radius with scores, pits and heavy furrowing; c) femur with scores, heavy furrowing and pits over fracture edge; d) tibiae with heavy pitting (photos by Denis Dainat, EPCC CERP Tautavel).*

*Figure 7 Restes de chevaux de l'Unité II modifiés par l'action des carnivores: a) humérus avec ponctuations et cassure de carnivore; b) radius avec entailles, ponctuations et rainures profondes; c) fémur avec entailles, rainures profondes et ponctuations sur le bord de fracture; d) tibias avec important rainurage (photos Denis Dainat, EPCC CERP Tautavel).*

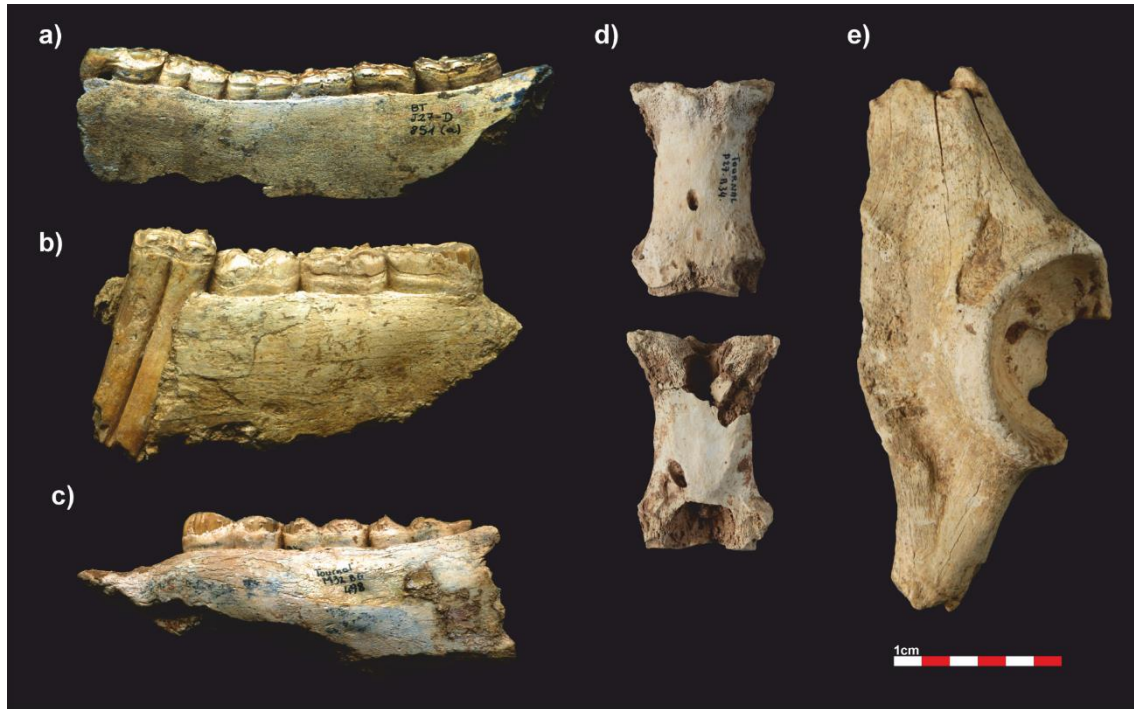


Figure 8 Horse remains from Unit II modified by carnivore action: a) mandible of old individual; b) mandible of prime adult with pitting; c) mandible of juvenile individual with two pits on fracture edge; d) first phalanx with marks of high digestions; e) coxal with pitting on the ilion and ischium extremes and scores at the acetabulum fossa (photos by Denis Dainat, EPCC CERP Tautavel).

Figure 8 Restes de chevaux de l'Unité II modifiés par l'action des carnivores: a) mandibule d'un vieil individu; b) mandibule d'un adulte avec ponctuations ; c) mandibule d'un individu juvénile avec deux piqûres au bord de la fracture; d) première phalange avec marques de digestion intense; e) Coxal avec ponctuations sur les extrémités de l'ilion et de l'ischion et entailles au niveau au niveau de la fosse acétabulaire (photos Denis Dainat, EPCC CERP Tautavel).

The pit measurements were treated statistically for Unit II, because this unit presented the majority of measurable modifications (Table 10). Unit III had one pit that could be measured, but Unit I had no measurable pits or score marks. With regard to the average dimensions of the pit and puncture marks, and considering their 95% confidence interval, the small size of the sample did not give a statistically significant result (Andrés et al., 2012) (Table 10; Figure 9). However, the size of the modifications suggests the action of at least one large carnivore (Andrés et al., 2012; Selvaggio and Wilder, 2001) (Figure 9).

		N°	Mean	95% confidence interval lower	95% confidence interval upper	SD	Min	Max
Pits cortical	Width	11	2.58	1.79	3.31	0.84	1.75	4.07
	Length	11	3.83	2.66	4.91	1.45	1.33	6.53
Pits cancellous	Width	8	4.49	2.51	6.41	1.88	2.07	6.82
	Length	8	7.14	4.26	8.8	2.78	4.11	11.98
Scores cortical	Width	104	2.01	1.21	2.38	1.22	0.53	8.13

Table 10 Dimensions (length and breadth) of tooth pits in the Unit II. Data include mean values, 95% confidence interval, standard deviation and minimum and maximum values documented at the sample.

Tableau 10 Dimensions (longueur et largeur) des ponctuations dentaires de l'Unité II. Les données comprennent les valeurs moyennes, l'intervalle de confiance à 95%, l'écart-type et les valeurs minimales et maximales documentées dans l'échantillon.

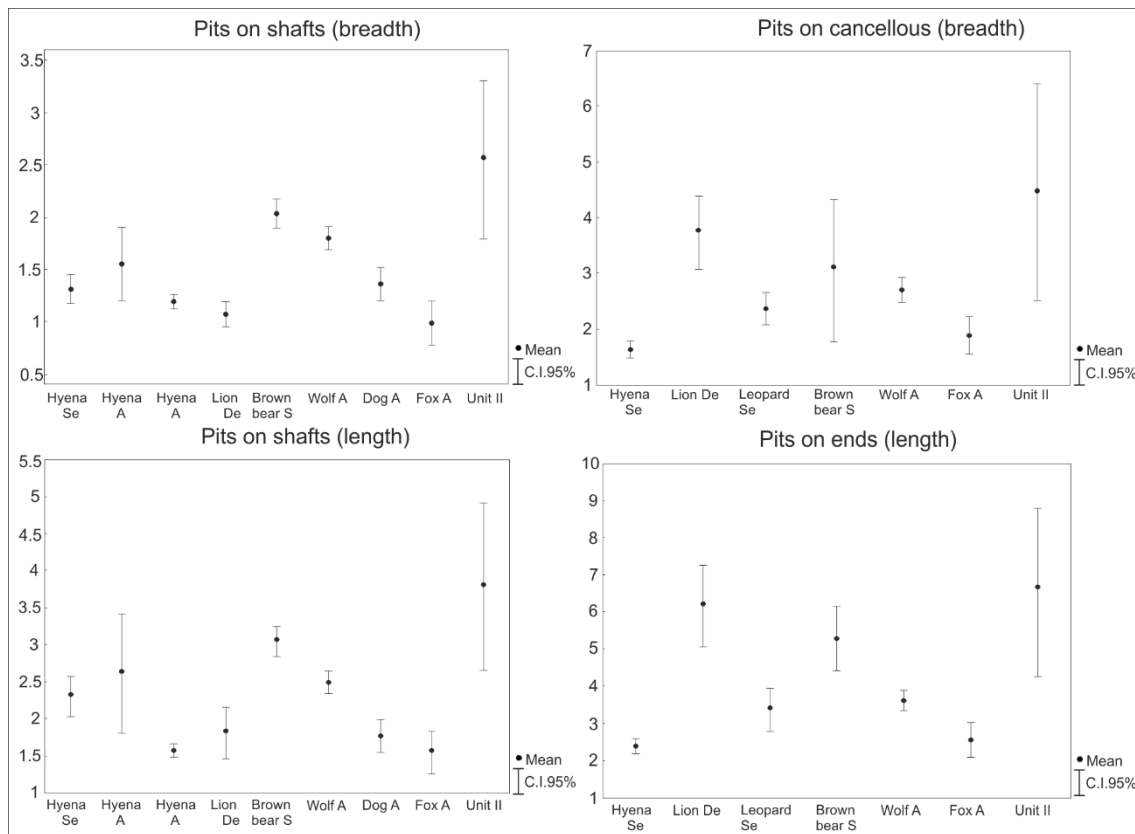


Figure 9 Mean percentages and one S.D. of tooth pit sizes stratified by bone type (dense cortical, cancellous), and by length and width. Data for sampled/specimens marked by A from Andrés et al. (2012), with D from Domínguez-Rodrigo and Piqueras (2003) and with S from Saladié et al. (2013).

Figure 9 Pourcentages moyens et écart-type de la taille des ponctuations dentaires présentés selon le type d'os (os cortical dense, os spongiex) e selon la longueur et la largeur. Données pour les spécimens marqués A d'Andrés et al. (2012), D de Domínguez-Rodrigo et Piqueras (2003) et S de Saladié et al. (2013).

The results of the taphotype analysis for Unit I are included in Table 11. Differences in bone damage between the assemblage from Unit II and the equid samples modified by lions and hyenas were statistically significant (Table 12). The bootstrapped femur CA showed that the taphotypes indicated equal damage in Dimensions 1 and 2 (inertia = 49.2%; inertia = 45.1%) (Supplementary material Table 1). The modifications identified in Unit II show similarities with hyena modifications, especially on the proximal femur (Figure 10a). The bootstrapped humerus CA revealed that taphotypes with greater proximal modifications have more influence in Dimension 1 (inertia = 44.6%), whereas humerus taphotypes with distal modifications in Dimension 2 (inertia = 30.1%) refer to different types of tooth marking (Supplementary material Table 2). This distribution separates the modifications seen in Unit II from lion modifications, although it shows a similar tendency between Unit II and hyenas, with high degrees of modifications (Figure 10b). The bootstrapped radius CA showed a two-dimensional solution, accounting for 100% of the inertia. Dimension 1 (inertia=80.9%) showed the high degrees of bone destruction in Unit II in contrast to low levels of modification by lions (Figure 11a) (Supplementary material Table 3). The bootstrapped tibia CA showed that taphotypes with greater modification have more influence on Dimension 1 (inertia=43.9%), corresponding to captive hyenas and lions, whereas tibia taphotypes with lower

modifications influence Dimension 2 (inertia=30.1%), corresponding to Taranguire lions and the Unit II assemblage (Figure 11b) (Supplementary material Table 4). These results indicate that the modifications of long bones in Unit II are similar to the modifications generated by hyenas. Even in cases where similarities with hyena modifications were not observed, the modifications in Unit II were still different to modifications caused by lions.

CSI		
Element	Unit II	
Humerus	h4 (2), h15 (7)	
Femur	f4 (2), f6, f15 (8)	
Radius	r0 (2), r4 (2), r6 (2), r11 (2), r12 (3), r15	
Ulna	u9, u12	
Tibia	t0, t2 (2), t3 (3), t4 (7), t6 (2), t15 (3)	
CSII		
Element	Portion	Unit II
Humerus	Proximal	hp1_3, hp6, hp7, hp5_6_7, hp5_6_8, hp5_6_7_8
	Distal	hd2, hd5_6_7_8
Femur	Proximal	fp0, fp2, fp4, fp1_2, fp2_4, fp1_2_3_4, fp5_6_7_8
	Distal	fd0, fd1_2, fd2_4, fd1_2, 3, 4, fd3_4_5_6_7_8, fd5_6_7_8
Radius	Proximal	rp0, rp3, rp5, rp7, rp5_6_7_8
	Distal	rd0, rd1, rd3, rd5, rd5_6_7_8
Ulna	Proximal	up0, up2_7_8
	Distal	ud0
Tibia	Proximal	tp0, tp1, tp3, tp5, tp1_2, tp1_2_3, Tp2_4, tp5_6_7_8, tp6_8
	Distal	td0, td2, td4, td8, td1_2_4, td2_4, td5_6_7_8
N° epiphyses		30

Table 11 Description of CSI and CSII taphotypes (Domínguez-Rodrigo et al., 2015) for Bize-Tournal Units and number of epiphyses identified. In brackets number of remains with the same modification.

Tableau 11 Description des taphotypes CSI et CSII (Domínguez-Rodrigo et al., 2015) pour les unités de Bize-Tournal et le nombre d'épiphyses identifiées. Entre parenthèses nombre de restes avec la même modification.

Element	X <sup>2</sup>	df	p
Femur	136.54	84	0.0002559
Humerus	162.26	78	7.285e-08
Radius	69.223	28	2.388e-5
Tibia	213.14	111	1.968e-8

Table 12 Chi-square analyses of taphotypes samples.

Tableau 12 Analyses du X<sup>2</sup> des échantillons de taphotypes.

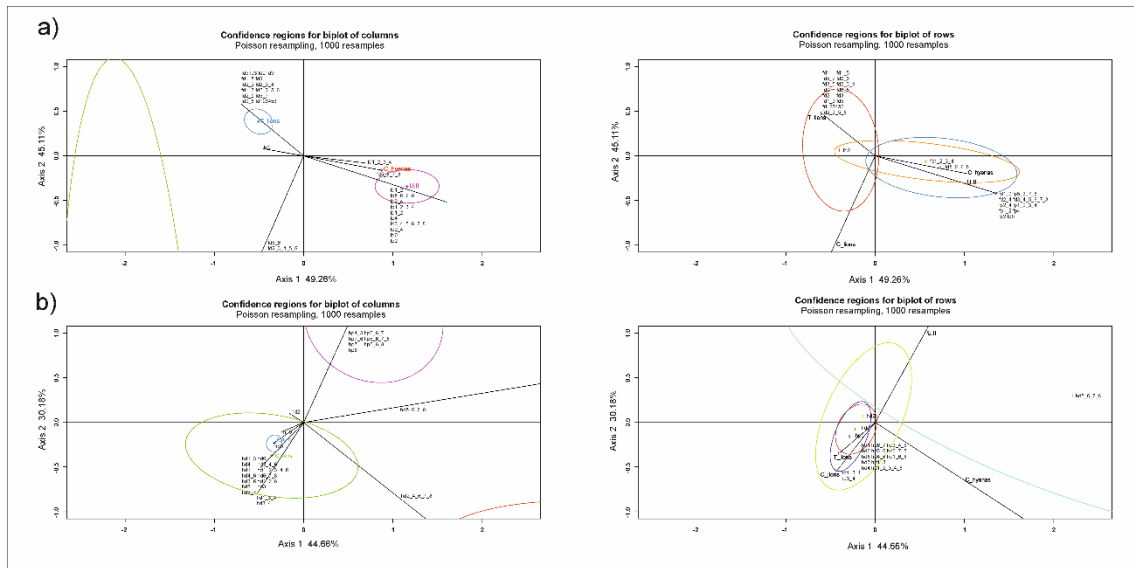


Figure 10 Biplots of the bootstrapped CA of each meat-bearing long bone showing the relationship between carnivore and unit II with respect to the taphotypes that determine them: a) femur; b) humerus. Ellipses with 95% confidence intervals for carnivore (left) and taphotypes (right) are also displayed. Length of the axes shows the importance of the contribution of each variable to the inertia.

Figure 10 Biplots de l'ACP (par bootstrap) du chaque os long porteur de viande montrant la relation entre carnivore et unité II vis-à-vis des taphotypes qui les déterminent: a) fémur ; b) humérus. Des ellipses avec des intervalles de confiance à 95% pour les carnivores (à gauche) et les taphotypes (à droite) sont également affichées. La longueur des axes montre l'importance de la contribution de chaque variable à l'inertie.

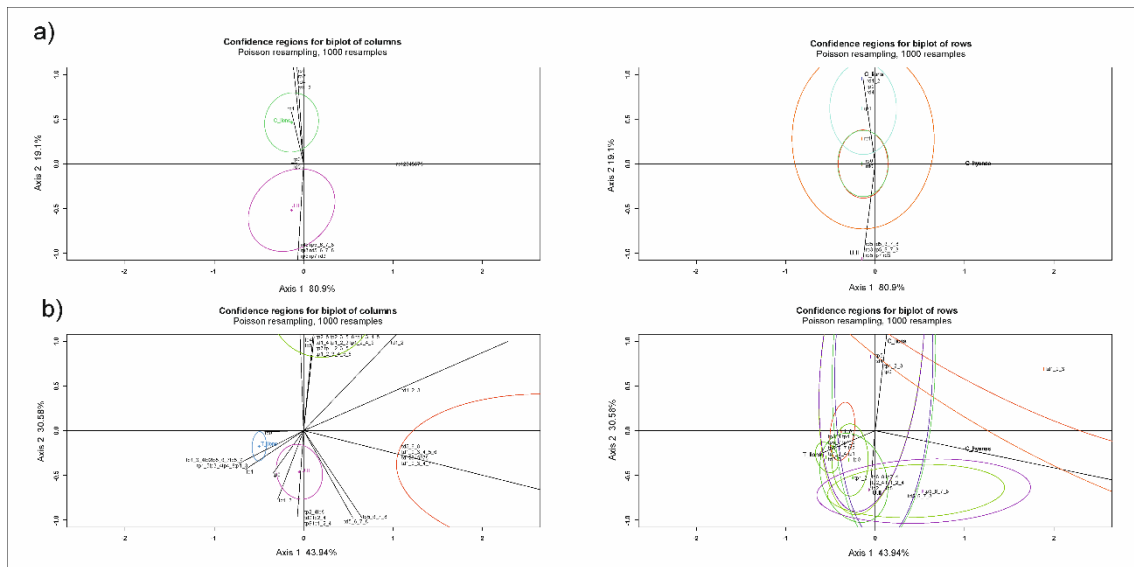


Figure 11 Biplots of the bootstrapped CA of each meat-bearing long bone showing the relationship between carnivore and unit II with respect to the taphotypes that determine them: a) radius; b) tibia. Ellipses with 95% confidence intervals for carnivore (left) and taphotypes (right) are also displayed. Length of the axes shows the importance of the contribution of each variable to the inertia.

Figure 11 Biplots de l'ACP (par bootstrap) du chaque os long porteur de viande montrant la relation entre carnivore et unité II vis-à-vis des taphotypes qui les déterminent: a) radio ; b) tibia. Des ellipses avec des intervalles de confiance à 95% pour les carnivores (à gauche) et les taphotypes (à droite) sont également affichées. La longueur des axes montre l'importance de la contribution de chaque variable à l'inertie.

Anthropogenic modifications were scarce in Units II and III, and non-existent in Unit I. Cut marks were identified on six specimens in Unit II and five in Unit III (Table 13). Anthropogenic bone breakage was not identified. In Unit II, the cut marks were on long, flat bones, and in Unit III only at long bones. The cuts were exclusively slice marks (Figure 13).

In Unit II, cut marks were located on two femurs, two tibias, one mandible, and one coxa (Table 13). In Unit II defleshing activities were identified (Figure 12): one femur showed a slice mark on the cranial side of the midshaft and on the inferior part of the supracondylar fossa, the first probably related to the extraction of the vastus intermedius muscle, and the second with the extraction of gastrocnemius muscle; the tibia had an incision on the popliteus line and lateral edge, both related to the extraction of popliteus muscle; the coxa had cut marks on the inferior edge related to the extraction of the iliac muscle; finally, on the mandible, the cut marks were documented on the labial face, below M2, related to the extraction of the masseter muscle. In Unit III, cut marks were found on two humeri, two tibias, and one femur (Table 13). The distribution of cut marks on the Unit III remains indicated defleshing as the only butchering activity: the tibia remains presented slice marks on the popliteus line and on the medial side of the midshaft, related to the extraction of the popliteus muscle or medial flexor muscle; the humeri presented an incision on the epicondylar ridge, related to extraction of the anconeus muscle, and posterior midshaft for the extraction of the coracobrachialis muscle; the femur had cut marks on the posterior side of the midshaft, related to the extraction of the vastus intermedius muscle.

In both units, the long limb bones with cut marks also presented green bone breakage features. This combination of cut marks and green breakage has been related to early access to animal carcasses by humans (Capaldo, 1997; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo and Pickering, 2003; Selvaggio, 1998, 1994).

In Unit II, two remains with cut marks also presented carnivore tooth marks: one femur with scooping-out, and one coxal bone with pitting. In Unit III, none of the specimens with cut marks presented carnivore modifications.



	Element	Number of remains with cut marks	Location	Cut marks morphology	Activity
Unit II	Mandible	1	Labial face	Slicing marks	defleshing
	Coxa	1	lower edge of the neck of the ilium	Slicing marks	defleshing
	Femur	2	Supracondylar fossa/lateral edge	Slicing marks	defleshing
	Tibia	2	Popliteus line/lateral edge	Slicing marks	defleshing
Unit III	Humerus	2	Epicondylar crest	Slicing marks	defleshing
	Femur	1	Trochanter minor	Slicing marks	defleshing
	Tibia	2	Popliteus line	Slicing marks	defleshing

*Table 13 Number of remains with cut marks by type of element, location, morphology of marks and butchering activities.*

*Tableau 13 Nombre de restes avec traces de découpe par type d'élément, emplacement, morphologie des marques et activités de boucherie.*

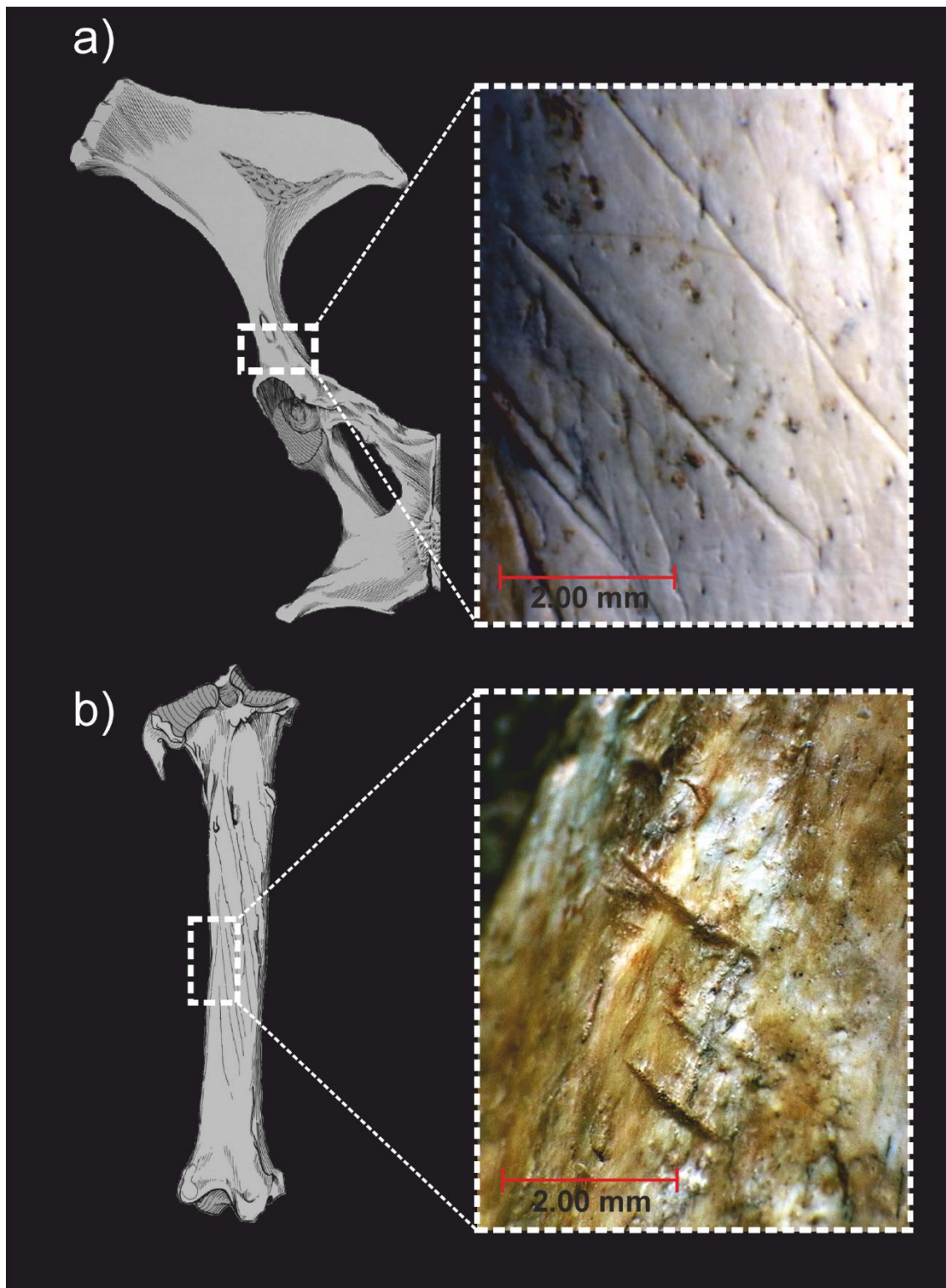


Figure 12 Examples of cut marks from Unit II: a) slicing marks over lower edge of the neck of the ilium of a coxal; b) slicing marks over popliteus line of a tibia. (Photos by Juan Marín, IPH; Drawings modified from Pales and Lambert, (1971).

Figure 12 Exemples de marques de découpe de l'unité II : a) traces de découpe sur le bord inférieur du col de l'ilion d'un coxal ; b) traces de découpe sur la ligne poplitée d'un tibia. (Photos de Juan Marín, IPH ; dessins modifiés de Pales et Lambert, 1971).

## 4.2. Post-depositional modifications

The most common post-depositional modifications in Unit I were sediments cemented onto bones (31.4%), followed by manganese oxides stains (25.5%), and rounding (23.5%). In addition, polishing (19.6%) and fissures (17.6%) were identified. In Unit II, rounding (32.8%), fissures (32.8%), and concretions (32.8%) presented the greatest proportions, followed by polishing (28.6%) and manganese oxide (20.2%). Trampling (2.2%) was also identified. Finally, in Unit III, concretions (25.7%) were the most common post-depositional modification, followed by fissures (17.1%), rounding (16.7%), and polishing (16%). Manganese oxide stains (9.3%) and trampling were identified on 0.4% of the specimens.

## 5. Discussion

The analysis of horse remains from Units I, II, and III from Bize-Tournal Cave has provided information of the origin and processes that affected the formation of the faunal assemblages. The results indicate that hominins played a minor role in the taphonomic history of the horse specimens. The main accumulator and modifier seem to have been carnivores, particularly in the formation of the Unit II assemblage. Finally, the major post-depositional modifications were concretions and rounding, due to the action of water flow, of diverse intensities, that affected part of the assemblages.

Previous research point to hominins as the principal accumulators of horses, and in Unit II shared with a primary and secondary of carnivores (Magniez, 2010, 2009; Magniez and Boulbes, 2014). According to these proposals, the equid carcasses were brought back in large portions after primary treatment at the kill site to discard the axial skeleton. Horse family groups were hunted from summer to autumn, generating mortality profiles dominated by prime adults. Carnivore modifications are common on bones from Mousterian and Aurignacian units, but the majority have been explained as a product of secondary access to carcasses by carnivores after the hominids abandoned the site. Those assemblages were only slightly affected by natural post-depositional processes (Magniez, 2009, 2010; Magniez and Boulbes, 2014).

Alternating carnivore and hominin occupations would indicate short human occupations (Aura et al., 2002; Daujeard and Moncel, 2010; Stiner, 1991a; Valensi, 2000). According to Costamagno and colleagues (Costamagno et al., 2006), the presence of carnivore tooth marks in the bone assemblages indicates short occupations; this should be considered an additional argument that corroborates other evidence of short-term occupation. Long-term residential camps, such as the French sites of Baume des Peyrards, show a specialised hunting spectrum while short-duration sites, such as Payre-F, Baume Flandin, and Le Figuier (France), show a varied faunal spectrum (Daujeard and Moncel, 2010). According to these criteria and the results from this work, we agree that the hominin occupations were short, even expedite, in the three units. However, we cannot

underestimate the role of carnivores, particularly hyenas, in the accumulations and/or modification of Units I, II, and III at Bize-Tournal Cave.

Multiple specialists have proposed a predominance of juvenile and subadult hyena as a factor characterising hyena dens (Cruz-Uribe, 1991; Klein et al., 1991; Stiner, 1991a). However, the research of Pickering (Pickering, 2002) and Kuhn et al. (Kuhn et al., 2010) highlighted the fact that an abundance of juvenile individuals together with an abundance of coprolites were the most convincing features for classifying a hyena accumulation. A predominance of juvenile individuals has been observed in present-day dens of striped hyena in the desert of Jordan, brown hyena in the Mashatu Reserve (Botswana), and spotted hyena in the Namib-Naukluft Park (Namibia) (Kuhn et al., 2010). It has also been evidenced in archaeological hyena dens from Grotta di Guattari (Italy) (Stiner, 1991b), the sites of Equus Cave and Swartklip (South Africa) (Cruz-Uribe, 1991; Klein et al., 1991), Manot Cave area D (Israel) (Orbach and Yeshurun, 2019), Nad Kacakem Cave and Bad Wildungen hyena dens (Germany) (Diedrich, 2013), at the French sites of Fouvent (Fourvel et al., 2014), La Chauverie and Camiac (Discamps et al., 2012) and on the Iberian Peninsula at Furninha Cave (Portugal) (Brugal et al., 2012), Cova del Gegant (Spain) (Samper Carro and Martínez-Moreno, 2014), and El Buho Cave (Sala et al., 2012), among others. These characteristics were recorded in previous works on Bize-Tournal Cave. In Units I, II, and III, carnivore remains (Unit I: NISP=14; Unit II: NISP=443; Unit III: NISP=72) represent 33% of MNI in Unit I, 34% in Unit II, and 28% in Unit III (Magniez, 2009). The hyena mortality profiles indicate that the three age groups were present in the same proportions (Magniez, 2009). Additionally, a great number of coprolites were found in Unit I (NR=125), Unit II (NR=389), and Unit III (NR=67).

The horse remains found in the Bize-Tournal units are dominated by skulls and long limb bones, especially metapodials, with low percentages of axial skeleton (except for coxa in Unit II) and compact bones. The scarcity of axial elements and compact bones is consistent with work on actualistic studies and fossil assemblages that have been modified by carnivores (Capaldo, 1998; Marean et al., 1992; Pickering et al., 2003). These anatomical profiles are similar at other sites inhabited by hyenas in a similar manner (Brugal et al., 1997; Diedrich, 2011b; Fosse, 1996, 1995; Fourvel et al., 2014; Fourvel and Fosse, 2017; Stiner, 1991b). Modern spotted hyenas also transport zebra carcasses, resulting in a similar overrepresentation of distal long limb bones, as well as large quantities of teeth from crushed skulls (Kruuk, 1972).

In addition, it has been proven that this species has the capacity to transport large animal elements (Egeland et al., 2008; Kruuk, 1972, 1970; Lam, 1992; Pokines and Peterhans, 2007). Present-day spotted hyenas can move a complete carcass over long distances to protect the prey from other carnivores (Kruuk, 1972). This supports the fact that these animals would have been able to transport the horse segments to Bize-Tournal Cave.

The mortality profiles identified for horses in the three units are: prime-adult dominated (Unit I); catastrophic (Unit III); and attritional (Unit II), no different to those generated by present-day carnivores (Stiner, 1990) (Figure 13). A prime-adult-dominated mortality profile has been identified for present-day spotted hyena assemblages (Kruuk, 1972). The profiles identified in Unit II and Unit III are similar to those generated by cursorial hunters, like hyenas (Cruz-Uribe, 1991; Kruuk, 1972). Additionally, the same type of mortality profile has been observed at various archaeological and palaeontological sites with carnivore bone accumulation, like Fouvent (France) (Fourvel et al., 2014), Llonin Cave (Spain) (Sanchis et al., 2019), and Level TD6.3 of Gran Dolina Cave (Saladié et al., 2017). The eruption pattern and wear stages of juvenile dentition indicate that the juvenile horses in Unit I died during the end of summer and beginning of autumn, while those from Units II and III died in various periods of the year. Previously, it was proposed that reindeer hunting involved the capture of isolated individuals (Magniez, 2009). The wide seasonal range observed for horses could indicate a similar scenario.

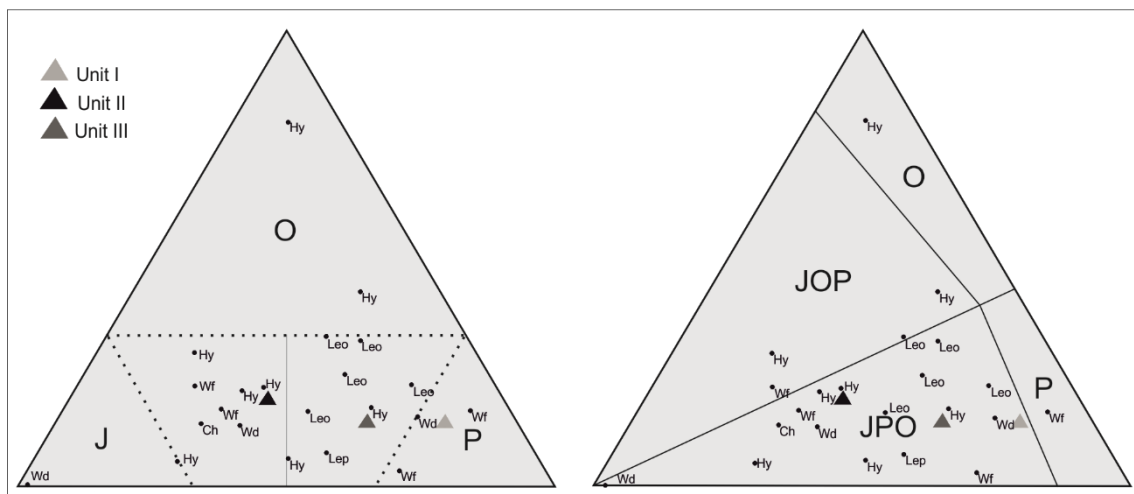


Figure 13 Mortality profiles for Bize-Tournal units and current carnivore samples from Stiner (1990). Hy=Hyena; Wf=Wolf; Tr=Tiger; Leo=Lion; Ch=Chita; Lep=Leopard.

Figure 13 Profils de mortalité pour les unités de Bize-Tournal et échantillons de carnivores actuels d'après Stiner (1990). Hy=Hyène; Wf= Loup; Tr=Tigre; Leo=Lion ; Ch=Guépard; Lep=Léopard.

Another aspect of hyena assemblages to consider is the low proportion of long limb bone epiphyses with respect to the abundance of diaphyses (Egeland et al., 2008; Pickering, 2002), and the relative abundance of shaft cylinders (Kuhn et al., 2010; Prendergast and Domínguez-Rodrigo, 2008). The results of the shaft/epiphysis ratio and percentage of change analysis indicate a scenario of moderate competition between carnivores. Cruz-Uribe (Cruz-Uribe, 1991) indicated that an elevated presence of limb bones with relatively complete shafts along with a lack of epiphyses is a good indicator of hyena accumulations. In all units the proportion of long bones with complete circumferences was very high. Additionally, cylinders were numerous in Unit II, with a total number of 68 remains. However, according to Kuhn et al. (Kuhn et al., 2010) cylinders alone indicate carnivore involvement in the formation of the assemblage, not exclusively hyenas, because lions and leopards could produce similar cylindrical fragments.

Moreover, the bone surface modification analysis of the horse specimens from Units I, II, and III shows that the assemblages were principally modified by carnivores. Magniez (2009, 2008) points to the possibility that carnivores had secondary access to animal carcasses abandoned by hominins in all the units, although their activity was greatest in Unit II. Use of the same space by hominins and carnivores is well attested (Brain, 1981; Domínguez-Rodrigo and Lezana, 1996; Kruuk, 1972; Prendergast and Domínguez-Rodrigo, 2008; Saladié et al., 2017), so it is common to find elements modified by both agents (Egeland et al., 2008). However, only on two specimens from Unit II was there coincidence between anthropogenic and carnivore modifications on the same remain. These were a coxa and a femur: the cut marks were related to defleshing; while the carnivore modification involved pitting on the two fragments, which could indicate posterior scavenging of elements abandoned by hominins. The low percentage of remains with co-occurrence of anthropogenic and carnivore modifications has been interpreted as a signal of great independence between the two groups, linked to a low level of competition (Egeland et al., 2008). In addition, the absence of anthropogenic bone breakage compared with the enormous number of remains fractured by carnivores, supports the idea that the majority of the elements were transported and accumulated by carnivores. However, the hyenids could destroy the anthropogenic traces and altered a first human breakage.

The types of modifications, their distribution on the bones, and the tooth mark measurements evidence that a large carnivore was involved during the formation of the assemblage. The taphotype analysis indicates that the consumption of epiphyses, especially femur and humerus, were closer to the action of hyenas, rather than large felids. Furthermore, the presence of numerous digested bones, including a phalanx, and even teeth, indicates the activity of a durophagous carnivore with a metabolism capable of assimilating the nutrients from these bones (Brain, 1981; Kruuk, 1972; Pickering, 2002). Pitting is also characteristic of carnivore den sites or resting places (Binford, 1981).

We cannot rule out the possibility that part of the assemblages from Units I, II, and III of Bize-Tournal Cave could have resulted from the ravaging of bones left behind by human groups. Indeed, some remains with both carnivore- and hominin-induced modifications indicate that this scenario was possible. However, the absence of anthropogenic bone breakage and the low percentages of cut marks, along with the large quantity of carnivore modifications, does not support this assertion for the majority of the assemblages. The anatomical distribution, like that seen in other carnivore accumulations, and the mortality profiles, especially in Units II and III, indicate that the main bone accumulation agents were carnivores. In addition, in Unit II, it seems that hyenas were solely responsible for the formation of the horse assemblage, with possible secondary action by other carnivores. An interesting point is that although the volume of horse remains in the Mousterian units differed with respect to the Aurignacian Unit, we found no great differences in the composition of the three samples. The anatomical profiles, dominated by cranial and distal long limb bones, the taphonomic signal, with a high percentage of

carnivore damage and little evidence of human activities, indicate that the use of the cave by Mousterian and Aurignacian groups did not change with respect to the accumulation of horses. This would indicate that the contribution of carnivores, especially hyenas, and their modifications was likely to have been similar, with sporadic hominin occupation.

## **6. Conclusions**

Assemblages generated by hyenas are characterised by abundant coprolites and juvenile hyena remains, an abundance of carnivore bone breakage, the presence of cylinders, digested bones, and damage like scoring, pitting, punctures, furrowing, scooping-out, and principally U-shaped prey mortality profiles. Analysing the horse remains from Units I, II, and III from Bize-Tournal Cave has enabled us to identify most of these characteristics, particularly in Unit II. The anatomical distribution is similar to that seen in other carnivore accumulations, and the mortality profiles, especially in Units II and III, indicate that the main agents of bone accumulation were carnivores. The type, distribution, and features of the modifications, together with the taphotype analysis indicate that large durophagous carnivores were involved in the formation of the assemblage, probably hyenas.

Hominins played a minor role in the horse accumulations, although part of the assemblage could have resulted from the ravaging of bones left behind by human groups. No great differences were found in the composition and features of the three units. The systematic analysis of the bone splinters of the studied levels contributed to complete the study of horse remains. The accumulation of horses in Bize-Tournal Cave during the Mousterian and Aurignacian did not change and was characterised by sporadic hominin occupation. This would indicate that the horse remains were introduced and modified in the cave, mainly by carnivores. In this context, it must be considered that carnivores have a more important role than suggested in the previous studies where the impact was clearly identified on the bones of megaceros, deer and ibex.

## **7. Acknowledgements**

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**Table 1: Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for femur.**

Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil)

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
fd0	-0.385	0.174	949	44	0.064	0.280	27	1	975
fd1	-0.594	0.000	613	5	0.471	0.000	385	4	998
fd1_2	1.362	0.000	883	28	-0.422	0.000	85	3	968
fd1_2_3_4	0.579	0.528	912	25	-0.064	0.120	11	0	923
fd1_2_3_4_5_6	-0.594	0.000	613	5	0.471	0.000	385	4	998
fd1_3	-0.594	0.000	613	11	0.471	0.000	385	7	998
fd1_5	-0.594	0.000	613	11	0.471	0.000	385	7	998
fd2	-0.594	0.000	613	16	0.471	0.000	385	11	998
fd2_3	-0.594	0.000	613	5	0.471	0.000	385	4	998
fd2_3_4	-0.594	0.000	613	5	0.471	0.000	385	4	998
fd2_3_4_5_6	-2.270	0.000	172	77	-4.984	0.000	828	403	1000
fd2_3_5_6	-0.594	0.000	613	5	0.471	0.000	385	4	998
fd2_4	1.362	0.000	883	28	-0.422	0.000	85	3	968
fd2_5	-0.594	0.000	613	5	0.471	0.000	385	4	998
fd3	-0.594	0.000	613	16	0.471	0.000	385	11	998
fd3_4_5_6_7_8	1.362	0.000	883	28	-0.422	0.000	85	3	968
fd3_5	-0.594	0.000	613	11	0.471	0.000	385	7	998
fd5	-0.594	0.000	613	95	0.471	0.000	385	65	998
fd5_6	-2.270	0.000	172	77	-4.984	0.000	828	403	1000
fd5_6_7_8	0.741	0.346	463	82	-0.131	0.138	15	3	477
fd5_7	-0.594	0.000	613	5	0.471	0.000	385	4	998
fd9	-0.594	0.000	613	5	0.471	0.000	385	4	998
fp0	1.362	0.000	883	110	-0.422	0.000	85	12	968
fp1_2	1.362	0.000	883	28	-0.422	0.000	85	3	968
fp1_2_3_4	1.362	0.000	883	110	-0.422	0.000	85	12	968
fp2	1.362	0.000	883	28	-0.422	0.000	85	3	968
fp2_4	1.362	0.000	883	28	-0.422	0.000	85	3	968
fp4	1.362	0.000	883	28	-0.422	0.000	85	3	968
fp5_6_7_8	1.362	0.000	883	83	-0.422	0.000	85	9	968

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	0.872	0.000	92	11	-0.161	0.000	3	0	95
C_lions	-1.931	0.319	185	166	-4.057	2.049	815	801	1000
T_lions	-0.505	0.064	635	224	0.383	0.054	365	141	1000
U.II	1.158	0.139	916	598	-0.343	0.079	80	57	996

## Table 2: Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for humerus.

Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil)

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
hd0	-0.213	0.098	837	31	-0.076	0.116	106	6	943
hd1	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd1_2_3_4_6	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd1_3	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd1_3_4	-0.432	0.000	15	5	-0.545	0.000	24	12	39
hd1_6_8	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd2	-0.129	0.245	152	1	0.067	0.425	42	0	194
hd3	-0.398	0.000	366	11	-0.343	0.000	271	12	637
hd3_4	-0.432	0.000	15	3	-0.545	0.000	24	6	39
hd3_4_6	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd3_4_6_7_8	6.047	0.000	703	505	-3.926	0.000	296	315	1000
hd3_6	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd4	-0.398	0.000	366	7	-0.343	0.000	271	7	637
hd4_6	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd5_6_7_8	2.221	1.564	982	272	0.299	0.786	18	7	1000
hd6	-0.398	0.000	366	9	-0.343	0.000	271	10	637
hd6_7	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd6_7_8	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hd8	-0.398	0.000	366	2	-0.343	0.000	271	2	637
hp0	-0.276	0.117	340	12	-0.156	0.190	109	5	449
hp1_3	0.946	0.000	234	12	1.707	0.000	763	60	997
hp5_6_7	0.946	0.000	234	12	1.707	0.000	763	60	997
hp5_6_7_8	0.946	0.000	234	37	1.707	0.000	763	179	997
hp5_6_8	0.946	0.000	234	12	1.707	0.000	763	60	997
hp6	0.946	0.000	234	25	1.707	0.000	763	119	997
hp7	0.946	0.000	234	12	1.707	0.000	763	60	997
hp7_6	0.946	0.000	234	12	1.707	0.000	763	60	997

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	5.000	1.877	778	690	-2.668	0.856	222	291	1000
C_lions	-0.357	0.436	27	14	-0.370	0.203	29	22	55
T_lions	-0.329	0.035	486	111	-0.233	0.041	243	82	729
U.II	0.782	0.306	312	186	1.160	0.285	686	605	998

### Table 3: Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for radius.

Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil)

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
rd0	-0.135	0.142	1000	6	-0.002	0.194	0	0	1000
rd1	-0.135	0.406	186	1	0.282	0.515	814	18	1000
rd1_2	-0.135	0.000	20	0	0.955	0.000	980	69	1000
rd3	-0.135	0.000	16	0	-1.066	0.000	984	86	1000
rd4	-0.135	0.000	20	0	0.955	0.000	980	69	1000
rd5	-0.135	0.000	16	0	-1.066	0.000	984	86	1000
rd5_6_7_8	-0.135	0.000	16	0	-1.066	0.000	984	86	1000
rp0	-0.135	0.145	999	6	0.004	0.189	1	0	1000
rp1	-0.135	0.191	45	2	0.619	0.262	955	174	1000
rp12345678	7.416	0.000	1000	982	0.000	0.000	0	0	1000
rp2	-0.135	0.000	20	0	0.955	0.000	980	69	1000
rp3	-0.135	0.000	16	0	-1.066	0.000	984	86	1000
rp5	-0.135	0.000	16	0	-1.066	0.000	984	86	1000
rp5_6_7_8	-0.135	0.000	16	0	-1.066	0.000	984	86	1000
rp7	-0.135	0.000	16	0	-1.066	0.000	984	86	1000

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	7.416	0.000	1000	982	0.000	0.000	0	0	1000
C_lions	-0.135	0.123	78	9	0.464	0.136	922	473	1000
U.II	-0.135	0.198	63	8	-0.518	0.189	937	527	1000

### Table 4: Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for tibia.

Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil)

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
td0	-0.368	0.057	606	62	-0.009	0.134	0	0	606
td1_2	1.350	1.242	570	58	1.168	0.721	426	63	996
td1_2_3	1.898	1.503	859	77	0.692	0.915	114	15	973
td1_2_3_4_5_6	3.545	0.000	890	268	-0.737	0.000	38	17	929
td1_2_3_4_7	3.545	0.000	890	134	-0.737	0.000	38	8	929

td1_2_4	-0.058	0.000	2	0	-0.666	0.000	212	14	214
td1_4	0.252	0.000	14	1	2.120	0.000	963	69	976
td12345678	3.545	0.000	890	134	-0.737	0.000	38	8	929
td2	-0.058	0.000	2	0	-0.666	0.000	212	7	214
td2_3	-0.600	0.000	276	4	-0.253	0.000	49	1	325
td2_4	-0.058	0.000	2	0	-0.666	0.000	212	7	214
td4	-0.038	0.242	2	0	0.830	0.724	914	42	916
td5_6_7_8	0.457	0.506	132	16	-0.676	0.152	289	49	421
td5_6_8	3.545	0.000	890	134	-0.737	0.000	38	8	929
td8	-0.058	0.000	2	0	-0.666	0.000	212	14	214
tp0	-0.282	0.083	323	15	-0.328	0.165	437	30	760
tp1	-0.540	0.066	339	28	-0.299	0.087	104	12	443
tp1_2	-0.239	0.195	90	2	-0.528	0.255	443	13	533
tp1_2_3	0.097	0.295	8	0	0.727	1.016	444	16	452
tp1_2_3_4_5_6	0.252	0.000	14	1	2.120	0.000	963	69	976
tp1_2_3_5	0.252	0.000	14	1	2.120	0.000	963	138	976
tp1_2_4_5	0.252	0.000	14	1	2.120	0.000	963	69	976
tp1_3	-0.600	0.000	276	8	-0.253	0.000	49	2	325
tp1_3_4	-0.600	0.000	276	8	-0.253	0.000	49	2	325
tp1_3_4_5	0.252	0.000	14	1	2.120	0.000	963	69	976
tp1_5	-0.600	0.000	276	4	-0.253	0.000	49	1	325
tp2	-0.600	0.000	276	4	-0.253	0.000	49	1	325
tp2_3_5_8	0.252	0.000	14	1	2.120	0.000	963	69	976
tp2_4	-0.058	0.000	2	0	-0.666	0.000	212	7	214
tp2_5	0.252	0.000	14	1	2.120	0.000	963	69	976
tp3	0.097	0.280	8	0	0.727	0.996	444	16	452
tp3_4	-0.600	0.000	276	4	-0.253	0.000	49	1	325
tp4_8	-0.600	0.000	276	4	-0.253	0.000	49	1	325
tp5	-0.038	0.241	2	0	0.830	0.709	914	42	916
tp5_6_7	-0.600	0.000	276	8	-0.253	0.000	49	2	325
tp5_6_7_8	0.543	0.610	188	19	-0.677	0.184	293	42	481
tp5_7	-0.600	0.000	276	4	-0.253	0.000	49	1	325
tp6_8	-0.058	0.000	2	0	-0.666	0.000	212	7	214

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	2.942	0.777	929	831	-0.510	0.376	28	36	957
C_lions	0.209	0.247	20	11	1.467	0.264	961	793	980
T_lions	-0.498	0.033	393	156	-0.175	0.067	49	28	442
U.II	-0.048	0.106	3	1	-0.461	0.125	244	143	246

## **Chapter 8. Discussion**



## Discussion

The Neanderthal subsistence strategies can be summarized as complex processes which include procurement and storage of raw materials, the intensive use of vegetal resources, use of fire and the ability to hunt a wide range of preys (Stiner and Kuhn, 1992; Mellars, 1996a; Villaverde et al., 1996; Patou-Mathis, 2000; Vallverdú et al., 2005, 2010; Moncel et al., 2008, 2019; Zilhão and Villaverde, 2008; Peresani et al., 2011; Blasco and Fernández Peris, 2012; Stiner, 2013; Yravedra and Cobo-Sánchez, 2015; White et al., 2016; Mallol et al., 2019; Rendu et al., 2019; Sanz et al., 2019). We want to contribute to this framework through the study of faunal assemblages of three sites of the Southwest of Europe, the Bize-Torunal cave, the Abri du Maras and Abric Romaní rock shelters. As each of the papers that form part of this doctoral thesis has a specific discussion, in this section we propose to discuss the different studies on faunal groups.

### 8.1. Assemblage formation

Reconstruct the taphonomical history of an assemblage is essential to know which agents and processes took part in its formation. The objectives and interests of zooarchaeology are focused on knowing the anthropogenic role in the origins of faunal assemblages. Matching the human activity with other agents, such as carnivores, permit us to know some features of the past human group's ecology. Behavioural inferences from the study of the assemblages resulting from the carnivore and human interactions can give us important clues about the ecological relationship between both predators (Saladié et al., 2018).

Archaeological sites are in most cases palimpsest result of an indeterminate number of occupation events, through materials deposition and reduction processes (LaMotta and Schiffer, 1999; Bailey, 2008; Bailey and Galanidou, 2009). The redundant use of occupied space with identical functions is called reuse, while reoccupation implies repeated use of the same place, but with activities that are not correlated with each other. The segregation and identification of the reoccupation processes are only to be observed in sites with high archaeological resolution (Yellen, 1977; Binford, 1981b; Brooks and Yellen, 1987; O'Connell, 1987). Among the studied sites, the Abric Romaní has high sedimentation rates (Bischoff et al., 1988, 1994) which permit sometimes the palimpsest dissection (Gabucio, 2014). This is the case of the level P of Abric Romaní, which archaeostratigraphic resolution that permitted us to observe the site reoccupation in different events, that used the site in some cases as residential camps and others as ephemeral hunting camps (Marín et al., 2019). It is not rare that Pleistocene hunter-gatherers reoccupied the same place with different objectives since the lower



Pleistocene (Valensi, 2000; Saladié et al., 2011a; Carbonell, 2012; Niven, 2013; Romandini et al., 2014; Rodríguez-Hidalgo et al., 2015, 2017).

Through the study of faunal remains from Abric Romaní, Abri du Maras and Bize-Torunal we have observed two types of sites. In the first instance, sites in which human activity is dominant, as the level P of Abric Romaní and the level 5 of Abri du Maras, sites where carnivore activity is the resulting ravaging of bones abandoned by humans, in an ecological interaction of commensalism. In this scenario, the carnivores modify the assemblage generated and abandoned by the hominin groups (Saladié et al., 2018). These types of sites are usually located in open site places, rock shelters and in the more open and external areas of a cave, which offered refuge but are not enough closed environment to being used as a den by carnivores. The impact of carnivore activity over the assemblages of Abri du Maras and Abric Romaní is limited, as the frequencies of their modifications show, even when they are related to brief human occupations. Humans usually abandon carcasses parts that could be profitable by carnivores, such as epiphysis or vertebra bodies. Carnivores are attracted by the smell of the spoils, scavenging the abandoned elements on the living floors. When we tackle a succession of short occupations, carnivore induced modifications are expected to range between 5 and 15% of specimens regarding total bone frequencies between 5 and 15% of specimens (Blumenschine, 1995; Capaldo, 1997). However, in the assemblages with the common use of fire, as the Abric Romaní, Neanderthals were able to intensely exploited animal carcasses, cooking or burning the remaining portions, which would considerably reduce the interest of carnivores in prowling in their settlements. According to the taphonomical history of both assemblages, we can assert that they were entirely produced by human activity and that carnivore activity was thus very scarce.

The horse assemblage of Unit I, II and III from Bize-Torunal cave represent the second type of archaeological site identified. This assemblage is included within the category of deposits and sites in which carnivore activities are dominant over hominin activity, and whose formation is firstly related with its use as dens or lairs (Brugal and Fosse, 2004; Stiner, 2010; Fourvel and Fosse, 2017). Normally, these types of sites are in caves and enclosed galleries. However, within these assemblages, the presence of hominin activities could present different features. First, there are sites in which the relevance of human and carnivore activity is similar, although the occupation, deposition and modification events were independent (Saladié et al., 2018). Secondly, there are sites in which the superposition of human and carnivore events were independents. In third and last place, sites used as lairs or dens by carnivores, where the human occupation is occasional and independent (Brugal and Fosse, 2004; Daujeard and Moncel, 2010b; Diedrich, 2010; Fourvel et al., 2012, 2014; Saladié et al., 2018; Rusch et al., 2019; Picin et al., 2020). The Mousterian levels of Bize-Torunal cave resemble the first type of site described because, despite the scarce of human modification, lithic remains were

abundantly found in these levels (Chacón, 2009). Besides, we should consider the great proportion of carnivore activity over horse remains over the scarcity of human modifications. Also, there is a great abundance of carnivore remains specially hyenas (*Crocuta crocuta*) and bears (*Ursus speleaeus/Ursus arctos*) (Magniez, 2008, 2009; Magniez and Boulbes, 2014). The great part of hyena remains belongs to young individuals, which together with to the abundance of coprolites suggest the use of the cave as hyena den (Pickering, 2002).

Some researchers have considered that in sites resulting from carnivore activities, but with human presence, it is possible to evaluate the intensity of carnivore occupation concerning a greater or lesser abundance of their modifications, allowing to infer longer occupation events by carnivores and shorter occupation by humans or vice versa (Stiner, 1991b; Valensi, 2000; Aura Tortosa et al., 2002; Daujeard and Moncel, 2010b). If we consider this proposal, the horse remains of Bize-Tournal indicate a greater intensity and more persistence carnivore occupations made during independent events than human occupations. These assemblages can, therefore, be interpreted as the result of the alternate of occupation of both agents, which shared the same site but not the resources found in there.

According to the classification proposed by Stiner (2013) we have been able to identify assemblages resulting from the occupation of different lengths. As we said, the assemblage of Bize-Tournal could be related to short-term occupation events by Neanderthals, that sporadically visited the cave. On the contrary, in the complete sequence of Abric Romaní we observed a great variability on this sense, the spatial patterns in the site correspond to functional campsite organized around isolated external hearths and campsites with many external connected hearths by refitting and sleeping and resting areas (Vaquero and Pastó, 2001; Vaquero, 2008; Vallverdú et al., 2010). In the short-term occupation events, it is possible to identify and isolate specific activity areas (Vallverdú et al., 2005), besides the remains are grouped mainly around hearths.

The sublevels identified in the level P of Abric Romaní, sublevel Pa and Pb, are one more example within the sequence of this spatial and occupational pattern. In these sublevels, it has been observed that the occupation events in which horses and deers were hunted are accumulated in different areas of the shelter surface, around combustion structures well defined. Although the occupations have distinct functions (residential occupations and hunting halts), both were short-term occupations, which could range from a few days to a few weeks. In the different levels of Abric Romaní, it has also been observed that the lithic remains support the existence of different length of occupations too. Indeed, according to Vaquero and colleagues (Vaquero et al., 2012), the variability of the lithic industry assemblages increased when the length of the assemblage formation grows. Besides, the presence of tool kits is normally abundant in

short-term occupation, as in sublevel Pa, where besides the different lithic remains present a higher degree of retouch (Martín-Viveros et al., 2020).

Instead, in level 5 of Abri du Maras the occupations were associated with one complete season, during summer, when Neanderthals pursuit reindeers and horses. So, we can assume that the site was occupied in long-term occupation events. This circumstance has been observed at other levels of the sequence proposing the seasonality may be related to the timing of reindeer movement, during their migratory movement in autumn (Daujeard et al., 2019). In level 5, the taxa more abundant was the reindeer too and considering the pattern of death of these animals the seasonal hunt for reindeer in level 5 can be also suggested.

The specific variability included in the archaeological assemblages has been used to identify the length of the occupations has been used the specific variability that includes the archaeological assemblages. Daujeard and Moncel (2010) observe that in different Neanderthals sites of the Rhone valley the short-term events were characterized by certain variability in ungulate preys, opposite to a trend of a specialized hunt in the long-term occupations. However, when applying a different index to measure the diversity and homogeneity of the assemblages of level P and level 5, the values obtained are similar. The taxonomic samples of both sites are dominated by the presence of medium and large ungulates. Both sites highlight the presence of cervids, the reindeer in the Abri du Maras and the red deer in the Abric Romaní. They are followed by horses and then by large bovids, the bison in the Abri du Maras and the auroch in the Abric Romaní. In addition, as is typical of the anthropogenic assemblages, at both sites the scarcity of carnivore remains stands out. Indeed, if we consider the specific features of level P, we observed that the occupation related to horse capture have specialized hunting despite they were short-term occupations, probably during a few days.

It should be noted that the sedimentary rate has allowed us to separate two clear sub-levels. Without this differentiation, it would have been difficult or impossible to segregate the occupations related to the capture of horses and those related to the capture of deer. Trends in the anatomical profiles of these taxa have already been seen at other levels of this site (e.g. Fernández-Laso et al., 2010; Rosell et al., 2012b; Modolo and Rosell, 2017) without this issue having been resolved in previous studies. According to the data we have observed that the spectrum of prey of the Neanderthals the Abric Romaní and the Abri du Maras may be linked to other circumstances, such as the time of year or the availability of resources, rather than to the length of the occupations.

## 8.2. Discard and transport

To evaluate the discard and transport activities we should refer to the anatomical profiles of ungulates presents in the archaeological sites. These studies also serve as indicators of economic aspects in the foraging systems of past human groups, allowing us to infer certain social features from these forager groups (White, 1952, 1953b, 1954, 1955; Perkins and Daly, 1968; Binford, 1978; Stiner, 1994, 2010; Saladié et al., 2011a; Rodríguez-Hidalgo et al., 2017).

Before the analysis of anatomical profiles in archaeological sites, some other issues must be considered. First, we must consider the differential survivorship of some elements and portion, and the destruction of other parts due to attritional processes by different agents (Marean and Cleghorn, 2003a). Secondly, a low MNE could affect the statistical results removing or providing them of statistical significance (Faith and Gordon, 2007a). Finally, the mixture of singular events, common in the accumulative palimpsest, could involve imprecise, incorrect or ambiguous results (Marín et al., 2017; Yeshurun and Bar-Oz, 2018). In this sense, the studies of Monahan (1998) over the Hadza assemblages, pointed to archaeological assemblages that could not reflect an exclusive transport model, but the total sum of multiple transport events superimposed.

If we evaluate the anatomical profiles of the Abric Romaní and Abri du Maras assemblages, the results are very similar among them. There is a predominance of the long bone shafts and teeth specimens. In both assemblages, the post-cranial axial skeleton is very scarce or nonexistent. Traditionally the absence of post-cranial axial skeleton has been explained by their abandon in the kill/butchering sites (White, 1953b; Perkins and Daly, 1968). However, Marean and colleagues (1992) proved that the activity of agents such as the hyenas over the assemblages could generate similar anatomical profiles to the called schleep effect (Perkins and Daly, 1968). Subsequent revaluations (Marean and Cleghorn, 2003a; Cleghorn and Marean, 2004) suggest that many taphonomic processes could act in the same way. Therefore, the taphonomic processes could affect the anatomical profiles, specially regarding the abundance of low survival elements. In the case of Abric Romaní, it was proposed that this model resulted from the abandon of trunk for large size animals in the kill site, meanwhile lighter animals (medium and small sizes) were transported completely to the site (Saladié and Aïmene, 2000; Fernández-Laso et al., 2010; Rosell et al., 2012b, 2012a, 2019; Modolo and Rosell, 2017). However, the anatomical representation pattern among the different weight size categories is very similar considering the scarce of the post-cranial axial skeleton. Indeed, in the Abric Romaní and Abri du Maras assemblages, independently of their species or weight category the elements of the trunk and the compact bones have small representation rates compared to the cranial and long bones remains

representation. However, the presence of some remains of the trunk or compact bones indicates that they were sometimes transported to the site, although it is not possible to assess how common their transport was. These elements could be transported as part of the complete trunk or in smaller portions, as have been observed in the transport performed by some current hunters-gatherers (Binford, 1978; Monahan, 1998; Lupo, 2001). Their condition of low survival elements does not allow us to evaluate how frequent their transport was. Considering that the carnivore activity is scarce at the Abri Romaní and in the Abri du Maras and the bone preservation is good as diagenetic processes are also non-destructive, we consider that Neanderthal activity could be the most predominant in bone destruction processes. This activity could be in the form of consumption, the intentional use of these elements as fuel or their destruction during cleaning or space maintenance (Théry-Parisot and Costamagno, 2005; Vallverdú et al., 2005, 2012; Costamagno and Rigaud, 2013; Gabucio et al., 2014a).

To interpret and evaluate the high survival elements representation from an economic point of view in the Abri Romaní and Abri du Maras assemblages we use Spearman's correlation index between %MAU and SFUI, and the Shannon diversity index according to Faith and Gordon (2007). The results of the Abri Romaní analysis indicated an unconstrained transport strategy for animal carcasses, implying the transport of complete carcasses, independently of the element economic values.

The transport strategies developed by Hadza groups have been one of the most studied and discuss examples of actual animal carcasses transport strategies (Bunn, 1986, 1993; O'Connell et al., 1988a, 1990; Monahan, 1998; Lupo, 2001). According to these observations, the Hadza develop even six transport strategies. They go from the transport of complete carcasses, including the maximization of the transport of elements rich in medullar marrow. For this reason, we applied the method of Faith and Gordon (2007) to faunal assemblages from two Hadza campsites. The results obtained are similar to the archaeological assemblages of Abri Romaní, opening the possibility that anatomical profiles of the mentioned above levels could result from the sum of different and variable transport events. Besides, results indicate that the diversity of carcass transport strategies could generate anatomical profiles similar to the unconstrained transport or transport of complete carcasses, according to Faith and Gordon (2007). The specific study of the assemblage of Abri Romaní sequence indicates that the transport wasn't homogeneous. For example, the existence of one remain of rhino transported to the shelter in the level M (femur diaphysis) could reflect the transport of a few remains of a single carcass. If we consider the economic value and the low processes and transport costs, their presence in the assemblage could be related to a gourmet strategy. The duality in the transport of complete carcasses or the selection of high ranked elements could enter in contradiction or could respond to variations in Neanderthal

behaviour, linked to the availability of prey, the season of the year, the transport distance or the number of individuals in the group (Monahan, 1998).

In level P of Abric Romaní, the seasonal capture of deer and horses in different moments of the year, the spatial distance of the main accumulation of these two species, and the differences in occupation types related to these conclude a bulk transport strategy for red deer and an inverse model in the transport of horses. This strategy has been also identified too for the transport of reindeer and red deer in level 5 of Abri du Maras. The bulk strategy is specially developed by hunter-gatherer groups when meat demand is high, so they try to transport as much meat as possible to the camp (Binford, 1978; Schoville and Otárola-Castillo, 2014). It also has been related to the transport distance, assuming that the selectivity in transport grows in direct relation with the increase of transport distance (Binford, 1978; Monahan, 1998; Lupo, 2001; Cannon, 2003; Morin et al., 2016). However, the sample of horse from level P of Abric Romaní showed an inverse model to the transport of deer, because the cranial elements are among the most-represented elements. Enloe (2004) asserted that inverse utility curves to bulk strategies could be located in assemblages in which the high and medium utility elements have been extracted from the kill site to their later consume in another place. Thus, these strategies were related to the transport of elements of moderate and high utility values. A similar scenario to what we propose from horses in level P.

The application of the same method to level 5 of Abri du Maras and level P of Abric Romaní indicates that variability is remarkable in the transport strategy developed by Neanderthal groups. However, in the different assemblages of Abric Romaní sequence as well as in level 5 of Abri du Maras exist a positive correlation between the representation of elements and UMI (Morin, 2007). This tendency supports the idea of carcasses elements transport is related to the marrow content and, therefore, the element's food utility. The diversity of the transport strategies have not been apart from the economic return of each element, being the unsaturated fatty acids present in marrow a common resource in Neanderthal diets (Morin et al., 2016, 2019).

A remarkable feature of the anatomical profiles of the horses from Abric Romaní and the Abri du Maras is that the remains belonging to the heads are in many cases the best represented (Figure 4). This profile highlights specially if we compare it to cervids anatomical profiles which, although present variability, are dominated by appendicular bones. Although, there are some exceptions, as in the anatomical profiles from level K of Abric Romaní dominated by red deer mandibles and the sublevel 5.3 of Abri du Maras dominated by reindeer skull (Figure 5). The anatomical profiles of large bovids are variable in both sites, as a result of the low values of MNE, it shows the dominance of appendicular bones, except in levels K and L of Abric Romaní (Figure 6).

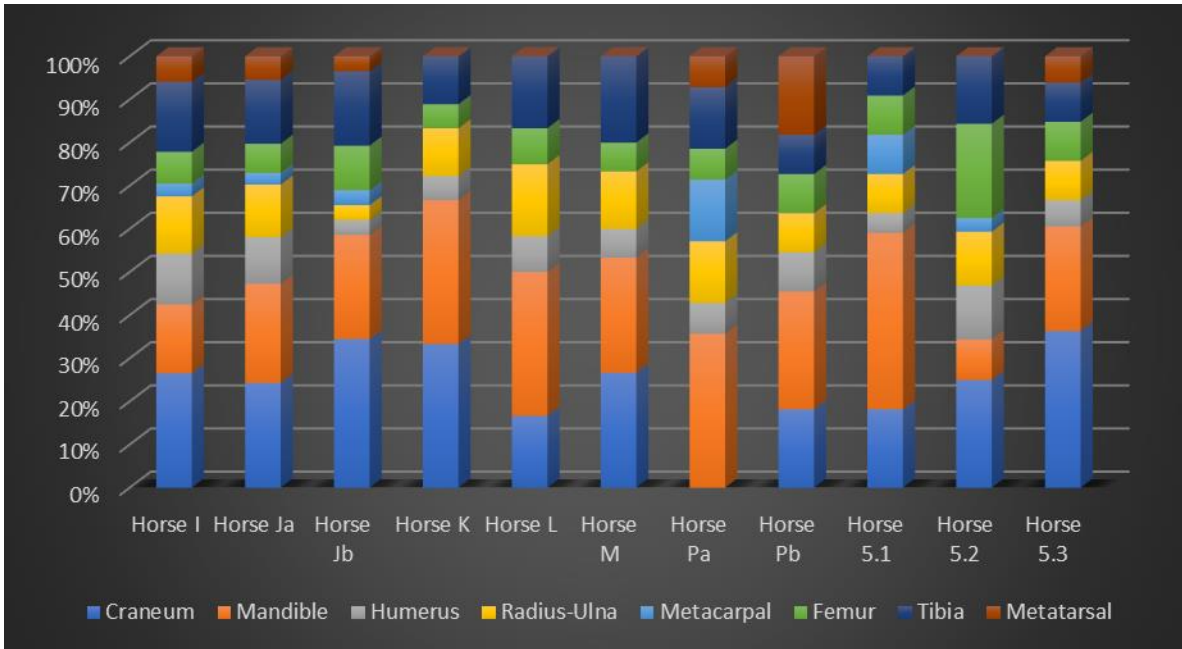


Figure 4 %MAU distribution of horses in the main levels of Abric Romaní and Abri du Maras.

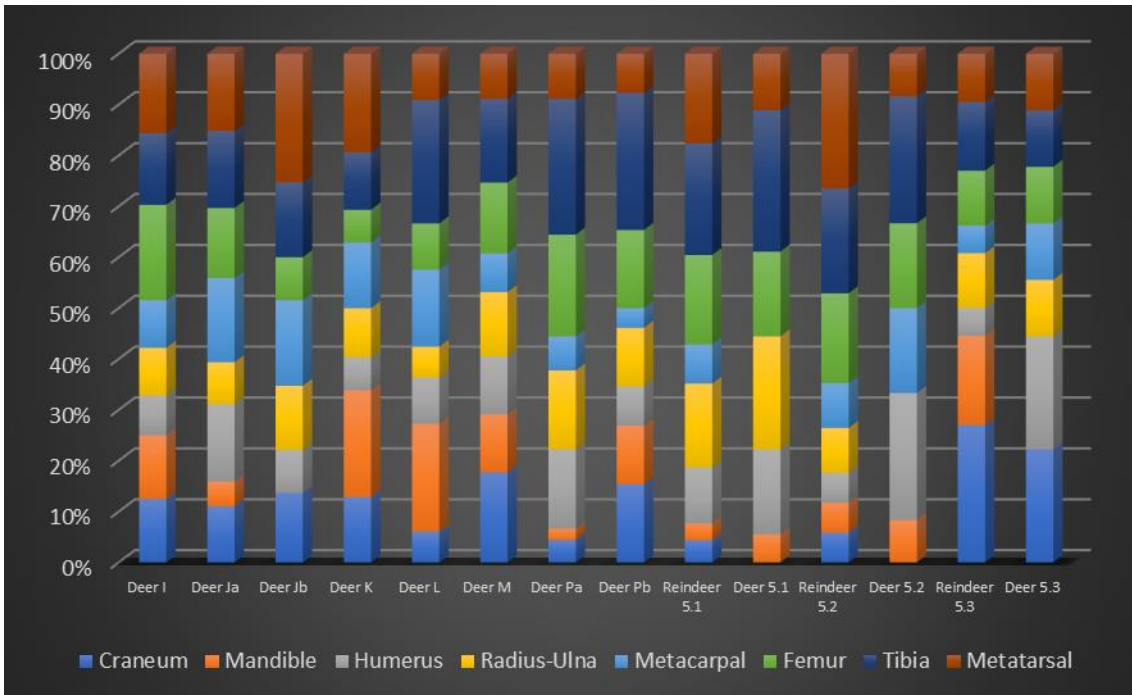


Figure 5 %MAU distribution of cervids in the main levels of Abric Romaní and Abri du Maras.

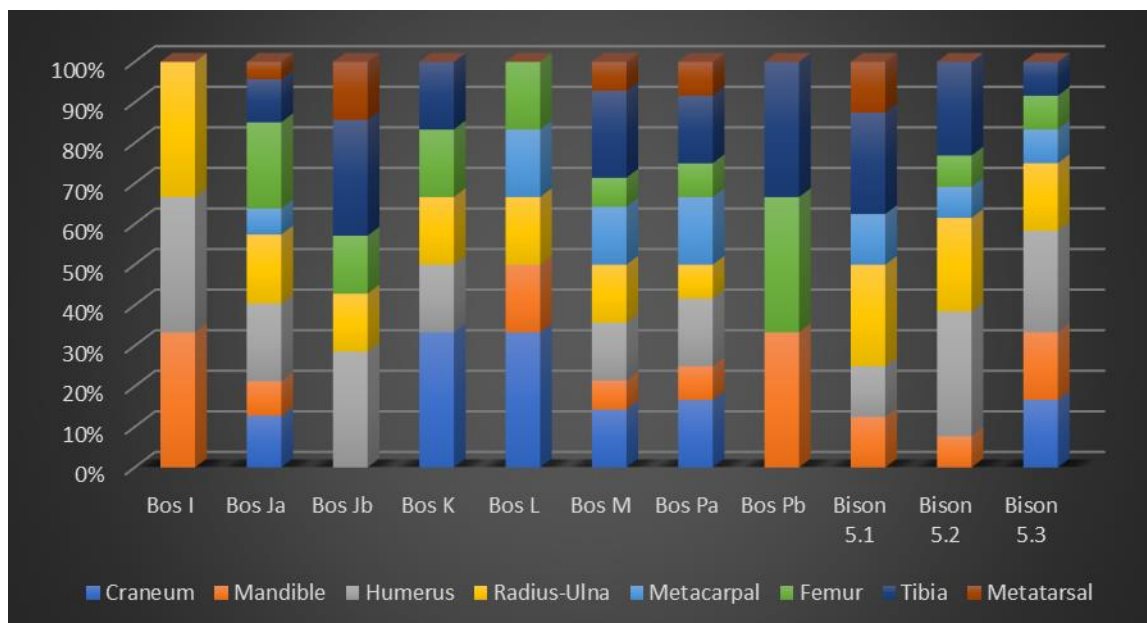


Figure 6 %MAU distribution of bovids in the main levels of Abric Romaní and Abri du Maras.

Marean and Frey (1997) suggest that the heads abundance pattern could be related to methodological bias, the result of the excluding of long bone shaft fragmented from the analysis. However, in this work shaft portions were never excluded shaft portions. A great representation of head could also be related too with differential destruction of the elements producing causing a greater survival of the horse dental pieces against the selenodont animals (Klein and Cruz-Uribe, 1983; Marean, 1997; Outram, 2001). However, horse and cervid teeth do not show differences in their conservation. If any taphonomic processes take part in bone conservation, it's should act concerning the animal age (Marean, 1997), implying better preservation of adult individuals versus young animals. However, in the Abric Romaní there is a greater proportion of young individuals of cervids than horses, and in the Abri du Maras a similar proportion, which allowed us to dismiss the post-depositional destruction of head abundance.

Another scenario that could explain the dominance of head remains and low food return elements in horses would be that their contribution is the result of scavenging events (Trinkaus, 1989; Stiner, 1990). Two strategies could be considered two strategies in this scenario, a passive scavenging or confrontational scavenging (O'Connell et al., 1988a; Bunn, 2001). The high presence of heads and the presence of the distal part of extremities was interpreted by Binford (1981b) and Blumenshine (1991) as clear evidence of the animal resource supply by means of passive scavenging. Firstly, it should be noted that at both sites the proximal and intermediate appendicular elements are abundant. Besides, in both Abric Romaní and Abri du Maras assemblages human modifications are abundant, specially slicing marks over long bones shafts and anthropogenic bone breakage (Table 1), and there is also a scarcity of carnivore tooth



marks. Indeed, modification's frequency and distribution are related to primary accesses to animal carcasses and the principal main muscular packages (Domínguez-Rodrigo, 1997). As we have seen, slicing marks over long bones shaft fragment, including proximal and intermediate bones, stand out. One way to access a great amount of flesh is the confrontational scavenging based on the robbery of prey captured by other carnivores. In these cases, the Neanderthals could have acceded to a greater amount of nutrients and the resulting butchering processes would be similar to the obtained by hunting. However, if this would have been the scenario, we would have found the common mortality profiles common among the prey of carnivores, which are generally characterized by attritional and catastrophic profiles (Schaller, 1972; Klein, 1982; Stiner, 1990; Cruz-Uribe, 1991). In this work, the horse's mortality profiles are dominated by a prime adult profile, which allows us to discard that the accumulations were the result of confrontational scavenging. Besides, this strategy is not much productive considering the high risk of large carnivore it implies (Treves and Naughton-Treves, 1999).

		Ja	Jb	K	L	M	Pa	Pb	5.1	5.2	5.3	Unit II
Cut marks	NSP	311	61	86	29	208	86	15	196	64	41	4
	%NSP	14,3	9,7	3,4	2,9	9,5	18,9	13,3	14,9	9,3	6,4	1,6
Bone breakage	NSP	763	149	274	34	308	52	13	148	47	58	2
	%NSP	35	23,7	10,6	3,4	14,1	11,4	5,5	11,2	6,8	9,1	0,8
Tooth marks	NSP	34	4	27	4	8	37	6	7	1	8	133
	%NSP	1,6	0,6	1,1	0,4	0,4	8,1	5,3	0,5	0,1	1,3	51,8

**Table 1** Number of remains and percentage of long bone specimens with cut marks, anthropogenic bone breakage and carnivore tooth marks of different assemblages of Abric Romaní and Abri du Maras.

So, we can dismiss that the abundance of horse skulls was an artefact product of bias and discuss other possible origins. One of them is that it is a result of their transport of the heads and the type of settlement recorded. Marean (1997) indicated that the head's transport of animal hunted could be affected by three main factors related among them. The first would be the animal weight, assuming that heads of small and medium animals should be transported more often than the heads of large animals. The next factor would be the size of the human group, which indicates that larger the hunting group is more easily the head will be transported. The transport of animals of the size of a horse was with any doubt cooperative. The needing of at least 10 individuals for the transport of complete carcasses of horse size (Monahan, 1998; Lupo, 2001), shows that cooperation among individuals during the development of hunting events was a fact for Pleistocene hominins (Stiner, 2009; Stiner et al., 2009; Saladié et al., 2011a).

The studies about the occupations of level N from Abric Romaní indicate that the Neanderthal group that used the site could be formed of a minimum of 8 to 12 individuals (Vallverdú et al., 2010). In other studies of the European record the size of

the Neanderthals groups calculated present similar numbers than for level N (Hayden, 2012; Duveau et al., 2019). Finally, the transport distance factor predicts that as the distance increase more possibilities for heads to be abandoned exits, specially for large animals. Although we cannot evaluate the original transport distance of horses, we can assume that it should have been trips that allowed the transport of heads, as they are present in the site when it was used as a hunting camp or residential place independently. Therefore, the distances between the kill site and the Abric Romaní and Abri du Maras should have been relatively short. This fact would have eased the transport of horse skull than the other species (Schoville and Otárola-Castillo, 2014).

The fatty tissues contained in the skull are totally or partially encased in the bone, as occurred with the marrow in the appendicular bones (Stiner, 1994). From a technical point of view, heads are relatively easy to separate from the trunk, in contrast with the difficult to preceding the fat-rich trabeculae of the spine (Yellen, 1977, 1991; Binford, 1978; Speth, 1987; Stiner, 1994). However, when crania are processed, the contents of some parts and tissues require considerable processing time to their preparation as food. Head parts are often valued by foragers, specially if the prey is in poor physical conditions at the time of death (Stiner and Kuhn, 1992; Miracle, 1996). The horse's head is less susceptible to depletion of the fat contained within the skull in times of nutritional stress of the animals when compared to other anatomical parts (Stiner, 1994; Lupo, 1998). Besides, all these resources are more profitable by the use of fire during their processing (Niven, 2007, 2013). Therefore, since the heads are resistant and require considerable processing time (Marean and Cleghorn, 2003a; Cleghorn and Marean, 2004), there are many incentives to transport them to protected sites, such as the Abric Romaní and the Abri du Maras.

The data from the study of anatomical profiles from Abric Romaní and level 5 of Abri du Maras, indicate that the transport was closely related to different objectives and features. Without doubts, the food utility of elements is a main constant in the assemblages. This could be observed in the long-term residential places and short-term and functional occupations. However, other features as the size of the hunting group and the transport distance should have had a fundamental role in the transport decision and therefore were key pieces in the transport strategies developed by Neanderthals groups.

### 8.3. Resource provisioning: prey selection and hunting

In the Mediterranean basin, the archaeological sites dominated by one single species are uncommon, unlike the Atlantic and North Europe where are more abundant. One feature of the Mediterranean ecosystem that may have influenced a higher diversity of preys is the existence of more fragmented landscapes than those recorded in the Atlantic region. In the Mediterranean region exists a greatest diversity of ecosystem in relatively short

distances, integrating coastal zones, coastal plains, river valleys and mountain environments (Valensi, 2000; Aura Tortosa et al., 2002; Carbonell, 2012; Moncel and Daujeard, 2012; Finlayson et al., 2019; Mallol et al., 2019; Rusch et al., 2019). In the Abric Romaní and the Abri du Maras stand up the relevance of one or two taxa, although neither are monospecific sites. Besides, if we consider the seasonality patterns identified in both sites a certain seasonal specialization could be suggested in prey catchment. In the Abri du Maras we have established that reindeer is the most represented taxa on three sublevels, although their abundance is reduced downwards the sublevels (Daujeard et al., 2019). The progressive reduction of the importance of reindeer in favour of an increase of horse and red deer, specially within level 5.3 where it accounts for 20.5% of NISP has been observed. Most levels of Abric Romaní are dominated by deer, followed in importance by horses, although in some assemblages this pattern is reversed.

Neanderthals were able to observe, learn and predict the behaviour of their preys has been assumed, therefore it is reasonable to expect that they could increase encounter rates with some species by planning hunting events (Dusseldorp, 2009). This would explain prey catchment seasonality observed in level P of Abric Romaní and level 5 of Abri du Maras. Prey selection is not always related exclusively with the taxa, since it can also depend on other factors as animal age or sex (Klein and Cruz-Urbe, 1983; Stiner, 1990). Stiner (1990) proposed that a high presence of adult individuals may be related to hunting activities, being these age groups represent the population reproductive core. We have observed this fact among the horse assemblages of Abric Romaní, dominated by prime adults. Follow the Stiner's (1990) proposal, the catastrophic and attritional mortality profiles could indicate animal procurements by scavenging. However, recently it has been proved that although human groups often capture prime adult, this was not always the case, and variability that may be related to the hunting tactics employed could also produce specific mortality profiles (Niven, 2013; Bunn and Gurtov, 2014; White et al., 2016; Rodríguez-Hidalgo et al., 2017).

In the Abric Romaní and Abri du Maras sequences, we have established differences among the horse, red deer and reindeer profiles. As we have seen, horses present a prime adult mortality profiles within all levels. However, following the method of Discamp and Costamagno (2015) we could observe that horse juvenile individuals are not completely absent from most of the assemblages. In the Abri du Maras assemblages the presence of juvenile horses is higher (MNI=28%) than respect to juvenile reindeers (MNI=20%), although the proportion of both taxa is similar. It could be related to the type of population group exploited. For example, the hunting of single male horses' groups should generate a greater proportion of prime adult individuals. Meanwhile, the hunt of female groups should generate assemblages with a higher presence of juvenile individuals, specially during the birth season. Between deer assemblages, greater

variability in mortality profile has been observed, including juvenile dominated profile and attritional, although the death age profiles are situated preferentially in the catastrophic and prime dominated areas.

Considering the behavioural predictability of some animals and the transient nature of occupation we could indicate that taxa exploitation was strongly linked to seasonal practices. In some cases, both strategies overlap in season. When hunting season does not overlap, and two clear moments of occupation are described, seasonally limited prey availability can be deduced. It could be the case of sublevels Pa and Pb. However, when moments at death are seasonally simultaneous, as in the case of level Ja, M, 5.1, 5.2 and 5.3, permit us to indicate that animals were intentionally hunted according to age and taxa. So, despite the availability and encounter rates, we can suggest that prime adult profiles were the result of selective hunting, and catastrophic and attritional profiles the result of non-selective hunting. Ambush hunting should allow hunters to be more selective about their choice (Binford, 1978). However, Bunn and Gurtov (2014) exposed that ambush hunting of prey implies an increment in the capture of prime adults (around 70% of individuals). In the Abri du Maras, this could be the case for the reindeer hunting in all levels and the horse in level 5.1 and 5.3, and it could be related to encounter rates instead of selectivity. The presence of other mortality profiles could be related to the intentional searching of animals of different ages or with the use of other tactics. Recently, it has been proved that archaic hominins, like *Homo erectus*, had physical skills to develop persistence running hunting (Hora et al., 2020), which could generate attritional and young dominated mortality profiles.

The Young dominated profile is another observed scenario which may correspond to an intentional selection linked to the birth season. Abric Romaní Level I showed a young dominated mortality profile for red deer, which represented 71% of the individuals. Therefore, exploitation seems to be specifically aimed at obtaining this type of prey. The young deer accumulation of level I was recovered in a specific activity area of the shelter (Vallverdú et al., 2005). This specific accumulation suggests a specialized seasonally hunting activity, probably during a single occupation event. The small size a low corporal fatty tissues of young individuals implies that these animals were low ranked animals than an adult deer (Speth, 2013). Speth and Clark (2006) discussed that an increment of young individuals could not be a seasonal sign of their abundance in the environment, proposing to be a sign of resources intensification or broad-spectrum diet in response to overexploitation of species. When high ranked animals are scarce in the environment hunters-gatherers exploit low ranked animals (Miracle, 1996; Munro and Bar-Oz, 2004; Speth and Clark, 2006). However, a diet intensification could also imply the exploitation of a wider range of species, something not observed at level I. Therefore, the young individual hunt could not reflect resources scarcity, because these animals could be appreciated by complementary reasons to their food utility. Binford

(1978) observed different hunting events of some Nunamiut groups where young individuals were killed to obtain soft leather for clothing. Besides, in Denmark, late Mesolithic sites (Rowley-Conwy, 1995; Richter and Noe-Nygaard, 2003; Magnell et al., 2020) a high proportion of young deer between 0 to 6 months could be related with the demand of soft and spotted hides of the young animals (Magnell et al., 2020). Within the European Neanderthal record the hunting of different species for specific resources, as leathers, are not unknown. A specific bear hunting has been identified to obtain their skins for clothing or leather, as well as meat and other food (Auguste, 1992, 2003; Bratlund, 1999; Gaudzinski-Windheuser and Roebroeks, 2011; Romandini et al., 2018). Lithic use-wear analyses at Abric Romaní show that worked skins existed within the sequence, with work on fresh leather being more common (Martínez Molina, 2005). Also, lithic functionality studies in level Ja relate denticulates and notches to the hardening of hides (Vaquero et al., 2012).

In summary, Neanderthals groups of the Mediterranean basin exploited the ungulates of their environment, specially cervids and horses according to the Abric Romaní and the Abri du Maras. Unlike other sites in the same region, such as Bolomor Cave, Gibraltar or the Abri du Maras itself, at level 4.1 or level O of the Abric Romaní (Sanchís and Fernández Peris, 2008; Hardy and Moncel, 2011; Blasco and Fernández Peris, 2012; Gabucio et al., 2014a; Blasco et al., 2016; Daujeard et al., 2019) we have not documented the exploitation of small prey. Carnivores such as bears, which were intensively exploited in the Fumane cave in Italy, Biache-Saint-Vaast in France and the Taubach site in Germany (Auguste, 1992, 2003; Bratlund, 1999; Gaudzinski-Windheuser and Roebroeks, 2011; Romandini et al., 2018) were also absent. Mortality profiles and seasonality of horses versus deer and reindeer found in the Abric Romaní and Abri du Maras indicate specialized seasonal exploitation of certain species.

## 8.4. Neanderthal mobility

The hunter-gatherer mobility in their environment is a fundamental part of their socio-economic system and responds to the aim of optimizing and securing resource exploitation (Audouze, 2006). According to available data from mobility features of current hunter-gatherers groups (e.g. Binford, 1980; Kelly, 1983), the mobility of past human groups has been studied, considering different aspects as group size (Vallverdú et al., 2010; Lalueza-Fox et al., 2011; Duveau et al., 2019), the type of settlement (Boyle, 2000; Patou-Mathis, 2000; Daujeard and Moncel, 2010b), raw materials procurement (Fernandes et al., 2008; Gómez de Soler et al., 2019), Neanderthal anatomy (Verpoorte, 2006; MacDonald et al., 2009; Higgins, 2014) and even genetic and demographic studies to understand the distribution of population dynamics at a territorial level (Mellars and French, 2011). All these research agree that Neanderthals lived organized in small social groups in territories with low population densities (Pettit,

1997; Henrich, 2004; Vallverdú et al., 2010; Lalueza-Fox et al., 2011; Mellars and French, 2011; Duveau et al., 2019). However, two main hypotheses about their territorial mobility have been proposed. One considers that Neanderthals were only able to develop residential mobility in small territories, becoming highly mobile groups (Verpoorte, 2006; MacDonald et al., 2009; Roebroeks and Verpoorte, 2009; Walker and Churchill, 2014; Churchill et al., 2016). Against this hypothesis, it has been proposed that Neanderthals were also able to develop, in certain periods and geographical areas, settlements and mobility strategies typical of logistically organized groups, in medium and large regional territories (Patou-Mathis, 2000; Vallverdú et al., 2005; Delagnes and Rendu, 2011; Niven et al., 2012; Marín-Arroyo, 2013; Turq et al., 2017; Marín et al., 2019).

Many European sites contain great assemblages resulting from redundant human activity and with wide chronological ranges, suggesting intentionality among Neanderthals in the repeated occupation of certain places and probably also in the search for food (Dusseldorp, 2009). According to the obtained data, consisting of the superposition of occupation events, in many cases seasonal, the Abric Romaní and Abri du Maras were two of these sites. As we have said, the possibility to exploit different biotopes and their resources should be a justifying reason for the recurrent use of the same space within a territory. Level P of Abric Romaní has been the assemblage proportionating more information in this respect. The results suggest that Neanderthals of sublevels Pa and Pb developed logistic mobility. The differences in the occupied surface and seasonality of the animal hunt allowed us to propose two types of low-intensity occupations, as a short-term residential camp for the capture of deer and as a hunting camp for horse hunt, to supply of resources to another aggregation site.

The study of lithic raw materials also supports that these sublevels are the result of logistical mobility. In both assemblages, outcrop chert distance ranging from 16 to 26 km from the site has been determined, indicating a regional catchment and a logistical mobility range. Considering that Neanderthal lived in small social groups (Pettit, 1997; Henrich, 2004; Vallverdú et al., 2010; Lalueza-Fox et al., 2011; Duveau et al., 2019) some researchers consider that this forced them to exploit small territories through high residential mobility (Dusseldorp, 2009; MacDonald et al., 2009). Although during Middle Palaeolithic the resource provisioning tends to be local, there are a growing number of examples in southern and central Europe indicating that the most common raw material provisioning was on a regional scale (5-30 km) (e.g. Fernandes et al., 2008; Moncel et al., 2008b; Eixea, 2018; Gómez de Soler et al., 2019). Remains that come from distances within large regional ranges (100-200 km) have been also identified, showing the existence of large expansive territories during the Middle Paleolithic (Féblot-Augustins, 1993; Conard and Adler, 1997; Slimak and Giraud, 2007; Spinapolice, 2012; Real et al., 2018). The sublevel Pa and Pb, are examples of the same

space reoccupation, used for distinct activities in different seasonal moments which support Neanderthals developed logistic management of their territory. In the centre and east Europe, the low frequency of residential camp and the abundance of a transitory camp has been related to the dominance of a multidirectional logistic mobility strategy (Patou-Mathis, 2000). Numerous sites in centre and east of Europe with specific features, as temporal hunting halts or stands (Scladina, Chokurcha I, Vindija) and kill/butchering sites (Kabazi II, Tata) has been related by Patou-Mathis (Patou-Mathis, 2015) with the existence of great provisioning territories and a logistic mobility strategy.

Following the data to our disposal, the catchment territories in the Mediterranean basin were on a regional scale (e.g. Fernandes et al., 2008; Moncel et al., 2008b; Eixea, 2018; Gómez de Soler et al., 2019). Among these sites, we must consider the assemblages of level P of Abri du Romaní and level 5 of Abri du Maras. In most cases, the occupation never exceeded more than one complete season, although we have identified more reduced temporal occupation at level P. This type of occupation is typical of groups with high territorial mobility, being logistics the predominant strategy. However, mixed scenarios cannot be discarded in which residential mobility, or groups moving from patch to patch of resources, could be combined with short-term occupations in settlements that were logistically supplied, suggesting a certain ductility of Neanderthals mobility in each period and region.

## **Chapter 9. Conclusions**





## Conclusions

Neanderthals are the main agent in the Abric Romaní and Abri du Maras sequence during assemblage formation, including the level P and level 5 studied for this thesis. At both sites, carnivore interactions were scarce supporting a commensalism relationship between humans and carnivores, in which they scavenged the spoils abandoned by Neanderthals. Carnivore activity was scarce as a result of the intensive exploitation of faunal remains by Neandertals. Both taphonomical agents did not share resources regularly at the Units I and II of Bize-Torunal. However, at this site, there was an alternate of site occupation. In this sense, the hyena was the main agent in the assemblage formation.

Through the study of different assemblages from the three sites, we have identified: ephemeral and expeditious occupations, as in the case of Bize-Tournal; short-term occupations within a logistic mobility system, probably for a few days or weeks, as in the case of level P of Abric Romaní; and long-term occupation events, even for a complete season, as in the case of level 5 of Abri du Maras. The three sites were repeatedly visited by Neanderthal groups. The Abric Romaní was used as a hunting camp and residential camp. In the sequence of this site, an alternate of short-term and long-term occupations has been identified, the Abri du Maras site was used mainly as a residential campsite, where Neanderthals developed the most of domestic activities and exploited the surrounding environment.

The predictability of resources coupled with its temporal disposition in the environment implies that its exploitation takes place within a temporal and spatial range, strengthening the use of a repeated capture strategy over time, adapting it to the migratory movements of each species. In the cases of Abric Romaní and Abri du Maras the faunal assemblage is the product of primary access to animal carcasses by Neanderthal through hunting activities. At both sites, the hominins were specialized in obtaining large and medium-sized ungulates, specially cervids (common deer and reindeer) and horses. The mortality profiles and seasonality show specialized behaviours at both sites. Prime adult exploitation, specially for horses, could have been developed probably by cooperation, through simple predation during selective ambush hunting episodes. The tactics which generated catastrophic and attritional profiles could imply the encounter or non-selective ambush hunting, or even the endurance hunting.

The transport of animal carcasses showed wide variability, which is reflected in the presence of all the high survival elements from a skeleton. However, the statistical proxies indicated that: elements are not uniformly distributed in the same proportions

and that the different skeletal portions are not present in the same frequencies, suggesting that the carcasses were not always transported completely. According to the diversity of elements and their correlation with food utility, the elements were transported according to their food return, ranking those from high and moderate utility. In this way, even in mixed skeletal profiles, we can see how there is intentionality at maximizing the quantity and value of the element transported. However, the distance between the kill site and the camps were factors that conditioned the different strategies developed at events. However, other existing constraints could not be inferred from an archaeological point of view.

## Conclusions

Les Néandertaliens sont le principal agent d'accumulation de la séquence de l'Abric Romani et de l'Abri du Maras pendant la formation des assemblages, en particulier le niveau P (Abric Romani) et le niveau 5 (Abri du Maras) analysés dans ce travail de thèse doctorale. Sur les deux sites, les interactions avec les carnivores étaient rares avec la présence d'une relation de commensalisme entre l'homme et les carnivores, dans laquelle ces derniers pouvaient récupérer les restes alimentaires abandonnés par les Néandertaliens. L'exploitation intensive des restes de la faune par les Néandertaliens réduisaient l'accès aux carcasses par les carnivores. Les deux agents taphonomiques accumulateurs pouvaient partager les ressources carnées des unités I et II de Bize-Torunal. Cependant, dans ce site, les deux accumulateurs occupaient en alternance le site. En ce sens, l'hyène était l'agent principal d'accumulation de la formation des assemblages osseux.

L'étude de différents assemblages fauniques des trois sites nous a permis d'identifier : les occupations éphémères et de très courtes durées, comme dans le cas de Bize-Torunal ; des occupations de courte durée dans le cadre d'un système de mobilité logistique, probablement de quelques jours ou semaines, comme dans le cas du niveau P de l'Abric Romani ; et des événements d'occupation à long terme, pouvant s'étirer sur une saison complète, comme dans le cas du niveau 5 de l'Abri du Maras. Les trois sites ont été visités à plusieurs reprises par des groupes de Néandertaliens. L'Abric Romani a été utilisé comme camp de chasse et comme campement résidentiel. Dans la séquence de ce site, il a été identifié une alternance d'occupations à court et à long terme, le site Abri du Maras a été principalement occupé comme campement résidentiel, où ils ont développé la plupart des activités domestiques et de Néandertaliens exploiter le milieu environnant.

Dans les cas de l'Abric Romani et de l'Abri du Maras, l'assemblage osseux est le produit de l'accès primaire aux carcasses des animaux par la chasse par les Néandertaliens. Sur ces deux sites, les hominines se sont spécialisés dans l'obtention d'ongulés de grande et moyenne taille, en particulier les cervidés (cerfs et rennes) et les chevaux. Les profils de mortalité et la saisonnalité des abattages montrent des comportements spécialisés sur les deux sites. L'exploitation des adultes, en particulier des chevaux, pourrait soit être acquis par coopération ou par simple prédation lors d'épisodes de chasse sélective en embuscade. Les profils catastrophiques et attritionnels identifieraient une chasse à la rencontre ou une chasse en embuscade non sélective, voire une chasse d'endurance.

Les résultats sur le transport des carcasses ont montré une grande variabilité, avec la présence de tous les éléments squelettiques au sein des assemblages. Cependant, les analyses statistiques indiquent que : les éléments sont inégalement distribués dans les mêmes proportions et que les différentes parties du squelette ne sont pas présentes dans les mêmes fréquences. Ceci suggère que les carcasses n'ont pas toujours été transportées entières. Selon la diversité des éléments, leur corrélation avec l'utilité alimentaire, les éléments ont été transportés en fonction de leur valeur nutritionnelle, en classant ceux d'utilité élevée à modérée. De cette façon, même dans des profils squelettiques mixtes, on peut voir comment il y a eu une intention de maximiser la quantité et la valeur nutritionnelle de l'élément transporté. Cependant, la distance entre le lieu d'abattage et les sites d'occupation ont été des facteurs qui ont conditionné les différentes stratégies développées dans chacun des événements. Cependant, il existe d'autres contraintes qui ne peuvent pas être déduites d'un point de vue archéologique.

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